United States
Department
of Agriculture

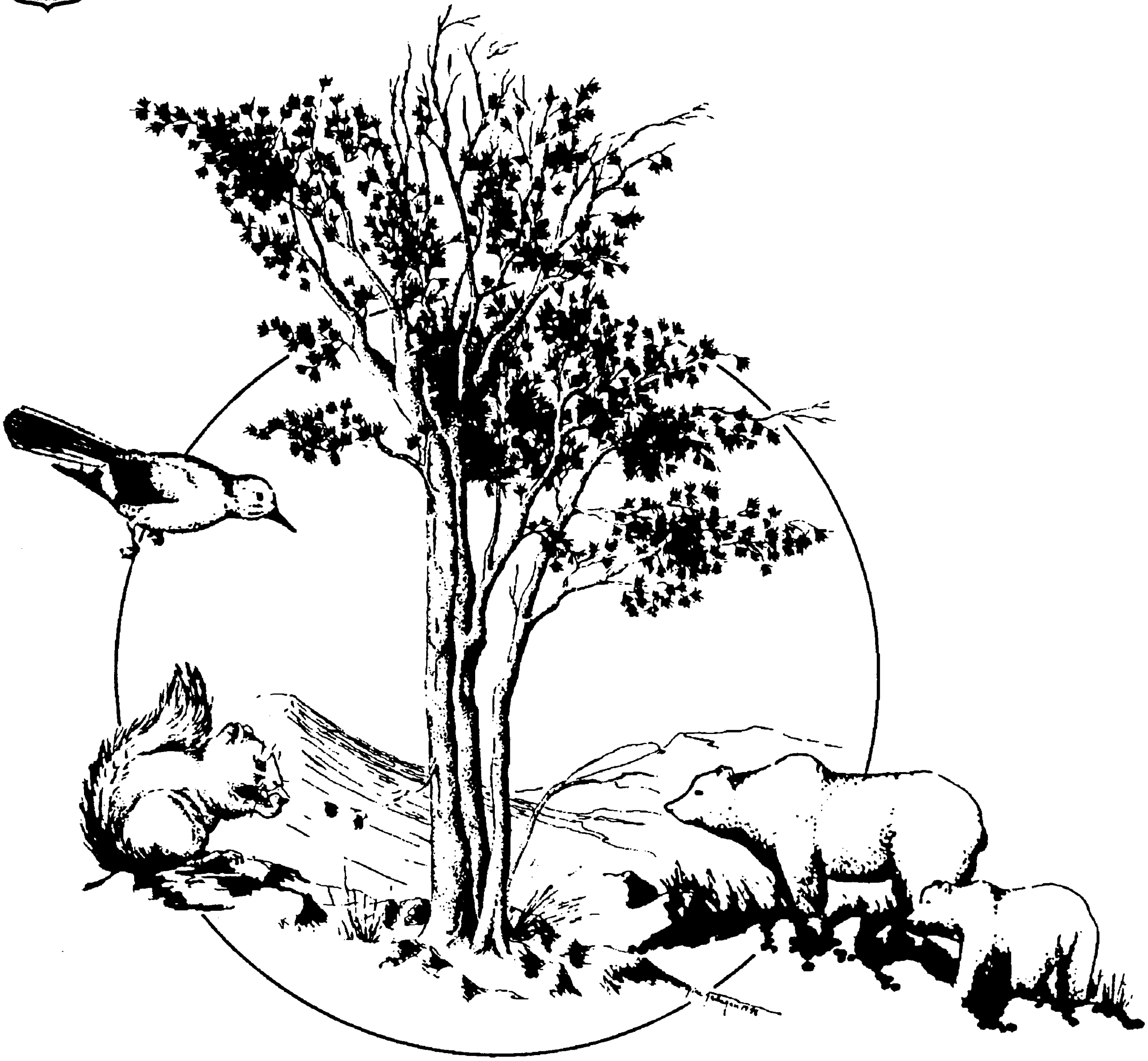
Forest Service

**Intermountain
Research Station**

General Technical
Report INT-270

June 1990

Proceedings—Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource



Intermountain Research Station
324 25th Street
Ogden, UT 84401

Proceedings—Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource

Bozeman, MT, March 29-31, 1989

Compilers:

Wyman C. Schmidt, Project Leader
Kathy J. McDonald, Clerk-Typist

Intermountain Research Station, Forest Service
U.S. Department of Agriculture

Symposium Sponsors:

Forest Service
  Northern Region
  Intermountain Research Stat
National Park Service
Montana State University
Society of American Foresters

SAF 90-03

FOREWORD

"New Perspectives in Forestry" is a recently coined term that describes the need for holistic approaches to forest management practices. It recognizes the broad range of resources that must be accounted for in forest management activities. Forest managers have long recognized this need and have responded accordingly—to a lesser degree in forests where a single resource value predominates and to a greater degree in forests where the various resource values are about equal. However, in nearly every case, the knowledge base needed for holistic management is incomplete and not readily available to those who must make the tough management decisions. This has particularly been the case for those ecosystems whose resources have had little demand in the past but whose values are rapidly being recognized. Whitebark pine ecosystems fit that definition and were the subject of a preliminary workshop February 24, 1987, and of a major symposium March 29-31, 1989, at Montana State University, Bozeman. This proceedings is a product of the 1989 symposium "Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource."

This symposium explored the ecology and management of high-mountain ecosystems of western North America where whitebark pine and its associated flora and fauna predominate—a subject of rapidly emerging recognition and importance. This was the first symposium that examined in depth these fragile high-mountain areas so important for their total complement of resource values. Specific objectives of the symposium were to ferret out and present the best information available for these relatively unexplored forests—forests that harbor the grizzly bear, mountain sheep, and elk; that provide late-season water for the valleys below; that provide expansive views and solitude for the high-mountain visitor; and, to a lesser extent, provide some of the wood products for North America.

Some striking similarities to European and Asian ecosystems were pointed out, and we in North America can learn much from our colleagues who research and manage the ecosystems in Eurasia. While our high-elevation ecosystems in North America have seen little occupancy and use to date, those in Eurasia have a long history of use and abuse as pointed out by Drs. Ives, Holtmeier, Lanner, and Ross in their papers. Much of what is learned there will likely be applicable in North America.

Happily, far more information was available about whitebark pine ecosystems than we envisioned at the outset of planning for this symposium, and the 52 papers and 14 poster synopses document that fact. About 150 people attended all or part of the symposium and 25 went on the postsymposium field trip into whitebark pine forests at Big Sky, MT.

The symposium program consisted of five major sessions: (1) High-Mountain Resources of the World, (2) High-Mountain Resources of North America, (3) Ecology of Whitebark Pine Forests, (4) Management Implications, and (5) Where Do We Go From Here?

The symposium was sponsored by the Forest Service, U.S. Department of Agriculture; National Park Service, U.S. Department of the Interior; Montana State University; and the Society of American Foresters, with designation as a SAF Regional Technical Conference.

The symposium was planned by:

Co-Chairmen:

Wyman C. Schmidt, Project Leader and Research Silviculturist, Intermountain Research Station, Bozeman, MT

Richard Kracht, Forest Silviculturist, Gallatin National Forest, Bozeman, MT

Coordinators:

Steve Arno, Research Forester, Intermountain Research Station, Missoula, MT

Kathy Hansen-Bristow, Associate Professor of Geography and Earth Sciences, Montana State University, Bozeman, MT

Wendel Hann, Regional Ecologist, Northern Region, Forest Service, Missoula, MT

Dave Mattson, Wildlife Biologist, Interagency Grizzly Bear Team, Bozeman, MT

Melanie Stocks, Events and Promotion Specialist, Montana State University, Bozeman, MT

Tad Weaver, Plant Ecologist, Biology Department, Montana State University, Bozeman, MT

I want to acknowledge the planning committee members, and the organizations that supported them, for their imaginative, enthusiastic, and dedicated efforts in the planning and conduct of this symposium. Also, I wish to acknowledge Gina Gahagan who designed the logo; Stephan Custer, Robert Breazeale, Laurence Lassen, Carter Gibbs, Robert Gibson, and Stewart Coleman who served as moderators; and a particular thanks to Kathy McDonald who processed all of the papers for this proceedings.

The world faces many environmental problems with acid rain, global warming, air pollution, and other factors affected by human activities. There are strong indications in the world literature that high-mountain ecosystems are particularly vulnerable to these disturbances and may indeed prove to be a sensitive monitor of subtle changes in the environment. The knowledge presented at this symposium should prove to be a springboard for accelerated research and intelligent management of these high-mountain ecosystems.

—WYMAN C. SCHMIDT
Project Leader and Research Silviculturist

CONTENTS

SESSION 1

High-Mountain Resources of the World

Wyman C. Schmidt
Session Coordinator

The papers in this section examine worldwide ecosystems that are similar to the high-mountain whitebark pine ecosystems of North America, providing an international perspective at a time of increasing concerns with changes in global environments. The primary purpose is to learn from the research and management of "Old World" ecosystems that have had many centuries of use and abuse, and attempt to capitalize on the knowledge gained there to better manage high-mountain ecosystems of the "New World" in North America. Papers in this session dealt with European and Asian findings and provided a glimpse into the future of high-mountain biological research in North America.

HIGH-MOUNTAIN FORESTS OF THE WORLD: ENVIRONMENTAL SIMILARITIES AND RESOURCE USE ISSUES

Jack D. Ives

ABSTRACT

The high-mountain forests of the world display remarkable similarities, at least from a physiognomic point of view (the inner tropics excepted). The lapse rate, in terms of its impact on the length and warmth of the growing season, is the most significant control on the upper limits of growth of these forests for any particular latitude. The principal environmental characteristics include: low temperature, high radiation receipts, azonal soils, high gradients, and potential slope instability, as well as relative inaccessibility.

Over much of the "Western" world inaccessibility and low growth rates of these forests have reduced their direct economic importance; dependency on fuelwood virtually ended some decades ago. This is not the case in Third World countries, where the manner of over-exploitation by subsistence peoples is closely following that which was typical of the Alps, for instance, throughout the Middle Ages and into the first decades of the present century. The most important resources of these forests relate to recreation and wildlife reserves, watershed management, and defense against mountain hazards. Efficient forest management is often hindered by the persistence of anachronistic forest laws that stand in urgent need of reappraisal and adjustment. Hand in hand with this, is the need for a much fuller understanding of two aspects of the dynamics of the mountain forest environment: (1) the history of deforestation (and natural reforestation); and (2) the actual physical impacts of deforestation, and especially the perceived distant downstream impacts.

ENVIRONMENTAL SIMILARITIES

The physical environment and associated resources of the world's high-mountain forests embrace an enormous topic of great complexity. In detail, upper montane forest belts and their forest-alpine tundra ecotones display considerable variation in terms of their floristics, topography, climate, soils, and in the histories of their resource use, as well as in their current status. Nevertheless, some useful generalizations can be made for the purpose of this conference on the whitebark pine ecosystems.

Temperature constraint is one common denominator of the world's upper montane forest belts. It is necessary to consider the progressive reduction in the length and warmth of the growing season with increasing altitude. On a global scale this "standard" lapse rate is the ultimate control on the altitude to which tree species can maintain themselves. It displays itself in simplified form by the regular reduction in the elevation of the highest surviving trees from the subtropics to polar latitudes (fig. 1). The 10 °C mean isotherm for the warmest month is frequently used as a surrogate for timberline but, as is generally understood, this isotherm conceals a great amount of complexity. And even this gross simplification breaks down between the tropics where, across the Equator in its extreme form, summer occurs every day and winter every night. In the inner continental interiors, such as the eastern Pamirs, and the Hoggar and Tibesti of the southern Sahara, extreme aridity prohibits establishment of any form of mountain forest belt. Nonetheless, on a world scale, the work of Arno and Habeck (1972), Hansen-Bristow and Ives (1985), Tranquillini (1979), Troll (1973), Wardle (1974), and others, can be combined by relating upper timberline in some very broad manner to temperature—in effect, the length and warmth of the growing season. This leads to a low latitude-high altitude to high latitude-low altitude energy continuum. A caution is needed even here, however, in that some tree species have the ability to live a very long time, especially those equipped to endure wind deformation and to reproduce assexually by layering. Thus it is necessary to be aware that the actual upper tree species limit, and the forest-alpine tundra ecotone as a whole, have the ability to withstand a degree of climatic vicissitude and may not necessarily be in synchroneity with the present climate, however that may be defined (Ives and Hansen-Bristow 1983). This has important implications for high-altitude forest management.

Any consideration of the functioning and manipulation (resource use) of high-mountain forests must relate to the temperature constraint on forest growth at altitude, which has several vital consequences. First, growth rates are progressively reduced with increasing altitude. In conjunction with steep slopes, however, this restraint is associated with azonal soils, frequently of low nutrient value. Thus, ecosystem manipulation based on short-term economic considerations can result in long-term environmental and economic losses. At issue here is the potentially very long recovery period, if recovery is at all possible, following disturbance. Witness the

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Jack D. Ives is President, International Mountain Society and Professor and Chairperson, Department of Geography, University of California, Davis, CA 95616.

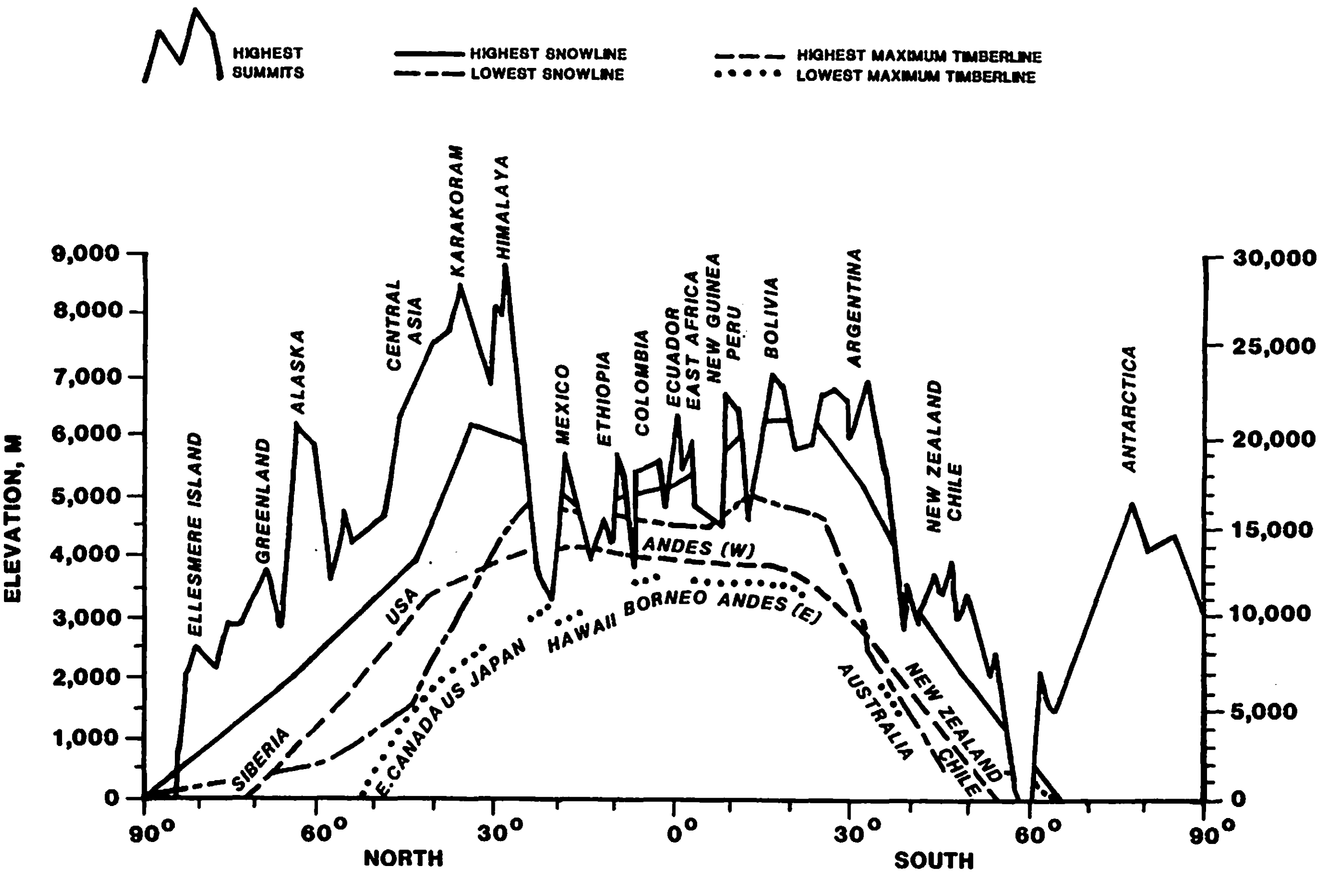


Figure 1—Global cross-section of the alpine regions, showing the highest summits, snowline, and timberline (Ives and Barry 1974; partly after Swan 1967).

lack of success in restoring timberlines in the Alps, despite much research and great expense in high-altitude planting.

These considerations are of particular value where climatic climax forests prevail—in other words, in the comparatively little disturbed high-mountain forest belts of North America. For much of the rest of the world upper timberlines have been extensively disturbed by human intervention, sometimes over thousands of years. This leads into the issue of the associated resources of the high-mountain forest belts: an issue beset with value judgments and resource-use conflicts.

RESOURCE USE ISSUES

Societies have undergone significant changes in the values placed on high-mountain forests. These changes have occurred over both long and short periods of time, and they also occur in space, in the sense that very different sets of values are placed on montane forest resources in different parts of the world today.

These changes in the value placed on high-mountain forest resources relate to the second common denominator—relative inaccessibility. In subsistence societies, such as the Alps of the Middle Ages, and the Himalaya and Andes of today, the forests both were, and are, closely integrated with subsistence living. Thus they provided multiple subsistence products, fuelwood not necessarily being the most important, together with a vital array of secondary products, such as wild game, berries, fruit, mushrooms, and open grazing for domestic animals. In many mountain areas it was the growing pressure on grazing land, to provide for increases in human populations, that led to extensive, even catastrophic, lowering of the upper timberlines. This is particularly well documented for the Alps.

From the perspective of present management of high-mountain resources in many developing mountain countries (the so-called Third World) a serious problem has arisen. This results from conflicts between aid agencies and governments, and mountain subsistence communities, in terms of how the forests are perceived. There is a "Western," or Eurocentric, view that regards the forests as a "sustainable resource," whereas many, although by no means all, mountain subsistence communities regard them as a "convertible resource." Thus, as long as mountain farmers view their forests as an opportunity for expansion of arable farming through forest clearance, it would appear that grandiose schemes for reforestation imposed from "outside" will have little chance of success.

The remainder of this paper will be devoted to a discussion of some of these issues. Brief case studies are presented to illustrate the complexity of high-mountain resource use issues on a global scale.

The Alps

As already mentioned, the Alps have experienced massive forest manipulation over many centuries. Deforestation of the upper montane forest belt, especially on *adret* (sunny) slopes, has resulted in progressive lowering of the timberline between 200 and 600 m (Tranquillini 1979). Periodic natural disasters, such as snow avalanches, mudflows, landslides, and floods, were recognized long ago to be related to unwise deforestation.

Several, if intermittent, attempts were made to control the loss of forest cover, but with limited success. Nevertheless, continued environmental deterioration resulted in the initiation of a series of forest laws in the closing decades of the last century that have been strengthened progressively up to the present (Price 1988). Switzerland, for instance, has a more extensive forest cover today than it had 90 years ago. However, during these last nine decades, the Swiss in particular, and residents of the entire Alpine region in general, have radically changed their perceived priorities of various upper montane forest uses. Subsistence use and export of commercial timber have virtually ceased. Esthetics, watershed management, and protection against natural hazards have come to dominate.

The irony is that current forest management is severely hindered by what were originally progressive forest laws and what are now anachronisms. The situation is made the more complex by the continued expansion of tourism, especially winter sports, and second home construction, and by the recent forest dieback, at least in part associated with atmospheric pollution. It is a remarkable fact that the cost of harvesting timber in the Alps is so high today that Finland has become a major source of lumber for Swiss mountain chalets.

The Rocky Mountains

Price's (1988) comparative study of the Swiss and Colorado forest laws and their impacts brings to light a number of fascinating points. The forest laws of the United States developed along lines very similar to those of Switzerland, both in terms of objectives and timing. More specifically in Colorado, pressure on the montane forests in the latter half of the last century derived predominantly from the mining boom and widespread firing, both natural and deliberate; this caused extensive official concern eventually resulting in enactment of a series of forest laws.

Once again, however, the majority of forest users today perceive the forests of the Rocky Mountains as valuable primarily for recreation, watershed management, wilderness, and wildlife preservation. There remain serious conflicts, nevertheless, in terms of ski resort and second home development and an economically marginal, but subsidized, timber industry. The controversy over fire suppression, at least in part, must be regarded as being exacerbated by now anachronistic forest laws.

The Nepal Himalaya

The World Bank (1979), many individuals (Eckholm 1976; Myers 1986), and many other agencies, have reiterated so often that Nepal will have no accessible forest cover by the year 2000 that this view of impending environmental disaster has had a momentous impact on foreign aid policy. The issue is a particularly fascinating one because a series of virtually "sacred" truisms has been used to convince governments, United Nations agencies, non-government organizations, and the conservationist public at large, that the "ignorant" and overly fecund mountain subsistence farmer, because of the supposed extensive deforestation, is responsible for massive damage to the life-support base of several hundred million people on the Ganges and Brahmaputra plains. This concern reached a crescendo in September 1988 when reportedly unprecedented flooding in Bangladesh, which put more than 60 percent of the entire country under water, was blamed in large part on the irresponsible mountain farmer. The Government of Japan is reportedly offering to collaborate with the United States and Bangladesh to reduce, or even prevent, future flooding through a series of massive infrastructural interventions, entailing the expenditure of billions of dollars. This would include extensive reforestation in the Himalaya, major headstream storage reservoirs, barrages, main channel canalization, and construction of artificial levees.

Unfortunately, the assumptions upon which such albeit preliminary policy formulation is based are at least largely unproven, or even totally false. This highly controversial statement is too complicated for adequate discussion here. It is the topic of a new book—"The Himalayan Dilemma: Reconciling Development and Conservation" (Ives and Messerli 1989). Yet some general statements are warranted.

Our claims concerning unproven, even false, assumptions are based upon an array of individual, small-scale studies that led to the serious questioning of the validity of many widely assumed cause-and-effect relationships that go to the heart of any attempt to evaluate the resource management approaches to high-mountain forests.

In many areas of the Himalaya, where reasonably reliable information is available, it appears that deforestation has not been a dramatic post-1950 phenomenon associated with the population explosion, as is so often stipulated (fig. 2). Deforestation in the Middle Mountains of Nepal (the region of major population concentration throughout history), and in many other parts of the Himalaya, was well advanced by the beginning of the 18th century and accelerated due to the imposition of government policy after the militant unification of Nepal under the House of Gorkha in 1769. Rapid conversion of mountain forest land to terraced agriculture was set in motion by the taxation structure, and continued throughout the last century. It appears, however, that by the 1930's most convertible forest land had been converted; the last 50 years have seen little change in forest area, although considerable depauperation of the remaining forest has occurred (Griffin 1988; Mahat and others 1986).

There is little reliable evidence to causally link deforestation, soil erosion, and landslide incidence (Ives and Messerli 1989, chapter 5), and there is even less support for the widely held assumption that land-use changes in the mountains have had serious impacts on the plains (Ives and Messerli 1989, chapter 6) (fig. 3). It has been claimed that Bangladesh is flooded because it periodically rains a lot (Hamilton 1987)! This seemingly outrageous statement demands the introduction of a number of others:

1. Deforestation on steep mountain slopes, particularly in tropical and subtropical regions, does not necessarily lead to increased soil erosion and slope instability—what rather is at issue is the manner of forest cutting and the alternative uses to which the cleared land may be put (fig. 4).
2. Despite widespread claims to the contrary, general Third World mountain deforestation is not a recent phenomenon.
3. Flooding and siltation on the flood plains of great mountain rivers, such as the Ganges, the Brahmaputra, and the Yangtze, are largely inevitable natural processes that have occurred throughout geological time. Recent deleterious impacts, if influenced to any extent by human activities, are more likely due to human intervention on the flood plains themselves, rather than to land-use changes in the upper catchments.
4. Deforestation is not necessarily "BAD."
5. Development of mountain resources requires sensitive understanding of the desires, objectives, and indigenous environmental knowledge of the local people.

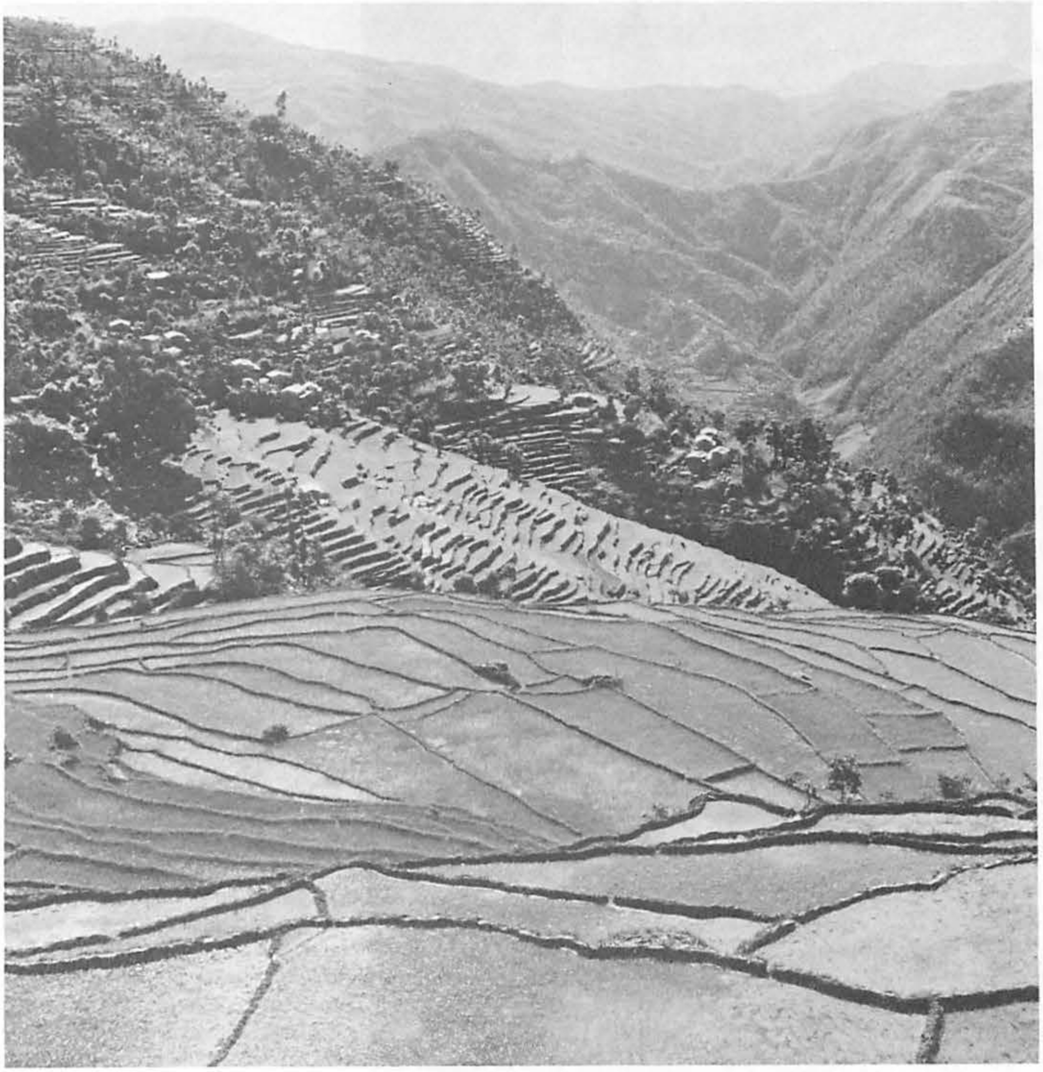
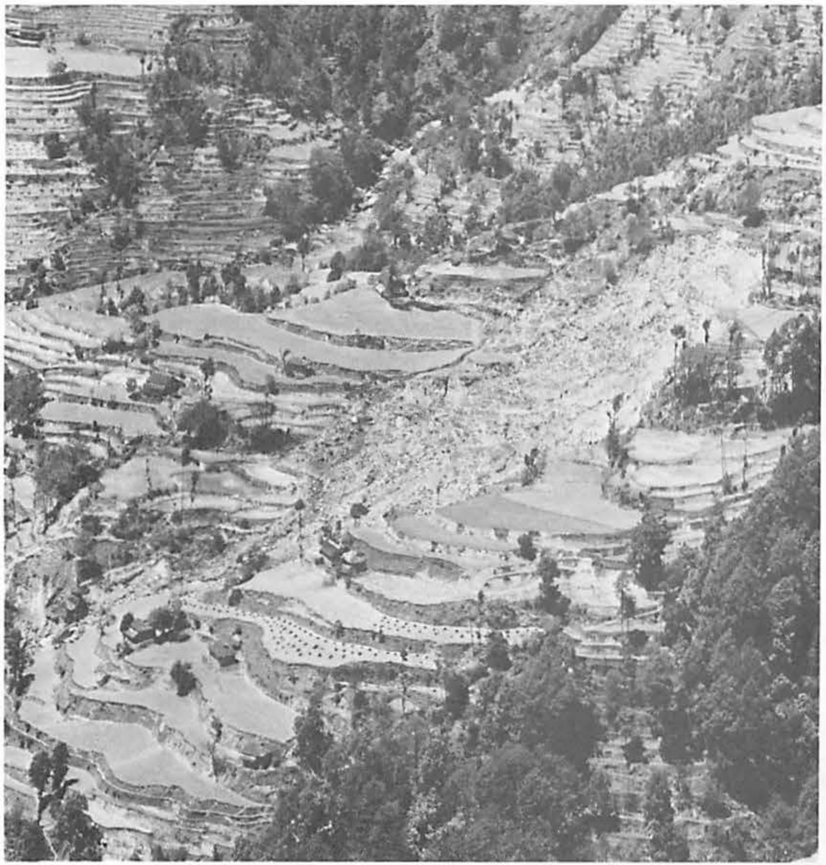
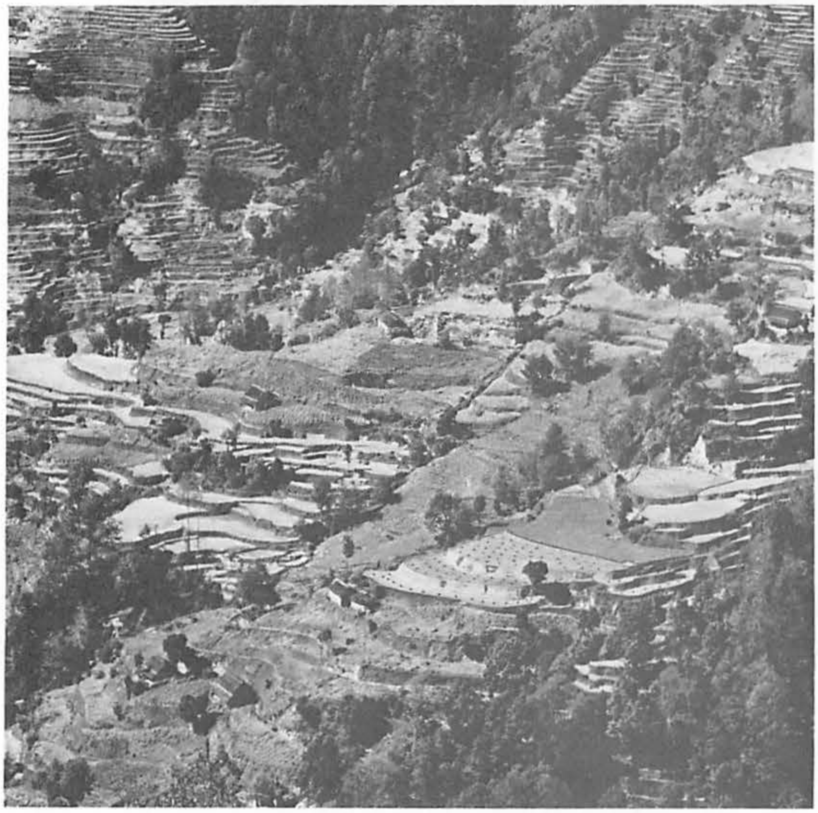


Figure 2—Sindhu Palchok District, Nepal Middle Mountains, near Chautara. Is deforestation really bad? The densely wooded steep slopes in the distance give an indication of what the foreground would have looked like before human impacts initiated in the 18th century. Now these magnificently constructed and tended khet, or irrigated, terraces grow multiple crops of paddy rice and winter wheat. They also represent an excellent soil conservation approach to steep mountain slopes without outside aid or interference.



A



B

Figure 3—(A) Photograph from the Trisuli Road below Kakani, in the Nepal Middle Mountains. The landslide occurred during the preceding monsoon season, (1978) and was regarded as exceptionally unstable and likely to enlarge. (B) The same view as shown in (A), but taken in October 1987. It is now almost impossible to determine the location of the landslide and it is unlikely that, without access to photo (A), the visiting "expert" would ever understand the land-use history of this site. Several houses, visible in A, have been moved or pulled down and the forms of many of the undamaged terraces have changed markedly. This is a very dynamic landscape.

Figure 4—This hillside, Lalitpur outside the Kathmandu Valley, was previously photographed from the air in 1981 by Brian Carson. His picture showed more than a hundred landslides caused by torrential rain. Many of the landslide scars still can be seen but only very faintly. They are largely revegetated and careful inspection is needed. A casual visitor to the area would probably notice nothing unusual.

The Hengduan Mountains, Northwestern Yunnan

Many of the dire predictions for environmental collapse ascribed to the Himalaya have been used to categorize the high-mountain and plateau forest lands of southwest China. In 1985, 10 weeks were spent undertaking detailed biogeographic and geomorphic research in the Yulongxue Shan (Jade Dragon Snow Mountains) of northwestern Yunnan (Ives 1985; Ives and Messerli 1989). Somewhat similar conclusions were obtained to those outlined for the Nepal Himalaya. In this case it was concluded that much of the widespread deforestation of the Yunnan Plateau, attributed to Chairman Mao Tsedung, the Great Leap Forward, and the Cultural Revolution, actually represents centuries, if not more than a thousand years, of progressive conversion of forests to agriculture. In the higher mountains a very complex situation was at least partially unraveled. Replication of high-quality photographs, taken in the 1920's and 1930's by Dr. Joseph F. Rock and kindly made available by the National Geographic Society, facilitated direct comparisons of forest cover over a 50- to 60-year period (fig. 5). In some specific localities forest cover was more luxurious and forest canopy more complete in 1985 than in Rock's time; in other localities there was little discernable difference (fig. 6); and in yet others serious and recent deforestation had occurred (figs. 7 and 8). In part, this can be explained by differences in relative accessibility, but it is also related to management policies of local leaders (fig. 9).

These general remarks are in no way intended to indicate that China does not face serious land-use problems in the important forest region of the southwest. Rather they support the claim that there is a need for development of a much longer historical perspective. The lesson to be learned, once again, is that mountains, and mountain peoples, are extremely diverse from region to region and that generalization and simplification are fraught with the risk of producing inaccurate conclusions. In addition it raises a challenge to the tendency for overdramatizing environmental catastrophe without first obtaining reliable data.

CONCLUSIONS

What can be learned from the foregoing, admittedly all too brief, commentaries on widely scattered areas of the high-mountain forests of the world? How is this relevant to concerns about the ecology and management of the whitebark pine ecosystems?

It would seem evident that we are still lacking high-quality, replicable information about high-mountain forest ecosystems, and this is likely as true for Montana as it is for the Alps and the Himalaya. It follows that, in view of the limited available resources for effective research, a rigorous intellectual approach is needed for the identification of vital gaps in knowledge so that the research resources that are available can be used most effectively. A corollary is that a much more efficient system for sharing information and experience is required. A succession of conferences to follow this one should be seriously considered.

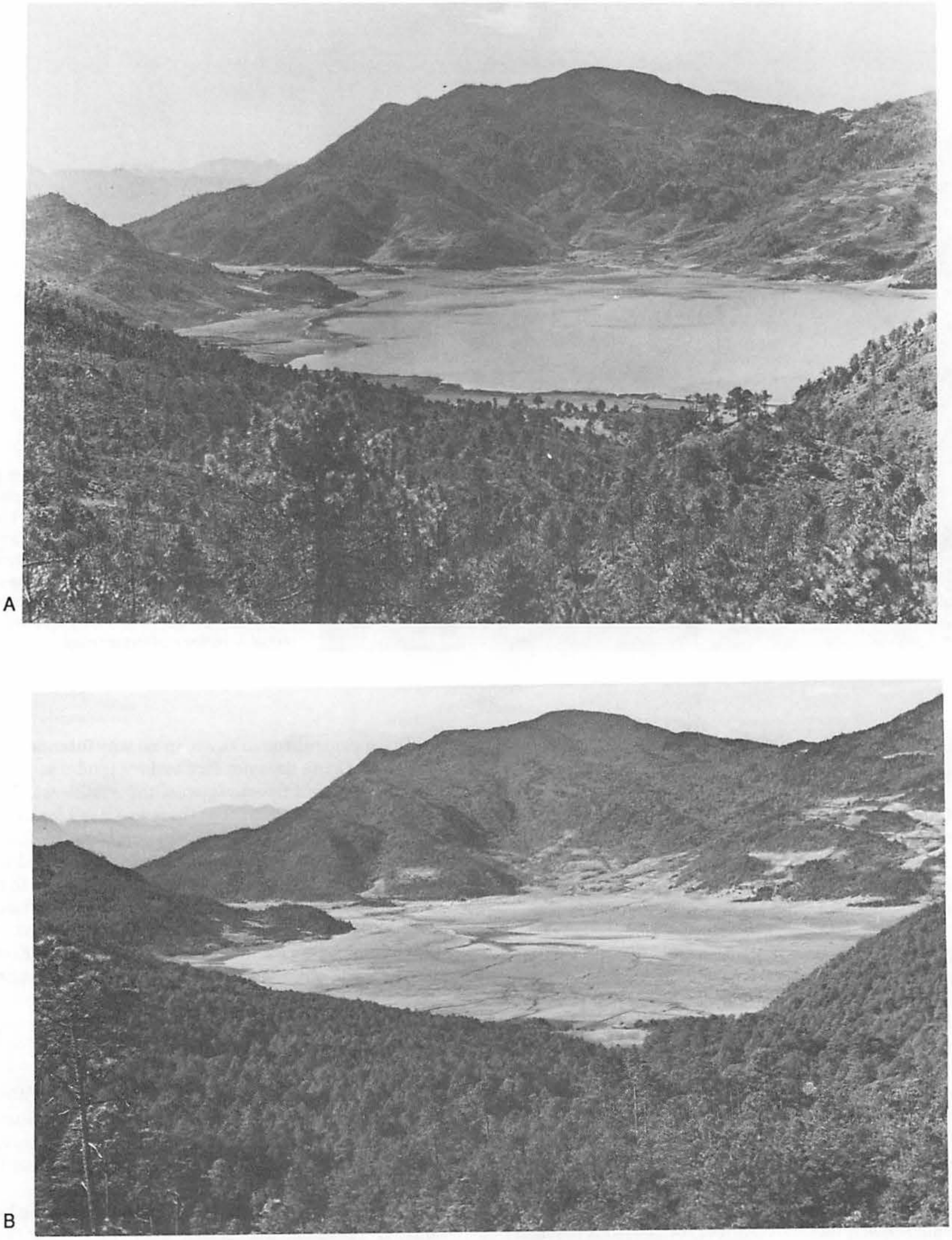
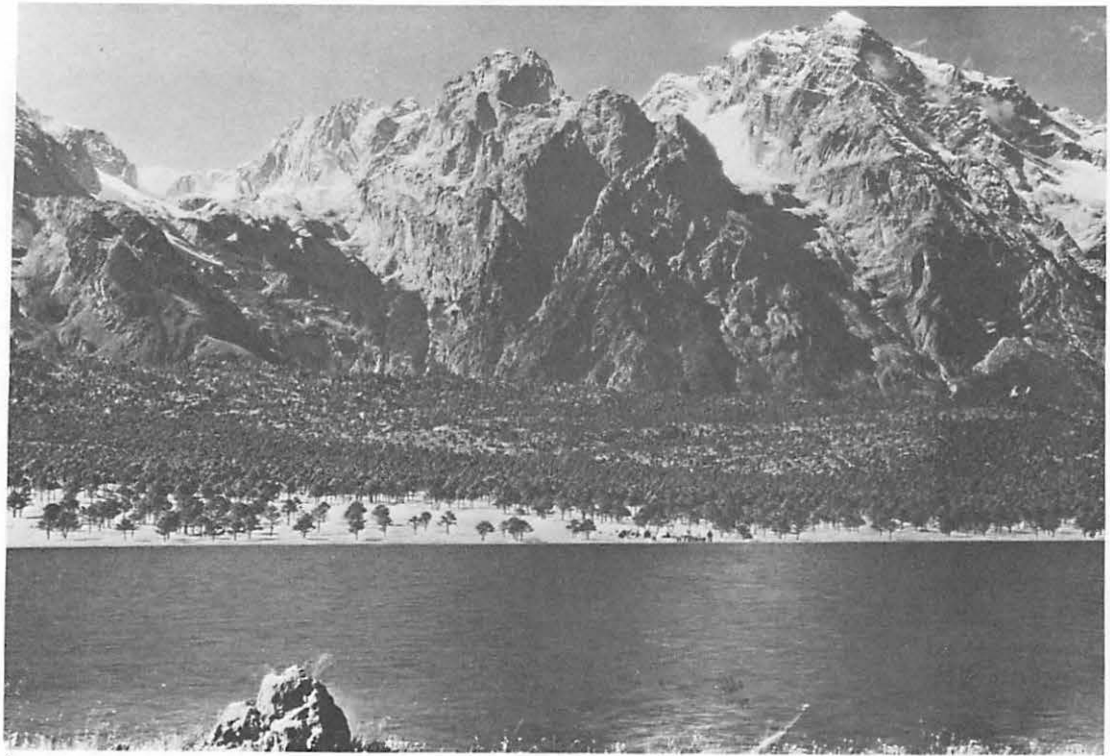


Figure 5—(A) Photograph taken in 1928 by Dr. Joseph F. Rock, Lijiang autonomous county, northwestern Yunnan. The time is postmonsoon and the doline is partly filled with water forming a shallow lake; it is usually dry by the following spring. Note the rather poor condition of the forests, both in the foreground, and especially on the steep slope on the right, and on the opposite side of the lake. (Courtesy, Dr. Barry C. Bishop, National Geographic Society). (B) Replicate of photograph shown as (A) taken in April 1985 by the author. The lake is now dry because of the season. Note the closed crown cover on the steep hillslope to the right. Also, despite the considerable distance, it is clear that the forests on the far side of the lake are more extensive and more luxuriant than they were in 1928.



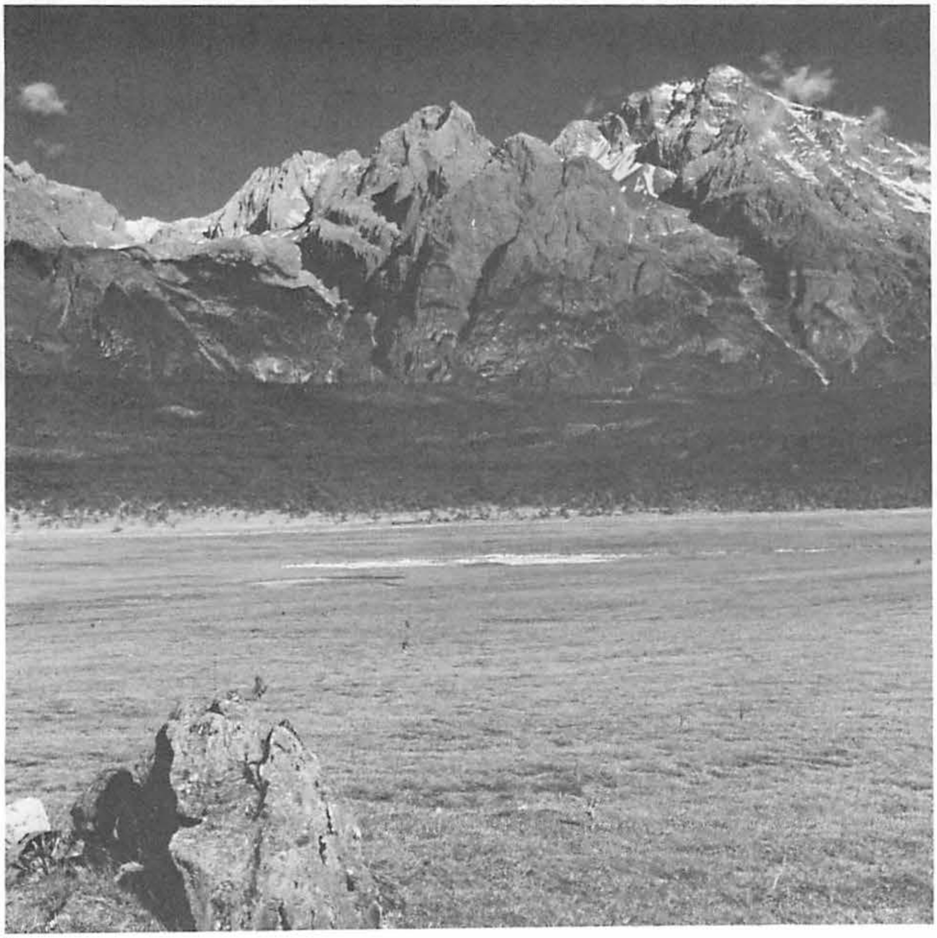


Figure 6—(A) The east face of the Yulongxue Shan, northwestern Yunnan, as seen by Dr. Joseph F. Rock in 1928. Rock's camp is situated on the far side of the karst lake. The forest cover in the middle ground is somewhat open and immature, being cut over and fired from time to time. (Courtesy Dr. Barry C. Bishop, National Geographic Society). (B) The same scene as that shown in (A), but taken in April 1985 by the author. The lake is now dry. The conspicuous rock in the foreground greatly aided the location of Rock's camera position. The forest in the middle ground is in approximately the same condition although most of the trees are only 25 to 40 years old (based on tree ring count); the area is being actively harvested today. Most of the trees of Rock's time were subsequently felled.

Figure 7—Hengduan Mountains, northwestern Yunnan, People's Republic of China. With the recent (post-1979) improvement in housing, additional pressures have been put on the forests nearest the villages. This view in Lijiang autonomous county looks across the Jinsha Jiang (Yellow River) onto heavily impacted mountain slopes. Note the numerous skid trails, some converting into gullies, with the more inaccessible slopes retaining a much fuller forest cover.

Figure 8—Large sections of the Yunnan Plateau have been totally deforested and soil erosion has proceeded to such an extent that the C-horizon has disappeared exposing the bedrock. This scene is traversed by the main road between Kunming and Dali, which is lined with eucalypts. Only on sheltered valley floors has enough soil been preserved to permit agriculture. Natural climax vegetation would be closed-crown monsoon rain forest. This deforestation, however, occurred hundreds of years ago, if not more than a thousand.

Figure 9—A once densely forested section of the high Yunnan Plateau between the Jinsha Jiang and the Mekong trench. Lack of coordination between loggers and transport authorities resulted in many square kilometers of logs being left on the ground to rot. In contrast to figure 8, this is modern, and very destructive, deforestation.

It also seems arguable that much that pervades the popular press, as well as some of the scientific literature, may be based upon misconceptions, false assumptions, even manufactured data. There is the need to challenge unproven assumptions in the context of good research that should lead to better management of high-mountain ecosystems. Mountains, even those without indigenous cultures of many centuries standing, are some of the world's most complex biophysical systems. Therefore, superficial generalization can lead to ill-founded conclusions, and in turn, misconceived management policies. It follows that the mountain researcher has a responsibility to enter the political arena and help correct false impressions that are being generated among the public at large.

The earlier remarks, suggesting a lack of relationship between deforestation and soil erosion, implying that deforestation is not necessarily "BAD," therefore, it might be "GOOD," are not intended as relevant to the whitebark pine ecosystems. What I would urge, however, is that, in our evaluation of high-mountain resource management issues, we must avoid mixing value judgments, old wives' tales—or "sacred cows," if you will—and scientifically based conclusions. But we must also recognize that society's values change with time and vary widely from one part to another of our present-day world. There is a need to demonstrate, unemotionally, that forest laws, or land management regulations in general, frequently do not keep pace with the changing values; this in turn has important implications for effective management. Additionally, the prospects for long-term environmental and economic losses that can ensue from unsound manipulation of these cold-stressed mountain forest ecosystems must be presented forcefully to the decision makers concerned.

REFERENCES

Arno, S. F.; Habeck, J. R. 1972. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Ecological Monographs. 42: 417-450.

Eckholm, E. 1976. Losing ground. New York: Worldwatch Institute, W. W. Norton and Co., Inc.

Griffin, D. M. 1988. Innocents abroad in the forests of Nepal. Canberra, Australia: Anutech Pty Ltd.

Hamilton, L. S. 1987. What are the impacts of Himalayan deforestation on the Ganges-Brahmaputra lowlands and delta? Assumptions and facts. Mountain Research and Development. 7(3): 256-263.

Hansen-Bristow, K. J.; Ives, J. D. 1985. Composition, form, and distribution of the forest-alpine tundra ecotone, Indian Peaks, Colorado, U.S.A. Erdkunde. 39: 286-295.

Ives, J. D. 1985. Yulongxue Shan, Northwest Yunnan, People's Republic of China: a geoecological expedition. Mountain Research and Development. 5(4): 382-385.

Ives, J. D.; Barry, R. G., eds. 1974. Arctic and alpine environments. London: Methuen: 3.

Ives, J. D.; Hansen-Bristow, K. J. 1983. Stability and instability of natural and modified upper timberline landscapes in the Colorado Rocky Mountains, U.S.A. Mountain Research and Development. 3(2): 149-155.

Ives, J. D.; Messerli, B. 1989. The Himalayan dilemma: reconciling development and conservation. London and New York: Routledge and United Nations University. 295 p.

Mahat, T. B. S.; Griffin, D. M.; Shepherd, K. R. 1986. Human impact on some forests of the Middle Hills of Nepal. I: Forestry in the context of the traditional resources of the state. Mountain Research and Development. 6(3): 223-232.

Myers, N. 1986. Environmental repercussions of deforestation in the Himalayas. Journal of World Forest Resource Management. 2: 63-72.

Price, M. F. 1988. Mountain forests as common-property resources: management policies and their outcomes in the Colorado Rockies and the Swiss Alps. Boulder, CO: University of Colorado. Thesis.

Swan, L. W. 1967. Alpine and aeolian regions of the world. In: Wright, H. E., Jr.; Osburn, W. S., Jr., eds. Proceedings, VII congress International Association for Quaternary Research. Arctic and Alpine Environments. 10: 29-54. Bloomington: Indiana University Press.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. Ecological Studies No. 31. New York: Springer-Verlag.

Troll, C. 1973. Upper timberlines in different climatic zones. Arctic and Alpine Research. 5: A3-A18.

Wardle, P. 1974. Alpine timberlines. In: Ives, J. D.; Barry, R. G., eds. Arctic and alpine environments: London: Methuen: 371-402.

World Bank. 1979. Nepal: development performance and prospects, a world bank country study. Washington, DC: World Bank, South Asia Regional Office.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Lawrence McHargue)—In view of some similarities in both terrain and climate, are any of the pines of the Central Asian mountains as long-lived as *Pinus* spp. around the Great Basin?

A.—I have no direct information with which to answer this question, nor have I been able to find anything in the literature. But now that the Central Asian mountains are becoming much more accessible, it would be most interesting to find out.

Q. (from Ray Brown)—You mentioned that one of the best things we in western countries could do for people in high-mountain regions of the Third World would be to leave them alone. However, we have learned a great deal about such things as revegetation techniques for alpine-subalpine disturbances, natural successional processes in these life-zones, and methods of selecting adaptive native plant species for revegetation practices. Don't you think we could initiate a program wherein we, on both sides, could demonstrate and teach what we have learned, and also learn from them new approaches and techniques? If not, why not?

A.—I have to agree that such a course ought to be very worthwhile. I am not so much dedicated to the isolation of mountain minority groups in the Third World, as to the need to treat them, both collectively and individually, as equals. In such circumstances the learning process would be two-way. Foreign aid would then progress from being a charity (a humiliating experience) to gift-exchange (an elevating experience). As "mountaineers" we should be enthusiastic about the latter! My remarks that provoked this eminently reasonable question were essentially a reaction to the nearly pervasive imposition of "outside" and "appropriate" (so often inappropriate) technologies that have frequently caused more harm than good, despite the sincerity and goodwill associated with them.

Q. (from Harry Hutchins)—How can we work with local cultures to improve subalpine forests in areas such as Tibet and Yunnan, China?

A.—I think that there is a good chance to work with local cultures in Tibet and Yunnan, despite the current political difficulties. It first would be necessary to achieve a sensitive collaboration on two fronts, both with the Chinese authorities and the local people. I think that the former would be relatively easy in many situations; the latter more difficult. However, the recent work of Drs. M. Goldstein and C. Beall, as anthropologists working with the nomads on the Tibetan Plateau (see National Geographic Magazine, June, 1989) is cause for considerable optimism. I am implying here that much of the "environmental" problem is political at several levels; it is necessary to break through the communication difficulties and to find a truly appropriate approach.

Q. (from Tad Weaver)—Why have agricultural terraces been deserted in the Soviet Pamirs? Is there similar desertion elsewhere?

A.—The abandonment of agricultural terraces in the Soviet Pamirs was primarily a 1930's to 1960's phenomenon. During this period marginal mountain peoples were attracted to the commune and state farms of the lowlands in response to the labor shortage with the development of irrigated agriculture (cotton and fruit). Widespread mountain depopulation occurred. Since 1986 a reverse flow has developed, the impacts of which will be extremely interesting to follow.

BIOLOGY, TAXONOMY, EVOLUTION, AND GEOGRAPHY OF STONE PINES OF THE WORLD

Ronald M. Lanner

ABSTRACT

*Stone pines (*Pinus *subsection* Cembrae*) are morphologically defined by wingless seeds and cones that remain closed at maturity, retaining their seeds within. These characteristics have been attributed to selection by the nutcracker (*Nucifraga *spp.), which caches seeds of these pines, causing them to regenerate from subsoil caches. Arguments are presented in support of retaining* Pinus pumila *Regel and* P. albicaulis *Engelm. in* Cembrae. *New data are presented on seed retention in* P. koraiensis *cones. Stone pines are shown to have similar environmental tolerances and successional roles.*

INTRODUCTION

The Stone pines are those species of section *Strobus* that have five-needled fascicles, wingless seeds, and cones that remain closed at maturity (subsection *Cembrae* Loud.) (Little and Critchfield 1969). They are whitebark pine (*Pinus albicaulis* Engelm.), Swiss stone pine (*P. cembra* L.), Korean stone pine (*P. koraiensis* Sieb. and Zucc.), Japanese stone pine (*P. pumila* Regel), and Siberian stone pine (*P. sibirica* Du Tour). The uniting of these species into a group or subsection has been common practice since Shaw did so in "The Genus Pinus" (1914). It is not without controversy, as we shall later see.

Winglessness is a common trait in the subgenus *Strobus* (fig. 1), though it is rare among the hard or yellow pines of subgenus *Pinus*.

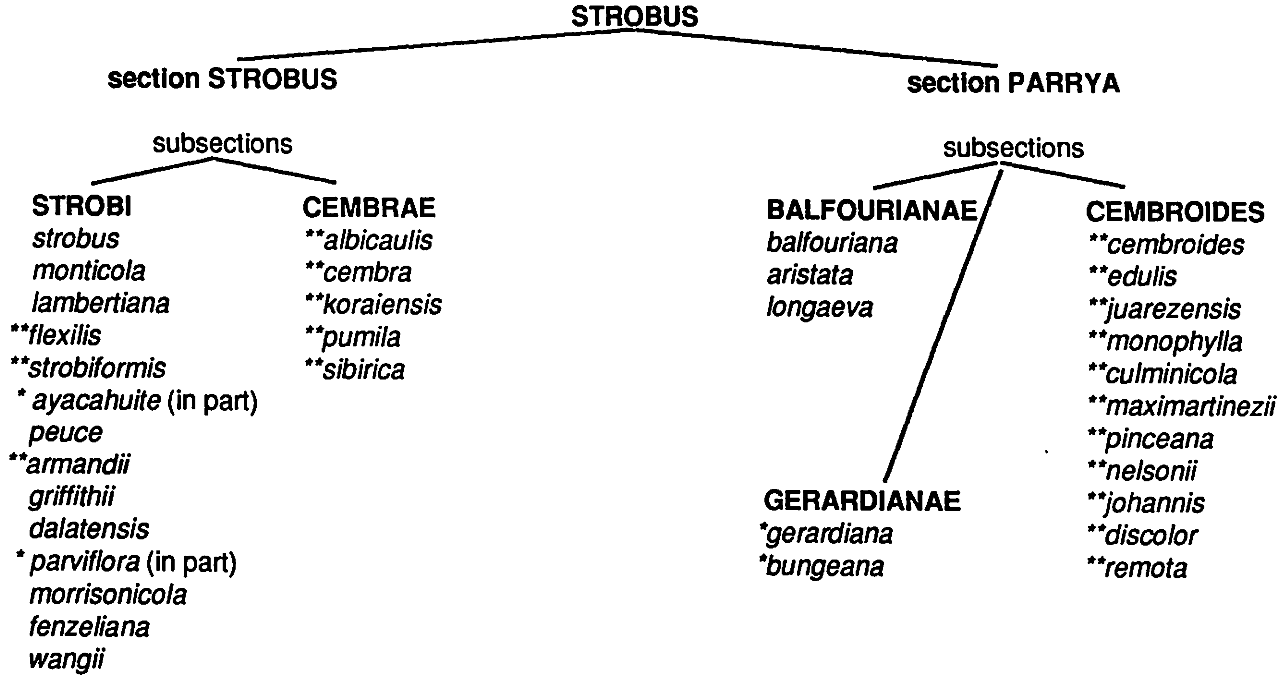


Figure 1—Distribution of wingless-seeded (**) and nearly wingless-seeded (*) pines within subgenus *Strobus*.

Paper presented at the symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Ronald M. Lanner is Professor, Department of Forest Resources, Utah State University, Logan, UT.

The "indehiscence" of cones (Little and Critchfield 1969; Shaw 1914) is, in contrast, absent from all other pine subsections, and it is this characteristic that really sets the stone pines apart.

It sets them apart not only in the taxonomic sense, as a diagnostic morphological feature, but in a more profound sense as well. This strange cone, and the wingless seeds within, provide an essential link to those corvids of the genus *Nucifraga*—the nutcrackers—that have played a central role in the biology, taxonomy, evolution, and geography of these fascinating pines. That is a very long story, and one that cannot be comprehensively covered in this paper. Instead, I will discuss just a few of the issues regarding the *Cembrae* that have received relatively little attention, with the objective of showing the essential coherence of this group of species.

BIOLOGY

In the only detailed report on the behavior of stone pine cones, Lanner (1982) showed that many undisturbed *albicaulis* cones remain on the tree and retain their seeds at least until the following July, long enough for the seeds to become inviable. The cone scales become loose in the fall, but do not part enough to allow seeds to fall out. Failure of the scales to reflex is apparently due to the absence of a layer of coarse tracheid strands beneath the adaxial surface—as first pointed out by Shaw (1914)—which, in other pines' cones, shrinks longitudinally, pulling the scale open (Harlow and others 1964). The absence of that tissue also makes the cone scales brittle and easy to break off, despite the formidable appearance lent by their massive apophyses. When they are broken off, the fracture zone is usually just distal to the midpoint of the subtended seeds, so most of the seeds remain in place, held in the "core" of the cone. Thus scale removal displays their seeds to the animal that removes the scales (Lanner 1982). These morphological and anatomical traits (fig. 2) facilitate the harvest and dispersal of *albicaulis* seeds by Clark's nutcracker (*Nucifraga columbiana* Wilson), as described in detail by Tomback (1978). Prior to ripening, the cones are pulpy, and can be pecked apart by nutcrackers feeding on the immature seeds.

The visibility of exposed stone pine seeds may be enhanced by conspicuous dark-brown to black markings (about 3 by 4 mm) on the hilum. These prominent "eyes" are not found in *albicaulis*, but occur on seeds of *koraiensis* from Japan (fig. 3), *sibirica* from Symansky Pass, Siberia, and *cembra* from the Austrian Alps. Sketches by Saito (1983a; 1985) show them in Japanese *pumila* as well.

Following harvest, nutcrackers cache many whitebark pine seeds in the soil, allowing those not later recovered or destroyed by predators to germinate. Thus the cone characteristics of *albicaulis* help ensure its regeneration. In a comparative study that assessed the role of nutcrackers and other animals in *albicaulis* regeneration, resident mammals and birds other than nutcrackers "did not have the requisite behaviors to systematically disperse or establish whitebark pine, and the pine was therefore dependent on the nutcracker for its regeneration" (Hutchins and Lanner 1982).

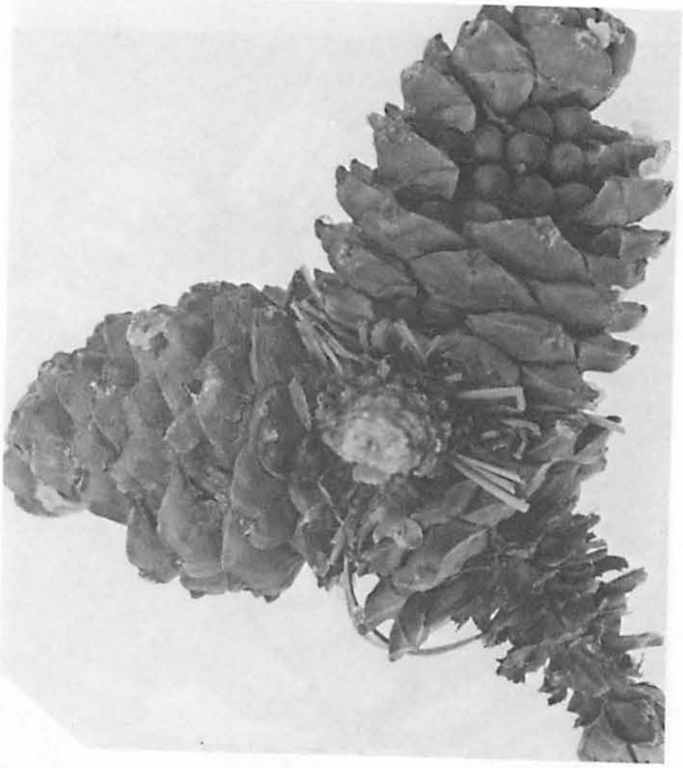


Figure 2—Mature *Pinus albicaulis* cones that are intact (left), partially divested of scales so as to expose the seeds within (upper right), and completely divested of scales and seeds, showing fragility of fracture zones (lower right). (From Lanner 1982.)

The situation appears similar among the other stone pines. *Pinus cembra* has been studied in detail by a number of investigators (Crocq 1978; Holtmeier 1966; Mattes 1982; Oswald 1956) in the Alps of Austria, Switzerland, and France. Its relationship there with the European nutcracker (Common names of subspecies of *N. caryocatactes* follow Dement'ev and others [1954]). *N. caryocatactes* ssp. *caryocatactes* is strikingly similar to the *albicaulis*-Clark's nutcracker mutualism. According to Oswald (1956) natural reproduction of *cembra* without the nutcracker is "scarcely conceivable." Mattes (1982) referred to the nutcracker as "an essential help in reforestation." In Poland, where specific studies of nutcrackers appear not to have been made, the nutcracker's role as a "sower" of *cembra* has been recognized (Myczkowski and others 1975). A difference between *cembra* and *albicaulis* is that seeds of the former are cached on stumps and in trees as well as in the soil (Holtmeier 1966; Mattes 1982). Seeds of *sibirica* are cached beneath moss polsters (Konev 1952).

Studies in the Soviet Union have shown an almost identical situation in the Urals and across much of Siberia, where the Siberian nutcracker (ssp. *macrorhyncos*) harvests and stores the seeds of *P. sibirica*, a

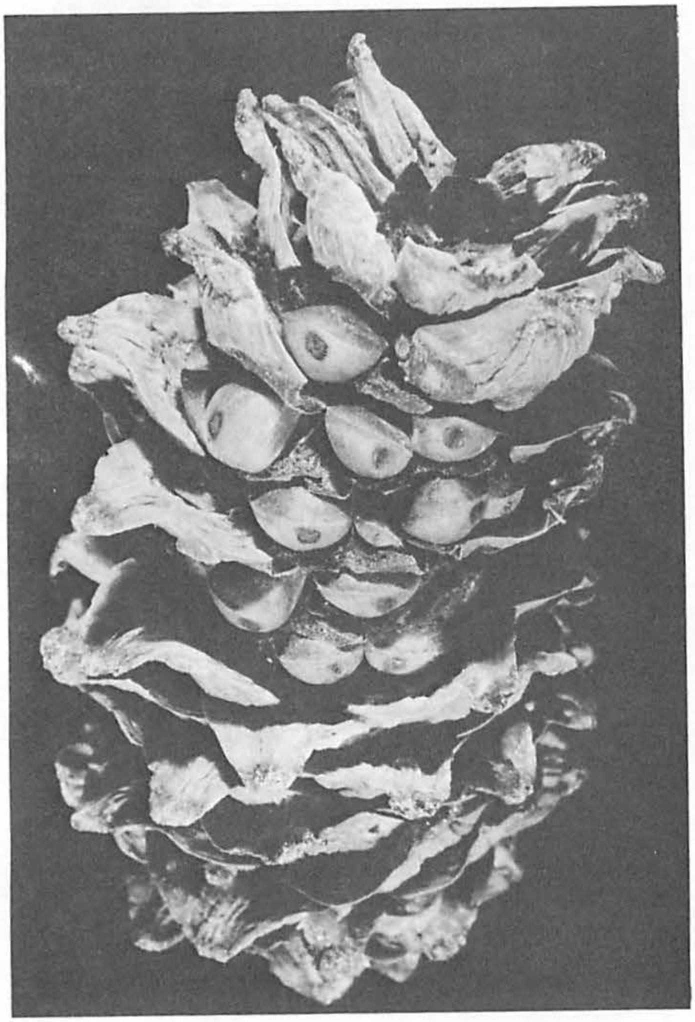


Figure 3—"Eyes" formed by the dark hilum of *Pinus koraiensis* seeds exposed by removal of cone scales.

species of economic value for its edible nut crops as well as its timber. Turcek and Kelso (1968) documented the extensive Russian literature on this subject.

In the Far East research has been less active. Little information is available, for example, on the harvest and storage of *P. koraiensis* seeds by the Siberian nutcracker, which is found throughout the range. This was true of *pumila* until the recent studies of Saito (1983a; 1983b; 1985), performed in a mountainous area of northern Hokkaido. Not surprisingly, Saito reported Japanese nutcracker (ssp. *japonicus*) behavior and *pumila* ecology almost exactly like that reported in Europe and North America, with allowances for such differences as the often-prostrate habit of the local stone pine species. According to Saito, the Japanese nutcracker is "the most effective disseminator of seeds of the (Japanese stone) pine" (Saito 1983a).

The strength of the stone pine-nutcracker interaction is dramatically illustrated by events—published here for the first time—in the lake district of southern Finland during the past two decades. Finland has numerous plantations of *sibirica* that were established as a hedge against crop failures when that country was under the Russian czars, apparently a common practice in Scandinavia and Russia (Holzer 1972). In 1968 Siberian nutcrackers invaded from the east, and a population of 10 to 15 pairs subsequently settled in Punkaharju. Ornithologists from nearby Savonlinna have observed these birds breeding in the vicinity, and congregating among the stone pines each fall, where they harvest pine nuts. Regeneration of *sibirica* has been observed some distance from the seed stands, presumably due to nutcrackers transporting and caching the seeds (Koski 1987; Vaisanen 1987).

The interaction of stone pines with nutcrackers has important biological consequences for the trees. To the degree that regeneration depends on seed caching by nutcrackers, site is determined by the bird's caching preference. Thus the tree will seldom have the opportunity to establish on a site not used for caching; but it will frequently have that opportunity on sites where nutcrackers do make seed caches. Caching does not automatically lead to seedling establishment, but merely creates the potential. Sites on which stone pines become established should be regarded as a sub-set of sites on which nutcrackers cache seeds. When sites within the range of both organisms lack stone pines it may be due to a lack of caches, or failure of cached seeds to become established.

Regeneration of stone pines from seed caches results, characteristically, in multiple germinations that lead to a high frequency of clumped stems (table 1). Clumping data have been reported for all the stone pines except *P. koraiensis*. The occurrence of many of a stone pine's stems in clumps has genetic implications. Furnier and others (1987) found that *albicaulis* trees within a clump were far more closely related to each other than to trees of other clumps, probably because they originated from seeds of the same cone; they were sibs or half-sibs. Such a genetic structure can potentially lead to heavy inbreeding, but this has not yet been examined.

Because nutcrackers cache seeds in an array of sites exhibiting a variety of physical and vegetational conditions, they become a factor in successional development. For example, *albicaulis* colonizes burned-over areas and rocky outcrops; or it may grow up through the gaps of an older canopy consisting of *albicaulis* and Engelmann spruce (*Picea engelmannii*), thereby acting as both a pioneer and a climax species (Lanner 1980). In a study of *albicaulis* establishment on the meadows of Squaw Basin in Togwotee Pass, WY, Snethen (1980) showed that this species was a pioneer on rocky outcroppings and moraines, and that only after pine groves had become established did Engelmann spruce grow up in their shade. Eventually the shade-tolerant spruce dominated the canopy, but nutcrackers continued to cache *albicaulis* seeds in the forest, maintaining large seedling and sapling populations of that species. The net effect of nutcracker activity in Snethen's study area was to accelerate secondary succession from a sagebrush (*Artemisia*)-grass mixture to a spruce-pine forest. As individual tree groves expanded, they formed a near-continuous cover, the shade of which supported numerous plants and animals not present in the sagebrush-grass vegetation type. In this

Table 1—Frequencies of multistem clumps among stone pines (*Pinus*, subsection *Cembrae*)

Tree species	Place and reference	Number of trees in sample	Trees in multistem clumps	Stems per clump
		n	*Percent*	*Range*
P. albicaulis	Wyoming, USA			
	(Lanner 1980)	1,270	47	2-8
P. cembra	Alps, France			
	(Crocq 1978)	167	89	2-11
		156	70	2-6
	(Lanner 1988)	154	66	2-6
	Alps, Switzerland			
	(Mattes 1982)	345	31	2->7
		214	39	2->7
P. pumila	Hokkaido, Japan			
	(Saito 1983a)[1]	69	94	2-19
P. sibirica	Sayan Mts., Siberia, USSR			
	(Konev 1952)[2]	ca. 3,600	—	2-23

[1] Saito's (1983a) data are based on seedlings, therefore avoiding errors that could be incurred due to layering of branches in this species.

[2] Percent of trees in multistem clumps cannot be calculated from Konev's (1952) data.

sense the nutcracker was a builder, or "edificator" of ecosystems in the sense of Reimers (Turcek and Kelso 1968). Reimers (1953) reported on the reforestation of *sibirica* by nutcrackers following fire and large-scale defoliation. Zykov (1953) pointed out the establishment of this species on the tundra margin.

Several authors have reported *P. cembra* in European larch (*Larix decidua*) stands, forming an understory. In Wyoming, whitebark pine sometimes becomes an understory in lodgepole pine (*Pinus contorta*) stands or in groves of quaking aspen (*Populus tremuloides*).

The environments in which the various stone pine species grow bear a striking resemblance. *Albicaulis* is found "in the highest elevation forest and at timberline" in a climatic zone that is "cold, windy, snowy, and generally moist" (Arno 1989). It is commonly associated with Engelmann spruce.

Pinus cembra was described by Plaisance (1977) as "an Alpinist . . . on bare rock to 2,400 m (7,900 ft), braving storms, snow, ice, wind." It too has a spruce associate, *Picea abies*.

Mirov (1967) stated that *sibirica*, which grows "in plains, in river valleys, and in the mountains of northern European Russia and Siberia" also occurs up to timberline in the Altai Mountains. According to Malyshev (1960) it reaches 1,950 m (6,400 ft) in the rugged Eastern Sayans, where its creeping, flat-topped growth resembles that of *pumila* growing in the alpine zone. Its common spruce associate is *Picea obovata* (Haddock 1977).

Pinus pumila "grows on very cold sites . . . in exposed and windy places" and cannot survive climates with hot summers (Saho 1972). Again, there is a spruce—*Picea glehnii*—associated with it in Hokkaido (Saito1985), and probably *Picea obovata* in Kamchatka.

Pinus koraiensis is found on a wide range of sites, from the relatively mild summer-rain region of Korea to the subarctic forest zone where it experiences temperatures as low as –35 °C (Hyun 1972). In Japan it is associated with *Picea jezoensis*.

It is beyond the scope of this paper to catalog the birds and mammals common to stone pine forests, but in addition to nutcrackers, chipmunks, squirrels, jays, and other animals typical of northern coniferous forests worldwide are common inhabitants of stone pine forests.

TAXONOMY AND EVOLUTION

Critchfield (1986) recently summarized the most commonly cited classifications of the white pines, including the stone pines, so there is no need to do so here. Instead, I will review and rebut Critchfield's reasons for rejecting the stone pines as a cohesive group of species sharing a common ancestor; and for suggesting that *pumila* and *albicaulis* do not belong with the "core species" of the *Cembrae*.

Critchfield (1986) expressed skepticism that the *Cembrae* really share "indehiscent" cones. He wrote:

"The indehiscent cone does not necessarily remain tightly closed at maturity" and detailed information on this point is "sparse and contradictory." He pointed out that in *albicaulis*, cone scale separation occurs "sometimes;" and that it is "usual" in *koraiensis* and *pumila*. This is misleading. I reported (Lanner 1982) that *albicaulis* cone scales become "loose enough to be displaced about 1-2 mm with slight pressure on the apophyses . . . upper scales frequently part as much as 8 mm, allowing seeds inside to be seen, *but not enough to let seeds fall out when the cone is turned or shaken*" (emphasis added). This is the important point, because the retention of seeds in the cone has been suggested as a nutcracker-selected characteristic that facilitates harvest of the seeds (Lanner 1982).

With regard to *koraiensis*, of which little has been written, I report here unpublished data of which Critchfield was unaware:

In December 1981 I experimented with mature 1981 *koraiensis* cones provided by the Kanto Forest Tree Breeding Institute at Mito, Japan. On many cones, several seeds were visible between slightly parted scales, especially in the distal area.

Experiment 1. Twenty-five cones each from lots Ohtaki-101, -104, -116, and -123 were rotated while being shaken. From these 100 cones only 11 of an estimated 8,140 seeds shook loose (0.14 percent).

Experiment 2. On 10 cones each from lots Ohtaki-101 and -123, 10 scales from mid-cone were broken off by finger pressure. The number of exposed seeds held in the cone core was counted. Cones were shaken and rotated, and the fallen seeds counted.

In lot 101, 160 seeds were exposed by removing scales; 41 of these (26 percent) were shaken loose. In lot 123, 131 seeds were exposed, of which 50 (38 percent) were shaken loose.

I conclude that *koraiensis* cones remain closed tightly enough to retain all but a minor portion of their seeds. (In February 1989, more than 7 years after being picked, they had opened no further). The majority of seeds are retained in the cone even after scale removal and vigorous shaking.

With regard to *pumila*, Saito (1983b) stated unequivocally: "The mature cones remain closed and do not release their seeds." Critchfield (1986) did not question the seed-retention abilities of *cembra* or *sibirica* cones, but should such questions arise in the future, the following should be noted: Crocq (1978) described how nutcrackers break off *cembra* cone scales one by one and added: "a dozen seeds or more are thus exposed." As for *sibirica*, I have found, in a cone from Symansky Pass, that seeds do not fall out when the cone is turned even after the scales are removed. It should be pointed out that these observations merely confirm Shaw's (1914) unequivocal characterization of all the *Cembrae* as having "indehiscent" cones that are "inert under hygrometric changes and may always be recognized in herbaria by their persistent occlusion . . .". Critchfield's (1986) skepticism of the effectiveness of these cones in retaining their seeds has, therefore, little basis.

Critchfield (1986) relied on de Ferré (1966) for findings that suggest *pumila* has closer affinities to *parviflora* than to the *Cembrae*. But de Ferré's conclusions are hardly definitive. For example, she wrongly stated that *parviflora*, like *pumila*, is wingless. This is not so (see below). De Ferré (1966) pointed out that *pumila* and *parviflora*, unlike *cembra* and *sibirica*, have folds in the walls of their mesophyll parenchyma cells, as do all other pines (Critchfield 1986). A later study of mesophyll cells showed that of three subtypes of cells with folds among *Cembrae* and *Strobi* species, *pumila* and *albicaulis* were of subtype 1, *koraiensis* and *armandii* of subtype 2, and *strobus* and *flexilis* of subtype 3 (Litvintseva 1974). And in a study of pollen morphology, Kuprianova and Litvintseva (1974) placed *pumila* with *cembra* and *sibirica*. De Ferré (1966) also found that both *pumila* and *parviflora* have warty epidermal cells and thick-walled subepidermal cells; but they differed in needle resin duct diameter and presence of sclerified fibers in the central cylinder. When cone-scale umbos and mucros are the criteria, *pumila* is again placed with *cembra* and *sibirica*, with *parviflora* ancestral to many of the *Strobi* (Klaus 1980).

There is similar interspecific variation among the *Cembrae* species in oleoresin composition and in heartwood phenolics. Using the latter characteristic as a common denominator, Critchfield combined *koraiensis*, *cembra*, and *albicaulis* with *ayacahuite* and *flexilis*. He suggested this group has phylogenetic significance but admitted "it is not readily compatible with any other proposed scheme of white pine relationships." In fact, it appears that "affinities" are in the eye of the beholder, and are determined by the characteristics chosen for study.

It seems risky to connect *pumila* closely to *parviflora* because of the unsettled nature of *parviflora*, which is regarded by many Japanese specialists as consisting of two species, *P. pentaphylla* Mayr in the north and *P. himekomatsu* Miyabe and Kudo in the south (Saho 1972). Numata (1974) referred to *P. parviflora* var. *pentaphylla*, *P. pentaphylla*, and *P. pentaphylla* var. *himekomatsu* within the covers of the same book! The southerly taxon, *himekomatsu*, has large seeds with reduced wings. The northern, *pentaphylla*, has large seeds with longer wings that are, however, stubbier than wings typical of wind-dispersed *Strobus* pines. According to Saito (1986), Japanese nutcrackers disseminate the seeds of *pentaphylla*. I predict that further study will show *himekomatsu* to be a nutcracker-dispersed species; and that its relationship to *pentaphylla* will be analogous to that of *flexilis* to *strobiformis* (Lanner 1980).

Let us now examine Critchfield's reasons for linking *albicaulis* to the *flexilis* complex. He stated that except for its cones, *albicaulis* "closely resembles" *flexilis*, but this overlooks clear differences in bark characteristics and pollen cone color. In addition to similarity in the number and placement of their accessory needle resin canals, *albicaulis* and *flexilis* share three other characteristics (Critchfield 1986):

1. Their needles have few or no marginal teeth.
2. Their needles have many stomata on abaxial surfaces.
3. The transition of vascular tissue arrangement occurs in the base of the hypocotyl rather than in the vicinity of the cotyledons, according to de Ferré (1965).

But as Critchfield pointed out, none of these traits is unequivocal. Marginal teeth, for example, are "sometimes sparse or obscure" in *pumila* and in three other white pines. Abaxial stomates also are found in *strobiformis* and *monticola*. In addition, the pinyons provide an example of an unquestioned subsection (*Cembroides*) in which some species lack abaxial stomates (*P. juarezensis, P. discolor)* while others have them (*P. edulis, P. cembroides)*. The vascular organization that characterizes *albicaulis* and *flexilis*, which occurs only in "a minority of their seedlings," occurs also in *monticola, ayacahuite*, and *aristata*. On the other hand, *albicaulis* and *flexilis* have the same pollen type (Kuprianova and Litvintseva 1974), and they share umbo and mucro characters (Klaus 1980).

Crossing results are equally inconclusive. Although *albicaulis* and *flexilis* commonly occur together at intermediate elevations (for example at 2,400-2,600 m [7,900-8,540 ft] in Togwotee Pass, WY), no suspected hybrids have been reported. Bingham and others (1972) reported 20-50 attempted crosses of *albicaulis* x *flexilis* resulted in less than one filled seed per cone. The hybridity of these seeds was not authenticated. Critchfield (1986) added that in seven of 14 other crosses, seven mature cones were produced. Four of these yielded sound seeds that were intermediate to the parents in germination characteristics. But the putative hybrids resembled *albicaulis* in their slow growth rate at the Institute of Forest Genetics, Placerville, CA. They subsequently languished and died, their hybridity never having been established (Critchfield 1989).

Critchfield (1986) therefore concluded that the proposed monophyletic origin of the *Cembrae*-type cone is undermined; that *P. pumila* is most closely allied to the *P. parviflora* group; and that *P. albicaulis* stems from the *P. strobiformis-P. flexilis* line. This required him to postulate that the indehiscent cone "has evolved independently at least twice in Eurasia . . . and once in North America . . . ." In other words, the *Cembrae* pines are end-products of convergent evolution in independent lineages.

Despite Critchfield's formidable argument, I think there is still a strong case that the *Cembrae* cone evolved once, under the selective pressure of an early nutcracker progenitor, and that speciation following that event has resulted in *albicaulis, cembra, koraiensis, pumila*, and *sibirica* (Lanner 1980; 1982). I base this argument on two grounds:

First, the cones of the *Cembrae* pines, whose unusual features have been interpreted as adaptations to nutcracker seed harvest (Lanner 1982), are similar in such detail that postulated origins in three gene pools on two continents grossly violate the concept of parsimony usually striven for in science. Second, in other cases where seed-retaining cones have evolved, convergence has not occurred.

For example, within the subsection *Cembroides*, the pinyon pines, every species has cones that hold their seeds in the seed cavities with flange-like fragments of spermoderm (fig. 4). This characteristic is unknown in other pines, and is perhaps the defining morphological characteristic of this ecologically and geographically coherent group.

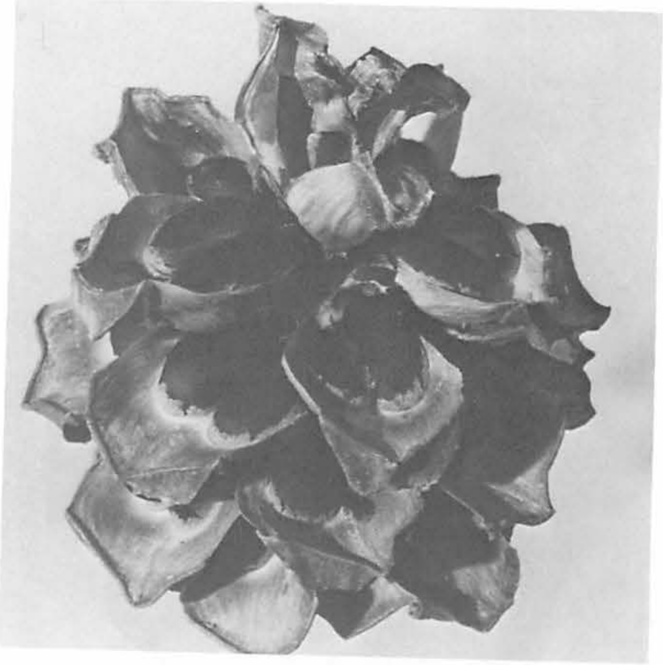


Figure 4—*Pinus monophylla* cone showing the flange-like extensions of cone-scale tissue preventing seeds from falling.

The two nearly-wingless-seed species of subsection *Gerardianae* have evolved different seed-wing adaptations to retain seeds in the cone. *Pinus gerardiana* has reduced wings that adhere to the lower surface of the scale above. This was first noted by Shaw (1914), and I have confirmed it in a large number of cones from the Himalaya. In *P. bungeana*, the tip of the greatly reduced wing adheres to the upper surface of *its own scale* (fig. 5). This wing-tip is membraneous, but wing tissue forms a thick wreath around the seed.

Only one other white pine has seeds that are retained in the cone—*P. parviflora* (fig. 6). It has "seeds with a large nut and a short broad wing, often temporarily adherent to the cone-scale and breaking apart at the fall of the nut . . . . The frequent but not invariable retention of the seed-wing in the cone is due to adhesion. Many seeds fall with their wings intact, others break away from the wing which, after awhile, loosens and also falls" (Shaw 1914). This appears to be the least effective of the seed-retention mechanisms. Yet, that of *pumila*, which Critchfield views as an offshoot of *parviflora*, is an example of the most effective. *Pinus pumila* has completely wingless seeds, and an indehiscent cone; *parviflora* has winged seeds and cones that open normally. I think it is reasonable to regard the various seed-retention mechanisms—those of the *Cembrae* pines, the pinyons, *gerardiana, bungeana*, and *parviflora*—as having evolved independently. All the *Cembrae* are known to be "Bird Pines," as are several of the pinyons (Vander Wall; Vander Wall and Balda 1977, 1988) and *parviflora* var. *pentaphylla* (Saito 1986). The nutcracker subspecies *N. macella* occurs with *bungeana* (Dement'ev and others 1954). *Pinus gerardiana* has not yet been found subject

Figure 5—Cone of *Pinus bungeana* showing adherence of the narrow seed-wings to the cone scale. The seed-wing at right center has become separated from its seed during handling, but still adheres to the cone scale.

Figure 6—Cone of *Pinus parviflora* showing adherence of the tip of the seed-wing to the cone scale surface. These seed-wings have become separated from their seeds, perhaps due to handling.

to avian seed dispersal, but a nutcracker subspecies (*multipunctata*) is endemic to this pine's distribution area (fig. 7).

After considering the evidence summarized above, Critchfield (1986) commented that "the contradictions between reproductive characters, vegetative morphology, crossing data, and biochemical variations appear to be irreconcilable, and to undermine most classifications of the species within section *Strobus*." His solution is to seek common characteristics unrelated to coevolved cone and seed adaptations. This, of course, can only fragment the *Cembrae*. I would prefer to regard those cone and seed characteristics, consistent within the *Cembrae*, as evidence of speciation from a common ancestor. In other words, I see the nutcracker progenitor as the ultimate architect of these pines. The numerous solutions to the problem of the seed-retaining cone suggest that they vary with the gene pool that is challenged, and it seems unlikely that *Cembrae*-type cones, having evolved once, would do so again.

A final comment on the origin of *albicaulis*: elsewhere I (Lanner 1980) have argued that the patterns of variation in nutcrackers and stone pines are similar. Dement'ev and others (1954) recognized 10 subspecies of the Eurasian nutcracker, while Clark's nutcracker has no recognized subspecies. Eurasia holds four stone pines of which all but little-known *koraiensis* have several named botanical forms, varieties, or subspecies. In contrast, *albicaulis*, the only North American stone pine, has none. These patterns are consistent with a long occupation of Eurasia by both bird and pine, and a recent arrival of both across the Bering land bridge. Amadon (1944) offered other reasons for regarding *Nucifraga* as being of Old-World origin. My conclusion may be arguable, but the important point is that the evolution of stone pines cannot be profitably discussed without also considering the nutcracker.

GEOGRAPHY

Pinus albicaulis is North American; the other stone pines are Eurasian. The eastern range of *albicaulis* is mainly in the Northern Rocky Mountains of western Wyoming, western Montana, central and northern Idaho, western Alberta, and British Columbia. Outliers to these populations occur in northern Nevada and northeastern Oregon. A second series of populations extends southwards down the Coast Mountains of British Columbia through the Cascades and Sierra Nevada, as far south as the headwaters of the Kern River overlooking the Owens Valley, CA. There are outliers in the Warner and Siskiyou Mountains, CA (Critchfield and Little 1966).

Pinus cembra is usually regarded as alpine in distribution, because its most famous stands are in Switzerland, Austria, France, and the Dolomitiche and Bergamasche Alpi of Italy. But there is a *cembra* presence in extreme northwestern Yugoslavia, and there are significant populations farther east in the Carpathians. These include stands in the High Tatra of Poland and Czechoslovakia, and an archipelago-like scattering of stands in the Gorgany Mountains of the Ukrainian SSR and in several

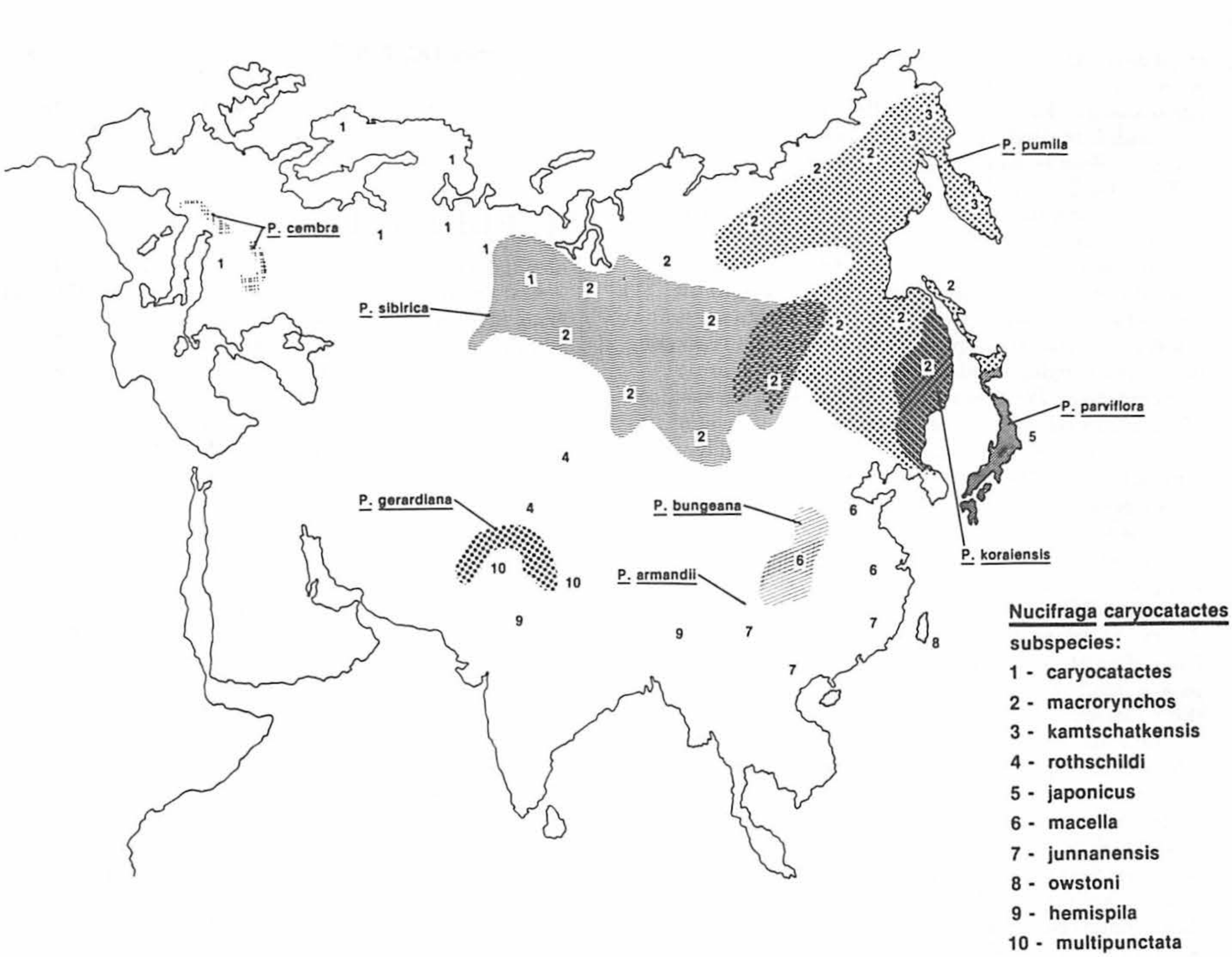


Figure 7—Geographic ranges of Eurasian wingless-seeded and nearly-wingless-seeded *Strobus* pines (after Critchfield and Little 1966) and subspecies of the Eurasian nutcracker (after Dement'ev and others 1954).

mountain ranges in Romania's Carpatil Meridionali ("Transylvanian Alps"): the Rodnei, Calimanilor, Fagarasului, Busegi, Sebesului, Retezatului, and Banat (Myczkowski 1975).

Pinus koraiensis extends from around Sovetskaya Gavan' in southeastern Siberia (Primorskiy Kray) south along the east face of the Sikhote Alin mountains on the coast of the Sea of Japan, into North Korea, and westward into Manchuria (Kirin and Heilungkiang). There are outliers in high mountains of South Korea and in central Honshu and Shikoku in Japan (Critchfield and Little 1966; Hyun 1972).

Pinus pumila is the only pine of section *Strobus* found north of latitude 70° N, approaching to within about 100 km (60 mi) of the Arctic Ocean at the Kolyma River delta. It is also the farthest-ranging *Strobus* pine, and is exceeded in this respect among pines only by *P. sylvestris*. Its range includes the coast of the far eastern USSR from about Khatyrka on the Bering Sea, around the Kamchatka Peninsula along the Sea of Okhotsk, and south along the Sea of Japan nearly to Vladivostok. Inland it ranges across eastern Siberia to the Lena River and Lake Baikal, even entering Mongolia. It is in the Kurile Islands, Sakhalin, and south through Hokkaido and Honshu to just south of Tokyo. There are outliers in North Korea and Manchuria (Critchfield and Little 1966; Saho 1972).

Pinus sibirica extends from the Urals and western Siberia east across the Central Siberian Plateau to the Aldanskoye Upland. It occurs widely in northern Mongolia from Lake Uvs east to Uuldza. It grows throughout the Altai Territory and Eastern and Western Sayans of Krasnoyarsk Territory, in the Irkutsk region and the Transbaikal. There are outliers on the Kola Peninsula near Murmansk, about 1,000 km (600 mi) from the main range in the northern Urals (Critchfield and Little 1966).

An aspect of stone pine geography that may be worthy of attention is that of range overlap with other wingless-seeded pines. If species are sympatric, and if their cone crops do not fail in the same years, then avian seed dispersers would be insulated against seed-crop failure in either species. For example, the Rocky Mountain range of *albicaulis* is often paralleled at lower elevations by that of the wingless-seeded *flexilis*. In years when *albicaulis* in Togwotee Pass, WY, has borne no cones, I have seen large flocks of nutcrackers foraging among *flexilis* trees in woodlands within 10 km (6 mi) and beyond. Though it has not been shown that the same birds feed alternately upon the two pines, the availability of both within the reach of a mobile bird species strongly suggests so. Vander Wall (1988) has recently shown how nutcrackers utilize two wingless-seeded pine species in similar circumstances. *Pinus monophylla*'s range, at the east foot of the Sierra Nevada, also parallels, at lower elevations, that of *albicaulis*. Tomback (1978) has described how nutcrackers forage on both species as well as the winged-but-large-seeded *P. jeffreyi* that grows with *albicaulis*.

Pinus koraiensis and *pumila* are in close proximity in the Primorskiy region of southeast Siberia: *koraiensis* is along the coast and lower slopes, and in interior valleys, while *pumila* is in the higher regions. In central Honshu, Japan, the community type in which *koraiensis* was found had a characteristic elevation of 2,080 m (6,900 ft), while *pumila* scrub occupied elevations over 2,400 m (7,900 ft) (Franklin and others 1980).

Pinus pumila is also widely sympatric with *sibirica* in a huge area—about the size of the Scandinavian Peninsula—surrounding Lake Baikal and extending northeast to the Aldan and Stanovoy Mountains. High-elevation forms of *sibirica* have been reported from the Altai, the Sayans, northern Mongolia, and the Transbaikal region. They include *P. sibirica* f. *humistrata* (Middendorf) Novac, f. *coronans* (Litv.) Krylov, f. *depressa* Kom., and f. *turfosa* Gorodkov (Pravdin 1963). Pravdin (1963) pointed out that the recognition of these "forms" may reflect an interest in plants growing in bogs and on high mountains, and that proper study of intraspecific variation in *sibirica* has been lacking.

Pinus cembra alone among the *Cembrae* pines is not sympatric with any other wingless-seeded *Strobus* pine. In none of the cases of sympatry cited here has there been an indication of interspecific hybridization.

It seems noteworthy that a very hungry nutcracker could, theoretically, eat its way through nearly 6,400 km (4,000 mi) of stone pines from Chelyabinsk to the Bering Sea! While such an event may have a low probability, it does focus the mind on the immensity of the nutcracker-established stone pine forest of northern Asia; and the general lack of appreciation of the ubiquity of the pine-corvid mutualism.

ACKNOWLEDGMENTS

Cones were kindly provided by the following colleagues: W. B. Critchfield, Institute of Forest Genetics, Placerville, CA; G. Georgeades, Strybing Arboretum, San Francisco, CA; S. R. Frost, U.S. National Arboretum, Washington, DC; T. S. Elias, Cary Arboretum, Millbrook, NY; H. Egger and K. Holzer, Forstliche Bundesversuchsanstalt, Vienna, Austria; Director, Kanto Forest Tree Breeding Institute, Mito, Japan; and M. P. Gupta, Himachal Pradesh Forest Department, Simla, India.

REFERENCES

Amadon, Dean. 1944. The genera of Corvidae and their relationships. American Museum Novitates. 1251: 1-21.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Bingham, R. T.; Hoff, R. J.; Steinhoff, R. J. 1972. Genetics of western white pine. Res. Pap. WO-12. Washington, DC: U.S. Department of Agriculture, Forest Service. 18 p.

Critchfield, William B. 1986. Hybridization and classification of the white pines (*Pinus* section *Strobus*). Taxon. 35(4): 647-656.

Critchfield, William B. 1989. [Personal communication]. February 10. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station.

Critchfield, William B.; Little, Elbert L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.

Crocq, C. 1978. Ecologie du Casse-noix (*Nucifraga caryocatactes* L.) dans les Alpes francaises du sud. Marseille, France: Universite d'Aux-Marseille. 189 p. Thesis.

de Ferré, Y. 1965. Structure des platules et systématique du genre *Pinus*. Bull. Societe de l'histoire Naturale, Toulouse. 100: 1-50.

de Ferré, Y. 1966. Validité de l'espèce *Pinus pumila* et affinités systématiques. Bull. Societe de l'histoire Naturale, Toulouse. 102: 351-356.

Dement'ev, G. P.; Gladkov, N. A.; Sudilovskaya, A. M. and others. 1954. Birds of the Soviet Union. Translated from Russian and published for Smithsonian Institute and National Science Foundation by Israel Program for Scientific Translation. 5: 93-103.

Franklin, J. F.; Maeda, T.; Ohsumi, Y.; Matsui, M.; Yagi, H. 1980. Subalpine coniferous forests of central Honshu, Japan. Ecological Monographs. 49(3): 311-334.

Furnier, G. R.; Knowles, P.; Clyde, M. A.; Dancik, B. P. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution. 41(3): 607-612.

Haddock, P. G. 1977. [Letter to Ronald M. Lanner]. Nov. 1. 1 leaf. Vancouver, BC: University of British Columbia.

Harlow, William M.; Coté, W. A., Jr.; Day, A. C. 1964. The opening mechanism of pine cone scales. Journal of Forestry. 62: 538-540.

Holtmeier, Friedrich-Karl. 1966. Die ökologische Funktion des Tannenhähers im Zirben-Lärchenwald und an der Waldgrenze des Oberengadins. Journal für Ornithologie. 107(3/4): 337-345.

Holzer, Kurt. 1972. Intrinsic qualities and growth-potential of *Pinus cembra* and *Pinus peuce* in Europe. In: Biology of rust resistance in forest trees: Proceedings of a NATO-IUFRO advanced study institute; 1969 August 17-24; Moscow, ID. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture, Forest Service: 99-110.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Hyun, Sin Kyu. 1972. White pines of Asia: *Pinus koraiensis* and *Pinus armandii*. In: Biology of rust resistance in forest trees: Proceedings of a NATO-IUFRO advanced study institute; 1969 August 17-24; Moscow, ID. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture, Forest Service: 125-149.

Klaus, Wilhelm. 1980. Neue Beobachtungen zur Morphologie des Zapfens von *Pinus* und ihre Bedeutung fur die Systematik, Fossilbestimmung, Arealgestaltung und Evolution der Gattung. Plant Systematics and Evolution. 134: 137-171.

Konev, G. I. 1952. Natural nests (clusters) of the cedar-pine in subalpine cedar stands. Agrobiologiia. 3: 140-142. (Russian)

Koski, V. 1987. [Letter to Ronald M. Lanner]. September 15. 1 leaf. Vantaa, Finland: Finnish Forest Research Institute.

Kuprianova, L. A.; Litvintseva, M. V. 1974. The group *cembra* of the genus *Pinus*, its volume and relationships according to palynological data. Botanicheskii Zhurnal. (Leningrad). 59(5): 630-644. (Russian)

Lanner, Ronald M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: Dancik, B. P.; Higginbotham, K. O., eds. Sixth North American forest biology workshop proceedings; 1980 August 11-13; Edmonton, AB. Edmonton, AB: University of Alberta: 15-45.

Lanner, Ronald M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research. 12: 391-402.

Lanner, Ronald M. 1988. Dependence of Great Basin bristlecone pine on Clark's nutcracker for regeneration at high elevations. Arctic and Alpine Research. 20(3): 358-362.

Little, Elbert L., Jr.; Critchfield, William B. 1969. Subdivisions of the genus *Pinus* (pines). Misc. Publ. 1144. Washington, DC: U.S. Department of Agriculture, Forest Service. 51 p.

Litvintseva, M. V. 1974. Characteristics of needle parenchymal cell structure in species of the group *cembra* genus *Pinus*. Botanicheskii Zhurnal. (Leningrad). 59(10): 1501-1505. (Russian)

Malyshev, L. I. 1960. A mistaken opinion concerning the occurrence of spreading pine (*P. pumila* [Pall.] Rgl.) in the Sayan Mountains. Botanicheskii Zhurnal. (Leningrad). 45: 737-739. (Russian)

Mattes, Hermann. 1982. Die Lebensgemeinschaft von Tannenhäher und Arve. Eidgenossiche Anstalt fur das forstliche Versuchswesen, Berichte, 241. 74 p.

Miror, N. T. 1967. The genus *Pinus*. New York: Ronald Press. 602 p.

Myczkowski, S. 1975. Geographical distribution. In: Bialobok, Stefan, ed. Stone-pine (*Pinus cembra* L.). Translated from Polish for U.S. Department of Agriculture and National Science Foundation. National Technical Information Service TT-73-54045: 19-44.

Myczkowski, S.; Bednarz, Z.; Lesinski, J. 1975. Ecological outline. In: Bialobok, Stefan, ed. Stone-pine (*Pinus cembra* L.). Translated from Polish for U.S. Department of Agriculture and National Science Foundation. National Technical Information Service TT-73-54045: 71-95.

Numata, M. 1974. The flora and vegetation of Japan. Tokyo: Kodansha Scientific Books; Amsterdam: Elsevier Scientific Publishing Company. 294 p.

Oswald, Helfried. 1956. Beobachtungen uber die Samenverbreitung bei der Zirbe (*Pinus cembra*). Allgemeine Forstzeitung. 67(15/16): 200-202.

Plaisance, G. 1977. Pin cembro. La forêt privée. 144: 67-70, 72.

Pravdin, L. F. 1963. The selection and the seed production of the Siberian stone pine. In: Shimanyuk, A. P., ed. Fruiting of the Siberian stone pine in East Siberia. Akad. Nauk SSSR Trudy Instituta Lesa i Drevesiny. 62: 1-20.

Reimers, N. F. 1953. The food of the nutcracker and its role in the dispersal of the cedar-pine in the mountains of Khamar-Daban. Lesnoe Khozyaistvo. No. 1: 63-64.

Saho, Haruyoshi. 1972. White pines of Japan. In: Biology of rust resistance in forest trees: proceedings of a NATO-IUFRO advanced study institute; 1969 August 17-24; Moscow, ID. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture, Forest Service: 179-199.

Saito, Shin-ichiro. 1983a. On relations of the caching by animals on the seed germination of Japanese stone pine, *Pinus pumila* Regel. Bull. Shiretoko Museum. 5: 23-40.

Saito, Shin-ichiro. 1983b. Caching of Japanese stone pine seeds by nutcrackers at the Shiretoko Peninsula, Hokkaido. Tori. 32: 13-20.

Saito, Shin-ichiro. 1985. Alpine vegetation of the Japanese stone pine, *Pinus pumila* Regel, and other shrubby species on the ridges between Mt. Onnebetsu-dake and Mt. Chinishibetsu-dake, Shiretoko Peninsula, easternmost Hokkaido. Koshunai, Bibai, Japan: Hokkaido Forest Experiment Station. 262: 223-295.

Saito, Shin-ichiro. 1986. [Postcard to Ronald M. Lanner]. December 18. Koshunai, Japan: Hokkaido Forest Experiment Station.

Shaw, George Russell. 1914. The genus *Pinus*. Publ. Arnold Arboretum No. 5. Cambridge, MA: Riverside Press. 96 p.

Shaw, George Russell. 1924. Notes on the genus *Pinus*. Journal of the Arnold Arboretum. 5: 225-227.

Snethen, K. L. 1980. Whitebark pine (*Pinus albicaulis*) invasion of a subalpine meadow. Logan, UT: Utah State University. 76 p. Thesis.

Tomback, Diana F. 1978. Foraging strategies of Clark's nutcracker. Living Bird. 16: 123-161.

Turcek, Frantisek J.; Kelso, Leon. 1968. Ecological aspects of food transportation and storage in the Corvidae. Communications in Behavorial Biology Part (A)1: 277-297.

Vaisanen, R. A. 1987. [Letter to Ronald M. Lanner]. November 30. 1 leaf. Helsinki, Finland: University of Helsinki.

Vander Wall, S. B. 1988. Foraging of Clark's nutcracker on rapidly changing pine seed resources. The Condor. 90: 621-631.

Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecological Monographs. 47: 89-111.

Zykov, I. V. 1953. The kedrovka in Siberian forests. Priroda. No. 7: 112-114.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from R. H. Smith)—Do you think "buried" seeds germinate and survive better than wind-disseminated seeds? Therefore, is the winglessness actually an advantage to stone pines?

A.—However a seed is disseminated, it is most likely to germinate successfully if it is covered with soil. Small winged seeds may frequently find themselves wedged into tiny cavities in the soil microtopography, large seeds less frequently unless animals put them in the soil. Obviously both systems work well enough.

Q. (from Earle F. Layser)—Bristlecone pine has a winged seed. It is widely dispersed on mountain tops, crags, etc. in the Southern Rockies. Why does it seem to have a similar pattern as stone pine in its occurrence at high elevation (obviously not strictly wind dispersed)?

A.—Great Basin bristlecone, though it has a small, winged seed, is indeed often dispersed and established by Clark's nutcracker at high elevations. See my recent article in Arctic and Alpine Research 20: 358-362, August 1988.

Q. (from Doug Turner)—Do pine seeds undergo any needed changes while in the crops of nutcrackers or are the seeds able to germinate if humans plant them? Any speculation or evidence of why nutcrackers fly so far to cache in burns if they can successfully cache under unburned canopies?

A.—No changes are known to occur to seeds while they are in the nutcracker's pouch. Sometimes the seeds are there for only a few minutes. We urgently need more information on nutcracker behavior, so until we get it you will have to either guess at their motives or ask them about it.

Q. (from Tad Weaver)—In tree islands, what comes first - *Pinus* or *Abies*? What's your evidence?

A.—My only experience is with establishment of groves in Squaw Basin, WY. Here Karen Snethen (1980) found whitebark pine pioneering on moraines, and Engelmann spruce later coming in under the pines. See her master's thesis for evidence in the form of chronosequences.

DISTURBANCE AND MANAGEMENT PROBLEMS IN LARCH-CEMBRA PINE FORESTS IN EUROPE

Friedrich-Karl Holtmeier

ABSTRACT

Cembra pine (Pinus cembra) *and larch* (Larix decidua) *form the uppermost forests in the Central Alps. Due to human influences, the timberline became lower and the species composition and structure of these forests changed. In general they are over-aged. As a consequence of the modern decline of pasturing, the natural succession from larch to cembra pine forest has been revived. In places it may be hampered by the larch bud moth, which may kill young cembra pines in the understory. Abandoned alpine pastures are invaded mainly by cembra pines. The larch-cembra pine forest as well as high-altitude afforestations and the invading cembra pines must be managed with the objective to restore the climatic timberline and to produce well-structured forests.*

INTRODUCTION

In Europe cembra pine (*Pinus cembra*), which is closely related to whitebark pine (*Pinus albicaulis*), is common only in the Alps (fig. 1). In the Tatra and southern Carpathian Mountains, cembra pine is restricted in occurrence. Therefore, this paper focuses on the Alps.

The Alps extend from west to east for about 1,000 km (746 mi). Their width ranges between 150 km (93.2 mi) in the west to about 250 km (155 mi) in the middle and eastern parts. The Alps are deeply dissected and characterized by rugged topography. The mountain rim is exposed to moisture-carrying air currents from northern, western, and southern directions. Thus, the climate of the outer ranges is rather maritime compared with the Central Alps, which are sheltered from these maritime influences (fig. 2).

Consequently, the upper timberline occurs from about 1,600 to 1,800 m (4,980 to 5,906 ft) in the outer ranges and from 2,200 to 2,400 m (7,218 to 7,873 ft) in the central region. In the outer mountains the montane and subalpine forests are dominated by spruce (*Picea abies*) and in places by beech (*Fagus sylvatica*), while cembra pine is found there only as relict stands in the upper subalpine belt and at the upper forest limit. Above the subalpine spruce forest occurs a more or less unbroken belt of prostrate mountain pine (*Pinus mugo*). This mountain pine belt is quite different from the krummholz belt in the high mountains of the western United States, because the prostrate growth form of *P. mugo* is genetically predetermined and not the result of the actual climatic environment (Holtmeier 1973, 1981).

In the Central Alps, the uppermost forests are formed by cembra pine and European larch (*Larix decidua*); spruce is common only at lower elevations. In general the range of cembra pine does not extend below 1,700 m (5,577 ft), because the species cannot successfully compete with spruce. Cembra pine is almost excluded from the outer ranges, which are characterized by heavy snow fall and long melting periods, because it is highly susceptible to snow fungi infections.

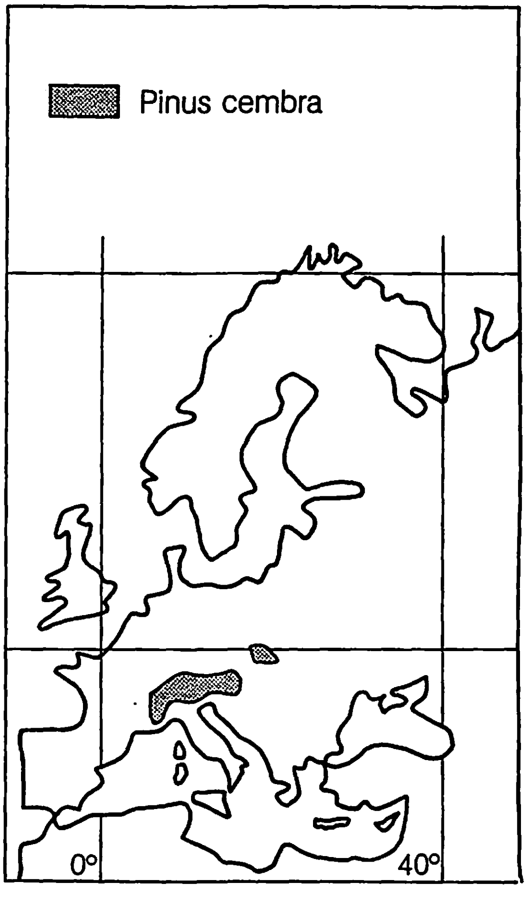


Figure 1—Distribution of cembra pine (*Pinus cembra*) in Europe.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Friedrich-Karl Holtmeier is Professor of Landscape Ecology and Geography, Institut fur Geographie, University of Munster, Federal Republic of Germany.

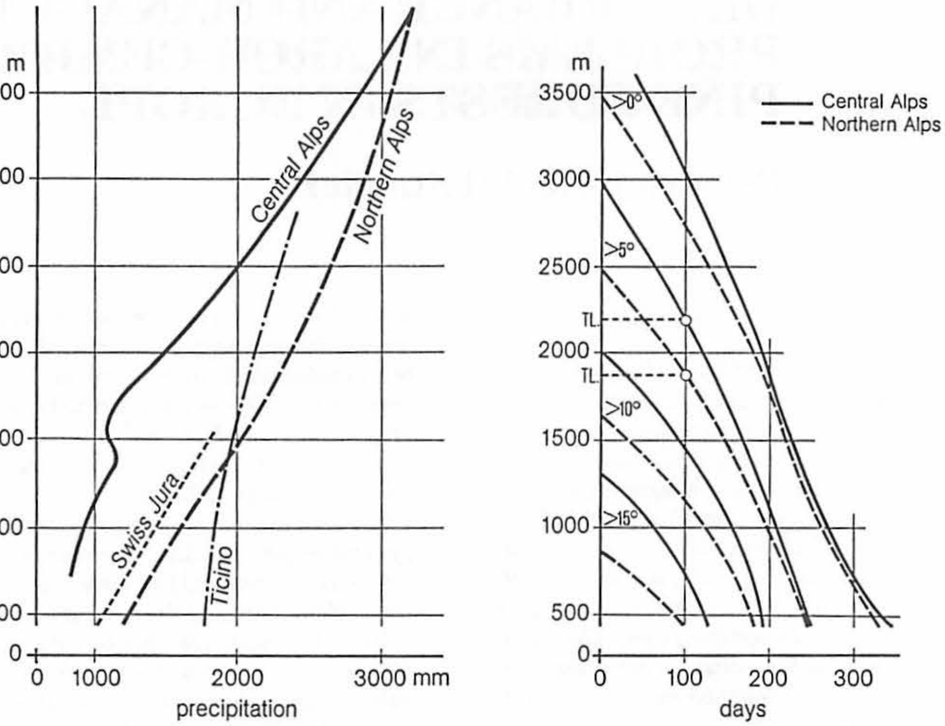


Figure 2—Annual amount of precipitation (left) and number of days with mean temperatures above 0, 5, 10, and 15 °C (right) in the Central Alps and in the outer ranges (after Ellenberg 1978).

Following Pleistocene glaciation, dissemination of seeds by the European thickbilled nutcracker (*Nucifraga caryocatactes caryocatactes*) (fig. 3) probably enabled cembra pine to spread from its refugial areas in the lowlands close to the southern Alps and the Carpathian Mountains and quickly resettle the high mountains. Some good evidence suggests that cembra pine spread faster than spruce (Mattes 1978, 1982).

There is no mountain pine belt above the larch-cembra pine forests. Mountain pine and green alder (*Alnus viridis*), which is another true krummholz species, are confined to avalanche tracks and similar sites unsuitable to upright tree growth.

The Alps, like many other high-mountain regions of Eurasia, were already settled in prehistoric time, which means there was persistent use of the mountain forests throughout history. Many of the forests were heavily grazed or cleared for agriculture and alpine pastures. Others were destroyed by ore mining, salt works, and charcoal production, especially during the Middle Ages. Overgrazing of the alpine vegetation caused severe soil erosion, which also was harmful to the subalpine forest below. As a consequence of these activities, not only did the upper timberline become lower, but also the species composition and structure of the mountain forests changed considerably. In many central alpine valleys, larch could spread at the cost of cembra pine. The situation in the Upper Engadine serves as a good example of human history and ecological changes in the Central Alps.

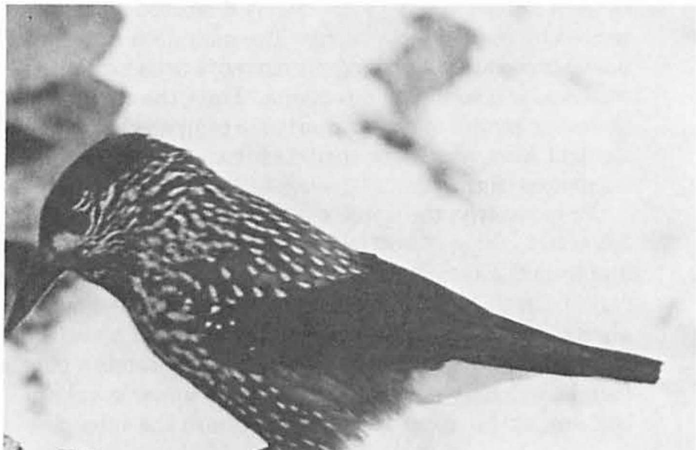


Figure 3—European thickbilled nutcracker at a winter feeding place.

THE UPPER ENGADINE FORESTS

The Upper Engadine is located in the eastern part of Switzerland and comprises the uppermost drainage area of the Inn River. The bottom of the main valley is situated at an altitude of 1,700 to 1,800 m (5,185 to 6,300 ft); the tributary valleys climb up to 2,300 m (7,546 ft). The highest peaks' elevations are about 4,000 m (13,123 ft).

Due to the geographical location and the high mass-elevation of the Engadine, the climate is rather continental. Although lowered by human disturbances by about 150 to 300 m (492 to 984 ft), the upper limit of the larch-cembra pine forest is located at about 2,200 to 2,300 m (7,217 to 7,546 ft) at places. Solitary crippled trees may still be found at and even above 2,500 m (8,202 ft) (Holtmeier 1965, 1967).

Distribution Patterns

The Engadine larch-cembra pine forests belong to the so-called silicate type (*Larici-Cembretum*, Ellenberg 1978; *Larici Pinetum cembrae*, Oberdorfer 1970), which is common to the crystalline Central Alps. Depending on the local site conditions, the forests display subtypes that can be distinguished by the different plant communities of the understory vegetation (grasses, dwarf shrubs). Thus, the uppermost cembra pine forests, which are relatively open, are characterized by *Rhododendron ferrugineum* and *Vaccinium myrtillus* (*Larici-Cembretum rhododendretosum ferruginei*) (fig. 4). Cembra pine regenerates vigorously there if not destroyed by red deer or livestock. Larch seedlings are very rare. The soil is a Ferro Orthic

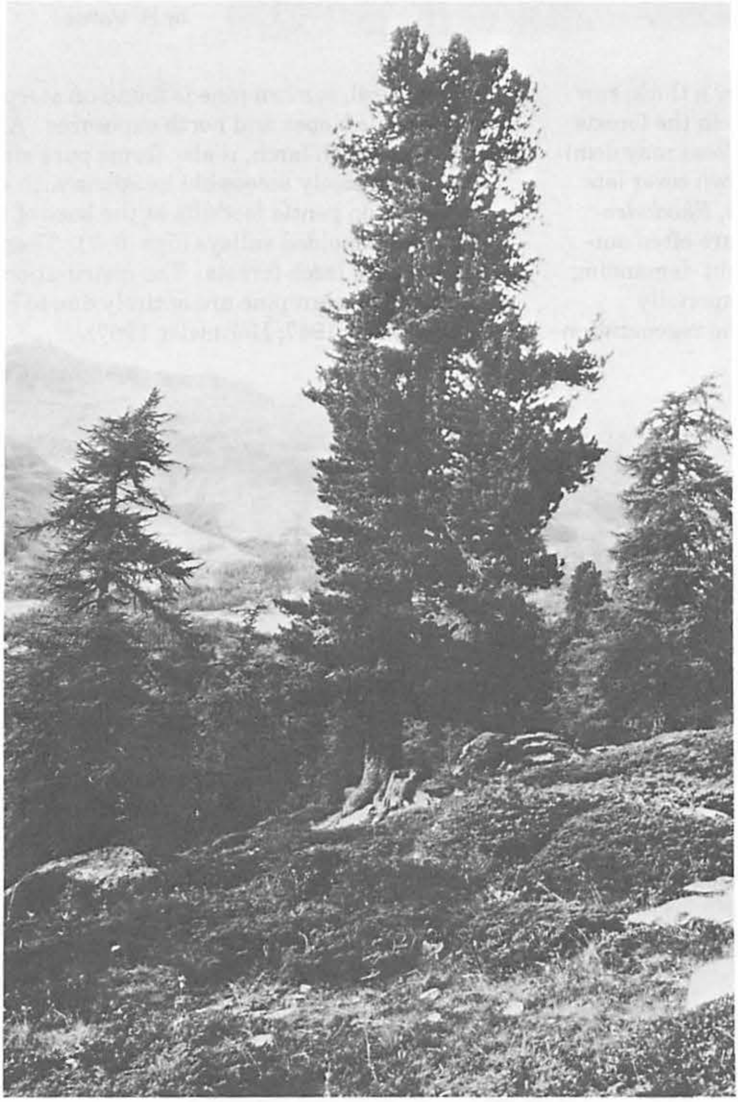


Figure 4—Open larch-cembra pine forest with dwarf shrubs (*Rhododendron ferrugineum, Vaccinium myrtillus*) as understory vegetation. Upper Engadine, northwest-facing slope of the main valley at 2,200 m (6,710 ft).

Figure 5—Cembra pine regenerates successfully in the dwarf shrub vegetation (background) but is almost excluded by *Calamagrostis villosa* (foreground). God da la Stretta, 1,830 m (5,582 ft). Photo by H. Mattes.

Podzol (FAO terminology), characterized by a thick, raw humus layer with high moisture capacity. In the forests below 2,000 m (6,562 ft), *Calamagrostis villosa* may dominate the undergrowth, especially if the crown cover lets the sunlight pass to the forest floor. There, *Rhododendron, Vaccinium*, and other dwarf shrubs are often outcompeted and replaced by warmth- and light-demanding species. However, the dense grass cover especially *Calamagrostis villosa*, not only hampers the regeneration of larch, but of cembra pine also (fig. 5).

In general, cembra pine is found on steep, rocky, and inaccessible slopes and north exposures. Although usually mixed with larch, it also forms pure stands. Larch prevails in easily accessible locations with southern exposures and on gentle foothills at the base of the steep walls of glacially molded valleys (figs. 6, 7). There we find extensive pure larch forests. The distribution patterns of larch and cembra pine are entirely due to human disturbances (Auer 1947; Holtmeier 1967).

Figure 6—Distribution pattern of cembra pine and larch. Pure larch forest covered the valley bottom and the talus cones at the base of the steep walls of this glacially molded valley. Pure cembra pine stands are confined to rocky, inaccessible sites. Roseg Valley, view to southwest.

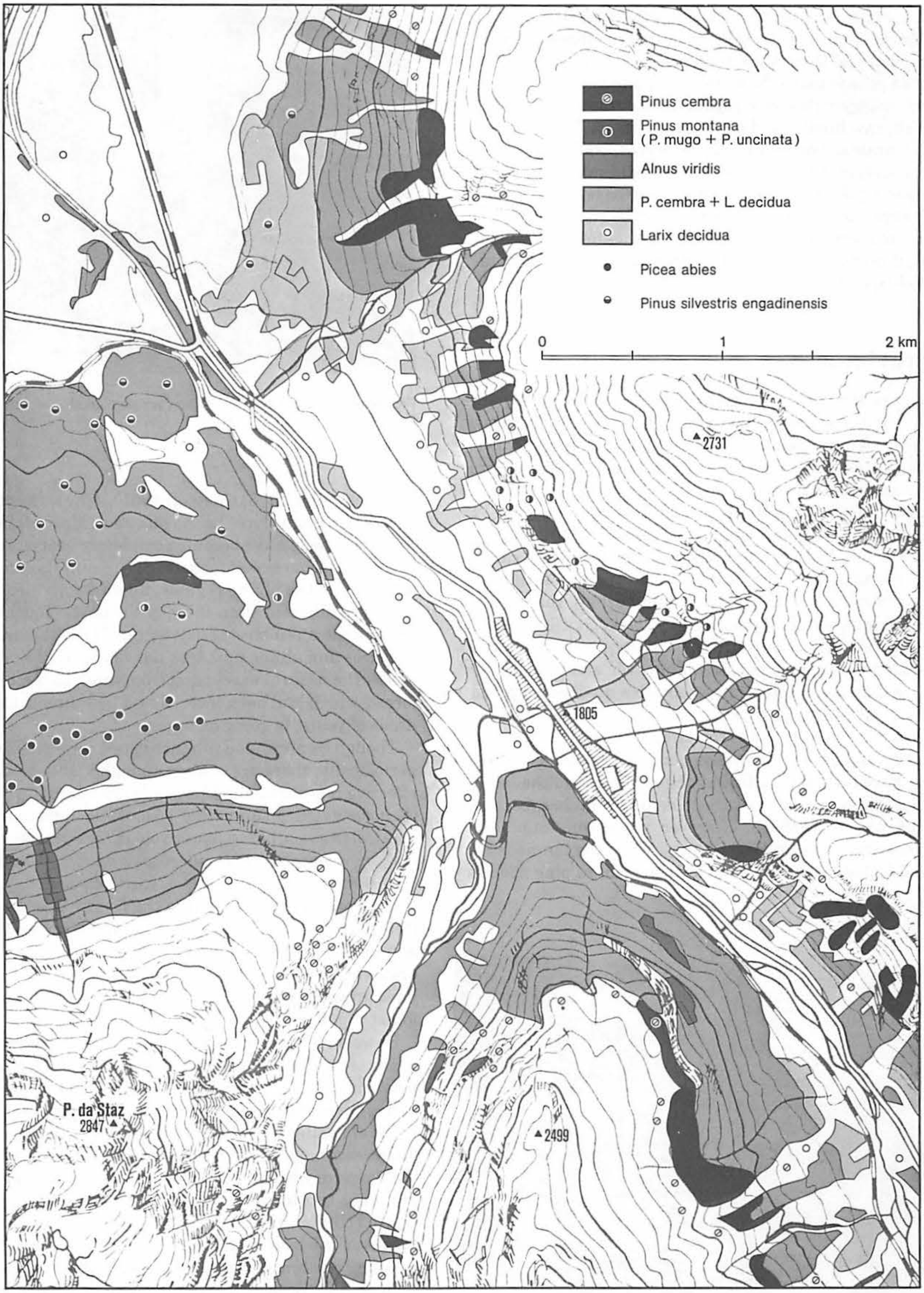


Figure 7—Distribution of the tree species in the Bernina Valley, Upper Engadine.

Under natural conditions larch, which is a shade-intolerant species, prevails in the pioneer stages of forest succession and then is gradually replaced by cembra pine. Cembra pine is more shade-tolerant, and because of its heavy, energy-rich seeds, regenerates successfully, even in thick, raw humus and dense plant cover. Thus, pure larch stands are expected only on screes, boulder fans, talus cones, and similar sites rich in bare mineral soil and lacking dense grass, dwarf shrubs, or both.

However, although cembra pine can be regarded as typical of advanced successional stages of forest development, it may also occur as a pioneer species on bare boulder fields, on moraines, or in front of retreating glaciers (fig. 8).

Disturbances

Cembra pine not only hampers the regeneration of larch, but it also prevents the growth of herbs and grasses on the forest floor because of its dark, shade-giving crown and slowly decaying needle litter. As a result, the cembra pine was systematically eliminated by people on sites suitable for grazing and restricted to inaccessible sites and northern exposures (figs. 6, 7). In addition, its soft wood was used for different purposes, such as wood carving, construction of wood trunks, furniture, and artifacts. Also, cembra pine suffered more from burning than deciduous larch, which is protected by thick, cork-like bark and may refoliate after burning. Finally, larch was favored by grazing, because the plant cover was frequently destroyed by trampling; thus, a suitable seedbed (exposed mineral soil) was provided.

Cyclic mass outbreaks of the larch bud moth (*Zeiraphera diniana*), which nowdays occur at intervals of 8 to 9 years, have been intensified by the expansion of the larch forests. These outbreaks very seldom kill larches, because they are able to refoliate. However, young cembra pines in the understory may be destroyed when the larvae leave the defoliated larch crowns to feed on cembra pine needles (Baltensweiler 1975; Campell 1955). Thus, the natural succession might have been retarded. Most of the former pasture forests have become completely over-aged (fig. 4).

Figure 8—Pioneer cembra pines invading the lateral moraine of the Morteratsch Glacier (Upper Engadine). Elevation 2,100 m (7,350 ft).

Figure 9—Cembra pines invading an ungrazed larch forest (2,000 m; 6,100 ft).

As a consequence of modern changes in the economic structure of the alpine regions, human activities today are quite different than those of the past. Tourism has become the main base of existence. Thus, the use of forest pastures and alpine pastures has declined. In many places the natural succession from larch to cembra pine forest, which had been interrupted by humans for hundreds of years, is going on again.

Though cembra pine produces good cone crops only periodically, there are always enough viable seeds for effective regeneration. The seeds are spread by squirrels (*Sciurus vulgaris*) and other rodents such as the common vole (*Microtus arvalis*), bank vole (*Clethrionomys glareolus*), by woodpeckers (*Dendrocopus major*), willow tits (*Parus montanus*), nuthatches (*Sitta europaea*), and by the European nutcracker into the former pasture-forests (Mattes 1985). Although these animals feed on the seeds, abundant quantities are left to guarantee vigorous regeneration of cembra pine. Dense groves of cembra pines have grown up below the canopy of the ungrazed larch forest (fig. 9).

However, this process may be slowed by damage caused to the terminal shoots and needles of the young cembra pines in the understory by the caterpillars of the larch bud moth and by secondary parasites such as different kinds of beetles (for example, *Pissodes pinii, Pityogenes bistridentatus, Pityophterus knotecki, Ips amitius*). Thus, the trees may become crippled or killed. In general, cembra pines shorter than 5 m (15.25 ft) are most seriously injured (Baltensweiler and Rubli 1984). The mass outbreaks of the larch bud moth seem to be more harmful to young cembra pines than to mature larch trees. Nevertheless, high proportions of larch can only be maintained by removal of the dense grass and dwarf shrub vegetation on the forest floor and by exposing the mineral soil. Otherwise, in the long run, larch is going to be replaced by cembra pine on most sites.

Natural Reforestation of Alpine Pastures

Just as conspicuous as the revived succession in the larch-cembra pine forest is the invasion of abandoned or rarely grazed alpine pastures. Surprisingly, it is cembra pine, not larch, that is most successful in resettling these areas (Holtmeier 1965, 1967). This is primarily caused by the dense grass and dwarf shrub vegetation that prevents the light larch seeds from reaching a suitable seed bed. Seeds of cembra pine are approximately 90 times heavier than larch seeds (Auer 1947).

The heavy, wingless seeds of cembra pine (fig. 10) are chiefly spread by the European nutcracker, which places food caches of nuts in the soil, rotten trunks, and in other suitable places, particularly at sites on small ridges, spurs, knobs, and rocky outcrops (Holtmeier 1966; Mattes 1978, 1982). Thus, the distribution of cembra pine depends more on the nutcracker's home range or area of activity than on the distance from the seed trees in the subalpine forest. In contrast, the occurrence of larch seedlings declines rapidly with increasing distance from the mother tree, as is characteristic of windborne tree seeds (Holtmeier 1974; Kuoch 1965).

Many of the seeds hoarded by nutcrackers remain unused and thus may give rise to cembra pine seedling clusters (fig. 11). Almost no cached cembra pine nuts are lost to mice. Above the timberline only the common vole (*Microtus arvalis*) is common at places. However, the common vole prefers dense plant communities such as *Deschampsia* meadows, which provide sufficient protection from predators. The nutcracker does not establish seed caches in these plant communities (Mattes 1978, 1982).

It is not only the distribution of seeds over relatively great distances, but also the specific choice of locations or the food caches that makes the nutcracker and cembra pine an important factor in natural high-altitude reforestation. This must be viewed in relation to the drastic environmental change that took place when the uppermost forest belt was destroyed by humans in the past. Above the closed forest, tree growth is impeded more by unfavorable site conditions than one would expect at the present level of the timberline. When the forest was removed, the windflow near the soil surface and the amount of solar radiation became strongly influenced by the local topography.

Sites vary in their exposure to solar radiation, wind velocity and directions, height and duration of the snow cover, length of the growing season, distribution of the soil temperature, soil moisture, and other factors. At present, sites relatively favorable to tree growth are near sites without trees. At exposed sites, which lack snow cover or are only occasionally covered with snow in winter, young trees suffer from desiccation, frost damage, and ice particle abrasion (fig. 12). On leeward slopes and in other places characterized by heavy snow accumulation, the growing season may be too short and evergreen conifers such as cembra pine are heavily damaged or even killed by snow fungi (for example, *Herpotrichia juniperi, H. coulteri, Phacidium infestans, Lophodermium pinastri*). In addition, thick, raw humus layers, typical of cool and moist north-facing sites, may prevent germination of seeds and growth of seedlings. And finally, the mycorrhizal flora was reduced by past disturbance and thus nutrient uptake by the seedlings may be considerably hampered. Even in the long-term, successful natural restocking will be confined to the favorable localities.

The sites chosen by the nutcracker for its food caches appear to be relatively favorable to successful growth of seedlings and saplings. Furthermore, the distribution of young cembra pines in tree clusters is advantageous

Figure 10—Cone and seeds of cembra pine.

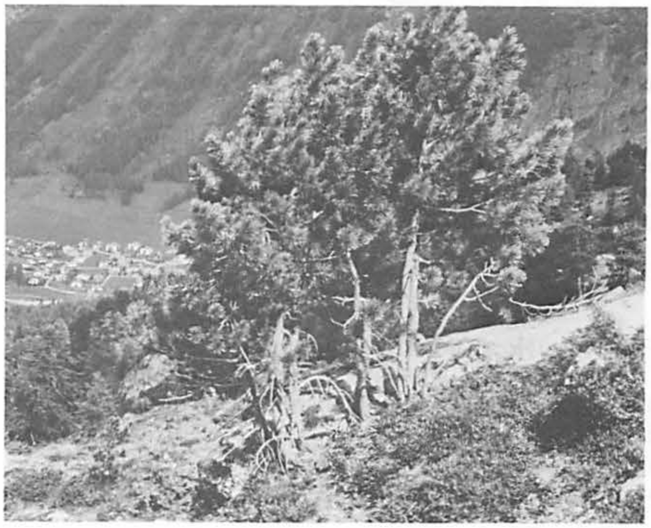


Figure 11—Cembra pines that rose from a nutcracker's seed cache. Muottas da Celerina, Upper Engadine, at about 2,250 m (6,883 ft).

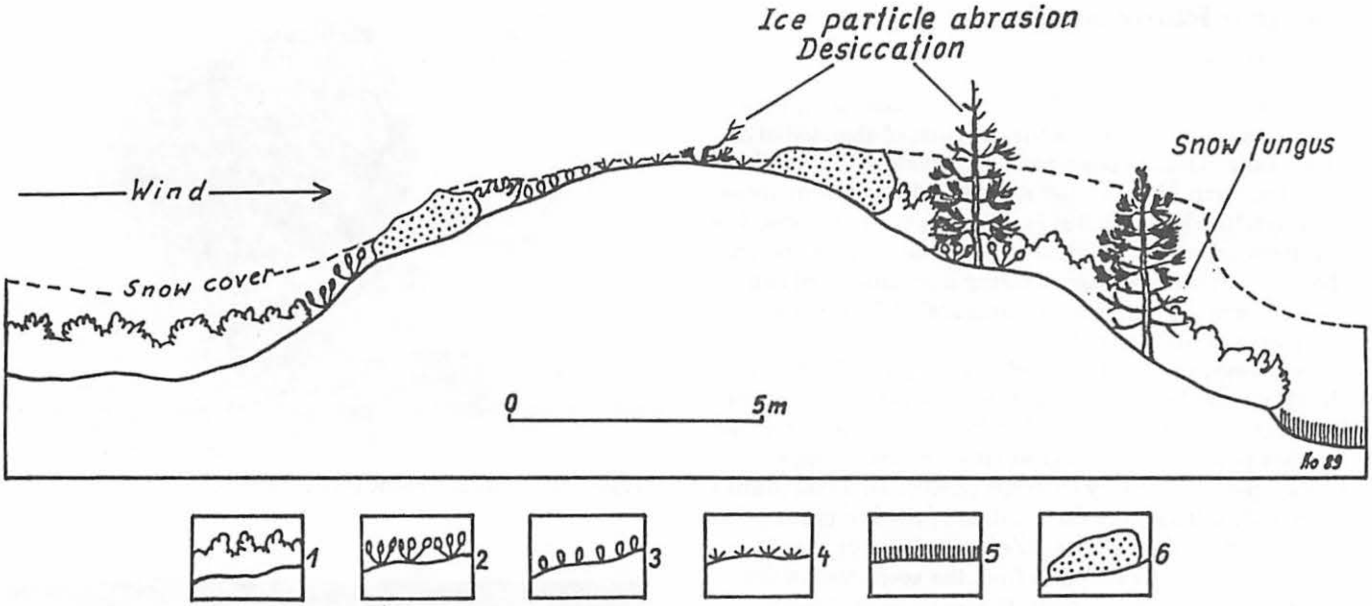


Figure 12—Influence of wind and snow cover on the distribution of ground vegetation and on young cembra pines in abandoned alpine pastures (schematic, following the conditions on the northwest-facing slope of the upper Engadine main valley (Holtmeier 1965, 1971)). (1) *Rhododendron ferrugineum*; (2) *Vaccinium myrtillus*; (3) *Vaccinium uliginosum, Empetrum nigrum*; (4) *Loiseleuria procumbens*, lichens (*Alectoria ochroleuca, Thamnolia vermicularis, Cladonia* spp.), *Juncus trifidus*; (5) *Trichophorum caespitosum, Eriopherum scheuchzeri, Carex* spp.; (6) boulder.

to those saplings growing up in the center of the clusters. Those trees are fairly well protected by the outer saplings from injurious climatic influences such as desiccation and ice blast—at least for a while. Nevertheless, as time goes on, many of the trees will succumb to root competition and also to snow fungi.

Fungi infections often become a detriment to cembra pines even on sites exposed to wind that, previous to seedling establishment, had little snow cover in winter (fig. 13). As seedlings grow taller, they begin to influence local windflow, and as a result snow accumulations near the soil surface (fig. 14). Thus, more snow will be accumulated within the tree clusters, and the duration of the snow cover may increase greatly.

The invasion of former alpine pastures, especially by cembra pine, cannot be compared to the invasion of natural subalpine meadows by trees in many mountain ranges in the western United States. The changes in the Alps are caused by cessation of disturbances; the changes in montane North America may be the result of more favorable climatic conditions.

Figure 13—Cembra pines planted by the nutcracker above the closed forest on the northwest-facing slope of the Upper Engadine main valley at 2,270 m (6,924 ft). The lower needles have been destroyed by *Phacidium infestans* after tree growth resulted in increased snow accumulations.

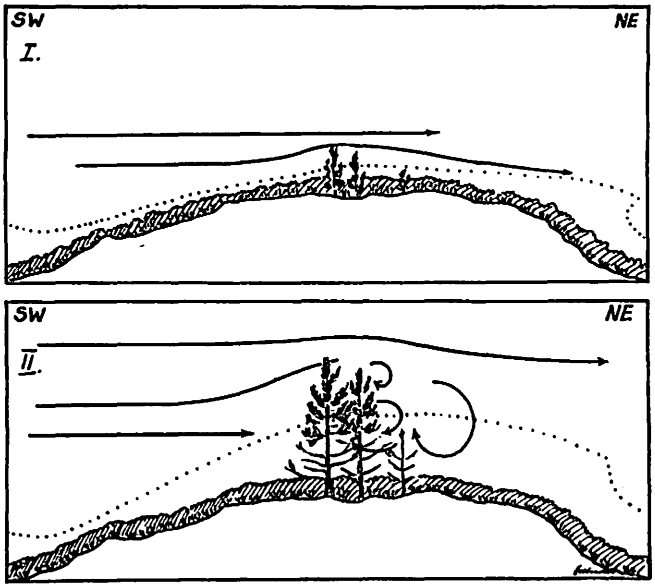


Figure 14—Influence of growth of cembra pines on windflow and snow accumulation.

MANAGEMENT OF THE LARCH-CEMBRA PINE FORESTS

It is clear that in the Engadine, as in the Alps in general, no forests remained untouched by humans. The use of the land has completely changed in modern times, but the legacy of disturbance and deforestation still has profound effects. Due to the extensive deforestation and over-utilization of the remaining forests, natural catastrophies such as avalanches, torrential floods, soil erosion, and land slides have increased and become a permanent threat to the people living in the mountain valleys. About 60 percent of the avalanches, for example, are released within the deforested area above the timberline. Maintenance of the remnant forests by careful silvicultural treatment and reforestation up to the climatic limit of tree growth, combined with fence construction when necessary, have proved to be the best way to reduce such catastrophies.

The first efforts to restore the uppermost forests were made about 130 years ago. Many of these early high-altitude afforestations failed completely because the environmental conditions, such as local climate, soil, and plant competition, had not been understood. However, it is evident that it is insufficient to protect the existing critical forests from commercial timber harvesting and to reforest the mountain slopes as high as possible. The forests should be managed to produce natural forest structure (age classes, density, coverage, etc.) and a variety of successional stages (Campell 1955; Mayer 1979).

In practice, opinions concerning specific silvicultural methods may differ considerably and recommendations can only be given with regard to the local situation. In the upper subalpine forests in the Engadine, cembra pine must be treated as part of the larch-cembra pine forest ecosystem. Natural succession in the ecosystem depends on the competition between cembra pine and larch.

For practical reasons, it seems appropriate to first look at the contiguous forest and then at the reforestation above the contemporary human-caused timberline. On the level foothills at the bottom of the glacial valleys and on the lower, sun-exposed slopes where open, over-mature larch forests still prevail, the cyclic mass outbreaks of the larch bud moth cause the most serious problems in developing a well-structured and healthy forest. Direct control of the larch bud moth with insecticides and bacteria has proved unsatisfactory. Also, there is increasing opposition by the public to chemical control. The best result could probably be achieved by appropriate silvicultural management (Baltensweiler 1975; Baltensweiler and Rubli 1984).

Thus, at sites not threatened by avalanches, high stem density and a rotation age of 150 to 200 years could reduce forest damage, because the larch bud moth populations grow most quickly in over-aged, open, and warm larch forests. Additionally, larch should be controlled for the benefit of cembra pine. Since the growth of cembra pine in the understory of the larch forests may be impeded by the larvae of the larch bud moth, a mixed forest, which consists of stands of pure larch and stands of cembra pine, might be most successful.

Most of the uppermost forests are over-mature, open, and consequently very sensitive to disturbances by windthrow, avalanches, and snow slides. Due to the short growing season, trees grow very slowly, and only occasional regeneration occurs. Luxuriously growing dwarf-shrubs and grasses hamper not only the natural regeneration of larch, but also of cembra pine. Big snow masses accumulate within the scattered tree stands. In clearings less wide than the height of the surrounding trees, the energy balance becomes negative because the incoming solar radiation is intercepted by the trees while the loss of out-going, long-wave radiation is almost unimpeded. Increased snow accumulation and negative energy balance result in delayed snow melt. Thus, scattered seedlings and saplings of cembra pine are more often damaged by snow fungi than trees in dense forests that offer more protection against snow (fig. 15). Consequently, the objective of silvicultural management must be to improve conditions for the regeneration of larch, which does not suffer from snow fungi. If necessary, the dense ground vegetation should be removed to provide suitable seed beds. In addition, larch should be planted. In the course of time the deposition of snow will be reduced by the closing crown cover. Thus, cembra pines in the understory, less threatened by snow fungi, could better survive.

To minimize the risk of disturbance and simultaneous decay of over-mature forests, a great variety of successional stages should be produced by silvicultural measures. Ongoing regeneration of larch trees, for example, can only be maintained if the bare mineral soil is exposed within the forest openings.

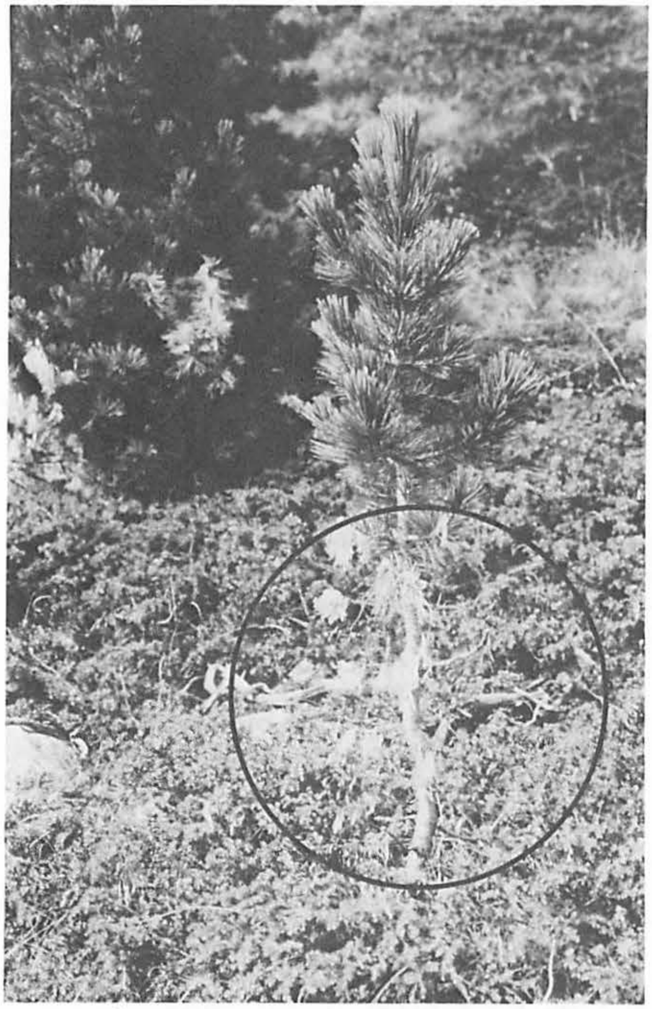


Figure 15—Young cembra pine that lost almost half of its needle foliage (circled) by *Phacidium infestans* activity. Morteratsch Valley, Upper Engadine at 2,170 m (6,618 ft).

The ongoing natural invasion of abandoned alpine pastures, especially by cembra pine, should be aided by management. This process will not succeed without help, because only a continuous compact, uneven-aged forest belt reaching as high as possible provides sufficient protection. Thus, in many areas the forest must be brought back by active management. However, the disturbance-caused lower timberline has become as formidable an ecological barrier as the natural climatic timberline had been before (Holtmeier 1965, 1974, 1987). Consequently, reforestation has to be carried out with respect to the local site patterns. That means excluding all sites from afforestation that are unfavorable to tree growth at the beginning of the effort—sites characterized by low solar radiation, low soil temperature, and long-lasting snow cover. If necessary, afforestation must be combined with artificial constructions such as avalanche walls and snow fences.

It has become obvious that cembra pine and larch are the species most appropriate for high-altitude afforestation in the Alps. Within plantations at timberline level in the Dischma Valley (west of the Engadine), after 8 years the survival rate was 71 percent for cembra pine and 81 percent for larch. Only 59 percent of mountain pine survived (Schönenberger 1985). The lower survival rate of cembra pine compared to larch was due to increasing fungi infections. Dense groups of 50 to 100 cembra pine trees should be planted. The distance between the individuals should not exceed 50 to 100 cm (1.6 to 3.2 ft). The groups should be separated by glades 6 to 8 m (19.7 to 24.3 ft) wide (Schönenberger 1986). This distribution will favor the accumulation of snow within the glades, thus keeping the risk of fungi infections low in the tree groups. However, reports from the Dischma Valley study site stated that adult cembra pines on wind-exposed spurs were heavily infected by *Phacidium infestans*. Two other fungi, *Ascocalyx abietina* and *Scleroderris lagerbergii*, seem to have become increasingly injurious to cembra pine during the last 20 years. Damages caused by *Ascocalyx* are most common on cool and moist north-facing sites and in gullies with late-melting snow cover (Schönenberger 1985).

Large populations of game animals and continued livestock grazing are other threats to forest regeneration. Cembra pine is very sensitive to browsing and trampling by red deer (*Cervus elaphus*) and livestock (fig. 16). Sheep, especially, are a most detrimental factor. Larch may more easily recover from damages caused by browsing animals. Winter feeding has reduced annual losses of red deer by starvation, resulting in unnaturally large populations. This never would have been possible in an undisturbed natural environment. Thus, all kinds of grazing should be excluded from the forest and areas that are being invaded by trees.

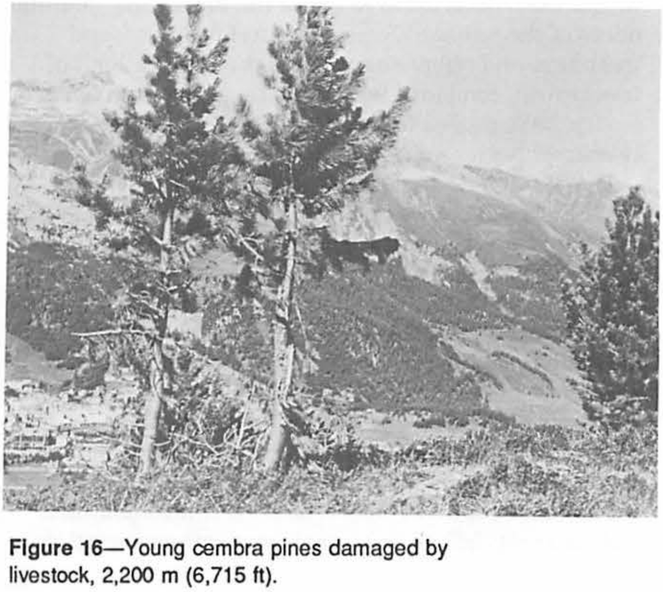


Figure 16—Young cembra pines damaged by livestock, 2,200 m (6,715 ft).

CONCLUDING REMARKS

I will leave it at that. The history of the high-altitude forest has roughly been outlined with special reference to cembra pine's ecology and role in the successional development of the forest. Disturbances and management problems of cembra pine in the larch-cembra pine forests of the Engadine have been discussed. It is obvious that the present ecological situation of cembra pine can be understood only if the numerous historical human influences on the forest ecosystem are considered. It is also evident that the situation in the Alps is quite different from that of most of the high-mountain forests of the western United States, where the first serious human influences do not date back more than 200 years.

The larch-cembra pine forests are now avalanche-protection forests, almost without exception. Thus, cembra pine must be managed to restore the climatic timberline and to produce well-structured, healthy forests to ensure their long-term vitality and protective function (fig. 17).

REFERENCES

Auer, Christian. 1947. Untersuchungen uber die natürliche Verjüngung der Lärche im arven-Lärchenwald des Oberengadins. Mitteilungen der schweizerischen Anstalt für das forstliche Versuchswesen. 25: 7-140.

Baltensweiler, Werner. 1975. Zur Bedeutung des Grauen Lärchenwicklers (*Zeiraphera diniana* Gn.) für die Lebensgemeinschaft des Lärchen-Arvenwaldes. Mitteilungen der schweizerischen Entomologischen Gesellschaft. 48: 5-12.

Baltensweiler, Werner; Rubli, Dieter. 1984. Forstliche Aspekte der Lächenwickler-Massenvermehrungen im Oberengadin. Mitteilungen der Eidgenössischen Anstalt für das forstliche Versuchswesen. 60: 148 p.

Campell, Eduard. 1955. Der Lärchen-Arvenwald. Ertragreiche Nadelwaldgesellschaften im Gebiete der schweizerischen Alpen. Beiheft zum Bündner Wald. 5: 14-26.

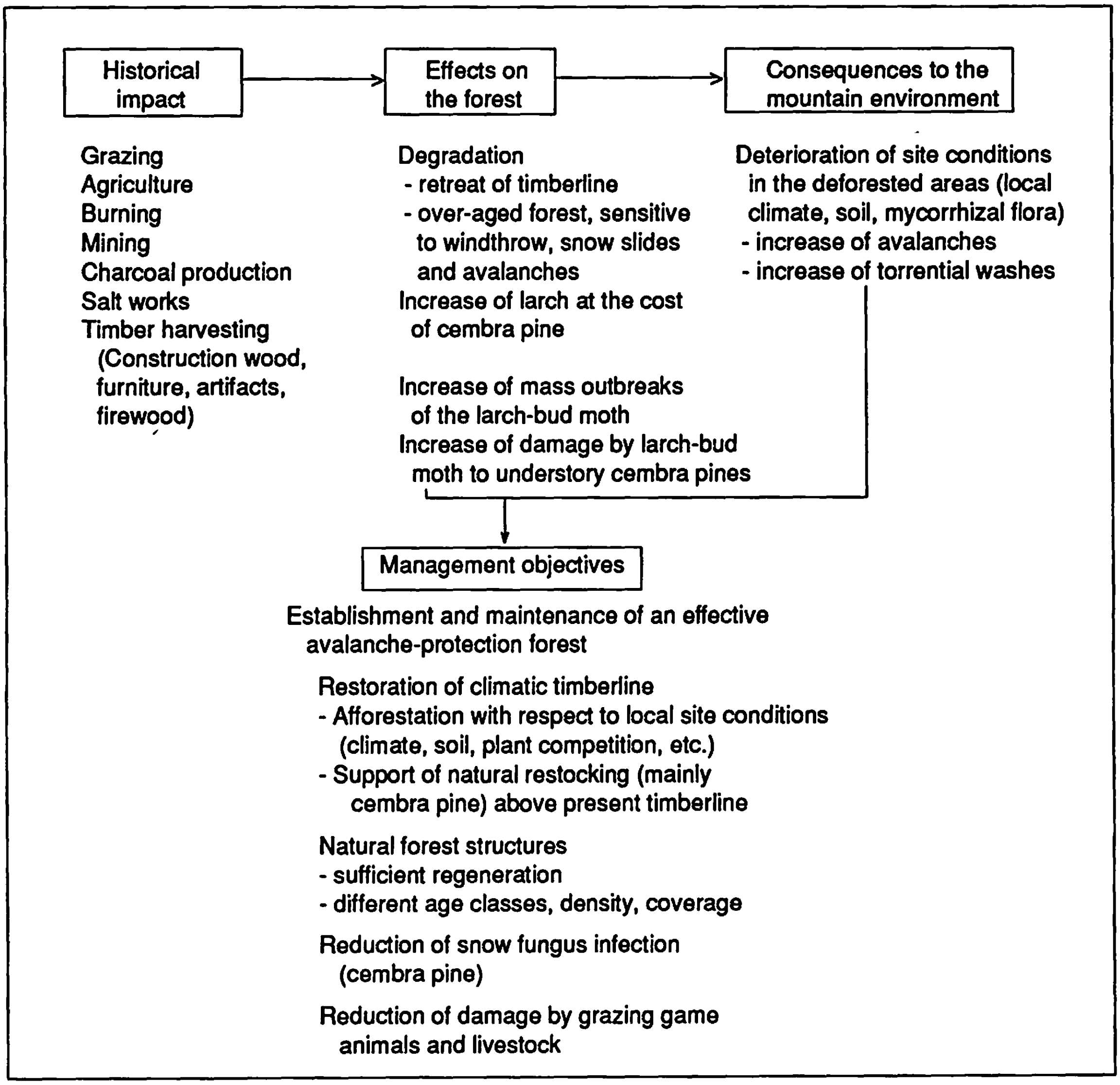


Figure 17—Synopses of human impacts, effects, and management possibilities to restore the larch-cembra pine timberline and maintain a healthy forest.

Ellenberg, Heinz. 1978. Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. 2d ed. Stuttgart: Verlag Eugen Ulmer. 981 p.

Holtmeier, Friedrich-Karl. 1965. Die Waldgrenze im Oberengadin in ihrer physiognomischen und ökologischen Differenzierung. University of Bonn, FRG. 163 p. Dissertation.

Holtmeier, Friedrich-Karl. 1966. Die ökologische Funktion des Tannenhähers im Zirben-Lärchenwald und an der Waldgrenze im Oberengadin. Journal für Ornithologie. 4: 253-260.

Holtmeier, Friedrich-Karl. 1967. Die Verbreitung der Holzarten im Oberengadin unter dem Einfluss des Menschen und des Lokalklimas. Erdkunde. 21: 249-258.

Holtmeier, Friedrich-Karl. 1973. Geoecological aspects of timberlines in Northern and Central Europe. Arctic and Alpine Research. 5(3): 45-54.

Holtmeier, Friedrich-Karl. 1974. Geoökologische Beobachtungen und Studien an der subarktischen und alpinen Waldgrenze in vergleichender Sicht (nördliches Fennoskandien/Zentral-alpen). Erdwiss. Forschung. 8: 130 p.

Holtmeier, Friedrich-Karl. 1981. What does the term "krummholz" really mean? Observations with special reference to the Alps and the Colorado Front Range. Mountain Research and Development. 1(3/4): 253-260.

Holtmeier, Friedrich-Karl. 1987. Der Baumwuchs als klimaökologischer Faktor an der oberen Waldgrenze. Münstersche Geographische Arbeiten. 27: 145-154.

Kuoch, Richard. 1965. Der Samenanfall 1963/64 an der oberen Fichtenwaldgrenze im Sertigtal. Mitteilungen der schweizerischen Anstalt für das forstliche Versuchswesen. 41(3): 53-85.

Mattes, Hermann. 1978. Der Tannenhäher im Engadin - Studien zu seiner ökologie und Funktion im Arvenwald. Münstersche Geographische Arbeiten. 2: 87 p.

Mattes, Hermann. 1982. Die Lebensgemeinschaft von Tannenhäher und Arve. Eidgenössische Anstalt für das forstliche Versuchswesen. Berichte. 241: 74 p.

Mattes, Hermann. 1985. The role of animals in cembra pine forest regeneration. Proceedings 3rd IUFRO Workshop P.1.07-00; 1984 September 3-5; Riederalp, Schweiz; Eidgenössische Anstalt für das forstliche Versuchswesen. Berichte. 270: 195-205.

Mayer, H. 1979. Ökosystem Lawinenschutzwald. In: Proceedings IUFRO Seminar: Mountain Forests Avalanches; 1978; Davos: 281-299.

Oberdorfer, Erich. 1970. Pflanzensoziologische Exkursions-flora für Süddeutschland. 3d ed. Stuttgart: Verlag Eugen Ulmer. 987 p.

Schönenberger, Walter. 1985. Performance of high altitude afforestations under various site conditions. Proceedings 3rd IUFRO Workshop P.1.007-00; 1984 September 3-5; Riederalp, Schweiz; Eidgenössische Anstalt für das forstliche Versuchswesen. Berichte. 270: 233-240.

Schönenberger, Walter. 1986. Rottenaufforstung im Gebirge. Schweizerische Zeitschrift für Forstwesen. 137 (6): 501-509.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Richard G. Krebill)—Is *Pinus cembra* as heavily damaged by the blister rust as is *Pinus strobus*?

A.—There is almost no damage by the blister rust to *Pinus cembra*, which seems to be very resistant.

Q. (from Ward W. McCaughey)—Do larch and cembra pine grow as well in mixed as in pure stands? Does cembra pine, growing in pure stands, develop a straight bole?

A.—Larch and cembra pine grow as well in mixed as in pure stands. That depends on the site conditions and the human interferences described in my paper. Pure stands of cembra pine are normally found on steep, rocky, and inaccessible slopes. Larch prevails on gentle terrain, exposed to the south, and easily accessible where cembra pine was eliminated by humans.

The bole appearance depends to a great extent on the age of the trees and on site conditions. In dense stands straight boles may prevail. However, trees that originated from seed caches of nutcrackers are usually multistemmed. Very old trees display a candelabrum-like growth form.

THE FUTURE OF HIGH-MOUNTAIN BIOLOGICAL RESEARCH

Eldon W. Ross

ABSTRACT

The emerging importance of the Nation's high-mountain forests for nontimber uses, such as watershed, recreation, and wildlife, is discussed. Attention is focused on the fragility of these ecosystems and the need for silvicultural options to maintain their presence and values. The need to better understand these complex ecosystems through research is reviewed.

I appreciate the opportunity to join you at this unique meeting. It is my understanding that this may well be the first ecology and management meeting in the United States devoted solely to high-mountain resources. Your timing for such a meeting is very appropriate. Scientifically, these resources are not as well understood as other forest systems. For an array of reasons, we have not adequately explored the various silvicultural options available to use in managing high-mountain forests. But of even more importance is a lack of appreciation of the numerous values and benefits of high-mountain systems by both the general public and, to a lesser extent, by some land managers.

In the next few days, you will review what is known about selected ecosystems and individual forest types that characterize portions of western high-mountain forests. You will review their early history and some of the many factors shaping current stand structures. By the end of this meeting, you will have provided a basis for reexamining the information needs necessary for managing this complex resource in the future, and your information will provide a sound basis for maintaining the health of high-mountain forests.

High-mountain forests are not like the major forest types now under management at lower elevations. Some of the oldest living trees and stands are to be found in these forests. Yet this system is rather fragile. The reported decline in the spruce-fir forests of the Eastern United States and the high-elevation forests of Europe certainly suggests this fact. A slight shift in the degree of stress, be it caused by humans or natural, can accelerate the decline of such ecosystems. We may argue over the causes of these declines, but they are taking place. In the next few years, a number of major research initiatives will be directed toward establishing the relationship between environmental changes and forest conditions.

In both Europe and the United States, high-mountain forests are now considered mainly as multiple-use forest resources. Their real value lies not in traditional forest products, such as timber or fiber, but in their value as wildlife habitats, recreational areas, water resource management units, and as sensitive environmental indicators. The consequences of the various uses are not adequately known and attention must be paid to possible negative impacts on these ecosystems.

Their value as a major catchment for snow may well prove to be a prime reason for their careful management in the future. In the last few years, some areas of Europe had to relearn that high-mountain forests are a major source of protection from the massive movement of snow. Thus, their value as protection forests will determine the extent and type of management, if any, that will be applied.

As wildlife habitat, the mountain forests are somewhat unique. Their value as a wildlife habitat is well known to some but is still undervalued by many. During their different seasons, mountain forests provide an everchanging array of food sources as well as shelter. Many of the wildlife species spend only a portion of their time in these forests. Yet it is often a critical portion of time in terms of reproduction and maturation. How more intensive management and use, especially recreation, will impact on the maintenance of viable wildlife populations must be a priority research item. Strengthening management strategies for maintaining rare and endangered species that are associated with the high mountains must also receive additional attention. Some of these issues you will address in your section on animal interactions. Such research needs to be directed at an array of different mountain ecosystems.

With our highly mobile society and the apparent increasing desire for a broader array of recreational opportunities, we are beginning to experience wider use of high-mountain forests. People pressures will be manageable in wilderness areas. However, there are already demands to increase the number of ski slopes and some are now under construction in once untouched mountain forests. What will be the impact on the ecological stability of the remaining stands? What will be the impact on the protection value of reduced forest cover? These are research areas we must be willing to support now if we are to continue wise use. Lest you feel this is an academic subject, let me remind you of events in the Italian Alps in the last few years. The number of summer mudflows and snow avalanches has increased with expanded recreational development at higher elevations. Firm evidence is in hand that the ecological stability of the protection forest has been greatly reduced through thinning operations designed to create trails and additional ski slopes. Even

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Eldon W. Ross is Associate Deputy Chief for Research, Forest Service, U.S. Department of Agriculture, Washington, DC.

in Europe with its relatively long history of mountain silviculture, I suspect much still remains to be learned. Yet, what is our current level of knowledge of appropriate European silvicultural practices that we could apply?

Finally, I would like to review briefly a viewpoint suggesting that high-mountain forests, because of their ecological sensitivity to their environment, are a barometer of climate change. Currently, a number of concerns exist in the scientific community and the general public. Those concerns include global warming caused by the rise in carbon dioxide levels from the use of fossil fuels as well as other gases—the so-called "Greenhouse Effect"—or the depletion of the ozone layer, which also contributes to a possible warming trend. We also have the presence of acid rain and related issues of pollution. To be sure, all of the facts related to these various issues are not available and we certainly can and will argue about what is really happening. Still, there are some indications that suggest we need to get on with focused research on sensitive ecosystems that will permit us to at least develop a rational level of understanding of what is happening. The first indication of forest decline was found in the high-mountain spruce-fir forests of Yugoslavia before it became apparent in lower elevations. To a degree, this also appears to be the case for the so-called spruce-fir forest decline in New England and decline in high-mountain forests of the Southeast. The causes for these forest declines are not known nor have current published research results completely clarified the situation. In West Germany, where the decline of European white fir and Norway spruce forests has received considerable attention, a review of earlier records suggests that in at least some forest regions, the declines were first apparent at higher elevations before they were detected in lower elevations. If we accept the premise that high-mountain ecosystems tend to be fragile and have limited elasticity to respond to change, then this early response to additional stress is not surprising.

If this concept that high-mountain forests are, in fact, a useful indicator of climate changes or environmental stresses, is correct then what type of research would prove useful? As noted earlier in this meeting, there are a number of descriptive ecological studies of at least the whitebark pine ecosystem. Certainly, we need a better understanding at the community level. This suggests the need to expand our studies to still other high-mountain systems and determine if there are some common ecological patterns. We need to strengthen our understanding of the genetic patterns of these systems, including the relative level of gene flow, if any, between related systems. Finally, I suspect that physiologically, high-mountain species will prove to be very different and interesting in their ability to respond to, and cope with, environmental changes. Research in Austria has for some time been focusing on certain aspects of comparative physiological studies of mountain species. Such research does suggest that high-mountain species do, in fact, have physiological coping mechanisms somewhat different from nonmountain species. How we can apply such information generally is not clear, nor have we adequately established the relationship of individual physiological responses to the interrelationships among competing species in a community. Mountain biological systems may be an ideal situation for establishing such relationships. Such complex questions clearly demonstrate the need to integrate the knowledge developed by different scientific disciplines.

There is great competition for research funding, but in establishing priorities for future programs we should not forget that high-mountain ecosystems are extremely important and deserve much more of our research attention.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Ron Lanner)—Should not special efforts be made to preserve, in place, high-elevation forests, as a research resource? Is the Forest Service going to do so?

A.—I certainly agree that high-elevation sites should be made available as a research resource. Currently the Forest Service is in the process of identifying different forest types or areas with unique features to be set aside as Research Natural Areas (RNA's). A number have already been designated and surely some of them will be high-mountain ecosystems. If you desire to know the location of specific RNA's or to conduct research on them you should contact the responsible Station Director or Regional Forester.

Q. (from Anonymous)—Will the Forest Service really give sustained support to high-mountain resources research?

A.—As I noted in my presentation there is strong competition for research funding. While we may have the desire to sustain long-term research programs in such areas as the high-mountain forests, we constantly have to re-evaluate our priorities. Therefore, it is very important that the public has a high awareness of the importance of such research. This is where you can help. Anytime you have an opportunity to address the importance of research in high-mountain forests in public gatherings or brief Congressional delegations, you should do so.

Q. (from Diana Tomback)—In view of the fragility of the high-mountain ecosystems, do you foresee any policy protecting these ecosystems from any commercial impact in National Forest and wilderness areas in the near future?

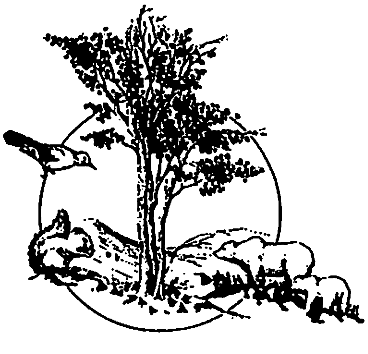
A.—There will certainly be increasing pressure for commercial development in high-mountain resources. We are already seeing increased requests for development of winter recreation. Officially designated Wildernesses are, of course, already protected from further development; however, nonwilderness areas in National Forests are available for multiple use. Good research is the key element in establishing sound future policy on use of these areas. The better we understand the high-mountain ecosystems, the better we will be able to manage development.

SESSION 2

High-Mountain Resources of North America

Richard Kracht
Session Coordinator

The United States and Canada have much in common with the geology and biology in the high mountains of the West that span the borders of these two countries—both can benefit from the knowledge gained on either side of the border. This session aimed at describing what resources result from this commonly shared environment and how resources are viewed under different public land management objectives.



LATE QUATERNARY HISTORY OF WHITEBARK PINE IN THE ROCKY MOUNTAINS

Richard G. Baker

ABSTRACT

The fossil record of whitebark pine (Pinus albicaulis) *is still sketchy. Only two fossil sites older than the last glacial advance contain whitebark pine pollen and macrofossils, but they show that it was present in the Yellowstone National Park region for over 100,000 years. The history of whitebark pine during the last 15,000 years in parts of the Rocky Mountains is fairly well understood.* Pinus albicaulis *apparently survived the last glaciation in protected areas throughout much of the Northern Rocky Mountains. It was well adapted to colonizing the treeless sites with mineral soils that prevailed during late-glacial times (about 15,000 to 10,000 years ago). Whitebark pine remained abundant, probably as a subalpine forest species, in many areas at the beginning of the early Holocene (about 10,000 to 8,000 years ago). During "Altithermal" warming in the middle Holocene of the Rocky Mountains (about 8,000 to 4,000 years ago), the species apparently was confined to high-altitude sites, and it has not substantially recovered during the slightly cooler climates of the late Holocene (the last 4,000 years).*

INTRODUCTION

To understand the ecology and distribution pattern of any plant species, it is useful, if not essential, to know its history through the study of fossil remains. When extensive fossil records became available for many species in both the eastern and southwestern United States, new concepts of community evolution and biogeography were mandated (Davis 1983; Spaulding and others 1983; Thompson 1988; Watts 1983; Webb 1988). Unfortunately, the fossil record is incomplete; for most species and most regions, such information is not available. The fossil record for whitebark pine (*Pinus albicaulis*) in the northwestern United States and Canada has been investigated during the past two decades, and the resulting paleoecological and paleogeographical information may help in understanding its present status. The purpose of this paper is to outline the evidence of the Late Quaternary occurrence of whitebark pine as it is known from the fossil record. The longest records and strongest evidence come from Yellowstone National Park and surrounding areas near the southeastern margin of its range, and these sequences will be emphasized. Other records from northern Montana, Idaho, Washington, and Alberta, Canada, will also be discussed.

The past distribution of whitebark pine can be inferred from (1) the present distribution, (2) the occurrence of high percentages of haploxylon pine pollen, (3) high PAR (pollen accumulation rate) values of haploxylon pine pollen (measured in grains per square centimeter per year), and (4) the occurrence of needles or other macrofossils of pine.

Using present distribution of whitebark pine or any other species to infer past ranges is the most speculative approach. It has often been suggested, for example, that the disjunct occurrence of trees like eastern white pine (*Pinus strobus*) and larch (*Larix laricina*) in the Midwest was a relict of the last (Wisconsinan) glacial episode; fossil evidence indicates that they are late Holocene immigrants (Davis 1979; Webb 1988).

Pollen percentages are a more useful though still imperfect method of studying past pine distribution. There are numerous pollen sequences in some areas of the Rocky Mountain region. The problem is in identifying pine pollen to species (Hansen and Cushing 1973). Two studies that deal with identification of conifer pollen do differentiate species of pine in the Northern Rocky Mountains (Bagnell 1975; Weir and Thurston 1977), using the scanning electron microscope. Virtually all routine pollen analysis, however, is done with a light microscope, and thus few palynologists use the criteria of Bagnell (1975) and Weir and Thurston (1977) in identifying pine to species. In fossil pollen studies, identifications are generally only to the subgeneric level, and many are only to the genus level.

Few pine species presently grow in the Northern Rocky Mountains, and the assumption is often made that only these species have been present during late Quaternary time. Support for this argument comes from the American Southwest, where there is strong evidence that several pine species moved vertically up and down mountain slopes and did not show major geographic shifts during this period (Thompson 1988). In the Northern Rocky Mountains, macrofossil studies suggest that the same type of movement occurred at least during the last

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Richard G. Baker is Professor of Geology and Botany, and Director, Iowa Quaternary Studies Group, University of Iowa, Iowa City, IA 52242.

15,000 years. *Pinus albicaulis* and limber pine (*P. flexilis*) are the only haploxylon pines in most of the Rocky Mountain region, though western whitepine (*P. monticola*) is present in northern Idaho and Montana. The co-occurrence of haploxylon-type pine pollen with *Picea* and *Abies* may help to distinguish *P. albicaulis* from *P. flexilis* and *P. monticola*, which have different associations in this region today. Studies of the modern pollen rain in Yellowstone and Grand Teton National Parks indicate that haploxylon/diploxylon pine pollen ratios are highest at high elevations at or near treeline, and are associated with peaks in spruce (*Picea*) and fir (*Abies*) pollen. Ratios are lowest in lodgepole pine (*Pinus contorta*) forests, and are intermediate and associated with Douglas-fir (*Pseudotsuga*) pollen at lower treeline, where *P. flexilis* occurs (Baker 1976; Barnosky 1987).

PAR values are more precise in determining the local presence of a taxon. PAR values reflect the actual deposition rate of pollen through time. Generally, these values are very low or zero when a taxon is absent, and they jump rapidly to high values when the taxon arrives at a site. Calculation of PAR requires an accurate chronology established by radiocarbon dating or varve record to provide the deposition rate, and few studies in the Rocky Mountains have used this method.

Studies of plant macrofossils are also not common, but where available, they establish more firmly the local presence of the tree. Fossil needles of *P. albicaulis* can be determined on the basis of morphology: they have both dorsal and ventral stomata, distinguishing them from *P. monticola*, and strongly thickened endodermal cells compared with *P. flexilis*. Even if this latter distinction cannot be made (perhaps because of poor preservation), the association of whitebark/limber pine needles with those of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) in the Central and Northern Rocky Mountains would suggest that whitebark pine was present on ecological grounds. In this region limber pine is associated with the lower treeline and whitebark pine with the upper treeline. A cautionary note is needed, however, because in the Southern Rocky Mountains, where whitebark pine is absent, limber pine grows at the upper treeline.

The modern distribution of *P. albicaulis* is likely controlled by a number of factors, of which climate is probably most important. Arno and Hoff (1989) have summarized climatic factors that characterize modern *P. albicaulis* stands. The general distribution follows boundaries of airmasses that determine when precipitation occurs (Mitchell 1976). Whitebark pine grows in areas of mainly high winter precipitation and dry summers in interior locations, and of both summer and winter precipitation in the Sierra and Cascade Ranges.

The Quaternary climatic history of the Yellowstone National Park region has been summarized by Porter and others (1983) and Richmond (1986a, 1986b). The region has a long and complex history of glaciations and interglaciations extending back to over 2 million years. Since the last (Sangamonian) interglaciation ended about 120,000 yr B.P., the Wisconsinan Glaciation (about 120,000-10,000 yrs B.P.) occurred, but glaciers were not extensive during that entire interval. Part of that period was dominated by nonglacial climatic episodes that ranged from warm to cold, based on both physical and biological evidence (Baker 1986; Richmond 1986a). As the last Wisconsinan glaciers retreated, a period of cool climate persisted prior to postglacial warming; this interval is herein called the "late-glacial" (15,000-10,000 yrs B.P.). The Holocene follows the late-glacial, and is used in this paper to mean the relatively warmer period during the last 10,000 years, with the exact timing of the warming depending on geographic position and altitude.

YELLOWSTONE NATIONAL PARK REGION

Although *Pinus albicaulis* probably arose from ancestral stock (in the Subgenus Strobus, Section Strobus, Subsection Cembrae) tens of millions of years ago during the Tertiary Period (Axelrod 1986), apparently no fossils referable to that stock are known in North America. In fact, I do not know of any published fossil records of whitebark pine older than Late Quaternary.

Earliest Records

Several unpublished pollen sequences have been completed from Early to Late Pleistocene sediments by E. B. Leopold, J. P. Bradbury, and W. Mullenders (Richmond 1978). Although no separation of pine pollen is made in these reports, association with spruce and fir would suggest that whitebark pine may have been present.

The earliest published records known from the Quaternary date back only to the waning stages of the previous (Illinoian) glacial period, approximately 140,000 yr B.P. The lowest exposed levels of a deltaic section along Beaverdam Creek in the southeastern part of Yellowstone National Park (fig. 1) contain pollen of spruce, fir, and haploxylon pine along with that of juniper, sagebrush, grass, and sedge (Baker 1981). This pollen assemblage strongly resembles much younger late-glacial assemblages in the Yellowstone Park region, and indicates a cold, near-treeline environment. No macrofossils were recovered from this section, but it is likely that the pine is whitebark pine.

Somewhat higher in the same deltaic sequence, overlying a very warm-climate pollen sequence, haploxylon pine pollen and needles are associated with pollen and macrofossils of spruce, fir, Douglas-fir, poplar, and dwarf birch (Baker 1986). This assemblage is much more heterogeneous, and the pine could be either whitebark or limber pine. Poor needle preservation precluded sectioning to determine which species was represented.

Another climatic fluctuation began an estimated 80,000 yr B.P. (Richmond 1986a) and is recorded by the sequence at Grassy Lake Reservoir, near the southwest corner of Yellowstone National Park (Baker 1986) (fig. 1). Pollen percentages of total pine are low (<30 percent) at

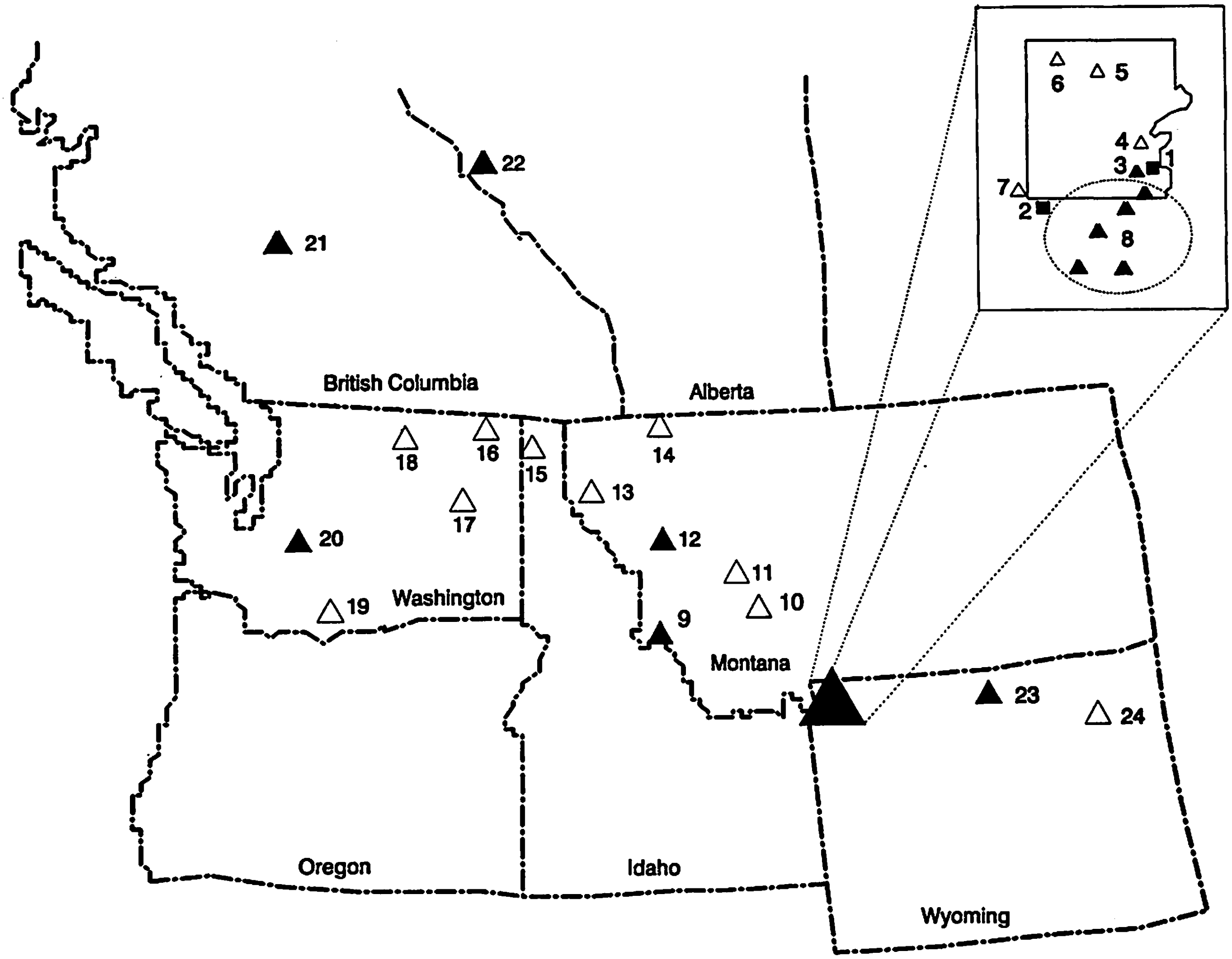


Figure 1—Location of sites considered in this paper. Squares (in the Yellowstone area inset) = sites older than 50,000 years B.P.; triangles = sites younger than 20,000 years B.P.; open markers indicate that pollen only was studied; filled markers indicate that both pollen and macrofossils were studied. 1-Beaverdam Creek (Baker 1981, 1986; Baker and Richmond 1978); 2-Grassy Lakes Reservoir (Baker 1986); 3-Buckbean Fen (Baker 1970, 1976); 4-Cub Creek Pond (Waddington and Wright 1974); 5-Blacktail Pond (Gennett and Baker 1986); 6-Gardiner's Hole (Baker 1983); 7-Cub Lake (Baker 1983); 8-group of five sites studied by Barnosky (1987); 9-Lost Trail Pass Bog (Mehringer and others 1977); 10-Forest Lake site (Brant 1980); 11-Telegraph Creek site (Brant 1980); 12-Sheep Mountain Bog (Mehringer 1985); 13-Teepee Lake (Mack and others 1983); 14-Guardipee Lake (Barnosky 1989); 15-Hager Pond (Mack and others 1978b); 16-Big Meadow (Mack and others 1978a); 17-Waits Lake (Mack and others 1978c); 18-Bonaparte Meadows (Mack and others 1979); 19-Carp Lake (Barnosky 1984, 1985); 20-Davis Lake (Barnosky 1981); 21-Castle Peak site (Clague and Mathewes 1989); 22-Wilcox Pass site (Beaudoin and King 1989); Watchtower and Excelsior sites (Luckman and Kearney 1986); Lake O'Hara (Reasoner and Hickman in press); 23-Sherd Lake (Baker 1983; Burkart 1976); 24-Antelope Playa (Margraf and Lennon 1986).

the base, indicating that pine trees were scarce to absent at the site, but the percentages are strongly dominated by haploxylon pine pollen. Spruce, sagebrush, grass, and sedge pollen are dominant. In the overlying zone, spruce pollen percentages and macrofossils rise first, followed shortly by those of whitebark pine type and fir, and last by those of lodgepole pine. This sequence also is similar to late-glacial sequences and indicates vegetational change from tundra to open parkland and finally to forest. Apparently spruce was the first migrant in the area, with whitebark pine following shortly after.

A second, stratigraphically younger sequence along Beaverdam Creek (fig. 1) extends from 70,000 yr B.P. to possibly 50,000 yr B.P. This thick section of laminated lake sediments records cold tundra conditions for nearly the entire period represented. An apparently short-lived interval near the base has peaks in haploxylon pine, spruce, and fir pollen (Baker and Richmond 1978). The same interval at a nearby section contained needles of spruce and whitebark pine (Baker 1978). Apparently trees were scarce during this long, cold period, but they were near enough to colonize local habitats during this earlier, slightly warmer interval.

The interval from about 50,000 to 15,000 yr B.P. is very poorly known. No known sequences in Yellowstone National Park contain sediments of this age, and during much of that time the Park was almost completely covered by a Late Wisconsinan ice cap (Pierce 1979; Porter and others 1983). Elsewhere, few long records from unglaciated areas in the Rocky Mountains and Pacific Northwest are available. Sites in western, west-central, and southern Washington date back more than 20,000 yr B.P. and record very cold conditions. There, however, the first pine to colonize was lodgepole, not whitebark, pine (Barnosky and others 1987; Heusser 1983, 1985). Another sequence that extends back more than 20,000 yr B.P. is from the Chuska Mountains of New Mexico (Wright and others 1973), well beyond the present range of whitebark pine. Some of the most reliable identification of pollen from several species of pine was performed there (Hansen and Cushing 1973), and no evidence of whitebark pine was found.

A different type of record provides paleoecological information from full-glacial and late-glacial time from the American Southwest (Spaulding and others 1983; Van Devender and others 1987). Packrats build nests and middens of local plant materials, which accurately represent the surrounding vegetation. Preservation of plant macrofossils in ancient nests is superb, and they have been used extensively in the arid mountains and deserts to provide key information on the distribution of many plant species, including several pines. Unfortunately, whitebark pine has not been recorded in these middens.

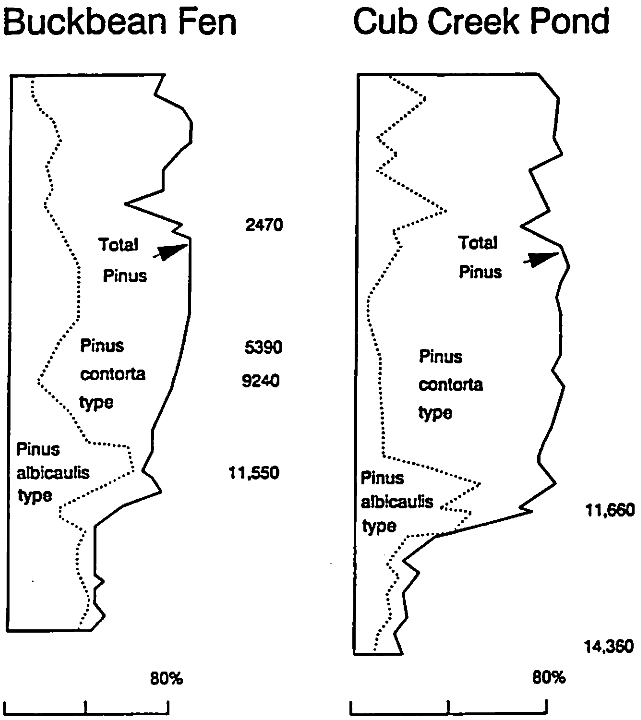


Figure 2—Total pine and whitebark pine-type pollen percentages from Buckbean Fen and Cub Creek Pond, Yellowstone National Park. Modified from Baker 1976 and Waddington and Wright 1974.

Late-Glacial and Holocene Records

Several sites in and near Yellowstone National Park contain late-glacial (about 15,000 to 10,000 yr B.P.) and early Holocene (about 10,000 to 8,000 yr B.P.) remains of whitebark pine. The record at Buckbean Fen (fig. 1) (elevation 2,380 m) is typical (Baker 1970, 1976). Prior to about 12,000 years ago sagebrush (*Artemisia*) and other shrubs and herbs dominated the pollen sequence. Pollen percentages of *Pinus* were low, but the dominant type was haploxylon, probably *P. albicaulis* (fig. 2). Macrofossils indicate that common juniper, (*Juniperus communis*), dwarf birch (*Betula glandulosa*), and open-ground subalpine and alpine herbs were present. Together these data indicate that an open landscape of tundralike vegetation prevailed. Engelmann spruce and whitebark pine may have been present in locally favorable microhabitats. Engelmann spruce, whitebark pine, and poplar (probably balsam poplar) were the first trees to migrate onto raw mineral soils of the deglaciated area. As the climate became warmer about 11,500 years ago, the pollen and macrofossil record indicates that *P. contorta* immigrated into the area, and a mixed forest of *P. albicaulis* and *P. contorta* covered the region. By about 10,000 yr B.P. pine dominance in the pollen and macrofossil record shifted from *P. albicaulis* to *P. contorta*, indicating that whitebark pine was gradually phased out, and *P. contorta* forests became dominant as they are today. During the late-Holocene, even though *Picea* and *Abies* pollen and macrofossils became more abundant, *P. albicaulis* did not return to this site (Baker 1970, 1976).

The other sites in Yellowstone National Park (fig. 1) show similar pollen sequences. These sites include Cub Creek Pond (elevation 2,485 m) (Waddington and Wright 1974), Gardiners Hole (elevation 2,215 m) (Baker 1983), Blacktail Pond (elevation 2,018 m) (Gennett and Baker 1986), and Cub Lake (elevation 1,840 m) (Baker 1983). The late-glacial pollen spectra at all these sites are similar to that at Buckbean Fen, with high percentages of nonarboreal pollen, and maxima of spruce and fir percentages and of whitebark-pine-type/lodgepole-pine-type pollen ratios. Although macrofossils are not available for these sites, the pollen sequences indicate comparable late-glacial paleoenvironments, even at low elevations.

The late-glacial to Holocene transition at 10,000 yr B.P. also is similar, with a rapid rise in total pine, mostly haploxylon, followed by a period of whitebark pine and lodgepole pine dominance. *Pinus contorta* is dominant during the middle and late Holocene, though *P. albicaulis* pollen rises slightly in the late Holocene at Cub Creek Pond (fig. 2), the highest elevation site sampled in the Park. Presumably *P. albicaulis* was confined to timberline sites during the middle Holocene, and remained at relatively high elevations during the late Holocene.

Barnosky (1989a) has studied several sites ranging in elevation from 2,073 m to 2,634 m between the southern boundary of Yellowstone National Park and Jackson Hole, WY (fig. 1). She has used pollen percentages and pollen accumulation rates, as well as macrofossils, to establish patterns of colonization after deglaciation. Her work indicates that a period of treeless vegetation followed deglaciation, as in Yellowstone National Park. Subsequently, *P. engelmannii* arrived at most sites, followed shortly by *P. albicaulis* and *A. lasiocarpa*. In early Holocene time *P. contorta* and *Pseudotsuga menziesii* forests prevailed, and low levels of haploxylon pine pollen suggest that whitebark pine was confined to exposed sites at high elevations.

Pinus albicaulis is not present today in the Bighorn Mountains in eastern Wyoming (figs. 1 and 3), and pollen analysis from three sites there suggests that it never grew there during the last 13,000 years (Baker 1983; Burkart 1976). It also never occupied the Wyoming basins during late-glacial times; at least the Powder River Basin (figs. 1 and 3) was apparently covered by late-glacial steppe (Markgraf and Lennon 1986). There is an excellent record of whitebark pine in the Bitterroot Mountains (fig. 1) to the west of Yellowstone National Park (Bright n.d.; Mehringer and others 1977). Both *P. albicaulis* and *P. engelmannii* pollen and needles appear about 11,500 yr B.P. at Lost Trail Pass Bog (elevation 2,152 m) and were codominants with *P. contorta* and *A. lasiocarpa* during the early Holocene. After a mid-Holocene warm period about 8,000 to 4,000 yr B.P., when an open forest of *Pseudotsuga* was apparently present, closed forests of *P. albicaulis*, *P. contorta*, *A. lasiocarpa*, and *P. engelmannii* returned to the site and remain to the present time.

NORTHERN ROCKY MOUNTAINS AND ADJACENT AREAS

Brant (1980) found pine pollen curves similar to those in Yellowstone National Park at two sites in west-central Montana (fig. 1). Haploxylon/diploxylon pine pollen ratios were highest during the late-glacial period, when total pine percentages were relatively low, and both haploxylon and diploxylon pines were present during the early Holocene (fig. 3). Whitebark pine apparently was not abundant during the late Holocene, although it is still present

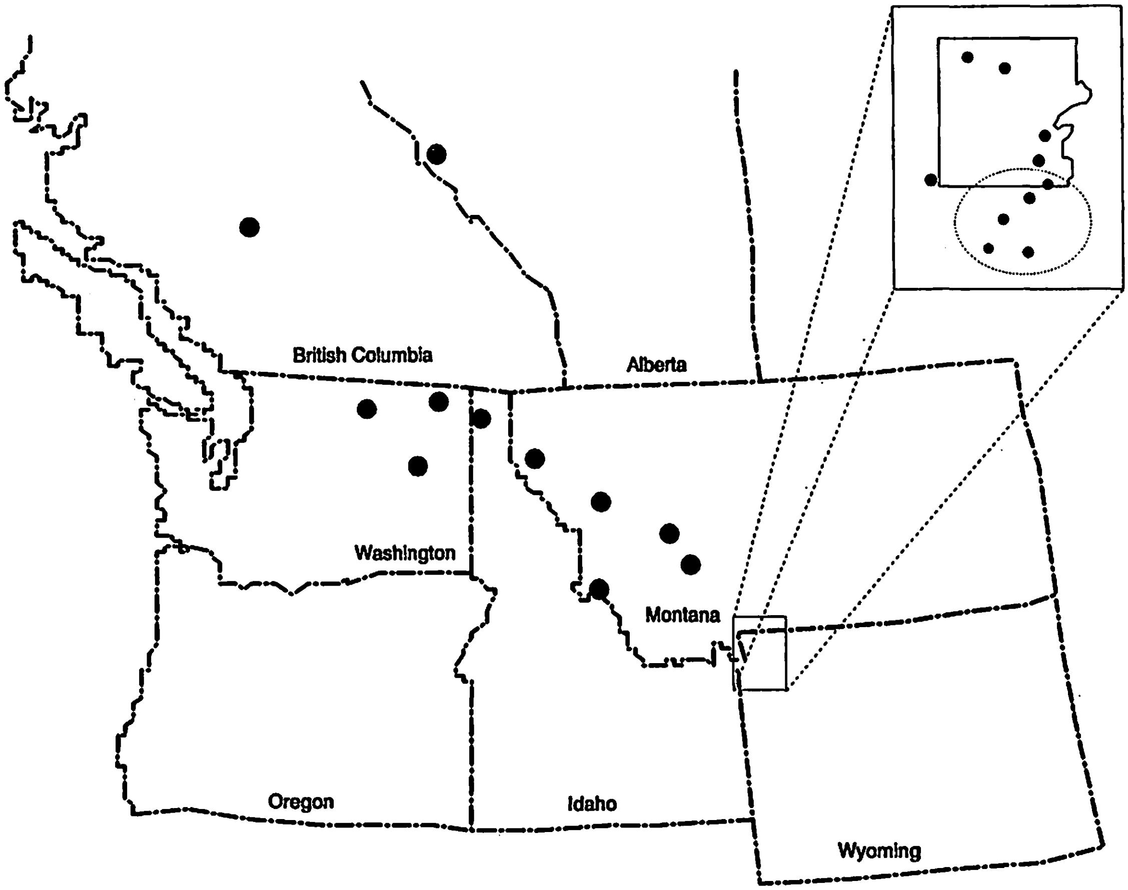


Figure 3—Sites where *Pinus albicaulis* was present between15,000 and 8,000 years B.P.

there. A very similar sequence occurs farther northwest at Sheep Mountain Bog (elevation 1,920 m) in northwest-central Montana (Mehringer 1985), where the high ratios of haploxylon/diploxylon last until about 9,500 yr B.P. Needles of whitebark pine confirm the tree's presence in this lower elevation site (Mehringer 1989). At this site, as at Lost Trail Pass Bog, haploxylon pine pollen remains at moderate levels throughout the Holocene. Both *P. flexilis* and *P. albicaulis* occur in the area at present; in the middle and late Holocene, limber pine may also have contributed to the haploxylon pine pollen rain.

Apparently the Great Plains adjacent to the Northern Rocky Mountains were not tree covered in late-glacial time, despite the lowering of treelines and forest zones (figs. 1 and 3). Pine pollen percentages are predominantly diploxylon and suggest that lodgepole pine was important in the nearby mountains, but that the trees were not present at Guardipee Lake east of Glacier National Park during the last 12,000 years (Barnosky 1989b).

A number of sites between the Northern Rocky Mountains and the Cascade Range provide pollen, but not macrofossil evidence for the past distribution of whitebark pine (see summaries in Baker 1983; Barnosky and others 1987; Heusser 1983, 1985; Mehringer 1985). *Pinus monticola*, *P. flexilis*, and *P. albicaulis* are all present today in the Northern Rocky Mountains, so the identification of *P. albicaulis* on pollen morphology alone is less certain in these studies. Nevertheless, it is the most likely contributor of haploxylon pine pollen in the late-glacial and early Holocene, based on other conifers present at that time.

Several sites in northwestern Montana and northern Idaho (fig. 1) show that both haploxylon and diploxylon pine pollen were part of the late-glacial pollen flora (fig. 3), along with *Picea* and *Abies* (Mack and others 1978a, 1978b, 1978c, 1979, 1983). The haploxylon pine pollen probably represents mostly whitebark pine, although some *P. monticola* pollen has been found according to Mack and others (1978b). The diploxylon pine pollen is thought to represent *P. contorta*, as opposed to *P. ponderosa*, which also grows there today. These conifers were apparently present in an open parkland, judging by the large amount of nonarboreal pollen in the late-glacial.

From the west side of the continental divide to the east flank of the Cascade Range in Washington (fig. 1), a number of sites indicate that a steppelike environment with scattered pine was present in the late-glacial and early Holocene (Barnosky and others 1987; Mehringer 1985). At the west end of this transect the pine pollen is mostly diploxylon. Apparently whitebark pine was rare or absent along the base and eastern slope of the Cascade Range. However, a recent report on fossil logs at timberline in southern British Columbia (figs. 1 and 3) indicates that *P. albicaulis* grew in the southern Canadian Cordillera 9,000 years ago (Clague and Mathewes 1989). In fact, timberline was 60 to 130 m higher at that time in the Pacific Northwest. Few, if any, pollen studies in the Cascades indicate that whitebark pine was present there. Whitebark pine was not present in a very careful study of plant macrofossils from the flanks of Mt. Rainier, for example (Dunwiddie 1986). Further careful work on the source of the pine pollen in that area is needed. The presence of both haploxylon and diploxylon pine pollen in the northeastern Washington highlands suggests that mixed *P. albicaulis-P. contorta* parklands were present there shortly after deglaciation. It is likely that *P. albicaulis* has been present, if not abundant, ever since in that area.

Recent studies in the Canadian Rocky Mountains (fig. 1) also indicate the early Holocene presence of *P. albicaulis* (fig. 3) (Beaudoin and King 1989; Kearney and Luckman 1983; Luckman and Kearney 1986; Luckman and others 1984; Reasoner and Hickman in press). It is the only high-altitude haploxylon pine in the region, and all sites investigated are in alpine meadows near the upper treeline. Both pollen and macrofossils (needles) of *P. albicaulis* were present shortly after deglaciation. Apparently whitebark pine survived glaciation locally and was able to colonize new sites effectively. It was relatively abundant during the early Holocene, became less common during the warmer middle Holocene, and again increased in abundance in the late Holocene.

DISCUSSION

From the fossil evidence, it seems clear that *P. albicaulis* was an important early invader on deglaciated ground throughout the Central and Northern Rocky Mountains. Its present ecology is well suited to such an environment. Arno and Hoff (1989) described its present treeline position, where it is well adapted to mineral soils and open, sunny habitats. These conditions must have been prevalent over large areas during late-glacial time.

The fossil records show that whitebark pine established much of its modern range by at least 10,000 yr B.P. (fig. 3). It seems likely that the tree survived glaciation in protected habitats in most areas. Present distribution of whitebark pine is heavily dependent on Clark's nutcrackers, which are almost solely responsible for dispersal of the tree (Hutchings and Lanner 1982; Tomback 1978). These birds collect, transport, and bury its seeds in caches. The common occurrence of many boles of whitebark pine is ample evidence of the effectiveness of these birds as agents of dispersal. It is likely that Clark's nutcrackers coevolved with the pines long before the last glaciation, and thus they would have been effective in the rapid dispersal of whitebark pine from sites where it survived full-glacial conditions. Similar relationships are present between fagaceous trees and blue jays in eastern North America, and blue jays have been cited as an important factor in the rapid dispersal of oaks in the early Holocene (Johnson and Webb in review).

During the early Holocene, whitebark pine apparently remained abundant in many areas, along with spruce, fir, and lodgepole pine. *P. albicaulis* probably occupied both of its present niches (climax at treeline and seral in spruce-fir-whitebark pine forests) (Arno 1986). Warm conditions during the middle Holocene may have been responsible for the apparent decline of whitebark pine. In a few places, pollen sites near treeline indicate that the tree became more abundant again during the late Holocene, but it never seems to have returned to its early Holocene prominence. If warmer climate was responsible for middle Holocene decline, then global warming from the "greenhouse effect" could be very detrimental to the future of the whitebark pine ecosystem.

ACKNOWLEDGMENTS

I thank C. W. Barnosky and P. J. Mehringer for sharing unpublished information, and Barnosky, L. A. Brant, and L. J. Maher for reviewing the manuscript.

REFERENCES

Arno, S. F. 1986. Technical commentary: whitebark pine cone crops—a diminishing source of wildlife food? Western Journal of Applied Forestry. 1: 92-94.

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Axelrod, D. I. 1986. Cenozoic history of some western American pines. Annals of the Missouri Botanical Garden. 73: 565-641.

Bagnell, C. R., Jr. 1975. Species distinction among pollen grains of *Abies*, *Picea*, and *Pinus* in the Rocky Mountain area (a scanning electron microscope study). Review of Palaeobotany and Palynology. 19: 203-220.

Baker, R. G. 1970. Pollen sequence from Late Quaternary sediments in Yellowstone Park. Science. 168(3938): 1449-1450.

Baker, R. G. 1976. Late Quaternary vegetation history of the Yellowstone Lake Basin, Wyoming. Professional Paper 729E. Washington, DC: U.S. Department of the Interior, Geological Survey.

Baker, R. G. 1978. [Unpublished data]. Iowa City, IA: University of Iowa, Geology Department. 1 p.

Baker, R. G. 1981. Interglacial and interstadial environments in Yellowstone National Park. In: Mahaney, W. C., ed. Quaternary paleoclimate. Norwich, England: Geo Books: 361-375.

Baker, R. G. 1983. Holocene vegetational history of the western United States. In: Wright, H. E., Jr., ed. Late Quaternary environments of the United States. Vol. 2, The Holocene. Minneapolis, MN: University of Minnesota Press: 109-127.

Baker, R. G. 1986. Sangamonian (?) and Wisconsinan paleoenvironments in Yellowstone National Park. Geological Society of America Bulletin. 97: 717-736.

Baker, R. G.; Richmond, G. M. 1978. Geology, palynology, and climatic significance of two pre-Pinedale lake sediment sequences in and near Yellowstone National Park. Quaternary Research. 10: 226-240.

Barnosky, C. W. 1981. A record of late Quaternary vegetation from Davis Lake, southern Puget Lowland, Washington. Quaternary Research. 16: 221-239.

Barnosky, C. W. 1984. Late Pleistocene and early Holocene environmental history of southwestern Washington State, U.S.A. Canadian Journal of Earth Science. 21: 619-629.

Barnosky, C. W. 1985. A record of late-Quaternary vegetation from the southwestern Columbia Basin, Washington. Quaternary Research. 23: 109-122.

Barnosky, C. W. 1987. Late-glacial and postglacial vegetation and climate of Jackson Hole and the Pinyon Peak highlands, Wyoming. Unpublished report on file at: University of Wyoming-National Park Service Research Center, Laramie, WY. 35 p.

Barnosky, C. W. 1989a. [Letter to R. G. Baker]. February 24. On file at: Geology Department, University of Iowa, Iowa City, IA.

Barnosky, C. W. 1989b. Postglacial vegetation and climate in the northwestern Great Plains of Montana. Quaternary Research. 31: 57-73.

Barnosky, C. W.; Anderson, P. M.; Bartlein, P. J. 1987. The northwestern U.S. during deglaciation; vegetational history and paleoclimatic implications. In: Ruddiman, W. F.; Wright, H. E., Jr., eds. North American and adjacent oceans during the last deglaciation. The Geology of North America, K-3. Boulder, CO: Geological Society of America: 289-318.

Beaudoin, A. B.; King, R. H. 1989. Late quaternary vegetation history of Wilcox Pass, Jasper National Park, Alberta. Unpublished paper on file at: Geology Department, University of Iowa, Iowa City, IA.

Brant, L. A. 1980. A palynological investigation of postglacial sediments at two locations along the Continental Divide near Helena, Montana. University Park, PA: Pennsylvania State University. 162 p. Dissertation.

Bright, R. C. [No date]. Postglacial history of Lost Trail Pass Bog, Montana: the "macrofossil" record. Minneapolis, MN: University of Minnesota, Bell Museum of Natural History. 24 p.

Bukart, M. R. 1976. Biostratigraphy and late Quaternary vegetation history of the Big Horn Mountains, Wyoming. Iowa City, IA: University of Iowa. 70 p. Dissertation.

Clague, J. J.; Mathewes, R. W. 1989. Early Holocene thermal maximum in western North America: new evidence from Castle Peak, British Columbia. Geology. 17: 277-280.

Davis, A. M. 1979. Wetland succession, fire, and the pollen record: a midwestern example. American Midland Naturalist. 102: 86-94.

Davis, M. B. 1983. Holocene vegetational history of the eastern United States. In: Wright, H. E., Jr., ed. Late-Quaternary environments of the United States. Vol. 2, The Holocene. Minneapolis, MN: University of Minnesota Press: 166-181.

Dunwiddie, P. W. 1986. A 6000-year record of forest history on Mount Rainier, Washington. Ecology. 67: 58-68.

Gennett, J. A.; Baker, R. G. 1986. A late-Quaternary pollen sequence from Blacktail Pond, Yellowstone National Park, Wyoming, U.S.A. Palynology. 10: 61-71.

Hansen, B. S.; Cushing, E. J. 1973. Identification of pine pollen of late Quaternary age from the Chuska Mountains, New Mexico. Geological Society of America Bulletin. 84: 1181-1199.

Heusser, C. J. 1983. Vegetational history of the northwestern United States including Alaska. In: Wright, H. E., Jr.; Porter, S. C., eds. Late-Quaternary environments of the United States. Vol. 1, The Late Pleistocene. Minneapolis, MN: University of Minnesota Press: 239-258.

Heusser, C. J. 1985. Quaternary pollen records from the interior Pacific Northwest coast: Aleutians to the Oregon-California boundary. In: Bryant, V. M., Jr.; Holloway, R. G., eds. Pollen records of late-Quaternary North American sediments. Dallas, TX: American Association of Stratigraphic Palynologists Foundation: 141-165.

Hutchings, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Johnson, W. C.; Webb, T., III. [In review]. The role of blue jays in the postglacial dispersal of fagaceous trees in eastern North America. Journal of Biogeography.

Kearney, M. S.; Luckman, B. H. 1983. Postglacial vegetational history of Tonquin Pass, British Columbia. Canadian Journal of Earth Sciences. 20: 776-786.

Luckman, B. H.; Jozsa, L. A.; Murphy, P. J. 1984. Living seven-hundred-year-old *Picea engelmannii* and *Pinus albicaulis* in the Canadian Rockies. Arctic and Alpine Research. 16: 419-422.

Luckman, B. H.; Kearney, M. S. 1986. Reconstruction of Holocene changes in alpine vegetation and climate in the Miligne Range, Jasper National Park, Alberta. Quaternary Research. 26: 244-261.

Mack, R. N.; Rutter, N. W.; Bryant, V. M., Jr.; Valastro, S. 1978a. Late Quaternary pollen record from Big Meadow, Pend Oreille County, Washington. Ecology. 59: 956-966.

Mack, R. N.; Rutter, N. W.; Bryant, V. M., Jr.; Valastro, S. 1978b. Reexamination of postglacial vegetation history in northern Idaho: Hagar Pond, Bonner County. Quaternary Research. 10: 241-255.

Mack, R. N.; Rutter, N. W.; Valastro, S.; Bryant, V. M., Jr. 1978c. Late Quaternary vegetation history at Waits Lake, Colville River Valley, Washington. Botanical Gazette. 139: 499-506.

Mack, R. N.; Rutter, N. W.; Valastro, S. 1979. Holocene vegetation history of the Okanogan Valley, Washington. Quaternary Research. 12: 212-225.

Mack, R. N.; Rutter, N. W.; Valastro, S. 1983. Holocene vegetation history of the Kootenai River Valley, Montana. Quaternary Research. 20: 177-193.

Markgraf, V.; Lennon, T. 1986. Paleoenvironmental history of the last 13,000 years of the eastern Powder River Basin, Wyoming, and its implications for prehistoric cultural patterns. Plains Anthropologist. 31: 1-12.

Mehringer, P. J., Jr. 1985. Late-Quaternary pollen records from the interior Pacific Northwest and Northern Great Basin of the United States. In: Bryant, V. M., Jr.; Holloway, R. G., eds. Pollen records of late-Quaternary North American sediments. Dallas, TX: American Association of Stratigraphic Palynologists Foundation: 167-189.

Mehringer, P. J. 1989. [Letter to R. G. Baker]. February 17. On file at: Geology Department, University of Iowa, Iowa City, IA.

Mehringer, P. J., Jr.; Arno, S. F.; Petersen, K. L. 1977. Postglacial history of Lost Trail Pass Bog, Bitterroot Mountains, Montana. Arctic and Alpine Research. 9: 345-368.

Mitchell, V. L. 1976. The regionalization of climate in the western United States. Journal of Applied Meteorology. 15: 920-927.

Pierce, K. L. 1979. History and dynamics of glaciation in the northern Yellowstone National Park area. Professional Paper 729-F. Washington, DC: U.S. Department of the Interior, Geological Survey. 90 p.

Porter, S. C.; Pierce, K. L.; Hamilton, T. D. 1983. Late Wisconsin mountain glaciation in the western United States. In: Wright, H. E., Jr.; Porter, S. C., eds. Late-Quaternary environments of the United States. Vol. 1, The Late Pleistocene. Minneapolis, MN: University of Minnesota Press: 71-114.

Reasoner, M. A.; Hickman, M. [In press]. Late Quaternary environmental change in the Lake O'Hara region, Yoho National Park, British Columbia. Palaeogeography, Palaeoclimatology, Palaeoecology.

Richmond, G. M. 1978. [Unpublished data]. On file at: Geology Department, University of Iowa, Iowa City, IA.

Richmond, G. M. 1986a. Stratigraphy and chronology of glaciations in Yellowstone National Park. In: Sibrava V.; Bowen, D. Q.; Richmond, G. M., eds. Quaternary glaciations in the Northern Hemisphere, Vol. 5, Quaternary Science Reviews. Oxford, UK: Pergamon Press: 83-98.

Richmond, G. M. 1986b. Tentative correlation of the Cordilleran ice-sheet in the Northern Rocky Mountains. In: Sibrava, V.; Bowen, D. Q.; Richmond, G. M., eds. Quaternary glaciations in the Northern Hemisphere, Vol. 5, Quaternary Science Reviews. Oxford, UK: Pergamon Press: 129-134.

Spaulding, W. G.; Leopold, E. B.; Van Devender, T. R. 1983. Late Wisconsin paleoecology of the American Southwest. In: Wright, J. E., Jr.; Porter, S. C., eds. Late-Quaternary environments of the United States. Vol. 1, The Late Pleistocene. Minneapolis, MN: University of Minnesota Press: 259-293.

Thompson, R. S. 1988. Western North America. Vegetation dynamics in the western United States: modes of response to climatic fluctuations. In: Huntley, B.; Webb, T., III, eds. Vegetation history. Dordrecht, The Netherlands: Kluwer Academic Publishers: 415-458.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird. 16: 123-160.

Tomback, D. F. 1981. Notes on cones and vertebrate-mediated seed dispersal of *Pinus albicaulis* (Pinaceae). Madrono. 28: 91-94.

Van Devender, T. R.; Thompson, R. S.; Betancourt, J. L. 1987. Vegetation history of the deserts of southwestern North America; the nature and timing of the late Wisconsin-Holocene transition. In: Ruddiman, W. F.; Wright, H. E., Jr., eds. North American and adjacent oceans during the last deglaciation. The Geology of North America. K-3. Boulder, CO: Geological Society of America: 323-352.

Waddington, J. C. B.; Wright, H. E., Jr. 1974. Late Quaternary vegetational changes on the east side of Yellowstone Park, Wyoming. Quaternary Research. 4: 175-184.

Watts, W. A. 1983. Vegetational history of the eastern United States 25,000 to 10,000 years ago. In: Wright, H. E., Jr.; Porter, S. C., eds. Late-Quaternary environments of the United States. Vol. 1, The Late Pleistocene. Minneapolis, MN: University of Minnesota Press: 294-310.

Webb, T., III. 1988. Eastern North America. In: Huntley, B.; Webb, T., III, eds. Vegetation history. Dordrecht, The Netherlands: Kluwer Academic Publishers: 385-414.

Weir, G. H.; Thurston, E. L. 1977. Scanning electron microscopic identification of fossil Pinaceae pollen to species by surface morphology. Palynology. 1: 157-165.

Wright, H. E., Jr.; Bent, A. M.; Hansen, B. S.; Maher, L. J., Jr. 1973. Present and past vegetation of the Chuska Mountains, Northwestern New Mexico. Geological Society of America Bulletin. 84: 1155-1180.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Lawrence McHargue)—Does the recent history of whitebark pine in the Sierra Nevada parallel that in the Rocky Mountains?
A.—It is difficult to say for two reasons. One, there are many more species of pine today in the Sierras, and this causes greater uncertainty in the identification of pine pollen to species. Second, work in the Sierras is still in its infancy, and few detailed studies are available. People from the University of Arizona and from Northern Arizona University are working there, so we may soon have some answers.

Q. (from Anonymous)—Do you ever check: (a) current pollen catch with stand composition? and (b) differential degradation of pollen?
A.—(a) Several studies have related pollen rain to several different quantitative measures of stand composition, but these were mostly in the Eastern United States. We have done this qualitatively in Yellowstone, but quantitative stand data were not available. This is a very worthwhile project, and I hope that workers in the Rocky Mountains will soon be doing this. (b) Palynologists are very aware of differential degradation of pollen. Many taxa are simply never preserved, because their pollen wall is not resistant. For example, Juncaceae pollen is never found in the fossil record. Other pollen taxa have variable preservation. *Populus* is commonly cited here. It is often found where preservation is good, but it is one of the first pollen types to degrade under less-than-perfect conditions.

Q. (from Wendel Hann)—Why do you think whitebark pine has not spread into similar environments in Colorado?
A.—I really do not know. It may be climate, effective moisture, temperature, or possibly some combination may be limiting. Another possibility is that the distance between mountain ranges between Wyoming and Colorado is too great for Clark's nutcrackers to cover. It is a long way from the Wind River Range to the Snowy Range, or from the Wyoming Ranges to the Uinta Range. It is increasingly apparent, though, that many taxa in the Rocky Mountains did not move great distances horizontally during the last glaciation. Many moved up or down the mountain slopes. The reasons for this are also unclear.

Q. (from Mike Simpson)—How far can pollen travel to be deposited in one of your sections?
A.—Individual pollen grains can travel thousands of kilometers, but most of the pollen that accumulates in an area originates within a few tens of kilometers. In mountainous regions, several studies show that there is considerable vertical transport as well. Nevertheless, it is generally possible to recognize present-day communities from their modern pollen rain.

Q. (from Stephen Harvey)—How do you assume that *Artemisia* pollen is from shrubby species rather than subalpine species such as *A. michauxiana*?
A.—I do not assume that at all. I feel that both lowland and subalpine-alpine *Artemisia* pollen are represented, especially in late-glacial samples. Samples from modern tundra contain relatively high percentages of *Artemisia*, but not nearly as high as those from 15,000 to 10,000 years B.P. In both sets of samples, there are pollen types from such strictly lowland plants as greasewood (*Sarcobatus*), other chenopods, and Mormon tea (*Ephedra*) so it is likely that lowland *Artemisia* also is present. Modern pollen studies show that in many mountain ranges, strong winds blow pollen grains up from below. On the other hand, high-elevation species also are likely to be represented; they are close at hand, and pollen from other taxa of high-altitude plants is also present. I do not think that the source of *Artemisia* pollen is an either/or situation.

HIGH-MOUNTAIN RESOURCES ON NATIONAL FOREST LANDS

John W. Mumma

ABSTRACT

The high-mountain ecosystems are a component of National Forest lands that help make the National Forest System unique in its values. These ecosystems, characterized by whitebark pine, have a complex set of values. People have historically used these ecosystems for a range of commodity and noncommodity values. Common uses have included timber; livestock grazing; mining; camping; hiking; horseback riding; viewing wildlife, plants, and scenery; fishing; and hunting. Because of their unique environments, high-mountain ecosystems also have an important value in maintaining a diversity of plant and animal life. The value of these lands as watersheds and for producing water has not been recognized at the level deserved. Demands for all the products and values of these lands will increase. National Forest land managers and the public will need to use an integrated approach to develop, implement, and monitor management of these areas.

The value of whitebark pine as a food source for grizzly bears, and the complex relationship among grizzly bears, squirrels, and the Clark's nutcracker, is an example of the type of chain of effects that must be considered in management prescriptions. The potential loss of whitebark pine to blister rust is a problem that we must face and do our best to overcome.

INTRODUCTION

This paper will provide an overview of the high-mountain ecosystems of National Forest lands, a look at some of the important resources and values related to these ecosystems, and a discussion of key management issues.

LAND AREA

There are approximately 162 million acres of land in the National Forest System (USDA 1987). Of this, about 13 million acres are in high-mountain ecosystems, within the geographic range of whitebark pine (*Pinus albicaulis*). This is about 8 percent of the National Forest System. States that have National Forest high-mountain environments within the geographic range of whitebark pine include Washington, Oregon, California, Nevada, Idaho, Montana, and Wyoming (Arno and Hoff 1989). The total area of high-mountain ecosystems in National Forests, which includes high-elevation ecosystems outside the range of whitebark pine, would be considerably more.

The 13 million acres is a rough estimate. Inventory data for the National Forests is fairly limited in these environments, for several reasons. The primary reason is that these environments are usually not intensively managed and there has not been a demand in the past for refined inventory data. A second reason is that much of this land is unroaded and designated as wilderness or semiprimitive management areas. In addition, it is difficult to aggregate inventory data over such a large area.

In the future we will have better inventory data and a better geographic data base system to help store and summarize that information. The National Forest System is rapidly moving into the era of "information management." With systems such as stand exam (USDA, Forest Service, Northern Region, 1987) and ecodata (Hann and Jensen 1988) we can provide detailed vegetation and site data for different types of ecosystems. Our stand and soil survey map data bases linked to a geographic information system will provide us information at the geographic level that will serve for both small- and large-scale analysis. By the year 1991, the Northern Region plans to have a fairly complete data base for all lands. Most of the other Regions in the Forest Service have similar objectives.

DIVERSITY OF ECOSYSTEMS

Although there are roughly 13 million acres of high-elevation National Forest ecosystems within the geographic range of whitebark pine, only a small part of it is dominated by whitebark pine. The majority of this land is dominated by other high-elevation species. Other common subalpine tree species include subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), spruce (*Picea engelmannii* and *Picea glauca*), mountain hemlock (*Tsuga mertensiana*), and alpine larch (*Larix lyallii*). Nonforest communities, dominated by a wide variety of herbaceous and shrub species, are also common in the subalpine and alpine zones. This wide range of flora and site conditions within these ecosystems provides for a wide diversity in plant and animal life.

A diversity of disturbance is also an integral component of the high-elevation ecosystems. Fire has played a dominant role in shaping the landscapes of the subalpine zone (Fischer and Bradley 1987; Fischer and Clayton 1983). In many of these ecosystems the interval between natural fires may be long, but the influence in shaping communities and in creating a variety of successional communities can be seen many years after a fire. Insects also play a

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

John W. Mumma is Regional Forester, Northern Region, Forest Service, U.S. Department of Agriculture, Missoula, MT 59807.

key role along with fire. Although the mountain pine beetle kills mature lodgepole pine, it sets the stage for a stand-consuming fire. Natural regeneration of lodgepole pine is highly fire dependent, since it requires an ash or mineral seedbed and the cones often require heat treatment to release the seeds. Thus, the continuance of the lodgepole species depends on the disturbance factors that destroy the mature species.

The environment of high-elevation ecosystems itself causes continual disturbance to the vegetation. Freezing temperatures during any month of the year, wind damage, and snow damage can change communities and initiate successional change. Avalanche areas usually contain a distinct complex of communities that only occur due to the environment created from repeated disturbance.

In many areas of high-elevation ecosystems the communities are developing for the first time on substrate that is forming from primary succession after glacial retreat, flooding, erosion, or debris slides. Soils of these ecosystems are usually poorly developed and slopes are often steep. This great complexity of environments results in an equally large complexity of communities.

Animal communities in these ecosystems also often have complex relationships. Due to the severe environments, animals and plants have developed complex interrelationships that aid their ability to survive and reproduce. The interesting relationship among the Clark's nutcracker, squirrels, grizzly bears, and whitebark pine is a classic example of this type of intricate ecological relationship.

The diversity of the high-elevation ecosystems is exemplified by whitebark pine and the diversity of associated plants and sites where it occurs. Whitebark pine can be found as a common component with lodgepole pine on moist, lower elevation subalpine fir habitat types (Cooper and others 1987; Pfister and others 1977; Steele and others 1981). It is also found on high, subalpine ridgetops growing in open parklike stands associated with species such as mountain big sagebrush (*Artemisia tridentata vaseyana*) or Idaho fescue (*Festuca idahoensis*). At timberline, whitebark pine can be found with alpine species such as mountain heath (*Phyllodoce empetriformis*) and alpine willow (*Salix arctica*).

POSTSETTLEMENT USE AND IMPACTS

The great diversity of animal and plant communities and the rugged landscapes of the high-mountain ecosystems result in a wide variety of resources and values. During the early settlement of the late 1800's and the early 1900's, the primary resources that were valued by society were the potentials for mineral development and forage for domestic sheep. Since the mid-1900's, there has been a steady trend of society to emphasize a different set of values for these ecosystems. These values are more noncommodity in nature, such as hiking, camping, and viewing wildlife or scenic features.

During the period of extensive, and often heavy, sheep grazing in the West, which lasted from the middle 1800's to the early 1900's, many of these lands were severely impacted. At the same time, mining operations with associated widespread cutting of timber for mine shafts and lumber and poorly designed roads often led to severe impacts on the land and watersheds. Time, improved management, and rehabilitation have healed many of the problems resulting from these past impacts.

There has been a more subtle effect than that of mining or grazing on the high-mountain ecosystems, related to settlement by Europeans, that has caused a significant change in the resource values. This is the effect of fire suppression. In the ecosystems where natural fire frequencies were quite long, 50 to 70 years of fire suppression has not had a significant effect. In other ecosystems where the natural fire frequency is short to moderate, there has been a significant effect (Gruell 1983). The result of a departure from this natural fire frequency has been an increase in mature timber types, a shift of nonforest types to forest types, and a decrease in diversity of structural classes across the landscape. The resulting increase in fuels and fuel continuity can lead to significant problems when wildfires occur, as was evidenced by the 1988 fire season. The change in communities has also resulted in a reduction in habitat values for many animal species that depend on forage from early successional stages, such as elk and grizzly bears. A planned program of prescribed fire and fuels management should reestablish the natural balance.

An additional subtle impact of Europeans has been the introduction of exotic insects, diseases, plants, and animals. In the high-elevation ecosystems the introduction of blister rust, which attacks whitebark pine, and the introduction of exotic weeds have resulted in significant problems. Blister rust is causing a significant reduction of whitebark pine in many National Forests. This poses a challenge to managers and researchers to develop strategies to aid whitebark pine in regeneration and survival in the face of this exotic disease.

The introduction of exotic plant species by livestock, people, horses and mules, and other means is a significant problem and is causing a reduction in resource values. A good example of a plant species that historically has been introduced by domestic sheep to high-elevation lands is mountain knotweed (*Polygonom phytolacefolium*). Kentucky bluegrass (*Poa pratensis*) and dandelion (*Taraxacum officinale*) are two species that many people think of as being naturalized. In a sense they are, in that they have filled most of the niches that are available. However, the cost in loss of niches, and therefore diversity of native species, is significant. As time passes and other species, such as spotted knapweed (*Centaurea repens*) and leafy spurge (*Euphorbia esula*) fill their niches, they may also be accepted. The management of these species may well prove to be a much more difficult challenge to researchers and land managers than the fire management situation.

PRESENT USE AND IMPACTS

Mining, livestock grazing, and limited timber harvest are still important resource uses of high-mountain National Forest lands. However, the emphasis relative to the importance of the high-mountain resources, the types of resource use, and the impacts has changed significantly within the last 30 years. At present, one of the most important uses of these lands is for recreation. Because of the diversity and rugged beauty of high-elevation lands, people find a lot of enjoyment in various activities in these areas. These activities include camping; hiking; horseback riding; picnicking; photography; viewing landscapes, plants, and animals; rock and mineral collecting; fishing; and hunting.

Along with the increase in recreational use, there have been associated impacts. Many of the high-elevation ecosystems are very fragile. People and their recreational stock or equipment can cause damage, just as mining and domestic sheep caused damage during the early days. This damage occurs at campsites, on trails, and along lakes, streams, and rivers. People also continue to aid the spread of exotic plants. Management of people and their recreational activities is a significant challenge that integrates sociology with resource management.

Of equal importance as recreation on the high-elevation lands is their value as watersheds. These lands provide catchment basins, sediment filters, and storage for water that is used at lower elevations during the summer. This water is critical in many areas for municipal use, irrigation, fisheries, industrial use, power development, and recreation.

The high-mountain lands of the National Forests play a key role in maintenance of biological diversity. The grizzly bear is probably one of the more well-known users of these ecosystems that is important to biological diversity. In drier areas, whitebark pine is a key food source for grizzly bears during the fall. The loss of whitebark pine due to the exotic blister rust disease not only is reducing the diversity of whitebark pine, but could hamper the grizzly bear recovery effort. Many other rare plants and animals are key components of diversity in these ecosystems. The common plants and animals and maintenance of their genetic diversity must be just as much a consideration for managers and researchers. At a larger scale, the diversity of communities or the landscape mosaic is an important resource, not only for wildlife and esthetics, but to provide ecosystem stability.

Air quality is a resource. It is a resource that is very difficult to manage because the pollutants that can degrade air quality can come from sources over which we have no control. The degradation of the ozone layer and the increase in CO_2, which could result in climatic change, are also effects that are difficult to manage. These are problems that we must deal with in large-scale cooperative efforts if we are to maintain environmental quality.

Wilderness, semiprimitive areas, and other natural areas are also a resource. These areas provide more than just recreation, watershed, and wildlife values. They provide a land system that is very important from other aspects. Because the management philosophy is to maintain natural systems, these areas provide excellent baselines for understanding ecological functions and values and can be used to evaluate effects of human activities on lands managed for products. They are also a reservoir for biotic diversity and provide a natural laboratory for scientific investigation of the natural world. Of most importance may be their value as an outdoor classroom for people young and old to learn about the natural world and how they fit in that world.

MANAGEMENT OF HIGH-MOUNTAIN ECOSYSTEMS

The National Environmental Policy Act of 1969 and the National Forest Management Act of 1976 have significantly changed the way National Forest activities are analyzed and evaluated. Forest Plans have been or are being completed for all the National Forests. These plans specify how the Forests will be managed for a 10-year period and set general direction for long-term management. The plans are developed with strong public involvement looking at a broad range of alternatives. Once the plan is complete the process of implementation begins, which takes a closer look at how and where projects will be carried out with continued public involvement.

Based on these plans, much of the lands that are high-elevation ecosystems will be managed as wilderness, semiprimitive recreation and wildlife areas, and developed recreation areas. Some of these lands are being managed for production of livestock, minerals, and timber values. However, projects are analyzed and planned using an integrated approach that assures that ecosystem quality is maintained or enhanced. In many cases road construction, timber management, and livestock grazing are used to improve access or vegetation composition for recreation, wildlife, and watershed purposes. Fire management plans are developed for each Forest and for specific wildernesses. These plans are designed to use fire as a tool to maintain the natural mosaic of communities and fuels.

The key to good management in these ecosystems is to have biologically and socially sound objectives supported by a thorough analysis. This analysis must be supported by a good inventory of the site, vegetation, and animal characteristics. The team members that conduct the analysis need to have a thorough understanding of the ecosystem relationships in reference to the types of site conditions, disturbances, and uses that are being planned. With this type of approach we can manage the National Forests to produce the desired values and maintain environmental quality.

REFERENCES

Arno, Stephen J.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Cooper, Stephen V.; Neiman, Kenneth E.; Steele, Robert; Roberts, David W. 1987. Forest habitat types of northern Idaho: a second approximation. Gen. Tech. Rep. INT-236. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 135 p.

Fischer, William C.; Bradley, Anne F. 1987. Fire ecology of western Montana habitat types. Gen. Tech. Rep. INT-223. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 95 p.

Fischer, William C.; Clayton, Bruce D. 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. Gen. Tech. Rep. INT-141. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 83 p.

Gruell, George E. 1983. Fire and vegetative trends in the Northern Rockies; interpretations from 1871-1982 photographs. Gen. Tech. Rep. INT-158. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 117 p.

Hann, Wendel J.; Jensen, Mark. 1988. Chapter 4—ecodata sampling methods. Forest Service Handb. 2090.11 R-1. Interim Directive No. 1. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 250 p.

Pfister, Robert D.; Kovalchik, Bernard L.; Arno, Stephen F.; Presby, Richard C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 117 p.

Steele, Robert; Pfister, Robert D.; Ryker, Russell A.; Kittams, Jay A. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 138 p.

U.S. Department of Agriculture, Forest Service. 1987. Land areas of the National Forest system. Forest Service Pub. FS-383. Washington, DC: U.S. Department of Agriculture, Forest Service. 88 p.

U.S. Department of Agriculture, Forest Service Northern Region. 1987. Timber management data handbook. Forest Service Handb. 2409.21h R-1. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 550 p.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Anonymous)—In your talk you referred to integrated management of National Forest lands. With the functional emphasis on specific resources, such as timber or wildlife, do you feel the Forest Service can actually conduct management in an integrated manner?

A.—During the development of the Forest Service and even now, there has often been a heavy emphasis on specific resource functions. However, with the completion of Forest Plans, we have a commitment to implement management in an integrated manner. It is difficult to move a large organization through rapid change, but we plan to meet that challenge, and become a better-rounded integrated management organization.

HIGH-MOUNTAIN RESOURCES OF NATIONAL PARK SERVICE LANDS

Don G. Despain

Resources are usually thought of as those raw materials that are put through some manufacturing process to yield a product needed or useful to mankind. Such a definition cannot be applied to the high-mountain lands administered by the National Park Service. The management goal of the Park Service is to maintain ecosystems as uninfluenced by modern technology as possible. However, there are a number of "commodities" produced in the high country used by a number of species for maintenance and growth.

The high-elevation areas are summer ranges for large mammals. Temperatures are cool and grass is produced abundantly in the moist meadows at these elevations. Whitebark pine (*Pinus albicaulis*) produces a large, oil-rich seed important to squirrels, Clark's nutcrackers, and grizzly bears. The cool climate also attracts large numbers of backpackers and campers, and mountainous cliffs and peaks draw many mountain climbers.

On lands outside the Parks (and often adjacent to them) the management objectives call for exploitation of resources such as timber. Even in wilderness areas, practices such as livestock grazing and hunting are used to harvest some of the resources. One special contribution of the National Parks is providing a benchmark against which the effects of other, more-extractive management practices may be judged.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Anonymous)—In order to ensure "naturalness" what measures is the NPS undertaking to reduce the impacts of high-intensity recreation that are characteristic of NPS lands?

A.—I can not presume to speak for the entire Park Service and am not too sure that I can speak for Yellowstone National Park. However, I can make a few personal observations. First, high intensity does not characterize all recreational use of NPS lands. Only 1 percent of Yellowstone is developed, and only the developed areas are sites of high-intensity recreation activity. The rest of the Park is backcountry, and even our backcountry use is largely limited to trails and designated campsites. I do not want to imply that this use does not affect the "naturalness" of the Park. It does. I guess it depends on whether you want to see the cup 95 percent full or 5 percent empty.

There are a number of regulations in force that limit what recreationists and others (including researchers) can do within the Park boundaries. Activities that alter the environment are generally discouraged. Where fishing pressure is high, catch-and-release fishing regulations are in place, and the fish populations are responding phenomenally well. Strict regulations regarding food storage at campsites have been instituted and enforced to keep bears from being unduly impacted by the visitors and vice versa. It appears now that the bears are returning to a more natural distribution. Overnight backcountry use is allowed by permit only, and the number of people at any one site is restricted. The number of climbers on popular climbing routes in other Parks is regulated to keep the natural environment as intact as possible. Some areas are intensively used. The frontcountry campgrounds are nearly full every night during the peak summer season. The developed areas are visited by enormous numbers of people. We do not operate under the pretense that places like Old Faithful and other developed areas are natural, but we try to keep the 99 percent that is not developed as "natural" as possible. For the most part, I think we are doing a pretty good job. Periodically we receive complaints that there are so many restrictions a person can not really enjoy camping and hiking in Yellowstone.

Q. (from Ron Hamilton)—Do you consider the management activities carried on in the adjacent National Forests surrounding Yellowstone an "experiment"?

A.—Yes! Our knowledge of this fragile, interconnected ecosystem—the environment, the organisms involved, and their relationships and interactions—is so rudimentary and fragmentary that I think we are a long way from managing it with any certainty of the outcome of our actions. Ecology is still a new science. We are still developing tools with which to look at our activities. The public furor over forest management practices is fueled to a certain extent by some ecologists and other scientists. That criticism is not entirely unjustified. This is not to say that the Forest Service is derelict. We have to manage according to the best available knowledge and political realities. I mean only to say that the best available knowledge is not sufficient enough to allow us to abandon the control areas or to assume that our management practices are anything but experiments. We still desperately need areas like the Park Service natural areas and others to act as benchmarks against which the results of our activities can be assessed. Until we can predict with a high degree of certainty the final outcome of our actions in all parts of the ecosystem we need to regard our management actions as experimental.

Summary of remarks presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Don G. Despain is Research Biologist, Yellowstone National Park, WY 82190.

DISTRIBUTION AND ECOLOGY OF WHITEBARK PINE IN WESTERN CANADA

R. T. Ogilvie

ABSTRACT

In the Provinces of British Columbia and Alberta, whitebark pine (Pinus albicaulis) *extends from latitude 49° to 55° N., through the Rocky Mountains, the Columbia Mountains, the Interior Plateau, the Cascade Mountains and the Coast Mountains. The species is usually restricted to the upper subalpine forest, occurring most abundantly at timberline, where it grows with Engelmann spruce* (Picea engelmannii) *and subalpine fir* (Abies lasiocarpa) *in the eastern mountains, and with mountain hemlock* (Tsuga mertensiana) *in the western ranges. It rarely forms stands with alpine larch* (Larix lyallii), *the other timberline tree in the southeastern ranges of these mountains. Whitebark pine occurs at 2,000 to 2,450 m above sea level in the eastern ranges, and 1,800 to 2,000 m in the western Coast and Cascade Mountains. Typical habitats are ridge crests and upper steep southwest-facing slopes with high wind-exposure and shallow snow. The growth form varies with altitude and habitat, ranging from tall, single-stemmed upright trees to dwarf single-stemmed bush krummholz and multistemmed krummholz. Limited age-class analyses show broad age-ranges and abundant young age-classes. The soils are shallow and rocky on colluvial and glacial till parent materials; their moisture regime varies from dry to mesic. Soil reaction varies from predominantly basic and calcareous to acidic. Regosols, Brunisols, and Podzols are the major soil profile types. In drier habitats, whitebark pine occurs in the* Juniperus communis, Arctostaphylos uva-ursi, *and* Shepherdia canadensis *vegetation-types; in the more mesic, snowier habitats it occurs in the* Vaccinium scoparium, Cassiope mertensiana, Phyllodoce glanduliflora, *and* P. empetriformis *vegetation-types.*

INTRODUCTION

Whitebark pine (*Pinus albicaulis* Engelm.) is one of the neglected coniferous species of western Canada. It has restricted distribution and sparse abundance; it is remote and difficult to access, and is of minor commercial importance. Although listed in botanical floras and tallied in forestry inventories, this species has received slight attention from botanists and foresters alike. Information on the distribution and ecology of whitebark pine in western Canada is scattered over a wide variety of sources: herbarium collections, field notes, graduate student theses, published and unpublished survey reports, and biophysical and resource inventories. Many of the sources deal with the subalpine forest as an entity, and the information on whitebark pine is peripheral. Where appropriate I have cited the source of information. Other sources of information on the species are in an Additional Readings section following the References section.

DISTRIBUTION

Figure 1 shows the distribution of whitebark pine in British Columbia and Alberta. This map is based on collections in the herbaria of the Royal British Columbia Museum, the University of British Columbia, the University of Victoria, and the Canadian Forestry Service, Victoria. Additional distributional data were provided by the Canadian Forestry Service from their records of fungal and insect collections on whitebark pine. These data were correlated with the map published by Krajina and others (1982).

In western Canada, whitebark pine is restricted to Alberta and British Columbia, extending from latitude 49° to 55° N. and from longitude 114° to 128° W. It is a species restricted to high mountains, occurring in several physiographic regions (Holland 1964). Whitebark pine is present in numerous ranges of the Coast Mountains, but primarily on their drier eastern slopes. In the Cascade Mountains it occurs in the Skagit Range, the Hozameen Range, and the Okanagan Range. On the Interior Plateau the species has scattered distribution on the isolated mountain peaks and ranges. This pine occurs extensively in the main ranges of the Columbia Mountains: the Monashee, Cariboo, Selkirk, and Purcell Ranges. The major occurrence of whitebark pine is in the Rocky Mountains on both sides of the Continental Divide, in the Border, Kootenay, Main, and Front Ranges.

The environmental diversity of these different mountains is considerable. The climate varies from the more maritime conditions of the Coast and Cascade Mountains to the dry continental climate of the Interior Plateau and the Rocky Mountains and the moister continental climate of the Columbia Mountains. In addition, the latitudinal differences are significant. The southernmost peaks of the eastern Cascade, Interior Plateau, Columbia, and Rocky Mountains have a pronounced summer-dry climate, with much of the growth water originating from snowmelt. In contrast, at the northern extremities of these mountains the climate is more boreal, with lower summer temperatures, and little or no moisture deficit.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

R. T. Ogilvie is Curator of Botany, Royal British Columbia Museum and Biology Department, University of Victoria, Victoria, BC, Canada V8V 1X4.

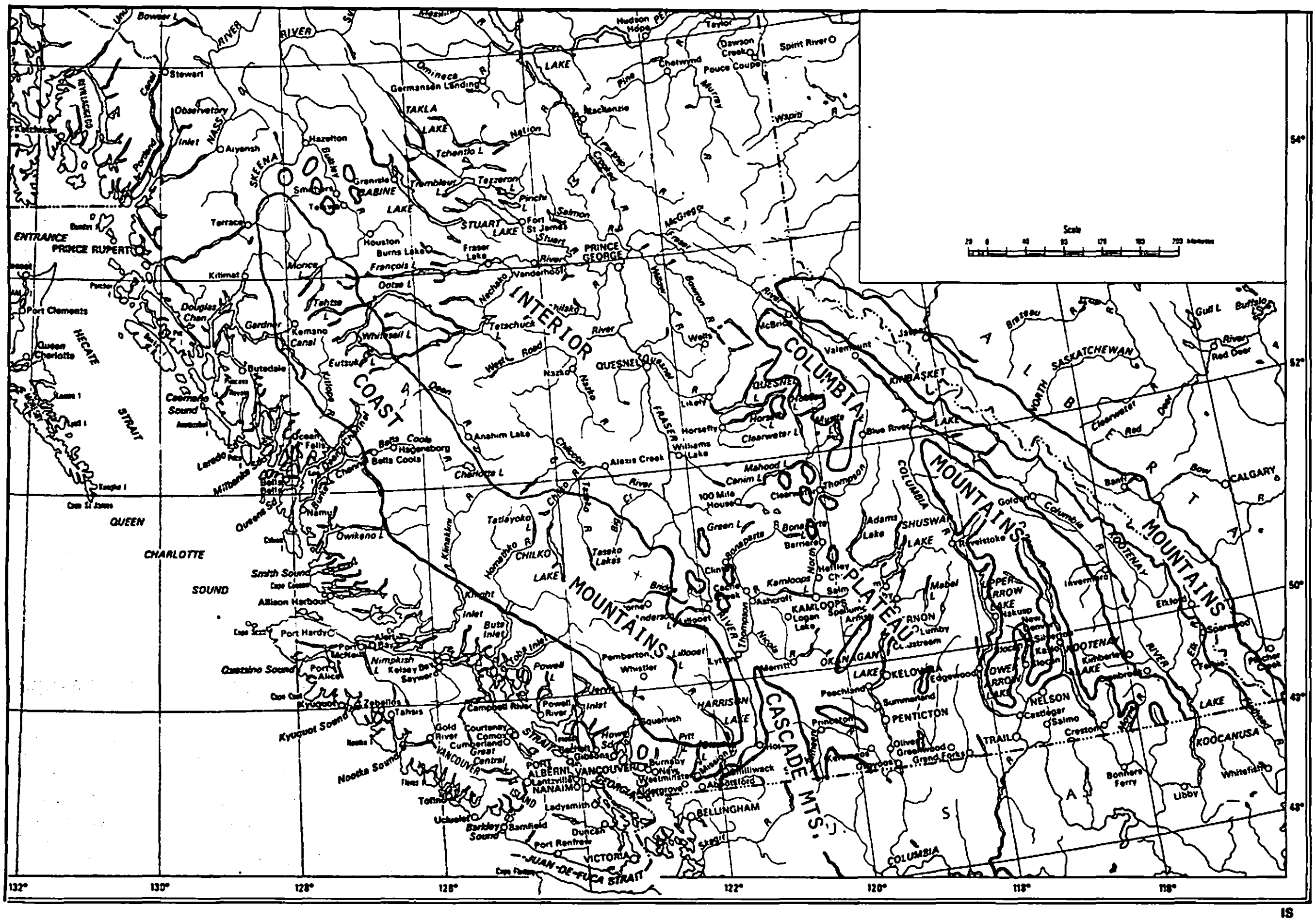


Figure 1—Whitebark pine (*Pinus albicaulis*) in western Canada.

ALTITUDINAL RANGE

Whitebark pine is typically an upper subalpine species, occurring most abundantly at timberline. It may grow as scattered trees as much as 700 m below timberline, and extend 300 m above timberline as small individuals less than 50 cm tall. On the west slope of the northern Rocky Mountains, valley bottom stands of whitebark pine occur at approximately 1,067 m elevation (Brayshaw 1989). On the lee side of the northern Coast Mountains, whitebark pine forms two altitudinal bands, one along the valley bottom at 900 m, and the other in the upper subalpine at 1,300 to 1,600 m (Pojar 1978; Yole and others 1989).

The upper altitudinal occurrence of whitebark pine krummholz is given in table 1 for the different mountain ranges of western Canada. These values for the altitudinal range of whitebark pine are consistent with the generalized geographic patterns of timberline: the species occurs at higher elevations in the southern mountain ranges and in the more continental and drier mountains.

Table 1—The upper altitude of whitebark pine in western Canada

Mountain range	Locale within range	Elevation limit
		Meters
Rocky Mountains	southern	2,300-2,400
	central	2,200
	northern	2,100
Columbia Mountains	Purcell Mountains	2,100-2,300
	Selkirk Mountains	2,000-2,200
	Monashee Mountains	2,200
	Cariboo Mountains	1,600
Interior Plateau	Okanagan Highlands	2,300
	Thompson Plateau	2,000-2,200
	Fraser Plateau	1,900-2,000
	Nechako Plateau	1,700
Cascade Mountains	Okanagan Range	2,200
	Hozameen Range	1,900-2,100
	Skagit Range	2,100-2,200
Coast Mountains	southern	2,000
	central	1,900
	northern	900 and 1,300-1,600

GROWTH FORM

The growth form of whitebark pine varies with altitude and habitat. In the more favorable habitats at lower elevations, the upright single-stemmed tree form occurs. Typically, these trees are short, attaining only 12- to 15-m heights. Exceptionally tall trees grow in southwestern Alberta and adjacent southeastern British Columbia at 1,676 m elevation, with trees 24 to 33 m tall and 51 to 79 cm diameter at breast height (Day 1967). Day reported that these trees were being logged and milled for pine lumber. The ages of these trees were over 250 years; other age measurements reported from Alberta are +300 years and 405 years (Baig 1972). This upright, single-stemmed tree form grows in mixed stands of hybrid spruce (*Picea engelmannii* x *Picea glauca*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta* var. *latifolia*). Stands of large, saw-timber-size whitebark pine also occur in the central Purcell Mountains at approximately 1,524 m elevation (Brayshaw 1989).

At higher elevations in the timberline zone, whitebark pine grows in a flat-topped candelabra form and a multistemmed form. Krummholz colonies of whitebark pine grow in the exposed, highest part of timberline. This form consists of a prostrate, multistemmed, low scrubby growth, with a few short upright flag stems (Baig 1972; Ogilvie 1978a). Signs of repeated injury and mortality of terminal branches from winter frost-drought (Tranquillini 1979) are indicative that the candelabra, multistemmed, and krummholz growth forms are environmentally induced, although a genetic basis comparable to mugo pine (*Pinus mugo*) in the European Alps has been speculated for these forms by Clausen (1963, 1965) and Crawford (1989).

LONGEVITY

Maximum ages of whitebark pine have been reported from dendrochronological studies of timberline trees in the central Rocky Mountains (Luckman and others 1984). In Mount Robson Park, BC, (lat. 52°42' N., long. 118°21' W.) 17 isolated whitebark pines at timberline (1,760 m) were aged by ring counts. Two trees had more than 450 annual rings, one snag had 520 rings, and the oldest tree had 713 rings, which when extrapolated to the center pith was an estimated 743 to 763 years. In Jasper Park, AB, (lat. 52°14' N., long. 117°14' W.) a single whitebark pine at upper treeline (approximately 2,200 m) had 550 annual rings. At the same locality, several dead standing snags of Engelmann spruce (*Picea engelmannii*), subalpine fir, and whitebark pine were dated by ^{14}C at between 900 to 1,160 yr BP (Jozsa 1989; Luckman and others 1984).

AGE COMPOSITION AND STAND DYNAMICS

Very few age analyses have been made of whitebark pine stands in western Canada. Day (1967) reported the results of a regeneration survey in two 5-acre mature stands of mixed spruce, subalpine fir, and lodgepole pine. Although there were only two parent trees of whitebark pine, the advanced regeneration (60 to 90 cm tall) of whitebark pine exceeded that of lodgepole pine, indicating that the former is a more successful competitor under closed stands with heavy shade and root competition.

Baig (1972) reported age analyses of six mature stands of mixed whitebark pine, Engelmann spruce, subalpine fir, and lodgepole pine in Alberta. All of the stands contained whitebark pine regeneration; two stands had subalpine fir regeneration, and only one stand had spruce regeneration. Whitebark pine had the largest number of individuals per stand, the broadest age range, and the oldest individuals. The dynamic trends of these stands indicate either pure whitebark pine stands, mixed whitebark pine and subalpine fir, or whitebark pine and spruce.

Many more age analyses are needed of stands from the different mountain systems to clarify the role of whitebark pine in relation to the other subalpine trees such as Engelmann spruce, subalpine fir, mountain hemlock (*Tsuga mertensiana*), and alpine larch (*Larix lyallii*).

GEOLOGY

The bedrock is highly variable in the different mountain systems in which whitebark pine occurs (Farley 1979; Holland 1964). In the Rocky Mountains, where whitebark pine has its major occurrence, the predominant rocks are sedimentary, consisting of limestones, sandstones, and shales. The Purcell Mountains consist of complex, folded limestones and quartzites with granitic intrusions. The Selkirk Mountains have complex, folded, erosion-resistant quartzites and limestones, gneiss, volcanics, and granitic intrusions. The Monashee Mountains are underlain by sedimentary and metamorphic gneissic rocks and volcanic intrusives. The Cariboo Mountains have folded and faulted, erosion-resistant quartzites and granitic rocks. Folded, intercalated volcanic and sedimentary rocks, and flat-lying lava flows, underlie the Interior Plateau. The Cascade Mountains are composed of folded and metamorphosed sedimentary and volcanic rocks with granitic intrusives. Batholithic intrusions of granites and gneisses predominate throughout the Coast Mountains.

SOILS

Soil parent materials derived from these rocks included bedrock debris at various stages of weathering, colluvium, and glacial tills. Very coarse fluvial and glacio-fluvial parent materials are reported by Pojar (1978) and Yole and others (1989) for valley bottom stands of whitebark pine in the northern Coast Mountains. The soil profile types are Lithic Regosols: (L-H), (Ah), *C*; Dystric and Eutric Brunisols: (L-H), *Ah*, *Bm*, C; and Orthic Humo-Ferric Podzols: *L-H*, Ae, *Bfh*, C (Canadian Society of Soil Science 1976; Canadian Soil Survey Committee 1978; Clayton and others 1977). The soil profiles are typically shallow, rocky, and coarse. Soil moisture conditions vary from dry to mesic. Whitebark pine in the Rocky Mountains is frequently associated with calcareous and basic soils, although some soil profiles are acidic.

Detailed soil profile descriptions and classifications are given in Achuff and others (1984a, 1984b), Coen and Holland (1976), Coen and Kuchar (1982), Coen and others (1977), Holland and Coen (1982), Lea (1984a), Sneddon and others (1972a, 1972b), van Ryswyk (1969), and Yole and others (1989). Discussions of problems in classifying and mapping subalpine and alpine soils are presented in Knapik (1978), Luttmerding and Shields (1978), and Valentine (1978).

General ecological descriptions of whitebark pine are given by Angove and Bancroft (1983), Krajina (1969), and Krajina and others (1982). According to these sources, whitebark pine occurs on xeric to mesic, nutrient-rich (subeutrophic) soils, is adapted to low temperatures, has high frost resistance, and low shade tolerance, and grows on high-nutrient soils rich in calcium and magnesium. Yole and others (1989) report very low nutrient status (oligotrophic to submesotrophic) for the soils of whitebark pine in the northern Coast Mountains. Soil pH and calcium content are given for whitebark pine soils in the Rocky Mountains by Baig (1972) and Smyth (1989a, 1989b). Approximately two-thirds of the soil profiles are calcareous and basic or circumneutral. Additional soil nutrient analyses (N, P, K, Ca, Mg, SO_4, and CEC) have been made by Smyth (1989a, 1989b).

STAND COMPOSITION

Throughout the Rocky Mountains, Columbia Mountains, and the Interior Plateau, whitebark pine forms stands with Engelmann spruce, subalpine fir, and the successional lodgepole pine. Occasionally, whitebark pine may extend to lower elevations in contact with hybrid spruce, in the Rocky Mountains and Selkirk Mountains. Although whitebark pine is sympatric with alpine larch in the southern Rocky Mountains, southern Purcell Mountains, and Cascade Mountains, the two species rarely form mixed stands, because they occupy different habitats. Generally, whitebark pine grows on drier, well-drained, southerly and westerly slopes, with shallow snow cover; in contrast, alpine larch occupies more mesic habitats with finer soils, on northerly and easterly slopes, and in deep snow accumulation areas. The geographic range of whitebark pine also overlaps with limber pine (*Pinus flexilis*) in the southern Rocky Mountains of Alberta and British Columbia. However, the two species are ecologically separated; limber pine grows at lower elevations in the foothills and front ranges well below the occurrence of whitebark pine.

In the Coast Mountains and the Cascade Mountains, whitebark pine forms stands with mountain hemlock, subalpine fir, Engelmann spruce, and lodgepole pine. In these mountains, whitebark pine may grow adjacent to stands with Alaska-cedar (*Chamaecyparis nootkatensis*) and Pacific silver fir (*Abies amabilis*), although they do not form mixed stands. In the northern Coast Mountains, the stands have an open canopy of whitebark pine, subalpine fir, lodgepole pine, and mountain hemlock, with seedlings and regeneration of all of these species (Pojar 1989; Yole and others 1989). In the northern Selkirk Mountains, whitebark pine also grows with mountain hemlock, subalpine fir, and hybrid spruce.

VEGETATION TYPES

There is considerable diversity in the species composition of whitebark pine stands. Whereas forest-line and tree-island stands appear discrete and clearly demarcated, the highest timberline stands have very open vegetation with widely spaced plants and widely spaced krummholz and dwarf trees. Problems arise in the delineation of such stands, and decisions may be difficult as to whether a patch of vegetation is part of a krummholz colony or a separate entity within a vegetation mosaic of krummholz and alpine meadow or krummholz and alpine heath.

One of the widespread whitebark pine vegetation types is the *Juniperus communis* series of dry habitats. Some of the major associated species are russet buffaloberry (*Shepherdia canadensis*), shrubby cinquefoil (*Potentilla fruticosa*), and bearberry (*Arctostaphylos uva-ursi*). This vegetation is widespread in the Rocky Mountains of Alberta (Baig 1972; Corns and Achuff 1982) and British Columbia (Achuff and others 1984a; Kuchar 1978; Lea 1984a, 1984b; Smyth 1987, 1989b). This vegetation also occurs in the southern Selkirk, Monashee, and Cascade Mountains, and in the Chilcotin Range of the east slope of the southern Coast Mountains (Selby 1980; Selby and Pitt 1984). A series of floristically related communities, also in dry habitats, occurs in the southern Rocky Mountains: the *Shepherdia canadensis* type (Lea 1984a, 1984b), the *Arctostaphylos uva-ursi* type (Smyth 1987, 1989b), and the *Festuca scabrella* type (Smyth 1987, 1989b).

Another widespread series of vegetation types are the heath communities of mesic, snow-accumulation habitats. The *Vaccinium scoparium* vegetation type occurs in the Rocky Mountains of Alberta (Baig 1972; Corns and Achuff 1982; Kuchar 1978; Ogilvie 1963, 1978a, 1978b) and adjacent British Columbia (Krajina 1969; Lea 1984a, 1984b; Smyth 1987). The *Phyllodoce glanduliflora, P. empetriformis* vegetation is common in the Rocky Mountains (Achuff and others 1984a; Baig 1972; Ceska 1989a, 1989b; Corns and Achuff 1982; Krajina 1969; Kuchar 1978; Ogilvie 1963, 1978a, 1978b) and in the Selkirk Mountains (Achuff and others 1984b). The *Cassiope mertensiana* vegetation type occurs in the Rocky Mountains (Achuff and others 1984a; Baig 1972; Ceska 1989a, 1989b; Krajina 1969; Kuchar 1973, 1978; Ogilvie 1963, 1978a, 1978b) and in the Selkirk Mountains (Achuff and others 1984b). The *Vaccinium membranaceum* vegetation type occurs in the Rocky Mountains (Achuff and others 1984a; Baig 1972; Corns and Achuff 1982; Kuchar 1978) and in the Selkirk Mountains (Achuff and others 1984b). A distinctive lichen community occurs on the east slope of the northern Coast Mountains. *Cladina rangiferina* and *Cladonia* spp. form the main ground cover under a sparse shrub layer with *Vaccinium membranaceum* and *Cassiope mertensiana* (Pojar 1978, 1989; Yole and others 1989).

The distinctive *Xerophyllum tenax* vegetation type occurs in the Rocky Mountains of southwestern Alberta (Baig 1972; Kuchar 1973; Ogilvie 1963, 1978a) and adjacent southeastern British Columbia. The *Dryas octopetala* vegetation type in wind-exposed, snow-free habitats is described from the southern Rocky Mountains of British Columbia (Lea 1984a, 1989b).

Within the subalpine and forest-line zone the *Rhododendron-Menziesia* vegetation type occurs in the southern Rocky Mountains of Alberta (Kuchar 1973) and southeastern British Columbia (Lea 1984a, 1984b) and in the northern Rocky Mountains of British Columbia (Ceska 1989a, 1989b). The tall willow-forb (*Salix* spp.-*Valeriana*) vegetation types are reported from the Rocky Mountains of Alberta (Baig 1972) and southeastern British Columbia (Kuchar 1978; Lea 1984a, 1984b).

PALEOECOLOGY

In a review of the main species encountered in the late Quaternary pollen record, Ritchie (1987) discussed the problem that none of the five western Canadian pines can be identified at the species level. Although our five-needle pines—whitebark pine, limber pine (*Pinus flexilis*), and western white pine (*P. monticola*)—have the distinctive *Haploxylon* pollen, they are not separable at the species level. Macrofossils are the only means of species identification. Until recently there had been no paleobotanical record of whitebark pine in western Canada.

In 1987, John Clague and Rolf Mathewes found buried logs of whitebark pine on the eastern slope of the southern Coast Mountains in British Columbia (Clague and Mathewes 1989; Mathewes 1988; Mathewes and Clague 1989). The age of the logs ranges between 8,200 to 9,100 yr. B.P., and associated with the logs are pollen and macrofossils of russet buffaloberry. The logs occur between 60 and 130 m above the present timberline, indicating a higher timberline and warmer climate at that time.

FUTURE STUDIES

As mentioned in the introduction to this paper, very little research has been done specifically on whitebark pine in western Canada. Research in most areas is needed for better understanding of this species.

The diversity of growth forms at timberline warrants attention. Population studies are required to determine the occurrence of altitudinal, latitudinal, geographic, and coastal versus continental races and ecotypes. Demographic analyses of whitebark pine stands are needed to understand its growth dynamics in relation to other timberline species, as well as to provide basic information for stand management. Soil chemistry studies are required to ascertain the relationship of whitebark pine to soil nutrients and to specific substrates such as limestone. Knowledge of the behavior of whitebark pine at the extremities of its range—in the Coast Mountains and in the northern Rocky Mountains and Interior Plateau—is of special interest since it can provide insight into the primary factors governing whitebark distribution and habitat relations.

ACKNOWLEDGMENTS

I would like to thank Wyman Schmidt and Tad Weaver for their invitation to contribute to the Symposium, and Wyman Schmidt especially for his patience and consideration in the preparation of this paper. I thank T. Christopher Brayshaw, Adolf Ceska, Ted Lea, and Jim Pojar for providing valuable field observations, records, and plot data on whitebark pine. I am indebted to Mirza Baig and Clint Smyth for the use of data from their theses research. I thank Rich Hunt, Canadian Forestry Service, for providing computerized data of their collections of diseased whitebark pine. I am grateful to Rolf Mathewes for making available the abstract and draft copy of his and John Clague's papers on the discovery of the early Holocene whitebark pine logs. I thank Les Jozsa, who provided field data and comments on his dendrochronology research. I am indebted to Stephen Arno, T. Christopher Brayshaw, and Jim Pojar who reviewed an earlier draft of this paper and provided valuable comments. For her careful and expeditious typing of the manuscript, I thank Carolyn Kenzie.

REFERENCES

Achuff, P. L.; Holland, W. D.; Coen, G. M.; Van Tighem, K., eds. 1984a. Ecological land classification of Kootenay National Park, British Columbia. Vol. 1: Integrated resource description. Edmonton, AB: Environment Canada and Alberta Institute of Pedology. 373 p.

Achuff, P. L.; Holland, W. D.; Coen, G. M.; Van Tighem, K., eds. 1984b. Ecological land classification of Mount Revelstoke and Glacier National Parks, British Columbia. Vol. 1: Integrated resource description. Edmonton, AB: Environment Canada and Alberta Institute of Pedology. 261 p.

Angove, K.; Bancroft, B. 1983. A guide to some common plants of the southern Interior of British Columbia. Land Management Handbook No. 7. Victoria, BC: British Columbia Ministry of Forests. 225 p.

Baig, M. N. 1972. Ecology of timberline vegetation in the Rocky Mountains of Alberta. Calgary, AB: University of Calgary, Department of Biology. 444 p. Thesis.

Brayshaw, T. C. 1989. [Personal communication]. May. Victoria, BC: Royal British Columbia Musuem.

Canadian Society of Soil Science, Nomenclature Committee. 1976. Glossary of terms in soil science. Publ. 1459. Ottawa, ON: Canada Department of Agriculture. 44 p.

Canadian Soil Survey Committee. 1978. The Canadian system of soil classification. Publ. 1646. Ottawa, ON: Canada Department of Agriculture. 164 p.

Ceska, A. 1989a. [Personal communication]. May. Victoria, BC: Royal British Columbia Museum.

Ceska, A. 1989b. Vegetation and habitat data of whitebark pine stands in the Rocky Mountains of northern British Columbia. Unpublished field data supplied to author by A. Ceska.

Clague, John J.; Mathewes, Rolf W. 1989. Early Holocene thermal maximum in western North America: new evidence from Castle Peak, British Columbia. Geology. 17: 277-280.

Clausen, J. 1963. Tree lines and germ plasm—a study in evolutionary limitations. Proceedings, National Academy of Sciences. 50: 860-868.

Clausen, J. 1965. Population studies of alpine and subalpine races of conifers and willows in the California High Sierra Nevada. Evolution. 19: 56-68.

Clayton, J. S.; Ehrlich, W. A.; Cann, D. B.; Day, J. H.; Marshall, I. B. 1977. Soils of Canada. Vol. 1: Soil report. Ottawa, ON: Canada Department of Agriculture. 243 p.

Coen, G. M.; Epp, P. F.; Tajek, J.; Knapik, L. 1977. Soil survey of Yoho National Park, Canada. Alberta Soil Survey Rep. No. 37. Edmonton, AB: Agriculture Canada and Alberta Institute of Pedology. 208 p.

Coen, G. M.; Holland, W. D. 1976. Soils of Waterton Lakes National Park and interpretations. Informational Report NOR-X-65. Edmonton, AB: Department of the Environment, Canadian Forestry Service, Northern Forest Research Centre.

Coen, G. M.; Kuchar, Peter. 1982. Biophysical (ecological) inventory of Yoho National Park, British Columbia, Canada. Edmonton, AB: Agriculture Canada.

Corns, I. G. W.; Achuff, P. L. 1982. Vegetation type descriptions. In: Holland, W. D.; Coen, G. M., eds. Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol. 2: Soil and vegetation resources. Publ. SS-82-44. Edmonton, AB: Alberta Institute of Pedology, University of Alberta.

Crawford, R. M. M. 1989. Studies in plant survival: ecological case histories of plant adaptation to adversity. Studies in ecology, Vol. 11. Oxford, England: Blackwell Scientific Publications. 296 p.

Day, R. J. 1967. Whitebark pine in the Rocky Mountains of Alberta. Forestry Chronicle. 43(3): 278-282.

Farley, A. L. 1979. Atlas of British Columbia. Vancouver, BC: University of British Columbia Press.

Holland, S. S. 1964. Landforms of British Columbia—a physiographic outline. Bull. No. 48. Victoria, BC: British Columbia Department of Mine and Petroleum Resources. 138 p.

Holland, W. D.; Coen, G. M., eds. 1982. Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol. 2: soil and vegetation resources. Publ. SS-82-44. Edmonton, AB: Alberta Institute of Pedology, University of Alberta.

Joza, L. A. 1989. [Personal communication]. June. Vancouver, BC: Forintek Canada, Western Laboratory.

Knapik, L. J. 1978. Aspects of classification of alpine and subalpine soils. In: Luttmerding, H. A.; Shields, J. A., eds. Proceedings of the workshop on alpine and subalpine environments. Victoria, BC: British Columbia Ministry of Environment: 56-73.

Krajina, V. J. 1969. Ecology of forest trees in British Columbia. Ecology of western North America. Vol. 2, No. 1. Vancouver, BC: University of British Columbia. 147 p.

Krajina, V. J.; Klinka, K.; Worrall, J. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Vancouver, BC: University of British Columbia, Faculty of Forestry. 131 p.

Kuchar, Peter. 1978. The vegetation of Yoho National Park. Calgary, AB: Parks Canada, Western Region. 385 p.

Lea, E. C. 1984a. Biophysical resources of the East Kootenay area: Volume 1—vegetation. Tech. Rep. 5. Victoria, BC: British Columbia Ministry of Environment. 75 p.

Lea, E. C. 1984b. Biophysical resources of the East Kootenay area: Volume 3—vegetation groups and types. Unpublished technical report on file at: British Columbia Ministry of Environment, Victoria, BC. 156 p.

Luckman, B. H.; Jozsa, L. A.; Murphy, P. J. 1984. Living seven-hundred-year-old *Picea engelmannii* and *Pinus albicaulis* in the Canadian Rockies. Arctic and Alpine Research. 16(4): 419-422.

Luttmerding, H. A.; Shields, J. A., eds. 1978. Proceedings of the workshop on alpine and subalpine environments, April 1976. Victoria, BC: British Columbia Ministry of Environment. 172 p.

Mathewes, Rolf W. 1988. Higher postglacial alpine timberlines in the eastern Coast Ranges of British Columbia. Abstract. Botany British Columbia Working Group Newsletter. 3: 5.

Mathewes, Rolf W.; Clague, John J. 1989. Early Holocene thermal maximum: new evidence from Castle Peak, British Columbia. Abstract. Ottawa, ON: Canadian Committee on Climatic Fluctuations and Man.

Ogilvie, R. T. 1963. Ecology of the forests in the Rocky Mountains of Alberta. Research Rep. No. 63-A-12. Ottawa, ON: Canada Department of Forestry. 57 p.

Ogilvie, R. T. 1978a. The alpine and subalpine in the Rocky Mountains of Alberta. In: Luttmerding, H. A.; Shields, J. A., eds. Proceedings of the workshop of alpine and subalpine environments; 1976 April. Victoria, BC: British Columbia Ministry of Environment: 33-48.

Ogilvie, R. T. 1978b. Vegetation mapping methodology: mapping of alpine and subalpine vegetation in the Rocky Mountains, Alberta. In: Luttmerding, H. A.; Shields, J. A., eds. Proceedings of the workshop on subalpine and alpine environments; 1976 April. Victoria, BC: British Columbia Ministry of Environment: 97-104.

Pojar, J. 1978. Vegetation of ecological reserve proposal No. 306, Nanika Lake. Unpublished paper on file at: British Columbia Ministry of Environment, Ecological Reserves Unit. Victoria, BC.

Pojar, J. 1989. [Personal communication]. May. Smithers, BC: Ministry of Forests, Research Section.

Ritchie, J. C. 1987. Postglacial vegetation of Canada. Cambridge, England: Cambridge University Press. 178 p.

Selby, C. J. 1980. Alpine and subalpine vegetation in the southern Chilcotin Mountain rangelands of British Columbia. Vancouver, BC: University of British Columbia, Department of Plant Science. 162 p. Thesis.

Selby, C. J.; Pitt, M. D. 1984. Classification and distribution of alpine and subalpine vegetation in the Chilcotin Mountains of southern British Columbia. Syesis. 17: 13-41.

Smyth, C. R. 1987. Seed production, dispersal, predation, and germination of seven high elevation Rocky Mountain legume species. Victoria, BC: University of Victoria, Department of Biology. 169 p. Thesis.

Smyth, C. R. 1989a. [Personal communication]. February. Victoria, BC: University of Victoria, Department of Biology.

Smyth, C. R. 1989b. Vegetation, soils, and habitat data of whitebark pine stands in the Rocky Mountains of southeastern British Columbia. Unpublished field data supplied to author by C. R. Smyth.

Sneddon, J. I.; Lavkulich, L. M.; Farstad, L. 1972a. The morphology and genesis of some alpine soils in British Columbia, Canada. 1. Morphology, classification and genesis. Soil Science Society of America Proceedings. 36: 100-104.

Sneddon, J. I.; Lavkulich, L. M.; Farstad, L. 1972b. The morphology and genesis of some alpine soils in British Columbia, Canada. 2. Physical, chemical and mineralogical determinations and genesis. Soil Science Society of America Proceedings. 36: 104-110.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. New York: Springer-Verlag. 137 p.

Valentine, K. W. G. 1978. Alpine and subalpine soils in British Columbia. In: Luttmerding, H. A.; Shields, J. A., eds. Proceedings of the workshop on alpine and subalpine environments. Victoria, BC: British Columbia Ministry of Environment: 49-55.

van Ryswyk, A. L. 1969. Forest and alpine soils of south-central British Columbia. Pullman, WA: Washington State University. Dissertation.

Yole, D.; Lewis, T.; Inselberg, A.; Pojar, J.; Holmes, D. 1989. A field guide for identification and interpretation of the Engelmann spruce-subalpine fir zone in the Prince Rupert Forest Region, British Columbia. Land Management Handbook No. 17. Victoria, BC: British Columbia Ministry of Forests. 83 p.

ADDITIONAL READINGS

Brink, V. C. 1959. A directional change in the subalpine forest-heath ecotone in Garibaldi Park, British Columbia. Ecology. 40: 10-16.

Brooke, R. C.; Peterson, E. B.; Krajina, V. J. 1970. The subalpine mountain hemlock zone. Ecology of western North America, Vol. 2, No. 2. Vancouver, BC: University of British Columbia: 148-349.

Carl, G. C.; Hardy, G. A. 1945. Flora and fauna of the Paradise Mine area, British Columbia. Annual Report 1944. Victoria, BC: Province of British Columbia, Provincial Museum of Natural History and Anthropology: 18-38.

Carl, G. C.; Guiguet, C. J.; Hardy, G. A. 1952. A natural history survey of the Manning Park area, British Columbia. Occasional Papers No. 9. Victoria, BC: British Columbia Provincial Museum. 130 p.

Chuang, C. C. 1972. A preliminary checklist of the flora of Yoho National Park. Unpublished manuscript on file at: Yoho National Park, Field, BC.

Chuang, C. C. 1975. Inventory of flora of Mount Robson Park. Unpublished report on file at: British Columbia Provincial Museum, Victoria, BC. 31 p.

Eady, K. 1971. Ecology of the alpine and timberline vegetation of Big White Mountain, British Columbia. Vancouver, BC: University of British Columbia, Department of Botany. 239 p. Thesis.

Goward, T. 1985. *Ahtiana*, a new lichen genus in the Parmeliaceae. The Bryologist. 88(4): 367-371.

Haber, Erich; Soper, James H. 1980. Vascular plants of Glacier National Park, British Columbia, Canada. Syllogeus No. 24. Ottawa, ON: National Museums Canada. 34 p.

Hamet-Ahti, Leena. 1965. Vascular plants of Wells Gray Provincial Park and its vicinity, in eastern British Columbia. Annales Botanici Fennici. 2: 138-164.

McAvoy, B. 1931. Ecological survey of the Bella Coola region. Botanical Gazette. 92: 141-171.

Meidinger, D. V.; Hope, G. D.; McLeod, A. J. 1984. Classification and interpretation of some ecosystems of the Rocky Mountain Trench, Prince George Forest Region, British Columbia. Land Management Rep. No. 22. Victoria, BC: British Columbia Ministry of Forests. 294 p

Shaw, C. H. 1916. The vegetation of the Selkirks. Botanical Gazette. 61: 476-494.

Ulke, Titus. 1934. A flora of Yoho Park, British Columbia. Biological Laboratory Contribution No. 14. Washington, DC: Catholic University of America. 90 p.

Ulke, Titus. 1935. List of the vascular plants of the Horsethief Creek-Purcell Range, British Columbia. Canadian Field-Naturalist. 49: 49-55, 71-76.

Utzig, G.; MacDonald, D.; Comeau, P. 1978. Ecological classification for the Nelson Forest District: second approximation. Nelson, BC: British Columbia Ministry of Forests. 33 p.

Vold, T.; Fenster, R. F.; Ovanin, T. K.; Woods, G. P. 1980. Soil and vegetation resources of the Pend d'Oreille Valley, British Columbia. APD Bull. 2. Victoria, BC: British Columbia Ministry of Environment.

SESSION 3

Ecology of Whitebark Pine Forests

Steve Arno and David Mattson
Session Coordinators

This session provided state-of-the-art physical and biological information about the high-mountain ecosystems of whitebark pine. Included are papers describing geology, climate, fire, succession, seeds and seedlings, insects and diseases, ecological interactions of birds, squirrels, and grizzly bears, and modeling. Invited and volunteer papers provide a surprising amount of qualitative and quantitative information about high-mountain ecosystems and serve as the basis for management implications in the session that follows.

GEOLOGY, GEOMORPHOLOGY, AND SOILS WITHIN WHITEBARK PINE ECOSYSTEMS

Katherine Hansen-Bristow
Clifford Montagne
Ginger Schmid

ABSTRACT

Whitebark pine (Pinus albicaulis) *stands grow on a variety of soil parent material lithologies (crystalline, volcanic, sedimentary [sandstone, argillite, limestone, interbedded sandstone and shale]) and surficial materials (glacial till, mass failure, colluvium, and residuum). The distribution of whitebark pine on calcareous parent materials appears to be limited to the Northern Rocky Mountains, from Canada into southern Montana.*

Landforms within whitebark pine ecosystems result from the interaction of bedrock type and structure with surficial processes of mountain environments (freeze-thaw, mass failure, mass wasting, and glaciation). Those landforms include ridge tops and dissected mountain slopes, glacial trough walls and moraines, cirque headwalls and basins, landslides, hogback ridges, talus slopes, rock glaciers, and rock slides. In most cases, whitebark pine is found on landforms with good drainage and relative stability.

Because of severe climate that limits biological activity, soils of whitebark pine ecosystems are minimally developed and highly influenced by underlying parent material. Soil textures range from sandy to loamy and fine loamy, often with abundant rock fragments (skeletal). Soil reaction is usually acidic, except on calcareous substrates. Many of these soils are classified as Cryochrepts and Cryoboralfs. Nutrient levels may generally be low in comparison with most forest soils.

INTRODUCTION

Whitebark pine (*Pinus albicaulis*) ecosystems are found predominantly at the highest elevations of forest growth, a result of the ability of this pine to tolerate the harsh climate at elevations where other tree species are not as dominantly competitive. Within these high elevations the precise location of whitebark pine stands is partially determined by the sites' geology, geomorphology, and soils.

This paper will provide generalized, cited information on the geology, geomorphology, and soils of high elevations of western North America where whitebark pine ecosystems may occur. Specific field and laboratory data from previous studies illustrate geologic, geomorphic, and soils relationships. Data have been cited from habitat and cover type maps of the Gallatin National Forest, Forest Service, U.S. Department of Agriculture, soil surveys, and from communication with staff of the Beaverhead, Bridger-Teton, Deerlodge, Flathead, Kootenai, and Gallatin National Forests. Literature searches provided relevant sources of data; however, there is little published material on this subject.

GENERAL GEOGRAPHY

In the Rocky Mountains, whitebark pine extends from British Columbia and Alberta, through Montana, Idaho, and Utah, to the Wind River Range in Wyoming. Whitebark pine also extends from the British Columbia coastal ranges through the Cascade and Sierra Nevada ranges. It occurs in isolated mountain ranges in Nevada, California, Oregon, and Washington (Arno and Hoff 1989) (fig. 1).

The high-elevation settings in which whitebark pine ecosystems are found are characterized by geography common to many mountain environments. Specific distributional information is available for selected stands within the general range of whitebark pine (table 1). As shown, whitebark pine is found on a wide variety of aspects and on wide-ranging slopes. In accordance, however, with expected latitudinal controls on the elevation of upper treeline species, the pine is found at highest elevations in the southern sites of the Sierra Nevada and the Bridger-Teton National Forest, WY. At more northerly locations, the pine's upper elevational limit may be depressed by both snow and lower energy budgets, resulting in its lower distribution.

At many tree-line and tree-limit sites, trees reach their maximum elevational limits on convex rather than concave slopes. Nocturnal temperature inversions often produce inverted tree lines at concave sites; in contrast, convex sites may have a warmer microclimate that extends the length of the growing season (Hansen-Bristow 1986). In some of the harshest microclimates, however, the uppermost trees are found at slope concavities where

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Katherine Hansen-Bristow is Associate Professor of Earth Sciences and Clifford Montagne is Associate Professor of Plant and Soil Science, Montana State University, Bozeman, MT 59717. Ginger Schmid is a Ph.D student of Geography, University of California, Davis, CA 95616.

Figure 1—The distribution of whitebark pine illustrates its widespread occurrence in western North America (from Arno and Hoff 1989).

Table 1—Available data on some site characteristics of some whitebark pine stands (derived from Baig 1972; Clausen 1965; Holland and Coen 1982; Lueck 1980; Steele and others 1983; Winthers 1989)

Site	Slope	Aspect	Elevation
	Percent		*m (ft)*
Banff and Jasper National Parks, Canada			
- whitebark dominated	10-75	NW to NE SW to SE	2,000-2,280 (6,560-7,480)
- whitebark codominant or subdominant	37-70	Wide variety	1,720-2,320 (5,645-7,610)
Flathead National Forest, MT	20-90	NE	1,675-2,440 (5,500-8,000)
Gallatin National Forest, MT	0-45	Wide variety	2,075-2,620 (6,810-8,600)
Bridger-Teton National Forest, WY	5-90	S and W	2,400-3,050 (7,875-10,000)
Cascade Mountains (Bachelor Butte, OR)	—	Wide variety	2,350-2,530 (7,710-8,300)
Sierra Nevada Mountains (Slate Creek, CA)			
- whitebark dominated	—	N	3,050-3,190 (10,010-10,456)
		S and E	3,200-3,350 (10,500-10,990)
- whitebark subdominant		S and E	3,050-3,200 (10,010-10,500)

winter snow accumulation provides insulation and protection from wind-blown ice crystals and winter desiccation. These snow-accumulation sites also provide moisture for growth. Because pines illustrate a superior adaptation to unshaded sites (more drought and radiation tolerant) (Wardle 1974), they often play a pioneering role at high elevations, occupying open meadow sites. They often serve as nuclei for establishment of other tree species. Such is the case at Logan Pass, MT, within Glacier National Park, where old whitebark pines, surrounded by younger subalpine fir, have formed "tree islands" (Habeck 1969).

GENERAL GEOLOGY, GEOMORPHOLOGY, AND SOILS

The lithology and structure of rock within a mountain environment tend to control landscape development (through the resistance and strength of its constituent material) and, therefore, influence a site's potential to support tree growth. Outliers and ridges are often associated with resistant crystalline rocks, such as granite or quartzite, while valleys may more often be formed in weak and friable rocks, such as limestone or shale (Price 1981).

Lithology—Mountains with whitebark pine include a variety of geologic types. The Cascades of Oregon and Washington are primarily volcanic while the Sierra Nevada is primarily igneous. Many of the mountains found in the continental interiors, such as much of the Central Rocky Mountains, are composed of ancient crystalline cores of Precambrian rock. Other ranges, such as the Northern Rocky Mountains, are composed chiefly of marine sediments, which have often been metamorphosed and injected with volcanic material. Coarse-textured bedrock lithologies often predominate. Where there are fine-textured lithologies, the surficial geologic materials usually have abundant coarse rock fragments. Acidic rock types are more prevalent than basic rock types.

Structure—A variety of geologic structures are found in environments occupied by whitebark pine. For example, the Northern Rocky Mountains are a major folded and faulted range, as exemplified by Montana's Lewis Overthrust in which Precambrian sedimentary rocks were uplifted and thrust over younger shales and sandstones. The Basin and Range mountains of the western United States result from tensional forces stretching the earth's crust and creating abrupt and spectacular fault scarps. The Sierra Nevada provides an example of a faulted range, dipping gently to the west, while the east-facing slopes rise abruptly as a fault line scarp.

Geomorphology

The landscapes of whitebark pine are influenced by both constructive and destructive processes and, therefore, these high-elevation sites are often characterized by a high rate of energy transfer, particularly where steep slopes prevail. Additionally, the type and rate of geomorphic processes are affected by the structure, form, climate, and composition of a particular mountain range. These factors result in a wide variety of environments and landscapes for whitebark pine.

Process—The high-mountain landscape is characterized by instability, variability, rapid physical weathering, and a continual transport of earth materials downslope. Many geomorphic processes are intensified in areas with steep slopes and a mountain-type climate. Low temperatures tend to be the dominant climatic feature at higher elevations, producing landscape regimes that are glacial, nivational, and periglacial (Embleton and King 1974; Price 1972; Washburn 1973).

Although many scales of geomorphic processes operate in mountains, large-scale features such as mudflows, landslides, and avalanches can reach catastrophic dimensions and do more geomorphic work in a matter of minutes than day-to-day processes can accomplish in centuries (Price 1981; Rapp 1960; Rapp and Fairbridge 1968). These processes often create both suitable and unsuitable sites for tree growth. For example, an avalanche slope is generally unsuitable for tree growth due to snow movement (Rapp 1959) and enhanced downslope drainage of cold air. In contrast, debris piles at the base of the avalanche slope may provide a shaded habitat for seedling survival.

Glaciation—Glacial processes, directly shaping the land with ice movement, produce some of the most distinctive and striking landscapes in the world. In sites where glacial erosion has occurred, such as bare cirque walls, trees are generally excluded. In contrast, soils on glacial and glacio-fluvial deposits often provide potential habitat for successful tree establishment and survival (Price 1981).

Periglacial—The entire periglacial system, characterized by low temperatures, frost action, mass wasting, and nivation, occupies large areas of mountain landscapes at high elevations, and is a dominant influence on whitebark pine distribution. Periglacial processes such as frost action (freezing and thawing of earth surfaces) form patterned ground (sorted and nonsorted circles, polygons, nets, steps, and stripes), and blockfields. Generally these landform surfaces are quite unstable, often to the point of elimination or prohibition of vegetative cover.

Mass wasting, achieving its greatest development in mountain landscapes because of steep slopes, great relief, and environmental variability, is the downslope movement of material due to gravity without the aid of a specific transporting medium (Price 1981). Many landforms resulting from mass wasting are the product of more than one type of motion, including creep, solifluction, mudflows, slumps, rockfalls, landslides, and debris avalanches, and often are unstable to the point of exclusion of trees.

Nivation, erosion within the narrow zone of the snowline area, creates hollows and depressions on the landscape. In many areas, benches, terraces, and rounded or flattened summits (altiplanation or cryoplanation terraces) are attributed to nivational processes (Price 1981). These processes often create more diverse microsites suitable for tree establishment due to substrate accumulations or shelter, once active erosion and deposition have ceased.

Soils

Soil development processes are functions of Jenny's Five Factors of Soil Formation (Jenny 1941)—climate, biological activity, relief or landscape position, geologic parent material, and time. High-elevation climates of whitebark pine ecosystems severely limit both biological activity and chemical weathering. Due to their position within usually mountainous landscapes, whitebark pine soils often occupy steep-slope landscape positions where erosion of various forms is the predominant surficial process. As mentioned earlier, many of the geologic parent materials at high elevations in western North America tend to produce coarse, sandy-textured, rock-fragment-rich soils. The bedrock chemistry is usually acidic. Due to landscape position, whitebark pine soils often occupy less stable slope positions where erosion predominates; therefore, soils of whitebark pine ecosystems tend to be young and minimally developed.

The five factors of soil formation limited by climate, biological activity, and coarse-textured geologic parent materials interact to produce minimally developed soils that are often low in plant-available water-holding capacity and nutrients. Whitebark pine soils are most often classified as Cryochrepts (cold-climate soils with light-colored surface horizons and minimally developed subsurface horizons). In some cases, whitebark pine soils are Cryoboralfs (cold-climate soil with light-colored surface horizons and clay accumulation in a subsurface horizon), Cryorthents (minimally developed cold-climate soils), or Cryoborolls (cold-climate soils with dark, organic-matter-enriched surface horizons) (Kuennen 1989).

GEOLOGY OF SPECIFIC ECOSYSTEMS

In Banff and Jasper National Parks of the Canadian Rockies, both calcareous (limestone and dolomite) and noncalcareous (sandstone, shale, siltstone) parent materials support whitebark pine (Baig 1972; Holland and Coen 1982). Many of the stands found in northwestern Montana are found in the Belt Supergroup, which includes metasediments of argillite, siltite, quartzite, and limestone. In southern Montana (Gallatin National Forest), whitebark pine stands are found on a variety of parent materials, including crystalline, volcanic, and sedimentary rocks (table 2) (fig. 2). Eighty-five percent of the whitebark pine stands sampled by Weaver and Dale (1974) in central and southern Montana were on igneous parent materials. In northern Wyoming, whitebark pine is found on a variety of bedrock types, including quartzite, sandstone, limestone, and dolomite.

A question exists concerning the distribution of whitebark pine and limestone substrates. Weaver and Dale (1974) commented that whitebark pine is definitely not found on limestone substrates, with the exception of its occurrence on Wheeler Ridge, near Bozeman, MT. In the Gallatin National Forest soil survey, 11 percent of the acres are mapped in *Abies lasiocarpa/Pinus albicaulis* habitat types (9.5 percent) and *Pinus albicaulis/Abies lasiocarpa* habitat types (1.5 percent). Limestone is associated with 11.5 percent of the mapped acres, but only 1.5 percent of the acreage has *Abies lasiocarpa/Pinus albicaulis* habitat types and limestone. *Pinus albicaulis/ Abies lasiocarpa* habitat types are not found associated with limestone. Arno's work (referred to in Pfister and others 1977) also indicated whitebark pine is not found on limestone. Whitebark pine is, however, found on limestone in the Canadian Rockies (Baig 1972; Holland and Coen 1982), the Flathead National Forest (Martinson and Basko 1988), and in the Bridger-Teton National Forest (Winthers 1989). Bamberg and Major (1968) mentioned stone pine (*Cembrae* or stone pine is a subsection of *Pinus*; it includes *albicaulis*) on calcareous parent material at three Montana locations: the Big Snowy Mountains, Siyeh Pass in Glacier National Park, and the Flint Creek Mountains. Whitebark pine also grows in limestone-derived soils in the Gravelly Range of southwestern Montana (Svoboda 1989). This relationship needs further study.

Figure 2—A whitebark pine stand in the Gallatin National Forest on metamorphic parent rock materials.

Table 2—Characteristics of Gallatin National Forest soil map units with whitebark pine as a habitat type species (PIAL-ABLA is *Pinus albicaulis-Abies lasiocarpa* habitat type, ABLA-PIAL/VASC is *Abies lasiocarpa-Pinus albicaulis/Vaccinium scoparium* habitat type) (from Davis and Shovic 1984)

Habitat type (percent of map unit)	Landform	Parent material	Slope	Aspect	Elevation	Soil classification
			Percent		*m (ft)*	
PIAL-ABLA (10-50)	Glacial troughs Cirque headwalls	Hard crystalline rocks	45+	Variable	2,500+ (8,200+)	Dystric and typic cryochrepts
PIAL-ABLA (5-30)	Talus slopes Rock glaciers Rock slides	Undifferentiated mixed colluvium	20-45	Variable	2,130-2,990 (7,000-9,800)	Rubble land
PIAL-ABLA (10-20)	Cirque basins	Hard crystalline rocks	0-20	E-NW	2,590+ (8,500+)	Dystric and litic cryochrepts
ABLA-PIAL/VASC (80)	Moraines	Glacial till-hard crystalline rocks	0-20	Variable	2,315-2,590 (7,600-8,500)	Dystric cryochrepts
ABLA-PIAL/VASC (80)	Moraines	Glacial till-volcanic rocks	0-20	Variable	2,375-2,590 (7,800-8,500)	Mollic cryoboralfs
ABLA-PIAL/VASC (75)	Moraines	Glacial till-hard crystalline rocks	45+	Variable	2,375-2,590 (7,800-8,500)	Dystric cryochrepts
ABLA-PIAL/VASC (70)	Rounded ridgetops	Hard crystalline rocks	0-20	Variable	2,375-2,590 (7,800-8,500)	Dystric cryochrepts
ABLA-PIAL/VASC (70)	Rounded ridgetops	Volcanic rocks	0-20	Variable	2,375-2,590 (7,800-8,500)	Mollic cryoboralfs
ABLA-PIAL/VASC (65)	Dissected mountain slopes	Hard crystalline rocks	45+	Variable	2,070-2,500 (6,800-8,200)	Dystric cryochrepts
ABLA-PIAL/VASC (65)	Dissected mountain slopes	Volcanic rocks	45+	Variable	2,375-2,590 (7,800-8,500)	Mollic cryoboralfs
ABLA-PIAL/VASC (60)	Moraines	Glacial till-volcanic rocks	45+	Variable	2,375-2,590 (7,800-8,500)	Mollic cryoboralfs
ABLA-PIAL/VASC (60)	Dipslopes	Folded sedimentary rocks (ss and shale)	10-20	North	2,440-2,680 (8,000-8,800)	Typic cryoboralfs
ABLA-PIAL/VASC (55)	Landflows	Mass failure deposits-weathered volcanics	0-20	Variable	2,375-2,590 (7,800-8,500)	Typic and mollic cryoboralfs
ABLA-PIAL/VASC (50)	Landflows	Mass failure deposits-weathered soft sedimentary rocks	0-20	Variable	2,375-2,620 (7,800-8,600)	Typic aquic mollic cryoboralfs
ABLA-PIAL/VASC (50)	Moraines	Glacial till-soft sedimentary rocks Limestone	0-20	N-NE	2,440-2,590 (8,000-8,500)	Mollic cryoboralfs

GEOMORPHOLOGY OF SPECIFIC ECOSYSTEMS

The majority of sites dominated by whitebark pine in Banff and Jasper National Parks are on colluvial slopes. Where whitebark pine is found on moraines and landslide deposits, it is often codominant or subdominant with subalpine fir, Engelmann spruce, and lodgepole pine (Baig 1972; Holland and Coen 1982).

In northwestern Montana (Kootenai and Flathead National Forests) whitebark pine is often found on glacially scoured sites. It is found in both cirque basins and on bedrock-dominated sideslopes. In addition, the soils there are subject to frost churning (Kuennen 1989). As displayed in table 2, in south-central Montana whitebark pine seems to exist on nearly all mountain landforms including glacial cirque basins, troughs, headwalls, moraines, landflows, and both dissected mountain slopes and rounded ridgetops (fig. 3).

Figure 3—A ridge in the Gallatin National Forest, MT, provides the setting upon which whitebark pine exist.

SOILS OF SPECIFIC ECOSYSTEMS

Characteristics of general forest soils can be compared with soils of whitebark pine sites (table 3). The usually lower pH and percent base saturation of whitebark pine site soils may be due to acidic, coarse-textured parent materials. Higher organic matter levels of whitebark pine soils may be related to the cool, dry, and windy decomposition-limiting climates of high elevations.

Soil pedon descriptions are available for 24 whitebark pine sites within Banff and Jasper National Parks (Baig 1972; Holland and Coen 1983). Half of these are sites dominated by whitebark pine (for example, *Pinus albicaulis-Picea engelmannii* or *Pinus albicaulis-Abies lasiocarpa*). The other half are sites where whitebark pine is codominant (*Pinus albicaulis-Abies lasiocarpa* and *Pinus albicaulis-Pinus contorta*) or subdominant (for example, *Abies lasiocarpa-Picea engelmannii-Pinus albicaulis*; *Abies lasiocarpa-Pinus albicaulis*; *Picea engelmannii-Pinus albicaulis*). Neither study documented any stands that are pure whitebark pine. The soils at all these sites are shallow with limited profile development.

Table 3—Properties of soils in whitebark pine ecosystems

	General forest		Whitebark pine sites				
Soil properties	**Gallatin NF, MT (Montagne and Munn 1980)**	**Gallatin NF, MT (Montagne and Munn 1980)**	**Montana and Wyoming (Weaver and Dale 1974)**	**Kootenai NF, MT (Kuennen 1989)**	**Wind River Range, WY (Reed 1976)**	**Banff and Jasper NP, AB (Holland and Coen 1983)**	**Banff and Jasper NP, AB (Baig 1972)**
	[1]*n* = 335	*n* = 19	*n* = 19	*n* = 7	*n* = 5	*n* = 31	*n* = 31
Percent sand	42	54	42	(silt loams)	—	54	51
	silt	34	35	49	—	38	35
	clay	24	11	9	—	8	16
pH	6.2	5.4	5.4	5.1	5.1	6.2	6.5
OM (percent)	2.3	2.9	6.1	4.2	—	3.0	2.2
Total N (percent)	.09	.000	—	.095	—	—	—
Ca (meq/100 g)	10.7	3.5	1.3	.4	8.2	1.1	—
Mg (meq/100 g)	2.5	.84	.6	.1	1.8	.3	—
Na (meq/100 g)	0.2	.07	.48	.4	—	.1	—
K (meq/100 g)	0.5	.40	.30	.2	.7	.1	—
CEC (meq/100 g)	21.2	16.0	—	15.5	—	5.3	—
BS (percent)	61.0	25.8	—	6.0	45.8	—	—
EC (mmhos/cm)	.48	.82	0.3	.12	—	—	—

[1] *n* = number of horizons analyzed.

Those with the highest degree of horizonation are found on sites where whitebark pine is codominant or subdominant. At these sites both AE and AB horizons are identified. Depth to C horizons ranged from 8 to 46 cm (3 to 18 inches) on the sites dominated by whitebark pine, and from 0 to 90 cm (0 to 36 inches) on all other sites. Textures in all horizons are silt loams, or coarser, with a majority of horizons being sandy loams. All are considered well drained with at least 20 percent (by weight) coarse fragments. Soils at the sites dominated by whitebark pine are classified as Dystric Brunisols and Regosols (Orthic, Cumulic, and Lithic). The other sites are classified as Dystric and Eutric Brunisols and Orthic Regosols (Brunisols are equivalent to Inceptisols, Regosols to Entisols).

Pfister and others (1977) summarized soil properties of whitebark pine-associated habitat types of the Forest Service's Northern Region (Montana and Northern Idaho) (table 4). In the northern Region, whitebark pine establishes on soils of high-elevation, subalpine-climate landscapes that are usually low in clay (with exception of some soils in the Gallatin and Beaverhead National Forests) and high in rock fragments (fig. 4). These soils are Cryochrepts, Cryoboralfs (clay rich), Cryoborolls, and Cryandepts (if influenced by volcanic ash) (Holdorf 1989).

In the Kootenai National Forest of northwestern Montana, whitebark pine exists on Cryochrepts (Typic, Andic, and Lithic) and Cryandepts with loamy-skeletal textures of mixed mineralogy and relatively low pH (5.5 to 6.5) (fig. 5). Most of these soils have a volcanic ash-influenced surface layer found over metasedimentary residuum of the Belt Supergroup. Two example soils have horizons influenced by silt-loam volcanic ash found over gravelly and rocky subsoils. Levels of acidity (pH) range from 4.0 to 5.7 with a cation exchange capacity of 6 to 23 meq/100 g. Percent base saturations are 4 to 14 percent and the surface horizons have 5 to 8 percent organic matter. Amounts of extractable calcium, magnesium, sodium, and potassium are generally less than 1 ppm.

The Flathead National Forest draft soil survey (Martinson and Basko 1989) describes four mapping units within the upper subalpine forest that include whitebark pine. Like the Kootenai National Forest soils, these have volcanic ash surface layers, acidic pH's, and abundant coarse fragments. In these whitebark pine landscapes the cirque basins have Andic Cryochrepts (fig. 5) in soil accumulation positions and Entic Cryandepts (fig. 6) on the steeper sites. Whitebark pine-subalpine fir is the major habitat type, occupying over 35,615 ha (88,000 acres). The bedrock-dominated sideslopes have over 3,640 ha (9,000 acres) of mixed forests of whitebark pine, subalpine fir, Engelmann spruce, and lodgepole pine, with subalpine fir-whitebark pine/grousewortleberry as the major habitat type. Soils are Ochrepts consisting of volcanic-ash-influenced silt-loam surface horizons over bedrock.

Weaver and Dale (1974) summarized soil properties for 19 whitebark pine stands found mostly in central and southern Montana. These were thin soils, with a median pH of 5.4 and loam to silt-loam textures with low clay content (average clay, 8.5 percent). These soils have average extractable nutrient amounts of: P, 153; K, 121; Ca, 260; Mg, 72; and Na, 110 (in ppm).

Table 4—Soil properties of whitebark pine habitat types, Northern Region, Forest Service (Pfister and others 1977)

	Habitat type		
	ABLA-PIAL/ VASC	PIAL/ABLA	PIAL
	($n = 22$)	($n = 15$)	($n = 5$)
Mean percentage surface rock	4	13	2
Mean percentage bare soil	1	6	3
Mean pH of upper soil	5	4.9	6
Mean percentage gravel	26	45	25

Figure 4—Whitebark pine is found in Montana and Idaho on soils that are usually low in clay and high in rock fragments.

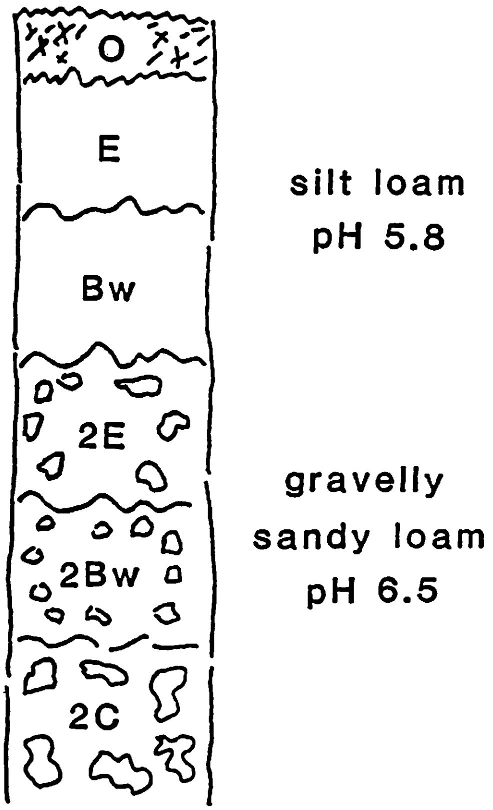


Figure 5—A typical soil profile of whitebark pine stand in the Kootenai National Forest, MT (typical soil classification is an Andic Cryochrept, loamy-skeletal, mixed).

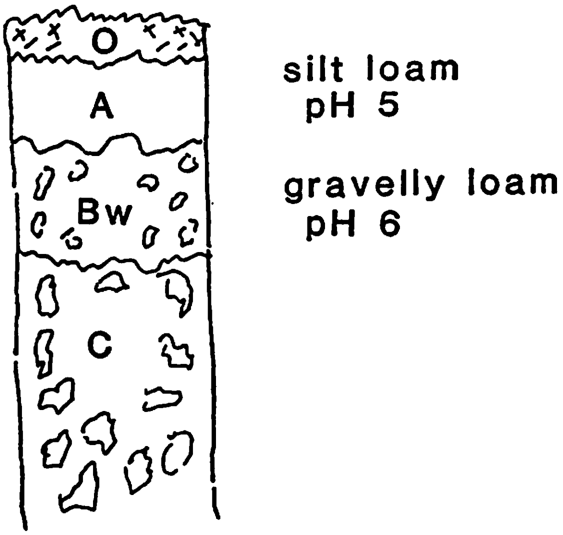


Figure 6—A typical soil profile of an Entic Cryandept.

The Gallatin National Forest soil survey (Davis and Shovic 1984) described soils in three whitebark pine-associated habitat types (table 5) reflecting the variety of bedrock parent materials within that forest. Dystric Cryochrepts (moderately acidic) are found on Precambrian crystalline rock, while volcanic and sedimentary parent materials develop more base-rich and more clay-rich Alfisols (Mollic and Typic Cryoboralfs) and Mollisols (Argillic and Typic). These sites have short growing seasons (most with less than 50 frost-free days) and may be droughty in summer.

The Beaverhead National Forest in southwestern Montana has whitebark pine on both clayey limestone (Mollic Cryoboralfs in the Gravelly Range) and nonlimestone-derived soils. Other whitebark pine sites have acidic soils (Dystric Cryochrepts) formed in glacial till and in residuum from sandstone, gneiss, and granite (Svoboda 1989).

In the Wind River Range at the southeastern limit of whitebark pine (Steele and others 1983), whitebark pine habitat types are found on coarse (sandy loam), rock-fragment-rich, Typic or Lithic Cryochrepts. These soils are developed on parent materials of residuum and glacial till from granitic and gneissic bedrock. Average soil pH's for these three habitat types range from 5.6 to 6.2.

In the Bridger-Teton National Forest south of Jackson, WY, whitebark pine habitat types occupy soils that are developed in slope-wash mantles over residuum and bedrock. Map units are complexes of Alfisols

Table 5—Properties of soils associated with whitebark pine in the Gallatin National Forest, MT (from Montagne and Munn 1980)

	Habitat type ABLA/PIAL	Habitat series ABLA/PIAL	Habitat type groupsDystric Cryochrepts in habitat groups with PIAL
	(*n* = 12)	(*n* = 15)	(*n* = 19)
Bulk density	1.34	1.35	1.3
Percent sand	35	43	54
Percent silt	45	40	39
Percent clay	20	17	11
Available water (cm)	3.8	3.4	2.8
Percent organic matter	2.6	2.8	2.9
pH	6.7	6.4	5.4
Cation exchange capacity (meq/100 g)	20	19	16
N (total percent)	0.07	0.057	0
P (available ppm)	148	120	90
K (extractable ppm)	176	156	155
Ca (extractable meq/100 g)	14	11.1	3.5
Mg (extractable meq/100 g)	1.6	1.3	0.84
Percent base saturation	56	46	26

(Mollic Cryoboralfs), Inceptisols (Typic Cryochrepts), and Mollisols (Typic Cryoborolls), all with a loamy-skeletal, mixed mineralogy. These soils are gravelly to very cobbly loams with pH's mostly near 6, but as high as 8.

SUMMARY

The distribution of whitebark pine at upper timberline is influenced, to some degree, by the geology, geomorphology, and soils of these high-elevation environments. Whitebark pine is found on a variety of geologic parent materials including sedimentary deposits, crystalline metamorphics, and volcanics. Presence of the pine on calcareous parent material appears to be limited to the northern extent of whitebark pine distribution in North America.

The landforms of whitebark pine environments are influenced by mountain building and high-elevation surficial processes. Whitebark pine grows on a variety of slope angles and aspects. Soils under whitebark pine tend to be shallow with minimal horizon development and are classified mainly as Cryochrepts and Cryoboralfs. Whitebark pine soils are predominantly coarse textured with an abundance of coarse fragments and low nutrient levels. These soils will be acidic except in northern areas where whitebark pine is found on calcareous substrates.

The information presented in this paper has been gathered from a review of published whitebark pine studies and through contact with Forest Service personnel. There is minimal information compiled about the soil-related environment of whitebark pine. We hope the summarization presented here will help direct further research on the geology, geomorphology, and soils of whitebark pine.

ACKNOWLEDGMENTS

We wish to thank all of the Forest Service and Soil Conservation Service personnel for their assistance in helping us compile this material. Special thanks are extended to Drs. William Locke and John Montagne for their valuable review comments on the manuscript, to Joan Montagne for cartographic assistance, and to the staff of both the Department of Earth Sciences and the Department of Plant and Soil Sciences at Montana State University for assistance in manuscript preparation.

REFERENCES

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Baig, M. N. 1972. Ecology of timberline vegetation in the Rocky Mountains of Alberta. Calgary, AB: University of Calgary. 446 p. Dissertation.

Bamberg, S. A.; Major, J. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions in Montana. Ecological Monographs. 38: 127-167.

Clausen, J. 1965. Population studies of alpine and subalpine races of conifers and willows in the California high Sierra Nevada. Evolution. 19 (1): 56-58.

Davis, C. E.; Shovic, H. F. 1984. Soil survey of the Gallatin Forest area southwestern Montana. Interim Draft Rep. Bozeman, MT: U.S. Department of Agriculture, Forest Service, Gallatin National Forest. 362 p.

Embleton, C.; King, C. A. M. 1974. Glacial and periglacial geomorphology. London: Edward Arnold Publishers. 608 p.

Habeck, J. R. 1969. A gradient analysis of a timberline zone at Logan Pass, Glacier Park, Montana. Northwest Science. 43: 65-73.

Hansen-Bristow, Katherine J. 1986. Influence of increasing elevation on growth characteristics at timberline. Canadian Journal of Botany. 64: 2517-2523.

Holdorf, Herb. 1989. [Personal communication]. February. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region.

Holland, W. D.; Coen, G. M., eds. 1982. Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol. 1: Summary. Publ. No. M-83-2. Vol. 2: Soil and vegetation resources. Publ. No. SS-82-44. Edmonton, AB: Alberta Institute of Pedology, University of Alberta. 540 p.

Jenny, H. 1941. Factors of soil formation. New York: McGraw-Hill. 281 p.

Kuennen, Lewis. 1989. [Personal communication]. Libby, MT: U.S. Department of Agriculture, Forest Service, Kootenai National Forest.

Lueck, D. 1980. Ecology of *Pinus albicaulis* on Bachelor Butte, Oregon. Corvallis, OR: Oregon State University. 90 p. Thesis.

Martinson, A. H.; Basko, W. J. 1988. Soil survey of the Flathead National Forest area, Montana (draft). Kalispell, MT: U.S. Department of Agriculture, Forest Service.

Montagne, C.; Munn, L. 1980. Statistical summaries of soil characterization and site data, Gallatin National Forest. USFS Contract R1-11-80-30. Bozeman, MT: Montana State University, Plant and Soil Science Department. 365 p.

Pfister, Robert D.; Kovalchik, Bernard L.; Arno, Stephen F.; Presby, Richard C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Price, Larry W. 1972. The periglacial environment, permafrost, and man. Res. Pap. 14. Washington, DC: Association of American Geographers. 88 p.

Price, Larry W. 1981. Mountains and man. Berkeley, CA: University of California. 506 p.

Rapp, A. 1959. Avalanche boulder tongues in Lappland. Geografiska Annaler. 41: 34-48.

Rapp, A. 1960. Recent developments of mountain slopes in Karkevagge and surroundings, northern Scandinavia. Geografiska Annaler. 42: 71-200.

Rapp, A.; Fairbridge, R. W. 1968. Talus fan or cone: scree and cliff debris. In: Fairbridge, R. W., ed. Encyclopedia of geomorphology. New York: Reinhold: 1107-1109.

Reed, Robert M. 1976. Coniferous forest habitat types of the Wind River Mountains, Wyoming. American Midland Nauralist. 95 (1): 159-173.

Steele, Robert; Cooper, Stephan V.; Ondov, David M.; Roberts, David W.; Pfister, Robert D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

Svoboda, Dan. 1989. [Personal communication]. March. Dillon, MT: U.S. Department of Agriculture, Forest Service, Beaverhead National Forest.

Wardle, P. 1974. Alpine timberlines. In: Ives, Jack D.; Barry, Rogar G., eds. Arctic and alpine environments. London: Methuen: 371-402.

Washburn, A. L. 1973. Periglacial processes and environments. London: Edward Arnold. 320 p.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation, and production. American Midland Naturalist. 92: 222-230.

Winthers, E. 1989. [Personal communication]. Jackson, WY: U.S. Department of Agriculture, Forest Service, Bridger-Teton National Forest.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Ray W. Brown)—The soils and geologic materials you described were similar to severely disturbed sites at high elevations (especially in the Beartooth Mountains of Montana and Wyoming and in the Rocky Mountains of Colorado) where *P. albicaulis* is absent. Would you be willing to say, in view of the types of geologic materials and soils that whitebark pine grows on, that this species is early successional and that it may be useful in revegetation as a colonizer?

A.—We agree that the soils and geologic materials upon which whitebark pine is found are very similar to those at disturbed high-elevation sites (they are young, thin, often rocky, and relatively nutrient poor). We further agree that this species may be early successional at these sites, and may even maintain itself as a pure stand at its upper most elevations. Because there is a critical need to revegetate and rehabilitate many severely disturbed sites at high elevations, we recommend a strong emphasis be placed on research aimed toward successful artificial planting and use of whitebark pine as a colonizer in these areas. This effort will require a detailed study of the specific site characteristics where the pine is naturally regenerating, of the seed germination requirements of the pine, and of techniques of planting that will assure establishment and survival.

Q. (from Stephen Harvey)—How about presenting elevation as "elevation below timberline," thereby avoiding latitude problems?

A.—Actual elevational occurrences provide the important perspective of the influences of latitude (radiation budgets and snow influence, in particular) on the geographic extent of whitebark pine. Presenting elevation as "elevation below timberline" would be useful for understanding the local extent of the pine; however, much of the data on the elevation of timberline are either lacking or have been determined by a variety of means. For example, timberline has been defined as the upper unit of trees greater than 2 m tall, as the upper limit of sexual reproduction, and as the extreme upper limit of tree growth. This variety of interpretations leads often to erroneous comparisons of studies.

Q. (from Friedrich-Karl Holtmeier)—With regard to microbial activity and to the pedo-ecological conditions, it would be interesting to learn something about the C/N ratio. Did you investigate this point? If yes, what were the results?

A.—Carbon-nitrogen ratios could provide some interesting insights into soil pedogenic conditions in whitebark pine ecosystems. None of the data available to us, however, included C/N ratios, so we were unable to investigate this relationship. Further research with whitebark pine soils should consider the importance of C/N ratios.

CLIMATES OF SUBALPINE PINE WOODLANDS

T. Weaver

ABSTRACT

The climate of whitebark pine (Pinus albicaulis) *woodlands is generally cold (average daily maxima and minima in January are -2 and -11 °C, respectively) and snowy 1 to 3 m maximum pack) in winter and warm (July average temperatures are 21 and 4 °C, respectively) and dry (July to September precipitation averages 102 mm and individual months can be rain free) in summer. The tree's lower altitudinal limit probabily is set by the competition of trees better able to compete for necessary resources such as light, water, and nutrients. In contrast its upward extension may be limited zonally by summer frosts and locally by desiccation. While the presence of one stone pine species is apparently a good indicator of an equivalent climate for other stone pine species, its presence does not indicate an identical climate and may therefore not indicate an equivalent climate for nonpine species with different climatic requirements.*

INTRODUCTION

Climate is a major determinant of plant (or community) presence, and due to this linkage, particular climax communities suggest particular climates and vice-versa. Extant vegetation and climatic data cannot, however, predict each other perfectly because other factors also affect dominance; these include propagule availability, substrate, biotic (for example, grazer or pathogen) or abiotic (for example, fire or windthrow) disturbance, and time. While they are less than universal, good predictions can be had by stratifying out the confounding factors one by one, that is, by focusing on one biotic region, one substrate, only undisturbed stands, and only mature stands.

Plant or community indicators of climate have been useful historically to new settlers of unexplored, undisturbed, and uninstrumented areas. And they are still useful in areas too complex to instrument economically. Climate-vegetation relationships have been studied at the world and continental levels by ecologists including Clements (1916), Holdridge (1947), Schimper (1903), Walter (1973), Walter and others (1975), and Whittaker (1975). The work is naturally extended to mountain regions where managers wrestle with moderately large land units containing "a world of variation." Work relevant to the Northern Rocky Mountains includes that of Baker (1944), Callison and Harper (1982), Daubenmire (1956), Harper and others (1980), Holdridge (1947), Price and Evans (1937), and Weaver (1980).

This paper describes and compares climates of pine woodlands near timberline. Its objectives are: (1) to characterize the climate of whitebark pine (*Pinus albicaulis*) communities with respect to factors important to the tree and its associates, (2) to compare the climate of whitebark pine woodlands with those of communities immediately above and below them with the object of generating hypotheses to explain the distribution of each type, and (3) to compare the whitebark pine climate with the climates of Eurasian stone pines as a test of the hypothesis that stone pine woodlands indicate similar climates worldwide.

METHODS

The climates of whitebark pine woodlands were characterized by summarizing data (CDOT 1961-70; Leeson 1989; Losleben 1983; and USDC 1951-80) collected in stands representative of the community. The temptation to include data from stations not in whitebark pine woodlands, but in some imagined "whitebark zone," was resisted because the heterogeneity of high-altitude microclimate makes it probable that such data would misrepresent the vegetation studied. While use of a longer record would have been desirable, data were summarized for 10 years, because few stations have a longer record and use of the same record length facilitates comparison of extremes. Ecologists consulted on the choice of stands are listed under "Acknowledgments." Data from Kings Hill, MT, Crater Lake, OR, and Old Glory Mountain, BC, were complete. Temperature data were unavailable from Ellery Lake; thus I violated my approach and substituted temperature data from a site (White Mountain I = Crooked Creek [3,123 m]) without whitebark pine, but with similar latitude, longitude, and altitude, and a more continental climate. Data from the Sunshine Station at Banff were gathered for avalanche forecasting, and only those from 1978 were sufficiently complete for my application.

Whitebark pine climates are contrasted with those of adjacent vegetation types. Instrumented subalpine fir environments with occasional or seral whitebark pine appear at Yellowstone Lake, WY, and Cooke City, MT (Despain and Rankin 1989). Alpine stations would ideally be paired with whitebark woodland sites from the same region—as the Lake or Cooke and Kings Hill sites almost are—but no data from alpine stations other than Niwot Ridge, CO, and White Mountain, CA, were available.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

T. Weaver is Plant Ecologist, Department of Biology, Montana State University, Bozeman, MT 59717.

While White Mountain II (Barcroft, 3,837 m) temperature data probably represent conditions above whitebark krumm- holz reasonably, the White Mountains are far drier than mountains usually containing whitebark pine. Data from Niwot Ridge, CO, undoubtedly represent conditions above whitebark krummholz better (Billings 1989).

Climates of environments dominated by closely related stone pines (Lanner, this proceedings; Mirov 1967) were compared with those of whitebark pine by summarizing data from stations in those types. Decade-long data sets from three *Pinus cembra* sites were supplied by Tranquillini (1989). Since *Pinus sibirica* and *Pinus pumila* occupy more homogeneous "plains areas," I felt reasonably confident in summarizing data from stations chosen with the help of Critchfield and Little (1966), Lieth (1988), and Mirov (1967). Stations used to represent *Pinus sibirica* were Serov (24), Surgut (28), Kolpasevo (30), Jenisejsk (32), Irkutsk (34), Tura (41), Kirensk (47), and Krasnojarsk (73). Stations used to represent *Pinus pumila* were Anadyr (13), Apuka (14), Petropavlovsk-Kamcatskij (37), Vitujsk (48), Jakutsk (49), Verchojansk (51), Ochotsk (53), and Zyranka (54). The numbers following each place name indicate the station number in Muller's (1982) compendium of climatic data.

Some climatic parameters were studied as indices of "killing conditions." Absolute maximum and minimum temperatures and absolute maximum and minimum monthly precipitation recorded in a decade suggest long-term values, but these undoubtedly underestimate extremes experienced by long-lived trees (Gumbel 1954).

Other parameters are reported as indices of average conditions likely to have a greater influence on the performance (for example, photosynthesis, respiration growth, and seed yield) of established trees: mean monthly maximum and minimum temperatures, mean annual precipitation, and mean summer (July to September) precipitation. While data from a 10-year record are minimal for estimating extremes, a decade of observations should reasonably represent average conditions.

RESULTS

Data for describing extreme conditions in the climates of three whitebark pine woodlands (Ellery Lake, CA, Crater Lake, OR, and Kings Hill, MT) and two krummholz stands (Old Glory, BC, and Banff, AB) are presented in table 1. The seasonal progression of temperature and precipitation data for one woodland (Kings Hill) and one timberline (Old Glory) site are presented graphically in figures 1 and 2.

Data comparing the climates of sites in which whitebark pine woodlands are climax with forest sites below them and alpine tundra sites above them also appear in table 1. Data from stands representative of subalpine fir forests below the whitebark pine zone (Cooke City, MT, subalpine fir with occasional and seral whitebark pine), whitebark pine woodland (Kings Hill, MT), krummholz (Old Glory Mountain, BC), and alpine tundra (Niwot Ridge, CO) above the range of the tree are compared in figures 1 and 2.

Data comparing the climates of *Pinus albicaulis* (whitebark pine), *Pinus cembra*, *Pinus sibirica*, and *Pinus pumila* appear in table 2.

THE CLIMATE OF WHITEBARK PINE WOODLANDS

The climate of woodlands where whitebark pine dominates (latitude 37° to 47° N.) is interpolated from data gathered in the Sierra (Ellery Lake, CA), the Cascades (Crater Lake, OR), and the Rocky Mountains (Kings Hill, MT). I summarize the data from all three stands with a description (following paragraph) organized around the passage of seasons in a whitebark pine woodland; please refer to table 1 to develop a feeling for regional variation in the woodland climate.

The average January day warms from a nightly low of –11 °C (–14 to –8 °C) to a high of –1 °C (–3 to 1 °C). The snow pack maximizes at 1 to 3 m in February to April and shields roots, decomposers, and small animals from hard frosts. Melt-out proceeds rapidly in May, when swelling buds and newly exposed organisms may experience frosts as cold as –10 to –19 °C. While the average July day warms from a low of 4 °C (3 to 5 °C) to a high of 21 °C (19 to 22 °C), the probability of a frost (0 °C) is still about 7 percent. Because the coarse soils of whitebark pine sites are usually more than saturated by snow melting in May to June, large differences in winter snowpack between sites or seasons are dissipated by runoff and probably go unexpressed in summer production. Production above a minimum set by the site's soil water holding capacity may be supported by July to September rains whose total deposits range from 25 mm to 180 mm (average 92 mm). The rain is deposited in five to 11 monthly showers, of which over half are so small (less than 2.5 mm) that they are probably useful only to insects and nonvascular plants (Weaver 1985). While snow showers occur in September and October, snow does not accumulate permanently until near the first of November.

CHANGES IN CLIMATE ACROSS THE WHITEBARK PINE ZONE

In the Northern Rocky Mountains, USA, whitebark pine is absent from foothill grasslands, Douglas-fir (*Pseudotsuga menziesii*) forests, and the lower part of a subalpine zone largely dominated by fir (*Abies lasiocarpa* at climax) and pine (*P. contorta* at subclimax). The species appears as an occasional and seral tree in the upper half of the subalpine zone, dominates woodlands just below timberline, is often important in krummholz, and is absent again in the alpine tundra. One would ideally describe changes in climate along this altitudinal-vegetational gradient by summarizing data from weather stations arranged along two to three geographically well-separated transects across the gradient (Marr 1961; Price and Evans 1937). In the absence of such data, changes in climate across the gradient are demonstrated on a synthetic gradient, that is, with graphs comparing, one by

Table 1—Climate[1] of high-altitude environmental types of the western United States

	Environmental type and location[2]								
	High-elevation fir		**WB woodland**			**WB timberline**		**Alpine**	
	Lake	**Cooke**	**Ellery**	**Crater**	**Kings**	**Glory**	**Sunshine**	**Niwot**	**White**
	WY	**MT**	**CA**	**OR**	**MT**	**BC**	**AB**	**CO**	**CA**
Temperature (°C)									
Abs. minimum	–44	–39	–32	–29	–38	–38		–38	–37
Abs. May min	–19	–16	–19	–13	–10	–13		–26	–17
Jan. mean min	–18	–16	–13	– 8	–14	–12	–21	–17	–12
Jan. mean max	–5	–6	1	1	–3	–7	–15	–10	– 5
July mean min	4	3	3	4	5	6	1	4	2
July mean max	22	23	19	20	22	14	17	12	12
Abs. max	33	29	26	32	31	27	30	21	20
July frost days	4	3	6	4	2	3		1	6
Precipitation[3] (mm)									
Mean annual	559	672	604	1,611	755	757		1,059	497
July–Sept.	130	159	68	89	120	130		137	86
Driest summer month	7	9	0	0	15	1		1	0
Wettest summer month	127	118	87	136	90	150		95	114
Summer shrs >0.02	11	11	5	6	11	10	10	11	4
Summer shrs >2.54	6	7	2	4	7	5	5	6	2
Snow[4]									
Months >0 cm		7		8	7	7			7
>30 cm		4		6	6	5			5
>50 cm		4		6	4	5			4
Mean max (cm)		102F		290M	135M	173A			81M
Location									
Latitude (°N)	44	45	37	42	46	49	51	40	37
Longitude (°W)	110	109	119	122	110	119	115	105	118
Altitude (ft)	7,700	7,553	9,545	6,475	7,300	7,700	7,042	12,165	12,470
(m)	2,369	2,324	2,937	1,992	2,246	2,369	2,167	3,743	3,837
Decade	61-70	70-79	71-80	61-70	51-60	61-70	1978	71-80	61-70

[1] Climatic descriptions are based on a decade specified near the bottom of the table; standard error of the means would be smaller and extremes larger if a longer period had been used. Because summer data from Sunshine are available for 1978 only, only 1978 data are reported.

[2] Stations are Yellowstone Lake, WY, Cooke City, MT, Ellery Lake, CA, and White Mountain I, CA, Crater Lake, OR, King's Hill, MT, Old Glory Mountain, BC, Sunshine-Banff, AB, Niwot, CO, and White Mountain II, CA. Because no temperature data were recorded at Ellery Lake, temperature data were taken from a White Mountain Station with a similar latitude (37), longitude (108), and altitude (3,123 m).

[3] Precipitation (mm) is reported for the entire year, the dry season (July to September), the driest summer month in the decade, and the wettest summer month in the decade. The average number of showers (>2.5 mm = 0.1 inch and >0.025 mm = 0.01 inch) is reported for the June to September period.

[4] The duration of snow pack greater than 0 cm, 30 cm, and 50 cm is reported along with the maximum depth reported and its month (February, March, April).

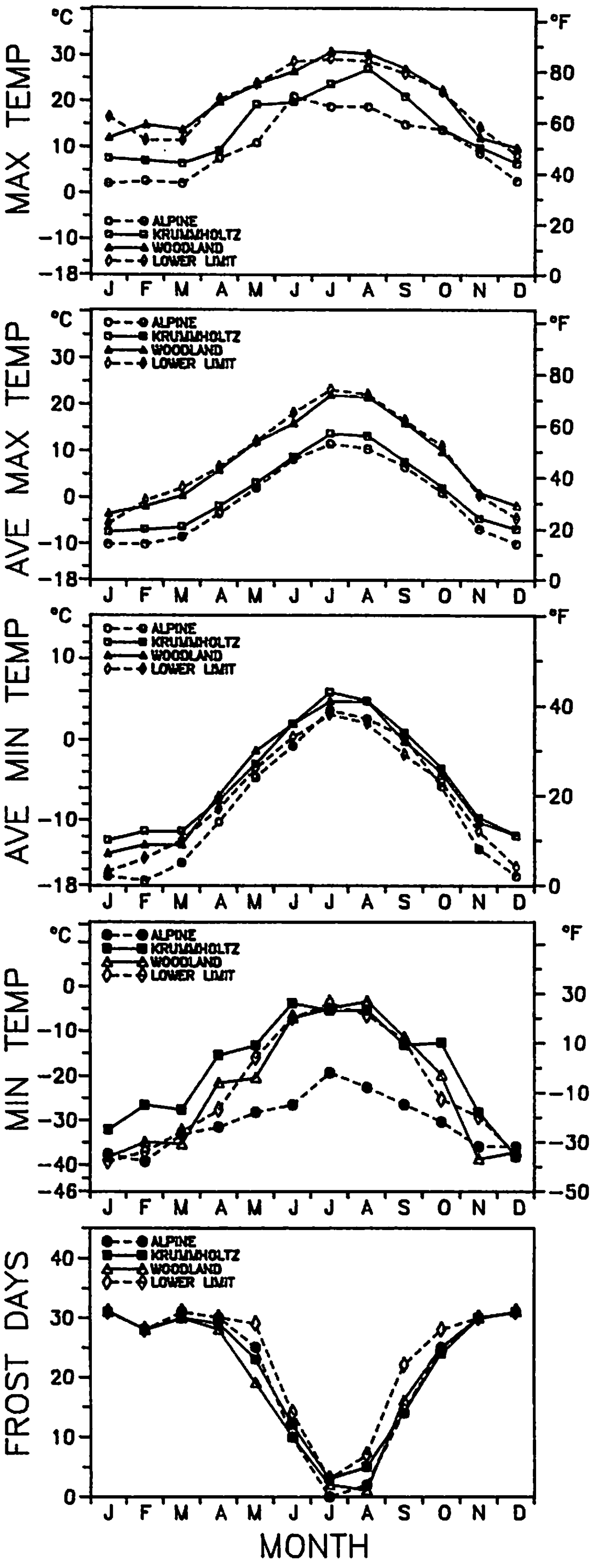


Figure 1—Comparison of temperature data from tundra, timberline, woodland, and high subalpine forests. Monthly data are summarized over a 10-year period and plotted against time. The data plotted come from the Niwot Ridge, Old Glory Mountain, King's Hill, and Cooke City weather stations; data from other comparable stations appear in table 1.

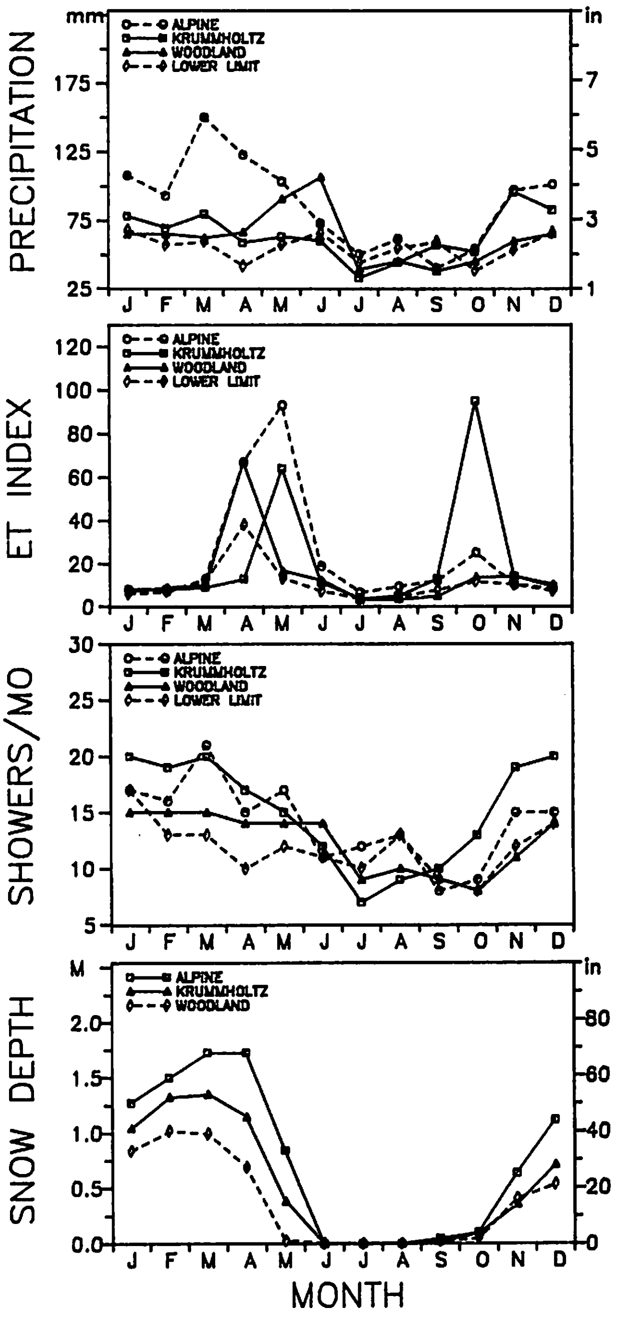


Figure 2—Comparison of precipitation data from tundra, timberline, woodland, and high subalpine forests. Monthly data are summarized over a 10-year period and plotted against time. A P/T index value of 1 indicates a relatively droughty season (Daubenmire 1956; Walter and others 1975); no alpine point falls below 5; timberline and fir types have 2 near-droughty (I = 2 to 5) months, and the woodland had 3 near-droughty months. The data plotted come from the Niwot Ridge, Old Glory Mountain, King's Hill, and Cooke City weather stations; data from other comparable stations appear in table 1.

Table 2—Climate[1] of stone pine communities of North America and Eurasia

	Species and location			
	P. albicaulis **North America**	***P. cembra*** **Euro-Alps**	***P. sibirica*** **Siberia**	***P. pumila*** **N. China**
Temperature[2] (°C)				
Abs. min	–34 ± 2	–23 ± 1	–55 ± 2	–52 ± 4
May min	–16 ± 2	–10 ± 1	–18 ± 2	–21 ± 2
Jan. mean min	–14 ± 2	–8 ± 0	–27 ± 2	–30 ± 8
Jan. mean max	–5 ± 3	–1 ± 1	–19 ± 2	–24 ± 9
July mean min	4 ± 1	5 ± 1	12 ± 1	8 ± 0
July mean max	18 ± 1	14 ± 1	21 ± 1	15 ± 2
Abs. max	29 ± 1	27 ± 2	37 ± 1	33 ± 1
Precipitation[3] (mm)				
Total	[2]931 ± 229	939 ± 9	432 ± 21	[2]407 ± 137
Summer	102 ± 14	323 ± 36	187 ± 11	143 ± 43
Summer dry month	4 ± 4	45 ± 16	8 ± 2	4 ± 2
Summer wet month	116 ± 16	214 ± 15	181 ± 8	165 ± 25
June-Sept. showers (No.)	8 ± 1		14 ± 1	1 ± 1

[1] Values presented are mean ± one standard error. Sample size is 4 for *P. albicaulis* (except average max and mins for January and July, *n* = 5), 3 for *P. cembra*, 8 for *P. sibirica*, except for average max and mins for January and July, *n* = 4), and 8 for *P. pumila* (except for average max and mins for January and July, *n* = 4).

[2] Temperature data (°C) are the mean ± one standard error. Absolute temperatures are recorded for 10 years in *P. albicaulis* and *P. cembra*; records for the Asian pines are longer (and unspecified).

[3] Precipitation (mm) data are total (sum of all months), summer (July, August, plus September), driest summer month (July to September) recorded, wettest summer month (July to September) recorded, and average number of showers in June toSeptember. High variances in total precipitation for *P. albicaulis* and *P. pumila* are reduced to 705 ± 51 mm and 274 ± 37 mm by omission of the Crater Lake and Petropavlovsk stations, respectively.

one, the annual course of nine factors at Cooke City, MT (subalpine fir with seral whitebark), Kings Hill, MT (woodland), Old Glory Mountain, BC (treeline = upper krummholz), and Niwot, CO (alpine). The reader should refer to table 1 to become convinced that the stations presented do reasonably represent other stations in their zones and, thus, that the comparison of data from these sites accurately represents climatic changes that would occur on a gradient across a whitebark pine woodland at any single location.

In the following discussion the climates of high-altitude vegetation zones will be related primarily to whitebark pine performance. A reader wishing to relate the data to other organisms or phenomena can do so by using community characteristics (for example, seral whitebark, whitebark woodland, whitebark krummholz, or above whitebark's range) as indicators of the position of a different phenomenon (for example, performance of another organism) in the climatic gradient.

Whitebark pine is most likely excluded from low-altitude grasslands and forests by high temperatures or scarcity of water. While temperatures at lower altitudes are warmer [average July maxima are 28, 26, 25, and 20 °C in foothill grasslands, Douglas-fir forests, low subalpine fir forests, and whitebark woodlands, respectively (Weaver 1980) (table 1)], high seedling photosynthesis at temperatures as high as 30 to 35 °C (Jacobs and Weaver, this proceedings) as well as the survival of specimen trees in lawns in the foothill grassland zone argue against temperature control. Lesser precipitation [380, 580, and 755 mm in foothill grasslands, Douglas-fir forests, and whitebark woodlands (Weaver 1980 and table 1)] and longer droughts [drought indices of 1.8, 0.3, and 0.0, respectively (Weaver 1980)] probably exclude whitebark pine from the grassland and Douglas-fir zones.

It seems unlikely that whitebark pine is excluded from lower parts of the subalpine fir zone by drought, since warmer (25 versus 20 °C) and perhaps rainier (82 versus 60 to 75 mm) conditions in the lower subalpine zone compensate to produce an equally drought-free condition (0.0 month drought index, Weaver 1980). If drought stresses and substrates are, in fact, similar, it seems likely that the lower limit of whitebark pine forests is set by competition rather than by climate (Arno and Weaver, this proceedings).

We reason, from the preceding, that the lower limit of whitebark dominance is set by conditions that limit the performance of its competitors upslope. The expectation that low temperatures probably eliminate whitebark competitors from the higher subalpine woodland zone is supported by the observation that whitebark pine and spruce range farther down into cold-air pockets than do lodgepole pine or subalpine fir. Two climatic differences between whitebark woodlands and subalpine forests below them seem contrary to this expectation: average minimum temperatures are higher and frost days are fewer in the higher altitude forest (fig. 1). I believe that the conclusion suggested—that whitebark woodlands require warm nights—is spurious and that the data result from a correlation between the presence of the tree, coincidental climatic data, and topographic-edaphic conditions which actually control locally. In the high subalpine zone the tree often grows on steep, rocky ridges from which cold air drains (yielding the warm night condition) and on which excessive drainage occurs (causing drought better tolerated by whitebark pine than subalpine fir). A scan of the other climatic data available (figs. 1 and 2) shows no differences—in either "killing factors" (absolute maximum or minimum temperatures) or factors likely to affect growth and competitiveness (average maximum temperatures, average mean temperatures, or drought months)—between the climates of climax whitebark woodlands and subjacent subalpine fir forests with whitebark subclimates.

Above the whitebark pine woodlands the tree gives way, via krummholz, to alpine tundra. The low stature of tundra vegetation makes the possibility of its competitive domination of forest trees seem unlikely. One therefore hypothesizes that one or more physical factors control tree distribution (Arno 1984; Tranquillini 1979) and looks to climatic data to clarify some possibilities. First, temperature effects. On our synthetic temperature gradient the small drop—relative to the temperature range observed within whitebark pine communities—in absolute high, average maximum, and average minimum temperatures from whitebark to alpine sites is so small that control by high or average temperatures (heat sums) seems unlikely (fig. 1). The far larger drop in absolute lows across the woodland-alpine gradient—and especially so in summer—suggests that growing season frosts could be an important factor in the final elimination of whitebark from high-altitude sites (fig. 1). This conclusion is supported by the absence of whitebark pine from the depths of frost pockets. As to mechanism, Tranquillini (1979) argued that, while early summer frosts may deform them, trees are more likely killed by winter desiccation, desiccation due to a cuticle inadequacy attributed to a short growing season. The climatic feature controlling cuticle development may be frosting (correlated with lows) rather than inadequate heat sums (correlated with averages) since opening and closing of the photosynthetic season is largely induced by frosts (Tranquillini 1979). Second, neither precipitation nor a drought index that ignores wind flow, become more unfavorable as one ascends from whitebark pine woodland to the tundra above. Third, other factors—such as high wind [contributing to desiccation through blasting and water transports (Hadley and Smith 1986; 1987)] and bleaching radiation (Tranquillini 1979)—for which we add no data, may contribute, in concert, to the disappearance of trees. Fourth, whether one factor or several acting in concert prohibit trees, the fact that timberline vegetation changes faster on the altitudinal gradient than any postulated climatic factor is nicely explained by the observation that, until the canopy begins to open, trees provide mutual shelter (Tranquillini 1979). This explanation applies to all factors from frost damage to frost-free period, degree days, wind blasting, desiccation, UV damage, or other factors considered by Tranquillini (1979) and Arno (1984).

Snow data (fig. 2) show that snow depth and duration generally increase with altitude. While the shielding of roots from hard frosts is probably important to trees, I doubt that the small differences observed control tree distribution. On the other hand, deep, long-lying snow undoubtedly benefits low organisms (for example, seedlings including those of whitebark pine, low plants, decomposers, and small animals) by shielding them from frost or predators—and may hinder them by crushing or supporting snow mold. It simultaneously affects large animals by covering their foodstuffs. Benefits and disbenefits are magnified on wind scour and wind deposit sites both above and below timberline.

Rain shower numbers in the Rockies range from 20 per month in winter to 10 per month in summer (fig. 2); summer showers are half as common on the Sierra-Cascade axis (table 1). Summer shower numbers vary little with altitude (Weaver 1985) and vary little between high-altitude types. About half of the showers at this altitude deposit less than 2.5 mm (table 1). While showers less than 5 mm may be important to mosses, lichens, and small animals ranging from insects to squirrels, their shallow penetration and rapid evaporation from both plants and soil render them largely ineffective to most vascular plants (Weaver 1985).

STONE PINE CLIMATE

Two stone pines (*Pinus sibirica* and *Pinus pumila*) dominate vast areas in northern Eurasia and two stone pines appear in high-altitude woodlands in the Alps (*Pinus cembra*) and the Rocky Mountains (*Pinus albicaulis*) (Crichfield and Little 1966). Their close relationships and ecological similarities (Mirov 1967) invite comparison of their climates as a test of the hypothesis that similar communities indicate similar climates.

While winter temperatures are especially low in stone pine communities of northern Eurasia, summer temperatures are similar in areas dominated by all four trees. Since the trees are dormant at midwinter, transplanted *Pinus albicaulis* and *Pinus cembra*, which normally experience absolute lows of only –21 to –38 °C, might tolerate the –34 to –67 °C lows experienced by their near-relatives of northern Eurasia. Frost danger is much more similar during the growing season; for example, at a hypothetical bud break in May absolute lows are all in the –10 to –21 °C range. Absolute highs are higher on Eurasian plains than in subalpine woodlands (table 2). Average maximum temperatures in July are slightly warmer in pine communities of the Eurasian plains (15 and 21 °C) than in pine communities of more southerly mountains (14 and 18 °C). Average minimum temperatures in July are also higher on the Eurasian plains (8 and 12 °C) than in subalpine woodlands (4 and 5 °C).

Although precipitation regimes differ considerably among stone pine habitats, the water regimes are apparently equivalent. In contrast to whitebark pine's winter wet/summer dry climate, all the Eurasian pines experience a winter dry/summer wet climate. In all four regions, however, snow accumulates over winter, melting snow saturates the soil, and excesses run off. Thus, wherever soil water-holding and drainage properties are similar, runoff should eliminate any effect of the large differences in October-June precipitation (603 to 829 mm for *Pinus albicaulis*, 616 mm for *Pinus cembra*, 245 mm for

Pinus sibirica, and 264 mm for *Pinus pumila*) and provide similar starting conditions. Stored soil water must provide survival water during occasional summer months in which rainfall provides as little as 0 to 13 mm, regardless of the region and community type. To the extent that moss-lichen-insect biotas are controlled by temperature and superficial moisture (numbers of June to September showers) these biota may differ little between stone pine communities.

Comparison of production data among these forests should suggest the degree to which growth—as opposed to survival—is limited by water availability. While growing season water availability differs considerably among regions (July to September precipitation for *Pinus albicaulis*, *Pinus pumila*, *Pinus sibirica*, and *Pinus cembra* is 102 mm, 143 mm, 187 mm, and 323 mm, respectively), there is probably little difference in other factors likely to control growth. Temperatures are similar (table 2). Nutrient availabilities are unlikely to differ systematically among regions so large. And underlying genetics (as suggested by taxonomic status) are similar.

I conclude that, while stone pine woodlands in one region indicate very similar climatic conditions, the degree of climatic similarity may decline with increases in the distance between the regions considered. Climatic differences increase as one compares stone pine climates in Montana with others in Montana, Oregon, and Eurasia. The climates appear, however, to be equivalent for stone pines; that is, effective growing season temperatures and water availabilities seem so similar as to permit success in transplanting. These equivalences should apply to other species with similar requirements, but they deteriorate for very different organisms: a person moving from a stone pine community in Montana to one in Eurasia will have to buy a warmer coat and a bigger umbrella. Indicator organisms are, then, good indicators of equivalencies for their near relatives, but relatively poorer indicators of conditions needed for the success of increasingly different species.

ACKNOWLEDGMENTS

I am grateful to ecologists who discussed the stone pine climates with me and helped me choose weather stations representative of whitebark pine forests, vegetation above and below whitebark pine forests, and other stone pine forests. University, USDA Forest Service (USFS), and USDI National Park Service (NPS) consultants from North America included S. Arno (USFS, Missoula, MT), P. Acuff (University of Alberta, Edmonton), M. Barbour and D. Ryerson (University of California, Davis), D. Billings (Duke University, Durham, NC), J. Bock (University of Colorado, Boulder), D. Despain and R. Rankin (NPS, Mammoth, WY), J. Halfpenny (University of Colorado, Boulder), K. Harper (Brigham Young University, Provo, UT), J. Jarvis (NPS, Sedro Wooley, WA), C. Johnson (USFS, Enterprise, OR), D. Knight (University of Wyoming, Laramie), B. Leeson (Parks Canada, Calgary, AB), J. Milestone (Crater Lake, OR), W. Moir (USFS, Fort Collins, CO), N. Stephenson (NPS, Three Rivers, CA), and J. Wagtendonk (NPS, El Portal, CA). Consultants from Europe included H. Lieth (University of Onsabrück, Germany), K. Holtmeier (University of Munster, Germany), and W. Tranquillini (University of Innsbruck, Austria). I am grateful to S. Harvey and J. Jacobs for constructing the graphs and to S. Arno, D. Ryerson, and N. Stephenson for reviewing an earlier draft of the paper.

REFERENCES

Arno, S. 1984. Timberline: mountain and arctic forest frontiers. Seattle, WA: The Mountaineers. 304 p.

Baker, F. 1944. Mountain climates of the western United States. Ecological Monographs. 14: 223-254.

Billings, D. 1989. [Personal communication.] Durham, NC: Duke University.

Callison, J.; Harper, K. 1982. Temperature in relation to elevation in the Uinta mountains, Utah. Encyclia. 59: 21-27.

Canadian Department of Transport. 1961-1970. Monthly record of meterological measurements in Canada. Toronto, ON: Canadian Department of Transport, Meterological Branch.

Clements, F. 1916. Plant succession: an analysis of the development of vegetation. Publ. 242. Washington, DC: Carnegie Institute of Washington. 512 p.

Crichfield, W.; Little, E. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.

Daubenmire, R. 1956. Climate as a determinant of vegetation distribution in eastern Washington and northern Idaho. Ecological Monographs. 26: 131-154.

Despain, D; Rankin, R. 1989. [Personal communication]. October. Yellowstone National Park, Mammoth, WY.

Gumbel, E. 1954. Statistical theory of extreme values and some practical applications. National Bureau of Standards Applied Mathematics Series #33. Washington, DC: U.S. Government Printing Office. 51 p.

Hadley, J.; Smith, W. 1986. Wind effects on needles of timberline conifers: seasonal influence on mortality. Ecology. 67: 12-19.

Hadley, J.; Smith, W. 1987. Influence of krummholz mat microclimate on needle physiology and survival. Oecologia. 73: 82-90.

Harper, K.; Woodward, R.; McKnight, K. 1980. Interrelationships among precipitation, vegetation, and streamflow in the Uinta Mountains, Utah. Encyclia. 57: 58-86.

Holdridge, L. 1947. Determination of world plant formations from simple climatic data. Science. 105: 367-368.

Leeson, B. 1989. Banff meterological records from several winters and one summer, 1978. Unpublished records on file at: Parks Canada, Natural History Research, Calgary, AB.

Lieth, H. 1988. [Personal communication]. December. Onsabrück, West Germany: University of Onsabrück.

Losleben, M. 1983. Climatological data from Niwot Ridge, East Slope, Front Range, Colorado (1970-1982). Boulder, CO: University of Colorado, Institute of Arctic and Alpine Research. 193 p.

Marr, J. 1961. Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Studies in Biology. 8: 1-134.

Mirov, N. 1967. The genus *Pinus*. New York: Ronald Press. 602 p.
Muller, M. 1982. Selected climatic data for a global set of standard stations for vegetation science. The Hague: Junk. 306 p.
Price, R.; Evans, R. 1937. Climate of the west front of the Wasatch Plateau in central Utah. Monthly Weather Review. 65: 291-301.
Schimper, A. 1903. Plant geography on a physiological basis. Oxford: Clarendon Press.
Tranquillini, W. 1979. Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European Alps. Berlin: Springer-Verlag. 137 p.
Tranquillini, W. 1989. [Personal communication]. January. Innsbruck, Austria: University of Innsbruck.
U.S. Department of Commerce. 1951-1980. Climatological data. Washington, DC: U.S. Department of Commerce.
Walter, H. 1973. Vegetation of the earth in relation to climate and ecophysiological conditions. New York: Springer-Verlag. 237 p.
Walter, H.; Harnickell, E.; Mueller-Dombois, D. 1975. Climate-diagram maps of the individual continents and the ecological climatic regions of the earth. Berlin: Springer-Verlag. 36 p. and 9 maps.
Weaver, T. 1980. Climates of vegetation types of the Northern Rocky Mountains and adjacent plains. American Midland Naturalist. 103: 392-398.
Weaver, T. 1985. Summer showers: their sizes and interception by surface soils. American Midland Naturalist. 114: 409-413.
Whittaker, R. 1975. Communities and ecosystems. New York: MacMillan. 385 p.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from R. Brown)—Is summer or winter desiccation more limiting to the distribution of whitebark pine?

A.—My study is correlative and therefore generates hypotheses rather than testing them. Altitudinally, I speculate that whitebark is excluded from grasslands, but not from subalpine forests and alpine tundra, by summer drought. Tranquillini (1979) argued that the upper limit of *Pinus cembra* is set by winter desiccation, possibly because of inadequate cuticle; a similar explanation for whitebark's distribution is not inconsistent with the data presented. Geographically, I speculate that whitebark's dominance declines to the north and west when more water-demanding competitors are supported, to the east when mountain sites with climates cool enough to exclude competitors or moist enough to support the tree disappear, and to the south when high-altitude sites become too dry, probably in the summer (Arno and Weaver, this proceedings).

Q. (from L. McHargue)—Is summer rainfall important to whitebark pine and, if so, would you expect especially resistant ecotypes in the summer-dry Sierra Nevada?

A.—Whitebark must maintain a minimal water content in the summer. Its dominance is greatest in summer-dry regions, and in these regions it must depend for survival water on soil water stored during the winter. Near and north of the Canadian border (Arno and Weaver, this proceedings) summer rainfall becomes more plentiful; since ecotypes (ecoclines) develop along most environmental gradients, I would expect some ecotypic variation with respect to late-season activity across the north-south range of the tree.

Q. (from M. Merigliano)—Might the near-absence of whitebark pine on interior Great Basin ranges—as opposed to the Cascade-Sierra axis—be due to the clear, sunny rather than more overcast winter days?

A.—Tranquillini suggests that upper timberline is controlled by winter desiccation. On this basis, one might expect the timberline in a region with clear, sunny winter days to be lower than that of a cloudier region. If timberline were pushed down to levels with summer warmth great enough to support competing trees, whitebark might be squeezed out.

Q. (from R. Krebill)—You have described the present climates of sites now occupied by whitebark pine. Are those climates the same as the climates the stands established in? Are whitebark stands "in sync" with today's environment?

A.—Weather varies from day to day and year to year; climate (average weather) varies from decade to decade and century to century (consider the little ice age, the hypsithermal, and the Wisconsin glaciation); and the difference between the two depends on the life span of the observer. In the Northern Rocky Mountains, I see reproduction throughout the altitudinal range of whitebark pine and I presume it exists throughout the geographic range of the species. If so, from the viewpoint of whitebark pine, the regional climate has not changed significantly and the tree is "in sync." Global warming of 1 to 5 °C, predicted by some (not all) current climatic models, may be comparable to that which occurred during the hypsithermal, and while it might not drive the tree from the region, it would surely induce a redistribution.

USING WIND-DEFORMED CONIFERS TO MEASURE WIND PATTERNS IN ALPINE TRANSITION AT GLEES

Robert C. Musselman
Gene L. Wooldridge
Douglas G. Fox
Bernadette H. Connell

ABSTRACT

The Glacier Lakes Ecosystem Experiments Site (GLEES) is a high-elevation ecosystem in the Snowy Range west of Laramie, WY, that is perceived to be highly sensitive to changes in chemical and physical climate. Deposition of atmospheric chemicals to this ecosystem is, in part, governed by the wind pattern. The GLEES has numerous wind-swept areas where the coniferous vegetation growth pattern is characteristically wind deformed or krummholz. Studies conducted in 1988 determined direction and degree of wind deformation of Engelmann spruce (Picea engelmannii) *and subalpine fir* (Abies lasiocarpa) *trees. Where both species occurred together, their wind deformation was similar. Limber pine* (Pinus flexilis) *occurred as scattered, isolated individuals on exposed ridges with extensive deformation, but because of its sparse occurrence was not useful in determining windspeed and direction in the GLEES. Engelmann spruce and subalpine fir tree deformation patterns were used to determine wind fields, which were compared with measured meteorological data at GLEES.*

INTRODUCTION

In recent years, forest managers have been faced with questions concerning the impact on sensitive ecosystems of atmospheric deposition of air pollutants from new or proposed point sources. Air quality legislation, written to prevent significant deterioration of present air quality in Class I or wilderness areas, requires forest managers to determine potential impact of pollutant sources on the ecosystems they manage. Alpine and subalpine wilderness ecosystems are thought to be particularly sensitive to increased atmospheric deposition. The existence of these high-elevation ecosystems is already fragile; any additional stress might have a large negative impact on their growth and survival. Few data are available to determine the potential effects of increased atmospheric deposition on such sensitive ecosystems.

A study area has been established in southeastern Wyoming to examine the effects of atmospheric deposition on alpine and subalpine ecosystems. The Glacier Lakes Ecosystem Experiments Site (GLEES) is a 200-ha alpine and subalpine watershed on the Medicine Bow National Forest, about 70 km west of Laramie, WY. The following site characteristics make it ideal for studying the effects of atmospheric deposition on wilderness ecosystems.

1. High elevation (3,400 m) typical of many western U.S. wilderness ecosystems
2. Management to preserve its natural state, but not a statutory wilderness area restricting research use
3. Exposed, slowly weathering bedrock, with shallow immature soils having low base saturation
4. Habitats similar to western wilderness ecosystems, with alpine and subalpine types dominated by spruce-fir; wind deformed spruce, fir, and willow; extensive meadow; and cushion plants
5. Low pollution impact at present, yet ecosystem is sensitive to any additional stress such as atmospheric pollutants
6. Lakes with low acid neutralizing capacity
7. Short growing seasons with cool temperatures and summer frosts
8. Deep snowpack that accumulates atmospheric pollutants
9. Complex terrain with rapid changes in topography
10. Persistent, high winds

Windspeed and wind direction are climatological components that exert major influence on alpine and subalpine ecosystems. Winds interact with terrain, producing local changes in wind direction, turbulent zones, and windspeeds over and through the surface vegetation. They determine precipitation patterns, snow distribution, snow pack accumulation, and resultant vegetation type and growth form. Atmospheric deposition will likely be greatest in areas where windspeeds are low, and turbulence is enhanced. Low windspeed allows particulates to settle. With greater turbulence, gaseous pollutants have greater potential for absorption or plant uptake, due to increased vertical mixing.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT., March 29-31, 1989.

Robert C. Musselman is Research Plant Physiologist; Gene L. Wooldridge is Meteorologist; Douglas G. Fox is Chief Meteorologist; and Bernadette H. Connell is Research Forester, all with the Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Fort Collins, CO.

Meteorological data on wind direction and speed are expensive and difficult to obtain at remote, high-elevation sites. A surrogate for wind instrumentation has been the use of asymmetric tree deformation to indicate direction and speed of prevailing wind. Direction of wind is indicated by compass direction of the deformation. Speed is calculated from empirical equations derived from actual windspeed data and amount of tree deformation in areas where both weather monitoring and tree deformation data are available.

The relationship between windspeed and deformation varies with tree species. Some species are more susceptible to deformation than others. Deformation is caused by ice crystal abrasion and desiccation of leaf bud and foliage tissue on the windward side of the tree (Holtmeier 1980). This tissue is killed, causing a slow development of surviving buds and branches on the lee side of the tree. Such selective upwind mortality leads to growth and development of branches and foliage primarily on the protected, lee side of the tree. As branch development and growth become dominant on the lee side of the tree, the tree becomes asymmetric. The degree of asymmetry or deformation is related to the speed of the wind. Season of high wind is also important, since plant tissue differs in sensitivity to wind abrasion with stage of development. Data from GLEES indicate that wind direction varies little with season. Although windspeeds are highest during the winter and spring months, winds are still strong during sensitive stages of plant growth. Measurement of amount of tree deformation also will give a long-term integrated estimate of snow depth at individual tree locations, as indicated by snow cover effects on tree growth and development.

The objectives of this study were to determine wind direction, windspeed, and snow depth in the GLEES watershed from tree deformation indices. The resulting information will be used to estimate areas of greatest impact from atmospheric deposition. Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are the dominant coniferous species in the watershed. Scattered individuals of limber pine (*Pinus flexilis*) also occur. Limber pine rarely fruits in the watershed, and young trees are rare. For Engelmann spruce and subalpine fir, seedling trees are evident in the lower, subalpine portions of the watershed; but most reproduction near alpine appears to be vegetative by layering.

EXPERIMENTAL METHODS

Tree deformation indices have been developed to estimate windspeed. The Griggs-Putman technique (Robertson 1987) rates degree of deformation on a scale of 1 to 8, with 1 indicating no deformation and 8 indicating deformation such that tree growth is flattened against the ground in what is often referred to as "krummholz" form. This method uses regression techniques with constants from empirical data to calculate windspeed. The Wade-Hewson deformation ratio (Wade and Hewson 1979) measures the asymmetry of the crown and the down-wind bending of the trunk. The tree is photographed perpendicular to the maximum deformation, and analyzed using a grid overlay on the photo to measure deformation angles. Tree ring analysis can also be used to estimate windspeed (Robertson 1986). Tree sections are measured for ring width on the lee and windward side of the trunk, with ring width wider on the lee or branched side. This technique is less sensitive as an indicator of wind deformation than the others, and requires destructive sampling.

In many mountainous areas, maximum snow depth occurs early in the snow season, often as early as January (Schild and Gliott 1981), with additional snowfall settling and compacting the snowpack. Therefore, the portion of the tree exposed to wind desiccation and snow or ice crystal abrasion remains somewhat constant throughout the coldest part of the winter. This maximum depth of snowpack on trees can be measured by observed differences between snow-covered and snow-free portions of the crown resulting from the long period of exposure to their snowy or snow-free environment.

Snow depth is estimated on trees by two contrasting methods, depending on the density of the canopy. In dense canopies with deep snow, brown felt blight (*Herpotrichia juniperi*) develops on snow-covered foliage resulting in death of the needles. This is indicated by areas of dead, fungus-covered needles, or defoliated branches near the base of larger trees. The top of the dead area generally marks the maximum snow depth. The other method relates directly to wind deformation, caused by ice abrasion at the top of the snow pack (Hadley and Smith 1986; Holtmeier 1985). Beneath the snowpack, asymmetric deformation does not occur. Above the snowpack, often delineated by a sharp line of a few centimeters, tree deformation becomes evident. This indicator of snow depth is much more distinct than the snow mold technique, but is not useful in dense canopies where wind abrasion and deformation may occur only in the tops of the tree crowns. Some evidence of the depth of the snowpack is also indicated by the bending of branches downward from the weight and settling of the snowpack; but subalpine conifers are remarkably resilient in resisting this type of damage.

For this study, the GLEES was divided into 100-meter grid mapping units, with a tree sampled for deformation near each grid intersection. Individual trees near each grid point, considered typical of that area in amount of deformation, were selected as sample points. This scale of sampling was considered adequate to identify areas of different atmospheric deposition potential within the watershed. Individual trees sampled were identified on aerial photos for precise location of windspeed and direction data within the watershed. Wind direction was determined by measuring compass direction of the primary orientation of asymmetry or bending. Windspeed was calculated using both the Griggs-Putman and Wade-Hewson index methods described above. Snow depth was estimated from tree deformation markers at the lower portion of the tree trunk.

RESULTS AND DISCUSSION

Results of the study indicated that tree deformation indices for Engelmann spruce and subalpine fir were useful for estimating wind direction, windspeed, and snow depth at the GLEES. Wind direction was consistent, generally from a westerly direction at all sites within the watershed. The wind direction indices reflected local patterns of topography, with wind generally following parallel to a steep ridge bordering the watershed, but with some minor channeling around smaller ridges and knolls. Some convergence was evident in a small valley, and slight divergence of flow was evident where it passed over a ridge line as it exited the watershed.

The windspeed calculations for both the Griggs-Putnam and Wade-Hewson index methods provided similar windspeed values for individual trees. Because of their similarity, an average of the two methods was used as the estimate of windspeed at each data point in the watershed. The windspeed data, derived from individual trees based on their deformation indices, varied from 3 to 11 m/sec at different sites throughout the watershed, with an average watershed windspeed of 7.4 m/sec. The data derived from tree deformation indices are consistent with limited (1-year) data from a meteorological tower located within the watershed. The meteorological tower data indicate an average windspeed of 9.4 m/sec at that particular site. Tree deformation at a grid point located 20 m southeast of the tower indicated an identical windspeed of 9.4 m/sec. This degree of accuracy is perhaps coincidental, but demonstrates the usefulness of tree deformation as a surrogate for meteorological instrumentation.

The snow depth estimations from height of fungal injury and initiation of tree deformation indicated that snow depth varied from less than 0.5 m to over 4.5 m within the watershed. The average snow depth within the watershed estimated from tree indices in this study was 1.9 m. Precipitation data recorded from a raingauge located within the watershed from 1979 to 1988 have indicated an average maximum seasonal snowfall of about 2.1 m. This estimate is based on a 20-percent adjustment for observed collection inefficiency of raingauges located in windy sites (Sommerfeld and others in preparation). This correction may be low, particularly for snowfall at high wind sites (Sturges 1986). It also does not account for snowpack settling. On the other hand, the tree deformation index of snow depth is also likely low, since trees would be deformed to the lowest point on the trunk during low snowfall years. The techniques used for identifying snow depth on trees in this study would indicate this minimum height of snow accumulation on the tree trunk.

Engelmann spruce and subalpine fir tree species were useful to estimate wind direction, windspeed, and snow depth. These species occurred at sufficient frequency to allow adequate coverage of all areas of the watershed except the highest elevation alpine meadows, talus slopes, and snowfields. These treeless areas, on the lee side of the large ridge bordering the watershed, accumulate large amounts of snow and appear to experience high windspeeds. Tree deformation indices indicated increases in windspeed moving upslope toward these areas.

Engelmann spruce occurred most frequently in the lower subalpine portions of the watershed. However, the species did occasionally occur as krummholz at the higher elevations. Subalpine fir was most abundant in the upper portions of the watershed near alpine, where it was extensively wind deformed as krummholz. Individuals of subalpine fir also occasionally occurred at the lower elevations. Where both species occurred together, no difference was noted in the degree of wind deformation. At higher elevations, both species formed ribbons and hedges (Holtmeier 1978, 1980, 1982), wave patterns typical of high-wind areas in the Rocky Mountains. Engelmann spruce and subalpine fir krummholz forms were indistinguishable at a distance.

Limber pine deformation was not useful for determining wind and snow depth parameters in the watershed. Limber pine did not occur in lower elevation or protected areas where subalpine fir and Engelmann spruce were more abundant and less wind deformed. Limber pine was found primarily as widely scattered, isolated individual mature trees on ridgetop sites. Occasionally, it occurred as isolated, scattered individuals in the higher elevation areas of the extensive krummholz mats of Engelmann spruce or subalpine fir. Although almost always wind deformed at the exposed sites where it occurred, its scattered distribution prevented observations sufficient to determine wind direction and speed throughout the watershed. Since no rooting of the species was evident, extensive mat or wave patterns typical of Engelmann spruce and subalpine fir did not occur with limber pine. The inability of limber pine to reproduce vegetatively by layering likely contributed to its limited distribution in the watershed.

On the exposed sites where limber pine did occur, it was often extensively wind deformed; windspeed, direction, and snow depth could be determined from those individual trees. In areas where it might occur in denser, more widespread stands, it may be useful to estimate windspeed and direction. However, since it did not occur in more protected areas of the GLEES, sensitivity of the species to deformation at lower windspeeds could not be determined. At a few exposed sites at the GLEES, limber pine, Engelmann spruce, and subalpine fir occurred together. At these high-wind sites, limber pine appeared to indicate wind deformation patterns similar to those of the spruce and fir.

Limber pine and whitebark pine (*Pinus albicaulis*) are closely related species that occur in similar habitats. It is expected that whitebark pine would respond similarly to limber pine in susceptibility to wind deformation. Whitebark pine has been documented to occur in krummholz form (Arno and Hoff 1989; Tomback 1986). Although rooting of krummholz whitebark pine by layering can occasionally occur (Arno and Hoff 1989), vegetative reproduction of the species in krummholz is rare. Reproduction of the species is predominately from seed transported to timberline sites by birds (Tomback 1986). Local seed production in krummholz stands is low, and seeds produced have lower germination capacity than nonkrummholz stands (Tomback 1986). Scavenging of seed cones by birds and mammals is high in these sites (Tomback 1986). Thus the distribution of whitebark pine in sites subject to wind deformation is limited compared to distribution of Engelmann spruce and subalpine fir, which readily spread in krummholz stands by layering.

As with limber pine, only where whitebark pine occurs at least as densely as that required here (100-m or smaller grid) would it be useful as a surrogate to determine windspeed and wind direction data in a watershed. Another closely related species, European stone pine (*Pinus cembra*), grows in similar habitats and is commonly wind deformed. This species has been used to relate deformation to windspeed and direction in mountainous terrain (Holtmeier 1985).

The 100-m grid was sufficient to delineate wind direction, which changed little throughout the watershed, and proved adequate for windspeed. Refinement of windspeed would have been possible with survey at a closer grid pattern. The snow depth determinations appeared to be the least precise. Snow depth varied on a very small micro-relief scale, and changed with the particular tree chosen for sampling. Amount of tree deformation and direction changed little at a given site. This suggests that more precise snow depth delineation might have been possible from sampling at a finer scale of resolution. We were, however, able to refine the precision of the snow depth measurements for the watershed using a series of aerial photos of snow fields during melt to determine where areas of adjacent, similar snow depth might occur. In such cases, care was taken not to compromise the integrity of the snow depth data from tree deformation indices. For example, aerial photographs suggested that isopleths of particular snow depths may have closed in certain areas where they might have been drawn parallel.

The snow depth estimates from tree indicators provided data that generally corresponded with topographic features, such as lower snow depth on windswept ridges, and greater depth in the lee of ridges, where upslope conditions prevailed, and on the windward side of large open areas such as lake surfaces. However, a regression of windspeed on snow depth/tree as indicated by tree deformation indices was not significant. This was likely due to the lack of precision by tree indicators of snow depth, and the sensitivity of snow depth to small changes in topography. Maps showing wind direction, windspeed, and snow depth within the watershed are being published elsewhere (Wooldridge and others in preparation).

This study has demonstrated the usefulness of tree deformation indices to estimate wind direction, windspeed, and snow depth in situations where meteorological instrumentation is not available or too costly to obtain such data. Engelmann spruce and subalpine fir were useful tree species to indicate these parameters at the GLEES, a small alpine, subalpine ecosystem in southeastern Wyoming sensitive to atmospheric deposition. The data obtained in this experiment will be useful for determining areas of maximum atmospheric deposition in the watershed, and will be useful in modeling water and chemical transport through the different subcatchments of this ecosystem.

REFERENCES

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Hadley, J. L.; Smith, W. K. 1986. Wind effects on needles of timberline conifers: seasonal influence on mortality. Ecology. 67(1): 12-19.

Holtmeier, F. K. 1978. Die bodennahen Winde in dem Hochlogen der Indian Peaks section (Colorado Front Range). Munstersche Geogfraphische Arbeiten. 3: 5-47.

Holtmeier, F. K. 1980. Influence of wind on tree-physiognomy at the upper timberline in the Colorado Front Range. NZFS FRI Tech. Pap. 70 Wellington, NZ: New Zealand Forest Service: 247-261.

Holtmeier, F. K. 1982. "Ribbon-Forest" unf "Hecken" - streifenformige Verbreitungsmuster des Baumwuchses an der oberen Waldgrenze in den Rocky Mountains. Erdkunde. 36(3): 142-153.

Holtmeier, F. K. 1985. Climatic stress influencing the physiognomy of trees at the polar and mountain timberline. In: Proceedings, 3rd IUFRO workshop; 1984. Berichte. Eidgenossische Anstalt fur das Forstliche Versuchswesen. 270: 31-30.

Robertson, A. 1986. Estimating mean windflow in hilly terrain from tamarack (*Larix laricina* [Du Roi] K. Koch) deformation. International Journal of Biometeorology. 30(4): 333-349.

Robertson, A. 1987. The use of trees to study wind. Arborcultural Journal. 11: 127-143.

Schild, M.; Gliott, S. 1981. Shnee- und Lawinen-verhaltnisse im schweizerischen Alpengebiet. (Schnee und Lawinen in den Schweizer Alpen Winter) 1979/80, Nr. 44: 42-92.

Sommerfeld, R. A.; Musselman, R. C.; Wooldridge, G. L. [In preparation]. A comparison of estimates of snow input to a small alpine catchment. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Sturges, D. L. 1986. Precipitation measured by dual gages, Wyoming-shielded gages, and in a forest opening. In: Cold regions hydrology: Proceedings of symposium July 1986; Fairbanks, AK. Bethesda, MD: American Water Resources Association: 387-396.

Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madrono. 33(2): 100-110.

Wade, J. E.; Hewson, F. W. 1979. Trees as a local climate indicator. Journal of Applied Meteorology. 19: 1182-1187.

Wooldridge, G. L.; Musselman, R. C.; Fox, D. G.; Connell, B. H.; Sommerfeld, R. A. [In preparation]. Wind patterns and snow depth in high altitude complex terrain as determined from coniferous wind deformation. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Richard Baker and Earle F. Layser)—Your preconference paper title and abstract mentioned whitebark pine, while your paper and talk referred to limber pine. Isn't the Snowy Range outside the range of whitebark pine?

A.—The species that occurs at our study site in the Snowy Range has few individuals; these rarely produce cones. No seedlings appear to be present at the site. No cone fragments were visible under the trees. We were able to locate three cones that closely resembled those of whitebark pine. When the preconference abstract was written, we had tentatively identified the species as *Pinus albicaulis* based upon these cone characteristics. However, further examination of the specimens, and considering the small number of cone samples and the location of the trees outside the range of *Pinus albicaulis* and within the range of *Pinus flexilis*, we identified the species in the paper and in the presentation as *Pinus flexilis*.

Q. (from Friedrich-Karl Holtmeier)—Did your different tree species respond in the same way to different windspeeds; do they really display the same growth form at a similar windspeed?

A.—Engelmann spruce and subalpine fir response to wind deformation at specific locations was remarkably similar. Where both tree species occurred at the same site, tree deformation indices were the same. We could not distinguish between the two species based upon tree deformation. Limber pine appeared to respond similarly to the other two species at the few sites where it occurred with Engelmann spruce and/or subalpine fir. However, these sites were located on ridgetops where windspeeds and subsequent deformation were always higher (6-8 on the Griggs-Putnam scale). Response of limber pine at the lower windspeeds is not known. Because of the sparse occurrence of limber pine, it was not used to determine wind direction, windspeed, or snow depth in this study.

Q. (from Wendel Hann)—How do the wind/ice abraided stems of whitebark grow to the size they get before they are wind damaged? For example, why doesn't the wind take the buds off and keep them low in height?

A.—Evidence suggests that the most wind desiccation and ice abrasion damage to conifer foliage occurs in a very small zone above the snow surface. If the tops of trees are able to survive a few seasons to reach beyond this level, then the probability of survival increases. Survival during this period of time is determined by a season or two of (1) mild winters where ice abrasion and desiccation are less severe; or (2) abnormally deep snowpack where the tops are protected by snowcover. The tree top may survive once it grows beyond the few centimeters at the surface of the snowpack where conditions are most severe. However, deformation still occurs, primarily from desiccation on the windward side of the stem.

AUTECOLOGY OF WHITEBARK PINE

Ward W. McCaughey
Wyman C. Schmidt

ABSTRACT

*Whitebark pine (*Pinus albicaulis*) is an unusual species with limited information available on its basic biology. This paper consolidates information on the autecology of whitebark pine, including mechanisms of flowering and fruiting, cone production, seed characteristics and dissemination, regeneration, vegetative reproduction, growth and morphology, rooting, shade tolerance, longevity, and phenology. General habitat requirements are addressed in terms of climate, soils, elevation and topography, and plant associates. The distributional range of whitebark pine is discussed along with specifics on its physical characteristics and habitat requirements.*

INTRODUCTION

Whitebark pine (*Pinus albicaulis* Engelm.) was first described by botanists in the mid 1800's and classified by Engelmann in 1863 (Bailey 1975; Engelmann 1863). Its seeds have been found to be an important food source for grizzly (*Ursus arctos horribilis*), black bears (*Ursus americanus*) (Craighead and others 1982; Kendall 1983), birds (Tomback 1982; Vander Wall and Hutchins 1983), red squirrels (*Tamiasciurus hudsonicus*), and small mammals (Hutchins and Lanner 1982). Whitebark pine is also considered valuable for watershed protection, wildlife cover, ornamental use, and esthetics. It has minor significance as a timber producing species.

Whitebark pine grows in high-elevation forests and at timberline in western North America. In some areas such as Montana, Idaho, and western Wyoming whitebark forests occupy up to 10-15 percent of the forest cover (Arno 1986). Research on whitebark pine has been minimal but interest in this species is growing.

Autecological information is limited for whitebark pine. This paper describes the distribution of whitebark along with the climate where it grows, the soils it grows on, its reproductive cycle, growth characteristics, light requirements, insect and disease problems, and plant associates.

DISTRIBUTION

Whitebark pine grows from northern British Columbia to south-central California and from the Pacific coastal range to the Wind River range in Wyoming (fig. 1). There are two major distributions in western North America, a western and an eastern population (Critchfield and Little 1966).

The western population extends from about latitude 55° N. along the lower Fraser River in western British Columbia, southward into the Cascades, through Washington and Oregon, and on into the Sierras in California. In northern California the distribution is less continuous but farther south in the Sierra Nevada of central California it again becomes continuous forming extensive stands at and below tree line. The southern limit of whitebark is in the region of Mount Whitney between latitude 36° and 37° N.

The eastern population of whitebark pine extends southward from near latitude 55° N. in British Columbia and follows the principal ranges of the northern Rocky Mountains (Critchfield and Little 1966). Whitebark is found in the higher mountains of western Montana and central Idaho and extensively in the Yellowstone region of south-central Montana and northwestern Wyoming. The Wind River range of western Wyoming represents the southern and eastern limit of the eastern population of whitebark except for some disjunct stands in northeastern Nevada.

The eastern and western populations are separate except for a connection by isolated stands in southern British Columbia and northeastern Washington. Between the two distributions whitebark occurs in the Blue and Wallowa Mountains of northeastern Oregon and in small isolated ranges in northeastern California, south-central Oregon, and northern Nevada (Arno and Hoff 1989). There are also outlier stands of the eastern population in the Big Horn and Wind River ranges of Wyoming and in the Sweetgrass Hills in Montana (Thompson and Kuijt 1976).

The distribution of whitebark pine can be divided between Canada and the United States. In most of its distribution in Canada, whitebark north of latitude 50° N. is a minor component of the high-elevation forests (fig. 1). In the United States, whitebark often is a major component in the subalpine forests, sometimes forming pure stands.

Whitebark pine is a timberline tree found on the highest summits throughout its range. It grows at elevations of 6,000 to 7,000 ft toward its northern limits, from 5,500 to 9,300 ft in Oregon, 7,000 to 11,000 ft in California, and at 5,000 to 10,000 ft in Idaho and Montana (Sudworth 1908).

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Ward W. McCaughey is Forester and Wyman C. Schmidt is Project Leader and Research Silviculturist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Bozeman, MT 59717.

Figure 1—Distribution of whitebark pine.

CLIMATE

Whitebark pine grows from high-elevation alpine to montane forest sites at its lower elevational limits. It is most abundant on warm-dry exposures in moist mountain ranges and is prevalent on cool-moist sites in semi-arid ranges (Arno and Hoff 1989). At whitebark's upper elevational limits, it grows under extreme seasonal changes with daily temperatures ranging from lows near –60 °F in winter to over 100 °F in summer (Sudworth 1908). Summer temperatures are cool with July temperatures ranging from 55 to 59 °F in pure whitebark stands and from 50 to 54 °F in adjacent timberline zones (Weaver and Dale 1974). Average temperatures exceed 32 °F in the months between May and October yet frosts can occur in any month. The average frost free season was 32 days for whitebark stands near Kings Hill in the Little Belt Mountains of eastern Montana (Weaver and Dale 1974).

Heavy snowfall, fierce winds, and a short growing season are characteristics of whitebark pine habitats. Wind gusts can exceed 73 mph on most sites, especially on ridgetops (Arno and Hoff 1989). Most precipitation comes in the form of snow anytime from October to May, although snow can occur in any month in the higher elevation stands. Rain is the prevalent form of precipitation from June through September with intense afternoon thundershowers periodically providing small amounts of moisture (Arno 1970).

In the northern latitudes, mean annual precipitation ranges between 24 and 71 inches in stands where whitebark is a major component. Rainfall is minimal in the southern portion of whitebark's distribution south of latitude 47° N. causing a droughty period during mid-to-late summer (Arno and Hoff 1989).

SOILS

Mountain soils are characterized by young soils such as entisols and inceptisols that have minimal horizon development from weathering. Pure whitebark pine stands typically occur on young inceptisol soils characterized by weakly differentiated horizons (USDA 1975). Entisols also have developed on high benches and rolling ridgetops where sand and gravel have accumulated (McCaughey 1988). These are the youngest soils with almost no horizon development. They have developed since the Pleistocene glacial period less than 12,000 years ago (Mehringer and others 1977). Because of their short period of development, inceptisol soils, such as Typic Cryochrepts, are fragmental with only minimal horizon development.

Where whitebark pine forms climax communities, it is often found on soils composed of coarse talus, exposed bedrock, or lava flows (Arno and Hoff 1989). These soils sometimes have scattered pockets of fine material that may support other conifer species such as subalpine fir. Climax stands may also occur on mollic soils (Pfister and others 1977) or on other better developed soils where the limiting factor preventing other conifers is short-cool growing season or inadequate moisture. Volcanic ash deposits in some areas develop into Andic Cryochrepts or Typic Cryandepts that support the more productive spruce-fir-whitebark stands (Arno and Hoff 1989).

A short, cool growing season is typical of the whitebark pine ecosystem. Soil temperature regimes within the whitebark zone are considered cryic, having a mean annual temperature higher than 32 but lower than 47 °F. Productivity is low in most high-elevation whitebark pine stands. Cool temperatures reduce chemical weathering and activity by nitrogen-fixing and other microbiotic organisms thus tying up most of the nutrients in the form of litter and debris on the forest floor. Weaver and Dale (1974) found that compared to Montana agricultural soils, whitebark soils were low in potassium, calcium, magnesium, and sodium, but high in phosphorus. Like most forest soils, whitebark sites are acidic with upper horizon pH values ranging from 4.7 to 6.0 in Montana and 7.8 to 8.0 in Alberta (Arno and Hoff 1989; McCaughey 1988).

Whitebark prefers non-calcareous soils but can be found on limestone soils in Montana (Pfister and others 1977; Weaver and Dale 1974). In Canada whitebark grows on limestone substrates (Weaver 1989).

PHYSICAL CHARACTERISTICS

Needles

Whitebark pine is a five-needled pine. Bud burst occurs around mid-June and needles complete their growth by early July (Schmidt and Lotan 1980). Whitebark pine has five needles per fascicle. Individual needles are three sided; the outer side is convex, the inner sides are flat. When the inner flat surfaces of the five needles fit together the fascicle forms a (rod) circle in cross-section. Needles of whitebark are $1^1/_3$ to $2^3/_4$ inches long, yellow-green in color, and have one to four light colored stomatal lines on each of the flat surfaces (Harlow and others 1979; Hitchcock and others 1969).

When cones are absent whitebark pine is very difficult to distinguish from limber pine (*Pinus flexilis* James). Limber pine needles are about $2^1/_2$ inches long and similar in structure and color to whitebark. Cell wall thickness in the needle endodermis can be used to distinguish between whitebark and limber pine. In whitebark the outer tangential walls of the endodermis are thicker than the other cell walls; those of limber pine are of uniform thickness all the way around the cell (Harlow 1931). Examination of the number of needle resin ducts can be used for quick field comparison between whitebark and limber pine, although this procedure is less reliable (Ericson 1964; Hendrickson and Lotan 1971).

Bark

The bark of whitebark pine is thin with a conspicuous chalky-white cortical appearance (Bailey 1975; Hitchcock and others 1969). The smooth or superficially scaly bark is rarely more than one half inch thick and is brownish white to creamy white on immature trees (Harlow and others 1979). The bark is rarely broken, even on older trees, except near the base. The lower bark is divided by narrow cracks creating very thin whitish or brownish scales that, after falling or breaking off, reveal a red brown inner bark (Sudworth 1908). Young twigs are pubescent while older twigs have smooth bark (Hitchcock and others 1969). The bark slips around the end of May and sticks, after summer growth, around mid-September (Schmidt and Lotan 1980).

Branches

Young trees have regular whorls of branches at right angles to the trunk, but in older trees upper whorls develop upward into long willowy stems. Branches are tough and flexible (Sudworth 1908).

Roots

Root length varies depending on the growth substrate and age of the tree. Whitebark pine germinants have a 2- to 7-inch tap root with several lateral and fine root hairs (Day 1967; McCaughey 1988). Older whitebark develop a characteristic deep and spreading root system. On glacial moraines in Wyoming, whitebark pine forms a pancake-like root system only 16 inches deep (Lanner 1981). This shallow rooting also occurs in high-elevation bogs (Arno and Hoff 1989).

Wood

Whitebark pine wood is soft, fine textured, and brittle with a light brown-colored heartwood. It is easy to saw, having a specific gravity ranging from 0.35 to 0.53, slightly heavier than subalpine fir and lodgepole pine (Day 1967; Keenan and others 1970). Whitebark pine is weaker than lodgepole pine except for compression perpendicular to grain and hardness (table 1).

Whitebark pine contains substantial amounts of solvent-extractable fractions (oils), polyphenol, and other byproducts that can be used for fuels, chemicals, and other industrial raw materials. Whitebark yields 10.1 percent oil and 19.6 percent polyphenol as well as turpentines and rosins (Carr and others 1986; Mirov 1967).

Tree Form

At timberline whitebark pine forms "krummholz" stands of shrublike trees. On more exposed sites whitebark is found as low cushion krummholz or with long prostrate, often twisted branches growing over rocks (Dallimore and Jackson 1948). This shrub form is caused by inadequate growing season length and warmth, preventing adequate growth, maturation, and minimal cuticular development of new shoots (Daubenmire 1954; Tranquillini 1979). The incompletely developed tissues allow excessive winter damage and tissue death resulting in the delimitation of upper timberline (Sowell and others 1982). Other factors that help create tree deformities of timberline trees are frost, ultraviolet and high intensity radiation, heat, wind, and snow blast damage (Baig 1972; Tranquillini 1979).

Below the krummholz zone whitebark grows in nearly pure stands of widely spaced trees with diffuse crowns. In these stands, whitebark grows from 30 to 90 ft tall and is often multistemmed (Arno and Hoff 1989; Eggers 1985; Weaver and Dale 1974). The multistemmed appearance is due in part to caching habits of the Clark's nutcracker

Table 1—Strength properties of whitebark pine at 12 percent moisture content (from Keenan and others 1970)

Strength property	Strength value
Static bending	
Modulus of rupture (psi)	8,340
Modulus of elasticity (psi)	1.20×10^6
Compression parallel to grain	5,244
Maximum crushing strength (psi)	702
Hardness	
Side (lb)	516
End (lb)	680
Shear parallel to grain (psi)	705
Tension perpendicular to grain (psi)	421
Cleavage (lb per inch width, length 3 inches)	213

(*Nucifraga columbiana*) and to natural branching habits of young whitebark (Lanner 1980; Lanner and Vander Wall 1980; Linhart and Tomback 1985; Tomback and Kramer 1980; Weaver 1989).

Whitebark has a tree form similar to lodgepole pine when grown in close competition with other species (Keenan and others 1970). Along the east slope of the Continental Divide, in northern Montana, height growth and bole diameters were identical for lodgepole pine and whitebark and from a distance it was hard to distinguish between them (McCaughey 1987). In these mixed stands, whitebark has multiple tops with forking occurring near the top of the tree.

REPRODUCTION

Flowering and Fruiting

Flowering occurs after the juvenile period, which varies greatly among conifers. The age at which flowering occurs for whitebark pine is around 20-30 years (Day 1967; Rehder 1940).

In conifers the reproductive flowers consist of pollen (staminate strobili) and seed (ovulate strobili) cones (Kramer and Kozlowski 1979). Whitebark pine is monoecious, containing both cone types on the same tree.

Whitebark pine has a 2-year flowering cycle. Initiation of flower and vegetative buds occurs during bud set in August (Allen 1941; Schmidt and Lotan 1980). Ovulate cones are sessile, occurring in clusters of two to five near the tip of upper crown branches. The staminate cones are distributed throughout the crown but most frequently on older branches in the lower crown on the current year's growth (Arno and Hoff 1989; Eggers 1985). The staminate cones are crimson red and ovulate cones dark purple. Limber pine by contrast has yellow staminate cones and green ovulate cones.

During their first full growing season staminate and ovulate cones of whitebark pine grow to a length of one-fourth inch and 1 inch respectively (McCaughey 1988). Ovulate cones are receptive to pollen when it is wind disseminated in mid-July, although this receptive period may be earlier at lower elevations (Arno and Hoff 1989; Schmidt and Lotan 1980). After pollination of ovulate cones, staminate cones fall off the tree while ovulate cones remain in place.

Growth of pollinated ovulate cones begins in June of the second summer following initiation of flower buds and continues until cones reach full size (1½ to 3½ inches) by early August (Arno and Hoff 1989; Kozlowski 1971; Schmidt and Lotan 1980). Seed continues to mature until mid-September or early October. Ripe cones are ovoid, dull purple to brown in color, resinous with thickened apophyses, have terminally armed umbos, and weigh roughly 1 to 2 oz (Harlow and others 1979; Krugman and Jenkinson 1974; Weaver and Forcella 1986).

Cone Production

Minimum seed bearing age is 20 to 30 years for whitebark pine with the interval between large crops being 3 to 5 years (Krugman and Jenkinson 1974). Throughout the Yellowstone ecosystem there were two moderate to heavy cone crops from 1980 to 1987 with overall cone production decreasing steadily during the 8-year period (Knight and others 1987). Declines in cone production in the Yellowstone ecosystem were attributed to mortality of whitebark pine trees due to the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Knight and others 1987). On the eastern slopes of the Sierra Nevada, Tomback (1978) observed moderate to heavy whitebark pine cone crops in 4 consecutive years from 1973 to 1976. Weaver and Forcella (1986) estimated an average of 1.17 cones/yd^2/yr over a 6-to-8 year period on 28 whitebark stands in Montana. Cone yields varied significantly between years within stands and generally high-yield years followed low-yield years.

Poor cone crops may be a function of weather-related factors rather than within-tree factors (Weaver and Forcella 1986). Temperature and precipitation have significant, but not dominant, effects on all stages of cone development throughout most of the year. Allen (1941) identified several factors responsible for poor cone crops in conifers: adverse weather conditions, insect damage, and abortions that may have been physiological.

Seed Characteristics

A whitebark pine cone contains about 75 wingless seeds each weighing approximately 0.005 oz. Seeds are light brown to light orange in color, and are around 0.3 inches long. There are between 2,200 to 4,500 seeds per pound (Krugman and Jenkinson 1974; McCaughey 1988). The large variation in the number of seeds per pound is due to differences in seed size and also may be due to seed maturity when harvested.

Seed Dissemination

Whitebark pine cones have cone scales that partly open exposing the wingless seeds (Eggers 1985; Hutchins and Lanner 1982; Lanner 1982; Tomback 1981). There has been no documented evidence that whitebark pine cones abscise and fall to the ground. If cones do fall as a result of being dislodged due to animal foraging, they disintegrate rapidly by decay and depredations by animals (Arno and Hoff 1989). Groups of whitebark pine germinants were observed around crumbled cones in southwestern Alberta (Day 1967).

When cones are protected from animal predation they remain attached (Hutchins and Lanner 1982; Lanner 1982). In a study by Lanner (1982), protected cones that remained attached and yielded 347 seeds 1 year after maturing had 93 percent of the seeds containing decayed endosperms, presumably from exposure to the weather. Whitebark pine cones are not found on trees because of nearly complete removal or destruction due to seed predators. Intact cones were found only infrequently on the ground, and they contained only white-coated empty seeds (Tomback 1981). In some areas most or all of a cone crop is harvested by seed predators (Hutchins and Lanner 1982; Lanner 1982).

The Clark's nutcracker and red squirrels are the major dispersers of whitebark pine seeds (Arno and Hoff 1989; Hutchins and Lanner 1982; Lanner 1980; Lanner and Vander Wall 1980; Tomback 1978; 1982). Nutcrackers have a sturdy pointed bill ideal for picking apart whitebark cones. Upper portions of cone scales are easily broken off along a thin fracture zone. The scale base does not break away from the core of the cone thus fully exposing the seeds for easy removal by the nutcracker (Lanner 1982). Nutcrackers extract the seed and store them in their sublingual pouch, a saclike modification on the floor of the mouth (Bock and others 1973). The nutcracker appears to discriminate between good, aborted, insect-infected, or diseased seeds by rattling each seed in its bill before depositing the seed in its pouch, which holds over 100 seeds (Hutchins and Lanner 1982; Tomback 1978; Vander Wall and Balda 1977).

Clark's nutcrackers have been observed to carry whitebark pine seeds up to 14 mi from the seed source, although typical caching sites are close to the harvest site (Hutchins and Lanner 1982; Tomback 1978; Vander Wall and Balda 1977).

Nutcrackers cache groups of 1 to 25 seeds, one-half to 2 inches deep, on a variety of sites (McCaughey 1988). Cache sites are found on both well-drained and moist substrate, including soil, forest litter, gravel, rubble, cracks and fissures on exposed rock, and pumice (Hutchins and Lanner 1982; Tomback 1978; 1982). It is estimated that one nutcracker stores from 22,000 to over 98,000 whitebark pine seeds in years when seed is available (Hutchins and Lanner 1982; Vander Wall and Balda 1977). Food requirement estimates indicate that nutcrackers may store three to five times as many seeds as needed (Tomback 1983).

Squirrels harvest cones and seeds from mid-July to early November (Eggers 1986; Hutchins and Lanner 1982; Smith 1968). Squirrels store whitebark cones in middens and extracted seeds in caches on the forest floor, greatly reducing widespread dissemination of seed.

There are a variety of secondary dispersers known to disseminate whitebark pine seed. Grizzly and black bears raid squirrel middens to obtain whitebark seeds for food. Black bears may climb trees to harvest cones (Craighead and others 1982; Hammon 1983; Tisch 1961). Only rarely do whitebark seeds pass through a bear's digestive tract intact, severely limiting the probability of dispersal in this manner (Mattson 1987; McCaughey 1987).

Other animals that harvest whitebark pine seed either from the cones directly or indirectly from the ground or other animal caches and may act as dispersal agents are: birds – William's sapsucker (*Sphyrapicus thyroideus*), hairy woodpecker (*Picoides villosus*), white-headed woodpecker (*P. albolarvatus*), mountain chickadee (*Parus gambeli*), white-breasted nuthatch (*Sitta carolinensis*), Cassin's finch (*Carpodacus cassinii*), red crossbill (*Loxia curvirostra*), pine grosbeak (*Pinicola enucleator*), Steller's jay (*Cyanocitta stelleri*), raven (*Corvus corax*), and the red-breasted nuthatch (*Sitta canadensis*); rodents – chipmunks (*Eutamias* sp.), deer mice (*Peromyscus maniculatus*), golden-mantled ground squirrel (*Spermophilus lateralis*), and the chickaree (*Tamiasciurus douglasi*) (Eggers 1986; Hutchins and Lanner 1982; Tomback 1978).

Germination

Seed Storage—Whitebark pine seeds vary in the length of time they can be stored under environmentally controlled conditions. Viability drops from an initial average of 50 percent down to 3 percent when stored from 11 to 20 years (Schubert 1954). Seed viability dropped from 24 percent at time of collection to 17 percent after being stored for 8 years, but dropped to 1 percent after 11 years of storage (Mirov 1946). Viability of seed, as related to storage time, is dependent on seed maturity when harvested, seed handling prior to storage, and methods and length of time of stratification for germination tests.

It is unknown how long whitebark pine seeds will remain viable under natural (cached) storage conditions. McCaughey (1988) found 1-year-old filled whitebark seeds buried within nutcracker caches containing germinants. Nearly 75 percent of these filled seeds germinated after stratification, indicating that whitebark seed remains viable for at least 2 years.

Seed Germination—Even under controlled conditions whitebark pine seed viability is highly variable, ranging from 0 to 75 percent. The recommended procedure for germinating whitebark pine seeds is to soak seeds in running tap water for 1 to 2 days and then, with moist seeds in plastic bags, stratify at 33 to 41 °F for 90 to 120 days (Krugman and Jenkinson 1974). The Coeur d'Alene Nursery in Idaho successfully uses the following procedures for both western white pine and whitebark pine:

A. Place seed in nylon mesh bags.
B. Soak seed for 48 hours in running tap water. Place nylon mesh bag in plastic bag.
C. Stratify for 100 days at 33 to 35 °F. Within that 100-day stratification time resoak the seed for 1 hour each week.
D. After 100 days, remove seed from stratification and surface dry.
E. Using a vacuum seeder, place 100 seeds on moist paper towels (kimpak) in each of four plastic trays.
F. Place trays in germinator and take counts.

Using these procedures, 1985 and 1987 seed lots (#6610 and #6653 respectively) of whitebark pine had 35 and 50 percent germination rates (USDA 1987).

Dormancy of whitebark pine seed is caused by embryo underdevelopment, physiological embryo dormancy, by the barrier of the seed coat and female gametophyte tissue to oxygen and water uptake, and possibly by deposition of growth inhibitors to the embryo by female gametophyte tissue (Pitel 1981; Pitel and Wang 1980).

Sulfuric acid treatment moderately improves germination of whitebark pine seeds; seedcoat clipping also increases germination. Sulfuric acid-treated seeds show a 6 percent improvement in germination and clipped seeds an 8 to 14 percent improvement over untreated seeds (Pitel and Wang 1980).

Seed dormancy can be reduced by increasing the length of time whitebark pine seeds are stratified. Germination increased from 0 to 4 percent for intact seeds and 0 to 30 percent for clipped seeds when stratification times increased from 20 to 60 days (Leadem 1985). Hoff (1980) obtained 34 percent germination of whitebark seed when seeds were first cold stratified for 150 days and then the seedcoat cracked. Whitebark pine germination increased to 78 and 90 percent when clipped and stratified for 30 and 60 days respectively (Pitel 1981). Under field conditions, germination was 8 to 14 percent for intact seeds when naturally stratified for nearly 200 days (McCaughey 1988). Under natural conditions whitebark seed is covered with snow from early November to late May creating a 180 to 210 day cold stratification period.

Germination of whitebark pine seed is influenced by seed placement and type of seedbed. Table 2 shows preliminary results of a natural regeneration study of whitebark pine under field conditions (McCaughey 1988). Shading of 0, 25, and 50 percent did not have a significant effect on germination.

In nature, whitebark pine germination begins immediately after snow melt and continues through early September (McCaughey 1988; Tomback 1987). Most of the late germination may actually have germinated earlier in the summer but because of the slow growth characteristics and depth of caching it was not visible until later. Most natural germination occurs in Clark's nutcracker caches, although minor amounts of germination may be due to natural seed dissemination from fallen cones. Germination from seeds scattered on the ground is minimal because of heavy predation by red squirrels, mice, and chipmunks (Hutchins and Lanner 1982; McCaughey 1988).

Seedlings

Whitebark pine germinants are large compared to those of its conifer associates. Germinants produce five to 12 cotyledons growing to heights ranging from 1 to 4 inches tall. Forking of the mainstem occurred on 17 percent of whitebark germinants; 10 percent had a single fork and 7 percent had two forks (McCaughey 1988).

Seedling survival of whitebark pine is affected by a variety of biotic and microsite factors. Several causes of conifer seedling mortality are drought, insolation, birds and rodents, animal trampling, frost heaving, damping off fungi, insects, and poor root development (Hard and Rice 1979; Harrington and Kelsey 1979; Shearer 1980).

Vegetative Reproduction

Whitebark pine vegetatively reproduces through layering of lower branches along the ground surface. In the Bitterroot Range of Montana vegetative reproduction was observed from layering of shrub-like whitebark (Arno 1981; Arno and Hoff 1989). Whitebark easily grafts on stock plants of whitebark and western white pine, although grafts grow fastest on western white pine (Johnson 1981).

Table 2—Percent germination of whitebark pine seeds placed on the surface and buried 2-4 cm on mineral and litter seedbeds (*n* = 360 seeds per seed placement seedbed combination)

Seed placement	Seedbed	
	Mineral	**Litter**
	- - *Percent germination* - -	
On surface	3.9	0.0
Buried 2-4 cm	14.7	8.8

GROWTH

Whitebark pine is a slow-growing tree when found at the upper limit of tree growth. It can compete with and even outgrow its conifer associates on better sites in southwest Alberta (Day 1967). Whitebark pine is long lived, surviving over 700 years and may attain 1,000 years (Arno and Hoff 1989; Luckman and others 1984). It tends to remain windfirm for longer periods than lodgepole pine (Day 1967; Luckman and others 1984).

Environment greatly affects growth of whitebark pine. At timberline, it grows extremely slowly, developing a shrublike appearance. In Wyoming, where whitebark forms climax stands, it attains heights from 30 to 90 ft tall with average stand diameters of 12 to 14 inches (Eggers 1986). The largest tree on record, based on height and diameter measurements, was 69 ft tall with a 105-inch diameter (AFA 1986). Several trees in Canada are from 80 to 100 ft tall with diameters ranging from 25 to 36 inches (Day 1967) and in northwest Montana whitebark trees from 100 to 110 ft tall are common in old stands on good sites (Arno 1989).

Growth and yield information is limited for whitebark because the species has typically occupied only a minor component in most commercial stands. Where whitebark forms a major component, stand productivity is usually low. In Montana, whitebark grows best in the *Abies lasiocarpa/Luzula hitchcockii* habitat type *Menziesia ferruginea* phase (Pfister and others 1977). Merchantable timber yield is low, about 10 to 20 ft^3/acre/yr in high elevation *Pinus albicaulis/Vaccinium scoparium* stands in Montana (Forcella and Weaver 1977). Yields were around 29 ft^3/acre/yr in the lodgepole pine-whitebark type in south-central Oregon (Hopkins 1979).

Biomass Production

Whitebark pine has a characteristic spreading crown when open grown and, in dense stands, has a crown shape similar to lodgepole pine's but with upswept upper crown development. There are several tree and stand characteristics of whitebark pine that interact in several ways resulting in varying biomass production depending on the situation (Weaver and Forcella 1977). Biomass production can be expressed as whole tree weight or as production of tree parts such as crown width (*CW*), live and dead crown weight, bole weight, foliage weight, and twig weight. Brown (1978) and Moeur (1981) developed several equations that predict biomass production of whitebark pine (table 3). Tree and stand characteristics used to develop prediction equations for biomass production are diameter at breast height (*D*), total tree height (*H*), crown length (*CL*), basal area of tree (*BA*), tree age (*A*), number of trees per acre (*TPA*), the relative diameter (*DREL=D/* quadratic mean stand diameter), and the crown ratio (*R*=[live crown length/*H*]*10).

LIGHT

Tolerance of whitebark pine to light competition is thought to change with stage of development. Whitebark is considered highly to somewhat shade intolerant during early juvenile growth but becomes more shade tolerant with age (Day 1967; Eggers 1986; Sudworth 1908). Whitebark pine has been rated very shade intolerant (Baker 1949), though McCaughey (1988) observed seedlings and saplings growing up through the canopies of subalpine fir and lodgepole pine indicating moderate tolerance at an early age. Arno (1989) has observed this moderate tolerance at all ages for whitebark pine. At later developmental stages, whitebark is less tolerant than subalpine fir, Engelmann spruce (*Picea engelmannii*), and mountain hemlock (*Tsuga mertensiana*) but more tolerant than lodgepole pine, limber pine, and subalpine larch (*Larix lyallii*) (Pfister and others 1977; Steele and others 1983).

INSECTS

There are a number of insects that damage whitebark pine. The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is the most important. Table 4 lists many of the insects that affect whitebark.

The mountain pine beetle displays host specificity between lodgepole pine and whitebark pine for the species in which it completed larval development. Extensive mortality in one or the other of the two host species does not result in comparable mortality in the other host (Baker and others 1971). Severe mortality in whitebark pine can occur during years when temperatures are favorable and beetle populations can increase (Baker and others 1971; McGregor and Cole 1985). Beetle populations usually build first in adjacent lower elevations where lodgepole pine is a major stand component and migrate up, eventually attacking the larger lodgepole pine and whitebark pine (McGregor and Cole 1985).

Table 3—Regression equations for predicting crown width, live and dead crown weight, bole and whole tree weight, foliage weight, and twig weights of whitebark pine (from: Brown 1978; Moeur 1981)

Tree component	Equation
Crown width (>3.5" *D*)	$\mathrm{LN}(CW) = -0.91984 + 1.08137\mathrm{LN}(D)$ $- 0.07299\mathrm{LN}(H) + 0.29786\mathrm{LN}(CL)$
Crown width (<3.5" *D*)	$\mathrm{LN}(CW) = 0.07049\mathrm{LN}(H) + 0.28283\mathrm{LN}(CL)$ $+ 0.04032\mathrm{LN}(BA)$ (Moeur 1981)
Crown weight (>3.5" *D*)	$\mathrm{LN}(WT) = 2.62251 + 2.08624\mathrm{LN}(D)$ $- 1.07705\mathrm{LN}(H) + 0.69082\mathrm{LN}(CL)$ $- 0.30885\mathrm{LN}(A) - 0.14210\mathrm{LN}(TPA)$ $+ 0.39924\mathrm{LN}(DREL)$
Crown weight (<3.5" *D*)	$\mathrm{LN}(WT) = -2.81317 + 1.47513\mathrm{LN}(D)$ $+ 0.22823\mathrm{LN}(A) - 0.13550\mathrm{LN}(TPA)$
Crown weight (live trees >1" *D*)	$WT = 0.65 + 0.06056(D^3) + 0.05477(D^2R)$
Crown weight (dead branches trees >1" *D*)	$WT = 0.001713(D^2CL) + 0.33$
Bole weight (<4" *D*)	$WT = 1.33 + 0.08614(D^2H)$
Whole tree (<15 ft *H*)	$WT = \mathrm{EXP}[-2.876 + 2.175\mathrm{LN}(H)]$
Foliage (indiv. branch)	$WT = -0.9265 + 2.292\mathrm{LN}(D)$
Branches (0 to 0.24" *D*)	$WT = -1.844 + 1.915\mathrm{LN}(D)$
Branches (0.25 to 0.99" *D*)	$WT = -1.008 + 2.664\mathrm{LN}(D)$
Branches (1 to 2.99" *D*)	$WT = -2.180 + 3.351\mathrm{LN}(D)$

Table 4—Known insect pests of whitebark pine (from: Arno and Hoff 1989; Bright 1968; Eggers 1986; Furniss and Carolin 1977; Hoff and McDonald 1977)

Species	Common name or type of insect
Dendroctonus ponderosa	Mountain pine beetle
Pityogenes knechtel	Secondary bark beetle
Pityogenes carinulatus	Secondary bark beetle
Pityogenes fossifrons	Secondary bark beetle
Pityophthorus aquilonius	Secondary bark beetle
Pityophthorus collinus	Secondary bark beetle
Ips spp.	Pine engraver
Argyrotaenia tabulana	Lodgepole needle-tier
Essigella gillettei	Aphid - needle feeder
Pineus coloradensis	Aphid - needle feeder
Puto cupressi	Mealy bug
Puto pricei	Mealy bug
Dioryctria	Cone worm
Eucosma	Cone worm
Conophthorus	Cone beetle
Conophthorus ponderosae	Cone insect

DISEASES

High-elevation stands of whitebark pine are not generally susceptible to most pathogens. White pine blister rust (*Cronartium ribicola*) introduced from Europe is the most serious disease affecting whitebark (Carlson 1978). Whitebark remains highly susceptible to white pine blister rust even on trees with disease-resistant parents (Hoff 1980). The severity and extent of an infection of blister rust depend mainly on weather patterns and to a lesser degree on the abundance of the alternate host *Ribes*. In the Yellowstone ecosystem of northwest Wyoming and south-central Montana blister rust incidence has remained at low levels even when *Ribes* populations are extensive in some areas. Ecological conditions in this area have probably limited rust spread (Carlson 1978). In the Pacific Northwest whitebark pine is the most susceptible of all host trees to white pine blister rust (Childs and Bedwell 1948). Extensive damage and mortality of whitebark pine to blister rust and secondary causes has been observed (Arno 1986).

There are a number of other pathogens that affect whitebark pine in a variety of ways. Table 5 lists most of the known pathogens found on whitebark pine.

HABITAT ASSOCIATES

Whitebark pine is found on a wide range of habitats. It occurs in 36 of the more than 50 forest habitat types in eastern Idaho-western Wyoming area, in 24 of 76 habitat/phase types in central Idaho, and in 46 of the 99 habitat/phase types in Montana (Pfister and others 1977; Steele and others 1981; 1983).

Little information is available on plant associates of whitebark pine at timberline. Where whitebark forms an overstory, the understory vegetation is usually dominated by *Vaccinium scoparium* (Weaver and Dale 1974). In the Rocky Mountains several other understory species commonly associated with whitebark pine are: *Hieracium gracile, Carex geyeri, Potentilla gracilis, Lupinus sericeus, Polygonum bistortoides, Castilleja rhexifolia, Poa alpina, Luzula hitchcockii, Phyllodoce empetriformis, Menziesia ferruginea, Xerophyllum tenax, Juncus parryi, Festuca idahoensis*, and *Erythronium grandiflorum*. The four most common associates of 57 plant species found in whitebark stands in Montana and Idaho were *Carex rossii, Abies lasiocarpa, Poa nervosa*, and *Arnica latifolia* (Forcella 1977). *Carex pensylvanica* and *Poa nervosa* are the most common undergrowth species in south-central Oregon (Hopkins 1979). In Alberta, *Juniperus communis* is the major understory plant associated with whitebark pine (Baig 1972).

Throughout whitebark's distributional range it grows in association with several tree species. Whitebark can be found growing with *Pinus contorta* var. *latifolia, Abies lasiocarpa, Picea engelmannii, Pinus flexilis, Pseudotsuga menziesii, Larix lyallii, Populus* spp., *Juniperus scopulorum, Abies magnifica* var. *magnifica, Abies magnifica* var. *shastensis, Pinus contorta* var. *murrayanna, Pinus monticola*, and *Pinus balfouriana* (Arno and Hoff 1989).

Table 5—Known pathogens of whitebark pine (from: Eggers 1986; Goward 1985; Hiratsuka and Funk 1976; Knutson and Tinnin 1981; Mathiasen and Hawksworth 1988; Smith 1972)

Species	Damage - affected area
Herpotrichia juniperi	Snow mold - foliage
Herpotrichia nigra	Snow mold - foliage
Neopeccia coulteri	Snow mold - foliage
Lophodermella	Needle cast - foliage
Lophodermium nitens	Needle cast - foliage
Bifusella linearis	Needle cast - foliage
Bifusella saccata	Needle cast - foliage
Gremmeniella abietina	Shoot blight - foliage
Cronartium ribicola	Blister rust - branch and stem
Arceuthobium americanum	Dwarf mistletoe - branch and stem
Arceuthobium cyanocarpum	Dwarf mistletoe - branch and stem
Lachnellula pini	Minor canker - branch and stem
Atropellis piniphila	Canker - branch and stem
Armillariella mellea	Shoestring root rot - root
Polyporus schweinitzii	Brown cubical butt rot - butt
Polyporus subacida	Spongy rot - butt
Phaeolus schweinitzii	Butt rot
Perenniporia subacida	Rot - root and butt
Phellinus pini	Decay - stem
Fomes annosus	Rot - root and butt
Ahtiana sphaerosporella	Lichen - bark

FIRE ECOLOGY

Wildfire plays an important role in creating the structure and plant diversity of the western forests. Little is known about how fire has shaped the subalpine and timberline habitats that contain whitebark pine. Fire intervals range from 60 to 300 years or more in the whitebark types of Montana (Arno 1980).

Lightning is the major cause of fires in most whitebark stands although accidental fires have resulted due to increased recreation activity in these forests (Arno and Hoff 1989). Fire intensity and resultant tree mortality are generally low in climax whitebark stands because of sparse ground fuels and cool-moist conditions. Fires are typically spotty in the pure whitebark types except when windy warm-dry conditions help fires spread both along the ground and through tree crowns (Arno and Hoff 1989).

Whitebark pine is considered a pioneering species on burned areas and is moderately fire resistant. Fire suppression over the past several decades has aided successional replacement of whitebark by shade-tolerant species thus reducing its distribution. Spreading surface fires help maintain whitebark communities on sites where they grow in association with subalpine fir and Engelmann spruce. Whitebark has a thin bark making it susceptible to fire injury from hot surface fires, but because of its open stand and low fuel characteristics it survives most surface fires. Subalpine fir and Engelmann spruce have properties that make them very vulnerable to fires of even low intensity (Crane and Fisher 1986; Fisher and Clayton 1983).

The mountain pine beetle and lower elevation forests play key roles in the fire ecology of whitebark pine. Mortality from the mountain pine beetle increases fuel loading, fire intensities, and crown fire potential. Fires starting in lower elevation forests, of higher density, spread up through climax whitebark communities to timberline (Arno and Hoff 1989). Open whitebark stands act as a firebreak unless stand and climate conditions are favorable for carrying the fire as was the case with the 1988 fires in Yellowstone National Park.

REFERENCES

Allen, G. S. 1941. A basis for forecasting seed crops of some coniferous trees. Journal of Forestry. 39: 1014-1016.

American Forestry Association. 1986. National register of big trees. American Forests. 92(4): 21-52.

Arno, S. F. 1970. Ecology of alpine larch (*Larix lyallis* Parl.) in the Pacific Northwest. Missoula, MT: University of Montana. 264 p. Dissertation.

Arno, S. F. 1980. Forest fire history in the Northern Rockies. Journal of Forestry. 78: 460-465.

Arno, S. F. 1981. [Unpublished observation]. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Fire Sciences Laboratory.

Arno, S. F. 1986. Whitebark pine cone crops - a diminishing source of wildlife food? Western Journal of Applied Forestry. 1(3): 92-94.

Arno, S. F. 1989. [Personal communication]. March 1989. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory.

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Baig, M. N. 1972. Ecology of timberline vegetation in the Rocky Mountains of Alberta. Calgary, AB: University of Calgary. 446 p. Dissertation.

Bailey, D. K. 1975. *Pinus albicaulis*. Curtis's Botanical Magazine. 180(111): 140-147.

Baker, B. H.; Amman, G. D.; Trostle, G. C. 1971. Does the mountain pine beetle change hosts in mixed lodgepole and whitebark pine stands? Res. Note INT-151. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 17 p.

Baker, F. S. 1949. A revised tolerance table. Journal of Forestry. 47(3): 179-182.

Bock, W. J.; Balda, R. P.; Vander Wall, S. B. 1973. Morphology of the sublingual pouch and tongue musculature in Clark's nutcracker. Auk. 90: 491-519.

Bright, D. E., Jr. 1968. Three new species of *Pityophthorus* from Canada (*Coleoptera: Scolytidae)*. Canadian Entomologist. 100: 604-608.

Brown, J. K. 1978. Weight and density of crowns of Rocky Mountain conifers. Res. Pap. INT-197. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 56 p.

Carlson, C. E. 1978. Noneffectiveness of *Ribes* eradication as a control of white pine blister rust in Yellowstone National Park. Forest Insect and Disease Management Rep. No. 78-18. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 6 p.

Carr, M. E.; Bagby, M. O.; Roth, W. B. 1986. High oil-producing and polyphenol-producing species of the northwest USA. Journal of American Oil Chemists Society. 63(11): 1460-1464.

Childs, T. W.; Bedwell, J. L. 1948. Susceptibility of some white pine species to *Cronartium ribicola* in the Pacific Northwest. Journal of Forestry. 46: 595-599.

Craighead, J. J.; Scaggs, G. B.; Sumner, J. S. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Wildlands Institute Monograph No. 1. Missoula, MT: University of Montana. 279 p.

Crane, M. F.; Fisher, W. C. 1986. Fire ecology of the forest habitat types of central Idaho. Gen. Tech. Rep. INT-218. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 86 p.

Critchfield, W. B.; Little, E. L. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.

Dallimore, W.; Jackson, A. B. 1948. A handbook of Coniferae including Ginkgoaceae. 3d ed. London: Edward Arnold and Co. 682 p.

Daubenmire, R. 1954. Alpine timberlines in the Americas and their interpretation. Butler University Botanical Studies. 11: 119-136.

Day, R. J. 1967. Whitebark pine in the Rocky Mountains of Alberta. Forestry Chronicle. 43: 278-282.

Eggers, D. E. 1986. Management of whitebark pine as potential grizzly bear habitat. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 170-175.

Engelmann, G. 1863. *Pinus albicaulis* Engelm. Transactions of the Academy of St. Louis. 2: 209.

Ericson, J. E. 1964. Field identification of whitebark and limber pines based on needle resin canals. Journal of Forestry. 62: 576-577.

Fisher, W. C.; Clayton, B. D. 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. Gen. Tech. Rep. INT-141. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 83 p.

Forcella, F. 1977. Flora, chorology, biomass and productivity of the *Pinus albicaulis - Vaccinium scoparium* association. Bozeman, MT: Montana State University. 99 p. Thesis.

Forcella, F.; Weaver, T. 1977. Biomass and productivity of the subalpine *Pinus albicaulis - Vaccinium scoparium* association in Montana. Vegetatio. 33: 95-106.

Furniss, R. L.; Carolin, V. M. 1977. Western forest insects. Misc. Publ. 1339. Washington, DC: U.S. Department of Agriculture, Forest Service. 654 p.

Goward, T. 1985. Ahtiana new-genus in the parmeliaceae. Bryologist. 88(4): 367-371.

Hammon, F. M. 1983. Food habits of black bears in the Greys River drainage, Wyoming. Laramie, WY: University of Wyoming and Wyoming Game and Fish Department. 50 p.

Hard, J.; Rice, J. 1979. Preliminary results of seedling damage surveys in young plantations of selected forests in Region 1. Report No. 79-10. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, Forest Insect and Disease Management. 5 p.

Harlow, W. M. 1931. The identification of the pines of the United States, native and introduced, by needle structure. Tech. Publ. 32. New York: New York State College of Forestry. 21 p.

Harlow, W. M.; Harrar, E. S.; White, F. M. 1979. Textbook of dendrology. 6th ed. New York: McGraw-Hill. 510 p.

Harrington, M. G.; Kelsey, K. G. 1979. Influence of some environmental factors on initial establishment and growth of ponderosa pine seedlings. Res. Pap. INT-230. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 26 p.

Hendrickson, W. H.; Lotan, J. E. 1971. Identification of whitebark and limber pines based on needle resin ducts. Journal of Forestry. 69(9): 584.

Hiratsuka, Y.; Funk, A. 1976. Additional records of *Gremmeniella abietina* in western Canada. Edmonton, AB: Department of the Environment, Canadian Forestry Service, Northern Forestry Research Centre. Plant Disease Reporter. 60(7): 631.

Hitchcock, C. L.; Cronquist, A.; Ownbey, M.; Thompson, J. W. 1969. Vascular plants of the Pacific Northwest. Part 1. Seattle: University of Washington Press. 914 p.

Hoff, R. J. 1980. [Personal Files]. Moscow, ID: U.S. Department of Agriculture, Forest Service, Forestry Sciences Laboratory.

Hoff, R. J.; McDonald, G. I. 1977. Differential susceptibility of 19 white pine species to woolly aphid *Pineus coloradensis*. Res. Note INT-225. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 1-6.

Hopkins, W. E. 1979. Plant associations of the Fremont National Forest. Publ. in Ecology. 79-004. Portland, OR: U.S. Department of Agriculture, Forest Service. 106 p.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Johnson, L. 1981. [Personal communication with Arno and Hoff]. In: Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Keenan, F. J.; Glavicic, M. R.; Swindle, P. W.; Cooper, P. A. 1970. Mechanical properties of whitebark pine. Forest Chronicle. 46(4): 322-325.

Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. In: Bears-their biology and management; Interagency conference on bear research and management. 1980 February; Interagency Association for Bear Research and Managment. 5: 166-173.

Knight, R. R.; Blanchard, B. M.; Mattson, D. J. 1987. Food habits. In: Yellowstone grizzly bear investigations. Annual Report 1987. Bozeman, MT: U.S. Department of the Interior, National Park Service. 80 p.

Knutson, D. M.; Tinnin, R. O. 1981. *Arceuthobium cyanocarpum* (limber pine dwarf mistletoe) in Oregon. Plant Disease. 65(5): 445.

Kozlowski, T. T. 1971. Growth and development of trees: volume I. Seed germination, ontogeny, and shoot growth. New York: Academic Press. 443 p.

Kramer, P. J.; Kozlowski, T. T. 1979. Physiology of woody plants. New York: Academic Press. 811 p.

Krugman, S. L.; Jenkinson, J. L. 1974. *Pinus* L. Pine. In: Schopmeyer, C. S., ed. Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture, Forest Service: 598-638.

Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. Sixth North American forest biology workshop proceedings 1980 August; Edmonton, AB. Edmonton, AB: University of Alberta: 14-48.

Lanner, R. M. 1981. [Personal communication with Arno and Hoff]. In: Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research. 12(2): 391-402.

Lanner, R. M.; Vander Wall, S. B. 1980. Dispersal of limber pine seed by Clark's nutcracker. Journal of Forestry. 78(10): 637-639.

Leadem, C. L. 1985. Seed dormancy in three *Pinus* species of the Inland Mountain West. In: Shearer, R. C., compiler. Proceedings—conifer tree seed in the Inland Mountain West; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 117-124.

Linhart, Y. B.; Tomback, D. F. 1985. Seed dispersal by nutcrackers *Nucifraga columbiana* causes multi-trunk growth form in pines. Oecologia (Berl.). 67(1): 107-110.

Luckman, B. H.; Jozsa, L. A.; Murphy, P. J. 1984. Living seven-hundred-year-old *Picea engelmannii* and *Pinus* *albicaulis* in the Canadian Rockies. Arctic and Alpine Research. 16(4): 419-422.

Mathiasen, R. L.; Hawksworth, F. G. 1988. Dwarf mistletoes on western white pine and whitebark pine in Northern California and Southern Oregon. Forest Science. 34(2): 429-440.

Mattson, D. J. 1987. [Personal communication]. February 1987. Bozeman, MT: U.S. Department of the Interior, Montana State University, Interagency Grizzly Bear Study Team.

McCaughey, W. W. 1987. [Unpublished observations]. Bozeman, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory.

McCaughey, W. W. 1988. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, Bozeman, MT.

McGregor, M. D.; Cole, D. M., eds. 1985. Integrating management strategies for the mountain pine beetle with multiple-resource management of lodgepole pine forests. Gen. Tech. Rep. INT-174. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 68 p.

Mehringer, P. F., Jr.; Arno, S.; Petersen, K. 1977. Postglacial history of Lost Trail Pass Bog, Bitterroot Mountains, Montana. Arctic and Alpine Research. 9(4): 345-368.

Mirov, N. T. 1946. Viability of pine seed after prolonged cold storage. Journal of Forestry. 44(3): 193-195.

Mirov, N. T. 1967. The genus *Pinus*. New York: The Ronald Press Co. 602 p.

Moeur, M. 1981. Crown width and foliage weight of Northern Rocky Mountain conifers. Res. Pap. INT-283. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 14 p.

Pfister, R. D.; Kovalchick, B. L.; Arno, S.; Presby, R. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Pitel, J. A. 1981. Improved germination of whitebark pine (*Pinus albicaulis* Engelm.) seeds. Unpublished report on file at: Environment Canada, Canadian Forestry Service, Petawawa National Forestry Institute, Chalk River, ON. 5 p.

Pitel, J. A.; Wang, B. S. P. 1980. A preliminary study of dormancy in *Pinus albicaulis* seeds. Bi-Monthly Research Notes. Ontario, AB: Environment Canada, Canadian Forestry Service, Petawawa National Forestry Institute. 36(1): 4-5.

Rehder, A. 1940. Manual of cultivated trees and shrubs hardy in North America. 2d ed. New York: Macmillan. 996 p.

Schmidt, W. C.; Lotan, J. E. 1980. Phenology of common forest flora of the Northern Rockies—1928-1937. Res. Pap. INT-259. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 20 p.

Schubert, G. H. 1954. Viability of various coniferous seeds after cold storage. Journal of Forestry. 52: 446-447.

Shearer, R. C. 1980. Regeneration establishment in response to harvesting and residue management in a western larch—Douglas-fir forest. Gen. Tech. Rep. INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 249-269.

Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecological Monographs. 38: 31-63.

Smith, Richard S., Jr. 1972. Needle casts of high-altitude white pines in California. Plant Disease Reporter. 56: 102-103.

Sowell, J. B.; Koutnik, D. L.; Lansing, A. J. 1982. Cuticular transpiration of whitebark pine (*Pinus albicaulis*) within a Sierra Nevadan timberline ecotone, USA Arctic and Alpine Research. 14(2): 97-103.

Steele, R.; Cooper, S. V.; Ondov, D. M.; Roberts, D. W.; Pfister, R. D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

Steele, R.; Pfister, R. D.; Ryker, R. A.; Kittams, J. A. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 138 p.

Sudworth, G. B. 1908. Forest trees of the Pacific slope. Washington, DC: U.S. Department of Agriculture, Forest Service. 455 p.

Thompson, L. S.; Kuijt, J. 1976. Montane and subalpine plants of the Sweetgrass Hills, Montana, and their relationship to early post-glacial environments of the Northern Great Plains. Canada Field Naturalist. 90(4): 432-448.

Tisch, E. L. 1961. Seasonal food habits of the black bear in the Whitefish Range of northwestern Montana. Bozeman, MT: Montana State University. 108 p. Thesis.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird. 16(1977): 123-160.

Tomback, D. F. 1981. Notes on cones and vertebrate-mediated seed dispersal of *Pinus albicaulis* (Pinaceae). Notes and News. Madrona. 28(2): 91-94.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51(2): 451-467.

Tomback, D. F. 1983. Nutcrackers and pines: coevolution or coadaptation? In: Nitecki, M. H., ed. Coevolution. Chicago; London: University of Chicago Press: 179-223.

Tomback, D. F. 1987. [Personal communication]. April 1987. Fort Collins, CO: Colorado State University, Department of Zoology and Entomology.

Tomback, D. F.; Kramer, K. A. 1980. Limber pine seed harvest by Clark's nutcracker *Nucifraga columbiana* in the Sierra-Nevada USA. Timing and foraging behavior. Condor. 82(4): 467-468.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. New York: Springer-Verlag. 137 p.

U. S. Department of Agriculture, Soil Conservation Service, 1975. Soil taxonomy. Agric. Handb. 436. Washington DC: U.S. Department of Agriculture, Soil Conservation Service. 754 p.

U.S. Department of Agriculture, 1987. [Information on file]. Coeur D'Alene, Nursery, Coeur D'Alene, ID.

Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecological Monographs. 47: 89-111.

Vander Wall, S. B.; Hutchins, H. E. 1983. Dependence of Clark's nutcracker, *Nucifraga columbiana*, on conifer seeds during postfledging period. Canadian Field-Naturalist. 97(2): 208-214.

Weaver, T. 1989. [Personal communication]. January 1989. Bozeman, MT: Montana State University, Department of Biology.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. American Midland Naturalist. 92: 222-230.

Weaver, T.; Forcella, F. 1977. Biomass of 50 conifer forests and nutrient exports associated with their harvest. Great Basin Naturalist. 37(3): 395-401.

Weaver, T.; Forcella, F. 1986. Cone production in *Pinus albicaulis* forests. In: Shearer, R. C., compiler. Proceedings—conifer tree seed in the Inland Mountain West; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 68-76.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from John Joy originally given to Diana Tomback)—On large burned over whitebark pine stands does regeneration come from seed cached prior to the fire, seed cached only after the fire, or both?

A.—I believe that the majority of the regeneration would come from seed cached after the fire but because I have found that seed can remain in the ground for at least 2 years and still germinate, "some" germination could come from previously cached seed.

Q. (from Ron Lanner)—Since nobody has ever published a definitive report of germination from a fallen cone nor even that cones abscise: how do you suppose these myths got started?

A.—Ron Lanner himself has published information on whitebark cones surviving on the tree and showing no signs of abscising. The myth probably came about when people were not finding cones on the trees. The immediate assumption is that the cones had fallen off. Again, they did not find the cones on the ground and assumed that they had fallen apart. They did not consider the possibility that animal predation (Clark's nutcracker and squirrels) could completely eliminate all cones from all trees.

Q. (from Bill Shuster)—Any idea on why the recent downward trend in cone production? What factors affect production in whitebark?

A.— Knight and others (1987) cited declines in productivity probably due to (1) infestations of the pine beetle, which were first noted in 1982; (2) the inherent cyclic nature of whitebark pine cone production, which results in extremes approximately every 7 to 10 years; and (3) the effects of persistent adverse climatic conditions (drought). Past studies indicate that temperature and precipitation have a significant, but not dominant, effect on all stages of cone development. Insects may also play a role in influencing cone production of whitebark pine.

Q. (from unknown source)—Is there a fairly reliable method to tell the difference between whitebark pine and limber pine, in the field, if there are no cones present?

A.—No. The only reliable way is to microscopically examine cell differences within cross sections of the needles. There are so many variables to consider when you try to determine what a tree is. The elevation: high elevation usually means it is whitebark unless it is on a limestone substrate; low elevation probably means the tree is limber pine. In the Bridger Mountains I have found whitebark and limber growing on the same site and without the cones I couldn't tell them apart.

Q. (from Diana Tomback)—You mentioned that single boled whitebark pine grew "in close competition" with lodgepole pine. Are you suggesting there is a cause-effect relationship for growth form? Or do some conditions producing dense lodgepole forests produce a multi-trunk form?

A.—I believe there is a cause and effect relationship occurring in dense stands of lodgepole pine on the growth form of whitebark pine. I have on rare occasions seen multi-trunked whitebark in dense stands of lodgepole pine. I believe that as stand density increases the *probability* of a single stemmed whitebark pine occurring increases.

Q. (from Maria Ash)—Your seedling photos mostly show the cotyledons and juvenile leaves of 1-year-old germinants. Is it possible that these 1-year-old seedlings could appear older (for example, more foliage with fascicles forming by the end of the first growing season)?

A.—Yes. Lammas growth does occur giving a 1-year-old seedling the appearance of being 2 years old.

Q. (from Earle Layser)—Do you think that the "isolated" occurrence that you showed for whitebark in the southern Selkirks in NE Washington are pockets or remnant stands that escaped from the extensive extreme fires that burned that area in the early 1900's?

A.—With little knowledge about the area I cannot give a good answer to this question. If the fires left pockets of whitebark pine then the burned areas should be capable of growing whitebark. If whitebark is naturally coming back onto the burned areas then it is very likely that the fires created the remnant stands. If not then the pockets are probably due to some past geologic event.

Q. (from Stephen Harvey)—Cones initiate in fall, develop in the following summer . . . please finish the progression.

A.—Differentiation into vegetative and reproductive buds occurs during the bud set period. Male and female cones develop during the first summer with male cones producing pollen which then pollinates the female cones. The female cone is a "first year cone" about 1 inch long. During the next summer the female cone "second year cone" grows to full mature size ($1^1/_2$ to $3^1/_3$ inches long).

WHITEBARK PINE COMMUNITY TYPES AND THEIR PATTERNS ON THE LANDSCAPE

Stephen F. Arno
Tad Weaver

ABSTRACT

Within whitebark pine's (Pinus albicaulis) *relatively narrow zone of occurrence—the highest elevations of tree growth from California and Wyoming north to British Columbia and Alberta—this species is a member of diverse plant communities. This paper summarizes studies from throughout its distribution that have described community types containing whitebark pine and the habitat types (environmental types based on potential vegetation) it occupies.*

Whitebark pine is most abundant and widespread in the semiarid inland mountain ranges of the northwestern United States and southwestern Canada, where it occurs in a continuum of environmental situations. It can be (1) a fire-dependent, early seral component of spruce-fir forests on moist sites; (2) a persistent seral or minor climax associate in drier forest habitats; (3) a major climax species or the only tree under still drier or more wind-exposed conditions; or (4) a major component or sole dominant of krummholz communities above tree line.

The timberline landscape is a mosaic of cover types including windswept fellfields and grassy balds, wet meadows, snowdrift communities, and krummholz (shrub-like conifers) and forest communities with various proportions of whitebark pine. Four factors explain much of the variation in cover types: (1) rugged topography, through its influence on microclimate; (2) differences in surface rockiness, ranging from boulder piles to moderately well-developed soils; (3) differences in substrate composition, with especially noteworthy changes occurring between calcareous and noncalcareous geologic parent materials; and (4) a patchwork of different disturbance histories in the aftermath of fires, bark beetle epidemics, blowdowns, or snow avalanches.

Whitebark pine communities also vary regionally, with changes in both climate and competing species. For example, in maritime mountain regions whitebark pine is unable to compete in the closed upper subalpine forest; it is, therefore, restricted to tree islands in the open heath parklands at timberline.

INTRODUCTION

Whitebark pine (*Pinus albicaulis*) is a prominent species in the upper subalpine forest and timberline zones on high mountains of western North America. Here, a great variety of tree-dominated and nonarboreal communities form a complex vegetational mosaic on the rugged landscape. While few studies have provided detailed descriptions of these communities or the causes of their distributional patterns, it is possible to list the major community types and to specify the principal factors controlling the mosaic. An understanding of this environmental complex is needed to guide land management. For example, to prevent undesirable changes in water, wildlife, and recreational resources, we must be able to recognize and manage the impacts of recreation, grazing, mining, timber harvest, air pollution, greenhouse effects, and advanced forest succession linked to fire suppression.

The presence and dominance of whitebark pine depend on its environmental tolerances and on its competitive abilities. Its tolerances restrict it to relatively cool sites without extended drought. Its relatively low capacity to compete (table 1) restricts it to harsh sites where growth of more competitive trees is hampered by physical factors or, on better forest sites, by disturbance. In this paper

Table 1—Comparative tolerance of shade or competition for species associated with whitebark pine in the Inland Northwest (after Minore 1979)

Tolerance	Species
Very tolerant	Subalpine fir (*Abies lasiocarpa*)
	Mountain hemlock (*Tsuga mertensiana*)
Tolerant	Engelmann spruce (*Picea engelmannii*)
Intermediate or intolerant	Whitebark pine (*Pinus albicaulis*)
Very intolerant	Lodgepole pine (*Pinus contorta* var. *latifolia*)
	Alpine larch (*Larix lyallii*)

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Stephen F. Arno is Research Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Intermountain Fire Sciences Laboratory, P. O. Box 8089, Missoula, MT 59807; Tad Weaver is Plant Ecologist, Biology Department, Montana State University, Bozeman, MT 59717.

we examine, first, the variation in potential climax vegetation reflecting the habitat type (Daubenmire and Daubenmire 1968; Pfister and Arno 1980) as it changes locally with microclimate or substrate and regionally with macroclimate. Then, we address the role of temporal changes in the vegetation on a site after disturbance, since whitebark pine is seral in many habitat types. We conclude with a brief outline of regional classification schemes.

ENVIRONMENTAL CONTROLS

The patterns of distribution and relative dominance of whitebark pine and its associates on the mountain landscape are strongly influenced by topography (Arno and Hammerly 1984; Habeck 1987; Pfister and others 1977; Steele and others 1981, 1983). For example, slope orientation profoundly affects microclimate; north and east aspects are relatively moist and cool while south and west aspects are drier and warmer. Also, at increasingly higher elevations growing seasons become shorter and cooler.

Because it is relatively cold tolerant and relatively noncompetitive, whitebark pine's importance increases with elevation. In the lower subalpine habitat types (fig. 1) whitebark pine occurs in small amounts and primarily as suppressed saplings. In the colder, upper subalpine habitat types the establishment and growth of competing conifers are reduced. This allows whitebark pine to assume dominance on many sites.

In moist sites of the upper subalpine zone (for example, cirque basins) whitebark pine is a minor component of subalpine fir-spruce (*Abies lasiocarpa-Picea engelmannii*) stands except where it becomes a pioneer dominant after a severe fire, avalanche, or other major disturbance. Its early seral success is possible because of whitebark pine's superior hardiness in the harsh microclimate of the disturbed site and its introduction by the seed caching Clark's nutcracker (Tomback and others, this proceedings). Within 150 to 200 years, vigorous fir and spruce begin to replace the pine.

Conversely, on relatively dry sites in the upper subalpine forest, whitebark pine is a long-persisting seral associate in the subalpine fir habitat types (potential climax; fig. 1). Lodgepole pine (*Pinus contorta* var. *latifolia*) is also a seral associate in many of these stands. On the driest sites, subalpine fir is absent, lodgepole pine is seral, and whitebark pine assumes the climax role (Steele and others 1983).

In the alpine timberline zone, above the upper limit of continuous forest, whitebark pine often occurs in pure or mixed groves or tree islands. Any trees that can survive are considered part of the climax community (Arno and Hammerly 1984; Pfister and others 1977). Whitebark pine and its arboreal associates occur in a continuum of lifeforms at timberline. These range from large, single-stem trees to stunted multistemmed trees to flagged krummholz (tall shrub form) and cushion krummholz. Because whitebark pine is hardier, it often produces a taller life form than the associated subalpine fir.

In addition to cold timberlines, whitebark pine occurs at dry timberlines, which are subalpine forest-herbland ecotones. At dry timberlines, it may be associated with inland Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) or limber pine (*Pinus flexilis*).

Rugged topography adds small-scale site variations to the general zonal patterns. For example, sharp ridge crests in the upper subalpine forest are exposed to severe wind, which favors whitebark pine relative to fir and spruce. Rugged topography and resulting vegetation patterns influence the distribution of snow, which in turn affects soil moisture, soil development, and potential

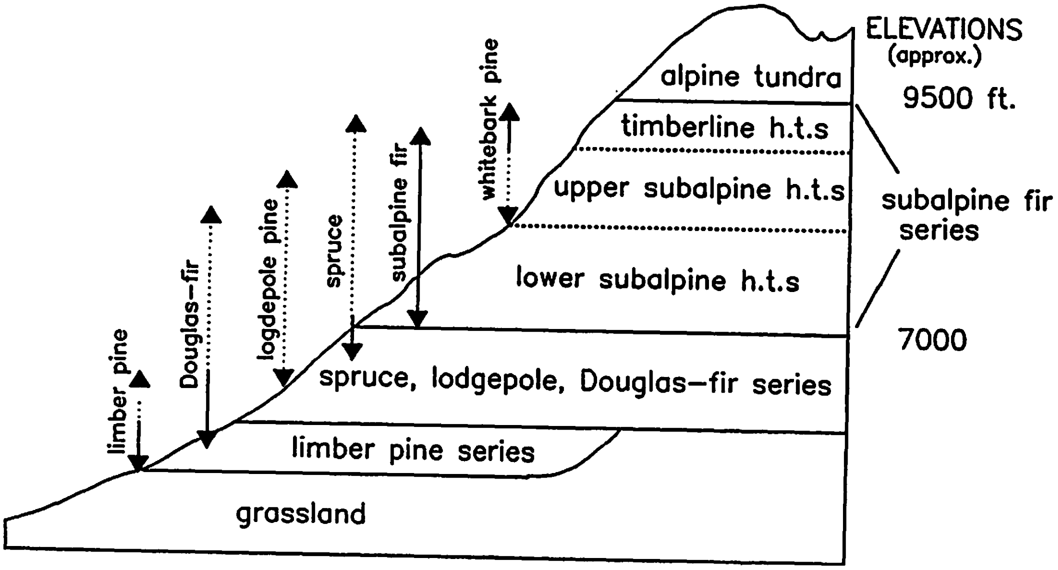


Figure 1—General elevational distribution of forest trees (arrows) and habitat type series (potential climax) on noncalcareous geologic types in south-central Montana. Solid portion of arrow indicates where a species is the potential climax, and dotted portion shows where it is seral. (Modified from Pfister and others 1977).

vegetation. Microsites receiving excessive snow often support wet meadow vegetation rather than trees. In contrast, microsites with deficient snow support semiarid grassland or other dry nonforest types. Sometimes contrasting snowdrift and dry microsites lie close to each other with a strip of whitebark pine in between, as in the "ridgetop ribbon forest" described by Arno and Hammerly (1984).

Edaphic factors also influence the distribution of whitebark pine in the rugged high-mountain terrain. For example, whitebark pine may be abundant on talus slopes or bedrock outcrops, but scarce on surrounding sites with deeper soils, where other conifers are more competitive.

Changes in substrate (surface geologic type) can also have a profound effect on whitebark pine communities. The contrast between calcareous (usually limestone) and noncalcareous substrates provides a dramatic example. Limestone often weathers to produce an excessively well-drained soil that limits growth of conifers (Goldin 1976; Pfister and others 1977). In especially dry regions (for example, in northern Nevada and eastern California), whitebark pine is largely confined to noncalcareous substrates (Harlow and Harrar 1958; Weaver and Dale 1974). In most regions, however, whitebark pine occurs on both calcareous and noncalcareous substrates. Calcareous sites support open pine stands with herbaceous undergrowth, while adjacent noncalcareous sites have dense mixed conifer stands with seral whitebark pine and an undergrowth of low *Vaccinium* (huckleberry or whortleberry) shrubs (Arno and Hammerly 1984; Pfister and others 1977).

REGIONAL VARIATIONS

On a larger scale, the composition and distribution of whitebark pine communities vary based on regional differences in climate, topography, and competitive relationships of subalpine tree floras. Whitebark pine communities are extensive and diverse in the drier inland mountain ranges. However, their abundance declines southward in California, perhaps in response to increasing length of summer drought. In wet regions, such as the crest of the northern Cascade Range and the British Columbia coastal ranges, whitebark pine occurs only in open timberline habitats and it is a minor constituent there. In these wet oceanic mountains, whitebark pine's growth is slow and its ultimate tree sizes are small. It is essentially absent from the dense upper subalpine forest, apparently because of an inability to compete with the shade-tolerant mountain hemlock (*Tsuga mertensiana*), subalpine fir, and Pacific silver fir (*Abies amabilis*). At these timberlines, dense heath (*Phyllodoce* and *Cassiope*) hinders conifer regeneration. Whitebark pine is a minor component of the conifer invasion that does occur in timberline heathlands during especially dry summers (Brink 1959; Franklin and others 1971).

Whitebark pine is abundant in regions having humid, snowy winters and long dry periods in summer, such as California's high Sierra Nevada and the inland mountains of the northwestern United States. Its abundance and vigorous growth in semiarid regions and on topographically dry sites suggest that it is more drought resistant than other northwestern subalpine trees.

The abundance of whitebark pine decreases as summer precipitation increases northward in the inland Northwest. For example, July-August precipitation in the upper subalpine zone averages about 2 inches (5 cm) in central Idaho, where the species is very abundant, and 5 to 6 inches in the latitude of Kootenay and Banff National Parks, where it is generally a minor component of the high-country vegetation (Arno 1970). Presumably this occurs because whitebark pine's competitors—subalpine fir, spruce, mountain hemlock (in the Selkirks), and (locally) alpine larch (*Larix lyallii*)—are more vigorous in the more humid environment. Physiological investigations of drought-sensitive alpine larch (Richards 1981; Richards and Bliss 1986) explain its inverse distribution. Despite extensive timberline habitat, alpine larch occurs only north of latitude 45.5° N., where it is confined to moist north-facing slopes. In contrast, northward into Canada it becomes abundant on southern exposures (Arno and Hammerly 1984).

Whitebark pine is absent from the high-desert mountains east and south of the Sierra Nevada, at least in part because this species is not as tolerant of year-round aridity as are limber pine and Great Basin bristlecone pine (*Pinus longaeva*). The current southern distributional limits of whitebark pine from California to the central Rockies may also result in part from inadequate seed distribution to isolated mountain habitats during alternating glacial and warm climates of the Pleistocene.

Thus, in the wettest mountain regions whitebark pine is narrowly confined to the timberline zone and to open rocky subalpine sites. In contrast, in drier regions where drought hampers competitors (notably in the dry-summer inland mountains of the northwestern United States), whitebark pine is often a major component of both the upper subalpine forest and the timberline zone, encompassing about 2,500 ft (760 m) in elevation. In the Sierra Nevada whitebark pine is generally confined to timberline but is often abundant there.

ROLE OF DISTURBANCE

Disturbances are important in shaping the structure of all whitebark pine communities, and natural disruptions are vital to the perpetuation of whitebark pine in the habitat types where it is seral. In the timberline zone, the climate is so harsh and limiting for tree growth that climatic disturbances (such as damaging winds, ice storms, snowloads, summer frost, and winter desiccation) prevent stand closure and thereby allow competition-intolerant species like whitebark pine to coexist indefinitely with their tolerant competitors (Arno and Hammerly 1984; Franklin and Dyrness 1973; Pfister and others 1977). Conversely, in subalpine forest habitats, whitebark pine's perpetuation depends upon occasional disturbances. Without disturbance, succession will lead to dominance by subalpine fir, spruce, or mountain hemlock.

In large portions of the inland northwestern United States, the area covered by seral whitebark pine communities has diminished in recent decades. Its decline is due to successional replacement linked to fire suppression and aggravated by epidemics of mountain pine beetle and white pine blister rust (Arno 1986; Kendall and Arno, this proceedings).

Prior to 1900, fires at intervals averaging between 50 and 350 years were widespread and were important in perpetuating seral whitebark pine communities (Arno 1986; Morgan and Bunting, this proceedings). These often burned in a patchy pattern with differential severities. Both light surface fires and stand replacing fires favor whitebark pine in relation to its shade-tolerant competitors. High-intensity, stand-replacing fires in thick subalpine fir-spruce forests often allow whitebark pine to become established as a result of nutcracker seed caching. After establishment, some of these seral whitebark pine communities have been perpetuated by low-intensity fires that killed understory fir and spruce.

As a result of fire suppression during the 1900's, natural fire cycles in seral whitebark pine communities have been postponed (Arno 1986), so this species is being replaced by its competitors. Even management programs that allow some natural fires to burn are probably insufficient for mimicking whitebark pine fire cycles of the past. The most effective fires in the highly discontinuous whitebark pine habitats (atop isolated high ridges) were ones that spread over large expanses—hundreds of thousands of acres. However, most whitebark pine habitats lie near developed or commercially utilized lands where such massive fires are not tolerable politically, even in wilderness areas or National Parks.

Fire suppression during this century has no doubt resulted in a decrease in the establishment of new whitebark pine communities. These young stands are needed to compensate for aging stands in which whitebark pine is being replaced successionally. Avalanches and severe blowdowns also create open microenvironments that allow whitebark pine to enter as a pioneer species. These disturbances are no substitute for fire, however, because they produce only small areas suitable for seral whitebark pine forests and they fail to reduce competition from understory trees and shrubs.

Mountain pine beetle epidemics are another influential natural disturbance that tends to kill overstory whitebark pines and enhance succession toward domination by subalpine fir (Bartos and Gibson, this proceedings; Kendall and Arno, this proceedings). Similarly, white pine blister rust, an introduced disease, severely injures and kills whitebark pine, hastening succession toward dominance by shade-tolerant conifers (Hoff and Hagle, this proceedings; Kendall and Arno, this proceedings).

COMMUNITY TYPES AND HABITAT TYPES

A variety of reports describe whitebark pine communities of almost every State and Province occupied by the tree (table 2). Whitebark pine habitats are abundant, diverse, and best documented in the inland northwestern United States (Cole 1982; Forcella 1977, 1978; Pfister and others 1977; Steele and others 1981, 1983; Weaver and Dale 1974; and other studies listed in table 2). Three remarkably consistent community complexes appear repeatedly in this region—extending from western Wyoming and northeastern Oregon to the southernmost portions of British Columbia and Alberta.

First, on the driest sites and in arid mountain ranges, communities dominated by whitebark pine (both seral and potential climax) are abundant. At the highest elevations, in cold-moist situations, the undergrowth is usually dominated by *Vaccinium scoparium*. Under progressively

Table 2—Principal publications and theses describing whitebark pine communities, listed by State and Province. Complete citations appear in the References section

Alberta	Achuff 1989; Baig 1972; Ogilvie, this proceedings
British Columbia	Achuff 1989; Brink 1959; McAvoy 1931; Ogilvie, this proceedings; Selby and Pitt 1984
California	Barbour 1988; Cooke 1940, 1955; Klikoff 1965; Sawyer and Thornburgh 1977; Taylor 1976; Vale 1977
Idaho	Steele and others 1981, 1983; USDA Forest Service 1989
Montana	Arno 1970; Craighead and others 1982; Forcella 1977, 1978; Pfister and others 1976, 1977; USDA Forest Service 1989; Weaver and Dale 1974
Nevada	Loope 1969
Oregon	Cole 1982; Franklin and Dyrness 1973; Hall 1973; Hopkins 1979; Jackson and Faller 1973; Lueck 1980
Washington	Agee and Kertis 1987; Arno 1970; del Moral 1979; Franklin and Dyrness 1973; Williams and Lillybridge 1983
Wyoming	Forcella 1977; Gruell 1980; Steele and others 1983;

drier conditions, the characteristic undergrowth changes to *Carex geyeri, Juncus parryi, Arnica cordifolia*, and, finally, *Festuca idahoensis*.

Second, in average mountain habitats of the inland Northwest, whitebark pine stands are codominated by subalpine fir and, at lower elevations, by lodgepole pine. The characteristic undergrowth ranges from *Phyllodoce empetriformis* and *Luzula hitchcockii* in moist situations to *Xerophyllum tenax, Vaccinium scoparium, Carex geyeri*, and *Ribes montigenum* on increasingly drier sites.

Third, moist subalpine forest sites often have whitebark pine as a seral component mixed with Engelmann spruce (*Picea engelmannii*), subalpine fir, and, at lower elevations, lodgepole pine. Alpine larch and mountain hemlock can be constituents in certain localities. Characteristic undergrowth includes numerous wet-meadow forbs and sedges, and the shrubs *Ledum glandulosum, Phyllodoce empetriformis, Menziesia ferruginea*, and *Rhododendron albiflorum*.

In the continental climate of western Wyoming and central Montana, whitebark pine is the potential climax tree in several subalpine forest habitat types as well as being a seral associate in several others (table 3). In the inland maritime climate found west of the continental divide in Montana, whitebark pine is seral except in the timberline zone (table 4).

Northward in the Rocky Mountains of Alberta and British Columbia, whitebark pine remains widespread but is less often a dominant species. Achuff (1989) and Ogilvie (this proceedings) provide detailed descriptions of whitebark pine communities in Canada. In Alberta, whitebark pine is most common in the timberline zone as a codominant with subalpine fir, spruce, and sometimes with alpine larch (Baig 1972). Characteristic undergrowth includes *Phyllodoce empetriformis* in moist sites along or near the Continental Divide (inland-maritime zone); *P. glanduliflora* in comparable sites in mountains farther inland (east); *Vaccinium scoparium* on well-drained sites, and *Juniperus communis* on the driest south-facing slopes.

The importance of whitebark pine increases from wet to dry sites in the Cascade Range. In the rain shadow of the Washington Cascades on the granitic Stuart Range, whitebark pine is abundant in the upper subalpine forest and the timberline zone. Timberline communities are dominated by whitebark pine on dry sites and warm aspects and by alpine larch in moist-cool situations (del Moral 1979) as they are in some moist mountain ranges of western Montana (Arno and Habeck 1972). In the Stuart Range, relatively moist whitebark pine-alpine larch communities have an undergrowth of *Vaccinium*

Table 3—High-elevation habitats of western Wyoming arranged approximately on a gradient of decreasing site moisture. Competitive status and abundance of whitebark pine and its associates are shown (modified from Steele and others 1983)

		Tree species[2]						
Site moisture	Habitat type[1]	*Pinus albicaulis*	*Abies lasiocarpa*	*Picea engelmannii*	*Pinus contorta*	*Pinus flexilis*	*Pseudotsuga menziesii*	*Populus tremuloides*
Wet								
	PIEN/VASC	(S)	c	C	(S)	(s)		
	PIEN/CALE	s	c	C	s			
	ABLA/VAGL, VASC	s	C	S	S			
	ABLA/VASC, PIAL	C	C	S	S		(s)	
	ABLA/VASC, VASC	s	C	S	S			
	ABLA/ARLA	(S)	C	S	(S)		(S)	(S)
	ABLA/THOC	s	C	S	S		S	(S)
	ABLA/JUCO	s	C	(S)	S	s	(S)	
	ABLA/RIMO, RIMO	s	C	S	(s)			
	ABLA/RIMO, PIAL	C	C	c				
	ABLA/ARCO, SHCA	s	C	s	S	s	s	s
	PIAL/VASC	C	c	c	C			
	PIAL/CAGE				(C)			
	PIAL/JUCO	C			C	s		
	PIAL/CARO	C	(c)	(c)	(C)	(s)		
	PIAL/FEID	C						
Dry								

[1] Abbreviations consist of the first two letters of the genus and species names. Undergrowth species are: ARCO = *Amica cordifolia;* ARLA = *A. latifolia;* CAGE = *Carex geyeri;* CALE = *Caltha leptosepala;* CARO = *Carex rossii;* FEID = *Festuca idahoensis;* JUCO = *Juniperus communis;* RIMO = *Ribes montigenum;* SHCA = *Shepherdia canadensis;* THOC = *Thalictrum occidentale;* VAGL = *Vaccinium globulare;* VASC = *V. scoparium.*

[2] C = climax dominant; S = seral dominant; c = minor climax species; s = minor seral species; () = in part of the habitat type only.

Table 4—Typical high-elevation forest zonation in west-central Montana showing the competitive status and abundance of whitebark pine and its associates (modified from Pfister and others 1977)

Elevational zone	Moisture	Habitat types[1]	Stand components[2] *Pinus albicaulis*	*Abies lasiocarpa*	*Picea engelmannii*	*Larix lyallii*	*Pinus contorta*	*Pseudotsuga menziesii*
Timberline zone	Dry sites	PIAL	C	—	—		—	—
		PIAL-ABLA	C	C	c			
	Moist sites	LALY-ABLA	C	C	c	C		
Upper subalpine forest	Dry sites	ABLA-PIAL/VASC	S^{300y}	C	s		—	—
		ABLA/LUHI	S^{250y}	C	s		S^{200y}	—
	Moist sites		S^{200y}	C	S^{400y}	s	s	—
Lower subapline forest	Dry sites	ABLA/XETE, VASC	s	C	s	—	S	s

[1] Abbreviations consist of the first two letters of the genus and species names. Undergrowth species are: LUHI = *Luzula hitchcockii*; VASC = *Vaccinium scoparium*; XETE = *Xerophyllum tenax*.

[2] C = climax dominant; S = seral dominant for number of years (as indicated) after fire or other disturbance; c = minor climax species; s = minor seral species.

myrtillus, which is ecologically similar to *V. scoparium* (del Moral 1979). With increasing dryness, whitebark pine communities have undergrowths characterized by *Lewisia columbiana*, *Phlox diffusa*, *Juniperus communis*, and *Penstemon davidsonii*.

In the excessively well-drained pumice of the Oregon Cascades, whitebark pine communities are characterized by sparse undergrowth. On sites with average moisture conditions, undergrowth is typically *Penstemon davidsonii*; in wetter microsites *Vaccinium scoparium* and *Luzula hitchcockii* are characteristic (Jackson and Faller 1973; Lueck 1980). On coarse volcanic substrates in south-central Oregon, Hopkins (1979) described two community types (= habitat types) in which whitebark pine and lodgepole pine are the climax dominants and the principal undergrowth is *Carex pensylvanica*, *Poa nervosa*, and *Penstemon laetus*.

Southward on the Cascade-Sierra Nevada axis, whitebark pine is common but largely confined to timberline communities in northern and central California. Subalpine fir and Engelmann spruce are essentially absent, and the timberline communities tend to be quite open, with only sparse, scattered undergrowth (Barbour 1988). These communities consist of mixtures of whitebark pine with mountain hemlock on moist sites and with Sierra lodgepole pine (*Pinus contorta* var. *murrayana*), western white pine (*Pinus monticola*), and foxtail pine (*P. balfouriana*) on drier sites.

The whitebark pine zone is often made up of an intricate pattern of community types dominated variously by tall or dwarf trees, shrubs, subalpine herbs, or alpine tundra plants. These community mosaics and their microenvironmental controls are little studied. One exception is del Moral's (1979) work in the Stuart Range. Another is Pfister and others' (1976) quantitative description and map of an extensive whitebark pine community mosaic in the Scapegoat Wilderness of northwestern Montana. Their map (fig. 17 in Craighead and others 1982) differentiated six habitat types and phases containing major amounts of whitebark pine and several habitat types in which whitebark pine is a minor component. The map units were characterized with constancy and coverage data for forest community types (both postfire and mature) as well as associated subalpine grassland, wet meadow, and avalanche community types (table 5). The topographic and edaphic controls of the major whitebark pine types (table 6) were identified as a guide for vegetation mapping throughout the study area. Many more similar studies are needed before we hope to understand the dynamics of whitebark pine community mosaics.

Table 5—Constancy (in percent + 10)—and average percent canopy cover, in (), for six habitat types in the Scapegoat Wilderness, MT, containing whitebark pine (from Pfister and others 1976; habitat types from Pfister and others 1977) (LUHI = *Luzula hitchcockii*; MEFE = *Menziesia ferruginea*; VASC = *Vaccinium scoparium*)

Habitat type and phase:	**ABLA-PIAL/ VASC**	**ABLA/LUHI- VASC**	**ABLA/LUHI- MEFE**	**PIAL-ABLA**	**PIAL-ABLA snowdrift**	**LALY-ABLA**
Computer map code:	**820**	**831**	**832**	**850**	**850D**	**860**
No. of sample stands:	**13**	**8**	**2**	**4**	**2**	**3**
TREES						
Abies lasiocarpa	9(39)	10(48)	10(65)	10(44)	5(4)	10(15)
Larix occidentalis						10(27)
Picea spp.	8(18)	8(27)	10(16)	8(7)	5(2)	7(13)
Pinus albicaulis	10(36)	10(30)	10(25)	10(47)	5(5)	10(15)
Pinus contorta	4(4)	1(10)				
Pseudotsuga menziesii	4(4)					
SHRUBS						
Alnus sinuata			5(4)			
Juniperus communis	4(7)			5(2)		
Ledum glandulosum		1(40)	10(10)			
Menziesia ferruginea	2(2)	4(3)	10(30)			
Ribes lacustre	3(1)	1(0)		2(0)		
Shepherdia canadensis	1(0)			2(0)		
Vaccinium caespitosum	1(0)					
Vaccinium globulare	2(30)	1(0)				
Vaccinium scoparium	7(38)	10(54)	10(45)	5(75)	5(10)	10(47)
PERENNIAL GRAMINOIDS						
Calamagrostis rubescens	2(10)					
Festuca idahoensis	1(20)			5(1)		
Luzula hitchcockii		10(11)	10(10)	8(2)		10(18)
PERENNIAL FORBS						
Cirsium foliosum	5(1)			8(1)		
Fragaria spp.	4(3)					
Heracleum lanatum	1(2)			2(0)		
Lomatium dissectum	1(0)					
Senecio triangularis	3(1)	1(0)		2(2)		
Thalictrum occidentale	4(22)	1(0)		8(17)		
Valeriana sitchensis	3(3)	3(2)		5(1)		
Viola orbiculata	1(0)		5(2)			
Xerophyllum tenax	8(38)	6(30)	5(30)			8(5)

Table 6—Topographical distribution of habitat types containing whitebark pine on noncalcareous and calcareous (limestone) substrates in the Scapegoat Wilderness, synthesized from Pfister and others (1976)

Environmental gradient	**Habitat type and phase (Pfister and others 1977)**	**Geologic substrate**			
		Noncalcareous		**Calcareous**	
		Elevation	**Aspect**	**Elevation**	**Aspect**
		Feet		*Feet*	
Warm/dry	PIAL and subalpine grasslands	[1]—	—	7,000-7,800	S
↑	ABLA-PIAL/VASC	—	—	7,000-8,000	all
	ABLA/LUHI-VASC	7,300-7,800	all	—	—
	ABLA/LUHI-MEFE	7,300-7,500	N&E	—	—
↓	PIAL-ABLA	7,800-8,300	NW,W, S, SE	8,000-8,500	all
Cold/wet	LALY-ABLA	7,700-8,600	N&E	—	—

[1] — = absent or scarce.

ACKNOWLEDGMENTS

The authors wish to acknowledge valuable technical advice provided by Peter Achuff, University of Alberta, Edmonton; Stephen V. Cooper, Ecological Consultant, Missoula, MT; Roger del Moral, University of Washington, Seattle; and R. T. Ogilvie, University of Victoria, Victoria, BC.

REFERENCES

Achuff, Peter L. 1989. Old-growth forests of the Canadian Rocky Mountain national parks. Natural Areas Journal. 9(1): 12-26.

Agee, James K.; Kertis, Jane. 1987. Forest types of the North Cascades National Park Service complex. Canadian Journal of Botany. 65(7): 1520-1530.

Arno, S. F. 1970. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Missoula, MT: University of Montana. 264 p. Dissertation.

Arno, S. F. 1986. Whitebark pine cone crops: a diminishing source of wildlife food. Western Journal of Applied Forestry. 1(3): 92-94.

Arno, S. F.; Habeck, J. R. 1972. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Ecological Monographs. 42: 417-450.

Arno, S. F.; Hammerly, Ramona P. 1984. Timberline—mountain and arctic forest frontiers. Seattle, WA: The Mountaineers. 304 p.

Baig, M. N. 1972. Ecology of timberline vegetation in the Rocky Mountains of Alberta. Calgary, AB: University of Calgary. Dissertation.

Barbour, M. G. 1988. Californian upland forests and woodlands. In: Barbour, M. G.; Billings, W. D., eds. North American terrestrial vegetation. New York: Cambridge University Press: 131-164.

Brink, V. C. 1959. A directional change in the subalpine forest-heath ecotone in Garibaldi Park, British Columbia. Ecology. 40: 10-16.

Cole, D. N. 1982. Vegetation of two drainages in Eagle Cap Wilderness, Wallowa Mountains, Oregon. Res. Pap. INT-288. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 42 p.

Cooke, W. B. 1940. Flora of Mount Shasta. American Midland Naturalist. 23: 497-572.

Cooke, W. B. 1955. Fungi of Mount Shasta (1936-1951). Sydowia, Annales Mycologici. 9: 94-215.

Craighead, J. J.; Sumner, J. S.; Scaggs, G. B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Wildlife-Wildlands Institute Monograph 1. Missoula, MT: University of Montana. 279 p.

Daubenmire, R.; Daubenmire, J. B. 1968. Forest vegetation of eastern Washington and northern Idaho. Tech. Bull. 60. Pullman, WA: Washington State University, Washington Agricultural Experiment Station. 104 p.

del Moral, R. 1979. High elevation vegetation of the Enchantment Lakes Basin, Washington. Canadian Journal of Botany. 57: 1111-1130.

Forcella, F. 1977. Flora, chorology, biomass and productivity of the *Pinus albicaulis-Vaccinium scoparium* association. Bozeman, MT: Montana State University. 99 p. Thesis.

Forcella, F. 1978. Flora and chorology of the *Pinus albicaulis-Vaccinium scoparium* association. Madrono. 25: 131-150.

Franklin, J. F.; Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 417 p.

Franklin, J. F.; Moir, W.; Douglas, G.; Wiberg, C. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arctic and Alpine Research. 3: 215-224.

Goldin, A. 1976. Effects of limestone soils on plant distribution in the Garnet Mountains, Montana. Missoula, MT: University of Montana. 115 p. Thesis.

Gruell, G. E. 1980. Fire's influence on wildlife habitat on the Bridger-Teton National Forest, Wyoming. Vol. I—Photographic record and analysis. Res. Pap. INT-235. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 207 p.

Habeck, J. R. 1987. Present-day vegetation in the Northern Rocky Mountains. Annals of the Missouri Botanical Gardens. 74(4): 804-840.

Hall, F. C. 1973. Plant communities of the Blue Mountains in eastern Oregon and southeastern Washington. R6 Area Guide 3-1. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 62 p.

Harlow, W.; Harrar, E. 1958. Textbook of dendrology. New York: McGraw-Hill. 555 p.

Hopkins, W. E. 1979. Plant associations of the Fremont National Forest. R6-Ecol-79-005. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 106 p.

Jackson, M. T.; Faller, A. 1973. Structural analysis and dynamics of the plant communities of Wizard Island, Crater Lake National Park. Ecological Monographs. 43: 441-461.

Klikoff, L. G. 1965. Microenvironmental influence on vegetational pattern near timberline in the central Sierra Nevada. Ecological Monographs. 35: 187-211.

Loope, L. L. 1969. Subalpine and alpine vegetation of northeastern Nevada. Durham, NC: Duke University. Dissertation.

Lueck, D. 1980. Ecology of *Pinus albicaulis* on Bachelor Butte, Oregon. Corvallis, OR: Oregon State University. 90 p. Thesis.

McAvoy, B. 1931. Ecological survey of the Bella Coola region. Botanical Gazette. 92: 141-171.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species—a literature review. Gen. Tech. Rep. PNW-87. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 72 p.

Pfister, R. P.; Arno, S. 1980. Classifying forest habitat types based on potential climax vegetation. Forest Science. 26: 52-70.

Pfister, R. P.; Kovalchik, B. L.; Arno, S.; Presby, R. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Pfister, R. P.; Kovalchik, B. L.; Ringleb, R. 1976. Scapegoat nonalpine vegetation. Unpublished report on file at: School of Forestry, University of Montana, Missoula, MT. 20 p.

Richards, J. H. 1981. Ecophysiology of a deciduous timberline tree, *Larix lyallii* Parl. Edmonton, AB: University of Alberta. 228 p. Dissertation.

Richards, J. H.; Bliss, L. C. 1986. Winter water relations of a deciduous timberline conifer, *Larix lyallii* Parl. Oecologia. 69: 16-24.

Sawyer, J. O.; Thornburgh, D. A. 1977. Montane and subalpine vegetation of the Klamath Mountains. In: Barbour, M.; Major, J., eds. Terrestrial vegetation of California. New York: John Wiley and Sons: 699-732.

Selby, C. J.; Pitt, M. D. 1984. Classification and distribution of alpine and subalpine vegetation in the Chilcotin Mountains of southern British Columbia. Syesis. 17: 13-41.

Steele, R.; Cooper, S. V.; Ondov, D.; Roberts, D.; Pfister, R. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

Steele, R.; Pfister, R.; Ryker, R.; Kittams, J. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 138 p.

Taylor, D. W. 1976. Vegetation near timberline at Carson Pass, central Sierra Nevada, California. Davis, CA: University of California. Dissertation.

U.S. Department of Agriculture, Forest Service. 1989. ECODATA database [computerized database that has 3,300 forest plots containing whitebark pine]. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Northern Region, Missoula, MT. Contact: Ecosystem Management Program, R.A.W.E., Northern Region, Federal Bldg., Missoula, MT.

Vale, T. R. 1977. Forest changes in the Warner Mountains, California. Annals of the Association of American Geographers. 67: 28-45.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. American Midland Naturalist. 92: 222-230.

Williams, C. K.; Lillybridge, T. 1983. Forested plant associations of the Okanogan National Forest. R6-Ecol-132b-1983. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 100 p.

WHITEBARK PINE ON THE MOUNT WASHBURN MASSIF, YELLOWSTONE NATIONAL PARK

David J. Mattson
Daniel P. Reinhart

ABSTRACT

Habitat distribution and stand dynamics of whitebark pine (Pinus albicaulis) *within the whitebark pine zone of the Mount Washburn massif, Yellowstone National Park were investigated as part of a study of relationships among grizzly bears, red squirrels, and whitebark pine. Distribution of whitebark pine and whitebark pine habitat types was positively associated with increased site coldness and wind exposure. Subalpine fir* (Abies lasiocarpa) *and Engelmann spruce* (Picea engelmannii) *were relatively intolerant of wind exposure. Whitebark pine and lodgepole pine* (Pinus contorta) *were principal seral species and competitors in the whitebark pine zone. Lodgepole pine replaced whitebark pine on the warmest sites of the zone. Whitebark pine was climax because of its ability to tolerate extreme site conditions rather than shade, and so was climax only on sites with the most extreme wind exposure at high elevations where other tree species could not survive. On the harshest sites whitebark pine recruitment into the overstory was near zero, but proportionately increased with site amelioration. Fire frequency in our study area was estimated to be 250 years, although stand replacement fires occurred somewhere in our study area at average 80-year intervals.*

INTRODUCTION

Relatively little is known about the autecology and stand dynamics of whitebark pine (*Pinus albicaulis*), especially in the lower portions of its zonal distribution where it grows in competition with other tree species. Forcella (1978), Forcella and Weaver (1977), and Weaver and Dale (1974) reported on the environment, productivity, and flora of whitebark pine-dominated stands in the Yellowstone area. However, their work was restricted to higher elevation stands where other tree species were a minor component and not a competitive factor.

In 1984 the Interagency Grizzly Bear Study Team (IGBST) initiated a study designed to investigate relationships among grizzly bears (*Ursus arctos horribilis*), red squirrels (*Tamiasciurus hudsonicus*), and whitebark pine. As part of this study, distribution and stand dynamics of whitebark pine were investigated in two study areas in the Yellowstone ecosystem. These study areas included the full spectrum of whitebark pine's zonal and habitat distribution.

In this paper we report results from our Mount Washburn study area that pertain to habitat distribution and competitive relationships of whitebark pine and stand dynamics within the whitebark pine zone. The whitebark zone is defined here as the geographical and elevational zone where whitebark pine is represented from variously isolated to nearly exclusive. Reinhart and Mattson (this proceedings) report results that pertain to red squirrel habitat relationships within the whitebark pine zone.

STUDY AREA

Our study area was located in Yellowstone National Park on the Mount Washburn massif, at 44°45' latitude. The study area was between 8,000 and 9,600 ft elevation and encompassed most of the elevational distribution of whitebark pine and most major habitat types of the whitebark pine zone in the Yellowstone area.

METHODS

We delineated and mapped stands using 1:20,000 color aerial photographs and USGS 15-ft topographic maps. We identified stands by discernible differences in stand structure and composition and by marked topographic clines. Each stand was classified according to standard habitat type (Steele and others 1983) and successional cover type (Despain 1986) classifications. (For habitat type and cover type nomenclature and acronyms used in this paper see appendixes A and B).

We sampled each stand with five to 26 systematically placed variable-radius standard forest inventory plots (Husch 1963:160). We used basal area factors of 20 and 40, and measured the diameter of all trees in the plot. Each tree was identified by species and whether dead or alive. Age and 10-year growth increment were recorded for each species and diameter class at each plot from increment cores. Stem densities and basal area were calculated by standard procedures for variable radius plots (Husch 1963).

We also calculated mortality rates by stem-diameter classes. These rates were based on approximately 10 years of mortality preserved in standing dead stems. Some bias in our calculated mortality rates was because

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

David J. Mattson is Wildlife Biologist and Daniel P. Reinhart is Wildlife Technician, Interagency Grizzly Bear Study Team, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717.

of movement of some live stems into a larger diameter class, while historical mortalities of those cohorts were attributed to the next smaller diameter class. Because of this likely bias and because mortality was spread over an extended time, calculated mortality rates are better viewed as an index, or at best a 10-year rate.

Stand and disturbance ages were estimated from examination of individual tree ages. Age was corrected for breast height by adding 20 years (Bunting 1989; Cole 1989). The oldest trees in a stand, regardless of species, were considered to best reflect stand age. Ages of stand disturbances were assumed to correspond to the oldest stand or individual tree ages.

We calculated several synthetic indices for our analysis of species and type distributions with respect to environment factors. Site radiation (*SR*) was derived from scaling (0 to 1.0) June 22 solar radiation (X_1) on site:

$$SR = (X_1 - 733)/100 \tag{1}$$

June 22 radiation (cal/cm²/day) was taken from tables that incorporated the effects of slope and aspect (Buffo and others 1972). Site warmth (*SW*) incorporated effects of elevation (X_2 in meters) and *SR* by adding *SR* and an inverse of scaled elevation (*E*):

$$E = (2896 - X_2)/609.6 \tag{2}$$

$$SW = E + SR \tag{3}$$

Wind exposure (*WE*) was also indexed by incorporating the effects of aspect and slope. Frequency of winds >5 mph by aspect class was taken from Dirks and Martner (1982), from their Upper Rendezvous site. Frequencies were applied to individual stands based on their aspect and multiplied by the sine of degrees of site slope. The resulting value (X_3) was scaled from 0 to 1.0 to derive *WE*:

$$WE = (X_3/100) - 0.09)/19.91 \tag{4}$$

Site favorability (*SF*), which was not used in this paper but was used by Reinhart and Mattson (this proceedings), was the difference of *SW* and ½ weighted *WE*:

$$SF = SW - \tfrac{1}{2}\,WE \tag{5}$$

RESULTS

Species Distribution

We examined distributions of the four major tree species in our study area with respect to site warmth and summer wind exposure. Distributions of whitebark pine and lodgepole pine (*Pinus contorta*) were typically more sensitive to site warmth; distributions of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) were more sensitive to wind exposure (fig. 1). Whitebark pine basal area increased with site coldness; this was most pronounced between warmth indices 1.25 and 1.00, and was highest on the coldest sites with moderate wind exposure. Lodgepole pine basal area increased with site coldness, most dramatically between warmth indices of 1.15 to 1.30. Basal areas of both subalpine fir and Engelmann spruce decreased with wind exposure to near zero on the most wind-exposed sites. Basal area of subalpine fir also decreased on the coldest and increased on the warmest protected sites. Engelmann spruce exhibited maximum local basal area on the coldest protected sites, where basal areas of both subalpine fir and lodgepole pine decreased, and at warmth indices between 1.00 and 1.25, where the most pronounced transition from lodgepole pine to whitebark pine occurred.

The distribution of whitebark pine basal area with respect to site warmth was exponential (fig. 2), with less variation in basal area on warmer sites. The lowest basal areas of whitebark pine occurred on sites with warmth indices >1.25. Only two of these warmest sites had whitebark pine basal area >50 ft²/acre.

Cover Type Distributions

Cover types reflect the relative stand structure of tree species and follow the descriptions of Despain (1986). Distribution of cover types followed environmental distribution of individual species (fig. 3). Lodgepole pine cover types were restricted to warmer, lower elevation sites. Whitebark pine cover types occurred on the coldest or highest elevation sites. Midsuccessional (LP2 and WB2) cover types occupied sites with greater summer radiation compared to later-successional cover types. Climax whitebark pine stands (WB), not shown in figure 3, were restricted to more open, high-elevation sites with high wind exposure.

Habitat Type Distributions

Distribution of habitat types (h.t.'s) in the whitebark pine zone was clearly associated with summer wind exposure (fig. 4). The whitebark pine (PIAL) series and the ABLA/SPBE h.t. were restricted to sites with high wind exposure (see appendix A for h.t. nomenclature). Only a few stands of the ABLA/VASC-PIAL phase and ABLA/THOC h.t. occurred on sites with high wind exposure; otherwise these and the ABLA/VAGL-VASC and ABLA/VASC-VASC types were restricted to sites with low to moderate exposure.

Among h.t.'s associated with high wind exposure, the ABLA/SPBE type was restricted to lower elevation sites of the whitebark pine zone with less incident radiation, and the PIAL series to higher elevations. Within the PIAL series, the PIAL/FEID h.t. was characteristic of cold sites and an as yet undefined, tentatively identified, PIAL/THFE h.t. was characteristic of warmer sites.

Distribution of habitat types on sites with lower wind exposure exhibited greater overlap (fig. 4). Distribution of the ABLA/VASC-VASC and ABLA/THOC types and the ABLA/VASC-PIAL and ABLA/VAGL-VASC types, respectively, overlapped considerably along elevation and summer radiation gradients. Core distribution of the ABLA/VASC-VASC and ABLA/THOC types was on the warmest sites of the whitebark pine zone. Core distribution of the ABLA/VAGL-VASC type overlapped almost completely with the ABLA/VASC-PIAL type on cool sites of the zone; the coldest sites were found exclusively on the ABLA/VASC-PIAL habitat type.

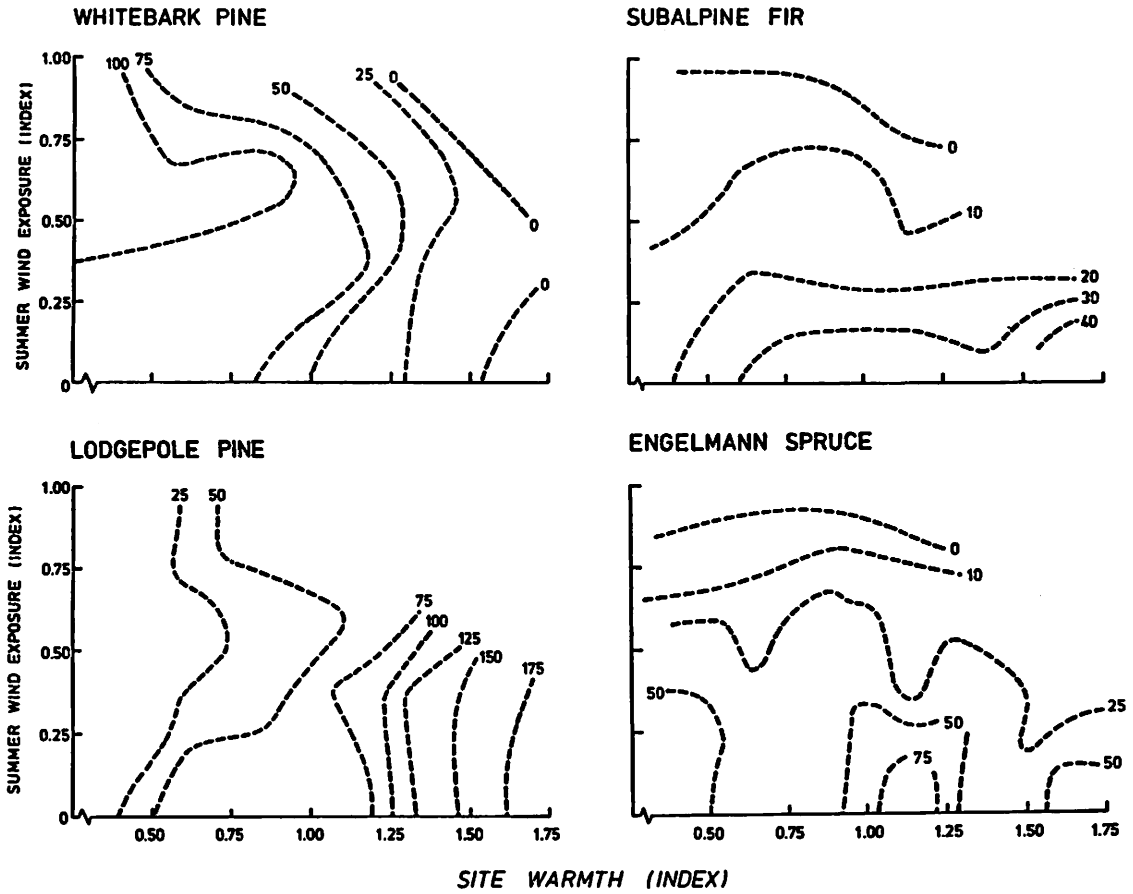


Figure 1—Basal area (ft²/acre) distribution of four major study area species with respect to site warmth and summer wind exposure.

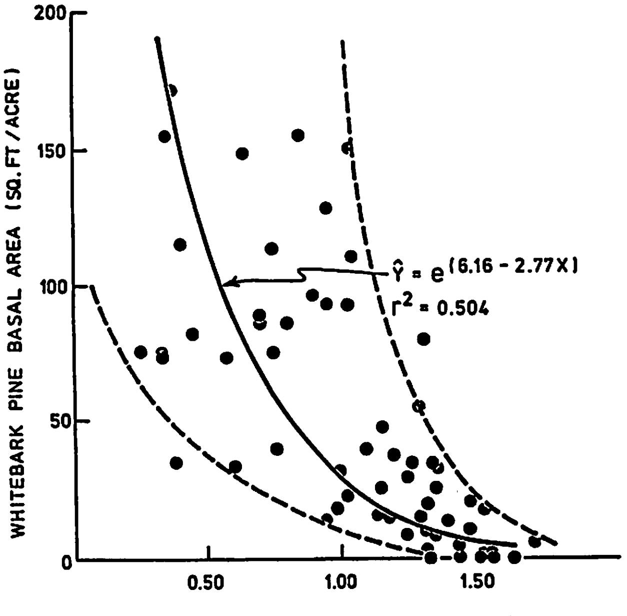


Figure 2—Relationship of whitebark pine basal area, on sites with low to moderate summer wind exposure, to site warmth.

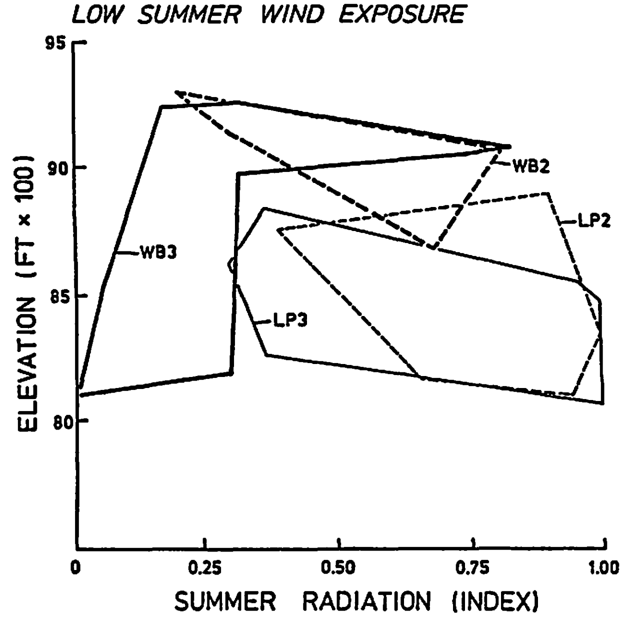


Figure 3—Distribution of cover types with respect to summer radiation and elevation, for sites with low to moderate summer wind exposure.

Growth and Age by Diameter Class

Cross-sectional growth rates of all four species tended to decline with increased diameter (fig. 5). This trend was most evident for Engelmann spruce and subalpine fir. Among all but the largest trees (≥19.7 inches d.b.h.) subalpine fir and Engelmann spruce were growing faster than whitebark pine and lodgepole pine. Among medium-diameter trees (9.8 to 13.8 inches d.b.h.) subalpine fir tended to be growing faster than Engelmann spruce.

Several distinctive patterns were evident in the distribution of ages with respect to diameter class. Among all but the largest trees, subalpine fir was consistently younger at a given diameter than the other three species. Among the smallest trees, the four species were clearly differentiated by age, with lodgepole the oldest and subalpine fir the youngest. These ages were a logical and inverse reflection of growth over a generally increasing period of time with increasing size, and suggested that among the smallest trees historical growth was greatest in subalpine fir and least in lodgepole pine. At the largest diameters a reverse pattern was evident among Engelmann spruce, whitebark pine, and lodgepole pine. This reverse pattern suggested that in the first years lodgepole pine grew the fastest and Engelmann spruce the slowest. Subalpine fir was anomalous, but was represented by very few large-diameter individuals.

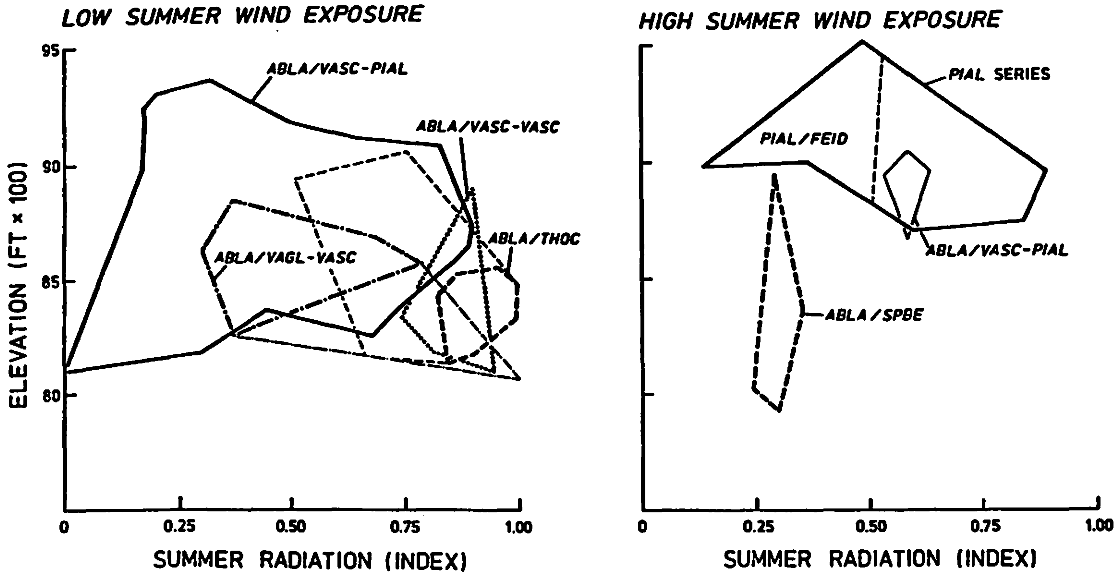


Figure 4—Distribution of habitat types with respect to summer radiation, elevation and summer wind exposure. Core and peripheral distributions of the Abla/Thoc and Abla/Vagl-Vasc types are denoted by thick and thin lines, respectively.

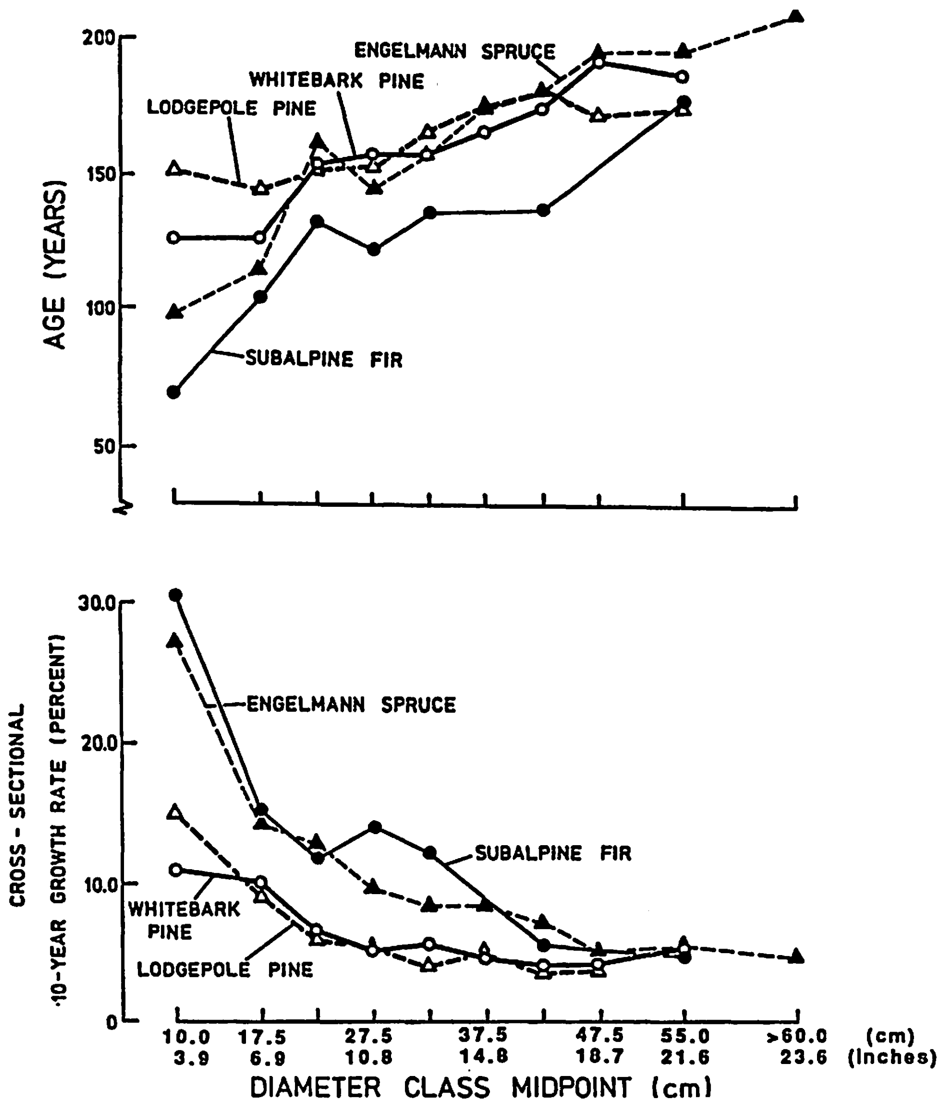


Figure 5—Mean age and cross-sectional growth rate of four major study area tree species with respect to diameter class.

Mortality and Stem Density of Whitebark Pine

Mortality of whitebark pine exhibited several patterns among size classes and habitat types (fig. 6). Averaged over all size classes, mortality was lowest in the PIAL series and highest on typically wet spruce-fir sites. In general, mortality rates irregularly decreased with increased stem diameter in all types. In the ABLA/VASC-PIAL and spruce-fir types, mortality peaked three times among small-, medium-, and large-diameter trees, respectively.

Stem densities and distribution of whitebark pine stems among size classes varied among types (fig. 6). Highest stem densities, especially among medium-diameter trees (5.9 to 15.7 inches d.b.h.), occurred in the PIAL series and ABLA/VASC-PIAL phase. Comparable densities of large-diameter (>15.7 inches d.b.h.) whitebark pine occurred in all of the types. Proportionately more small-diameter (<5.9 inches d.b.h.) stems occurred in, progressively, the PIAL series, ABLA/VASC-PIAL phase, mesic h.t.'s, and spruce-fir stands. By inference, proportionate recruitment of whitebark pine into the overstory also progressively increased in the same order among these types.

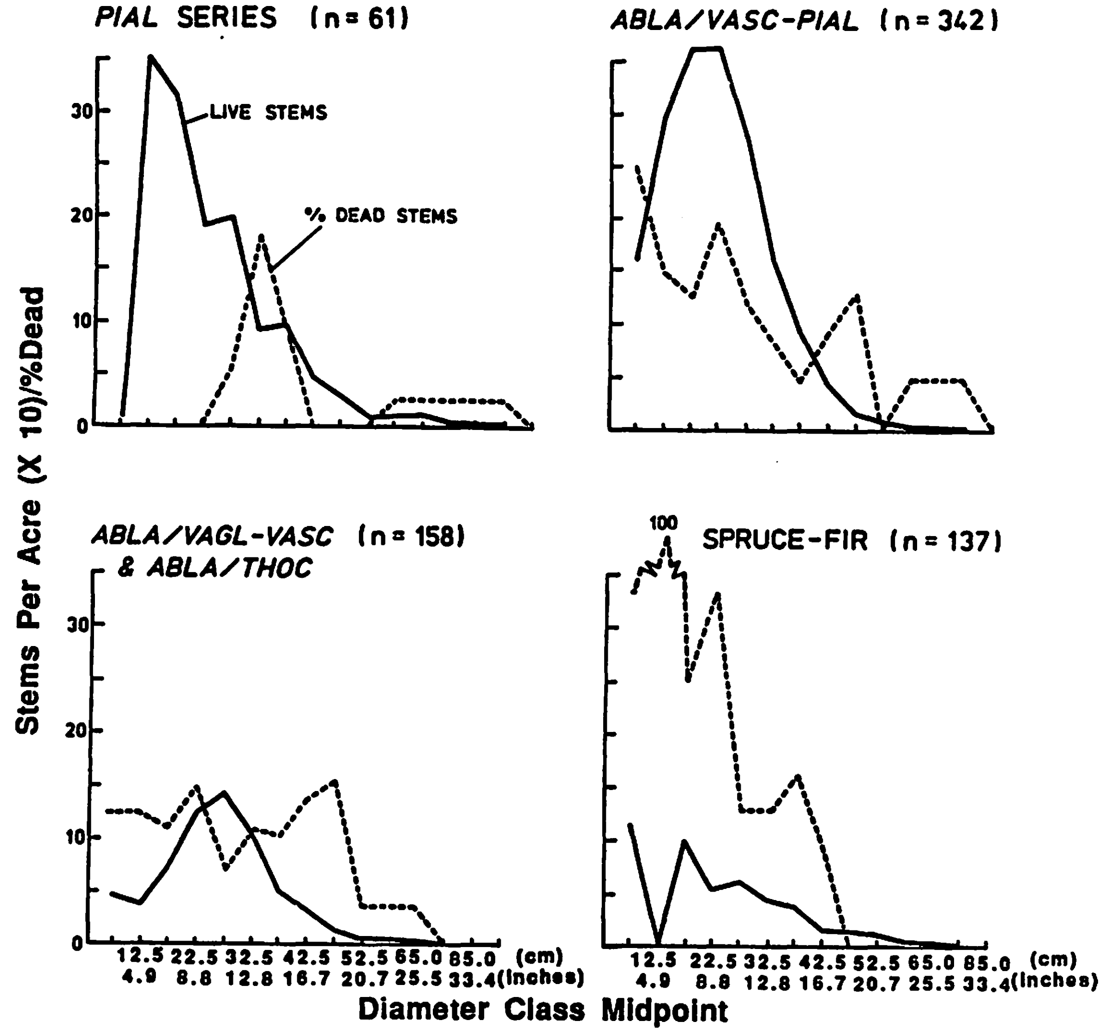


Figure 6—Mean stems per acre and percent dead stems of whitebark pine with respect to diameter class, for major study area cover and habitat types.

Basal Areas by Cover and Habitat Types

Average total basal area was relatively uniform for most habitat and cover types except for the PIAL series (table 1). In this series, total basal area was roughly one-half that of the other types, and consisted mostly of whitebark pine.

Whitebark pine basal area varied considerably among habitat and cover types (table 1). Whitebark pine basal area was typically highest in mid-successional cover types, and all cover types of the PIAL series and ABLA/VASC-PIAL phase. Lowest whitebark pine basal area occurred in spruce-fir cover types, and in the ABLA/THOC, ABLA/CACA, and ABLA/VASC-VASC types.

Stand Ages

Our study area included 82 stands approximately 150 to 310 years old (fig. 7). The majority of stands were between 180 and 270 years old. Roughly one-half of our study area burned in 1988.

We examined stand age distributions for the different successionally defined cover types (fig. 7). Although the late successional types (LP3 and WB3) included more older and fewer younger stands than the mid-successional types (LP2 and WB2), there was considerable overlap. The climax spruce-fir (SF) type also included a number of stands in the same age range as mid- and late-successional types, but typically included the oldest study area stands. Identification of the successional cover types of a stand in the whitebark pine zone is apparently more based on differences in stand species composition than on stand age.

Table 1—Total and whitebark pine basal area of habitat types and cover types of the Mount Washburn study area

			Basal area (ft^2/acre)				
			Total		Whitebark pine		
Habitat type	**Cover type**	***n***	$\bar{X}$	S_x	$\bar{X}$	S_x	**Percent of total**
PIAL series	WB2	3	106.7	—	83.6	—	78.0
	WB	4	98.0	34.0	84.9	35.7	86.0
ABLA/?[1]	WB3	4	134.1	39.2	64.0	22.2	48.0
ABLA/VASC-PIAL	WB2	6	186.8	34.0	121.5	39.2	65.0
	WB3	14	211.7	45.3	108.9	27.9	51.0
	LP2	3	210.8	—	28.7	—	14.0
	LP3	5	240.0	40.9	31.8	17.4	13.0
	SF	6	230.0	52.3	41.8	17.4	18.0
ABLA/VASC-VASC	LP2	5	219.5	34.8	9.6	5.7	4.5
ABLA/VAGL-VASC	LP3	6	191.2	20.5	42.7	32.2	22.0
	SF	2	220.8	—	4.4	—	2.0
ABLA/THOC	LP2	5	220.4	46.6	5.2	8.3	2.5
	LP3	4	211.2	36.6	19.6	24.0	9.0
ABLA/CACA	SF	3	239.1	—	25.7	—	11.0

[1] These stands could be a high-elevation variant of the ABLA/THOC h.t., but material identified as *Thalictrum occidentale* is in question and could be *T. fendleri*.

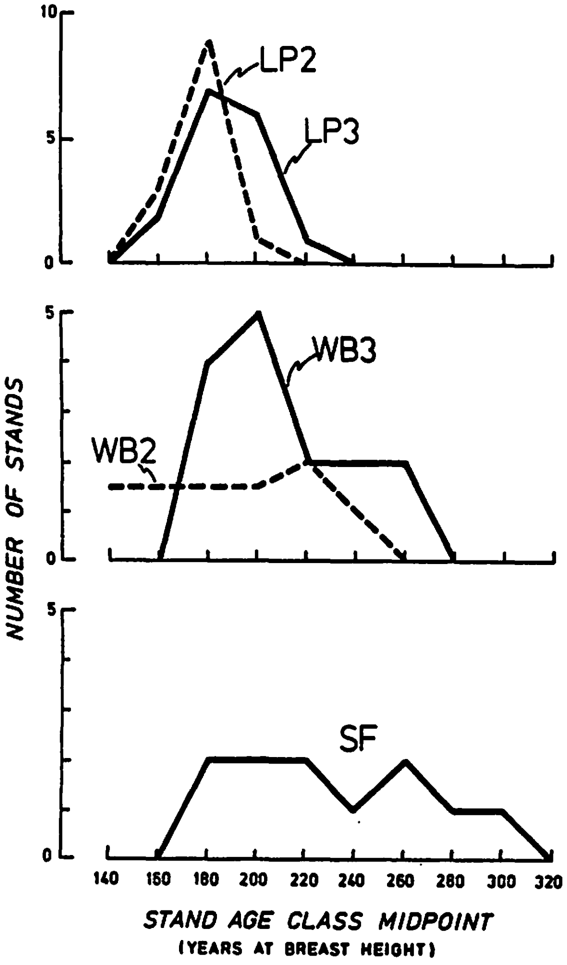


Figure 7—Frequency of stands with respect to stand age at breast height.

Tree Ages

We sampled individual tree ages on variable radius plots. For any given size class we sampled species relative to their proportionate representation. However, we sampled larger trees with proportionately much greater intensity than smaller trees. In figure 8 the relative pattern of species was significant, but absolute frequencies by age class merely reflected our sampling intensity.

We were able to assess two phenomena by species age-class frequencies in our study area (fig. 8): (1) relative rates of establishment after stand replacement and (2) approximate dates of stand replacement disturbances. The timing of peak frequencies for each species suggested that establishment and growth of whitebark pine to breast height (4 ft) lagged approximately 10 years behind that of lodgepole pine, and that establishment and growth of Engelmann spruce lagged 10 to 20 years behind that of whitebark pine. Subalpine fir patterns showed no easily identifiable relationship with the other species patterns, although there were proportionately more young subalpine fir compared to the other three species. Among the oldest stands, relative abundance of trees reversed from the order [lodgepole (1), whitebark pine (2), and Engelmann spruce (3)] characteristic of younger stands. From all tree ages we were also able to detect four stand-replacement fires in our study area (fig. 8). Using all tree ages, historic disturbances dated to approximately 1820, 1790, 1730 to 1760, and 1670.

DISCUSSION

The nature and limited geographic scope of our study imposed certain constraints on our analysis and conclusions. We did not sample young or very old stands. We were therefore unable to analyze growth of the tree species through time and address certain aspects of stand dynamics more definitively. We also did not include many stands on east and south aspects due to the location of our transects on primarily west exposures. South aspects, however, were characterized by a paucity of forest cover. We were also unable to take exhaustive age data due to study priorities and limited available time. However, within these constraints we were able to glean a considerable amount of valuable information from our data.

Whitebark Pine Autecology

Whitebark pine and lodgepole pine were distinguished from subalpine fir and Engelmann spruce by their greater occurrence on drier sites associated with increased wind exposure, that is, on sites with steeper slopes and higher mean summer windspeeds. We used summer rather than winter windspeeds in our analysis because of their stronger apparent relationship to tree species distributions in our study area. Whitebark pine was further distinguished from lodgepole pine by its greater apparent tolerance of cold, although not necessarily frosty, sites.

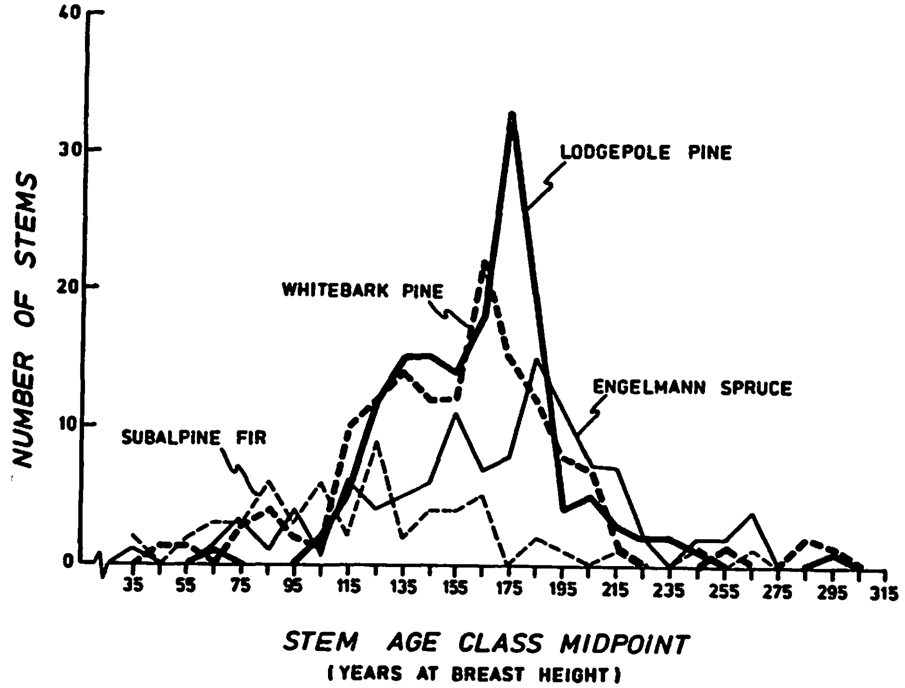


Figure 8—Frequency of stems with respect to stem age at breast height, for four major study area tree species.

With increasing elevation or colder exposures whitebark pine replaced lodgepole pine. The greatest rate of transition from whitebark to lodgepole pine occurred in association with the warmest sites of the whitebark pine zone. Subalpine fir and Engelmann spruce appeared to be less sensitive to site warmth, although abundance of subalpine fir declined and Engelmann spruce increased on the coldest sites.

Lodgepole pine and whitebark pine exhibited characteristics typical of early successional or relatively shade-intolerant species. Initial growth and establishment of both these species appeared to be greater than that of Engelmann spruce. In mid- to late-successional stages in our study area, general growth of the pines was slower than spruce and fir growth, although dominant large-diameter pines appeared to grow as well as comparable size spruce and fir. Differences in growth rates and apparent rates of establishment between lodgepole and whitebark pine could be attributed to differential distribution of whitebark pine on colder and presumably less productive sites, given that we agglomerated stands from the entire whitebark pine zone for our analysis of growth. On the other hand, slightly better apparent growth under closed-canopy conditions and lag in initial growth and establishment of whitebark pine compared to lodgepole pine could indicate greater shade tolerance—hence a tendency toward intermediate successional status for whitebark pine.

Arno and Habeck (1972) and Arno and Hoff (1989) ascribed greater shade tolerance to whitebark pine than to lodgepole pine. Similarly, Knowles and Grant (1983) considered the ecologically related limber pine (*Pinus flexilis*) to be intermediate in successional status between lodgepole pine and Engelmann spruce. Given this context, we suspect that our results are best interpreted as corroborating those earlier observations that whitebark pine is intermediate in shade tolerance between Engelmann spruce and lodgepole pine, although more similar in tolerance to lodgepole pine.

Sudworth (1967) commented that whitebark pine was more shade tolerant on deeper, moist soils at lower elevations than on drier, shallower soils near timberline. Greater environmental stress would logically impair the physiological efficiency of a species; in a tree this would very likely be manifested as a higher light compensation point (Kozlowski 1979; Kramer and Kozlowski 1960; Tranquillini 1979). Our results suggest that recruitment of whitebark pine into the overstory is proportionately least on the harshest sites of the Pial series and progressively greater with site amelioration; recruitment appears to be proportionately greatest on the mesic or lower elevation habitat types of the whitebark pine zones. These results corroborate the hypothesis that whitebark pine is more shade tolerant with site amelioration.

This tendency contrasts with the proclivity of whitebark pine to dominate a site. In our PIAL series, where whitebark pine is the climax dominant, whitebark does not appear to replace itself with great frequency. Other studies of near-pure stands of whitebark pine and ecologically related species—limber pine and Siberian stone pine (*Pinus sibirica*)—also show a lack of recruitment in mature stands (Iroshnikov and others 1963; Jackson and Fuller 1973; Knowles and Grant 1983). In the PIAL series, persistence of whitebark pine is probably dependent on stand gaps, widely dispersed in time and space, and on stand-replacement fires (Arno 1980; Fischer and Clayton 1983).

Our results suggest that lodgepole pine and whitebark pine are major competitors during early stages of stand development. Engelmann spruce also appears to be a major component of the initial stand, but at the same time appears to be more opportunistic and less competitive in these early stages. Whitebark pine has the apparent advantage over lodgepole pine on increasingly colder sites. We hypothesize that the absence of whitebark pine from forest overstories on warmer sites within the whitebark pine zone or at lower elevations is due largely to competitive exclusion, especially by lodgepole pine. Critchfield and Allenbaugh (1969) offered some anecdotal support for this hypothesis. At a latitude 3° farther south than our study area, they observed whitebark pine well represented as low as 6,400 ft in a mountain range without any other pine species. In two other mountain ranges at the same latitude, they observed whitebark pine to be common only down to 8,400-ft elevation, and replaced at lower elevations by limber pine. In our study area, whitebark pine is similarly well represented down to 8,200-ft elevation. In the absence of its other hypothesized major competitor, lodgepole pine, whitebark pine may very well be capable of attaining stand dominance on warmer sites.

Whitebark pine appears to be climax in a limited habitat characterized by high wind exposure and high elevations. Arno and Habeck (1972), Arno and Hoff (1989), Jackson and Fuller (1973), Steele and others (1983), and Sudworth (1967) also associated near-pure stands of whitebark pine with sites exposed to wind and sun. Climax subalpine limber pine stands in the Colorado Front Range are similarly associated with exposed drier sites (Peet 1981).

Climax status of whitebark pine appears to be by default. Whitebark pine apparently tolerates conditions associated with extreme wind exposure better than its competitors (Steele and others 1983), and is not climax in the classic sense of having greater shade tolerance (Emlen 1973:354). Stem frequencies of whitebark pine relative to diameter in the PIAL series do not exhibit the "inverse-J" pattern usually associated with a climax species (Whipple and Dix 1979). Basal area and overstory stem densities of whitebark pine are similar in the ABLA/VASC-PIAL phase and PIAL series. The two types are notably different by the absence of other tree species in the PIAL series. Whitebark pine, like lodgepole pine, appears to be climax because of its tolerance of extreme site conditions rather than competitive ability vis-a-vis other species under mature stand conditions (Despain 1983; Pfister and others 1977; Whipple and Dix 1979).

Stand Dynamics and Classification

Stand-replacement fires burned somewhere in our study area at relatively frequent, average 80-year, intervals. Given that virtually all our study area was burned at least once in a 300-year period and we found few 300-year-old stands, we speculate that our entire study area had a fire cycle of approximately 300 years' duration. This fits within the roughly 60- to 300-year fire frequency cycle documented for the whitebark pine zone by Arno (1980).

Our data suggest the prevalence of succession by "initial floristic composition" rather than "relay floristics" (Mueller-Dombois and Ellenberg 1974:395) in the tree strata of our study area. Subalpine fir increases markedly in the understory with stand age, but is represented at stand initiation, and rarely achieves stand dominance due to a prolonged seral stage relative to fire frequency. Relative composition of the overstory only begins to change markedly approximately 200 years after stand initiation.

Caution should be used when inferring successional status from cover type designations in the whitebark pine zone. Our classification of stands according to successional cover types was apparently determined as much by initial stand composition as by stand age (successional status). Stands classified as spruce-fir (SF) did not reflect progression to climax, but rather wetter or more protected sites and variants of habitat types where initial establishment of spruce and fir was favored. Similarly, some stands classified as mid-successional WB2 types merely reflected conditions where establishment of whitebark pine was favored over sites with comparably aged stands classified as late-successional WB3 types. These aberrations reflect the persistent expression of initial floristic composition in stands of a zone where growth and turnover of individuals are relatively slow.

THE FUTURE

Much of the discussion presented here is speculative. Researchers have enough collective information at this point to generate well-founded hypotheses, but few definitive studies to test them and, from their conclusions, to direct management. To further test our hypotheses and speculations, we especially need comparative physiological studies that deal with whitebark pine and its potential competitors and survey studies that can provide additional data for modeling efforts. Our future management of whitebark pine and its seed crops for a host of vertebrate species will only be as good as our understanding of its habitat and competitive relationships.

REFERENCES

Arno, Stephen F. 1980. Forest fire history in the Northern Rockies. Journal of Forestry. 78(8): 460-465.

Arno, Stephen F.; Habeck, James R. 1972. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Ecological Monographs. 42: 417-450.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Buffo, Fred; Fritschen, Leo J.; Murphy, James L. 1972. Direct solar radiation on various slopes from 0 to 60 degrees north latitude. Res. Pap. PNW-142. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 74 p.

Bunting, S. 1989. [Personal communication]. March 29. Moscow, ID: University of Idaho, Moscow, ID.

Cole, D. 1989. [Personal communication]. March 15. Bozeman, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Critchfield, William B.; Allenbaugh, Gordon L. 1969. The distribution of Pinaceae in and near northern Nevada. Madrono. 19(1): 12-26.

Despain, Don G. 1983. Nonpyrogenous climax lodgepole pine communities in Yellowstone National Park. Ecology. 64(2): 231-234.

Despain, Don G. 1986. Habitat type and cover type as a base for grizzly bear habitat mapping and evaluation. In: Proceedings—Grizzly bear habitat symposium; 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 230-233.

Dirks, Richard A.; Martner, Brooks E. 1982. The climate of Yellowstone and Grand Teton National Parks. Occ. Pap. 6. Washington, DC: U.S. Department of the Interior, National Park Service. 26 p.

Emlen, J. Merritt. 1973. Ecology: an evolutionary approach. Reading, MA: Addison-Wesley Publishing. 493 p.

Fischer, William C.; Clayton, Bruce D. 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. Gen. Tech. Rep. INT-141. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 83 p.

Forcella, Frank. 1978. Flora and chorology of the *Pinus albicaulis-Vaccinium scoparium* association. Madrono. 25: 139-150.

Forcella, F.; Weaver, T. 1977. Biomass and productivity of the subalpine *Pinus albicaulis-Vaccinium scoparium* association in Montana, USA. Vegetatio. 35(2): 95-105.

Husch, Bertram. 1963. Forest mensuration and statistics. New York: The Ronald Press. 474 p.

Iroshnikov, A. I. 1963. Fruit bearing of stone pine forests in the northwestern part of the eastern Sayan. In: Shimanyuk, A. P., ed. Fruiting of the Siberian stone pine in East Siberia. Academy of Science of the USSR Siberian Department. Trans. of the Institute of Forest and Wood Processing. Israel Program for Science Translations, Jerusalem, 1966. 62: 98-109.

Jackson, M. T.; Fuller, Adolph. 1973. Structural analysis and dynamics of the plant communities of Wizard Island, Crater Lake National Park. Ecological Monographs. 43: 441-461.

Knowles, Peggy; Grant, Michael C. 1983. Age and size structure analysis of Engelmann spruce, ponderosa

Knowles, Peggy; Grant, Michael C. 1983. Age and size structure analysis of Engelmann spruce, ponderosa pine, lodgepole pine, and limber pine in Colorado. Ecology. 64(1): 1-9.

Kozlowski, Theodore. 1979. Tree growth and environmental stress. Seattle, WA: University of Washington Press. 192 p.

Kramer, Paul J.; Kozlowski, Theodore T. 1960. Physiology of trees. New York: McGraw-Hill. 642 p.

Mattson, David J.; Despain, Don G. 1985. Grizzly bear habitat component mapping handbook for the Yellowstone ecosystem. Unpublished handbook. Yellowstone National Park, WY: U.S. Department of the Interior, National Park Service; U.S. Department of Agriculture, Forest Service. 37 p.

Mueller-Dombois, Dieter; Ellenberg, Heinz. 1974. Aims and methods of vegetation ecology. New York: John Wiley and Sons. 547 p.

Peet, P. K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. Vegetatio. 45(1): 3-75.

Pfister, Robert D.; Kovalchik, B. L.; Arno, Stephen F.; Presby, Richard C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Steele, Robert; Cooper, Stephen V.; Ondov, David M.; Roberts, David W.; Pfister, Robert D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

Sudworth, George B. 1967. Forest trees of the Pacific slope. New York: Dover Publications, Inc. 455 p.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. New York: Springer-Verlag. 137 p.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. The American Midland Naturalist. 92(1): 222-230.

Whipple, Stephen A.; Dix, Ralph L. 1979. Age structure and successional dynamics of a Colorado subalpine forest. The American Midland Naturalist. 101(1): 142-158.

APPENDIX A—HABITAT TYPE NOMENCLATURE AND ACRONYMS (STEELE AND OTHERS 1983; THIS STUDY)

Acronym	Common name	Scientific name
PIAL series	Whitebark pine series	*Pinus albicaulis* series
PIAL/FEID h.t.	Whitebark pine/Idaho fescue h.t.	*P. albicaulis/Festuca idahoensis* h.t.
PIAL/THFE h.t.	Whitebark pine/Fendler's meadowrue h.t.	*P. albicaulis/Thalictrum fendleri* h.t.
ABLA/VASC-PIAL phase	Subalpine fir/grouse whortleberry-whitebark pine phase	*Abies lasiocarpa/Vaccinium scoparium-P. albicaulis* phase
ABLA/VASC-VASC phase	Subalpine fir/grouse whortleberry-grouse whortleberry phase	*A. lasiocarpa/V. scoparium-V. scoparium* phase
ABLA/VAGL-VASC phase	Subalpine fir/globe huckleberry-grouse whortleberry phase	*A. lasiocarpa/V. globulare-V. scoparium* phase
ABLA/THOC h.t.	Subalpine fir/western meadowrue h.t.	*A. lasiocarpa/Thalictrum occidentale* h.t.
ABLA/SPBE h.t.	Subalpine fir/shiny-leaf spiraea h.t.	*A. lasiocarpa/Spiraea betulifolia* h.t.

APPENDIX B—SUCCESSIONAL COVER TYPES (DESPAIN 1986; MATTSON AND DESPAIN 1985)

Lodgepole Pine Types

COVER TYPE—30 (LP0)

Recently burned or harvested lodgepole pine stands in the grass to seedling/sapling stage before canopy closure. Approximately 0-40 years postfire.

COVER TYPE—31 (LP1)

Closed canopy of even-aged, usually dense, lodgepole pine where trees are younger and shorter than those of neighboring stands. Young pole successional stage. On outwash at West Yellowstone, it is represented by islands of scattered short trees next to islands of scattered larger trees. Approximately 40-100 years postfire.

COVER TYPE—32 (LP2)

Closed canopy dominated by lodgepole pine. Overstory still largely intact. Mature lodgepole pine successional stage. Understory usually small to medium Engelmann spruce and subalpine fir seedlings and saplings but also may be mostly lodgepole pine. Approximately 100-300 years postfire.

COVER TYPE—33 (LP3)

Canopy quite ragged, predominately of overmature lodgepole pine but containing some Engelmann spruce, subalpine fir, and whitebark pine in the pole-sized class. Old-growth lodgepole pine successional stage. Understory of small to large spruce and fir seedlings and saplings. Three hundred plus years postfire.

COVER TYPE—34 (LP)

Canopy dominated by overmature lodgepole pine beginning to break up. Understory of lodgepole pine and whitebark pine. Stands usually on rhyolite and multiaged. Lodgepole is climax or persistent seral species. Three hundred plus years postfire.

Whitebark Pine Types

COVER TYPE—50 (WB0)

Recently burned whitebark pine stands usually near upper timberline where whitebark pine clearly dominates reproduction.

COVER TYPE—51 (WB1)

Even-aged, closed whitebark pine stands where trees are younger and shorter than those of neighboring stands. Trees are small pole sized.

COVER TYPE—52 (WB2)

Closed canopy dominated by whitebark pine. Overstory still largely intact. Trees pole to mature sized. Understory usually small to medium Englemann spruce and subalpine fir seedlings and saplings but may be mostly whitebark pine. Approximately 100-300 years postfire.

COVER TYPE—53 (WB3)

Stands dominated by mature whitebark pine and may also contain considerable Engelmann spruce, subalpine fire, or lodgepole pine. Understory is a combination of Engelmann spruce, subalpine fir, and whitebark pine.

COVER TYPE—54 (WB)

Stands of mature to overmature whitebark pine where the reproduction is nearly all whitebark pine.

COEVOLUTION OF WHITEBARK PINE AND NUTCRACKERS: IMPLICATIONS FOR FOREST REGENERATION

Diana F. Tomback
Lyn A. Hoffmann
Sharren K. Sund

ABSTRACT

Clark's nutcracker (Nucifraga columbiana) *is the primary disperser of the large, wingless seeds of whitebark pine* (Pinus albicaulis). *The seed-storing habits of nutcrackers influence whitebark pine distribution, site preference, and population structure. In the northern Rocky Mountains, periodic fires followed by seed dispersal by nutcrackers regenerate seral whitebark pine communities. Data from two burns in the Bitterroot National Forest, Montana, show similar whitebark pine regeneration patterns and densities but different subalpine fir densities. Seed dispersal by nutcrackers may give whitebark pine a competitive edge over subalpine fir in very large burns, particularly where wind patterns are unfavorable for subalpine fir seed dispersal.*

INTRODUCTION

The seeds of most conifers are disseminated by wind, but the large, wingless seeds of whitebark pine (*Pinus albicaulis* Engelm.) are disseminated primarily by Clark's nutcracker (*Nucifraga columbiana* Wilson) (Hutchins and Lanner 1982; Tomback 1978, 1982). Dispersal is effected by the seed-storing habits of the bird, which profoundly influence many aspects of the biology of the pine. In this paper we briefly review salient features of the ecological interaction between whitebark pine and the nutcracker, emphasizing the role of the nutcracker in forest regeneration. We also illustrate the importance of seed dispersal by nutcrackers in maintaining seral whitebark pine communities in the northern Rocky Mountains with recent data on postfire forest regeneration in the Bitterroot National Forest of western Montana.

THE NUTCRACKER-PINE INTERACTION

Eight of the 100 or so pine species are known to be dispersed by two birds of the family Corvidae, the Clark's nutcracker of western North America and the Eurasian nutcracker (*N. caryocatactes* [L.]) of Europe and Asia. The known nutcracker-dependent pines of the United States are the Colorado pinyon (*P. edulis* Engelm.) and the singleleaf pinyon (*P. monophylla* Torr. and Frem.) (Vander Wall and Balda 1977; Vander Wall 1987), whose seeds also are dispersed by the pinyon jay (*Gymnorhinus cyanocephalus* Weid) (Ligon 1978; Vander Wall 1987), limber pine (*P. flexilis* James) (Lanner and Vander Wall 1980), and whitebark pine (Hutchins and Lanner 1982; Tomback 1978, 1981, 1982). Dependence on birds for seed dispersal apparently has resulted in character convergence among pines of different taxonomic affinities; all have large, wingless seeds and, with the exception of limber pine, seed retention in cones (Lanner 1980, 1982; Tomback 1983). In the pinyon pines, seeds are held in place by bracts in dehisced cones; in whitebark pine, the ripe cones are indehiscent. Because large, wingless seeds and seed retention increase foraging efficiency of nutcrackers, the birds first deplete seeds from pines with these traits before moving to sympatric wind-dispersed species (Tomback 1978; Vander Wall and Balda 1977; but see Tomback and Linhart 1990).

The nutcrackers are also morphologically adapted to the interaction. Their sturdy, long, pointed bills are used to open pine cones and extract seeds (Tomback 1978; Vander Wall and Balda 1977). They also use their bills to dig sites for seeds in mineral soil; and they thrust seeds into place in sandy soil or loose substrates (Tomback 1978). By means of the sublingual pouch, a saclike extension of the floor of the mouth (Bock and others 1973), a nutcracker may transport up to 150 whitebark pine seeds at a time (Tomback 1982). Each nutcracker recovers its own seed stores by means of a remarkable spatial memory (Kamil and Balda 1985; Tomback 1980; Vander Wall 1982).

The historical origin of nutcracker-dispersed pines, previously discussed by Lanner (1980), Tomback (1983), and Tomback and Linhart (1990), is briefly summarized here. Whitebark pine is the only North American pine in the subsection Cembrae (Critchfield and Little 1966). The other four Cembrae pines, the stone pines of Europe and Asia, depend on the Eurasian nutcracker for seed dispersal (Turcek and Kelso 1968). *Nucifraga* and Cembrae pines probably coevolved in Eurasia, and forms ancestral to Clark's nutcracker and the whitebark pine crossed the Bering Strait land bridge into North America (Lanner 1980; Turcek and Kelso 1968). In North America, seed-storing jays probably influenced the evolution of limber pine (Lanner 1980) and the pinyon pines (Tomback 1983).

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Diana F. Tomback is Associate Professor, Department of Biology, University of Colorado at Denver, Denver, CO 80204. In 1987 and 1988, Lyn A. Hoffmann and Sharren K. Sund were Graduate Research Assistants in the same department. Currently, Lyn A. Hoffmann is a Graduate Student, Department of Range Science, and Sharren K. Sund is Research Associate, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523.

As a consequence of range expansion by either the birds or the pines, nutcrackers found these pines to be attractive food sources. If this sequence of events is correct, the relationship between the Clark's nutcracker and whitebark pine was coevolved; the relationship with the other New World wingless-seed pines was initially coadapted (based on adaptations evolved for other mutualists) (Tomback 1983).

Assuming that seed dispersal by wind is an ancestral state, Lanner (1980) suggested a connection among seed dispersal by birds, wingless seeds, xeric or high-elevation environment, and large seed size. Large seed size under stressful conditions allows rapid, early growth (Baker 1972). It is possible that ancestral pines encountered rigorous semiarid and subalpine environments, either by climatic change or by range expansion, and evolved larger seeds. This, in turn, decreased the effectiveness of anemochory and attracted seed-storing jays or nutcrackers (Tomback 1983). If the sites selected by the birds were incompatible with the germination and growth requirements of a pine, the pines could not evolve bird-dependence. However, if the sites were compatible with some genotypes, seed wings might decrease in size and bird-dependency evolve (Tomback 1983). This evolutionary scenario and proposed genetic mechanisms are discussed at length in Tomback and Linhart (1990). Why winglessness and bird-dependency are not as prevalent in the pine subgenus *Pinus* (yellow or hard pines) as they are in the subgenus *Strobus* (white or soft pines) remains unclear.

SEED DISPERSAL BY NUTCRACKERS

Nutcrackers have a year-round diet of fresh and stored pine seeds, supplemented by insects and various plant foods (Giuntoli and Mewaldt 1978; Tomback 1978). Stored seeds are used during winter and spring months when other foods are scarce (Tomback 1978) and are fed, almost exclusively, to nestlings and dependent juveniles (Mewaldt 1956; Tomback 1978; Vander Wall and Hutchins 1983).

With respect to quantities of seeds dispersed and the burial of seeds at cache sites, nutcrackers are highly efficient seed dispersers. In late summer and fall, a single nutcracker may store between 32,000 (Tomback 1982) and 98,000 (Hutchins and Lanner 1982) whitebark pine seeds. Seeds are buried under 1 to 3 cm of soil in clusters of 1 to 15 seeds with a mean of 3 or 4 seeds per site (table 1). Tomback (1982) estimated that a population of 25 nutcrackers stored about 800,000 seeds within a

Table 1—Cache and cache site characteristics of Clark's nutcracker. Modified from Tomback and Linhart (1990)

Characteristic			**Characteristic**		
No. of seeds per cache			**Characteristics of storage slopes**		
$\bar{X}$	**S.D.**	**Range**	**Exposure**	**Slope**	**Substrate**
3.7	2.9	1-15 (a)	SE,S,SW,WSW	22-30°	pumice or gravel (f)
3.2	2.8	1-14 (b)	southern	25-33°	loose gravel (e)
4.2	3.1	1-5 (c)	**Microhabitats of cache sites**		
4.0	2.7	1-14 (d)	Base of trees or under canopy, near logs, in small plants, open substrate. (b,e,f)		
Cache depth (cm)			Forest litter, among tree roots, in trees. (f)		
$\bar{X}$	**Range**				
2.0	1-3 (a)		In moss. (b)		
about	2-3 (b)		Barren ledges and fissures on rock walls. (g)		
Distance seeds transported (km)					
7.5, 22 (e)			In forest floor of burned and live krummholz pine. (h)		
2.5, 4.5, 8-10, 12.5 (f)					
3.5 (b)			Steep slopes among rocks and vegetation, and cracks in granite (ESE,NW). At edges of meadows among grasses, sedges and rocks. (i)		

Reference	***Pinus***	**Geographical location**
(a) Tomback (1982)	*albicaulis*	eastern California
(b) Hutchins and Lanner (1982)	*albicaulis*	western Wyoming
(c) Lanner and Vander Wall (1980)	*flexilis*	northwestern Utah
(d) Vander Wall and Balda (1981)	*edulis*	northern Arizona
(e) Vander Wall and Balda (1977)	*edulis*	northern Arizona
(f) Tomback (1978)	*albicaulis*	eastern California
(g) Tomback and Kramer (1980)	*flexilis*	eastern California
(h) Tomback (1986)	*albicaulis*	eastern California
(i) Tomback and Knowles (1984)	*albicaulis*	western Wyoming

50-ha area (16,000 seeds/ha) in the California Sierra Nevada range. Vander Wall and Balda (1977) estimated that a population of 150 nutcrackers stored between 3 and 5 million Colorado pinyon seeds in their San Francisco Mountains study area in northern Arizona. According to calculations by Vander Wall and Balda (1977) and Tomback (1982), the number of seeds stored per bird represents several times its energy requirements during the period the seeds are used.

Nutcrackers may bury caches near parent trees, or they may travel distances of a few to 22 km (table 1), often with substantial changes in elevation (Tomback 1978; Vander Wall and Balda 1977). The sites selected for seed storage are on forest floor, above treeline, on rocky outcrops, in meadow edges, in clearcuts, and in burns. Often, a steep, south-facing slope may be used by a local population of birds (table 1). Seed storage in south-aspect or wind-blown sites probably ensures that some caches are snow-free in winter and spring. Placement of caches at different elevations relates to later seasonal altitudinal movements (Tomback 1978). Caches not recovered by nutcrackers may germinate in spring and summer, producing clusters of seedlings (Tomback 1982).

The seed shadow (seed dispersal pattern) of a wind-dispersed conifer typically conforms to a negative exponential distribution; most seeds land within 20 to 50 m of the parent tree, and few seeds travel beyond 60 to 250 m (McCaughey and others 1986). The seed shadow of whitebark pine may also resemble a negative exponential distribution (Sund 1988; Sund and others 1989; Tomback and others 1989a), but because of the distances that nutcrackers travel and the variety of sites used for seed storage, the seed shadow is far more extensive and unpredictable than that of wind-dispersed conifers (Tomback and Linhart 1990). One nutcracker may disperse seeds from one stand of trees to different areas. Within these areas, more than one nutcracker may store seeds, each bird with seeds from a different stand of trees. Nutcrackers may disperse seeds far from other trees, resulting in "outlying" individuals and a pioneering status for whitebark pine. In addition, by caching seeds at high elevations, nutcrackers may maintain timberline at the highest climatic limits for whitebark pine (Mattes 1982; Tranquillini 1979).

POPULATION STRUCTURE OF WHITEBARK PINE

The population structure of whitebark pine differs in many respects from that of wind-dispersed conifers, because of the foraging and caching behaviors of nutcrackers. First of all, whitebark pine, limber pine, and Swiss stone pine (*P. cembra* L.) are known to grow in a "multi-trunk" form (Clausen 1965; Holtmeier 1988; Lanner 1980). This form appears to be a single tree with two or more trunks sometimes fused at or above the base. The frequency of occurrence of this growth form and mean number of trunks per tree vary geographically (table 4 in Tomback and Linhart 1990). Protein electrophoresis confirms that most of these multi-trunk trees contain two or more distinct genotypes (Furnier and others 1987; Linhart and Tomback 1985; Tomback and others 1989b); this supports the suggestion by Lanner (1980) that each trunk of a multi-trunk tree may originate from one seed of a multi-seed nutcracker cache. The consequence of this growth form is an extremely clumped population dispersion pattern (individuals often occur in small clumps).

To complicate matters, not all multi-trunk trees consist of more than one genotype. For one of the six (17 percent) multi-trunk whitebark pine trees analyzed by Linhart and Tomback (1985) and 12 of 35 (34 percent) analyzed by Furnier and others (1987), only one genotype per tree was found. Perhaps if they had examined more gene loci, additional distinct genotypes would be identified; however, it is more likely that some multi-trunk trees were of only one genotype. This possibility was recently discussed for a disjunct population of limber pine in which 88 of 106 (83 percent) multi-trunk trees consisted of one genotype (Schuster and Mitton 1988). In most cases, there were no aboveground morphological clues to the origin of the growth form. Schuster and Mitton (1988) suggested that damage to the leader shoot may result in the growth of side branches into main trunks and also that some individuals may have a genetic predisposition for release from apical dominance. Both effects may vary with biotic and abiotic conditions. Consequently, the genetic makeup of multi-trunk trees cannot be assumed without genetic analysis.

The complexities of growth form in whitebark and limber pine necessitate clear terminology in discussions. We propose the following: single-trunk tree (typical of conifers), multi-trunk tree (single genotype), and tree cluster (multiple genotypes). If the genetic makeup of a tree is unknown and such information is relevant, the point should be clearly stated. For example, the tree might be described as a multi-trunk tree of unknown genetic composition or of unknown origin.

In addition, the genetic relationships among individuals within a tree cluster differ from those between tree clusters, because nutcrackers usually harvest a number of seeds from the same parent tree. Tomback (1988a) estimated that 73 to 93 percent of caches contain two or more sibling or half-sibling seeds, and caches usually contain a mix of related and nonrelated seeds. Electrophoretic analysis indicated that individual whitebark pine trees in a cluster were genetically more similar to each other than to trees in nearby clusters (Furnier and others 1987). This finding was confirmed for limber pine as well by Schuster and Mitton (1988).

Furthermore, because more than one nutcracker may cache seeds in a given area (Tomback 1978), and each nutcracker may harvest seeds from different stands, the genetic structure among tree clusters may be randomized (Furnier and others 1987; Tomback and Linhart 1990). In fact, Furnier and others (1987) did not find a family structure (a relationship between genotype and distance) similar to that of wind-dispersed conifers among tree clusters in two whitebark pine stands, nor did Schuster and Mitton (1989) find a family structure within several limber pine populations. The family structure of wind-dispersed conifer populations comes from shorter, more predictable seed dispersal distances (Knowles 1984; Linhart 1989; Linhart and others 1981).

ROLE OF NUTCRACKERS IN FOREST REGENERATION

Climax Communities, Primary and Secondary Succession

Climax communities are relatively open and favorable to establishment of the moderately shade-tolerant whitebark pine (Arno and Hoff 1989). By caching seeds in forested sites (Tomback 1978), nutcrackers maintain climax communities of whitebark pine. In some montane regions, such as the Sierra Nevada, most of the whitebark pine occurs in climax stands at subalpine and treeline elevations. Fire is of limited importance, typically consuming less than 0.5 ha of forest per burn (Tomback 1986). In the northern Rocky Mountains where fire is more important, whitebark pine alone or with subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) forms climax communities at treeline elevations and on exposed subalpine sites (Arno and Hoff 1989).

The tendency of nutcrackers to disperse seeds at a distance from parent trees indicates that whitebark pine may become established in new environments as they arise. Examples include the invasion of the shores of subalpine lakes when water levels decrease and the invasion of subalpine meadows (Dunwiddie 1977). An unusual example involves the Swiss stone pine. The Morteratsch Glacier of the Engadine Valley of Switzerland has retreated about 1 km since 1900 and, on the exposed, bare lateral morraines, Swiss stone pines are already established (Tomback 1988b). This is an illustration of primary succession, according to some definitions (Smith 1986), initiated by a bird.

Nutcrackers are attracted to open sites for seed caching and will fly great distances to use them (Tomback 1978). McCaughey (1987) observed nutcrackers caching quantities of whitebark pine seeds in a recent clearcut. Studies of regeneration following fire indicate the efficacy of nutcrackers in seeding burns, even areas several kilometers from a seed source (Sund 1988; Sund and others 1989; Tomback 1986; Tomback and others 1989a).

Examples of Postfire Regeneration

Alpine Timberline: Cathedral Peak, Yosemite National Park—On exposed, high-elevation sites, whitebark pine assumes a shrublike or elfinwood growth form (Clausen 1965) sometimes referred to as krummholz. In 1975, a lightning strike ignited a fire on the west slope of Cathedral Peak, Yosemite National Park, elevation 3,337 m, that severely burned 2 ha of a krummholz whitebark pine stand. In 1979, regeneration was surveyed along a series of 2-m belt transects totalling 790 m in length and representing about 8 percent of the area of the burn (Tomback 1986). The density of seedling sites per transect ranged from 0.015/m^2 to 0.027/m^2 with an overall density of 0.020/m^2. At each regeneration site there were one to four seedlings (from germination of seeds within a nutcracker cache) with a mean of 2.6 (S.D. = 0.74). Tomback (1986) observed nutcrackers transporting whitebark pine seeds up from cone-bearing stands of erect trees on the lower west and east slopes and caching them in the burn.

Because krummholz conifer forms typically produce few cones and the seeds have low germination capacity (Tranquillini 1979), it is likely that most of the seedlings in the burn originated from trees of the erect growth form from lower elevations (Tomback 1986). Assuming that this is true, the question remains whether the regenerating trees will be krummholz in form, and, if so, whether they will be genetically differentiated by selection from the populations of parent trees or whether the krummholz growth form is primarily the product of the severe environment. Previous studies of Engelmann spruce and subalpine fir show differences in peroxidase proteins between the krummholz and erect tree forms (Grant and Mitton 1977).

Seral Whitebark Pine Community: Bitterroot National Forest—Throughout the Northern Rocky Mountains, periodic fire followed by seed dispersal by nutcrackers historically renewed seral whitebark pine communities; however, the fire suppression practices of the last 80 years have lengthened the interval between fires (Arno 1980, 1986). In the absence of fire, shade-tolerant subalpine fir, sometimes in combination with Engelmann spruce or mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.), replaces whitebark pine (Arno 1986; Arno and Hoff 1989). Because of diminishing whitebark pine populations, the status of whitebark pine in several large-scale burns is currently of concern.

CASE STUDIES: THE SLEEPING CHILD BURN AND SADDLE MOUNTAIN BURN

In 1987 and 1988, we examined forest regeneration in the Sleeping Child and Saddle Mountain Burns, respectively, Ravalli County, Bitterroot National Forest, western Montana. The primary elevational range for whitebark pine in this region is 2,290 to 2,620 m (Arno and Hoff 1989; Pfister and others 1977). At lower subalpine elevations (2,130 to 2,290 m), occasional islands of whitebark pine occur on exposed or rocky areas. Forest regeneration patterns observed in the Sleeping Child Burn were compared with patterns in the Saddle Mountain Burn. The two study areas were selected for similarities in time elapsed since fire, severity of the fire, and the relationship between whitebark pine seed source and topography. Details concerning the studies are reported elsewhere (Sund 1988; Sund and others 1989; Tomback and others 1989a).

Study Areas

The Sleeping Child Burn resulted from an uncontrollable lightning-ignited fire in 1961 that consumed about 11,350 ha of forest on the west slope of the Sapphire Range (fig. 1). Fuel accumulation from a mountain pine beetle (*Dendroctonus ponderosae* Hopk.) epidemic in the 1930's contributed to the severity of the burn (Lotan 1976). Lodgepole pine (*Pinus contorta* Dougl.) dominated the lower subalpine at the time of the fire (Lotan 1976; Lyon and Stickney 1976).

Figure 1—Sleeping Child Burn, Bitterroot National Forest, western Montana. View toward the west along the ridge study area.

The primary whitebark pine seed source is continuous stands of mature trees at elevations above 2,250 m on the northeastern edge of the burn. In these stands, subalpine fir, Engelmann spruce, and lodgepole pine also provide seed sources for regeneration. Analysis of two plots in these stands indicated that whitebark pine and subalpine fir were the most common species (Sund 1988; Sund and others 1989). Potential seed sources for subalpine fir, spruce, and lodgepole pine also occur on the other perimeters of the burn and on small forest islands in the burn.

The principal study area was a 3.7-km long ridge that is contiguous with the unburned forest on the east edge and extends nearly due west into the northern center of the burn (fig. 2). Elevation along the ridge decreases from 2,482 m to 2,173 m with increasing distance from the edge of the burn. A second study area, following the Skalkaho-Rye Creek Road and then Paint Creek Road south through the center of the burn (fig. 2), was selected to measure regeneration at distances up to 8 km from the whitebark pine seed source and at elevations as low as 2,100 m.

The Saddle Mountain Burn, in the Bitterroot Mountains near Lost Trail Pass, resulted from an uncontrollable lightning-strike fire in 1960 that destroyed about 1,240 ha of forest (fig. 3). Running northeast to southwest in the longest dimension, the burn ranges from about 2,475 m to 1,950 m elevation (fig. 4). Relatively flat in profile, the northeastern 2 km of the burn fluctuate around 2,100 m elevation, with a hill near the northeast end. The southwestern 1.2 km of the burn increase steeply in elevation (fig. 4). The whitebark pine seed source is at the southwest edge of the burn above 2,250 m elevation in stands where whitebark pine and subalpine fir are equally common and lodgepole pine and Engelmann spruce are present in small numbers (Tomback and others 1989a). Additional seed sources for lodgepole pine, spruce, subalpine fir, and Douglas-fir (*Pseudotsuga menziesii* [Beissn.] Franco) occur within about 0.5 km of the lower perimeter.

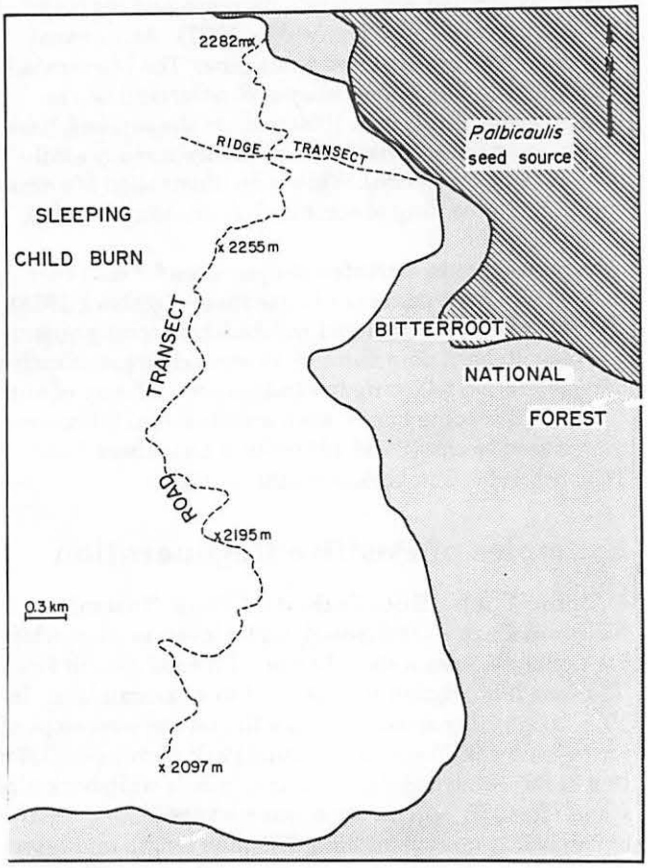


Figure 2—Sleeping Child Burn: ridge and road study areas. The dark, striped area indicates forest above 2,250 m elevation where continuous stands of whitebark pine provide the seed source for regeneration.

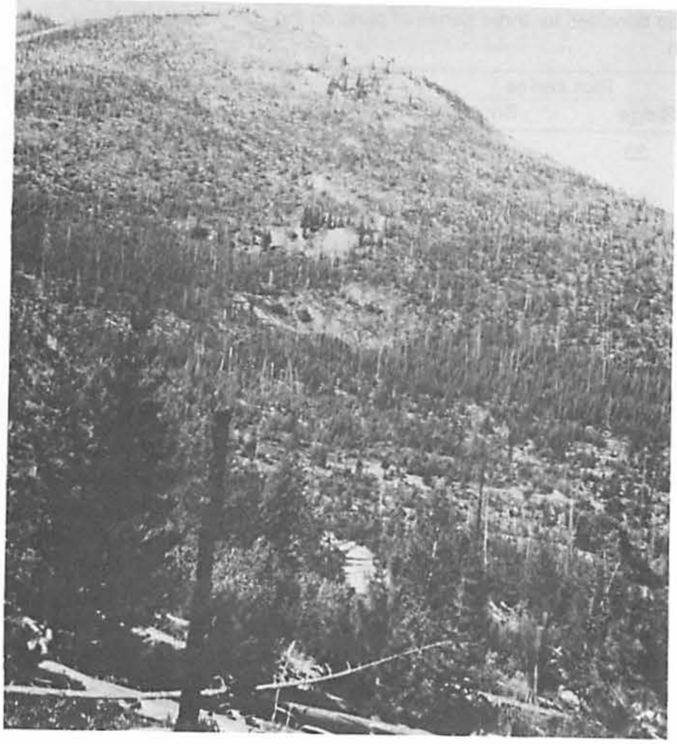


Figure 3—Saddle Mountain Burn, Bitterroot National Forest, western Montana. View toward the southwest end of the study area.

Methods

In the Sleeping Child Burn, fieldwork was conducted from August 3 to 26, 1987. On the ridge study area, plots were established every 150 m along a 3.6-km transect beginning 50 m from the whitebark pine seed source. For each ridge plot, a plot on the south and north aspects of the ridge was also established to compare the influence of aspect on regeneration abundance. Altogether, 63 plots were studied: 21 north, 19 south, and 23 ridge. The plot sizes ranged in set increments from 50 by 1.25 m to 50 by 12 m with respect to local densities of whitebark pine (for details, see Sund 1988; Sund and others 1989). Along the road transect 14 plots, 30 by 1.5 m to 30 by 10 m in area, were established on suitable north aspect sites. The plots ranged from 0.9 to 8 km from the whitebark pine seed source.

We sampled regeneration in the Saddle Mountain Burn from August 1 to 9, 1988. Two parallel transects A and B, separated by 10 m, began at the steep, southwest edge of the burn and continued 3.2 km northeast (fig. 4). On the steep part of the burn, plots were established every 100 m along each transect for a total of 16 plots. On the flat part of the burn, plots were established every 50 m along transect A, for a total of 15 plots, but every 100 m along the B transect for a total of 10 plots. All 41 plots were 50 m long with belt widths up to 20 m (for details, see Tomback and others 1989a).

For both burns, plot measurements included elevation, aspect, slope angle, and distance from the whitebark pine seed source. All seedlings and trees on the plots were counted. "Regeneration site" refers to the location on a plot of a seedling or tree. For whitebark pine, a single regeneration site might represent more than one seedling or tree. In such cases, cluster size was determined by separating stems or trunks at or below ground level. All whitebark pine seedlings or trees were aged in the Sleeping Child Burn, and representatives of different height classes were aged in the Saddle Mountain Burn. In both areas, representatives of height classes for the other conifer species were also aged (for details, see Sund 1988; Sund and others 1989; Tomback and others 1989a).

Results and Discussion

In the Sleeping Child Burn, a total of 455 whitebark pine, 60 subalpine fir, 37 Engelmann spruce, and 436 lodgepole pine trees were encountered in the ridge area study plots (table 2). At 48 percent (217) of the whitebark pine sites, seedlings or trees occurred in clusters of 2 to 8, with a mean of 1.91. The oldest trees (total age) recorded

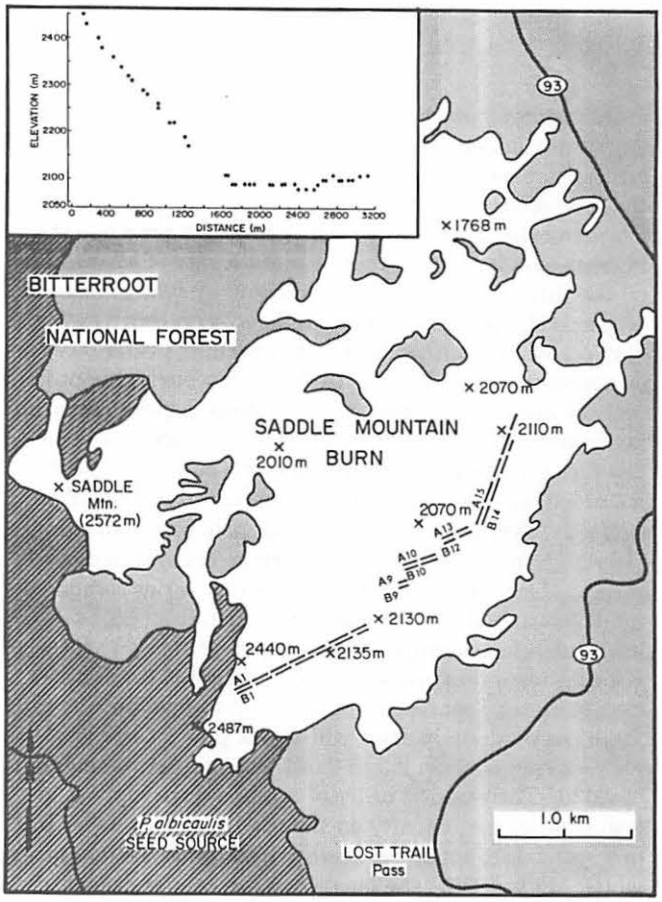


Figure 4—Saddle Mountain Burn. Path of parallel A and B transects through the burn. The dark, striped area indicates forest above 2,250 m where continuous stands of whitebark pine provide the seed source for regeneration. The stippled area indicates unburned forest around the perimeter of the burn. On the inset graph of elevation versus aerial distance from the whitebark pine seed source, each point represents a single study plot ($n = 41$).

Table 2—Sample sizes and 1987 conifer regeneration densities for three series of plots on the ridge study area in the Sleeping Child Burn

	Plot series			
	North	Ridge	South	Total
No. plots	21	23	19	63
No. regeneration sites				
whitebark pine	271	119	65	455
subalpine fir	33	21	6	60
Engelmann spruce	19	16	2	37
lodgepole pine	115	186	135	436
Area sampled (m^2)				
whitebark pine	3,500	5,750	6,225	15,475
others	3,250	4,625	4,350	12,225
Plot densities (sites/m^2)				
Range				
whitebark pine	0.006-.512	0.000-.192	0.001-.110	0.000-.512
subalpine fir	.000-.080	.000-.032	.000-.032	.000-.080
Engelmann spruce	.000-.024	.000-.056	.000-.008	.000-.056
lodgepole pine	.000-.176	.000-.296	.000-.296	.000-.296
Mean, standard deviation				
whitebark pine	0.140,.145	0.044,.060	0.025,.032	0.070,.104
subalpine fir	.014,.019	.006,.010	.002,.008	.008,.001
Engelmann spruce	.006,.008	.004,.012	.001,.002	.004,.009
lodgepole pine	.031,.046	.051,.080	.036,.069	.040,.066

for each species were 21 years for whitebark pine, 24 years for fir and lodgepole pine, and 20 years for spruce. Regeneration apparently began soon after the burn, because at the time of sampling 26 years had elapsed since the fire. On the north aspect plot series, whitebark pine had the highest plot density and mean plot density of all conifers on the three plot series, 0.512 sites/m^2 and 0.140 sites/m^2, respectively (table 2). The high density on this aspect may result from either nutcracker caching preferences or environmental conditions. In fact, whitebark pine prefers moister areas in the more arid montane regions (Arno and Hoff 1989). The highest mean fir and spruce plot densities also occurred on the north aspect, but the highest mean lodgepole pine plot density occurred on the ridge (table 2). Whitebark pine and lodgepole pine had similarly high mean densities on the ridge and south plot series. Mean densities for all three plot series combined indicated the following density ranking, from highest to lowest: whitebark pine, lodgepole pine, fir, and spruce. Because sampling areas differed among the conifer species, statistical comparisons are of limited value.

On the road study area, whitebark pine site density per plot ranged from 0.0 to 0.067 sites/m^2, with a mean of 0.020. The ranking order of conifers from highest to lowest mean plot density on the road study area was fir, lodgepole pine, spruce, and whitebark pine. Although whitebark pine was the least common conifer, its densities were on average comparable to those on the ridge and south plot series. This suggests that nutcrackers are in fact transporting seeds a long distance from the seed source.

Scatterplots of plot densities for the ridge study area versus distance from the whitebark pine seed source reveal interesting differences in regeneration patterns (fig. 5). For lodgepole pine, densities increase with increasing distance from the whitebark pine seed source but with decreasing distance from regenerated stands of lodgepole pine in the lower subalpine forest zone. Regression analysis indicated a highly significant relationship ($r = 0.482$, df = 61, $P < 0.001$). Because much of the lower subalpine zone was dominated by lodgepole pine at the time of the fire, the restocking came from seeds in serotinous cones on site (Lotan 1976). Throughout the burn, young lodgepole pine trees are already producing cones and are a secondary seed source.

Although density increases slightly but nonsignificantly with distance on the spruce scatterplot (fig. 5), the curve is nearly flat with a dip at about 3,000 m. It is possible that seeds are blown into the ridge study area from both the higher and lower elevation seed sources. On the road transect there is, in fact, an increase in spruce density with distance from the whitebark pine seed source (Tomback and others 1989a).

The scatterplot for subalpine fir shows a negative relationship (fig. 5), suggesting that the primary fir seed source for the ridge is the high-elevation seed source. A regression analysis of density versus distance from the whitebark pine seed source is significant ($r = -0.355$, df = 61, $0.01 > P > 0.001$). Along the road transect, there is an increase in fir density with distance from the whitebark pine seed source, indicating that lower elevation forests are also contributing to fir regeneration (Tomback and others 1989a).

For whitebark pine, the scatterplot is a pronounced negative exponential curve, with a long tail of low densities beginning about 2 km. The regression analysis shows a highly significant relationship between density and distance ($r = -0.592$, df = 61, $P < 0.001$). Whitebark pine density also decreases with distance from the whitebark pine seed source along the road transect, as expected if the high-elevation source is the primary seed source ($r = -0.374$, df = 12, NS). The fact that whitebark pine

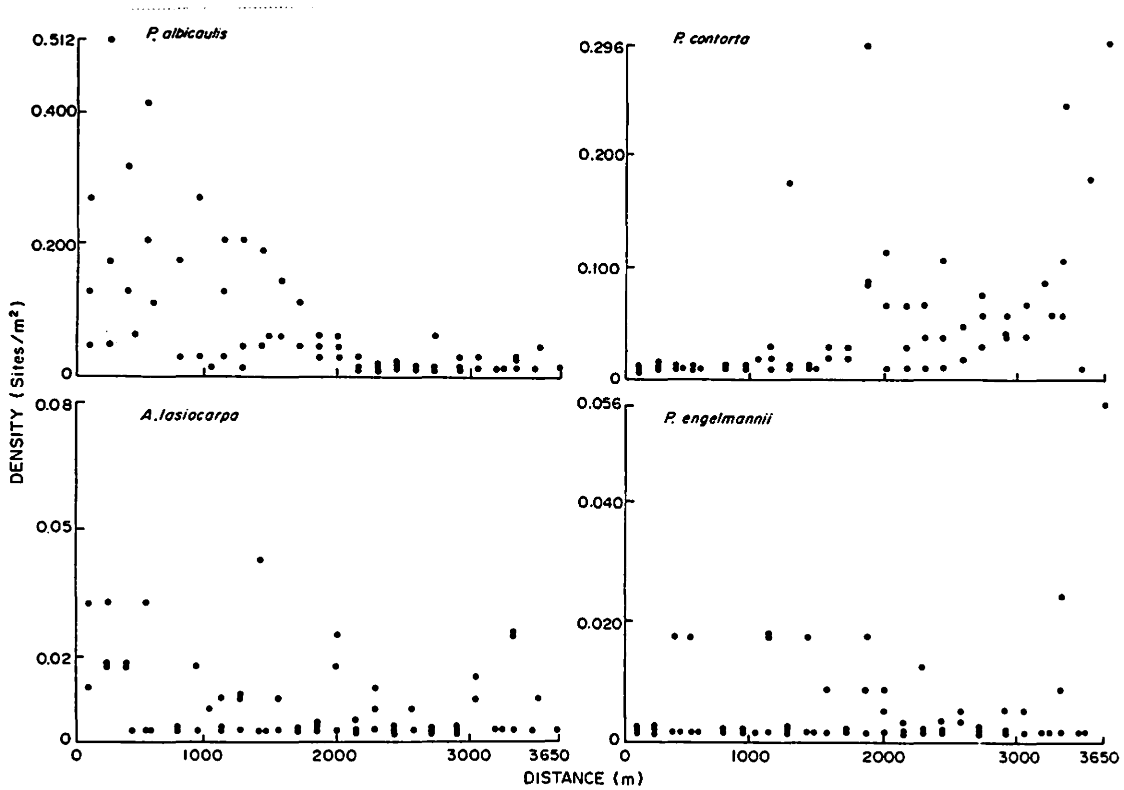


Figure 5—For the ridge study area of the Sleeping Child Burn, scatterplots of regeneration density versus distance from the whitebark pine seed source for four conifer species. Clockwise from left: whitebark pine, lodgepole pine, Engelmann spruce, and subalpine fir.

is regenerating up to 8 km from the single seed wall is an illustration of the seed dispersal effectiveness of Clark's nutcrackers.

A more meaningful regression analysis of the relationship between density (Y) and distance (X) for whitebark pine is based on a plot of $\log_{10}$ density versus distance. The result is a highly significant linear relationship ($r = -0.692$, df = 61, $P < 0.001$) described by the following regression model:

$$\log_{10}Y = -0.0005X - 0.806$$

This model may be used to formulate an equation to describe the negative exponential regeneration curve:

$$Y = (0.156)E^{-0.0005X}$$

where E is 10.

Regression analysis also indicates a significant relationship between whitebark pine plot density and elevation ($r = 0.608$, df = 61, $P < 0.001$). Unfortunately, the confounding effects of distance from the seed source and elevation cannot be separated statistically. Although some effects from elevation, perhaps in conjunction with site aspect, cannot be ruled out, whitebark pine grows well at elevations of 2,100 m and above in the Bitterroot National Forest (Arno 1988; Arno and Hoff 1989). Therefore, confounding elevation effects are unlikely on the ridge and road study areas.

In the Sleeping Child Burn, seed dispersal by nutcrackers has given whitebark pine a clear advantage over subalpine fir, the major climax species in seral communities in the upper subalpine. In particular, dispersal of whitebark pine seeds into the burn occurs even if wind patterns are unfavorable; dispersal of fir seeds from the same seed source can be impeded. The prevailing winds in the region during the time that conifers release seeds are from the west (Finklin 1983); the direction that subalpine fir seeds must travel from the seed source into the burn is toward the west. This may well account for the fact that the densities of whitebark pine are higher than those of fir on all aspects. Additional factors might include the greater tolerance of whitebark pine for open sites (Arno and Hoff 1989) and the occurrence of some whitebark pine regeneration in clusters; the loss of one seedling or tree at a site may still result in a mature tree. Of particular note, whitebark pine regeneration has extended 8 km or more into the burn from a single seed wall.

The advantage to whitebark pine in the Sleeping Child Burn may be explained by the size of the burn, wind patterns, and the difficulty of long-distance seed dispersal for the other conifers. The smaller Saddle Mountain Burn may provide some test of this hypothesis. There, we sampled 164 whitebark pine and 175 fir trees on 41 plots and 49 spruce, 286 lodgepole pine, and 29 Douglas-fir trees on

Table 3—Sample sizes and 1988 conifer regeneration densities for the Saddle Mountain Burn (Tomback and others 1989a)[1]

	Conifer species				
	WP	SF	ES	LP	DF
Number of sites	164	175	49	286	29
Area sampled (m²)	10,410	5,980	1,580	1,170	1,580
Density per plot (sites/m²)					
Range	0-0.160	0-0.280	0-0.200	0-1.24	0-0.160
Mean	0.042	0.046	0.030	0.323	0.019
SD	0.051	0.684	0.044	0.355	0.032

[1] WP = whitebark pine, SF = subalpine fir, ES = Engelmann spruce, LP = lodgepole pine, and DF = Douglas-fir, SD = standard deviation.

31 plots (table 3). At 43 percent of the whitebark pine sites, regeneration was in clusters of two to 10 seedlings or trees, with a mean of 1.98 per site. The oldest trees sampled were 21 years for whitebark pine, 16 years for fir, 22 years for spruce, and 17 years for lodgepole pine and Douglas-fir. Mean plot densities indicated the following ranking of conifers, from highest to lowest: lodgepole pine, whitebark pine and subalpine fir nearly equal, spruce, and Douglas-fir (table 3). A comparison of whitebark pine and fir densities for plots that were equal in sampling area (n = 27) indicated no difference (Mann-Whitney U test). As for the Sleeping Child Burn, the prevalence of lodgepole pine in the Saddle Mountain Burn may be the consequence of its prefire dominance in the area.

Relationships between density and distance from the whitebark pine seed source for all conifers resemble those for the Sleeping Child Burn. For lodgepole pine, the regression analysis of density versus distance indicates a trend toward increasing densities with distance (r = 0.320, df = 29, P = 0.079). This is consistent with primary seed sources and more favorable sites at lower elevations, as observed for the Sleeping Child Burn. In the case of Douglas-fir, density also increases with distance from the whitebark pine seed source, reaches the highest values between transect distances of 1,100 and 2,200 m, and then decreases. Douglas-fir is a lower subalpine and montane-elevation species (Pfister and others 1977); its distribution in the burn probably reflects the location of seed sources, wind patterns, and site suitability. The spruce scatterplot is nearly flat, with a sharp spike in density between transect distances of 1,700 m and 2,100 m. The explanation for Douglas-fir applies to spruce as well. Again, the scatterplot for subalpine fir indicates a strong inverse relationship between density and distance (fig. 6). This relationship is highly significant (r = –0.498, df = 39, P < 0.001), suggesting that the residual forest on the southwest edge of the burn is the principal seed source for this species.

For whitebark pine, the pattern of regeneration follows a negative exponential curve, as in the Sleeping Child Burn (fig. 6). The relationship between density and distance is highly significant (r = –0.822, df = 38, P < 0.001); however, the linear model based on $\log_{10}$ density is barely significant (r = –0.301, df = 38, P = 0.059):

$$\log_{10}Y = -0.0002X - 1.065.$$

The model for the negative exponential regeneration curve is

$$Y = (0.086)E^{-0.0002X}$$

where E is 10. Again, the effects of distance and elevation cannot be separated statistically (density versus elevation, r = 0.884, df = 38, P < 0.0001).

The slopes and intercepts of the linear models based on $\log_{10}$ whitebark pine density versus distance were compared for both burns (Greybill 1976). There were no significant differences between the models, suggesting that they may be used for management purposes or regeneration simulations in process models for comparable burns (Keane and others, in press; Keane and others, these proceedings).

In the smaller Saddle Mountain Burn, whitebark pine and subalpine fir have comparable regeneration densities. Because the mean plot density for subalpine fir is much higher in the Saddle Mountain Burn than in the Sleeping Child Burn, one or more factors must cause relatively higher numbers of subalpine fir seeds to land in the burn. In fact, the prevailing winds from the west in late summer (Finklin 1983) favor the dissemination of subalpine fir seeds into the burn from the seed source at the southwest edge. This and the smaller size of the burn probably

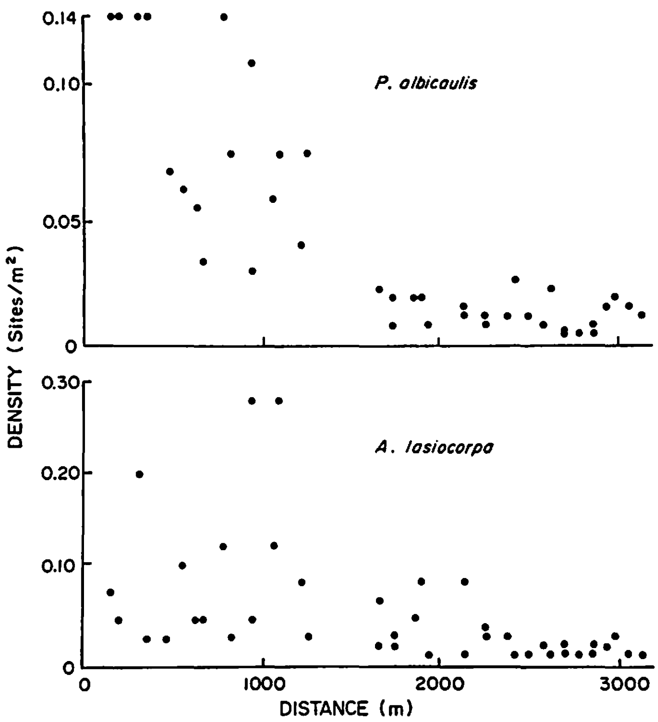


Figure 6—For the Saddle Mountain Burn, scatterplots of regeneration density versus distance from the whitebark pine seed source for whitebark pine (*P. albicaulis*) and subalpine fir (*Abies lasiocarpa*).

result in higher densities of subalpine fir seeds available for regeneration. The mean plot density for whitebark pine in the Saddle Mountain Burn is nearly identical to the mean plot density of the ridge plot series in the Sleeping Child Burn, suggesting that nutcracker seed dispersal activity may be the same. Comparison of regeneration patterns between the two burns indicates that whitebark pine may have an advantage over subalpine fir in situations where seed dispersal by nutcrackers is greatly superior to that of wind. Examples include (1) very large burns, where seed dispersal by nutcrackers extends greater distances than seed dispersal by wind, (2) areas where prevailing wind patterns are against the direction of the burn, and (3) burns where a seed source is more than 1 km from the perimeter of the burn.

ACKNOWLEDGMENTS

Discussions with Yan Linhart contributed greatly to the synthesis in the first part of the paper. We thank Steve Arno, Jim Brown, and Bob Keane for helpful discussions and advice concerning the whitebark pine regeneration studies. Steve Arno, Bob Keane, and Bill Schuster provided helpful comments on a draft manuscript. Mike Reuss contributed software expertise, Jan Driscoll advised us on statistics, and Ron Langley helped with statistical analysis. Funding (to DFT) and logistic support for the Sleeping Child and Saddle Mountain Burn fieldwork were provided by the Intermountain Research Station, Forest Service, U.S. Department of Agriculture.

REFERENCES

Arno, S. F. 1980. Forest fire history in the northern Rockies. Journal of Forestry. 78: 460-465.

Arno, S. F. 1986. Whitebark pine cone crops—a diminishing source of wildlife food? Western Journal of Applied Forestry. 1: 92-94.

Arno, S. F. 1988. [Personal communication]. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Fire Sciences Laboratory.

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. Ecology. 53: 997-1010.

Bock, W. J.; Balda, R. P.; Vander Wall, S. B. 1973. Morphology of the sublingual pouch and tongue musculature in Clark's nutcracker. Auk. 90: 491-519.

Clausen, J. 1965. Population studies of alpine and subalpine races of conifers and willows in the California High Sierra Nevada. Evolution. 19: 56-68.

Critchfield, W. B.; Little, E. L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.

Dunwiddie, P. W. 1977. Recent tree invasion of subalpine meadows in the Wind River Mountains, Wyoming. Arctic and Alpine Research. 9: 393-399.

Finklin, A. I. 1983. Weather and climate of the Selway-Bitterroot Wilderness. Moscow, ID: University Press of Idaho. 144 p.

Furnier, G. R.; Knowles, P.; Clyde, M. A.; Dancik, B. P. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution. 41: 607-612.

Giuntoli, M.; Mewaldt, L. R. 1978. Stomach contents of Clark's nutcracker collected in western Montana. Auk. 95: 595-598.

Grant, M. C.; Mitton, J. B. 1977. Genetic differentiation among growth forms of Engelmann spruce and subalpine fir at tree line. Arctic and Alpine Research. 9: 259-263.

Greybill, F. A. 1976. Theory and application of the linear model. North Scituate, MA: Duxbury Press. 704 p.

Holtmeier, F. K. 1988. [Personal communication]. Münster, FRG: Institute für Geographie, Westfälischen Wilhelms-Universität Münster.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Kamil, A. C.; Balda, R. P. 1985. Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). Journal of Experimental Psychology: Animal Behavior Processes. 11: 95-111.

Keane, R. E.; Arno, S. F.; Brown, J. K.; Tomback, D. F. [In press]. Modelling stand dynamics in whitebark pine forests. Ecological Modelling.

Knowles, P. 1984. Genetic variability among and within closely spaced populations of lodgepole pine. Canadian Journal of Genetics and Cytology. 26: 177-184.

Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: Proceedings of sixth North American forest biology workshop; Edmonton, AB: University of Alberta: 14-48.

Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research. 12: 391-402.

Lanner, R. M.; Vander Wall, S. B. 1980. Dispersal of limber pine seed by Clark's nutcracker. Journal of Forestry. 78: 637-639.

Ligon, J. D. 1978. Reproductive interdependence of piñon jays and piñon pines. Ecological Monographs. 48: 111-126.

Linhart, Y. B. 1989. Interactions between genetic and ecological patchiness in forest trees and their dependent species. In: Bock, J. E.; Linhart, Y. B., eds. Evolutionary ecology of plants. Boulder, CO: Westview Press: 1-31.

Linhart, Y. B.; Mitton, J. B.; Sturgeon, K. B.; Davis, M. L. 1981. Genetic variation in space and time in a population of ponderosa pine. Heredity. 46: 407-426.

Linhart, Y. B.; Tomback, D. F. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. Oecologia. 67: 107-110.

Lotan, J. E. 1976. Cone serotiny—fire relationships in lodgepole pine. In: Proceedings; Tall timbers fire ecology conference no. 14 and Intermountain fire research council fire and land management symposium; 1974; Tallahassee, FL: 267-278.

Lyon, L. J.; Stickney, P. F. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. In: Proceedings; Tall timbers fire ecology conference no. 14 and Intermountain fire research council fire and land management symposium; 1974; Tallahassee, FL: 355-375.

Mattes, H. 1982. Die Lebensgemeinschaft von Tannenhäher und Arve. Birmensdorf, Switzerland: Swiss Federal Institute of Forest Research. 74 p.

McCaughey, W. W. 1987. [Personal communication]. Bozeman, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory.

McCaughey, W. W.; Schmidt, W. C.; Shearer, R. C. 1986. Seed-dispersal characteristics of conifers in the Inland Mountain West. In: Proceedings—Conifer tree seed in the Inland Mountain West symposium; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 50-62.

Mewaldt, L. R. 1956. Nesting behavior of the Clark nutcracker. The Condor. 58: 3-22.

Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Schuster, W. S. F.; Mitton, J. B. 1988. Discerning individuality: genetic analyses of multi-trunk trees and fused clusters of trees in limber pine. Boulder, CO: University of Colorado at Boulder; Department of Environmental, Population, and Organismic Biology. Working draft.

Schuster, W. S. F.; Mitton, J. B. 1989. [Personal communication]. Boulder, CO: University of Colorado at Boulder, Department of the Environmental, Population, and Organismic Biology.

Smith, R. L. 1986. Elements of ecology. 2d ed. New York: Harper and Row. 677 p.

Sund, S. K. 1988. Post-fire regeneration of *Pinus albicaulis* in western Montana: patterns of occurrence and site characteristics. Denver, CO: University of Colorado at Denver. 63 p. Thesis.

Sund, S. K.; Tomback, D. F.; Hoffmann, L. A. 1989. Post-fire regeneration of *Pinus albicaulis* in western Montana: patterns of occurrence and site characteristics. Denver, CO: University of Colorado at Denver, Department of Biology. Working draft.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. The Living Bird. 16: 123-161.

Tomback, D. F. 1980. How nutcrackers find their seed stores. The Condor. 82: 10-19.

Tomback, D. F. 1981. Notes on cones and vertebrate-mediated seed dispersal of *Pinus albicaulis* (Pinaceae). Madroño. 28: 91-94.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51: 451-467.

Tomback, D. F. 1983. Nutcrackers and pines: coevolution or coadaptation? In: Nitecki, N. H., ed. Coevolution. Chicago, IL: University of Chicago Press: 179-223.

Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madroño. 33: 100-110.

Tomback, D. F. 1988a. Nutcracker-pine mutualisms: multi-trunk trees and seed size. In: Ouellet, H., ed. Acta XIX Congressus Internationalis Ornithologici, Vol. I. Ottawa: University of Ottawa Press: 518-527.

Tomback, D. F. 1988b. Observations from the Engadine Valley, Switzerland. Unpublished observations on file at: University of Colorado at Denver, Department of Biology, Denver, CO.

Tomback, D. F.; Carsey, K.; Powell, M. 1989a. The genetic analysis of multi-trunk *Pinus cembra*. Unpublished data on file at: University of Colorado at Denver, Department of Biology, Denver, CO.

Tomback, D. F.; Hoffmann, L. A.; Sund, S. K. 1989b. Post-fire regeneration patterns of a bird-dispersed pine, *Pinus albicaulis* in western Montana. University of Colorado at Denver, Department of Biology, Denver, CO: Working manuscript.

Tomback, D. F.; Knowles, J. W. 1984. Observations in the Wind River Range, Wyoming. Unpublished observations on file at: University of Colorado at Denver, Department of Biology, Denver, CO.

Tomback, D. F.; Kramer, K. A. 1980. Limber pine seed harvest by Clark's nutcracker in the Sierra Nevada: timing and foraging behavior. The Condor. 82: 467-468.

Tomback, D. F.; Linhart, Y. B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. [In press].

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. Berlin, Heidelberg: Springer-Verlag. 137 p.

Turcek, F. J.; Kelso, L. 1968. Ecological aspects of food transportation and storage in the Corvidae. Communications in Behavioral Biology. Part A. 1: 277-297.

Vander Wall, S. B. 1982. An experimental analysis of cache recovery in Clark's nutcracker. Animal Behaviour. 30: 84-94.

Vander Wall, S. B. 1987. [Personal communication]. Logan, UT: Utah State University.

Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. Ecological Monographs. 47: 89-111.

Vander Wall, S. B.; Balda, R. P. 1981. Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. Zeitschrift für Tierpsychologie. 56: 217-242.

Vander Wall, S. B.; Hutchins, H. E. 1983. Dependence of Clark's nutcracker, *Nucifraga columbiana*, on conifer seeds during the postfledging period. Canadian Field-Naturalist. 97: 208-214.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Wyman Schmidt)—If one wanted to attract nutcrackers to an area to have them do the seeding for you, what stand and site conditions would be most favorable?

A.—The sites used by Clark's nutcracker are extremely diverse. In fact, there seem to be few that they never use.

My impression, though, is that nutcrackers prefer more open situations with sparse ground cover.

Q. (from Richard Baker)—(1) Do Clark's nutcrackers migrate? (2) If so, would they ever carry whitebark pine seeds greater distances, such as, from one mountain range to another? (3) If so, why hasn't whitebark pine gotten to Colorado?

A.—(1) Nutcrackers remain at montane elevations all year, unlike those species that migrate south for the winter. However, nutcrackers periodically "irrupt" in great numbers from a montane region if there has been a widespread cone crop failure. Many search through the mountains for food, and flocks have been found hundreds of miles outside their range in some years, in such places as Carmel, CA. Annually, nutcrackers in some montane regions also undergo altitudinal migration, moving downslope in late fall and returning to the higher elevations in late spring.

(2) Nutcrackers are known to carry pine seeds 22 km or more, but it is unlikely that a bird would transport seeds hundreds of kilometers (an extreme case of "take-out food"?).

(3) We really don't know for a fact that whitebark pine has not been in the Colorado Rockies historically. Perhaps environmental conditions are now such that it cannot occur there; perhaps in the current conditions, limber pine is a serious competitor? Possibly, if conditions were to change, there would be a slow southward migration of whitebark pine. Alternatively, there may be a geographic barrier, such as distance, to continuous seed dispersal by nutcrackers. Some people have suggested that whitebark pine has a remnant distribution. If this is the case, range expansion to favorable, high-elevation locations may be impossible.

Q. (from Anonymous)—I missed the number of seeds stored per day.

A.—I estimated that each nutcracker in the Sierra Nevada stored around 850 seeds per day, for a total of about 35,000 whitebark pine seeds per season.

Q. (from Jack Losensky)—Have you found any indication of birds caching at the same site more than one time; are there sites with more than 30 seeds?

A.—I have never encountered a cache of more than 15 seeds or a germinated cache of seeds with more than 17 seedlings. It is unlikely that more than one bird would use the same site.

Q. (from Bill Shuster)—Have you identified any predation on nutcracker caches?

A.—In a series of experiments to determine the extent of cache predation, I buried caches of various sizes. Large and small caches were taken alike for a total of 85 percent loss. This is described in my 1980 paper in "The Condor." I believe *Peromyocus* was responsible.

PHYSICAL AND CHEMICAL TREATMENTS TO IMPROVE GERMINATION OF WHITEBARK PINE SEEDS

J. A. Pitel
B. S. P. Wang

ABSTRACT

Seeds of whitebark pine (Pinus albicaulis *Engelm.*) *were x-rayed, and those with full embryos were selected for the experiment. For intact seeds, no germination was observed for unstratified seeds; 23 percent germination was obtained for seeds stratified for 60 days. Treatment with* GA_3 *was not effective in improving germination of intact seeds. Following sulfuric acid scarification, unstratified seeds had 4.7 percent germination, while those stratified for 60 days had 41.3 percent germination. The best treatment to improve germination was clipping the seeds—excising a small piece of the seedcoat and gametophyte from the radicle end, exposing the root tip. With this treatment, germination rates of 61.3 percent and 90.7 percent were observed for unstratified and 60-day-stratified seeds, respectively. Some causes of dormancy of the seeds are discussed.*

INTRODUCTION

Whitebark pine (*Pinus albicaulis* Engelm.) occurs in subalpine areas in the northern Rocky Mountains and Coast Mountains of British Columbia through the Cascade Range to the southern Sierra Nevada. In Canada, the species has some importance in reclamation projects. The wood is also cut locally for lumber and mine timbers.

In a previous study with this species (Pitel and Wang 1980), results with three seedlots showed that embryo underdevelopment was the primary cause for poor germination. Only 19 to 30 percent of the seeds had embryos that were 75 to 100 percent full. Because of this, seed germination did not increase very much following cold or warm stratification or after various physical and hormone treatments. Another seedlot acquired recently (provided by Dr. Ray J. Hoff, Intermountain Research Station, Moscow, ID) was found to be very interesting as, unlike the previous three seedlots examined, more of the seeds contained fully developed embryos. The purpose of this study was to determine if this seedlot would respond more favorably to treatments with sulfuric acid, clipping, gibberellic acid, and cold stratification.

MATERIALS AND METHODS

Whitebark pine seeds of the 1974 crop, obtained from Gisborne Peak, near Priest River, ID, were classified according to the size and development of the embryos and endosperms (Simak 1980), and then surface-sterilized with calcium hypochlorite (4 percent available chlorine). For each experiment treatment, three replicates of 50 seeds (with mature embryos) were used. Physical treatments included soaking in concentrated (97 percent) sulfuric acid for 3.5 hours, followed by stratification for 30 and 60 days; and by clipping unstratified and 30- and 60-day-stratified seeds at the radicle end, removing a piece of the seedcoat and gametophyte tissue sufficient to allow exposure of the root tip.

Seeds were stratified at 4 °C in the dark under moist, aerated conditions. For hormone treatment, intact and sulfuric-acid-treated seeds were placed in a solution of gibberellic acid (GA_3 at 500 mg/L) for 24 hours. Germination was at 20 °C in continuous light for 30 days. Germination is based on seeds selected for fully developed embryos and gametophytes. Seeds were considered to have germinated if the radicles were at least 5 mm long, and showed geotropic curvature. Seeds were x-rayed with Kodak "M" films at 20 KV, 3 mA, 80 seconds, and 56 cm focus to film distance.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Jack A. Pitel and Ben S. P. Wang are Research Scientists, Petawawa National Forestry Institute, Chalk River, ON, K0J 1J0.

Table 1—Percentage distribution of different embryo and female gametophyte types present in whitebark pine seeds from Idaho

Seed class	Female gametophyte type	Embryo type	Percentage
O	shrunken or full	absent	11.0
III A	full	50-75% full	37.5
IV A	full	75% to full	47.0
III B	shrunken	50-75% full	1.5
IV B	shrunken	75% to full	3.0

RESULTS AND DISCUSSION

Analysis by x-radiography showed that 84.5 percent of the seeds obtained from Idaho contained embryos that were larger than half of the embryo cavity. Most of these were seeds with full embryos. The percentage of seed included for each of the embryo and endosperm classes is described in table 1. The large proportion of seeds with full or almost full embryos indicated that embryo underdevelopment would not be a significant factor affecting the germination of this seedlot, as was the case in the previous study (Pitel and Wang 1980).

In contrast to the seeds from Idaho, seeds recently obtained (1986 crop) of whitebark pine from a high-elevation site (longitude 114 °37'; latitude 50 °06'; 2,164 m) in the Rocky Mountains Forest Reserve, AB, provided by the Alberta Forest Service, showed a very high percentage of empty and underdeveloped seeds. Following an attempt to upgrade the seed quality by flotation in cyclohexane (fig. 1) and x-radiography, only 10 percent of the seeds were found to have 50 to 100 percent fully developed embryos, according to the anatomical development classification of Simak (1980) (table 2). Figures 2 and 3 indicate that separation of many poor quality seeds can be achieved by use of cyclohexane. Pentane gave similar results. Because of the poor quality of the seeds from the Alberta source, we decided not to include this seedlot for physical and chemical treatments. Further studies of Canadian whitebark pine seeds with special reference to their anatomical development, upgrading of seed quality by pentane (Barnett 1971), and physical and physiological treatments for improving germination are planned.

Although the seeds from Idaho had a large percentage of mature embryos, none of the intact seeds germinated (table 3). Stratification for 60 days increased germination to 23.3 percent. The increased germination following cold stratification suggests the presence of physiological embryo dormancy. This is usually overcome after certain metabolic events that may result in decreased inhibitor and increased growth promoter content, increased energy charge, activation of the genome, and increased protein synthesis (for example, see Khan 1982). Gibberellic acid was not effective in improving the germination of intact whitebark pine seeds.

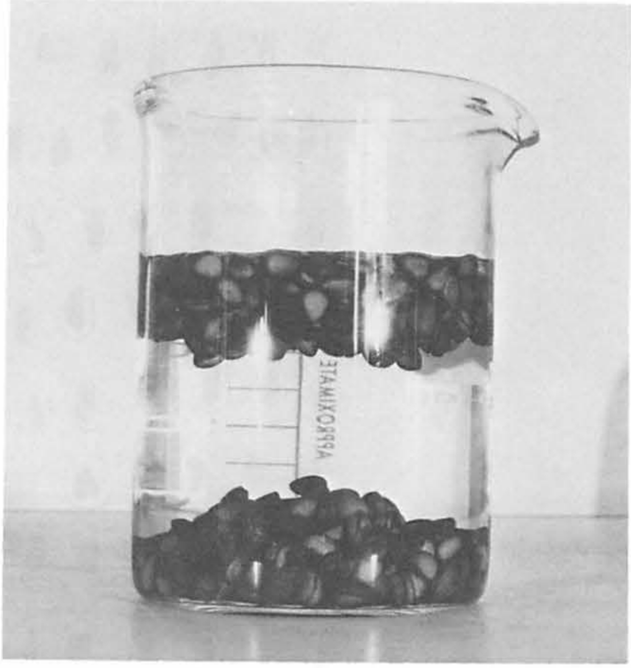


Figure 1—Separation of whitebark pine seeds into sinkers and floaters by use of cyclohexane.

Table 2—Percentage distribution of embryo size and female gametophyte development of Alberta whitebark pine seeds (based on 1,034 seeds x-rayed)

Seed class	Female gametophyte type	Embryo type	Percentage
O	shrunken or full	absent	27.9
II A	full	less than 50%	57.1
III A	full	50-75% full	7.3
IV A	full	75% to full	2.2
II B	shrunken	less than 50%	5.0
III B	shrunken	50-75% full	0.5
IV B	shrunken	75% to full	0.0

Table 3—Percentage germination using various cold stratification and physical and hormone treatments on whitebark pine seeds obtained from Idaho

Seed treatment	Days of stratification					
	Control^{0}	GA$_3$	Control^{30}	GA$_3$	Control^{60}	GA$_3$
Intact seeds	0	0	16.7	19.3	23.3	26.7
Sulfuric acid treated	4.7	14.7	20.7	18.0	41.3	32.7
Clipped	61.3	—	78.7	—	90.7	—

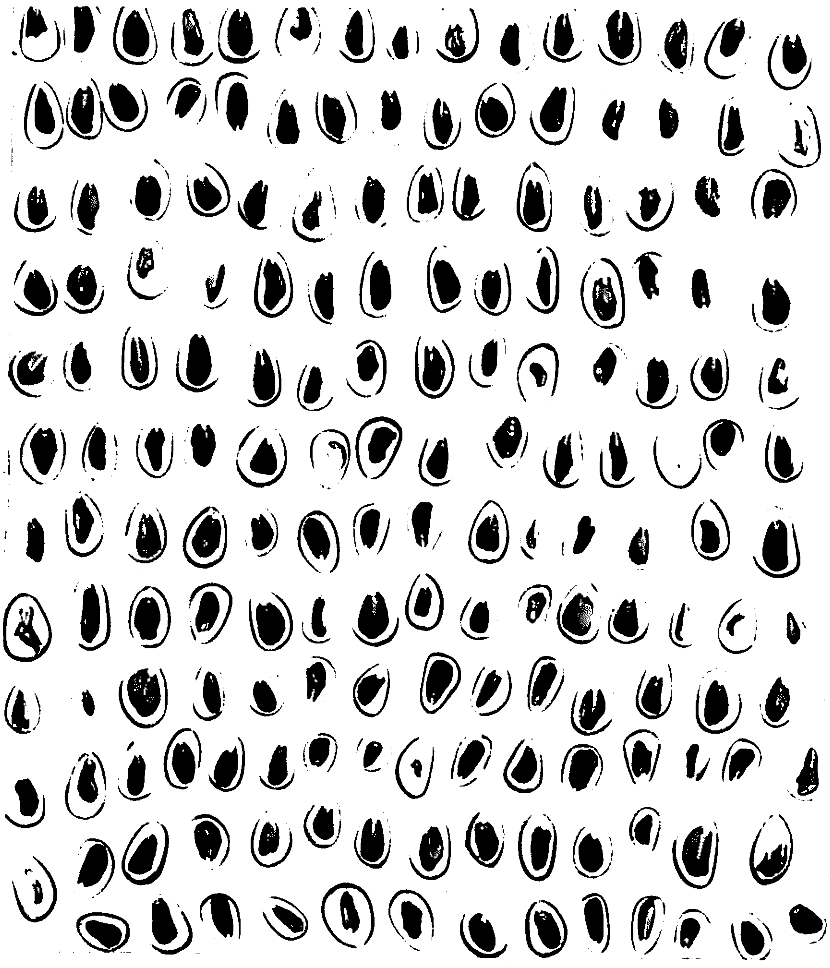


Figure 2—Analysis by x-radiography of seeds that floated following cyclohexane separation.

Treatment of seeds with sulfuric acid improved germination of both unstratified and stratified seeds. Germination of 41.3 percent was obtained after 60 days of stratification. These results suggest that the seedcoat is also a factor involved in the dormancy of whitebark pine seeds, either by restricting water and oxygen uptake, by mechanical restraint, or both. Treatment with sulfuric acid and gibberellic acid improved germination over that of the controls only for unstratified seeds.

Clipping resulted in the greatest improvement in germination. Unstratified seeds that were clipped had a germination rate of 61.3 percent. If the seeds were stratified for 30 and 60 days, germination increased to 78.7 percent and 90.7 percent, respectively. Sufficient seeds were not available for analysis by treatment with a combination of gibberellic acid and clipping. However, as shown in table 3, gibberellic acid had no effect on intact seeds, and even if most of the seedcoat was removed with sulfuric acid, germination only improved slightly.

Our results indicate that if the seeds have a high proportion of developed embryos, good germination can be obtained if treated as shown in table 3. Further studies are needed to clarify the exact cause of dormancy. It may be the result of a combination of physiological embryo dormancy and mechanical restraint, limited oxygen supply, and growth inhibitors imposed by the seed coat and female gametophyte tissue.

However, for whitebark pine seeds obtained from Canadian sources to date, the low percentage of seeds with fully developed embryos and gametophytes is the primary cause of poor germination. Studies are in progress to improve this situation by first identifying the best seed lots in British Columbia and Alberta and then upgrading the seed quality by flotation, such as with n-pentane. Treatment by warm stratification is being done to try to increase embryo size. Physical and chemical treatments (such as potassium nitrate and growth promoters) will be combined with methods to overcome possible physiological dormancy, such as cold stratification or alternating temperatures.

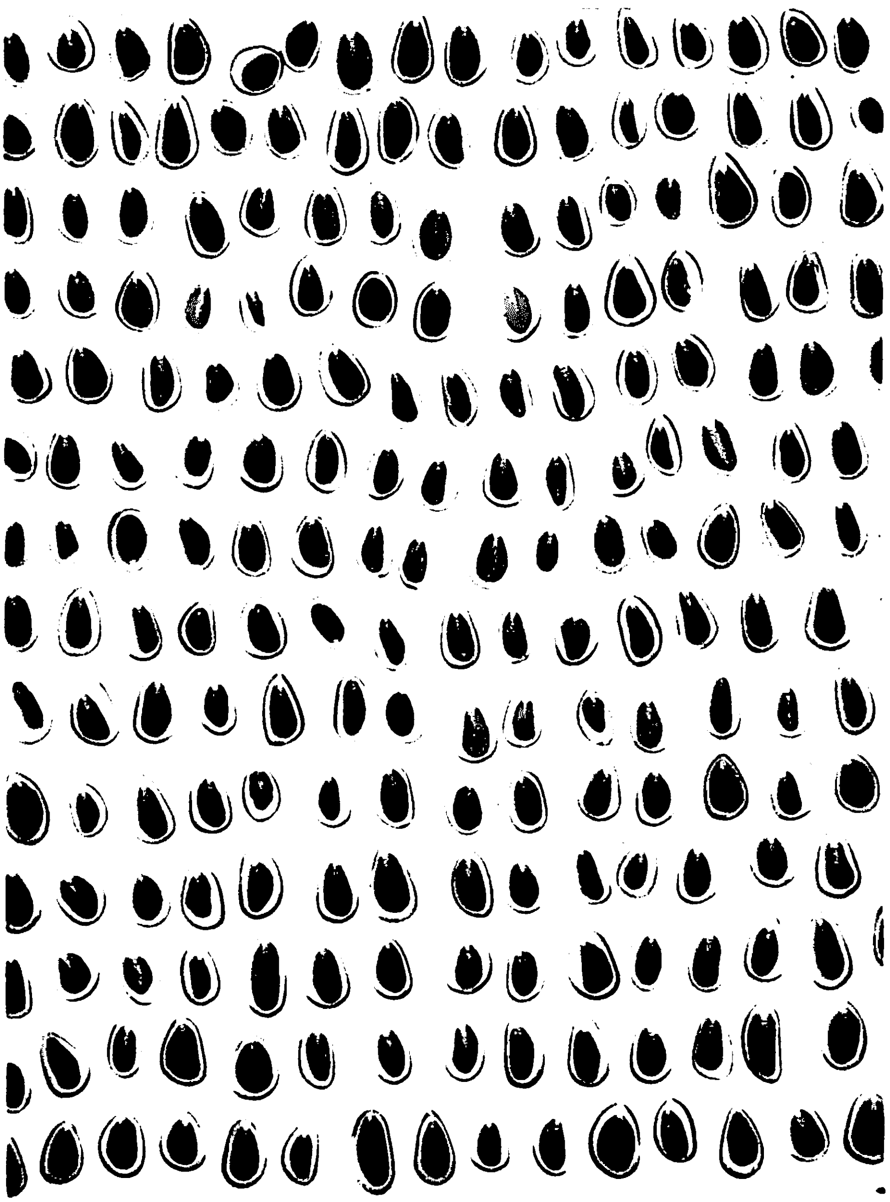


Figure 3—Analysis by x-radiography of seeds that sank following cyclohexane separation.

REFERENCES

Barnett, J. P. 1971. Flotation in ethanol reduces storability of southern pine seeds. Forest Science. 17: 50-51.

Khan, A. A. 1982. The physiology and biochemistry of seed germination and dormancy. Amsterdam and London: Elsevier: 29-50.

Pitel, Jack A.; Wang, Ben S. P. 1980. A preliminary study of dormancy in *Pinus albicaulis* seeds. Bi-Monthly Research Notes. No. 36. Ottawa, ON: Canada Department of the Environment, Canadian Forestry Service: 4-5.

Simak, Milan. 1980. X-radiography in research and testing of forest tree seeds. Rapporter No. 3. Umea, Sweden: The University of Agricultural Sciences, Department of Silviculture. 34 p.

EFFECTS OF TEMPERATURE AND TEMPERATURE PRECONDITIONING ON SEEDLING PERFORMANCE OF WHITEBARK PINE

J. Jacobs
T. Weaver

ABSTRACT

Four experiments explored the effects of temperature on the germination and seedling performance of whitebark pine (Pinus albicaulis). *While 1 month of stratification increased germination from 5 percent to about 40 percent, longer stratification periods (to 8 months) did not improve germination. Germination occurred throughout the 10 to 40 °C range with a broad optimum near 30 °C. Root growth occurred throughout the 10 to 45 °C range with an optimum near 30 °C. Long exposure (5 months) to low temperature (1.5 °C) lowered the temperature threshold for both germination and root growth. The apparent temperature range (perhaps 0 to 35 °C) and optimum (20 °C) for net photosynthesis at light saturation were lower than for germination and growth. While no preconditioning effect of light level (200 to 800 uE/M2*S) on the photosynthetic capacities of mature leaves was seen, photosynthesis increased progressively from needles preconditioned with winter, spring (5 °C day to 5 °C night), summer (15 °C day to 5 °C night), and abnormally warm (25 °C day to 15 °C night) temperatures.*

INTRODUCTION

The establishment of whitebark pine (*Pinus albicaulis* Engelm.) on a site must depend on its response to quantities of energy (light and heat), materials (water and nutrients), and destructive forces (fire, herbivory, and trampling) present at the site (Hutchinson 1957). The trees' response might depend, as well, on preconditioning with respect to water (May and others 1962), temperature (Tranquillini 1979), or even destructive forces (Ryan 1983).

The object of our research was to explore the effects of one environmental phenomenon, temperature, on whitebark pine's readiness to germinate, germination, root growth, and photosynthesis. The magnitude of temperature preconditioning effects was studied on one of these processes, net photosynthesis.

METHODS

Seed Source

Seeds for studies of stratification, germination, root growth, and photosynthesis were collected from an *Abies lasiocarpa-Vaccinium scoparium* habitat type near Jardine, MT (Palmer Mountain, 2,652 m) in the autumn of 1987. They were stored under dry 20 °C conditions.

Stratification Time

To determine the effects of stratification time on germination rate, filled seeds were stratified for 0, 1, 2, 3, 5, or 8 months and germination rates were compared (Jacobs 1989). All seeds were x-rayed before stratification and empty seeds were discarded. To minimize the danger of fungal attack during stratification, the seeds were surface sterilized by soaking in 40-percent Clorox for 10 minutes and rinsing 10 times in distilled water to remove the Clorox (Wenny and Dumroese 1987). The seeds were then placed in nylon bags and soaked in clear running tap water for 48 hours. The imbibed seeds were surface dried, lightly dusted with Spurgon fungicide (Tetrachloro-para-benzoquinone 98 percent) and placed between two moistened blotter papers in plastic germination boxes (14 by 13 by 3.5 cm), 100 seeds per box. The seeds were stratified in a refrigerator (1.5 °C) for 0 to 8 months. When the stratification was complete, the stratification-germination boxes were transferred to a germination chamber (25 °C day, 15 °C night, and a 10-hour photoperiod). Germination occurred over a period of 1 to 3 months. After germination ceased, percent germination was calculated.

Germination Rates

To determine the effect of temperature on germination rate, the germination rates of seeds stratified at 1.5 °C for 2 to 3 months were compared at temperatures ranging from 5 to 50 °C (Jacobs 1989). Stratified seeds were placed on a temperature gradient bar with a temperature range of 5 to 50 °C and germinating seeds were counted over a period of 2 weeks. The temperature gradient bar was similar to that of Barbour and Racine (1967): three aluminum plates (one per species) 90 by 14.5 by 0.7 cm lay parallel and connected by tubes with 50 °C water

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

J. Jacobs is Forest Ecology Associate and T. Weaver is Plant Ecologist, Department of Biology, Montana State University, Bozeman, MT 59717.

passed through at one end, and 4 °C isopropyl alcohol at the other. Each bar was coated with lacquer (to minimize Al^{+++} exposure) and a moist blotter. The blotter paper was kept moist by immersing its warm end in a tray of water, and by the condensation of water on its cold end. The bars were covered with plastic wrap and a plexiglass box top to minimize evaporation and temperature fluctuation. Stratified seeds were lined up across the bar in columns of 10, and with the columns 5 cm apart. Treatment temperatures were measured by placing the tip of a thermocouple on the blotter paper at each seed column. Seeds germinating in each temperature treatment were counted every 48 hours for 2 weeks. The experiment was replicated on three dates (July 15, 1988; December 2, 1988; and February 27, 1989).

Root Growth Rates

To determine the effects of temperature on root growth rates, the root growth rates of plants growing under cool temperatures were compared with those of plants growing under warmer conditions (Jacobs 1989). The seeds were stratified in a refrigerator (1.5 °C) for 1 to 3 months. When the stratification was complete, the stratification-germination boxes were transferred to a germination chamber (25 °C day, 15 °C night, and a 10-hour photoperiod). Freshly germinated seeds were transferred to the temperature gradient bar to measure root growth rates at temperatures ranging from 4 to 48 °C. The bar was coated with lacquer (to minimize Al^{+++} exposure), a moist blotter, and, 1 mm above the blotter, a glass plate. Each bar was tilted at a 45° angle so the roots would grow geotropically straight down between the blotter and the glass and in a region of constant temperature. The blotter paper was kept continuously moist by immersing its warm end in a tray of water, and by the condensation of water on its cold end. The bars were covered with a plexiglass box top to minimize evaporation and temperature fluctuation. Root lengths were measured when seeds were placed on the bar and every 48 hours thereafter for 8 days. Bar temperatures at sites where the roots grew were measured by inserting a thermocouple between the glass plate and the blotter paper. The experiment was replicated on four dates (April 26, May 6, June 1, and June 22, 1988).

Photosynthetic Rates

Seeds collected in 1984 were stored, stratified, planted, and started in the Coeur d'Alene nursery. We obtained 2-year-old *Pinus albicaulis* seedlings as bare root stock in October of 1987. The seedlings were transferred to 3.8- by 20.3-cm "conetainer" tubes in a soil composed of equal volumes of Fort Ellis loam, sand, and peat; steam pasteurized at 180 °F; and maintained in a greenhouse at 15 °C and natural photoperiod over winter. In March 1988, seedlings were transferred to a vernalization room (5 °C night/9 °C day) to prevent breaking dormancy.

Seedlings were preconditioned for 35 days (April 19 to May 24, 1988) at three day-night temperature combinations and two light levels. Temperatures in the three growth chambers were 25 °C day/15 °C night (hotter than field conditions), 15 °C day/5 °C night (similar to July-August), and 5 °C day/5 °C night (similar to April-May) (Weaver 1980, this proceedings). In each temperature regime six seedlings received light levels equal to 33 percent of full sun (800 uE/M2*S = micro-Einsteins PAR (= micro moles of photosynthetically active radiation) per meter squared per second and simulating light levels in an open stand) and six seedlings received 10 percent of full sun (200 uE/M2*S and simulating understory conditions in a fully shaded spot, Wellner 1948). Light was provided with fluorescent and incandescent light (twelve 60-watt incandescent, and sixteen 6-ft cool white fluorescent tubes) shaded, in the low-light case, with steel screen. Light levels measured in a mature whitebark pine stand (52 percent cover, Weaver and others, this proceedings) were 250-1,619 uE/M2*S in sun spots and 140-230 uE/M2*S in full shade. The photoperiod was 14 hours, equivalent to the photoperiod 1 month before bud break (lat. 45° N., May, Long 1969; Schmidt and Lotan 1980). In spite of the short days, seedlings in the 25 °C day-15 °C night and 15 °C day-5 °C night chambers broke bud dormancy during preconditioning; the resultant growth was clipped off so only year-old needle photosynthesis and respiration were measured. The base of each conetainer tube was submerged in 2 cm of water to prevent water stress.

Photosynthetic rates of seedlings given the six preconditioning treatments were measured, via CO_2 exchange, at four temperatures (0, 15, 25, and 35 °C) and five light levels (dark, 210, 420, 1,050, and 1,580 uE/M2*S) between May 24 and June 14. Six 5-cm-diameter by 15-cm-long plexiglass chambers, one for a seedling from each preconditioning treatment, were cemented side-by-side in a rectangular water jacket. The air was mixed by turbulence as it flowed from top to bottom of the tubular chamber. Chamber air temperatures were maintained by pumping water from a water bath through the water jacket surrounding the chambers. The roots were outside the chambers and therefore near room temperature (21 °C). A thin copper-constantan thermocouple was inserted into a *Pinus albicaulis* needle and placed in the chamber as an index of leaf temperature. The chambers were lighted with a xenon lamp and light levels were regulated using wire screens. Plumbers' "bolwax" was used to seal the conetainers into the chambers and to seal the soil-root systems out of the chambers.

CO_2 flux density was measured with an Analytical Development Company open system IR gas analyzer. Air from the ceiling of a hallway was pumped through copper tubing in the water bath to adjust its temperature, through a silica gel to dry it, and split for reference and analysis air. Both reference and analysis air were, thus, very dry. The reference air was passed through a flow regulator and to the reference port of the gas analyzer. The analysis air went to a manifold that directed it to the six chambers with the seedlings. The analysis air was directed through one of the six chambers at a time, to a flow regulator, and then to the analysis port of the gas analyzer. Flow rate for reference and analysis air was maintained at 150 mL/minute. The difference between reference and analysis air was checked with an empty chamber at the beginning and end of each day to verify that the CO_2 concentrations were equal.

The experiment was replicated six times. Each run began at 0 °C and progressed through four temperature steps to 35 °C; the plants were allowed 1 hour to equilibrate after each adjustment. Within each temperature level net photosynthesis was measured at irradiation levels including dark (for respiration), four light levels up to 1,580 uE/M2*S, and a second end-of-run measurement of dark respiration; the plants were allowed to equilibrate 20 minutes between changes in light levels. Since it took 2 days to complete one replication (run through the four temperatures and five light levels), the seedlings were returned to their preconditioning chambers for the night.

Whole-seedling photosynthetic rates were converted to leaf area rates by dividing whole seedling photosynthesis by the total leaf area of the seedling. All the needles were plucked from the seedling and run through a Licor optical planimeter to measure the projected area (Kvet and Marshall 1971). In contrast to a platelike leaf—whose total area is calculated by doubling projection areas—a needle is a three-sided triangular prism formed by division of a cylindrical needle bundle into five needles. Since the cylinder splits from the tip down, each needle is curved outward from the axis so that the projectable area is roughly equivalent to a radial section (0.5 diameter by ht) through the needle bundle cylinder. Assuming this, one sees that total needle area is proportional to projectable area as needle radius is to needle circumference [that is, r (for one radial side) + r (for the second radial side) + $2*pi*r/5 = 1.256r$ (for the circumferential side)] so total needle area can be calculated by multiplying projected area by 3.256. We recognize that total leaf area overestimates functioning leaf area and therefore underestimated absolute photosynthetic rates (Carter and Smith 1985), but believe the units are adequate for comparisons designed to determine the effects of light and temperature levels.

Statistical analysis of the data was by analysis of variance across the six replications with a Newman-Kuels comparison of means (Snedecor and Cochran 1980).

RESULTS AND DISCUSSION

Stratification

Exposure to moist cold is a dormancy-breaking requirement for many species including almost half of the pines (Schopmeyer 1974). Since whitebark pine usually exhibits low germination rates in standard tests, we tested the hypothesis that the 1-month stratification time usually applied is less effective than a stratification time approximating the 5 to 8 months received naturally (Weaver 1980). Germination rates were 4 percent, 68 percent, 38 percent, 41 percent, 52 percent, and 38 percent for seeds stratified for 0, 1, 2, 3, 5, and 8 months, respectively. We conclude that stratification beyond 1 month does little to increase germination and speculate that a short stratification time has been naturally selected, because it prevents fall germination without any chance of delaying spring germination. This conclusion is bolstered by parallel tests (Jacobs 1989) that show 1-month stratification times were required for species from high (long-winter) altitudes (whitebark pine), middle altitudes (lodgepole pine), and low (short-winter) altitudes (limber pine). We speculate that the low germination rates observed are due in part to seed defect and in part to other dormancy mechanisms that reserve live seed for succeeding years (McCaughey 1989 [whitebark pine]; Perry 1989 [lodgepole pine]).

Temperature and Germination

Our tests show that, newly stratified whitebark pine seeds, germinate at temperatures ranging from 10 to 40 °C and that, while germination rates of specific lots of 10 seeds vary from 0 to 50 percent at most temperatures in this range, germination rates tend to be slightly higher in the 25 to 35 °C range than at cooler or warmer temperatures (fig. 1A). Germination of middle-altitude lodgepole pine and low-altitude limber pine occurred in the same 10 to 40 °C range as the high-altitude whitebark pine. During our stratification studies we saw that, if seeds are kept under cold conditions (1.5 °C) for longer periods of time (over 5 months), most dormancy-broken seeds will germinate. Since stratification is probably completed in the early winter, germination in moist forest soils is likely under temperature and/or endogenous control for most of the winter. If so, germination is expected in the spring near the time of snow melt.

Temperature optima may drop slightly with decreases in altitude from 25 to 35 °C for whitebark, 15 to 35 °C for lodgepole, and 15 to 25 °C for limber pine (Jacobs 1989). We speculate that, because lower temperatures precede the warmer temperatures of late spring, seeds with a lower optimum probably germinate first and are deeper rooted at the onset of any summer drought. If so, natural selection at lower, drier altitudes, where limber pine was collected, probably favors a lower temperature optimum than that favored at higher moister altitudes where whitebark pine predominates.

Temperature and Root Growth

Our tests show that, in newly stratified whitebark pine seeds, root growth can occur at temperatures between 10 and 45 °C and that, at the temperature optimum (25 to 35 °C), root extension of new germinants is 5 to 15 mm per day (fig. 1B). Root growth of high-altitude whitebark pine, middle-altitude lodgepole pine, and low-altitude limber pine has similar ranges (10 to 45 °C) and optima (30 °C) (Jacobs 1989). During our stratification experiments we also saw that, if seeds germinate after long (5 months) cold (1.5 °C) storage, root growth will occur at temperatures below the range reported. We conclude that in nature, germination must produce roots near snow melt, most growth occurs at suboptimal temperatures, and high-temperature stress is rare or nonexistent for most roots. This assertion is supported by soil temperature data at 5 cm depth from level grasslands just below the conifer zone at Bozeman, MT, and Casper, WY (NOAA 1985). Of the 6 months with average maximum

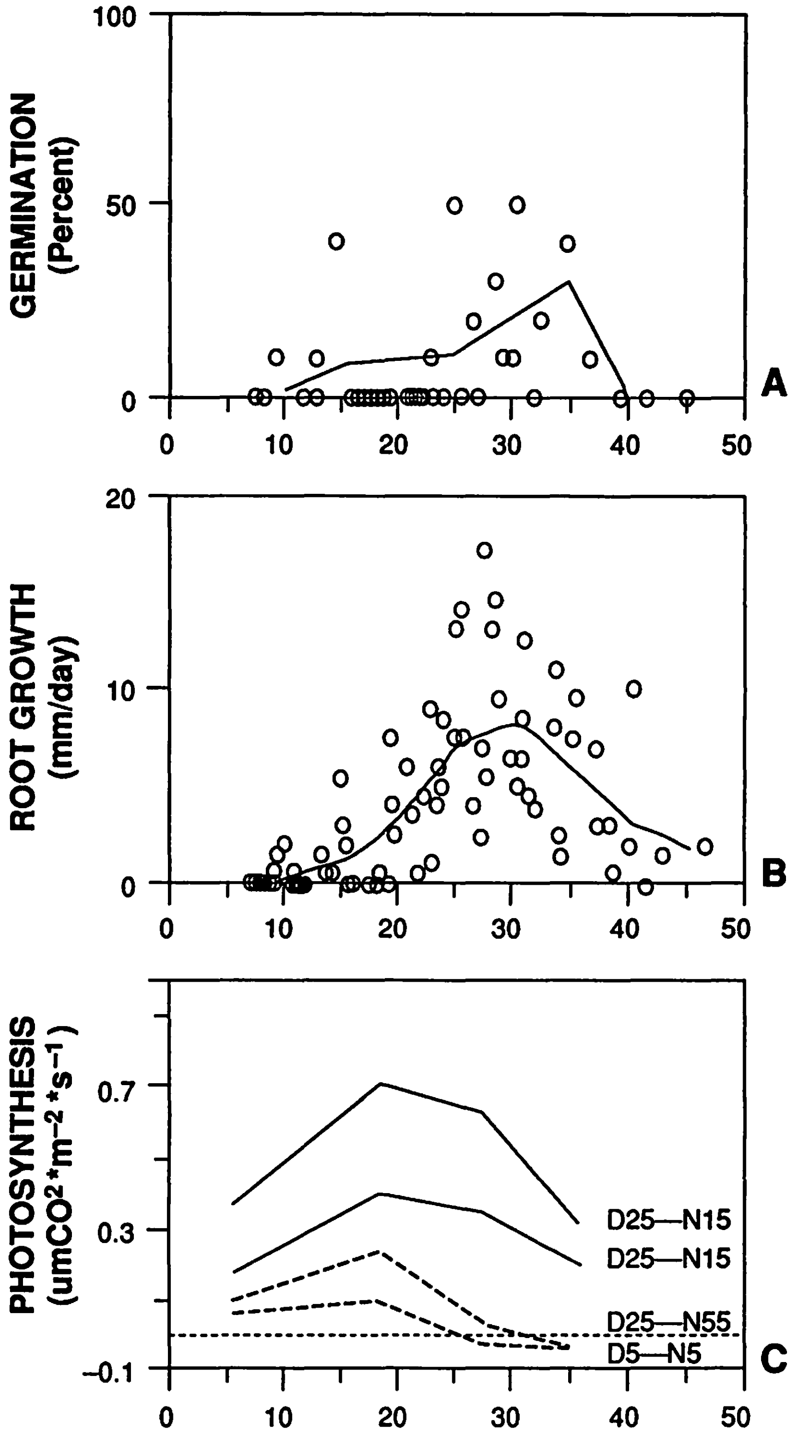


Figure 1—Effect of temperature on seed germination, root growth, and net photosynthesis: (A) Percent germination in 33 lots of 10 seeds tested at temperatures between 5 and 45 °C. The line passes through the median of non-zero values. (B) Initial growth rates (mm/day) of 71 roots grown at temperatures between 5 and 50 °C; the line passes through the median of non-zero values. (C) Photosynthetic rates at saturation for plants preconditioned at spring (5 °C day to 5 °C night), summer (15 °C day to 5 °C night), and warmer than natural (25 °C day to 5 °C night) conditions. Plants preconditioned under the hot conditions (solid lines) and low light (200 uE/M2*S) had higher photosynthetic rates (upper solid line) than the chlorotic plants preconditioned under high light (800 uE/M2*S).

temperature above 10 °C, only 3 have average maximum temperatures above 20 °C and maximum temperatures of 30 °C are reached rarely, if at all. If maximum temperatures almost never exceed 30 °C at 5 cm, the inhibition of root growth observed there (Weaver 1981) is more likely due to drought than high temperature; both factors may be important in more superficial layers.

Photosynthetic rates for ecologically and genetically related *Pinus cembra* increase fourfold as average soil temperatures rise from 0 to 8 °C (Tranquillini 1979); the increase in photosynthesis with increases in average soil temperature may indicate the daily duration of root activity; that is, hours above a root growth minimum of 10 °C.

Temperature and Photosynthesis

Net photosynthesis rises with increasing light from 0 to a maximum near 1,050 uE/M2*S for seedlings preconditioned under naturally occurring conditions. *Pinus contorta* (Dykstra 1974) and *Picea engelmannii* (Hadley and Smith 1987) were also light saturated at about 50 percent of full sun. While we saw no consistent difference in photosynthetic rates of mature leaves preconditioned for 1 month at 200 or 800 uE/M2*S, shade leaves might have been formed if branches had been shaded during needle initiation (Jacobs 1989).

Net photosynthesis at light saturation probably occurs at all above-freezing temperatures. It occurs at –4 °C in *Pinus cembra*, a close ecologic, taxonomic, and genetic relative (Tranquillini 1979), and in whitebark pine was shown to occur at 5 °C, was maximum near 20 °C, and declined significantly above 20 °C (fig. 1C). The temperature optimum for photosynthesis of *Pinus contorta* is also near 20 °C (Dykstra 1974). Dark respiration increased slightly from 5 °C (0.13 μmole m^{-2}sec^{-1}) to 30 °C (0.19 μmole m^{-2}sec^{-1}) and rose significantly as 35 °C (0.32 μmole m^{-2}sec^{-1}) was approached (Jacobs 1989). Despite the fact that both germination and root growth occur in the soil at temperatures lower than air temperature, both apparently have higher temperature cardinal points (minimum 10-optimum 30-maximum 40 °C) than does photosynthesis (0 min, 25 opt, and 35-40 °C, fig. 1)— a process proceeding at air temperature.

Net photosynthetic rates of whitebark pine are affected by temperature preconditioning (reviewed for other timberline species by Tranquillini 1979). Studies of photosynthesis of *Pinus cembra* (Tranquillini 1979) showed no photosynthesis during the winter months and *Pinus albicaulis* probably behaves similarly. Warming from winter to simulated spring (day 5 °C-night 5 °C) and summer (day 15 °C-night 5 °C) temperatures increased photosynthetic rates from 0.00 to 0.06 and 0.19 μmole m^{-2}sec^{-1}, respectively (fig. 1C). Further warming, to temperatures of 25 °C day-5 °C night, not even experienced in dry grasslands below, increased photosynthetic rates to 0.38-0.69 μmole m^{-2}sec^{-1} (fig. 1C). The increase in net photosynthetic rates with higher temperature preconditioning must be primarily due to increases in gross photosynthesis or decreases in photorespiration—because differences in preconditioning temperature caused no difference in dark respiration rates. Light preconditioning had no effect on photosynthetic rate under spring or summer conditions; under warmer than natural preconditions, however, net photosynthesis of plants preconditioned with low light (200 uE/M2*S) was significantly higher than that of plants preconditioned with higher light levels (800 uE/M2*S).

Acclimatization (preconditioning) results suggest that—with adequate water and with competitor reduction, perhaps by fire or management—whitebark pine might survive under the warmest temperature conditions in our region. The trees may have used this capability in surviving the hypsithermal, a warm dry postglacial period, that deforested some of the highest sites in our region (for example, the Bighorn and Beartooth Mountains). This possibility is supported by the vigorous growth of trees transplanted from high forests to lawns in the valley below where their success surely depends on both heavy watering and the elimination of less cold-tolerant competitors such as *Pinus ponderosa*, *Psuedotsuga menziesii*, and *Abies lasiocarpa* (Arno and Weaver, this proceedings).

ACKNOWLEDGMENTS

This study was funded by Intermountain Research Station, Forest Service, U.S. Department of Agriculture, under Agreement No. INT-87284.

REFERENCES

Barbour, M. G.; Racine, C. H. 1967. Construction and performance of a temperature-gradient bar and chamber. Ecology. 48(5): 861-863.

Carter, G. A.; Smith, W. K. 1985. Influence of shoot structure on light interception and photosynthesis in conifers. Plant Physiology. 79: 1038-1043.

Dykstra, G. F. 1974. Photosynthesis and CO_2 transfer of lodgepole pine seedlings in relation to irradiation, temperature, and water potential. Canadian Journal of Forest Research. 4: 201-206.

Hadley, J.; Smith, W. 1987. Influence of krummholz mat microclimate on needle physiology and survival. Oecologia. 73: 82-90.

Hutchinson, G. E. 1957. Concluding remarks. Cold Springs Harbor Symposium on Quantitative Biology. 22: 415-426.

Jacobs, J. 1989. Temperature and light effects on seedling performance of *Pinus albicaulis*. Bozeman, MT: Montana State University. 39 p. Thesis.

Kvet, J.; Marshall, J. 1971. Assessment of leaf area and other assimilating plant surfaces. In: Sestak, J. [and others], eds. Plant photosynthetic production-manual and methods. The Hague: Junk Publications: 517-555.

Long, L., ed. 1969. The world almanac. New York: Newspaper Enterprise Association. 932 p.

May, L.; Milthorpe, E.; Milthorpe, F. 1962. Presowing hardening of plants to drought. Field Crop Abstracts. 15: 93-98.

McCaughey, Ward W. 1989. [Personal communication]. Bozeman, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory.

NOAA. 1985. Climatological data for Wyoming and climatological data for Montana. Asheville, NC: U.S. Department of Commerce, National Oceanic and Atmospheric Administration.

Perry, D. 1989. [Personal communication]. October. Corvallis, OR: Oregon State University.

Ryan, C. 1983. Insect induced chemical signals regulating natural plant protection responses. In: Denno, R.; McClure, M. Variable plants and herbivores in natural and managed systems. New York: Academic Press: 43-60.

Schmidt, Wyman C.; Lotan, James E. 1980. Phenology of common forest flora of the Northern Rockies—1928 to 1937. Res. Pap. INT-259. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 20 p.

Schopmeyer, C. S. 1974. Seeds of woody plants of the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture, Forest Service. 883 p.

Snedecor, G. W.; Cochran, W. G. 1980. Statistical methods. 7th ed. Ames, IA: Iowa State Press. 507 p.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. Berlin: Springer-Verlag. 137 p.

Weaver, T. 1980. Climates of vegetation types of the Northern Rocky Mountains and adjacent plains. American Midland Naturalist. 103: 392-398.

Weaver, T. 1981. Distribution of root biomass in well-drained surface soils. American Midland Naturalist. 107: 393-395.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. American Midland Naturalist. 92: 222-230.

Wellner, C. A. 1948. Light intensities related to stand intensity in mature stands of the western white pine type. Journal of Forestry. 46: 16-19.

Wenny, David L.; Dumroese, R. Kasten. 1987. Germination of conifer seed surface sterilized with bleach. Tree Planters' Notes. 38(3): 18-21.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from P. Kolb)—Do shaded seedlings have lower compensation points than sun-grown seedlings?

A.—Our growth chamber lights were not as bright as sunlight (1,600 uE/M2*S) so different light levels really refer to a light shade (800 uE/M2*S)—rare in the field—and a deep shade (200 uE/M2*S). Plants preconditioned in deeper shade usually had slightly lower compensation points (Jacobs 1989), but I doubt that the differences were statistically significant. It would be interesting to compare compensation points of sun and shade needles in the field.

Q. (from P. Kolb)—Why are photosynthetic rates of your shade-conditioned seedlings higher than those of your sun-conditioned seedlings?

A.—Light preconditioning had no differential effect on plants grown under normal spring (5 °C day-5 °C night) or summer (15 °C day-5 °C night) conditions. Plants grown at high temperature (25 °C day-15 °C night) with relatively high light levels (800 uE/M2*S) were chlorotic and therefore demonstrated lower photosynthetic rates than plants preconditioned at lower light levels (200 uE/M2*S).

Q. (from D. Mattson)—How does photosynthetic performance of whitebark pine under different light and temperature conditions compare with that of associated conifers (*Abies lasiocarpa*, *Picea engelmannii*, or *Pinus contorta*)?

A.—Lodgepole (Dykstra 1974) and Engelmann spruce (Hadley and Smith 1987) are similar to whitebark in light saturation levels (50 percent of full sun) and temperature optima (20 °C). Your question would be answered best with one experiment comparing all four species with uniform methods. Even these data would provide only a partial explanation of shade and temperature tolerance, as information on photosynthesis should be integrated with information on other processes (such as, respiration rates) to understand the carbon balance (growth) of the tree. Models integrating a variety of environmental factors will be required to predict the distribution and growth of whitebark pine; the models of Tranquillini (1979) and Keene (this proceedings) are relevant.

BIOTIC AND MICROSITE FACTORS AFFECTING WHITEBARK PINE ESTABLISHMENT

Ward W. McCaughey
T. Weaver

ABSTRACT

To enhance establishment of future whitebark pine (Pinus albicaulis) *forests, information is needed on the physical and biological factors affecting whitebark seed germination and seedling establishment. This paper summarizes the first-year results of field examinations designed to evaluate predator and seedbed factors affecting whitebark pine establishment. Predator effects were estimated by recording seedling emergence under four levels of predator exclusion (free predator access, rodents excluded, birds excluded, and both rodents and birds excluded). Rodents ate or removed 100 percent of available surface-sown seeds. Emergence was higher on plots excluding rodents only and significantly higher on plots excluding rodents and birds. Seedling emergence did not differ significantly between mineral (although numerically higher) and litter seedbeds.*

The effects of three seedbed factors were also examined by comparing seedling emergence under three light levels (open, 25, and 50 percent shade cover), two seedbed conditions (mineral and litter), and two sowing depths (on surface and 0.8 to 1.6 inches beneath surface). Buried seeds had significantly higher emergence rates than did surface-sown seeds. Even though the first season was hot and dry, 78 percent of seedlings survived.

INTRODUCTION

In the Northern Rocky Mountains, whitebark pine (*Pinus albicaulis* Engelm.) is important for watershed protection, esthetics, ornamental planting, and wildlife food and cover. Relatively pure whitebark pine stands provide cover in timberline and subtimberline zones little occupied by other tree species (Arno and Hoff 1989). Whitebark seeds are an important food source for grizzly (*Ursus arctos horribilis*) and black bear (*Ursus americanus*) (Craighead and others 1982; Kendall 1983; Knight and others 1987) and a supplemental food source for birds (Tomback 1982; Vander Wall and Hutchins 1983) and other small animals (Hutchins and Lanner 1982). Despite these merits, it forms only a minor component of forest communities that are commercially harvested. It has minimal significance for timber production because of its slow growth and generally poor form characteristics (Arno and Hoff 1989). Information on regeneration of whitebark is sparse because of its low commercial value and previously unrecognized alternative uses.

Current environmental conditions apparently favor whitebark pine mortality over establishment. Fire suppression practices over the past few decades have allowed successional replacement of whitebark by shade-tolerant fir and spruce (Arno 1986). Whitebark pine is highly susceptible to the introduced European disease white pine blister rust (*Cronartium ribicola*) even on trees with disease-resistant parents (Hoff 1980). Extensive mortality occurs in areas where the alternate host *Ribes* is abundant. The native mountain pine beetle (*Dendroctonus ponderosae* Hopkins) devastates stands of mature whitebark pine during years when climatic factors are favorable for beetle survival (Amman 1982). Mortality from the mountain pine beetle releases late-successional species such as subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*).

The probability of natural regeneration of whitebark pine in wildlife-sensitive areas likely is decreasing and there is a need to reverse that trend. However, little is known about germination success rates of whitebark pine under natural conditions (Eggers 1986). Weaver and Dale (1974) examined established regeneration of whitebark pine in undisturbed climax communities of whitebark pine. Whitebark pine reproduction was apparently most successful in openings created by fallen trees or incomplete initial seeding of whitebark. Seedling survival within nutcracker caches was as high as 56 percent the first year and 25 percent by the fourth year, but the actual germination percent of all seeds "sown" by the nutcracker is unknown (Tomback 1982).

Management of whitebark pine forests will require management of competitors, disease, and the tree itself. Wildfires or prescribed burns may be needed to maintain whitebark in areas where it is seral. Exotic diseases must be managed, and where fire or disease mortality cannot be reduced, regeneration must be increased to compensate. Studies of the regeneration process will contribute to this establishment.

This paper reports first-year results of a study designed to determine the effects of biotic and microsite factors on seed survival, seedling emergence, and seedling survival,

---

Paper presented at the symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Ward W. McCaughey is Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Forestry Sciences Laboratory, Bozeman, MT 59717; T. Weaver is Plant Ecologist, Department of Biology, Montana State University, Bozeman, MT 59717.

and on subsequent seedling survival for the first 3 years after germination. Five objectives of this study are to:

1. Determine differences in seed loss due to bird and small mammal predators when seed is surface sown (simulating tree dispersal) rather than buried 0.8 to 1.6 inches in soil (simulating burial by Clark's nutcracker [*Nucifraga columbiana]*).
2. Compare seed emergence and seedling establishment between surface-sown seeds and seeds buried 0.8 to 1.6 inches in soil.
3. Compare seed emergence and seedling establishment on mineral, litter, and burned seedbeds.
4. Compare emergence and seedling establishment under 100, 50, and 25 percent of full sunlight.
5. Record survival rates and factors limiting survival of natural seedlings for the 3-year period following germination.

STUDY AREA AND METHODS

The experimental site is classified as an *Abies lasiocarpa-Pinus albicaulis/Vaccinium scoparium* habitat type (Pfister and others 1977) recently occupied by a lodgepole pine forest. Its soils are classified as Typic Cryorthent, sandy skeletal and well drained. Soil pH values range from 4.7 to 5.5. The elevation is 8,700 ft MSL with 0 to 25 percent slopes and a northeast aspect.

The study area is located within section 14, township 9 south, range 9 east on the Gardiner Ranger District of the Gallatin National Forest just north of Yellowstone National Park (fig. 1), and near the southwestern corner of the Absaroka Beartooth Wilderness approximately 5.5 air miles east of Gardiner, MT.

Study plots were established on a 15-acre clearcut that is connected on one side to a large clearcut (50 acres) called the Palmer Coop timber sale. The Palmer Coop sale was harvested during the winter of 1985-86. Approximately 17,000 to 20,000 board feet per acre of timber were harvested from the sale area and 10 to 15 tons per acre of slash were left on the site. The species and percents of volume harvested were: live lodgepole pine (*Pinus contorta*)-75 percent, dead lodgepole-13 percent, Engelmann spruce-4 percent, subalpine fir-4 percent, and whitebark pine-4 percent. The study area is bordered by mature timber of similar composition on the south, west, and north sides.

Study Design

A factorial design (table 1) was used to evaluate the effects of seed predators, light levels, seedbed conditions, and seed sowing depths on the germination and survival of whitebark pine. Three subsites (replicates) were subjectively chosen within the clearcut as representative, similar, and suitable for plot establishment. The subsites had minimal amounts of logging slash, large areas of undisturbed litter, and represented the total stand conditions. Figure 2 is a schematic plot representation of one replication of each predator exclusion (EA = exclude all predators, ER = exclude rodents only, EB = exclude birds only, EN = exclude none)-shade level-seedbed condition-sowing depth combination. Plots were randomly located in each replicate.

The burned seedbed level for the seedbed condition factor was not used for the 1988 analysis because wet weather conditions in 1987 delayed burning and we could not establish plots. Mineral seedbed plots were located on scarified skid trails or hand-scalped when scarified areas could not be found.

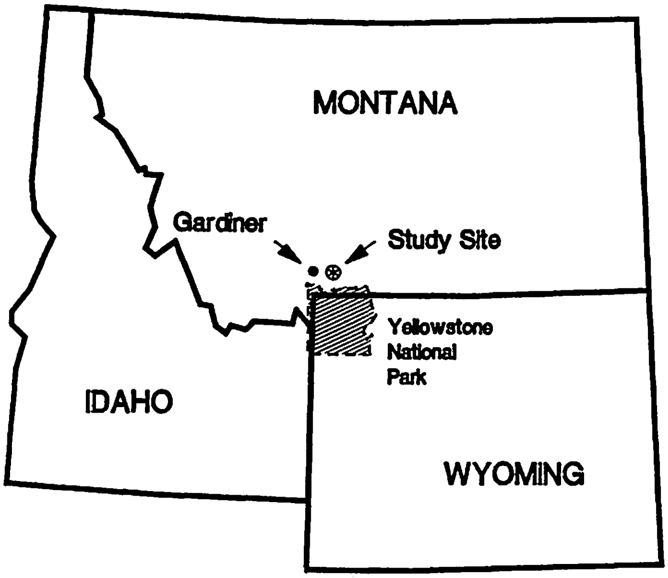


Figure 1—Study site location. Gallatin National Forest, Section 14, Township 9 south, Range 9 east, Montana Principal Meridian.

Table 1—Factors and factor levels

Factor	Levels
1. Predator exclusion	4
a. Exclude birds and rodents (EA)	
b. Exclude rodents only (ER)	
c. Exclude birds only (EB)	
d. Exclude none (EN)	
2. Shade level	3
a. No shade	
b. 25 percent shade	
c. 50 percent shade	
3. Seedbed condition	3
a. Mineral (1988 analysis)	
b. Litter (1988 analysis)	
c. Burned (1989 analysis)[1]	
4. Sowing depth	2
a. Surface sown	
b. Seed buried (0.8-1.6 inches)	
5. Replication	3

[1] First-year results did not include a burned seedbed treatment.

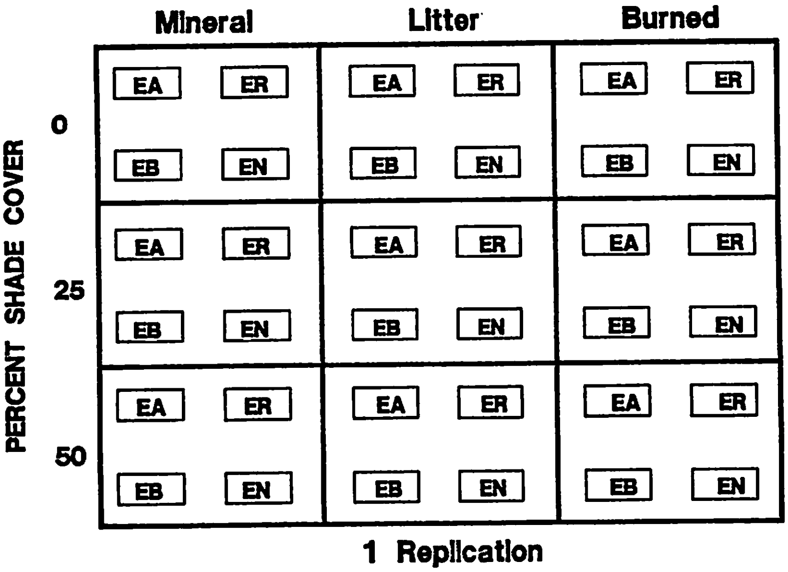


Figure 2—Schematic layout of study design showing all the treatment combinations in one of three replications. In the field, treatment combinations were located randomly.

Plot Layout

Within each subsite, 24 plots were established to represent all combinations of four predator exclusion levels, three shade levels, two seedbed conditions, and two sowing depths (fig. 2). Plots were rectangular (1.6 by 6.5 ft) oriented north-south. The south half (1.6 by 3.25 ft) of each plot was seeded in the fall of 1987 and the north half was seeded in the fall of 1988.

Each plot was subdivided into 40 subplots measuring 3.9 by 4.29 inches. Within each subplot two seeds were planted, one surface sown and one buried. The surface-sown seed was placed on the ground surface in the north half of each subplot. The buried seed was placed 0.8 to 1.6 inches below the surface level in the south half of each subplot. The buried seed was covered by the appropriate seedbed material (mineral soil or forest litter).

A total of 5,760 whitebark pine seeds were planted in 1987. The seed was collected in 1985 from trees at the same elevation as the study area and only 0.25-mile distant. All seeds were x-rayed and only filled seeds were planted.

Shade levels were imposed with slatted roofs. Four 6-ft-tall steel posts were installed at the corners of an imaginary 4- by 8-ft rectangle overtopping but slightly to the south of each plot to be shaded. A 4- by 8-ft-long wood frame was constructed with 2- by 4-inch lumber and attached to the steel posts 40 inches above the ground. A 4- by 8-ft section of wood snow fence was suspended on the wood frame. The 50 and 25 percent shade levels were simulated by either leaving all the wood slats in the snow fence or by eliminating every other slat, respectively.

Screen wire was used to exclude seed predators from the plots. Plots exposed to all predators were unscreened. Plots protecting seeds from all predators were completely covered using hardware cloth with 0.25-inch square holes (fig. 3a). Plots for protecting seed from birds only were covered by screen with 2- by 3-inch wide holes (fig. 3b). Plots excluding small mammals only were completely enclosed by a 30-inch high fence of 0.25-inch hardware cloth. The rodent fence was designed to exclude rodents but allow avian predators to fly into the plots. The top of the fence therefore had an 8-inch lip, bent outward from the plot. A 6-inch piece of tin flashing had to be attached to the underside of the lip to effectively exclude rodents (fig. 3c). The bottoms of screens were buried 4 to 6 inches deep on plots excluding birds and rodents and plots excluding rodents only. The bottom edge of the buried screen had a 2-inch lip bent outward from the plot to minimize the chance of rodents tunneling under the screen. Screening techniques for the control of seed predation were suggested by Curt Halverson, Fish and Wildlife Service, U.S. Department of the Interior, Fort Collins, CO.

Measurements

Counts of whitebark pine emergence were made periodically on all plots. Counts started on June 16, 1988, just 3 weeks after snowmelt. Seedling counts were measured and recorded weekly until the first of August and bimonthly from August to the first of October. Emergents were marked with colored plastic toothpicks; different colors indicated the week they emerged. A hypothetical cause and week of mortality were assigned to all seedlings that died.

Gravimetric soil moisture was measured on 6 of the 24 germination plots at each of the three replicates. These six plots comprised one plot from each combination of mineral and litter seedbed and 0, 25, and 50 percent shade cover. Soil from the upper 2 inches of the A horizon was collected in gravimetric soil cans and sealed for transport from the field to the laboratory. Percent soil moisture was determined with gravimetric methods (Soil Survey Staff 1975).

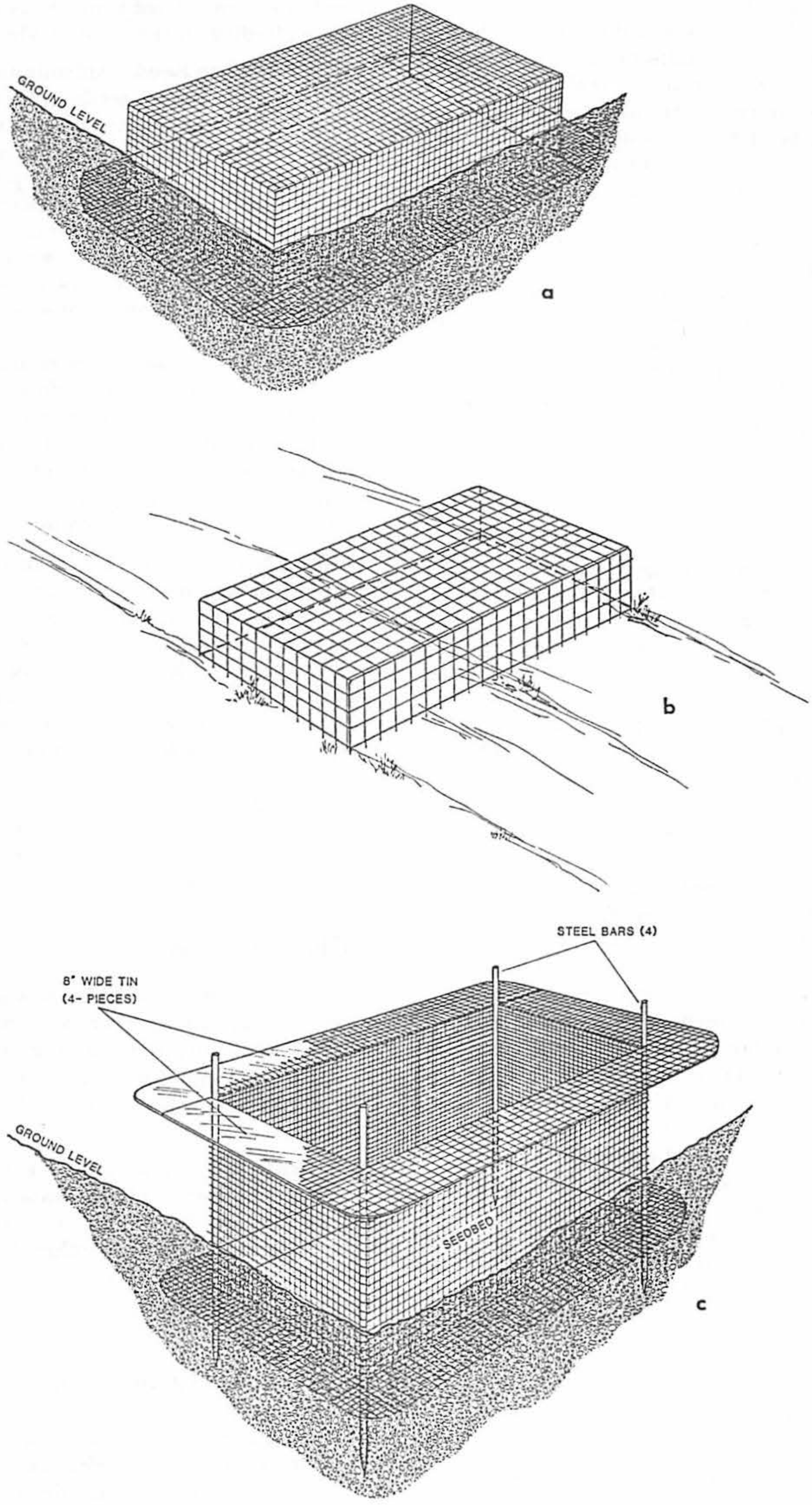


Figure 3—Cages for: (a) excluding birds and mammals, (b) excluding birds only, and (c) excluding mammals only.

Subsurface soil temperatures were measured with Taylor minimum-maximum thermometers at the same seedbed-shade plots where soil moisture collections were taken on replicates 1 and 3. Soil temperatures in replicate 2 were measured with temperature probes connected to electronic microprocessors designed for continuous collection of environmental conditions. Minimum and maximum soil temperatures were measured at a soil depth of 1 inch (the level where seeds were buried). Temperatures were measured and recorded weekly, daily, and sometimes hourly throughout the 1988 summer.

Maximum surface temperatures were measured weekly with wax (Big Three Industries-tempil) pellets, which melt at specific temperatures. Tempils used for this study were designed to melt at 100, 106, 113, 125, 138, 150, 163, 175, 188, and 200 °F. Tempils were placed on one of the mineral and litter seedbeds on each of the 0, 25, and 50 percent shade plots for a total of six plots on each replicate.

Data Analysis

The proportion of whitebark emergents on each subplot was used as the dependent variable for analysis of emergence differences between predator exclusion levels, shade levels, seedbed conditions, sowing depth, and factor interactions. Proportion of emergence is defined as the number of emergents divided by the number of seeds sown (40). Empty plots were counted as $^1/_{4n}$ $n = 40$ to prevent distortion of the analysis by small numbers (Mosteller and Youtz 1961). The transformation, arc sine of the square root of the proportion of germination, was used to stabilize variation due to proportions (Snedecor and Cochran 1980).

The statistical analysis system (SAS) was used to analyze whitebark pine emergence data. Analysis of variance was used to test for significance of main factors and interactions on seedling emergence and survival. Anova was also used for evaluation of soil moisture and temperature data. The "F" statistic was used to determine the significance of factors and their interactions on germination of whitebark pine. Tukey's standardized range test (Snedecor and Cochran 1980) was used to statistically test differences in emergence among factor levels. Unless otherwise stated references to significant results indicate the 0.05 level.

Predation on whitebark pine seed was analyzed separately from microsite factors affecting whitebark germination. Seed predation was assessed using results from the exclude birds only (EB), exclude no predators (EN), exclude rodents only (ER), and exclude birds and rodents (EA) treatments. The EA and ER treatments were used in analysis of variance to assess whitebark emergence differences between shade levels, seedbed conditions, and sowing depths.

SEED PREDATION

Birds and rodents were the two important predators on whitebark seed considered in this study. The Clark's nutcracker is considered the major bird species consuming whitebark seed. Chipmunks (*Eutamia* spp.), deer mice (*Peromyscus maniculatus*), and golden-mantled ground squirrels (*Spermophilus lateralis*) were assumed to be the main rodent consumers (Lanner 1980; Tomback 1981). Insects were considered a minor predator and were not seen feeding on or removing whitebark pine seed.

Surface-Sown Seed—Animals ate or removed 100 percent of surface-sown seeds on EB and EN treatments within 5 days after sowing. No seeds were removed from ER and EA treatments, indicating that birds were not randomly searching for whitebark pine seeds and screening effectively excluded rodents. Exclosures may have discouraged seed foraging by birds; however, birds, including the Clark's nutcracker, were observed sitting on exclosures of ER treatments and shade structures. No birds were seen foraging for seeds on any plots. Despite observations of birds sitting on the mammal-excluding cages, no seeds were removed from plots open to birds. It is assumed that surface-sown seeds on EB and EN treatments were eaten or removed by rodents while bird predation was, at best, minimal. Hutchins (1989) believes that random foraging by Clark's nutcrackers is highly unlikely since their efforts appear to be toward finding their own seed caches.

Buried Seed—Animal predation of buried whitebark pine seeds was evidenced by depressions on mineral soil and litter seedbeds at buried seed locations on all EB and EN plots. There was no evidence of disturbance at buried seed locations on ER treatments; therefore, it is assumed that there was no seed predation of buried seeds by birds. Seeds were untouched on EA treatments, indicating that rodent and bird predation was eliminated. Emergence from buried seeds occurred on EB and EN treatments, indicating that rodents did not find all available buried seeds. There was no significant difference in the mean number of whitebark emergents per plot between EB (0.67) and EN (0.86) treatments.

EMERGENCE

Emergence of whitebark pine was significantly affected by replicate, predator exclusion method, seedbed condition, and sowing depth (table 2). Four two-factor interactions showed significant relationship to whitebark pine emergence. Shading did not affect whitebark pine emergence.

Replicates—There were significantly fewer whitebark pine emergents per plot in replicate 3 (0.79) than in replicates 1 (3.08) or 2 (3.71) (table 3). This difference may be attributable to soil changes within the study area. Soil moisture in replicate 3 was nearly always less than in replicates 1 and 2 during the early summer when the emergence rate was highest (figs. 4 and 5).

The soil on replicate 3 was classified as a Typic Cryorthent, sandy skeletal with a 6-inch A horizon containing 54 percent sand over a C horizon of 60 percent sand. Soils on the other replicates have not been fully classified but appear to have a weak B horizon below a thicker A horizon indicating a different classification. Moisture may be the limiting factor for emergence on replicate 3 considering the high sand content of the soil profile and the shallow A horizon. The A horizon in replicates 1 and 2 was thicker and hand textural analysis indicated less sand and more silt and clay.

Table 2—Significance (Anova probability) of effects on seedling emergence of four treatments (predation, seedbed, sowing depth, and shade) and significant interactions. Before analysis, percent germination data were transformed by the arc sine of the square root (Snedecor and Cochran 1980). Analysis of variance results showing significance of biotic and microsite factors and two-way interactions of the arc sine transformation of the square root of germination proportion for the predator exclusion treatments, exclude rodents and birds and exclude rodents only

Source	DF	Mean square	F value	Significance
MAIN FACTORS				
*Rep*licate	2	0.1487	20.94	[1]*
*Pre*dator exclusion	1	.1648	23.20	*
*See*dbed condition	1	.0692	9.74	*
*Sow*ing depth	1	.7385	103.96	*
*Sha*de level	2	.0119	1.67	
INTERACTIONS				
Rep x Sow	2	.0656	9.23	*
Pre x See	3	.0335	4.72	*
Pre x Sow	3	.0530	7.46	*
Sha x See	2	.0255	3.59	*
Rep x Pre	6	.0058	.81	
Rep x Sha	4	.0029	.41	
Rep x See	2	.0039	.55	
Pre x Sha	6	.0165	2.32	
Sha x Sow	2	.0002	.03	
See x Sow	1	.0001	.02	
Error	45	.0071		

[1]* indicates significance at the 0.95 confidence level.

Table 3—Mean number of emergents per plot by replicate, predator exclusion, shade level, seedbed condition, and sowing depth on plots excluding rodents and birds (EA) and excluding rodents only (ER)

Replicate	Mean	Predator exclusion	Mean	Shade level	Mean	Seedbed condition	Mean	Sowing depth	Mean
				Percent					
1	[1]3.08 (a)	EA	3.69 (a)	0	1.96 (a)	Mineral	3.17 (a)	Surface	0.50 (a)
2	3.71 (a)	ER	1.36 (b)	25	3.04 (a)	Litter	1.89 (b)	Buried	4.56 (b)
3	0.79 (b)			50	2.58 (a)				

[1] Similar and dissimilar letters in parentheses represent nonsignificant and significant differences respectively.

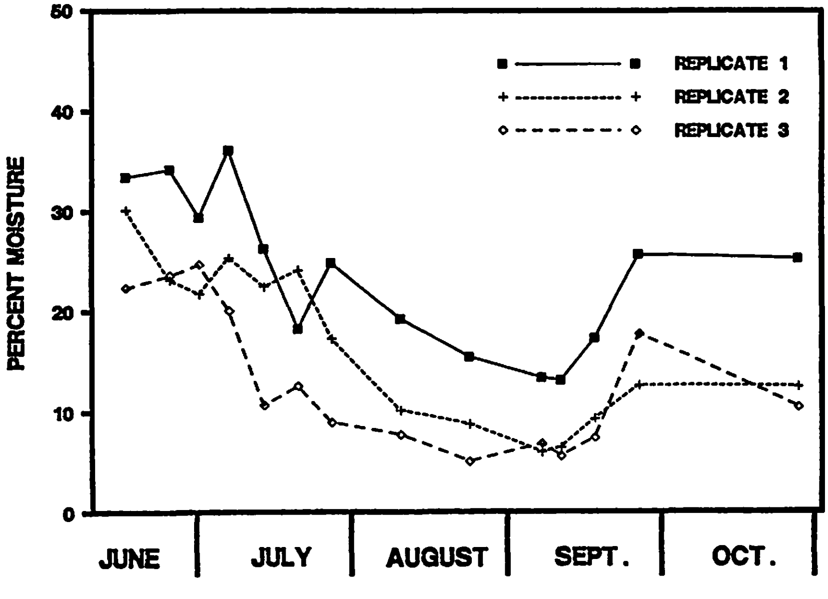


Figure 4—Percent moisture in top 2 inches of soil by replicate.

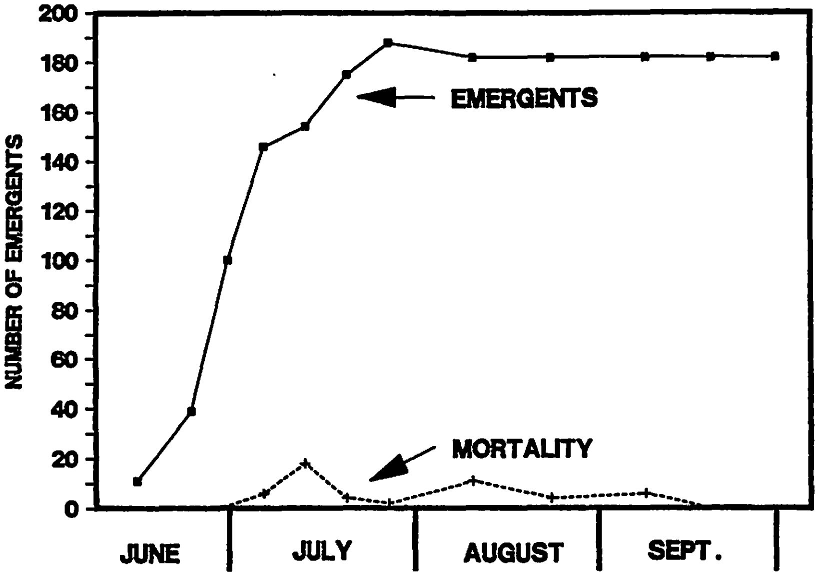


Figure 5—Total number of living emergents and current deaths of whitebark pine over time—1988. The data include germinants from all predator exclusion methods, shade cover levels, seedbed conditions, and sowing depths.

Predator Exclusion—Whitebark pine emergence was significantly affected by screen design differences between the EA and ER treatments (table 2). The mean number of seedlings per plot was 3.69 for EA treatments and 1.36 on ER treatments (table 3). The difference in emergence between the EA and ER treatments can probably be attributed to within-plot microclimate differences. The EA treatment had hardware cloth with 0.25-inch-square holes about 4 inches above the ground level and totally enclosing the plot. The metal cloth may have provided extra shade-reducing daytime temperatures; the overtopping of the screen may have increased night temperatures. A subsample of each treatment combination will be monitored in 1989 for soil temperature and solar radiation differences.

Seedbed Condition—Seedbed condition significantly affected whitebark pine germination throughout the summer (table 2). There was an average of 3.17 germinants per plot on mineral soil seedbeds versus 1.89 on litter by the end of the summer.

Most conifers germinate best on mineral seedbeds (Seidel 1979; Zasada and others 1978). When mineral soil is exposed to eliminate competing vegetation, more light, moisture, and nutrients are available for seedling growth (Schmidt and others 1976). Although no quantitative measure of competing vegetation was taken, reduction of competition may be the reason for better germination of whitebark pine on mineral seedbeds.

Sowing Depth—Sowing depth significantly affected regeneration of whitebark pine on plots (exclude rodents and birds and exclude rodents only) where seed was protected from animal predation. Emergence from buried seed was significantly higher (4.56 emergents per plot) than from surface-sown seeds (0.50 emergents per plot) (table 2).

There are no documented studies on germination differences between various sowing depths of whitebark pine seed. Most conifer seeds germinate on the surface following wind dispersal. The Clark's nutcracker caches whitebark pine seed at a depth of 1 to 1½ inches on a variety of ground surfaces such as mineral soil, litter, and gravel (Lanner 1980). Germination of buried seeds appears to be the evolved regeneration method of whitebark pine (Tomback 1983).

Shade Cover—Shade was not a significant factor affecting emergence of whitebark pine seed (table 2). Germination of whitebark pine was generally higher for shaded than nonshaded treatments, ranging from 3.04, 2.58, to 1.96 germinants per plot with 25, 50, and 0 percent shade cover, respectively (table 3). Whitebark pine is rated intermediate to intolerant of shade (Arno and Hoff 1989). The shade created by the shade coverings is dead shade. The slats of the snow fence cause alternate strips of shade and full sunlight. This type of dead shade may not be enough, even at the 50 percent shade cover level, to affect emergence. A better measure of individual plot shading will be examined in 1989 with solar radiation monitoring.

INTERACTIONS

Four two-factor interactions of microsite variables significantly affected whitebark pine emergence (table 2). The interactions were replicate by sowing depth, predator exclusion by seedbed condition and by sowing depth, and shade cover by seedbed condition (fig. 6). The replicate by sowing depth interaction showed similar trends for all replicates; however, replicate 3 showed a steep reduction in the absolute difference in mean number of emergence per plot between buried and surface-sown seed (fig. 6a). Few buried seeds emerged and no seeds emerged on the surface. This change in absolute difference may be attributed to soil-moisture variation in replicates as described earlier.

The interaction of predator exclusion treatment by seedbed condition showed less absolute difference in mean number of whitebark pine emergents per plot between mineral and litter seedbed under the ER treatment

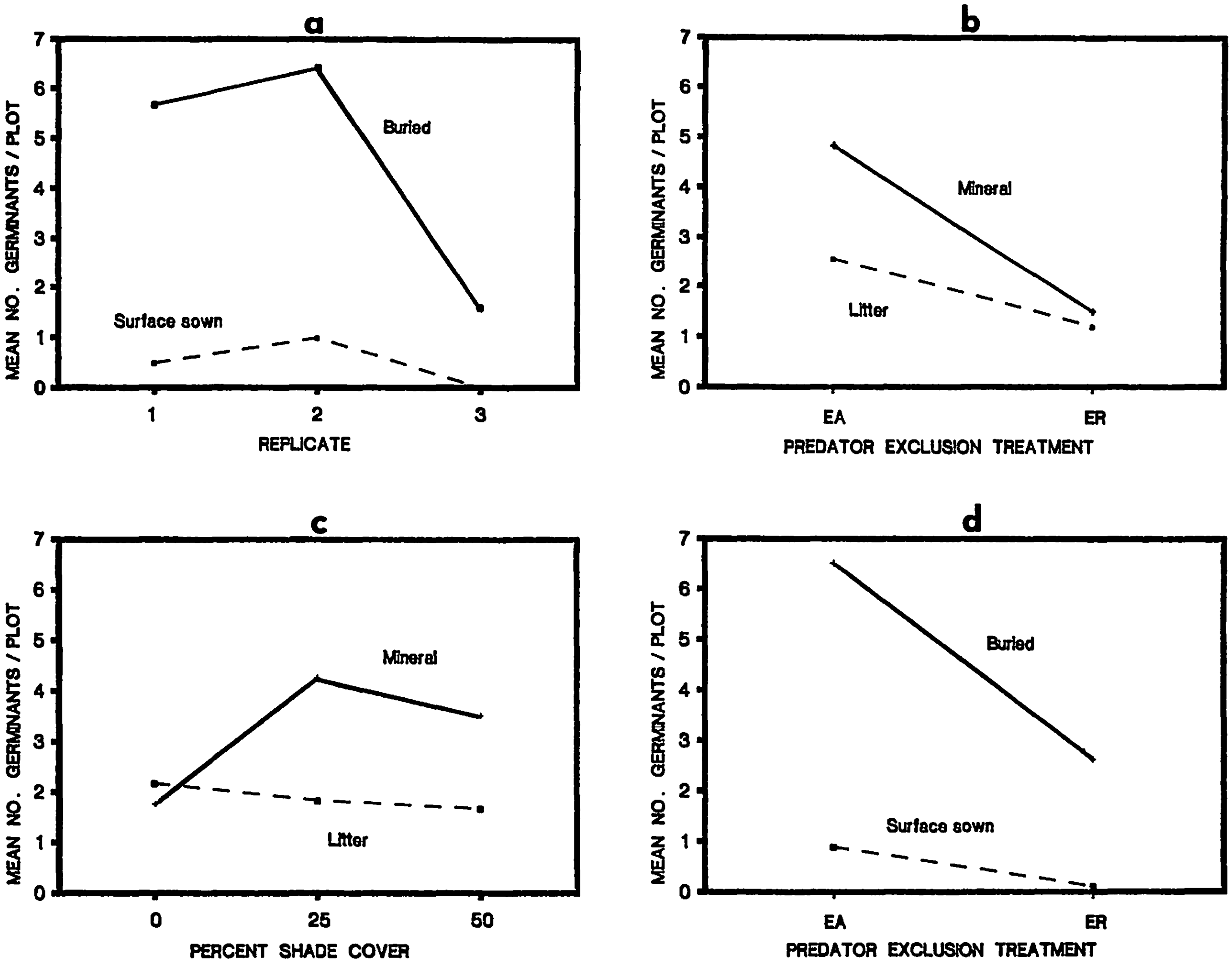


Figure 6—Mean number of whitebark pine germinants per plot for analysis of variance interactions: (a) replicate by sowing depth, (b) predator exclusion treatment by seedbed condition, (c) percent shade cover by seedbed condition, and (d) predator exclusion treatment by sowing depth.

(fig. 6b). The change in absolute values may be caused by microclimate differences between predator exclusion treatments due to effects of metal screen exclosures. Increased measures of microsite differences in 1989 may help explain this interaction of predator exclusion treatment and seedbed condition.

Shading was not a significant factor affecting whitebark pine emergence, but the interaction of shading and seedbed condition was (table 2). There were significant differences in emergence between mineral and litter seedbeds under 25 and 50 percent shade cover, but not at 0 percent shading (fig. 6c). This indicates that shading as little as 25 percent improves whitebark emergence on mineral soil; however, no shading level significantly affected emergence on litter seedbeds.

The predator exclusion treatment by sowing depth also showed less absolute differences in mean number of whitebark pine emergents per plot between buried and surface-sown seeds under the ER treatment (fig. 6d). Screening differences between predator exclusion treatments may again be the reason for the absolute value changes.

MORTALITY

Whitebark pine emergence rates were high from mid-June through the end of July, slowed, and then leveled off in August (fig. 5). Germinants continued to emerge until the first of September, but total number of survivors remained about the same because of compensating mortality.

Mortality of whitebark pine emergents did not begin until the first of July and continued at a low level until the first of September (fig. 7). Two causes of mortality were identified: (1) insolation (indicated by scorching of seedling stem at ground surface), and (2) drought. Animal, fungi, and insect mortality were not apparent

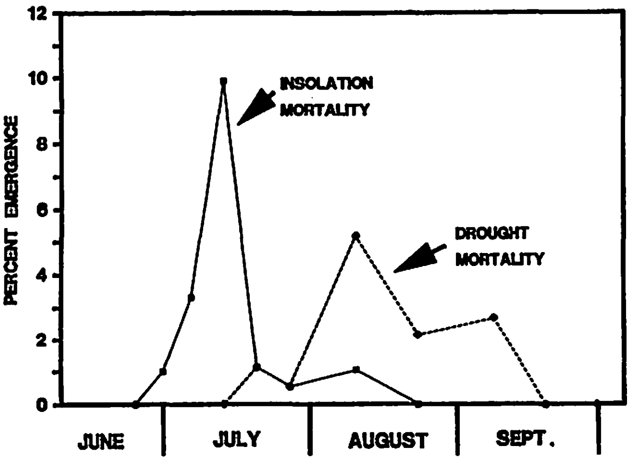


Figure 7—Percent insolation and drought mortality of whitebark pine seedlings over time—1988. Percent mortality represents the percent of living seedlings that died in the period.

on any of the whitebark seedlings examined. Insolation mortality of seedlings began early in the season when day lengths were the longest and ended by early August (fig. 7). Insolation-caused mortality was highest on nonshaded mineral seedbeds; these beds also had the highest absolute (98 °F) and highest mean (78 °F) subsurface temperature. Drought mortality began around the third week in July and continued until the first of September.

Twenty-five and 50 percent shade cover reduced total seedling mortality (table 4). Total mortality did not vary with shade level; however, shading greatly influenced the mortality type for whitebark pine seedlings on mineral and litter seedbeds. Insolation mortality of seedlings was highest on mineral and litter seedbeds with no shade cover; shading of as little as 25 percent greatly decreased insolation mortality (table 4). Because shading reduced soil moisture (fig. 8), we tentatively attribute its effect to reduction of soil temperature. Our explanation is apparently countered by the relatively warm temperatures observed on littered soils receiving 50 percent shade.

Table 4—Mortality of whitebark pine emergents on mineral and litter seedbeds under 0, 25, and 50 percent shade. Mortality is the percent of emergents in each category that died (212 total germinants)

Percent shade cover	Seedbed condition	Hypothetical mortality cause		
		Insolation	Drought	Total
		Percent		
0	Mineral	33	11	44
	Litter	23	6	29
25	Mineral	6	8	14
	Litter	0	29	29
50	Mineral	5	12	17
	Litter	9	22	31

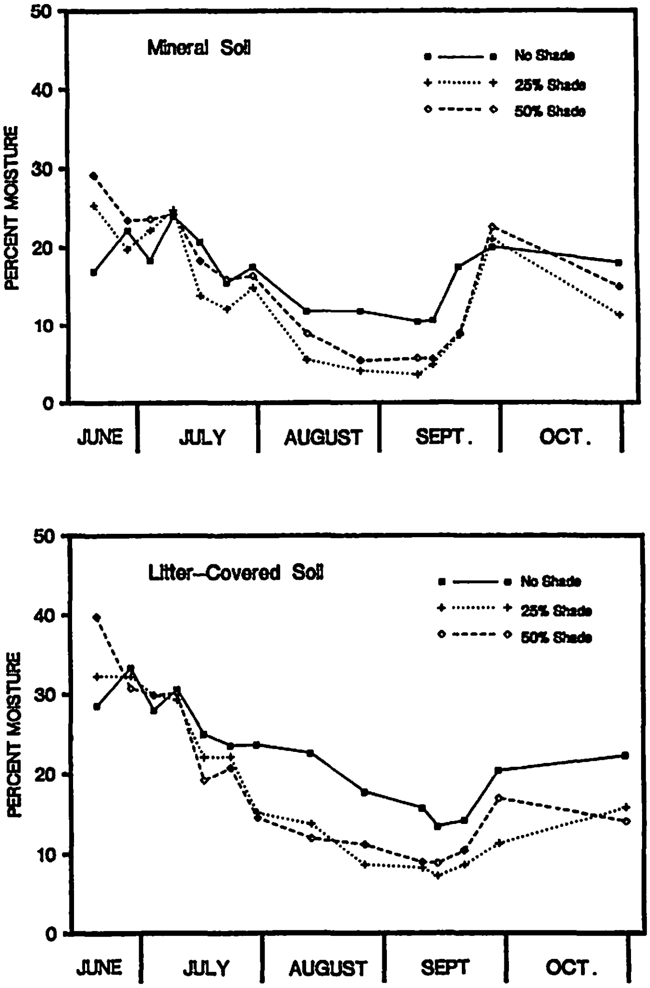


Figure 8—Percent moisture in top 2 inches of soil on a mineral and litter seedbed.

Drought mortality of whitebark pine seedlings was lowest on nonshaded plots. This is consistent with the fact that nonshaded plots were moister than shaded plots during the mid-summer weeks when most drought mortality was occurring (fig. 8). Low canopy catch may account for higher soil moisture values on open plots.

SOIL TEMPERATURE AND MOISTURE

Regardless of shading, surface temperatures were higher on litter seedbeds than mineral soils under 0, 25, and 50 percent shade cover (table 5). Surface temperatures were higher on litter seedbeds possibly because of increased light reflectance off light-colored needles and because of an insulating effect reducing downward heat transmittance.

Minimum subsurface temperatures were warmer with increased shade cover, indicating a moderating effect of screening on temperature (table 6). Mineral seedbeds had relatively low minimum temperatures and high maximum temperatures; litter mulch moderated soil temperature.

Table 5—Maximum surface temperatures recorded on mineral and litter seedbeds under 0, 25, and 50 percent shade cover

Seedbed condition	N	Percent shade cover 0	25	50
		°F		
Mineral	3 x 6	150	138	138
Litter	3 x 6	163	150	163

Table 6—Minimum-maximum soil temperatures at a depth of 1 inch on mineral and litter seedbeds under 0, 25, and 50 percent shade cover. Values without parentheses are June through September absolutes. Values in parentheses are mean minima and maxima for the summer

Seedbed condition	Temperature	Percent shade cover 0	25	50
		°F		
Mineral	Minimum (Mean min)	11 (34)	17 (37)	19 (33)
	Maximum (Mean max)	98 (78)	83 (68)	84 (73)
Litter	Minimum (Mean min)	16 (35)	18 (35)	20 (35)
	Maximum (Mean max)	81 (73)	75 (67)	82 (69)

Soil moisture decreased steadily from mid-June through mid-September and rose again with late September rains (fig. 8). Soil moisture remained highest on unshaded plots on mineral and litter seedbeds; this may be due to interception or deflection of rain by shade covers. There was little difference between plots shaded to either 25 or 50 percent.

A typical September storm (Weaver 1989) partially replaced soil moisture. Soil moisture declined again in late September to early October on mineral seedbeds but increased slightly on litter seedbeds. The increase in soil moisture in September indicates that small amounts of precipitation fell during that time and litter had a positive effect on holding that moisture.

SUMMARY

Rodents are the main predators of whitebark pine seed when it is available on the forest floor or buried. All surface-sown seeds were eaten or carried off when rodents had access to them. Nearly all accessible buried seeds were eaten or removed; however, some did germinate. Seeds available only to birds were undisturbed, indicating no open foraging for seeds by avian predators. Birds were seen sitting on several exclosures, but none were seen foraging for seed inside exclosures open to birds. All seeds were undisturbed and able to emerge on treatment plots that excluded all predators and excluded rodents only. Emergence was highest for treatments excluding all predators, probably due to microclimate changes caused by the exclosure structure. The overtopping screen probably modified the microsite climate by holding heat in during the nights and reducing daytime temperatures.

Emergence of whitebark pine seeds was slightly higher on shaded plots. Emergence was highest on the 25-percent and second highest on the 50-percent shade cover plots. It is unknown why emergence was highest on the 25-percent shade cover plots. Perhaps whitebark pine seeds need some shade (25 percent) for setting up the proper conditions for germination; too much sun or shade (0 to 50 percent) may be detrimental.

Emergence of whitebark pine was significantly higher on mineral than on litter seedbeds. This was highly evident for treatments protecting seeds from all predators and may be confounded by the shading effect from the exclosure structure. Emergence was significantly higher on shaded-mineral than on shaded-litter seedbeds. There was no difference in emergence between seedbed types under open conditions.

Sowing depth of seed had the greatest influence on emergence of whitebark pine. Emergence of buried seeds was significantly higher than that of surface-sown seeds when seeds were undisturbed and available to germinate (fig. 7). Surface germination of whitebark does occur when seeds are undisturbed but is highly unlikely because of near-complete seed loss due to small-mammal foraging. Mammals took or consumed most buried seeds on plots where seeds were available to them; however, some seeds were missed and did germinate. Mammals would probably not have found as many buried seeds, increasing the number of emergents, had surface-sown seeds not been in close proximity acting as an attractant.

Mortality of whitebark pine emergents varied by cause throughout the summer. Insolation mortality was highest in early July but was not a factor after early August. Insolation mortality was highest on mineral seedbeds under no shade even though surface temperatures were highest on litter seedbeds. Drought mortality was highest during August and September when soil moisture was lowest. Drought mortality was highest on litter seedbeds under shaded conditions where soil moisture was the most limiting.

REFERENCES

Amman, G. D. 1982. Characteristics of mountain pine beetles reared in four pine hosts. Environmental Entomology. 11(3): 590-593.

Arno, S. 1986. Whitebark pine cone crops—a diminishing source of wildlife food? Western Journal of Applied Forestry. 1(3): 92-94.

Arno, S.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Craighead, J. J.; Scaggs, G. B.; Sumner, J. S. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Wildlands Institute Monograph 1. Missoula, MT: University of Montana. 279 p.

Eggers, D. E. 1986. Management of whitebark pine as potential grizzly bear habitat. In: Proceedings—grizzly bear habitat symposium; 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 170-175.

Hoff, R. J. 1980. [Personal files]. Moscow, ID: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory.

Hutchins, H. E. 1989. [Personal communication]. March. Grand Rapids, MN: Itasca Community College, Department of Forestry.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. Interagency conference on bear research and management. In: Bears—their biology and management. Calgary, AB: International Association of Bear Management. 5: 166-173.

Knight, R. R.; Blanchard, B. M.; Mattson, D. J. 1987. Yellowstone grizzly bear investigations: Annual report of the interagency study team—1987. Bozeman, MT: U.S. Department of the Interior, National Park Service.

Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: Sixth North American forest biology workshop proceedings. Edmonton, AB: University of Alberta: 14-48.

Mosteller, F.; Youtz, C. 1961. Tables of the Freeman-Tukey transformations for the binomial and Poisson distributions. Biometrika. 48(3 and 4): 433-440.

Pfister, R. D.; Kovalchick, B. L.; Arno, S.; Presby, R. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Schmidt, W. C.; Shearer, R. C.; Roe, A. L. 1976. Ecology and silviculture of western larch forests. Tech. Bull. 1520. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 96 p.

Seidel, K. W. 1979. Regeneration in mixed conifer shelterwood cuttings in the Cascade Range of Eastern Oregon. Res. Pap. PNW-264. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 29 p.

Snedecor, G. W.; Cochran, W. G. 1980. Statistical Methods. 7th ed. Ames, IA: Iowa State University Press. 507 p.

Soil Survey Staff. 1975. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. Agric. Handb. No. 436. Washington, DC: U.S. Department of Agriculture. 682 p.

Tomback, D. F. 1981. Notes on cones and vertebrate-mediated seed dispersal. Madrono. 28(2): 91-94.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51(2): 451-467.

Tomback, D. F. 1983. Nutcrackers and pines: coevolution or coadaptation? In: Niteck, M. H., ed. Coevolution. Chicago and London: University of Chicago Press: 179-223.

Vander Wall, S. B.; Hutchins, H. E. 1983. Dependence of Clark's nutcracker, *Nucifraga columbiana*, on conifer seeds during postfledgling period. Canadian Field-Naturalist. 97(2): 208-214.

Weaver, T. 1989. [Personal communication]. Bozeman, MT: Montana State University, Department of Biology.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in Central Montana: environment, revegetation, and production. American Midland Naturalist. 92: 222-230.

Zasada, J. C.; Foote, M. J.; Deneke, F. J.; Parkerson, R. H. 1978. Case history of an excellent white spruce cone and seed crop in Interior Alaska: cone and seed production, germination, and seedling survival. Gen. Tech. Rep. PNW-65. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 53 p.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Ken Gibson)—Though we haven't studied insect predation in whitebark pine to a great extent, it has been observed. Did you notice any in your studies? If so, was it significant?

A.—Of the seed that was surface sown and protected from large predators 99 percent was still visible after 1 year. The 1 percent that was missing was on litter seedbeds and could have been removed due to insect predation, although I did not see that. I was attributing the missing seed to the possibility that from snow and rain they had fallen down through the litter and were no longer visible. I did not want to disturb the sites for fear of disrupting germination.

Q. (from Mike Merigliano)—Did you account for the possible heat retention effect of the animal barrier and sun shade screens on seedling survival?

A.—I assumed the sun shade screen would hold some heat similar to that of what an overtopping tree crown would. I did not expect the screening, because of its open nature, to cause much of an effect. Obviously, the screening that completely enclosed some plots was having a substantial effect on heat retention. This coming summer I will be looking at this in more detail.

Q. (from Ray W. Brown)—What is known about pH limits of whitebark pine, and its tolerance to low pH during germination?

A.—I do not have an answer to this question. I have not seen literature referring to this subject. This would be a perfect laboratory experiment that could be done very quickly.

Q. (from Harry Hutchins)—What influence do you feel your enclosures and your scent have on attracting rodents to your caches?

A.—The enclosures likely have a great influence on attracting rodents because if they found seed there they would likely key on this point and check out all the enclosures. My scent would probably also be an attractant to rodents because of their natural curiosity. I am not sure how you could effectively test the influence of human scent as an attractant.

STAND DEVELOPMENT IN WHITEBARK PINE WOODLANDS

T. Weaver
F. Forcella
D. Dale

ABSTRACT

Analysis of density data from stands in the Northern Rocky Mountains shows that, while seedlings establish at the rate of over 1,000/ha x year in whitebark pine-grouse whortleberry (Pinus albicaulis-Vaccinium scoparium) *forests of all ages, stem numbers in the canopy thin to 400 at 30 years, 150 at 200 years, and 100 at 300 to 600 years. Indices of productive potential, cover, and total circumference rise to an asymptote at about 100 years. Total basal area rises from 0 to 60 m^2/ha at about 200 years, the aggregate basal area of trees with diameters over 20 cm rises from 0 to 40 m^2/ha at about 250 years, and tree height maximizes (12 m) at 200 years. It is hypothesized that further growth in productive potential (that is leaf and/or root area) is prevented by limited supplies of water or a nutrient, further growth in basal area is prevented by lack of a nutrient (probably not carbon, hydrogen, oxygen, or nitrogen) and further growth in height is prevented by scarcity of water.*

INTRODUCTION

Ecologists often describe plant succession by comparing communities existing on a series of sites that are considered environmentally identical, but differ widely in age (Boggs and Weaver, in preparation; Cooper 1923; Cowles 1899; Crocker and Major 1955; Olsen 1958). Chronosequence studies in secondary seres in the whitebark pine-grouse whortleberry (*Pinus albicaulis-Vaccinium scoparium*) environments (= habitat types or HT's, Arno and Weaver, this proceedings; Pfister and others 1977; Weaver and Dale 1974) have demonstrated little change in understory vegetation (Weaver and Dale 1974), large increases in biomass (Forcella and Weaver 1977), and small increases in productivity (Forcella and Weaver 1977, 1986). Field data from these studies are reworked here to (1) describe the dynamics of tree establishment, stand closure, and competition and (2) to generate hypotheses to explain the control of productivity, maximum standing crop, and tree height.

METHODS

To characterize succession in whitebark pine woodlands we compared 47 stands of diverse ages in one environmental type (*Pinus albicaulis-Vaccinium scoparium* [Daubenmire and Daubenmire 1968; Pfister and others 1977]). Each stand was aged by coring three trees representative of the dominants, that is, trees that were neither new reproduction nor representatives of an earlier generation; the ages ranged from 29 to 643 years. The stands sampled were broadly representative of stands found in Montana, Wyoming, and Idaho (Forcella 1978; Forcella and Weaver 1977; Weaver and Dale 1974).

Tree densities were estimated by counting individuals in representative areas at each site. Trees in the 19 stands considered in the first study (Weaver and Dale 1974) were sampled with a 500-m^2 circular plot ($r = 12.6$ m). To guarantee a complete count, we counted seedlings in a 1- by 30-m plot whose center coincided with that of the circle. Trees and seedlings in the 28 stands sampled in the second study were counted in a 600-m^2 area consisting of three 6.67- by 30-m plots (Forcella and Weaver 1977).

Trees in the first and second studies were tallied into 10-cm and 5-cm diameter at breast height (d.b.h.) classes, respectively. These data were used directly in comparison of seedling survival among stands of differing age. Total circumferences were calculated by assuming that all trees in a size class had a diameter equal to the midpoint of the class, multiplying for each individual ($\pi \times D$), and summing across individuals. The use of midpoints introduced a downward bias in the smallest size classes in a stand and an upward bias in the largest size classes. Calculation of total basal areas also involved the use of midpoints, multiplication ($\pi \times r^2$), and summation across all trees in the plot. We did not correct for the additional small error due to the fact that the basal area of a midpoint tree is less than the average basal area of trees at the top and bottom of that size class.

Canopy cover was estimated as the percentage of 30 points, observed overhead through a vertical periscope (Weaver and Dale 1974), which were covered by trees. Tree heights were measured with a Bitterlich "relaskop."

Cone production in the year of observation was estimated by multiplying an estimate of branch tip density

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

T. Weaver is Plant Ecologist, Department of Biology, Montana State University, Bozeman, MT 59717; F. Forcella is Research Agronomist, North Central Soil Conservation Research Lab, Agricultural Research Service, U.S. Department of Agriculture, Morris, MN 56267; D. Dale is Head, Department of Forestry, Salish-Kootenai College, Pablo, MT 59855.

in the canopy (#/m^2) by the average number of cones on a sample of branch tips. Cone production in earlier years was estimated by multiplying branch tip density by estimates of cone production made from counts of cone scars at nodes representing the previous 4 years (Weaver and Forcella 1986). Seed production was estimated by multiplying cone number by the average number of seeds in a cone (75 ± 28, Weaver and Forcella 1986).

RESULTS AND DISCUSSION

The dynamics of *Pinus albicaulis* in whitebark pine woodlands were studied by examining a chronosequence based on 47 stands with ages ranging from 29 to 650 years. Readers preferring different units will remember that there are 10,000 m^2/ha and 2.47 acres/ha.

Seedling Establishment

Cone production rose from 0 cones/ha in newly established stands to an average of about 10,000 cones/ha in stands over 100 years old. Figure 1a presents 5-year averages of cone production. Cone production was variable among stands (for example, 0.5 to 5 cones/m^2 annually in the 100- to 200-year stage) as well as among years (Weaver and Forcella 1986). If each cone contained 75 seeds (Weaver and Forcella 1986), seed production ranged from 370 to 3,700 seeds/ha annually in stands over 150 years old.

Median seedling density was 1,000 to 1,500 seedlings/ha during the first 300 years of stand development (fig. 1b) and quite variable among stands in any age class (for example, 0 to 5,000 among 100- to 200-year communities). The large seedling number in young stands must be due to long distance dispersal, probably by Clark's nutcracker (Hutchinson and Lanner 1982; Linhart and Tomback 1985), because whitebark pine seeds are both too heavy for wind dispersal and unlikely to have survived in the seed bank since the stand replacing event (Harper 1977). The consistency of seedling densities across stands of increasing age suggests that nutcracker cache density may not vary significantly among stands with different ages.

Competition and Thinning

Total whitebark pine density falls exponentially from 4,000 individuals/ha at 30 years to 1,500 at 200 years and 1,000 at 400 years (fig. 1d). We attribute this decline to self-thinning; while seedlings established with mean areas of 2 to 3 m^2 cannot compete significantly, 200- to 300-year-old trees apparently require mean areas averaging about 10 m^2. The decline in tree density with time is exponential because the growth of young trees is exponential and the area saturated by a tree is proportional to its size.

Seedling fate is a second indicator of the time of resource (that is, space) saturation in developing whitebark pine woodlands. Seedlings establish at rates of 1,000 to 1,500 individuals/ha^2 in stands of all ages (fig. 1b).

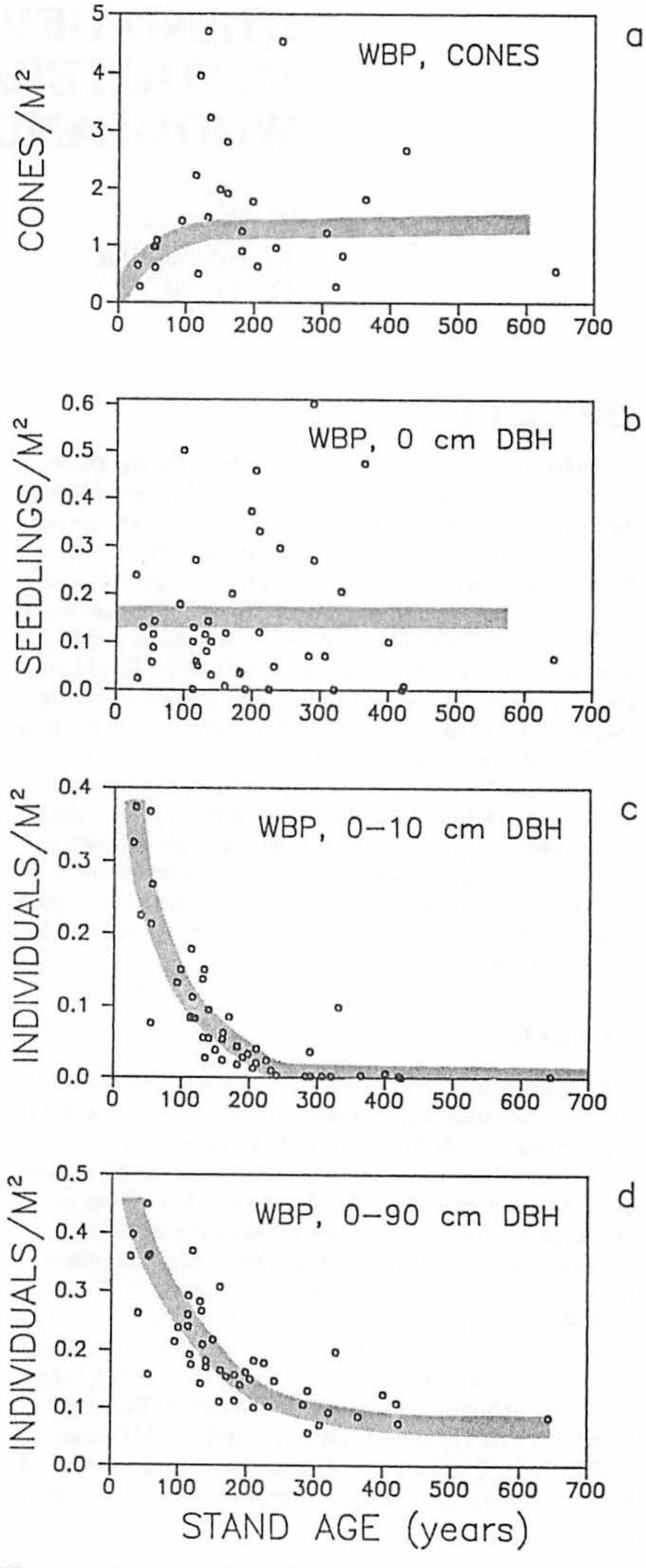


Figure 1—Change in whitebark pine density with stand age (0 to 650 years): (a) cones with an average of 75 seeds, (b) seedlings, (c) 0- to 10-cm d.b.h. saplings, and (d) all individuals. While seedling number remains constant, establishing trees (0 to 10 cm d.b.h.) fail in stands older than 250 years, established trees self-thin through 350 years. The line is hand-fit through medians calculated across centuries.

In stands less than 100 years old many individuals reach heights of 1.5 m, as indicated by tree counts in the 0- to 5- and 0- to 10-cm d.b.h. classes (fig. 1c). The simultaneous presence of seedlings and absence of 0- to 5-cm (and 0- to 10-cm) d.b.h. trees in stands older than 150 (250) years indicates that, while there are noncompetitive "safe sites" for seedlings in all stands, the "safe sites" in stands older than approximately 100 years are not large enough to support growth from the seedling to the sapling stage. Since the probability of reproductive success is diminishingly small for those seedlings that regularly establish in clearings of less than 10 m^2, we conclude that the sites are, in fact, only apparently "safe." That is, tree establishment is only apparent and its appearance is an artifact of the short time period humans easily comprehend.

The sum, across all trees in the stand, of tree circumference is a third indicator that resource use becomes complete in most whitebark pine woodlands at about 100 years. Circumference is a good index of leaf area because it is strongly correlated with the amount of vascular tissue supplying water and nutrients to the leaves (Marshall and Waring 1986; Shinozaki and others 1964). It must be an equally good index of root area because it is strongly correlated with the amount of phloem delivering photosynthate to absorbing organs. Whether saturation is due to canopy closure (full utilization of light) or complete exploitation of the soil resources (water and minerals), we can expect total circumference to grow exponentially (or, at least linearly) from stand establishment to near site saturation and then level out. Our expectation is realized (fig. 2a): initial circumference (even under very high seedling densities) is near 0, rises to about 750 m/ha (= 0.1 m/m^2) soon after 100 years, and remains constant through the next 500 years. Regardless of whether the population is light or water-nutrient limited, growth of one individual after saturation (100 years in whitebark pine) can only occur when resources are released by the death of another individual (Valentine 1988).

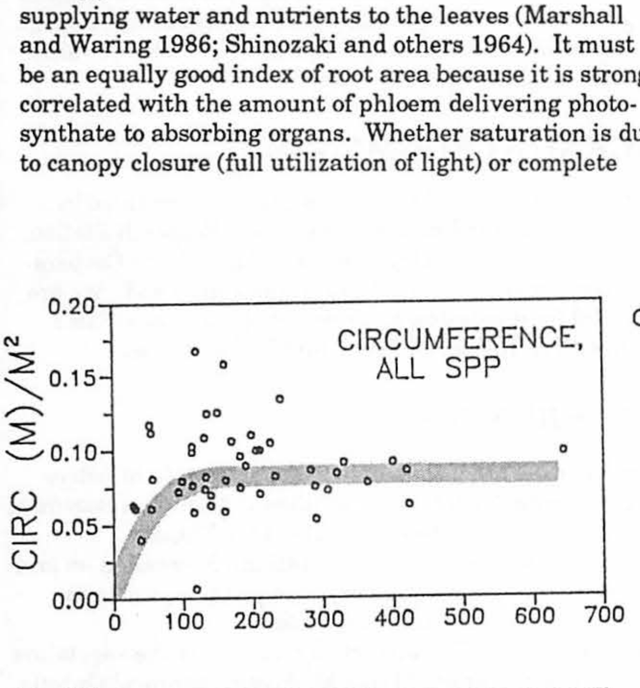


Figure 2—Indices of resource saturation and productive potential (a) aggregate circumference and (b) canopy cover increase to about 150 years and equilibrate there. The line is hand-fit through medians calculated across centuries.

Factors Limiting Production

Community production can be limited by resource availability. Among resources, lack of heat (temperature) surely limits production in the winter through its influence on both water-nutrient availability and enzyme activity. Warmer and moist conditions may result in nutrient limitation in the spring (Weaver and Forcella 1979), and relatively dry conditions probably cause water limitation in the summer (Weaver 1980).

The productive potential of a community also depends on its "factory size"—its leaf or root area. Factory size might be limited by either light or a soil (water or a nutrient) resource. While the former is often assumed (and as a result, trees are often ranked according to their "shade tolerance"), ditching tests suggest that root competition is often the actual controlling factor (Watt and Fraser 1933). Whitebark pine woodlands consist of open stands with an initial canopy cover of 0 percent, which grows to a limit of 60 percent in 100 to 150 years, and remains constant at that level for the next 200 to 300 years (fig. 2). Since, in saturated stands, canopy coverages are only 60 percent and since forest floor light levels (200 to 1,600 uEm^{-2}s^{-1}) are well above those required for whitebark pine photosynthesis (200 uEm^{-2}s^{-1} at compensation and 1,000 uEm^{-2}s^{-1} at saturation, Jacobs and Weaver [this proceedings]), we deduce that stand saturation in whitebark pine is more likely due to complete exploitation of a soil resource (water or a nutrient element) than to exhaustion of the light supply.

Factors Limiting Maximum Standing Crop

The rate of production is initially low, grows with increases in foliage cover, and halts at stand saturation (about 100 years), because leaf or root surfaces are maximized. In contrast, basal area accumulation continues to a maximum (60 m^2/ha) at 200 to 250 years and levels there (fig. 3a). The upper limit for standing crop must be due to one of three factors: excessive respiratory mass, a resource limit, or a structural limit. First, the most immediate limiting factor is probably the accumulation of a respiratory mass sufficient to consume all current photosynthesis (Odum 1969). Second, since the canopy is not saturated at maturity, however, the ultimate limiting factor must be either a nonlight resource or a structural deficiency. The limiting factor cannot be temperature

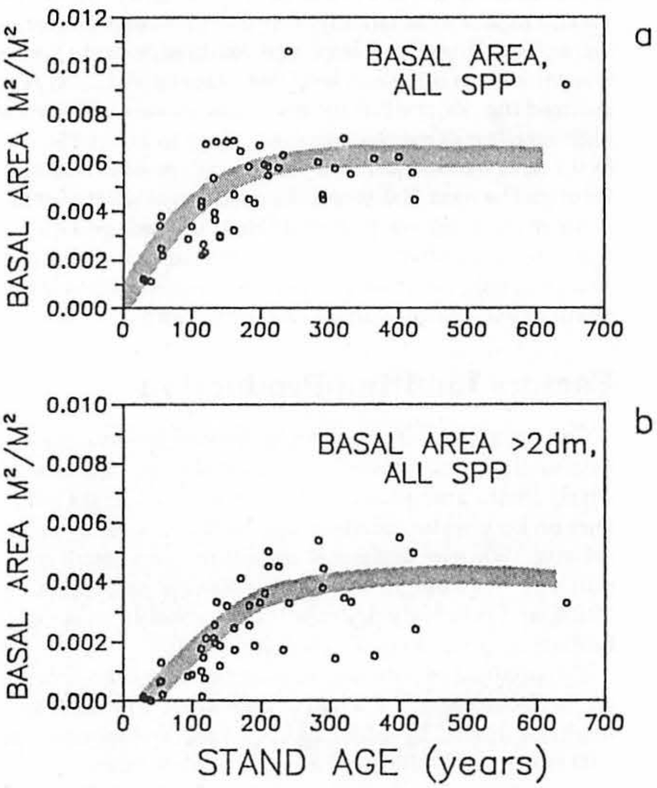


Figure 3—Standing crop, indexed by basal area (a) total and (b) trees larger than 20 cm d.b.h., increases to about 250 years and equilibrates. Tree heights equilibrate at about 200 years (12 M, Weaver and Dale 1974). The line is hand-fit through medians calculated across centuries.

because air temperature does not change systematically during stand development and, while soil temperature might be reduced by canopy shading, if this effect were controlling it should be maximized at canopy closure (100 years, not 250 years). The limiting factor cannot be water, because, while drought may stop growth each summer, precipitation in the following winter and spring will allow resumption of growth (not observed) if no other factor limits. The limiting resource is most likely the supply of an important nutrient—and probably not carbon, hydrogen, oxygen, or nitrogen, because supplies of these elements are constantly delivered from the atmosphere. The reader may question the inclusion of nitrogen in the list of elements available from the atmosphere; we do so because we believe researchers underestimate both nitrogen losses (production of decomposition-recalcitrant organic matter, and fire) and compensating nitrogen imports (Aradottir 1984; Boggs and Weaver, in preparation; Johnson and others 1983; Weaver and others 1978). Third, a structural limit would exist if nutrient supplies were sufficient to allow the growth of larger trees with the consolidation of more productive potential, but physical damage prohibited it. We doubt that it is physical control because the trees in whitebark pine woodlands can be relatively large, because little wind deformation occurs, because wind-snow breakage is uncommon, and because seedlings occupying openings fail to establish.

Total biomass depends on tree height as well as basal area. Tree heights increase linearly to 12 m at 200 years and then level off (Weaver and Dale 1974). Maximum tree height is most likely determined by water availability at the shoot tip and is therefore a product of the drying power of the air, the conductivity of the stem, and the water supplying power of the soil.

Harvestable Production

With few exceptions (Losensky, this proceedings), the height and form of whitebark pine trees encourage the reservation of forests dominated by it for wildlife, watershed cover, recreational, and esthetic purposes rather than timber production. If logging is contemplated, the manager needs a measure of basal area against time for trees large enough to log (for example, over 20-cm d.b.h.). Figure 3b shows that the basal area of trees large enough to log levels later (about 250 years) and at a lower value (40 m²/ha) than total basal area.

ACKNOWLEDGMENTS

Support for the field work reported was provided by NSF grant 29908X and Intermountain Research Station, Forest Service, U.S. Department of Agriculture Cooperative Agreement #12-11-202-12, Supplement #33. We are grateful for discussion and reviews of many associates including R. Keene, D. Perry, and H. Valentine.

REFERENCES

Aradottir, A. 1984. Ammonia volatilization from native grasslands and forests of southwest Montana. Bozeman, MT: Montana State University. 48 p. Thesis.

Boggs, K.; Weaver, T. [In preparation]. Succession on arid region river deposits: system composition, structure, and biomass-elemental dynamics.

Cowles, H. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Botanical Gazette. 27: 95-117; 167-202; 281-308; 361-391.

Cooper, W. 1923. The recent ecological history of Glacier Bay, Alaska. Ecology. 4: 93-128.

Crocker, R.; Major, J. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. Journal of Ecology. 43: 427-448.

Daubenmire, R.; Daubenmire, J. 1968. Forest vegetation of eastern Washington and northern Idaho. Tech. Bull. 60. Pullman, WA: Washington Agricultural Experiment Station. 104 p.

Forcella, F. 1978. Floristics and chorology of the *Pinus albicaulis-Vaccinium scoparium* association. Madroño. 25: 139-152.

Forcella, F.; Weaver, T. 1977. Biomass and productivity of the subalpine *Pinus albicaulis-Vaccinium scoparium* association in Montana, USA. Vegetatio. 35: 95-105.

Harper, J. 1977. Population biology of plants. New York: Academic Press. 892 p.

Hutchinson, H.; Lanner, R. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Johnson, C.; Rowe, R.; Weaver, T. 1983. Effect of irrigation on N_2-fixation by free-living prokaryotes in two grasslands. Proceedings of Montana Academy of Science. 42: 32-38.

Linhart, Y.; Tomback, D. 1985. Seed dispersal of nutcrackers causes multi-trunk growth form in pines. Oecologia. 67: 107-110.

Marshall, J.; Waring, R. 1986. Comparison of methods of estimating leaf-area index in old-growth Douglas-fir. Ecology. 67: 975-979.

Odum, E. 1969. The strategy of ecosystem development. Science. 164: 262-270.

Olsen, J. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Botanical Gazette. 119: 125-170.

Pfister, R.; Kovalchik, B.; Arno, S.; Presby, R. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Shinozaki, K.; Yoda, K.; Hozumi, K.; Kira, T. 1964. A quantitative analysis of plant form—the pipe model theory. Japanese Journal of Ecology. 14: 97-105.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European Alps. Berlin: Springer-Verlag. 137 p.

Valentine, H. 1988. A carbon-balance model of stand growth: a derivation employing pipe-model theory and the self-thinning rule. Annals of Botany. 62: 389-396.

Watt, A.; Fraser, G. 1933. Tree roots in the field layer. Journal of Ecology. 21: 404-414.

Weaver, T. 1980. Climates of vegetation types of the northern Rocky Mountains and adjacent plains. American Midland Naturalist. 103: 392-398.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. American Midland Naturalist. 92: 222-230.

Weaver, T.; Forcella, F. 1979. Seasonal variation in soil nutrients under six Rocky Mountain vegetation types. Journal of Soil Science Society of America. 43: 589-593.

Weaver, T.; Forcella, F. 1986. Cone production in *Pinus albicaulis* forests. In: Shearer, R., ed. Proceedings—conifer tree seed in the Inland Mountain West symposium. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 285 p.

Weaver, T.; Forcella, F.; Strobel, G. 1978. Phyllosphere nitrogen fixation in vegetation of the northern Rocky Mountains. Proceedings of Montana Academy of Science. 38: 78-84.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from R. Brown)—Do you know of studies of water relations—for example, the diurnal course of plant water status or transpiration rates—for whitebark pine?

A.—While Tranquillini (1979) provided extensive discussion of water relations in closely related *Pinus cembra*, I know of no studies of water relations in whitebark pine. In this paper I have speculated that water stress limits late summer production, but not maximum standing crop, in whitebark pine woodlands. In answering your question (of my climate paper) about factors limiting the distribution of whitebark pine I speculated that the southern limit of the tree's range might be set by summer drought.

Q. (from M. Cole)—According to your basal area graphs, standing crop is initially zero and increases asymptotically with time. The graphs also show considerable variance. Do you think the variance could be explained by plotting a series of site class curves in each graph?

A.—The variance you observe strongly suggests that while we selected stands representative of the *Pinus albicaulis-Vaccinium scoparium* woodland climax there is "site class" variance in the indicated habitat type. While it would be well represented by site class curves, I have no independent site class data to enable me to draw such curves; can you suggest an approach I haven't thought of?

OCCURRENCE OF MULTIPLE STEMS IN WHITEBARK PINE

T. Weaver
J. Jacobs

ABSTRACT

Depending on the stand, Montana-Wyoming whitebark pines (Pinus albicaulis) *may have multiple stems in 8 to 79 percent of the trees. The clumps had one to 11 stems with stand medians between two and three. Multiple stems may arise from several seeds germinating together, from basal branching, or both. Median stem number and maximum stem number per clump decrease with stand age, probably due to both within-clump and between-clump competition. While declines are slight in open woodlands, clumps almost disappear in closed forests. The presence of clumps is correlated with stand density in other conifers as well.*

INTRODUCTION

While most trees tend to be single stemmed, a few (such as *Quercus*, *Populus*, *Salix*, and *Sequoia*) are often multiple stemmed (Elias 1980). Stem number in trees must be determined by two factors: (1) the tendency to form, at one point, stems that are genetically identical (from, for example, spontaneous basal branching or wound-induced branching), maternally related (poly-embryony or seeds cached from one tree), or less strongly related (seed cached from different trees) individuals and (2) the tendency of multiple stems to survive at that point.

Whitebark pine (*Pinus albicaulis*) has long been noted for its tendency to occur in clumps with stems fused, or not fused, at the base (Harlow and Harrar 1958; Sudworth 1908). Multiple-stem origin (factor 1) was originally attributed to branching (Sudworth 1908), then to branching and/or seed caching (Weaver and Dale 1974), and most recently almost exclusively to seed caching (Lanner 1980; Linhart and Tomback 1985). The importance of stem survival (factor 2) in the determination of the number of stems in a clump has received little attention. The objectives of this note are to demonstrate the multiple-stem phenomenon for the whitebark pine of subalpine woodlands, to examine evidence for the mode of multistem initiation, and to open discussion on the effect of survival of the stems in a clump.

METHODS

Clump sizes were observed in 19 stands located in 10 subranges of the Rocky Mountains between latitude 43.5° and 46.5° N. All stands were subtimberline woodlands with canopies dominated by whitebark pine and understories dominated by grouse whortleberry (*Vaccinium scoparium*); none of the stands was krummholz. In each stand, the number of stems was counted on each tree in a representative 500-m^2 (12.6-m [41.3-ft] radius) circular plot. The stand was aged by coring three representative dominant trees. Canopy cover was estimated by determining, with a periscope, the percentage of 33 points that was covered. The locations, climate, soils, and vegetation of the study areas, as well as the sampling methods, are described in greater detail by Weaver and Dale (1974).

The 52 seedlings observed for basal branching were planted one-seed-per-pot and grown under normal nursery conditions for 2 years. The seeds were collected just north of Yellowstone National Park in the Palmer Creek-Bear Creek drainage at an altitude of 2,677 m (8,700 ft).

THE PHENOMENON

Observations in 19 woodland stands—neither krummholz nor forest stands—in the Rocky Mountains between latitude 43.5° and 46.5° N. (table 1) support five descriptive statements about clumping in whitebark pine.

1. There were both single-stemmed and multiple-stemmed trees in every stand.
2. There were more multiple-stemmed than single-stemmed clumps in 37 percent of the stands.
3. Clumps with more than seven stems were rare in stands over 150 years old. The fact that the smaller stems in older clumps were often dead suggests that weaker associates were competitively excluded (Lanner 1988).
4. Over half of the clumps were multiple stemmed in stands with cover less than 48 percent and less than half the clumps were multiple stemmed in stands with cover greater than 60 percent. Competition associated with stand closure probably selected against stems in clumps, since competition from the time of establishment would give clumped stems a relatively small height and would allow them to be overtopped and outcompeted by trees outside the clump.
5. These forest trees had one to 11 stems with a median averaging 2.36. Clumps containing as many as 22 stems have been reported in open subalpine stands of the Sierra Nevada (Tomback 1989).

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

T. Weaver is Plant Ecologist and J. Jacobs is Forest Ecology Associate, Department of Biology, Montana State University, Bozeman, MT 59717.

Table 1—Stem number in *Pinus albicaulis* clumps appearing in 19 Montana-Wyoming stands. The stands are arranged in order of arboreal cover

Tree cover	Basal area	No. clumps per plot	Stand age	Single stemmed	Percentage of trees by stem number class										
					1	2	3	4	5	6	7	8	9	10	11
Percent	*m²/ha*		*Yr*	*Percent*											
21	5.1	43	40	21	21	23	26	12	7	5	2	4			
27	10.8	67	133	45	45	34	10	6	3	0	1	0	1		
33	12.7	50	116	48	48	28	12	10	0	2					
45	23.5	37	190	43	43	45	3	3	3	0	3				
48	13.5	32	210	65	65	13	13	3	6						
48	17.2	50	140	48	48	30	8	8	2	4					
50	11.5	26	290	92	92	8									
51	21.0	23	420	35	35	48	13	0	4						
55	15.3	34	160	59	59	29	9	3							
57	12.7	33	140	30	30	27	16	18	3	0	3	0	0	0	3
63	20.2	46	400	61	61	37	2								
66	13.4	72	113	53	53	21	14	7	3	1	0	1			
66	13.4	61	170	90	90	3	2	2	3						
67	15.3	68	113	56	56	21	12	7	1	3					
75	17.3	53	210	53	53	26	11	6	2	2					
78	17.8	54	225	61	61	23	9	7							
84	13.1	58	99	53	53	28	3	5	7	0	2	0	2		
84	17.3	43	289	60	60	28	6	4	0	2					
85	23.5	30	283	63	63	14	13	3	7						

CLUMP INITIATION

Many multistemmed whitebark pine clumps undoubtedly arise from different seeds deposited at one spot, most likely by nutcrackers (Hutchins and Lanner 1982), but occasionally by squirrels and chipmunks or, conceivably but rarely, by a cone falling intact (Linhart and Tomback 1985). One can easily demonstrate this by pulling clumps and counting entirely separate stems. We suggest that mature trees arising through this mechanism may be recognized by the acute angles between the stems of trees competing with each other; this form is illustrated by Linhart and Tomback (1985).

We give two lines of evidence that some whitebark pine clumps arise by spontaneous basal branching and note that damage to apical meristems by insects, vertebrates, or climate might also stimulate basal branching. First, of seedling clumps pulled in the field, some consist of single trees with a single root system. Second, nursery seedlings, planted one-seed-at-a-time, often have multiple stems. For example, seedlings grown from one lot of seeds were branched at the base in over 84 percent of the cases and exhibited stem frequencies even higher than those seen in natural stands of the region (tables 1 and 2). The developmental tendency of whitebark pine to branch at the base may be related to its tendency to branch profusely and widely at higher nodes—a tendency that has led dendrologists to contrast the "lyrately branching" form of whitebark pine with the conical form of most other Rocky Mountain conifers (Harlow and Harrar 1958).
We suggest that obtuse basal branching, as well as strong crown branching, indicates a morphologic tendency of individuals that normally grow in open stands to optimize energetically through extensive branching. Such branching is energetically efficient because it develops a large canopy with minimal competition among branches and a minimal investment in trunk biomass. We suggest that—although forces such as crushing snow might sometimes spread clumps of genetically distinct individuals obtusely—obtuse basal branching often, or usually, indicates a genetically uniform clump.

Genotypic analysis of multistemmed clumps should shed light on the relative contributions of basal branching and the germination of clumped seeds to multiple stemming in particular whitebark pine stands. Analyses made in two Alberta stands (Furnier and others 1987) and one Wyoming stand (Linhart and Tomback 1985) show:
(1) that while 58, 70, and 83 percent, respectively, of the clumps examined had mixed origins, as many as 42, 30, and 17 percent may have arisen by branching alone, and (2) that, while most clumps are of mixed origin, 22, 19, and 46 percent, respectively, of the stems in the mixed clumps were genetically undistinguished from their neighbors and may well have arisen by branching. Genotypic analysis may have misclassified some distinct stems as branches; this is unlikely in studies based on 11 loci (Furnier and others 1987), and somewhat more likely in studies based on only four loci (Linhart and Tomback 1985).

Table 2—Branching of pine seedlings grown under greenhouse conditions

Species	Sample size	Percent of seedlings with "X" branches				
		1	2	3	4	5
Pinus albicaulis	52	15	15	58	6	6
Pinus contorta[1]	198	90	10	0	0	0

[1] In contrast to *Pinus albicaulis* branches, the branches of *Pinus contorta* were weak and not competitive with the main stem.

SURVIVAL OF STEMS IN CLUMPS

We observed that while multiple-stemmed trees are common in open woodlands just below timberline, they are rare in denser forests a few tens of meters lower. We attribute the difference not to sources of multistems, but to the survival of clumped stems. In a closed forest, trees in a clump should be at a disadvantage. Trees in a clump are very dense, and the clump can be expected to self-thin if other trees are nearby. One might even expect all trees in the clump to disappear, since their competition with each other will reduce the likelihood that any one will grow fast enough to stay in the canopy. On the other hand, if the stand is open—due to its occupation of a marginal habitat where "safe sites" for establishment are few or if the stand is thinned—we expect the multistem habit to be most energetically efficient.

Multistems are most efficient in open stands because (1) single stems have less circumference than multiple stems of equal cross-sectional area, (2) leaf area is proportional to circumference (Marshall and Waring 1986; Shinozaki and others 1964), and therefore (3) branched crowns require less photosynthate per unit of leaf area for support than single stems do. For example, simple geometry shows that two-, three-, four-, and five-stemmed trees have 140, 172, 200, and 222 percent of the circumference (our leaf area index) of a single-stemmed tree with the same cross-sectional area (our index of photosynthetic cost). One wonders whether the basal area differences underestimate differences in structural costs, since clumped trees growing in open stands are generally shorter than relatives growing in closed stands. This seems unlikely since the shorter trees of clumps will have longer, more costly, radial reaches in both shoot and root zones; such compensation has been demonstrated in juniper (Weaver and Lund 1982). While hormonal coordination might allow single-genotype clumps to outperform multiple-genotype clumps or conjoined stems in a clump to outperform single-stemmed trees, we have no evidence for either hypothesis. Nor do we have estimates of the possible impacts of clumping on group function—whether they might be positive (by transpiration reduction through mutual shelter or water supply increases due to snowdrift creation) or negative (by evaporation of rain or snow from a large canopy).

If competition significantly affects the degree of multistemming in open versus closed stands of whitebark pine, we might expect the same phenomenon in stands of other tree species. With or without "cache-planting," one sees that clumping is most common in open stands. In contrast to its forest form, thick-barked Douglas-fir (*Pseudotsuga menziesii*) is often clumped at lower timberline and along rocky ridges at higher altitudes, probably as a result of damage to apical meristems and survival of multiple stems or perhaps nutcracker caching (Lanner 1988). Typically single-stemmed lodgepole becomes multistemmed at lower timberline in areas such as meadow borders in northwestern Yellowstone National Park, due to survival of multiple stems arising after leader damage or germination of seeds from a cone that fell intact. While subalpine fir (*Abies lasiocarpa*) is strongly single stemmed in forests, its lower branches root and layer to form tight clumps in mountain meadows (Billings 1969) and krummholz sites (Marr 1977). The tendency of pines in open stands of warmer environments such as *Pinus edulis* (Vanderwall and Balda 1977), and *Pinus ponderosa* and *Pinus flexilis* of Montana, to branch low and profusely, but without multistemming, may be an adaptation to decrease exposure to groundfire and/or high soil-surface temperatures.

CONCLUSIONS

From the above we conclude that:

1. Multiple stems could arise from basal branching, from multiple establishment of seeds deposited near each other, or both.
2. Either basal branching or seed caching could yield more stems per clump than normally occur in mature whitebark pine stands.
3. Whether it arises through basal branching or seed caching, stem number is ultimately controlled by competition among members of a clump (and declines therefore with clump age) and competition between adjacent clumps (and declines therefore with canopy closure).
4. Branching seems to account for 31, 26, and 46 percent of total multiple stemming in three particular whitebark pine stands. We speculate that branching may dominate in woodlands where most clumps are obtusely branched and may be less important in woodlands where most clumps are acutely branched.

REFERENCES

Billings, W. 1969. Vegetation pattern near alpine timberline as affected by fire-snowdrift interaction. Vegetatio. 19: 192-207.

Elias, T. 1980. The complete trees of North America. New York: Van Nostrand and Reinhold. 948 p.

Furnier, G.; Knowles, P.; Clyde, M.; Dancik, B. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution. 41: 607-612.

Harlow, W.; Harrar, E. 1958. Textbook of dendrology. New York: McGraw-Hill. 55 p.

Hutchinson, H.; Lanner, R. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Lanner, R. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: Dancik, B.; Higgenbotham, K., eds. Proceedings—6th North American forest biology workshop. Edmonton, AB: University of Alberta: 15-48.

Lanner, R. 1988. Dependence of Great Basin bristlecone pine on Clark's nutcracker for regeneration at high elevations. Arctic and Alpine Research. 20: 358-362.

Linhart, Y.; Tomback, D. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. Oecologia. 67: 107-110.

Marr, J. 1977. The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. Ecology. 58: 159-164.

Marshall, J.; Waring, R. 1986. Comparison of methods of estimating leaf-area index in old-growth Douglas-fir. Ecology. 67: 975-979.

Shinozaki, K.; Yoda, K.; Hozumi, K.; Kira, T. 1964. A quantitative analysis of plant form—the pipe model theory. Japanese Journal of Ecology. 14: 97-105.

Sudworth, G. 1908. Forest trees of the Pacific slope. Washington, DC: U.S. Department of Agriculture. 455 p.

Tomback, D. 1989. [Personal communication]. October. Denver, CO: University of Colorado at Denver, Department of Biology.

Vanderwall, S.; Balda, R. 1977. Coadaptations of the Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. Ecological Monographs. 47: 89-111.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. American Midland Naturalist. 92: 222-230.

Weaver, T.; Lund, R. 1982. Diameter-weight relationships for juniper from wet and dry sites. Great Basin Naturalist. 42: 72-76.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Dave Mattson)—Nutcracker-dispersed trees that were not multistemmed might support the branching hypothesis, what about *Pinus sibirica* and *Pinus pumila*?

A.—*Pinus edulis* and *Pinus flexilis*, from the lower timberline, are nutcracker-dispersed trees that are mostly single stemmed. It is not clear to me either why companion seedlings fail to establish or why the tree fails to branch lower; perhaps fire or high surface heat select against multiple stems. Clumping seems more characteristic of cooler-moister woodlands and may be due, as in *Pinus albicaulis*, to a combination of caching and basal branching. While multiple stems have been reported in *Pinus sibirica and Pinus pumila*, I do not know whether and under what conditions it is important; at this symposium Tomback and Holtmeier both described clumping in closely related *Pinus cembra*. Lanner (1988) described clumping in wing-seeded conifers (*Pinus longaeva* and possibly *Pseudotsuga menziesii*) dispersed by nutcrackers.

Q. (from Cathy Stewart)—Are the single stems typical of closed-canopy forests due to lack of caches or to competitive thinning?

A.—I see both single-stem and multiple-stem reproduction in relatively dense stands. I would therefore attribute the lack of mature multiple-stem clumps to thinning induced by within-clump and between-clump competition.

Q. (from Ron Lanner)—If branching occurs at both the base and the crown of whitebark pine trees, why is it rare on the lower trunk?

A.—Our seedlings branched naturally and it is obvious that upper crowns branch naturally. I agree that branches on the lower trunk are rare, but have no solid explanation for their absence there; browsing or sand and snow blowing near the ground surface may contribute.

XYLEM RESIN MONOTERPENES OF WHITEBARK PINE IN THE SIERRA NEVADA AND SOUTHERN CASCADES

R. H. Smith

ABSTRACT

A preliminary study was made of the xylem monoterpenes of whitebark pine in the southwestern portion of its range to determine local and regional variation in components and composition. Three stands were sampled: Mount Rose, Nevada—43 trees; Mount Shasta, California—62 trees; Paulina Mountains, Oregon—23 trees.

The mean, maximum, and minimum of β-pinene, 3-carene, myrcene, and limonene varied greatly between stands. The greatest differences were between the Mount Rose stand and the two Cascade stands. 3-carene was usually the highest percentage in individual trees; but myrcene was highest in some trees. Other components occurring in small amounts were α-pinene, camphene, β-phellandrene, and terpinoline.

The overall frequency distribution of each of the four variable components suggested high, medium, and low classes to characterize the amounts in individual trees and to express total tree composition with four digits. When so classified, about 95 percent of the trees at Mount Rose differed from trees at Mount Shasta. The compositional types at Mount Shasta and in the Paulina Mountains were somewhat similar, but they differed markedly in frequency.

Thus, it is concluded that there is appreciable difference among the three stands in the frequency of genes or alleles for the expression of xylem resin monoterpenes.

INTRODUCTION

Five pine species are placed under the subsection *Cembrae*: one in North America, *Pinus albicaulis* Engelm. (whitebark pine), and four in Eurasia, *P. sibirica* DuTor., *P. cembra* L., *P. pumila* Regel., and *P. koraiensis* Sieb. and Zucc. Mirov (1961) reported that the xylem monoterpene of whitebark pine is almost completely 3-carene while that of the four Eurasian species consists of α-pinene and ß-pinene with smaller amounts of 3-carene and limonene. Local and regional variation was not reported by Mirov because the sampling and analytical procedures of that time were long and cumbersome, and to explore local and regional variation would have been a substantial undertaking. It was also difficult with those older procedures to determine the presence of small amounts of components. Though early studies were thus limited, they did provide an excellent basis for further research.

More recently, through the use of improved techniques for examining large numbers of small samples, considerable local or regional variation in xylem monoterpene composition has been found in many pines of western North America: *P. muricata* D. Don (Forde 1964), *P. torreyana* Parry (Zavarin and others 1967), *P. radiata* D. Don (Williams and McDonald 1962), *P. aristata* Engelm. (Zavarin and others 1976), *P. coulteri* D. Don, *P. washoensis* Mason and Stockwell, *P. ponderosa* Laws., *P. contorta* Dougl., (Smith 1967, 1977, 1983), and *P. monophylla* Torrey and Frem. (Smith and Preisler 1988). In a preliminary study considerable variation was found in the young progeny of six pine species of Mexico (Smith 1982).

I know of no report on the intraspecific variation of the xylem monoterpenes of whitebark pine. This paper reports a preliminary study of the local and regional variation of the xylem monoterpenes of whitebark pine in the southwestern portion of its range. Such information could be of value in refining the description of the species and in research on its specificity to bark beetle attack.

METHODS AND MATERIALS

Three stands of whitebark pine were sampled for xylem resin (fig. 1, table 1). This portion of the tree's range is characterized by small, widely separated stands at high elevation. Diameter of the trees sampled ranged from 10 cm to 45 cm; most were 15 cm to 20 cm. All trees were probably greater than 40 years old. Each tree was tapped at a height of 1.5 m with a 1.4-cm bit. The tap hole was at a slight upward angle, and went through the bark and phloem and for about 8 mm into the xylem. A 5-cc shell vial was fitted into the tap hole to collect the resin. Two to three days later the vials were removed and corked.

An aliquot of 0.1 to 0.5 cc of the sample of resin and an approximate equal amount of chromatographic grade pentane were combined in a 1-cc screw cap vial. These prepared samples were refrigerated at 0 °C except when being processed.

The prepared samples were analyzed for monoterpene content by gas liquid chromatography (Smith 1977), using a thermal conductivity detector, a ß, ß' oxydipropionitrile column, and a sample size of about 1.0 µl. The results of the analysis were recorded by a reporting integrator and were expressed as normalized composition—each component was calculated as a percentage of the total monoterpene in the sample. Peaks were identified by a combination of relative retention time, introduction of internal

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

R. H. Smith (retired) was Research Entomologist, Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Berkeley, CA 94701.

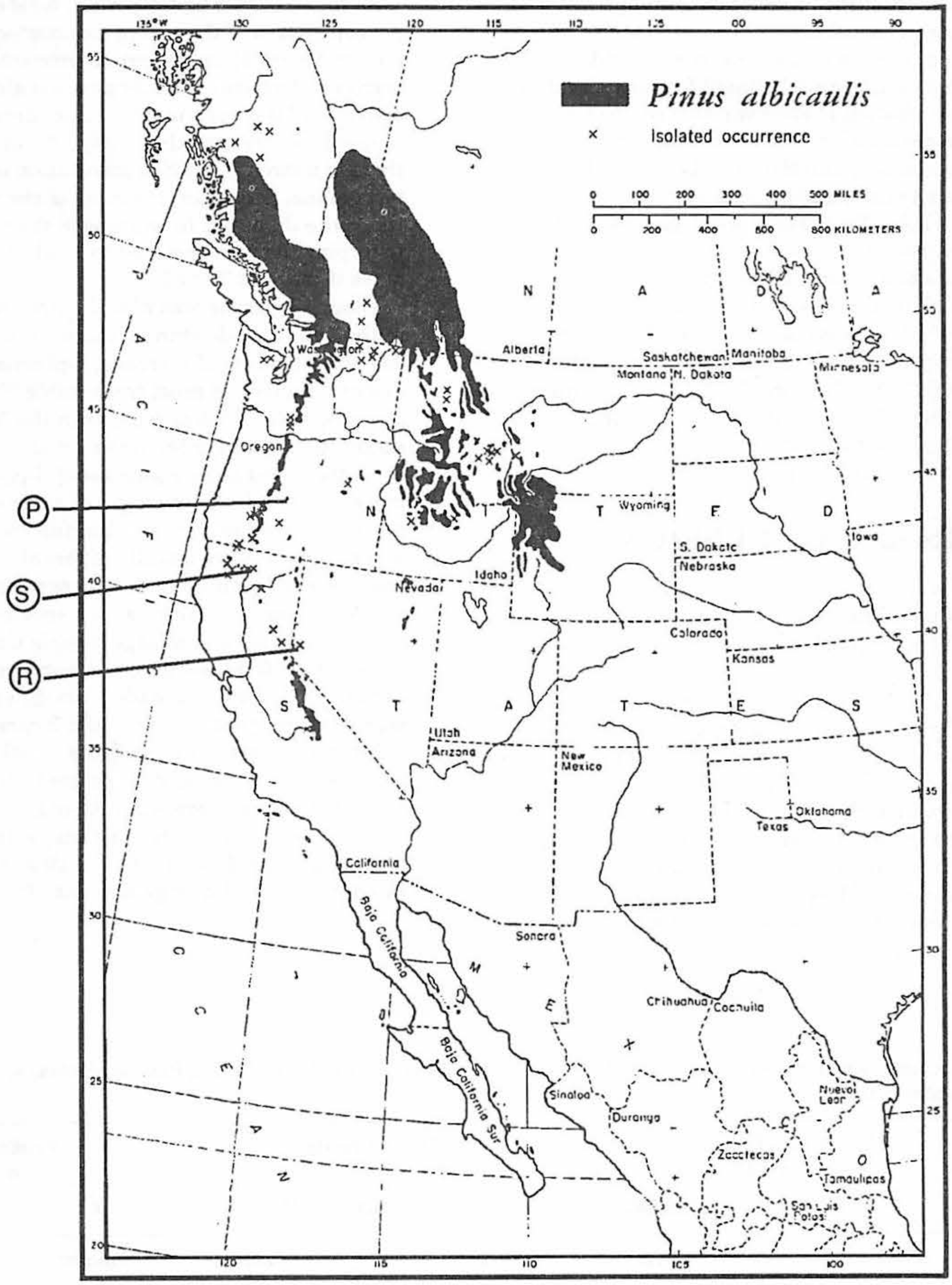


Figure 1—Location of three stands of whitebark pine sampled for xylem resin monoterpenes, P = Paulina Mountains, S = Mount Shasta, R = Mount Rose. Distribution taken from Critchfield and Little (1966).

Table 1—Number of trees sampled and sampling dates for three study locations

Number of trees sampled	Locale	National Forest	Mountain range	Date sampled
43	Mount Rose	Toiyabe	Sierra Nevada	September 1986
62	Mount Shasta	Shasta-Trinity	Cascades	August 1987
23	Paulina Mountains	Deschutes	Cascades	June 1988

standards, and from the experience of analyzing large numbers of resin samples.

Average composition and the maximum and minimum for each component were calculated for each stand. The frequency distribution of each variable component was plotted. The modes of each of the multimodal distributions were estimated, and their limits were defined when the distribution of a component for all three stands was viewed as a whole. Since there were, generally, three modes in the distribution of four of the components, numerical values of 0, 1, and 2 were given to the low, medium, and high modes, respectively. The percentage composition of each tree was converted to a four-digit value, one digit for each of the four variable components, by applying the 0, 1, 2 definition. The normalized distribution of the kinds of composition was then calculated for each stand, and the three stands were compared on the basis of the frequency of types of composition.

RESULTS AND DISCUSSION

The three whitebark pine stands differed considerably in average composition of xylem monoterpenes and in the range of the components (table 2). However, no composition of any tree in the three stands resembled that which Mirov (1961) reported for the other four species of *Cembrae*. The two Cascade plots differed much more from the Sierra Nevada plot than they differed from each other. However, there were noticeable differences between the two Cascade plots. Although in a normalized analysis a change in one component can cause a change in another, the total monoterpene content of whole resin was fairly constant. Thus, the normalized system is a close approximation of the absolute amounts, and the differences observed can be considered real.

As Mirov (1961) had reported, 3-carene was the principal component of the xylem monoterpenes of whitebark pine at Mount Rose, but small amounts of α-pinene, myrcene, limonene, and terpinoline along with trace amounts of ß-pinene and ß-phellandrene were also found in nearly all trees in this study. As with other pines, there is a strong, positive association of 3-carene and terpinoline. However, the ratio of the two components was quite different; in whitebark the ratio of 3-carene to terpinoline was about 10 to 1, whereas in most other pines it is about 20 to 1.

Though 3-carene was also the principal component in the two Cascade stands, there were considerable and variable amounts of myrcene, ß-pinene, and to a limited extent limonene in most trees (table 2). The ratio of 3-carene to terpinoline was, as in the Mount Rose trees, about 10 to 1, and there was a small amount of α-pinene, in all trees and a trace amount of ß-phellandrene in most trees. Although the averages of several components were about the same in the two Cascade stands, the maximum and minimum were usually different. This could have been caused by differences between the two stands in the size of the sample. That is, in a species so variable, it may be necessary to have a large sample size—from my experience 70 to 100 trees—to consistently estimate the range of variation. The two Cascade plots differed markedly in the mean and range of ß-pinene and 3-carene (table 2). The difference between the two plots in sabinene is caused by one tree at Paulina with 23 percent sabinene. As in several other pines, there was a strong positive relationship between sabinene and terpinoline, with nearly a one-to-one ratio. Therefore, the tree with a large amount of sabinene also had a large amount of terpinoline.

Table 2—Xylem resin monoterpenes of *Pinus albicaulis* in three stands: Mount Rose, Mount Shasta, Paulina Mountains; $\overline{X}$ = mean, SD = standard deviation

	Mount Rose $n = 43$			Mount Shasta $n = 62$			Paulina Mountains $n = 23$		
Component	$\overline{X}$	SD	Max/Min	$\overline{X}$	SD	Max/Min	$\overline{X}$	SD	Max/Min
	Percent[1]		*Percent*	*Percent*[1]		*Percent*	*Percent*[1]		*Percent*
α-pinene	1.9	0.59	4/1	2.7	1.24	8/2	2.9	1.14	5/0
ß-pinene	.3	.16	1/*	4.6	7.35	39/*	11.4	6.87	20/0
3-carene	83.2	5.35	94/70	54.0	9.37	82/40	45.1	13.70	68/8
sabinene[2]	.0	—	—	.0	—	—	1.0	4.69	23/0
myrcene	6.1	4.79	18/*	28.1	10.46	44/1	27.8	11.43	69/16
limonene	1.0	1.11	5/0	3.6	3.35	11/0	3.4	3.52	14/0
ß-phellandrene	.4	.25	1/0	.3	.44	1/0	1.3	3.18	16/0
γ-terpinene	*	—	—	*	—	—	*	—	—
terpinoline	6.9	2.42	14/0	6.0	1.21	11/4	6.8	3.45	20/2

[1] = normalized.

[2] = all in one tree at Paulina.

* = trace, less than 0.1.

Three trees at Paulina are of note, the one high in sabinene discussed above, one high in myrcene, and one high in ß-phellandrene. The normalized percent composition of these three trees was:

Component	Percent composition Tree 1	 Tree 2	 Tree 3
α-pinene	2.6	3.6	4.9
ß-pinene	11.3	trace	21.1
3-carene	8.1	23.9	21.2
sabinene	23.0	0.6	trace
myrcene	25.3	68.8	26.0
limonene	8.9	trace	6.8
ß-phellandrene	trace	trace	16.1
terpinoline	20.0	4.0	4.1

Are these three trees unusual, or are there other similar trees in other parts of the species distribution?

The three stands differ markedly in the frequency distribution of four variable components: ß-pinene, 3-carene, myrcene, and limonene (fig. 2). All four frequency distributions have a tendency to be tri-modal, when all three stands are viewed together. The best approximation of the three modes and the intervals that describe them is given in table 3. The similarity and differences between the two Cascade plots are clearly evident from the frequency distributions (fig. 2).

The types of monoterpene composition in each stand—obtained by converting the composition of each tree to a four-digit value using table 3 and then normalizing the types of composition for each of the three stands—shows

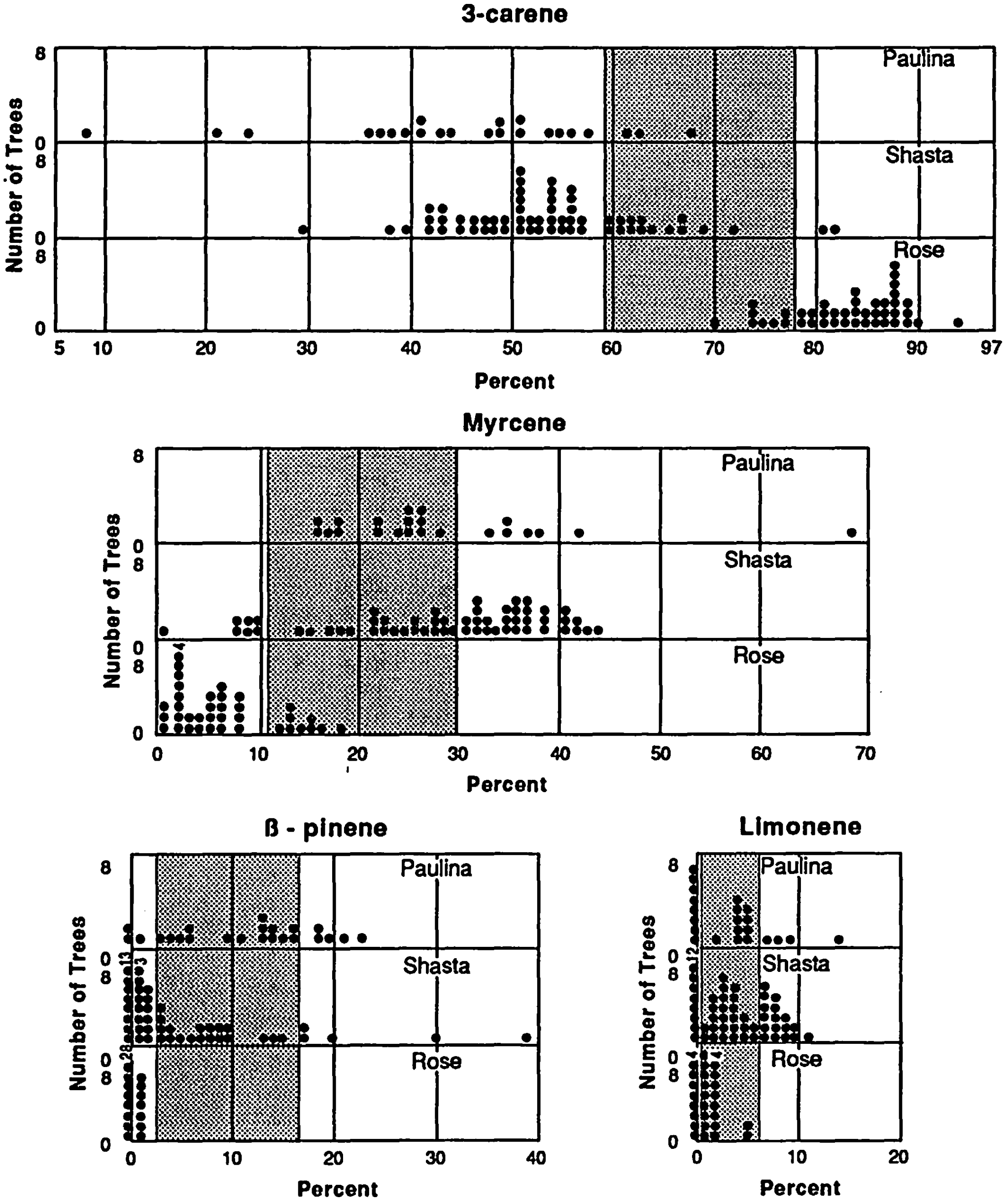


Figure 2—Frequency distribution of 3-carene, myrcene, ß-pinene, and limonene in three stands of whitebark pine: Paulina Mountains, Mount Shasta, Mount Rose. Numbers at top of a line of plotted points are the additional number of points for that percentage. The medium mode is shaded for the distribution of each component.

that each stand is sharply different from each other (tables 4 and 5). Again, the large difference between the Sierra Nevada plot and the two Cascade plots is clearly evident (fig. 2 and tables 4 and 5), and the substantial difference between the two Cascade plots is also clearly evident. That is, the types of composition found in the two Cascade plots are somewhat similar, but their frequencies are quite different.

The coefficient of determination between the stands was very low (about 0.1), though one might question the use of this analysis because of the large differences in the numbers of trees in the three stands. Even without the coefficient of determination, the differences between stands is clearly evident. The two Cascade plots are clearly different in the frequency of types, and the Sierra Nevada stand is clearly different from the two Cascade plots in both the kinds of and frequencies of compositional types. Likewise, the numbers of compositional types in the three stands are very different, with only four types at Mount Rose, 13 types at Paulina, and 21 types at Mount Shasta.

These differences in means, ranges, and in the kinds and frequency of compositional types suggest that there are major genetic differences between the Cascade and Sierra Nevada stands and minor genetic differences between the two Cascade stands. It should be reemphasized

Table 3—Intervals for low-, medium-, and high-frequency modes of the four variable components of whitebark pine xylem monoterpenes, β-pinene, 3-carene, myrcene, limonene

Mode	Code value	Component β-pinene	 3-carene	 myrcene	 limonene
		Percent			
Low	0	0-3	0-58	0-10	0
Medium	1	4-16	59-78	11-30	1-6
High	2	17-100	79-100	31-100	7-100

Table 4—Coded types of xylem monoterpene composition of whitebark pine and the average actual composition of these coded types for 128 trees

Coded type[1]	N	Actual composition[2] α-p	 cam	 β-p	 car	 sab	 myr	 lim	 β-ph	 γ-t	 ter
		Percent[3]									
0011	1	2.5	—	2.2	56.0	—	29.2	3.7	0.3	0.4	5.4
0012	4	1.7	*	.3	54.2	—	28.3	9.4	*	.5	5.6
0020	11	2.5	0.1	.7	49.3	0.1	41.2	*	.5	.1	5.5
0021	14	2.4	*	1.5	51.8	*	34.7	3.4	.3	.1	6.4
0022	4	2.3	*	.6	42.3	—	41.8	7.0	.3	.1	5.6
0110	9	1.8	.1	.4	74.3	—	13.8	.2	.5	—	8.9
0120	1	1.9	.3	.8	60.0	—	31.3	.5	.3	—	4.7
0111	3	1.7	*	.5	63.4	—	23.0	3.5	.2	.2	7.5
0112	5	1.6	.1	.2	61.9	—	21.5	8.6	*	.2	5.7
0200	6	2.4	.3	.4	84.7	—	4.6	.2	.3	.1	6.8
0201	29	1.9	*	.3	85.1	—	4.0	1.4	.3	*	7.0
0210	2	1.5	*	.3	79.5	—	12.6	.3	.2	—	5.5
1010	3	3.2	*	12.3	53.8	*	23.6	*	.3	—	6.7
1011	4	2.8	.1	10.8	49.7	*	23.0	4.9	1.0	*	7.6
[4]1012	6	2.6	*	11.2	43.2	3.8	21.0	9.9	.3	—	8.4
1020	7	4.3	*	10.1	44.4	*	35.6	*	.3	—	5.1
1021	1	2.5	*	5.4	41.1	*	41.9	4.5	.6	—	3.9
1110	2	1.8	*	9.5	63.1	*	17.6	*	.4	—	7.7
1101	3	2.5	*	8.1	67.2	—	9.6	4.8	.7	—	6.7
1111	2	2.1	.1	5.0	64.5	*	16.4	3.4	.4	—	7.8
1112	1	2.7	*	6.6	60.7	—	16.7	6.7	.3	—	6.5
2001	2	5.8	.2	34.4	48.0	—	4.5	2.1	.2	—	4.8
2010	3	4.2	*	19.3	47.0	*	22.2	*	.4	—	6.1
2011	4	4.3	.2	18.8	42.3	*	25.7	2.9	.6	—	5.0
2012	1	4.9	*	21.1	26.2	*	26.0	6.8	16.1	—	4.1

[1] From left to right: β-pinene, 3-carene, myrcene, limonene; see table 3 for values of code numbers.

[2] From left to right: α-pinene, camphene, β-pinene, 3-carene, sabinene, myrcene, limonene, β-phellandrene, γ-terpinene, terpinoline.

[3] Average for the normalized composition for the trees in each type.

[4] One tree with 23 percent sabinene and 20 percent terpinoline.

Table 5—Frequency distribution of coded types of xylem monoterpene composition in three stands of whitebark pine; see table 4 for actual composition of coded types

Coded type	Stand		
	Paulina Mountains	Mount Shasta	Mount Rose
	Percent[1]		
[2]0011	—	1.6	—
0012	—	6.5	—
0020	4.3	16.1	—
0021	8.7	19.4	—
0022	—	6.5	—
0110	—	1.6	18.6
0120	—	1.6	—
0111	4.3	3.2	—
0112	—	8.1	—
0200	—	3.2	9.3
0201	—	—	67.4
0210	—	—	4.7
1010	8.7	1.6	—
1011	13.0	1.6	—
1012	[3]13.0	4.8	—
1020	13.0	6.5	—
1021	4.3	—	—
1110	4.3	1.6	—
1101	—	4.8	—
1111	4.3	1.6	—
1112	—	1.6	—
2001	—	3.2	—
2010	8.7	1.6	—
2011	8.7	3.2	—
2012	[4]4.3	—	—

[1] Normalized for each stand.

[2] From left to right: α-pinene, 3-carene, myrcene, limonene.

[3] One tree with 23 percent sabinene and 20 percent terpinoline.

[4] Tree also has 16 percent β-phellandrene.

that the study was limited to a small portion of tree range. And it is apparent that with such large local variation, larger numbers of trees are needed at both the Mount Rose and Paulina Peak stands to improve the analyses. Obviously, too, a survey of the rest of the species distribution would be useful.

REFERENCES

Critchfield, W. B.; Little, E. L. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.

Forde, Margot B. 1964. Geographic variation in the turpentine of Bishop pine. New Zealand Journal of Botany. 2: 44-51.

Mirov, N. T. 1961. Composition of the gum turpentines of pines. Tech. Bull. 1239. Washington, DC: U.S. Department of Agriculture, Forest Service. 158 p.

Smith, Richard H. 1967. Variations in the monoterpene composition of the wood resin of Jeffrey, Washoe, Coulter, and lodgepole pine. Forest Science. 13: 246-252.

Smith, Richard H. 1977. Monoterpenes of ponderosa pine xylem resin in western United States. Tech. Bull. 1532. Washington, DC: U.S. Department of Agriculture, Forest Service. 48 p.

Smith, Richard H. 1982. Xylem monoterpenes of some hard pines of western North America. Res. Pap. PSW-160. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 7 p.

Smith, Richard H. 1983. Monoterpenes of lodgepole pine xylem resin: a regional study in western United States. Forest Science. 29: 333-340.

Smith, R. H.; Preisler, H. K. 1988. Xylem monoterpenes of *Pinus monophylla* in California and Nevada. Southwestern Naturalist. 33: 205-214.

Williams, A. L.; McDonald, I. R. C. 1962. Variation of turpentine composition in five population samples of *Pinus radiata*. New Zealand Journal of Science. 5: 486-495.

Zavarin, Eugene; Hathaway, Wilhelmina; Reichert, Thomas; Linhart, Yan B. 1967. Chemotaxonomic study of *Pinus torreyana* Parry turpentine. Phytochemistry. 6: 1019-1023.

Zavarin, Eugene; Snajberk, Karl; Bailey, Dana. 1976. Variability in the essential oils of wood and foliage of *Pinus aristata* and *Pinus longaeva*. Biochemical Systematics and Ecology. 4: 81-92.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Ron Lanner)—How does *Pinus albicaulis* compare to *P. flexilis* in monoterpenes?

A.—Within the limits of my data, the two species are distinctly different. None of the 128 *P. albicaulis* examined had more than 8 percent α-pinene, with an average of about 2.5 percent. Of the 10 trees of *P. flexilis* examined, none had less than 28 percent α-pinene, with an average of about 55 percent. *Pinus albicaulis* can be separated from *P. monticola* on the same basis.

FIRE EFFECTS IN WHITEBARK PINE FORESTS

Penny Morgan
Stephen C. Bunting

ABSTRACT

Although whitebark pine (Pinus albicaulis) *forests frequently burn, little is known about the patterns of regeneration, growth rates, and successional development of these forests as they are influenced by fire frequency. This paper presents such data collected from seral whitebark pine stands in the Shoshone National Forest, WY.*

Cross-sections were collected from fire-scarred whitebark pines. Fires have occurred often in the past, and the larger trees often survive low-intensity fires. Many trees have been scarred by more than one fire. Young whitebark pine trees populate recent burns. Relative ages and growth rates of whitebark pine and associated conifers have been determined. On sites where it is seral, whitebark pine is gradually replaced by subalpine fir (Abies lasiocarpa) *and Engelmann spruce* (Picea engelmannii) *in the absence of fire. Frequent fires prevent or slow the replacement of whitebark pine by these more shade-tolerant and less fire-resistant conifers.*

Based on a composite of samples and a synthesis of the literature, successional patterns in seral whitebark pine forests are documented. Fires rejuvenate and maintain the productivity of seral whitebark pine stands. Fires are thus important to regeneration and long-term maintenance of seral whitebark pine forests.

INTRODUCTION

Whitebark pine (*Pinus albicaulis*) is an important species in subalpine ecosystems throughout the Northern Rocky Mountains. It is an early successional species in many habitat types (Pfister and others 1977; Steele and others 1981, 1983) and may occur in both pure and mixed stands.

In substantial areas of the species' natural distribution, whitebark pine populations are declining in abundance (Arno 1986). White pine blister rust (*Cronartium ribicola*) has reduced many stands in the Northern Rocky Mountains. Mountain pine beetle (*Dendroctonus ponderosae*) has also affected populations in some areas. Seral whitebark pine stands are being replaced by more shade-tolerant species, particularly subalpine fir (*Abies lasiocarpa*).

Fire may play an important ecological role in seral whitebark pine stands. Whitebark pine regeneration is favored in the open conditions created by fires or other large-scale disturbances, but little is known about the role of fire in the maintenance and management of whitebark pine. We studied successional patterns relative to fire history in two habitat types. Specific objectives were to:

1. Collect and interpret detailed fire history data.
2. Identify past regeneration patterns for whitebark pine and determine their relationship to fire history.
3. Analyze stand age and size structure of whitebark pine and associated conifer species in stands where whitebark pine is seral.

LITERATURE REVIEW

Whitebark pine is a subalpine white pine of the Northern Rocky, Sierra Nevada, and Cascade Mountains. Loope and Gruell (1973) found whitebark pine from 2,400 and 3,050 m, often in nearly pure stands just below timberline. It is most common on thin soils of igneous origin (Harlow and Harrar 1969), but may occupy other soils (Weaver and Dale 1974). It may be small, scrubby, and multistemmed (krummholz) near timberline or can attain commercial size and good form in mixed stands at lower elevations.

The stands are open, with large whitebark pines often occurring in clumps (Weaver and Dale 1974). Stands may be even or multiaged. Whitebark pine occurred in 36 of 50 habitat types identified in eastern Idaho and western Wyoming by Steele and others (1983). Whitebark pine may occur as a seral stage dominant or in pure or mixed climax stands.

Whitebark pine is an important source of food for wildlife in the Greater Yellowstone Ecosystem. Red squirrels, grizzly bears, and Clark's nutcrackers are particularly dependent on the large, high-protein seeds produced by whitebark pine, but numerous other birds and rodents also eat the seeds (Craighead and others 1982; Eggers 1986; Hutchins and Lanner 1982; Tomback 1982).

Arno (1986) calculated a mean fire-free interval of 30 to 41 years with a range from 4 to 78 years for fires occurring in large stands (100 to 300 ha) in upper subalpine habitat types where whitebark pine is a seral species and replaced at climax by subalpine fir. For small areas less than 1 ha, Arno and Petersen (1983) found mean fire-free intervals to vary between 72 and 94 years. Romme (1982) estimated a fire-free interval of about 300 years for much of the lodgepole pine forest of Yellowstone National Park, and this interval may reflect conditions of the adjacent whitebark pine forests as well.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Penny Morgan is Assistant Professor, Department of Forest Resources, and Stephen C. Bunting is Professor, Department of Range Resources, University of Idaho, Moscow, ID 83843.

Whitebark pine is a pioneer on burns (Weaver and Dale 1974) and may dominate for 225 years or more (Loope and Gruell 1973). Whitebark pine trees grow slowly in both diameter and height (Weaver and Dale 1974). Although whitebark pine has thin bark, it often occurs on dry sites in open stands, which reduces fire intensity and, consequently, the tree's vulnerability to fire (Fischer and Clayton 1983). The common associates of whitebark pine are, in order of increasing fire resistance: subalpine fir, Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*). Douglas-fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) are relatively fire resistant and are occasionally associated with whitebark pine at its lower elevational limit. The most common associates in the Yellowstone region are subalpine fir and lodgepole pine.

METHODS

The Russell Peak study area is located approximately 25 km northwest of Cody, WY, in the Crandall Ranger District, Shoshone National Forest. The study area is about 750 ha in area with elevations from 2,300 to 2,800 m. Soils are immature and primarily formed from andesite and volcanic breccia of the Wapiti Formation (Pierce and Nelson 1971).

The majority of the seral whitebark pine stands in the study area occur on *Abies lasiocarpa / Vaccinium scoparium or Abies lasiocarpa / Arnica cordifolia* habitat types (Steele and others 1983). To determine the response of the species through time, sample stands were selected to represent a variety of successional stages on these two habitat types.

Eight mid-seral and two late-seral stands were sampled. Macroplots were 50 by 50 m (0.25 ha) in size. All trees greater than 1.4 m in height of all species were aged by taking an increment core at breast height. A subsample of trees was cored at both the base and 1.4 m to determine an adjustment, by species, for total age. Basal diameter of all saplings, those individuals less than 1.5 m and greater than 0.5 m in height, was recorded on the macroplot. A subsample of saplings was cored at the base or cross-sectioned to determine an age-height relationship. Density of seedlings, those individuals from 0 to 0.5 m in height, was estimated within five 2- by 20-m belt transects. Obtaining the total age of all trees on the plot allowed analysis of stand dynamics.

At three locations within a 100-ha sample area, cross-sections were collected from trees with multiple fire scars. All three locations had a minimum of three trees with multiple fire scars and were located near sample plots. Cross-sections were sent to the Laboratory of Tree-Ring Research at the University of Arizona for analysis. Cross-sections were sanded and cross-dated using the skeleton plot technique (Stokes and Smiley 1968; Swetnam and others 1985). Based on characteristic cell structure, scars were classified as having high or medium probability of resulting from fires, or as scars probably created by other means, such a windthrow or black and grizzly bear feeding. Skeleton plots were made for each cross-section, and in some cases for two or more radii per tree. The skeleton plots were compared among the whitebark pine cross-sections and to two different tree-ring chronologies from the Yellowstone region, a Douglas-fir and limber pine series from Gardiner, MT (Drew 1975). Unfortunately these chronologies did not cross-date satisfactorily with the whitebark pine specimens. However, cross-dating was observed on the skeleton plots among the whitebark pine cross-sections.

Fire scars were dated by their position within dated annual rings (Arno and Sneck 1977; Dieterich and Swetnam 1984). Relative positions of scars within annual rings were also noted where possible, so that inferences regarding seasonal timing of past fires might be made (Barrett 1981; Dieterich and Swetnam 1984). Many scars of varying severity were found on the cross-sections. Only those scars that had a high probability of being caused by fire were used to estimate the fire-free intervals (FFI). These scars were selected through inspection of the tree, the morphology and shape of the scar, and subsequently developed woody tissue.

RESULTS

Data from the 10 stands sampled near Russell Peak indicate a variety of tree compositions. The combined data for all stands show that most of the whitebark pine in the area regenerated 100 to 300 years ago (fig. 1) and is presently declining in abundance (fig. 2). General successional patterns and fire history data for stands on the two habitat types are similar and are presented together here. Subalpine fir, which established in the past 200 years, is beginning to dominate many sites. Lodgepole pine and Engelmann spruce are present in small amounts only and do not comprise a significant amount of any stand.

Scars from 14 trees found within a 100-ha area in the general area of Russell Peak were dated. The FFI prior to 1875 was estimated to be 29 years, based on an average of all intervals between fires on individual cross-sections. The average FFI for the three groups of cross-sections varied from 13 to 46 years. Fire was relatively common within the Russell Peak area prior to 1850. The last fire that can be documented occurred in 1867.

The fire scar data indicate that in the Russell Peak region fires were much more common from 1700 to 1850 than they have been since 1850. More than 40 probable fire scars formed during this period in the 14 whitebark pine sampled. Most of the fires were small, as they scarred only one tree. There were, however, some years in which more than one tree was scarred in two or more of the three fire-history data locations. When two or more scars were dated to the same year, it was assumed that the fire affected a larger area than when only one tree was fire scarred. Our data indicate that such large fires occurred in 1595, 1672, 1693, 1721, 1810, 1825, 1836, 1848, and 1858. The average interval between these fires is 33 years with a range of 10 to 77 years. No such large-scale fire can be documented after 1858.

Even the more conservative 33-year FFI in the Russell Peak region is extremely short for whitebark pine survival. Whitebark pine grows slowly and may not achieve reproductive maturity until at least age 50 (Morgan and

Bunting 1989); most trees do not produce large numbers of seeds until at least age 70. Even if many mature whitebark pine trees survived the fires, it is doubtful that the species could persist with fires occurring so frequently. We are limited by having few trees dating prior to 1750, but it appears that fires were more frequent in the Russell Peak area between 1780 and 1850 than prior to 1780. The reasons for this are not evident but may be related to American Indian movements, climatic changes, or random variation in natural ignition. The frequent fire occurrence between 1780 and 1850 significantly lowers the average FFI and may not reflect the long-term conditions under which the species existed in prehistoric periods.

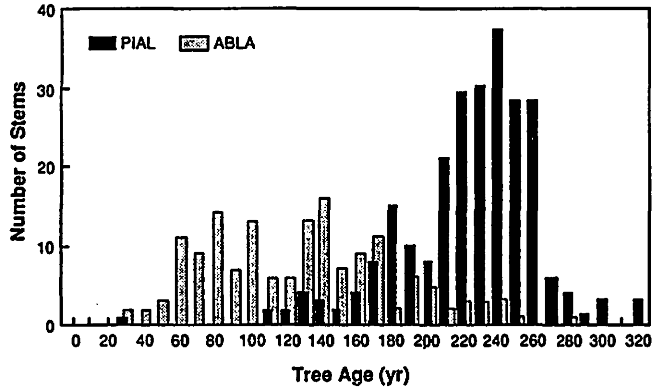


Figure 1—Combined distribution of whitebark pine (PIAL) and subalpine fir (ABLA) trees by 10-year age classes for 10 stands on the Shoshone National Forest, WY.

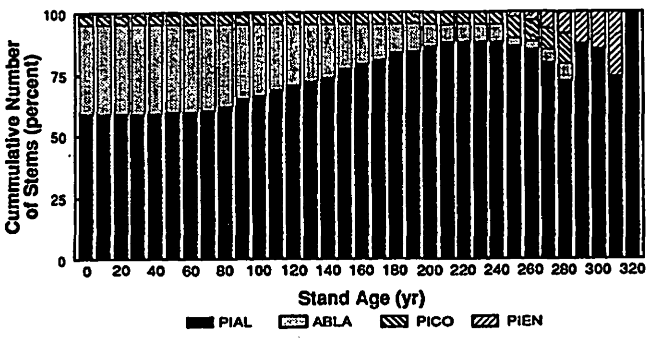


Figure 2—Percentage of the 10 sampled stands in the Shoshone National Forest, WY, comprised of the major conifer species, whitebark pine (PIAL), subalpine fir (ABLA), lodgepole pine (PICO), and Engelmann spruce (PIEN) through time.

No scars of any origin were found in the Russell Peak area dating after 1894. These data suggest that sources of scars, which include fires and grizzly bears, have been reduced since the late 1800's. At that time, an expanding range livestock industry in western Wyoming may have resulted in both killing of grizzly bears as predators and less frequent fires due to removal of the fine fuels by grazing. The American Indian was also displaced during this period. The other possibility is that the region has undergone a slight climatic change that has made fires less likely to occur.

The reduced fire frequency in the last 130 years has allowed subalpine fir to regenerate in abundance (figs. 1 and 2). Fewer fires have probably limited the opportunity for successful regeneration of whitebark pine. Fires create more open stands and expose mineral soil, which are necessary for establishment of whitebark pine seedlings. Whitebark pine can regenerate in duff or under a closed overstory but seldom succeeds in becoming a mature individual under these conditions.

Fires apparently occurred during different seasons of the year (table 1). Fires were relatively evenly distributed throughout the growing season for whitebark pine. Large fires, those that scarred more than one tree, occurred more frequently late in the growing season or when whitebark pine was dormant. Thus, most fires that occur are small, burning only one or a few trees, and they occur at any time during the growing season. Occasionally, such as in 1805, 1810, 1819, 1828, and 1858, large-scale fires apparently occurred in mid- to late summer or early fall.

The majority of the stands had significant amounts of subalpine fir regeneration. Stand 5 is typical (fig. 3). This stand was classified as an *Abies lasiocarpa/Arnica cordifolia* h.t. Most of the whitebark pine trees are over 200 years old and predate a series of fires that burned in the stand in the late 18th and early 19th centuries. The lodgepole pine present in the stand also predates these fires. Most subalpine fir has become established since the last fire, which occurred in 1867. No fires can be documented in the stand after 1867. There is a gap in conifer regeneration between 160 and 200 years ago. This gap coincides with a period when fires were very frequent in the stand, occurring in 1789, 1794, 1798, 1805, and 1810. The short FFI during this period probably prevented all conifer regeneration on the site. The period between 1829 and 1845 also had short FFI with the occurrence of four to five fires during this time. The canopy is now closed and few conifers have established in the last 50 years (an established conifer is defined as one greater than 1.5 m tall).

Our data show that whitebark pine frequently survives fires, since we found fire-scarred trees in virtually every stand we sampled. We hypothesize that the stands are likely to burn only when they are very young, when there is sufficient fine fuel in the form of herbaceous understory vegetation, or late in the successional development, when there is sufficient regeneration of subalpine fir and an accumulation of downed and dead woody fuel in the stand. Topography and structure of the adjacent stands may also be important based on limited field observations of areas that did and did not burn in the Yellowstone area fires of 1988.

Table 1—Distribution of fire occurrence by season in the Russell Peak area, Shoshone National Forest, WY, as determined by the method of Dieterich and Swetnam (1984) where the position of the scar within the growth ring is noted

Probability that fire caused scars	Season of fire[1]			Number of fires
	Early	Late	Dormant	
	- - - - - - - *Percent* - - - - - - -			
Highly probable	48	19	33	33
Probable	38	22	40	58

[1]Relative to growing season for whitebark pine.

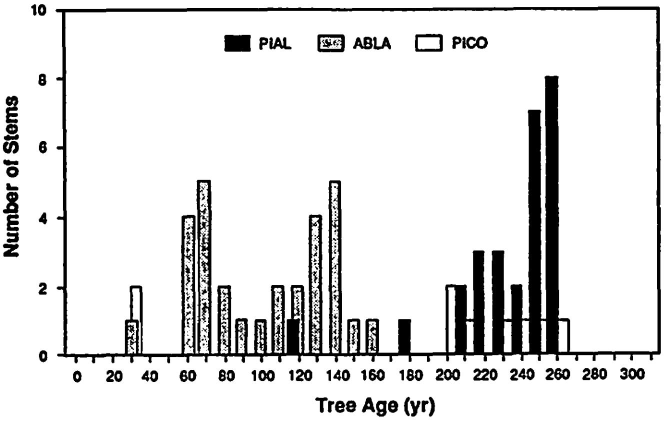


Figure 3—Distribution of whitebark pine (PIAL), subalpine fir (ABLA), and lodgepole pine (PICO) by age in stand number 5 in the Russell Peak area, Shoshone National Forest, WY.

SUMMARY AND CONCLUSIONS

Our data indicate that fire was much more common in the Russell Peak area of the Shoshone National Forest 150 to 300 years ago and had an average FFI of less than 50 years. Few fires have occurred there since 1850, and there is no evidence of any since 1900. Whitebark pine is seral to subalpine fir on most of the area, and the absence of fire has resulted in an increase in the abundance of subalpine fir. Few whitebark pine trees greater than 1.5 m in height were observed in the closed-canopy stands. If the current trend in regeneration continues, whitebark pine will continue to decline in abundance.

Fire may be very important in maintaining healthy, productive populations of whitebark pine in the face of competition from less fire-resistant tree species. In the absence of fire, cone production of whitebark pine may decrease as more shade-tolerant and less fire-resistant trees increase in abundance, thereby competing with or replacing whitebark pine. If this trend continues throughout the Yellowstone region, there will be fewer whitebark pine seeds available for wildlife or for regeneration of new whitebark pine stands.

The likelihood of fire occurrence changes with the development of the forest stand. The probability of fire spread is initially high following high-intensity fires due to the increase in the herbaceous component of the plant community. Although whitebark pine regenerates readily following high-intensity, stand-replacing fires, the trees are not likely to survive subsequent fires that occur while they are still small and easily killed. As the stand develops, the likelihood of fire is reduced because the fine fuels are suppressed by the conifer overstory. During this period the probability of a high-intensity, stand-replacing fire is low. However, low-intensity surface fires may occur. Fire likelihood and severity increase as subalpine fir becomes established in the stand, creating a fire ladder. Thus the more advanced successional stages become susceptible to stand-replacing fires.

ACKNOWLEDGMENTS

We are indebted to the many people who contributed to this research project. In particular we would like to thank Steve and Nathan Arno, who helped collect the fire history cross-sections, and Tom Swetnam, who supervised the tree-ring analysis. Personnel of the Bridger-Teton and Shoshone National Forests and Yellowstone National Park also assisted us.

REFERENCES

Arno, S. F. 1986. Whitebark pine cone crops—a diminishing source of wildlife food. Western Journal of Applied Forestry. 1: 92-94.

Arno, S. F.; Petersen, T. D. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. Res. Pap. INT-301. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 28 p.

Arno, S. F.; Sneck [Davis], K. M. 1977. A method for determining fire history in coniferous forests in the Mountain West. Gen. Tech. Rep. INT-42. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 28 p.

Barrett, S. W. 1981. The role of Indian-caused fires in the ecology of western Montana forests. Missoula, MT: University of Montana. 198 p. Thesis.

Barrett, S. W.; Arno, S. F. 1988. Increment-borer methods for determining fire history in coniferous forests. Gen. Tech. Rep. INT-244. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 15 p.

Craighead, J. J.; Sumner, J. S.; Scaggs, G. B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Monogr. No. 1. Missoula, MT: University of Montana, Wildlife-Wildlands Institute. 84 p.

Dieterich, J. H.; Swetnam, T. W. 1984. Dendrochronology of a fire-scarred ponderosa pine. Forest Science. 30: 238-247.

Drew, L. G. 1975. Tree ring chronologies of western America. V. Washington, Oregon, Idaho, Montana and Wyoming. Chronology Series 1. Tucson, AZ: University of Arizona, Laboratory of Tree-Ring Research. 45 p.

Eggers, D. E. 1986. Management of whitebark pine as potential grizzly bear habitat. In: Proceedings—grizzly bear habitat symposium; 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 170-175.

Fischer, W. C.; Clayton, B. D. 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. Gen. Tech. Rep. INT-141. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 83 p.

Harlow, W. M.; Harrar, E. S. 1969. Textbook of dendrology. New York: McGraw-Hill. 512 p.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Loope, L. L.; Gruell, G. E. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. Quaternary Research. 3: 425-443.

Morgan, P.; Bunting, S. C. 1989. Unpublished data on file at: Forest Resources Department, University of Idaho, Moscow, ID.

Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Pierce, W. G.; Nelson, W. H. 1971. Geologic map of the Beartooth Butte Quadrangle, Park County, Wyoming. Map GQ-935. Washington, DC: U.S. Department of the Interior, Geological Survey.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs. 52: 199-221.

Steele, R.; Cooper, S. V.; Ondov, D. M.; Roberts, D. W.; Pfister, R. D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

Steele, R.; Pfister, R. D.; Ryker, R. A.; Kittams, J. A. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 138 p.

Stokes, M. A.; Smiley, T. L. 1968. Introduction to tree-ring dating. Chicago, IL: University of Chicago Press. 73 p.

Swetnam, T. W.; Thompson, M. A.; Sutherland, E. K. 1985. Using dendrochronology to measure radial growth of defoliated trees. Agric. Handb. 639. Washington, DC: U.S. Department of Agriculture, Forest Service. 39 p.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51: 451-467.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation, and production. American Midland Naturalist. 92: 222-230.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from T. W. Weaver)—You gave data from two stands (one with spruce-fir regeneration and one without). Please argue for and against their occupying the same habitat type.

A.—Argument against being same habitat type:
The existence of a stand for 150 years without the development of a subalpine fir codominant or subdominant layer in the absence of fire or other disturbance is good evidence that the site is not suitable for subalpine fir and is, therefore, probably not an *Abies* habitat type.

Argument for being the same habitat type:
There were a number of mature subalpine fir within the general area, and three within the boundary of the stand. In addition, there were a large number of small subalpine fir (less than 1.5 m in height) distributed throughout the stand, which indicates that the species could exist on the site, although it may require a long time for the species to dominate.

Q. (from Roger Andrascile)—Why couldn't you use recently fallen trees to get fire history rather than damage standing live trees—why use the chainsaw technique?

A.—Dead trees cannot be used unless they can be crossdated with other trees in the sample or with an existing tree-ring chronology to obtain accurate dates. We did use some dead trees in the study. The increment core technique of Barrett and Arno (1988) is a nondestructive method to determine fire history but is not as accurate for determining the occurrence of buried scars or scars that are only a few years apart. For most of our research on whitebark pine (manuscript in preparation) this method was used, but we wanted to check the increment core technique against a more accurate standard. It is also possible to take partial sections from standing live trees without killing the tree, which we did in some cases.

Q. (from Don Despain)—How did you distinguish older bear-feeding scars from fire scars?

A.—Bear scars tend to be longer (some may be 2 m long) and narrower than fire scars, but cause would often be difficult to distinguish on the very old scars we were sampling in this study. This would particularly be a problem with single scars. We felt, however, that multiple scars on the same tree would not likely be caused by bears, since once a portion of the tree was scarred the cambium would be dead and not attractive to bears. Once scarred by bears, trees could be easily reinjured by fire.

Q. (from Wyman Schmidt)—Did the bear stripping of the whitebark pine appear to be related to age, size, stand density, tree vigor, or other site or stand factors?

A.—The bear stripping was not specifically studied, but most stripped trees were greater than 25 cm in diameter and often the largest trees in a stand. It occurred in stands of varying density and topographic position. We do not recall any other relationship of bear stripping to site or stand factors.

INSECTS OF WHITEBARK PINE WITH EMPHASIS ON MOUNTAIN PINE BEETLE

Dale L. Bartos
Kenneth E. Gibson

ABSTRACT

*Few insects that live on whitebark pine (*Pinus albicaulis*) are considered pests or potential pests. Those that inhabit cones can cause reductions in reproduction of the tree by destroying seed crops. Decreases in food for animals ranging from squirrels to grizzly bears may also result.*

*A single insect species, mountain pine beetle (*Dendroctonus ponderosae*) (MPB), may cause serious damage to whitebark pine over much of its range by killing mature trees. Through periodic epidemic outbreaks, the resultant tree killing causes reductions in seed cones and so decreases food supplies for various animals. Excessive mortality of whitebark pine can lead to increases in other tree species, and decreases in whitebark pine, in some future stands.*

A survey of MPB damage in the whitebark pine zone was conducted in Yellowstone National Park, Gallatin National Forest, and Flathead National Forest from 1983 to 1988. Preliminary results show 22 to 44 percent of the whitebark pine had been killed by MPB during the recent past. Losses were strongly related to elevation—decreasing mortality with increasing elevation. Losses were heaviest in the lodgepole pine-whitebark pine ecotone. Implications of such losses are discussed.

INTRODUCTION

Whitebark pine (*Pinus albicaulis* Engelm.) occurs at high elevations in the mountainous west of North America (Arno and Hoff 1989). This is a long-lived tree that grows very slowly on moist to dry sites. Like other trees, the whitebark pine provides habitat for various insect species. Most of these insects do not have serious effects on whitebark pine. An exception is mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins [Coleoptera: Scolytidae]) which occasionally occurs in epidemic proportions. Insects associated with whitebark pine have not been studied in any detail and, therefore, revelant literature is quite sparse.

Seeds from whitebark pine are not only important for regeneration of the trees but are also important as a food source for various animals (grizzly bears to squirrels). Whitebark pine cones can be invaded by cone worms (*Dioryctria* spp. and *Eucosma* spp.) and by cone beetles (*Conophthorus* spp.), but these insects have been virtually unstudied. Other species than those reported in the literature have been observed (Dewey 1989), such as midges and a seed chalcid (*Megastigmus* spp.). Cone and seed insects would probably affect whitebark pine as they do other conifer species, for example, causing years of light cone crops following a heavy cone crop year. More detailed work on cone and seed insects would show their importance to the whitebark pine system.

Foliage insects can cause stress in attacked trees by causing a decline in their growth rate. Aphids (*Essigella gillettei* Hottes) are known to feed on needles; mealybugs (*Puto cupressi* Coleman and *P. pricei* McKenzie) are found on branches and trunks (Arno and Hoff 1989). Arno and Hoff (1989) also state that the lodgepole needletier (*Argyrotaenia tabulana* Freeman), which is very destructive in lodgepole pine stands, can also infest whitebark pine.

Several secondary beetles (*Ips, Pityogenes,* and *Pityophthorus*) are known to attack the boles of whitebark pine. The Monterey pine ips (*Ips mexicanus* Hopkins) and two Pityogenes (*P. carinulatus* LeConte and *P. fossifrons* LeConte) are reported to infest the bole of whitebark pine (Furniss and Carolin 1977). Bright (1968) working in British Columbia described two species of *Pityophthorus* (*P. aquilonius* Bright and *P. collinus* Bright) that are found in whitebark pine.

Mountain pine beetle is the most destructive bark beetle in western North America (Furniss and Carolin 1977) because it can kill apparently healthy trees. This is the one insect that has the most impact on whitebark pines. Between 1911 and 1942 there was widespread destruction of lodgepole pine (*Pinus contorta* Douglas) forests by MPB in Idaho and Montana. These outbreaks were at lower elevations and moved upwards into the whitebark pine zone where "ghostlike forests" were created by the numerous dead snags that resulted (Ciesla and Furniss 1975) in about 1937. A similar situation occurred on the Flathead National Forest (NF) of Montana in the 1970's where epidemics developed in the lodgepole pine forests and then moved into the whitebark pine zone (Arno and Hoff 1989).

There are several instances of whitebark pine being invaded by MPB from epidemic populations that occur in lower elevation lodgepole pine. Baker and others (1971)

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Dale L. Bartos is Operations Research Analyst, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Logan, UT 84321; Kenneth E. Gibson is Entomologist, Northern Region, Forest Service, U.S. Department of Agriculture, Missoula, MT 59807.

conducted a study in western Wyoming to see if this scenario held true. In situations where both lodgepole and whitebark pine existed together, MPB killed proportionally more lodgepole than whitebark pine. In part, Baker and others (1971) attributed this to phloem thickness with the larger diameter trees (those with thicker phloem) being taken. Another part of their study described how cooler temperatures at the higher elevations caused little mortality by MPB in either lodgepole or whitebark pine. In part, the colder temperatures at the higher elevations reduced MPB survival and therefore lessened the number of trees killed.

Crossover of MPB from one host species to another has been detailed by Amman (1982). It is generally believed that insects invade species similar to the ones in which they developed (Allee and others 1949). However, both Amman (1982) and Wood (1963) stated that this rule probably holds under endemic (low population levels) situations only; during "full blown" epidemics MPB will select any acceptable host. Thus, we observe the movement of MPB from lodgepole into whitebark pine in the ecotonal zone with further movement into pure whitebark pine stands when epidemic conditions exist throughout vast lodgepole pine stands at lower elevations (Parker 1973).

As just described, a variety of insects occur in whitebark pine; however, none have the impact that MPB does. Therefore, it is the purpose of this paper to detail the effect of MPB on whitebark pine with particular emphasis on the northern Rocky Mountain region. Recent past epidemics and current work will be used to complete the picture of the effect of MPB on the whitebark pine ecosystem.

RECENT HISTORY

To better understand the interrelationship of MPB and whitebark pine we can look at the infested acres in the Northern Region of the USDA Forest Service during the past 10 years. Particular interest will be placed on the Gallatin and Flathead National Forests and surrounding areas.

Infested areas were determined by using aerial sketch mapping. Usually, this method does not record low level (endemic) populations of MPB. Mountain pine beetle activity peaked in the Northern Region during 1981. The following acreage was reported as infested lodgepole pine (predominantly lodgepole pine but other species did occur): Gallatin National Forest, 455,000 acres; Beaverhead National Forest, 119,000 acres; Flathead National Forest, 209,000 acres; and Yellowstone National Park, 965,000 acres.

Our reference to whitebark pine stands means that whitebark pine does occur but is not necessarily the dominant species. There were 32,000 acres of whitebark pine infested with MPB in 1983 in the Gallatin National Forest. This acreage has declined precipitously with only 500 acres infested in 1986 and none since then. The MPB epidemic has probably "run its course" in this area.

Similar trends were observed on other areas adjacent to the Gallatin National Forest. At the turn of the decade, there were about 10,000 acres of MPB-infested whitebark pine reported for the Beaverhead National Forest; during the past several years no additional infested acreage was reported. A similar trend was observed on the Custer National Forest but of a lesser magnitude. In 1981, there were 1,600 acres infested with only 150 acres by 1986. Again, none have been reported during the last 2 years.

Yellowstone National Park is an area of special concern because of recent fires and the destruction of endangered grizzly bear habitat. Similar trends were observed there with 34,000 acres being infested in 1983, however, no acreage has been reported the last few years. There are small populations of MPB, however, in some limber pine (*Pinus flexilis* James) stands near Mammoth.

In 1980, MPB infestation on the Flathead National Forest was 96,500 acres of whitebark pine. Infestations of whitebark pine dropped to 1,500 acres in 1986 and to only 100 acres last year. There has been no new acreage of infested whitebark pine observed in Glacier National Park for the past 3 years, however, earlier in 1980 there were 15,000 acres reported for whitebark pine and 292,000 acres for lodgepole pine.

AREA DESCRIPTIONS

Between 1983 and 1988, on-the-ground surveys were conducted to determine the extent of MPB in whitebark pine and surrounding tree types. These determinations were made on three areas: Gallatin National Forest, Flathead National Forest, and Yellowstone National Park.

Gallatin National Forest

In 1983, 211 data collection points were established at selected sites on the Gallatin National Forest. Fifty-six distinct stands were selected within three elevational zones (5,400-8,500 ft). These collection points were located on the Hebgen Lake, Bozeman, and Gardiner Ranger Districts (fig. 1). Eleven stands were found at lower elevations, in which Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) dominated; 25 stands were found at midelevations, in which lodgepole pine dominated, and 20 stands were found at high elevations, in which whitebark pine dominated. Even in the low-elevation stands, lodgepole pine was a major component. All stands were selected where whitebark pine occurred and where MPB was active or had been active in the recent past.

Yellowstone National Park

In 1987, 30 data collection points were established within the whitebark pine zone in Yellowstone National Park. The stands selected were mixed lodgepole and whitebark pine and occurred at about 8,300 ft elevation. All collection points were in the southwestern portion of Yellowstone National Park just west of Yellowstone Lake. Due to lack of ground access into high-elevation whitebark pine stands and the observation that most past beetle activity was confined to lodgepole pine stands, data were not collected from these high-elevation stands.

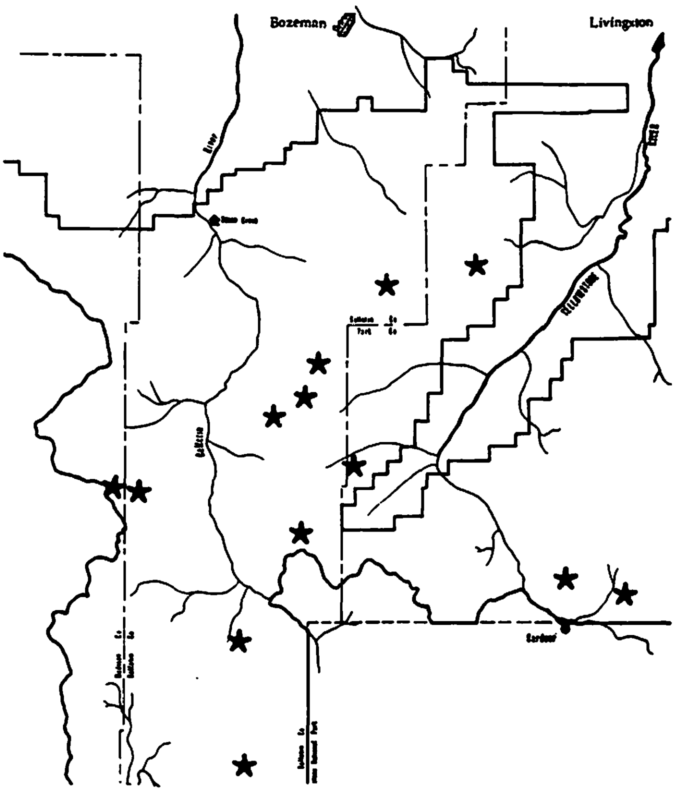


Figure 1—Map of Gallatin National Forest in southern Montana showing stand locations where sampling for MPB infestations was conducted during 1983.

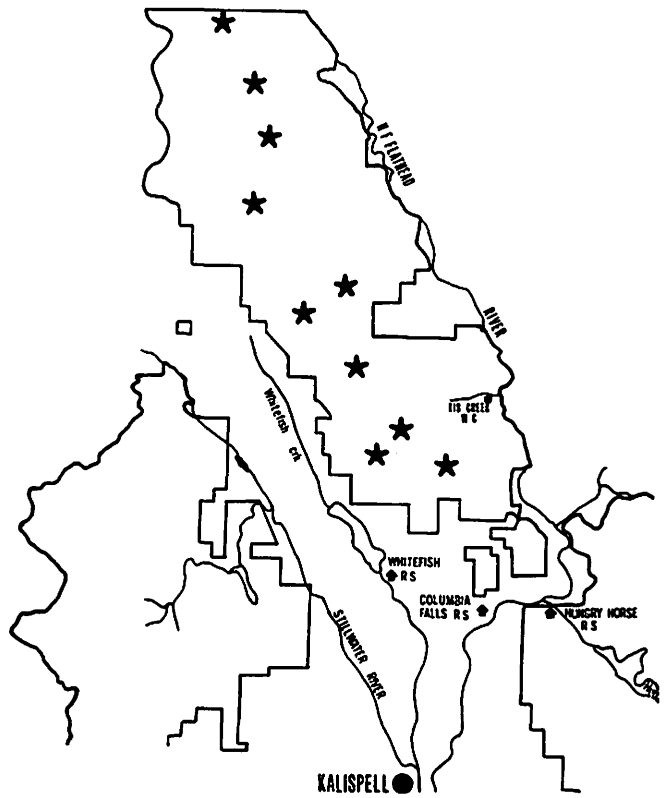


Figure 2—Map of Flathead National Forest in northern Montana showing stand locations where sampling for MPB infestations was conducted during 1988.

Flathead National Forest

To obtain data from a different geographical area, whitebark pine stands affected by MPB on the Flathead National Forest were sampled in 1988. Selected stands ranged in elevation from 5,500 to 6,600 ft, and were located exclusively on the Glacier View Ranger District in the Whitefish Mountain Range (fig. 2). Ten stands were visited—the northernmost was about 6 air miles south of the Canada-United States border and the southernmost was approximately 5 air miles north of Whitefish, MT. Number of plots per stand varied; a total of 80 plots was sampled. Stands were generally of mixed species; subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) dominated, and all fit the criteria for the subalpine fir habitat type.

METHODS

Number and spatial arrangement of the plots established in each area were determined by the size and shape of the stand visited. Whenever possible, a minimum of 10 plots was located in each stand. These plots were generally located at 5-chain intervals along a compass line coinciding with the long axis of the stand. Occasionally, plots were established on parallel lines 5 chains apart. The initial plot in each series was located randomly, but it was at least 2 chains within the stand's boundary.

On each plot, various stand and site data were collected to relate ecological factors to pest-caused damage. At each plot center, a variable radius plot (BAF 10) was established using a Spiegel Relaskop R. Each "in" tree, equal to or greater than 5 inches d.b.h. (diameter breast height) was recorded by species and d.b.h. In addition, each tree was assigned one of the following "damage" codes:

0 = undamaged, healthy tree
1 = unknown mortality
2 = current year MPB-caused mortality
3 = previous year MPB-caused mortality
4 = older MPB-caused mortality
5 = unsuccessful MPB attack
6 = current year MPB strip attack
7 = older MPB strip attack
8 = current secondary beetle-caused mortality
9 = older secondary beetle-caused mortality
10 = secondary beetle strip attack
49 = spike top usually white pine blister rust
50 = other damage

Heights and ages were measured on the first two dominant or codominant trees of each species encountered on the plot. The observer was at the center of the plot and turned in a clockwise direction starting from the direction of travel; trees were recorded as they were encountered.

The center of the variable-radius plot also served as the center for a 1/300-acre (6.8-ft diameter) fixed-radius plot on which were collected regeneration data. Only the four "best" trees (greater than 6 inches tall and less than 5 inches d.b.h.) were recorded.

In addition to the stand data, the following site data were recorded for each plot: elevation, slope, and aspect. At each plot, a "downed fuel inventory" was conducted to assess the amount and size of materials contributing to the fuel load on the site. Observations regarding presence and abundance of various wildlife species were noted. Evidence of big game (trails, droppings, shed antlers) was recorded by species. In addition, habitats (such as snags or caves), sightings, or other indications of non-game mammals and birds were tallied. Sampling was done to determine the amount (on a dry weight basis) of understory vegetation as a critical component of the system.

RESULTS AND DISCUSSION

The 1988 distribution map of MPB activity in the Northern Region (fig. 3) shows the greatest intensity of tree killing by MPB to occur in the northwestern part of Montana near the Canadian border. Mountain pine beetle activity is strongest in the lodgepole pine type with very little recorded in the ponderosa pine, western white pine, or whitebark pine type (fig. 4). One might say that there is nothing to worry about concerning the whitebark pine; however, Amman (1982), Parker (1973), and Wood (1963) stated there is strong evidence that any whitebark pine stands that occur above lodgepole pine stands could definitely be in danger of attack or devastation. Even if the whitebark pine stands are not in close association with lodgepole pine they are still at risk because infestations can occur during warmer than average years in the absence of lodgepole pine infestations (Baker and others 1971).

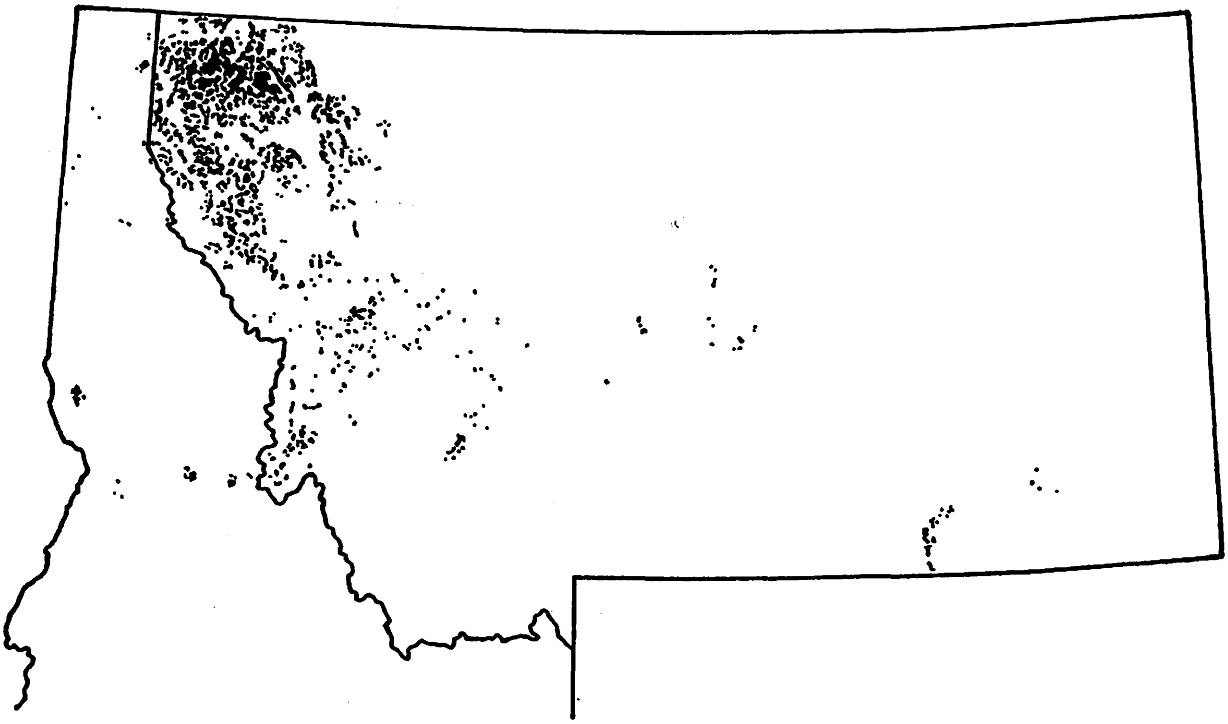


Figure 3—A map of the Northern Region showing the location of MPB infestations for 1988.

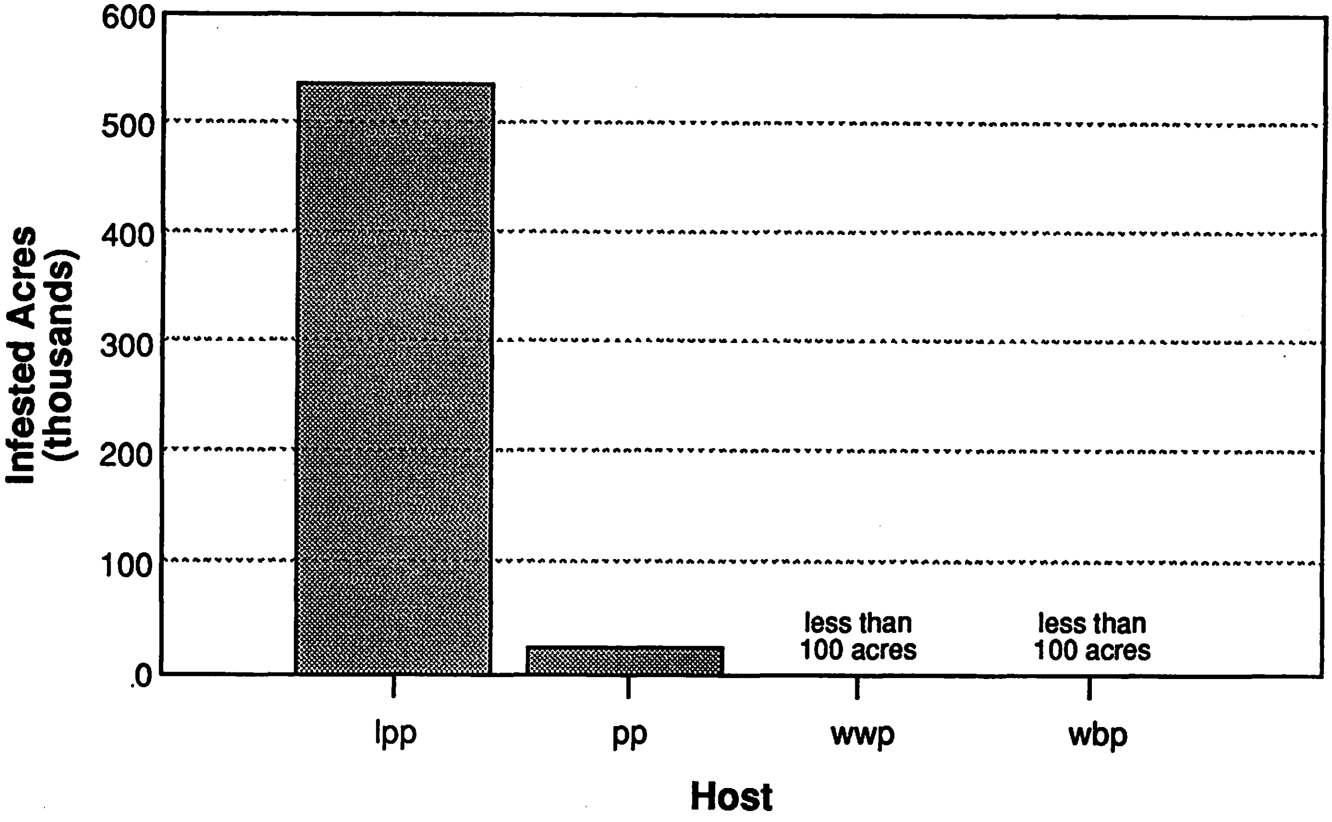


Figure 4—Acreage of MPB infestations in the Northern Region for 1988 for four host species: lodgepole (lpp), ponderosa (pp), western white (wwp), and whitebark pine (wbp).

Gallatin National Forest

Surveys during 1983 found MPB and unknown agents were the major killing agents of both lodgepole pine and whitebark pine across all 56 stands sampled (table 1). Mortality of lodgepole pine varied between 10 and 62 percent for the various size classes considered. Highest mortality was observed in the largest trees, 12 inches and larger d.b.h., while the least mortality was seen in the 5- to 9-inch d.b.h. category.

Similar trends were observed in the whitebark pine on the Gallatin National Forest (table 1). Where whitebark pine dominated, the most mortality occurred in the largest trees—23 percent of the 12 inch and larger. Even at the lowest elevations sampled, where Douglas-fir dominated, there was 60 percent mortality, caused by secondary beetles, of the 5- to 9-inch d.b.h. whitebark pine trees.

It should be noted that less than 10 percent of the MPB attacks at the time of the survey were current which shows most MPB activity occurred prior to the sample year and supports the fact that MPB activity peaked on the Gallatin National Forest in 1981. This information further substantiates what Arno and Hoff (1989), Ciesla and Furniss (1975), and Parker (1973) observed of outbreaks occurring in the lower lodgepole pine zone and moving up into the whitebark pine zone.

With almost a quarter of the dominant trees being killed in the whitebark pine zone, what effect will this mortality have on future forests? There will definitely be a reduction in the cone crop for the immediate future because the most mature trees were killed. It is safe to say that whitebark pine reproduction might suffer some and that one food source (pine nuts) for animals will be diminished. There may be a shift in the ecotonal zone between lodgepole pine and whitebark pine as a result of this mortality. Will the whitebark pine zone expand into the lower lodgepole pine area or vice versa? It is conceivable that the remaining whitebark pine may become more vigorous because of the "natural thinning" by MPB of both whitebark and lodgepole pine.

Yellowstone National Park

In our survey of Yellowstone National Park, MPB-caused mortality was not observed for the sample year or previous years. Accessibility to other high-elevation whitebark pine stands was not possible, therefore, the survey was limited. Furthermore, it was observed that most of the past beetle activity was confined to lower elevation lodgepole pine stands. Almost a million acres of lodgepole pine was infested in Yellowstone National Park in 1981. This was one of the main contributing factors to the tremendous fuel loads that existed in the National Park for the fire season of 1988.

Table 1—Summary of whitebark pine and lodgepole pine mortality due to mountain pine beetle for Gallatin National Forest for 1983

Elevational zones	No. of stands surveyed	Dominant tree species	D.b.h. classes		
			5-8.9 inch	9-11.9 inch	12 + inch
Killing agent/species[1]			*Percent mortality*		
Low elevation	11	Douglas-fir			
MPB/LPP			14.5	38.4	61.7
SEC/LPP			0.0	2.2	0.6
UNK/LPP			16.0	3.8	0.0
Total LPP			30.5	44.4	62.3
SEC/WBP			59.5	0.0	0.0
Mid elevation	25	Lodgepole pine			
MPB/LPP			16.3	38.9	53.2
SEC/LPP			6.1	2.1	1.6
UNK/LPP			2.2	0.6	1.5
Total LPP			24.6	41.6	56.3
High elevation	20	Whitebark pine			
MPB/LPP			0.0	5.5	39.3
SEC/LPP			5.6	4.3	5.0
UNK/LPP			6.9	0.0	0.0
Total LPP			12.5	9.8	44.3
MPB/WBP			0.8	5.3	19.1
SEC/WBP			1.4	5.0	2.2
UNK/WBP			0.7	1.7	2.0
Total WBP			2.9	12.0	23.3

[1] MPB = mountain pine beetle
SEC = secondary beetles
UNK = unknown agent
LPP = lodgepole pine
WBP = whitebark pine.

Flathead National Park

Stands were sampled in northern Montana to give a more complete picture of the effects of MPB on whitebark pine in the Northern Region. A summary of 80 plots that were sampled (table 2) shows a range of live whitebark pine 5-inch d.b.h. and larger varied between 1 tree/acre to 87 trees/acre. An average of 27 percent of the stand was composed of live whitebark pine and this varied between 1 and 63 percent for the 10 stands sampled. Percent mortality for the whitebark pine was between 14 and 97 percent with most of the kill occurring prior to 1987. Only a little mortality was recorded for 1987 and hardly any for 1988. This helps validate what was observed on the Gallatin National Forest and in Yellowstone National Park.

Effects of MPB on whitebark pine was directly connected to the peak infestation for the Region. Most of the mortality seen occurred between 1981 and 1987. If MPB infestations continue to decline, the remaining whitebark pine in the Northern Region will not likely succumb to MPB, at least in the near future.

Miscellaneous Observations

Total understory vegetation (current growth of shrubs, forbs, grasses, and grasslike species) was sampled to determine, in part, fine fuels that exist in the stands. On the Gallatin National Forest understory vegetation was sparse with values ranging from 166 to 1,217 lb/acre. Farther north on the Flathead National Forest, understory growth was considerably more with values of 1,090 to 1,748 lb/acre. Understory values of 166 lb/acre imply impoverished sites; and 1,748 lb/acre imply moderately stocked understory.

In the 10 areas sampled on the Flathead National Forest, most regeneration observed was subalpine fir. Next in occurrence was Engelmann spruce. On only four of the 10 areas sampled was whitebark pine regeneration noted, and then it was always in the minority. We did not observe whether this was due to lack of seeds or merely a successional pattern typical of subalpine fir habitat types.

Table 2—Summary of whitebark pine (WBP) mortality due to mountain pine beetle (MPB) for Flathead National Forest for 1988

Stand number	Green WBP 5 inch+	1988 MPB attacks	1987 MPB attacks	Older MPB attacks	Stand green WBP	WBP mortality	Secondary attacks	Blister rust damage
	Number/acre				*Percent*		*Number/acre*	
1	25.6	0.0	0.0	8.0	63	24	0.0	0.3
2	38.8	0.0	0.0	15.6	52	29	0.0	4.8
3	48.3	0.0	32.3	136.8	51	78	34.9	9.1
4	9.6	1.2	0.0	0.4	13	14	0.0	0.0
5	86.9	0.0	14.2	32.7	44	35	8.1	0.0
6	29.0	0.0	35.0	8.3	13	60	0.0	20.8
7	20.5	0.0	19.9	22.5	11	67	0.0	0.0
8	1.2	0.0	9.9	29.3	1	97	0.0	0.0
9	9.8	0.0	2.3	28.1	6	94	0.0	0.0
10	6.1	0.0	0.0	56.0	4	90	17.0	0.0
Average	27.3	0.1	13.4	36.2	27	65	6.5	4.7

CONCLUSIONS

In the Northern Region, whitebark pine was killed as a result of the epidemic MPB populations that peaked in this area during the early 1980's (an exception was Flathead National Forest, which peaked in 1986). Most information we have suggests that whitebark pine stands were infested by MPB populations originating in lower elevation lodgepole pine stands. This conclusion is substantiated by the literature. However, MPB can, and sometimes does, kill whitebark pine in the absence of adjacent infestations in lower elevation lodgepole pine stands.

For the most part, if we want to reduce mortality in whitebark pine stands it appears that we need to suppress MPB populations in lodgepole pine stands that occur at lower elevations. Thinning of lodgepole pine stands on the Kootenai, Lolo, and Flathead National Forests shows basal area reductions can significantly reduce losses to MPB (McGregor and others 1987). Such population reductions by stand manipulation should reduce the likelihood of MPB outbreaks in the higher elevation whitebark pine stands.

We suggest the following as ways of better understanding the interrelationship of pests and whitebark pine:

1. Monitor the effects of insect pests (not just MPB) in whitebark pine stands in other geographical locations in the Region.
2. Obtain more accurate information on the impacts of cone and seed pests on whitebark pine.
3. Gain a better understanding of the association between MPB and secondary bark beetles in whitebark pine stands.

REFERENCES

Amman, G. D. 1982. Characteristics of mountain pine beetles reared in four pine hosts. Environmental Entomology. 11(3): 590-593.

Allee, W. C.; Emerson, A. E.; Park, O.; Park, T.; Schmidt, K. P. 1949. Principles of animal ecology. Philadelphia: W. B. Saunders Co. 837 p.

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Baker, B. H.; Amman, G. D.; Trostle, G. C. 1971. Does the mountain pine beetle change hosts in mixed lodgepole and whitebark pine stands? Res. Note INT-151. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 7 p.

Bright, D. E., Jr. 1968. Three new species of *Pityophthorus* from Canada (Coleoptera: Scolytidae). Canadian Entomologist. 100: 604-608.

Ciesla, W. M.; Furniss, M. M. 1975. Idaho's haunted forests. American Forests. 81(8): 32-35.

Dewey, Jerald E. 1989. [Personal communications]. March 27. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region.

Furniss, R. L.; Carolin, V. M. 1977. Western forest insects. Misc. Publ. 1339. Washington, DC: U.S. Department of Agriculture, Forest Service. 654 p.

McGregor, M. D.; Amman, G. D.; Schmitz, R. F.; Oakes, R. D. 1987. Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. Canadian Journal of Forest Research. 17: 1234-1239.

Parker, D. L. 1973. Trends of mountain pine beetle outbreaks in mixed stands of preferred hosts. Insect and Disease Prevention and Control Office Report. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region. 8 p.

Wood, S. L. 1963. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Great Basin Naturalist. 23: 1-117.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from David Charlet)—Is work being done on improving rearing techniques of predatory wasps for introduction as a means of biological control?

A.—The only parasitic wasp of importance affecting MPB populations is the Braconid, *Coeloides brunneri* Viereck. It may exert a small amount of control on endemic beetle populations, however, at epidemic levels, it is probably of little consequence. Artificial rearing of this wasp has not been successful. To our knowledge, no work is currently being done in that area. Efforts are better spent trying to manipulate the host rather than the pest populations.

Q. (from Ron Lanner)—How much is known about the effects of white pine weevil on *Pinus albicaulis*?

A.—In our experience, the only host of the white pine weevil (*Pissodes strobi* Peck) in the Intermountain West is Engelmann spruce. Lodgepole pine is affected by a closely related species, *P. terminalis* Hopping. We have never observed, nor seen recorded in the literature, *P. terminalis* infesting whitebark pine.

Q. (from Jim Jacobs)—(a) Is whitebark pine a preferred host for beetles or do they choose it when all else is consumed, and is whitebark pine susceptible to blue stain fungus? (b) What percent of seeds are consumed by worms and do you think nutcrackers can recognize them?

A.—(a) Whitebark pine is not the *most* preferred host of MPB, but it will readily infest it, as it does virtually any pine species within its range. In order of preference (as judged by occurrence of damage caused), the beetles' choice of host is probably lodgepole pine, ponderosa pine, western white pine, whitebark/limber pine, and ornamental (exotic) pines. This scenario may be only applicable in the Intermountain West; in the Sierra Nevada, this list may vary somewhat. Yes, whitebark pine is susceptible to blue stain fungi. (b) We have not surveyed cone crops in whitebark pine stands nearly enough to estimate what proportion of the seeds may be affected by coneworms, cone beetles, midges, or seed chalcids. All, however, have been recorded as affecting whitebark pine seeds. This is an area where work is sorely needed. We would not hazard a guess as to whether or not nutcrackers can recognize infested seeds.

Q. (from Anonymous)—How much of the whitebark pine mortality from MPB occurs in endemic situations versus epidemic? (Also) can beetles overwinter in whitebark pine stands? What effect does tree vigor/phloem thickness have on susceptibility to beetle attack?

A.—We have little information on endemic MPB populations in whitebark pine stands. Beetles do kill some older, weaker individuals in endemic situations, but it is likely part of the "background" or naturally occurring mortality. Yes, MPB can overwinter in whitebark pine stands. Tree vigor—as exhibited by young healthy trees—is important in protecting them from endemic beetle populations. It is of less importance in full-scale epidemics. Also, phloem thickness is critical to the beetle as it is the food of the developing larvae. Trees with phloem too thin to support developing broods are seldom attacked.

DISEASES OF WHITEBARK PINE WITH SPECIAL EMPHASIS ON WHITE PINE BLISTER RUST

Ray Hoff
Susan Hagle

ABSTRACT

Whitebark pine (Pinus albicaulis) *has few endemic diseases that do much harm. White pine blister rust* (Cronartium ribicola *J. C. Fisch. ex Rabenh.), an exotic disease brought here from Europe, is the most damaging disease. It is epidemic over most of the range of whitebark pine.*

There have been 23 diseases reported for whitebark pine, including stem and branch cankers, needle casts, seed and cone diseases, stem and root decays, and dwarf mistletoes. Significant damages from most diseases have been observed only in localized areas. White pine blister rust is the only disease that is widespread and damaging over most of the range of whitebark pine, with the exception of high-dry areas such as in Yellowstone National Park.

Pruning and excising cankers are good management options for saving trees infected by white pine blister rust, but only on moderately hazardous sites. On high-hazard sites, the only option is to utilize resistance. Resistance is common in whitebark pine. Several methods for using resistance to restock decimated areas are presented.

INTRODUCTION

Whitebark pine (*Pinus albicaulis* Engelm.) grows over a large geographic area, but within this area it is restricted to a fairly narrow ecological zone (Arno and Hoff 1989). However, forests adjacent to whitebark pine habitats vary widely. On the coast, adjacent forests are wet and warm; in the Rocky Mountains they are dry and cold. Consequently, whitebark pine is subjected to many different pest problems. The rate of infection by white pine blister rust appears to depend on the amount of inoculum produced in adjacent forests. If those forests are not conducive to the disease, then there is little infection. Some pathogens, such as the canker fungus *Lachnellula pini* and the foliar fungi *Bifusella saccata* or *Herpotrichia coulteri*, prefer high-elevation sites on which whitebark pine grows.

Nonetheless, except for local epidemics that occur from time to time, whitebark pine is relatively free of diseases. The only widespread and serious disease is white pine blister rust (caused by *Cronartium ribicola* J. C. Fisch. ex Rabenh.). The disease was introduced to western North America in 1910.

The purpose of this paper is to review both known and potential diseases of whitebark pine, with major emphasis placed on white pine blister rust, and offer recommendations for management of whitebark pine that would aid its survival in rust-decimated stands.

NONRUST DISEASES OF WHITEBARK PINE

Other than white pine blister rust, the most damaging pathogen is probably limber pine dwarf mistletoe, (*Arceuthobium cyanocarpum* Coulter & A. Nels.). Numerous diseases have been reported afflicting whitebark pine (Hagle and others 1987; Hepting 1971; Hiratsuka and Funk 1976; Smith 1978). Some, particularly old-growth diseases such as heartrots or butt rots, are likely to be less important in managed stands. Others, like annosus root rot, may become more damaging in managed stands. Seed and cone pathogens such as *Siroccocus* blight, may become important if artificial regeneration is used. Both pathogens known to cause damage and those considered potentially damaging to whitebark pine are presented in table 1.

STEM AND BRANCH CANKERS

Gremmeniella abietina (*Gremmeniella abietina* (Lagerberg) Morelet =*Scleroderris lagerbergii* Gremmen =*Crumenula pinea* (Karst.) Ferd.& Jorg.; anamorph =*Brunchorstia pinea* (Karst.) Hoehn.) has aroused a great deal of interest since its discovery in Ontario, Canada, and the northeastern United States. This fungus was found to cause serious damage to pine plantations in those areas. Mortality rates exceeding 50 percent were measured in many young pine plantations (Skilling and Cordell 1966). The fungus had long been known to cause similar damage to plantations in Europe.

Three strains of the fungus are now known to occur in North America (Skilling and others 1984). The one referred to as the "North American strain" has been present at least since the early 1950's. This fungus has a

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Raymond Hoff is Principal Plant Geneticist and Project Leader, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Moscow, ID 83843; Susan Hagle is Pathologist, Timber, Cooperative Forestry, and Pest Management, Northern Region, Forest Service, U.S. Department of Agriculture, Missoula, MT 59807.

Table 1—Pathogens of whitebark pine

Pathogen	Disease or other name
Stem and branch cankers	
Cronartium ribicola	White pine blister rust
Gremmeniella abietina	*Scleroderris lagerbergii*
Lachnellula pini	*Dasyscypha pini*
L. agassizii	
L. arida	
L. flavovirens	Branch dieback
Atropellis piniphila	
Needlecasts and blights	
Bifusella saccata	
Lophodermella arcuata	
Bifusella linearis	
Lophodermium nitens	
Lophodermium pinastri	
Herpotrichia coulteri	Brown felt blight
Seed and cone diseases	
Sirococcus strobilinus	*Sirococcus* blight
Calocypha fulgens[1]	Seed or cold fungus
Stem and root decays	
Perenniporia subacida	Feather root rot
Phaeolus schweinitzii	Root and butt rot
Heterobasidion annosum	*Annosus* root rot
Armillaria ostoyae	*Armillaria* root rot
Dwarf mistletoe	
Arceuthobium cyanocarpum	Limber pine dwarf mistletoe
A. tsugense	Hemlock dwarf mistletoe
A. americanum	Lodgepole pine dwarf mistletoe
A. laricis	Larch dwarf mistletoe

[1] Not reported infecting whitebark pine but high potential for damage expected, based on ecology.

relatively narrow host range, infecting only the genus *Pinus*. Cankers caused by this strain are generally restricted to the lower branches of a tree and are usually damaging only to small trees.

The fungus referred to as the "European strain" appears to have greater potential for damage. It has been recognized as a distinct strain in the northeastern United States since the early 1970's. It has a broad host range including *Pinus*, *Picea*, *Abies*, *Larix*, *Tsuga*, and *Pseudotsuga*. Cankers occur at all heights in trees, on both stems and branches. Infection can take place at any age.

A third strain has been described that has characteristics intermediate between the North American and the European. The relationship between the North American and European strains of *G. abietina* is not understood, but it appears that they have been separate strains for a considerable time, based upon the great differences in ecology.

One collection of *G. abietina* on whitebark pine has been reported. This collection was made at Apex Mountain near Penticton, BC, in 1968. Hiratsuka and Funk (1976) speculated that the fungus collected on whitebark pine was an endemic form of the pathogen with little potential for serious damage.

Because *G. abietina* is known to have considerable potential for damage and has the ability to infect whitebark pine, it should be considered a potentially damaging parasite. Care should be taken to avoid moving the European or intermediate strains of the fungus into whitebark pine habitats. With the current interest in active management of whitebark pine, there is potential for infection of nursery-grown seedlings possibly leading to transport of the pathogen into natural whitebark pine stands.

Lachnellula pini (Brunch.) Dennis = *Dasycypha pini* (Brunch.) Hahn & Ayers has a circumpolar distribution at high elevations and northern latitudes. It causes a resinous canker of whitebark pine that has been confused with white pine blister rust in the Pacific Northwest. Stillinger (1929) surveyed western white pine stands in the Inland Empire and found that those most heavily infected by *L. pini* occur at relatively high elevations—4,500 to 6,000 ft.

Hahn and Ayers (1934) recorded three collections of *L. pini* on whitebark pine in British Columbia. These were in Mt. Revelstoke National Park, 4,000 to 5,000 ft elevation; Flat Creek, east of Revelstoke at 6,000 to 7,500 ft elevation; and D'Arcy, 3 miles west at 6,000 ft elevation. These observations were consistent with results of growth studies in which they found optimal *in vitro* growth of *L. pini* occurred at temperatures between 38 and 42 °F. They concluded that "we may be dealing with a parasite peculiarly specialized as regards the necessary environment for its existence, and for this reason limited in its present distribution."

Lachnellula pini is not observed to grow beyond the canker after death of the branch or stem. Fruiting is localized in the immediate area of the canker. It is not, however, an obligate parasite because abundant fruiting continues even after the branch or stem has died.

Stillinger (1929) reported high levels of damage to western white pine stands caused by *L. pini* cankers. Whitebark pine was not included in his survey, but whitebark pine may be similarly affected on high-elevation sites in the Inland Empire.

Three other species of *Lachnellula* are known to be locally damaging to whitebark pine stands. *Lachnellula agassizii* (Ber. & Curt.) Dennis is parasitic, causing cankers on branches and stems (Smerlis 1973). The anamorph of this species, *Naemospora*, is observed fruiting at canker margins along with *L. agassizii*. *Lachnellula arida* (Phill.) Dennis is also a parasite that causes cankers on branches and stems (Funk 1981). *Lachnellula flavovirens* (Bres.) Dennis is considered to be a facultative parasite that causes cankers and dieback of branches (Frajo-Apor 1976; Smerlis 1973).

Atropellis piniphila (Weir) Lohman & Cash was described by Lohman and Cash (1940) as causing a canker on several pine species including whitebark pine. This fungus is best known from lodgepole pine on which it causes extensive damage in the northern Rocky Mountains of the United States and Canada (Hopkins 1985; Lightle and Thompson 1973). Black radial staining occurs in the wood adjacent to cankers, and the bark external to cankers adheres tightly to the stem thus creating problems for pulping. Mortality is a secondary concern, although mortality rates can be high in some severely infected stands. At greatest risk for mortality are young trees growing on sites with histories of *Atropellis* damage.

NEEDLECASTS AND BLIGHTS

Bifusella saccata (Darker) Darker has been reported on whitebark pine and limber pine (*P. flexilis*) (Staley 1964). It is found at elevations above 9,000 ft on whitebark pine in the southern Sierra Nevada (Bega 1979). It is reported as rarely occurring on whitebark pine in British Columbia, where it is observed to fruit on dead tips of green needles (Funk 1985).

Lophodermella arcuata (Darker) Darker was reported to cause a needlecast of whitebark pine in British Columbia (Hunt and Ziller 1978). Severe defoliation of a sugar pine (*P. lambertiana* Dougl.) plantation greatly reduced terminal growth (Burleigh and others 1982). Within a heavily infected plantation, individual trees that were apparently resistant were found. The disease was damaging in occasional, isolated trees in limber pine stands in Colorado (Staley 1964).

Bifusella linearis (Peck) Hoehn. is reported to cause a common needlecast disease of whitebark pine (Bega 1979; Funk 1985; Hunt 1981). Two- to 3-year-old needles are killed and cast. Because the fungus is restricted to older foliage, it is not considered to cause a serious disease.

Lophodermium nitens Darker is a common needlecast-causing fungus on whitebark pine (Darker 1932; Funk 1985; Hunt 1981). Hunt (1981) considered the fungus to be a weak pathogen, attacking only the older foliage.

Lophodermium pinastri (S. ex H.) Chev. is also found on whitebark pine needles, but is probably present as a saprophyte.

Brown felt blight caused by *Herpotrichia coulteri* (Peck) Bose kills snow-covered foliage and causes branch dieback or, in the case of seedlings, death. This disease is widespread and common owing to the snowpack found in whitebark pine habitats.

SEED AND CONE DISEASES

Siroccocus strobilinus Preuss causes a seed-borne disease of many conifers including whitebark pine. The disease damages seedlings in nurseries and in natural stands. Losses in nurseries are due both to seedling mortality and to culling for deformity. The fungus is thought to infect fully formed seed, but the mechanism is not known (Sutherland 1987b). Nursery production of whitebark pine is likely to be accompanied by some level of damage from *Siroccocus* blight. The frequency of occurrence of this disease in natural whitebark pine regeneration is not known.

Calocypha fulgens (Pers.) Boud. (anamorph = *Geniculodendron pyriforme* Salt) referred to as the seed or cold fungus, causes pre-emergence seed losses in numerous conifer species including eastern white pine (*P. strobus* L.). This seed-borne fungus spreads from diseased to healthy seeds during cold periods. The mycelium of the fungus grows through forest duff. Cones that contact the duff are subject to infection. Thus cones on the ground or in squirrel caches or, perhaps in the case of whitebark pine, seeds cached by nutcrackers, may be infected.

Sutherland (1987a) reported losses of 25 percent of stored seed of spruces, Douglas-fir (*Pseudotsuga menziesii* Mirb.), and grand fir (*Abies grandis* [Dougl.] Lindl.) in British Columbia due to this fungus. In Ontario, bareroot nurseries' seed germination of numerous conifer species was reduced by as much as 98 percent. Cool soil conditions were most commonly associated with high losses to *C. fulgens*. Rates of isolation of the fungus from spruce seedlots in Washington and Oregon were sufficiently high for Sutherland to conclude that the disease has potential to impede natural regeneration of Engelmann spruce (*Picea engelmannii* [Parry] Engelmann) in certain areas of the western United States (Sutherland 1987a).

Fruiting bodies of this fungus are widespread and common in the early spring in the Rocky Mountains and Pacific Northwest (Tylutki 1979). The habitat requirements of *C. fulgens* and its potential for damage in both natural stands and nurseries may have serious implications for whitebark pine regeneration.

STEM AND ROOT DECAYS

Perenniporia subacida (Pk.) Donk and *Phaeolus schweinitzii* (Fr.) Pat. have been locally damaging in old stands of whitebark pine. *Phellinus pini* (Thore:Fr.) Pilat. causes a heartrot of whitebark pine that is also common in some locations. All these pathogens are likely to be significant only in old stands. Regeneration of whitebark pine stands is not likely to lead to significant carryover or intensification of damage from these pathogens.

Heterobasidion annosum (Fr.) Bref. = *Fomes annosus* = *Fomitopsis annosa*; anamorph = *Spiniger meineckellus* (A. J. Olson) Stalpers is another matter. This fungus is one of the most aggressive root pathogens; it responds to stand harvest by infecting cut stumps, presenting even greater problems with each succeeding generation of susceptible hosts. Numerous environmental factors play a role in determining whether *H. annosum* will increase with timber harvest and whether damage from this pathogen will continue over the life of the stand. The frequency of root infection in the existing stand may greatly influence the potential for damage in a succeeding rotation. *Heterobasidion annosum* is a common pathogen of subalpine fir (James 1979). It causes direct mortality of infected trees or, perhaps more commonly, it rots the tap root and develops into a butt rot. In either case, infected roots of subalpine fir can serve as a food and inoculum base for infection of whitebark pine. The frequency with which whitebark pine is infected by *H. annosum* in natural stands has not been investigated. Mature western white pine were commonly found to have root and butt rot caused by *H. annosum* before white pine blister rust lead to their wholesale removal from forest stands in the Inland Empire (Ehrlich 1939).

Direct stump surface infection by spores of *H. annosum* is considered a major means of spread and intensification of this fungus in forest stands (Edmonds and others 1984; Hunt and others 1976; Rishbeth 1951; Wallis and Ginns 1976). Temperature and moisture conditions in whitebark pine habitats are likely to be suitable for both sporulation and infection by *H. annosum*. Spring and fall temperature and moisture conditions are generally regarded as best for growth, sporulation, and infection in north temperate zones where *H. annosum* is known to be damaging.

Soil characteristics have been found to play a great role in determining the longevity of stand damage from this fungus following tree cutting in the southeastern United States. Soils with poor internal drainage and high seasonal water tables were found to not support long-term infestations by *H. annosum* (Anderson and others 1980; Froelich and others 1977). The fungus is believed to have limited tree-to-tree movement in such soils. Trees that are immediately adjacent to infected stumps may be killed at a high rate in the decade following tree cutting, but the fungus spreads little to other live trees.

Heterobasidion annosum is mentioned as a known pathogen of whitebark pine by Hepting (1971), but no references to published reports of the fungus infecting this tree species are offered. Webb and Alexander (1985) did not list whitebark pine among the known hosts for *H. annosum*. Root pathogens of whitebark pine have probably received less attention than other, more readily observable, pests of this species. With this in mind, it is prudent to regard the fungus as a pathogen that will almost certainly infect whitebark pine and may have considerable potential for damage in managed stands.

Likewise, *Armillaria* root rot has been listed as a disease of whitebark pine without reference to the extent or severity of the infection. *Armillaria ostoyae* (Romagnesi) Herink is not specifically known to be a pathogen of whitebark pine, but can be assumed to infect this species because it is generally considered to be the predominant pathogenic *Armillaria* on western conifers.

Whitebark pine habitats are outside the temperature/moisture combination range that we normally consider to be *Armillaria*-prone, but subalpine firis occasionally damaged by this pathogen. The frequent association of whitebark pine with subalpine fir probably exposes whitebark pine to inoculum of *A. ostoyae*. *Armillaria* may result in locally important damage, but it is more likely to be an infrequent killer of scattered, individual trees.

DWARF MISTLETOE

Limber pine dwarf mistletoe (*Arceuthobium cyanocarpum* Coulter & A. Nels.) infects and sometimes kills whitebark pine. This parasitic plant occurs in scattered locations from the southern Sierra Nevada to the mountains of Montana, Idaho, Wyoming, Colorado, Utah, and Nevada (Hawksworth and Wiens 1972). One location is known in Oregon, in Deschutes County (Hawksworth and Wiens 1984).

Limber pine and Great Basin bristlecone pine (*P. longaeva* D. K. Bailey) are the principal hosts of this species of dwarf mistletoe; whitebark pine is considered both a primary (Mathiasen and Hawksworth 1988) and secondary (Hawksworth and Wiens 1972) host. Other unusual hosts include western white pine (*P. monticola* Dougl.), ponderosa pine (*P. ponderosa* Laws.), Rocky Mountain bristlecone pine (*P. aristata* Engelm.), foxtail pine (*P. balfouriana* Grev. & Balf.), and mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.) (Hawksworth and Wiens 1972; Hawksworth and Wiens 1984; Scharpf 1984).

Heavy mortality of whitebark pine resulting from limber pine dwarf mistletoe infections has been reported only from Mount Shasta, CA, where Cooke (1955) referred to infested stands as "ghost forests." Stands in this area were surveyed by Mathiasen and Hawksworth (1988). They had an average of 96 percent of whitebark pine infected with 58 percent dead. Most of the dead trees had evidence of past heavy dwarf mistletoe infection.

Arceuthobium tseugense (Rosendahl) G. N. Jones (hemlock dwarf mistletoe) is known to infect whitebark pine in the Crater Lake region of Oregon where it causes considerable damage (Hawksworth and Wiens 1972). *Arceuthobium americanum* Nutt. ex Engelm. occasionally infects whitebark pine when it grows in association with infected lodgepole pine. Likewise, *A. laricis* (Piper) St. John is known to occasionally infect whitebark pine when it grows among infected western larch (Hawksworth and Wiens 1972).

WHITE PINE BLISTER RUST

The disease that has the most impact on whitebark pine is white pine blister rust. Blister rust is a stem rust limited to the white pines. It is native to Eurasia, and all species of white pines on those continents are moderately to highly resistant to the fungus. However, it is exotic to North America, and it follows that all North American white pines are highly susceptible. Whitebark pine appears the most susceptible.

The white pine blister rust fungus was brought to western North America in 1910, arriving with a boatload of blister rust-infected eastern white pine (*Pinus strobus* L.). The seedlings were shipped by the nurseries of Pierre Sebire and Son, Ussy, France. The point of introduction was Point Grey, near Vancouver, BC. The disease was not noticed until 1921 (Boyce 1922). In the fall of that year, blister rust was observed in several stands in southwestern British Columbia and northwestern Washington. By 1922, cankers were found 100 mi north of Vancouver, in eastern British Columbia, and eastern Washington. By 1927, cankers were observed near the southern limit of western white pine in Idaho.

To get a better idea of just when the fungus entered a specific site, Lachmund (1926a) reconstructed the early history by dating backwards from cankers—something that is fairly easy to do and usually correct within a year or two. The evidence is good that the rust infected trees 130 mi northwest of Vancouver, 110 mi north, and 70 mi east, by 1913. In 1917 or 1918, the rust infected trees of the interior pine regions, including the Canoe, Revelstoke, and Beaton regions of British Columbia, Butte Inlet, 150 mi north of Vancouver, BC, and 100 mi to the south in the Puget Sound region. Further, the infection observed in Idaho in 1927 was dated to a 1923 infection. So, in just 13 years, blister rust had become established throughout the range of western white pine and in a high proportion of the range of whitebark pine. By 1965, the fungus seemed to have reached the ecological limit of its range.

The first infected whitebark pine was reported in the University of British Columbia Arboretum (Davidson 1922) and in a botanical garden in England (Spaulding 1923). Infection of whitebark pine, in a natural setting, was first observed in the coast range of British Columbia, 100 mi north of Vancouver (Lachmund 1926b). This observation was in a mixed stand of whitebark pine and western white pine. At least at this site, whitebark pine appeared to be seven to 10 times more susceptible than western white pine. Childs and others (1938) reported infection of whitebark pine in the Mount Hood area of Oregon, and Gynn and Chapman (1951b) found cankers in Yellowstone National Park that dated back to a 1945 infection.

The first thing foresters did when they discovered the disease was to destroy the trees that were infected. But with a fast-moving disease like this one, it became obvious that this approach would not work. The fungus also requires an alternate host to complete its life cycle. It must go from pine to currants or gooseberries (*Ribes*) and then back to pine. No problem—just remove the *Ribes* bushes. And so they tried! Table 2 shows the number of bushes removed from eastern Washington, Idaho, Montana, and Wyoming from 1923 to 1965 (USDA 1953, 1965).

In 1965, foresters gave up attempts to eradicate *Ribes* bushes. Most *Ribes* spp. are high survivors and, thus, not easy to get rid of. Next, chemicals were used on the pine host. Some at first seemed to hold promise of killing the fungus, but these too ended up not working well enough. The outlook for white pines was bleak.

Impact of Blister Rust on Natural Stands

Table 3 lists the published data, including survey data from official Forest Service files (Northern Region), that we found on the infection level of blister rust in natural stands (Bedwell and Childs 1943; Berg and others 1975; Brown 1966; Carlson 1978; Gynn and Chapman 1948, 1952a, 1952b; Toko and Dooling 1968). Figure 1 indicates locations of these stands. These data are not current; most of the surveys were conducted at least 20 years ago. Also, in most cases the ages of the stands were not indicated. Stand age greatly influences rate of infection, so comparisons of rates of infection without consideration of stand age are not very meaningful. Observations indicate that the infection levels and mortality in northern Idaho and Montana may be more severe now than they were in the 1960's. These old survey data do substantiate the general observation that whitebark pine is highly susceptible to blister rust and is impacted heavily where environmental conditions are conducive to the blister rust. They also indicate that damage can be very light where environmental conditions are not conducive to the disease. Further, it seems reasonable to conclude that the degree of infection on whitebark pine decreases southward for all parts of its range—throughout the Cascade-Sierra Nevada chain, the Bitterroot Mountains, and along the Continental Divide of the Rocky Mountains.

Table 2—Number of *Ribes* bushes eradicated in eastern Washington, Idaho, Montana, and Wyoming between 1923 and 1965

Area	Years of eradication	Number of *Ribes* bushes
Total area	1923-1965	468,420,720
Yellowstone National Park	1945-1965	10,222,300
Glacier National Park	1939-1965	4,630,900
Grand Teton National Park	1950-1965	181,700

This is especially evident in Yellowstone National Park where there have been extensive surveys (table 4), even in areas where there are substantial populations of *Ribes* (Toko and Dooling 1968). This limitation is probably due to a somewhat dry and perhaps cold climate, together with a decrease in low elevation sources of inoculum.

Carlson (1978) reported survey results from 29 stands in Yellowstone National Park. Four of 29 stands were found to have blister rust infections. Rate of infection ranged from 0 to 6 percent of trees. Nine stands were found to have *Ribes* populations. *Ribes* importance, expressed as: (*Ribes* cubic foot volume per acre) x (Total *Ribes*/total plots sampled), ranged from 0 to 1,041. Three stands with natural *Ribes* population densities (no eradication history) had *Ribes* importance values of 1,041, 211, and 20. Even with relatively high *Ribes* values, the infection rates (percent trees infected) were low: 5, 0, and 6 percent, respectively. The remaining noneradicated stands had values of 7, 1, and 0.04, and five had values of 0.00.

In another survey of Yellowstone (Berg and others 1975), infection was closely related to elevation (table 5). Of 325,641 trees (whitebark and limber pines combined) inspected over an area of 2,246,000 acres, 959 trees were infected.

The general conclusion drawn from these surveys was that the Yellowstone environment may be poorly suited to blister rust infection. It is a cool, dry climate which, according to R. G. Krebill (1971) is only marginally suitable for blister rust teliospore germination.

In western white pine stands where this disease is devastating, individuals that are not infected stand out like a green thumb. In 1950, a program was started with the aim of determining whether this apparent resistance in western white pine was genetic or if somehow these trees were escapees—even though they were surrounded by trees that had, at times, thousands of cankers. The trees turned out to be genetically resistant. A breeding program was started with the purpose of producing new varieties of western white pine resistant to blister rust. Within the research work surrounding this program, one of the studies had the specific objectives of (1) comparing the resistance level of western white pine with other North American white pines and Eurasian white pines and (2) comparing the kinds of resistance that were observed in western white pine to those of the other pines cited above.

Table 3—Percent infection of whitebark pine by blister rust

Stand name	Area No.	Data years	No. of trees per stand	No. of trees infected	Percent infected
90 miles N Vancouver, BC	1	1937	11	11	100
90 miles N Vancouver, BC	1	1937	21	21	100
Marmot Pass, WA	2	1937-39	26	24	92
Hyas Lake, WA	3	1937-39	9	8	89
Mt Rainier, WA	4	1951	602	331	55
Mt Rainier, WA	4	1952	297	154	52
Mt Wilson, OR	5	1937-39	17	12	71
Frog Lake, OR	6	1937-39	10	10	100
White River, OR	7	1937-39	23	88	
Salmon River, OR	8	1937-39	17	16	94
Quarles Peak, ID	9	1937-39	37	22	59
Windy Peak, ID	10	1937-39	17	12	71
York Creek, AB	11	1960	—	—	100
Glacier Park, MT	12	1948	2,585	48	2
Glacier Park, MT	12	1952	677	45	7
Glacier Park, MT	12	1968	—	—	45
Blackfoot IR, MT	13	1965	1,315	782	60
Gallatin NF, MT	14	1966	496/6	4	0-5
Gallatin NF, MT	14	1966	14/1	10	71
Gallatin NF, MT	14	1966	262/3	261	98-100
Custer NF, MT	15	1966	48/1	34	71-80
Custer NF, MT	15	1966	185/2	159	81-90
Yellowstone Nat. Park, WY	16	1966	?/7	—	0-.6
Yellowstone Nat. Park, WY	16	1975	325,641	959	0.3
Yellowstone Nat. Park, WY	16	1968	?/17	—	0-10
Yellowstone Nat. Park, WY	16	1968	?/1	—	21-30
Yellowstone Nat. Park, WY	16	1966	?/5	—	24
Shoshone NF, WY	17	1966	3,517/30	0	0
Shoshone NF, WY	17	1966	108/1	7	6
Bighorn NF, WY	18	1966	878/7	0	0
Bighorn NF, WY	18	1966	450/2	8	2
Bighorn NF, WY	18	1966	370/2	184	41-50
Bighorn NF, WY	18	1966	90/2	65	71-80
Bighorn NF, WY	18	1966	223/1	200	90
Wind River IR, WY	19	1966	50/3	0	0

See figure 1 for location of stand.

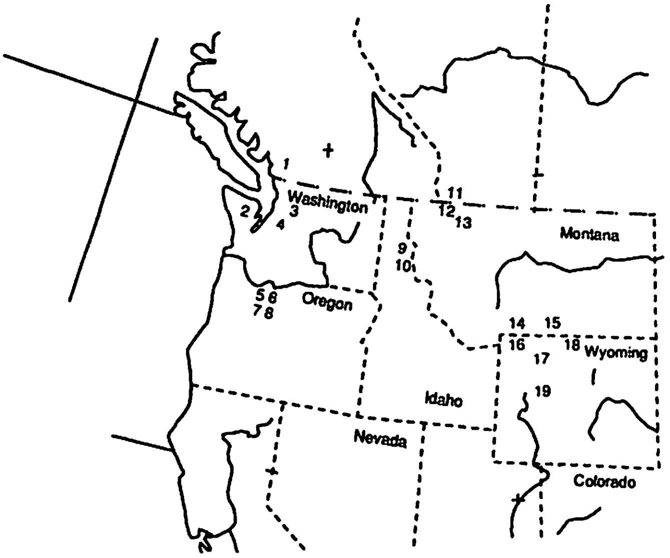


Figure 1—Location of stands listed in table 3.

Table 4—Level of infection on whitebark pine and corresponding *Ribes* populations in Yellowstone National Park

Stand number	Trees infected	*Ribes*/acre
	Percent	*Number*
30	0.0	[1]0.0
29	.0	[1].1
22-23	.0	[1]2.0
35-37	.2	[1]3.0
10	.2	7.0
28	.3	[1]3.0
21	.6	4.0
18	1.8	4.0
9	3.3	61.0
38	3.7	105.0
14	4.6	58.0
2-4	7.5	70.0
46	23.7	91.0

[1] *Ribes* eradication 5 or more years prior to survey.

Table 5—Blister rust infection by elevation in Yellowstone National Park

Percent of all infections	Elevation
	Feet
44	Below 7,500
25	7,500-8,000
23	8,000-8,500
6	8,500-9,000
2	Above 9,000

Blister Rust Resistance in Whitebark Pine

That whitebark pine is very susceptible to blister rust was obvious to field observers; this was especially obvious where whitebark and western white pine were in a mixed stand. Several studies were completed that compared resistance among many of the white pines from throughout the world. Bingham (1972) summarized these data (table 6), and it was no surprise that whitebark pine was again rated as "most susceptible."

The research was directed toward producing new varieties of western white pine that not only had high resistance, but also had the kinds of resistance that are stable—varieties that would not be vulnerable to new races of the rust fungus. Therefore, there was interest in what mechanisms were present in the highly resistant white pines especially, where blister rust was native. The thinking was that if a certain mechanism or combination of mechanisms worked in resistant species where white pine blister rust was endemic, it would have an even better chance of surviving here—even though there were different environmental conditions involved.

Part of the collection of white pines in this study were seedlings from three phenotypic resistant whitebark pines. Although these three trees were not a very big sample, it was hoped that they would provide an idea of what was possible for whitebark pine in terms of resistance. Ultimately, 207 seedlings were generated, which was a pretty good sample. Results of the study were reported by Hoff and others (1980). They indicated that resistance in whitebark pine had increased substantially since introduction of blister rust (table 7). In the test reported, whitebark pine ranked ninth out of 16 species tested. The only North American species to rank higher was resistant collections of western white pine, a strong indication of good potential for control via resistance.

Table 6—Blister rust resistance of 14 white pines, rated as most resistant (1) to least resistant (11)

Species	Average ranking
Pinus armandii	1
P. cembra	1
P. aristata	2
P. wallichiana	2
P. koraiensis	2
P. peuce	3
P. sibirica	4
P. parviflora	5
P. strobiformis	6
P. strobus	7
P. flexilis	8
P. monticola	9
P. lambertiana	10
P. albicaulis	11

Table 7 also shows rankings of the species for six mechanisms of resistance. A brief description of the life cycle of blister rust in the pine host may be helpful. A fungus spore germinates on the surface of the leaf, enters the leaf through a stomate, and grows down the leaf, within the vascular tissue, and into the stem. After reaching the stem, it grows vertically and laterally. Fruiting of the fungus causes the most damage to the tree by physically disrupting the vascular tissues.

The first operational resistance mechanism was one that prevented the fungus from entering a leaf; it was called "no needle infection." Thirty-three percent of the seedlings of whitebark pine were in this category (33 percent of the seedlings were clean—no needle infections and no stem infections). The average over all species was 37 percent, range 1 to 96 percent. The second reaction observed was in the number of needle spots. Spots were counted and presented as number per lineal meter of needle tissue. Whitebark pine had 6.7 spots per meter; the average was 5.9 percent, range 0 to 28 percent.

Next, it was noticed that the needles with spots from some trees fell off before the fungus could reach the stem. This reaction was called "premature needle shed." After adjusting for previous resistance—the no needle infection

Table 7—Species ranked by average ranking for six mechanisms of resistance

Species	Mechanism of resistance						Rank
	NNI[1]	NSN[2]	PNS[3]	FSS[4]	BR[5]	A&C[6]	
Pinus koraiensis	2	2	4	1	1	4	2.3
P. sibirica	3	2	3	3	7	2	3.3
P. parviflora	1	1	10	9	2	1	4.0
P. cembra	4	4	2	2	6	6	4.0
P. armandii	6	6	3	5	3	11	5.7
P. monticola	9	8	2	6	4	5	5.7
P. peuce	5	2	8	6	6	8	5.8
P. wallichiana	7	5	5	3	5	14	6.5
P. albicaulis	8	10	1	4	7	13	7.2
P. strobiformis	13	9	9	8	9	3	8.5
P. morrisonicola	10	9	10	9	4	11	8.8
P. chiapensis	11	9	6	9	8	14	9.5
P. lambertiana	14	7	7	7	11	12	9.7
P. flexilis	12	11	8	7	10	10	9.7
P. ayacahuite	15	13	10	9	11	7	10.8
P. strobus	15	12	9	9	12	9	11.0

[1] NNI = no needle infection
[2] NS = needle spots per meter of secondary foliage
[3] PNS = premature needle shed
[4] FSS = fungicidal short shoot
[5] BR = bark reaction
[6] A&C = alive and cankered.

reaction—whitebark pine percentage was 38 percent. These trees had needle spots in June, 9 months after inoculation, but never developed cankers. The average was 11 percent, range 0 to 38 percent; whitebark pine rated the best of all species for this trait. The next reaction observed was caused by the interaction of the fungus and host when fungus growth down the needle reached the short shoot. This reaction seemed to produce a toxin that killed the fungus, hence it was called the "fungicidal short shoot" reaction. Again, after adjusting for the previous resistance mechanisms (no needle infection and premature needle shed), the whitebark pine occurrence rate was 7 percent. These seedlings had needle spots in June and September, 9 and 12 months after inoculation, but they also did not develop cankers. The average was 6 percent, range 0 to 90 percent. After entering the stem, other defense reactions occur that also kill the fungus. There appear to be several kinds, but they have been lumped into a single category called "bark reactions." Again, after adjusting for previous mechanisms of resistance, whitebark pine was 6 percent (seedlings never had normal cankers); the average was 7 percent, range 0 to 40 percent. The last reaction reported noted the ability of seedlings to remain alive even though they had normal cankers. This trait was called "alive and cankered" (also referred to as tolerance). Whitebark pine rated low, with only 8 percent of the seedlings alive 3 years after inoculation; the average was 21 percent, range 5 to 50 percent.

The increase in resistance of whitebark pine appears due mainly to four traits: (1) no needle infections, (2) premature needle shed, (3) fungicidal short shoot, and (4) bark reactions. Again, assuming that the three phenotypic resistant whitebark pine in this test are representative of other phenotypic whitebark pine, it seems reasonable to hope that the species is on its way to becoming resistant to blister rust.

Management of the Whitebark Pine-Blister Rust System

Management of whitebark pine in the face of blister rust is largely dependent on the relative rust hazard of the site. In some areas, such as Yellowstone National Park, where the fungus appears to be at its ecological limit, nothing needs to be done—unless global warming causes a climate change that becomes favorable to the fungus. In areas where there is high mortality, resistance appears the only option. For areas with moderate hazard, pruning and excising of cankers is a viable option.

Hagle and others (1989) produced management guidelines for blister rust control in western white pine. If one reads the document with the silvics of whitebark pine in mind, many of the recommendations can be used almost directly with only minor modification. Even though whitebark pine is more susceptible than western white pine, the cankers grow more slowly (Bedwell and Childs 1943). When high-elevation whitebark pine was compared to the main altitudinal range of western white pine, the cankers grew about half as rapidly. Therefore, in stands of whitebark pine and western white pine with equal hazard, pruning and excising of cankers should be even more effective in whitebark pine stands. Dooling (1974) evaluated the effectiveness of pruning to save relic limber pine in Yellowstone National Park. He found it to be a viable option in the localized high-use area that was treated. Only cankered branches were removed to preserve the visual quality of trees, and some of the trees required climbing for complete pruning. There were as many as 150 cankers in some trees. Acres treated were 1,367 at an average of 4 acres/person/day. The cost in 1972-73 was $20 per acre. Current costs for pruning western white pine stands range from $50 to $80; excision of cankers on pruned trees adds about $10 to $20 per acre.

Phenotypically resistant whitebark pine are fairly common; nearly every severely infected stand has a few. So there would be little problem in setting up a scheme to produce seedlings that are resistant to blister rust. Some schemes are fairly cheap; others are costly. The basic format is: (1) Collect seed from resistant individuals and either directly sow or plant seedlings in natural sites. (2) Make grafts of resistant phenotypes and plant those. (It has been noted that grafting on western white pine stock causes the whitebark pine scion to grow faster [LeRoy Johnson, personal communication]. With Swiss stone pine [*P. cembra* L.], Holzer (1975) reported that grafting on blue pine [*P. wallichiana* A. B. Jacks.] or Scotch pine [*P. sylvestris* L.] resulted not only in better growth, but in more flowers). (3) Cross breed several resistant individuals (this would assure cross pollination as compared to the above, which are probably selfs that are slow growing). (4) For both 1 and 3 above, the seedlings could be artificially inoculated with blister rust and only resistant seedlings would be planted.

A more difficult problem is to decide how far to transfer seed. We know of no data on the genetic parameters for adaptation of this species over its range. Since it appears that the evolution of this species has been greatly influenced by birds and the environment in which whitebark pine grows is uniformly severe, it would seem that adaptation would be fairly broad. So far, the known genetics of whitebark pine bear this out. Furnier and others (1987) found in an allozyme analysis that trees within clumps were more closely related than trees among clumps. This means that when a bird cached seed, it was most likely gathered from a single tree, or a cluster of trees. They found, however that there was no difference in the genetic relation among clumps, as compared to clumps collected at different sites. This means that the birds were just as likely to go long distances to cache seed as they were to cache close to the collection site. Therefore, the seed is apparently distributed over a broad area, causing good mixing of genes over that large area. Nonetheless, there probably is a photoperiod effect over the range of whitebark pine, and differences are likely in insect and disease resistance among provenances or geographic areas. A conservative recommendation, until the patterns of adaptive variation are assessed, would be to stay within a particular mountain range, for example, the Bitterroots, Cabinets, or Selkirks. Each of these areas would be treated as separate populations with resistance selections located and crossed within each. If future data show no appreciable differentiation two or more of the populations would be lumped.

REFERENCES

Anderson, R. L.; Fisher, V.; Mistretta, P. 1980. How to recognize *annosus*-prone forest sites. Forest Farmer. October 7: 17.

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Bedwell, J. L.; Childs, T. W. 1943. Susceptibility of whitebark pine to blister rust in the Pacific Northwest. Journal of Forestry. 41: 904-912.

Bega, R. V., tech. coord. 1979. Diseases of Pacific Coast conifers. Agric. Handb. 521. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 206 p.

Berg, M. J.; Carlson, C. E.; Lounsbury, L. P.; Dooling, O. J. 1975. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Northern Region, State and Private Forestry, Missoula, MT. 15 p.

Bingham, R. T. 1972. Taxonomy, crossability, and relative blister rust resistance of 5-needled white pines. In: Biology of rust resistance in forest trees: proceedings of a NATO-IUFRO advanced study institute; 1969 August 17-24. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture: 271-280.

Boyce, J. S. 1922. White pine blister rust in the Pacific Northwest. Phytopathology. 12: 448.

Brown, D. 1966. White pine blister rust survey in Montana and Wyoming. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Northern Region, State and Private Forestry, Missoula, MT. 10 p.

Burleigh, J. R.; Wood, W.; Sebesta, P. 1982. Growth retardation of plantation-grown sugar pine by *Lophodermella arcuata*. Plant Disease. 66: 680-682.

Carlson, C. 1978. Noneffectiveness of *Ribes* eradication as a control of white pine blister rust in Yellowstone National Park. Rep. 78-18. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, State and Private Forestry. 4 p.

Childs, T. W.; Bedwell, J. L.; Englerth, G. H. 1938. Blister rust infection on *Pinus albicaulis* in the Northwest. Plant Disease Reporter. 22: 139-140.

Cooke, W. B. 1955. Fungi of Mount Shasta (1936-1951). Sydowia Annals Mycologica. 9: 94-215.

Darker, G. D. 1932. The Hypodermataceae of conifers. Contributions from the Arnold Arboretum of Harvard University. I. 158 p.

Davidson, A. T. 1922. White pine blister rust in British Columbia. In: Proceedings, third western white pine blister rust conference. Portland, OR. U.S. Department of Agriculture, Division of Forest Pathology, Bureau of Plant Industry: 9-22. Mimeo.

Dooling, O. J. 1974. Evaluation of pruning to reduce impact of white pine blister rust on selected areas in Yellowstone National Park. Rep. 74-19. Missoula, MT: U.S. Department of Agriculture, Forest Service, State and Private Forestry, Northern Region. 5 p.

Edmonds, R. L.; Leslie, K. B.; Driver, C. H. 1984. Spore deposition of *Heterobasidion annosum* in thinned coastal western hemlock stands in Oregon and Washington. Plant Disease. 68: 713-715.

Ehrlich, J. 1939. A preliminary study of root diseases in the western white pine type. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Rocky Mountain Forest and Range Experiment Station. 77 p.

Frajo-Apor, A. 1976. Physiologische und parasitilogische Untersuchengen an *Lachnellula flavovirens* (Bres.) Dennis. European Journal of Forest Pathology. 6: 360-371.

Froelich, R. C.; Kuhlman, E. G.; Hodges, C. S.; Weiss, M. J.; Nichols, J. D. 1977. *Fomes annosus* root rot in the south. Guidelines for prevention. Atlanta, GA: U.S. Department of Agriculture, Forest Service, Southeastern Area, State and Private Forestry. 16 p.

Funk, A. 1981. Parasitic microfungi of western trees. Victoria, BC: Environment Canada, Canadian Forestry Service, Pacific Forest Research Centre. 190 p.

Funk, A. 1985. Foliar fungi of western trees. Victoria, BC: Agriculture Canada, Canadian Forestry Service, Pacific Forest Research Centre. 159 p.

Furnier, G. R.; Knowles, P.; Clyde, M. A.; Dancik, R. P. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution. 41: 607-612.

Gynn, J. D.; Chapman, C. M. 1948. Blister rust control, Glacier National Park, 1948. In: White pine blister rust control in the Northwest region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine: 80-85.

Gynn, J. D.; Chapman, C. M. 1949. Blister rust control, Glacier National Park, 1949. In: White pine blister rust control in the Northwest region. Spokane WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine: 77-82.

Gynn, J. D.; Chapman, C. M. 1950. Blister rust control, Yellowstone National Park, 1950. In: White pine blister rust control in the Northwest region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine: 92-94.

Gynn, J. D.; Chapman, C. M. 1951a. Blister rust control, Mount Rainier National Park, 1951. In: White pine blister rust control in the Northwest region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine: 64-66.

Gynn, J. D.; Chapman, C. M. 1951b. Blister rust control, Yellowstone National Park, 1951. In: White pine blister rust control in the Northwest region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine: 70-73.

Gynn, J. D.; Chapman, C. M. 1952a. Blister rust control, Glacier National Park, 1952. In: White pine blister rust control in the Northwest region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine: 57-60.

Gynn, J. D.; Chapman, C. M. 1952b. Blister rust control, Mount Rainier National Park, 1952. In: White pine blister rust control in the Northwest region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine: 54-56.

Hagle, S. K.; McDonald, G. I.; Norby, E. A. 1989. Western white pine and blister rust in northern Idaho and western Montana: alternatives for integrated management.

Gen. Tech. Rep. INT-261. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 35 p.

Hagle, S. K.; Tunnock, S.; Gibson, K. E.; Gilligan, C. J. 1987. Field guide to diseases and insect pests of Idaho and Montana Forests. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, State and Private Forestry. 123 p.

Hahn, G. G.; Ayers, T. T. 1934. *Dasyscyphae* on conifers in North America. III. *Dasyscypha pini*. Mycologia. 26: 479-502.

Hawksworth, F. G.; Wiens, D. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). Agric. Handb. 401. Washington, DC: U.S. Department of Agriculture, Forest Service. 34 p.

Hawksworth, F. G.; Wiens, D. 1984. Biology and classification of *Arceuthobium*: an update. In: Hawksworth, F. G.; Scharpf, R. F., tech. coords. Biology of dwarf mistletoes: Proceedings of the symposium; 1984 August 8; Colorado State University, Fort Collins, CO: Gen. Tech. Rep. RM-111. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 2-17.

Hepting, G. H. 1971. Diseases of forest and shade trees of the United States. Agric. Handb. 386. Washington, DC: U.S. Department of Agriculture, Forest Service. 658 p.

Hiratsuka, Y.; Funk, A. 1976. Additional records of *Gremmeniella abietina* in western Canada. Plant Disease Reporter. 60: 631.

Hoff, R. J.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology. 10: 307-316.

Holzer, Kurt. 1975. Genetics of *Pinus cembra* L. Annales Forestales. 6: 139-158.

Hopkins, J. 1985. *Atropellis* canker. For. Pest Leafl. 25 (Rev.). Victoria, BC: Agriculture Canada, Canadian Forestry Service, Pacific Forestry Centre. 4 p.

Hunt, R. S. 1981. Pine needle casts and blights in the Pacific region. For. Pest Leafl. 43. Victoria, BC: Environment Canada, Canadian Forestry Service, Pacific Forest Research Centre. 7 p.

Hunt, R. S.; Cobb, F. W., Jr.; Parmeter, J. R., Jr. 1976. *Fomes annosus* stump colonization and fungus development in the California mixed conifer type. Canadian Journal of Forest Research. 6: 159-165.

Hunt, R. S.; Ziller, W. G. 1978. Host-genus keys to the *Hypodermataceae* of conifer leaves. Mycotaxon. 6: 481-496.

James, R. L. 1979. *Fomes annosus* on white fir in Colorado. Plant Disease Reporter. 63: 129-130.

Johnson, LeRoy. 1964. Grafting whitebark pine or western white pine stock. Personal communication.

Krebill, Richard G. 1971. Conditions for teliospore germination in Yellowstone. National Park Environment. Inhouse report, Forest Service meeting.

Lachmund, H. G. 1926a. Studies of white pine blister rust in the West. Journal of Forestry. 24: 874-884.

Lachmund, H. G. 1926b. Western blister rust investigations, 1926. In: Proceedings, western white pine blister rust conference. Mimeo. Portland, OR: U.S. Department of Agriculture, Division of Forest Pathology, Bureau of Plant Industry. 12-19.

Lightle, P. C.; Thompson, J. H. 1973. *Atropellis* canker of pines. Forest Pest Leaflet 138. Washington, DC: U.S. Department of Agriculture, Forest Service, Washington Office. 6 p.

Lohman, M. L.; Cash, E. K. 1940. *Atropellis* species from pine cankers in the United States. Journal of the Washington Academy of Science. 30: 255-262.

Mathiasen, R. L.; Hawksworth, F. G. 1988. Dwarf mistletoes on western white pine and whitebark pine in northern California and southern Oregon. Forest Science. 34: 429-440.

Rishbeth, J. 1951. Observations on the biology of *Fomes annosus*, with particular reference to East Anglian pine plantations II. Spore production, stump infection, and saprophytic activity in stumps. Annals of Botany. 15: 1-22.

Scharph, R. F. Host resistance to dwarf mistletoes. In: Hawksworth, F. G.; Scharph, R. F., tech. coords. Biology of dwarf mistletoes symposium: Proceedings; 1984 August 8; Fort Collins, CO. Fort Collins, CO: Colorado State University; 1984: 70-76

Skilling, D. D.; Cordell, C. E. 1966. *Scleroderris* canker on National Forests in upper Michigan and northern Wisconsin. Res. Pap. NC-3. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 10 p.

Skilling, D.; Kienzler, M.; Haynes, E. 1984. Distribution of serological strains of *Gremmeniella abietina* in eastern North America. Plant Disease. 68: 937-938.

Smerlis, E. 1973. Pathogenicity tests of some discomycetes occurring on conifers. Canadian Journal of Forest Research. 3: 7-16.

Smith, R. S., Jr. 1978. Needle diseases. In: Bega, R. V., tech. coord. Diseases of Pacific Coast conifers. Agric. Handb. 521. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 42-68.

Smith, Richard S., Jr. 1972. Needle casts of high-altitude white pines in California. Plant Disease Reporter. 56: 102-103.

Spaulding, P. 1923. Foreign studies of white pine blister rust. Abstract. Phytopathology. 13: 45.

Staley, J. M. 1964. A survey of coniferous foliage diseases (other than rusts) in Colorado. Plant Disease Reporter. 48: 562-563.

Stillinger, C. R. 1929. *Dasyscypha fuscosanquinea* Rehm on western white pine, *Pinus monticola* Dougl. Phytopathology. 19: 575-584.

Sutherland, J. R. 1987a. The seed or cold fungus. In: Sutherland, J. R.; Miller, T.; Quinard, R. S. Cone and seed diseases of North American conifers. North Amer. For. Comm. Publ. 1. Victoria, BC: U.S. Department of Agriculture, Forest Service, International Forestry Staff, Washington Office: 28-33.

Sutherland, J. R. 1987b. *Sirococcus* blight. In: Sutherland, J. R.; Miller, T.; Quinard, R. S. Cone and seed diseases of North American conifers. North Amer. For. Comm. Publ. 1. Victoria, BC: U.S. Department of Agriculture, Forest Service, International Forestry Staff, Washington Office: 34-41.

Thomas, G. P.; Bourchier, R. J.; Lowman, A. A. 1959. Rust diseases. In: Annual report forest insects and disease survey for 1959. Victoria, BC: Canadian Department of Agriculture, Science Service, Forest Biology Division: 90-91.

Toko, H. V.; Dooling, O. J. 1968. An evaluation of the blister rust control program of the National Park Service in the Rocky Mountain area. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Northern Region, State and Private Forestry, Missoula, MT. 8 p.

Tylutki, E. E. 1979. Mushrooms of Idaho and the Pacific Northwest: Discomycetes. Moscow, ID: The Idaho Research Foundation, Inc.; The University Press of Idaho. 133 p.

U.S. Department of Agriculture, Forest Service. 1953. White pine blister rust control: Northwestern project, 1952-1953. Spokane, WA: U.S. Department of Agriculture, Forest Service, Northern Region: 83-89.

U.S. Department of Agriculture, Forest Service. 1965. White pine blister rust control, 1954-1965. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region: 31, 36, 38, 53, 55, 57, 64, 66, 70, 72, 77, 81.

Wallis, G. W.; Ginns, J. H., Jr. 1976. *Annosus* root rot in Douglas-fir and western hemlock in British Columbia. For. Pest Leafl. 15. Victoria, BC: Environment Canada, Canadian Forestry Service, Pacific Forest Research Centre. 4 p.

Webb, R. S.; Alexander, S. A. 1985. An updated host index for *Heterobasidion annosum*. Information Series No. 85-2. Blacksburg, VA: Virginia Polytechnic Institute and State University. 27 p.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Bill Shuster)—Looking at a whitebark pine snag, can you determine if it died of blister rust?

A.—If a tree died from blister rust, there will be scars from the cankers that caused its death. Look first at the base for large basal scars and then look higher on the stem and branches for cankers.

Q. (from Wendel Hann)—If you select for resistant phenotypes, how much chance is there of also selecting for undesirable characteristics such as poor growth or survival?

A.—We have looked for those kinds of associations in western white pine, but have not seen any yet. We certainly would expect correlations of some kind, so far we can be thankful that none are obvious.

Q. (from Dick Krebill)—What percentage of whitebark pine in natural stands is likely to be resistant to blister rust? What is the chance for a new resistant population developing via natural selection without human intervention?

A.—We do not know the proportion of resistant trees. Bingham in the 1950's did a survey with western white pine and he found one tree with no cankers out of about 10,000 in the most heavily infected stands. But that is not the total picture. Trees can have cankers and still be resistant. Bob Keine ran the whitebark pine model using 5 percent resistance. At that level, there was no regeneration. He agreed to run other percentages—10 percent, 15 percent, 20 percent—until a regeneration effect is evident. He will put that in his paper in the question section.

Q. (from Kate Kendall)—I have estimates of severe whitebark pine mortality from blister rust in Glacier National Park. What was your information source for blister rust mortality in Glacier National Park?

A.—Toko and Dooling (1968, unpublished, in cited literature) reported a 1967 survey of a 45-year-old whitebark pine stand near Oldman Lake in Glacier Park in which 45 percent of the trees were infected. Two other surveys, one in 1947 and the other in 1951, of whitebark pines about 25 years old around Oldman Lake were reported in blister rust annual reports from 1948 and 1952 (Gynn and Chapman, in cited literature). A total of 2,585 and 677 trees were examined with 2 and 7 percent, respectively, infected. The Toko and Dooling survey was conducted by USDA Forest Service, State and Private Forestry, Pest Management personnel, and the second was conducted by Park Service personnel. These were surveys in what was referred to as the Old Man Lake Control Unit. The park was broken up into five control units designated as Park Headquarters, Lake McDonald, East Glacier, Two Medicine, and Oldman Lake. Oldman Lake was the only unit that had whitebark pine in the survey sample. The others had limber and western white pines. These are the only data for Glacier Park that we were able to locate. On the basis of your and other people's impressions of the situation, a current resurvey is needed.

Q. (from Anonymous)—Blister rust seems to be more common in areas of greater multiple use (grazing, lumbering) and lower in protected areas (National Parks). Could human activities be partly responsible for the spread of the disease?

A.—Blister rust mortality is high in Rainier National Park and Garibaldi National Park in Canada, and it is probably high in Glacier National Park (although we do not have survey records to show this).

However, once the fungus is in an area, intensification is local and depends mostly on the local climate, white pine populations, and *Ribes* populations. *Ribes* are seral species—early invaders of disturbed sites. They accomplish this, not by having wind transported seeds, but by having very tough seed coats and tremendous capacity for dormancy (200 or more years). This means that they can wait in a dormant condition for the next suitable disturbance. In natural forests, this disturbance would normally have been fire. Stirring or burning the duff in which *Ribes* seeds are stored stimulates germination. Human activity can greatly increase populations of *Ribes* in and near whitebark pine stands, thus influencing disease development.

HISTORICAL USES OF WHITEBARK PINE

B. John Losensky

ABSTRACT

The historical use of whitebark pine for lumber and other products is reviewed. While whitebark pine exhibits favorable wood qualities, its size and location generally precluded active management and past use was more incidental or one of convenience. This paper focuses on the Butte/Anaconda area of Montana. Records of historical use on private and public ownerships are limited and incomplete; however, the best documentation was in conjunction with mining and ore reduction activity. Present-day use continues to be incidental, with limited attention directed at management of the species. Recent harvest records are presented for Federal ownership.

INTRODUCTION

Eastern white pine, a distant cousin of whitebark pine, was eagerly sought and reserved for masts for the Royal Navy by the British during colonial days (Dana 1956). The resulting friction between the colonies and British authorities helped spark the War of Independence and the establishment of the United States of America. Whitebark pine has no such claim to fame. Descriptions of the tree often refer to it as a high-elevation tree of no commercial value (Elias 1987). Its wood is not preferred for any special uses, and in most cases the tree would have been overlooked except for a quirk of fate that placed some of the best-developed stands in the same neighborhood as major deposits of gold, silver, and copper. Thus the past use of whitebark pine is the result of its proximity to a wood market rather than an interest in its wood properties. As can be seen in table 1, whitebark pine has better wood properties than its associates Engelmann spruce and subalpine fir. Its general form, small size, and isolated location normally preclude its use, however.

LOCATION

Whitebark pine is common at higher elevations on warm aspects and ridgetops and is less abundant on sheltered north-facing slopes. It can be found in the British Columbia coastal mountains, the Olympic Mountains, and on the western slope of the Cascades in Washington and northern Oregon, but is more prominent in the Cascades of southern Oregon and northern California. In these locations the tree is generally of poor form and confined to the high ridgelines. In the Rocky Mountains it is a scattered tree, but it becomes a major component in Montana and central Idaho and parts of Alberta, Canada. Here it may form stands of relatively tall, straight trees particularly on moist, north slopes. It is abundant in western Wyoming and may develop good form there also (Arno and Hoff 1989; Day 1967).

Table 2 shows the percent of whitebark pine in the various drainages in the Deerlodge National Forest (USDA n.d.) as compiled from cruises made at the turn of the century. While logging had occurred on much of the area before the cruises were conducted, they do provide an estimate of the amount of whitebark pine present in the original stands.

A cruise conducted in the 1920's as part of a land exchange proposal north of Anaconda indicated that 15 percent of the volume was whitebark pine (USDA 1932). The major portion of this part of the exchange was in Lost Creek; minor amounts were in Antelope and Modesty

Table 1—Wood properties of whitebark pine and associated species (Forbes 1956; Hall and Maxwell 1911; Hazen (n.d.); Keenan 1970)

Species	Heat value	Modulus of rupture	Specific gravity	Weight per ft³
	million btu	*psi*		*lb*
Douglas-fir	19.2	9,600	0.43	30
Lodgepole pine	18.6	9,400	.41	29
Western white pine	17.3	9,500	.38	27
Engelmann spruce	14.7	6,000	.33	23
Fir	16.6	6,300	.37	26
Whitebark pine	16.6	8,150	.42	26

Table 2—Percent of whitebark pine by drainage on the Deerlodge National Forest

Drainage	Percent of whitebark pine
Race Track Creek	5
Lost Creek	21
Foster Creek	13
Warm Spring Creek	13
Storm Lake	7
Twin Lakes	8
Barker Creek	30
Deep Creek	19
Seymour Creek	2
La Marche Creek	17
Fishtrap Creek	17
Mudd Creek	9
Forest average	6

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

B. John Losensky is Forest Ecologist, Lolo National Forest, Forest Service, U.S. Department of Agriculture, Missoula, MT 59801.

Creeks. The percentage of whitebark pine is similar to that found in the earlier work. Since these sources are the only known information on the extent of whitebark pine at the time of the mining development, I decided to use them recognizing that errors may be present because of past cutting activity.

HISTORICAL USE

To understand past use of whitebark pine, it is helpful to review early timber harvest policies for the public domain. Until organized lumbermen began to commercially exploit public timber, there was little concern over its use. As with mineral deposits, land, water, and grass, timber could be used by whoever claimed it. As supplies diminished around populated areas, the Federal Government attempted to pass and enforce legislation for its use. In 1849 Congress established the Department of the Interior and in 1850 the first Federal timber agents were appointed (Butcher 1967). These agents were directed to prohibit cutting of public timber. Because of the lack of money and subsequent inability to enforce the regulations, a compromise was developed in 1860 that required payment for illegally cut timber.

Through the 1870's various attempts were made to stop the illegal use of public timber with limited success. Because of extensive problems elsewhere, the Land Office generally ignored the early development of the lumber industry in Montana (Butcher 1967). During the early 1880's there was little interest in enforcing compliance and public timber was up for grabs. When President Cleveland came into office in 1885, renewed efforts to enforce Federal timber policies were attempted. With the establishment of the Forest Reserves in the 1890's and early 1900's, policies were implemented that provided for the orderly harvest of the timber resource. In time, depredations on the public lands were finally brought under control.

Pre-1860 Period

Prior to the arrival of European man, seed of whitebark pine was used principally as a food source by Native Americans. With the California gold rush, miners may have had an opportunity to utilize whitebark pine for firewood or other uses associated with mining activity; however, because it grew only on high ridges, and early mining activities were concentrated in the major stream bottoms, other woods would have been more commonly used. No references could be found that indicated other than minor isolated use of the tree in California. Placer mining progressed to Idaho and Montana in the 1850's and 1860's. As occurred in California, most of the first discoveries were placer gold deposits at lower elevations. Towns such as Idaho City, Pierce, and Orofino in Idaho and Bannack, Virginia City, and Helena in Montana attracted thousands to the new fields (Fisher and Holmes 1968). Wood for these early operations was obtained from low-elevation forests and had limited impact on whitebark pine.

1864-1882 Period

Along with the placer mines came the discovery of significant lode claims. In Montana and Idaho many of these hardrock mines were found at upper elevations in close proximity to stands of whitebark pine. As the placer mines gave way to hardrock mines, which required milling, a new era was introduced into the territory. Hardrock mines required substantial amounts of wood for mine supports, railroad tracks, mine buildings, mills for ore reduction, huge amounts for fueling steam engines used in the mines and the mills, and wood for use in ore reduction and the refining process (USDA 1932). In addition, hardrock mining and reduction required a large permanent labor pool; these workers needed houses and wood for heat. These requirements were met by the forest resources of the surrounding area, mostly from the public domain. Because the timber stands surrounding the mines contained whitebark pine, it was natural that it was utilized along with other species.

Butte-Anaconda Area

The development of the Butte-Anaconda area was destined to play a major role in the use of whitebark pine. Not only were major mineral deposits present, but whitebark pine was common in the higher elevation stands as shown in table 2. These trees were also of good form when compared to the normal whitebark pine stands.

In 1864 the Butte area was important for its placer gold activity centered around the original town of Silver Bow (Freeman 1900). By 1866 most of the placer activity was over, and by 1868 the gravel beds had played out. Silver ore had been discovered soon after the discovery of the placer gold, and attempts were made to mill the ore in 1867. These early attempts failed often because of a lack of knowledge in milling procedures (Freeman 1900). With these failures many of the people left for other camps. This 4-year period probably resulted in a minor impact on the timber resource near Butte. William Clark, one of the "Copper Kings," acquired four mines in Butte in 1872 and the Dexter Mill in the latter part of the 1870's (Malone 1983). Continued efforts were made between 1869 and 1874 to use the quartz ores in the Butte area but with little success. In 1875 a revival of interest occurred in the quartz claims in the Butte area when smelters were developed capable of effectively milling the ore (Freeman 1900). Clark built the Colorado Smelting and Mining Company operation in 1878 to process silver ore (Malone 1983).

Since there was no railroad into Montana, all the fuel for these operations plus lumber needed for construction came from local sources. This demand was met by the forests in the Flint Creek Valley and the area immediately adjacent to Butte, Philipsburg, and Argenta. By 1879 it is estimated that 42 mills were cutting 6,000 thousand board feet (mbf) of lumber annually in Montana to meet development needs (Butcher 1967). By 1880, 3,000 people were living in Butte and the first railroad from

Utah reached the area. This event played a significant role in the expansion of the mining industry as ores or refined metals could be sent to market much cheaper and quicker (Freeman 1900).

Around 1875 "heap roasting" of ores was begun. Large lumps of almost pure sulfide ore were intermixed with layers of logs. The size of the heaps could be up to a city block long, as wide as a city street, and as high as a man (Deer Lodge County History Group 1975; Macmillan 1973). Using these estimated sizes and assuming about one third of the stack was wood, about 200 cords went into each pile. These stacks burned 2 to 3 weeks, the ore was recovered, and a new stack built. Many of these stacks would be burning at the same time resulting in a tremendous amount of cordwood used each year for this one process (Macmillan 1973). Evidence indicating the amount of timber harvested around Butte during this period is limited. But based on stand ages near Butte, much of the available timber was removed by 1885 (Joy 1989). Whitebark pine probably made up less than 2 or 3 percent of the total volume.

Marcus Daly arrived in Butte in the 1870's and in 1882 acquired an interest in the Anaconda Mine, which eventually set the stage for the development of the mill at Anaconda and major exploitation of the timber resource of Montana. Wood was the principal fuel with minor amounts of coal used where locally available. Most of the timber lands were still in the public domain, although the Northern Pacific had acquired over 1,500,000 acres for constructing a railroad through Montana (Butcher 1967). Since there was no control of cutting on the public domain, no records were kept on the amount of timber harvested. Wood cutters continued to cut what was available, moving to the higher elevations and more distant sites as local sources were depleted. A story from a Mineral County paper quoted by Davis gives a good description of the period:

> The source of heat and power in those days was mainly dependent upon the efforts of the humble woodchopper, supplemented in a small measure by costly coke shipped from the Pennsylvania coal fields. But cordwood was the main and most dependable resource. The chopper appeared in thousands and he did this job so well that the hills and mountains surrounding Butte for a radius of many miles were completely stripped of their forest growth during the years preceding the utilization of coal and hydro-electric power. Everything that would burn was cut and fed into the mouths of the boilers and smelting furnaces and much of the natural beauty of hill and mountain was changed into desolation. . ..
>
> Cordwood was a staple product and poured into Butte and Anaconda in thousands of cords daily by wagons, sleighs, pack trains, and flumes, and went up in smoke from mine hoists, smelters, "heap" roasting of ores and stampmills, to say nothing of the baseburner and kitchen stove, for wood was the only resource in which to keep the "home fires" burning (Davis 1963).

While the total use of whitebark pine may have been limited during this period, use of the forests adjacent to Butte set the stage for the exploitation of whitebark pine in future years.

Butte-Anaconda Area, 1883-1896

A major change and expansion in smelting operations was under way. Silver ore gave way to copper and the mill at Anaconda was established (Anaconda Copper Mining Co. 1909). McCune and Caplice were given a contract to supply the mill at Anaconda with 300,000 cords of firewood at the rate of 75,000 cords per year (Deer Lodge County History Group 1975; Kelly 1983). Flumes were constructed in Mill and Willow Creeks to bring the wood to the mill (figs. 1 and 2). At first mules with pack saddles were used to bring the cordwood to the flume (fig. 3). Later a narrow-gauge railroad was built into the woods with a donkey engine and long cable used to pull the cars loaded with wood to the loading platforms at the flume (Kelly 1983) (fig. 4).

It is estimated that about 718,868 cords were removed from present-day National Forest lands during this period, or about 194,000 mbf (Kelly 1983; Newell 1980). The

Figure 1—Flume in French Gulch 1906.

Figure 2—End of flume in Mill Creek near Anaconda, MT, 1906.

Figure 3—Getting wood for the Colorado Smelter, Butte, MT.

Figure 4—Tram landing 1908.

majority of this volume was lodgepole pine, but based on cruises cited in table 2, an estimated 12,000 mbf of whitebark pine may have been cut. Since much of the volume was for firewood or stulls for the mines, tree size was not important and if whitebark pine was present, it probably was taken (Kelly 1983; USDA n.d.). In 1885 there were 300 mines, nine stamp mills to crush the quartz ores, and as many as seven copper smelters operating in and around the city of Butte in addition to the works at Anaconda (Macmillan 1973). All of these operations required wood for fuel. In 1883 the mill at Anaconda alone used about 200 cords per day. By 1891 this had increased to 360 cords per day. An upgrading of the mill increased use to 700 cords per day in the fall of 1891. This rate continued through 1892. Lumber requirements for the same period were 40,000 mbf in 1888 and 100,000 mbf for both 1891 and 1892.

The mills at Butte continued to process ore using heap roasting up until about 1894 when it was outlawed by the town. A report from 1890 indicated that about 25,000 tons of ore were constantly in the process of open-air roasting (Macmillan 1973). It was becoming necessary to go elsewhere to find lumber as cutting in the Butte area had depleted much of that resource. During this period the Northern Pacific Railroad was being constructed through Montana, and it also required large amounts of wood. To meet these needs and those of the Butte-Anaconda area, the Montana Improvement Company was formed in 1882 (Butcher 1967). The first mill was established at Bonner with logs coming from the Blackfoot drainage.

In 1884 cutting began in the Flathead Indian Reservation. Much of this volume was for the railroad construction, but portions found its way into the lumber market or the mines. In 1888 the lumber mills in Montana produced 150,000 mbf, a large portion of which went to the Butte-Anaconda operations (Butcher 1967).

1897-1905 Period

While placer mining began early in Idaho, hardrock mining in the whitebark pine environment was delayed until the 1890's. The Spring Creek area on the present-day Salmon National Forest was developed at this time, and a stamp mill was constructed on site. It is unclear how long this mine was active, but use extended into the early 1900's (Jacobsen 1989; Umpleby 1913). In several areas along the Continental Divide old wood ricks remain that had been cut for firewood for these mills. Many of these ricks contain large amounts of whitebark pine (Hamilton 1989), but no estimates of volume could be made.

Butte-Anaconda Area

There are few references to timber use during this period in the studies reviewed. If harvest continued at the same rate as in the previous period, approximately 500,000 cords may have been harvested in the immediate area. This may represent 8,000 mbf of whitebark pine. The new smelter was completed at Anaconda, which greatly increased the milling capacity; however, increased availability of coal may have precluded any major change in firewood needs (Deer Lodge County History Group 1975; Kelly 1983).

The use of electricity, which would eventually replace wood for fuel in many applications, was also increasing (Johnson 1988; Quivik 1988). The Alice Mine became the first mine in Butte to use electric lights in 1881, and by 1900 Butte mines used electricity for surface tramming. As early as 1890 a small dam on Georgetown Lake was supplying electricity for the mines at Granite, but technology to transmit the amounts of electricity required for the large mills was not available (Johnson 1988; Quivik 1988; Sorte 1960). Daly installed an onsite generation plant using coal at Anaconda about 1890 (Quivik 1988). Coal needs were obtained from the towns of Storrs and Aldridge in the Bozeman area (Chadwick 1973). By the 1900's steam generation plants were running in Butte and a hydroelectric plant had been installed on the Big Hole River near Divide. Additionally, power was being produced at Canyon Ferry on the Missouri River and brought to Butte on relatively low-voltage lines. In 1905 Anaconda Company acquired the plant at Ennis and enlarged it for additional electricity production (Johnson 1988).

Butte-Anaconda Area, 1906-1915

Major changes in the operation of the mills and ownership and control of the timber resource occurred during this period. In 1906 all smelting operations in Butte were moved to Great Falls with the exception of the Butte Reduction Works operated by William Clark. He continued the business until 1910 when he finally sold his operations to Anaconda (Malone 1983). Wood for the Great Falls plant was brought from Kalispell as well as the Missoula area and was obtained from low-elevation stands of larch, Douglas-fir, and ponderosa pine.

In 1905 the Hell Gate Forest Reserve was established and in 1906 the Big Hole Reserve. The Deerlodge National Forest was formed from portions of these reserves in 1908. Starting in 1906, records are available on volume removed from these reserves. Unfortunately, species are not identified. One of the first sales was to W. R. Allen for 100,000 mbf in the French Gulch drainage (USDA n.d.). He built an extension to the McCune flume that crossed the Continental Divide into the Bighole drainage. The flume crossed the divide at about 7,000 ft elevation, which is generally near the lower limits of whitebark pine (Joy 1989). The flume covered about 18 miles, and had 29 trestles, the highest of which was 72 ft and spanned 775 ft (fig. 5). Most of the timber cut was for firewood and stulls for the mine (fig. 6). Cutting occurred throughout the year with the floating season from May to November (Newell 1980). Many problems occurred with this sale, often the result of Forest Service inexperience in administration of a sale of this size. At first the logger was allowed to select what he wanted. In late 1906 cutting rules were developed with clearcuts 150 ft wide interspersed with 75-ft leave strips. Later this design was divided into 75-ft^2 alternate blocks. Windfall was a major problem with this design. In 1909 a system was established using strips 100 to 150 ft wide. This approach resulted in many small unmerchantable trees being left. In 1910 the rule was changed to clearcutting in overmature stands and thinning in immature stands. Allen got a new contract for an additional 100,000 mbf, and cutting continued until 1917 when the contract expired. At that time operations were moved to lower elevations in the Flint Creek drainage where whitebark pine was less frequent (Newell 1980).

Cutting continued in other areas around the Butte-Anaconda area. An estimated 8,600 mbf of whitebark pine was harvested. This estimate was developed by using the percent of whitebark pine present by drainage (table 2) for sales over 7,000 ft elevation. This period marked the end of heavy cutting in the Butte-Anaconda area. The demand for firewood dropped significantly after 1912 as electrification was implemented in the mills. Between 1908 and 1910 a new dam was built at Rainbow Falls near Great Falls and a 100-kW line was built to the Butte-Anaconda area. This was one of the first long-distance transmissions of high voltage and permitted the mills to turn to more electrification (Quivik 1988). Up to this point all hoist operations, which represented a major energy demand at the mines, were supplied by steam. These were now converted to electricity.

Figure 5—Trestle on French Gulch Flume 1906.

Figure 6—Fuelwood and stull cutting, French Gulch 1908.

1916-1940 Period

During the early 1930's "tie hackers" for the Chicago, North Western, and Burlington Northern Railroads cut ties in the Dunoir area west of Dubois, WY. Whitebark pine is found on these sites mixed with lodgepole pine. It has a good form, and it was harvested along with the other species present. No estimates of this use are available, however (Houston 1989).

Table 3—Estimated whitebark pine use in the Butte-Anaconda area between 1860 and 1940

Time period	Estimated whitebark pine harvest
	(thousand board feet)
1860-1882	3,000
1883-1896	12,000
1897-1905	8,000
1906-1910	3,200
1911-1915	11,400
1916-1920	800
1921-1925	180
1926-1930	180
1931-1935	60
1936-1940	10
Total	38,830

Butte-Anaconda Area

Between 1914 and 1923 the annual requirement for wood products in the Butte-Anaconda market was 400,000 stulls, 55,000 converter poles, 130,000 lagging poles, and 3,000 cords of firewood for area home use (USDA 1932). Volumes continued to decline with most of the harvest in latter years going for home fuel.

The area north of Anaconda was described as having most of the accessible material removed by 1924. The Anaconda Copper Mining Company's needs came chiefly from the Big Blackfoot Drainage (USDA 1932). Of the 35,000 acres evaluated by the proposed exchange, 28,000 were listed as logged and 3,800 acres burned. Much of the area was clearcut and most of the marketable-sized material was taken. By 1919 coal was the principal fuel used in the smelting process (Anaconda Copper Mining Co. 1919). Natural gas came to the area in 1932 and further reduced dependency on wood and coal (Kelly 1983).

Summary of Whitebark Pine Use

It is evident that significant use was made of whitebark pine between 1860 and 1940. A major portion of the volume came from the public domain during a period of laissez-faire attitude in the country. No attempts were made to record use, and figures available represent information that was collected by government agents years after the fact. Table 3 presents an estimate of use of whitebark pine between 1860 and 1940 for the Butte-Anaconda area; it does not include other parts of Montana. These areas may account for an additional 500 mbf.

As a check of these figures, a rough survey of cutover lands in the Butte-Anaconda area was conducted. Using volumes presented in the Deerlodge National Forest Plan (USDA 1987), an estimated 100,000 mbf of whitebark pine may have been utilized. These values suggest that total use may be somewhere between 40,000 mbf and 100,000 mbf. Based on the fragmentary information for the ACM Company during the period from 1882 to 1925, it is estimated that 4.7 billion board feet of wood was used by their operation alone. In addition some 50,000 mbf was used for home heating. Before 1906 an unestimated amount was used by the other mining operations not controlled by Anaconda. While these figures are only rough estimates, they provide an expression of the magnitude of timber activity found around the Butte-Anaconda area and the role whitebark pine played in that use.

RECENT USE

Presently, the role of whitebark pine in timber harvest is insignificant. Harvest activity continues to occur in this type in Montana, Idaho, and Wyoming. Most whitebark pine harvest is in conjunction with spruce or subalpine fir with which it is growing. Cutting during the past 20 years has occurred in northwestern Wyoming in the Bridger-Teton National Forest, but it has been incidental to regular timber harvest and amounts are included with other species. The extent of this cutting could not be determined. A similar condition was found in Idaho where cutting in the type has occurred in the Salmon and possibly the Payette National Forests. Significant acres of the type were killed by mountain pine beetle in the 1930's and 40's in Montana and Idaho. Where accessible, much of this material is currently being used for firewood or house logs. Again no records have been kept to determine the extent of this activity (Jacobsen 1989). Regeneration efforts are geared to replacing the stands with spruce or lodgepole pine and whitebark pine regenerates through natural regeneration.

An estimated 900 acres of whitebark pine type have been harvested in the Northern Region. Table 4 provides a breakdown by forest, which indicates that most harvest has occurred in the Gallatin and Deerlodge National Forests. Much of the type has been allocated to noncommodity uses in recent National Forest planning efforts. Similar information is not available for the Intermountain Region as it is lumped in with other types. California and the Pacific Northwest Regions have no reported use of the type. Indications are that the trees in these areas are of poorer form and, therefore, have been ignored in timber activity. Limited investigations were made on utilization of whitebark pine in Canada. A report by Day suggested that some large stands are found in Alberta in the Crowsnest Forest. Some of these stands contain 10 percent or more of large whitebark pine (Day 1967), which has been harvested and sold along with the lodgepole pine.

Table 4—Acres harvested in the whitebark pine type by National Forest in the Northern Region

Montana forests	Acres	Idaho forests	Acres
Bitterroot	29	Clearwater	1
Beaverhead	91	Kootenai	42
Custer	7	Nezperce	8
Deerlodge	176		
Flathead	37		
Gallatin	402		
Helena	22		
Kootenai	42		
Lolo	67		

CONCLUSIONS

While it is quite evident that significant amounts of whitebark pine have been used in the past and minor amounts are still being cut, there has never been a real interest in whitebark pine lumber or management for whitebark pine. If turn-of-the-century mining activity had been adjacent to the timber types found in the Kalispell, Missoula, or Bitterroot Valley areas, whitebark pine would probably have been ignored. Its use has been based on convenience and its association with other tree species. Use of whitebark pine will probably never reach the heights it experienced at the turn of the century and its place in the future may be that of providing food for wildlife. We still have much to learn about the tree itself.

REFERENCES

Anaconda Copper Mining Company. 1919. The Anaconda reduction works. [No publisher shown]. 32 p.

Anaconda Copper Mining Company's Staff. 1909. A brief description of the Washoe Smelter, Anaconda Copper Mining Company, Anaconda, MT: Standard Publishing Co. 32 p.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Butcher, Edward Bernie. 1967. An analysis of timber depredations in Montana to 1900. Missoula, MT: University of Montana. 118 p. Thesis.

Chadwick, R. A. 1973. Coal. Montana's precious treasure. Montana: The Magazine of Western History. 23(3): 18-31.

Dana, Samuel T. 1956. Forest and range policy: its development in the United States. New York: McGraw-Hill. 455 p.

Davis, Jean. 1963. Shallow diggin's. Caldwell, ID: The Caxton Printers. 375 p.

Day, R. J. 1967. Whitebark pine in the Rocky Mountains of Alberta. Forestry Chronicle. 43(3): 278-282.

Deer Lodge County History Group. 1975. Under the shadow of Mount Haggin: the story of Anaconda and Deer Lodge County from 1863 to 1976. Deer Lodge, MT: [Publisher unknown].

Elias, Thomas S. 1987. The complete trees of North America. New York: Gramercy. 948 p.

Fisher, Vardis; Holmes, O. L. 1968. Gold rushes and mining camps of the early American west. Caldwell, ID: The Caxton Printers. 466 p.

Freeman, Harry C. 1900. A brief history of Butte, Montana. Chicago, IL: The Henry O. Shepard Co. 123 p.

Forbes, Reginald D. 1956. Forestry Handbook. New York: The Ronald Press Company. 1166 p.

Hall, William L.; Maxwell, Hu. 1911. Uses of commercial woods of the United States: II Pines. Bulletin 99. Washington, DC: U.S. Department of Agriculture, Forest Service. [Pages unknown].

Hamilton, Ron. 1989. [Personal communication]. January 25. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region, Regional Office.

Hazen, Jon H. [n.d.]. The woodheat handbook. Boise, ID: Idaho Office of Energy. [Pages unknown].

Houston, Kent E. 1989. [Personal communication]. March 16. Cody, WY: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Shoshone National Forest.

Jacobsen, Robert L. 1989. [Personal communication]. January 26. Salmon, ID: U.S. Department of Agriculture, Forest Service, Intermountain Region, Salmon National Forest.

Johnson, Carrie. 1988. Electrical power, copper, and John D. Ryan. Montana: The Magazine of Western History. 38(4): 24-37.

Joy, John. 1989. [Personal communication]. January 20. Butte, MT: U.S. Department of Agriculture, Forest Service, Northern Region, Deerlodge National Forest.

Kelly, Matt J. 1983. Anaconda: Montana's copper city. Butte, MT: Artcraft. 75 p.

Keenan, F. J. 1970. Mechanical properties of whitebark pine. Forestry Chronicles. 46(4): 322-325.

Macmillan, Donald. 1973. A history of the struggle to abate air pollution from copper smelters of the Far West 1885-1933. Missoula, MT: University of Montana. 380 p. Dissertation.

Malone, Michael P. 1983. Midas of the West: the incredible career of William Andrews Clark. Montana: The Magazine of Western History. 33(4): 2-17.

Newell, Alan S. 1980. Historic resources study: Mount Haggin Area, Deer Lodge County, Montana. Unpublished report prepared for: Montana Department of Fish, Wildlife and Parks. Missoula, MT: Historical Research Associates. 94 p.

Quivik, Fredric L. 1988. Early steel transmission towers and energy for Montana's copper industry. Montana: The Magazine of Western History. 38(4): 67-69.

Sorte, Donald L. 1960. The Hope Mining Company of Philipsburg. Missoula, MT: University of Montana. 96 p. Thesis.

Umpleby, J. B. 1913. Geology and ore deposits of Lemhi County, Idaho. Bulletin 528. Washington, DC: U.S. Department of the Interior, Geological Survey.

U.S. Department of Agriculture, Forest Service. [n.d.]. Atlas of timber harvest on the Deerlodge Forest from 1906. Unpublished maps on file at: U.S. Department of Agriculture, Forest Service, Deerlodge National Forest, Butte, MT.

U.S. Department of Agriculture, Forest Service. 1932. Mines Timber Company, Deerlodge sales. On file at: Historical Research Associates, Missoula, MT. [pages unknown].

U.S. Department of Agriculture, Forest Service. 1987. Forest plan Deerlodge National Forest. On file at: U.S. Department of Agriculture, Forest Service, Deerlodge National Forest, Butte, MT. 342 p.

BERRY PRODUCTION IN THREE WHITEBARK PINE FOREST TYPES

T. Weaver
K. Kendall
F. Forcella

ABSTRACT

In the whitebark pine/whortleberry (Pinus albicaulis/ Vaccinium scoparium) *habitat type of southwestern Montana, whortleberry plants produced seven to 69 berries/*m^2 × *yr in 1974. In subalpine fir* (Abies lasiocarpa) *habitat types of northwestern Montana, huckleberry plants* (Vaccinium globulare) *may produce from 13 to 228 berries/*m^2 × *yr. While removal of competing trees increases production, thinning the understory apparently reduces berry production in direct proportion to the shrubs removed; there is no compensatory production indicative of shrub-shrub competition in fully vegetated plots. Fifty- to 100-fold variation in production among years in* Vaccinium globulare *berry production is attributed to variation in weather conditions.*

INTRODUCTION

Vaccinium species are common associates of whitebark pine (*Pinus albicaulis*). Whortleberry (*Vaccinium scoparium*) dominates the understories of relatively dry high-altitude forests in which whitebark pine is either climax (*Pinus albicaulis/Vaccinium scoparium* and *Abies lasiocarpa-Pinus albicaulis/Vaccinium scoparium* HT's) or seral (*Abies lasiocarpa/Vaccinium scoparium* HT). Lower in whitebark pine's altitudinal range, and especially on relatively moist sites near the Canadian border, one also finds huckleberry (*Vaccinium globulare*) in communities including *Abies lasiocarpa/Xerophyllum tenax-Vaccinium globulare* HT (Martin 1979). Habitat type (HT) and plant association names follow Pfister and others 1977.

Vaccinium berries are important foods of bears (black and grizzly), birds (Clark's nutcracker, Cassin's finch, flickers, ravens, and robins), small mammals (squirrels, redbacked voles, and deer mice), and humans; and their production is therefore of interest to wildlife managers. This note summarizes our observations on the variation in berry production with changes in habitat type, overstory cover, shrub cover, and year.

METHODS

Two independent studies were conducted, one in the Madison Range of southwestern Montana near Bozeman, and the other in the Glacier National Park and Whitefish Range in northwestern Montana.

Whortleberry fruit densities in the understories of five *Pinus albicaulis/Vaccinium scoparium* forests in the Madison Range study were determined by counting the berries in m^2 quadrats placed at alternate meters along the center line of 10- by 30-m plots sampled in a study of forest productivity (Forcella 1977; Forcella and Weaver 1977). Berry density was also recorded in a clearcut ski-run between the two forest stands measured on Lone Mountain (Madison Range near Bozeman, MT). All berry counts were made during August of 1974.

Huckleberry fruit densities were measured in relatively young forests on *Abies lasiocarpa-Pinus albicaulis/ Vaccinium scoparium* and *Abies lasiocarpa/Xerophyllum tenax-Vaccinium globulare* habitat types in the Rocky Mountains of Glacier National Park and in the adjacent Whitefish Range. Whitebark comprised relatively low percentages (4 to 40 percent) of the forest canopies, both because whitebark pine is being eliminated from the stands by white pine blister rust (Hoff and Hagle, this proceedings; Kendall and Arno, this proceedings) and because whitebark is never fully dominant in the relatively moist climate of the area (Arno and Weaver, this proceedings). Annual counts (1983-88) were made in seven forests; 20- by 20-cm plots were placed at 50 points located by pacing from permanent stakes along specified compass lines. While *Vaccinium scoparium* was present in some of these plots, its berries were never counted.

AVERAGE BERRY PRODUCTION IN WHITEBARK PINE STANDS

Average whortleberry production ranged from seven to 69 berries/m^2 in five closed *Pinus albicaulis/Vaccinium scoparium* stands observed in southwestern Montana during the summer of 1974 (table 1). Because July-August precipitation in 1974 was 132 percent of normal and precipitation in the preceding August was 119 percent of normal (USDC 1973-1989), these yields are probably average or above average. The average whortleberry weighed (dry) 0.0075 g.

During the 1983-88 period, huckleberry production averaged 45 to 228 berries/m^2 in three *Abies lasiocarpa-Pinus albicaulis/Vaccinium scoparium* stands and 13 to

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

T. Weaver is Plant Ecologist, Department of Biology, Montana State University, Bozeman, MT 59717; K. Kendall is Research Biologist, Glacier National Park, West Glacier, MT 59936; F. Forcella is Research Agronomist, North Central Soil Conservation Research Lab, Agricultural Research Service, U.S. Department of Agriculture, Morris, MN 56267.

Table 1—*Vaccinium* berry production (berries/m^2) in three habitat types

Environmental type (HT)[1]	Location[2]		Year	Arboreal cover	Wortleberry		Huckleberry	
					Cover	Berries	Cover	Berries
				Percent	*Percent*	*Per m^2*	*Percent*	*Per m^2*
PIAL/VASC[3]	Madison	1LM	1974	73	42 ± 3	68 ± 9	none	present
	Madison	1-2	1974	0	48 ± 4	372 ± 47	_	_
	Madison	2LM	1974	97	44 ± 4	52 ± 9	_	_
	Gravelly	10MM	1974	52	31 ± 3	69 ± 10	_	_
	Elkhorn	11	1974	40	21 ± 2	7 ± 2	_	_
	Tobacco Rt	14	1974	56	50 ± 3	15 ± 4	_	_
ABLA-PIAL/VASC[3]	Lewis	2DF	1983-1988	4	0	not counted	60	135 ± 65
	Lewis	3MB	1983-1988	22	26		30	45 ± 15
	Apgar	6HM	1983-1988	0	30	_	35	228 ± 141
ABLA/XETE-VAGL[4]	Whitefish	1MO	1983-1988	24	35	_	50	34 ± 7
	Whitefish	2MO	1983-1988	44	60	_	35	13 ± 5
	Lewis	1MB	1983-1988	16	35	_	52	64 ± 14
	Lewis	1TM	1983-1988	42	0	_	70	33 ± 7

[1] Habitat types are *Pinus albicaulis/Vaccinium scoparium*, *Abies lasiocarpa-Pinus albicaulis/Vaccinium scoparium*, and *Abies lasiocarpa/Xerophyllum tenax-Vaccinium globulare* (Pfister and others 1977).

[2] Locations are given by mountain range and site number. PIAL/VASC sites are described in more detail by Forcella 1977.

[3] *Vaccinium scoparium* (VASC) standard errors represent quadrat to quadrat variance, $n = 15$.

[4] *Vaccinium globulare* (VAGL) standard errors represent year to year variance, $n = 50$.

64 berries/m^2 in four *Abies lasiocarpa/Xerophyllum tenax-Vaccinium globulare* stands in northwestern Montana. Huckleberry weights (dry) range from 0.02 to 0.11 g and average 0.06 g (Stark 1990).

OVERSTORY-UNDERSTORY COMPETITION

Removal of the whitebark canopy in an area between stands 1LM and 2LM resulted in a sixfold increase in whortleberry fruit production (table 1). Regression of huckleberry production against overstory cover indicates exponential decreases in berry production with increases in overstory cover; the equation [berries/m^2 = 214 e (– 0.075 canopy cover)] explains 96 percent of the variance in the berry production data ($r^2 = 0.96$) and has a probability of 0.001. Removal of the tree canopy also increased huckleberry production in nonwhitebark forests (Minore 1972; Zager and others 1980).

The inhibition of berry production by tree canopies is often attributed to lack of light energy (Dahlgreen 1984; Martin 1983). Other hypotheses seem equally good. Since the failure of tree seedlings in closed forests is sometimes due to lack of water or nutrients rather than lack of light (Watt and Fraser 1933; Weaver 1974), and since the failure of seedlings in whitebark forests appears to be more likely due to edaphic than light factors (Weaver and others, this proceedings), berry production might also be limited by an edaphic factor. An additional possibility is that berry production might decrease with increases in canopy cover if lack of light inhibited pollinators or promoted flower- or fruit-attacking fungi.

COMPETITION AMONG SHRUBS

If berry plants compete, one expects the production per unit area covered to fall with increases in percent of shrub cover. The hypothesis of strong within-species competition among whortleberry plants is negated by the linear rise in berry production with increases in *Vaccinium* cover both in closed stands (berries/m^2 = 0.65 cover + 18.75, $r^2 = 0.56$) and in logged stands (berries/m^2 = 9.85 cover – 102, $r^2 = 0.66$, $p = 0.0$). In huckleberry stands neither we nor Martin (1983) found any correlation between shrub cover and berry production.

WEATHER AFFECTS HUCKLEBERRY PRODUCTION

Huckleberry fruit production varied considerably among years with notable lows across most stands in 1984 and 1987 (table 2). Year-to-year variance surely depends on a succession of weather-condition effects on flower initiation, pollination, winter kill, plant carbohydrate stores, and photosynthesis during the berry-filling period. The poor production observed across all stands in 1984 and 1987 suggests a common meteorological cause. We (1) hypothesize that water was the factor most likely responsible, (2) eliminate rainfall in the bearing season as a factor because, while 1984 was dry, 1987 was wet, and (3) speculate that the failed crops were due to drought during the flower bud initiation season, because the Augusts preceding both 1984 and 1987 were very dry (table 3).

Table 2—Annual variation in huckleberry berry production (in percent of maximum berry count/m^2)

Site	Max/m^2	1983	1984	1985	1986	1987	1988
2DF	410	60	15	11	100	0	11
3MB	95	48	19	89	34	0	100
6HM	512	100	18	99	29	0	21
1MO	58	86	21	48	45	47	100
2MO	29	86	3	31	14	31	100
1MB	95	77	57	100	88	3	771
1TM	51	86	10	94	100	55	47
Berry index[1]		17	36	19	21	36	20

[1] Berry yields were recorded in seven stands for 6 years. Yields were ranked across years by giving the high production a 1, the low production a 6. Ranks were summed across stands to index the productivity of each year. Productivities were similar in all years except 1984 and 1987 when high scores indicate poor crops.

Table 3—Precipitation (inches) in West Glacier, MT. Months with less then half of normal precipitation are asterisked

	Year:	1982	1983	1984	1985	1986	1987	1988	
Month	Berry index[1]:		17	36	19	21	36	20	Normal
May		1.40	0.96*	3.54	3.00	2.55	1.96	3.27	2.51
June		2.48	4.41	2.83	1.77	3.44	2.05	1.58*	3.42
July		2.58	4.70	.42*	.09*	3.02	3.32	1.56	1.44
August		.89	.52*	.73*	2.08	.54*	2.20	.36*	1.49
September		2.12	1.43	3.61	4.83	3.49	.33*	1.83	2.25

[1] High berry yield indices from table 2 indicate low yields in 1984 and 1987. While one summer was dry (1984) and the other one was wet (1987), both were preceded by dry Augusts.

ACKNOWLEDGMENTS

Forcella gathered the whortleberry data. Kendall gathered the huckleberry data with the help of R. Potter, L. Stoltz, and S. Kiser. Weaver prepared the manuscript. We are grateful for the support of Glacier National Park, Montana State University, and USDA Forest Service Contract #12-11-204-12, Supplement 33.

REFERENCES

Dahlgreen, M. 1984. Observations on the ecology of *Vaccinium membranaceum* Dougl. of the southeast slope of the Washington Cascades. Seattle, WA: University of Washington. 120 p. Thesis.

Forcella, F. 1977. Flora, chorology, biomass and productivity of the *Pinus albicaulis/Vaccinium scoparium* association. Bozeman, MT: Montana State University. 99 p. Thesis.

Forcella, F.; Weaver, T. 1977. Biomass and productivity of the subalpine *Pinus albicaulis-Vaccinium scoparium* association in Montana, USA. Vegetatio. 35: 95-105.

Martin, P. 1979. Productivity and taxonomy of the *Vaccinium globulare-Vaccinium membranaceum* complex in western Montana. Missoula, MT: University of Montana. 136 p. Thesis.

Martin, P. 1983. Factors influencing globe huckleberry fruit production in northwest Montana. International Conference on Bear Research and Management. 5: 159-165.

Minore, D. 1972. The wild huckleberries of Oregon and Washington: a dwindling resource. Res. Pap. PNW-20. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 20 p.

Pfister, R.; Kovalchik, B.; Arno, S.; Presby, R. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Stark, N. 1990. [Personal communication]. January. Missoula, MT: University of Montana, School of Forestry.

U.S. Department of Commerce. 1973-1989. Climatological data, Montana. Washington, DC: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Environmental Data Service.

Watt, A.; Fraser, G. 1933. Tree roots in the field layer. Journal of Ecology. 21: 404-414.

Weaver, T. 1974. Interference with grass production by interaction of oak and Aristida roots in the Carolina fall-line sandhills. Proceedings; Montana Academy of Science. 34: 27-29.

Zager, P.; Jonkel, C.; Habeck, J. 1980. Logging and wildfire influence on grizzly bear habitat in northwest Montana. International Conference on Bear Research and Management. 5: 124-132.

USE AND IMPACT OF DOMESTIC LIVESTOCK IN WHITEBARK PINE FORESTS

E. Earl Willard

ABSTRACT

The whitebark pine (Pinus albicaulis) *ecosystem has historically been important as summer range for livestock. These ranges supply nutritious, green forage to supplement the often-dry summer ranges of lower elevations. Many areas were grazed by huge herds in the late 1800's and early 1900's. These herds have been greatly reduced due to recognition of the unacceptable levels of disturbance to the soil and vegetation, leading to overall range improvement. This paper summarizes the impact of livestock grazing in the whitebark pine ecosystem, including a history of grazing, disturbance of soils and plant communities, changes in livestock numbers and grazing management, and a view of the future.*

INTRODUCTION

Whitebark pine (*Pinus albicaulis*) ranges occur in a cold, windy, snowy, and generally moist climatic zone at timberline (Arno and Hoff 1989). Stands occur in a mosaic of subalpine parklands and alpine meadows, often remote and on steep, rugged terrain.

A combination of high precipitation, unstable soils, fairly steep slopes, and a short growing season with extreme weather variations makes proper livestock grazing very difficult on such ranges (Mueggler 1962). Blizzard conditions commonly occur in timberline types in all months except July and August (Pfister and others 1977). Since the snow is slow to melt in the spring, the soil is slow in warming and plant growth is delayed; the growing season is short (Thilenius 1975). Thus, livestock use the whitebark pine zone as summer range.

One problem with maintaining livestock on high-elevation ranges too late into the season (mid to late September) is the chance of heavy snowfall. Early fall snowstorms are disadvantageous in two ways: (1) the obvious danger of high losses of animals, and (2) the danger of heavy trampling damage to the soil where the soil has been moistened by snow, but where it is not yet solidly frozen (Thilenius 1975).

Some sites such as drainage bottoms, wet meadows, and grassy slopes are preferred by livestock, while forested sites and steep slopes are less preferred (Willard and others 1983). Water is often located in drainage bottoms and unevenly distributed. When cattle water in the bottoms, they tend to spend more time on the lower slope as the slope becomes steeper. For example, Mueggler (1965) found that on a 10 percent slope, 75 percent of cattle use is likely to be within 810 yd of the foot of the slope; on a 60 percent slope, 75 percent of cattle use will probably occur within 35 yd of the bottom. Thus, livestock grazing distribution is usually uneven on such ranges.

Jardine and Anderson (1919) reported that each class of livestock uses the high-mountain ranges differently. Cattle prefer open grassy parks and meadows close to water and shade. Horses prefer high, open grass ridges; compared with cattle they will travel longer distances to water. Sheep will penetrate and utilize small areas of fallen timber; they can easily utilize areas that can be ridden through on horseback, and if quietly handled they will use areas that a horse cannot get through. Horses will use grass range not well suited to sheep and too far from water or too rough for full use by cattle.

Sheep are the principal livestock now using the subalpine zone, since most breeds of cattle are poorly adapted to the colder, windy climate (Thilenius 1975). Horse use is significant in wilderness areas, mostly by recreationists' and government administrative stock.

Livestock forage in the whitebark pine ecosystem varies considerably, depending on the local climate, associated vegetation types, and past grazing. Some dry-site whitebark pine stands in semiarid regions have open, grassy understories, but undergrowth is sparse in Sierra Nevada stands (Arno and Hoff 1989). Common juniper (*Juniperus communis*), practically worthless as livestock forage, is a major understory plant in Alberta stands (Baig 1972). Steele and others (1981) stated that forage production may sustain light grazing, but in many areas grazing abuse has decimated the forage and exposed the soil; vegetation recovers slowly and, in some areas, soil loss may preclude complete restoration.

Pfister and others (1977) reported that the major understory species in Montana of value to livestock include *Calamagrostis canadensis, C. rubescens, Carex geyeri*, and *Xerophyllum tenax*. Forage production is low in these stands. However, forb and grass growth may be luxuriant

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

E. Earl Willard is Professor of Range Resources Management, School of Forestry, University of Montana, Missoula, MT.

in certain timberline areas, particularly those east of the Continental Divide on better soils. These ranges are presently grazed very little in Montana (Willard and others 1983).

Steele and others (1981) reported that *Arnica cordifolia* is often the dominant forb in the undergrowth in Idaho; livestock seldom find much forage in the understory but may use these sites for bedding and shelter. Whitebark pine stands farthest from areas of heavy grazing may have an undergrowth dominated by *Festuca idahoensis* or *Stipa occidentalis*. Understory species vary considerably and range from *Festuca idahoensis* on dry, exposed sites to *Carex geyeri* and *Vaccinium scoparium* on more mesic sites.

Franklin and Dyrness (1973) reported that on associated alpine meadows in Oregon and Washington, the major community of importance to livestock is the *Festuca viridula/Lupinus latifolius* community. It is snow-free for a period of 3-4 months. Other communities are of very limited value to livestock.

Mueggler (1962) stated that subalpine herblands that are natural openings on high-elevation slopes and ridges in northern Idaho form only a small part of the range area, yet furnish an important part of the summer forage. Such areas in good condition produce abundant grasses and forbs, but they are very sensitive to grazing abuse.

EARLY GRAZING—THE WESTERN COMMONS

Galbraith and Anderson (1971) reported that cattle were driven from Washington in 1858 to the British Columbia gold mines near Kamloops. Soon, other herds were driven to the Cariboo mining district. The preferred ranges on public lands in British Columbia became badly overgrazed before the Grazing Act was passed in 1919.

During the period of 1850 to 1890, there was rapid expansion of cattle and sheep ranching onto open range in Oregon and Washington. Sheep in great numbers were moved into eastern Oregon and across the Columbia River into Washington beginning in 1892. Sheep were far less expensive than cattle to feed and care for on the range. The market was limited, so the sheep quickly multiplied until the market eventually improved. Sheep numbers rose spectacularly from 1865 to 1901. This was the period of trail herding, when as many as 600,000 sheep were trailed from California and Oregon to stock ranges farther east (Thilenius 1975). Sheep numbers peaked in the western United States around 1910.

Livestock were first introduced into Montana in the mid 1800's. By 1880, approximately 400,000 sheep were reported in the Montana Territory. In the early 1890's, sheepmen gained a foothold on the ranges, especially in the northwestern States. In some States, especially Wyoming, Montana, and Idaho, sheepmen gradually forced the cattle interests from many of their old ranges (Barnes 1926), and many cowmen turned to raising sheep. Sheep in Montana increased to nearly 6 million by 1906.

Sheep were moved up the mountains into the subalpine/alpine zone—more or less following the snow line—for summer grazing. High mountain ridges were often a cloud of dust for most or all of the summer. Intense competition occurred between herders to be first to move their bands onto preferred mountain ranges. No sheepman chose to save forage for future use, knowing it would be sought out by another herder with a hungry band of stock. It was common practice to graze everything into the ground before the sheep were moved down the mountain in the fall. The situation was graphically described by Barnes (1926):

> Every spring the herds of sheep followed the melting snows into the high mountain meadows just as soon as the ground was uncovered. The hungry sheep fed on new plant growth, and their sharp hoofs trampled and cut up the sod until bare wastes took the place of grassy meadows and bunchgrass hillsides. From the pinnacles the owners watched with jealous eyes each other's progress into the high ranges. By day the cloud of dust that rose above the migrating herds, and by night the fires built to keep off the predatory animals, showed the advance of the rival herds.

END OF OPEN RANGE ERA

Much of the whitebark pine ecosystem is located on public lands. The first major act to control grazing on these lands was the reservation of large acreages in National Forests, which provided for grazing controls and grazing fees. The first forest reserve was established in 1891; many others were established by 1900. Grazing control on these forest reserves between 1900 and 1905 was difficult (Dana 1956). Sheep grazing was at first forbidden in all reserves outside Washington and Oregon. The policy was changed in 1901 to allow sheep in those portions of reserves where it could be shown that sheep grazing would not be detrimental.

Initially, horse and cattle grazing were regarded as less detrimental than sheep grazing, so they were subjected to little control on forest reserves. In 1900, however, permits were required for all classes of livestock. Jardine and Anderson (1919) reported that in 1907 approximately 18,500 permits were issued for the grazing of cattle and horses on the National Forests; by 1917 the number had increased to approximately 32,000. In 1907 approximately 1,250,000 head of cattle and horses were grazed, and in 1917 over 2 million were grazed.

In 1906, grazing fees were adopted on forest reserves to help bring grazing under control. These permits were issued for a specific number of animal unit months (AUM's) of grazing on a specified area. These were granted to ranchers who owned enough property to support the animals when they were not on the forest reserve. Thus, public land grazing permits were tied to individual private ranches. Excessive livestock grazing and trespass grazing within forest reserves continued to be a major problem for many years. These were slowly reduced, but the practices had become deeply entrenched.

GRAZING IMPACTS

Infiltration and Sediment Yield

Research is limited relative to hydrologic impacts of livestock grazing in the whitebark pine ecosystem. However, extensive evidence is available that shows the negative hydrologic impacts of excessive grazing in other vegetation types. Livestock influence infiltration rates and sediment production on watersheds by removing the soil's protective cover and compacting the soil. An adequate vegetative cover is generally accepted as the most important factor in maintaining adequate infiltration and preventing erosion.

Meeuwig (1971) stressed the importance of maintaining vegetation and litter cover for adequate infiltration and soil stability on rangelands in Utah, Idaho, and Montana. On a subalpine watershed in Utah, Meeuwig (1960) reported that heavy grazing reduced vegetative cover and created a serious flood source area.

Mueggler (1962) stated that many subalpine herblands in northern Idaho and northeastern Washington are seriously depleted because they have been grazed too heavily by cattle and sheep during the short summer grazing period. He indicated that forage depletion, sheet erosion, and gullying are evident in many areas. These areas now produce only a fraction of their potential forage. However, the most serious result of overgrazing was expressed as loss of the soil mantle.

Plant Community Indicators

Range condition and trend on high-elevation ranges are recognizable by certain signs or indicators that can be detected by observing the soils and vegetation on a site. These indicators not only provide an insight into changes that may have occurred during the past because of livestock grazing, but also suggest what may be expected to occur in the future if the manner of grazing is not altered (Ellison and others 1951).

Jardine and Anderson (1919) stated that overgrazing for an extended period leaves signs that are readily recognized. These signs were listed as follows: (1) the predominance of annual forbs and grasses, with a dense stand of such species and lack of variety in species; (2) the predominance of plants that have little or no value for any class of stock; (3) the presence of dead and partly dead stumps of shrubs; (4) noticeable damage to tree reproduction; and (5) erosion and bareness.

Ellison and others (1951) stated that three characteristics of high-mountain vegetation are especially important to consider in judging range condition and trend on high-elevation ranges:

1. On range in good condition, the vegetation, along with the litter it produces, effectively protects the site against soil erosion, especially since the cover tends to be greater on high-mountain range than on lowland range. Bare spots are neither naturally large nor permanent on such sites.
2. Vegetation of high-mountain sites in good condition usually supports many kinds of plants.
3. There is a dominance by perennial plant species. If annuals are present, they make up only a small part of the community. Conspicuous annuals in high-mountain vegetation indicate the range is not in good condition.

Sampson (1919) described four vegetation types or stages in plant succession on high-mountain ranges in Utah. These stages, listed in order from the most disturbed to climax, include the following: (1) early maturing annuals and weak perennials; (2) perennial herbs, chiefly forbs with some aggressive grasses and shrubs; (3) aggressive perennial grasses in abundance with perennial herbs and shrubs; and (4) deep-rooted or densely tufted perennial grasses, growing almost to the exclusion of other plants. These stages have been widely studied by numerous workers on subalpine grasslands, and the validity of this classification has been generally accepted (Pickford and Reid 1942).

The climate of alpine and subalpine rangelands is adequate for luxuriant plant growth. Thus, whenever the perennial plant cover of a site is less than normal, even though it may be adequate to prevent accelerated erosion, an unsatisfactory condition is indicated by two conditions (Reid and Pickford 1946): (1) reduced cover reflects a lower production of forage, and (2) the site becomes more xeric. A range in good to excellent condition is more mesic than one in poor to fair condition. When the climax dominant plants are lost from a dry site, the site is slower to progress to a climax condition than when it is a mesic or wet site.

Meadows at timberline in good to excellent condition support a dense sod of perennial grasses and sedges with few perennial forbs and essentially no annuals (Reid and Pickford 1946). Severely overgrazed meadows have a reduced cover of plants that is mostly annuals. Intermediate seral stages have a mixture of perennial grasses and sedges, perennial forbs, and annuals. Thus, increased range deterioration is indicated as perennial forbs and annuals increase.

Pickford and Reid (1942) also described these high-elevation communities in climax condition as dominated by grasses, with a small amount of forbs present. They indicated that as range condition declines, the perennial forbs and sagebrush increase on the site. Since the drier sites decline in range condition more readily than wetter sites (Reid and Pickford 1946), sagebrush first shows up on these dry sites and is an indicator of range deterioration.

Sheep tend to prefer forbs over grasses, thus an overgrazed sheep range would be characterized mostly by low value grasses (Ellison 1954). As overgrazing continues, the less-preferred perennial grasses decline so that unpalatable forbs and annuals predominate. Dominance by rhizomatous species represents an intermediate level of range condition (Ellison and others 1951).

Plant Species Indicators

Subalpine rangelands in eastern Oregon and Washington that support chiefly *Stipa columbiana* and forbs indicate unstable soil and vegetation conditions (Pickford and Reid 1942) caused by overgrazing. These can be used as indicators of excessive grazing on these sites.

Annuals that are indicative of overgrazing on high-elevation ranges in the Intermountain region include *Lepidium, Polygonum, Amaranthus,* and *Descurainia* (Ellison and others 1951). *Madia,* where it is a strong competitor, is considered to indicate a poorer condition than the other annuals.

Reid and Pickford (1946) described the vegetation on overgrazed sites in eastern Washington and Oregon. *Poa pratensis, Koeleria cristata, Bromus carinatus, Agropyron trachycaulum, Achillea lanulosa, Potentilla, Aster occidentalis,* and *Taraxacum officinale* are found on such sites. Dense stands of *Wyethia* are an indicator of poor condition. Annuals that are found on disturbed sites include *Polygonum douglasii, Gilia, Gayophytum,* and *Madia.*

Festuca idahoensis appears to be a major dominant species on high, open ridges. Branson and Payne (1958) found that this grass decreased with excessive sheep grazing in the Bridger Mountains of Montana. Morris (1961) considered *Festuca idahoensis* to be a decreaser in Cabin Creek and Sage Creek in southwestern Montana. Kuramoto and Bliss (1970) reported that *Festuca idahoensis* is the most important species in the mesic grass type and dry grass-forb type of the Olympic Mountains, WA; reduced abundance of this species was said to indicate regression from climax condition.

Plant species most abundant on heavily grazed sheep range include *Stipa lettermani, Agropyron trachycaulum, Achillea lanulosa, Aster,* and *Taraxacum officinale* (Ellison 1954).

Branson and Payne (1958) used exclosures to compare vegetation on protected sites to those grazed by sheep in the Bridger Mountains of Montana. They found that sheep grazing led to a decrease of *Festuca idahoensis, Stipa columbiana,* and *Potentilla,* and only a slight decrease in *Bromus carinatus.*

Morris (1961) summarized the climax vegetation and successional pattern for an upper elevation range in southwestern Montana. *Festuca idahoensis* and *Stipa columbiana* are the two dominant species. *Bromus carinatus* and *Agropyron trachycaulum* are present but subdominant. *Melica bulbosa* is infrequent in the climax. Forbs make up approximately 25 to 35 percent of the composition, and include *Lingusticum, Senecio, Hieracium, Delphinium,* and *Mertensia. Achillea* and *Lupinus* are present in lesser amounts.

Regressive succession to a distinctly weed stage due to excessive grazing appears to follow this pattern (Morris 1961): *Festuca idahoensis* and *Stipa columbiana* are among the first to disappear, while *Bromus carinatus* and *Agropyron trachycaulum* increase. *Senecio* and *Ligusticum* are replaced by *Helianthus,* which, along with *Bromus carinatus* and *Agropyron trachycaulum,* make up a distinct community. Further regression of the community results in an increase in *Aster engelmannii,* annual forbs, and *Melica bulbosa.* The soils are unstable and excess runoff occurs on weed types or when *Bromus carinatus* and *Agropyron trachycaulum* are the major grass species.

The successional status of *Artemisia tridentata vaseyana* is difficult to establish. Morris and others (1976) indicated that it is probably a seral species that increases its range and density on disturbed sites.

A range may have been overgrazed in the past but may now be improving in condition. The abundance of individual plants in each of the age classes (seedling, young, middle-aged, and old plants) indicates whether a species is maintaining itself, or is increasing or decreasing. A mixture of age classes indicates that a species is maintaining itself in the stand. Improvement may be assumed when the climax species are increasing, and when gullies and other former bare spots are being revegetated (Ellison and others 1951).

Soil Indicators

A stable soil is required for satisfactory range condition on any area where a soil mantle has previously developed. Soil erosion always means a downward trend; thus, range improvement can only occur where the soil is stable (Ellison 1949).

Pickford and Reid (1942) studied the subalpine grasslands of eastern Oregon and eastern Washington. They reported that soil removal by accelerated erosion was an indicator of overgrazing on green fescue (*Festuca viridula*) communities.

Ellison and others (1951) described the evidences of an unstable soil from studies in Utah, Idaho, Washington, and Oregon. They found these signs included rill marks, pedestaled pebbles and plants, tiny alluvial deposits, and gully development. They concluded that small rocks, pebbles, and bunchgrasses on the soil surface protect it from the erosive impact of raindrops, while the surrounding unprotected soil is washed away. Thus, the rocks, pebbles, and bunchgrasses become elevated on low pedestals of soil. Pedestaling was found to be especially useful to indicate current accelerated erosion when storms are of such moderate intensity as not to form gullies or alluvial deposits.

There is no evidence that frost heaving causes pedestals. Frost loosens the soil, may move rocks or pebbles to the soil surface, and can "heave" grass seedlings from the soil and onto the soil surface. However, it is highly unlikely that frost heaving will raise a deep-rooted, fibrous-rooted bunchgrass onto a pedestal.

Substantial evidence demonstrates the negative impacts of excessive grazing on soils in numerous vegetation types. Flory (1936) found that soils on ungrazed, overgrazed, and severely grazed range sites had pore space of 68.1, 51.1, and 46.5, percent, respectively. Lodge (1954) reported that heavy livestock grazing resulted in soil compaction and reduced moisture-holding capacity; higher successional plant species were replaced by lower successional species that are more competitive under drier conditions.

Willard and Hermann (1977) studied soil water infiltration rates on various range sites in Montana to assess soil compaction by cattle grazing at various times of the year. Infiltration rates were generally highest on ungrazed sites, followed by those sites grazed in winter (when soils are frozen) and fall (when soils are dry). Infiltration rates were lowest on sites grazed during the spring when the soils were wet. Increased soil compaction was associated with increased soil surface erosion and regressive plant succession.

Gullies

Rainfall alone cannot account for the presence of an active gully system cutting into the soil mantle on high-elevation watersheds. Ellison and others (1951) stated that the presence of a soil mantle and a gully system cannot both be normal: the two are irreconcilable. They indicated that the same is true for occurrences of unvegetated soil surfaces, wind-scoured depressions, accelerated soil movement, soil movement by trampling, pedestaling of plants, and widespread accumulation of gravel at the soil surface. On high-elevation ranges these are not compatible with development of a soil mantle on a slope.

Gullies are developed through excessive surface runoff. Bare, steep slopes on a gully generally indicate it is active and the watershed is poorly vegetated. Conversely, when the watershed plant cover is adequate, the gully slopes will be less steep and plants will be establishing both on the slopes and in the channels.

Lichen Lines

The growth of lichens on rocks can often be used as an indication of soil loss around the rock. Lichens grow on the aboveground portions of a rock, usually in the more moist positions on shaded sides and near the ground surface. Soil loss around these rocks can often be detected by observing lichen lines where the soil has been removed at the base of the rock. The lichens are very slow in moving onto the barren areas on the lower rock, thus leaving characteristic "lichen lines" in eroded areas (Ellison and others 1951).

Pocket Gopher Activity

The obvious diggings of pocket gophers on high-elevation ranges leads one to question the influence that these animals have on the soils and vegetation, and whether the gopher influences are natural or are an indirect result of over-grazing. Morris (1961) stated that the amount of gopher activity is directly related to a decline in range condition. He found that as the amount of *Festuca idahoensis* decreased and the amount of forbs together with *Bromus marginatus* and *Agropyron trachycaulum* increased, the amount of gopher activity increased.

Because of the subterranean habitat of gophers, they mostly feed underground. Their food includes fleshy plant parts (taproots, rhizomes, tubers, and corms) found while excavating their runways. Gophers may actually cause an increase in grasses and sedges by feeding on other plant species. Ellison and Aldous (1952) found that *Agropyron* and *Stipa columbiana* increased markedly where gophers were present. They concluded that there is no evidence that gophers have caused a reduction in total production; they may actually have promoted increased production slightly.

No evidence was found by Ellison (1946) that gophers destroy sufficient vegetation to cause accelerated erosion on high-mountain ranges. He also found no evidence that the tunnels of gophers concentrate overland flow sufficiently to create gullies, unless, possibly, abnormal surficial runoff is induced by other causes.

It is generally assumed, then, that pocket gophers only become excessive in numbers and contribute to range deterioration when the normal environment is altered by heavy livestock grazing. There is little or no evidence to contradict this view (Morris 1961).

CURRENT LIVESTOCK MANAGEMENT

Resource values of the whitebark pine ecosystem include water storage and yield, recreation, ecological diversity, wildlife, minerals, small amounts of firewood, and livestock grazing. Concerns with resource value conflicts between livestock grazing and other values, along with changes in livestock economics and grazing policy, have led to a general decline in livestock numbers in the whitebark pine ecosystem from the early 1950's to the present. In general, range condition is improving as livestock numbers are reduced and better management is applied.

High-elevation ranges are more suited to sheep than cattle grazing. However, sheep numbers have declined as cattle numbers have increased throughout the West. For example, from 1925 to 1982, sheep numbers in Montana declined from approximately 2.2 million to 0.6 million, while cattle numbers increased from about 1.1 million to 2.9 million (U.S. Bureau of the Census 1983). These changes have generally led to a decreased demand for high-elevation grazing.

Numerous grazing allotments in National Forests are currently vacant; many have been for 25 years of more. These allotments are being closed because of the absence of suitable range, changes in use from sheep to cattle, and resource conflicts. Many of the sheep allotments were closed in the 1950's and 1960's for resource protection on high-elevation ranges.

in wilderness areas is for packstock. For example, there are about 17,000 acres in packstock allotments in wilderness in the Bitterroot National Forest (USDA Forest Service 1987). The Flathead National Forest had 2,664 AUM's allocated to recreationists' stock and government administrative stock in wilderness in 1980 (USDA Forest Service 1985).

FUTURE OF GRAZING IN THE WHITEBARK PINE ECOSYSTEM

Various factors will interact to determine the future of livestock grazing in the whitebark pine ecosystem. These factors are mostly negative on public lands and mixed on private lands. Factors on public lands will include the following: wilderness designation of new areas, increased emphasis on recreation, conflicts between livestock and big game, increase in grizzly bears and introduction of wolves, improved riparian area management, and increased stress for range improvement. Factors important on private lands will include cost/benefits of producing livestock, availability of herders and riders, use of sheep to control weeds, and development of fee hunting of big game as an alternative to livestock production.

Livestock grazing in the whitebark pine ecosystem is expected to continue to decline on public lands and will probably remain constant on private lands. Since whitebark pine occurs mostly on public lands, most of the livestock grazing will be reduced within this ecosystem.

CONCLUSIONS

The whitebark pine ecosystem has been an important source of livestock foraging since the late 1800's. The large bands of sheep that grazed these ranges during the "open range" period caused considerable, sometimes irreversible, damage to the soils and natural vegetation. As these lands have come under management, the grazing pressure has been reduced, many allotments have been closed, and partial recovery has occurred.

In judging the impacts of present management, it is important to determine range condition and trend. These can be determined by using plant community and soil indicators. A range overgrazed in the past may now be improving in condition; conversely, a range in good condition may be deteriorating. The abundance of plants in each age class indicates whether a species is maintaining itself, or is increasing or decreasing. Improvement implies an increase in climax plant species and active revegetation of gullies and other former bare spots.

With the growing concern for protecting the whitebark pine ecosystem, along with an increase in poisonous plants, establishment of wilderness areas, decreased interest in herding livestock, and difficulty of ready access to these areas, there has been a steady decline of livestock grazing in this ecosystem. Conflicts with other uses will probably lead to further declines in livestock use.

REFERENCES

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Baig, M. N. 1972. Ecology of timberline vegetation in the Rocky Mountains of Alberta. Calgary, AB: University of Calgary. Dissertation.

Barnes, W. C. 1926. The story of the range. Washington, DC: U.S. Department of Agriculture; reprinted, 1926, from Part 6 of the Hearings before a Sub-committee of the Committee on Public Lands and Surveys, United States Senate, Sixty-ninth Congress, First Session, pursuant to Senate Resolution 347. 60 p.

Branson, F. A.; Payne, G. F. 1958. Effects of sheep and gophers on meadows of the Bridger Mountains of Montana. Journal of Range Management. 11(4): 165-169.

Dana, S. T. 1956. Forest and range policy: its development in the United States. New York: McGraw-Hill. 455 p.

Ellison, L. 1946. The pocket gopher in relation to soil erosion on mountain range. Ecology. 27(2): 101-104.

Ellison, L. 1949. Establishment of vegetation on depleted subalpine range as influenced by macroenvironment. Ecological Monographs. 19(2): 95-121.

Ellison, L. 1954. Subalpine vegetation of the Wasatch Plateau, Utah. Ecological Monographs. 24(2): 89-184.

Ellison, L.; Aldous, C. M. 1952. Influence of pocket gophers on vegetation of subalpine grassland in central Utah. Ecology. 33(2): 177-186.

Ellison, L.; Croft, A. R.; Bailey, R. W. 1951. Indicators of condition and trend on high range-watersheds of the Intermountain Region. Agric. Handb. 19. Washington, DC: U.S. Department of Agriculture. 66 p.

Flory, E. L. 1936. Comparison of the environment and some physiological responses of prairie vegetation and cultivated maize. Ecology. 17: 67-103.

Franklin, J. F.; Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 263-264, 273 and table 40.

Galbraith, W. A.; Anderson, E. W. 1971. Grazing history of the Northwest. Journal of Range Management. 24(1): 6-12.

Jardine, J. T.; Anderson, M. 1919. Range management on the National Forests. Bull. 790. Washington, DC: U.S. Department of Agriculture. 98 p.

Kuramoto, R. T.; Bliss, L. C. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. Ecological Monographs. 40(3): 317-347.

Lodge, R. W. 1954. Effects of grazing on the soils and forage of mixed prairie in southwestern Saskatchewan. Journal of Range Management. 7(4): 166-170.

Meeuwig, R. O. 1960. Watersheds A and B—a study of surface runoff and erosion in the subalpine zone of central Utah. Journal of Forestry. 58: 556-560.

Meeuwig, R. O. 1971. Soil stability on high-elevation rangeland in the intermountain area. Res. Pap. INT-94. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 10 p.

Morris, M. S. 1961. An ecological evaluation of the nonforested areas in the subalpine zone of Cabin Creek, Tepee Creek, and Carrot Basin on the Gallatin National Forest. Unpublished paper on file at: University of Montana, School of Forestry, Missoula, MT. 7 p.

Morris, M. S.; Kelsey, R. G.; Griggs, D. 1976. The geographic and ecological distribution of big sagebrush and other woody *Artemisias* Montana: Proceedings; 1976; Montana Academy of Sciences: 56-79.

Mueggler, W. F. 1962. Range resources and management problems in northern Idaho and northeastern Washington. Res. Pap. 68. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 30 p.

Mueggler, W. F. 1965. Cattle distribution on steep slopes. Journal of Range Management. 18(5): 255-257.

Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 15; 18, fig. 6; 77-80; 106-114; 157, appendix C-1.

Pickford, G. D.; Reid, E. H. 1942. Basis for judging subalpine grassland ranges of Oregon and Washington. Circ. 655. Washington, DC: U.S. Department of Agriculture. 37 p.

Reid, E. H.; Pickford, G. D. 1946. Judging mountain meadow range condition in eastern Oregon and eastern Washington. Circ. 748. Washington, DC: U.S. Department of Agriculture. 31 p.

Sampson, A. W. 1919. Plant succession in relation to range management. Bull. 791. Washington, DC: U.S. Department of Agriculture. 76 p.

Steele, R.; Pfister, R. D.; Ryker, R. A.; Kittams, J. A. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 80-83.

Thilenius, J. F. 1975. Alpine range management in the western United States-principles, practices, and problems: the status of our knowledge. Res. Pap. RM-157. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 32 p.

U.S. Bureau of Census. 1983. Census of agriculture, 1982, Volume 1, Montana. Washington, DC: U.S. Government Printing Office. 302 p.

U.S. Department of Agriculture, Forest Service 1987. Final environmental impact statement, Bitterroot National Forest land and resource management plan. n.p.

U.S. Department of Agriculture, Forest Service 1985. Final environmental impact statement, Flathead National Forest land and resource management plan. n.p.

Willard, E. E.; Hermann, L. 1977. Grazing study in the Missouri breaks. Montana Forest and Conservation Experiment Station Special Report. Missoula, MT: Univeristy of Montana. 77 p.

Willard, E. E.; Bedunah, D. J.; Hann, W. J. 1983. Forage and livestock in western Montana. In: O'Loughlin, J.; Pfister, R. D., compilers and editors. Management of second-growth forests: the state of knowledge and research needs: 1983 March 14; Missoula, MT. Missoula, MT: University of Montana, School of Forestry, Montana Forest and Conservation Experiment Station: 187-208.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Linda Meriglaino)—What evidence do you have to support that pocket gophers only come in after excessive grazing?

A.—It was not my intent to imply that pocket gophers are not present before excessive grazing occurs. Rather, pocket gophers are present only in small numbers on high elevation grasslands in good to excellent condition. As indicated by the studies reviewed in this paper, pocket gophers eat fleshy underground plant parts, not fibrous roots of grasses. Thus, the climax grasses must be reduced by excessive livestock grazing to allow forbs and rhizomatous grasses to enter the stand in such density to support high densities of pocket gophers.

Q. (from Sandy Kratville)—If we do receive increased horse use of high elevation ranges - what would you recommend to reduce impacts to these areas?

A.—The best way to reduce horse use and associated disturbances is to reduce the number of horses and the amount of time they spend on a specified area. This can be partially accomplished by regulating the number of horses using a particular trail system, and by limiting the time they spend on each of the meadows and grasslands; reduce the number, disperse them to the extent possible, and keep them moving.

EXOTIC INVASION OF TIMBERLINE VEGETATION, NORTHERN ROCKY MOUNTAINS, USA

T. Weaver
J. Lichthart
D. Gustafson

ABSTRACT

Thirty-five exotic species were found in vegetation characteristic of Northern Rocky Mountain timberlines. At least 20 percent were intentionally introduced along roadsides. The diversity of invading exotics declined from subalpine to alpine vegetation. While exotic diversity generally increased with increasing disturbance, severe trampling excluded some species from road-shoulder sites. The exotics of greatest concern to wildland managers are Phleum pratense *(timothy) and* Poa pratensis *(Kentucky bluegrass) because they establish widely, spread vigorously, and usually escape early detection. Control of any exotic should involve its eradication and simultaneous introduction of desirable competitors to minimize reinvasion.*

INTRODUCTION

Timberline in the Northern Rocky Mountains is usually bordered above by alpine vegetation (Bamberg and Major 1968; Johnson and Billings 1962) and below by either subalpine forests—often subalpine fir-whortleberry (*Abies lasiocarpa-Vaccinium scoparium*, Daubenmire and Daubenmire 1968; Pfister and others 1977)—or subalpine meadows—often Idaho fescue-wheatgrass (*Festuca idahoensis-Agropyron caninum*, Mueggler and Stewart 1980). Whitebark pine often occurs at and below timberline and tends to dominate on relatively dry sites (Arno and Weaver, this proceedings). Since vegetation tends to vary continuously along environmental gradients, we believe that our observations of exotic weed invasion of adjacent forest, meadow, and tundra vegetation types also will apply to most timberline and whitebark pine vegetation types with similar understories.

Our studies of exotic invasion of major vegetation types of the Northern Rocky Mountains have concentrated on two questions:

1. Which exotics are capable of invading each environmental zone—habitat type (HT, Daubenmire 1968, 1970)?
2. Within an environmental zone, how much disturbance is required for success of the exotic; that is, does the plant require continuous disturbance or can it invade even undisturbed vegetation?

METHODS

To determine which exotics can invade major environmental zones of the Northern Rocky Mountains (question 1), we listed those present in each of 16 environmental types (= habitat types, HT's) ranging from dry grasslands up through forests to the alpine (Weaver and others 1989). Three of these HT's are found at timberline (*Abies lasiocarpa-Vaccinium scoparium* forests, *Festuca idahoensis-Agropyron caninum* meadows, and alpine tundra; Weaver and others 1989) and therefore represent whitebark pine understories. We sampled only roadside sites because these have a high probability of inoculation; that is, species absences there are likely due to the physical-biological environment rather than lack of seed. Ten sites were examined in each environmental zone (HT). At each site the five disturbance conditions described below were examined to ensure that exotics specific to any disturbance condition were included. As it turned out, this site reconnaissance—which examined far larger areas—identified few exotics not found in specific plots used to answer our second question.

Knowledge of the environmental zones (HT's) an exotic can occupy does not reveal the degree to which the plant will dominate the HT considered; will it occupy only highly disturbed areas or will it spread to undisturbed vegetation? To determine the capacity of an exotic to spread (question 2), we sampled sites experiencing the range of disturbance conditions (DC's) expected in the HT: constant heavy disturbance, periodic light disturbance, one-time heavy disturbance followed by primary succession, one-time light disturbance followed by secondary succession, and no disturbance. These DC's appear at roadsides in the form of shoulder, ditch slope, cutbank, logged right-of-way, and undisturbed vegetation of our National Parks, respectively. Exotic dominance was sampled in each DC in a 0.5- by 25-m macroplot running parallel to the road. Presence was recorded in each macroplot for plot constancy calculations; constancy indicates regional ubiquity and is calculated as the percent of the 10 sites in an environmental zone and across all disturbance conditions (HT) or a disturbance zone within

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

T. Weaver is Plant Ecologist and J. Lichthart and D. Gustafson are Ecologists, Department of Biology, Montana State University, Bozeman, MT 59717.

an environmental zone (HT-DC) occupied by the plant. Presence was also recorded in five 0.5- by 5-m subplots for frequency calculations; frequency indicates local ubiquity and is measured, for example, as the percent of five subplots in a macroplot occupied by the species. Cover was measured with 75 points lowered along the centerline of the macroplot; it indicates the degree to which the ground surface is covered by a particular species.

PRESENCE BY HABITAT

Our studies of vegetation above and below timberline suggest that 34 exotic species tolerate timberline environments of the Northern Rocky Mountains and show that these species differ considerably in the consistency of their presence among sites in an environmental type (constancy; table 1, column 2). Exotic diversity (richness)

Table 1—Constancy and infected site frequency of exotic species in three environmental types and five disturbance conditions. The species are listed in approximate order of their abilities to invade closed vegetation

	Constancy[2]	Disturbance condition[3] (infected site frequencies > 20 percent)				
Exotic species[1]	F.M.A.	Shoulder-constantly	Ditch-periodic	Roadcut-once (1°)	Logged-once (2°)	Climax-never dist.
Phleum pratense	99.99.36	FM	FM	FM		M
Poa pratensis	99.99.00	FM	FM	FM	F	M
Polygonum aviculare	60.60.00	FM	FM		F	M
Taraxacum officinale	99.99.91	FMA	FMA	FM	F	M
Descurainia pinnata	00.50.00		M	M		M
Festuca rubra	00.00.09					A
Madia glomerata	60.50.00	FM	FM	FM	F	
Lychnis alba	10.00.00			F		
Thlaspi arvense	00.10.00			M		
Tragopogon dubius	10.10.00		M	F		
Trifolium hybridum	99.90.00	FM	FM	FM		
Trifolium repens	90.30.00	FM	F	M		
Agrostis alba	60.40.00	FMA	FM	F		
Bromus inermis	50.99.36	FMA	FM	F		
Dactylis glomerata	50.00.00	F	F	F		
Matricaria matricari.	60.20.00	FM	FM	M		
Medicago lupulina	80.60.00	FM	FM	F		
Melilotus officinalis	40.70.00	F	FM	F		
Agropyron repens	30.00.00	F	F			
Arabis glabra	20.00.00	F	F			
Festuca pratensis	30.10.09	A	FM			
Plantago major	20.00.00	F	F			
Poa compressa	20.50.27	MA	FM			
Cirsium arvense	10.00.00		F			
Cirsium vulgare	10.00.00		F			
Lactuca serriola	10.00.00		F			
Medicago sativa	10.00.00		F			
Rumex crispus	20.00.00		F			
Tanacetum vulgaris	10.00.00		F			
Capsella bursa-past.	30.00.00	M				
Verbascum thapsus	10.00.00	F				
Alyssum alyssoides	20.00.00					
Rumex acetosella	00.00.36					
Trifolium pratense	20.00.00					

[1] Column 1 lists all exotics found in three HT's—a forest (F = *Abies lasiocarpa-Vaccinium scoparium*, Pfister and others 1977), a subalpine meadow (M = *Festuca idahoensis-Agropyron caninum*, Mueggler and Stewart 1980), and alpine tundra (Johnson and Billings 1962). Eleven alpine sites were sampled along the Beartooth Highway; 10 mountain meadows and 10 subalpine fir forests were sampled in and around Grand Teton National Park. Nomenclature follows Hitchcock and Cronquist (1973); abbreviated names are *C. bursa-pastoris* and *M. matricarioides*.

[2] Column 2 gives the constancy of each species in the forest (F), meadow (M), and alpine tundra (A) environments; that is, the percent of sites at which the exotic species was present in the area encompassed by five 0.5- by 25-m plots, one in each disturbance zone. In two cases a species, not present in the plots, was recorded outside; site constancies were slightly higher than plot constancies in these cases: *Taraxacum* 99.99.99 and *Bromus inermis* 50.99.45. Column 2 can be summarized by counting numbers of present exotics (cn > 10 percent, 30.17.07), common exotics (cn > 30 percent, 13.12.04), and universal exotics (cn > 30 percent, 05.05.01) in the forest, meadow, and alpine environments, respectively.

[3] Columns 3 through 7 indicate the disturbance conditions where, at infected sites, the species had a frequency higher than 20 percent; that is, the species occurred in more than 20 percent of the 1- by 5-m plots sampled at infected sites in that disturbance condition. The disturbance conditions considered include undisturbed (Climax-never dist.), secondary succession on cleared right-of-way (Logged once (2°)), primary succession on roadcuts (Roadcut-once (1°)), periodically disturbed ditch slope (Ditch-periodic), and constantly disturbed road shoulder (Shoulder-constantly). The environments where the frequency exceeded 20 percent are indicated by F (forest), M (meadow), and A (alpine tundra).

declines from 30 species in subalpine forests to 17 species in subalpine meadows, to seven species in alpine tundra. Wildland managers should notice that 20 to 30 percent of the high-frequency exotics (table 1, columns 3 through 7) have been intentionally introduced in roadside seedings.

Vaccinium scoparium (whortleberry) dominates the understories of the major forest habitats, such as *Abies lasiocarpa-Vaccinium scoparium, Pinus albicaulis-Vaccinium scoparium, Abies lasiocarpa-Pinus albicaulis-Vaccinium scoparium* (Pfister and others 1977). In this vegetation we found 30 exotic associates, of which 13 occurred in over 30 percent of the stands and five occurred in over 80 percent of the stands (table 1).

Festuca idahoensis-Agropyron caninum meadows occupy drier sites in the subalpine zone and serve as an understory in *Pinus albicaulis-Festuca idahoensis* woodlands. These meadows contained 17 exotic species, of which 12 occurred at over 30 percent of the sites, five occurred at over 80 percent of the sites, and only two—*Descurainia pinnata* (tansey mustard) and *Thlaspi arvense* (pennycress)—were not observed as colonizers in whortleberry understories (table 1).

Alpine vegetation appears around and among trees—whitebark pine (*Pinus albicaulis*), subalpine fir, and Engelmann spruce (*Picea engelmannii*) at upper timberline. In this vegetation we found seven exotic species, of which four appeared in over 30 percent of the stands, one appeared in over 80 percent of the stands, and only two, *Festuca rubra* (red fescue) and *Rumex acetosella* (sheep sorrel), were not observed in whortleberry understories (table 1).

PRESENCE BY DISTURBANCE CONDITION

Exotic species that invade undisturbed climax vegetation are of greatest concern to managers opposed to the modification of natural vegetation. We recorded no exotic colonization of forests with undisturbed whortleberry understories (table 2); the absence of exotics in closed forest stands is probably due to the high sun requirements of the plants introduced. Six exotic species were present in over 30 percent of the meadow sites occupied by the exotic species (table 3). Three species, *Festuca rubra, Poa compressa* (Canada bluegrass), and *Taraxacum officinale* (dandelion), were present in over 30 percent of the occupied alpine sites (table 4). Most of these colonizers had frequencies over 20 percent; that is, they occurred in over 20 percent of the 0.5- by 5-m quadrats sampled. Throughout this section, and in tables 2, 3, and 4, disturbed site constancy is expressed on the basis of infected sites because our object is to express the capacity of species present to invade variously disturbed zones. If readers want to calculate conventional constancies they can use disturbed site constancy and total constancy (from table 1) to do so; for example, if the disturbed site infected-constancy were 50 percent and the total constancy were 50 percent the disturbed site total-constancy would be 25 percent.

Exotic species that colonize secondary succession sites such as logged or burned sites are also of concern because large areas are involved and their dominance might slow succession. Of 13 invaders found on logged *Abies lasiocarpa-Vaccinium scoparium* sites, six had constancies over 30 percent and four had frequencies of 20 percent or more (table 2). While this disturbance condition does not exist in meadow and alpine sites, it exists potentially (unstudied) in high-altitude whitebark or limber pine (*Pinus flexilis*) woodlands.

Topsoil removal leading to primary succession, while less common than the community destruction considered above, does occur on roadcuts, riverbanks, and landslides. Fourteen, 10, and two exotic species had constancies over 30 percent on roadcuts in forest, meadow, and alpine zones respectively (tables 2, 3, and 4). Sixteen species had frequencies of over 20 percent on primary succession sites in at least one environmental type (table 1). Two exotics—*Lychnis* (campion) and *Thlaspi* (pennycress)—that were restricted to primary succession sites in our sample are known to occupy repeatedly disturbed sites elsewhere.

Ditch slopes are periodically influenced by humans; they may be mowed, watered, sanded, lightly compacted, sprayed with herbicide, or salted. Twenty-eight, 13, and four species had constancies over 30 percent on infected sites in forest, meadow, and alpine respectively (tables 2, 3, and 4). Infected site frequencies of 20 percent or more were observed for 20 species in this disturbance condition (table 1).

Road shoulders are constantly disturbed by people with heavy trampling, mowing, watering, sanding, heavy compaction, herbicides, or salt. Twenty-two, 15, and six species had constancies over 30 percent on infected sites in forest, meadow, and alpine zones, respectively (tables 2, 3, and 4). Infected site frequencies over 20 percent were observed for 21 species in this disturbance condition (table 1).

Numbers and frequencies of species generally increase as one moves from undisturbed to regularly disturbed sites (right to left in tables 1 to 4). We believe such increases occur primarily because resources are more available to individuals on more disturbed sites—both because competition is increasingly reduced and because supplements, especially runoff water, begin to appear. Diversity increases might also be due to a constant reintroduction of species, such as *Chenopodium album* (lambsquarter), which are unlikely to reproduce or spread away from the road. At timberline, half of the exotics such as *Plantago major* (broadleaf plantain) are restricted to high-resource, low-competition shoulder and ditch sites (table 2).

Due to the interaction of disturbance and trampling, the increase in species richness ceases when one moves to the road shoulder (tables 1 to 4). Further increases in water and sun, decreased competition, or continual introduction support the increase of several species such as *Capsella bursa-pastoris* (shepherdspurse), *Chenopodium album* (lambsquarter), and *Verbascum thapsas* (mullien).

Table 2—Exotic invasion of five disturbance zones in ABLA-VASC forests as indexed by percent constancy, percent frequency, and percent cover at infected sites. Blanks separated by periods indicate zeros

	Disturbance zone[1] and presence[2]				
	Shoulder-constantly	Ditch-periodic	Roadcut-once (1°)	Logged-once (2°)	Climax-never dist.
Exotic species[2]	cn fq cv	cn fq cv	cn fq cv	cn fq cv	cn fq cv
Verbascum thapsus	99.20. 0.	. . .	. . .	. . .	. . .
Agropyron repens	33.27. 2.	99.40. 5.	. . .	. . .	. . .
Alyssum alyssoides	50.10. 0.	50.10. 0.	. . .	. . .	. . .
Arabis glabra	99.20. 0.	99.30. 1.	. . .	. . .	. . .
Capsella bursa-past.	67.20. 0.	33. 7. 0.	. . .	. . .	. . .
Chenopodium album	50.10. 0.	50.10. 0.	. . .	. . .	. . .
Festuca pratensis	33.13. 0.	67.33. 2.	. . .	. . .	. . .
Matricaria matricari.	83.53. 1.	67.30. 2.	. . .	. . .	. . .
Plantago major	99.40. 1.	99.50. 1.	. . .	. . .	. . .
Cirsium arvense	. . .	99.40. 0.	. . .	. . .	. . .
Cirsium vulgare	. . .	99.20. 0.	. . .	. . .	. . .
Lactuca serriola	. . .	99.20. 0.	. . .	. . .	. . .
Medicago sativa	. . .	99.99.12.	. . .	. . .	. . .
Poa compressa	. . .	99.30. 1.	. . .	. . .	. . .
Rumex crispus	. . .	99.20. 1.	. . .	. . .	. . .
Tanacetum vulgare	. . .	99.20. 0.	. . .	. . .	. . .
Lychnis alba	. . .	. . .	99.40. 0.	. . .	. . .
Tragopogon dubius	. . .	. . .	99.20. 0.	. . .	. . .
Agrostis alba	99.53. 7.	83.57.13.	67.23. 0.	17. 7. 0.	. . .
Bromus inermis	99.64. 8.	80.60. 6.	80.56. 5.	60.16. 1.	. . .
Dactylis glomerata	99.48. 4.	99.48. 4.	40.28. 0.	20. 4. 0.	. . .
Madia glomerata	67.33. 1.	83.63. 4.	83.43. 1.	33.20. 0.	. . .
Medicago lupulina	63.55. 3.	75.50. 2.	50.30. 2.	13. 5. 0.	. . .
Melilotus officinalis	99.50. 2.	75.75. 5.	75.60.17.	25.15. 1.	. . .
Phleum pratense	90.82. 7.	90.68. 5.	80.50. 1.	30. 6. 0.	. . .
Poa pratensis	90.74.11	90.54. 3.	40.30. 1.	30.20. 0.	. . .
Polygonum aviculare	83.47. 2.	67.47. 2.	67.17. 0.	50.23. 0.	. . .
Taraxacum officinale	99.76. 5.	99.82. 4.	80.64 . 3.	80.48. 2.	. . .
Trifolium hybridum	80.54. 7.	60.58. 9.	80.60. 7.	40.16. 0.	. . .
Trifolium pratense	50.10. 0.	50.10. 0.	0. 0. 0.	50.10. 0.	. . .
Trifolium repens	44.31. 3.	89.62. 9.	44.18. 0.	11. 7. 0.	. . .

[1] Site and type of disturbance were: constantly and heavily disturbed road shoulder (Shoulder-constantly), periodically and lightly disturbed ditch (Ditch-periodic), once heavily disturbed with soil removal (Roadcut-once 1°), once moderately disturbed without soil removal (Logged-once 2°), and undisturbed climax (Climax-never dist.).

[2] Exotic presence at infected sites is reported with constancy (cn = percent of infected sites occupied), frequency (fq = percent of 0.5- by 5-m subsites occupied at infected sites), and cover (cv = percent of ground covered at infected sites). Data are based on 10 sites sampled in the Grand Teton National Park area.

Simultaneously, trampling at the road shoulder eliminates brittle-stemmed species such as *Cirsium* (thistle), *Lactuca* (lettuce), and *Tanacetum* (tansey) that would undoubtedly thrive in its absence. Species that do survive on roadshoulders seem to do so (Dale and Weaver 1974) via flexibility (as with grasses and clovers, especially bluegrass, timothy, clover, and sweetclover), stemless forms (such as plantain, dandelion, and mullien), creeping forms (such as knotweed), and avoiding destruction with short life cycles or growth in the off-season (as illustrated by rockcress and shepherdspurse).

MANAGEMENT

As noted above, the exotics of greatest concern are those capable of leaving the roadsides and invading little-disturbed or undisturbed native vegetation. For the upper forest and alpine zones these include *Phleum pratense* (timothy), *Poa pratensis* (Kentucky bluegrass), *Polygonum aviculare* (prostrate knotweed), *Taraxacum officinale* (dandelion), *Descurainia pinnata* (tansey mustard), and *Festuca rubra* (red fescue). *Phleum pratense* and *Poa*

Table 3—Exotic invasion of five disturbance zones in FEID-AGCA meadows as indexed by percent constancy, percent frequency, and percent cover at infected sites. Dashes indicate a nonexistent zone and blanks separated by periods indicate zeros

	Disturbance zone[1] and presence[2]				
	Shoulder-constantly	Ditch-periodic	Roadcut-once (1°)	Logged-once (2°)	Climax-never dist.
Exotic species[2]	cn fq cv	cn fq cv	cn fq cv	cn fq cv	cn fq cv
Chenopodium album	99.40. 0.	. . .	. . .	- - -	. . .
Agrostis alba	25.20. 1.	99.30. 1.	. . .	- - -	. . .
Bromus inermis	80.50. 4.	80.36. 2.	. . .	- - -	. . .
Festuca pratensis	. . .	99.40. 0.	. . .	- - -	. . .
Tragopogon dubius	. . .	99.20. 1.	. . .	- - -	. . .
Matricaria matricari.	50.30. 1.	50.30. 1.	50.20. 1.	- - -	. . .
Poa compressa	60.28. 2.	60.32. 2.	20. 4. 0.	- - -	. . .
Trifolium hybridum	78.44. 2.	78.60. 5.	67.24. 1.	- - -	. . .
Trifolium repens	67.27. 1.	33. 7. 0.	33.27. 1.	- - -	. . .
Thlaspi arvense	. . .	. . .	99.20. 0.	- - -	. . .
Descurainia pinnata	20.12. 0.	40.20. 1.	40.32. 1.	- - -	80.28. 1.
Madia glomerata	40.20. 0.	80.56. 1.	40.28. 0.	- - -	40.12. 0.
Melilotus officinalis	71.17. 1.	57.20. 0.	14.11. 0.	- - -	14. 6. 0.
Phleum pratense	60.32. 0.	99.60. 1.	70.40. 1.	- - -	60.30. 0.
Poa pratensis	90.76. 3.	90.68. 3.	70.40. 3.	- - -	50.22. 0.
Polygonum aviculare	33.20. 2.	83.40. 2.	0. 0. 0.	- - -	33.23. 0.
Taraxacum officinale	90.88. 7.	99.88. 5.	99.60. 1.	- - -	60.32. 0.

[1] Site and type of disturbance were: constantly and heavily disturbed road shoulder (Shoulder-constantly), periodically and lightly disturbed ditch (Ditch-periodic), once heavily disturbed with soil removal (Roadcut-once 1°) once moderately disturbed without soil removal (Logged-once 2°), and undisturbed climax (Climax-never dist.)

[2] Exotic presence at infected sites is reported with constancy (cn = percent of infected sites occupied), frequency (fq = percent of 0.5- by 5-m subsites occupied at infected sites), and cover (cv = percent of ground covered at infected sites). Data are based on 10 sites sampled in the Grand Teton National Park area.

Table 4—Exotic invasion of five disturbance zones in the alpine tundra environment, as indexed by percent constancy, percent frequency, and percent cover at infected sites. Dashes indicate a nonexistent zone and blanks separated by periods indicate zeros

	Disturbance zone[1] and presence[2]				
	Shoulder-constantly	Ditch-periodic	Roadcut-once (1°)	Logged-once (2°)	Climax-never dist.
Exotic species[2]	cn fq cv	cn fq cv	cn fq cv	cn fq cv	cn fq cv
Festuca pratensis	99.20. 0.	. . .	. . .	- - -	. . .
Bromus inermis	75.25. 0.	25. 5. 0.	. . .	- - -	. . .
Phleum pratense	50.10. 0.	50.10. 0.	25. 5. 0.	- - -	. . .
Poa compressa	67.40. 0.	33. 7. 0.	0. 0. 0.	- - -	33. 7. 0.
Taraxacum officinale	90.62. 1.	80.60. 1.	40.10. 0.	- - -	10. 2. 0.
Rumex acetosella	50. 5. 0.	50.15. 0.	25.15. 0.	- - -	75.15. 0.
Festuca rubra	. . .	. . .	99. 0. 0.	- - -	99.40. 0.

[1] Site and type of disturbance were: constantly and heavily disturbed road shoulder (Shoulder-constantly), periodically and lightly disturbed ditch (Ditch-periodic), once heavily disturbed with soil removal (Roadcut-once 1°) once moderately disturbed without soil removal (Logged-once 2°), and undisturbed climax (Climax-never dist.)

[2] Exotic presence at infected sites is reported with constancy (cn = percent of infected sites occupied), frequency (fq = percent of 0.5- by 5-m subsites occupied at infected sites), and cover (cv = percent of ground covered at infected sites). Data are based on 10 sites sampled in the Beartooth Plateau area.

pratensis are of special concern because they often dominate the areas they occupy. Because we sampled along long-established roads, we believe that most invaders that have occupied the region for long periods of time have been introduced, have been naturally tested, and are unlikely to invade further. Any plants currently establishing in the region, however (like, but probably not including leafy spurge [*Euphorbia esula*]), have not been tested naturally and could conceivably become important at timberline. While most new introductions fail to establish, some establish in limited areas and small numbers and, presumably after either a "fitting mutation" or some natural or human-caused environmental change, spread widely (Krebs 1985). Plants that have only established well on roadsides in timberline environments are of little concern in this vegetation zone (because they occupy little area and have been well tested for escape), but should perhaps be controlled if roadsides through this zone serve as corridors for invasion of other habitats. Control of any exotic species should involve both elimination and simultaneous introduction of a desirable competitor to minimize reinfection.

ACKNOWLEDGMENTS

The project was designed by T. Weaver; field sampling was done by B. Woods (below timberline) and J. Lichthart (above timberline); data analysis and interpretation are due primarily to T. Weaver and D. Gustafson. The field work was supported by National Park Service grant CX125-4-A038.

REFERENCES

Bamberg, S.; Major, J. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. Ecological Monographs. 38: 127-167.

Dale, D.; Weaver, T. 1974. Trampling effects on vegetation of the trail corridors of Northern Rocky Mountain forests. Journal of Applied Ecology. 11: 767-772.

Daubenmire, R. 1968. Plant communities. New York: Harper and Row. 300 p.

Daubenmire, R. 1970. Steppe vegetation of Washington. Tech. Bull. 62. Pullman, WA: Washington Agricultural Experiment Station. 131 p.

Daubenmire, R.; Daubenmire, J. 1968. Forest vegetation of eastern Washington and northern Idaho. Tech. Bull. 60. Pullman, WA: Washington Agricultural Experiment Station. 104 p.

Hitchcock, C.; Cronquist, A. 1973. Flora of the Pacific Northwest. Seattle, WA: University of Washington Press. 730 p.

Johnson, P.; Billings, W. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. Ecological Monographs. 32: 105-135.

Krebs, C. 1985. Ecology, the experimental analysis of distribution and abundance. New York: Harper and Row. 800 p.

Mueggler, W.; Stewart, W. 1980. Grassland and shrubland habitat types of western Montana. Gen. Tech. Rep. INT-66. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 154 p.

Pfister, R.; Kovalchik, B.; Arno, S.; Presby, R. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Weaver, T.; Gustafson, D.; Lichthart, J.; Woods, B. 1989. Distribution of exotics in the Northern Rocky Mountains by environmental type (HT) and disturbance condition (DC). Biol. Rep. 41. Bozeman, MT: Montana State University. 91 p.

USE OF FOREST ECOSYSTEM PROCESS MEASUREMENTS IN AN INTEGRATED ENVIRONMENTAL MONITORING PROGRAM IN THE WIND RIVER RANGE, WYOMING

G. J. White
G. A. Baker
M. E. Harmon
G. B. Wiersma
D. A. Bruns

ABSTRACT

Three forest ecosystem processes—conifer needle retention, canopy litterfall, and litter decomposition—were measured as part of an integrated environmental monitoring program at a high-elevation site dominated by whitebark pine (Pinus albicaulis) *and Engelmann spruce* (Picea engelmannii). *Whitebark pine demonstrated much lower needle retention rates and slightly slower decomposition rates relative to Engelmann spruce. Studies to date reflect low productivity at this site and will provide baseline data against which future monitoring data may be compared.*

INTRODUCTION

This paper reports on forest ecosystem process measurements at an integrated environmental monitoring site located in a high-elevation, whitebark pine/Engelmann spruce (*Pinus albicaulis/Picea engelmannii*) system in the Wind River Mountains of western Wyoming. Ecosystem process measurements emphasized include conifer needle retention, canopy litterfall, and litter decomposition rates. Nutrient analyses were also conducted on conifer needles and litter samples. The primary objectives of this paper are: (1) to describe the rationale for applying these measurements to a monitoring program, (2) to summarize and discuss the data collected to date, and (3) to compare data with those collected at other remote sites.

This study represents an extension of previous monitoring and research conducted at other remote sites including national and international Biosphere Reserves and U.S. National Parks and wilderness areas (for example, Bruns and others 1982, 1984; Wiersma and others 1984; Wiersma and Otis 1986). In addition to the Wind River program, other sites that have been studied include Olympic National Park in Washington (Brown and Wiersma 1979), Noatak National Preserve and Biosphere Reserve in Alaska (Wiersma and others 1986), and Torres del Paine National Park in southern Chile (Bruns and Wiersma 1988a; Wiersma and others 1988). The basic objective of each of these monitoring programs is to provide the baseline data necessary to define the "natural" conditions at the site. This in turn allows better interpretation of the impacts of human activities on the system. A further goal of the Wind River monitoring program is to field test guidelines established by the U.S. Department of Agriculture, Forest Service, for monitoring the condition of remote, wilderness ecosystems (Fox and others 1987).

SYSTEMS APPROACH

An integrated, multimedia systems approach has been implemented in the Wind River monitoring program (Bruns and Wiersma 1988b). The design of the program is based on a watershed/drainage basin perspective (for example, Likens 1985; Minshall and others 1985), and links together key aspects of the forest, soil, stream, and lake components along selected pathways within the system (Bruns and Wiersma 1988b). This approach begins with the development of a simple conceptual design of the system to be monitored. This conceptual design is translated into a schematic diagram such as that shown in figure 1. Such diagrams are intended as heuristic tools for identifying system compartments of primary concern, delineating potential pollutant pathways through the system, and identifying potential critical pollutant receptors. This allows us to view the problem as one of pollutant sources and pathways to critical receptor components of the ecosystem. The ultimate goal of such a program is to identify a list of pollutant and ecosystem measurements capable of providing good, quality-assured data against which future observations may be compared, allowing us to assess the relative condition of the system.

The integrated ecosystem approach to environmental monitoring used in the Wind River monitoring program

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Gregory J. White is Senior Scientist, G. Bruce Wiersma is Director, Dale A. Bruns is Scientific Specialist, Center for Environmental Monitoring and Assessment, Idaho National Engineering Laboratory, Idaho Falls, ID 83415; Gail A. Baker is Research Scientist and Mark E. Harmon is Research Associate, Forestry Sciences Laboratory, Oregon State University, Corvallis, OR 97731.

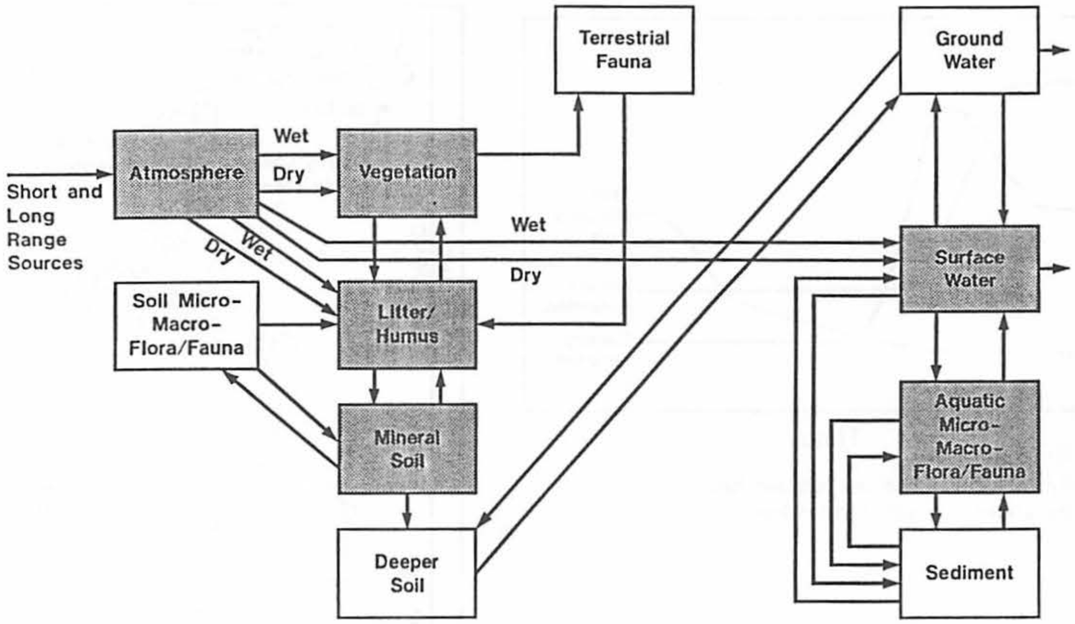


Figure 1—Conceptual approach to monitoring sensitive wilderness systems. Shaded compartments are included in the monitoring program.

involves the collection of two basic types of information: analyses of multimedia environmental samples, and measurement of terrestrial and aquatic ecosystem processes identified as potential indicators of pollutant impact to the system. Components examined in the monitoring program include the atmosphere, soils, aquatic chemistry, aquatic biology, salmonid fish, and vegetation. Specific methods and procedures used are provided elsewhere (Bruns and Wiersma 1988b; Bruns and others 1987, 1988; Fox and others 1987). The emphasis of this paper is on the portion of the program involving the measurement of forest ecosystem processes.

FOREST ECOSYSTEM PROCESSES

The measurement of parameters related to various ecosystem processes can be used to monitor changes in ecosystem condition (Baker and others 1986). To function adequately as an indicator of pollutant impact, an ecosystem parameter should satisfy the following criteria: (1) it should adequately reflect a process or function of the ecosystem, (2) it should respond to the input of an environmental pollutant in some predictable manner, (3) it should be measurable through time, (4) a small natural variability should be associated with it, and (5) the precision associated with the measurement of the parameter should be adequate to observe departures from the norm (Hinds 1984; McShane and others 1983). Needle retention, canopy litterfall, and litter decomposition rates were chosen because they appeared to meet these criteria, and because they had been established in previous investigations on ecosystem response to atmospheric pollutants.

Premature needle loss and the associated change in litterfall rate have been shown to be related to the input of air pollutants either due to the direct action of the pollutant on needle or leaf surfaces or due to damage to root systems caused by increased soil acidity (Mann and others 1980; Ulrich 1981; Williams 1980). Litter decomposition may also be affected due to heavy metal inputs (Coughtrey and others 1979; Strojan 1978), pH changes (Moloney and others 1983), or indirectly in response to changes in litterfall characteristics resulting in litter input containing higher nitrogen concentrations relative to lignin (Melillo and others 1982). The potential for disruption of nutrient cycles or primary productivity may therefore increase. Increases in tree mortality have also been associated with airborne pollution in North America and Europe (Freedman and Hutchison 1980).

The methodologies used to measure forest ecosystem processes in this program have been previously used in the Hoh Rain Forest of Olympic National Park (Baker and others 1986). Changes in needle retention, litterfall, and litter decay rates can result in changes in productivity and mortality. Observation of these processes allows the establishment of a broader basis on which to explain changes in the system. The range of natural variability in an ecosystem is an important consideration in the design of a monitoring program (Miller 1984). It may be difficult to distinguish between natural ecosystem variability and pollutant-induced change in the presence of extreme environmental conditions, short periods of pollutant exposure, or early stages of pollutant input. In such cases, the use of parameters with known and predictable fluctuations as indicators would aid in making that distinction.

A hypothetical response of needle retention, canopy litterfall, and tree mortality in response to the input of atmospheric pollutant is shown in figure 2. In response to pollutant input, conifer needle retention rates have been shown to decline significantly (Mann and others 1980; Williams 1980), typically with the youngest needles showing the greatest impact (Ulrich 1981). In response to the decrease in needle retention times, litterfall rates

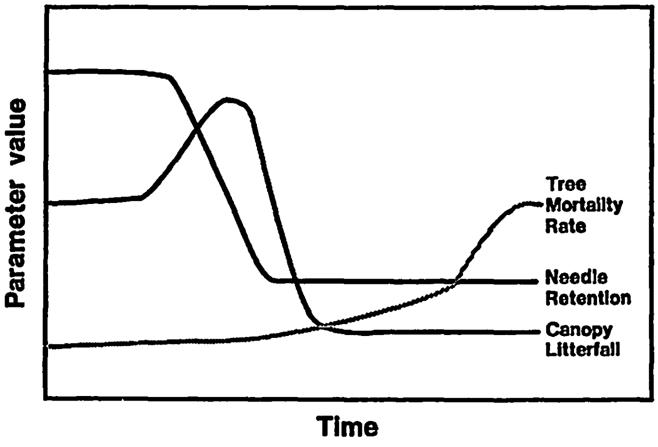


Figure 2—Hypothetical interactions between forest ecosystem parameters to input of atmospheric pollutants.

would be expected to increase initially, before decreasing and ultimately leveling off at a lower level. Similarly, the reduction in active photosynthetic area associated with decreased needle retention would be expected to contribute to the overall mortality rate of the stand, although other factors would undoubtedly impact the mortality rate as well.

Litter decomposition rate also plays an important role in nutrient recycling in forest ecosystems, and is influenced by many factors (Fogel and Cromack 1977). Alterations in nutrient release rates, therefore, may have an impact on tree growth and survival. Decomposition rate is not shown on figure 2, due to the difficulties associated with predicting the response of litter decomposition rates to the input of atmospheric pollutants. Pollutant input can have a detrimental effect on the organisms responsible for much of the decay, resulting in a decrease in the total rate of decay. The lignin-nitrogen ratio of the needles shed by the conifers may also play a significant role. If the response of the trees in the canopy is to prematurely shed younger needles, the lower lignin/nitrogen ratios typically associated with younger foliage may contribute to an increase in the decay rate of the litter (Melillo and others 1982).

The intent of the model proposed in figure 2 is to integrate ecosystem response to atmospherically deposited pollutants in remote areas. The long-term goal of this study is to test these and other hypotheses against future changes in pollutant levels.

STUDY SITE

The study site is located at Nancy Lake, in the upper portion of the Hobbs Lake watershed within the Bridger Wilderness Area of the Bridger-Teton National Forest, WY (fig. 3). Nancy Lake is located at an elevation of 3,140 m (10,400 ft), and is approximately 2 ha (5 acres) in surface area. Soils at the study area are thin, and the area is sparsely forested with Engelmann spruce and whitebark pine, interspersed with small numbers of subalpine fir (*Abies lasiocarpa*). Some environmental monitoring previously had been conducted by the Forest Service in the area (USDA FS 1984). The study site was originally chosen because of the presumed sensitivity of high-mountain ecosystems to atmospheric pollutants, the presence of other ongoing complementary monitoring projects, relatively easy access to the site, and potential for the area to receive measurable pollutant input from energy development activities upwind (fig. 3). As such, the Wind River Mountains provide an ideal location for an integrated monitoring project (Wiersma and others 1985).

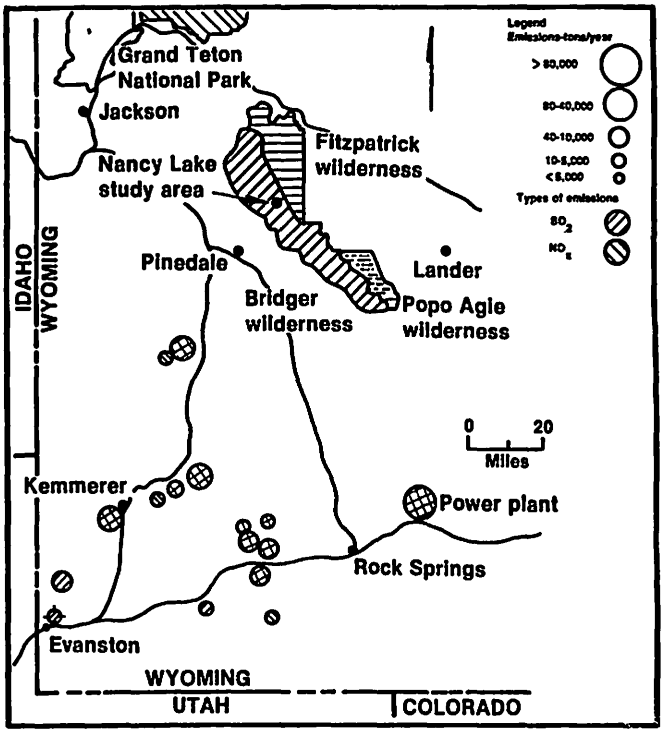


Figure 3—General location of the Wind River study site. Permitted point sources for SO_2 and NO_2 are also shown. Map based on USDA Forest Service (1984).

METHODS

Permanent Reference Stands

Two permanent 0.25-ha (0.6-acre) study plots were established within different forest patches during the 1987 field season. The plots are referred to as BR-1 and BR-2, and were chosen to reflect the basic forest types found in the Nancy Lake area. These forest types fit into the habitat types described by Steele and others (1983); BR-1 represents the *P. engelmannii/Vaccinium scoparium* type and BR-2 represents the *P. albicaulis* phase of the *A. lasiocarpa* type. Plot boundaries were surveyed with compass and meter tapes. Diameters of all trees greater than 1-cm diameter at breast height (d.b.h.) were measured, and these trees were tagged.

Conifer Needle Retention

Branches were selected for use in determining needle retention from whitebark pine and Engelmann spruce, the two dominant tree species found in the area. Single branches were sampled from five trees of each species, for each stand. Each branch was placed in a plastic bag, labeled, and was returned to the laboratory for counting. All were placed in a refrigerated room within 36 hours of collection, and were counted within 4 days of collection. Subsamples of needles from the branches sampled were analyzed for nutrient concentrations.

In the laboratory, three secondary branches were selected from each primary branch for needle retention counts. The secondary branches were divided into single-year growth increments, starting with the most recent growth and proceeding through the oldest segment for which needles were still present. Because the spruces were found to retain their needles for up to 30 years, only the first 5 years and two randomly selected, older needle age classes were sampled for each branch. This reduced the time required to count the needles while still providing an estimation of needle loss over the longer time frame. For each age class counted, measurements were made of twig length, number of needles present, and the number of needles absent as determined by the presence of residual needle scars. The fraction of needles remaining on the segment was then calculated for each segment by dividing needle number by the sum of the needle number and the number of residual needle scars. In the case of whitebark pine, fascicles and fascicle scars were counted.

Canopy Litterfall

The method used to determine litterfall rates was modified from Baker and others (1986). Twelve pairs of litter collection buckets were placed in each reference stand. The area of an individual bucket was 0.066 m^2 (0.72 ft^2). Material falling into the buckets was collected in nylon mesh liners. Three bucket pairs were placed randomly in each of four quadrants within each stand. One bucket pair in each trio was "fixed"; it always remained in the same location. The other two pairs were randomly relocated within the quadrant at the beginning of each sampling period. This fixed and movable bucket system allowed for the determination of both spatial and temporal variability of litterfall while minimizing the total number of buckets required (Reiley and others 1969). Bucket pairs were used to provide samples for the determination of both nitrogen/lignin ratio and trace element analysis (Baker and others 1986).

Litter bucket samples were collected three times each during the 1987 and 1988 field seasons. Samples were returned to the laboratory for processing. The samples were dried at 50 °C for 48 hours and weighed. Major components (needles, cones, fine branches) were separated. Each category was weighed separately and pooled for the season. These samples were analyzed for lignin and nitrogen concentration by methods described by Goering and Van Soest (1970) and Isaac and Johnson (1976), respectively.

Litter Decay Rates

Annual decay rates were determined for various species using litter bags (Crossley and Hoglund 1962; Singh and Gupta 1977). Litter from species indigenous to this study area was collected for this portion of the study just prior to abscission. These species included whitebark pine, Engelmann spruce, subalpine fir, and willow (*Salix* spp.). Leaves from Pacific dogwood (*Cornus nuttallii*) and needles from western white pine (*Pinus monticola*) were also used. These additional species were collected in Oregon, and were selected to provide a wider range of lignin and nitrogen concentrations.

Litter was weighed and placed in 20- by 20-cm polyester bags of 1-mm mesh size. Each bag contained approximately 10 g (dry weight) of litter. Subsamples of each species were used to determine moisture, lignin, and nitrogen content. The litter bags were placed in the field in August 1987 and were collected in August 1988. After collection, the remaining litter was removed from each bag, ovendried, and weighed. Litter loss was expressed as a rate constant (k), as well as a percentage (Jenny and others 1949; Olson 1963).

Elemental Analyses

In association with the 1987 needle retention study, needle samples were collected for elemental analysis from whitebark pine, Engelmann spruce, and subalpine fir. Litterfall samples collected during the 1987 and 1988 field seasons were also analyzed to determine concentrations of various elements. Litter bucket samples collected in June 1988, representing the overwinter accumulation of litter, were not used for elemental analysis due to the uncertainties associated with the effects of snowpack and other factors on the litter. Elemental analyses were performed by spark source emission spectroscopy (Alexander and McAnulty 1981).

RESULTS

Needle Retention

The results of the 1987 needle retention study are shown in figure 4. Data from both stands are combined because no significant difference was found between stands. Eighty percent of the whitebark pine needles observed were lost over a 12-year period. In contrast, Engelmann spruce retained over 75 percent of its needles during the same time frame, and did not reach the 50 percent loss level until the 14th year.

Chemical analysis indicated that both species had their highest nitrogen content in the needles of the current year (table 1). The nitrogen content of spruce needles was initially higher than that of the pine, but this difference decreased as needle age increased. All needle age classes of whitebark pine contained higher lignin content than corresponding age classes from Engelmann spruce.

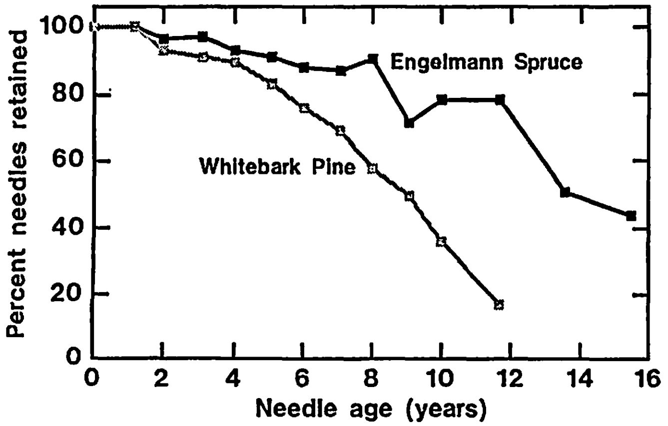


Figure 4—Needle retention for whitebark pine and Engelmann spruce, Nancy Lake, WY, 1987.

Canopy Litterfall

The 1987 and 1988 litterfall data for the two permanent stands are shown in table 2. These data indicate that the litterfall rates during 1988 were substantially higher than those of 1987. In both years, the total litterfall rate for BR-2 exceeded that of BR-1. In both stands, the dominant component of the litterfall was conifer needles.

Litter Decay

The initial nitrogen content of litter used ranged from 0.61 percent for whitebark pine to 1.18 percent for willow. Lignin is highest in the two pine species, and is lowest in the dogwood (table 3). Litter decomposition rate constants (k) were determined for each species by dividing the natural logarithm of the fraction of litter remaining by the time the litter remained in the field (years), and are shown in table 4. Of the species used in the study, decomposition of Pacific dogwood was the most rapid; the decomposition rate was slowest for western white pine.

Analysis of variance for the litter decay rates indicates that there were highly significant differences in decay rates between species, but not between stands (BR-1 and BR-2). The regression between the annual decay rate constants (k) determined for the six species used in this experiment and their respective lignin/nitrogen ratios was highly significant ($p < 0.001$):

$$k = 1.453(\text{lignin/nitrogen})^{-0.564}$$
$$r^2 = 0.93$$

The relationship between the decay constants and the lignin/nitrogen ratio of the species used for the Nancy Lake study site is shown in figure 5.

Table 1—Lignin and nitrogen content of conifer needles of seven different age classes, Nancy Lake, WY, 1987

	Whitebark pine		Engelmann spruce	
Needle age	N	Lignin	N	Lignin
Year		*Percent*		
<1	1.93	13	2.08	5
1	1.21	16	.74	10
2	1.30	17	.66	9
3	1.21	19	.66	9
6	1.06	12	.65	9
10	.84	14	.63	8
13	.92	13	(1)	(1)

[1] Insufficient sample volume for analysis.

Table 2—Litterfall data, Nancy Lake study site, 1987-1988

Collection date	Days in field	Total litter mass g/m²		Seasonal litterfall rate g/ha day	
		BR-1	BR-2	BR-1	BR-2
08/12/87	32	7.2	7.4		
09/16/87	35	3.5	10.7		
10/06/87	20	2.6	9.3		
Seasonal Total	87	13.3	27.4	1,500	3,150
07/18/88	19	13.9	12.4		
08/30/88	43	8.4	16.3		
Seasonal Total	62	22.3	28.7	3,600	4,630

Table 3—Initial lignin and nitrogen content of litter used in the determination of decay rates percent

	Lignin		Nitrogen		Lignin/N
Species	Mean	Stan. dev.	Mean	Stan. dev.	ratio
Pacific dogwood	6.2	0.20	0.87	0.20	7.1
Willow	21.4	1.51	1.18	.07	18.0
Engelmann spruce	13.4	.15	.74	.03	18.0
Subalpine fir	20.5	.70	.77	.05	26.0
Whitebark pine	23.4	2.02	.61	.02	38.0
Western white pine	27.0	3.48	.37	.01	73.0

Table 4—Decay constants for litter of six tree and shrub species, Nancy Lake, WY, 1988 (per year)

	Stand BR-1		Stand BR-2	
Species	Mean	Stan. dev.	Mean	Stan. dev.
Pacific dogwood	0.487	0.186	0.471	0.029
Willow	.284	.047	.266	.019
Engelmann spruce	.262	.038	.255	.020
Subalpine fir	.220	.023	.276	.035
Whitebark pine	.202	.032	.228	.047
Western white pine	.111	.019	.121	.019

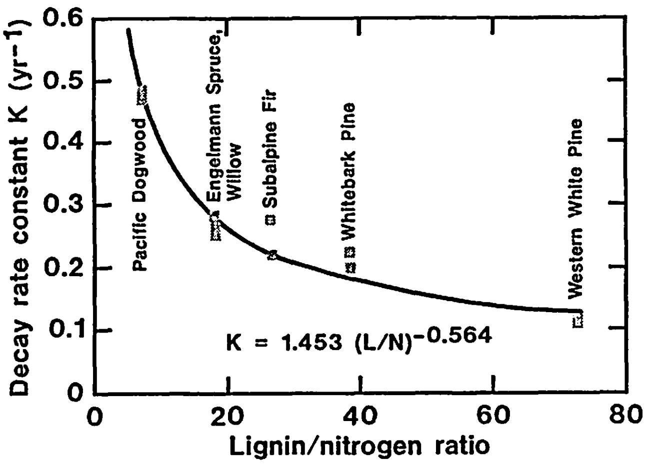


Figure 5—Relationship between decay rate constant and lignin/nitrogen ratio for six species, Nancy Lake, WY, 1987-88.

Elemental Analyses

Results of the analyses of litterfall samples and conifer needles for selected nutrients (P, K, Ca, and Mg) are shown in table 5.

DISCUSSION

The data collected during the 1987 and 1988 field seasons provide an indication of the recent status of these ecosystem processes at the Nancy Lake study site. Future measurements of these parameters can be compared with these baseline values to observe changes in the system. Additional data sets are required before we can adequately determine whether needle retention, canopy litterfall, and litter decomposition meet the five criteria described above for use as indicators of pollutant input.

Needle Retention

Needles of both whitebark pine and Engelmann spruce are retained for longer periods of time at this high-elevation system than are those of conifers observed in more temperate forests of the Pacific Northwest (Baker and others 1986). Many of the spruce examined at the Nancy Lake site retained needles for up to 30 years; this represents extremely long retention times for spruce needles (Harlow and Harrar 1958). We hypothesize that this extended retention rate represents a response to the shorter growing seasons or poor soil development characteristic of these high-elevation sites, where branch elongation and growth of new photosynthetic tissue are restricted. Preliminary data from a study designed to examine the relationship between needle retention rate and elevation in the Nancy Lake area seem to support the hypothesis (White and Wiersma, in preparation). The trees in the Nancy Lake area appear to have responded to the environmental conditions of the site by maintaining their needles for longer time periods. The older needles present do show signs of age or exposure to the harsh environmental stresses naturally present at the site (Bruns and others 1988).

Canopy Litterfall

Canopy litter input is a more difficult parameter to assess due to the limited collection period and to the problems associated with collecting accurate data during the winter months. These problems included damage to the collection buckets from snowpack and animals. The severe drought conditions prevalent in the area during 1988 may have resulted in annual litter input rates that were abnormally high for this area. Additional data are necessary to determine the extent of the natural variability associated with this parameter. The annual input rates determined for the two stands are extremely low compared with those of more temperate forest sites in the

Table 5—Concentrations of selected nutrients in conifer needles and litter samples, Nancy Lake, WY, 1987-1988 (all values in parts per million)

		Litterfall samples			
Collection date	**Stand**	**P**	**K**	**CA**	**MG**
August 1987	BR-1	2,800	2,830	4,790	972
	BR-2	2,460	2,410	2,990	1,330
September 1987	BR-1	1,530	2,900	5,160	835
	BR-2	1,270	1,680	3,450	1,330
October 1987	BR-1	1,160	2,120	5,920	769
	BR-2	989	1,690	6,280	1,110
July 1988	BR-1	2,560	2,440	7,200	961
	BR-2	1,600	1,970	6,180	1,260
August 1988	BR-1	1,890	2,250	11,800	685
	BR-2	1,450	1,750	8,365	1,220

		Conifer needles			
Collection date	**Species**	**P**	**K**	**CA**	**MG**
July 1987	Whitebark pine	1,710	2,180	7,600	1,420
July 1987	Engelmann spruce	1,240	2,580	15,400	767
July 1987	Subalpine fir	1,460	2,060	15,400	766

Pacific Northwest (Baker and others, in preparation; McShane and others 1983). This reflects the relatively low productivity expected in a forest with a limited growing season. The difference in litterfall rates found between the two stands can primarily be attributed to the presence of the many small firs in the understory of BR-2. Other possible contributing factors include differences in relative canopy cover, basal area factor, and the number of stems per acre between the two stands.

Litter Decomposition

Decomposition rates have been shown to be dependent on the initial ratio of the concentrations of lignin and nitrogen in the litter, with litter containing high relative concentrations of lignin expected to exhibit the slowest decomposition rates (Melillo and others 1982). This relationship was observed in the Nancy Lake decomposition data shown in figure 5. Decay rates, however, are also a function of climatic factors. The relationship between decay rates and lignin/nitrogen ratios from Nancy Lake is compared with those of other sites in figure 6. These sites represent a wide variety of climatic conditions, and include sites in Washington State (Harmon and others, in press), North Carolina (Cromack and Monk 1975), and Puerto Rico (La Caro and Rudd 1985). At any given lignin/nitrogen ratio, the decay rate constant is less at the Nancy Lake site than at other sites. This phenomenon appears to be due to a more harsh climate characteristic of the Wind River range.

Elemental Analyses

A cursory review of the nutrient concentration data from conifer needles and litter samples indicates that the levels of these nutrients in litter are similar in both stands (table 4). With respect to the needles, it is interesting that whitebark pine needles were found to have only about half the calcium content of either Engelmann spruce or subalpine fir while possessing almost twice the concentration of magnesium. Comparison of the differences in calcium content of green needles versus that of litter collected during the same time frame (August 1987), indicates that a significant reabsorption of calcium from needles prior to abscission may be occurring. A more detailed review of the nutrient concentration data will be provided along with that of other chemical elements in these and other environmental media in a future report (Wiersma and others in preparation).

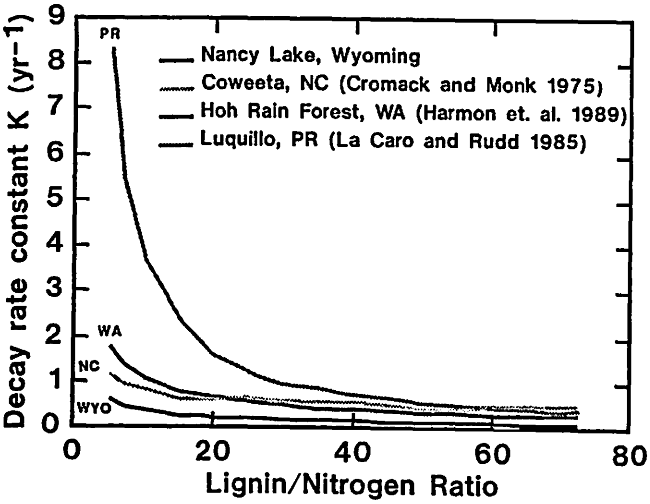


Figure 6—Comparison of relationship between decay rate constant and lignin/nitrogen ratio for sites of varying climatic conditions.

ACKNOWLEDGMENTS

This project was supported by the Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, through an interagency agreement with the U.S. Department of Energy. The Exploratory Research and Development Program at the Idaho National Engineering Laboratory, Idaho Operations Office, U.S. Department of Energy, under DOE Contract No. DE-AC07-76ID01570, is acknowledged for its support in the development of the study site and the implementation of the initial pilot studies.

Multimedia trace element analyses for this project were conducted at the Department of Energy Laboratory of Biomedical and Environmental Sciences at the University of California at Los Angeles. Lignin and nitrogen analyses were performed at the University of Alaska Experimental Station.

Special thanks are given to T. O'Rourke, C. Staley, K. Wright, C. Gautier, B. Smith, and S. Greene for their assistance in the field work of this project, and to T. O'Rourke, K. Wright, K. Finley, D. Beutler, D. Varacalle, and R. Sherwood for their contributions in the laboratory.

REFERENCES

Alexander, G.; McAnulty, C. 1981. Multi-element analysis of plant related tissue and fluids by optical emission spectroscopy. Journal of Plant Nutrients. 3: 51-59.

Baker, G. A.; Harmon, M. E.; Greene, S. E. 1986. A study of selected ecosystem processes potentially sensitive to airborne pollutants. In: Flug, M., ed. Proceedings—conference on science in the national parks: physical processes and water resources; 1986 July 13-16; Fort Collins, CO. Fort Collins, CO: Colorado State Univeristy: 119-138.

Baker, G. A.; Harmon, M. E.; Wiersma, G. B. [In preparation]. Seasonal litter input in the Hoh Rain Forest, Olympic National Park, Washington: physical components and chemical composition. Corvallis, OR: Oregon State University.

Brown, K. W.; Wiersma, G. B. 1979. Pollutant monitoring in Olympic National Park Biosphere Reserve. Proceedings of the second conference on scientific research in the national parks; 1979 November 26-30; San Francisco, CA. Corvallis, OR: Oregon State University, Forest Research Laboratory: 77-82.

Bruns, D. A.; Baker, G. A.; Clayton, J. L.; Greene, S. E.; Harmon, M. E.; Minshall, G. W.; O'Rourke, T. P.; Smith, B. G.; Staley, C. S.; White, G. J.; Wiersma, G. B. 1988. Integrated environmental monitoring at remote ecosystems: first annual report. Report EGG-CEMA-8185. Idaho Falls, ID: EG&G Idaho, Inc. 177 p.

Bruns, D. A.; Minshall, G. W.; Brock, J. T.; Cushing, C. E.; Cummins, K. W.; Vannote, R. L. 1982. Ordination of functional groups and organic matter parameters from the Middle Fork of the Salmon River, Idaho. Freshwater Invertebrate Biology. 1(3): 2-12.

Bruns, D. A.; Minshall, G. W.; Cushing, C. E.; Cummins, K. W.; Brock, J. T.; Vannote, R. L. 1984. Tributaries as modifiers of the river continuum concept: analysis by polar ordination and regression models. Archiv für Hydrobiologie. 99: 208-220.

Bruns, D. A.; Wiersma, G. B. 1988a. Stream ecosystem monitoring at a remote biosphere reserve: Torres del Paine National Park, Chile. Bulletin of the North American Benthological Society. 5: 52.

Bruns, D. A.; Wiersma, G. B. 1988b. Research plan for integrated ecosystem and pollutant monitoring at remote wilderness study sites. Informal Report EGG-EES-7951. Idaho Falls, ID: EG&G Idaho, Inc. 50 p.

Bruns, D. A.; Wiersma, G. B.; White, G. J.; Staley, C. S.; Sanders, R. D.; Rogers, R. D.; Miley, D. 1987. Preliminary results and research protocol for environmental functioning and response to energy related emissions. Internal Technical Report ST-ES-02-87. Idaho Falls, ID: EG&G Idaho, Inc. 65 p.

Coughtrey, P. J.; Jones, C. H.; Martin, M. H.; Shales, S. W. 1979. Litter accumulation in woodlands contaminated by Pb, Zn, Cd, and Cu. Oecologia. 39: 51-60.

Cromack, K., Jr.; Monk, C. D. 1975. Litter production, decomposition, and nutrient cycling in a mixed hardwood watershed and a white pine watershed. In: Howell, F. G.; Gentry, J. B.; Smith, M. H., eds. Mineral cycling in southeastern ecosystems: Proceedings of a symposium; 1974 May 1-3; Augusta, GA. CONF-740513. Washingrton, DC: U.S. Energy Research and Development Administration: 609-624.

Crossley, D. A., Jr.; Hoglund, M. P. 1962. A litter bag method for the study of microarthropods inhabiting leaf litter. Ecology. 43: 571-573.

Fogel, R.; Cromack, K. 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Canadian Journal of Botany. 55: 1632-1640.

Fox, D.; Bernabo, J.; Hood, B. 1987. Guidelines for measuring the physical, chemical, and biological conditions of wilderness ecosystems. Gen. Tech. Rep. RM-146. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 48 p.

Freedman, B.; Hutchinson, T. C. 1980. Long-term effects of smelters at Sudbury, Ontario on surrounding forest communities. Canadian Journal of Botany. 58: 2123-2140.

Goering, H. K.; Van Soest, P. J. 1970. Forage fiber analysis apparatus, reagents, procedures, and some applications. Agric. Handb. 379. Washington, DC: U.S. Department of Agriculture, Forest Service. 20 p.

Harlow, W. M.; Harrar, E. S. 1958. Textbook of dendrology. New York: McGraw-Hill. 512 p.

Harmon, M. E.; Baker, G. A.; Spycher, G.; Greene, S. E. [In press]. Early decomposition of leaf litter in a *Picea-Tsuga* forest, Olympic National Park, Washington, USA. Forest Ecology and Management.

Hinds, W. T. 1984. Towards monitoring of long-term trends in terrestrial ecosystems. Environmental Conservation. 11: 11-18.

Isaac, R. A.; Johnson, W. C. 1976. Determination of total nitrogen in plant tissue, using the block digestor. Journal of the Association of Analytical Chemists. 59: 98-100.

Jenny, H.; Gessel, S. P.; Bingham, T. 1949. Comparative study on decomposition rates of organic matter in temperate and tropical regions. Soil Science. 68: 419-432.

La Caro, F.; Rudd, R. L. 1985. Leaf litter disappearance rates in Puerto Rican montane rain forest. Biotropica. 17: 269-276.

Likens, G. E. 1985. The aquatic ecosystem and air-land-water interactions. In: Likens, G. E., ed. An ecosystem approach to aquatic ecology, Mirror Lake and its environment. New York: Springer-Verlag: 430-435.

Mann, L. K.; McGlaughlin, S. B.; Shriner, D. S. 1980. Seasonal physiological responses of white pine under chronic air pollution stress. Environmenal and Experimental Botany. 20: 99-105.

McShane, M. C.; Carlile, D. W.; Hinds, W. T. 1983. The effect of sample size on forest litterfall collection and analysis. Canadian Journal of Forest Research. 13: 1037-1047.

Melillo, J. M.; Aber, J. D.; Muratore, J. F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology. 63: 621-626.

Miller, D. R. 1984. Distinguishing toxic effects. In: Sheehan, P. J.; Miller, D. R.; Butler, G. C.; Bourdeau, P., eds. Effects of pollutants at the ecosystem level. Report #22. Scientific Committee on Problems of the Environment (SCOPE). New York: John Wiley and Sons: 15-22.

Minshall, G. W.; Cummins, K. W.; Petersen, R. C.; Cushing, C. E.; Bruns, D. A.; Sedell, J. R.; Vannote, R. L. 1985. Developments in stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences. 42: 1045-1055.

Moloney, K. A.; Stratton, L. J.; Klein, R. M. 1983. Effects of simulated acidic, metal-containing precipitation on coniferous litter decomposition dynamics. Ecology. 63: 621-626.

Olson, J. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology. 44: 322-331.

Reiley, J.; Machin, D.; Morton, A. 1969. The measurement of microclimatic factors under a vegetation canopy—a reappraisal of Wilm's method. Journal of Ecology. 57: 101-108.

Singh, J.; Gupta, S. 1977. Plant decomposition and soil respiration in terrestrial ecosystems. The Botanical Review. 43: 449-528.

Steele, R.; Cooper, S.; Ondov, D.; Roberts, D.; Pfister, R. 1983. Forest habitat types of eastern Idaho and western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S.

Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

Strojan, C. L. 1978. Forest leaf litter decomposition in the vicinity of a zinc smelter. Oecologia. 32: 203-212.

Ulrich, B. 1981. Air pollution and forest decline. Environmental Science Technology. 17: 246-256.

USDA Forest Service. 1984. Air quality and acid deposition potential in the Bridger and Fitzpatrick Wilderness. Proceedings of a workshop: 1984 March; Fort Collins, CO: Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region. 292 p.

White, G. J.; Wiersma, G. B. [In preparation]. Relationship between conifer needle retention rate and elevation at a high-elevation site in western Wyoming. Idaho Falls, ID: EG&G, Idaho, Inc.

Wiersma, G. B.; Bruns, D. A.; Sanders, R. D.; Rogers, R. D.; Lemmon, E. C.; Wright, R. B.; Breckenridge, R. P. 1985. Preliminary results and research protocol for environmental functioning and response to energy related emissions. Internal Tech. Rep. ST-ES-02-85. Idaho Falls, ID: EG&G Idaho, Inc. 58 p.

Wiersma, G. B.; Frank, C. W.; Case, M. J.; Crockett, A. B. 1984. The use of simple kinetic models to help design environmental monitoring systems. Environmental Monitoring and Assessment. 4: 233-255.

Wiersma, G. B.; O'Rourke, T. P.; Bruns, D. A.; Boelke, C.; Johnson, A.; McAnulty, L. 1988. Integrated monitoring project at Torres del Paine National Park, Chile—methodology and data report—1984 through 1986. Informal Tech. Rep. EG-EES-7966. Idaho Falls, ID: EG&G Idaho, Inc.

Wiersma, G. B.; Otis, M. D. 1986. Multimedia design principles applied to the development of the global integrated monitoring network. In: Cohen, Y., ed. Pollutants in a multimedia environment. New York: Plenum Publishing: 317-332.

Wiersma, G. B.; Slaughter, C.; Hilgert, J.; McKee, A.; Halpern, C. 1986. Reconnaissance of Noatak National Preserve and Biosphere Reserve as a potential site for inclusion in the Integrated Global Monitoring Network. Washington, DC: U.S. Department of State, Man and the Biosphere Program. 84 p.

Wiersma, G. B.; White, G. J.; Bruns, D. A. [In preparation]. Distribution of trace elements in various environmental media at a remote, high-elevation site in western Wyoming. Idaho Falls, ID: EG&G Idaho, Inc.

Williams, W. T. 1980. Air pollution disease in the California forests: a base line for smog disease on ponderosa and Jeffrey pines in the Sequoia and Los Padres National Forests, California. Environmental Science Technology. 14: 179-182.

STONE PINES AND BEARS

David J. Mattson
Charles Jonkel

ABSTRACT

Bears use stone pine (subsection Cembrae) seeds throughout the Northern Hemisphere, primarily Pinus sibirica, P. pumila, *and* P. koraiensis *in Eurasia, and* P. albicaulis *in North America. Bears make the greatest use of pine seeds in eastern Siberia and in the Northern Rocky Mountains of the United States. The pine seeds are important to bears because of their high nutritional value. During years of poor pine seed crops, Yellowstone area grizzly bears are trapped and killed more often; in Siberia, brown bears wander more and become more predatory.*

Grizzly use of pine seeds in the Yellowstone area is variable among years, in accord with the erratic seed production. Virtually all seeds used by bears are extracted from red squirrel caches. In many areas, the whitebark pine has nearly disappeared as a result of the double onslaught by white pine blister rust and mountain pine beetle infestations. This important food for some bears and populations has been nearly eliminated, and may not be available to bears despite human intervention for hundreds of years. Because the trees are so thinly distributed, silvicultural treatments hold little promise of appreciably enhancing pine seed availability to bears.

INTRODUCTION

The seeds of whitebark pine (*Pinus albicaulis*) and other stone pines (subsection Cembrae) are a high-quality wildlife food characterized by high triacerglycerol content (Craighead and others 1982; Hutchins and Lanner 1982; Mealey 1980; Shcherbina and Larionova 1963) and energy concentration comparable to that of fleshy fruits (Craighead and others 1982; Mealey 1980). Large seed size contributes to efficiencies of use by numerous species of birds and mammals (Hutchins and Lanner 1982; Tomback 1983). Because the cones are typically indehiscent (Arno and Hoff 1989; Lanner 1982), seeds remain concentrated in the cones and contribute to efficiencies of use, especially by red squirrels (*Tamiasciurus hudsonicus*) and bears (*Ursus* spp.). Where bears eat the entire cone, the fleshy pulp of the cone also contributes to their diet (Jonkel 1967).

Whitebark pine and other stone pine seeds are high-quality bear food for reasons in addition to their high energy content. Stone pine seeds mature by August and are available from then until bears hibernate (Hutchins and Lanner 1982; Iroshnikov 1963; Kendall 1983). This period corresponds with the critical hyperphaegic state during which bears accumulate the fat necessary to sustain them through hibernation and subsequent hypophaegia (Nelson and others 1983). Because of their high digestible lipid content, pine seeds very likely contribute more to efficiencies of body fat accumulation by bears than foods high in protein or sugar content (Allen 1976; Brody and Pelton 1988; Hadley 1985). Because of their durable nature, pine seeds can overwinter in or out of cones and provide high-quality food for bears the next spring and summer. Whitebark pine seeds and cones also contain estrogenic compounds (Jonkel 1967; Jonkel and Cowan 1971). These compounds could influence reproduction in bears, but effects are undocumented and the precise roles played by estrogens in delayed implantation are as yet unknown.

Bear use of stone pines is disadvantaged by frequent poor cone crops. Craighead and Mitchell (1982) recorded bumper cone crops of whitebark pine only 2 of 12 years in the Yellowstone National Park area and 2 of 7 years in the Scapegoat Mountains of Montana. In recent years we recorded good crops 2 and poor crops 4 out of 12 years in the Yellowstone area. Data from Weaver and Forcella (1986) suggested an average 2-year interval between poor crops and 6-year interval between good crops of whitebark pine in the Rocky Mountains during the 1970's. In Siberia, Nesvetailo (1987) estimated 10 good and 10 poor Siberian stone pine crops during a 58-year period. Together these observations suggest an average 2- to 6-year interval between both good and poor stone pine crops. It is also clear that this cycle is highly irregular among years, regions, and habitat types.

In areas where bears depend on stone pine seeds for fattening, and where there are typically few fleshy fruits available, years of poor pine seed crops result in increased conflict between bears and humans. In the Yellowstone area there is a predictable and dramatic increase in adult female bear deaths and management actions against bears during poor seed crop years (Blanchard, this proceedings). Similarly, in Siberia poor stone pine seed crops result in increased attacks on humans and increased livestock and agricultural crop depredations (Stroganov 1962; Ustinov 1965). This increased conflict probably results not only from an increased number of poor-condition bears (Ustinov 1965), but also because of the many human foods available in bear habitat that constitute high-quality alternatives to native fruit and seed crops (Mattson, in press).

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

David J. Mattson is Wildlife Biologist, Interagency Grizzly Bear Study Team, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717; Charles Jonkel is Leader, Border Grizzly Project, University of Montana, Missoula, MT 59812.

DISTRIBUTION OF USE

In common with other stone pines (including *P. sibirica, P. pumila,* and *P. koriaensis*), whitebark pine is used by bears wherever it is abundant (fig. 1). In North America this occurs south of the Canadian border in the cordillera of the western United States. Farther north, whitebark pine is only an incidental part of the forest vegetation (Arno and Hoff 1989).

Within the range of stone pines, bear use of stone pine seeds ranged from near zero in Glacier National Park, MT, (Kendall 1986) and the Mission Mountains of Montana (Mace and Jonkel 1986) to 18.3 percent and 28 percent of total sampled fecal volume in Yellowstone (Mattson and others, in preparation) and the Lake Baikal area of Ulan-Ude, U.S.S.R. (Ustinov 1965; Vereschagin 1976), respectively (table 1). Peak use consistently occurred from September through November. A secondary peak usually occurred in the spring, in association with use of overwintered pine seeds following large crops the previous fall. This pattern of use is typified by Yellowstone data for the years 1977-87 (fig. 2). When feeding on pine seeds, bears tend to consume the seeds to the near-exclusion of all other foods. This was consistently reflected in high mean percent volumes of pine seeds in scats—percent volume divided by percent frequency (fig. 2).

There is a remarkable correspondence between the current southern limit of the main distribution of brown bears (*Ursus arctos*) and stone pines (fig. 1). This correspondence almost certainly does not reflect dependence of either species on the other. More likely human (*Homo sapiens*) intolerance has relegated brown bears to the comparatively inhospitable and harsh environments characterized by stone pines (Mattson, in press). Nonetheless, within this area of overlap, stone pine seeds are an important food for numerous Asian and North American bear populations (Aune and Kasworm, in press; Bergman 1936; Bromlei 1965; Craighead and others 1982; Kendall 1983; Kistchinski 1972; Novikov 1956; Stroganov 1962; Ustinov 1965, 1976; and others), especially where there were few, irregularly available fleshy fruits (Mattson and others, in preparation).

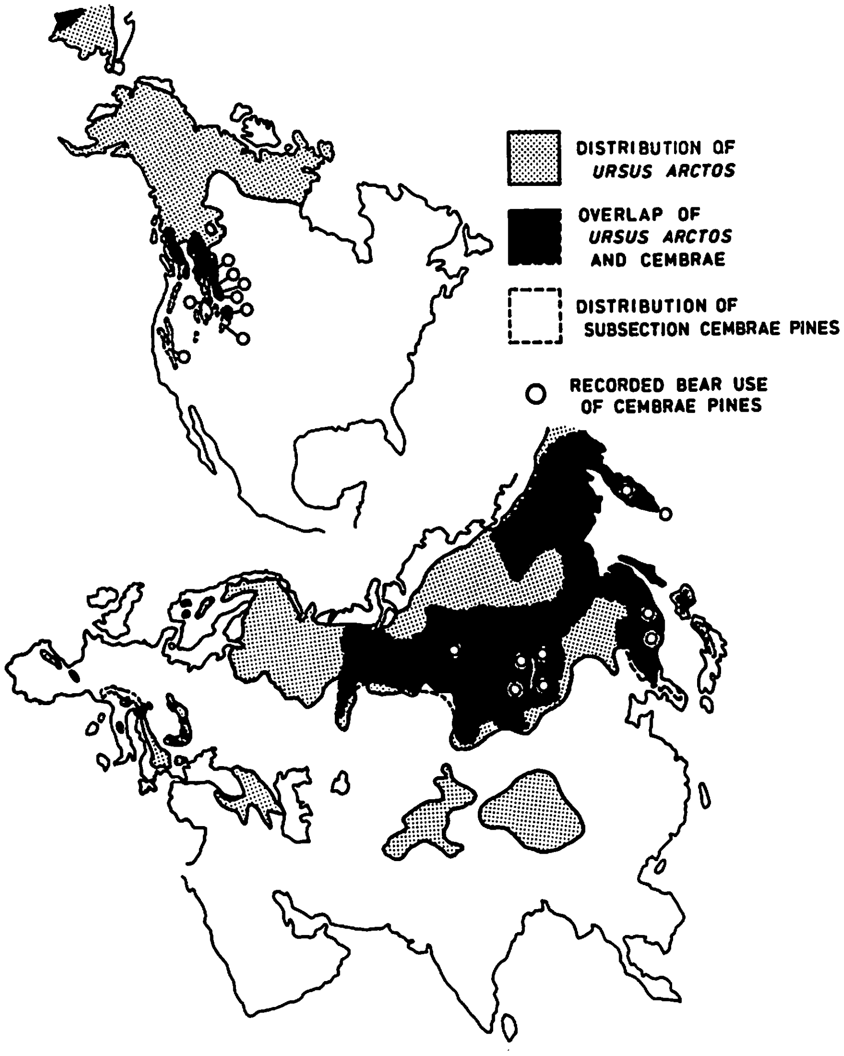


Figure 1—Distribution of brown bears (*Ursus arctos*) and stone pines (subsection Cembrae), and recorded instances of substantial stone pine seed use by bears (*Ursus* spp.) (Clevenger and others 1987; Critchfield and Little 1966; Elgmork 1987; Patnode and LeFranc 1987; Yi-Ching 1981; Zunino 1975).

Table 1—Percent frequency (%F) and volume (%V) of stone pine seeds in bear scats from study areas in the Rocky Mountains, Sierra Nevada, and Siberia

	Total scat collection		Maximum month or season		
Study area	**%F**	**%V**	**%F**	**%V**	**Month or season**
Rocky Mountains					
Glacier NP, BC[1]	—	—	2	tr	Fall
North Fork of the Flathead, MT[2/11]	4.0	1.2	19.2	11.3	September
South Fork of the Flathead, MT[2]	.7	.4	—	—	
Glacier NP, MT[3]	0	0	—	—	
Mission Mtns, MT[2]	.3	.1	—	—	
East Front, MT[2/4]	14.6/5.1	12.6/4.5	33.3	31.0	October
Yellowstone, MT&WY[5]	30.3	18.4	42.8	39.2	October
Grays River Mtns, WY[6]	—	—	22.5	15.0	Fall
Sierra Nevada					
Yosemite NP, CA[7]	3	1	17	7	Fall
Siberia					
Kamchatka[8]	—	14	—	—	
Primore[8]	—	6	—	—	
Ussuri[9]	—	5.3	—	25.0	November
Baikal[8/10]	—	28	—	100.0	October

[1] Mundy (1963).
[2] Mace and Jonkel (1983).
[3] Kendall (1986).
[4] Aune and Kasworm (in press).
[5] Mattson and others (in preparation).
[6] Irwin and Hammond (1985).
[7] Graber and White (1983).
[8] Vereschagin (1976).
[9] Bromlei (1965).
[10] Ustinov (1965).
[11] Husby and others (1977).

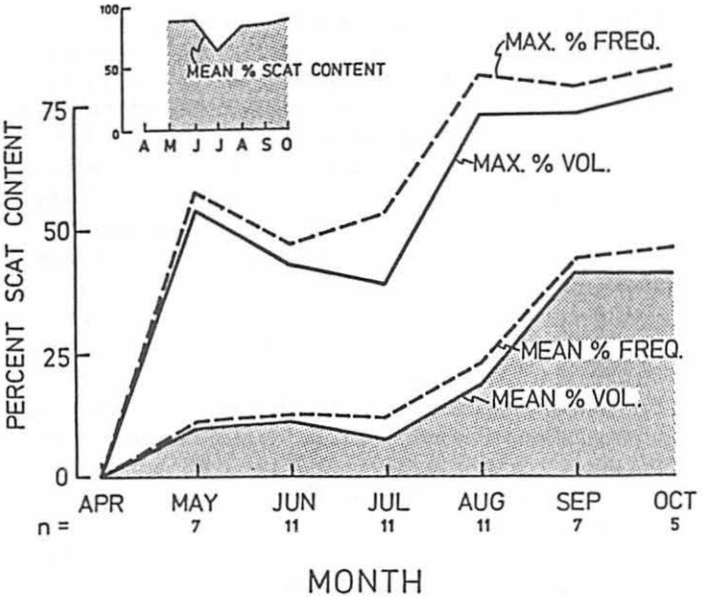


Figure 2—Percent frequency and volume of whitebark pine seeds in scats collected in the Yellowstone area, by month, 1977-87 (*n* = number of years). Inset diagram depicts mean percent pine seed volume in scats of occurrence, by month.

ACQUISITION OF PINE SEEDS

Bears employ several strategies to acquire stone pine seeds depending on the presence of rodent intermediaries, the density and stature of stone pine forests, and the bear's ability to climb. Black bears (*Ursus americanus* and *Selenarctos thibetanus*) are more adept climbers than brown bears (Herrero 1978) and are more likely to climb trees to consume seeds in the canopy, or to break limbs off and subsequently consume the seeds on the forest floor (Barnes and Bray 1967; Bromlei 1965; Mealey 1975; Stroganov 1962). In northwestern Montana, bears commonly climbed trees to acquire whitebark pine cones. These bears often had no hair on their entire front legs after a fall spent feeding on pine seeds (figs. 3 and 4). Pitch that built up on the feet and legs from clawing small whitebark pine trees peeled off when caked with dirt and debris, taking all the hair along.

Brown bears seem generally restricted to acquiring seeds that have fallen or been brought down to the forest floor by other animals. Scavenging on fallen cones is apparently common in Siberia (Bromlei 1965). In the Rocky Mountains, forest floor scavenging on cones is rare (Mattson, personal observation; Aune and Kasworm, in press). In the Yellowstone area only 3 percent of 193 instances where bears were known to have used pine seeds involved scavenging on fallen cones. These few

Figure 3—The front feet of this black bear are caked with pitch from feeding on whitebark pine cones and seeds (1959 photo by C. Jonkel).

Figure 4—Cracking of the pitch, debris, and hair mat on this young black bear's front foot show the extent of whitebark pine cone and seed feeding by this bear, and the process whereby bears lost the hair from their front legs (1959 photo by C. Jonkel).

instances occurred in stands where whitebark pine comprised approximately 76 percent of total stand basal area ($\overline{X}$= 46.7 ± 10.6 m^2/ha), and following extreme weather that knocked cones out of the trees. Taylor (1964) similarly mentioned bears concentrating at and scavenging on cones on the forest floor in an area where whitebark pine cones were wind-thrown by a "violent storm." Bears also consumed cones directly from the canopy of dwarfed stone pines, commonly in Kamchatka (Bergman 1936; Kistchinski 1972) and less frequently near timberline in northwest Montana and Yellowstone (Mattson and Jonkel, personal observation; Craighead and others 1982; Jonkel 1967; Tisch 1961).

In most areas where brown bears make substantial use of stone pine seeds, rodents are a critical link. In the Rocky Mountains red squirrels preferentially harvest whitebark and limber pine seeds (Hutchins and Lanner 1982) and cache them in middens, typically in intact cones (Hutchins and Lanner 1982; Kendall 1983). Bears subsequently search out these middens and excavate the whitebark pine cones. This commonly occurs in the Yellowstone area (Kendall 1983) and along the East Front of the Rocky Mountains in Montana (Aune and Kasworm, in press; Schallenberger and Jonkel 1980). Excavation of squirrel middens by bears to obtain seed and fruits is also known from northern Idaho (whitebark pine seeds) (Kendall 1989), Yosemite National Park (whitebark pine seeds) (Graber and White 1983), and northern Minnesota (hazelnuts [*Corylus cornuta*]) (Rogers 1989). In the Yellowstone area, 97 percent of 196 pine seed feeding sites involved excavation of squirrel middens. A similar high percentage of squirrel midden use was characteristic on the East Front of Montana (Aune and Kasworm, in preparation; Schallenberger and Jonkel 1980).

In Siberia, the Siberian chipmunk (*Eutamias sibiricus*) appears to be the primary rodent intermediary between stone pine seeds and bears. As in North America, stone pine seeds are a preferred food of both chipmunks and squirrels (*Sciurus vulgaris*) in Siberia (Ognev 1940). Siberian chipmunks commonly make stone pine seed caches of 1.5 to 2 kg in size (up to 6 kg) for winter and spring consumption (Ognev 1940). And as in the Rocky Mountains, bears search out and excavate these rodent caches in spring and late fall (Bromlei 1965; Novikov 1956; Ognev 1940; Stroganov 1962; Ustinov 1976).

The much greater use of chipmunk rather than squirrel caches by Siberian bears is puzzling. In his monograph on Eurasian mammals, Ognev (1940) suggested that chipmunks commonly attained much higher densities than squirrels in the range of Siberian stone pines. He quoted an estimate for one area of only 0.14 squirrel "nests"/km of transects. This compared with 0.11 to 0.14 squirrel middens/km in pure whitebark pine stands of the Yellowstone area (Reinhart and Mattson, this proceedings). Significantly, virtually no bear use of squirrel middens was observed in pure whitebark pine stands of the Yellowstone area. This suggests that when squirrels are at such low densities bears use relatively few squirrel caches. By all indications Siberian squirrels more often cache cones in hollow trees, through elevated openings, than do squirrels in the Rocky Mountains. This would further complicate acquisition of squirrel caches by Siberian bears.

Bears are remarkably adept at extracting seeds from cones in the Yellowstone area; few cone remnants are ingested along with the seeds (Kendall 1983). One way that bears achieve this is by scraping away the cone scales with their claws and lapping up the seeds with their tongues from among the debris (Kendall 1983). Typical bear feces that result from consumption of pine seeds consist almost wholly of broken seed coats (Kendall 1983; Tisch 1961). Very few seeds pass through intact, and it is doubtful that bears serve as a significant dispersal agent for whitebark pine in most of the Rocky Mountains (Hutchins and Lanner 1982). This is especially likely given the poor germination potential of unburied whitebark pine seeds (McCaughey, this proceedings).

Interestingly, Siberian brown bears are apparently prone to ingest more cone scales when scavenging pine seeds out of cones from the forest floor (Semechkin 1963). This may be a consequence of their greater use of individual seeds extracted from chipmunk caches. The scavenging of cones may also be marginally profitable, providing little incentive to invest the added time and energy required to break apart the cones and pick out the individual seeds.

Of the three main seed-acquiring techniques, the excavation of rodent caches is on average the most energetically efficient process for bears. Unless there is a bumper crop, bears will expend considerably more energy than they acquire by breaking major tree limbs and harvesting seeds from the relatively few cones on each limb. Similarly, unless there is an unusual weather event, very few cones will survive depredations of chipmunks, nutcrackers (*Nucifraga* spp.), and other avifauna and fall intact to the forest floor (Hutchins and Lanner 1982; Kozhevnikov 1963). Rodents increase the foraging efficiencies for bears by harvesting otherwise unavailable, intact cones and seeds from trees, then concentrating them in caches. Red squirrels will use caching sites or middens for many years (Reinhart and Mattson, this proceedings), which in turn facilitates their location by bears. In the Yellowstone area individual middens receive repeat use by bears in the same and different years (Mattson, personal observation; Kendall 1983). Bear depredations may be so heavy in some habitats that many squirrels may not survive (Mattson and Reinhart 1987; Reinhart and Mattson, this proceedings). In these situations midden locations may be less predictable due to higher turnover of individuals in the squirrel population.

CHARACTERISTICS OF PINE SEED FEEDING SITES

Topography

Bears exhibited different tendencies in their use of the landscape to acquire pine seeds depending on the year and study area. In the Yellowstone area, bears used mid-slopes and up-slopes to forage on pine seeds more than expected from distribution of all activity sites (fig. 5). However, they exhibited greater preference for mid-slopes during 1986, when using an overwintered crop, and up-slopes during 1987, when using a current year's crop. (Activity site and feed-site parameters were determined from visiting telemetry locations of radio-instrumented bears.) Greater use of mid- and up-slopes corresponded with the tendency for whitebark pine to occur at higher elevations in more wind-exposed habitats (Mattson and Reinhart, this proceedings). Interestingly, in the Yellowstone area bears used ridgetops relatively little for pine seed foraging; in past years, ridgetops were the main foraging area for bears in the Whitefish Range of northwestern Montana (Jonkel 1967).

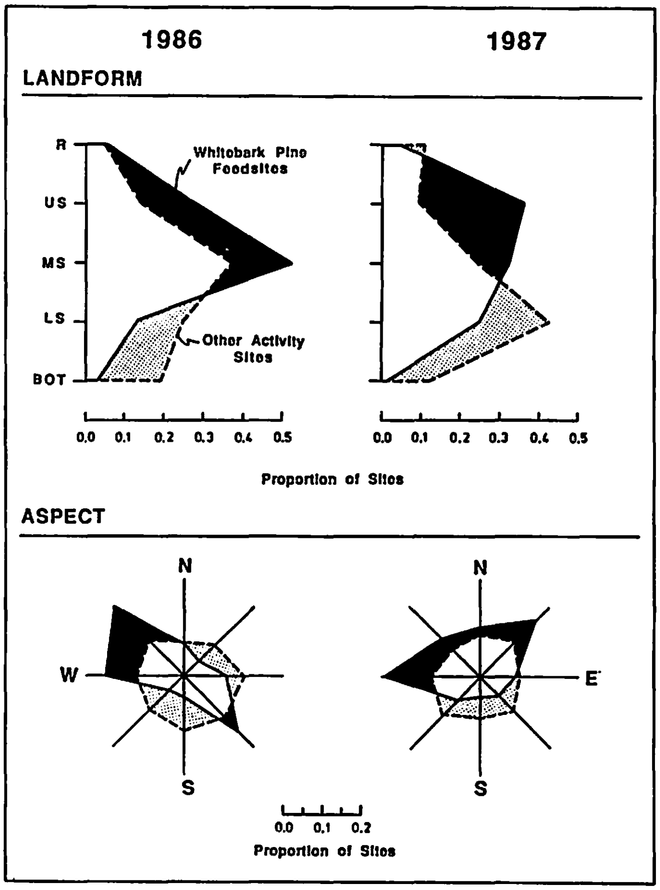


Figure 5—Proportionate distribution of whitebark pine seed feed sites and all other activity sites among landform and aspect classes in the Yellowstone area.

Distribution of pine seed feed sites among aspects varied considerably among years, regions, and landforms. In the Yellowstone area, greater than expected use of west and northwest exposures occurred during 1986, and of west, northwest, and northeast exposures during 1987 (fig. 5). Use of west exposures occurred most often on mid- and low slopes. On the East Front of the Rockies, northeast, east-southeast, southwest, and west-southwest exposures were used most for foraging on pine seeds (Aune and Kasworm, in press).

The distribution of use among aspects in Yellowstone appeared to be related to environmental factors, depending on landform. (We derived estimates for environmental variables from published data.) Use of up-slopes and ridges was negatively related to estimated summer radiation (Buffo and others 1972) and estimated relative frequency of summer winds >8 k/h (Dirks and Martner 1982, Upper Rendezvous site) (fig. 6). This suggests that more exposed and "droughty" conditions did not favor bear use of pine seeds in convex topography. This effect was most likely mediated through the abundance of red squirrels; site favorability for squirrels was negatively

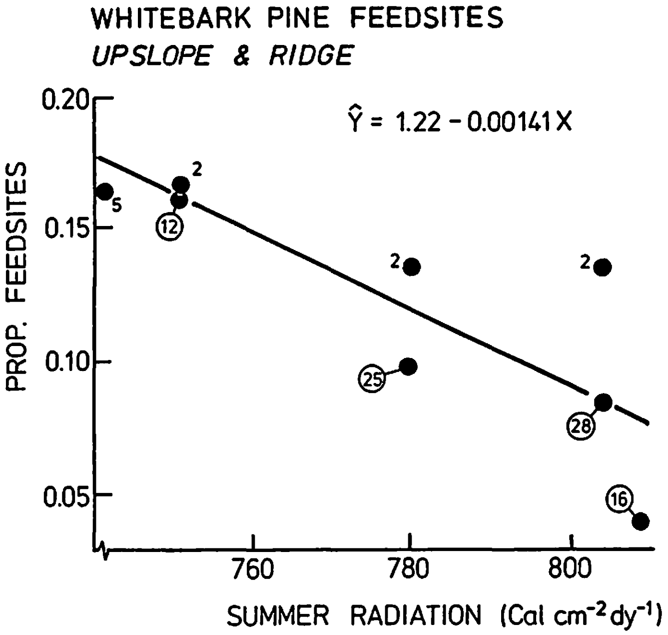


Figure 6—Relationship of proportionate pine seed feed-site distribution in Yellowstone among aspect classes, on convex landforms relative to summer radiation (June 22) and frequency of summer winds >8 k/h (numbers, with higher values circled).

related to wind exposure and positively related to stand basal area (Reinhart and Mattson, this proceedings). On mid- and low slopes, pine seed foraging increased exponentially with increased frequency of winter winds >8 k/h ($\hat{y} = 0.097 + 12.2\,x^4$, where y is the proportion of pine seed feed sites and x is the proportion of winter winds >8 k/h, in a given aspect class). This relationship was probably related to decreased or more irregularly drifted winter snowpack with increased winter wind exposure (Reinhart and Mattson, this proceedings). Given that spring and summer bear use of overwintered crops occurred more commonly on mid-slopes, a combination of shallower snowpack and more productive squirrel habitat probably favored early season bear use of overwintered squirrel caches on west slopes.

The elevational distribution of pine seed feed sites also varied among study areas and years, although in Yellowstone virtually all feed sites occurred above 2,425 m (8,000 ft) elevation (fig. 7). East Front feed sites averaged 455 m (1,500 ft) lower in elevation than Yellowstone feed sites, and partly reflected the 3° latitude difference in study areas (Aune and Kasworm, in press). The elevational distribution of pine seed feed sites was also much more dispersed on the East Front compared with Yellowstone. The much lower elevational range of East Front feed sites, between 1,515 and 1,879 m (5,000 and 6,200 ft), almost certainly reflected bear use of limber pine (*Pinus flexilis*) seeds. Bear use of limber pine seeds from squirrel caches was also recorded in Yellowstone, but only three times out of a total of 196 recorded instances of pine seed use.

Use of the overwintered Yellowstone pine seed crop during 1986 tended to occur at higher elevations than use of the current year's crops during 1979 and 1987 (fig. 7). The higher elevational distribution of feed sites during 1986 conformed more closely to the elevational distribution of whitebark pine (from the Mount Washburn massif; see Mattson and Reinhart, this proceedings) than did pine seed feed sites the other 2 years. This suggests that bears preferred stands with higher whitebark pine basal area when using overwintered seed crops.

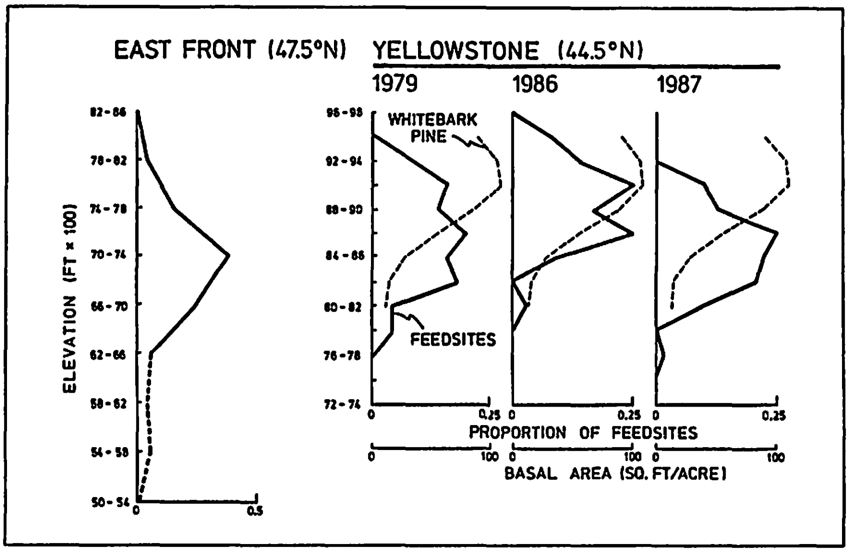


Figure 7—Proportionate distribution of East Front (Aune and Kasworm, in press) and Yellowstone (by year) pine seed feed sites by elevation, and mean whitebark pine basal area by elevation for the Yellowstone area (1 m = 3.28 ft; 1 m^2/ha = 0.2295 ft^2/acre).

Timber Overstory

There was a weak positive association between intensity of midden use by bears and whitebark pine basal area (table 2). This was more evident during use of an over-wintered crop during 1986, when bears tended to use more stands with higher whitebark pine basal areas compared to 1987 ($\chi^2 = 12.81$, df = 5, $P = 0.025$; number of feed sites relative to six categories based on whitebark pine basal area). This difference is understandable given that stands with higher whitebark pine basal areas would have a higher probability of providing over-wintered seeds. However, there was very little correlation between number of cones excavated from middens by bears and whitebark pine basal area ($r = 0.194$, $n = 69$, $P = 0.106$).

Whitebark pine basal area was apparently only one of several habitat parameters that determined the location and intensity of pine seed foraging by bears. This was further implied by the relatively low average basal areas and percent composition of whitebark pine in stands used by bears for foraging on pine seeds (table 3). Stands with high percent whitebark pine composition and whitebark pine basal area were generally not preferentially selected by bears in the Yellowstone area.

We recorded no use of younger aged, early successional stands by bears for foraging on whitebark pine seeds in the Yellowstone area. All stands used by bears were classified as mature to overmature and mid-successional to climax. This is not surprising, given the probable late age at which whitebark pine produce an appreciable number of cones under normal stand conditions. Although the relationship between cone production and stand age is not known for whitebark pine, this relationship is well described for the related and morphologically similar Siberian stone pine (Axelrod 1986). Generally, Siberian stone pines do not produce appreciable numbers of cones until stands reach 90 to 120 years of age. Under exceptional conditions appreciable cone production begins as early as 30 years and, depending on stand and site conditions, high levels of cone production last 150 to 300 years (Iroshnikov and others 1963; Kozhevnikov 1963). It is reasonable, therefore, to assume that most habitat types used by bears for foraging on whitebark pine seeds do not produce sufficient numbers of seeds to sustain bear use until stands reach approximately 100 ± 20 years of age.

Table 2—Whitebark pine basal area associated with different intensities of midden use by bears in the Yellowstone area, 1986 and 1987

	Intensity of use								
	Low			Moderate			High		
Year	n	$\bar{X}$	S_x	n	$\bar{X}$	S_x	n	$\bar{X}$	S_x
1986	5	10.1	5.0	15	13.8	17.1	14	19.0	27.1
1987	14	9.1	7.8	20	15.8	15.4	19	14.0	15.7

Habitat Types

The majority of pine seed use by bears in the Yellowstone and East Front study areas occurred in the ABLA/VASC-PIAL h.t. phase (table 4). (This same type was designated the ABLA-PIAL/VASC h.t. in the East Front study area; see Appendix A for habitat type nomenclature). Proportionate use of the ABLA/VASC-PIAL phase in the Yellowstone area varied from year to year, primarily as a result of different levels of use in mesic mid-elevation and drier high-elevation habitat types. The proportionate distribution of pine seed feed sites among all habitat types in the East Front and in Yellowstone during 1987 was remarkably similar. Very little use of the PIAL series was documented in both study areas. These observations suggest that bear foraging on pine seeds in the various drier portions of the Rocky Mountains occurs in similar habitats for probably much the same reasons.

We quantified bear use of different habitat types by two different use-density indices for the Yellowstone area (table 5). These calculations used data collected at bear feed sites in 1986 and 1987. The estimated density of excavated material (D x E) indexed the density of bear use in sites selected for use by bears. (A/F) x E was dimensionless and quantified overall density of bear feeding on pine seeds in a given type within the whitebark pine zone (>2,545 m); it was not specific to sites selected by bears. The second index was not calculated for high-elevation, dry habitat types because we lacked an estimate of availability for this type.

Values of the second index suggest that overall density of pine seed feeding by bears at elevations >2,545 m (the whitebark pine zone) was highest in lodgepole pine (LP) cover types of the ABLA/VASC-PIAL phase and lowest in the ABLA/VAGL-VASC and ABLA/VASC-VASC phases. Intermediate levels of use characterized whitebark pine (WB) cover types of the ABLA/VASC-PIAL phase and the ABLA/THOC and ABLA/CACA h.t.'s.

Table 3—Whitebark pine and total stand basal area ($\bar{X} \pm S_x$), and whitebark pine as a percent of total stand basal area and cover for whitebark pine seed feed sites in the Yellowstone area, 1986 and 1987

	Basal area (m²/ha)				Mean percent whitebark pine	Percent whitebark pine canopy cover	
	Total		Whitebark pine				
Year	$\bar{X}$	S_x	$\bar{X}$	S_x		$\bar{X}$	S_x
1986	49.4	22.3	14.9	20.5	30.2	—	—
1987	46.6	23.0	12.9	15.1	27.8	33.3	13.7

The degree to which bears were selecting specific sites to feed on pine seeds within a habitat type is suggested by the ratio of estimated midden use density at bear-selected sites to the ratio of observed to expected proportionate use (D/(A/F)). A high value suggests that although relatively few sites were used by bears within a type, those few sites received relatively high-density use because of favorable combinations of squirrel densities and whitebark pine basal area. This was especially true for the ABLA/CACA h.t., and to a lesser extent for the ABLA/VAGL-VASC and ABLA/VASC-VASC phases and spruce-fir (SF) cover types of the ABLA/VASC-PIAL phase. In other habitat types bear use of pine seeds was more uniform.

Bears used the ABLA/VASC-PIAL phase and high-elevation dry types (ABLA/ARCO and ABLA/RIMO h.t.'s) during 1986 and 1987 primarily to feed on pine seeds (fig. 8). Very little bear activity in the whitebark pine (PIAL) series was devoted to use of pine seeds, principally because very few squirrels reside in this type (Reinhart and Mattson, this proceedings); most bear activity in the PIAL series was described as travel. This assessment emphasizes the importance of the ABLA/VASC-PIAL phase and, in areas where this phase is less common, the drier high-elevation *Abies lasiocarpa* (ABLA) series types.

The ratio of whitebark pine basal area at sites used to forage on pine nuts and whitebark pine basal area at all other activity sites within a given habitat type is shown in figure 8. These data indicate that bears selected pine seed feed sites in the ABLA/VASC-VASC phase and ABLA/ THOC h.t. principally on the basis of locally greater whitebark pine basal area; use of these types for pine seed foraging was restricted to anomalous sites at higher elevations where mature whitebark pine occurred in appreciable amounts.

Table 4—Proportional use (P) of habitat types and habitat type groups by bears for foraging on whitebark pine seeds in the Yellowstone area and East Front of the Rockies (data from Aune and Kasworm, in press)

	Yellowstone							
	1979		1986		1987		East Front	
Habitat types	P	*n*	P	*n*	P	*n*	P	*n*
ABLA/VASC-PIAL	0.700	35	0.583	21	0.534	39	0.522	35
ABLA-PIAL/VASC								
High-elevation, subxeric	.120	6	.250	9	.082	6	.104	7
Mesic-subhydric, mid-elev.	.180	9	.194	7	.315	23	.313	21
Mid-lower elev., subxeric	.000	0	.000	0	.068	5	.060	4
Total *n* =		50		36		73		67

Table 5—Whitebark pine basal area, estimated squirrel densities, and parameters of bear use for whitebark pine feed sites in habitat types of the whitebark pine zone

Habitat types	(A) *n*	(B) Estimated squirrel density (*n*/km)	(C) Whitebark pine basal area m²/ha $\bar{X}$	S_x	(D) Estimated density of midden use (*n*/km)	(E) Excavated material (m³/midden) $\bar{X}$	S_x	(D x E) Estimated density of excavated material (m³/km)	(F) Expected frequency[1]	(A/F) Ratio, observed/ expected	(A/F x E) Density of excavated material (dimensionless)	D/(A/F)
ABLA/VASC-PIAL LP cover types	14	2.76	4.3	5.8	1.24	6.6	4.0	8.18	6.7	2.09	13.8	0.59
ABLA/VASC-PIAL WB cover types	37	2.05	20.1	17.0	1.59	5.6	6.9	8.86	27.5	1.34	7.5	1.18
ABLA/VASC-PIAL SF cover types	6	2.36	10.7	9.0	1.43	3.5	3.8	5.00	7.8	.77	2.9	1.86
High elev., dry[2]	13	.85	14.9	25.0	.58	7.0	8.0	4.06	—	—	—	—
Low elev., dry[3]	5	2.23	9.2	9.7	1.25	1.8	—	2.25	4.1	1.22	2.2	1.02
ABLA/CACA	4	3.62	9.2	15.4	2.07	7.4	—	15.32	6.7	.60	4.4	3.45
ABLA/THOC	19	2.62	10.2	11.5	1.56	5.3	5.1	8.21	18.2	1.04	5.5	1.50
ABLA/VAGL-VASC	4	1.32	5.7	6.9	.65	2.8	—	1.82	11.7	.34	1.0	1.91
ABLA/VASC-VASC	5	2.92	.9	2.0	1.00	2.3	3.9	2.30	9.9	.50	1.2	2.00
PIAL series	6	.14	40.2	4.4	.14	2.4	—	.34	7.3	.82	2.0	.17

[1] From Mount Washburn study area, Yellowstone National Park (*n* = 835).

[2] ABLA/ARCO, ABLA/RIMO h.t.'s.

[3] ABLA/SPBE, ABLA/JUCO, and ABLA/BERE h.t.'s.

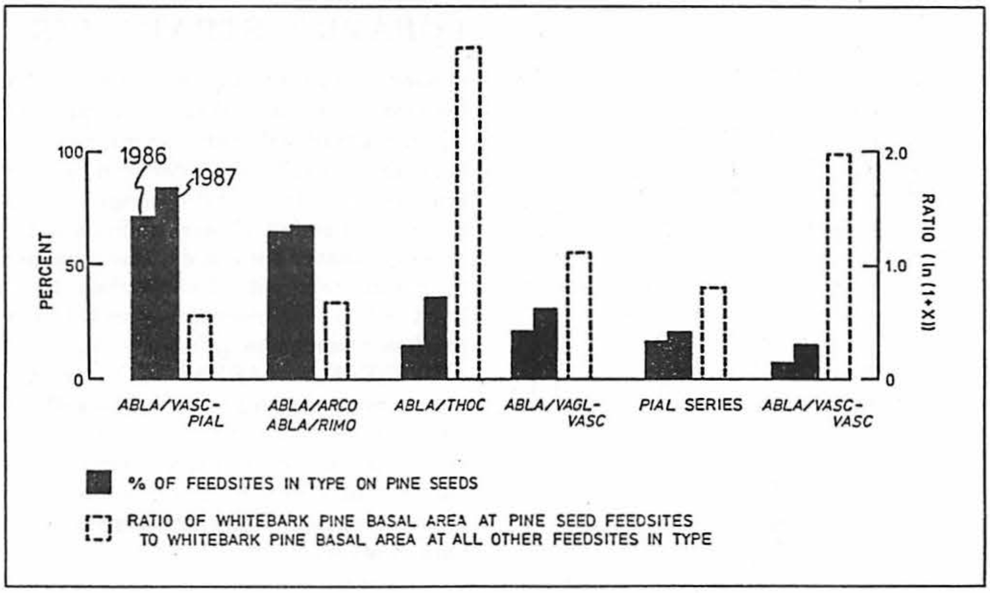


Figure 8—Percent of activity sites devoted to pine seed use in Yellowstone habitat types, for 1986 and 1987, and the ratio (ln (1 + X)) of whitebark pine basal area at pine seed feed sites to whitebark pine basal area at all other activity sites for 1986 and 1987 combined (1986, $n = 36$; 1987, $n = 73$ pine seed feed sites).

USE OF SQUIRREL MIDDENS

Most bear use of pine seeds in the Yellowstone area was from cones cached in squirrel middens. A major portion of bear excavations in middens were <2.0 m^3 in size, and could be characterized as incidental or exploratory (fig. 9). A few midden excavations ($n = 3$) were extensive (30 to 51 m^3). The number of cones excavated by bears per midden ($\hat{y}$) during 1987 was positively and significantly related to total excavated volume (x) ($\hat{y} = 33.2 + 13.6x$; $r^2 = 0.676$, $n = 52$, $F = 219.8$, $P < 0.000$); excavated volume reflected the relative number of seeds acquired by bears from a midden. The volume of excavated material did not vary significantly among middens from different habitat types.

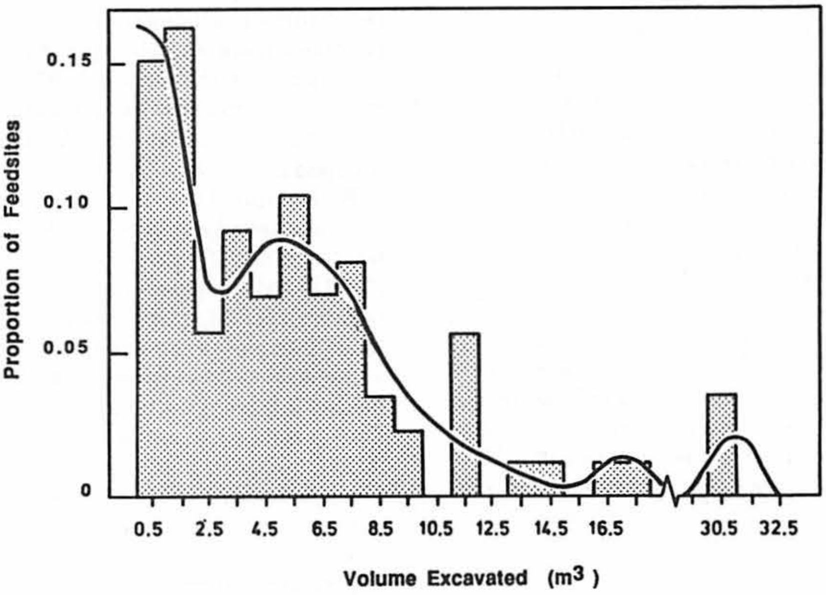


Figure 9—Proportionate distribution of Yellowstone pine seed feed sites, for 1986 and 1987 combined, with respect to estimated excavated volume ($n = 109$).

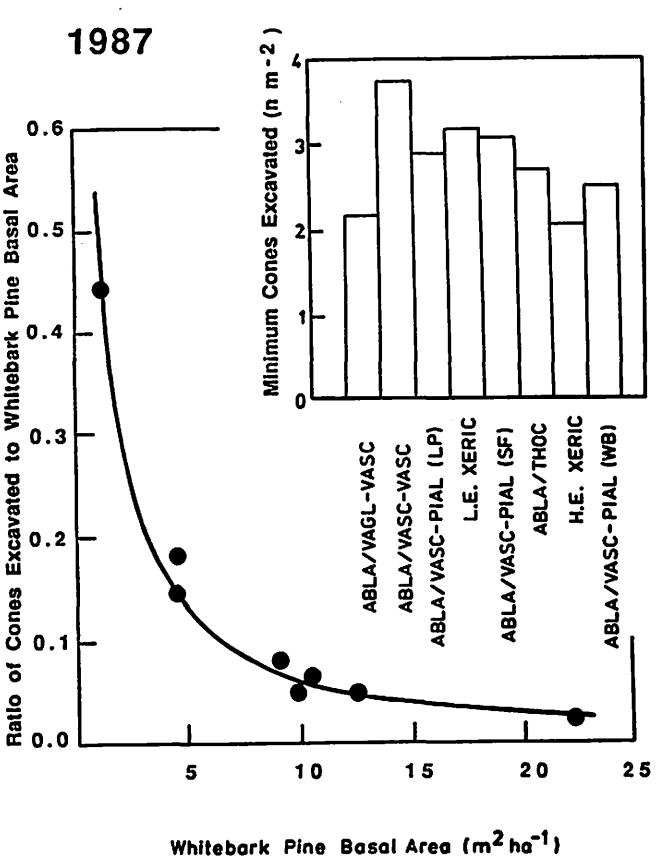


Figure 10—Relationship of the ratio of excavated cone density to whitebark pine basal area averaged for Yellowstone area habitat types, for 1987. Inset depicts mean estimated number of cones excavated/m^2 for Yellowstone area habitat types.

The apparent preferential harvest of whitebark pine cones by squirrels tended to minimize differences in the densities of whitebark pine cones in middens, relative to stand whitebark pine basal area. Absolute densities of cones excavated by bears in Yellowstone varied relatively little among habitat types (between 2 and 4 cones/m^2), regardless of characteristic whitebark pine basal area (fig. 10). This was reflected in an asymptotic increase in the ratio of excavated cone density to whitebark pine basal area as basal area decreased. At low densities of mature whitebark pine, fewer squirrels' territories contained cone-producing trees, and despite preferential caching of whitebark pine cones by squirrels, there were fewer middens with whitebark pine cones available to bears. This phenomenon was evident in the positive relationship between stand whitebark basal area (x, in m^2/ha) and the probability of a midden being excavated by a bear ($\hat{y}$) ($\hat{y} = (942.8 + 13.36\, X^{-2})$) (Mattson and Reinhart 1987).

FORAGING STRATEGIES

Bear pine seed foraging, squirrel midden densities, and whitebark pine abundance are clearly related. A chronology of the trade-offs between midden density and whitebark pine basal area is evidenced by bear use of the 1987 pine seed crop in the Yellowstone area (table 6). During the earliest period of bear use in July, the number of cones excavated per cubic meter of excavation was higher than during August. These earliest feed sites occurred in a few favored, lower elevation habitats on south and southeast exposures, primarily in the ABLA/SPBE, ABLA/BERE, and ABLA/JUCO habitat types. These types were restricted to anomalous sites above 2,425 m elevation, and were more common at lower elevations. Whitebark pine cones probably matured earlier in these habitats, and because of high whitebark pine basal areas, the resident squirrels may have started caching whitebark pine cones earlier than in other stands with relatively less whitebark pine. Use through the first half of August was oriented toward stands with higher whitebark pine basal area and lower squirrel densities. The density of excavated material and cones was comparatively low during this period, as would be expected with the low rate of caching during early phases of whitebark pine cone harvest by squirrels (Hutchins and Lanner 1982). Peak use of pine seeds occurred between the middle of August and the middle of September, when bears used stands with higher squirrel densities. Bears excavated a higher density of cones during the last half of August, compared with the previous month, despite the lowest average number of excavated cones per cubic meter of excavation. By this time squirrel caching was at a uniformly high level (Hutchins and Lanner 1982), and squirrel midden density was probably most limiting to bear use of pine seeds. Although densities of excavations and excavated cones remained high during the last half of September, use generally declined. By this time marginal habitats had probably been fully exploited, and bears turned to using other foods or pine seed sites with relatively more whitebark pine and fewer squirrels. Full exploitation of the modest 1987 pine seed crop (Blanchard, this proceedings) by bears probably occurred by the end of September; subsequent October bear use of pine seeds dropped to very low levels.

We examined the relationship of various measures of cone-use density in habitats selected by bears to relative fecal volumes of pine seeds for different 1987 time periods (fig. 11). Although we had few data points, the derived relationships suggest constraints on bear use of pine seeds that were related to minimum densities of available whitebark cones in favored habitats. Such relationships further suggest that bears did not forage on pine seeds during 1987 when densities were less than approximately 39 available cones/midden and 56 available cones/km. The relationship of mean cones excavated per investigated telemetry location (relative pine seed use as documented by feed-site investigation) to relative pine seed scat volume, suggests that at <9 excavated cones/investigated relocation, pine seed use was likely to go undetected by scat analysis, at least at the 1987 sampling intensity ($n = 472$).

Table 6—Whitebark pine basal area, estimated squirrel densities, and parameters of bear use for whitebark pine feed sites for seasonal time periods, 1987. Squirrel midden densities were estimated by a site favorability index (Reinhart and Mattson, this proceedings), and use of any given midden was predicted from stand whitebark pine basal area (Mattson and Reinhart 1987)

Time period	*n*	(A) Estimated squirrel density (*n*/km)	(B) Whitebark pine basal area m²/ha		Estimated density of midden use (*n*/km)	(D) Excavated material (m³/midden)		(C x D) Estimated density of excavated material (m³/km)	(E) Minimum No. of excavated cones (*n*/midden)		(C x E) Est. minimum density of excavated cones (*n*/km)	(E/D) Mean number of excavated cones per m³ of excavation
			$\bar{X}$	S_x		$\bar{X}$	S_x		$\bar{X}$	S_x		
07/15-07/31	7	2.04	22.3	17.5	1.66	1.8	0.9	2.99	37.3	7.5	61.9	20.7
08/01-08/15	14	2.04	16.1	16.1	1.44	5.0	5.1	7.20	75.5	76.4	108.7	15.1
08/16-08/31	19	2.80	11.4	15.7	1.73	6.5	8.7	11.24	81.2	91.0	140.5	12.5
09/01-09/15	24	2.42	9.1	9.9	1.38	4.8	4.2	6.62	116.6	103.7	161.0	24.3
09/16-09/30	2	1.98	9.2	—	1.13	2.6	—	2.94	50.5	—	57.1	19.4

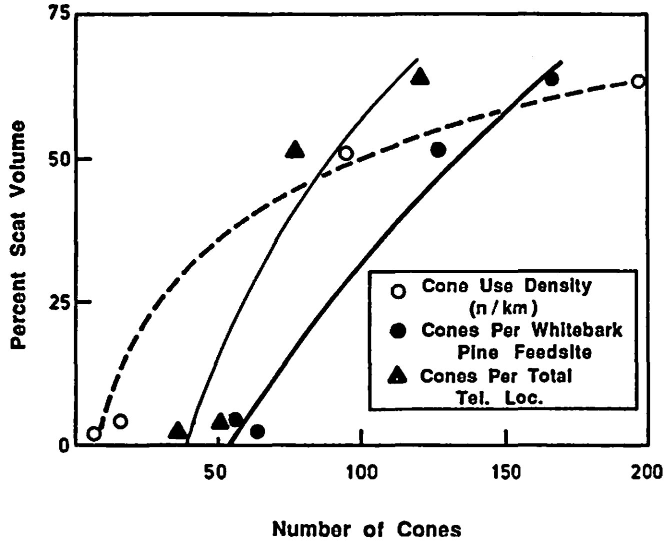


Figure 11—Relationships between percent scat volume, by month for 1987, and estimated excavated cone densities; per km, per whitebark pine seed feed site, and per telemetry location visited.

SUMMARY AND MANAGEMENT RECOMMENDATIONS

Stone pine seeds are a high-quality bear food because of their high triacerglycerol and energy content, relatively large size, and intermittent abundance. Wherever stone pines are relatively abundant, bears use them. Indehiscent stone pine cones are collected by arboreal rodents, principally red squirrels and Siberian chipmunks, into middens or caches. Preferential caching by these rodents, to a certain extent, minimizes the variation in stone pine seed production among sites and years. These rodents, therefore, are a key to the bear's ability to use pine seeds in most areas and to management of bear habitat for pine seed use.

Bears, midden locations and densities, the seasonal activities of squirrels, and whitebark pine abundance affect the seasonal foraging strategies of bears. Yellowstone bears were found to forage seeds primarily within the constraints of whitebark pine availability and squirrel midden densities. Bears made substantial use of stands with relatively low numbers of mature cone-producing whitebark pine, and were limited primarily by the absence of these trees altogether over substantial areas (more than approximately 1/2 ha). The greatest use of pine seeds typically occurred in LP cover types of the ABLA/VASC-PIAL phase because both squirrels and whitebark pine were relatively abundant in this type. At elevations >2,425 m, use of the ABLA/VAGL-VASC and ABLA/VASC-VASC h.t. phases was limited primarily by the lack of cone-producing whitebark pine, while use of the PIAL series was limited by lack of squirrels.

Management of bear habitat in drier portions of the Rocky Mountains for pine seed feeding depends on integrating squirrel and whitebark pine densities with bear foraging strategies. Stands of pure whitebark pine are of little use to most bears for pine seed foraging. However, these less fire-prone stands of pure whitebark pine may serve as important reservoirs of seed for dispersal by Clark's nutcrackers (*Nucifraga columbiana*) into burned areas.

Timber harvest has the potential to substantially impact bears through effects on squirrels and whitebark pine in habitats characterized by appreciable squirrel densities and mixed conifer species overstories that include whitebark pine. In many areas, stands and habitats important to bears for pine seed foraging occur at lower elevations of the whitebark pine zone and may contain few enough whitebark pine that their significance to bears is not recognized. Although whitebark pine is seral in much of the habitat used by bears to feed on pine seeds (Arno and Hoff 1989; Mattson and Reinhart, this proceedings), it may persist in stands for several hundred years as an appreciable cone producer. In addition, significant seed production is not likely to occur until trees are approximately 100 years old. Assuming 250 to 300 years to senescence of whitebark pine, 3 to 4 percent harvest of a landscape per decade would be sufficient to maintain productive whitebark pine stands. A few large-scale natural fires would serve the same purpose. Selective thinning of stands, even in favor of whitebark pine, would not necessarily benefit bears because a reduction in stand basal area under most circumstances predictably results in a reduction of red squirrel density (Reinhart and Mattson, this proceedings). Because squirrels require mixed-species conifer stands to achieve even moderate densities (Reinhart and Mattson, this proceedings), cutting and replanting stands to pure or near-pure whitebark pine has little promise of enhancing bear habitat, even in 100 years. In conclusion, there seems little that active timber management can do to augment bear use of whitebark pine in drier portions of the Rocky Mountains, although in areas where timber harvest has already occurred or is planned for other reasons, judicious planting of whitebark pine in mixtures with other tree species will very likely benefit bears in the future.

In northwestern Montana, whitebark pine has been seriously depleted by (1) extensive infections of white pine blister rust (*Cronartium ribicola*), (2) the massive mountain pine beetle (*Dendroctonus ponderosae*) outbreaks of the 1970's and 1980's, and (3) by extensive logging of old-growth whitebark stands, especially in the Whitefish Range. Extensive use of whitebark pine cones and seeds in this area by both black and grizzly bears, as during the 1950's and 1960's (Jonkel 1967; Kendall and Arno, this proceedings; Tisch 1961), does not occur any more.

Cutting practices that favor whitebark pine are urgently needed in northwestern Montana. The mechanics of whitebark pine regeneration are poorly understood; extensive periods (100 or 1,000 years) may be required before optimal conditions for reseeding and survival may occur. The elimination of old-growth stands, even though the trees are slowly dying from blister rust, may doom whitebark pine in its northern range and cause the permanent loss of an important bear food.

REFERENCES

Allen, W. F. 1976. Biochemical aspects of lipid storage and utilization in animals. American Zoologist. 16: 631-647.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Aune, Keith; Kasworm, Wayne. [In press]. East front grizzly studies: final report. Helena, MT: Montana Department of Fish, Widlife and Parks.

Axelrod, Daniel I. 1986. Cenozoic history of some western American pines. Annals of the Missouri Botanical Garden. 73: 565-641.

Barnes, Victor G., Jr.; Bray, Olin E. 1967. Final report: population characteristics and activities of black bears in Yellowstone National Park. Boulder, CO: Colorado Cooperative Wildlife Research Unit, Colorado State University. 199 p.

Bergman, S. 1936. Observations on the Kamchatkan bear. Journal of Mammalogy. 17(2): 115-120.

Brody, A. J.; Pelton, M. R. 1988. Seasonal changes in digestion in black bears. Canadian Journal of Zoology. 66: 1482-1484.

Bromlei, F. G. 1965. Bears of the south far-eastern USSR. Zdatel'stvo Akademii Nauk SSR, Moskva. (Translated from Russian, Indian National Scientific Documentation Centre, New Delhi, 1973). 138 p.

Buffo, Fred; Fritschen, Leo J.; Murphy, James L. 1972. Direct solar radiation on various slopes from 0 to 60 degrees north latitude. Res. Pap. PNW-142. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 74 p.

Clevenger, A. P.; Purroy, F. J.; de Burvaga, M. S. 1987. Status of the brown bear in the Cantabrian Mountains, Spain. International Conference on Bear Research and Management. 7: 1-8.

Craighead, John J.; Mitchell, John A. 1982. Grizzly bear. In: Chapman, Joseph A.; Feldhamer, George A., eds. Wild mammals of North America. Baltimore, MD: The Johns Hopkins University Press: 515-556.

Craighead, John J.; Sumner, J. S.; Scaggs, G. B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Wildlife-Wildlands Institute Monograph No. 1. Missoula, MT: University of Montana, U of M Foundation. 279 p.

Critchfield, William B.; Little, Elbert L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.

Dirks, Richard A.; Martner, Brooks E. 1982. The climate of Yellowstone and Grand Teton National Parks. Occ. Pap. No. 6. Washington, DC: U.S. Department of the Interior, National Park Service. 26 p.

Elgmork, K. 1987. The cryptic brown bear populations of Norway. International Conference on Bear Research and Management. 7: 13-16.

Finley, R. B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. In: Jones, J. D., ed. Contributions in mammalogy. Lawrence, KS: University of Kansas, Museum of Natural History: 233-273.

Graber, D. M.; White, M. 1983. Black bear food habits in Yosemite National Park. International Conference on Bear Research and Management. 5: 1-10.

Hadley, N. F. 1985. The adaptive role of lipids in biological systems. New York: John Wiley and Sons. 319 p.

Herrero, S. 1978. A comparison of some features of the evolution, ecology and behavior of black and grizzly/brown bears. Carnivore. 1(1): 7-17.

Husby, P.; Mealey, S.; Jonkel, C. 1977. Seasonal food habits of grizzly bears (*Ursus arctos horribilis* Ord) in northwestern Montana. In: Jonkel, C., ed.; Annual Report, Border Grizzly Project No. 2. Missoula, MT: Border Grizzly Project: 103-117.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Iroshnikov, A. I. 1963. Fruit bearing of stone pine forests in the northwestern part of the eastern Sayan. In: Shimanyuk, A. P., ed. Fruiting of the Siberian stone pine in East Siberia. Academy of Sciences of the USSR Siberian Department. Transactions of the Institute of Forestry and Wood Processing, Vol. 62. Izdatel'stvo Akademii Nauk SSR. (Translated from Russian; Israel Program for Scientific Translations, Jerusalem, 1966): 98-109.

Iroshnikov, A. I.; Lebkov, V. F.; Cherednikova, Yu S. 1963. Fruit bearing of stone pine forests of the Lena-Ilim interfluvial area. In: Shimanyuk, A. P., ed. Fruiting of the Siberian stone pine in East Siberia. Academy of Sciences of the USSR Siberian Department. Transactions of the Institute of Forestry and Wood Processing, Vol. 62. Izdatel'stvo Akademii Nauk SSR. (Translated from Russian; Israel Program for Scientific Translations, Jerusalem, 1966): 35-79.

Irwin, L. L.; Hammond, F. J. 1985. Managing black bear habitats for food items in Wyoming. Wildlife Society Bulletin. 13: 477-483.

Jonkel, Charles J. 1967. The ecology, population dynamics, and management of the black bear in the spruce-fir forest of northwestern Montana. Vancouver, BC: University of British Columbia. 170 p. Dissertation.

Jonkel, Charles J.; Cowan, Ian McT. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27. 55 p.

Kendall, Katherine C. 1983. Use of pine nuts by black and grizzly bears in the Yellowstone area. International Conference on Bear Research and Management. 5: 166-173.

Kendall, Katherine C. 1986. Grizzly and black bear feeding ecology in Glacier National Park, Montana: progress report. West Glacier, MT: Glacier National Park, Science Center. 42 p.

Kendall, Katherine. 1989. [Personal communication]. April. Glacier National Park, MT: U.S. Department of the Interior, National Park Service.

Kistchinski, A. A. 1972. Life history of the brown bear (*Ursus arctos* L.) in northeast Siberia. International Conference on Bear Research and Management. 2: 67-73.

Kozhevnikov, A. M. 1963. Fruit bearing of the Siberian stone pine in the western part of the Transbaikal. In: Shimanyuk, A. P., ed. Fruiting of the Siberian stone pine in East Siberia. Academy of Sciences of the USSR Siberian Department. Transactions of the Institute of Forestry and Wood Processing, Vol. 62. Izdatel'stvo Akademii Nauk SSR. (Translated from Russian; Israel Program for Scientific Translations, Jerusalem, 1966): 80-97.

Lanner, Ronald M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Resources. 12: 391-402.

Mace, Richard D.; Jonkel, Charles J. 1986. Local food habits of the grizzly bear in Montana. International Conference on Bear Research and Management. 6: 105-110.

Mattson, David J. [In press]. Human impacts on bear habitat use. International Conference on Bear Research and Management 8.

Mattson, David J.; Blanchard, Bonnie M.; Knight, Richard R. [In preparation]. Contents of Yellowstone grizzly bear scats, 1977-87.

Mattson, David J.; Reinhart, Daniel P. 1987. Grizzly bear, red squirrels, and whitebark pine: third year progress report. In: Knight, Richard R.; Blanchard, Bonnie J.; Mattson, David J. Yellowstone grizzly bear investigations: report of the Interagency Study Team, 1986. Bozeman, MT: U.S. Department of the Interior, National Park Service. 82 p.

Mealey, Stephen Patrick. 1975. The natural food habits of free ranging grizzly bears in Yellowstone National Park, 1973-1974. Bozeman, MT: Montana State University. 158 p. Thesis.

Mealey, Stephen Patrick. 1980. The natural food habits of grizzly bears in Yellowstone National Park, 1973-1974. International Conference on Bear Research and Management. 4: 281-292.

Mundy, Keith R. D. 1963. Ecology of the grizzly bear (*Ursus arctos* L.) in Glacier National Park, British Columbia. Edmonton, AB: University of Alberta. 102 p. Thesis.

Nelson, Ralph A.; Folk, Edgar J., Jr.; Pfeiffer, Egbert W.; Craighead, John J.; Jonkel, Charles J.; Steiger, Dianne L. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. International Conference on Bear Research and Management. 5: 284-290.

Nesvetailo, V. D. 1987. Long-term dynamics of cedar pine reproductive activity and radial growth in pine forest adjoining village in southern taiga subzone. Ekologiya. 18(6): 19-25. (Translated from Russian; Consultants Bureau, New York, 1988.)

Novikov, G. A. 1956. Carnivorous mammals of the fauna of the USSR. Keys to the fauna of the USSR. Zoological Institute of the Academy of Sciences of the USSR. No. 62. Izdatel'stvo Akademii Nauk SSR, Moskva. (Translated from Russian; Israel Program for Scientific Translations, Jerusalem, 1962.)

Ognev, I. V. 1940. Mammals of the USSR and adjacent countries. Volume IV. Rodents. Izdatel'stvo Akademii Nauk SSR, Moskva-Leningrad. (Translated from Russian; Israel Program for Scientific Translations, Jerusalem, 1966.) 429 p.

Patnode, Kathleen A.; LeFranc, M. N., Jr. 1987. Distribution. In: LeFranc, Maurice N.; Moss, Mary Beth; Patnode, Kathleen; Sugg, William C., eds. Grizzly bear compendium. Available from: Christopher Servheen, Grizzly Bear Recovery Coordinator. Missoula, MT: U.S. Department of the Interior, Fish and Wildlife Service and University of Montana: 3-12.

Pravdin, L. F. 1963. The selection and the seed production of the Siberian stone pine. In: Shimanyuk, A. P., ed. Fruiting of the Siberian stone pine in East Siberia. Academy of Sciences of the USSR Siberian Department. Transactions of the Institute of Forestry and Wood Processing, Vol. 62. Izdatel'stvo Akademii Nauk SSR. (Translated from Russian; Israel Program for Scientific Translations, Jerusalem, 1966): 1-20.

Roger, L. 1989. [Personal communication]. February. St. Paul, MN: U.S. Department of Agriculture, Forest Service.

Schallenberger, A.; Jonkel, C. J. 1980. Rocky Mountain East Front grizzly studies, 1979. Annual report. Border Grizzly Project Special Report No. 39. Missoula, MT: Border Grizzly Project. 207 p.

Semechkin, I. V. 1963. The method of calculating the productivity of stone pine forests by the remnants of cones on the ground. In: Shimanyuk, A. P., ed. Fruiting of the Siberian stone pine in East Siberia. Academy of Sciences of the USSR Siberian Department. Transactions of the Institute of Forestry and Wood Processing, Vol. 62. Izdatel'stvo Akademii Nauk SSR. (Translated from Russian; Israel Program for Scientific Translations, Jerusalem, 1966): 161-167.

Shcherbina, K. G.; Larionova, N. A. 1963. Variability of fat content in stone pine kernels. In: Shimanyuk, A. P., ed. Fruiting of the Siberian stone pine in East Siberia. Academy of Sciences of the USSR Siberian Department. Transactions of the Institute of Forestry and Wood Processing, Vol. 62. Izdatel'stvo Akademii Nauk SSR. (Translated from Russian; Israel Program for Scientific Translations, Jerusalem, 1966): 134-138.

Steele, Robert; Cooper, Stephen V.; Ondov, David M.; Roberts, David W.; Pfister, Robert D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

Stroganov, S. U. 1962. Carnivorous mammals of Siberia. Akademiya Nauk SSR. Sibirskoe Otdelemie, Biologicheskii Institut. Izdatel'stvo Akademii Nauk SSR, Moskva. (Translated from Russian; Israel Program for Scientific Translations, Jerusalem, 1969).

Taylor, R. A. 1964. Columbian ground squirrel and cambium found in grizzly bear stomachs taken in the fall. Journal of Mammalogy. 45(3): 476-477.

Tisch, Edward L. 1961. Seasonal food habits of the black bear in the Whitefish Range of northwestern Montana. Missoula, MT: University of Montana. 108 p. Thesis.

Tomback, Diana F. 1983. Nutcrackers and pines: coevolution or coadaptation? In: Nitecki, Matthew H., ed. Coevolution. Chicago, IL: The University of Chicago Press: 197-223.

Ustinov, S. K. 1965. K biologii buroge medvedya Vostochnoi Sibiri. Okhotnich'e-proryslovye zveri. Biologiya i khozyaistvennoe ispol'zevania No. 1, Moskov. Vet. Akad: 229-234. (in Russian).

Ustinov, S. K. 1976. The brown bear on Baikal: a few features of vital activity. International Conference on Bear Research and Management. 3: 325-326.

Vereschagin, N. K. 1976. The brown bear in Eurasia, particularly the Soviet Union. International Conference on Bear Research and Management. 3: 327-335.

Weaver, T.; Forcella, F. 1986. Cone production in *Pinus albicaulis* forests. In: Shearer, Raymond C., compiler. Proceedings-conifer tree seed in the Inland Mountain West symposium. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 68-76.

Yi-Ching, M. 1981. On the distribution of bears in China. Acta Theriologica Sinica. 1(2): 137-144.

Zunino, F. 1975. L'Orso bruno in Italia. Natura e Montagna. 4: 5-18. (in Italian.)

APPENDIX A. HABITAT TYPE NOMENCLATURE AND ACRONYMS (STEELE AND OTHERS 1983)

Acronym	Common name	Scientific name
PIAL series	Whitebark pine series	*Pinus albicaulis* series
ABLA/VASC-PIAL phase	Subalpine fir/Grouse whortleberry-Whitebark pine phase	*Abies lasiocarpa/ Vaccinium scoparium- P. albicaulis* phase
ABLA/VASC-VASC phase	Subalpine fir/Grouse whortleberry-Grouse whortleberry phase	*A. lasiocarpa / V. scoparium-V. scoparium* phase
ABLA/VAGL-VASC phase	Subalpine fir/Globe huckleberry-Grouse whortleberry phase	*A. lasiocarpa / V. globulare-V. scoparium* phase
ABLA/THOC h.t.	Subalpine fir/Western meadowrue h.t.	*A. lasiocarpa / Thalictrum occidentale* h.t.
ABLA/SPBE h.t.	Subalpine fir/Shiny-leaf spiraea h.t.	*A. lasiocarpa/Spiraea betulifolia* h.t.
ABLA/BERE h.t.	Subalpine fir/Oregon-grape h.t.	*A. lasiocarpa/Berberis repens* h.t.
ABLA/JUCO h.t.	Subalpine fir/Common juniper h.t.	*A. lasiocarpa/Juniperus communis* h.t.
ABLA/RIMO h.t.	Subalpine fir/Mountain gooseberry h.t.	*A. lasiocarpa/Ribes montigenum* h.t.
ABLA/ARCO h.t.	Subalpine fir/Heart-leaf arnica h.t.	*A. lasiocarpa/Arnica cordifolia* h.t.
ABLA/CACA h.t.	Subalpine fir/ bluejoint h.t.	*A. lasiocarpa/ Calamagrostis canadensis* h.t.

ELK AND MULE DEER USE OF WHITEBARK PINE FORESTS IN SOUTHWEST MONTANA: AN ECOLOGICAL PERSPECTIVE

Terry N. Lonner
David F. Pac

ABSTRACT

Summer-fall elk (Cervus elaphus nelsoni) *habitat use and relationships to logging were studied southwest of Butte in the Long Tom Creek area from 1971 to 1981 and mule deer* (Odocoileus hemionus hemionus) *population dynamics and habitat use were studied in the Bridger Mountains near Bozeman from 1971 to 1987. During these two studies elk and mule deer relationships to whitebark pine* (Pinus albicaulis) *communities were measured. Elk use of whitebark pine forests during the summer was incidental to the preferred use of high-mountain meadows. During fall, elk use of pure stands of whitebark pine at high elevations was negligible. However, fall elk use of whitebark pine was high when whitebark pine was associated with subalpine fir* (Abies lasiocarpa) *at lower elevations and there were high densities of tree regeneration. For female mule deer during summer and fall, forest cover types dominated by whitebark pine accounted for 15 and 3 percent of total habitat use, respectively. This value for adult males was 4 percent during summer. Insufficient data prevented an evaluation of habitat use by adult males during fall.*

Elk and mule deer selection of individual plant communities is discussed with reference to their mobility and broad ecological amplitude. The authors recommend that natural resource managers responsible for mobile, large mammal populations in mountain environments evaluate management alternatives from the perspective of how land uses will affect the entire ecological unit and its seasonal range components, regardless of public/private land ownership patterns. Management decisions thus made will be more successful in directing effective management of big game populations than decisions based on the importance of individual plant communities.

INTRODUCTION

Whitebark pine (*Pinus albicaulis*) forests are one of many habitat components found on elk (*Cervus elaphus nelsoni*) and mule deer (*Odocoileus hemionus hemionus*) summer-fall range in southwest Montana. These forests occur at the upper limit of the animals' summer-fall distribution. High-elevation zones occupied by whitebark forests provide a shorter period of occupancy for mule deer and elk than other habitats at lower elevations, due to weather conditions and site fertility. Most whitebark pine stands grow on weakly developed soils where nitrogen-fixing and other microbiotic activities are apparently restricted by low soil temperatures and high acidity (Arno and Hoff 1989).

Whitebark pine is often a dominant seral species of the upper subalpine and timberline habitat types that have been classified under the *Abies lasiocarpa* series and has been recognized as valuable for wildlife habitat, watershed protection, outdoor recreation, and esthetics (Arno and Hoff 1989; Pfister and others 1977). Forage production for livestock grazing and timber productivity are generally low where whitebark pine stands are prevalent. Silvicultural practices are frequently hampered by problems in road construction, harvesting, regeneration, and site protection.

In this paper we will present some pertinent results from research conducted on elk during the Long Tom Creek Elk Project (Lonner 1977), a research effort that was part of the Montana Cooperative Elk-Logging Study conducted from 1970 to 1985. Mule deer populations were studied in the Bridger Mountains from 1971 to 1987 as part of the Montana Statewide Deer Ecology Project. Data presented in this paper represent a portion of the results of the total study reported in detail by Pac and others (in preparation).

THE STUDY AREAS

Long Tom Creek

The Long Tom Creek study area (177 km^2) was located 20 km south of Anaconda, with the northwest corner in Deer Lodge County and the remainder in Silverbow County, MT (fig. 1). It served as spring, summer, and fall range for elk. The entire area was in public ownership; the Forest Service, U.S. Department of Agriculture, and the Montana Department of Fish, Wildlife and Parks (MDFWP) were responsible for administration of land management. The Beaverhead and Deerlodge National Forests accounted for 78 percent (94 km^2) and 9 percent (11 km^2) of the area, respectively. The remaining 13 percent (16 km^2) was managed by the MDFWP as part of the Mount Haggin Wildlife Management Area.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Terry N. Lonner is Assistant Chief, Research and Technical Services Bureau, and David F. Pac is Deer Research Biologist, Montana Department of Fish, Wildlife and Parks, Bozeman, MT 59717.

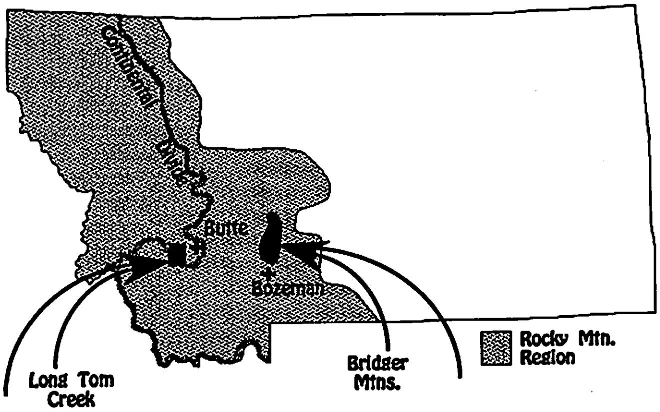


Figure 1—Location of the Long Tom Creek elk study area and Bridger Mountains mule deer study area in Montana.

Elevations ranged from 1,890 to 2,792 m, with moderate slope gradients except for a few areas that consisted of steep slopes and talus fields. The three prominent drainages on the study area (Johnson, Long Tom, and Jerry Creeks) were tributaries of the Big Hole River. Geologically, this area is probably a northward extension of the Pioneer Mountains. Numerous strongly scoured cirque basins as well as lateral, ground, and recessional moraines provide evidence of geologically recent glaciation in the valleys of both Long Tom Creek and Jerry Creek (Moore 1956). The Boulder Batholith formation occurs within the study area and sedimentary rocks of Proterozoic, Paleozoic, Mesozoic, and Cenozoic ages are also exposed in the area (Moore 1956).

The climate was generally mild during the summer and severe in winter, with the area usually under snow cover from November through May. The annual mean temperature ranged from 38.5 to 41.7 °F during 1972 to 1980, with wide fluctuations in daily and seasonal temperatures. Annual temperature extremes ranged from 88 and −19 °F in 1977 to 91 and −34 °F in 1979. Annual precipitation (1972 to 1980) ranged from 19 cm in 1974 to 49.7 cm in 1975. Fifty-five to 80 percent of the annual precipitation fell between April 1 and August 31 during the study (NOAA 1982). (Climatological data only approximate conditions on the study area because they were collected at the Divide weather station 15 km southeast of the study area at an elevation of 1,648 m.)

Vegetation in the area was dominated by lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine. There were 13 forest habitat types (Pfister and others 1977) identified in the study area, although only *Abies lasiocarpa-Pinus albicaulis/Vaccinium scoparium* (ABLA-PIAL/VASC h.t.), *Pinus albicaulis* h.t., (PIAL h.t.), and *Abies lasiocarpa/Vaccinium scoparium* (ABLA/VASC h.t.) were considered common. The ABLA/VASC h.t. was represented by the *Vaccinium scoparium* and *Thalictrum occidentale* phases. Three types were found occasionally: *Abies lasiocarpa/Calamagrostis canadensis* (ABLA/CACA h.t.), *Abies lasiocarpa/Luzula hitchcockii* (ABLA/LUHI h.t.)-VASC phase, and *Abies lasiocarpa/Calamagrostis rubescens* (ABLA/CARU h.t.). Five were found incidentally: *Pseudotsuga menziesii/Juniperus communis*, *Abies lasiocarpa/Vaccinium scoparium-Calamagrostis rubescens* phase, *Abies lasiocarpa/Xerophyllum tenax Vaccinium scoparium* phase, *Pseudotsuga menziesii/Calamagrostis rubescens*, and *Abies lasiocarpa/Linnaea borealis*.

Stands of limber pine (*Pinus flexilis*), Douglas-fir (*Pseudotsuga menziesii*), and alpine larch (*Larix lyallii*) also occurred in the area. Timber stands were aged as old as 325 years and ranged in stem density from scattered (200 trees/ha) to dense (7,900 trees/ha). Approximately 75 percent (90 km²) of the study area was occupied by trees with a moderately dense (30 to 70 percent) to dense (>70 percent) canopy cover. This timber was interspersed with numerous xeric and mesic meadows and talus outcrops. Scattered timber sites (areas with canopy coverage less than 30 percent), natural meadows, and clearcuts amounted to 4.6, 12.6, and 6.6 percent of the study area, respectively. A few small lakes or ponds also existed.

Idaho fescue (*Festuca idahoensis*) and other dry-site graminoids and forbs commonly dominated natural dry parks. Various sedges (*Carex* spp.), wet-site graminoids, several forb species, and a few shrubs, including Labrador tea (*Ledum glandulosum*), characterized wet sedge meadows. The older logged sites had very little conifer regeneration, but a diversity of grasses and forbs grew in them. The newly logged sites (cut in 1975 to 1977), especially the clearcuts, had little revegetation by the end of the study.

Before the study, clearcut logging occurred in six units totalling 421 ha in the Jerry Creek drainage. Logging during the study (1975-77) involved 12 clearcuts and one selective cut altering 242 ha and removing 8.17 mbf of timber within the Long Tom Creek portion of the study area. These 12 clearcuts ranged in size from 6.4 to 49.2 ha with an average of 19.2 ha; the selective cut was 14.2 ha.

The Bridger Mountains

This mountain range is located just north of Bozeman, MT (fig. 1). It is one of a series of isolated frontal ranges located along the eastern flank of the Rocky Mountain cordillera. The total study area occupied nearly 2,000 km² that encompassed all habitats used by seven relatively distinct mule deer population/habitat units (Pac and others 1984). Average annual precipitation varied between 35 and 127 cm along an elevation gradient ranging from 1,365 to 2,947 m.

Soil parent materials consisted of consolidated sedimentary strata including a prominent calcareous substrate forming the backbone of the main Bridger Divide (McMannis 1955). Noncalcareous sandy or loam soils at lower elevations along the west slope arose from ancient arkoses (granitelike sandstones) and older metamorphic rocks. Andesitic sandstones at lower elevations along the east slope gave rise to similar soil types. Shale strata scattered throughout parts of the area resulted in clay soils.

Important plant communities associated with deer winter ranges included shrub/grasslands dominated by big sagebrush (*Artemisia tridentata*), antelope bitterbrush (*Purshia tridentata*), Rocky Mountain juniper (*Juniperus* *scopulorum*), Idaho fescue, and bluebunch wheatgrass (*Agropyron spicatum*). Narrow stringers of Douglas-fir often occur along stream courses within the winter range boundaries.

Habitats used by deer during spring, summer, and fall are characterized by an extensive coniferous forest at middle elevations comprised of numerous habitat types in the *Pseudotsuga menziesii*, *Pinus flexilis*, *Abies lasiocarpa*, and *Pinus albicaulis* habitat series described by Pfister and others (1977). Subalpine plant communities consist of clumps of stunted conifer interspersed with grass/forb meadows. Important species included Idaho fescue, slender wheatgrass (*Agropyron caninum*), sticky geranium (*Geranium viscosissimum*), and tall larkspur (*Delphinium occidentale*). The alpine meadow community occurred in scattered patches on high-elevation ridgetops. Species composition was relatively diverse and included *Carex* spp., Indian milkvetch (*Astragalus aboriginum*), spring parsley (*Cymopterus bipinnatus*), and eight-petal dryas (*Dryas octopetala*). Environmental characteristics along the east and west slope of the Bridger Mountains were described by Bucsis (1974), Nyberg (1980), Pac (1976), Rosgaard (1981), Steerey (1979), and Wilkins (1957).

Approximately 90 percent of the 360 km^2 of mule deer winter range was privately owned. Much of the spring, summer, and fall ranges along both sides of the Bridger Divide is administered by the Forest Service (Gallatin National Forest). A checkerboard pattern of public and private ownership occurs in the timbered foothills along the east slope.

Our discussion of mule deer use of whitebark pine communities in the Bridger Mountains pertains to only one of seven population/habitat units that occurred in the total study area. We referred to that ecological unit as the Northwest Slope. Over a period of 16 years it contained all seasonal ranges used by a population that averaged 650 adult deer in late winter. This was the only unit that contained significant stands of whitebark pine, which covered 13.6 km^2 (7 percent) of the total 186-km^2 area included within the Northwest Slope. All whitebark stands were classified as belonging to either the PIAL h.t. or the ABLA-PIAL/VASC h.t. (Pfister and others 1977). To improve interpretation of habitat selection by deer, we also described plant communities according to vegetation cover types.

METHODS

Long Tom Creek Study

Elk distribution and habitat use were determined primarily from elk "sign" recorded while periodically and systematically walking 11 circuitous foot routes. Routes were charted on aerial photographs and marked on the ground with colored plastic flagging material tied onto trees. Length ranged from 4.8 to 14.5 km; the average was 9 km. The routes were divided into segments, each sampling a homogeneous cover type. Segments longer than 0.5 km were usually divided to provide better sensitivity in measuring elk spatial distribution over the study area. A total of 700 segments were delineated; they ranged in length from 10 to 860 m, and averaged 158 m ± SE 4.7.

Each segment of the route system was assigned at least a general cover type (park, open-scattered forest, clear-cut forest, medium-dense forest). Each segment with medium-dense forest was assigned a forest habitat type based on the Pfister and others (1977) classification system. Habitat types, however, often did not express the cover value of the forested segments. For each forested segment, tree densities were measured by species, diameter at breast height (d.b.h.), and height class. A cover type value from 1 to 5 was then assigned to each of these segments based on the amount of tree regeneration (all trees with a d.b.h. of less than 4 inches; seedlings were not counted). The five density classes of regeneration were: 1 (100 to 250), 2 (251 to 500), 3 (501 to 1,000), 4 (1,001 to 1,500), and 5 (1,500+ trees/acre). These five density classes of tree regeneration provided an index of hiding cover quality. This assumption was based on a signifi-cant relationship previously determined between sight distance (that distance at which approximately 90 percent of an elk is hidden) and regeneration density (Lonner 1977).

Routes were walked at least four times during summer and fall each year from 1972 through 1980. In 1973, 1974, and 1976 the routes were walked six, seven, and five times, respectively. It took about 1 week for two people to walk the entire route system. For analysis, data were organized so the replications completed each year represented three time periods: summer (June to mid-August), early fall or the rut (mid-August to late September) and fall (late September to late November). Only data from 1972 to 1976 were used for habitat analysis in this presentation.

Elk use during summer and early fall was the total number of fecal pellet groups counted since the last replication of the route system. Duplication of recording the same elk sign from one replication to another was avoided as much as possible. Elk sign during fall (October and November) could not be recorded directly due to snow cover. Therefore, during the first replication of the route system in June, elk use from the previous fall was determined by counting pellet groups with a form and consistency characteristic of the fall season.

All indexes of elk use for each segment were standardized by dividing the segment length into the total of fecal droppings; for example, if two fecal droppings were recorded for a particular segment that was 182 m long, the index of elk use was transformed into a ratio of 2/182 or 0.011.

Use of specific vegetation types was interpreted by statistically comparing the average use that occurred in each type during a particular season with the mean elk use of the route system for that season. Positive associations, or means significantly higher than the overall mean, indicate a preference or a concentration of elk use. Negative associations, or means significantly lower than the overall mean, may indicate an aversion or low concentration of elk use. Types listed as nonsignificant were those where elk use did not significantly deviate from the overall mean elk use.

However, elk use lower than the mean did not necessarily indicate an indifference or aversion to a particular habitat or cover type. Failure to select a particular habitat or cover type may only indicate that it may be available in excess of the needs of the elk during the time of the study.

Biotelemetry was also used to track radio-collared elk during the study, but these data were not used specifically for evaluating elk habitat relationships.

Bridger Mountain Study

A total of 46 individual cover types were defined according to dominant plant species as well as the structural characteristics of the overstory and understory layers. The distribution of individual cover types was mapped within the Northwest Slope population/habitat unit using 1:24,000 scale ortho-photo quads. This overlay map was digitized using the computer program GEOSCAN, a Houston Instruments Complot digitizing tablet, and Vax 11/780 computer.

Deer use of vegetation cover types during summer and fall was based on 1,466 aerial locations of 28 adult females and 13 adult males equipped with radio transmitters. All deer were relocated every 7 to 10 days. Sample size was not adequate to measure male use in fall.

In our analysis of deer habitat use, we employed computer-generated sampling plots or "scan circles." The conceptual basis for this method assumed that an animal location is not only related to the single vegetation cover type at that precise location; it may be significantly influenced by the mosaic of vegetation types within a prescribed area around the relocation point. We used a scan circle radius of 100 m to reflect the small seasonal home ranges of mule deer in this environment. We employed the GEOCALC computer software program written by Bill Hoskins for the Interagency Grizzly Bear Study, Bozeman, MT. This program used a dot grid method to calculate cover type areas within scan circles around deer and random relocation points.

For statistical analysis, individual cover types were combined into a hierarchical system. The primary stratum in the hierarchy described major vegetation zones along an elevation gradient. These consisted of steppe, montane forest, and subalpine/alpine. Secondary strata were categorized according to major structural differences in the overstory layer. The tertiary stratum in the hierarchy categorized forest cover types according to the dominant tree species in the overstory layer. Terminology generally follows standardized definitions (Hann and Jensen 1987).

Statistical comparisons of observed and expected use of cover types followed the technique described by Neu and others (1974) that employed a Bonferroni Z statistic.

RESULTS

Long Tom Creek Study

During the summer, elk use of the park cover type was significantly above the expected, while elk use of the medium-dense forest cover type was significantly below the expected (fig. 2A). Within this general type, ABLA/LUHI-VASC h.t. was the only forest type that received significant above-average elk use during the summer (fig. 2B). The whitebark pine habitat type received the least attention, but use was not significantly below the expected. Use of cover types within the two whitebark pine habitat types showed no statistical significance above or below the expected (fig. 2C).

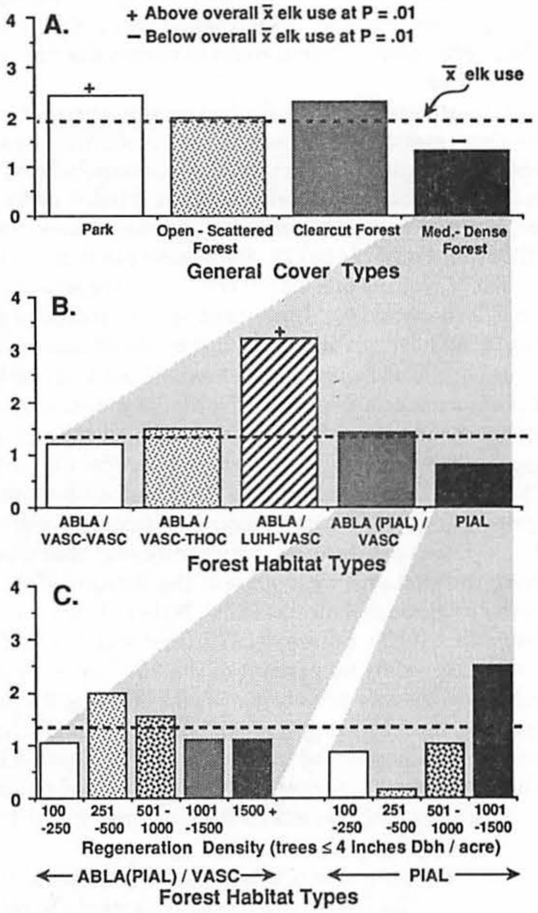


Figure 2—Summer elk use preference in the Long Tom Creek study area of: four general cover types (A), five forest habitat types (B), and regeneration densities with two forest habitat types with whitebark pine as a dominant tree species (C).

During the fall months, elk use of the open-scattered forest cover type decreased to a level significantly below the expected and elk use of the medium-dense forest cover type increased to a level that was similar to the expected (fig. 3A). Within this general cover type, elk use of four of the five forest habitat types was not different than expected. Elk use of the whitebark pine habitat type was significantly below the expected (fig. 3B). Elk use of cover types with the ABLA-PIAL/VASC and the PIAL habitat types was not different than expected except for a preference for cover type 5 within the ABLA-PIAL/VASC h.t. and a significant aversion to cover type 1 within the PIAL h.t. (fig. 3C).

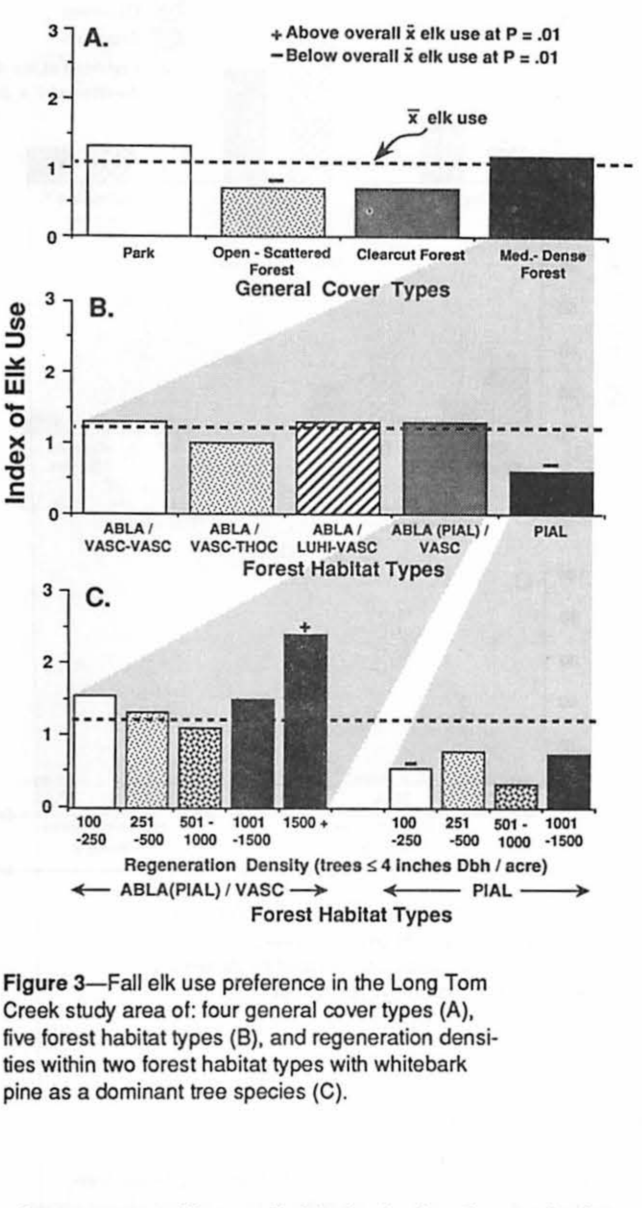


Figure 3—Fall elk use preference in the Long Tom Creek study area of: four general cover types (A), five forest habitat types (B), and regeneration densities within two forest habitat types with whitebark pine as a dominant tree species (C).

In summary, elk use of whitebark pine forests during the summer was incidental to the preferred use of high-mountain meadows. During fall, elk use of pure stands of whitebark pine at high elevations was negligible. However, elk use of whitebark pine was significant when whitebark pine was associated with subalpine fir at lower elevations and there were high densities of tree regeneration.

Bridger Mountain Study

During summer, more than 90 percent of all habitat use recorded for adult females occurred within the highly preferred montane forest zone (fig. 4A). Females avoided the steppe and subalpine/alpine zones. Much of their use was concentrated in two canopy classes of the mid-elevation forest, although only open-scattered canopy cover types were preferred (fig. 4B).

Although females preferred the two canopy classes of high-elevation forests during summer, total use was much less than mid-elevation forests (fig. 4B). Whitebark pine cover types in the high-elevation scattered and open forest were preferred and accounted for 7.3 percent of all use of vegetation types by adult females (fig. 4C). In the high-elevation medium-dense canopy forest, whitebark pine cover types were also preferred and accounted for 7.7 percent of all female use.

The montane forest continued to be very important to adult females during fall (fig. 5A). Adult female use of high-elevation forests declined sharply during the fall with a corresponding increase in use of mid-elevation forests with medium-dense canopies (fig. 5B). This change reflected snow accumulation at the high elevations. Combined use of all whitebark pine cover types did not exceed 3 percent during fall (fig. 5C) compared with a total of 15 percent in summer.

In summer, adult males preferred the montane forest, which accounted for 67 percent of all habitat use (fig. 6A). Males avoided the steppe and used the subalpine/alpine zone in proportion to its occurrence. Total male use of these two zones was substantially greater than that recorded for adult females. Males preferred the mid-elevation open-scattered canopy forests (fig. 6B), although

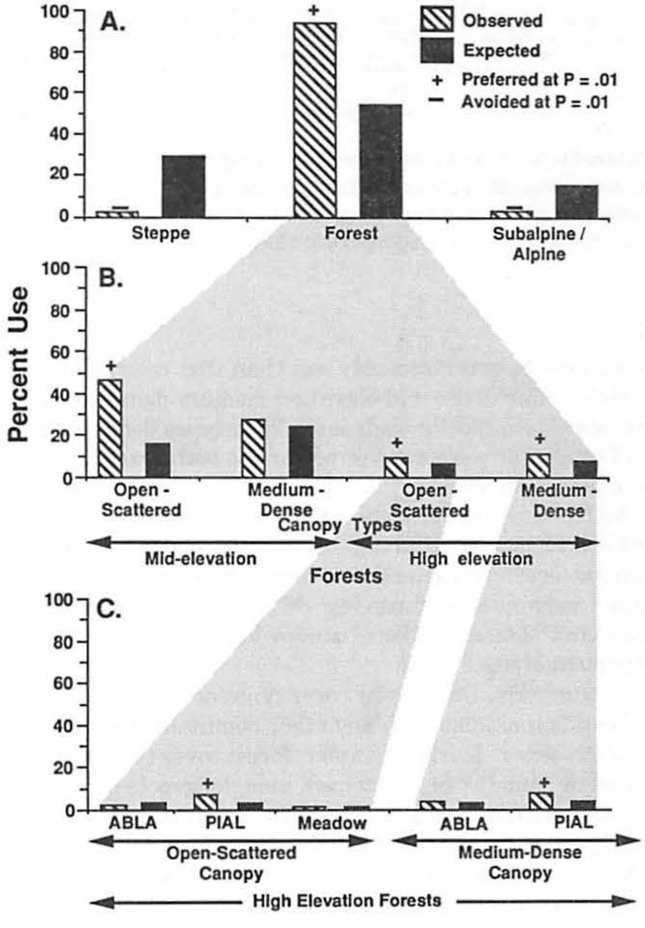


Figure 4—Adult female mule deer use during summer of: major vegetation zones (A), four categories of forest (B), and cover types categorized by dominant tree species in the high-elevation forest (C).

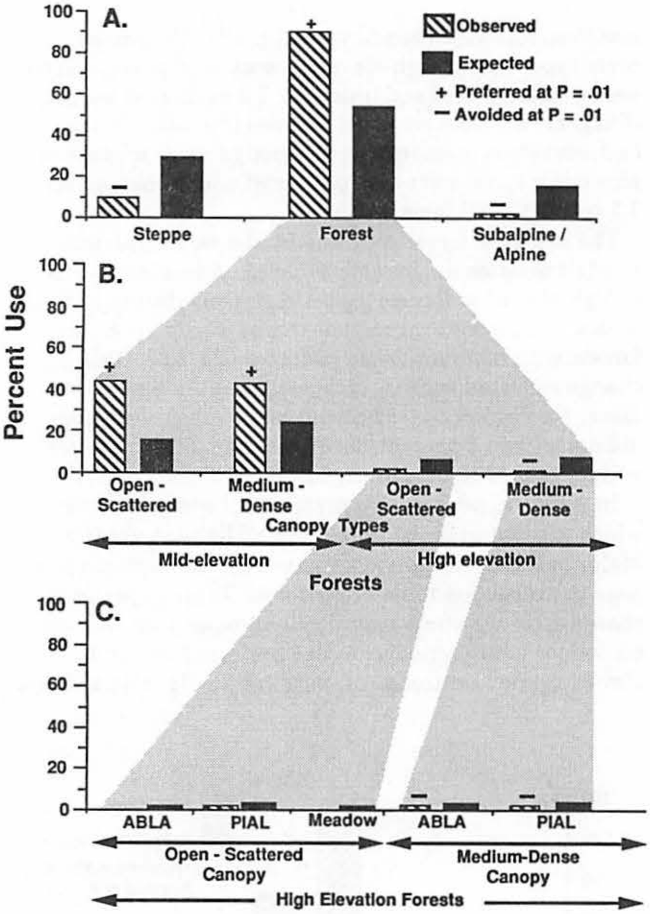


Figure 5—Adult female mule deer use during fall of: major vegetation zones (A), four categories of forest (B), and cover types categorized by dominant tree species in the high-elevation forest (C).

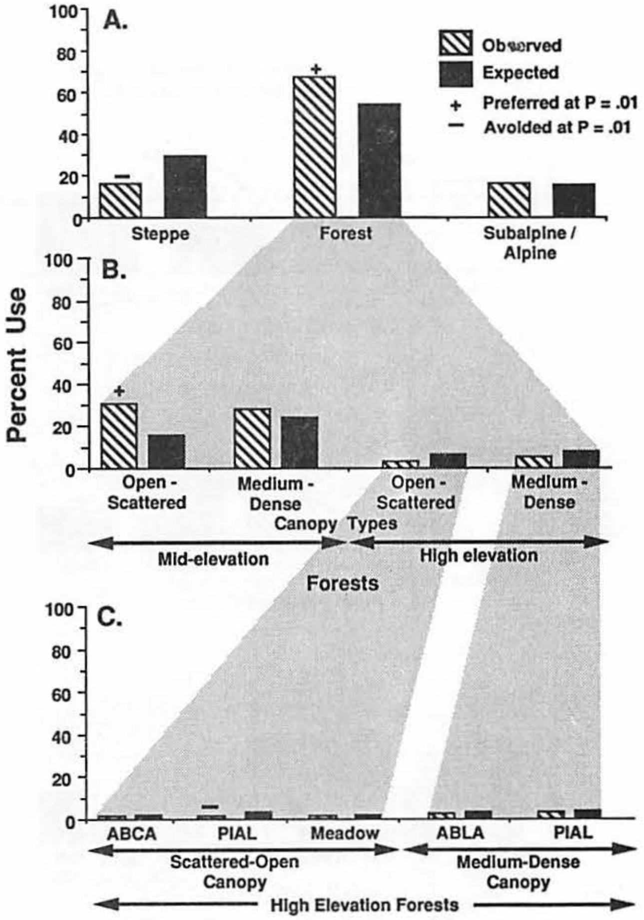


Figure 6—Adult male mule deer use during summer of: major vegetation zones (A), four categories of forest (B), and cover types categorized by dominant tree species in the high-elevation forest (C).

use by males was noticeably less than that recorded for females. Use of the mid-elevation medium-dense canopy forest was similar for each sex. Cover types dominated by Douglas-fir were most important to both sexes in the mid-elevation forests.

Male use of high-elevation forests in summer was not different than expected (fig. 6B). In the scattered-open canopy forest, whitebark pine cover types accounted for only 1 percent of total use (fig. 6C). Whitebark pine cover types in the medium-dense canopy forest accounted for 3 percent of use.

In summary, Douglas-fir cover types accounted for significantly more use than any other dominant tree species for both sexes. During summer, forest cover types dominated by Douglas-fir, whitebark pine, lodgepole pine, subalpine fir, and Engelmann spruce accounted for 58, 15, 12, 5, and 3 percent of total habitat use for adult females. These values for adult males were 48, 4, 9, 4, and 2 percent, respectively. During fall for adult females, this same ordering of use of forest cover types was 72, 3, 15, 0.5, and 0 percent. Insufficient data prevented an evaluation of habitat use by adult males during fall.

DISCUSSION

Animal selection of most vegetation communities appears related more to overstory and understory structure than to habitat types or individual species of plants (Lonner 1976). The broad ecological amplitude of animal species such as mule deer and elk causes difficulty in understanding and quantifying requirements for specific vegetation types such as whitebark pine communities or habitat types. Mobile animal species range freely over many vegetation types. It is implicit that difficulty will occur when a continuum of animal use is compared to a discrete classification system of vegetation, but it is important that big game habitat management plans and objectives recognize and address this dilemma.

A solution to this problem may be to express these relationships at a level of resolution above that of individual plant communities or habitat types. When evaluating elk or mule deer habitat relationships, the complete ecological unit or population/habitat unit that supports a migratory elk or mule deer population is the most critical entity to understand and quantify. An example of this is shown in figure 7 for the Northwest Slope mule deer population/

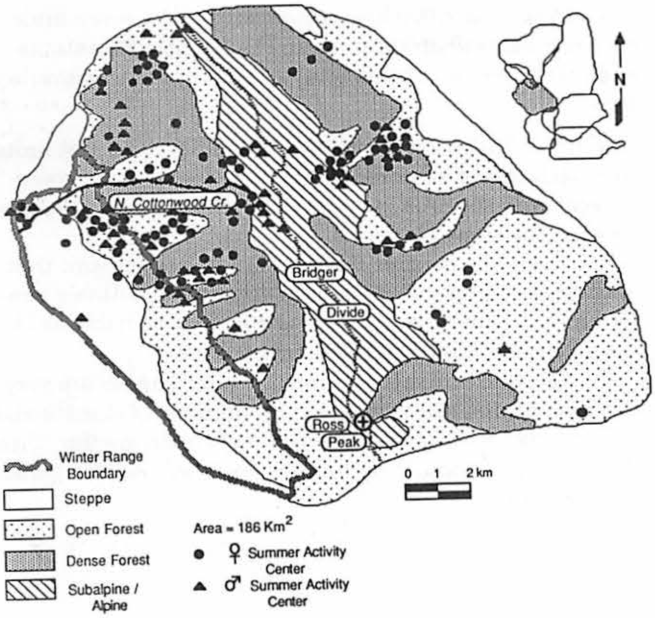


Figure 7—The Northwest Slope mule deer population/habitat unit in the Bridger Mountains.

habitat unit in the Bridger Mountains. This unit was based on the perimeter enclosing all relocations of individually marked deer associated with a particular winter range. Relocations of individual deer were summarized as activity centers.

This unit includes all seasonal ranges required to sustain the population. Each seasonal range, in turn, is usually comprised of a mosaic of individual plant communities. These lower order components have less individual importance to the welfare of an elk or deer population. At this level of habitat organization, mobile big game species can adjust to habitat changes much more easily than those that occur more broadly within the higher orders of organization.

We recommend that natural resource managers responsible for mobile, large mammal populations in mountain environments evaluate management alternatives from the perspective of how land uses will affect the entire ecological unit and its seasonal range components, regardless of public/private land ownership patterns. Management decisions made at this level of resolution will more successfully direct effective management of big game populations than decisions based on the importance of individual plant communities.

REFERENCES

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Bucsis, R. A. 1974. Ecological characteristics of the Armstrong mule deer winter range, Bridger Mountains, Montana. Bozeman, MT: Montana State University. 104 p. Thesis.

Hann, W. J.; Jensen, M. E. 1987. Ecosystem classification handbook—chapter 4: ecodata sampling methods. Handb. 12/87 R-1 Supplement 1. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region.

Lonner, T. N. 1976. Elk use-habitat relationships on summer and fall range in Long Tom Creek, Southwestern Montana. In: Proceedings, elk-logging roads symposium; 1976 December 16-17; Moscow, ID. Moscow, ID: University of Idaho: 101-109.

Lonner, T. N. 1977. Montana cooperative elk-logging study. JobII-B, Long Tom Creek study. Prog. Rep. January 1-December 31, 1976. Helena, MT: Montana Fish and Game Department: 25-68.

McMannis, W. J. 1955. Geology of the Bridger Range, Montana. Bull. Vol. 66. New York: Geological Society of America: 1385-1430.

Moore, G. T. 1956. Geology of the Mount Fleecer area. Bloomington, IN: Indiana University. 88 p. Dissertation.

Neu, C. W.; Byers, C. R.; Peek, J. M. 1974. A technique for analysis of utilization—availability data. Journal of Wildlife Management. 38(3): 541-545.

Nyberg, H. E. 1980. Distribution, movements, and habitat use of mule deer associated with the Brackett Creek winter range, Bridger Mountains, Montana. Bozeman, MT: Montana State University. 106 p. Thesis.

Pac, D. F. 1976. Distribution, movement, and habitat use during spring, summer and fall by mule deer associated with the Armstrong winter range, Bridger Mountains, Montana. Bozeman, MT: Montana State University. 120 p. Thesis.

Pac, D. F.; Mackie, R. J.; Jorgensen, H. E. 1984. Relationships between mule deer and forest in southwestern Montana. In: Wallmo, O. C.; Taber, R. D., eds. Fish and wildlife relationships in old growth forests: symposium of the northwest section of the Wildlife Society. 1982 April; Juneau, AK. Morehead City, NC: American Institute of Fishery Research Biologists: 321-328.

Pac, D. F.; Mackie, R. J.; Jorgensen, H. E. [In preparation]. Ecology of mule deer in mountain-foothill habitat: a study of population organization, behavior, and dynamics in a complex Northern Rocky Mountain environment. Bozeman, MT: Montana Department of Fish, Wildlife and Parks.

Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Rosgaard, A. I. 1981. Ecology of the mule deer associated with the Brackett Creek winter range in the Bridger Mountains, Montana. Bozeman, MT: Montana State University. 76 p. Thesis.

Steerey, W. 1979. Distribution, range use, and population characteristics of mule deer associated with the Schafer Creek winter range, Bridger Mountains, Montana. Bozeman, MT: Montana State University. 119 p. Thesis.

U.S. Department of Commerce, National Oceanic and Atmospheric Administration. 1982. Climatologic data 1912-1981. Washington, DC: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Environmental Data Service.

Wilkins, B. T. 1957. Range use, food habits, and agricultural relationships of the mule deer, Bridger Mountains, Montana. Journal of Wildlife Management. 21(2): 159-169.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Tad Weaver)—How much overlap occurs between adjacent mule deer population/habitat units in the Bridger Mountains?

A.—A total of 2,000 km^2 occurs within the seven mule deer population/habitat units in the Bridger Mountains and only 9 percent of this total area occurs within overlap zones.

Q. (from Tad Weaver)—If deer population/habitat units were obliterated across Montana and deer were allowed to recolonize the area, would the population/habitat units occur in the same places?

A.—Yes. The portion of a population/habitat unit that anchors it at a specific site is the location of suitable winter habitat. Summer range consists of mesic habitats in the general proximity of the winter range.

The location and distribution of winter ranges are very site specific and relate to special conditions of climate and topography. As long as these factors remain similar, then the location of population/habitat units will remain generally constant.

WHITEBARK PINE SEED DISPERSAL AND ESTABLISHMENT: WHO'S RESPONSIBLE?

Harry E. Hutchins

ABSTRACT

Whitebark pine (Pinus albicaulis) *has many characteristics that typify an animal-dispersed plant species. This paper outlines the role of individual animal species involved in the dispersal and establishment of whitebark pine seeds in Wyoming. Red squirrels harvested 63.7 percent of the seed, and Clark's nutcracker 36.1 percent in large forested tracts. Seeds from open-grown trees are almost entirely harvested by nutcrackers (99.4 percent) with less than 1 percent going to ground squirrels, chipmunks, Steller's jay, ravens, and other birds. The behaviors of animals that foraged on the pine seed and their influence on whitebark pine are discussed. Only Clark's nutcracker dispersed the seed in a way that might lead to the establishment of whitebark pine seedlings. Nutcracker caches on the open meadow ridges faced less predation than forest seed caches, so it appears to be more profitable for both the tree and the nutcracker to have seeds cached in the meadow.*

INTRODUCTION

Until recently whitebark pine (*Pinus albicaulis*) was thought to disperse its seeds by the cone falling to the ground and decaying. New trees would then establish in the rotting residue of the indehiscent cones (Day 1967), or the cone would simply disintegrate (Shaw 1914; Weaver and Dale 1974). But what of those lone sentinels on the sides of rocky cliffs and scattered individuals along subalpine moraines? Or the seedlings establishing under a lodgepole pine (*P. contorta*) forest canopy several miles from a mature whitebark pine tree?

When I first undertook this study the evidence began to mount implicating birds and mammals in the dispersal and subsequent establishment of whitebark pine (Tomback 1978; Vander Wall and Balda 1977). In this paper I will outline my findings concerning the animal species that were observed foraging on, and dispersing, whitebark pine seeds. These data will be supplemented by other authors who can add to this discussion. My observations were primarily made from July 1979 to September 1981 in the Rocky Mountains of Wyoming. Additional observations have been made on whitebark and other wingless-seeded pines from 1982 to 1987.

STUDY SITES

The study was primarily conducted at Squaw Basin, Bridger-Teton National Forest, WY. This area of high-elevation meadows offered distant views of bird activity, whitebark pine growing in both contiguous forest and open-grown situations, and an abundant cone crop for whitebark pine during 1980. Besides whitebark pine, the forest stands were composed of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and a minor amount of lodgepole pine. The moraine meadow ridges were pioneered by lone whitebark pine. This provided an opportunity to study two different types of communities—forest and meadow.

Observations of animal activity were also made at Surprise Lake (2,960 m, Grand Teton National Park, WY) and Mount Washburn (2,680 to 3,140 m, Yellowstone National Park, WY). These areas were similar to the Squaw Basin site except they lacked open-grown, cone-bearing trees. Details on the study sites can be found in Hutchins and Lanner (1982) and Vander Wall and Hutchins (1983).

METHODS

Several cone-bearing whitebark pines were chosen for observation in both continuous forest (red squirrels were present) and in open meadows at least several hundred meters from the nearest forest edge (these sites lacked squirrels). In each of these two types of sites, 1,005 whitebark pine cones were observed during the period from July 3 to November 2, 1980. The cones were scattered among several mature trees and were counted at 1- to 2-week intervals using a 15-25 by 60-mm spotting scope. Counts were made by standing in a specific marked location and mapping the cones on clear acetate. Changes in the cone map at each observation were recorded, including the partial removal of a cone. Cone count data were converted into seeds using an empirically derived value for the mean number of seeds per cone (50.4 seeds/cone) (Hutchins 1982). Partially consumed cones were tallied by estimating from the ground the percentage of seed remaining as described in Hutchins and Lanner (1982). The seed harvest data were then plotted against cumulative time for both forest and meadow sites (Hutchins and Lanner 1982).

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Harry E. Hutchins is Natural Resource Instructor, Itasca Community College, Grand Rapids, MN 55744.

At each observation date samples of seeds were collected to determine maturity and condition. The number of filled, discolored, insect-attacked, and second-year-aborted ovules were tallied. Mean dry weight of shelled seeds, seed coat thickness, and caloric content of shelled seeds were all obtained. Germination tests were also conducted with seeds collected at 10 collection dates during the 1980 field season.

Seedfall (caused by animal foraging) below the tree was estimated by placing five 1-m^2 wire mesh seed traps randomly below trees. The tops of the seed traps were designed to let seed fall through, but to exclude rodents. Data on the number of cones in the tree, the area of the tree crown, and the number of seeds falling per square meter were used to estimate the magnitude of seed fall.

Predation on seed caches of whitebark pine was also studied in 1979 and 1980. I simulated three types of caches: (1) seed that lands on the soil surface from foraging accidents, (2) seed cached at a depth of 3 cm simulating Clark's nutcracker (*Nucifraga columbiana*) activity, and (3) seed cached at 7-cm deep, which simulates the most shallow red squirrel seed cache. Each individual cache contained 10 seeds.

Animal/time/budget data were collected for the diurnal species found foraging in the whitebark pine ecosystem. Both quantitative and qualitative observations were made of the various activities and behaviors of the animals; these methods were detailed by Hutchins and Lanner (1982).

Red squirrel middens were also analyzed and compared with 25 random plots to determine tree establishment on these seed/cone caching areas. A split-plot Analysis of Variance and Least Significant Difference multiple mean test ($p = 0.05$ and 0.01) were performed on these data to identify significant differences. Tree seedlings were also studied to determine the year of establishment.

RESULTS

Seed Development

Hutchins and Lanner (1982) monitored seed development and found mean seed coat thickness and seed weight to be significantly greater during the August 31 to November 2 collecting period than before these dates. Clark's nutcrackers were unable to extract whole seed from a cone until August 13 due to the thin, fragile seed coats. The characteristic shell fragments of an unripened "nutcracker cone" were left as evidence of their foraging attempts (fig. 1). Thus, nutcrackers were unable to cache whole seed until after this date.

By September 7-10, the cones had dried and turned a dull brown from their previous moist, pitch-filled, purple color. Whitebark pine cones are often referred to as indehiscent, however, about 25 percent of the cones collected after September 7 parted their scales slightly (4 to 8 mm; $n = 141$). This still was not enough of an opening to allow the seeds to fall out of their own accord.

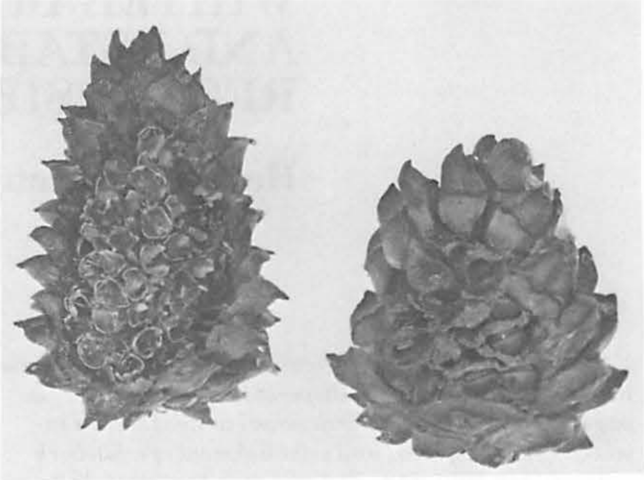


Figure 1—Typical Clark's nutcracker damage to whitebark pine cones. On the left, damage before the seed coat has developed; on the right, nutcracker damage from mid-September, after the cone had dried.

Seed Crop Depletion

Figure 2 (from Hutchins and Lanner 1982) shows that seed crop depletion followed a logistic curve ($r^2 = 0.99$ in the forest and $r^2 = 0.96$ in the meadow). Seed harvesting began somewhat earlier in the forest than in the meadow. In fact, about 50 percent of the seed crop had been harvested in the forest by August 31, while in the meadow this point was not attained until September 25. As seen on the graph, no seeds remained from this mast year in the forest stands by November 1. Only 0.1 percent of the seeds still resided in the tree crowns of the meadow trees, and these were no longer there when checked on June 27, 1981.

Even after several thousand hours in whitebark pine forests, I have never observed a whitebark pine cone falling from a tree without being aided by an animal. We have even bagged several cones in a double layer of hardware mesh to protect them from animals. Clark's nutcracker hammered right through the mesh to get at the seed after November when the cone crop was exhausted. Those that remained never abscised (Lanner 1982), as is sometimes mentioned in the literature. Analysis of seed traps below mature trees showed that 4.2 percent of the seed was dropped to the soil surface by foraging animals.

Seed Cache Predation

No seeds scattered in various locations on the soil surface of the forest or meadow survived to the following July in the simulated caching study (table 1). Seeds cached at nutcracker depth (3 cm) in the forest had a much greater predation rate than those cached in the meadow. Those seeds cached at the shallowest squirrel depth known (7 cm) had 100 percent survival of all artificial caches.

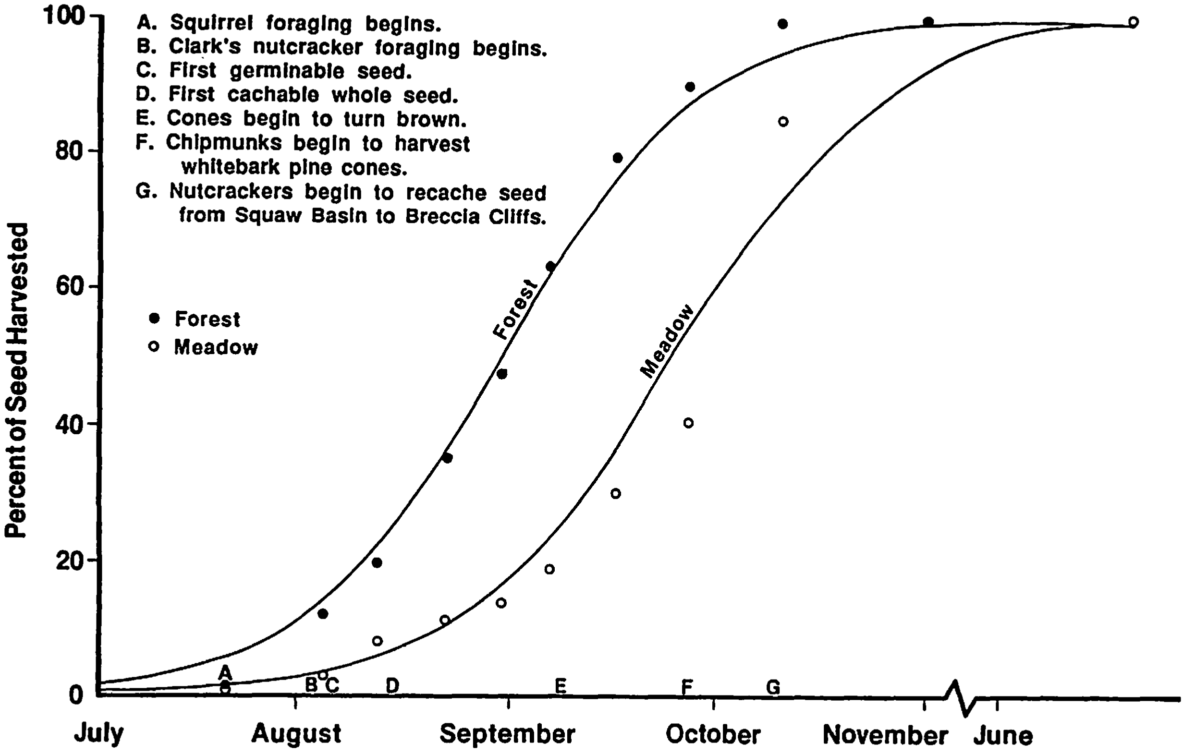


Figure 2—Seasonal course of whitebark pine seed harvest by vertebrates in Squaw Basin, WY, in 1980.

Animal Interactions With Whitebark Pine Seed

A variety of active diurnal animals were observed in or under whitebark pine trees. Many of these, however, were never observed foraging on whitebark pine seed. These nonforagers include: gray jay (*Perisoreus canadensis*), common flicker (*Colaptus auratus*), Cassin's finch (*Corapodacus cassinii*), rosy finch (*Leucosticte* spp.), pine siskin (*Spinus pinus*), dark-eyed junco (*Junco hymelis*), black-billed magpie (*Pica pica*), pine marten (*Martes americana*), coyote (*Canis latrans*), and weasel (*Mustela* spp.).

Table 1—Percent survival rates of simulated seed caches at three soil depths: surface, 3 cm (simulated nutcracker cache), and 7 cm (simulated squirrel)

	Surface	3 cm	7 cm
1979-80			
Forest (*n* = 3)[1]	0	43.3	100
Meadow (*n* = 3)	0	100.0	100
1980-81			
Forest (*n* = 12)	0	10.0	—
Meadow (*n* = 8)	0	62.9	—

[1] *n* = the number of cache replications, 10 seeds per cache.

Many feces of the mammal species listed above were examined, but no evidence of whitebark pine seeds was found. Gray jays were commonly found in the crowns of whitebark pine, but were only observed hawking insects and caching fresh carrion or boluses in pine branches. Dow (1965) found this species has little interest in pine seed during feeding trials, although Turcek and Kelso (1968) described its Eurasian cousin, the European jay (*P. infaustus*), as having been observed taking and caching Siberian stone pine (*Pinus sibirica*).

The other birds I have listed do not possess the anatomical adaptations or requisite behaviors to disperse seeds and thus promote establishment of whitebark pine—except possibly the magpie (Smith and Balda 1979). But in the thousands of hours I have spent observing animals in whitebark pine forests throughout its range, I have observed only two magpies, and both of these were flying swiftly over the trees toward lower elevations. Due to the rarity of this species in whitebark pine forests, any potential harvesting of seed would probably be unimportant.

Many species were found foraging on whitebark pine cones (table 2). At this point I would like to take a closer look at their role in the dispersal and establishment of this pine.

Clark's Nutcracker—Nutcrackers were the most common resident bird to visit the whitebark pine trees (Hutchins and Lanner 1982). They were scattered about whitebark pine stands in loose flocks foraging and caching seed of this tree. They are dependent on these caches year round (Giuntoli and Mewaldt 1978; Vander Wall and Balda 1977; Vander Wall and Hutchins 1983).

Nutcrackers were observed harvesting seed as early as July 13, 1979. During July, however, they appeared only to be testing the cones for ripeness and primarily feeding on the previous year's caches until mid-August. Seeds harvested at this time were lost to regeneration because the seed coats were broken and the seed was ungerminable until August 13. In 1980, the birds were able to successfully harvest whole, developed seed by August 15.

Table 2—Summary of animals known to forage on whitebark pine seed

Species	Date when foraging begins	Overlap with WBP range	Dependence on WBP in the subalpine
		Birds	
Clark's nutcracker	2nd week of July	all	high
Steller's jay	1st week of September	all	low
Common raven	1st week of September	all	low
White-headed woodpecker[1]	unknown	N. Cascades to Sierra Nevada	unknown
Hairy Woodpecker[1]	unknown	all	unknown
Williamson's sapsucker[1]	unknown	all	unknown
Mountain chickadee	1st week of September	all	low
Red-breasted nuthatch	1st week of September	all	low
White-breasted nuthatch[1]	unknown	all	unknown
Cassin's finch[1]	unknown	all	low
Red crossbill[1]	unknown	all	unknown
Pine grosbeak	1st week of September	all	low
		Mammals	
Red squirrel	2nd week of July	all except Cascades, Sierra Nevada	high
Chickaree[1]	unknown	CA, WA, OR	high (?)
Chipmunk	3rd week in September	all	low
Golden-mantled ground squirrel	3rd week in August	all	unknown
Black bear	anytime - raid middens	all except Nevada	high
Grizzly bear	anytime - raid middens	Rocky Mountains	high
New World mice, voles	unknown	all	unknown

[1]Foraging of these species has only been observed in the Sierra Nevadas.

Nutcrackers harvested seed from cones at increasingly faster rates (Hutchins and Lanner 1982) through early October, when seed became hard to find (fig. 2). Nutcrackers were never seen attempting to harvest Engelmann spruce or lodgepole pine even as the whitebark pine seed crop dwindled in October.

As the seed supply in the tree crowns was depleted, nutcrackers continued to search cones in the crown for stray seeds. I recorded one bird checking more than 50 cones for a period of 613 seconds without finding a single seed.

By November 2, it appeared nutcrackers were almost totally dependent upon their new seed caches, and would remain so until the following August. These caches were placed just below the soil surface (2 to 3 cm) and ranged in size from 1 to 14 seeds ($\bar{x} = 3.2 \pm 2.8$ seeds/cache) (fig. 3). These data agree closely with Tomback (1978) and Vander Wall and Balda (1977), but I found a much greater occurrence of single-seed caches than Tomback.

Caches were made in a variety of locations on the various study areas. Sometimes the birds marked their caches by placing small sticks or stones on them. More commonly the caches were left unmarked, at least as far as we humans are concerned. I observed caching in wet moss, at the base of trees, the base of annuals, the base of rocks, or not near any discernible landmark. The birds cached in the densely shaded forest or in open meadows; on northeast facing slopes where the snow may linger until August; or more commonly on the sunny, dry southwest-facing slopes. Tomback (1978) never observed caching in damp areas or on stream banks, and suggested that seed spoilage occurs on these wet sites. Hutchins and Lanner (1982), however, were able to successfully germinate seeds from a wet cone found buried in a squirrel midden.

Transport distances varied greatly. Seeds were placed as close as 50 m from the site of the harvested tree, or were transported at least 3.5 km to the Breccia Cliffs on the edge of the Squaw Basin site. With little seed left in the trees by mid-October, the birds began retrieving many of their caches made in the Squaw Basin meadows and recaching them on the southwest-facing slopes of the Breccia Cliffs.

Large flocks of nutcrackers would often cache seed together. At Mount Washburn a flock estimated at 150 birds was seen caching seed under an open-grown whitebark pine stand, with 10 to 15 birds within a 10-m^2 area. No aggression occurred among the birds during these observations.

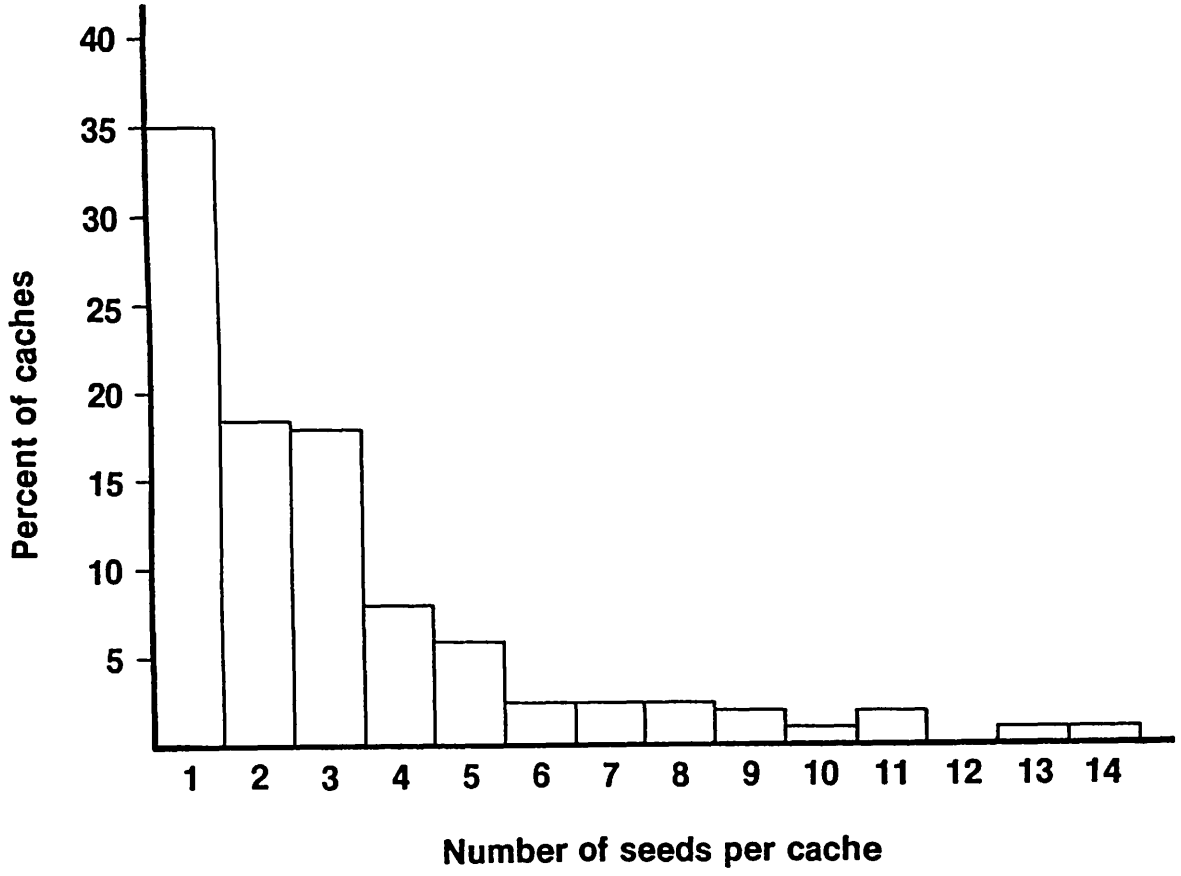


Figure 3—Clark's nutcracker cache size frequency. Data from 157 observations made at several locations in Wyoming.

By November 2, 1980, snow covered many of the caching areas for the winter. Nutcrackers were observed on several occasions successfully pecking through as much as 25 cm of snow and ice to retrieve a cache. The Togwotee Pass area may receive up to 1,500 cm of snow a year, yet the windswept ridges and south-facing slopes remain exposed enough for the birds to retrieve their caches. Caches on the northeast-facing slopes and under the forest canopy are more frequently used during June, July, and August, as the snow recedes from these sites last (Vander Wall and Hutchins 1983).

The number of seeds an individual nutcracker caches annually has been estimated in several studies. The numbers for whitebark pine range from 32,000 in the Sierras (Tomback 1982) to 98,000 in the Rocky Mountains (Hutchins and Lanner 1982). Because of the number of variables that must be considered (such as flight distances and the amount of available seed), these estimates vary a great deal from site to site and year to year.

Studies by Vander Wall and Balda (1977) and Tomback (1982) estimated that an individual bird caches several times more seed than it needs to survive through the winter and early spring. At that time other food items become available—although the nutcrackers continue to use their caches heavily until the new cone crop begins to mature. This leaves many unused caches for potential germination and establishment of whitebark pine seedlings (Hutchins and Lanner 1982).

Clark's nutcracker stands out from all the other potential seed dispersers in two major ways. First, it consistently disperses seed in a way that increases the chance of seedling establishment. The seed is placed just below the soil surface and hidden from seed predators (Hutchins and Lanner 1982; Lanner 1980).

Second, nutcrackers scatter caches across the landscape—both long and short distances from the source trees. Dispersal distances of up to 22 km have been observed by Vander Wall and Balda (1977). Also, the scattering of their caches again reduces predation.

Steller's Jay (*Cyanocitta stelleri*)—Unlike the Steller's jays of the southwestern and central Rocky Mountains, the birds of the Yellowstone ecosystem are shy and silent. Consequently, they are difficult to follow and observe. They are primarily solitary foragers and uncommon visitors to the whitebark pine forest. These birds did not forage for whitebark pine seed until early September when the cones dried and the scales separated slightly. Their bill structure does not approach the efficiency of the nutcracker's in prying apart cone scales to get to the seed (Vander Wall and Balda 1981), thus they were often only able to extract seed from cones that had been exposed by nutcrackers. These jays harvested seed from the ground (14 percent of their observed foraging time) as well as from the cones (24.5 percent). The seed was always placed between their feet and hammered with their bill to crack the hull, whereas nutcrackers primarily cracked the seed between their mandibles.

Observations showed Steller's jays either pouched their seed in their elastic esophagus for later caching, or consumed the seed by breaking it into small pieces. Thus, they could not possibly pass the seed through their digestive system and disperse it in that manner.

Although Steller's jays were observed caching whitebark pine seeds on seven occasions, none of these were in the soil. The birds placed the pine seeds in the crotch of a tree, a densely foliated witches-broom, or under dense lichen growth along a tree branch. The largest number of seeds I observed being pouched at one time by this species was five, although data from Vander Wall and Balda (1981) indicate these birds could hold up to 32 seeds per pouch load. Because this species does not cache whitebark pine seed in the soil, it is an improbable vector for seedling establishment.

As the snow melted, Steller's jays fed heavily on the sprouting spring beauties (*Claytonia lanceolata*), pulling the corm from the ground and consuming the plant just as it emerged. Some of these were possibly cached for later use.

Raven (*Corvus corax*)—A third corvid observed foraging on whitebark pine seed was the common raven. These birds had a great deal of difficulty extracting seed from whitebark pine cones with their thick, long bills. They dropped most of the seed when foraging (Hutchins and Lanner 1982). Caching of carrion was observed with this species, but no observations were made of seed caching. More observations of this species in whitebark pine communities need to be made to confirm my observations. Reimers (1959, cited in Turcek and Kelso 1968), described observations of ravens caching Japanese (*Pinus pumila*) and Siberian stone pine (*P. sibirica*), although it was not clear in what type of substrate.

Pine Grosbeak (*Pinicola enucleator*)—Pine grosbeaks primarily foraged on whitebark pine seed that had been exposed by Clark's nutcrackers breaking off cone scales. Their large conical beaks also enabled them to tear away cone scales to get at seed. Their foraging rates were very slow compared to the nutcrackers' due to their technique, and as a consequence, they had little influence on the depletion of the whitebark pine cone crop.

Grosbeaks are not known to cache food (Smith and Balda 1979; Vander Wall in press). During my observations, they cracked the seed coat and consumed the seed in the tree crown. It is unlikely that they could pass an intact seed through their digestive tracts.

Mountain Chickadee (*Parus gambeli*) and Red-Breasted Nuthatch (*Sitta canadensis*)—These two species occasionally searched through the whitebark pine cones during September after the seeds were exposed by nutcrackers. Both these species almost always dropped the seed from the tree crown because the seeds were too large for them to handle. Their unsuccessful foraging bouts contributed to seed found on the soil surface, which was later consumed by other animals. Neither bird species was observed caching whitebark pine seed, although they are known to cache seeds of smaller seeded conifer species under bark (Smith and Balda 1979).

Red Squirrel (*Tamiasciurus hudsonicus*)—Red squirrels are common residents of whitebark pine forests. In fact they were the second most commonly observed vertebrate next to the Clark's nutcracker (Hutchins and Lanner 1982). These mammals actively defend their territories (Smith 1968), and like nutcrackers, harvest whitebark pine cones and seeds as a fall and winter food source. Red squirrels were not observed in the meadows.

Red squirrels spent most of their foraging time (75.8 percent) on whitebark pine cones or recovering dropped whitebark pine seeds. Most of the rest of the observed foraging activities were collecting Engelmann spruce cones (11.3 percent) and harvesting seeds of herbaceous plants (12.9 percent).

Red squirrels began harvesting cones as early as nutcrackers harvested seeds (July 13, 1979), but did so more intensely during July while the nutcrackers relied more heavily on the previous year's caches (fig. 2). Their foraging rate is much higher than that of the other mammals discussed in this paper because they usually harvest an entire cone (50 or more seeds in one chunk).

Squirrels were observed pulling cones off the branches with their teeth 72 percent of the time ($n = 71$ observations), as opposed to cutting the subtending branch. Halvorson (1985) presented an interesting discussion on the effects of cone cutting by squirrels on tree growth and cone production. With whitebark pine, however, because squirrels seldom cut the branches, little change occurs in growth form or cone production.

Red squirrels often would leave cones on the ground below the tree where they were cut for up to 3 days before caching them in their middens. Seeds in cones were consumed until August 15 when squirrel activity turned more toward caching cones for a winter food supply. This date coincides with the onset of seed germinability of whitebark pine (fig. 2).

Cone caching began on August 4 at Squaw Basin. Caching of other conifer species began later with Engelmann spruce on August 18, 1980, subalpine fir on September 11, 1980, and lodgepole pine on September 27, 1980. All cones were stored on a midden ($n = 114$). These midden areas can be quite extensive and are composed of many years of cone debris above the soil surface (Finley 1969; Smith 1970). Of the time spent caching food, 61.4 percent was devoted to whitebark pine cones and 16.9 percent to whitebark pine seeds. Foraging on the cones of other conifers in the subalpine forest accounted for most of the rest of the caching time (7,304 seconds of observation). Some caching of mushrooms and herbaceous seed took place also.

A second stage of caching began about September 16, 1980. At this time, squirrels began to make large seed caches from whitebark pine cones by extracting seed from the cone, running several meters to place a seed in a deeply dug hole, and then returning to the cone to acquire another seed. This slow and inefficient process took 63.8 ± 36.5 sec/seed cached ($n = 34$). These seed caches were placed 6.5- to 40.0-cm deep ($n = 6$); four were observed between 11- and 11.5-cm deep. The number of seeds per cache ranged from 14-55 ($\bar{x} = 28.8 \pm 19.2$ seeds/cache; $n = 4$), although Kendall (1981) found up to 176 seeds in a single hole. I examined the seeds from two squirrel caches and found all the seeds sound.

Red squirrels actively chased Clark's nutcrackers from the trees above their territories and their middens. On two occasions, however, I watched nutcrackers steal whitebark pine seeds from squirrel middens.

Chipmunk (*Eutamias* spp.)—Chipmunks seldom visit whitebark pine tree crowns, but do occur on both open meadow and forested sites. Most of their time is spent on the ground, usually near cover plants like sagebrush (*Artemisia tridentata*). They preferred herbaceous plant parts (lupine seed and grasses) on my subalpine study sites until the third week of September when these plants died back and presumably lost much of their nutritive value. At that time, chipmunks clumsily foraged on the remaining whitebark cone crop (~10 percent in the forest, 40 percent in the meadow). They also foraged on the small amount of seed below the trees, which had been dropped by any of the species discussed earlier. Heller (1971) similarly found that in the Sierra Nevada this species devotes little time to foraging on whitebark pine.

I found no evidence of chipmunks caching whitebark pine seed. Broadbooks (1958) found the cache depth of western chipmunks (*Eutamias amoenus*) to average 28 cm. They use these types of caches as a winter and spring food source when they are periodically aroused during hibernation (Vander Wall in press). I examined chipmunk burrows to a depth of 20 cm without finding any evidence of them harvesting and caching whitebark pine seed.

Chipmunks are known to scatter-hoard smaller amounts of seed in shallower caches from 2 to 5 cm in depth (Vander Wall in press). There appears to be little information on the use of these caches, how long they last, and how commonly this type of caching occurs with the pines of the western United States.

Although this species is often assumed to play a significant role in afforestation of pines, no data support this conjecture for whitebark pine. In fact, the necessary information to support this idea is lacking for any of the pine species (Gordon 1943; MacClintock 1970; Shtil'mark 1963; Tevis 1953). Kawamichi (1980) reported scatter hoarding of oak acorns at more reasonable depths (3 cm) in Japan by the Siberian chipmunk (*Eutamias sibiricus*). This chipmunk is known to occur in Siberian stone pine forests (Shtil'mark 1963). Still, the limited amount of seed these animals harvest apparently precludes them from being significant to whitebark pine establishment in the Rocky Mountains.

Golden-Mantled Ground Squirrel—The golden-mantled ground squirrel also consumes a limited amount of whitebark pine seed. This species will rarely climb trees to feed on cones, but more commonly feeds on seeds that fall to the ground through foraging accidents.

Ground squirrels will make caches in the ground, but like those of chipmunks, these caches are about 20 cm deep (MacClintock 1970). This species also begins hibernation quite early in September and would not have time to acquire much seed for storage. As with the chipmunk, few studies have been performed to determine ground squirrel foraging and caching behavior.

A recent study in pinyon-juniper in Colorado provided no evidence for pinyon pine (*Pinus edulis*) seed (also large and wingless) being harvested by deer mice, chipmunks, pocket mice, or the golden-mantled ground squirrel (Haufler and Nagy 1984). In fact, all but the ground squirrel preferred arthropods.

Nocturnal Rodents—This group of animals, made up primarily of mice and voles (Cricetidae), must also be considered as potental dispersal agents of whitebark pine seed. They were not directly observed in this study, but possible evidence of their foraging on whitebark pine seed was discovered by the shelled seed left behind on my simulated cache experiments.

Surface seed caches simulating the seed found on the ground indicate it will not last long (table 1). Most of the seed in these caches was consumed within 2 weeks after placement under trees and the shelled seed was left behind. Almost all of the shells were left behind at the cache site, indicating little if any caching was done.

There are two primary places cricetid rodents may obtain whitebark pine seed: (a) from seed that falls to the ground and (b) a discovered nutcracker cache. A small amount of seed (~4 percent of the seed crop) was found to fall to the forest floor in the mast year of 1980. About 69 percent of this seed was determined not viable by examination of the contents inside the shell.

Nocturnal rodents may also find and recover nutcracker caches. Although the rodents may recache the seed, it was probably already placed in a suitable site for seedling establishment by Clark's nutcracker. Thus, even if these Cricetidae relocate the seed to another cache, their positive effect on the establishment of whitebark pine is questionable at best.

Abbott and Quink (1970), working with eastern white pine (*Pinus strobus*), showed most caches by these rodents were made less than 15 m from the seed source. Thus, the habit of whitebark pine trees pioneering open meadows and disturbed areas does not arise from cricetid caches. Their study also stated that of those caches not recovered by the time the seed germinated, the germinated seedlings were soon consumed by these animals. This information coupled with the small amount of seed available on the ground for these rodents, indicates they could rarely be responsible for seedling establishment. Future studies need to look at this group of potential dispersal agents more closely to further delineate their role in whitebark pine ecosystems.

Grizzly and Black Bears—Bears (*Ursus arctos* and *U. americana*) primarily obtain seed from squirrel middens (Kendall 1981, 1983), although black bears are known to also break branches to harvest the seed (Tisch 1961). I examined more than 10 fecal deposits packed solidly with whitebark pine shell fragments of grizzly bears and found a total of three seeds left intact. Many black bear scats were also examined, and only one seed remained undamaged. These scats were all found within 25 m of a squirrel midden. If these seeds germinated in the bear scats, they would produce an insignificant number of whitebark pine seedlings.

Percentage of Seed Harvested by Each Animal

Using raw data from this study and from long-term behavioral observations of nutcrackers by Steve Vander Wall (1981), I have estimated the percentage of the 1980 seed crop harvested by the animals in the Greater Yellowstone Ecosystem.

On forested sites, about 63 percent of the seed was harvested by red squirrels and 36 percent by Clark's nutcracker. The other 1 percent was harvested by all other animals combined (table 3).

The story is quite different on meadow sites that have too few trees for squirrels to exist. Here the nutcrackers harvested almost the entire crop of whitebark pine seed (99 percent).

I am uncertain to what extent these percentages might vary between years and different sites, but they do give an indication of what is occurring in Rocky Mountain whitebark pine communities in relation to seed crop harvest.

Table 3—Estimate of whitebark pine seed harvested by various animals in Wyoming

Species	Mean seeds extracted/ minute[1]	Minutes spent foraging/ day[2]	Foraging days/ season	Seeds harvested/ individual	Number of individuals visiting trees	Seeds harvested by all individuals Forest	Seeds harvested by all individuals Meadow[3]
						Percent	Percent
Clark's Nutcracker	7.9	180	91	129,402	448	36.3	99.4
Steller's Jay	.7	120	55	4,620	11	<.1	.1
Raven	.6	30	53	954	15	<.1	<.1
Noncorvids	.7	120	56	4,704	43	.1	.3
Red squirrel	43.4	240	84	874,944	116	63.5	—
Chipmunk	1.7	120	35	7,140	10	<.1	.1

[1] Seasonal average from observations made from August 15 to October 11, 1980.
[2] Estimate made from observed daily activity patterns.
[3] Meadow area lacks squirrels.

DISCUSSION

Even during years of heavy cone crops, animals harvest nearly all of the seed crop by early November in the Rocky Mountains (Hutchins and Lanner 1982; Vander Wall 1981). By this time, no cones remain on the trees and many of those bagged with hardware cloth have been broken into by squirrels and nutcrackers. Seeds do not have a chance to survive long enough on the ground and germinate as suggested by Day (1967) and others. The seeds and cones, which have been dropped to the ground, are eaten within 3 weeks by various foragers.

A species cannot depend on chance regeneration to survive. Obviously whitebark pine has been very successful in naturally regenerating itself over millions of years. Through seed trap studies, I estimated about 4 percent of the seed crop is dropped to the ground through foraging accidents and only 30.5 percent of that seed was viable. Most of the seeds we see on the ground have been discarded by nutcrackers and squirrels, or dropped accidentally by other seed-foraging animals. They usually discard seeds that are of little food value (Vander Wall and Balda 1977). Consequently, seeds falling from trees to the ground are few in number, and of poor quality. If whitebark pine relied upon this method of regenerating, the tree would be extinct today.

Surveys of middens versus random nonmidden plots show that the middens had a significantly lower number of stems in the regeneration size classes (table 4). This may be due to (1) near-constant digging and searching for cones and seed by squirrels in their food stores, (2) a deep litter layer from cone debris, which is a very poor seed germination bed, and (3) the ability of squirrels to more readily find their seed/cone stores within a limited storage area. Consequently, we can disregard red squirrels as agents of whitebark pine regeneration.

One tree species that was found to be more abundant on squirrel middens was subalpine fir—in fact, I found it easy to locate middens from a distance by a cluster of fir trees. The youngest fir tree found on 25 middens surveyed was 6 years old; the youngest whitebark pine was 30 years.

Squirrels harvest most of the whitebark pine seed in the forest and they are the major seed predator on forested sites. Red squirrels should not, however, be chastised for the destruction of the whitebark pine seed crop. We must remember their importance in collecting seed for grizzly and black bear use. The effect bears have on squirrel populations due to their midden raiding habits is unknown.

Table 4—Number of stems by diameter class (cm), comparing squirrel middens and random forest plots. Each surface was sampled by 25 10-m² plots

Tree species	Surface	<1 cm	1-9 cm
Whitebark	midden	7	13
pine	random	[1]72	[1]119
Engelmann	midden	3	9
spruce	random	[1]79	[2]16
Subalpine	midden	[2]67	14
fir	random	10	2

[1]Significance = 0.01 (LSD multiple mean test).
[2]Significance = 0.05 (LSD multiple mean test).

Nutcrackers are one of the most important biotic influences developing and changing subalpine communities. This species alone probably accounts for nearly all whitebark pine regeneration, except for chance happenings. Whitebark pine becomes established wherever the nutcracker caches the seed. I have found germinating seeds and observed caching in a wide variety of microhabitats, although nutcrackers may prefer certain sites. Several studies (Lanner 1982; Lanner and Vander Wall 1980; Snethen 1980; Tomback 1978; Vander Wall and Balda 1977) indicate south-facing slopes seem to be preferred. Where establishment actually occurs is another matter. Seedling establishment appears to be much more common on moister sites in the Rocky Mountains (Arno 1986; Arno and Hoff 1989; Vander Wall and Hutchins 1983) than in the Sierra Nevada (Tomback 1982).

As far as the bird and the tree are concerned, it is more profitable to cache in the open meadow. Less predation occurs on nutcracker caches in the meadow, and the small ridges are usually free of snow due to wind action. Consequently, the higher cache survival rate benefits tree regeneration as well as the survival of the nutcracker. This more than any factor may be why we see whitebark growing where we do—pioneering the exposed ridges, roadside cuts, burned sites (Lanner and Vander Wall 1980; Tomback 1986), and meadow swales.

Determining cache sites, however, can be difficult because nutcrackers will recache seeds. It appears that they forage on cones to get the seed out of the trees and down into the ground away from other seed eaters. Then as the seed crop becomes depleted in October, they spend their time recaching the seed over a much more dispersed area. This reduces loss to seed cache predators unlike the red squirrel cache loss to bears.

When nutcrackers forget where they placed a cache (Vander Wall 1982), or die, or a rodent does not discover the seed cache—it has a chance to germinate. By placing the seed in an excellent germination bed just below the soil surface (2-3 cm) and also hiding the seed from easy discovery by seed predators, the bird creates a new forest stand.

These whitebark pine trees modify the once-open subalpine landscape so other more shade-tolerant species such as Engelmann spruce and subalpine fir can establish themselves in this community (Arno 1989; Franklin and Dyrness 1973; Snethen 1980). The seed produced by whitebark pine attracts a large number of seed eaters (table 2), which in turn attract predators. During the summer/fall of 1980 at Squaw Basin, I recorded 10 hawk species (including the endangered peregrine falcon) and one owl species feeding among a large prey base of primarily seed eaters. After whitebark pines die, they become important to snag- and fallen-tree-dependent species as they decompose slowly. As previously discussed, both bear species consume large amounts of whitebark pine seed before denning in autumn. Also, whitebark pine often provides the only substantial

Table 5—Seed caching characteristics of animals that may potentially cache whitebark pine seed

Species	Substrate	Depth
Clark's nutcracker	soil	2-3 cm
Steller's jay	tree branch	—
Common raven	probably soil	?
Red squirrel	soil	6.5 - 40 cm
Douglas squirrel	probably soil	?
Chipmunk	soil	probably >20 cm (?)
Golden-mantled ground squirrel	soil	?

thermal and reproductive cover in an otherwise inhospitable environment. And all this ultimately goes back to Clark's nutcrackers—caching the seed of whitebark pine in a manner that leads to successful establishment of seedlings.

SUMMARY

Whitebark pine depends upon animal dispersal for regeneration. There are many dispersal agents of whitebark pine seed, but only a few promote whitebark pine seedling establishment (table 5). The preponderance of evidence lies in favor of Clark's nutcracker—which by itself is almost entirely responsible for whitebark pine regeneration. These long-distance dispersal agents should be the key focus in subalpine community management.

ACKNOWLEDGMENTS

I wish to thank Ron Lanner, Steve Vander Wall, Diana Tomback, and Susan Hutchins for taking time out of their busy schedules to review this manuscript—and keeping me on the right track. Curt Halvorson was a great help with the literature search on rodents.

Partial financial support for this study came from a NSF grant DEB-7802808 to Ron Lanner.

REFERENCES

Arno, S. 1986. Whitebark pine cone crops—a diminishing source of wildlife food? Western Journal of Applied Forestry. 1(3): 92-94.

Arno, S.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Abbott, H. G.; Quink, T. F. 1970. Ecology of eastern white pine seed caches made by small mammals. Ecology. 51: 271-278.

Broadbooks, H. E. 1958. Life history and ecology of the chipmunk (*Eutamias amoenus*) in eastern Washington. Misc. Publ. 103. Ann Arbor, MI: Univeristy of Michigan, Museum of Zoology: 5-42.

Day, R. J. 1967. Whitebark pine in the Rocky Mountains of Alberta. Forestry Chronicle. 43: 278-282.

Dow, D. D. 1965. The role of saliva in food storage by the gray jay. Auk. 82: 139-154.

Finley, R. B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. In: Contributions in mammalogy. Misc. Publ. 51. Lawrence, KS: University of Kansas, Museum of Natural History: 233-274.

Franklin, J. F.; Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 417 p.

Giuntoli, M.; Mewaldt, L. R. 1978. Stomach contents of Clark's nutcracker in western Montana. Auk. 95: 595-598.

Gordon, K. 1943. The natural history and behavior of the western chipmunk and mantled ground squirrel. Oregon State Monograph. Studies in Zoology. 5: 7-38.

Halvorson, C. H. 1985. Influence of vertebrates on conifer seed production. In: Shearer, Raymond C., compiler. Proceedings—conifer tree seed in the inland mountain west symposium. 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 201-222.

Haufler, J. B.; Nagy, J. G. 1984. Summer food habits of a small mammal community in the pinyon-juniper ecosystem. Great Basin Naturalist. 44(1): 145-150.

Heller, H. C. 1971. Altitudinal zonation of chipmunks (*Eutamias*): interspecific aggression. Ecology. 52(2): 312-319.

Hutchins, H. E. 1982. The role of birds and mammals in the dispersal and establishment of whitebark pine. Logan, UT: Utah State University. 67 p. Thesis.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Kawamichi, N. 1980. Food hoarding and seasonal changes of Siberian chipmunks. Japanese Journal of Ecology. 30(3): 211-220.

Kendall, K. C. 1981. Bear use of pine nuts. Bozeman, MT: Montana State University. 27 p. Thesis.

Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. In: Bears—their biology and management. Interagency conference on bear research and management. International Association for Bear Management: Calgary, AB: 5: 166-173.

Lanner, R. M. 1980. Avian seed dispersal in the ecology and evolution of limber and whitebark pines. In: Sixth North American forest biology workshop proceedings. Edmonton, AB: University of Alberta: 14-48.

Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research. 12(2): 391-402.

Lanner, R. M.; Vander Wall, S. B. 1980. Dispersal of limber pine seed by Clark's nutcracker. Journal of Forestry. 78(10): 637-639.

MacClintock, D. 1970. Squirrels of North America. New York: Van Nostrand Reinhold Co. 184 p.

Shaw, G. R. 1914. The Genus *Pinus*. Cambridge, MA: Riverside Press. 96 p.

Shtil'mark, R. R. 1963. Ecology of the chipmunk (*Eutamias sibiricus* Laxm.) in cedar forests of the western Sayan Mountains. Zoological Zhurnal. 42(1): 92-102. From Biological Abstracts. Vol. 45.

Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecological Monographs. 38: 31-63.

Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs. 40: 349-371.

Smith, C. C.; Balda, R. P. 1979. Competition among insects, birds, and mammals for conifer seed. American Zoologist. 19: 1065-1083.

Snethen, K. L. 1980. Whitebark pine (*Pinus albicaulis*) invasion of a subalpine meadow. Logan, UT: Utah State University. Thesis.

Tevis, L., Jr. 1953. Stomach contents of chipmunks and mantled ground squirrels in northeastern California. Journal of Mammalogy. 34: 316-324.

Tisch, E. L. 1961. Seasonal food habits of the black bear in the Whitefish Range of northwestern Montana. University of Montana, Missoula. 67 p. Thesis.

Tomback, Diana F. 1978. Foraging strategies of Clark's nutcracker. The Living Bird. 16: 123-161.

Tomback, Diana F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51: 451-467.

Tomback, Diana F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madrono. 33(2): 100-110.

Turcek, F. J.; Kelso, L. 1968. Ecological aspects of food transportation and storage in the Corvidae. Communications in Behavioral Biology. 1: 277-297.

Vander Wall, S. B. 1982. An experimental analysis of cache recovery in Clark's nutcracker. Animal Behaviour. 30: 84-94.

Vander Wall, S. B. [In press]. Food hoarding in animals. Chicago, IL: University of Chicago Press.

Vander Wall, S. B. [Personal communication]. July 1981. Research Biologist with Utah State University, Logan, UT.

Vander Wall, Stephen B.; Balda, R. P. 1977. Coadaptations of Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecological Monographs. 47: 89-111.

Vander Wall, Stephen B.; Balda, R. P. 1981. Ecology and evolution of food-storage behavior in conifer-seed caching corvids. Zeitschrift fur Tierpsychologie. 56: 217-242.

Vander Wall, Stephen B.; Hutchins, Harry E. 1983. Dependence of Clark's nutcracker, *Nucifraga columbiana*, on conifer seeds during the postfledging period. The Canadian Field Naturalist. 97(2): 208-214.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. American Midland Nautralist. 92: 222-230.

RED SQUIRRELS IN THE WHITEBARK ZONE

Daniel P. Reinhart
David J. Mattson

ABSTRACT

Reports results of a study of interactions among red squirrels (Tamiasciurus hudsonicus), *bears* (Ursus *spp.*), *and whitebark pine* (Pinus albicaulis) *from 1984 through 1987 in north-central Yellowstone National Park and in the vicinity of Cooke City, MT. This paper deals with results that pertain to habitat relationships of red squirrels in the whitebark pine zone. Indices of red squirrel activity and abundance were highest in the mesic and wet habitat types. Pure whitebark pine stands were apparently not favorable habitat for red squirrels. In the whitebark pine zone, cones of other conifer species were needed to offset yearly variations in whitebark pine cone production. Optimal red squirrel habitat in this zone consisted of stands with high tree species diversity, basal area, and environmental favorability. Annual fluctuations in red squirrel densities reflected yearly whitebark pine cone production in stands with a high whitebark pine component. Bears may play a role in regulating red squirrel abundance in whitebark pine stands.*

INTRODUCTION

Red squirrels (*Tamiasciurus hudsonicus*) are commonly associated with coniferous forests. They range extensively in the boreal regions of North America from Alaska to Arizona and from northern Quebec to the Appalachian Mountains (Smith 1970). Red squirrels are typically diurnal, solitary, and active throughout the year. Their diet consists primarily of the reproductive products of trees, fungi, and shrubs within the forests they occupy (C. Smith 1968). Although red squirrels are well adapted to live on a variety of foods available during the growing season (Ferron and others 1986), in the Rocky Mountains they must rely on stored conifer seeds for half the year (Finley 1969; Rusch and Reeder 1978). Conifer seed cones represent storable, high-energy packages that are relatively resistant to spoilage (Weigl and Hanson 1980).

Red squirrels subsist on a seasonal food supply on a year-round basis by caching and storing conifer seed cones gathered within established, defended territories. Gathering and storing cones occupy up to 80 percent of their daily activity from August through November (C. Smith 1968). Individual territories are nonoverlapping and contiguous within forest habitats and are defended from other red squirrels regardless of sex by vocalizations and by chasing intruder squirrels (Rusch and Reeder 1978; C. Smith 1968).

A large, centralized midden is a major feature of a red squirrel territory. Middens are sites traditionally used to cache and feed on cones and consist of large amounts of cone clippings. They occasionally extend into springs, bogs, and creek bottoms where added moisture helps preserve cones in a closed, more storable condition (Finley 1969).

In high-elevation mountain forests of western North America, whitebark pine (*Pinus albicaulis*) trees produce annually fluctuating crops of large, edible seeds (Forcella and Weaver 1986). These seeds are extensively used by wildlife such as Clark's nutcracker (*Nucifraga columbiana*), bears (*Ursus* spp.), and red squirrels (Kendall 1981; Tomback 1982). The large, edible seeds of whitebark pine are apparently preferred over other conifers by red squirrels and are readily cached when available (Hutchins and Lanner 1982). Whitebark pine seeds are also an important fall and spring food for grizzly bears (*Ursus arctos*) within the Yellowstone ecosystem and are obtained almost exclusively by raiding squirrel caches (Kendall 1981). During 1984 through 1987 the Interagency Grizzly Bear Study Team (IGBST) studied the interrelationships of grizzly bears, red squirrels, and whitebark pine. Habitat relationships of red squirrels within the whitebark pine zone are presented here.

STUDY AREA

Our study area consisted of the Mount Washburn massif in north-central Yellowstone National Park, and an area in the Gallatin National Forest near Cooke City, MT (fig. 1). Both areas were located in higher elevations of the subalpine zone on moderately steep topography. Elevations ranged from 2,360 m (7,800 ft), just below the lower elevational limits of whitebark pine distribution, to 2,865 m (9,400 ft) at the upper limits of erect tree growth.

Most study area timber cover was mature to overmature with some stands of pole-sized, even-aged trees. Whitebark pine occurred throughout the study area and was variously represented from dominant to scattered individuals. Whitebark pine was more prevalent in the Mount Washburn area than in the Cooke City area, where lodgepole pine (*Pinus contorta*) was a more common dominant.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Daniel P. Reinhart is Wildlife Technician and David J. Mattson is Wildlife Biologist, Interagency Grizzly Bear Study Team, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717.

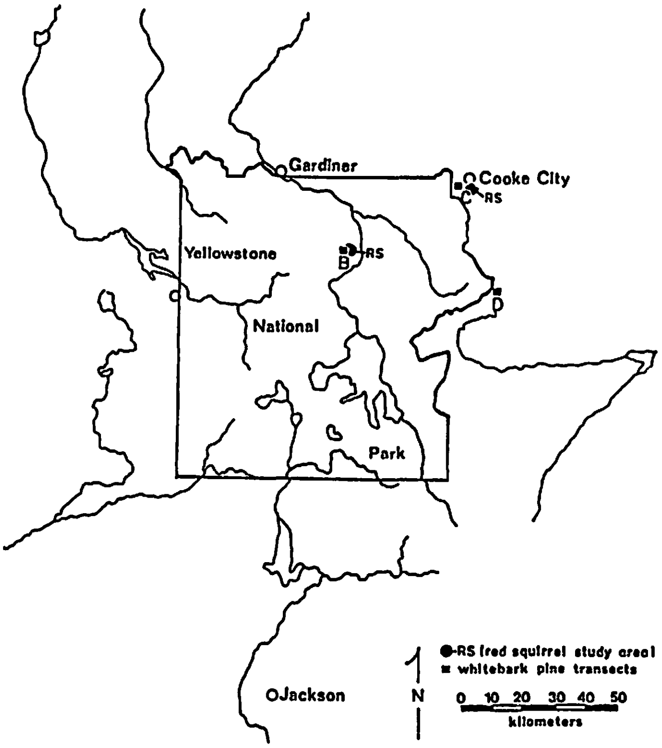


Figure 1—Location of red squirrel study areas (RS) and whitebark pine transects: Mount Washburn (B) and Cooke City (C).

The study area included five major habitat types described by Steele and others (1983). The *Pinus albicaulis* (PIAL) series habitat types prevailed at high elevations on west and south aspects. The *Abies lasiocarpa/Vaccinium scoparium-Pinus albicaulis* (ABLA/VASC-PIAL) and *Abies lasiocarpa/Vaccinium globulare-Vaccinium scoparium* (ABLA/VAGL-VASC) habitat type phases were the most common habitat types in our study area. The *Abies lasiocarpa/Vaccinium scoparium-Vaccinium scoparium* (ABLA/VASC-VASC) phase, *Abies lasiocarpa/Thalictrum occidentale* (ABLA/THOC), and *Abies lasiocarpa/Spiraea betulifolia* (ABLA/SPBE) habitat types occurred at low elevations. The wet site *Abies lasiocarpa/Calamagrostis canadensis* (ABLA/CACA) type was found near creek bottoms and seeps.

METHODS

We delineated homogeneous timber stands on USGS 15-ft topographic maps and 1:20,000 and 1:30,000 color aerial photographs. Line transects were laid out to intercept all stands so that no transects intersected and stand edge effect was minimized. Transects were laid out without bias toward timber stands or toward the monitored squirrel population. Transect lengths were determined from airphotos and corrected for slope.

Field work was conducted from mid-August to mid-September from 1984 through 1987. Beginning and end points were located using airphoto interpretation and marked with stakes. Two people walked all transects each year during daylight hours; one person maintained compass bearing and distance pacing, while the other person was responsible for observing and recording squirrel sign. Regular pauses were observed every 100 to 200 m in each stand for habitat evaluation.

All stands were identified by forest habitat type (Steele and others 1983) and forest cover type (Despain 1977; Mattson and Reinhart, this proceedings). In addition, between 5 and 26 systematically placed variable-radius overstory plots were taken in each stand (see Mattson and Reinhart, this proceedings).

Red squirrel data were collected annually while walking line transects (see Eberhardt 1978). Squirrel sign was referenced to transect locus and perpendicular distance from transect. All unduplicated sightings or vocalizations discerned from the transects and estimated to be within stand bounds were recorded. All individual squirrel middens observed from transects were noted and described as active or inactive based on the presence of cached cones, fresh cone clippings, or squirrels. Red squirrel activity was recorded between 0 to 60 m from transect lines. Bear activity and bear-excavated red squirrel middens were also noted.

We calculated two indices of relative squirrel abundance for habitat types and for habitat type-cover type combinations. We summed sightings and vocalizations and divided by total transect length to derive linear frequency of occurrence. Similarly, we divided total middens by transect length to derive linear frequency of middens.

Annual whitebark pine cone production for Cooke City and Mount Washburn study areas was obtained by counting cones on marked trees along predetermined whitebark pine cone transects (Blanchard, this proceedings).

RESULTS

Data were collected on up to 50 km of line transects per study year. Between 41 and 57 transects that sampled between 40 and 74 stands were walked annually on Mount Washburn. Between 15 and 22 transects surveyed between 51 and 65 stands near Cooke City.

Annual whitebark pine cone production varied widely in the study areas (fig. 2). Whitebark pine cone production was highest in 1985 and lowest in 1986. Cone crops in 1984 and 1987 were intermediate. Cooke City cone data were missing in 1984 and therefore extrapolated using simple linear regression. Actual cone production in 1987 was believed to be higher than the cone counts indicated because of earlier than normal cone maturation and harvest and late cone surveys (Blanchard, this proceedings).

Several patterns were evident by linear counts of vocalizations plus sightings and active middens (table 1, fig. 3):

1. Relatively little squirrel activity occurred in PIAL series habitats on Mount Washburn. These were mostly pure near-climax whitebark pine stands.

2. Moderate amounts of squirrel sign were found on the drier ABLA/SPBE type and in the ABLA/VASC-PIAL phase.

3. A higher incidence of red squirrel activity occurred in more mesic habitats represented by the ABLA-THOC habitat type and the ABLA/VAGL-VASC and ABLA/VASC-VASC phases and in the wetter sites of the ABLA/CACA habitat type.

We calculated annual variation of squirrel density indices for the major study area habitat types (table 1). On Mount Washburn (fig. 3A), annual variation in squirrel abundance generally reflected annual variation in whitebark pine cone production. This pattern was most evident in the ABLA/VASC-PIAL phase but was also apparent in the other more mesic habitat types. At Cooke City (fig. 3B), sequential years' variation of squirrel densities was not as pronounced as on Mount Washburn with the exception of the ABLA/VASC-PIAL phase where variation did reflect the whitebark pine cone crop.

Table 1—Mean densities (n/km) and coefficients of yearly variation of active red squirrel middens for habitat types of the two study areas

	Midden density			
	Mount Washburn		Cooke City	
Habitat type	X̄	C.V.	X̄	C.V.
ABLA/CACA	3.64	0.506	2.35	0.719
ABLA/THOC	3.20	0.233	1.63	0.355
ALBA/VAGL-VASC	2.60	0.079	1.92	0.250
ABLA/VASC-VASC	2.78	0.243	—	—
ABLA/VASC-PIAL, LP cover type	3.80	0.389	4.34	0.737
ABLA/VASC-PIAL, WB cover type	1.15	0.548	1.38	0.188
ABLA/SPBE	1.53	0.580	—	—
PIAL series	0.11	0.200	—	—

There were differences in the extent of variation among years between the two indices used to measure squirrel abundance (fig. 3). Linear densities of vocalizations and sightings varied more than linear densities of active middens. There was also an exponential increase in the density of vocalizations plus sightings relative to the increase in the density of active middens ($r^2 = 0.959$, $P < 0.001$) (fig. 4).

Average linear frequency of middens for different habitat types was positively related to average timber basal area ($r^2 = 0.675$, $P < 0.001$) (fig. 5). The ABLA/VASC-PIAL habitat type-whitebark pine cover type deviated the most from this relationship. Lodgepole pine cover types of the ABLA/VASC-PIAL phase fit the general relationship of basal area and squirrel density. At an average basal area of less than 67.7 m^2/ha (90 ft^2/acre), no resident squirrels occurred. Mean basal area for the PIAL series defined this extreme end point.

We also related a synthetic environmental variable, "site favorability," to mean squirrel midden abundance (fig. 6). Site favorability was an index that positively weighted direct solar radiation and negatively weighted wind exposure and elevation. Mattson and Reinhart (this proceedings) more fully described this variable. Squirrel abundance was lowest on the coldest, highest, and most wind-exposed habitat types ($r^2 = 0.792$, $P < 0.001$). Variation from this relationship was associated with overstory species diversity and higher basal areas of whitebark pine and Douglas-fir (*Pseudotsuga menziesii*). Habitat types with less squirrel densities included the PIAL series, which consisted of almost pure whitebark pine stands, and the ABLA/VASC-VASC phase, which consisted of predominantly pure lodgepole pine stands. The lodgepole pine cover type of the ABLA/VASC-PIAL phase and the ABLA/SPBE habitat type showed higher squirrel densities than expected by site favorability index. Higher levels were associated with moderate overstory diversity and relatively high basal areas of whitebark pine and Douglas-fir, respectively.

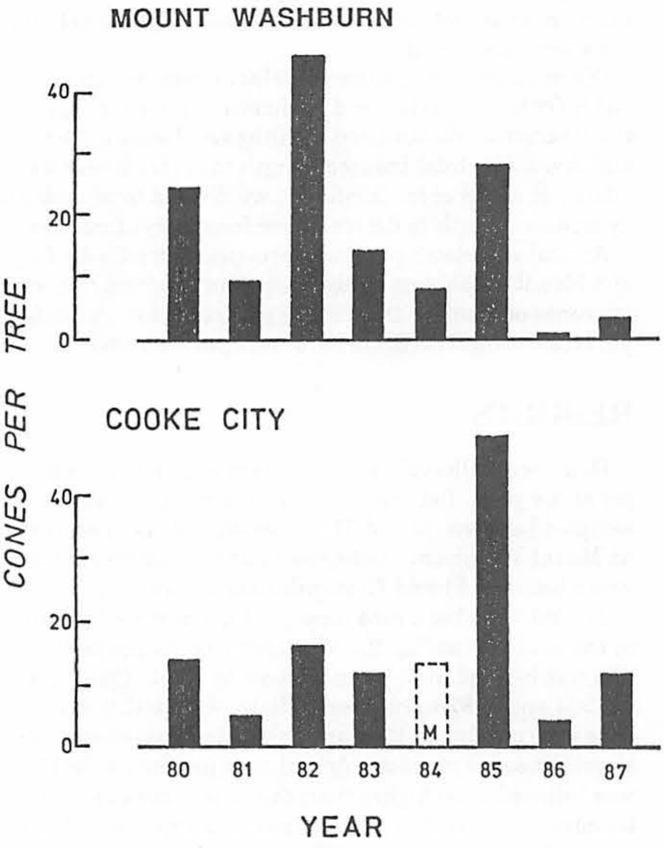


Figure 2—Whitebark pine cone production, 1980-1987, for the Mount Washburn and Cooke City study areas. Cone production for Cooke City in 1984 was extrapolated.

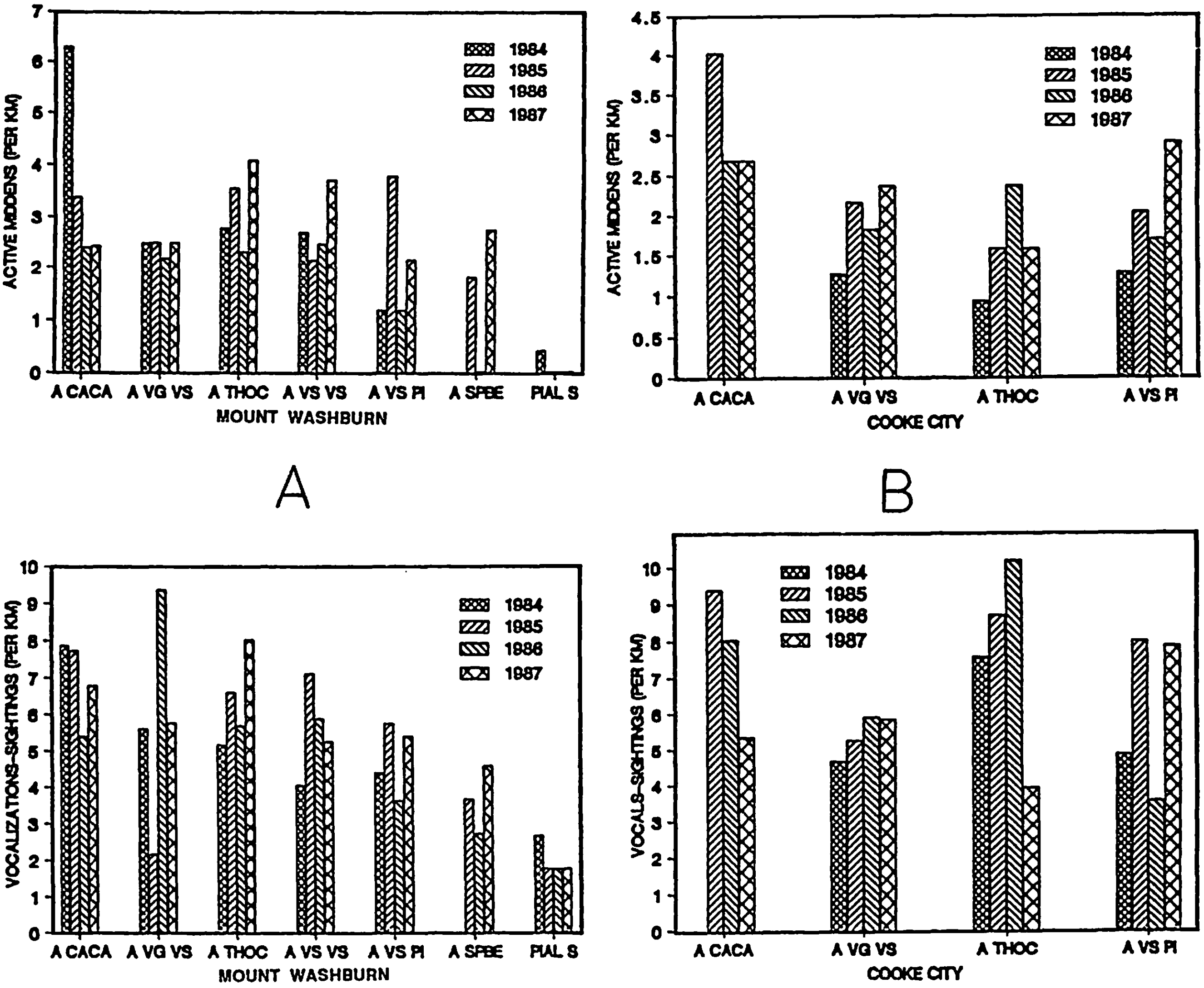


Figure 3—Linear densities of active squirrel middens and sightings + vocalizations for habitat types in the Mount Washburn (A) and Cooke City (B) study areas, 1984-1987.

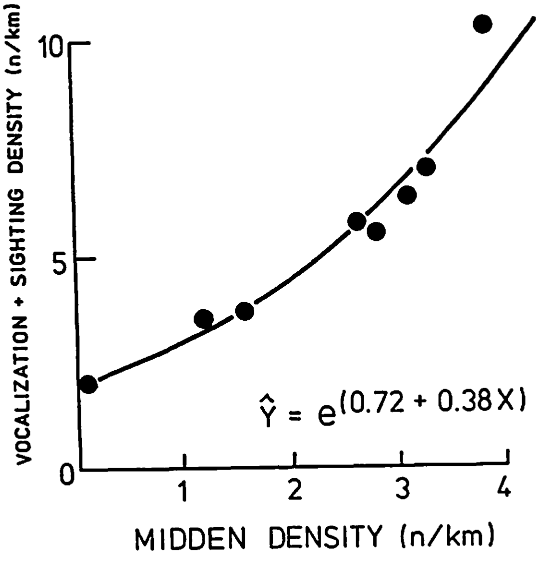


Figure 4—Relationship of average linear densities of squirrel middens and vocalizations + sightings for the Mount Washburn study area. Densities were averaged by habitat type and by habitat type and cover type for the ABLA/VASC-PIAL h.t.

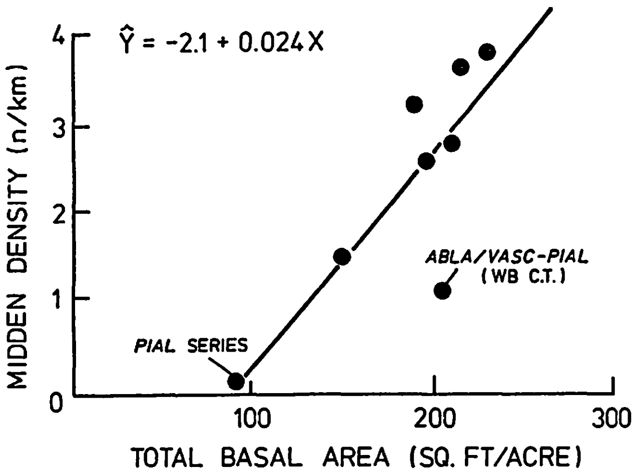


Figure 5—Relationship of active midden density and total timber basal area for the Mount Washburn study area.

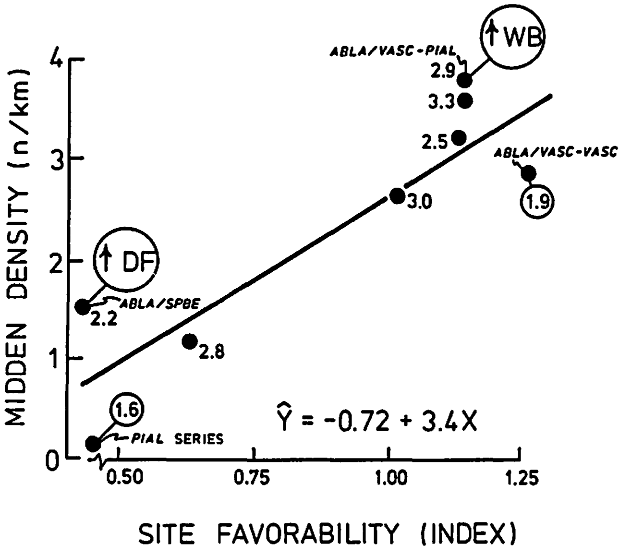


Figure 6—Relationship of active squirrel midden density and site favorability index for the Mount Washburn study area. Numbers at each datum are overstory diversity (e^H; Shannon and Weaver 1963) for the corresponding type.

DISCUSSION

Line transects have been used in previous studies to describe the relative abundance of wild populations (Burnham and others 1980; Eberhardt and others 1979; Hayne 1949). Indirect evaluation techniques have been useful measures of animal abundance when used to compare data between areas and time periods, or to associate habitat parameters with wildlife populations (Halvorson 1984). The following criteria should be met to reduce bias and variability in auditory and visual line transects of red squirrels (Eberhardt 1978; Halvorson 1984; Hayne 1949):

1. Sample design includes standardized methods that are repeatable.
2. Transects are laid out without bias toward the monitored population.
3. Time of day or season in relation to animal activity patterns does not vary over the course of the sampling period.
4. The effects of topography and cover on animal response to the observer are known.
5. Monitoring of a population is undertaken for a time period long enough to cover full cycles of population abundance.

This study of red squirrel populations appeared to have met these criteria. Red squirrel vocalizations could be heard between 0 to 60 m from transect lines, and usually occurred when the observer entered a red squirrel territory (C. Smith 1968). Red squirrels and middens were sighted between 0 to 40 m from the transect lines. There were no apparent differences in the frequency of squirrel calls or sightings related to time during daylight hours; stand boundaries and red squirrel territories were discrete so that topography changes were not critical to our evaluation. This study encompassed 4 years that included high, low, and intermediate whitebark pine cone crops. Although more years are needed to fully monitor red squirrel population trends (Halvorson 1984), some aspects of red squirrel habitat relationships can be addressed.

The high correlation of vocalization plus sighting densities with midden densities suggests that these two indices reflected the same phenomenon, and tends to corroborate the validity of each as a measure of squirrel abundance. The greater frequency of vocalization plus sighting densities relative to midden densities could have been a reflection of our greater sensitivity to red squirrel activity because of the greater detection range of vocalizations relative to middens. The exponential increase and greater variation of vocalizations and sightings with respect to middens could also reflect positive acoustical feedback similar to ruffed grouse (*Bonasa umbrellus*) behavior (Rogers 1981). With increasing squirrel densities (midden densities), there could have been an exponential increase in vocalizations triggered as a positive response to one squirrel's initial call. We suspect that this second explanation holds, and so considered squirrel midden abundance to be a more reliable indicator of squirrel density in our study area.

The whitebark pine zone apparently constitutes an extreme of the red squirrel niche. Pure whitebark pine stands, represented by the PIAL series habitat types, were not hospitable habitats for red squirrels. Factors that may contribute to the lack of red squirrels in pure whitebark pine stands include less total overstory basal area and species diversity, highly variable cone crops characteristic of whitebark pine, and the high, cold, harsh environments associated with these stands. The more mesic and wetter habitat types supported more red squirrels. These habitats had more overstory diversity, which in turn offered red squirrels other species' cone crops when whitebark pine seeds were not available. Lodgepole pine was an important conifer species to red squirrels. Although less preferred by red squirrels compared to some other tree species (Finley 1969), lodgepole pine played an important role in red squirrel habitat by providing a more consistent source of serotinous and thus more storable cones (C. Smith 1968).

Annual variation in red squirrel densities apparently reflected general whitebark pine cone crops in stands with a moderate to high proportion of whitebark pine. This was most evident in the ABLA/VASC-PIAL phase of both the Cooke City and Mount Washburn study areas. Although cone crops of other conifer species in mixed stands were not measured in this study, they apparently played an important role in the red squirrels' food supply, especially in years of poor whitebark pine cone mast (Finley 1969). In general, squirrel densities in all habitat types were more sensitive to whitebark pine crops in the Mount Washburn study area where whitebark pine was more prevalent than in the Cooke City study area. Two factors may explain greater yearly fluctuations in red squirrel densities in stands with a substantial amount of whitebark pine:

1. The food supply associated with large whitebark pine cone crops may allow the temporary establishment of more territories and squirrels in areas that did not previously support red squirrels.
2. Bear depredation of red squirrel caches may compound the effects of variable whitebark pine crops by further disrupting the squirrel population social status, by competing for food, and by occasionally eating red squirrels outright. Squirrel remains show up in grizzly bear scats containing whitebark pine seeds (Knight and others 1987).

Regulatory factors have been identified for red squirrel populations in other study areas. C. Smith (1968) suggested that territoriality allowed individual red squirrels the optimum conditions for harvesting, storing, and defending a seasonal food supply throughout the year. He further demonstrated that territory size was related to food supply, or was inversely proportional to habitat quality. Kemp and Keith (1970) found a strong correlation between white spruce (*Picea glauca*) cone crops and red squirrel population levels. However, M. Smith (1968) showed that red squirrel populations could survive a white spruce cone crop failure by caching surplus cones during good mast years.

Red squirrel populations in our study areas may be influenced by bear use and flexible habitat requirements of squirrels. Our study area included the edge of occupied red squirrel habitat. In the whitebark pine zone this edge varied with whitebark pine cone production. In years of unusually large whitebark pine crops, red squirrels occupied pure whitebark pine stands (Kendall 1981). However, this occupancy was probably shortlived. We found little sign of permanent red squirrel occupancy in stands with a high percentage of whitebark pine. Generally, with increased site favorability and species diversity, middens were characterized by increasing amounts of cone debris that indicated a longer history of occupancy. Red squirrels apparently established transient territories in whitebark stands during years of large cone crops because of the high forage quality of whitebark pine seeds. We are not sure how this was realized, but it was probably by the immigration of juveniles or extension of ranges by established squirrels into adjacent whitebark pine stands. Squirrels probably do not survive poor mast years in nearby pure whitebark pine stands because of frequent poor crops, the lack of alternative foods, and depredations by bears that possibly deprive them of an additional year's food. Ognev (1940) described a similarly dynamic situation for the European squirrel (*Sciurus vulgaris*) in the range of Asian stone pines (subsection Cembrae). He described transient territories and even mass "migrations" following years of crop failures.

More research is needed to better understand the relationships among whitebark pine, red squirrels, and bears, as well as how specific silvicultural treatments affect this system. Longer term study is required to assess red squirrel population responses to variable whitebark pine cone crops. In mixed and pure whitebark pine stands, red squirrel densities should be monitored, as should cone mast of all conifer species stratified by age and size classes. Study of red squirrel territory sizes with respect to different habitats or whitebark pine crops, as well as territory stability with respect to site favorability would provide valuable insight into red squirrel population regulation in this zone. More data are needed to assess the interaction between bears and red squirrel populations in the whitebark pine zone. This may be approached by relating levels of midden use by bears to annual variations in red squirrel densities and whitebark pine cone crops.

MANAGEMENT IMPLICATIONS

Timber management can potentially affect red squirrel population densities in the whitebark pine zone. Whitebark pine is not considered to be a valued commercial timber species (Arno and Hoff 1989). However, timber harvests do occur in stands that contain whitebark pine, primarily in stands of higher commercial value in the lower part of whitebark pine's elevational distribution. Basal area reduction by timber harvest in the whitebark pine zone will almost certainly reduce squirrel densities. Our results suggest this effect. Other studies in Alaska (Wolf and Zasada 1975) and Ohio (Nixon and others 1980) have also documented reduction in squirrel densities following reduction in basal area of seed-producing trees.

The strong link between red squirrels and grizzly bears (Kendall 1981; Mattson and Jonkel, this proceedings) in the whitebark pine zone merits the attention of resource managers. Management of grizzly bear habitat in the whitebark pine zone is partly contingent on management of red squirrel habitat and populations. Because of squirrel habitat requirements, management for both bears and squirrels logically revolves around maintenance of diverse-species, high-basal-area stands on favorable, more mesic sites of the zone. Forest managers should be cautious when applying silvicultural practices in whitebark pine forests to "enhance" grizzly bear habitat. Leaving seed-bearing whitebark pine trees in shelterwood cuts would reduce red squirrel densities by reducing overstory diversity and basal area. Planting whitebark pine seedlings following clearcutting may benefit long-term management of these stands, but will have little positive effect until these slow growing trees are mature enough to bear cones. Both practices would increase human access and activity. Increased risk of bear displacement and mortality would outweigh any gains achieved by overt forest manipulation.

REFERENCES

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Burnham, K. B.; Anderson, D. R.; Laake, J. L. 1980. Estimation of density from line transect sampling of biological populations. Wildlife Monograph 72. 202 p.

Despain, D. G. 1977. Forest successional stages in Yellowstone National Park. Infor. Pap. 32. Yellowstone National Park, WY: U.S. Department of the Interior, National Park Service. 3 p.

Eberhardt, L. L. 1978. Transect methods for population studies. Journal of Wildlife Management. 42: 1-31.

Eberhardt, L. L.; Chapman, D. G.; Gilbert, J. R. 1979. A review of marine mammal census methods. Journal of Wildlife Management. 63: 1-46.

Ferron, J.; Quellet, J. P.; Lemay, Y. 1986. Spring and summer time budgets and feeding behavior of the red squirrel (*Tamiasciurus hudsonicus*). Canadian Journal of Zoology. 64: 385-391.

Finley, R. B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. In: Contributions in mammalogy. Misc. Publ. 51. Lawrence, KS: University of Kansas, Museum of Natural History: 233-273.

Forcella, F.; Weaver, T. 1986. Cone production in *Pinus albicaulis* forests. In: Shearer, R. C., compiler. Proceedings—conifer tree seed in the inland mountain west symposium; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 68-76.

Halvorson, C. H. 1984. Long term monitoring of small vertebrates: a review with suggestions. In: Johnson, J. L.; Franklin, J. F.; Krebill, R. G., coords. Proceedings—research in natural areas; baseline monitoring and management. Gen. Tech. Rep. INT-173. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 11-25.

Hayne, D. W. 1949. An examination of the strip census method for estimating animal populations. Journal of Wildlife Management. 13: 145-157.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Kemp, G. A.; Keith, L. B. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology. 51(5): 763-779.

Kendall, K. C. 1981. Bear use of pine nuts. Bozeman, MT: Montana State University. 25 p. Thesis.

Knight, Richard R.; Blanchard, Bonnie M.; Mattson, David J. 1987. Yellowstone grizzly bear investigations: annual report of the Interagency Study Team, 1986. Bozeman, MT: U.S. Department of the Interior, National Park Service. 82 p.

Nixon, C. M.; McClain, M. W.; Donohoe, R. W. 1980. Effects of clearcutting on gray squirrels. Journal of Wildlife Management. 44: 403-412.

Ognev, I. V. 1940. Mammals of the U.S.S.R. and adjacent countries. Volume IV. Rodents. Izdatel'stvo Akademi Nauk' SSSR. Moskva-Leningrad. 429 p. Translated from Russian, 1966. Israel Program for Scientific Translations. Jerusalem.

Rogers, R. D. 1981. Factors affecting ruffed grouse drumming counts in southwestern Wisconsin. Journal of Wildlife Management. 45: 409-418.

Rusch, D. A.; Reeder, W. G. 1978. Population ecology of Alberta red squirrels. Ecology. 59: 400-420.

Shannon, C. E.; Weaver, W. 1963. The mathematical theory of communication. Urbana, IL: University of Illinois Press. 117 p.

Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecological Monographs. 38: 31-63.

Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs. 40: 349-371.

Smith, M. C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. Journal of Wildlife Management. 32(2): 305-317.

Steele, R.; Cooper, S.; Ondov, D.; Roberts, D.; Pfister, R. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

Tomback, D. F. 1982. Nutcrackers and pine: coevolution or coadaptation? In: Coevolution: Proceedings of the fifth annual spring systematics symposium; 1982 May 8; Chicago, IL. Chicago and London: University of Chicago Press: 179-223.

Weigl, P. D.; Hanson, E. U. 1980. Observational learning and the feeding behavior of the American red squirrel: *Tamiasciurus hudsonicus*: the ontogeny of optimization. Ecology. 61: 213-218.

Wolf, J. O.; Zasada, J. C. 1975. Red squirrel response to clearcut and shelterwood systems in interior Alaska. Res. Pap. PNW-255. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 7 p.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Ron Lanner)—How many years is a squirrel midden likely to remain active?

A.—Middens of cone scales and cores in addition to cached cones are conspicuous signs of a red squirrel territory. They range in size from 1 to 300 m^2. Large middens can be decades old and represent the accumulation of many successive generations of red squirrels (Finley 1969). The advantage of a long-used, traditional site midden is that stored cone clippings help maintain cached cones in a moist, more storable condition.

Midden use is apparently short lived in predominant whitebark pine stands compared to other more diverse sites. Active middens can be recognized from inactive middens by the presence of fresh cones, cone clippings, and red squirrels at midden sites. In the predominant whitebark pine stands, we found active middens were generally smaller and newer than in other more mesic habitats. The proportion of all encountered middens found to be inactive was also higher in stands with a higher whitebark pine component. This may represent higher annual fluctuations in red squirrel abundance. This is consistent with our findings that pure whitebark pine stands are not favorable habitats for red squirrels.

WHITEBARK PINE—AN IMPORTANT BUT ENDANGERED WILDLIFE RESOURCE

Katherine C. Kendall
Stephen F. Arno

ABSTRACT

Whitebark pine (Pinus albicaulis) *is a valuable wildlife resource in the western United States and southwestern Canada. Its large seeds are a preferred food for a variety of birds and mammals, especially Clark's nutcrackers* (Nucifraga columbiana), *red squirrels* (Tamiasciurus hudsonicus), *and bears* (Ursus *spp.*). *Whitebark pine communities provide food and shelter for nongranivorous species as well.*

In many areas, whitebark pine populations are being depleted by advancing forest succession and insect and disease epidemics. Extensive but unknown numbers of whitebark pine were lost to mountain pine beetle (Dendroctonus ponderosae) *in the Intermountain West in the 1970's and early 1980's. Dwarf mistletoe* (Arceuthobium *spp.*) *is a significant source of mortality in some parts of California, Oregon, Nevada, and Wyoming. White pine blister rust* (Cronartium ribicola) *has killed much of the whitebark pine in portions of the Inland Northwest.*

This paper summarizes available information on the status and health of whitebark pine and on its importance to wildlife. Widespread losses of this species have a variety of implications for management issues such as the restoration of grizzly bear (U. arctos horribilis) *populations. The need for better information on the status of whitebark pine is discussed.*

INTRODUCTION

Whitebark pine (*Pinus albicaulis*) is a valuable resource for a variety of birds and mammals in the western United States and southwestern Canada. Its large, wingless seeds are a preferred, high-energy food source, and whitebark communities provide other foods and shelter for several wildlife species inhabiting a harsh environment. The importance of whitebark pine to wildlife, however, has only recently been recognized. While useful research on red squirrels (*Tamiasciurus hudsonicus*), Clark's nutcrackers (*Nucifraga columbiana*), and bears (*Ursus* spp.) in whitebark pine communities has been conducted in the last decade, information is scarce on many aspects of wildlife ecology in these forests.

Recently, Arno (1986) warned that whitebark pine appears to be threatened by the effects of fire suppression and insect and disease epidemics. Because whitebark pine occupies cold, high-elevation sites, it grows and matures very slowly. Most trees are about a century old before they produce significant cone crops. Thus, whitebark pine stands are especially slow to recover from damage and slow to respond to management measures. In this paper, we summarize currently available information on the status and health of whitebark pine (little of which is published) and on the importance of whitebark pine to wildlife.

IMPORTANCE TO WILDLIFE

Whitebark pine forests appear to be significantly more productive, in terms of mass of seed produced per unit area, than most other temperate coniferous forests (Forcella 1977). The importance of whitebark pine as a wildlife food arises from the large size (0.1 to 0.2 g/seed; Krugman and Jenkinson 1974; McCaughey and Schmidt, this proceedings) and high lipid content (78 percent; Mealey 1980) of its seeds. The seeds are a concentrated, high-quality food source that can be stored for 12 months or more in squirrel middens or nutcracker caches; other high-elevation foods are more ephemeral. Typically, birds and mammals harvest almost all the viable seeds produced.

Red squirrels concentrate their foraging activities on whitebark pine seeds when they are available, virtually ignoring other foods. They are the most efficient of all whitebark pine seed predators because they can cut down and cache cones quickly. Squirrels also guard their caches from most other seed harvesters except bears. In a mixed stand of whitebark pine in Squaw Basin, WY, red squirrels accounted for 63 percent of all whitebark pine seeds taken by vertebrates (Hutchins and Lanner 1982). However, in nearly pure stands of whitebark pine, squirrel densities tend to be low (Mattson and Reinhart 1987) and Clark's nutcrackers harvest most of the seeds. Apparently, squirrel populations are highest where mature whitebark pine is mixed with other conifers. In these stands, alternate foods are available during years of low whitebark pine cone production.

Whitebark pine cones do not open and fall from the tree upon ripening in September. Cones are available to bears in some areas on stunted trees. Typically, however, bears obtain seeds from squirrel caches. The whitebark pine stands that are most valuable to bears, then, are those inhabited by large populations of red squirrels.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Katherine C. Kendall is Research Biologist, Glacier National Park, West Glacier, MT 59936; Stephen F. Arno is Research Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Missoula, MT 59807.

Whitebark pine seeds are an important autumn food for grizzly (*U. arctos*) and black (*U. americanus*) bears wherever whitebark pine is common in Montana and Wyoming. This has been confirmed for the Whitefish Range (Tisch 1961), East Front of the Rocky Mountains (Aune and Kaseworm in preparation), Scapegoat Wilderness (Craighead and others 1982), and Yellowstone National Park (Knight and others 1988).

Whitebark pine seed consumption by grizzly bears in the Yellowstone area is closely correlated with cone crop size (Knight and others 1988). During good cone crop years, Yellowstone bears feed almost exclusively on pine seeds in autumn (Knight and others 1985). Furthermore, seeds from the exceptionally heavy 1978 cone crop were the dominant bear food consumed in the spring and summer of 1979 (Kendall 1983). Good cone crops appear to be positively correlated with grizzly bear cub production and early weaning of young (Blanchard 1989; Knight 1989); poor whitebark pine cone crops are associated with increased grizzly bear mortalities and conflicts with humans (Knight and others 1988).

In the Soviet Union, brown bears (*U. arctos*) feed on the seeds of the closely related Siberian stone pine (*P. sibirica*). During years of massive cone crop failure, large numbers of emaciated bears make long migrations in search of food, frequently entering villages and killing livestock and occasionally attacking people (Pavlov and Zhdanov 1972; Ustinov 1972).

The Clark's nutcracker has evolved mutualistic relationships with pines that have large, wingless seeds. Whitebark pine is a preferred food for the nutcracker which, in turn, is responsible for most whitebark pine dispersal and regeneration. Nutcrackers cache seeds up to 14 mi away from a seed source (Vander Wall and Balda 1977). They bury more whitebark pine seeds than they require for winter and spring food, and many seed caches are in sites suitable for whitebark pine establishment (Tomback 1982). Nutcrackers are so dependent on whitebark pine and other conifer seeds that years of widespread cone crop failure cause nutcracker irruptions in which the birds may move hundreds of miles from their normal range (Davis and Williams 1964). Use of pine seed caches to feed nestlings and fledglings enables Clark's nutcrackers to nest earlier than other passerines, which must wait until insects are available for feeding. By the next winter, the more mature and experienced nutcracker offspring may be better able to survive (Tomback 1978).

Other birds and mammals are relatively minor consumers of whitebark pine seeds compared to the species discussed above (Hutchins and Lanner 1982; Tomback 1978). Golden-mantled ground squirrels (*Spermophilus lateralis*) and several species of chipmunk (*Eutamias* spp.) harvest seed from cones on the ground. Chipmunks also gather seed from cones in trees. The following birds are reported to feed on whitebark pine seeds: hairy and white-headed woodpeckers (*Picoides villosus* and *P. albolarvatus*), Williamson's sapsucker (*Sphyrapicus thyroideus*), mountain chickadee (*Parus gambeli*), white- and red-breasted nuthatches (*Sitta carolinensis* and *S. canadensis*), Steller's jay (*Cyanocitta stelleri*), raven (*Corvus* spp.), pine grosbeak (*Pinicola enucleator*), red crossbill (*Loxia curvirostra*), and Cassin's finch (*Carpodacus cassinii*).

The significance of whitebark pine to wildlife extends beyond its seeds as food. Its community structure is also valuable to wildlife. The openness and influence of fire in some whitebark pine stands provide conditions for abundant wildlife forage. Whitebark pine will grow in high-elevation, exposed sites where it modifies the microclimate and allows other less hardy vegetation to establish (Habeck 1969; Snethen 1980). In winter, blue grouse (*Dendragapus obscurus*) often roost at timberline in the dense protective crown of whitebark pine, which provides thermal and hiding cover. The grouse also feed on whitebark pine buds and needles (Arno 1970). Cavities in whitebark pine snags provide favored nest sites for mountain bluebirds (*Sialia currucoides*) and northern flickers (*Colaptes auratus*) (McClelland 1989).

Significant reductions in whitebark pine cone production may lower the wildlife carrying capacity of an area. Fewer whitebark pine seeds should result in fewer seed consumers and a decline in the number of their predators. Bears are both primary and secondary consumers in this system; they feed directly on pine nuts and on animals, such as red squirrels, that preferentially feed on pine nuts. In areas where whitebark pine is a major forest component, bears have been implicated as a factor in regulating red squirrel populations (Mattson and Reinhart 1987). Grizzly bears also prey on ungulates, especially elk (*Cervus canadensis*) calves (French and French in press). Because grizzly bear reproductive and mortality rates are correlated with whitebark cone crops in Yellowstone, long-term declines in cone production may lower bear population levels and could result in a decline in ungulate predation.

THREATS TO WHITEBARK PINE

Insect and disease epidemics and successional replacement by other conifers have reduced the numbers of whitebark pine throughout its range in the last 80 years (Arno 1986). In most communities (mixed stands) where whitebark pine provides food for squirrels and bears, it is a seral species perpetuated primarily by fire. Fire suppression has favored shade-tolerant conifers. Prior to the early 1900's, average natural fire intervals for whitebark pine stands were 50 to 350 years (Arno and Weaver, this proceedings; Morgan and Bunting, this proceedings), but under current management policies a seral whitebark pine stand would burn at 3,000-year intervals (Arno 1986).

Fire control has apparently increased the damaging effects of mountain pine beetle (*Dendroctonus ponderosae*) and dwarf mistletoes (*Arceuthobium* spp.), all native species, on whitebark pine. Even without the effects of fire suppression, mountain pine beetle epidemics killed large numbers of whitebark pine between 1909 and 1940 in Idaho and Wyoming (Arno 1970). With fire control, however, more extensive areas of old lodgepole pine (*P. contorta*) have developed. These support severe mountain pine beetle epidemics that spread to higher elevations and result in greater whitebark pine mortality than under natural fire regimes. Mountain pine beetles can also cause more mortality in the older whitebark pine stands that result from fire suppression.

Because dwarf mistletoe is controlled by stand-replacing fire, it is now more prevalent in undisturbed stands than in the past (Alexander and Hawksworth 1976). Whitebark pine is a principal host of limber pine dwarf mistletoe (*A. cyanocarpum*) and is heavily parasitized by leafless mistletoe (*A. americanum*) (Jackson and Faller 1973; Mathiasen and Hawksworth 1988). Both can reduce growth rates of heavily infected hosts, increase mortality rates, reduce seed and cone production, and increase vulnerability to other diseases and insects (Hawksworth and Wiens 1972).

White pine blister rust (*Cronartium ribicola* Fisch.), native to Europe, was accidentally introduced to western North America in 1910 and has since infected whitebark pine throughout its range (Hoff and Hagle, this proceedings). It attacks all North American five-needled pines, but whitebark pine is the most susceptible (Hoff and others 1980). The disease often first kills the upper, cone-bearing branches, and can eventually kill the entire tree. Seedlings and saplings are readily infected. Thus, white pine blister rust can significantly decrease whitebark pine seed production and regeneration (Arno and Hoff 1989). Blister rust infection also makes trees more susceptible and attractive to other diseases and insects, including mountain pine beetle. Blister rust control efforts, begun in the late 1930's, were largely unsuccessful and were abandoned in the 1970's.

Fires in whitebark pine stands normally are beneficial to regeneration of the species. Some large, severely burned areas, however, have failed to regenerate whitebark pine (fig. 1). The proposed Great Burn Wilderness in the Clearwater National Forest in northern Idaho, and the Lolo National Forest in western Montana supported extensive ridgetop stands of whitebark pine that were burned by the severe Great Idaho Fire in 1910 (Cohen and Miller 1978). Recent reconnaissance (by Arno) in different parts of this old burn revealed little or no regeneration of whitebark pine on sites (above 6,500 ft; 1,980 m) where snags confirm that it was once a dominant species. Other subalpine conifers have become reestablished (fig. 2). Two plausible explanations for the negligible reestablishment of whitebark pine are: (1) inadequate whitebark pine seed source survived the 1910 fire and (2) white pine blister rust has killed most of the seedlings and much of the seed source.

Moderate levels of whitebark pine mortality may benefit some species of wildlife. Mortality from mountain pine beetle, mistletoe, and blister rust opens the forest canopy. This may result in increased undergrowth vigor and forage production. For instance, berry production is often negatively correlated with canopy closure. Forcella (1977) studied the productivity of 28 stands in the *P. albicaulis-Vaccinium scoparium* association with varying amounts

Figure 1—Remains of a nearly pure whitebark pine stand killed in the Great Idaho Fire of 1910. Site is in the upper subalpine zone (Pfister and others 1977); the poorly developed postfire regeneration is composed of lodgepole pine and subalpine fir. Scene is at about 7,300 ft (2,225 m) elevation on Granite Peak, on the Idaho-Montana divide 8 air miles northwest of Lolo Pass. (Photo by S. Arno.)

Figure 2—Along the Idaho-Montana divide 7 miles northwest of figure 1 (west of Kid Lake). Large snags are mostly whitebark pine that survived a low-intensity fire in the mid-1800's but were killed in the severe 1910 fire. Regeneration of subalpine fir and lodgepole pine has been successful at the more moderate elevations in the foreground (about 6,500 ft; 1,980 m); but very little regeneration has taken place above 7,000 ft (2,130 m) (background) where nearly pure whitebark pine groves formerly existed. (Photo by S. Arno.)

of tree canopy cover. He identified three significant wildlife foods other than pine nuts: *V. scoparium* berries, *Carex geyeri*, and *Arnica* spp. He found, however, that whitebark pine produced 2 to 35 times as many kcal/m^2/yr of wildlife forage as these other species and was by far the most important wildlife food source in all stands studied.

EXTENT OF DECLINE

Because whitebark pine has limited value in timber production, data on its status are sparse. Foresters may have difficulty distinguishing between whitebark and limber pine, and many are unfamiliar with the remote high-mountain country where whitebark pine is found. Insect and disease surveys often fail to cover the whitebark pine zone or lump information on whitebark pine with other species. Therefore, available information is sketchy and relies on personal observation. Nevertheless, we believe there is enough evidence to justify concern for the perpetuation of whitebark pine as an important wildlife resource.

Some indirect evidence for a decline in whitebark pine comes from a comparison of past and recent bear studies and observations. R. Daubenmire (1989) encountered squirrel caches of whitebark pine cones that had been excavated by bears in the Selkirk Range of northern Idaho in the 1940's. A 1984 bear study in the Selkirks found no squirrel caches of whitebark pine cones and no whitebark pine seeds in bear scats, although three scats contained a small number of western white pine (*P. monticola*) seeds (Almack 1989). During a black bear study in the southern Whitefish Range of northwestern Montana in the early 1960's, all bears handled in the autumn showed signs of feeding on whitebark pine seeds (Jonkel 1989) (fig. 3). Whitebark pine seeds occurred in 30 percent of fall bear scats collected during that study (Tisch 1961) but in no bear scats observed in this area in the 1980's (Hadden 1989; Jonkel 1989; Kendall, personal observation). In the Mission Range, south of Flathead Lake, MT, most bear droppings observed during fall between 1925 and the late 1930's were entirely composed of whitebark pine seeds (Cheff 1984). Observations of

Figure 3—Black bear captured during a bear ecology study in the southern Whitefish Range, MT, in the early 1960's. The hair on its paws and stomach is matted with pitch from handling whitebark pine branches and cones. All bears trapped in autumn showed similar signs of feeding on whitebark pine seeds, but this has not been seen in the 1980's. (Photo by Charles Jonkel.)

grizzly bears and excavated squirrel middens were common in the whitebark pine zone during this time. No bear feeding activity on whitebark pine has been reported in this area in recent years. More of this sort of comparative information would be helpful.

Mountain Pine Beetle

Some of the only quantitative information on mountain pine beetle mortality in whitebark pine comes from the Northern Region, Forest Service, U.S. Department of Agriculture (headquarters at Missoula, MT). In the Flathead National Forest in this Region, 225,000 acres of whitebark pine suffered some mortality from mountain pine beetle 1975-1988 (Gibson 1988). Most of this occurred in the Whitefish Range, which lost one-half to two-thirds of its whitebark pine in the last 10 years to the combined effects of mountain pine beetles and white pine blister rust (Wilson 1988). Damage to whitebark pine stands ranged from very little mortality to almost 100 percent loss. The mountain pine beetle epidemic in the Whitefish Range originated from a severe infestation in lodgepole pine in adjoining Glacier National Park. Between 1979 and 1985, over 25,000 acres of whitebark pine, primarily in the North Fork of the Flathead River drainage, were infested with mountain pine beetle (Gibson 1988). Much of the whitebark pine in this area was killed, including the oldest whitebark pine trees known in the Park (DeSanto 1989).

Aerial surveys of mountain pine beetle infestations in the Forest Service Intermountain Region (headquarters at Ogden, UT) are for commercial timber only. Thus, substantially more whitebark pine mortality occurs than is indicated in insect damage figures (Knapp 1989). Heavy infestations in the Bridger-Teton and Targhee National Forests are killing large but unknown numbers of whitebark pine. For example, Knapp (1989) estimated that 50 to 75 percent of the whitebark pine on Signal Mountain was killed in recent years. Mountain pine beetle infestations are implicated in whitebark pine cone production decline in the Yellowstone ecosystem between 1980 and 1987 (Knight and others 1988).

The Forest Service Rocky Mountain Region (headquarters at Denver, CO) includes expanses of whitebark pine in the Absaroka and Wind River Ranges of western Wyoming (Steele and others 1983). Little is known about mountain pine beetle damage in those stands except that mortality has been high along the Continental Divide in the Wind River Range (Lister 1989).

In the Forest Service Pacific Northwest Region (headquarters at Portland, OR) whitebark pine is abundant at high elevations along and east of the Cascade Crest in Washington and in the highest mountains of central and eastern Oregon (Arno and Hammerly 1984). It is identified on mountain pine beetle survey maps but is not distinguished from western white pine when damage figures are tallied. It is known that a mountain pine beetle outbreak in northeastern Oregon killed substantial amounts of whitebark pine in the 1970's (Bridgewater 1989).

Dwarf Mistletoe

The few references available on whitebark pine infection by dwarf mistletoe indicate it causes significant mortality in some areas. Cooke (1955) reported "ghost forests" of whitebark pine resulting from dwarf mistletoe on the northwest slopes of Mount Shasta, CA. In the same area, Mathiasen and Hawksworth (1988) found that 96 to 98 percent of the whitebark pine was infected and half had been killed by limber pine dwarf mistletoe. Heavy infections of whitebark pine were also reported in the Copper Mountains, Elko, NV, and near South Pass, Fremont County, WY (Mathiasen and Hawksworth 1988). Whitebark pine has dominated the crater rim community of Wizard Island, Crater Lake National Park, OR, for several centuries. However, recent mortality (45 percent of standing whitebark pine stems less than 4 inches d.b.h. were dead) and little regeneration have diminished the population (Jackson and Faller 1973). Because many living whitebark pine are heavily parasitized by leafless mistletoe, this was suggested as the primary cause of mortality.

White Pine Blister Rust

White pine blister rust is a major source of whitebark pine mortality in areas humid enough to support the spread of spores from one host (*Ribes* spp.) to the other (whitebark pine). Whitebark pine is afflicted by blister rust wherever it is found with infected western white pine. Blister rust has caused heavy losses of whitebark pine from the crest of the northern Cascade Range in Washington to Glacier National Park, MT, and south to Lewiston, ID (Arno, personal observation; Layser 1989). In drier climates, such as the Yellowstone area, whitebark pine is experiencing only minor mortality from blister rust.

Some of the most severe blister rust damage to whitebark pine has occurred in the Forest Service Northern Region, especially in the Cabinet Mountains in northwestern Montana and the Selkirk Range and Bitterroot Mountains (Selway and North Fork of the Clearwater drainages) in northern Idaho (fig. 4) (Arno, personal observation; Hagle 1988). For example, observations and photographs by Arno (1984) indicate that more than 90 percent of the whitebark pine along the Selkirk Crest east of Priest River Experimental Forest was killed by blister rust by the early 1980's. This, no doubt, explains the absence of seeds in bear scats in the Selkirks discussed earlier. A substantial amount of whitebark pine was killed by blister rust in the Whitefish Range, MT, including an area south of Werner Peak in which virtually all the whitebark pine is now dead (Wilson 1988). In the past, this area produced large cone crops that attracted bears. Whitebark pine was a major component of high-elevation forests in portions of Glacier National Park, but blister rust has killed significant numbers, especially on the east side of the park where more than 90 percent has been lost (Buchholtz 1989). Extensive whitebark pine mortality has occurred since the 1930's in the Mission Mountains due to blister rust and mountain pine beetle. Since 1960 there has been continual blister rust mortality of whitebark pine on Desert Mountain south of West Glacier, MT (Schmidt 1989), whereas southward near Observation Peak in the Bob Marshall Wilderness, whitebark pines are just beginning to die from this disease (Keane 1988).

In Washington and Oregon, whitebark pine is damaged by white pine blister rust, but there is no measure of the extent of the problem (Russell 1989). Blister rust has caused significant whitebark pine mortality in the Crater Lake area of Oregon (Harvey 1989). In the Olympic Range, whitebark pine inhabits only the northeastern portion, but some stands, for example, at Constance Pass, have been killed by white pine blister rust (Arno and Hammerly 1984). Whitebark pine is common in northeastern Washington and has died or is dying in many places from blister rust (Layser 1980).

In California, whitebark pine occurs primarily in designated Wildernesses, and there are no quantitative data on distribution or mortality. White pine blister rust had infected whitebark pine in northern California by the 1950's. Increasing amounts of blister rust have been found in the Sierra Nevada in central California in the last 10 years. The rust is beginning to attack sugar pine (*P. lambertiana*) and western white pine at midelevations, so whitebark pine will probably be next (DeNitto 1989). A similar pattern is developing in the Lake Tahoe Basin and on the Lassen National Forest. Western white pine is beginning to contract blister rust, and whitebark pine is expected to follow suit (Kinloch 1989).

IMPLICATIONS FOR MANAGEMENT AND RESEARCH

Widespread loss of whitebark pine has a variety of implications for wildlife management. For example, it may limit efforts to restore grizzly bear populations in areas where, in the past, whitebark pine seeds were an important food. In the Selway-Bitterroot Wilderness, northern Cascade Range, and the Cabinet, Selkirk, and Mission Mountains, grizzly bear and whitebark pine numbers are greatly reduced. With other historically important food sources for bears gone or diminished—for example, depletion of salmon (*Oncorhyncus* spp.) and forage lost to agriculture—whitebark pine cone crops may be a factor in the continued survival or restoration of grizzly bear populations. Yet, this food source (and its decline) is often overlooked in bear habitat evaluations.

Current trends suggest continuing losses of whitebark pine in many areas. Lodgepole pine established after the 1910 fires will be vulnerable to mountain pine beetle attack 10 to 15 years from now (Gibson 1988). Intense infestations are likely to result in high mortality of whitebark pine. Extensive fires and drought create conditions favorable for bark beetle infestations. Mountain pine beetle populations increase in fire-scorched and drought-weakened trees and then spread to adjacent trees.

National Park managers are charged with conserving natural ecosystems including pristine genetic pools. Because white pine blister rust is not native to North America and is causing significant ecological changes, blister rust is of special concern to National Park management. The possibility of an experimental program in

Figure 4—Typical whitebark pine mortality caused by blister rust and possibly mountain pine beetle in the northern portion of the Selway-Bitterroot Wilderness, ID. Scene is on Beaver Ridge, 9 air miles southeast of Lolo Pass. (Photo by S. Arno.)

National Parks to enhance whitebark pine's natural resistance by selecting for resistant genotypes has not yet been considered, but should be.

Our extensive contacts with scientists familiar with whitebark pine communities and the effects of insects and diseases have left little doubt that there is cause for concern about the continuing productivity of this tree. Although a downward trend in whitebark pine abundance is apparent, it is also clear that better information is needed. The first step should be to conduct comprehensive surveys to assess the extent of damage to whitebark pine throughout its range and in various habitat types. Whitebark pine stands should be included in insect and disease surveys.

Additional information on wildlife ecology in whitebark pine communities is also needed. Because of whitebark pine's reliance on Clark's nutcrackers for seed dispersal, it would be useful to know if nutcrackers are no longer attracted to whitebark pine stands with little cone production or at what level of cone production there is not enough seed to cache or virtually all pine nuts are recovered by seed predators.

We must develop management techniques to counteract the problems besetting whitebark pine. We need to find ways to reintroduce fire or mimic its effects in allowing establishment of seral whitebark pine. Techniques for widespread propagation of whitebark pine are needed for a variety of site conditions.

Simulation modeling confirms the observational evidence of decline in whitebark pine in the inland Northwest (Keane and others, this proceedings). Whitebark pine's status as an important mast producer is precarious or already lost in many areas. Wildlife concerns alone make massive cone reductions unacceptable.

Whitebark pine was dominant over a much larger area in the early 1900's than today. A continuation of current successional patterns and mortality trends bodes poorly for whitebark pine. Unless resistant strains can be developed and introduced in large quantities, white pine blister rust will further reduce whitebark pine cone production in moist regions. Whitebark pine often occurs in small geographically isolated populations, which can be destroyed by blister rust or endangered by successional replacement. This, coupled with longer fire intervals, could result in local extinctions and loss of genetic variation. As we seek to mitigate the effects of human activities on wildlife populations, we should make rejuvenation of whitebark pine stands an urgent priority.

ACKNOWLEDGMENTS

We thank D. Tomback, P. Zager, R. Lanner, and E. Layser for their helpful reviews of a previous draft of the manuscript and the many people who provided unpublished data and other information included in this paper.

REFERENCES

Alexander, M. E.; Hawksworth, F. G. 1976. Fire and dwarf mistletoes in North American coniferous forests. Journal of Forestry. 74(7): 446-449.

Almack, Jon. 1989. [Personal communication]. February 17. Sedro Wooley, WA: Washington Department of Wildlife, North Cascades National Park.

Arno, Stephen F. 1970. Ecology of alpine larch (*Larix lyallii*) in the Pacific Northwest. Missoula, MT: University of Montana. 264 p. Dissertation.

Arno, Stephen F. 1984. [Observations and photographs]. On file at U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Missoula, MT.

Arno, Stephen F. 1986. Whitebark pine cone crops: a diminishing source of wildlife food? Western Journal of Applied Forestry. 1(3): 92-94.

Arno, Stephen F.; Hammerly, R. P. 1984. Timberline—mountain and arctic forest frontiers. Seattle, WA: The Mountaineers. 304 p.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Aune, Keith; Kaseworm, Wayne. [In preparation]. East front grizzly studies— final report. Helena, MT: Montana Fish, Wildlife, and Parks.

Bailey, D. K. 1975. *Pinus albicaulis*. Curtis's Botanical Magazine. 180(3): 140-147.

Blanchard, Bonnie. 1989. [Personal communication]. March 14. Bozeman, MT: U.S. Department of the Interior, National Park Service, Interagency Grizzly Bear Study Team.

Bridgewater, Dave. 1989. [Personal communication]. January 25. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Forest Pest Management.

Buchholtz, Curt. 1989. [Personal communication]. March. Estes Park, CO: Rocky Mountain Nature Association.

Cheff, Bud. 1984. What has happened to the Montana grizzly? [Unpublished manuscript]. Charlo, MT: Outfitter, rancher. Manuscript on file at: U.S. Department of the Interior, National Park Service, Glacier National Park, Science Center. 8 p.

Cohen, Stan; Miller, Don. 1978. The big burn—the Northwest's forest fire of 1910. Missoula, MT: Pictorial Histories Publishing Company. 88 p.

Cooke, W. B. 1955. Fungi of Mount Shasta (1936-1951). Sydowia, Annales Mycologici. 9: 94-215.

Craighead, J. J.; Sumner, J. S.; Scaggs, G. B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Wildlife-Wildlands Inst. Monogr. 1. Missoula, MT: University of Montana. 279 p.

Daubenmire, Rexford. 1989. [Letter to Steve Arno]. February. On file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Missoula, MT.

Davis, J.; Williams, Laidlaw. 1964. The 1961 irruption of the Clark's nutcracker in California. Wilson Bulletin. 76(1): 10-18.

DeNitto, Greg. 1989. [Personal communication]. January 18. Redding, CA: U.S. Department of Agriculture, Forest Service, Shasta-Trinity National Forest.

DeSanto, Jerry. [retired], 1989. [Personal communication]. February. Babb, MT: National Park Service, Glacier National Park.

Forcella, F. 1977. Flora, chorology, biomass and productivity of the *Pinus albicaulis-Vaccinium scoparium* association. Bozeman, MT: Montana State University. 99 p. Thesis.

French, Steve P.; French, Marilyn G. [In press]. Predatory behavior of grizzly bears on elk calves, 1986-88. International Conference Bear Research and Management.

Gibson, Ken. 1988. [Personal communication]. December 8. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, Cooperative Forestry and Pest Management.

Habeck, James R. 1969. A gradient analysis of a timberline zone at Logan Pass, Glacier Park, Montana. Northwest Science. 43(2): 65-73.

Hadden, Dave. 1989. [Personal communication]. February. Former graduate student, School of Forestry, University of Montana, Missoula, MT.

Hagle, Sue. 1988. [Personal communication]. December 8. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, Cooperative Forestry and Pest Management.

Harvey, Bob. 1989. [Personal communication]. January 18. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Forest Pest Management.

Hawksworth, F. G.; Wiens, D. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). Agric. Handb. 401. Washington, DC: U.S. Department of Agriculture, Forest Service. 234 p.

Hoff, R.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology. 10: 307-316.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Jackson, M. T.; Faller, A. 1973. Structural analysis and dynamics of the plant communities of Wizard Island, Crater Lake National Park. Ecological Monographs. 43: 441-461.

Jonkel, Charles. 1989. [Personal communication]. March 13. Missoula, MT: University of Montana, School of Forestry.

Keane, Robert E. 1988. [Personal communication]. December 8. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region and Intermountain Research Station.

Kendall, Katherine C. 1983. Use of pine nuts by black and grizzly bears in the Yellowstone area. International Conference Bear Research and Management. 5: 166-173.

Kinloch, Bohun. 1989. [Personal communication]. January 18. Berkeley, CA: U.S. Department of Agriculture, Forest Service, University of California-Berkeley.

Knapp, Andy. 1989. [Personal communication]. January 18. Boise, ID: U.S. Department of Agriculture, Forest Service, Intermountain Region, Forest Pest Management.

Knight, Richard R. 1989. [Personal communication]. March 14. Bozeman, MT: U.S. Department of the Interior, National Park Service, Interagency Grizzly Bear Study Team.

Knight, Richard R.; Blanchard, Bonnie M.; Mattson, David J. 1985. Yellowstone grizzly bear investigations. Report of the Interagency Study Team, 1983 and 1984. Bozeman, MT: U.S. Department of the Interior, National Park Service. 41 p.

Knight, Richard R.; Blanchard, Bonnie M.; Mattson, David J. 1987. Yellowstone grizzly bear investigations. Annual Report 1986. Bozeman, MT: U.S. Department of the Interior, National Park Service. 82 p.

Knight, Richard R.; Blanchard, Bonnie M.; Mattson, David J. 1988. Yellowstone grizzly bear investigations. Annual Report 1987. Bozeman, MT: U.S. Department of the Interior, National Park Service. 80 p.

Krugman, S. L.; Jenkinson, J. L. 1974. *Pinus* L. Pine. In: Schopmeyer, C. S., ed. Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture, Forest Service: 598-638.

Layser, Earl. 1980. Flora of Pend Oreille County, Washington. Pullman, WA: Washington State University, Cooperative Extension. 144 p.

Layser, Earl. 1989. [Personal communication]. February 8. Prineville, OR: U.S. Department of Agriculture, Forest Service, Ockoco National Forest.

Lister, Ken. 1989. [Personal communication]. January 18. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Forest Pest Management.

Mathiasen, Robert L.; Hawksworth, Frank G. 1988. Dwarf mistletoes on western white pine and whitebark pine in northern California and southern Oregon. Forest Science. 34(2): 429-440.

Mattson, David J.; Reinhart, Daniel P. 1987. Grizzly bear, red squirrels, and whitebark pine: third year progress report. In: Knight, R. R. and others. Yellowstone grizzly bear investigations. Annual Report 1986. Bozeman, MT: U.S. Department of the Interior, National Park Service: 36-45.

McClelland, B. Riley. 1989. [Personal communication]. February. West Glacier, MT: U.S. Department of the Interior, National Park Service, Glacier National Park, Science Center.

Mealey, Stephen P. 1980. The natural food habits of grizzly bears in Yellowstone National Park, 1973-1974. International Conference Bear Research and Management. 4: 281-292.

Pavlov, M. P.; Zhdanov, A. P. 1972. On migrations and aggressive behavior of brown bears in the Siberian Taiga. In: Proceedings of conference on bear ecology, morphology, protection and utilization. Moscow, USSR: Soviet Union Academy of Sciences. 64-66.

Pfister, Robert D.; Kovalchik, Bernard L.; Arno, Stephen F.; Presby, Richard C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Russell, Ken. 1989. [Personal communication]. January 18. Olympia, WA: Washington Department of Natural Resources, Pest Management.

Schmidt, Wyman C. 1989. [Personal communication]. January 26. Bozeman, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Snethen, Karen L. 1980. Whitebark pine (*Pinus albicaulis* Engelm.) invasion of a subalpine meadow. Logan, UT: Utah State University. 76 p. Thesis.

Steele, R.; Cooper, S. V.; Ondov, D.; Roberts, D.; Pfister, R. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

Tisch, Edward L. 1961. Seasonal food habits of the black bear in the Whitefish Range of northwestern Montana. Bozeman, MT: Montana State University. 108 p. Thesis.

Tomback, Diana F. 1978. Foraging strategies of Clark's nutcrackers. Living Bird. 16: 123-161.

Tomback, Diana F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51: 451-467.

Ustinov, S. K. 1972. Cannibalism and attacks on humans by brown bears in eastern Siberia. In: Proceedings of conference on bear ecology, morphology, protection and utilization. Moscow, USSR: Soviet Union Academy of Sciences: 85-87.

Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecological Monographs. 47: 89-111.

Weaver, T.; Forcella, F. 1986. Cone production in *Pinus albicaulis* forests. In: Shearer, R. C., compiler. Proceedings—conifer tree seed in the Inland Mountain West symposium; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 68-76.

Wilson, George. 1988. [Personal communication]. December 13. Columbia Falls, MT: U.S. Department of Agriculture, Forest Service, Glacier View District, Planning Coordinator.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Penny Morgan)—Is a major effort to regenerate whitebark pine justified given the loss of whitebark pine as a resource, especially where we can document loss due to white pine blister rust?

A.—Given the importance of whitebark pine to wildlife, regeneration efforts definitely warrant consideration. Other values include whitebark pine's role in the hydrologic cycle and as a structural component of timberline communities, as well as its esthetic qualities. There is not currently enough information on many aspects of whitebark pine and white pine blister rust to decide if a major effort is justified. The first step toward answering this question should be to get better information on the status of whitebark pine throughout its range and in a variety of habitat types.

Q. (from Anonymous)—What is the cone crop frequency of whitebark pine? Is it different throughout its range?

A.—Little information is available on annual variation in whitebark pine cone production. According to Bailey (1975), whitebark pine stands tend to cone profusely and simultaneously over large areas at infrequent intervals with very little cone production in the intervening years. However, good cone crops may be produced more frequently in the southern parts of its range. In a Sierra Nevada study area, moderate to heavy whitebark pine cone crops were produced in each of 4 years cone production was rated (Tomback 1978). Data from the greater Yellowstone area suggest that while excellent cone crops are infrequent, moderate as well as poor cone crops are common (Knight and others 1987). Annual cone production was estimated for 29 whitebark pine stands in the northern Rockies (Weaver and Forcella 1986). Excellent cone years were preceded in 20 of 29 cases by average or poorer cone years. Poor cone years were not significantly correlated with yields in any previous year. There is no information on cone crop periodicity in the northwest range of whitebark pine where it is more immediately threatened by disease and successional replacement.

SIMULATING DISTURBANCES AND CONIFER SUCCESSION IN WHITEBARK PINE FORESTS

Robert E. Keane
Stephen F. Arno
James K. Brown
Diana F. Tomback

ABSTRACT

*Infestations of white pine blister rust (*Cronartium ribicola*) and successional replacement by more shade tolerant conifers can reduce whitebark pine populations. This could adversely affect wildlife species dependent on whitebark pine cone crops including the red squirrel (*Tamiasciurus hudsonicus*), grizzly bear (*Ursus arctos horribilis*), and black bear (*Ursus americana*). The ecological process model FIRESUM (a FIRE SUcession Model) was adapted to whitebark pine (*Pinus albicaulis*) forests and used to simulate effects of long-term successional trends on different seral and climax whitebark pine communities in relation to (1) high severity (crown) fires and fire suppression scenarios, (2) near and far-distant seed sources, and (3) disease epidemics. FIRESUM is a gap-phase model that was used to simulate tree establishment, growth, and mortality on a 400-m^2 (0.1-acre) plot. Live and dead fuel accumulations, fire behavior and frequency, fuel reduction, and insect- and disease-caused tree mortality were also modeled. Tree establishment and growth in the model are influenced by temperature, water stress, site quality, and light conditions. An additional submodel was included in FIRESUM to simulate the Clark's nutcracker's (*Nucifraga columbiana*) important role in regenerating whitebark pine through seed-caching activities. A test of the FIRESUM model revealed its ability to predict basal areas within 15 percent of those values obtained from inventory data from actual postfire stands.*

INTRODUCTION

Whitebark pine (*Pinus albicaulis*) is a common tree species of upper subalpine forests and timberlines in the western United States and southwestern Canada. While this species is of limited use for timber, it is highly valued as a food source for wildlife and as cover for snow retention and watershed protection (Arno and Hoff 1989; Day 1967; Forcella and Weaver 1977). Whitebark pine is a component of stands comprising about 10-15 percent of the forested landscape in the Rocky Mountains of Montana, Idaho, and northwestern Wyoming. Most of these whitebark pine stands have not been commercially exploited. However, the species' abundance appears to be threatened by the individual and combined effects of fire suppression, insects, and diseases (Arno 1986). Modeling the effects of these factors on whitebark pine might aid in developing management strategies for maintaining vigorous populations of this species. In addition, modeling will help us understand important ecological relationships in whitebark pine forests.

This paper presents results of an application of process modeling to investigate the effects of fires and diseases on long-term stand dynamics in whitebark pine forests. The computer model FIRESUM (a FIRE SUccession Model) was modified and used for this investigation (Keane and others 1989). The model was used to simulate tree dynamics for four natural and management scenarios using actual field data as inputs. Effects of seed source distance on tree regeneration were also simulated using FIRESUM. Model results were compared with actual field data sampled from two whitebark pine sites.

FIRESUM is a gap-replacement, ecological process model (Shugart and West 1980) following the approach used for JABOWA (Botkin and others 1972) where individual trees are grown deterministically using an annual time step, difference equation. Tree growth and regeneration are affected by several site factors including light, water, tree densities, and temperature. Tree regeneration and mortality are modeled stochastically using Monte Carlo techniques (Keane and others 1989). To simulate whitebark pine regeneration it was essential to modify FIRESUM to account for the role of birds in seed dispersal. Mortality from major insects and diseases was also included in the modeling process.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Robert E. Keane is a Quantitative Ecologist working with the Intermountain Research Station and the Northern Region, Forest Service, U.S. Department of Agriculture, Missoula, MT; Stephen F. Arno is a Research Forester and James K. Brown is a Project Leader, Intermountain Research Station; Diana F. Tomback is Associate Professor, Department of Biology, University of Colorado, Denver.

WHITEBARK PINE ECOLOGY

Whitebark pine is a long-lived, slow-growing tree of high-elevation forests from California and Wyoming north into southern Canada (Arno and Hoff 1989; Day 1967). Throughout most of its range, whitebark pine occurs on two kinds of sites: (1) alpine timberlines and very dry sites where it usually is the climax tree species, and (2) upper subalpine forests where it occurs as a seral species often associated with subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), mountain hemlock (*Tsuga mertensiana*), and Engelmann spruce (*Picea engelmannii*) (Arno 1986).

The seeds of whitebark pine are wingless, large (1,180 seeds/kg), and, like most pine seeds, nutritious (Botkin and Shires 1948; Lanner 1982; Mattson 1987; Schopmeyer 1974). These characteristics make the seeds highly desirable to many species of wildlife including the red squirrel (*Tamiasciurus hudsonicus*) (Smith and Follmer 1972), Clark's nutcracker (*Nucifraga columbiana*) (Forcella and Weaver 1977; Tomback 1978), black bear (*Ursus americana*), and grizzly bear (*Ursus arctos horribilis*) (Eggers 1986; Kendall 1980; Mealey 1975). Red squirrels harvest whitebark pine cones and store them in caches or middens on the ground. These middens provide an important, energy-rich food for grizzly and black bears (Mattson 1987; Mattson and Reinhart 1986).

Clark's nutcrackers play a major role in the regeneration of whitebark pine by being the primary means of dispersal for the large, wingless seeds (Hutchins and Lanner 1982; Lanner 1982; Tomback 1982). The nutcrackers harvest seeds from cones on trees and cache these seeds in the surface soil. Seeds not reclaimed by the nutcracker before late spring may germinate and grow into seedlings.

Probably the agents most damaging to whitebark pine are mountain pine beetle (*Dendroctonus ponderosae*), white pine blister rust (*Cronartium ribicola*), wildfire, and successional replacement by more shade-tolerant conifers (Arno and Hoff 1989). Mountain pine beetle killed many mature stands of whitebark pine in the northern Rockies during the years 1909-1940 and again during the 1970's (Arno 1970). Blister rust, an introduced disease, destroys trees in regions where the climate is moist enough to allow it to complete its life cycle. Blister rust is especially damaging to seedlings and saplings (Arno and Hoff 1989), and it also severely damages upper (cone-bearing) branches long before causing mortality in larger trees (Arno 1986). Consequently, epidemics of bark beetles and blister rust in whitebark pine stands jeopardize perpetuation of whitebark pine cone crops in many stands.

The cold, often moist, conditions in whitebark pine forests coupled with sparse fuels result in infrequent fires (50- to 300-year interfire periods) (Arno 1986). Whitebark pine is able to survive low severity fires that kill much of the competing subalpine fir. This creates small openings favorable for regeneration. High severity fires, usually originating from lower elevation forest stands, kill whitebark pines, but the species often becomes more abundant in the postburn community as a result of nutcracker seed dispersal (Arno 1986). Fire suppression favors successional replacement of whitebark pine with subalpine fir on sites where whitebark pine is a seral species.

MODEL DESCRIPTION

FIRESUM is a computer program written in FORTRAN 77 containing 45 subroutines and a main driver program (Keane and others 1989). The model was originally developed from the SILVA model of Kercher and Axelrod (1984) which modeled stand dynamics in ponderosa pine-Douglas-fir forests (Keane and others in press a). Each subroutine in FIRESUM simulates an ecological process and is composed of a specific algorithm driven by a set of associated parameters. Figure 1 presents a modified flow chart showing the names of the important subroutines. FIRESUM models stand dynamics on a 400-m^2 (0.1-acre) simulation plot. Actual field data from two sites were used to construct the initial simulation stand. Modification of FIRESUM to simulate whitebark pine stand dynamics required the alteration or addition of several algorithms, and the revision of nearly all model parameters. Because routines in FIRESUM are described in detail by Keane and others (1989), only the five most important processes and the new whitebark pine regeneration routines are discussed in this paper.

Growth Process (Subroutine GROW)

Tree growth is modeled by an annual increase in tree diameter at breast height (1.37 m above ground) using annual time-step difference equations. In these equations (table 1), an optimal diameter increase for a tree species (DI) is reduced by four growth reduction factors. The factors (numbers between 0 and 1) model effect of light (rAL), crowding (rN), water stress (rW), and growing season warmth (rC) on tree growth. Process parameters are shown in table 2.

Regeneration Process (Subroutine BIRTH)

Trees are established on the simulation plot if two criteria were met. First, degree-days had to exceed a minimum number of degree days (DMIN) for the species under consideration, and second, the actual to potential evapotranspiration ratio (AET:PET) had to be greater than the minimum value (WSO) for the species (table 2) (Keane and others 1989; Kercher and Axelrod 1984).

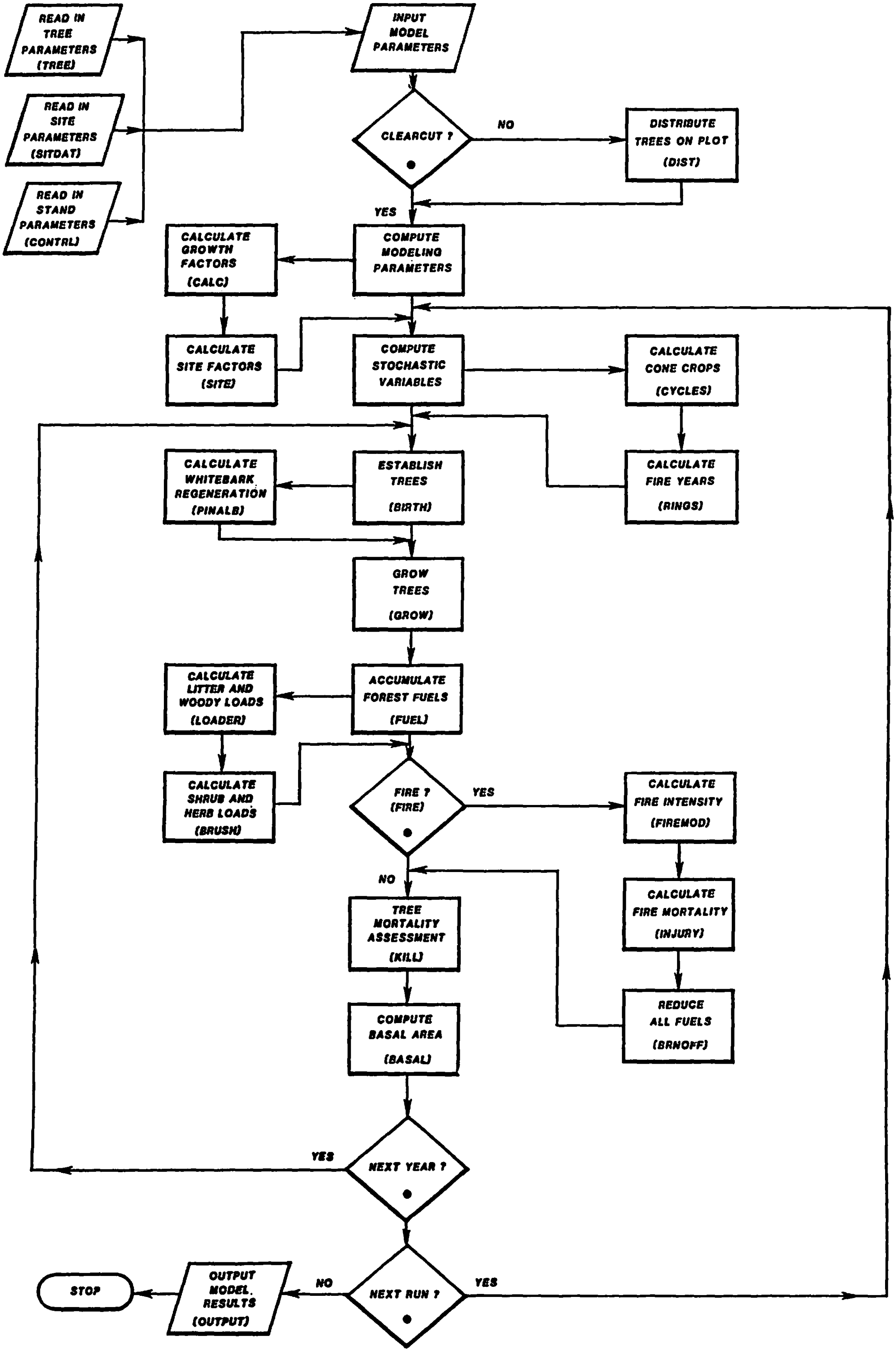


Figure 1—Simplified flow chart for the process model FIRESUM. Names of the FORTRAN subroutines are in parentheses.

Table 1—Descriptions of important equations and algorithms used in the subroutines of FIRESUM

Sub-routine	Important FIRESUM equations	Source or explanation
GROW	$DI = \frac{G\,D\,[1-(DH/D_m H_m)]}{274 + 3b_2D - 4b_3D^2}$ rAL rN rW rC	Botkin and others (1972)
	DI = annual diameter increment (cm)	
	G = growth parameter calculated in FIRESUM	
	D = tree diameter (cm)	
	$H = 137 + b_2D - b_3D^2$ (cm)	Ker and Smith (1955)
	D_m = max. dia. for a species (cm)	b_2, b_3 derivation shown in
	H_m = max. height for a species (cm)	Botkin and others (1972)
	rAL, rN, rW, rC = growth reduction factors $0.0 < \text{value} < 1.0$	Kercher and Axelrod (1984)
	$AL = AL_0\, e^{-k*\mathrm{LAI}}$	Kercher and Axelrod (1984)
	AL_0 = available light (full sunlight) standardized to zero	
	k = extinction coefficient (0.426)	Keane and others (1989)
	LAI = sum of leaf area indices for all trees taller than one in question	
	$\mathrm{LA} = \frac{[(CW * \mathrm{PFOL}) / CD] * SV}{\mathrm{PLA}}$	
	CW = crown weight (g)	Brown (1976)
	PFOL = proportion CW that is foliage	Brown (1978)
	CD = needle density (g/cc)	Assumed to be 0.5 g/cc
	SV = needle surface area:volume ratio	Lopushinsky (1970), Brown (1970), Minore (1979)
	PLA = all sided to projected leaf area conversion factor	Kaufmann and others (1982)
	$\mathrm{rAL} = 1 - e^{[-4.64(AL-0.05)]}$ shade tolerant species	Botkin and others (1972)
	$\mathrm{rAL} = 2.24\{1 - e^{[-1.136(AL-0.08)]}\}$ shade intolerant species	Botkin and others (1972)
	$\mathrm{rN} = 1.0 - (\mathrm{BAR}/\mathrm{BARMAX})$	BARMAX from Pfister and others (1977)
	BAR = current basal area of plot (square meters)	
	BARMAX = maximum attainable basal area for plot	
	$\mathrm{rW} = 1 - [(1 - \mathrm{APR}) / (1 - \mathrm{WSO})]^2$	Kercher and Axelrod (1984)
	APR = annual AET:PET ratio for simulation site	Used Thorthwaite and Mather (1957) equations
	WSO = lower limit of tolerance in APR	Calculated from actual weather data
	$\mathrm{rC} = \frac{[(\mathrm{DEGD} - \mathrm{DMIN})(\mathrm{DMAX} - \mathrm{DEGD})]^V}{[(\mathrm{DOPT} - \mathrm{DMIN})(\mathrm{DMAX} - \mathrm{DOPT})]^V}$	Reed and Clark (1979)
	DEGD = degree-days for simulation site	
	DMIN = minimum degree-days defining a species' range	DMIN, DMAX, DOPT determined from weather data
	DMAX = maximum degree-days defining a species' range	
	DOPT = degree-days needed for optimal species growth	
	V = species-specific constant	Keane and others (1989)

(con.)

Table1—(Con.)

Subroutine	Important FIRESUM equations	Source or explanation
BIRTH	rSRF = Exp $(a + b\,DS)$	McCaughey and Schmidt (1985)
	rSRF = seed source distance reduction factor	
	a, b = species specific constants	
	DS = distance from seed wall	
	rALs = $e^{(-0.8\ \mathrm{LAI})}$ for shade-intolerants	Based on unpublished data
	rALs = $e^{(-0.25\ \mathrm{LAI}-1.0)}$ for moderate shade tolerants	
	rALs = $1 - e^{(-0.25\ \mathrm{LAI}-0.2)}$ for shade tolerants	
	PSUR = 1.0 − $a\,DD$	Boyce (1985)
	PSUR = proportion of surviving seedlings	
	a = species specific constant	
	DD = duff depth (cm)	
KILL	P_r = 4 / AGEMAX	Botkin and others (1972)
	$P_S = P_S + 0.2 - 0.2\,P_S$	Derived from unpublished data
	$P_f = \dfrac{1}{1+\mathrm{EXP}[-1.941+6.32(1-\mathrm{EXP}(BT))+0.000535C^2]}$	Ryan and Reinhardt (1988)
	P_r = random or background mortality	
	P_S = stress mortality	
	P_f = fire mortality	
	BD = bark thickness (cm)	
	C = percent of crown scorched (%)	
	AGEMAX = maximum attainable age (yr)	

Table 2—Parameter values for whitebark pine forest species implemented in FIRESUM[1]

Parameter symbol (units)	Tree species[2]				
	PIAL	PICO	LALY	ABLA	PIEN
H_m (cm)	3,657.000	4,115.000	3,048.000	4,175.000	5,456.000
D_m (cm)	182.000	110.000	168.000	126.000	234.000
AGEMAX (years)	1,000.000	350.000	800.000	250.000	300.000
DMIN (deg-days)	800.000	1,500.000	800.000	1,003.000	1,003.000
DOPT (deg-days)	3,000.000	3,000.000	3,000.000	3,800.000	3,800.000
DMAX (deg-days)	5,200.000	6,500.000	5,200.000	6,200.000	6,200.000
Shade tolerance	M	I	I	T	M
SV (cm^2/cm^2)	57.600	64.700	184.000	70.000	54.200
PLA (m/m)	3.540	3.540	3.540	2.040	2.040
WSO (proportion)	.330	.400	.750	.650	.650
Pc (probability)	N/A	.318	.368	.333	.167
hc (years)	1.000	2.000	1.000	2.000	3.000
BC (proportion)	.015	.014	.031	.015	.022
DKF (proportion)	.057	.044	.201	.034	.034
DKL (proportion)	.112	.112	.200	.067	.067
LTD (proportion)	.550	.660	.650	.650	.650
DKD (proportion)	.221	.221	.321	.221	.221
AINC (cm)	.006	.016	.007	.008	.008
Lc (percent)	50.000	40.000	45.000	80.000	80.000
NYR (years)	7.000	3.000	1.000	7.000	6.000

[1] Sources for model parameters are listed in Keane and others (1989). Variables not defined in text or table 1 are shown in Keane and others (1989).

[2] PIAL-whitebark pine, PICO-lodgepole pine, LALY-alpine larch, ABLA-subalpine fir, PIEN-Engelmann spruce.

If these criteria were met, the size of the cone crop was then evaluated. The procedure described below is used for every species in the model except whitebark pine. Since whitebark pine seed is dispersed by the Clark's nutcracker, its regeneration algorithm is presented in detail later in this paper.

Each year a species (not including whitebark pine) can have a good or poor cone crop, and trees are established only in the year following good cone crop years. Cone crop years are computed stochastically using Monte Carlo techniques discussed in Kercher and Axelrod (1984).

The actual number of trees established on the simulation plot (FNJ) for a species is calculated from the equation:

$$FNJ = SPM * PTREE * PSUR * rSRF * rALs \qquad (1)$$

where SPM is the maximum number of seedlings that can become established on a square meter (10.8 ft^2), 0.87 was used for this investigation (Keane and others, unpublished data); PTREE is number of seed trees for the species under consideration divided by the total number of seed trees for all species (Keane and others 1989); and PSUR is a reduction factor (table 1) simulating the proportion of seedling survival as a function of duff depth (Boyce 1985; Keane and others 1989). The reduction factor rSRF models the effect of distance to seed source on seedling establishment (table 1). Equations used to compute rSRF for each tree species are a modification of the dispersal curves of McCaughey and others (1986) (fig. 2). Lastly, rALs is a reduction factor simulating seedling survival under various light conditions as a function of leaf area and shade tolerance (Keane and others 1989). All new trees, including whitebark pine trees, are established as saplings of 1.0 cm diameter at breast height (d.b.h.) and 1.37 m tall. These new trees are included after a lag period of 25-50 years depending on the site.

Whitebark pine regeneration is computed in subroutine PINALB, which models the effects of seed crop, nutcrackers, and light on whitebark regeneration. Four cone crop classes are used in PINALB: none, poor, moderate, and good, with each class having an associated probability of occurrence (p_w) and a crop reduction factor (rCONFAC) (table 3). Cone crop class is determined stochastically using random number generation. The number of cones on a whitebark pine tree (CPT) is computed using the equation:

$$CPT = CMAX * rCONFAC * rCRF \qquad (2)$$

where CMAX is the maximum number of cones per tree (table 3) and rCRF is another crop reduction factor that is a function of tree age (fig. 3a). The total number of cones produced on the simulation plot (CONES) is calculated by

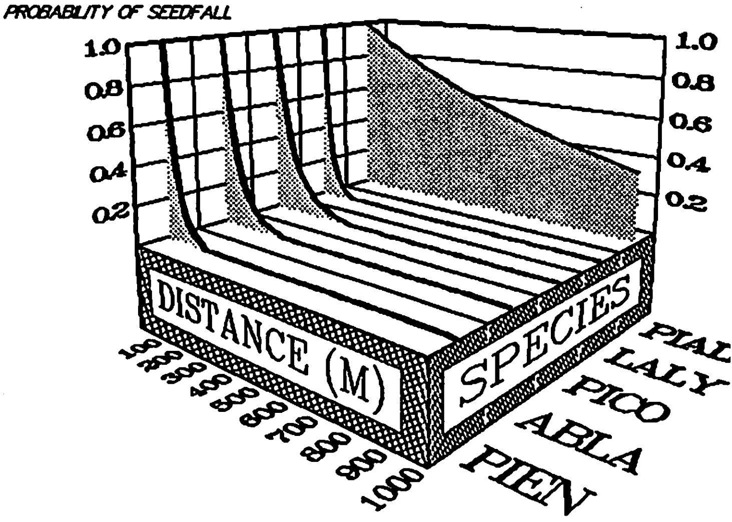


Figure 2—Seed dispersal curves for several tree species. Probability of seedfall describes the chances a seed will fall to the ground at various distances. Whitebark pine (PIAL) curve from Tomback and others (1989); all other curves were derived from McCaughey and others (1986). Symbol definitions include ABLA: subalpine fir, and PIAL: whitebark pine, LALY, subalpine larch, PIEN: Engelmann spruce, and PICO: lodgepole pine.

Table 3—Parameters used in the whitebark pine regeneration algorithm and associated references

Symbol	Description and reference	Class	Value
p_w	Probability of cone crop class	Good	0.2175
	Mattson (1986),	Moderate	0.3152
	Weaver and Forcella (1986)	Poor	0.3152
		None	0.1521
CMAX	Maximum number of cones/tree Arno and Hoff (1989), Mattes (1984)		80.0000
rCONFAC	Reduction factor for cone crop class	Good	– 1.0000
		Moderate	– 0.6700
		Poor	– 0.3300
		None	– 0.0000

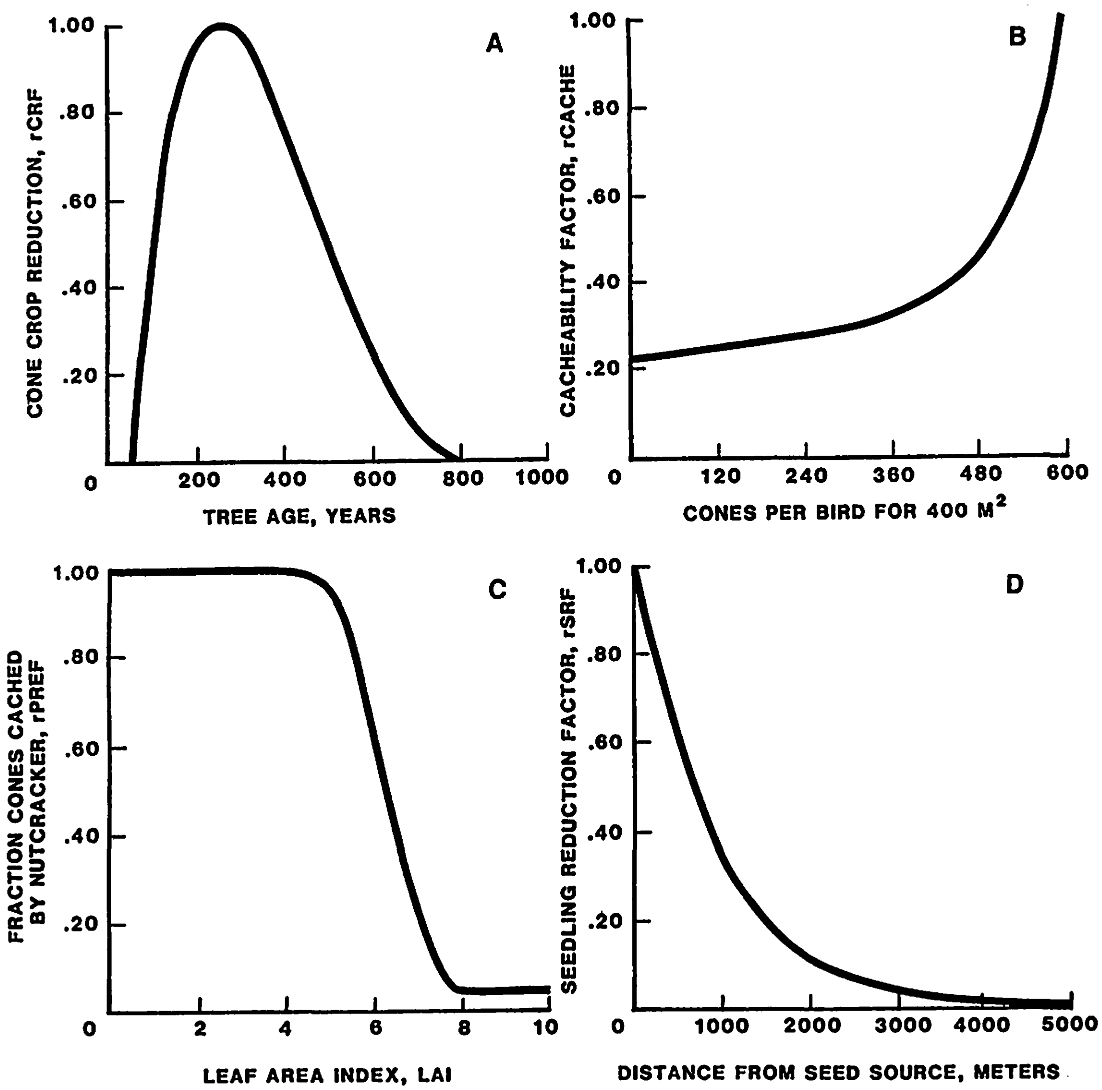


Figure 3—Reduction factors used for modeling whitebark pine regeneration with respect to whitebark pine seed dispersal by nutcrackers. Factor rCRF is the cone reduction factor (A), rCACHE is the caching frequency reduction factor (B), rPREF is the site preference reduction factor (C), and rSRF is the seedling reduction factor for distance from seed source (D).

summing the cones per tree across all cone-bearing trees on the plot. A cone-bearing tree is a tree at least 60 years of age or 20 cm d.b.h. (Arno and Hoff 1989). The total number of whitebark pine seeds (NSEED) is computed by multiplying CONES by the number of seeds per cone (SPC), taken to be 68.8 for this study (Weaver and Forcella 1986).

It is assumed all whitebark pine seeds are dispersed by the Clark's nutcracker (Hutchins and Lanner 1982; Tomback 1982) and the number of seeds imported to the site is equal to the number exported. Because the seed import:export ratio may vary across sites, it is assumed site conditions for the simulation plot are similar to surrounding areas. Although a cluster of seedlings can emerge from a nutcracker cache, we considered the mature tree, single or clustered form, to function as a single tree (Linhart and Tomback 1985). The total number of seedlings (TNS) established on the plot is computed from:

$$\mathrm{TNS} = \left[\frac{\mathrm{NSEED} * (1 - \mathrm{PFIND}) * (1 - \mathrm{PCONS})}{\mathrm{SPCAC}}\right] * (\mathrm{rCACHE} * \mathrm{rPREF} * \mathrm{rSRF} * \mathrm{rALs}) \qquad (3)$$

where PFIND is the proportion of seeds reclaimed by the nutcracker during the following winter and spring (assumed as 0.8) (Tomback 1982), PCONS is the proportion of seeds eaten by the nutcracker during caching season (calculated as 0.11 from Tomback 1982), and SPCAC is the average number of seeds per cache (=3.7) (Tomback 1978). The last four terms in the equation are regeneration reduction factors (numbers between 0 and 1).

The reduction factors in the equation above account for the more important factors influencing dispersal and survival of whitebark pine seedlings. Frequency of nutcracker visitation is modeled using rCACHE or cacheability. This function (fig. 3b) is dependent on the number of cones per bird (CPB) calculated by dividing the total cones (CONES) by the number of nutcrackers which is an input to FIRESUM. Factor rPREF models the appeal of the site to nutcrackers and uses leaf area index as the driving variable (fig. 3c). The more shaded a site becomes (high LAI) the less appealing the site is for nutcracker caching (extrapolated from Tomback 1978, 1982). The relationship of distance to seed source and caching intensity is modeled using rSRF. This function (fig. 3d) shows seeds may be carried up to 5,000 m from a seed source (Tomback and others 1989). Lastly, rALs simulates the effect of light conditions on seedling survival as previously presented for all other tree species. Because Clark's nutcrackers consistently cache whitebark pine seed 1-3 cm below duff surface (Tomback 1982), duff depth was assumed to be an unimportant factor affecting whitebark pine regeneration.

The absence of seed trees for a species on the plot presents a special case in FIRESUM. Distances to seed source from simulation plot by species are input into the model. The factor rSRF and the number of seed trees are computed annually for each species. However, the value of rSRF only enters into the seedling equation(s) when all seed trees of that species are eliminated from the simulation plot, because of beetle epidemic or successional replacement, for example. It is assumed in FIRESUM that the seed source of eliminated species composes 5 percent of the total seed crop trees outside the simulation plot (Keane and others, in press a) for all tree species but whitebark. In the absence of whitebark pine seed trees, the number of seeds carried to the site is 10 percent of CMAX times SPC. If all trees are killed on the plot, such as after a crown fire, the composition of the seed source stand is assumed to be identical to the preburn simulation stand.

Mortality Process (Subroutine KILL)

Trees die in FIRESUM from four types of mortality that are modeled as an annual probability of death. The first type is called random or background mortality. This probablity (P_r in table 1) is the chance of death from endemic disturbances, such as windthrow, a tree experiences each year of its life (Keane and others 1989). The second type, stress mortality, results from severe stress over long periods because of limited light, water, or crowding conditions. The probability of stress death (P_s in table 1) is a function of diameter growth increment and is only considered when a tree's annual growth increment becomes less than a threshold value (AINC in table 2). The third type of tree mortality is from fire. When a fire occurs on the simulation plot it kills trees by scorching foliage and killing cambium. Ryan and Reinhardt (1988) developed FIRESUM's empirical fire mortality equation, which uses percentage crown scorched (Van Wagner 1972) and bark thickness as independent variables (P_f in table 1). This equation is used for all tree species.

Insect and disease epidemics account for the last type of mortality. Currently, FIRESUM simulates only mountain pine beetle and white pine blister rust infestations. The year in which the beetle or rust infestation starts is input by the user. Tree mortality after the start of an epidemic is modeled as an annual probability of death. Since the objective of this study was to model the effects of blister rust infestations, the mountain pine beetle algorithm will not be discussed.

Once a blister rust epidemic begins, each whitebark pine has a probability of infection assumed as 0.60 (Keane and others, unpublished data). If a tree becomes infected, the probability of death from blister rust (P_i) is computed annually using the equation:

$$P_i = e^{-0.15 * \mathrm{DBH}} \qquad (4)$$

where DBH is the tree diameter (cm). A tree remains infected all its life and, once infected, its cone crop is reduced by 90 percent. Whitebark pine's resistance to blister rust is modeled as a probability of resistance (= 0.05 based on consultation with Ray Hoff [Hoff 1987]). Each established tree is determined to be either resistant or nonresistant based on Monte Carlo techniques using the probability of resistance. Blister rust kills only whitebark pine for all simulations.

Fuel and Fire Processes (Subroutines FUEL and FIRE)

Six dead and two live fuel components are modeled in FIRESUM: four dead downed woody (litter, 1 -, 10 -, and 100-hour timelag), dead shrubby, dead herbaceous, live shrub, and live herbaceous. Loadings for these components are computed annually and used to determine fire intensity (Keane and others 1989). Litter and duff loadings are dynamically modeled in FUEL using compartments (Keane and others 1989; Kercher and Axelrod 1984).

Fires are simulated in FIRESUM by computing fire intensity, flame length, and scorch height from fuel loadings and weather conditions using the FIREMOD subroutine developed by Albini (1976). FIREMOD uses Rothermel's (1972) model to compute the fire behavior characteristics. Fire occurrence is input by the user for a specific year, selected intervals, or stochastic intervals. After a fire occurs, duff, litter, and woody fuel loadings are reduced in subroutine BRNOFF using regression equations from Brown and others (1985). Fire weather conditions and fuel moistures are also inputs to the model. The values used in this study were taken from data measured for a hot day in August after a 2-week dry period. These are the conditions under which most fires occur in whitebark pine forests.

Table 4—Site descriptions of the two stands used in the testing and evaluation of FIRESUM

Site location	Elevation	Aspect class	Slope	Disturbed age	Rust infest.	Beetle kill
	Meters		*Percent*	*Year*		
One Horse Ridge (PIAL h.t.)	2,634	Southwest	21	96	Little	Yes
One Horse Ridge (ABLA h.t.)	2,329	Northeast	70	99	Little	No

METHODS

Field Data Collection

Site, vegetation, and climate data were collected at two whitebark pine sites on One Horse Ridge in the Bitterroot Mountains southwest of Missoula, MT (table 4). The ridgetop site is a whitebark pine habitat type (PIAL h.t.) in which whitebark pine is the indicated climax species as described by Pfister and others (1977). This site has a southern aspect and is substantially drier than the north-slope site, which is a subalpine fir habitat type (ABLA h.t.) in which whitebark pine is a major seral tree species. The ABLA h.t. site represents intermediate moisture conditions for a whitebark pine site.

Field data were obtained by sampling methodologies discussed in detail in Keane and others (in press a, b). In summary, at each site, vegetation and environmental data were gathered for both a mature stand and an adjacent young stand that had arisen after a stand-replacement wildfire in the late 1800's (young stands were 99 years old). Sample plots were 400 m^2 and located in representative portions of the stands. The following variables were measured for each stand: stand age, tree density and diameters, aspect, slope, elevation, and fuel loadings. Weather data for these sites were extrapolated from historical weather data from similar whitebark pine sites (Arno 1970) and modified using the climate model MTCLIM (Hungerford and others 1989).

Simulation Framework

The model FIRESUM was used to investigate the effects of fire and blister rust on seral and climax whitebark pine sites using nearby and distant seed sources. First FIRESUM was calibrated using data collected by Keane and others (in press b) in climax and seral whitebark pine stands. Then sample data from the mature stands on both One Horse Ridge sites were used as inputs to the model to create initial simulation stands. Sampled site and climate data were also model inputs. Then, the following natural and management scenarios were simulated for both sites:

1. No fires—complete fire suppression.
2. Crown fire at year 150—a stand-removing wildfire is initiated at simulation year 150.
3. Blister rust infection at year 150—a blister rust epidemic is initiated at simulation year 150 with no fires throughout the simulation period.
4. Blister rust infection at year 100, crown fire at year 150.

The crown fire scenario was conducted for two conditions: nearby and distant seeds sources. The distant seed sources were input as 3,000 m from the simulation plot. This attempts to replicate the differences between small and large burns. Results of each scenario and seed source distance effects were compared.

Model Verification

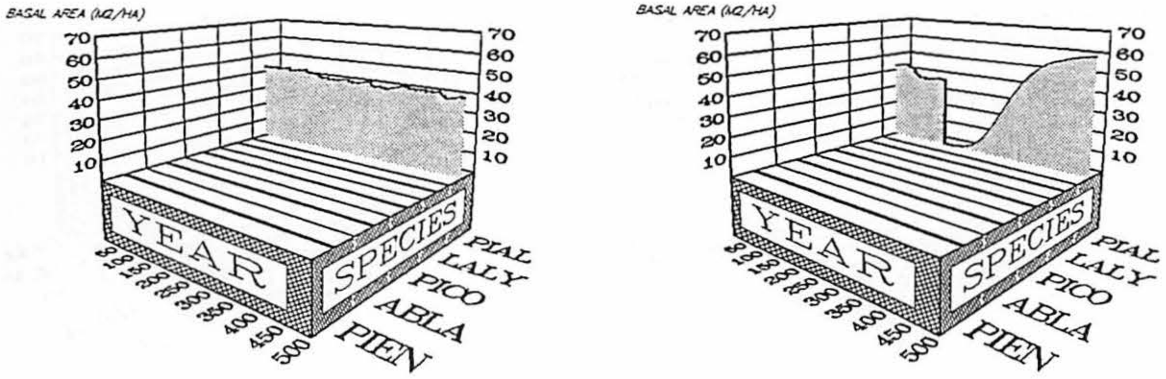
The mature stand data from the two sample sites were used as inputs to FIRESUM. Subsequent predictions at simulation year 99 were then compared with data collected in the young stands (age 99) at each site (Keane and others, in press a). The variables compared were basal area by tree species and fuel loadings.

RESULTS AND DISCUSSION

Simulations compare consequences of four natural and management scenarios for the One Horse Ridge PIAL h.t. and ABLA h.t. sites (figs. 4 and 5, respectively). These results show successional trends for a close or nearby seed source (small burn) for all tree species. Simulation results for distant seed sources (large burn) after crown fires on the two sites are also presented (fig. 6). A detailed technical discussion of FIRESUM performance is provided by Keane and others (1989).

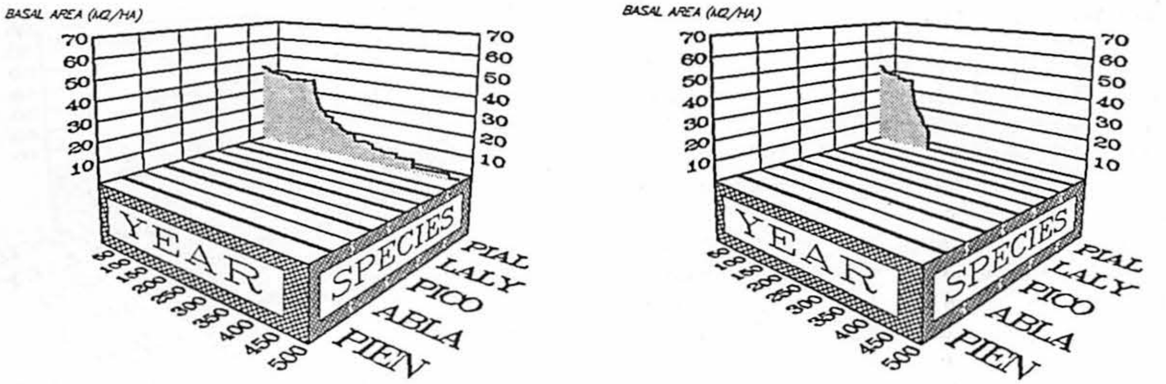
Model Results

Fires simulated in FIRESUM were crown fires that killed and consumed all trees on the simulation plot. Actual or "real world" fires moving through these plots would often be of low to moderate intensity (flame lengths of 0.5-1.5 m or 1-3 ft, 1- to 4-m scorch heights) because of the sparse fuel loadings. Simulated surface fires ranged from 250 to 300 kW/m fireline (1.9- to 3.88-m scorch heights) on the ABLA h.t. site and 180 to 250 kW/m fireline (1.1- to 2.3-m scorch heights) on the PIAL h.t. site. These fires were not capable of igniting the crown and destroying all trees on the simulation plot. Therefore, it was assumed the crown fire did not originate on the simulation plot but was carried there from other stands.



(a) NO FIRE SCENARIO

(b) CROWN FIRE YEAR 150



(c) BLISTER RUST YEAR 150

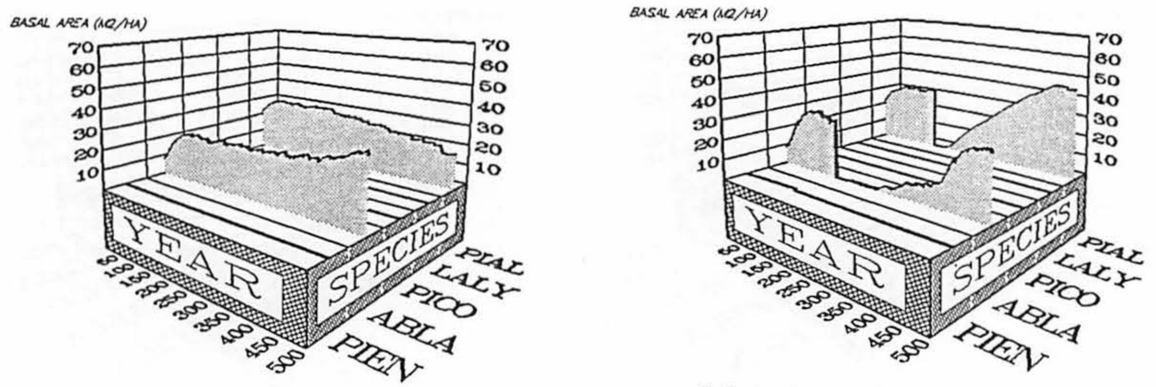
(d) BLISTER RUST 100 – CROWN FIRE 150

Figure 4—Basal area predictions for tree species on the One Horse Ridge PIAL h.t. Four scenarios are shown: (a) no fires (fire suppression), (b) crown fire at year 150, (c) blister rust epidemic at year 150, (d) blister rust at year 100 and crown fire at year 150. Symbol definitions include ABLA: subalpine fir, and PIAL: whitebark pine, LALY, subalpine larch, PIEN: Engelmann spruce, and PICO: lodgepole pine.

Simulated woody fuel loadings were much greater on the ABLA h.t. site (0.29 to 0.39 kg/m^2) compared with those on the PIAL h.t. site (0.19 to 0.23 kg/m^2). Predicted duff depths and fuel loadings varied greatly by scenario. Simulated leaf areas averaged around 1.5 to 2.6 m^2/m^2 for the PIAL h.t. site and 3.0 to 6.9 m^2/m^2 for the ABLA h.t. site.

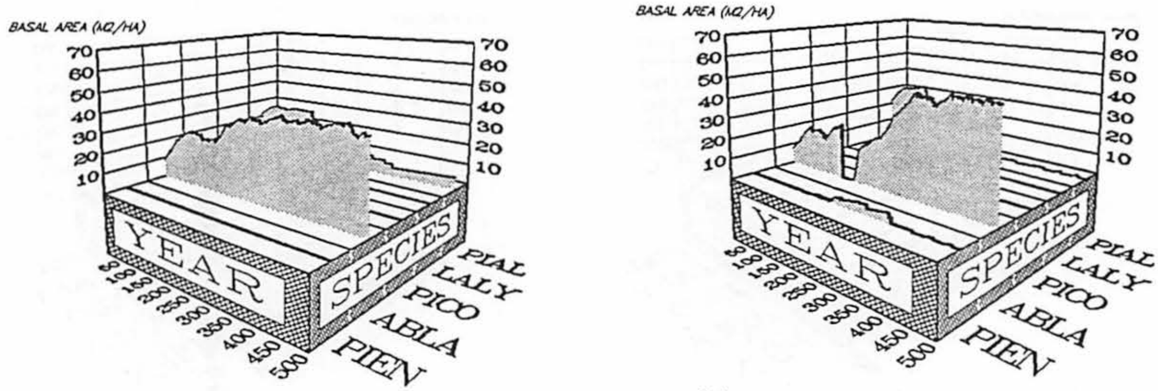
No Fire Scenario—Results from the fire suppression scenario differ between the two whitebark pine sites (figs. 4a and 5a). With the exclusion of fire, whitebark pine (PIAL) remains the dominant species on the PIAL h.t. site. On the ABLA h.t. site, PIAL is replaced successionally by the more shade-tolerant subalpine fir (ABLA). There is also a corresponding decline in whitebark pine cone production on the ABLA h.t. site (table 5). Maximum fuel loadings for these stands tended to be similar (0.216 kg/m^2 for PIAL h.t. and 0.362 kg/m^2 for ABLA h.t.) indicating a potential for high severity wildfires after many decades of fire suppression. In the model simulation, the moist ABLA h.t. site was able to support small quantities of Engelmann spruce (PIEN) and lodgepole pine (PICO), although this is not evident in the graph (fig. 5b) because of the small basal area values. The composition and basal area of PIAL for the PIAL h.t. site (fig. 4a) correspond with those observed by Pfister and others (1977) for the whitebark pine (PIAL) habitat type. Average duff depth was much greater for the ABLA h.t. site (3.2 to 5.4 cm) when compared with the PIAL h.t. site (0.8 to 2.2). This is mainly due to the smaller leaf areas on the PIAL h.t. site indicating a smaller amount of needlefall.

Crown Fire Scenario—Successional trends after crown fires are somewhat similar between sites (figs. 4b and 5b). On the PIAL h.t. site, whitebark pine became well established within 25-40 years after fire and this species reached preburn basal areas after 150 years of simulation. On the ABLA h.t. site, whitebark pine became established after 25-35 years but attained prefire basal area much quicker (70-80 years). The shade tolerant ABLA was eliminated from the ABLA h.t. site by crown fire and did not become a significant component in the stand until a century after the fire (fig. 5b). On the ABLA h.t. site, even though a crown fire occurred at year 150, the average number of cones per year for all 500



(a) NO FIRE SCENARIO

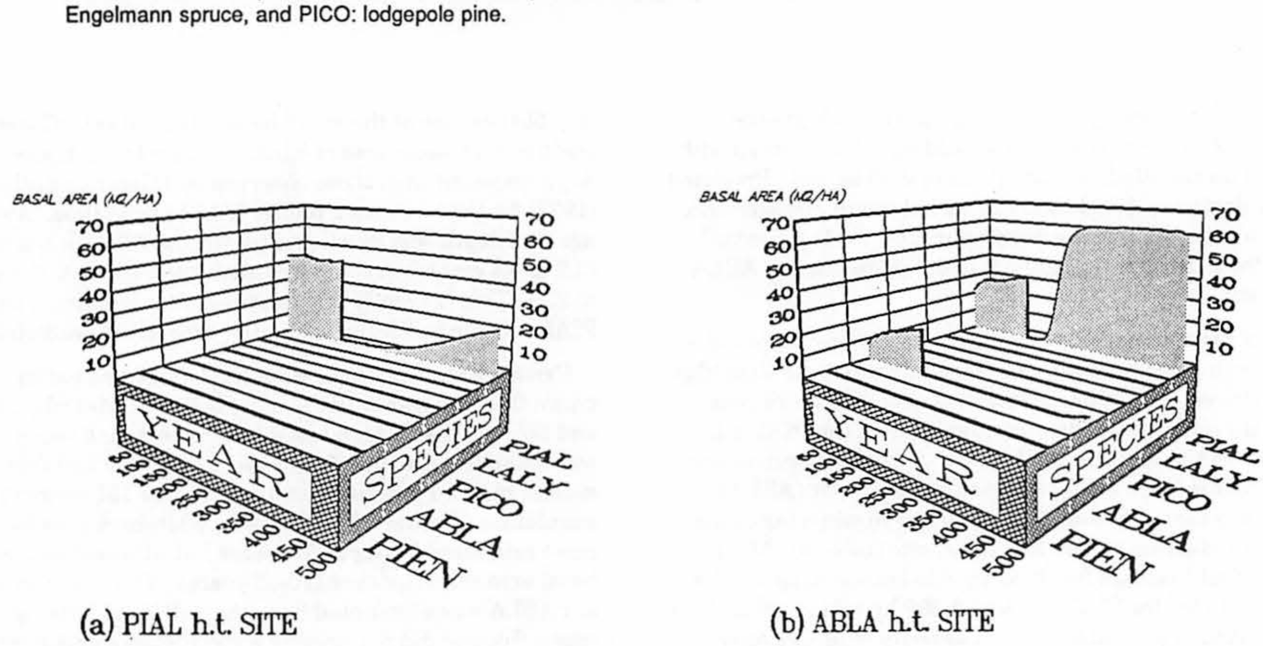
(b) CROWN FIRE YEAR 150



(c) BLISTER RUST YEAR 150

(d) BLISTER RUST 100 – CROWN FIRE 150

Figure 5—Basal area predictions for tree species on the One Horse Ridge ABLA h.t. site where whitebark pine is the major seral tree species. Four scenarios are shown: (a) no fires (fire suppression), (b) crown fire at year 150, (c) blister rust epidemic at year 150, (d) blister rust at year 100 and crown fire at year 150. Symbol definitions include ABLA: subalpine fir, and PIAL: whitebark pine, LALY, subalpine larch, PIEN: Engelmann spruce, and PICO: lodgepole pine.



(a) PIAL h.t. SITE

(b) ABLA h.t. SITE

Figure 6—Basal area predictions for tree species on the One Horse Ridge PIAL h.t. and ABLA h.t. sites when the seed source after fire is 3,000 m from the simulation plot. Two scenarios are shown: (a) PIAL h.t. site-crown fire year 150, (b) ABLA h.t. site-crown fire year 150. Symbol definitions include ABLA: subalpine fir, and PIAL: whitebark pine, LALY, subalpine larch, PIEN: Engelmann spruce, and PICO: lodgepole pine.

Table 5—Average number of whitebark pine cones produced each year on the simulation plot for the 500-year simulation period

Scenario	Average cones/year	
	PIAL h.t. site	ABLA h.t. site
1 - No fires (fire suppression)	166	102
2 - Crown fire year 150	134	219
3 - Blister rust year 150	109	55
4 - Blister rust year 100-Crown fire year 150	44	42

years of this scenario was greater than all years in the no fire scenario (table 5).

Duff depths (1.9 to 3.5 cm) and fuel loadings (0.201 to 3.120 kg/m^2) for the ABLA h.t. site were much less than those predicted for the no fire scenario. This is a result of the decrease in ABLA and the corresponding increase in PIAL. PIAL tends to cast less foliage and dead branches than ABLA, probably because of its smaller leaf area. The decrease in leaf area (2.2 to 4.3 m^2/m^2) was also evident in the simulation results for the ABLA h.t. site when compared to the no fire scenario.

Blister Rust Scenario—Blister rust infections resulted in severe reductions of whitebark pine over long periods (greater than 500 years) for both sites (figs. 4c and 5c). Whitebark pine decreased throughout the simulation and is expected to be absent from the PIAL h.t. site by simulation year 750 (fig. 4c). The long, gradual decline of whitebark pine is the consequence of the great longevity of the species. On the ABLA h.t. site, subalpine fir replaced whitebark pine as the dominant tree species (fig. 5c). On both sites, the whitebark pine cone crop declined markedly as a result of the blister rust (table 5).

Duff depths and fuel loadings decreased on the PIAL h.t. site (0.5 to 0.9 cm and 0.14 to 2.1 kg/m^2) and increased on the ABLA h.t. site (4.7 to 5.9 cm and 0.29 to 0.40 kg/m^2) when this scenario is compared with the no fire and crown fire scenarios. This is because of the decline of PIAL on PIAL h.t. site and increase in ABLA on the ABLA h.t. site.

Blister Rust-Crown Fire Scenario—This scenario illustrates the probable effects of crown fires in the blister-rust-infected whitebark pine stands common in Washington, northern Idaho, and northwestern Montana. Whitebark pine trees are unable to regenerate on the PIAL h.t. site due to the blister rust (fig. 4d). Consequently, trees never become established on the site and it is converted to high-elevation grassland or alpine tundra. Blister rust also prevented whitebark pine regeneration on the ABLA h.t. site (fig. 5d), but subalpine fir (ABLA) was able to regenerate, grow, and become the dominant tree species.

Distance to Seed Sources—The distance from seed source to simulation plot dictates the composition of whitebark pine sites (fig. 6). Comparing nearby (fig. 4b) and distant (fig. 6a) seed sources for the PIAL h.t. site reveals that the recovery time after fire is much greater when the seed source is distant. Whitebark pine on the ABLA h.t. site (fig. 6b) is the only species able to become established and grow when the seed sources are 3 km away. This is a result of the great distance Clark's nutcrackers will fly to cache whitebark pine seed (see fig. 2). Only nearby seed sources (fig. 5b) provide for the prompt establishment of subalpine fir.

Verification Results

Test results show FIRESUM predictions seem to be comparable to conditions measured at the disturbance stands (table 6) after 99 years of simulation. Predicted whitebark pine basal area for the PIAL h.t. and ABLA h.t. sites is within 10 percent and 27 percent of the

Table 6—Verification results of the model FIRESUM for two whitebark pine sites[1]

Variable	PIAL h.t.		ABLA h.t.	
	Observed	Predicted	Observed	Predicted
Whitebark pine basal area	16.80	15.10	7.40	10.20
Subalpine fir basal area	0.10	0.00	0.40	1.20
1-hour time-lag fuel loading	0.08	0.06	0.06	0.11
10-hour time-lag fuel loading	0.08	0.06	0.06	0.11
100-hour time-lag fuel loading	0.30	0.25	0.21	0.93
Duff depth	1.75	1.43	1.10	1.50

[1] Units for basal area values are in meters squared per hectare, fuel loadings are in kilograms per meter squared, and duff depths are centimeters.

observed values, respectively (table 6). However, the observed and predicted fuel loadings differ; this could be a result of inaccurate decomposition parameters and calibration data. FIRESUM seems to overpredict basal areas for all tree species. This is probably because of the inadequacy of FIRESUM to model the harshness of the microenvironment for tree establishment and growth in these high-elevation stands.

CONCLUSIONS

FIRESUM modeling results indicate that the combined effects of fire suppression and blister rust infections could severely reduce whitebark pine populations (figs. 4 and 5) and their cone crops (table 5). This may affect population levels of red squirrels, Clark's nutcrackers, bears, and perhaps other animals inhabiting or utilizing high-elevation forests. White pine blister rust reduces and may eventually eliminate whitebark pine cone crops as a significant food source in some areas (table 5 and figs. 4c and 5c).

The ability of whitebark pine to colonize large burns is much greater than that of subalpine fir due to seed dispersal by nutcrackers (fig. 6).

Possible methods of increasing whitebark pine populations and cone crop levels may be inferred from these simulation results. Allowing crown fires to occur on sites where whitebark pine is a seral species may increase whitebark pine populations. In areas where blister rust mortality is prevalent, planting rust-resistant whitebark pine might help perpetuate this species in sufficient amounts to provide a continued food source for wildlife.

These FIRESUM results are only a first approximation of modeling for whitebark pine forests. Although forecasts seem to agree with data collected from field studies (Arno 1986; Pfister and others 1977), we plan to continue testing the model against actual stands and refine our characterizations of whitebark pine forest succession. Many parameters and equations in FIRESUM have not yet been accurately quantified for high-elevation ecosystems. In addition, we wish to identify and characterize any important ecological processes in the high-elevation forests that are not presently simulated in FIRESUM, such as the quality and quantity of sunlight.

ACKNOWLEDGMENTS

We would like to thank the following who helped develop the whitebark pine version of FIRESUM: Ken Gibson and Sue Hagle of the Northern Region, Forest Service, and Ward McCaughey, Wyman Schmidt, Raymond Hoff, Sally Hejl, and Gene Amman of the Intermountain Research Station, Forest Service; Penny Morgan and Steve Bunting, University of Idaho, Moscow; Hans Zuuring and Brian Steele, University of Montana, Missoula.

REFERENCES

Albini, Frank A. 1976. Computer-based models of wildland fire behavior: a user's manual. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 45 p.

Arno, Stephen F. 1970. Ecology of alpine larch (*Larix lyallii*) in the Pacific Northwest. Missoula: University of Montana. 264 p. Dissertation.

Arno, Stephen F. 1986. Whitebark pine cone crops: a diminishing source of wildlife food? Western Journal of Applied Forestry. 1(3): 92-94.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Botkin, C. W.; Shires, L. B. 1948. The composition and value of pinon nuts. New Mexico Experimental Station Bull. 344: 3-14.

Botkin, D. B.; Janak, J. F.; Wallis, J. R. 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology. 60: 849-872.

Boyce, R. B. 1985. Conifer germination and seedling establishment on burned and unburned seedbeds. Moscow: University of Idaho. 71 p. Thesis.

Brown, James K. 1970. Ratios of surface area to volume for common fire fuels. Forest Science. 16: 101-105.

Brown, James K. 1976. Predicting crown weights for eleven Rocky Mountain conifers. Oslo Biomass Studies, June 1976. IUFRO Congress. 9 p.

Brown, James K. 1978. Weight and density of crowns of Rocky Mountain conifers. Res. Pap. INT-197. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 56 p.

Brown, James K.; Marsden, Michael A.; Ryan, Kevin C.; Reinhardt, Elizabeth D. 1985. Predicting duff and woody fuel consumed by prescribed fire in the northern Rocky Mountains. Res. Pap. INT-337. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 23 p.

Day, R. J. 1967. Whitebark pine in the Rocky Mountains of Alberta. Forestry Chronicle. 43(3): 278-283.

Eggers, D. E. 1986. Management of whitebark pine as potential grizzly bear habitat. In: Proceedings, grizzly bear habitat symposium: 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Experiment Station: 170-175.

Forcella, F.; Weaver, T. 1977. Biomass and productivity of the subalpine *Pinus albicaulis-Vaccinium scoparium* association in Montana, U.S.A. Vegetatio. 35: 95-105.

Hoff, Ray. 1987. [Personal communication]. November 8. Moscow, ID: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Hungerford, Roger D.; Nemani R. R.; Running, Stephen W. 1989. MTCLIM: a mountain microclimate simulation model. Res. Pap. INT-414. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 53 p.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.

Kaufmann, M. R.; Edminster, C. B.; Troendle, C. A. 1982. Leaf area determinations for subalpine tree species in the central Rocky Mountains. Res. Pap. RM-238. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 7 p.

Keane, Robert E.; Arno, Stephen F.; Brown, James K. 1989. Documentation of the ecological process model FIRESUM—a fire succession model for western conifer forests. Gen. Tech. Rep. INT-266. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 76 p.

Keane, Robert E.; Arno, Stephen F.; Brown, James K. [In press a.] Modeling cumulative fire effects in ponderosa pine/Douglas fir forests. Submitted to Ecology.

Keane, Robert E.; Arno, Stephen F.; Brown, James K.; Tomback, Diana F. [In press b.] Modeling stand dynamics in whitebark pine forests. Submitted to Ecological Modeling.

Keane, Robert E.; Arno, Stephen F.; Brown, James K.; Tomback, Diana F. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Missoula, MT.

Kendall, K. C. 1980. Bear-squirrel-pine nut interaction. In: Yellowstone grizzly bear investigations. Annual Report 1978-1979. Bozeman, MT: U.S. Department of the Interior, National Park Service: 51-60.

Ker, J. W.; Smith, J. H. G. 1955. Advantages of parabolic expression of the height-diameter relationship. Forestry Chronicle. 31: 235-246.

Kercher, J. R.; Axelrod, M. C. 1984. A process model of fire ecology and succession in a mixed-conifer forest. Ecology. 65(6): 1725-1742.

Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research. 12: 391-402.

Linhart, Y. B.; Tomback, D. F. 1985. Seed dispersal by nutcrackers causes multi trunk growth form in pines. Oecologia. 67: 107-110.

Lopushinsky, W. 1970. Relationship of needle surface area to needle volume in ponderosa pine and lodgepole pine. Res. Note PNW-126. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 4 p.

Mattes, H. 1984. The role of animals in Cembra pine forest regeneration. In: Turner, H.; Tranquillini W. eds. Proceedings, Third IUFRO workshop, establishment and tending of subalpine forest: research and management. 270: 197-205.

Mattson, D. J. 1987. Habitat dynamics and their relationship to biological parameters of the Yellowstone grizzly bear, 1977-83. Progress report. Bozeman, MT: Interagency Grizzly Bear Study Team. 28 p.

Mattson, D. J.; Reinhart, D. P. 1986. Grizzly bear, red squirrels, and whitebark pine: second year progress report. Bozemzn, MT: Report submitted to Interagency Grizzly Bear Study Team. 38 p.

McCaughey, Ward W.; Schmidt, Wyman C.; Shearer, Raymond C. 1986. Seed dispersal characteristics of conifers of the Inland Mountain West. In: Shearer, Raymond C., compiler. Proceedings—conifer tree seed in the Inland Mountain West symposium; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 50-61.

Mealey, S. 1975. The natural food habits of free ranging grizzly bears in Yellowstone National Park 1973-1974. Bozeman, MT: Montana State University. Thesis.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species: a literature review. Gen. Tech. Rep. PNW-87. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 48 p.

Pfister, Robert D.; Kovalchik, B.; Arno, Stephen F.; Presby, R. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Reed, K. L.; Clark, S. G. 1979. SUCcession SIMulator: a coniferous forest simulator. Model documentation. Bull. No. 11. Seattle: University of Washington, Coniferous Biome Ecosystem Analysis. 96 p.

Rothermal, Richard C. 1972. A mathematical model for predicting fire spread in wildland fuels. Res. Pap. INT-115. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 40 p.

Ryan, Kevin C.; Reinhardt, Elizabeth D. 1988. Predicting postfire mortality of seven western conifers. Canadian Journal of Forest Research. 18: 1291-1297.

Schopmeyer, C. S. 1974. Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture, Forest Service. 884 p.

Shugart, H. H.; West, D. C. 1980. Forest succession models. Bioscience. 30(5): 308-313.

Smith, C. C.; Follmer, D. 1972. Food preferences of squirrels. Ecology. 53: 82-91.

Thornthwaite, C. W.; Mather, J. R. 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Drexel Institute of Technology Publications in Climatology. 10: 180-311.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird. 16: 123-161.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51: 451-467.

Tomback, D. F.; Hoffmann, L. A.; Sund, S. K. 1989. Seed dispersal in whitebark pine. Submitted to Ecology.

Van Wagner, C. E. 1972. Height of crown scorch in forest fires. Canadian Journal of Forest Research. 3: 373-378.

Weaver, T.; Forcella, F. 1986. Cone production in *Pinus albicaulis* forests. In: Shearer, Raymond C., compiler. Proceedings—conifer tree seed in the Inland Mountain West symposium; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 68-76.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Jerry Covault)—Your model says a stand-replacement fire (one less than 3,000 m from seed source) would have PIAL come back. Katherine Kendall pointed out that this situation in the Great Burn did not result in the reestablishment of PIAL. Is the model wrong?
A.—No. The Great Burn was an extremely intense fire burning many acres of forest and leaving large continuous landscapes devoid of trees. History tells us that during the period after the burn, many sheep were brought to the area by rail and were grazed extensively throughout the burn. The sheep could have prevented or delayed whitebark pine establishment. The blister rust may have also had an effect on the species establishment. If we knew all factors involved I think we could model the results of the Great Burn fire and get relatively accurate results.

Q. (from Dave Mattson)—Where did you get cone production figures for PIAL and ABLA habitat types?
A.—Cone production figures were computed from data that you collected from your sample stands in the Yellowstone area. Checks of your figures were taken from work by Weaver and Forcella (1986) and Arno and Hoff (1989).

Q. (from Don Despain)—Does your model account for seeds already on the site, those that don't need to disperse in?
A.—Yes. The model puts seed on the simulation plot before the first simulation year.

Q. (from Dick Baker)—For your high elevation (PIAL h.t.) in the blister rust-crown fire scenario I was surprised to see that the site converted to a grassland. What happened to the nutcracker dispersal capability for 350 yrs?
A.—Nutcrackers still cached seeds on the simulation plot, but due to adverse site conditions and the blister rust, the seedlings were unable to grow to maturity.

Q. (from Ray Hoff)—What happens when you add some resistance to blister rust for whitebark pine in your model?
A.—I did model 5 percent resistance in the whitebark pine (each tree established had a 5 percent chance of being resistant to the blister rust) and found that the severity of the site and nutcracker dispersal did not allow any of the resistant trees to grow to maturity.

Q. (from Anonymous)—Why didn't you model mountain pine beetle in your model?
A.—We did, but presented the results in another paper that was submitted for publication in the journal "Ecological Modelling." The paper was titled: "Modeling Stand Dynamics in Whitebark Pine Forests".

SESSION 4

Management Implications

Wendel Hann and Kathy Hansen-Bristow
Session Coordinators

Papers in this section examine the ecological background of the various resources of high-mountain ecosystems and their implications for management. Included are wildlife, livestock, fisheries, hydrology, recreation, and timber resources and how these interact with changes in biological diversity, fire behavior, and silvicultural practices. There is little experience in active management of whitebark pine ecosystems, so the management implications presented here are essentially charting new ground.

WILDLIFE RESOURCES AND HABITAT MANAGEMENT OBJECTIVES IN THE WHITEBARK PINE ECOSYSTEM

Dan Tyers

ABSTRACT

Several principles become apparent in managing for the wildlife resource in the whitebark pine (Pinus albicaulis) *ecosystem. First, much of the value placed upon this ecosystem is transferred to it because of its value to the grizzly bear—a high-profile species due to its listed status. Second, if management of the wildlife resource in the whitebark pine ecosystem is to be successful it must be integrated and carefully coordinated with other legitimate resources such as timber, recreation, and range. Third, for wildlife, this ecosystem cannot be managed as an island. It must be managed with sensitivity to the total habitat requirements of wildlife that use it.*

Grizzly bear, bighorn sheep, and moose management options are discussed as examples of programs that apply to these three principles.

It falls to wildlife biologists to develop management programs that express the importance of this ecosystem. In general, our understanding of the actual habitat requirements of wildlife as they relate to the whitebark ecosystem is often no more specific than an awareness that the area deserves special management consideration. Attempting to clarify and quantify the habitat requirements of each wildlife species in the whitebark ecosystem is a continuing effort. The level that we generally operate at usually results in setting the objective of simply preserving the integrity of the area.

INTRODUCTION

It seems to be generally recognized that our understanding of the habitat requirements of wildlife in the subalpine and timberline forests of the West is less well developed than it is for lower elevation forests (Arno and Hoff 1989; Raphael 1987; Thomas 1987). This would include forests where whitebark pine (*Pinus albicaulis*) is found. It has been suggested that this paucity of information is the result of a comparative lack of accessible and available resources in this ecosystem. Available resources generate management and research attention, which generates information. As resources become more finite and the demand for them expands even into the comparatively remote whitebark pine ecosystem, interest in these areas is being generated. Wildlife managers and biologists are left playing a catchup game to keep pace with the demand for information this interest has created.

Studies have shown that subalpine and timberline forests support low numbers of nongame species and low population sizes compared with other habitat types in the Rocky Mountains and in contrast with other coniferous forest systems in North America (Raphael 1987). This, however, belies the importance of the whitebark pine ecosystem. If the cumulative values from watershed, recreation, range, species diversity, and habitat for non- game and big game species could be assessed in a compounding fashion, then the value of the whitebark ecosystem is better represented (Hann 1987). This ecosystem particularly gains in importance in management priorities when some of the value of one of the animals that uses it, the federally listed grizzly bear (*Ursus arctos*), is transferred to it.

The value of the whitebark pine ecosystem to wildlife, in terms of what specific site and stand conditions optimize its value for a given species, is often not well quantified. As a result, wildlife management programs specific to whitebark are generally not very sophisticated. A generic response of simply attempting to protect whitebark forests for the wildlife resource is typical and often sufficient. It serves as a good "umbrella" management objective. The lack of specific information and the fragile nature of subalpine forests makes caution in management an appropriate response. Shallow, poorly developed soils with low fertility, severe climates, and a short growing season make them more vulnerable to the mistakes of managers (Arno and Hoff 1989; Thomas 1987).

However, more specific information is often needed to assist managers in developing programs for managing whitebark for wildlife. As better information becomes available it can be integrated into three basic principles.

MANAGEMENT PRINCIPLES

First, even though the boundaries of the whitebark pine ecosystem and grizzly bear distribution do not directly overlap, the national priority given to the grizzly gives it a driving force in the broad topic of wildlife management in whitebark pine areas. Second, a great deal can be accomplished for the wildlife resource if management objectives for this resource are carefully integrated with the management objectives of other resources. Although not the ideal situation, this can be done using basic concepts of wildlife management without the precise knowledge of the optimum site and stand characteristics for each species. Third, in general, the whitebark pine ecosystem represents only seasonally valuable range for wildlife. With this in mind, the whitebark pine ecosystem cannot be managed as an island for any species. In attempting to establish management objectives for a species that uses the whitebark pine ecosystem, all seasonally important ranges need to be considered.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Dan Tyers is District Wildlife Biologist, USDA Forest Service, Gallatin National Forest, Gardiner Ranger District, Gardiner, MT 59030.

For the practical application of these three principles, three species that use the whitebark pine ecosystem will be discussed: the grizzly bear, the Rocky Mountain bighorn (*Ovis canadensis*) sheep, and the Shiras moose (*Alces alces shirasi*). Our understanding of the specific habitat requirements of these (and other species) in the whitebark pine ecosystem is at different levels. When specific requirements are determined, they can be integrated into the three principles mentioned.

Grizzly Bears

The importance of whitebark to grizzlies is well documented (Kendall 1981; Mealy 1975). The unique relationship between whitebark, grizzlies, and red squirrels (*Tamiasciuius hudsonicus*) has also been documented (Kendall 1981; Mattson and Reinhart 1987). Mattson and Reinhart (1986) have taken our level of understanding further to describe the relationships between density and the probability of red squirrel midden use by grizzly bears, site and stand characteristics, and trends in squirrel activity and population levels. An understanding of these relationships is being fine tuned (Mattson 1989).

This information has provided us with a clearer understanding of what areas with whitebark specifically are important to grizzlies and why. In a management sense, this could conceivably assist in determining the location, timing, and appropriateness of vegetation manipulation—either timber harvest or prescribed burning. Reforestation through planting whitebark, as an additional option for vegetation manipulation to benefit grizzlies, can also be considered (McCaughey 1988).

Although this information is very useful by itself, it also has applicability in integrating recreation management with wildlife management. Mattson and Reinhart (1986) observed that the availability of nuts greatly influences numbers of grizzly/human conflicts and resulting management actions. Management actions were observed to be fewer during years of good nut production and higher when nut production was poorer. They stated that, in general, low pine nut production is positively correlated with high mortality rates for grizzly bears. It was their opinion that when nut production is assessed during July, the potential intensity of grizzly/human conflicts can be predicted. With an awareness of the location of the most productive areas for grizzly bears for foraging on whitebark pine nuts, managers can adjust recreation use patterns. With an awareness of the annual success of whitebark pine nut crops, managers can brace for trouble with increased patrols, tighter travel restrictions, or more public education. In this context, the whitebark pine resource suddenly becomes a very relevant topic at the field level of management.

Certainly, a management objective for meeting the habitat needs of the grizzly in the whitebark ecosystem would be to maintain or create site and stand conditions that optimize the area for the bear. However, there is another management objective that is overriding in its immediacy and in its demand for attention. It tends to permeate all management activities for all resources in grizzly country. Because of the grizzly's listed status and its propensity for conflict with humans, a wildlife management objective for the whitebark pine ecosystem (and any other area where the bear is present) is zero preventable grizzly bear mortalities. Time and dollars are invested in making attractants unavailable to bears, preventing bears from making the association between people and food, and avoiding conflicts between people and bears—all variations on the same theme of trying to keep the grizzly from an untimely death (USDA FS 1986). Accomplishing this is in one sense optimizing the habitat for the bear, although it does not meet the usual sense of the definition of habitat enhancement. The listed status of the bear and the value of the whitebark pine ecosystem to the bear make this an important management objective.

Bighorn Sheep

Bighorn sheep summer in and adjacent to timberline forests. They often migrate to and from winter ranges through these same forests and through subalpine forests as well. Wakelyn and Bailey (1983) summarized key habitat factors of bighorn sheep range. They included: (1) abundant, continuous forage to support a large dispersed group, (2) nearby escape terrain, and (3) good visibility. In habitats that afford good visibility, predator detection is increased allowing individuals to disperse further from escape terrain and more effectively use the forage resource. In addition, in habitats with good visibility sheep tend to form larger groups. In larger groups individuals spend less time alert and may forage more continuously under the comparative safety of the collective alertness of the whole group. Forest succession may degrade bighorn habitat by reducing the quantity and quality of available forage and by reducing visibility.

Bighorn seasonal ranges are connected by traditionally used migration corridors. These corridors are predictably adjacent to the best escape terrain. This is often along rocky ridges where whitebark is present. Good visibility along migration routes is equally important and can also be degraded by forest and shrub succession. Wakelyn and Bailey (1983) concluded that sedentary populations either lacking in additional seasonal ranges or suitable migration corridors have "bleak futures" as they are more susceptible to disease and predation.

Whitebark forests in advanced successional stages where visibility is poor and forage more limited due to the proliferation of other conifer species have progressed past the point of providing optimum habitat for bighorn sheep. Early successional stage timberline and subalpine forests are of more value to sheep. The influence of fire and its alteration of these forest types favor sheep. Gruell (1983) concurred that sheep, as a grass- and forb-eating herbivore without strong requirements for abundant cover, are favorably influenced by the results of fire. Therefore, a management objective for bighorn sheep in the whitebark pine ecosystem would be to maintain early successional stages, specifically in the timberline zone. Because of the low market value of timber in these areas and their general inaccessibility, particularly next to rocky escape terrain, timber harvest as a means of returning to early successional stages is not usually viable.

However, manipulation of timberline and subalpine forests with whitebark by fire is not a panacea for meeting the habitat requirements of bighorn sheep populations. Suitable summer range in or adjacent to the whitebark pine ecosystem is most often not the limiting factor.

Healthy populations (relatively large, mobile groups) need a variety of seasonal ranges linked by migration corridors. The year-round range of a bighorn may include up to nine seasonal ranges. Each migration corridor between seasonal ranges is potentially a weak link that can jeopardize a bighorn population. Forests with whitebark are only a part of a bighorn sheep population's range. The quality of winter range well away from the whitebark pine ecosystem is more often the issue. While management objectives for bighorn sheep in whitebark types should be to optimize security from predators and optimize available forage, they should be conducted with the awareness that areas with whitebark are only part of a more complex habitat. Careful coordination with other land use activities is critical in all parts of a population's range. This is particularly true because the winter range of bighorn sheep, unlike the summer range, is more easily reached by humans and so is more susceptible to degradation.

Shiras Moose

Moose are traditionally associated with early successional stages and deciduous browse species. However, Loope and Gruell (1973) observed that the moose population in northwestern Wyoming has increased with advancing forest succession. Gruell (1980) stated that moose numbers were low around the turn of the century when much habitat was in early succession with the influence of wildfires. Moose populations did not increase significantly until more advanced stages were reached 60 years or more after large wildfires. He attributed the increase to an increased availability of winter forage, especially subalpine fir. He indicated that subalpine fir appeared to be the primary and even exclusive diet in late winter. Subalpine fir has increased dramatically over a widespread area in the near absence of wildfires. Studies from other areas where tall growing deciduous trees and shrubs that reestablish rapidly after fire are well represented show moose benefiting from early successional stages. However, in northwestern Wyoming succession is slower, there are fewer tall deciduous shrubs and trees, and deep snows preclude the availability of browse present in early successional forests. Schladweiler (1973) found subalpine fir to be an important browse species of moose in southwestern Montana, particularly at higher elevations and in late-successional-stage forests. Stevens (1970) found relatively large numbers of moose in the Gallatin range wintering at high elevations in late-successional forests (spruce-fir).

Work being done on the Gardiner District of the Gallatin National Forest has resulted in similar conclusions (Tyers and others 1989). Moose in the drainages of the Yellowstone River on or adjacent to the northern winter range of Yellowstone National Park and the Gallatin National Forest spend most of the winter in late-successional forests. Their diet is primarily subalpine fir. The forests used are cover types (Mattson and Despain 1985): LP3—overstory of lodgepole pine with some Engelmann spruce, subalpine fir, and whitebark pine in the pole size class; an understory of small to large spruce and fir seedlings and saplings, 300 years plus post fire. SF—dominated by Engelmann spruce and subalpine fir in both overstory and understory; lodgepole pine, Douglas-fir, or whitebark pine may be present but are a minor stand component. WB3—dominated by mature whitebark pine and may also contain considerable Engelmann spruce, subalpine fir, or lodgepole pine; understory is a combination of Engelmann spruce, subalpine fir, and whitebark pine. DF3—ragged canopy of predominantly mature to overmature Douglas-fir but containing some Englemann spruce, subalpine fir, or whitebark pine in the pole-sized class, understory of small to large spruce and fir seedlings and saplings.

A common denominator in these cover types is the fact that they are late-successional stage forests with an understory of subalpine fir. A completion of the study and data analysis will further describe the microsites within those cover types the moose select. Density of subalpine fir saplings of a certain height will be important.

Another common factor with these cover types is that whitebark pine may be present, but as different age classes and in different quantities. Also, these cover types represent late-successional forests several hundred years removed from fire. In areas where whitebark is present in late-successional forests and moose are utilizing an understory of subalpine fir as a browse species, the return of these forests to an early successional stage through fire or timber harvest would be to the detriment of the moose.

Snow depth and consistency have an impact on moose use of winter habitats. Forests with closed canopies can be easier to travel in than open areas because of these variables (Jenkins 1985; Peek 1971). Telfer (1970) in New Brunswick reported late-winter moose activity largely restricted to dense conifer-dominated stands after the animals spent fall and early winter in more open stands. In Quebec, des Mueles (1964) found that moose also shifted to more dense types when snow accumulated to 77 to 86 cm. Peek (1971) found that shifts to more dense types occurred as a response to differences in snow hardness and density as well as depth. Work currently being done in the northern Yellowstone area (Tyers and others 1989) suggests that moose abandon the early winter foraging areas in willow communities in late January in favor of dense forests—often with whitebark pine in the overstory or understory. This is in response to contrasts in snow depth and consistency. In late winter dramatic differences exist in these variables in open areas versus dense forests. These open areas include early successional stage forests brought about by timber harvest or recent fire. Such areas show almost no use throughout the winter. Gruell's (1980) notion that deciduous browse is either unavailable because of snow depth, slow to appear, or of insufficient quantities holds true for timber sale units in the study area described.

A management objective for the Shiras moose in the whitebark ecosystem where snow depth and consistency and a lack of deciduous browse force an association between moose and dense forests would be to maintain winter range areas in late-successional stage and ensure the integrity of travel corridors. This would require close coordination with timber harvest activities where the two occurred in the same area.

DISCUSSION

I have attempted to demonstrate that, although our understanding of the habitat requirements of wildlife in the whitebark pine ecosystem is thought to be poor, we still have guidelines available to us for establishing management objectives for the wildlife resource. These guidelines represent different levels of sophistication and can be expressed as follows (proceeding from the simple to the more complex): (1) establish management activities on the premise that the whitebark pine ecosystem is a fragile and finite resource that should be protected from consumptive activities; (2) establish management objectives based on three basic principles: the needs of the grizzly bear dominate, the whitebark pine ecosystem is seasonally important range to different wildlife species and cannot be managed as an island for any given species that uses this ecosystem, and management activities must be integrated; (3) management objectives can be established based on a knowledge of the specific site and stand characteristics that optimize the value of the area for a given species.

REFERENCES

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

des Mueles, P. 1964. The influence of snow on the behavior of moose. Transactions of North East Wildlife Conference. 21: 17.

Gruell, G. E. 1980. Fire's influence on wildlife habitat on the Bridger-Teton National Forest, Wyoming. Volume II—changes and causes, management implications. Res. Pap. INT-252. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 35 p.

Gruell, G. E. 1983. Fire and vegetative trends in the Northern Rockies: interpretations from 1871-1982 photographs. Gen. Tech Rep. INT-158. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 113-122.

Hann, W. 1987. Resource values in whitebark pine ecosystems. In: Notes; mini-workshop on whitebark pine; 1987 February 24; Bozeman, MT: On file at: U.S. Department of Agriculture, Forest Service, Gallatin National Forest, Bozeman, MT.

Jenkins, K. J. 1985. Winter habitat and niche relationships of sympatric cervids along the North Fork of the Flathead River, Montana. Moscow, ID: University of Idaho. 183 p. Dissertation.

Kendall, K. C. 1981. Bear use of pine nuts. Bozeman, MT: Montana State University. 27 p. Thesis.

Loope, L. L.; Gruell, G. E. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. Quaternary Research. 3: 425-443.

Mattson, D. J. 1989. [Personal communication]. April. Bozeman, MT: U.S. Department of the Interior, National Park Service, Forestry Sciences Laboratory, Montana State University.

Mattson, D. J.; Despain D. G. 1985. Grizzly bear habitat component mapping handbook for the Yellowstone ecosystem. Mammoth Hot Springs, WY: U.S. Department of the Interior, National Park Service and U.S. Department of Agriculture, Forest Service. 39 p.

Mattson, D. J.; Reinhart, D. P. 1986. Grizzly bear, red squirrels and whitebark pine: third year progress report. In: Knight, R. R.; Blanchard, B.; Mattson, D. J. Yellowstone grizzly bear investigations 1985. West Yellowstone, WY: U.S. Department of the Interior, National Park Service: 36-44.

Mattson, D. J.; Reinhart, D. P. 1987. Significance of whitebark pine to wildlife. In: Notes; mini-workshop on whitebark pine; 1987 February 24; Bozeman, MT. On file at: U.S. Department of Agriculture, Forest Service, Gallatin National Forest, Bozeman, MT.

McCaughey, W. W. 1988. Determining what factors limit whitebark pine germination and seedling survival in high elevation subalpine forests. Unpublished paper. Study No. INT-4151-020. On file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, Bozeman, MT.

Mealy, S. P. 1975. The natural food habits of free-ranging grizzly bears in Yellowstone National Park, 1973-74. Bozeman, MT: Montana State University. 158 p. Thesis.

Peek, J. M. 1971. Moose-snow relationships in northeastern Minnesota. In: Proceedings of the symposium: snow and ice in relation to wildlife and recreation; 1971; Ames, IA. Ames, IA: Iowa State University: 34-49.

Raphael, Martin G. 1987. Nongame wildlife research in subalpine forests of the central Rocky Mountains. In: Management of subalpine forests: building on 50 years of research: proceedings of technical conference; 1987 July 6-9; Silver Creek, CO. Gen. Tech. Rep. RM-149. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 113-122.

Schladweiler, P. 1974. Ecology of Shiras moose in Montana. Big game research Project W-98-R and W-120-R final report. Helena, MT: Montana Department of Fish and Game. 100 p.

Stevens, D. R. 1970. Winter ecology of moose in the Gallatin Mountains, Montana. Journal of Wildlife Management. 34(1): 37-46.

Telfer, E. S. 1970. Winter habitat selection of moose and white-tailed deer. Journal of Wildlife Management. 34(3): 553-559.

Thomas, J. W. 1987. Do we know enough to manage subalpine wildlife habitat?—it all depends. In: Management of subalpine forests: building on 50 years of research: proceedings of technical conference; 1987 July 6-9; Silver Creek, CO. Gen. Tech. Rep. RM-149. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 123-125.

Tyers, D.; Singer, F.; Alt, K. 1989. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Gallatin National Forest, Gardiner Ranger District, Gardiner, MT.

U.S. Department of Agriculture, Forest Service. 1986. Charting the course—the Forest Service grizzly bear conservation program. FS 6200-28. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 100 p.

Wakelyn, L. A.; Bailey, J. A. 1983. [In: letter from John Mumma, Region 1 Director, to Gallatin Forest Supervisor] December 20. 15 leaves. On file at: U.S. Department of Agriculture, Forest Service, Gallatin National Forest, Bozeman, MT.

RESPONSE OF VEGETATION TO LIVESTOCK IMPACTS ON GREEN FESCUE SITES IN THE WHITEBARK PINE ECOSYSTEM

Charles G. Johnson, Jr.

ABSTRACT

Subalpine grasslands have been important for mid- to late-summer grazing by domestic sheep. Operations centered at base ranches in the canyons of the Snake River and valleys surrounding the Wallowa Mountains of northeastern Oregon. A serious degrading of these rangelands occurred near the turn of the century when sheep production was primary and concern for the natural resources was secondary. Following World War II, sheep use markedly declined with a responding rebound by vegetation that covered the scars of land abuse.

Pioneering range scientists used subalpine areas of the Wallowas to learn grassland successional relationships. Arthur Sampson studied the Standley Allotment between 1907 and 1911; Pickford and Reid selected Tenderfoot Basin for their 1938 investigation of depleted green fescue range. Their initial photographic work has been periodically retaken along with interpretation of successional trend.

The primary plant associations utilized by sheep in the subalpine areas of the Wallowa Mountains were dominated by green fescue (Festuca viridula *Basey). Classifying vegetation based on the potential of the site to produce a climax dominant grass is simplified by the pioneering secondary succession work accomplished by earlier investigators. The continued monitoring of green fescue sites will enable land managers to interpret severity of use with resulting plant compositional and productivity changes.*

INTRODUCTION

> Every mountainous part of the West has its particular breed of mountain bunchgrass; thus, green fescue is the mountain bunchgrass of the Blue Mountain country of northeastern Oregon and southeastern Washington. Lambs fed on these ranges are famous for condition and the high market prices they command. Few sights are more pleasing to the eye than high knolls and ridges covered with a fine stand of green fescue. The rich green hue of the foliage contrasts strikingly with the bright bluish-purple heads (USDA 1937).

Green fescue (*Festuca viridula* Basey) plant communities are found in the subalpine fir and whitebark pine zones occurring in parks, on open slopes and ridgetops, and as a part of a savanna beneath open-growing trees (Reid 1942).

Green fescue communities generally occur in exposed portions of the subalpine forest above 6,000 ft elevation. These grasslands exist on relatively dry sites within a high-precipitation zone (over 35 inches ppt/yr) that have been created by excessive wind transfer of winter snows, exposing these slopes to dessication (Daubenmire and Daubenmire 1968). Deep, finely textured soils capable of high water-holding capacity help compensate for wind dessication promoting the fescue on exposed, open slopes (Weaver 1979). Therefore, they support grasses and forbs in the absence of trees except for occurrence beneath whitebark pine in a savanna. These sites are often droughty in late summer when intense storms can provide highly erosive winds and torrential rains can cause severe sheet and gully erosion.

The species occurs in southern British Columbia and Alberta, the northern Rockies of western Montana and Idaho, along the Cascadian crest in Oregon and Washington, in the Sierras from Mount Lassen to Yosemite, and in the Wallowa and northern Blue Mountains of northeastern Oregon.

The grass plants form a dense sod with an extensive root system penetrating to depths of 3 ft and greater (USDA 1937). In good ecologic condition, green fescue communities are characterized by almost pure stands of grass, a dense foliage cover, and interstitial areas occupied by fescue root crowns and litter (Reid 1941). The forb composition of late-seral green fescue communities is often less than 20 percent (Johnson and Simon 1987).

Green fescue is well adapted to the severe climatic conditions prevailing at these subalpine elevations. In late seral stands, green fescue can average over 500 lb/acre. Communities in mid-seral stages of succession often contain a greater forb composition, which can provide up to 1,300 lb/acre. Late-seral green fescue stands in the Wallowa Mountains average almost 900 lb/acre of total herbage production (Johnson and Simon 1987).

Besides being very productive, green fescue is highly palatable and very nutritious. Sheep have been the primary class of livestock to historically use these high-elevation grasslands. They habitually prefer forbs, but avidly seek the succulent fescue and tend to graze this herbage more closely than that of other grasses (Sampson and Chase 1927). The deep extensive root system provides a stabilizing force to thwart erosion from high winds

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Charles G. Johnson, Jr. is Area Plant Ecologist for the Malheur, Umatilla, and Wallowa-Whitman National Forests, Forest Service, U.S. Department of Agriculture, Baker City, OR 97814.

and surface water runoff resulting from either rapid snowmelt or high-intensity storms. When degraded, green fescue loses its vigor, seedhead production is diminished, and seedling establishment is often poorer. The capability of green fescue communities to withstand trampling from heavy animal use is lessened. The result is an increase in forb and other graminoid composition coupled with a breaking down of the soil mat followed by rapid soil loss.

GRAZING IMPACTS—THE TENDERFOOT BASIN STUDIES

Tenderfoot Basin is located in the whitebark pine zone of the Wallowa Mountains at elevations ranging from 7,200 to 8,500 ft. By the turn of the century, the dominant green fescue communities were badly deteriorated from sheep abuse. Annual overutilization of the available forage from the practice of turning livestock onto the allotment too early in the season resulted in low plant vigor and a decline in vegetative cover. The Wallowa Mountains were used extensively as primary summer range for large sheep ranches. In the early part of this century, 380,000 sheep were estimated to have grazed annually in the subalpine portions of these mountains (Cole 1977). The Tenderfoot Basin area was selected by G. D. Pickford and E. H. Reid to study plant succession and effects of use on green fescue grasslands. A second area was selected for comparison where sheep use had been much lighter, resulting in a green fescue community of near-climax ecologic condition.

There were four 1,200-head bands of sheep grazing for 3 months in Tenderfoot Basin in 1916 with a carrying capacity of 6.4 sheep months/acre. By 1938, the area could sustain only 0.57 sheep for a month on an acre (Pickford and Reid 1938). The plant communities were characterized as having only 33 percent vegetative cover with needlegrasses dominating over fescue on pedestals resulting from severe soil loss (estimated at 428 tons/acre). Other sites were further degraded. Here vegetative cover was only 10 percent consisting of needlegrass six times more abundant than green fescue and dominated by perennial and annual forbs. Erosion pavement was prevalent between the pedestals. Soil loss was estimated at 927 tons/acre on these earlier seral sites (Strickler 1957).

In contrast, in near-climax stands, green fescue comprised 68 percent with lupine the only other associate. The grass sod was fairly continuous with no distinct hummocky appearance, exposed soil was less than 25 percent at the surface, and no erosion pavement was evident. This climax fescue grassland could carry 5.35 sheep on an acre for a month where the best stands at Tenderfoot Basin could only support 0.57 sheep (Pickford and Reid 1942).

SUCCESSIONAL CHANGE (1956)

Tenderfoot Basin was reexamined in 1956 following an 18-year period of lighter sheep use (Strickler 1957). The desirable forage species had increased in cover and production; most perennial forbs decreased in cover and vigor. Active erosion had ceased as desirable grasses began to colonize the erosion pavement. Pedestals were breaking down and depositing soil on the pavement, providing new growing sites for young grass plants. In 1938, the three major graminoids (fescue, needlegrasses, and sedges) produced an average of 630 lb/acre on the Tenderfoot Basin sampled sites. In 1956, the same sites produced an average of 1,530 lb/acre of these graminoids (Strickler 1961). Fescue cover increased from 11 to 32 percent over the time period.

What contributed to this reversal in succession? It was determined (Reid and others 1980) that accelerated erosion ceased and vegetative rehabilitation began when:

1. The number of sheep using Tenderfoot Basin was reduced;
2. A deferment period had occurred;
3. Allotment entry was regulated to coincide with range readiness;
4. Periods of nonuse occurred;
5. Sheep were permitted to graze freely;
6. Bedgrounds were used for only one night.

FESCUE DOMINANCE REESTABLISHED (1978)

After 40 years had elapsed from the period of overutilization, the Tenderfoot Basin study locations had responded with a new vegetative vitality that altered the community composition toward the climax stage of succession (Reid and others 1980). Total plant cover had continued to increase since 1956 under light impact from grazing animals. The needlegrasses, sedges, and forbs declined in percent composition. Green fescue had regained dominance over needlegrass in the established perennial bunchgrass locations and was more actively invading the bareground locations. Most pedestals had either collapsed or were less visible due to a "rounding" by the new vegetative covering.

The acceleration of change between 1956 and 1978 was principally created by the reduction in sheep months of grazing, deferment periods over the preceding 40 years, and the stabilizing period necessary for fescue seedling survival on the eroded soil. Another factor in the acceleration of change may have been increased activity by soil mycorrhizal fungi. Prior to that time continued soil disturbance restricted fungal formation.

MANAGEMENT OF SUBALPINE VEGETATION

The need to maintain foliar or litter cover is important to the protection of subalpine fescue sites. Utilization should be limited to 50 percent of the fescue plant; this would require a minimal stubble height of 3 inches (Pickford and Reid 1942). At this limit of utilization, sufficient seed stalks should remain for natural reproduction. Grazing should be limited to a 1- to 2-month season following fescue seedhead formation and ripening to allow for dissemination of viable seed.

Domestic cattle are injurious to green fescue communities. The weight of the animal creates severe erosive opportunities through displacement of the porous soils and separation of sod mats from trampling hooves. The fine-textured, porous soils are very susceptible to subsequent wind and water erosion. Sheep, properly tended, should promote fescue by preferentially grazing forbs and tamping fescue seed with their hooves. The lighter animal can move rapidly across the slopes and maximize utilization of the rangeland as a whole much more effectively than cattle (Johnson and Simon 1987).

Most of the subalpine areas where green fescue and high-elevation Idaho fescue communities (Hall 1973) occur are managed as portions of the National Wilderness Preservation System. Grazing by commercial permit has declined and appears to be continuing in decline. The major management concern for subalpine herbaceous vegetation will continue to be generated by people. As our population increases and these higher elevation sanctuaries are sought by the recreating public, degradation could increase where people and their animals congregate. Populations of native and introduced wild ungulates, if allowed to increase unchecked, can create some of the same degradation problems as were encountered by investigators in the Wallowa Mountains early in the 20th century.

REFERENCES

Cole, David N. 1977. Man's impact on wilderness vegetation: an example from Eagle Cap Wilderness, northeastern Oregon. Eugene, OR: University of Oregon. 307 p. Dissertation.

Daubenmire, R. F.; Daubenmire, J. B. 1968. Forest vegetation of southeastern Washington and northern Idaho. Tech. Bull. 60. Pullman, WA: Washington Agricultural Experiment Station. 104 p.

Hall, F. C. 1973. Plant communities of the Blue Mountains in eastern Oregon and southeastern Washington. R-6 Area Guide 3-1. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 62 p.

Johnson, Charles G.; Simon, S. 1987. Plant associations of the Wallowa-Snake province, Wallowa-Whitman N.F. R-6-Ecol-TP-225A-86. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 400 p.

Molina, Randolph J.; Trappe, J. M.; Strickler, G. S. 1978. Mycorrhiza fungi associated with *Festuca* in the western United States and Canada. Canadian Journal of Botany. 45(14): 1691-1695.

Pickford, G. D.; Reid, E. H. 1938. Range research progress report (1937-1938). Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 94 p.

Pickford, G. D.; Reid, E. H. 1942. Basis for judging subalpine grassland ranges of Oregon and Washington. Circular No. 655. Washington, DC: U.S. Department of Agriculture, Forest Service. 38 p.

Reid, E. H. 1941. Plant succession on subalpine grasslands as affected by livestock management. Northwest Science. 15(1): 3-5.

Reid, E. H. 1942. Important plants on National Forest ranges of eastern Oregon and eastern Washington. Range Research Report No. 1. Portland, OR: U.S. Department of Agriculture, Forest Service. 64 p.

Reid, E. H.; Strickler, G. S.; Hall, W. B. 1980. Green fescue grassland: 40 years of secondary succession. Res. Pap. PNW-274. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 39 p.

Sampson, A. W.; Chase, Agnes. 1927. Range grasses of California. Bull. 430. Berkeley, CA: University of California Printing Office. 94 p.

Strickler, G. S. 1957. Vegetation and soil condition changes in Tenderfoot Basin (1938-1956)—office report. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Strickler, G. S. 1961. Vegetation and soil condition changes on a subalpine grassland in eastern Oregon. Res. Pap. 40. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 46 p.

U.S. Department of Agriculture, Forest Service. 1937. Range plant handbook. PB-168-589. Washington, DC: U.S. Department of Agriculture, Forest Service. 419 p.

Weaver, T. 1979. Climates of fescue grasslands of mountains in the western United States. Great Basin Naturalist. 39(3): 284-288.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Anonymous)—Do you think that grazing domestic stock will ever be excluded from public lands?

A.—Not in the foreseeable future. Domestic livestock grazing is still a viable use of the forage resources of our National Forests. In many bunchgrass-dominated plant communities, a grazing animal stimulates tillering and invigorates the grass stand to produce new growth. Old growth is consumed with a resulting reduction in the buildup of material conducive to rodent infestations, disease, and fire susceptibility.

Q. (from Anonymous)—What effect did the drought of the 1930's have on your sites? How much of the state of the 1938 stands depended on the drought?

A.—I'm not sure we can determine the role of climate on the state of green fescue rangelands 50 years ago. Certainly the major factor leading to the condition of the rangelands then was overgrazing by domestic sheep.

Q. (from Anonymous)—Are there situations in subalpine meadows where forbs are an indicator of a healthy situation? What's wrong with forbs? Where should they be growing?

A.—There is nothing wrong with forbs in subalpine plant communities. From the successional point of view, we see forb increase with degradation of green fescue grasslands and ultimate domination by forbs in very denuded areas. The concept of late-seral (near-climax) communities having nearly forbless stands dominated by perennial bunchgrass is proposed through work in classifying green fescue stands where stability has occurred over time. Forbs provide a diverse offering to the grazing resource. We may wish to manage for mid-seral stands where green fescue is strongly associated with a forb component. If we are managing for recreational use, forb abundance is often highly desired by our high-country users.

STREAMS, LAKES, AND FISH IN WHITEBARK PINE ECOSYSTEMS

Ray J. White

ABSTRACT

Not only do streams, lakes, and fish occur in the whitebark pine (Pinus albicaulis) *ecosystem, but the streams and fish are important to ecosystems lying downslope and extending out into the mountain valleys. Many of the lakes support significant recreational fishing, but few of the streams do, although they may serve as spawning, juvenile rearing, and refuge areas. The primary fishes of interest are salmonids, certain kinds of which seem better adapted than others to high-altitude streams. The streams here tend to be an extraordinarily harsh environment due to steepness, coldness, ice conditions, and nutrient poverty—but in some regions may have a more dependable water supply than those farther downslope. Avalanches, ice, snow, boulder control, vegetation, beaver, and disturbance by livestock grazing may often play important roles in shaping stream channels in these areas. Many of the high lakes of the United States Rocky Mountains have been stocked with trout, char, or grayling, many kinds of which are exotic to the regions or drainages. Many of these lakes no longer contain their prestocking-era faunal composition. The lakes that are deep enough often have substantial salmonid populations, but growth tends to be slow, owing to infertility, cold, and 7 to 8 months of ice cover. Those near hiking, pack-trip, or vehicle trails are commonly overfished, but many are so remote that this is not a problem.*

INTRODUCTION

Streams and lakes exist as distinctive aquatic subecosystems nested in and closely interconnected with a hierarchy of larger, primarily terrestrial, ecosystems, such as those defined by small drainage (catchment) basins and clusters of larger basins. In some drainage basins and ecosystems, whitebark pine (*Pinus albicaulis*) is the predominant tree. This may or may not mean they are whitebark pine ecosystems.

The stream and lake subecosystems perform in special ways that are surely affected by whitebark pine and the associated biota. It is likely that no one has studied characteristics of streams and lakes in relation to whitebark pine specifically. The plant communities of whitebark pine forests must influence the chemistry of soils, hence of surface and subsurface runoff water that feeds streams and lakes. Streams and lakes in the forest may supply food for various members of the animal community, namely herbivores, such as moose (*Alces americanus*), and carnivores, such as osprey (*Pandion haliaetus*), mustelids, and bears. It is well known that fish can be very important in the diet of grizzly bears (*Ursus horribilis*). They feed heavily on cutthroat trout (*Oncorhynchus* [formerly *Salmo*] *clarki*) from Yellowstone Lake that migrate into the lower reaches of tributary creeks to spawn in late spring and early summer, however researchers in Yellowstone National Park have no evidence that bears eat fish in creeks at still higher elevations (Reinhart 1989). Although beaver (*Castor canadensis*) may not use whitebark pine, within some parts of the forests, they may strongly influence vegetation, soils, water levels, fish, and wildlife habitat. At this stage of our knowledge it may be most appropriate to discuss general characteristics and functioning of streams and lakes that are at about the same range of altitude as whitebark pine and to raise questions and highlight potentially important issues based on general information.

For this paper, I not only have reviewed literature, but have discussed the subject with limnologists, as well as with fishery biologists from State agencies and the Forest Service, U.S. Department of Agriculture, in Montana and Idaho, who deal with waters in the whitebark pine range. Interesting and potentially useful information exists that is not in the literature because the observations are not from formal study but are largely subjective.

The assigned topic, "water quality and fish," was changed because water quality is only one of several important general aspects of aquatic ecosystems affecting their performance and their fish. Other key aspects are water quantity (for example, streamflow discharge and lake volume), physical structure of the water body, and temporal regimens of variation in water quantity, water quantity, and physical structure. All are interrelated.

Because the needs for protecting water quality are fairly well known, and because matters of water quantity are covered by Farnes (this proceedings), I will concentrate on physical structure and its effects on fish. To consider stream quality and lake quality in their totalities is often much more effective than focusing narrowly on water quality. I am fond of pointing out that even if the water of a stream or lake is pure enough for human babies to drink, and even if it is at the same time sufficiently nutrient-rich and of the right temperature for growing lots of organisms, still, it cannot harbor many fish of desirable size if the container is the wrong shape.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Ray J. White is Associate Professor of Fishery Science, Department of Biology, Montana State University, Bozeman. Present address: Trout Habitat Specialists, 320 12th Avenue N, Edmonds, WA 98020.

The shapes of stream channels and lake basins are important to the suitability of these water bodies for other organisms as well. For example, the fineness of streambed texture (small-scale structure) can greatly affect the kinds and abundances of benthic fauna. Also, the steepness of side slopes of lake basins, as well as lake depth—hence darkness—can affect the abundance of rooted aquatic plants and all that depend on the plants.

What goes on in ecosystems containing whitebark pine, especially in regard to vegetation and soils, may greatly affect the shapes, water quantity, and water quality of streams and lakes. Conditions of the drainage basin's vegetative mantle will exert much control on inputs of water, sediments, and dissolved chemicals. Streambank vegetation is a major determinant of stream channel shape and of the stability of the bed and banks. In particular, the sloughing of trees and brush into channels forms jams and other large roughness elements that resist downward and lateral erosion of the stream and that provide hiding cover for fish and other orgainsms. There are obvious effects of drainage basin morphometry; slope steepness is important, as are the roles and effects of snow avalanches and landslides on the shapes and hydrology of streams and lakes.

In the sections that follow, I will discuss lakes separately from streams. One characteristic common to both types of aquatic systems and of special relevance within a forest is that, when not frozen, they have wet surfaces that catch small particles of organic debris. Of great importance to stream and lake ecosystems, particularly small ones such as found in alpine areas, is the amount of small debris from terrestrial vegetation—such as bits of bark and twigs, pollen grains, leaves, and needles—that enters and can be used by the aquatic biota. These fragments can be blown for great distances through the air and across surfaces of rock, ice, and crusted snow, but the wet surfaces of water bodies act as sticky traps for them. This material is then held within the stream or lake and does not soon, if ever, return to the terrestrial part of the larger ecosystem. Hence, streams and lakes receive far more allochthonous particulate organic input than would derive even from having a canopy of vegetation. In small headwater creeks in particular, the food web tends to be based far more on terrestrial organic detritus than on algal production (Vannote and others 1980).

The sport fishes adapted to life in high-mountain lakes are all salmonids—trouts, chars, and graylings. Before stocking was begun, the salmonids that naturally occurred in high-mountain waters within the range of the whitebark pine were the cutthroat trout, represented by several subspecies, each including many strains having special adaptations to local conditions; the arctic grayling (*Thymallus arcticus*); some varieties of redband or rainbow trout (*Oncorhynchus mykiss*, formerly *Salmo gairdneri*) west of the Continental Divide, and also on that side of the mountains, the river char known as bulltrout (*Salvelinus confluentus*). Few species of nonsalmonid fish occurred in high streams or lakes; sculpins (*Cottus* spp.), the longnose sucker (*Catostomus catostomus*), and the burbot (*Lota lota*) probably were the only ones. Stocked species have included cutthroat trout, arctic grayling, rainbow trout, brook trout (*Salvelinus fontinalis*—a char from eastern North America), golden trout (*O. aguabonita*) from California, and the European brown trout (*Salmo trutta*).

HIGH-ALTITUDE LAKES AND THEIR FISH

High lakes of the Rocky Mountains and other ranges on this and other continents are generally small, often locally numerous, have usually been formed in various ways by glacial action, and are always cold, thickly covered with ice and snow for most of the year, and relatively nutrient poor (Loeffler 1983; Rabe and Breckenridge 1985). The typical inaccessibility of mountain lakes to fish has meant that most were fishless, at least until people began extensive stocking.

In contrast to nearby streams, lakes now support almost all of the high country's recreational angling. On high Rocky Mountain trails, hikers or packtrippers who have fishing rods are almost always on the way to or from a lake, not a stream. Some people go into the mountains mainly for the fishing, but for many, that sport is incidental to other recreation. In the last few years, the proportion of mountain lake fishing that is incidental, as opposed to being the main objective, may have increased, according to the impressions of the few mountain lake anglers I polled on this matter.

By the late 1960's, overharvest of trout in wilderness lakes by backpackers was a major management headache for State of Idaho biologists. Therefore, the State's official informational booklet on mountain trails and lakes was discontinued, and now privately published trail guides may undermine that effort to reduce angling pressure (Gebhards 1988). Idaho's Sawtooth National Recreational Area has particularly heavy human use; lakes near trails are intensely fished, and remote lakes seldom fished. Outfitters are taking clients back into some of the remote lakes, and these are suffering problems caused by horse grazing.

Camping near lake shores may now be the foremost human use of alpine lakes, but fishing surely remains as an enhancement of the camping experience, as well as a major attraction . The plant-and-soil systems of the riparian zones of high lakes may be particularly fragile. It is obvious to all who have observed the effects of human activity, such as camping around high lakes, that damage to physical and vegetational conditions occurs as a result of trampling, wood-gathering, fire sites, waste disposal, and the use of pack animals. Chemical water quality of the lakes also can be affected by these activities (Taylor and Erman 1979).

In most high lakes of the Rocky Mountains, there would be no fishing had the fish—mainly trout but also grayling—not been introduced by humans. In the 1920's in Montana's Beartooth Range, for example, miners, packers, rod and gun club members, and government personnel began to stock fish in the mountains (Anderson 1984). For sustained fishing, repeated stocking was required because many of the lakes lacked spawning habitat. Most had no gravelly tributary or outlet streams, or lacked certain types of lakebed gravel formations. In the Beartooth

Range today, about 35 percent of the lakes contain fish, 25 percent lack fish but are probably capable of sustaining them, and 40 percent are unsuitable for fish (Anderson 1984).

The planting of trout and grayling in high lakes was often successful from an angling standpoint, when the lakes were relatively deep and nutrient rich. The practice was rather unsuccessful (fish grew poorly) in lakes that were too shallow or nutrient poor, or when, as was often the case, more fish were stocked than the food resources could sustain (Reimers 1979). The process of overcrowding and consequent stunting of salmonids introduced in high-mountain lakes also is common in the Alps (Pechlaner 1966, 1984).

Salmonid stocking may almost always have been a disaster for the pre-existing faunal community. In the few lakes having native populations of trout or grayling, the stocked trout of other species—or of other strains of the same species—would usually have exerted adverse competitive pressure (Moyle and others 1986). When the stocked species was able to breed substantially with the indigenous species, introgressive hybridization may often have eventually eliminated the former; this is common when rainbow trout are imposed on some strains of cutthroat trout (Behnke and Zarn 1976).

Not only do unmanaged high-mountain lakes tend to have few kinds of fish, if any, but, owing to recent (on the geologic time scale) formation of the lakes, poor accessibility, harsh climate, and low nutrient availability, the entire faunal community of such a lake tends to be poor, compared to lakes of similar dimensions at lower altitude. The typical natural, relatively simple, hence probably unresilient community, would have had some salamander, frog, or predatory invertebrate (insect or zooplankter) at the peak of the aquatic trophic pyramid—aside from water birds during the short, ice-free season.

When salmonids were suddenly thrust into such systems, they would within a few months or years deplete the invertebrates that were large enough to be of value to them (Pechlaner 1966, 1984; Reimers 1979). Predatory fish of any kind in ponds and lakes at any altitude become stunted (almost stop growing) when they become so numerous that the invertebrate population is kept size-selectively cropped down to the point that the only food organisms left are those so small that the fish's energy cost of capturing and eating such an organism exceeds the energy that can be gained from it. This process is so well known that the literature for it need not be cited. This was demonstrated in reverse when brook trout were transplanted from a densely populated mountain lake to a less crowded one and subsequently accelerated in growth (Rabe 1967).

Thus, especially in the nutrient-poor lakes so often found in alpine areas, the fish virtually eradicate the food supply, almost stop growing, and exist for years on the verge of starvation—which fish are good at, especially in very cold water. Perhaps in almost no high lakes, even if the supply of larger invertebrates has not been severely cropped off, do trout or grayling grow at rates that would generally be considered fast. This is because the water is continually so cold. Where food remains relatively plentiful, the slowly growing fish that survive eventually reach large size because in the cold they live much longer than in waters of normal temperature regimen.

The result in many high lakes has been extraordinarily large, long-lived trout. These are lakes that were rather lightly stocked, have been very lightly harvested, and are biologically productive. Examples of excellent fisheries in high lakes abound. A Beartooth Mountain lake accessible by a good but steep foot trail many kilometers long reportedly contained not only fair-sized cutthroat trout caught by anglers in summer, but also brook trout of 2 kg or more. The latter were apparently caught with regularity only in winter by very few fishermen using special bait and willing to wade through kilometers of hip-deep snow (Marcuson 1975). Some other lakes of that area yield cutthroat and brook trout that are commonly as large as 35 to 40 cm (personal observation of the author).

Greater lake productivity can be due to location in calcareous mountains and on south-facing slopes, as well as other conducive attributes (Johnson 1973; Rabe and Breckenridge 1985). Calcareous (limestone) formations are fossilized marine organisms and their products. Water flowing over and through such rock dissolves alkaline ions and other plant nutrients. The alkalinity also directly benefits trout and many other organisms by imparting near-neutral pH to the water and by buffering against swings in acidity and against toxicity of various dissolved metallic ions. As opposed to lakes of humid eastern North America, in which the limiting nutrient for biological productivity is usually phophorus, those of the arid West are most often nitrogen limited (Priscu 1985-87). High mountain lakes of the West appear to fit this pattern. In research now under way, most lakes of Montana's Beartooth Range are proving to be nitrogen limited. Fallout from the 1988 fires in Yellowstone National Park resulted in nutrient enrichment, as evidenced by microbial responses, in high, alpine lakes (Angelo 1989). In a sample of 10 high-mountain lakes in a once-remote wilderness area of California, there was significant positive correlation between percentage frequency of benthic plants and intensity of past recreational camping in the lake vicinity (Taylor and Erman 1979).

In the many nutrient-poor or overstocked high lakes, the fish also lead long lives, but starving, stunted, truly miserable lives, and do not reach large size. The classic account is that of a brook trout population stocked in a high Sierra Nevada lake, the last survivor of which lived into its 24th year, doubling the previous longevity record for the species. Its body length was only 25 cm, mostly accrued during its first 6 years of growth, 9 months of which were in a hatchery from which the lot was stocked at mean size of 6.6 cm (Reimers 1979). In various other types of waters, brook trout reach 25 cm in 2 to 3 years.

HIGH-MOUNTAIN STREAMS AND THEIR FISH

High-altitude streams are typically small, cold, and very steep with much shallow water rushing over beds of large stone. The steep reaches, however, often contain accumulations of boulders and large woody debris that form a stairstepped bed. Behind the obstructions, gravel deposits serve as spawning beds. Just below the steps plunge pools occur, which provide fish with resting sites protected from swift current and predators.

The multifaceted benefits to fish habitat of having many large roughness elements (mainly boulders and logs) in streams and the important role of woody debris in creating such roughness have recently become apparent (Lisle 1981, 1986). Important among these benefits is the creation of hiding cover (visual isolation from predators and competitors) and eddies where current is slow enough to enable fish to maintain position without undue expenditure of energy. Where whitebark pine predominates, the contribution of its logs and limbs to streams is a question of interest that has probably not yet been investigated.

Streambed steepness is also occasionally interspersed with mountain meadows and swamp pockets where gradient is less, where gravel and finer sediments accumulate to form the streambed, and where pronounced meandering courses form, having pools at the bends and riffles between bends. Stream-dwelling salmonids are adapted to the features associated with stairstepping in the steep reaches and meandering in the low-gradient reaches.

The populations of resident trout in these small, steep, cold waters often attract little angling because the fish are generally small. Many of the streams, however, are considered to be very important to the fisheries of downstream rivers and lakes, not only because they supply water and nutrients, but because they serve as spawning grounds for larger fish that migrate from the larger, warmer waters. They also provide rearing habitat for young offspring. In western Idaho, bull trout and westslope cutthroat trout (*O. clarki lewisi*) predominate in streams above about 2,000 m; juveniles of steelhead rainbow trout and chinook salmon (*O. tshawytscha*) are the primary inhabitants at lower altitudes (Anderson 1988).

Fish in alpine streams face many problems, natural and human caused. Due to the vagaries of drought and spells of ample flow, trout populations in headwaters tend to fluctuate greatly (Erman 1986). Many parts of high-altitude streams freeze completely in winter, and their fish must move to other areas or perish, although those of small enough size can survive where the streambed is composed of stones that offer interstices leading to subsurface water. Slushlike anchor ice, which typically forms on winter nights and disappears the next day, also is a special hazard. Artificial sources of damage to high-mountain streams probably derive from almost any type of human activity that occurs in or near the streams and their riparian zones. Notable in the past was the near eradication of beaver from streams. At present, in addition to recreation, significant artificial factors include livestock grazing, logging, mining, and a variety of construction and maintenance activities associated with dwellings, roads, trails, power lines, telephone lines, pipe lines, water storage dams, and diversions for water supplies.

Beaver constitute one of the major natural habitat influences for stream fish in the Rocky Mountains—a beneficial influence in most cases. Their dams and ponds contribute importantly to the stairstepped stream profile and diversity of channel form and flow. The ponds also trap and store organic matter that would otherwise flush out of the system sooner and not be as available to stream (and terrestrial) organisms. Roles of beaver in stream ecosystem functioning were discussed by Naiman and others (1986). Whether beaver ever relate directly to whitebark pine apparently is not discussed in the literature, but beaver definitely extend their activity into the altitudes of the whitebark pine range.

In eastern Idaho, western Wyoming, and southern Montana, beaver are often abundant at 1,800 to 2,500 m (Platts 1989). In whitebark pine areas, they use willow for dams and for food, particularly for winter food caches. In summer much of their diet may be herbaceous plants, which tend to thrive at high altitudes better than in lower zones that have prolonged dry periods. Although willow brush tends to be small at high altitudes, it suffices for beaver dams, which can be low and relatively weak because (1) large floods do not occur in headwaters, (2) heavy snow cover prevents the winter ice layer from becoming as thick as at lower altitude, and (3) the beaver need not flood as large an area to reach sufficient food, owing to the availability of herbaceous vegetation (Platts 1989). Donald Anderson (1989) reports that beaver impoundments are important to Idaho salmon at altitudes of 1,800 to 2,000 m.

REFERENCES

Anderson, Donald. 1988. [Personal communication]. McCall, ID: Idaho Department of Fish and Game.

Anderson, R. 1984. Beartooth country: Montana's Absaroka and Beartooth Mountains. Montana Geographic Series 7. Helena, MT: Montana Magazine, Inc. 84 p.

Angelo, R. 1989. [Personal communication]. March. Bozeman, MT: Montana State University, Department of Biology.

Behnke, R. J.; Zarn, M. 1976. Biology and management of threatened and endangered western trouts. Gen. Tech. Rep. RM-28. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 1-45.

Erman, D. C. 1986. Long-term structure of fish populations in Sagehen Creek, California. Transactions of the American Fisheries Society. 115: 682-692.

Gebhards, Stacey. 1988. [Personal communication]. Boise, ID: Idaho Department of Fish and Game.

Johnson, J. J. 1973. High lakes and stream survey report. Olympia, WA: U.S. Department of Agriculture, Forest Service, Olympic National Forest, and Washington State Game Department. 74 p.

Lisle, T. E. 1981. Roughness elements: a key resource to improve anadromous fish habitat. In: Hassler, T. J., ed. Propagation, enhancement, and rehabilitation of anadromous salmonid populations and habitat in the Pacific Northwest; Proceedings of a 1981 October 15-17 symposium. Arcata, CA: Humboldt State University: 93-98.

Lisle, T. E. 1986. Effects of woody debris on anadromous salmonid habitat, Prince of Wales Island, Southeast Alaska. North American Journal of Fisheries Management. 6: 538-550.

Loeffler, H. 1983. Aspects of the history and evolution of alpine lakes in Austria. Hydrobiologia. 100: 143-152.

Marcuson, D. E. 1975. [Personal communucation]. July. Red Lodge, MT: Montana Department of Fish, Wildlife and Parks.

Moyle, P. B.; Li, H. W.; Barton, B. A. 1986. The Frankenstein effect: impact of introduced fishes on native fishes in North America. In: Stroud, R. H., ed. Fish culture in fisheries management. Bethesda, MD: American Fisheries Society: 415-426.

Naiman, R. J.; Mellilo, J. M.; Hobbie, J. E. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology. 67: 1254-1269.

Pechlaner, R. 1966. Salmonideneinsätze in Hochgebirgsseen und Tümpel der Ostalpen. Verhandlungen, Internationale Vereinigung der Limnologie. 16: 1182-1191.

Pechlaner, R. 1984. Dwarf populations of arctic char (*Salvelinus alpinus*) in high-mountain lakes of the Alps resulting from under-exploitation. In: Johnson, L.; Burns, R., eds. Biology of the arctic char: Proceedings of the symposium; 1981 May; Winnipeg, MB. Winnipeg, MB: University of Manitoba Press: 319-328.

Platts, William. 1989. [Personal communication]. March. Boise, ID: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Priscu, John. 1985-87. [Personal communication]. Various dates. Bozeman, MT: Montana State University, Department of Biology.

Rabe, F. W. 1967. The transplantation of brook trout in an alpine lake. Progressive Fish-Culturist. 29: 53-55.

Rabe, F. W.; Breckenridge, R. M. 1985. Physical and chemical factors of glacial lakes in northern Idaho as related to potential productivity and natural area selection. Journal of the Idaho Academy of Science. 21: 1-16.

Reimers, N. 1979. A history of a stunted brook trout (*Salvelinus fontinalis*) population in an alpine lake: a life span of 24 years. California Fish and Game. 65: 196-215.

Reinhart, Daniel P. 1989. [Personal communication]. March. Bozeman, MT: U.S. Department of the Interior, National Park Service, Interagency Grizzly Bear Study Team.

Taylor, T. P.; Erman, D. C. 1979. The response of benthic plants to past levels of human use in high mountain lakes in King's Canyon National Park, California, U.S.A. Journal of Environmental Management. 9: 271-278.

Vannote, R. L.; Minshall, G. W.; Cummins, K. W.; Sedell, J. R.; Cushing, C. E. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences. 37: 130-137.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (Mike Merigliano)—If the exotic trout and other fishes are eliminated from the previously barren high-mountain lakes, would the original food chain reestablish itself in the original composition?

A.—This consideration, not covered in the brief oral presentation, is touched upon in the printed version. Referenced material indicates that populations of invertebrates—at least of some invertebrates—increase (and trout growth rates increase) as trout populations diminish. This is not to say, however, that the full species complement and proportional abundances of the community have been restored. Probably there has not been enough study for us to know whether full recovery of an original community ever takes place. One might expect some species that are highly vulnerable to predation by (and competition from) trout, that have low reproductive rates, and low interlake mobility, hence poor potential for recolonization, to remain absent for many years after disappearance of trout from a lake. In the absence of former components of the community, especially if they had been key species in the trophic system—or "keystone" species in other respects—the species that do recover would be unlikely to repopulate to the same relative abundance as before disruption of the community by the trout. The community could therefore not be said to have truly recovered.

SNOTEL AND SNOW COURSE DATA: DESCRIBING THE HYDROLOGY OF WHITEBARK PINE ECOSYSTEMS

Phillip E. Farnes

ABSTRACT

Snow survey measurements have been made in and near whitebark pine ecosystems in the Western United States and Canada for over 50 years. Within the past 15 years, automated SNOTEL (snow survey telemetry) sites have provided daily data on snow water equivalent, total precipitation, and temperature. This information, along with hydrologic relationships, is used to describe the various hydrologic environments occupied by whitebark pine. Variations in snowpack, snow water equivalent, annual precipitation, growing season precipitation, and potential water yield from these areas are presented. SNOTEL sites in the Western United States and similar sites in Alberta, British Columbia, and California that provide historic and current data on snow water equivalent, total precipitation, and air temperature in or near whitebark pine ecosystems are identified.

INTRODUCTION

Whitebark pine generally occupies the higher elevation zones of western alpine watersheds (Arno and Hoff 1989; Little 1971). These areas are also the main water-producing zones. Snow courses and SNOTEL (snow survey telemetry) or similar sites have been established in these zones to monitor the seasons' snowpack and the primary source of the water supply. Data from these sites are also useful in evaluating the climatic and hydrologic regimes of whitebark pine.

SNOW SURVEYS

Snow surveys started in the West near Mount Rose, NV, in 1906 (USDA SCS 1988a). However, the first major expansion to all western States occurred in the mid-1930's, as a result of unprecedented drought and water shortages. There are now approximately 1,500 snow courses in the Western United States and 300 in Alberta and British Columbia. The record for manual snow surveys, which include both snow depth and snow water content, now exceeds 50 years at many locations. Generally, snow surveys are made three to five times each year. Many of these snow courses are located in areas occupied by whitebark pine.

Snow pillows were first installed in the early 1960's. These containers hold an antifreeze solution and are placed on the ground surface. The weight of the snow on the pillow is transferred to sensors inside a shelter and recorded with onsite recorders or telemetered, using radio equipment. Usually, snow pillows are 10 to 12 ft in diameter and are made of nylon reinforced neoprene. They provide a continuous record of snow accumulation and melt. Recording and storage precipitation gauges are also installed to quantify the total precipitation at these locations.

Snow pillows are a part of a system of SNOTEL sites that now number about 550 in the Western United States, excluding California (Barton 1975; McMillan 1981). All SNOTEL sites gather snow water equivalent, total precipitation, and air temperature daily. Other data such as wind speed and direction, solar radiation, and soil temperature are collected at a few of these sites. There are about 110 similar sites in California and about 12 in British Columbia and Alberta.

The SNOTEL electronics are currently being upgraded with microprocessors that can be programmed to select, accumulate, or average data. At sites with the upgraded electronics, daily maximum and minimum temperatures are being selected and the average daily temperature is being calculated using 96 daily observations.

While the primary use of these data is to forecast water supplies, they can also be used to evaluate the climatic regime of the whitebark pine.

There are approximately 110 SNOTEL sites or other snow measuring sites where both precipitation and snow water content data are gathered that coincide with whitebark pine ecosystems. While these sites occur in Alberta, British Columbia, California, Idaho, Montana, Nevada, Oregon, Washington, and Wyoming, as shown in table 1, the majority of these sites are in Idaho, Montana, and Wyoming.

Those wishing to access these data or those who have questions should contact the Soil Conservation Service, U.S. Department of Agriculture, (SCS) snow survey staffs in the western States (USDA SCS 1988b). Cooperators can access the SCS's Centralized Forecast System (CFS) in Portland, OR, using a computer and modem. Both real-time and historic data for snow courses and SNOTEL sites are available. Depth and snow water equivalent are available for snow courses. Daily snow water equivalent,

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Phillip E. Farnes is Supervisory Hydrologist, Snow Survey Data Collection Office, Soil Conservation Service, U.S. Department of Agriculture, Bozeman, MT 59715.

Table 1—Sites in or near whitebark pine

State or Province	Number sites	Range of elevations	Range of average annual precipitation	Range of average maximum SWE
		Feet	.... *Inches*	
Alberta	6	6,960- 7,640	30- 43	17-31
British Columbia	5	5,540- 6,360	38- 58	16-36
California	8	9,800-11,450	30- 40	12-32
Idaho	18	5,560- 9,150	31- 88	22-71
Montana	32	5,930- 9,100	26- 85	10-50
Nevada	7	7,700- 8,800	24- 43	15-24
Oregon	9	5,315- 6,200	35-112	19-72
Washington	5	5,400- 6,500	51- 83	40-74
Wyoming	16	8,200-10,100	21- 48	9-33

precipitation, and air temperature are available for SNOTEL sites in Idaho, Montana, Nevada, Oregon, Washington, and Wyoming. In California, the Department of Water Resources is the responsible agency and can provide snow, precipitation, and temperature data. In Alberta and British Columbia, the Provincial governments can provide this information.

PRECIPITATION, SNOWPACK, AND WHITEBARK PINE

Data from these sites show that whitebark pine grows under a wide variation of average annual precipitations and snow water equivalents. Average annual precipitation varies from about 20 inches to over 100 inches. Average maximum seasonal snow water equivalents range from about 10 inches to over 70 inches (California 1987; USDA 1987 Annual Data Summaries for Idaho, Montana, Nevada, Oregon, Washington, and Wyoming; Alberta Environment 1986; Ministry of Environment 1985).

Some of the lower average annual precipitation amounts may be misleading because redistribution of snow by wind may create a more favorable moisture environment for this species. This is most evident in some areas in Wyoming where snow at higher elevations is redistributed into drifts around tree stands. These drifts increase soil moisture, modify soil temperature, and hold soil moisture to near field capacity levels later into the season. This redistribution of snow may also create a favorable microclimate for reproduction in these lower precipitation areas.

The amount and distribution of precipitation between complete snowmelt and fall freezeup may be the most critical factor in whitebark pine survival and growth. Since soils in whitebark ecosystems generally have low water holding capacity, the frequency of summer rain may be as important as the quantity of precipitation that falls. Also, condensation is very common in these altitudes during summer months, and it is possible that this enables these trees to lower their daily transpiration.

The date snowpack melts to zero at SNOTEL sites in or near whitebark pine areas averages mid to late June. In California, Nevada, and Oregon, the average date of complete melt can be as early as mid-May. Snowmelt at the higher elevation sites in Wyoming continues into mid-July on the average.

Average precipitation that occurs after all the snow has melted and prior to fall freezeup, usually in early September, varies from about 3 to 5 inches. However, a few sites show precipitation as high as 7 to 8 inches during the snow-free season. Very little runoff is generated from the precipitation falling during this snow-free period as most of the summer's precipitation enters the soil profile and subsequently is used by the vegetation or evaporates.

Lack of significant moisture over long periods may stress the whitebark pine since the water holding capacity of the soils is quite low. The amount and distribution of this precipitation could also be related to the success of pine nut production. Sustained growth and good nut production are probably optimum when there is adequate moisture available from the soil throughout the entire growing period for 2 or more consecutive years.

WATER YIELDS AND WHITEBARK PINE

Whitebark pine areas are usually in the heavier precipitation zones in areas that have scanty vegetation and on soils that have a low water holding capacity. These areas yield large per-unit runoff within any given watershed; the per-unit runoff is generally exceeded only by that from the alpine areas above timberline.

In areas of western Montana that have an average annual precipitation of 30 inches, about 35 percent of this annual precipitation (about 10 inches) eventually flows out of the watershed as streamflow. The efficiency increases to about 60 percent in the 70-inch precipitation zones where about 40 inches eventually become streamflow (Farnes 1978). Snowmelt runoff from whitebark pine areas occurs late in the runoff season and is some of the most valuable water for irrigation in drainages not having reservoir storage. The runoff from these high elevations usually coincides with large irrigation demands in June and July.

Management of these stands would probably have little effect on water yield or peak flows for any given watershed. The snow at high elevations is not usually melting or is melting very little when the peak flows are occurring from these watersheds. Any change in snow distribution related to management of existing whitebark pine stands would not cause any significant changes in peak flows at downstream locations. Removal of significant volumes of timber would reduce evapotranspiration and could result in small increases in runoff until regeneration is established. In windy areas, snow redistribution could be altered by stand management and could affect the runoff. Selective thinning in denser stands would increase snow throughfall and would increase the water yield from snowmelt. However, in most situations, the costs for such treatment would probably exceed any benefits accruing from the increased runoff. Each situation would need to be evaluated on its specific merits and objectives to determine whether it was economically and environmentally feasible to attempt to manage any given stand of whitebark pine for water yield enhancement.

REFERENCES

Alberta Environment, River Forecast Centre and Survey Branch. 1986. Water Supply Review and Snow Survey Summary 1985/1986. Edmonton, AB: Technical Services Division, Water Resources Managment Services. 100 p.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Barton, Manes. 1975. SNOTEL automated snow surveys. Proceedings—western snow conference; 1975 April; Coronado, CA. Fort Collins, CO: Western Snow Conference, 1975: 6-9.

California, State of, Department of Water Resources. 1987. Water conditions in California, fall report. October. Sacramento, CA: California Department of Water Resources. 48 p.

Farnes, Phillip E. 1978. Preliminary report hydrology of mountain watersheds. Bozeman, MT: U.S. Department of Agriculture, Soil Conservation Service. 7 p.

Little, Elbert L., Jr. 1971. Atlas of United States trees, Vol. 1, conifers and important hardwoods. Misc. Publ. 1146. Washington, DC: U.S. Department of Agriculture, Forest Service. Map No. 43W and 43N.

McMillan, George D. 1981. SNOTEL: a management tool for the future. Proceedings—western snow conference; 1981 April; St. George, UT. Fort Collins, CO: Western Snow Conference, 1981: 116-119.

Ministry of Environment, Water Management Branch. 1985. Summary of Snow Survey Measurements in British Columbia 1935-1985. Victoria, BC: Province of British Columbia. 193 p.

U.S. Department of Agriculture, Soil Conservation Service. 1987. Idaho annual data summary, water year 1987. Boise, ID: U.S. Department of Agriculture, Soil Conservation Service. 30 p.

U.S. Department of Agriculture, Soil Conservation Service. 1987. Montana annual data summary, water year 1987. Bozeman, MT: U.S Department of Agriculture, Soil Conservation Service. 41 p.

U.S. Department of Agriculture, Soil Conservation Service. 1987. Nevada annual data summary, water year 1987. Reno, NV: U.S Department of Agriculture, Soil Conservation Service. 26 p.

U.S. Department of Agriculture, Soil Conservation Service. 1987. Oregon annual data summary, water year 1987. Portland, OR: U.S Department of Agriculture, Soil Conservation Service. 28 p.

U.S. Department of Agriculture, Soil Conservation Service. 1987. Washington annual data summary, water year 1987. Spokane, WA: U.S Department of Agriculture, Soil Conservation Service. 22 p.

U.S. Department of Agriculture, Soil Conservation Service. 1987. Wyoming annual data summary, water year 1987. Casper, WY: U.S Department of Agriculture, Soil Conservation Service. 27 p.

U.S. Department of Agriculture, Soil Conservation Service. 1988a. Snow surveys and water supply forecasting. Agriculture Information Bulletin 536. Portland, OR: U.S Department of Agriculture, Soil Conservation Service. 28 p.

U.S. Department of Agriculture, Soil Conservation Service. 1988b. Snow survey and water supply products reference. Portland, OR: U.S. Department of Agriculture, Soil Conservation Service, West National Technical Center, Water Supply Forecasting Staff, Data Analysis Group. 192 p.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Wendel Hann)—Is there a difference in the way whitebark pine catches and shades snow compared to subalpine fir?

A.—In younger stands where shapes are similar, for example, tall and slender, the response is similar. As the crown of the whitebark pine begins to expand, there is a much larger surface area that intercepts snowfall and the shade of the larger crowns encompasses a much larger ground surface area that reduces melt rates of snowpacks in the shaded area.

RECREATION IN WHITEBARK PINE ECOSYSTEMS: DEMAND, PROBLEMS, AND MANAGEMENT STRATEGIES

David N. Cole

ABSTRACT

Whitebark pine ecosystems are an important element of many of the most spectacular high-elevation landscapes in the western United States. They occupy upper subalpine and timberline zones in the prime recreation lands of the Cascades, the Sierra Nevada, and the Northern Rocky Mountains. This paper explores the nature of the recreational opportunities that the whitebark pine ecosystem provides and the demand for those opportunities. Important management problems are described, as are strategies for minimizing problems and optimizing recreational opportunities.

Dispersed backcountry recreation is particularly important in whitebark pine ecosystems. Maintenance of natural-appearing landscapes is a critical management objective with this type of recreational use. The principal management challenges are to (1) provide opportunities to enjoy the landscape but concentrate and contain use wherever it regularly occurs, (2) design transportation systems and facilities to blend with the surroundings, (3) strive to improve site rehabilitation techniques, and (4) minimize the obtrusiveness of other forest uses.

RECREATION DEMAND AND OPPORTUNITIES

Most whitebark pine ecosystems are remote and inaccessible by road (Arno and Hammerly 1984). Consequently, the most common recreational activities are dispersed backcountry pursuits, such as backpacking, horsepacking, hike-in fishing, photography, nature study, and contemplation. A large proportion of these ecosystems—probably well over one-half—is protected as Wilderness, under the authority of the Wilderness Act, which expressly prohibits mechanized equipment, such as four-wheeled vehicles, motorcycles, snowmobiles, and even mountain bikes. This limits the range of recreation activities in most places.

Demand for outdoor recreation is great in whitebark pine ecosystems. The Cascades and Sierra Nevada are close to the population centers of the Pacific Coast, and the Northern Rocky Mountains are an important vacation destination. Wilderness acreage in these areas is abundant and large numbers of wilderness visitors are attracted to whitebark pine ecosystems. Eight of the 10 most heavily used wilderness areas in the United States have substantial amounts of whitebark pine (fig. 1). Within these wilderness areas, visitors are frequently attracted to these high-elevation forests. Visitors commonly hike or ride through lower elevations up to the higher elevation forests and meadows that are their primary destination. This tendency can be illustrated using data collected in the most popular portion of the Eagle Cap Wilderness, in the Wallowa Mountains of northeastern Oregon. In that area, about one-third of the landscape consists of whitebark pine forests, associated subalpine meadows, and spruce-fir forests in which whitebark pine is a component. However, 46 percent of the trail miles and 78 percent of the campsites are located in these ecosystem types (Cole 1977). Most wilderness visitors want to spend most of their time in these places.

The reasons why wilderness visitors are particularly attracted to whitebark pine ecosystems have not been studied. Four attributes of these ecosystems that likely attract large numbers of dispersed recreationists are esthetics, diversity, ease of hiking and camping, and good fishing. These landscapes are highly esthetic. Views of rugged peaks are often spectacular. At these elevations the peaks look close and the open stand structure provides more frequent vistas than the denser forests of lower elevations. Stunted whitebark pines and sun-bleached snags are highly attractive, particularly silhouetted or bathed in late evening's alpenglow.

Whitebark pine landscapes are also unusually diverse. Meadows and rock outcrops are frequently as abundant as the forests and invite exploration. Creeks babbling through the meadows and the wildflowers that fill the meadows add to the diversity and interest of these areas. So do glacial features, such as cirque lakes and waterfalls, that cascade over glacially carved steps. The relatively open and highly diverse landscape invites cross-country travel and dispersed camping. It is relatively easy to hike off trail and to find attractive campsites away from heavily trafficked places.

Finally, the fact that whitebark pine ecosystems frequently occupy glacially carved landscapes means that cirque lakes are common features. These lakes attract visitors both as an esthetic and logical destination area and because they frequently offer good fishing. Fishing is an important wilderness activity for many visitors. In many wilderness areas, more than one-half of all visitors spend some time fishing (Lucas 1980). Fishing quality is

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

David N. Cole is Project Leader and Research Biologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Missoula, MT 59807.

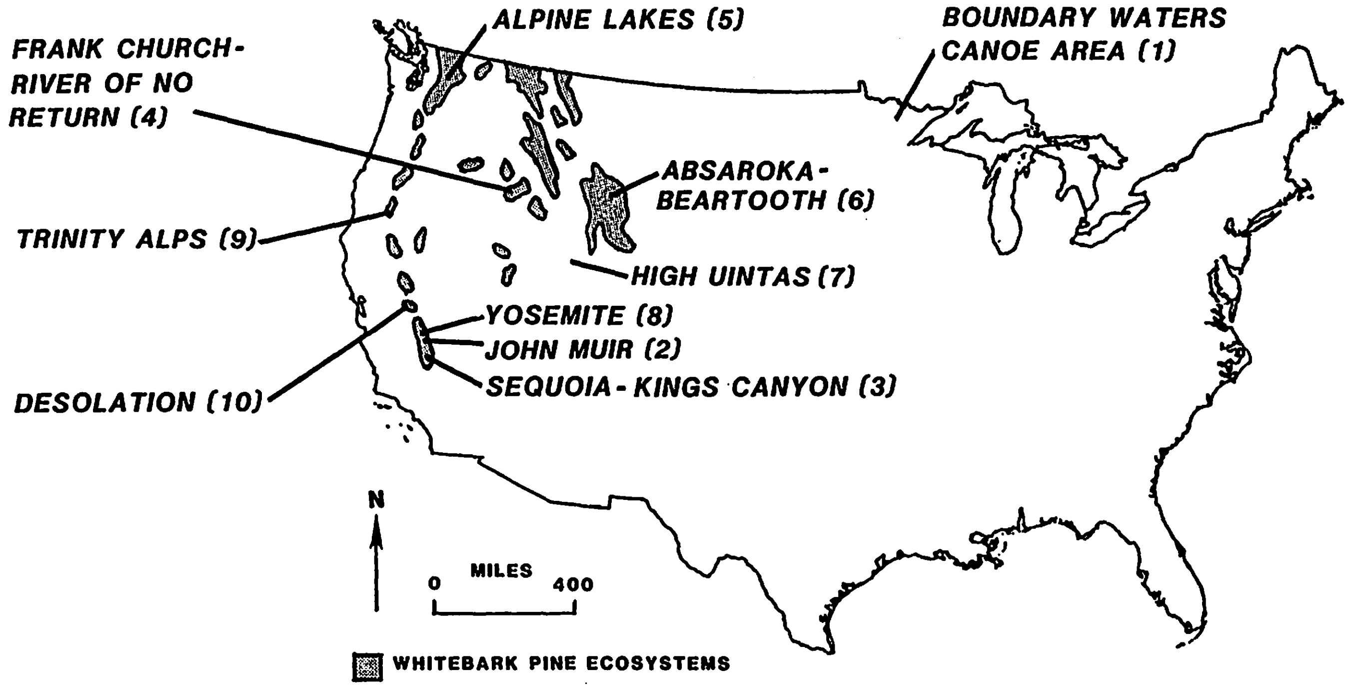


Figure 1—Eight of the ten most heavily-used wilderness areas in the country are in places with whitebark pine ecosystems. Numbers in parentheses are the rank of each wilderness area in terms of amount of use.

often an important consideration when selecting a wilderness destination and goes a long way toward explaining the popularity of whitebark pine ecosystems.

While backpacking, horsepacking, hiking, and fishing are probably the most common recreational opportunities that whitebark pine ecosystems provide, other types of recreation also are pursued. In the few places where roads access whitebark pine forests, scenic driving, picnicking, and roadside camping occur. The Tuolumne Meadows-Tioga Pass area in Yosemite National Park is a good example of a popular place offering this style of recreation. Snowmobiling and off-road-vehicle driving are well-established in some places and mountain biking is growing greatly in popularity. Demand for these experiences is high, again because of esthetics, diversity, and fishing. However, these opportunities are limited by road access and are not as unique to these ecosystems as is backcountry recreation. Finally, downhill and cross-country skiing occur in whitebark pine forests, but are not especially common there.

One theme common to all of these recreational pursuits is the importance of scenic quality and a landscape that has not been greatly altered by man. This latter concern is explicit in wilderness, where the Wilderness Act (P.L. 88-577) directs management to preserve wilderness such that it "appears to have been affected primarily by the forces of nature, with the imprint of man's work substantially unnoticeable." Scenic qualities and an environment that contrasts with civilization are important motivations for visiting wilderness (Lucas 1985; Stankey and Schreyer 1987). I would hypothesize that these motivations are also important to recreationists outside wilderness and more important in whitebark pine ecosystems than in most other ecosystems.

A major management concern, then, should be to minimize the evidence of human use. This means minimizing the impacts caused by recreational use and sensitive design of transportation routes and facilities to accommodate recreational use. It also means minimizing the obtrusiveness of other forest uses, such as timber harvesting, grazing, and mining.

COMMON MANAGEMENT PROBLEMS

The most common problems that recreation managers face in whitebark pine ecosystems are resource degradation and crowding as a result of intensive recreational use. Trail and campsite degradation, packstock impacts, development of user-created trails around lakeshores, litter, and loss of solitude are all significant problems in many places (Washburne and Cole 1983). These problems are not unique to whitebark pine ecosystems, but they may be particularly pronounced due to the popularity of those landscapes.

Two studies have evaluated the susceptibility of whitebark pine ecosystems to recreational impact. In the Eagle Cap Wilderness, campsite impacts in whitebark pine forests were pronounced. The undergrowth vegetation, primarily grouse whortleberry (*Vaccinium scoparium*), is quite fragile; the mean vegetation loss on the central part of campsites was 94 percent. This compares, for example, with neighboring sedge (*Carex nigricans*) meadows where the mean vegetation loss on campsites was only 40 percent (Cole 1981).

Dale (1973) studied trails in whitebark pine, lodgepole pine, and spruce-fir forests of the Lee Metcalf Wilderness, in the Madison Range in southwestern Montana. Trails in whitebark pine forest were not particularly deep, but they tended to be unusually wide, particularly when subjected to heavy use. Factors that might contribute to wider trails here include (1) rocky soils that tend to cause users to spread out, (2) sandy soils that are readily displaced laterally, and (3) open vegetation that makes walking side-by-side easier. Generally, the suitability of whitebark pine forests for trails appears to be good to moderate, while suitability for campsites is moderate to poor.

Two problems that are particularly pronounced in whitebark pine ecosystems are the impacts associated with the collection of fuelwood for campfires and widespread proliferation of user-created trails and campsites. Collecting and burning wood in campfires is a common practice in most wilderness areas. In popular places this practice leads to large areas denuded of all downed wood and extensive damage to standing trees, both dead and alive. Damage to trees, from broken off lower branches to felled saplings and hacked snags, presents obvious evidence of human impact. A forest floor totally devoid of downed wood also looks unnatural to many visitors. In addition to these esthetic impacts, there are undoubtedly ecological changes that result from this practice. Recent research suggests that removal of large woody residue on and in the soil may have serious consequences. Large decaying wood plays an important and irreplaceable role in the ecosystem—for example, in water and nutrient conservation and as a substrate for biological activity (Franklin and others 1981; Harvey and others 1979).

These problems are likely to occur wherever fuelwood consumption rates exceed the rate at which downed woody material is produced. Problems are particularly likely in whitebark pine forests because productivity is relatively low and consumption is often high, due to the popularity of these places as destination areas. In a few study areas in the Sierra Nevada, for example, Davilla (1978) found that whitebark pine wood litter production was very low compared with that of lodgepole pine and mountain hemlock. This led him to recommend that fuelwood never be collected in forests where the dominant tree is whitebark pine. In many national parks campfires are prohibited at higher elevations; however, campfires are seldom prohibited in wilderness areas administered by the Forest Service, U.S. Department of Agriculture (Washburne and Cole 1983). While it is very common to discourage the use of campfires (and encourage visitors to use stoves), it is uncommon to differentiate among ecosystems in terms of their productivity and therefore the importance of not having a campfire (Cole in press).

Another problem that is particularly pronounced but not unique to whitebark pine forests is the proliferation of campsites and user-created trail systems in popular destination areas. Proliferation reflects heavy use, ease of cross-country travel, and the large number of potential campsites in these ecosystems. For example, all campsites were inventoried in a 325-acre area around two popular lakes in the Eagle Cap Wilderness. More than 200 campsites were found (fig. 2). Virtually every site around Mirror Lake with the potential for camping showed some evidence of use. Also, the fact that recreational use in the area was spread over a very large number of sites did not mean that impact on these sites was negligible. More than half the campsites had experienced a moderate to great loss of vegetation (Cole 1982). In addition to all these campsites, numerous informal trails branched off from the constructed trails to other campsites and to circle the lakes. Created by users, many of these trails are poorly located and prone to erosion.

Impact problems are exacerbated by the difficulty of rehabilitating damaged recreation sites in whitebark pine forests. Rehabilitation is required wherever excessive or inappropriate use has occurred or whenever management objectives change. Much of the current rehabilitation work in wilderness is focused on campsites close to lakeshores. In the past, few wilderness areas had specific objectives about appropriate campsite locations; today objectives frequently stress maintaining lakeshores in as natural a condition as possible. It is also common to rehabilitate braided trails and trails that have been relocated either because they were inadequately constructed or poorly located.

Without assistance, trails and campsites in whitebark pine ecosystems will require decades—if not centuries—to recover. For example, campsites in a lodgepole pine-whitebark pine forest around heavily impacted Bullfrog Lake in Kings Canyon National Park were closed to overnight use in 1961. After 17 years of closure, soil compaction levels had returned to near-natural levels. Litter depth and volume, however, remained substantially below those found in undisturbed forest. Tree damage, vegetation loss, and user-created trails remained pronounced, although recovery had begun. Tree mutilations were often covered over with new growth and some of the trails were being recolonized (Parsons 1979; Parsons and DeBenedetti 1979).

Attempts to assist site rehabilitation in these ecosystems are challenging. It is difficult to effectively close sites to use, and without effective closure sites are not likely to recover (Cole and Ranz 1983). Even where assistance has been effective in establishing an initial plant cover on damaged sites, recolonization of the entire site may be slow. For example, the success of transplanting was followed over a period of 5 years on two campsites in the Eagle Cap Wilderness. Mean vegetation cover on these two sites increased from 6.3 and 10.8 percent in 1979 to 7.3 and 12.3 percent in 1984. This compares with a mean vegetation cover of about 60 percent on undisturbed sites. Most of this increase was a result of the original transplanting of plugs. While most transplants survived, they had not spread and did not contribute much to a gain in vegetation cover (Cole 1986).

A final problem is disposal of human waste. Toilet facilities are seldom provided in whitebark pine ecosystems because use frequently is dispersed and facilities often are considered inappropriate. Where heavy overnight use occurs, camping areas can be littered with feces and toilet paper. In addition to being an esthetic problem, this can pose a health hazard. It is difficult to clearly demonstrate a cause-and-effect relationship between inadequate disposal of human waste and disease;

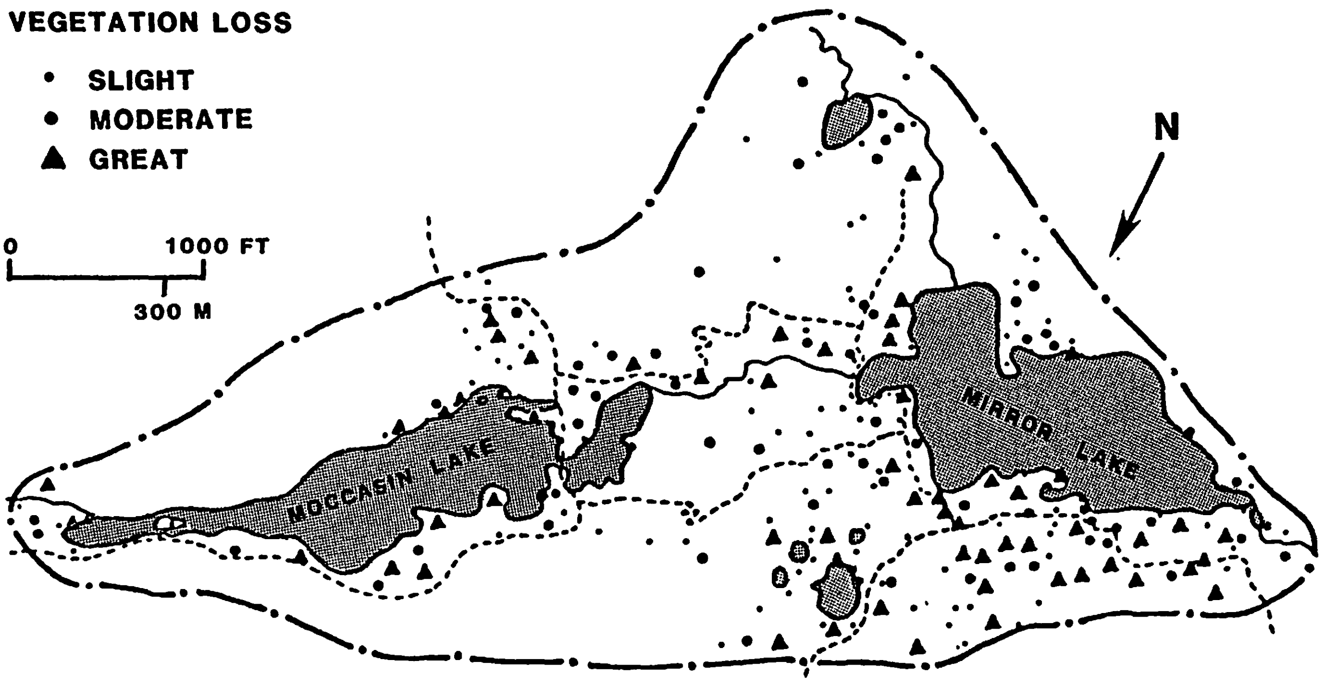


Figure 2—The distribution and degree of vegetation loss on campsites around Mirror and Moccasin Lakes in the Eagle Cap Wilderness, OR.

however, there is some evidence that *Giardia* spp. are more abundant in surface waters of frequently used recreational areas (Suk and others 1987). *Giardia* contamination is now a common problem in whitebark pine ecosystems.

MANAGEMENT STRATEGIES

Maintaining a natural-appearing landscape is the key to recreation management in whitebark pine ecosystems. Recreationists visiting these places expect to see little evidence of human use and impact. Characteristics of whitebark pine forests that make this difficult are inherently low productivity and low resilience. Once damage occurs, recovery takes a long time. Given the popularity of these places with backcountry recreationists, this low resilience means that management must be especially proactive. Management must strive to avoid problems rather than deal with them after they have occurred.

Four challenges face managers of whitebark pine ecosystems seeking to optimize recreational opportunities. First, it is important to concentrate and contain recreational use wherever it regularly occurs. Extremely low recovery rates make it imperative to minimize the number of places that are disturbed by recreational use. This is accomplished by confining as much use as possible to established trails and campsites. Overlooks should be designed to contain use and, if necessary, managers should harden heavily trafficked surfaces. Wilderness visitors should be encouraged to stay on constructed trails and use well-established or even officially designated campsites. Where packstock use is allowed, facilities for concentrating impact in small areas (for example, hitchrails or corrals) should be provided. The consequence of not pursuing this strategy is proliferation of impacts—a mistake that will require decades and centuries to correct.

Second, transportation systems and facilities can increase recreational opportunities in these ecosystems. Scenic byways and overlooks can add greatly to the enjoyment of motorized recreationists. Well-constructed trails, hitchrails, and toilets can add to the enjoyment of backcountry recreationists. Sensitive design is important, however. Cut slopes visible for miles—whether along roads or trails—are intrusive and detract from the natural environment. The challenge is to make certain that transportation systems and facilities blend into the natural-appearing landscape. This is particularly true inside wilderness, where the general philosophy is to provide facilities for purposes of safety and resource protection, but not visitor convenience.

The third challenge is to improve our ability to rehabilitate damaged sites. More experimentation with rehabilitation methods is needed. Rehabilitation efforts need to be documented and monitored; successes and failures need to be communicated to others. One example of a step in the right direction is a new rehabilitation program begun in whitebark pine and other ecosystems in Yosemite National Park. Experiments with seeding, nursery propagation, transplanting, and a variety of cultural treatments are under way. A controlled trampling experiment was conducted to evaluate the resistance of individual plant species and plant communities to trampling. Rehabilitation success is being monitored and results are being published in reports (Hadley and Moritsch 1988). Similar efforts are needed elsewhere.

The fourth challenge is to minimize the obtrusiveness of forest uses other than recreation. Timber harvesting, domestic livestock grazing, and mining are uses that can leave obvious disturbances on the landscape and detract from the esthetics of these places. Where these uses occur, every effort should be made to separate these uses from recreational uses. Buffer strips along trails and roads can screen places where disturbance is evident. Trails can also be rerouted away from these places. Grazing can be limited to times and places where recreational use is low.

A CONCLUDING REMARK

A final challenge I might mention is the challenge I experienced in trying to write this paper. Information on recreational opportunities and problems in specific ecosystem types is sorely lacking. Consequently I had few concepts or data to work with and no precedent to follow or even build upon. Biologists seem to have conveniently ignored recreation management, preferring to concentrate on management of more tangible commodities. Recreation managers and researchers too frequently ignore the unique opportunities and constraints that each ecosystem presents. Better cooperation between these two groups is needed to effectively manage whitebark pine and other ecosystems.

REFERENCES

Arno, Stephen F.; Hammerly, Ramona P. 1984. Timberline—mountain and arctic forest frontiers. Seattle, WA: The Mountaineers. 304 p.

Cole, David N. 1977. Man's impact on wilderness vegetation: an example from Eagle Cap Wilderness, northeastern Oregon. Eugene, OR: University of Oregon. 307 p. Dissertation.

Cole, David N. 1981. Vegetational changes associated with recreational use and fire suppression in the Eagle Cap Wilderness, Oregon: some management implications. Biological Conservation. 20(4): 247-270.

Cole, David N. 1982. Controlling the spread of campsites at popular wilderness destinations. Journal of Soil and Water Conservation. 37(5): 291-295.

Cole, David N. 1986. Ecological changes on campsites in the Eagle Cap Wilderness, 1979 to 1984. Res. Pap. INT-368. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 15 p.

Cole, David N. [In press]. Low-impact recreational practices for wilderness and backcountry. Gen. Tech. Rep. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Cole, David N.; Ranz, Beth. 1983. Temporary campsite closures in the Selway-Bitterroot Wilderness. Journal of Forestry. 81(11): 729-732.

Dale, Donn Richard. 1973. Effects of trail-use under forests in the Madison Range, Montana. Bozeman, MT: Montana State University. 96 p. Thesis.

Davilla, Bill. 1978. Firewood production, use and availability in the High Sierra. In: Stanley, J. T., Jr.; Harvey, H. T.; Hartesveldt, R. J., eds. A report on the wilderness impact study: the effects of human recreational activities on wilderness ecosystems with special emphasis on Sierra Club wilderness outings in the Sierra Nevada. San Francisco, CA: Sierra Club, Outing Committee: 94-128.

Franklin, Jerry F.; Cromack, Kermit, Jr.; Denison, William; [and others]. 1981. Ecological characteristics of old-growth Douglas-fir forests. Gen. Tech. Rep. PNW-181. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 48 p.

Hadley, Richard L.; Moritsch, Barbara J. 1988. Subalpine and montane revegetation in Yosemite. Park Science. 8(4): 20-21.

Harvey, A. E.; Jurgensen, M. F.; Larsen, M. J. 1979. Role of forest fuels in the biology and management of soil. Gen. Tech. Rep. INT-65. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 8 p.

Lucas, Robert C. 1980. Use patterns and visitor characteristics, attitudes, and preferences in nine wilderness and other roadless areas. Res. Pap. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 89 p.

Lucas, Robert C. 1985. Visitor characteristics, attitudes, and use patterns in the Bob Marshall Wilderness complex, 1970-82. Res. Pap. INT-345. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 32 p.

Parsons, David J. 1979. The recovery of Bullfrog Lake. Fremontia. 7(2): 9-13.

Parsons, David J.; DeBenedetti, Stephen H. 1979. Wilderness protection in the High Sierra: effects of a 15-year closure. In: Linn, R. M., ed. Proceedings of the first conference on scientific research in the national parks; 1976 November 9-12; New Orleans, LA. Transactions and Proceedings Series No. 5 Washington, DC: U.S. Department of the Interior, National Park Service: 1313-1318.

Stankey, George H.; Schreyer, Richard. 1987. Attitudes toward wilderness and factors affecting visitor behavior: a state-of-knowledge review. In: Lucas, Robert C., comp. Proceedings—national wilderness research conference: issues, state-of-knowledge, future directions; 1985 July 23-26; Fort Collins, CO. Gen. Tech. Rep. INT-220. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 246-293.

Suk, Thomas J.; Sorenson, Stephen K.; Dileanis, Peter D. 1987. The relation between human presence and occurrence of *Giardia* cysts in streams in the Sierra Nevada, California. Journal of Freshwater Ecology. 4: 71-75.

Washburne, Randel F.; Cole, David N. 1983. Problems and practices in wilderness management: a survey of wilderness managers. Res. Pap. INT-304. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 56 p.

TIMBER MANAGEMENT AND TARGET STANDS IN THE WHITEBARK PINE ZONE

Jimmie D. Chew

ABSTRACT

Regardless of the mixture of land management objectives, quantification of the type of stands that will meet these objectives, target stands, is needed. Quantification of target stands is essential as the starting point for the diagnosis of treatment needs and to achieve consistency over time in the interpretation of a given management direction.

To facilitate quantification of target stands a U.S. Forest Service Regional form has been developed. This form provides one format for identifying various essential attributes.

For many resource objectives the desired conditions include the aggregate conditions of a number of stands in a given area over time. A Data General computer program has been developed to assist with the summarization and graphic representation of many stands projected over time by the Stand Prognosis Model. The summary and representation can be linked to key attributes that are descriptive of the target stands or to area conditions.

INTRODUCTION

Timber management can mean many things to different people. Within the whitebark pine (*Pinus albicaulis*) forest types of the Northern Region, Forest Service, U.S. Department of Agriculture, the activities that we usually associate with timber management will generally be done with little or no emphasis on sustained production of wood products.

Instead of identifying our management activities in the whitebark pine zone as timber management, it is more appropriate to refer to them as forest management: the application of our knowledge of silvics and forest ecology to create and maintain the types of stands that will meet our management objectives over time.

NEED FOR TARGET STANDS

The desired future condition that we refer to when we talk about implementing National Forest plans has to be considered at both the level of the individual stand and their aggregates across the forest. For all of our management objectives we need stands that will provide the desired conditions over time. How can we utilize our knowledge to ensure that we have such stands? How can we get from plans to the desired type of stands on the ground? How can we communicate with different resource managers over time about the type of stands we need? How can we achieve an adequate degree of consistency in the application of a given management direction between National Forests within a Region?

The use of site-specific evaluations of present and future stand conditions and the description of characteristic stands that meet Forest plan objectives are necessary to answer these questions. An essential part of being able to transfer our management objectives to the ground is to quantify what types of stands are needed to meet these objectives. Only by a comparison of an existing stand to a target stand can we devise a treatment or determine if no treatment is appropriate. All too often a treatment is prescribed simply because it is possible to use it; not because it is needed to modify existing stand conditions to achieve long-term management objectives.

REGIONAL FORM FOR TARGET STANDS

To assist in the quantification of target stands the Northern Region has provided a standard format: Regional Form R1-FS-2470-24 (12/86). An example of its application has been taken from the Lewis and Clark National Forest in Montana (tables 1 and 2). The management objective addressed by these two target stands is for "timber production and livestock grazing." Each target stand represents the application of this resource objective to a specific set of habitat types each one featuring a different tree species and different density levels over time.

Target stands have not been defined for all ecosystems and resource management objectives, specifically not for whitebark pine. Nevertheless, we can identify some of the questions that must be answered to formulate a target stand for meeting important management objectives in whitebark pine ecosystem. For an objective of producing cones for grizzly bear food what should the stands be like? Do we want stands that are all whitebark pine? Or should they be a mixture of species? Should they have uniform spacing of trees, or clumpy spacing? How long will it take the stand to start producing an adequate number of cones for food? Will the stand need to be thinned to remove natural regeneration of spruce and subalpine fir in the understory? How do stands in the Gallatin National Forest compare to those in the Flathead National Forest in regard to these questions. Answers to these questions

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Jimmie D. Chew is Silviculturist, Northern Region, Forest Service, U.S. Department of Agriculture, Missoula, MT 59807

Table 1—Target stand description

Development stage	Age	Trees per ac	Basal area	QM dia	Structure	Height	Species	Growth	I&D	Forage	Remarks
Seedling	0-15	300-2000	-	0-1	Single story	0-8	LP	-	Dwarf Mstoe minor occurrence	B-400 H-100	DF, S-acceptable
Sapling	15-30	500-1600	-	2		8-25	LP	10		B-300 H-75	Begins providing game hiding cover
Pole	31-50	400-780	70-210	5		25-50	LP	20		B-200 H-50	
Imm. saw	51-70	200-300	130-240	8		50	LP			B-200 H-50	
Mature saw	71-110	200-300	180-240	10		65	LP	30		B-200 H-50	

MANAGEMENT AREA: MA-B
HABITAT TYPES: Abla/Vasc ^{730}, Abla/Libo-Vasc ^{663}, Psme/Libo-Caru ^{292}
PRIMARY RESOURCES: Timber and Livestock Grazing

Table 2—Target stand description

Development stage	Age	Trees per ac	Basal area	QM dia	Structure	Height	Species	Growth	I&D	Forage	Remarks
Seedling	0-20	200-1700	-	0-1"	Single story	0-4'	DF	-	Budworm Low, Root Rot Mod 15% Area	B-400 H-600	
Sapling	21-40	200-1200	-	2		5-25	DF	3	SBW Low RR - Low 5% Area	B-300 H-450	
Pole	41-70	200-700	40-140	6		25-30	DF	20	SBW Low RR-Low	B-200 H-300	
Imm. saw	71-100	200-400	80-175	9		30-50	DF	44		B-200 H-300	
Mature saw	101-130	150-280	100-180	11		50-55	DF	30		B-200	

MANAGEMENT AREA: MA-B
HABITAT TYPES: Picea/Sest ^{460}, Abla/Clps ^{770}, Psme/Juco ^{360,} Psme/Spbe ^{340}
PRIMARY RESOURCES: Timber with Livestock Grazing

are needed to quantify target stands that will meet our management objective of providing cones for grizzly bear food. Target stands for all other management objectives in the whitebark pine zone also need to be developed.

NEED FOR ANALYSIS OF STAND AGGREGATES

The desired future forest condition goes beyond what we describe for the individual stand. Creating a 5-acre stand to provide cones as food may be meaningless if it is the only such food source within an entire area. As we look at areas, they should be a collection of individual stands. As there is variability in the types of stands we can create, there is variability in how these stands respond to treatments over time. Evaluations of existing and future conditions over an area need to be as site specific as we can make them. This is perhaps more critical within the whitebark pine ecosystems than in many other forested ecosystems. Many of the presentations at this symposium have stressed how slowly whitebark pine ecosystems recover from impacts. Instead of using average responses over time, the Stand Prognosis Model (Wykoff and others 1982) allows us to generate site-specific values. We can evaluate our ability to meet given resource objectives in terms of the development of specific stands within a given area. The Northern Region has linked a Data General graphics package with the Prognosis output to provide area summaries for resource attributes. For example the acres within different stand structural stages can be displayed for specific future decades (fig. 1). The changes in these attributes are stand specific based upon stand projections that will change with various treatment scenarios.

In terms of whitebark pine forests and the grizzly bear food management objectives discussed above, we can assess specific stand attributes such as blister rust status, crown ratio, tree height, and stand density for their influence on cone production. We can produce graphs similar to figure 1 to represent the effect of our management choices on acres in various cone production stages over time (fig. 2 and 3). By projecting the subsets of stands relating to the different cone production stages of figure 2, we can develop a picture, decade by decade, of the efficiency of management in achieving our chosen desired future conditions. An example is shown in figure 4.

Other resource objectives might be given priority within the whitebark pine zone—for example, watershed enhancement. As in the approach outlined above, needed information would be developed to describe desired stand conditions that define target stands for achieving the water resource goals. Similarly, stand and area projections would be aggregated for the present and for future time periods to guide decisions and provide benchmarks for monitoring management performance.

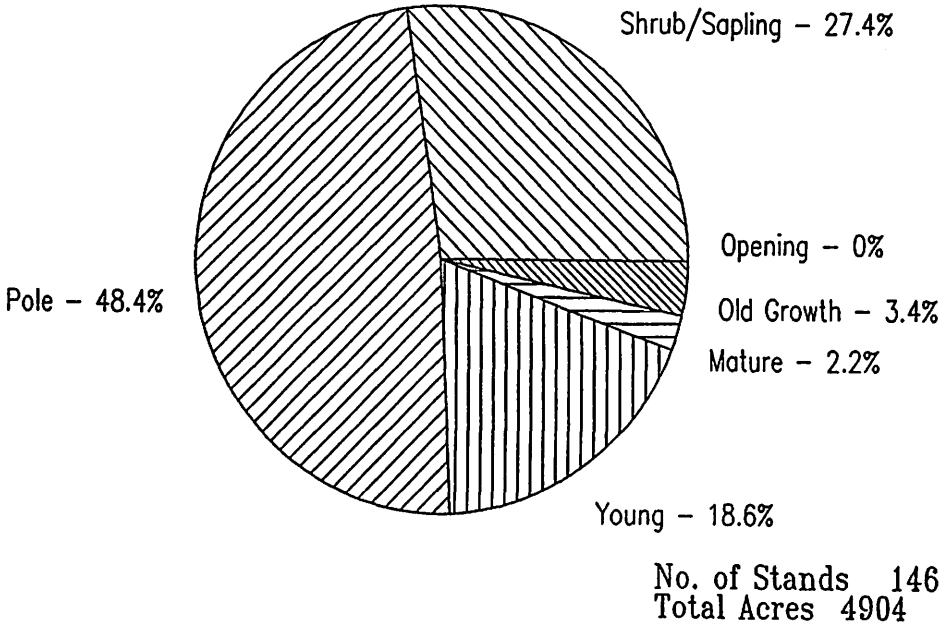


Figure 1—Stand structure stages of whitebark pine stands for wildlife habitat of the Gallatin National Forest for decade starting in 2021.

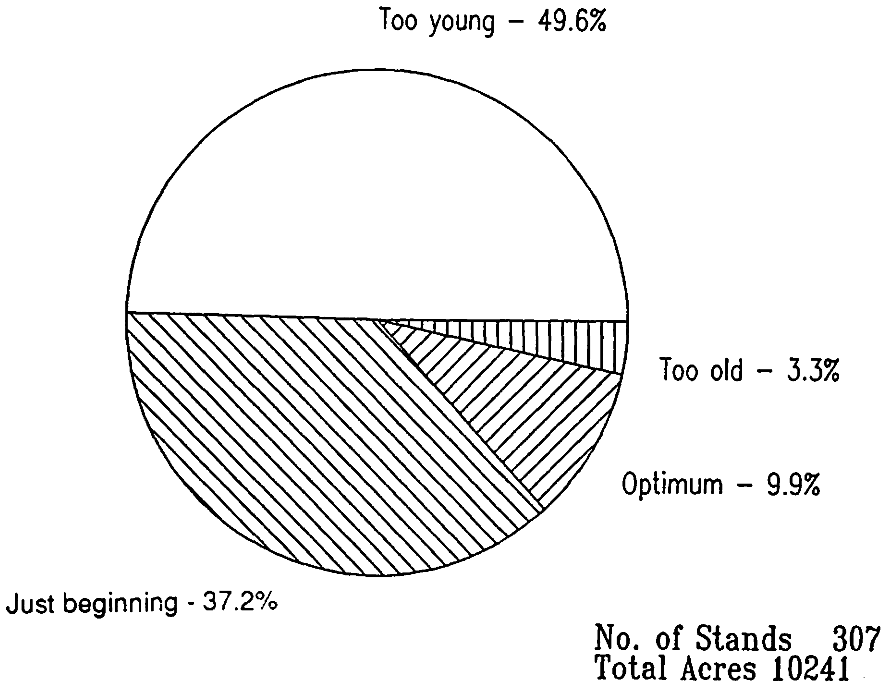


Figure 2—Projected percent of whitebark pine stands in various stages of cone production for the decade starting in 1990.

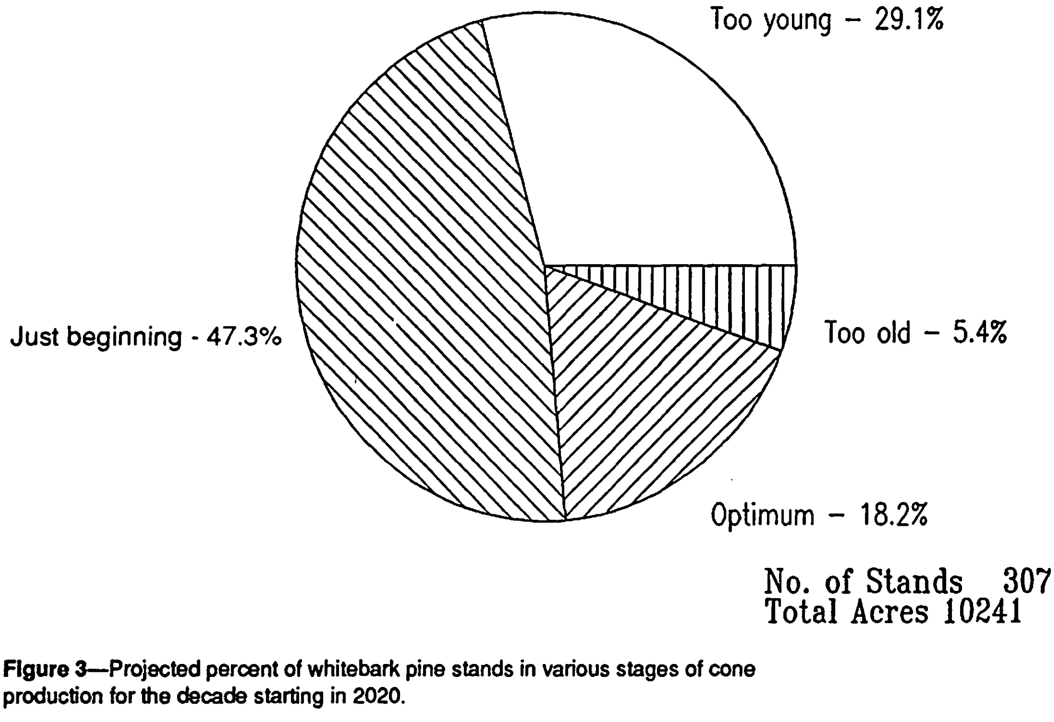


Figure 3—Projected percent of whitebark pine stands in various stages of cone production for the decade starting in 2020.

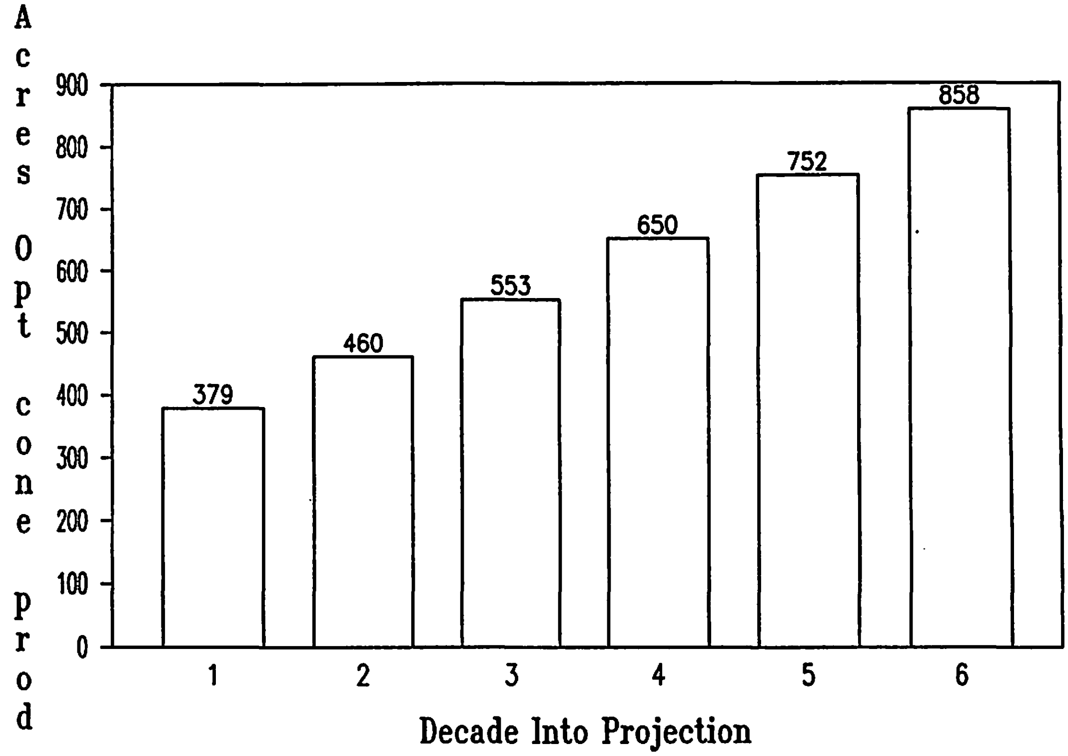


Figure 4—Projected acres of whitebark pine that will be optimum for whitebark pine cone production by decades. Projection is for 147 stands, 4,940 acres.

SUMMARY

Whether our management objectives are for watershed management, timber production, wildlife habitat, visual management, or any mixture of these resources, quantification of target stands is essential. Quantification of target stands provides the starting point for the diagnosis of treatment needs and consistency for the many resource managers involved in the interpretation of a given management direction over time. Without the quantification, it becomes difficult to monitor and judge the success of vegetative treatments and to rationally modify them to ensure meeting management objectives.

REFERENCES

Wykoff, William R.; Crookston, Nicholas L.; Stage, Albert R. 1982. User's guide to stand prognosis model. Gen. Tech. Rep. INT-133. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 112 p.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Earle F. Layser)—Is it not presumptuous for us to assume we can set objectives for these high-elevation forests? Do they not by their very nature dictate their own objectives?

A. The very nature of these forests sets limitations and defines potentials. What would be presumptuous would be that we, at this time, assume we know all there is to understand concerning the limitations of these high-mountain ecosystems.

THE ROLE OF GENETIC DIVERSITY IN WHITEBARK PINE CONSERVATION

Peter F. Brussard

ABSTRACT

Whitebark pine, like most other coniferous trees, has high levels of genetic variation. This has been demonstrated for allozymes, and can be inferred for recessive deleterious genes as well. The current levels of genetic diversity in different populations of whitebark are determined to a large extent by their history and degree of isolation. Populations consisting of many contiguous or semicontiguous stands will have the highest amounts of heterozygosity. Small, geographically isolated, populations will have the least because of the strong influence of founder effects and restricted gene flow. If events occur that reduce current levels of gene flow in whitebark pine populations, levels of inbreeding are likely to increase. This will result in increased expression of deleterious recessives which, in turn, will reduce rates of survivorship and reproduction. These events can be particularly critical in populations already challenged by parasites, disease, or climate change.

INTRODUCTION

Consideration of genetic factors is critical in developing a management plan for any species because genetic variability is important for both short-term population fitness and long-term adaptation to changing environmental conditions. As the effects of global warming become apparent during the next half century, both factors are likely to become extremely relevant to conservation planning (Peters 1988; Peters and Darling 1985). Unfortunately, populations may not begin to show symptoms of genetic decline until the F_2 generation; for long-lived species like whitebark pine this seems to be an impossibly long time frame. However, this also means that decisions made now regarding genetic management will have important consequences for the resource many years in the future.

GENETIC VARIATION IN OTHER SPECIES OF PINES

At this writing there is no published survey of genetic variation in whitebark pine (*Pinus albicaulis*). However, a recent review by Ledig (1986) pointed out that genetic variation in conifers in general and pines in particular is usually quite extensive, although there are some notable exceptions. Allozymes (polymorphic proteins) have been surveyed in 24 species of *Pinus* at between 4 and 59 loci per species. The proportion of these loci found to be polymorphic (P), under the criterion for polymorphism that the most common allele must occur in a frequency of less than 0.95, averages 0.53 ± 0.25 and ranges from 0 to more than 0.90 per species. The mean heterozygosity (H) for these species, calculated over this same range of loci, is 0.17 ± 0.09 and ranges from 0.0 in Torrey pine (*P. torreyana*) to 0.36 in loblolly pine (*P. taeda*) (data taken from table 1 in Ledig [1986]).

The average values for P and H in pines are higher than for most other plants and animals. For example, average P and H in vertebrates are 0.17 and 0.05, in invertebrates, 0.38 and 0.11, and in plants, 0.26 and 0.07, respectively (Nevo 1978). Although estimating levels of variation in entire genomes from the relatively small number of loci typically used (15-40) in the studies from which these figures are derived may be weak from a statistical standpoint (see Mitton and Pierce 1980), allozyme variants are generated and lost by exactly the same processes that generate and erode other kinds of genetic variation—mutation, drift, and selection. Thus, it is likely that species of pines with high levels of allozyme variability would also tend to be rich in other kinds of genetic variability. This seems to be true as well for polygenic traits such as growth rate, growth form, and wood characteristics and for genetic loads (Ledig 1986).

While certain types of genetic variation are important for both short-term population fitness and long-term adaptation, other variants, especially when occurring in homozygous form, may be deleterious. These deleterious alleles are referred to collectively as a population's genetic load, and expressed genetic load can significantly depress the population's overall levels of fertility and viability. Genetic load in conifers is often high; for example, depression in embryo viability following inbreeding is commonly reported (Namkoong and Bishir 1987). Ledig (1986) reported that embryonic lethal equivalents (recessive lethals that if dispersed among different embryos would cause, on average, one selective death) range from 0.3 to 9.4 per zygote and average 5.2 in eight species of *Pinus*;

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Peter F. Brussard is Professor and Chairman, Biology Department, University of Nevada-Reno, Reno, NV 89557.

the usual range is 1 to 4 in other plants, humans, and fruit flies. It should be noted that the total genetic load is actually much higher in pines because much additional mortality occurs after germination.

The high levels of genetic variation typical of pines are a consequence of many aspects of their life histories and reproductive biology. Most populations are exposed to heterogeneous selective pressures along major environmental gradients of elevation, exposure, and soil types. Timing of pollen release usually promotes outcrossing, and wind pollination provides opportunities for long-range gene flow. Furthermore, pines are long-lived and accumulate large numbers of somatic mutations; these mutations are transmitted to succeeding generations when somatic tissue is converted into germinal tissue. Ledig (1986) believes that this high mutational load drives the breeding system to outcrossing, which in turn protects all forms of genetic variation. The resulting high genetic load is expressed only under extreme inbreeding. The suggestion by Namkoong and Bishir (1987) that many of the genes that depress embryo viability in conifers may represent unique mutants, which will be eliminated by selection, is consistent with this idea.

Ledig (1986) has also summarized the patterns of distribution of genetic variation in various pine species. In general, he found that species of limited range have little variation, while widely distributed species tend to have more. However, there are many exceptions. For example, loblolly pine is wide ranging and highly variable, while red pine (*P. resinosa*) has a wide range and almost no detectable variation. Western white pine (*P. monticola*) is genetically uniform across most of its range, but is highly variable in California. Torrey pine is found only in two small populations, both of which lack genetic variation, but each population is genetically unique. Great Basin bristlecone pine (*P. longeava*) has a highly fragmented range, but it maintains high levels of variation with 90 percent of the total variation in the species found in any one population. Clearly, the current levels and distribution of genetic diversity in these species are complex functions of the species' dispersal history, population size, and degree of present range fragmentation.

GENETIC VARIATION IN WHITEBARK PINE

No survey of genetic variation has yet been done for whitebark pine throughout its range (McCaughey and Weaver, this proceedings), although such a survey is badly needed. A few relevant data are available, however. Furnier and others (1986) reported polymorphism at 9 out of 12 enzyme systems (75 percent) (or for 11 out of 20 presumed loci—[55 percent]) examined by electrophoretic techniques in two populations from Alberta. Linhart and Tomback (1985) used allozyme data to determine the genetic composition of multitrunked individuals in populations from Colorado and Wyoming. Their paper provided enough raw data for me to make an estimate of heterozygosity of 0.32 for the trees in one clump, although the small number of loci (*N*=4) and individuals (*N*=5) involved, plus the strong probability that all the individuals in the clump are siblings or half-siblings, make this estimate very tentative. Even with these limited data, however, it appears that whitebark pine has ample genetic variation, perhaps even more than the average for pines.

Because of its bird-mediated seed-dispersal mechanism, whitebark pine populations are likely to have a genetic structure different from those of wind- or gravity-dispersed species. Some data exist on this structure within clumps of trees, among clumps within populations, and among different populations. Furnier and others (1987) and Linhart and Tomback (1985) reported that clusters of two to 12 trees consist of at least some genetically different individuals. Weaver and Jacobs (this proceedings), however, present data showing that some clumps result from basal branching of the same genetic individual. Thus, trees with more than one trunk may consist either of a single genotype or more than one genotype (termed multitrunk trees and tree-clusters respectively by Tomback and others [this proceedings]). However, these differences cannot be determined without genetic examination.

Some of the individuals within tree-clusters are likely to be closely related because nutcrackers often gather and cache together seeds from the same parent tree. This was confirmed by Furnier and others (1987), who found that individual trees in a cluster were genetically more similar to each other than they were to trees in neighboring clusters. Further evidence is provided by Tomback (in press), who found that seed caches contained both related and nonrelated seeds and estimated with simulations that 73 to 93 percent of the caches contained two or more sibling or half-sibling seeds.

The close relatedness of trees within clumps evidently does not extend to clumps within stands. Furnier and others (1987) showed that individuals in neighboring clumps were not any more similar genetically than were individuals in distant clumps. Tomback and Linhart (1989) point out that such a pattern would be expected in a bird-dispersed species; one bird may disseminate seeds from a stand of trees to different areas, and within these areas, more than one nutcracker, each with seeds from different stands, may cache. Thus, gene flow among contiguous or semicontiguous stands of whitebark pine is probably rather widespread, resulting in large, diverse, and relatively homogeneous populations over fairly large areas due to the large home range of its dispersal agent and its wind pollination system.

Genetic heterogeneity probably increases on a larger geographical scale, however. Within its range, the distribution area of whitebark pine is highly fragmented, and gene flow is no doubt much less common among these units than within them. Furthermore, many small, isolated populations were probably established as a result of long-distance seed dispersal by nutcrackers (Wells 1983). Such establishment would lead to strong founder effects in these populations, and gene flow among them would be sporadic and uncommon. The net result of this fragmentation is likely to be a complex of genetically differentiated units within the main body of the species' range and highly heterogeneous and genetically depauperate populations in areas outside the main Rocky Mountain and Sierra Nevada cordilleras. Smith (this proceedings) presented data that support this supposition; he found appreciable differences in the frequency of genes coding for xylem resin monoterpenes between populations in Nevada, California, and Oregon.

GENETIC FACTORS AND WHITEBARK PINE CONSERVATION

The goal of conservation genetics is to maintain populations large enough to keep levels of inbreeding low and to maintain high levels of heterozygosity. This is not only because there is reasonable evidence that supports the idea that heterozygosity at certain loci leads to increased fitness, but also because even moderate inbreeding can cause large increases in the expression of a population's genetic load. This increased expression of lethal equivalents and other deleterious recessives generally leads to reduced vigor and reproductive output, and the population becomes more susceptible to various stresses such as insects, disease, or climate change. Thus, large reductions in stand size or even extensive fragmentation of existing large stands—especially to the extent that medium-range seed or pollen dispersal patterns are seriously disrupted—may eventually result in a general decrease in population fitness for the remaining trees due to increased levels of inbreeding. As fitness decreases, reproductive success may decline appreciably, and this may eventually result in the population's extinction.

How large must populations be to prevent such genetic problems? Levels of inbreeding and the rate of loss of genetic variation are determined by a population's genetically effective size, not by its census size. Effective population size can be thought of as the number of individuals actually contributing genes to the next generation. This number is a complex function of spatial structure, age structure, variance in breeding sex ratio, variance in reproductive success among individuals, and fluctuations in population size over time. Needless to say, there are no data on effective population sizes in whitebark pine, but many aspects of the species' biology suggest that it may be small relative to total population numbers. For example, most populations are highly age structured because of episodic recruitment. Spatial structuring of related individuals and seed caching by nutcrackers may result in a high variance in progeny survival, and previous disease epidemics or insect outbreaks may have resulted in substantial population bottlenecks.

Genetic problems are likely to be more severe in small, isolated populations. These populations will be lower in heterozygosity and more inbred due to founder effects and reduced gene flow, and as a consequence they may face rapid extinction when exposed to stressful conditions. However, a few of these populations may have survived previous bouts of inbreeding, become purged of their genetic loads, and developed local adaptations with high survival value.

A survey of genetic variation throughout the range of whitebark pine is a necessary first step for formulating a genetic management plan for the species and for identifying populations of high conservation concern. Next, long-term plans must be made to preserve these populations where they occur. Reliance on botanical gardens, test plantations, seed storage banks, DNA libraries, and other similar techniques for the preservation of genetic diversity in this or most other tree species is too uncertain and far too costly (Ledig 1989). Stand preservation will involve the conservation of the entire whitebark pine ecosystem, including, particularly, a healthy population of nutcrackers. Fortunately, whitebark pine populations are concentrated at high elevations, which are generally the areas most often preserved as wilderness or national parks. Thus, while loss of genetic variation may be less of a problem in whitebark pine than in some of its congeners whose habitats coincide with more immediately profitable land uses, loss of seed sources from blister rust and population senescence related to fire suppression may well result in a declining genetic base for the future.

ACKNOWLEDGMENTS

David Cameron, Diana Tomback, and Tad Weaver were kind enough to review and comment on this manuscript. Their help is greatly appreciated.

REFERENCES

Furnier, Glenn R.; Knowles, Peggy; Aleksiuk, Mary A.; Dancik, Bruce P. 1986. Inheritance and linkage of allozymes in seed tissue of whitebark pine. Canadian Journal of Genetics and Cytology. 28: 601-604.

Furnier, Glenn R.; Knowles, Peggy; Clyde, Mary A.; Dancik, Bruce P. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution. 41(3): 607-612.

Ledig, F. Thomas. 1986. Heterozygosity, heterosis, and fitness in outbreeding plants. In: Soule, Michael E., ed. Conservation biology: the science of scarcity and diversity. Sunderland, MA: Sinauer Associates: 77-104.

Ledig, F. Thomas. 1989. The conservation of genetic diversity in forest trees. BioScience. 38(7): 471-479.

Linhart, Yan B.; Tomback, Diana F. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. Oecologia. 67: 107-110.

Mitton, Jeffry B.; Pierce, Benjamin A. 1980. The distribution of individual heterozygosity in natural populations. Genetics. 95(4): 1043-1054.

Namkoong, Gene; Bishir, John. 1987. The frequency of lethal alleles in forest tree populations. Evolution. 41(5): 1123-1126.

Nevo, Eviatar. 1978. Genetic variation in natural populations: patterns and theory. Theoretical Population Biology. 13: 121-177.

Peters, Robert L. 1988. Effects of global warming on species and habitats, an overview. Endangered Species Update. 5(7): 1-8.

Peters, Robert L.; Darling, Joan D. S. 1985. The greenhouse effect and nature reserves. BioScience. 35(11): 707-717.

Tomback, Diana F. [In press]. Nutcracker-pine mutualisms: multi-trunk trees and seed size. In: Ouellet, H., ed. Acta XIX Congressus Ornithologici Internationalis.

Tomback, Diana F.; Linhart, Yan B. 1989. The evolution of bird-dispersed pines. 55 p. Editorial draft.

Wells, Philip V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecological Monographs. 53(4): 341-382.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Ron Lanner)—Since squirrels cause eventual death of most whitebark seeds on trees in closed mixed stands, should effective population size be adjusted to emphasize the importance of open-growing trees that maximize nutcracker harvest?

A.—Yes. This phenomenon will increase the variance in progeny contribution to the next generation and result in a substantial decrease in the ratio of genetically effective population size to census size.

Q. (from Dick Baker)—Would you recommend crossing isolated populations to preserve genetic diversity?

A.—Outcrossing is one way to replenish depleted genetic variation and decrease the level of inbreeding in isolated populations. However, outcrossing can also disrupt coadapted gene complexes that confer adaptation to local environments and consequently result in loss of fitness similar to that caused by inbreeding depression. This phenomenon is called "outbreeding depression." While there are no long-term deleterious consequences of outbreeding depression over the span of several generations, it can greatly increase the chance of population extinction during early generations if it is severe. Thus, outcrossing is not a universal panacea, especially in long-lived organisms such as whitebark pine.

Q. (from Dick Baker)—Whitebark pine has many disjunct populations, much like Great Basin bristlecone pine. Yet, genetic diversity seems to be much greater in whitebark pine, implying much longer isolation. Any idea why?

A.—I am not sure what you mean by "genetic diversity" in this context. If you mean genetic diversity in the sense of heterozygosity, Great Basin bristlecone has an H of 0.33 and a P of 0.79 (here P is calculated somewhat differently from the values presented in my paper), very near the high end of the scale. While an accurate H estimate for whitebark pine is currently unavailable, my very rough calculation of 0.32, along with P estimates of 0.55 to 0.75, puts it in the same ballpark as Great Basin bristlecone—certainly not very much greater.

If you mean "genetic diversity" in the sense of intrapopulation differentiation, once again accurate comparisons are not possible. It is true that Great Basin bristlecone has little genetic differentiation among its populations; the reason for this is to be found in its past history. This species occurred in essentially continuous stands throughout the Great Basin until about 12,000 years ago. Now it is reduced to remnant populations on mountaintops. Since these populations apparently have not experienced severe bottlenecks since the last glacial period, they have retained high amounts of intrapopulation variation. The present isolation of these Great Basin bristlecone populations evidently has not lasted long enough for much differentiation to occur among the remnant populations.

However, as I have suggested above, there is likely to be more differentiation among isolated populations of whitebark pine. This is because many of these populations probably originated from a few founding individuals carried to distant suitable habitats by birds. These founders would carry only a sample of the genetic diversity of the parent population with them, and the small post-establishment genetically effective population size would result in numerous fixations and losses of alleles by genetic drift. Thus, I predict that many isolated whitebark pine populations will be low in intrapopulation variation and high in interpopulation variation.

Q. (from Diana Tomback)—The dispersal of seeds by nutcrackers—a very mobile disperser—adds complexities to whitebark pine genetics. How would this affect conservation strategies for the species?

A.—Events that result in the reduction of nutcracker-mediated seed dispersal may have important genetic consequences of conservation concern. For example, widespread mortality in large whitebark pine populations from blister rust or pine beetle epidemics may leave only small, isolated fragments alive. These remaining fragments stand a good chance of becoming increasingly inbred if pollen flow and nutcracker visitation stop or decline appreciably; this in turn may lead to lowered fitness and perhaps eventually to extinction.

Likewise, small, isolated populations of whitebark pine probably receive some gene flow through occasional nutcracker-mediated seed dispersal. This trickle of gene flow may be enough to prevent a significant loss of genetic variation and extreme inbreeding in these populations. If nutcracker numbers decline, or if the species undergoes a range shift because of climate change, these populations will lose their only source of gene flow—with the consequences outlined above.

FIRE BEHAVIOR CHARACTERISTICS AND MANAGEMENT IMPLICATIONS IN WHITEBARK PINE ECOSYSTEMS

Richard J. Lasko

ABSTRACT

Fire is a significant element of alpine timberline ecosystems in the Northern Rocky Mountains. Fire behavior in these ecosystems is influenced by topographical, meteorological, and vegetative conditions that are characteristic of the alpine timberline. These characteristics and their relationships to fire behavior are analyzed.

INTRODUCTION

Managers are faced with a variety of challenges in the stewardship of high-elevation forests and timberlines in the Northern Rocky Mountains. The diversity of microhabitats and their distribution on the landscape in the alpine timberline compound the difficulties of prescribing management programs to achieve resource objectives. Success in these endeavors depends upon a clear understanding of the ecological processes that define the ecosystem. The ability to predict the behavior of fire, and its effects, is prerequisite to the management of any system where fire is a major ecological process.

The occurrence of fire in the alpine timberline in the Intermountain West is well documented (Forcella and Weaver 1977; Hawkes 1980; Heinselman 1985). Charred wood was found in the duff surrounding 300-year-old spruce in potentially fire-resistant, high-elevation cirque basins in northwestern Montana (Bigler 1976). Lightning is the primary cause, although, human-caused fires can enter the alpine timberline from lower elevations; or be introduced into this zone as human-ignited prescribed fire.

It is difficult to apply the concept of fire frequency to the alpine timberline because of the variety of microhabitats that occur. If fire regimes are characterized in this zone, they are usually described as having fire return intervals of 50 to 300 years (Arno and Hoff 1989). Both low-intensity and high-intensity fire have been documented in this zone (Billings 1969; Lasko 1987).

Accurate prediction of fire behavior depends on the skill and knowledge of the user and the degree of uniformity, or lack of uniformity, of the fuels and environmental conditions (Rothermel 1983). Although fire occurrence at the alpine timberline is amply documented, there is a lack of recorded observations of fire behavior. Characteristics of the microhabitats of this zone define fire behavior potentials and effects. Successful management of fire at the alpine timberline requires recognition of the microhabitats and an understanding of the ecosystem processes that led to their establishment.

THE FIRE ENVIRONMENT

While each microhabitat is unique in a microclimatological sense, broadscale climatological features are applicable to the alpine timberline. These general climatic attributes define the limits of fire in this zone. Climates of the alpine timberline are commonly described as having long, cold winters and short, cool growing seasons. Precipitation generally increases with elevation (Baker 1944) and quite frequently occurs as snow.

Relative Humidity—Diurnal patterns of relative humidity in the alpine timberline differ significantly from those in valley bottom sites (Furman 1978; Hayes 1941). In contrast to the valley bottom sites where humidities can often reach values of 80 percent or greater under frequent summer night-time inversion conditions, humidities seldom exceed 50 percent at the alpine timberline. This factor contributes to the drying of all fuel size classes, including the duff layer, thus increasing the ignition potential and length of the daily burning period.

Snowpack Influences—Distribution, depth, and duration of snow cover have significant effects in determining the patterns of vegetation on the landscape and the environment for the drying of fuels. Deeper snowpacks do not directly correspond to moister fuel conditions, especially in large-diameter fuels (McCammon 1976). However, deeper snowpacks increase the duration of snow coverage of fuels and vegetation, resulting in shorter growing and decomposition periods. Drought conditions, wind ablation, or early removal of snowpacks by warm spring rains can increase the amount of time that fuels are exposed to the drying conditions of the atmosphere, thus lengthening and increasing the severity of the fire season at these high-elevation sites.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Richard J. Lasko is Forester (Fire, Wilderness, and Ecology), Spotted Bear Ranger District, Flathead National Forest, Hungry Horse, MT 59919.

Fuels—Microclimatic conditions associated with alpine timberline do not encourage the decay of woody fuels. Downed trees that had been killed by fire were still present on a timberline site in Colorado 160 years after the fire (Billings 1969). Fuel inventories conducted in northern Idaho and Montana indicate that forested alpine timberline zones are characterized by accumulations of large-diameter downed and dead woody fuels. These inventories have indicated an average of 2 tons/acre of small-diameter materials (0.25 to 3 inches in diameter) and about 9 tons/acre of material over 3 inches in diameter (Fischer and Clayton 1983). Fuel loadings are expected to increase in northwestern Montana as a result of *Pinus albicaulis* mortality resulting from mountain pine beetle (*Dendroctonus ponderosae*) and white pine blister rust (caused by *Cronartium ribicola*).

Windfield—Alpine timberlines are directly influenced by regional air mass phenomena and associated gradient winds. Windspeeds often increase at high-elevation sites during night-time hours (Baughman 1981). The location and orientation of each particular site influences wind velocity. When ridgelines are oriented perpendicular to the airflow, a standing eddy can form on the lee side of the ridge. As gradient winds increase, lee waves and rotors may form and updrafts of up to 100 mi/h may occur (Scorer and Klieforth 1959). Fires may stall on the lee side of ridges due to the retrograde wind direction associated with these conditions.

MICROHABITATS AND FIRE BEHAVIOR

Fire Behavior Terminology—A brief discussion of fire behavior terminology is in order before proceeding with descriptions of plant associations and their fire behavior potentials. Surface fires refer to flaming fronts advancing in surface fuels within 6 ft of, and contiguous to, the ground (Rothermel 1983). Spot fires refer to small fires established by firebrands in advance of the main body of fire. Crown fires are grouped into three classes by Van Wagner (1977):

Passive Crown Fires—Trees torch as individuals, reinforcing the spread rate, but these are not basically different from surface fires.

Active Crown Fires—A solid flaming front develops in the crowns, but the surface and crown phases advance as a linked unit dependent upon each other.

Independent Crown Fires—Fires advance in the crowns independent of surface fire spread.

Characteristics of the microhabitats define fire behavior potentials and effects. As forests approach timberline the general pattern is that they decrease in density and height. As elevation increases, forests eventually break into scattered clumps of trees separated by meadow or park-like openings dominated by shrubs and other low-lying vegetation (Price 1981). Since standard terminology for the plant associations or microhabitats of the alpine timberline is nonexistent, I will rely on nomenclature used by Arno and Hammerly (1984) and Price (1981). Fire behavior characteristics of the microhabitats of the alpine timberline are summarized in table 1.

Upper Subalpine Forests—*Picea engelmannii* and *Pinus albicaulis* are usually codominant in the closed forests that form the lower reaches of the upper subalpine zone (Achuff 1989). *Abies lasiocarpa* is often present. Habitat types representative of this zone include *Pinus albicaulis-Abies lasiocarpa*, and *Pinus albicaulis*. The understory of these forests is strongly dominated by a low-lying shrub, *Vaccinium scoparium*, on many sites in the Northern Rocky Mountains (Weaver and Dale 1974). Forbs such as *Xerophyllum tenax* may also be present.

Table 1—Fire behavior characteristics of the alpine timberline

Microhabitat	Fuel conditions	Surface fire intensity	Crown fire potential[1]	Fire effects
Upper subalpine forest	Heavy loadings possible	High	High	Stand replacement
Open forests	Moderate to low	Low	Low	Favors *Pinus albicaulis*
Krummholz	Moderate	Moderate	High	Return to tundra
Groves	Light	Low	Low	Favors *Larix lyallii*
Ribbon forest	Moderate	Moderate	High	Return to tundra
Cirque basin	Heavy	High	High	Stand replacement
Tundra	Low	Low	Low	Remains as tundra

[1] Under extreme burning conditions and extended drought.

These forests generally occupy sites within or immediately above thermal belts and are subjected to extensive drying conditions. Tightly spaced canopies reduce the amount of precipitation reaching forest floor fuels and vegetation, contributing to increased ignition potential and fire intensity. The intensity of surface fires depends on the amount of downed woody material because the shrub layers are not especially flammable or dense enough to promote high fire intensities. Regeneration of *Abies lasiocarpa* and *Picea engelmannii*, if present, provides ladder fuels and contributes to passive and active crown fire activity. In dense stands, intermingled tree crowns increase the susceptibility of the forests to active and independent crown fire and subsequent stand replacement. Table 2 summarizes the relative fire resistance of alpine timberline conifers in the Northern Rocky Mountains. Following disturbance, regeneration of conifers generally occurs, but growth is slow—often requiring a period of 200 years for conifers to reach diameters of 16 inches (Bigler 1976).

Open Forests—Open stands of *Pinus albicaulis* and *Picea engelmannii* can sometimes be found at the upper reaches of the closed forest zone. Forest floor vegetation consists of low-lying grasses such as *Luzula hitchcockii*; shrubs such as *Vaccinium scoparium*; and forbs such as *Xerophyllum tenax*. Widely spaced tree canopies preclude the development of independent crown fires, but passive crown fire activity can occur with the presence of *Picea engelmannii* or *Abies lasiocarpa* saplings, which transport fires into the upper tree canopy. Surface spread is usually confined to large, downed woody debris, due to the absence of extensive duff and surface fuels. The widely spaced canopy also allows increased penetration of rainfall to the forest floor fuels.

Krummholz—This term describes a vegetation pattern of environmentally dwarfed forms of *Abies lasiocarpa*, *Picea engelmannii*, and *Pinus albicaulis* (Weaver and Dale 1974) that become treelike on favorable sites (Arno 1984). Under dry conditions these dense mats of vegetation can exhibit crown fire behavior in a nontraditional application of the term. Alpine tundra vegetation follows stand replacement fire on these sites and can persist for hundreds of years. Increased snow deposition may occur in unburned krummholz zones on the lee side of burned areas, resulting in additional krummholz mortality, eventually causing a return to alpine tundra vegetation in the unburned krummholz zone.

Ribbon Forest and Snowglade—On gentle slopes or plateaus the forest tends to occur in elongated strips aligned perpendicular to the normal winter wind direction. Ribbons are usually 10 to 20 m across and may be several hundred meters long. Ribbons are commonly composed of *Abies lasiocarpa* and *Picea engelmannii* (Billings 1969). *Larix lyallii* and *Pinus albicaulis* may also occur in the ribbons (Arno and Habeck 1972). Moist bands of subalpine meadow vegetation, large tussock-forming grasses and sedges, occupy intervening strips 25 to 75 m across and are the result of snow deposition on the lee sides of the forested ribbons. Fire activity is usually quite localized because of the intervening meadow vegetation (Billings 1969). Both crown and surface fires can occur in the ribbon forest. Low-intensity surface fires may modify the understory vegetation and have little effect on the coniferous ribbons; while crown fires have long-term effects. Succession back to the ribbon forest pattern usually requires several hundred years (Billings 1969).

Groves—Generally associated with *Larix lyallii* in the Northern Rocky Mountains, these small stands of trees usually occur on moderately cool exposures above the tree limit for other species of conifers (Arno 1972). Groves of *Larix lyallii* may also occupy bedrock and coarse talus sand within or adjacent to talus slopes (Arno 1972). Under extreme conditions fires can burn woody debris and depositions of litter occurring on talus slopes, but will not generally cause mortality in the groves. Fire-scarified seedbeds adjacent to the talus slopes can seed in rapidly with *Larix lyallii* seedlings (Arno 1972).

Tundra—This plant association grows above the climatic timberline and is characteristically dominated by low-growing (20 cm or less), perennial, herbaceous, and shrubby vascular plants, and extensive mats of cryptograms (Thilenius 1975). Fire does not appear to be influential in the tundra association (Thilenius 1975). Where tundra has extended below timberline as the result of past fires, larger downed woody debris may remain on these sites and serve as the mechanism of fire spread.

Table 2—Fire resistance of alpine timberline conifers (adapted from Flint 1925)

Species	Fire resistance	Bark	Stand habit	Branch habit
Abies lasiocarpa	Very low	Very thin	Moderate	Low and dense
Pinus albicaulis	Moderate	Thin	Open	High and open
Larix lyallii	Moderate	Thin	Open	Open
Picea engelmannii	Low	Thin	Dense	Low and dense

Cornice Lines—These snow deposition zones form along ridgelines and are composed of moist subalpine meadow vegetation, large tussock-forming grasses, and sedges. Surface firespread through these treeless strips is limited. This feature may prevent firespread across ridgelines under moderate burning conditions. The presence of a cornice line contributed to the confinement of the Charlotte Peak fire to the Holbrook drainage under severe burning conditions in 1985 in the Bob Marshall Wilderness (Lasko 1986).

Cirque Basins—Moist conditions and topographic features shelter these sites from all but the most severe episodes of external fire. *Pinus albicaulis* can be present, but the dominant coniferous species is *Picea engelmannii*. Shrubs such as *Menziesia ferruginea* commonly inhabit the forest floor and retard the spread of surface fire under most condtions. Under the severest of burning conditions, at the latter stages of stand succession when large amounts of downed woody debris are present, stand replacement crown fires can occur. Site characteristics generally allow the establishment of coniferous regeneration within 10 years of major disturbance. Two hundred years were required for trees to reach 18 inches in diameter in cirque basin stands above 5,000 ft elevation in northwestern Montana (Bigler 1976).

SUMMARY

Fire management programs create subtle yet long-lasting alterations in the alpine timberline. Fires less than 10 acres in size can alter vegetation patterns for hundreds of years. Continued elimination of fire from this zone delays its inevitable occurrence, increases fuel loadings, and ensures the severity of future fires. The desire of the public for a risk-free environment and the maintenance of existing landscapes, add to the complexity of the situation. A clear understanding of the role of fire is prerequisite to correct management of the timberline resource. Limited experience with the application of fire in the alpine timberline requires us to proceed with caution.

REFERENCES

Achuff, Peter L. 1989. Old-growth forests of the Canadian Rocky Mountain National Parks. Natural Areas Journal. 9(1): 12-26.

Arno, Stephen F.; Habeck, J. R. 1972. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Ecological Monographs. 42: 417-450.

Arno, Stephen F.; Hammerly, Ramona P. 1984. Timberline. Seattle: The Mountaineers. 304 p.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Baker, Frederick S. 1944. Mountain climates of the western United States. Ecological Monographs. 14(2): 223-254.

Baughman, Robert G. 1981. Why windspeeds increase on high mountain slopes at night. Res. Pap. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 6 p.

Bigler, Robert L. 1976. Age and size class distribution in the *Abies lasiocarpa/Luzula hitchcockii-Menziesia ferruginea* habitat type in northwestern Montana. Moscow, ID: University of Idaho, College of Forest, Wildlife and Range Science. 44 p. Thesis.

Billings, W. D. 1969. Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. Vegetatio. 19: 192-207.

Fischer, William C.; Clayton, Bruce D. 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. Gen. Tech. Rep. INT-141. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 83 p.

Flint, R. 1925. Fire resistance of northern Rocky Mountain conifers. Idaho Forester. 7: 7-10, 40-43.

Forcella, F.; Weaver, T. 1977. Biomass and productivity of the subalpine *Pinus albicaulis-Vaccinium scoparium* association in Montana, USA. Vegetatio. 35(2): 95-105.

Furman, R. William. 1978. Wildfire zones on a mountain ridge. Annals of the Association of American Geographers. 68(1): 89-94.

Hawkes, Brad C. 1980. Fire history of Kananaskis Provincial Park—mean fire return intervals. In: Proceedings: fire history workshop; 1980 October 20-24; Tucson, AZ. Gen. Tech. Rep. RM-81. Fort Collins, CO. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 42-45.

Hayes, G. Lloyd. 1941. Influence of altitude and aspect on daily variations in factors of forest-fire danger. Misc. Publ. 591. Washington, DC: U.S. Department of Agriculture, Forest Service. 37 p.

Heinselman, Miron L. 1985. Fire regimes and management options in ecosystems with large high-intensity fires. In: Proceedings—symposium and workshop on wilderness fire; 1983 November 15-18; Missoula, MT. Gen. Tech. Rep. INT-182. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 101-109.

Lasko, Richard J. 1987. Weather forecasts, fire behavior predictions, and the management of public safety in the Bob Marshall Wilderness. In: Ninth conference on fire and forest meteorology; 1987 April 21-24; San Diego, CA. Boston, MA: American Meteorological Society: 127-131.

McCammon, Bruce P. 1976. Snowpack influences on dead fuel moisture. Forest Science. 22(3): 323-328.

Price, Larry W. 1981. Mountains and man. Berkeley, CA: University of California Press. 506 p.

Rothermel, Richard C. 1983. How to predict the spread and intensity of forest and range fires. Gen. Tech. Rep. INT-143. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 161 p.

Scorer, R. S.; Klieforth, H. 1985. Theory of mountain waves of large amplitude. Quarterly Journal of the Royal Meteorological Society. 85(364): 131-143.

Thilenius, John F. 1975. Alpine range management in the western United States—principles, practices, and problems. Res. Pap. RM-157. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Van Wagner, C. E. 1977. Conditions for the start and spread of crown fires. Canadian Journal of Forestry Research. 7: 23-34.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. American Midland Naturalist. 92: 222-230.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from anonymous)—What do you see as the role of human-induced fires in the management of whitebark pine in wilderness systems, when considering mountain pine beetle and blister rust?

A.—The interactions between fire, mountain pine beetle, and white pine are ecosystem processes that the Wilderness Act was established to perpetuate with as little influence by humans as possible. The introduction (by humans) of nonnative organisms will alter or shift affected ecosystems. In the instance of blister rust the best we can do is probably document the effects on the ecosystem.

SILVICULTURAL MANAGEMENT ALTERNATIVES FOR WHITEBARK PINE

Douglas E. Eggers

ABSTRACT

Whitebark pine (Pinus albicaulis) *has received little management emphasis except in the past 10 years. Silvicultural treatment of whitebark pine is starting to draw increased interest as attention is focused on the species and its potential management. The objective of this paper is to summarize what is currently known about the silvicultural management of the species. There has been little written concerning silvicultural treatment in whitebark pine stands; however, there are some inferences that can be drawn by examining specific examples. These examples will be used to demonstrate that information does exist and that these existing data will probably need to be used to guide management while additional data are gathered and understanding is gained.*

SILVICULTURAL OBJECTIVES

The most important factor to keep in mind (and the one so often neglected) when examining silvicultural management alternatives for whitebark pine (*Pinus albicaulis*) is the need to identify clear, accomplishable, land management objectives. Daniel and others (1979) described the role of silviculture in forest and wildland management. Formulating silvicultural strategies requires the recognition of biological, managerial, and economic considerations. For example, objectives for recreation, water production, wildlife, or wood may require forests with different structures. Translating those objectives into specific kinds of stand structures and composition then becomes a matter of silvicultural application. This silvicultural application involves a basic understanding of principles that will in turn translate into recommended practices. This paper will not address different land management objectives other than showing how they may affect treatments. The assumption is made that the perpetuation of the whitebark pine component is desired.

In translating land management objectives into tangible, specific activities, it is important to define the subject using accepted forestry terminology. The terms used here are taken primarily from the Society of American Foresters' publication, "Terminology of Forest Science, Technology, Practice and Products" (Ford-Robertson 1971).

The first definition, silviculture, is fundamental to the rest that will be presented in this paper. Silviculture is defined as follows:

1. Generally, the science and art of cultivating (growing and tending) forest crops, based on a knowledge of silvics.
2. More particularly, the theory and practice of controlling the establishment, composition, constitution, and growth of forests (Ford-Robertson 1971).

The definition can be refined further to understand that silvics is: "The study of the life history and general characteristics of forest trees and stands, with the particular reference to locality factors, as a basis for the practice of silviculture" (Ford-Robertson 1971). Examination of the "theory and practice of controlling the establishment, composition, constitution, and growth" of whitebark pine based on what is known about its life history and general characteristics, using some specific references to locality factors, will be the focus of this paper. The specific examples given will utilize what is known of current stand structure and knowledge of stand history as well as ecological information to project the treatments necessary to produce the desired future conditions.

CONTROLLING ESTABLISHMENT

Controlling establishment involves "The process of developing a crop to the stage at which the young trees may be considered established; i.e., safe from normal adverse influences—e.g., frost, drought, weeds or browsing—and no longer in need of special protection or special tending, but only routine cleaning, thinning, and pruning" (Ford-Robertson 1971).

The process of developing a crop of whitebark pine to the stage that it is considered established or free to grow starts with regeneration. Daniel and others (1979) distinguished between silvicultural reproduction (regeneration) methods and silvicultural systems: a regeneration method describes the manner of cutting to ensure regeneration and a silvicultural system describes additionally the process for treating the resulting stand after establishment. Attention will be focused on regeneration rather than on silvicultural systems. The regeneration methods that could be used in whitebark pine stands, according to Arno and Hoff (1989), would be either even-aged or uneven-aged depending on site factors and management objectives. Even-aged regeneration methods are clearcutting,

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Douglas E. Eggers is Forest Silviculturist, Bridger-Teton National Forest, Forest Service, U.S. Department of Agriculture, Jackson, WY.

seed tree, and shelterwood. Uneven-aged regeneration methods are single tree and group selection. These various methods form a continuum, as described by Daniel and others (1979); the amount of site exposure that results ranges from the least, with single tree selection, to the greatest, with clearcutting.

The silvical characteristics of whitebark pine including irregular large cone crops, uncertain seed dissemination, and low seed germination, will narrow the range of silvicultural options that are feasible for any particular site.

There has been little management activity in northwestern Wyoming that has focused directly on whitebark pine. Only in recent years has there been much attention given to whitebark pine, therefore, there is not the amount or detail of data available that there is for some other species. However, observations have been made that should be valuable in evaluating the appropriateness of prescribing various regeneration methods. The types of data, such as timber inventory data, that exist for the Bridger-Teton National Forest, also exist for most other National Forests.

Arno and Hoff (1989) noted that whitebark pine often regenerates following wildfire and after clearcutting (with or without site preparation) on southern exposures or ridgetops. They also observed that to regenerate whitebark pine on moist sites, appreciable stand opening and localized site preparation would probably be necessary. Arno and Hoff (1989) found that whitebark pine can be regenerated artificially by using seedlings or seeds in mineral soil or at the soil-litter interface. Eggers (1986) has noted various artificial regeneration methods that could be utilized.

The author has made observations on a study site located in the Union Pass area of the Bridger-Teton National Forest that was set up in 1971 to evaluate several methods of harvesting mature lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and to compare postharvest treatments (Benson 1982). These observations have shown that whitebark pine seedlings are becoming established on this site. The greatest number of seedlings is located in the areas that received the treatment of clearcut, tractor pile, burn, and plant. This stand, prior to harvest, had over 1,500 stems/acre of whitebark pine under 5.0 inches d.b.h. These seedlings, which became established under the closed canopy of the predominately lodgepole pine stand over its 160-year life span, were of poor quality and arranged in a clumpy pattern (Benson 1982). The evidence would indicate that if there is whitebark pine in surrounding stands, within 10 to 15 years there will be some stocking of whitebark pine in clearcuts.

At this relatively moist, higher elevation (9,200 ft) where strong winds are experienced during the winter, it is probable that some seed dispersal takes place from seeds being blown along on crusted snow. There could be some dispersal by rodents or birds, however, the pattern of occurrence corresponds to that of seedlings of other species started from wind-borne seed. There were more seedlings observed on the north and northeast sides of the planted lodgepole pine, which would seem to indicate that some degree of shading may benefit establishment. The whitebark pine seedlings found in this area are single and not clustered as they would be if a whole cone disintegrated on the ground and the seeds germinated.

One of the factors that has contributed to the seedling establishment of all species in this area is the wet seasons that occurred during the mid-1980's. It is also interesting to note that observations made in late 1988, after one of the driest years on record, confirmed that a number of first- and second-year seedlings were still alive. This would indicate that after germination, vigorous rooting takes place, thereby aiding survival.

There have been questions raised on the value of releasing understory whitebark pine. My observations, made primarily in mixed species stands in which whitebark pine is a component, of the growth response of residual seedlings and saplings of whitebark pine after release have indicated that residual seedlings and saplings have responded little to release. The observations were made in clearcuts and in stands with various levels of partial cutting (some regeneration harvests and some intermediate harvest). This is an area that needs additional data to determine more of the specific characteristics of the residuals such as age at release and average growth prior to release.

The inference that can be drawn from these observations is that whitebark pine establishment is enhanced by bare mineral soil and an abundance of moisture. Germination is one of the most critical factors known at this time. Answers to the whys of poor germination are currently unknown. Pitel and others (1980) indicated that there appears to be a relationship between the completeness of development of the embryo and the condition of the seed coat that affects germination. The factors at work here are important, but personal observation has shown that more seedlings are visually evident after a wet season, particularly a wet spring, than any other time. More moisture is permeating the seed coat, thereby aiding germination, whatever the mechanism is for breaking down seed dormancy.

There are silvical characteristics important to establishment that can be controlled with some degree of predictability. Seed production, is one such characteristic. Flowering and fruiting is an integral part of seed production and can be influenced by the application of spacing control to produce trees with a higher proportion of crowns that are fully exposed to light (Daniel and others 1979). Techniques used in seed production areas such as thinning, fertilization (after foliar analysis), and protection from insects and other seed destroying agents could also be used.

Regeneration methods that recognize the basic silvical needs of the species will be the most successful. Additional examples are described by Arno and Hoff (1989), such as a rooting habit that develops a deep spreading system. The root system is well-anchored in the rocky substrate and is seldom disturbed despite the tree's large, exposed crown and the violent winds to which it is subjected. They also indicated that while whitebark pine had previously been reported as very intolerant, more recent observations show that it would be more accurate to classify it as intermediate in tolerance to shade.

Whatever regeneration method is chosen, the retention of healthy, windfirm seed trees with good phenotypic characteristics will aid in natural regeneration. It is important to realize that regeneration through natural regeneration alone will probably mean long regeneration periods. These regeneration periods may be decades, in comparison to a few years for such associated species as Engelmann spruce or lodgepole pine. The characteristic that whitebark pine is intermediate in tolerance would indicate that there will be some seedlings that become established.

Using the Bridger-Teton National Forest as an example, in the short term, if the whitebark pine component is to be increased or its range is to be extended, artificial regeneration will be necessary. If this option is chosen, it will be very expensive to carry out on an operational basis. It is not an easy solution, as described by Eggers (1986), but one that could be carried out if management emphasis and budget were committed to it.

CONTROLLING COMPOSITION

Composition is defined by the Society of American Foresters (Ford-Robertson 1971) as the "species composition of a forest crop or stand, the representation of tree species in it. This is expressed quantitatively as percent by volume or basal area of each species; percent by number only at the seedling stage."

The species composition that is desirable may be dependent on the land management objectives, but what is possible will be dependent on inherent characteristics such as site quality, habitat type capabilities, and presence or absence of pest agents. Whitebark pine, Society of American Foresters Cover Type 208, (Eyre 1980) is used to designate pure stands or mixed stands in which the species comprises a plurality of stocking. It is necessary to know the existing vegetation to formulate a better prescription for what is desired. For example, in the over 50 forest habitat types identified in the eastern Idaho-western Wyoming area, whitebark pine was found in 36. On the Bridger-Teton National Forest, whitebark pine occurs with lodgepole pine, limber pine (*Pinus flexilis* James), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and aspen (*Populus* spp.). The single-stemmed growth form is most commonly associated with a plurality of lodgepole pine. The multi-stemmed growth form is more commonly found with a plurality of whitebark pine at the extremes of environmental conditions. Common shrub and herbaceous associates are listed in "Forest Habitat Types of Eastern Idaho-Western Wyoming" (Steele and others 1983). This publication lists the percentage canopy coverage by species and the constancy or the percentage of stands in a habitat type that contain a given species.

Controlling the species composition begins with establishment, through the favoring of trees left for seed or artificial reforestation. The time between establishment and the next regeneration period can be used to perform a whole range of stand manipulations, generally termed intermediate treatments, to control the species composition. Cleaning, weeding, liberation, and improvement cuttings could be used at various stages of stand growth, singly or in combination, to achieve the land management objectives.

CONTROLLING CONSTITUTION

Constitution is the "structure, of a forest crop or stand, the distribution and representation of age and/or size classes" (Ford-Robertson 1971).

Land management objectives will guide the controlling of distribution of age and size classes of whitebark pine and specific stand structures: the relative proportion of overmature (declining in vigor, health, or soundness), mature (full development of height and seed production), saplings, and seedlings. Success requires an understanding of stand dynamics including succession, competition, and tolerance. This can be aided by the identification of habitat types as described in the previous section. The various pathways of succession are affected by the starting point. The progression toward climax vegetation will continue without treatment, but the character of the stand can be changed through treatment. The silviculturist can control the structure by applying various treatments including harvesting, site preparation, controlling species composition, and thinning. These choices will affect the ways individual trees and species will respond. These choices may range from broad to narrow in the short term depending on the character of the existing stands.

An illustration from the Bridger-Teton National Forest timber inventory information will help to put this into perspective. Examining the timber inventory plot data has given a profile of the existing condition of the whitebark pine resource:

Characteristic	**Average for whitebark pine**
d.b.h.	14.9 inches
height	51 feet
d.b.h. age	157 years
past 10 yrs. radial growth	0.25 inches (range 0.1 to 0.9)
best 10 yrs. radial growth	0.8 inches (range 0.25 to 2.25)
age of best growth	20 years
elevation	9,000 feet

These facts should help when writing prescriptions that will be able to be implemented. What does an analysis of these data show? It shows that for the Bridger-Teton National Forest, the whitebark pine is a mature/overmature resource that is currently growing slowly, but at younger ages is capable of growing as well as its associates.

CONTROLLING GROWTH

Growth is described as: "increment, accretion. The increase in girth, diameter, basal area, height, volume, quality or value of individual trees or crops" (Ford-Robertson 1971).

The definition of growth covers the whole range from individual trees to entire forest. Land management objectives should indicate the relative importance of various growth factors. This could mean quality or value in terms of such characteristics as multi-stemmed growth habit, foliar biomass, or consistently large seed crops.

There are basic standards that should be reviewed to be able to set realistic growth expectations. A number of these have been described in earlier sections. There are givens. For example, the height that a tree can reach at a certain age on a particular site is largely limited by soil and climatic factors. Different species respond differently to differing site quality. It is important to recognize that whitebark pine grows over a range of climatic conditions but is characterized by Arno and Hoff (1989) as growing in cold, windy, snowy, and generally moist conditions. They indicated that in moist mountain ranges, whitebark pine is most abundant on warm, dry exposures and in semiarid ranges it becomes prevalent on cool exposures and moist sites. The mean annual precipitation for most stands where whitebark pine is common is between 24 and 72 inches with about two thirds of the precipitation coming in the form of snow and sleet.

In considering environmental factors affecting growth of whitebark pine stands, two of the most important are insects and disease. The most damaging insect pest of whitebark pine is the mountain pine beetle (*Dendroctonus ponderosae* Hopkins). There has been a significant amount of mortality in mature stands throughout the northern Rocky Mountain area Arno and Hoff (1989). This insect may kill individual trees even at higher elevations but most whitebark pine tree killing in northwestern Wyoming occurs when beetle populations build up in lodgepole pine stands at lower elevations. Management in lower elevation stands may need to increase to lessen the impact on higher elevation stands. Mountain pine beetle has caused severe damage to some whitebark pine stands. The principal disease that causes damage to whitebark pine is white pine blister rust (*Cronartium ribicola*); it usually results in death in sapling and pole-sized trees and top killing in mature trees.

We also need to recognize that basic tree physiological principles are at work even though we may not know or recognize them all for whitebark pine. Examples are: the major reasons why understory may not respond after release are that poor root systems can't use the increased nutrients, low live crown ratio won't allow adequate food production, or advanced age decreases ability to respond.

In the area of growth, as in establishment, composition, and constitution, there are some specific examples from data collected in unmanaged stands that can be used to illustrate what is known. From these examples inferences can be drawn on the expectations from stand manipulations. The major growth factors that can be affected by management activities are: controlling composition and manipulating density.

The following examples from the Bridger-Teton National Forest will help to demonstrate:

The best whitebark pine height growth on the Bridger-Teton National Forest (as evidenced by the greatest number of plots with trees over 70 ft in height) was recorded at elevations between 8,300 and 9,100 ft.

The most prevalent habitat type for these plots was *Abies lasiocarpa / Vaccinium scoparium-Vaccinium scoparium* phase. The *Abies lasiocarpa* Series is the most prevalent on the Forest and *Vaccinium scoparium* is the most prevalent habitat type in the *Abies lasiocarpa* Series. The yield capability for this habitat type is quite broad, ranging from 20 to 90 cubic ft per acre per year (Steele 1982). The inventory data showed that on the above habitat types we can expect a tree that is 17 to 20 inches d.b.h. and over 70 ft tall to be between 150 and 175 years old. Trees that are over 30 inches d.b.h. and over 90 ft tall are usually at least 220 years old. One of the larger specimens recorded on the inventory plots was 38.1 inches d.b.h., 111 ft tall and 281 years old. We can also infer from the inventory that the growth pattern after establishment could follow the progression shown in table 1.

It will help lend perspective to the observations by recognizing that in terms of relative productivity, the Bridger-Teton National Forest has the highest overall productivity of any National Forest in the Intermountain Region of the Forest Service. The Bridger-Teton's average productivity potential is 63 ft^3/acre/yr, (USDA Forest Service 1980) which compares to an average of 64 ft^3/acre/yr for the Rocky Mountain area as a whole (USDA Forest Service 1982).

Table 1—Growth examples at various ages from Bridger-Teton National Forest inventory

Age	D.b.h.	Height
Years	*Inches*	*Feet*
25	5.3	21
40	10.8	41
70	12.6	67
100	13.7	71

CONCLUSIONS AND RECOMMENDATIONS

It would seem that whitebark pine is neither the mystical nor mysterious species that some have made it out to be, but one for which a broader base of knowledge is needed. The attention focused recently on whitebark pine due to its relationship with grizzly bear habitat has helped to add to the knowledge base. We need to use the information, such as timber inventory plot information, that is currently available until more site-specific information for particular stands is collected. By observing what has happened in stands that have been entered, a silviculturist should be able to determine appropriate ways to manipulate individual stands to meet land management objectives. These land management objectives need to be clearly stated in quantifiable terms. We can then work toward developing the types of stands that we desire, while recognizing that it will take a considerable amount of time to get them.

Future research and information needs:

1. Continue to refine nursery propagation techniques,
2. Continue the genetic work to determine variability in whitebark pine,
3. Delineate and define objectives for those stands that need management prescriptions, and gather the site data needed.

REFERENCES

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of white bark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Bailey, D. K. 1976. *Pinus albicaulis*. Curtis Botanical Magazine. 180(3): 141-147.

Benson, Robert E. 1982. Management consequences of alternative harvesting and residue treatment practices—lodgepole pine. Gen. Tech. Rep. INT-132. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 58 p.

Daniel, Theodore W.; Helms, John A.; Baker, Frederick. 1979. Principles of silviculture. New York: McGraw-Hill. 500 p.

Eggers, D. E. 1986. Management of whitebark pine as potential grizzly bear habitat. In: Contreras, G. P.; Evans, K. E., eds. Proceedings—grizzly bear habitat symposium. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 170-175.

Eyre, F. H., ed. 1980. Forest cover types of the United States and Canada. Washington, DC: Society of American Foresters. 148 p.

Ford-Robertson, F. C., ed. 1971. Terminology of forest science, technology practice and products. Washington, DC: Society of American Foresters. 349 p.

Pitel, J. A.; Wang, B. S. P. 1980. A preliminary study of dormancy in *Pinus albicaulis* seeds. Canadian Forest Service Bi-Monthly Research Notes. 36(1): 4-5.

Steele, Robert; Cooper, Stephen V.; Ondov, David M.; Roberts, David W.; Pfister, Robert D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

USDA Forest Service. 1980. Environmental consequences of timber harvesting in Rocky Mountain coniferous forests. Gen. Tech. Rep. INT-90. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 526 p.

USDA Forest Service. 1982. An analysis of the timber situation in the United States 1952-2030. Forest Resource Report No. 23. Washington, DC: U.S. Department of Agriculture, Forest Service. 499 p.

RECLAMATION PRACTICES IN HIGH-MOUNTAIN ECOSYSTEMS

Ray W. Brown
Jeanne C. Chambers

ABSTRACT

Mineral exploration, mining, road construction, and recreation have resulted in severe disturbances to many subalpine and alpine ecosystems throughout the mountainous West. Revegetation research has revealed several promising techniques that may lead to the rehabilitation of these disturbances. The selection and use of adapted native plant species representative of different seral stages are needed to provide optimum species and structural diversity in revegetated communities. Amendments such as fertilizer, organic matter, and surface mulching that ameliorate limiting adaphic and microclimatic conditions are essential.

INTRODUCTION

High-elevation mountainous regions of the western United States support vitally important ecosystems. They are the primary watersheds for agricultural, industrial, and metropolitan development as snow accumulation and water storage in these areas provide the main sources of summer runoff for western streams and rivers. The more gentle slopes and rolling plateaus of mountain regions also provide summer range for both livestock and wildlife, and these unique ecosystems offer stunning panoramas and remote wilderness solitude for recreationists. However, with the advent of modern technology many areas are being disturbed at an accelerated rate by human activities such as recreation, road construction, mineral exploration, mining, and other endeavors.

The impacts of disturbance on high-elevation lands threaten their important watershed, wildlife habitat, grazing, and recreational values. Revegetation of these disturbances is essential to minimize the consequences of erosion and loss of water quality, and to reestablish stable native ecosystems. However, conventional techniques of revegetation developed for more moderate climatic zones at lower elevations have largely been unsuccessful for disturbed high-mountain ecosystems. The rigorous climate at high elevations, coupled with the impacts of disturbance, dictate the use of techniques that have been designed for the unique conditions of high-elevation lifezones. Short, cool growing seasons, strong winds, frequent frosts, and a limited pool of adapted plant species severely complicate revegetation efforts. These constraints are compounded by the effects of disturbance that often result in spoil material that is acidic, low in essential plant nutrients, or contains toxic concentrations of heavy metals or other unsuitable constituents. Erosion, acid-water runoff, and sedimentation frequently result in the destruction of off-site plant communities, streams, and aquatic habitats, and the general deterioration of water quality.

In 1972 the Intermountain Research Station initiated an integrated research effort to develop revegetation techniques for high-elevation disturbances. Also, considerable interest was fostered in high-elevation revegetation problems throughout the West with the establishment of the High-Altitude Revegetation (HAR) Committee. Early attempts to revegetate disturbances at high elevations were frustrated by a lack of knowledge about the complexities of high-elevation environments and the effects of disturbances. However, during the last 15 to 20 years numerous promising techniques and approaches have been developed for the revegetation of these areas. The purpose of this paper is to summarize the nature of high-elevation environments, the effects of disturbance on them, and the more successful revegetation techniques available.

FACTORS LIMITING REVEGETATION

Climatic conditions of high-elevation regions are often limiting to successful revegetation of disturbances. Generally, high-elevation environments have low heat budgets that result in short, cool growing seasons (Billings 1974). Typical high-elevation growing seasons range from 45 to 90 days with average summer temperatures near 10 °C (Billings and Mooney 1968). Growing season temperatures frequently fall below 0 °C, and frost occurs throughout the growing season in many areas. Needle ice can uproot seedlings and contribute to surface soil erosion on disturbed sites throughout the growing season where soil water status is maintained at or near saturation (Brink and others 1967). At high elevations in the western United States precipitation occurs mainly as winter snow, but soil water availability is highly variable with

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Ray W. Brown is Plant Physiologist and Jeanne C. Chambers is Plant Ecologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Forestry Sciences Laboratory, 860 N. 1200 E., Logan, UT 84321.

season, location, and topography. For example, snow fields commonly accumulate on the lee sides of ridges while ridgelines may remain nearly snow free due to redistribution by wind. High winds are common in subalpine and alpine ecosystems, and can cause significant soil erosion and be physically and physiologically detrimental to plants. Also, wind coupled with high solar radiation flux densities in mountain life-zones can promote extremely high rates of evaporation and transpiration.

The type of disturbance imposes various limitations on successful revegetation. Severe disturbances result in the removal of surface soil horizons and expose the underlying geological materials. Less severe disturbances leave the surface soil in place but may result in the mixing of the surface and subsurface soil horizons (Chambers and others 1988). Natural causes of severe disturbances include geomorphological processes such as landslides or avalanches; human causes include such activities as road building and mining. Less severe disturbances result from causes such as freeze-thaw cycles (Johnson and Billings 1962), small-mammal burrowing and tunneling (Thorn 1982), and some human recreational activities. The two types of disturbances result in significantly different revegetation environments. Severe disturbances that remove surface organic horizons and leave mineral soils in place are often characterized by lower water and nutrient holding capacities. Disturbance in general can result in the loss of finer soil particles due to wind erosion.

Severe disturbances at high elevations can expose pyrtic materials that initiate a cycle of sulphide oxidation near the soil surface (Johnston and Brown 1979). This can result in low soil pH and increased availability of potentially toxic metals such as copper, iron, and aluminum. Plant establishment and growth, and thus, natural successional processes, can be severely limited. Runoff from such areas frequently causes mortality to offsite plant communities and seriously degrades water quality and aquatic ecosystems downslope.

A major limitation to successful high-elevation revegetation is knowledge about the selection and use of adapted plant species. The total flora of high-elevation ecosystems is relatively small compared with more moderate low-elevation life-zones, and the pool of adapted species suitable for revegetation is limited. Introduced plant species commonly used for revegetation in lower elevation areas are frequently unadapted and unsuccessful when used for revegetation of high-elevation disturbances. Brown and Johnston (1979, 1980) found that such introduced species as smooth brome (*Bromus inermis*) and intermediate wheatgrass (*Agropyron intermedium*) were no longer present 4 years after planting on a subalpine site that had been mined in southwestern Montana. However, native adapted species from the area such as tufted hairgrass (*Deschampsia cespitosa*) and alpine bluegrass (*Poa alpina*) increased in density, cover, and biomass production over the same period. The most important criteria used in selecting adapted species for revegetation, including observations of natural succession on disturbed areas, are discussed by Chambers and others (1984, 1988).

SELECTION OF ADAPTED PLANT SPECIES

Selecting plant species for revegetation that are suited to the limiting environmental factors characteristic of a disturbance is one of the most important aspects of successful reclamation. Adapted species are those capable of long-term survival and reproduction. One of the most promising methods of identifying adapted species for revegetation of high-elevation disturbances is to examine natural successional processes on local old disturbances such as road cuts and fills and gravel pits (Brown and Johnston 1980; Chambers and others 1984, 1988). Unfortunately, most native high-elevation plant species suited for revegetation are not commercially available and must be hand-collected. Collection of seed tends to be expensive, but use of locally adapted populations greatly enhances the chances for successful revegetation.

Species Selection

Research results suggest that reclamation success of high-elevation disturbances may be improved when mixtures of species are planted that represent different life histories and physiological traits. Typically, grasses are the most widely used group of plants in revegetation, yet heavily fertilized swards of high-nutrient adapted grasses often tend to form closed stands that exclude or inhibit the invasion of other species (Brown and others 1984). Research on plant succession on high-elevation disturbances suggests that inclusion of different lifeforms in seeding and planting mixtures, together with appropriate amendments, may increase species and structural diversity of revegetation communities and enhance rates of successional development (Chambers and others 1988). In addition, use of seed mixtures consisting of species with many different physiological and ecological characteristics improves the chances of stand survival in the event of catastrophic events such as insect infestations, disease, or drought (Brown and Johnston 1980).

In alpine environments many plant species adapted for revegetation of disturbances can be classified according to their frequency of occurrence in different successional stages (Chambers and others 1984, 1988). Initial colonizers of disturbed sites often exhibit broad ecological amplitudes, and are usually widely distributed in geographic area. At low elevations early colonizers tend to include a large complement of annual "weeds"; at higher elevations more desirable perennial species predominate. Early colonizers often have large and consistent seed production capabilities, effective seed dispersal mechanisms, high seed germination percentages, and high rates of growth and development. They may also be able to tolerate high concentrations of heavy metals, low pH, and other adverse disturbance conditions.

Late-seral species often have slower growth rates, lower seed production, and lower rates of seed dispersal than early seral species (Chambers and others 1988). For example, frequent colonizers such as tufted hairgrass typically produce large quantities of small-sized seeds with high viability and germination, have high seed longevity, high seed dispersal capability, high plant growth rates, and low root:plant biomass ratios (Chambers and others 1988). In contrast, species typical of late-seral communities such as alpine avens (*Geum rossii*), an alpine forb, produce small quantities of larger sized seeds with relatively short seed longevity, low seed dispersal capability, low growth rates, and high root:plant biomass ratio (Chambers and others 1988). Also, tufted hairgrass tends to have shallower, less extensive root systems and higher nutrient requirements than alpine avens (Chambers and others 1987c). Species adapted to low-nutrient sites, such as alpine avens, can ensure long-term stability on disturbances, but lower rates of production are to be expected (Chambers and others 1988). Listed below are native alpine and subalpine species that have been established successfully on disturbed sites from seeds (*), together with others that have favorable characteristics for revegetation (Brown and others 1978, 1988; Chambers 1987; Chambers and others 1984, 1988):

Grasses and Grasslike Plants—

**Agropyron trachycaulum* (slender wheatgrass)
**A. scribneri* (Scribner wheatgrass)
**Carex paysonis* (Payson sedge)
**Deschampsia cespitosa* (tufted hairgrass)
**Phleum alpinum* (alpine timothy)
**Poa alpina* (alpine bluegrass)
P. epilis (skyline bluegrass)
P. rupicola (timberline bluegrass)
**Trisetum spicatum* (spike trisetum)

Forbs—

**Achillea millifolium* (western yarrow)
Agoseris glauca (pale agoseris)
Arenaria obtusiloba (alpine sandwort)
Artemisia campestris (wormwood)
**A. scopulorum* (alpine sagebrush)
Cerastium arvense (mouse-ear chickweed)
C. beeringianum (alpine chickweed)
**Geum rossii* (alpine avens)
Lupinus argenteus (lupine)
**Potentilla diversifolia* (varileaf cinquefoil)
Senecio fremontii (Fremont's groundsel)
**Sibbaldia procumbens* (sibbaldia)
Smelowskia calycina (smelowskia)
Solidago multiradiata (low goldenrod)
Trifolium dasyphyllum (whiproot clover)
T. parryi (Parry clover)

Many of the species listed have broad ecological amplitudes and occur as frequent colonizers on alpine disturbances. Also, many have high reproductive rates and easily collectible seeds.

Seed Collection

Seed collection of adapted native species requires a knowledge of the phenology of plant development and the complex interactions with environment. Seed maturity and production are highly variable from year to year, and collection must be opportunistic to take advantage of good seed production years for different species. Several years may be required to collect sufficient seed of all species desired for a given revegetation project. Usually, seeds mature on the plant in the late summer or fall, and should be collected just prior to natural dispersal. The seeds are normally stored in dry, porous containers such as paper or cloth bags, and kept in a cool, dry environment maintained near 0 °C (Chambers and others 1987a). However, there is some evidence that seed longevity of high-elevation species is improved if seeds are stored at –18 °C at low moisture content (Billings and Mooney 1968).

Seed Mixtures and Planting Concerns

Seeding rates based on the number of viable seeds per unit area for each species used, instead of the more typical method of weight per unit area, allow rates to be determined on an individual species seed viability basis. This ensures that potential competition among species will be uniform over the area, provides optimum opportunity for survival of seedlings, and permits success or failure of each species in the mixture to be correctly assessed. The amount of seed applied for each species in a mixture may need to be adjusted for different seed lots collected from different locations and times because seed viability varies widely from year to year (Chambers in press).

Knowledge of seed germination requirements of species is essential to determine seeding methods and other revegetation techniques. Many species have small-sized seeds that cannot emerge from the soil if planted too deeply; species with larger sized seeds may require deep planting to avoid desiccation during dormancy and seedling development. Also, some species must be planted at or near the soil surface because of a requirement for light during germination (Chambers and others 1987b; Haggas and others 1987). Chambers and others (1987b) found that many alpine forbs require light for germination, but grasses have less specific requirements. Also, they found that wet cold stratification during the winter following fall seeding results in fewer days for germination and, consequently, an increased likelihood of seedling establishment the following spring.

Nutrient Requirements and Growth

Use of fertilizer is a common practice in revegetation, yet little is known about the growth responses to specific nutrient levels or nutrient requirements of native high-elevation plant species (Brown and Johnston 1979; Chambers and others 1988). Although highly site specific, nitrogen (N) and phosphorus (P) are usually the most limiting nutrients on disturbances, but individual species responses to these nutrients vary widely. The availability of these and other nutrients and the nutrient retention capacity of a soil are often determined by the severity of the disturbance (Tilman 1986). Chambers and others (1988) found that tufted hairgrass, a frequent early colonizer on alpine disturbances, responded more to N inputs, and that the typical late-successional species, alpine avens, respond more to P. They also showed that tufted hairgrass had greater rates of growth at all levels of N and P than alpine avens. This suggests that tufted hairgrass may have competitive superiority over alpine avens on disturbances and over broad ranges of available N and P.

However, factors other than fertility and growth rate may affect the interactions among species in a revegetation mixture. Low growth rates and high root:shoot ratios are important attributes of species adapted to low-nutrient environments. Including species in a seed mixture that are low-nutrient and low-growth-rate adapted together with those that are high-nutrient and high-growth-rate adapted can help ensure long-term stability on nonintensively managed reclaimed disturbances. It may be necessary to use moderate seeding and fertilizer rates and to seed low-growth-rate species in equal amounts with high-growth-rate species in such mixtures.

RECLAMATION METHODS

The immediate goal of revegetation is to provide protection and surface stability on disturbed sites, but esthetics and long-term site stability are also important concerns. The general principles of revegetation applicable to disturbances in all life-zones, such as shaping and contouring, fertilizing, seeding and planting, and mulching apply to high-elevation disturbances. However, under the severe environmental conditions unique to high elevations in the mountainous West, the more subtle aspects of timing, species selection, and microenvironmental concerns often determine the difference between success and failure in revegetation. A primary objective of revegetation is to ameliorate soil and microclimatic conditions that are limiting to the physiological tolerances of otherwise adapted plant species on that site. For remote area disturbances that will be managed at low intensity levels following revegetation, proper methods should lead to site conditions that promote natural succession by enhancing invasion and colonization of different microorganisms, plant lifeforms, and animal species. Ultimately, a plant community should be established that is commensurate with ecosystem dynamics of that area.

Contouring and Shaping

Mine spoil piles, old roadbeds, and other severe disturbance areas should be reshaped to conform to the original contour of the land as nearly as possible (Brown and Johnston 1979). Reshaping should minimize slope angles, sharp ridgelines, and undrained depressions that lead to wind-scour, excessive erosion or overland flow, and water accumulation. Contouring should be designed to promote optimum environmental conditions for plant establishment and growth. Spoil or soil materials containing toxic concentrations of heavy metals and acid-bearing wastes should be buried under the best growing medium available in areas where subsurface drainage is not likely to cause contamination or loss of water quality. Topsoil should be stored and replaced before reclamation wherever possible. Contouring and shaping work should be completed well in advance of planned revegetation to permit settling to occur before seeding and planting. Ripping compacted spoil material may be necessary to promote root aeration and growth, and to facilitate water and nutrient absorption.

Season and Timing of Revegetation

High-elevation disturbances should be revegetated in the fall. Timing of revegetation has been found to be extremely important to successful plant establishment (Brown and Johnston 1980; Chambers 1987). Transplant stock should be hardened to low fall temperatures and should be in a dormant condition during planting. Seed, transplants, and soil amendments should be applied as late in the growing season as possible so that cold temperatures prevent germination and growth. Severe frost damage to young seedlings and transplanted stock may result if planting is too early. Fall revegetation ensures that seeds and amendments will be in place when conditions are ideal for germination the following spring as snowmelt occurs. Fall seeding and planting can usually be accomplished when conditions are relatively dry and when the soil or spoil can be worked most easily.

Spring or summer revegetation can be detrimental to successful plant establishment on high-elevation disturbances. Most high-elevation areas remain inaccessible in the spring until large snowdrifts melt. By the time access and site conditions are suitable, the optimum conditions for seed germination and seedling development may be passed.

Nutrients and Other Soil Amendments

A complete soil analysis should be performed well before seeding and planting so that low levels of available plant nutrients and potentially limiting physical or chemical soil properties can be identified (Chambers and others 1987a; Jurinak 1982). Mine spoils and other disturbed sites are often deficient in required nutrients for higher plants, and may have low pH and toxic concentrations of heavy metals that limit plant establishment. Amounts and ratios of fertilizers should be determined from levels of nutrients already present in the soil, the nutrient retention and cycling capacity of the soil, and the particular requirements of plant species to be seeded. In general, soils with high percentages of organic matter and fine textures have greater nutrient retention capacities than coarse mineral soils low in organic matter. Consequently, one-time applications of fertilizer may have more long-term benefits in fine-textured soils with greater amounts of organic matter. To substantially increase levels of available plant nutrients in mineral soils, organic matter additions may be necessary. Nutrient levels in the soil should be balanced for both high- and low-nutrient-adapted species. It is important to add a proportion of low-nutrient-adapted species to the seed mixture for low organic matter mineral soils to ensure long-term site productivity.

Fertilizer should be distributed uniformly over the site in the proper proportions to achieve the desired ratio of N-P-K and other needed nutrients. Commercially available hand-operated distributors perform acceptably with granular fertilizers (Brown and Johnston 1979, 1980). Normally, rates of application on high-elevation disturbances range from about 50 to 110 kg of N per ha, but actual rates vary with specific sites and objectives. The site should be harrowed, raked, or rototilled to incorporate the fertilizer into the upper 15 to 30 cm of soil or spoil.

The incorporation of organic matter or mulch into the upper layer of soil or spoil is beneficial for both improved nutrient- and water-holding capacity. Materials such as steer manure, straw, hay, peat moss, and other organic matter have been used successfully (Brown and others 1976, 1978).

If the soil pH is lower than about 5.0, lime or calcium carbonate should be applied in sufficient amount to raise the pH to about 5.5 or 6.0. Soil pH above 5.5 ensures that residual nutrients and applied fertilizers will be available to the developing plants, and that aluminum concentrations will be unavailable for uptake. Soil acidity tests performed by soil testing laboratories can provide data that recommend liming or calcium carbonate application rates necessary to neutralize acidity (Jurinak 1982). This amendment should be applied at the same time as fertilizer, and should also be incorporated into the upper 15 or 30 cm of soil. Brown and Johnston (1980) used 2,240 kg/ha of hydrated lime on the McLaren Mine in southwestern Montana to successfully adjust soil pH above 5.0 before revegetation. However, exact quantities required vary widely with specific site conditions.

Seeding and Planting Methods

Seed mixtures of several species should be applied on the site after fertilizer and other amendments have been incorporated into the soil. Optimum seeding rates on high-elevation disturbances normally range from about 225 to 550 total seeds per m^2 depending on the species used and site conditions. Generally, the seed is distributed uniformly with a hand-operated distributor or broadcast by hand over the surface of the site, and then covered by light raking or harrowing. Brown and Johnston (1980) used a commercial seeder-packer on a subalpine mine site to cover the seed to a depth of about 1 cm. Packing ensures firm contact between the seed and the soil particles, which appears to enhance germination. Species requiring light for germination (Haggas and others 1987) should be applied on the surface separately after the other species are seeded and packed. Seeding should be done during relatively calm periods to minimize wind redistribution.

Transplanting offers an alternative to seeding, and in some cases may be desirable in combination with seeding. Plant survival rates tend to be high when transplanting is accomplished in the fall with dormant containerized stock, and when rigorous planting procedures are followed (Brown and Johnston 1980). Plants may be grown from seed in a greenhouse or nursery as tublings, and then transported to the site for hardening and planting. Additionally, sod pieces collected from old road cuts or other disturbances can be collected and transplanted directly on the disturbed site (Brown and others 1976, 1978). Although survival of transplants can be high, transplanting tends to be very expensive and should probably be restricted to small key disturbances where slopes are too steep for seeding and where erosion hazards are high.

Surface Mulching

Surface mulching is recommended following seeding to moderate the effects of wind redistribution of seed, reduce evaporation, and minimize the effects of frost on seedling development (Brown and Johnston 1979, 1980; Chambers and others 1988). Materials such as straw or hay held in place with either pinned netting or an emulsion agent have been used successfully (Brown and Johnston 1979, 1980; Chambers 1987). Surface mulches should lightly cover the soil, yet still allow light to penetrate to the soil surface (Brown and Johnston 1979).

RESEARCH NEEDS

Although techniques for revegetation of high-elevation disturbances appear to be successful, additional research is needed as these life-zones come under increasing pressure from a wide variety of uses. Identification of adapted native species and an understanding of their physiological tolerances and ecological characteristics remain some of the most urgent needs. We need a better understanding of successional processes on disturbances, including the effects of competition and of nutrient and water relations requirements and interactions. In addition, we need to understand the characteristics and long-term interactions that mycorrhizal and nitrogen-fixing symbionts have with other adapted species on disturbances.

Further research is needed on the long-term effects of various reclamation methods, including soil amendments, and the effects they have on species performance and interactions and on soil nutrient retention and cycling. Studies on soil weathering and development and the dynamics of heavy metals and other toxic materials as they interact with plants are needed. Present methods appear to be inadequate for successfully revegetating the most extreme acidic mine spoils in the alpine zone throughout the West. Thousands of hectares of abandoned pyritic mine dumps and tailing piles throughout the mountainous West are located in the headwaters of watersheds from which increasing demands are being made as metropolitan areas expand. These, together with new mines and other disturbances, are degrading water quality of streams, rivers, and reservoirs throughout the region. Clearly, reclamation research of high-elevation disturbances needs to be expanded and intensified.

REFERENCES

Billings, W. D. 1974. Arctic and alpine vegetation: plant adaptations to cold summer climates. In: Ives, J. D.; Barry, R. G., eds. Arctic and alpine environments. London: Methuen and Co: 403-443.

Billings, W. D.; Mooney, H. A. 1968. The ecology of arctic and alpine plants. Biology Review. 43: 481-529.

Brink, V. C.; Mackay, J. R.; Freyman, S.; Pearce, D. G. 1967. Needle ice and seedling establishment in southwestern British Columbia. Canadian Journal of Plant Science. 47: 135-139.

Brown, R. W.; Chambers, J. C.; Wheeler, R. M.; Neely, E. E.; Kelrick, M. I. 1988. Adaptations of *Deschampsia cespitosa* (tufted hairgrass) for revegetation of high-elevation disturbances: some selection criteria. In: High altitude revegetation workshop No. 8. Infor. Ser. 59. Fort Collins, CO: Colorado State University, Colorado Water Resources Research Institute: 147-172.

Brown, R. W.; Johnston, R. S. 1979. Revegetation of disturbed alpine rangelands. In: Johnson, D. A., ed. Special management needs of alpine ecosystems. Ser. 5. Denver, CO: Society for Range Management, Range Science: 76-94.

Brown, R. W.; Johnston, R. S. 1980. An assessment of revegetation techniques and species for alpine disturbances. In: High altitude revegetation workshop No. 4. Infor. Ser. 42. Fort Collins, CO: Colorado State University, Water Resources Research Institute: 126-146.

Brown, R. W.; Johnston, R. S.; Chambers, J. C. 1984. Responses of seeded native grasses to repeated fertilizer applications on acidic alpine mine spoil. In: High altitude revegetation workshop No. 6. Infor. Ser. 53. Fort Collins, CO: Colorado State University, Water Resources Research Institute: 200-214.

Brown, R. W.; Johnston, R. S.; Johnson, D. A. 1978. Rehabilitation of alpine tundra disturbances. Journal of Soil and Water Conservation. 33: 154-160.

Brown, R. W.; Johnston, R. S.; Richardson, B. Z.; Farmer, E. E. 1976. Rehabilitation of alpine disturbances: Beartooth Plateau, Montana. In: High altitude revegetation workshop No. 2. Infor. Ser. 21. Fort Collins, CO: Colorado State University, Water Resources Research Institute: 58-73.

Chambers, J. C. 1987. Disturbed alpine ecosystems: seedling establishment of early and late seral dominant species. Logan, UT: Utah State University. 148 p. Dissertation.

Chambers, J. C. [In press]. Seed viability of alpine species: variability within and among years. Journal of Range Management.

Chambers, J. C.; Brown, R. W.; Johnston, R. S. 1984. Examination of plant successional stages in disturbed alpine ecosystems: a method of selecting revegetation species. In: High altitude revegetation workshop No. 6. Infor. Ser. 53. Fort Collins, CO: Colorado State University, Water Resources Research Institute: 215-224.

Chambers, J. C.; Brown, R. W.; Johnston, R. S. 1987a. A comparison of soil and vegetation properties of seeded and naturally revegetated pyritic alpine mine spoil and reference areas. Landscape and Urban Planning. 14: 507-519.

Chambers, J. C.; MacMahon, J. A.; Brown, R. W. 1988. Seedling establishment in disturbed alpine ecosystems: implications for revegetation. In: High altitude revegetation workshop No. 8. Infor. Ser. 59. Fort Collins, CO: Colorado State University, Water Resources Research Institute: 173-191.

Chambers, J. C.; MacMahon, J. A.; Brown, R. W. 1987b. Germination characteristics of alpine grasses and forbs: a comparison of early and late seral dominants with reclamation potential. Reclamation Revegetation Research. 6: 235-249.

Chambers, J. C.; MacMahon, J. A.; Brown, R. W. 1987c. Responses of an early seral dominant alpine grass and a late seral dominant alpine forb to N and P availability. Reclamation Revegetation Research. 6: 219-234.

Haggas, L.; Brown, R. W.; Johnston, R. S. 1987. Light requirement for seed germination of Payson sedge. Journal of Range Management. 40(2): 180-184.

Johnson, P. L.; Billings, W. D. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. Ecological Monographs. 32: 102-135.

Johnston, R. S.; Brown, R. W. 1979. Hydrologic aspects related to the management of alpine areas. In: Johnson, D. A., ed. Special management needs of alpine ecosystems. Ser. 5. Denver, CO: Society for Range Management, Range Science: 65-75.

Jurinak, J. J. 1982. Overview of soils considerations in high altitude revegetation. In: High altitude revegetation workshop No. 5. Infor. Ser. 48. Fort Collins, CO: Colorado State University, Water Resources Research Institute: 128-135.

Thorn, C. E. 1982. Gopher disturbance: its variability by Braun-Blanquet vegetation units in the Niwot Ridge alpine tundra zone, Colorado Front Range, USA. Arctic and Alpine Research. 14: 45-51.

Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. Ecology. 67: 555-563.

LANDSCAPE- AND ECOSYSTEM-LEVEL MANAGEMENT IN WHITEBARK PINE ECOSYSTEMS

Wendel J. Hann

ABSTRACT

To provide adequate resource protection in alpine and subalpine areas, managers need to expand their perspectives and focus on ecosystem and landscape-level management. Single-resource and microsite focuses stymie integrated management and protection plans. A landscape perspective is outlined for the Northern Rocky Mountains, interpreting climatic, landform, topographic, and distribution factors and their relation to vegetation mosaics.

INTRODUCTION

The upper subalpine and alpine zone of the Northern Rocky Mountains has a unique natural vegetation mosaic. This mosaic of forested and nonforested communities differs from the montane forested and nonforested community mosaic that occurs in the next lower elevation zone. The alpine and subalpine community mosaic is a diverse complex of subalpine forest-dominated upland communities, shrub- or herb-dominated upland communities, shrub- or herb-dominated wetland communities, and talus, scree, or rock cliff areas, with sparse vegetation cover.

The types of community mosaics within the alpine/subalpine zone vary by geographic area and type of disturbance history, and are strongly correlated with topography and amount of soil development. A second process of importance is presettlement and postsettlement fire history. Differences between geographic areas exist, both in the natural potential for fire ignition and spread and in the history of fire suppression. A third process that produces different types of mosaics is disturbance by humans, which in this zone, typically includes timber harvest, roads, mining, effects of pollution, effects from recreation, and livestock grazing.

Managers and researchers face a difficult challenge in this zone. It is imperative that we take a landscape perspective and ecosystem management approach to maintain a diversity of productive and functioning ecosystems. Yet the nature of resource advocacy and studies that emphasize small, uniform areas stymie our ability to manage ecosystems at a broad-scale level with an integrated approach. Our basic management objective should be land stewardship that protects the basic ecosystem values of soil, water, air, biotic diversity, and ecological processes, while producing resources for public use. To protect these values and provide resources it is logical to move forward in understanding and implementing an ecosystem management approach at a landscape level.

The understanding of communities and their linkages at a landscape level is a developing science. This paper will provide a landscape perspective of subalpine and alpine ecosystems in the Northern Rocky Mountains, interpret some of the effects of human activities on the landscape mosaic, and identify challenges for managers and researchers to meet to provide sound land stewardship of these ecosystems.

PRIMARY FACTORS OF LANDSCAPE MOSAICS

The pattern, shape, size, and juxtaposition of communities on a landscape are formed or controlled by a variety of factors (Bailey 1988). These factors range from broad-level factors, such as change in climate, to site-specific factors, such as effects of fire, insects, or windthrow (Knight 1987). Broad-level and community-specific factors interact to result in a dynamic pattern of shifting community shapes and sizes. This spatial and temporal pattern is an important component in the development of management strategies.

Geographic and Climatic Patterns

Different geographic areas have different spatial and temporal patterns on their landscapes within the subalpine and alpine zones. Within the Northern Rocky Mountains there is a strong west-to-east longitudinal gradient and a strong south-to-north latitudinal gradient that create different patterns as a result of changing climate conditions (Arno and Hammerly 1984). From west to east, subalpine and alpine climates shift from inland-maritime, to semidesert, to continental influence. From south to north in the Northern Rocky Mountains the lower elevational limits of the subalpine and alpine zones tend to decrease with elevation. However, this can be strongly influenced by local relief and wind patterns.

Landform Patterns

Local landforms and valley to mountaintop relief strongly influence the climate of the subalpine and alpine zones (Arno and Hammerly 1984; Habeck 1987). The

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Wendel J. Hann is Ecologist, Northern Region, Forest Service, U.S. Department of Agriculture, Missoula, MT 59807.

present landform landscape is an interaction of the landforming process with the geological bedrock and previous landforms (Bailey 1988). In subalpine and alpine areas glaciation is a common important landforming process. Areas that had significant mountain glaciation that covered all aspects differ considerably from areas that had minor mountain glaciation or nivation snow basin action on north slopes, but were not glaciated on alpine plateaus or southerly aspects. Other areas on the northern end of the Northern Rocky Mountains that were strongly influenced by both continental and mountain glaciation have a different landform landscape.

Areas that have low-elevation valleys associated with high-elevation mountains appear to differ significantly in their subalpine and alpine landscape from those areas where the valleys are relatively high elevation and the relief difference from valley to mountaintop is not as great. Those areas that have large relief differences usually have sharper gradients in the alpine and subalpine zone and often have higher precipitation.

Topographic and Edaphic Patterns

Aspect, slope, and soil have a strong influence in the alpine and subalpine zone. The slope, aspect, and position of a community determine microclimatic influences that create a highly complex set of conditions across relatively small land areas. This results in an intricate pattern of variation within and between communities.

Many plants in the subalpine and alpine zone are on the edge of their ecological amplitude. Consequently, minor shifts in soil characteristics that change soil physical and chemical conditions can affect the ability of plants to survive and compete. This results in high variability within and between communities.

Natural Disturbance and Cycles

Natural disturbances and successional cycles, or sequences, cause dramatic changes in the spatial and temporal patterns of subalpine and alpine communities. Natural disturbances of fire, wind, drought, severe cold, erosion, animal herbivory, and mortality or reduction in vigor from insect or disease influences all interact to result in dynamic conditions in this zone. Vegetation composition over time, as a result of interacting plant species growth rates, competitive ability, and mortality, also changes over time as influenced by the various disturbance factors. In the subalpine and alpine zones, where plant growth rates are slow and competitive ability is low, disturbance factors are often harsh and play a strong role in maintaining a dynamic set of shifting conditions. But alpine plant communities have a relatively low ability to buffer against these changes, in comparison to lower elevation montane and valley systems.

Landscape Linkages

The mosaic of ecosystems in a landscape has linkages of: (1) snowmelt and water flow, (2) energy state and transfer, (3) nutrient state, cycling, and transfer, (4) animal habitat needs and movement, and (5) buffering from disturbance. In systems such as the subalpine and alpine zones, which are subjected to extreme environmental conditions, these linkages are critical for species and community survival. Changes in community juxtaposition or conditions can shift the environmental balance and negatively affect an associated community to the point where it can no longer survive. An example in the alpine and subalpine zones is the moist herbaceous communities typically associated with the lee side of a patch of subalpine trees or timberline krummholz trees. Removal of the patch of trees through fire or other disturbance eliminates the conditions for snow retention in the adjacent community, which changes the moisture, energy, and temperature conditions in that ecosystem.

Human Disturbance

Impacts from human developments, pollution, and disturbance to natural processes have been relatively low in the subalpine and alpine zones compared to other ecosystems. However, these zones are very sensitive to disturbance by humans, and the consequences are often highly visible. Primary human disturbances that have affected the subalpine and alpine ecosystems involve: (1) mining, (2) oil and gas development, (3) road construction, (4) direct fire suppression impacts, (5) indirect fire suppression effects, (6) domestic livestock grazing, (7) logging, and (8) air pollution and associated global climatic change. Because of the lack of buffering ability in subalpine and alpine ecosystems, the effects of these disturbances are longer, often more drastic, and tend to be more chain-reactive than in other more productive and less fragile ecosystems.

The principal effects of historic natural resource management and development on landscape patterns and linkages have tended to fragment communities that are naturally contiguous and reduce or eliminate corridors or environmental linkages between associated ecosystems (Franklin and Forman 1987; Knight 1987). In contrast, the consequence of fire suppression in relatively natural landscapes has been homogenization. Typical patterns of human developments are straight lines, squares, and rectangles compared to the more natural shapes of nature.

In Europe, long-term human developments have resulted in a lowering of the upper timberline, thus increasing the alpine zone (Douguedroit 1978; Plesnik 1978). This has been primarily caused by tree cutting for use in charcoal burning and by grazing. Some attempts have been made to reforest these areas with subalpine tree species. These attempts have been somewhat successful in establishing trees in this zone, but the resulting forests greatly lack the natural diversity of patterns and associated stability of linked communities.

In the Northern Rockies, historic logging, mining, and livestock overgrazing have locally removed forest subalpine communities and changed community patterns. However, these effects have not been broad scale. Revegetation of sites degraded by mining, roading, and overgrazing has been somewhat successful given the right conditions. It has become apparent that once the shallow topsoil is lost, revegetation of alpine and timberline ecosystems is very difficult. The change in snow accumulation/melt patterns and energy flow from tree removal and soil loss in these ecosystems often create a complete change in the potential vegetation that can grow on the sites.

Disturbances to subalpine forest vegetation from logging and overgrazing set succession back to an early stage. As long as the disturbance has replicated natural events, such as fire or big-game grazing, and no exotic plants have been introduced, succession will usually proceed in a relatively natural fashion. However, successional response in this zone is very slow, even when there has been no effect on soil and microclimate. This slow response usually does not meet management standards for regeneration or for livestock vegetation management trend. There is little that can be done to speed up this response on areas that have been impacted in the past. Future harvest treatments and grazing systems should be designed to better mimic natural disturbances and maintain soil productivity and microclimate conditions.

The results from fire suppression in the subalpine zone are broad scale. Natural fire frequency cycles are relatively long in this zone and successful ignitions are infrequent (Arno 1986; Fischer and Bradley 1987). Consequently, fire suppression has been relatively successful. Since fire frequencies are typically 100 to 300 years, the effects of fire suppression on individual communities have not caused a change from what is present naturally. The primary effect is that the amount of communities in an early seral stage compared to mid and late seral is much less. Consequently, the pattern of communities in this zone is becoming more homogenous; old communities are maintained, while adjacent communities that were once young are now becoming old.

Intensive development and management by humans usually result in a reduction of genetic and species diversity. In the subalpine and alpine zones of Europe this has been a significant result from long-term degradation of these environments (Douguedroit 1978; Plesnik 1978). Many species have become extinct, and the diversity of species in existing communities is much lower than in similar natural communities.

In the Northern Rocky Mountains there have been relatively few plant species extinctions in the alpine or subalpine zones that have been caused by human developments or management. In localized communities that have had severe impacts from mining, road building, or overgrazing there has been significant loss in species diversity. Where exotic species have been introduced, there is little chance for the native species to compete and reestablish dominance through succession.

There is little doubt that pollution is affecting our natural communities (Mintzer 1988; Perry and Maghembe 1989). There is ample evidence that acid rain and other pollutants are reaching all environments on earth. Some ecosystems have the ability to buffer these pollutants and will not be strongly affected. Ecosystems at extremes, such as the subalpine and alpine zones, that have little buffering ability, are typically the first to demonstrate effects of these pollutants. There is little agreement on how global climates may change. However, it is generally agreed that climates will become more extreme even if there is little change in the averages. The subalpine and alpine climates will be more sensitive to this change and communities may show the effects. These ecosystems should make excellent monitoring sites that would be sensitive to changes in air pollutant levels and climates.

EVALUATION AREAS

Three areas were selected on a west-to-east gradient at approximately 46 °N. latitude across the Northern Rocky Mountains. All areas have had varying degrees of mountain glaciation and have subalpine and alpine vegetation, with some communities dominated by whitebark pine (*Pinus albicaulis*). Areas were mapped and map photo interpretation types were correlated with available ground data. The furthest west area is an area on the south end of the Seven Devils Mountains of north-central Idaho, which lies between the Snake River to the west and the Little Salmon River to the east. The second area, which is in west-central Montana, near the Continental Divide, is in the Bitterroot Range, and is called the Piquette Mountain area. This area lies between the East Fork and West Fork of the Bitterroot River. The third area is in south-central Montana, west of the Boulder River, and is called the Meatrack-Carbonate area.

The three areas all have had historic sheep grazing impacts, but adequate areas were left ungrazed to compare disturbed to natural vegetation. All three areas also have had some disturbance from past exploratory mining, but this is relatively minor when compared to the size of the total area.

Table 1 shows a comparison of various environmental and landscape factors based on a preliminary assessment. A final assessment will be published at a later date based on additional ground data and correlation.

Climates of the three areas make a transition from strong maritime influence on the west to the continental climate of the Meatrack-Carbonate area on the east. The Seven Devils site has strong evidence of glacial cutting or deposition on most of the area. The Piquette Mountain area shows evidence of glaciation primarily on the northerly aspects and on south aspects at the highest elevations. Both of these areas have alpine communities that are on steep slopes or in cirque basins. The Meatrack-Carbonate area has strong evidence of glaciation on the north aspects and some south aspects, but large areas of high-elevation alpine plateaus remain above the glacial cirques.

The area with the highest relief is the Seven Devils area with a low of 1,600 ft at the Snake River to a high of about 8,500 ft. The other areas have differences of relief of about 5,000 ft; the Meatrack-Carbonate rises almost 2,000 ft higher than the Piquette Mountain area.

Potential vegetation indicated a strong dominance by forest communities in the Piquette Mountain area compared to approximately an even split between forest potential and nonforest potential on the Seven Devils area. The Meatrack-Carbonate area showed strong dominance by herbaceous communities. This is probably correlated with the low precipitation and continental climatic regime. The presence of subalpine shrub types, primarily

Table 1—Environmental and landscape factors for three subalpine/alpine areas in the Northern Rocky Mountains

Factor	Area Meatrack-Carbonate	 S. Seven Devils	 Piquette Mt.
Climate type	Inland-maritime	Inland-maritime	Continental
Valley elevation (ft)	1,600	3,500	5,500
High elevation (ft)	8,500	8,600	10,500
Percent mt. glaciation	85	50	35
Percent subalpine forest potential	45	60	30
Percent subalpine herb potential	15	15	30.
Percent subalpine shrub potential	15	5	0
Percent timberline krummholz	5	2	10
Percent alpine herb-shrub potential	5	3	15
Percent rock, scree, and cliff	15	15	15
SI(50) SAF ABLA/VASC HT	44	33	22
BA (ft^2) ABLA/VASC HT	115	145	175
Herb-shrub foliage production (lb)	955	785	1,060

mountain sagebrush (*Artemisia tridentata vaseyana*), appeared to be strong to the west and decreased to the east. All areas had approximately the same amount of rock, scree, and cliffs.

Site index and basal area of subalpine fir (*Abies lasiocarpa*) were evaluated on a subalpine fir/grouse whortleberry habitat type (Pfister and others 1977; Steele and others 1981) on all three areas for similar aspects. There is considerable difference in soils between the three areas. Site index (SI) generally decreased from west to east for subalpine fir, as would be expected, making the transition to a drier and more continental climate. Basal area generally increased from west to east, and no correlation can be drawn since this attribute is probably more highly correlated to past stand history than to the environment. Production of annual herb and shrub foliage (lb/acre) was evaluated on an elk sedge/Idaho fescue grassland type for all three areas. This value should generally increase in correlation with continental climate, but there was considerable difference in soils and precipitation.

A preliminary assessment of polygon shape and size was also conducted for the three areas. These preliminary values are presented in table 2.

Size and shape of polygons for different vegetation types were highly variable between the areas and showed no strong correlation with the west to east climatic trends. Size, shape, and juxtaposition appear to be highly correlated to local factors of landform, topography, soils, and historic disturbance. Table 3 shows a relative correlation of these factors for the three areas that were evaluated. Fire appears to be a much stronger component in the Seven Devils and Piquette Mountain areas compared to the Meatrack-Carbonate area. However, that may be an incorrect conclusion, since although fires may be less frequent in the Meatrack-Carbonate area, they may just as strongly control size and shape over the long term.

Methods for assessing these correlations are relatively rough and need to be refined to better identify controlling factors and explain variability. Statistical parameters to describe variability are difficult to assess, since none of the factors can be considered to have normal distributions. Frequency statistics appear to be the primary attributes that are descriptive and have meaning for making management assessments and recommendations.

Table 2—Polygon size and shape factors for three subalpine/alpine areas in the Northern Rocky Mountains

Factor	Area Meatrack-Carbonate	 S. Seven Devils	 Piquette Mt.
Polygon shape			
Subalpine forest types			
Mean size (acres)	45	80	20
Percent linear	30	45	15
Percent octagonal	35	20	40
Percent elliptical or oblong	25	25	30
Percent rotund	5	0	10
Percent irregular	5	10	5
Percent rectangular	0	0	0
Whitebark pine types			
Mean size (acres)	35	10	15
Percent linear	40	85	25
Percent octagonal	40	5	15
Percent elliptical or oblong	0	0	20

Table 3—Percent correlation of factors controlling polygon size and shape for three subalpine/alpine areas in the Northern Rocky Mountains

Factor	Area Meatrack-Carbonate	 S. Seven Devils	 Piquette Mt.
		Percent	
Geoclimatic	5	5	5
Landform	15	30	30
Topography	15	25	30
Soils	20	5	15
Disturbance	45	35	20

MANAGEMENT AND RESEARCH CHALLENGES

There are many challenges for management and research in the subalpine and alpine ecosystems. We need to evaluate our ability to manage ecosystems from a landscape and vegetation perspective. Do we have the technology and the philosophy to take this approach? Another way to ask this question is "do we see the ecosystem for the trees?" If we had all the data we needed to describe ecosystems from a landscape perspective, would we have the techniques to analyze those data? We need to develop the ability to assess natural mosaics relative to "human activity" mosaics and determine the positives and negatives of various combinations of vegetation types, their size and shape, their juxtaposition, and associated corridors or linkages.

Now more than ever, managers must develop an ecosystem philosophy for management. The number one objective for managers of public lands should be to provide land management and stewardship that protect and enhance basic values (soil, water, air, biotic diversity, natural processes), while producing resources for public use.

On the forefront of management and research challenges is the need to take an ecosystem and landscape approach to assessing management alternatives. Managers must develop their abilities to analyze ecosystems and develop integrated alternatives, rather than being advocates for their own specialty. Specific resource advocacy is a detriment to an ecosystem approach and results in interdisciplinary team members "whipsawing" each other from defensive to offensive, and alternatives to mitigation.

To develop effective management alternatives and understand their potential effects, management needs to be able to extrapolate to large-scale areas. Present research is often done at a micro scale, and management lacks the tools to interpret the results at a large scale. Research needs to develop the relationship between predicting results for a site to extrapolation for an ecosystem.

Research should begin developing technology to assess spatial and temporal changes and assess how these changes might affect resource outputs, community linkages, and ecosystem stability. Without this technology it will be difficult to develop viable ecosystem management alternatives that will provide for conservation of natural processes, landscapes, ecosystems, species, and genetic resources. With this technology managers can develop prescriptions for landscapes versus stands or communities.

To summarize, the challenge to managers is to expand their perspective to the ecosystem and be their own conscience for protection of basic ecosystem values. The challenge to researchers is to improve our ability to extrapolate results, and assess alternatives and affects, in the realms of both spatial and temporal landscapes.

REFERENCES

Arno, Stephen F. 1986. Whitebark pine cone crops—a diminished source of wildlife food? Western Journal of Applied Forestry. 1(3): 92-94.

Arno, Stephen F.; Hammerly, Ramona P. 1984. Timberline: mountain and arctic forest frontiers. Seattle, WA: The Mountaineers. 304 p.

Bailey, Robert G. 1988. Ecogeographic analysis: a guide to ecological division of land for resource management. Misc. Publ. 1465. Washington, DC: U.S. Department of Agriculture, Forest Service. 16 p.

Douguedroit, Annick. 1978. Timberline reconstruction in Alpes de Haute Provence and Alpes Maritimes, southern French Alps. Arctic and Alpine Research. 10(2): 505-517.

Fischer, William C.; Bradley, Anne F. 1987. Fire ecology of western Montana forest habitat types. Gen. Tech. Rep. INT-223. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 95 p.

Franklin, Jerry F.; Forman, Richard T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology. 1(1): 5-18.

Habeck, James R. 1987. Present-day vegetation in the Northern Rocky Mountains. Annals of the Missouri Botanical Garden. 74(4): 804-840.

Hungerford, Roger D.; Nemani, Ramakrishna R.; Running, Stephen W.; Coughlan, Joseph C. 1989. MTCLIM: a mountain microclimate simulation model. Res. Pap. INT-414. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 52 p.

Knight, Dennis H. 1987. Chapter 4. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. In: Turner, Goigel, ed. Landscape heterogeneity and disturbance. Ecological Studies 64. New York: Springer-Verlag: 59-82.

Mintzer, Irving. 1988. Global climate change and its effects on wildlands. Presented at 4th World Wilderness Congress, 1987. Golden, CO: Fulcrum, Inc: 56-67.

Perry, David A.; Maghembe, Jumanne. 1989. Ecosystem concepts and current trends in forest management: time for reappraisal. Forest Ecology and Management. 26: 123-140.

Pfister, Robert D.; Kovalchik, Bernard L.; Arno, Stephen F.; Presby, Richard C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Plesnik, P. 1978. Man's influence on the timberline in the west Carpathian mountains, Czechoslovakia. Arctic and Alpine Research. 10(2): 491-504.

Steele, Robert; Pfister, Robert D.; Ryker, Russell A.; Kittams, Jay A. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 138 p.

SESSION 5

Where Do We Go From Here?

Tad Weaver and Wyman C. Schmidt
Session Coordinators

This session served as a wrap-up for the symposium and described how the Forest Service and National Park Service, who manage the preponderance of whitebark ecosystem lands in the United States, view the management and goals for these lands. It also includes an examination of the knowledge gaps and research needs that became apparent as a result of the symposium as well as some highlights of what was learned.

INTEGRATING WHITEBARK PINE INTO NATIONAL PARK MANAGEMENT GOALS

C. J. Martinka
K. A. Keating
C. H. Key

ABSTRACT

Various relationships between ecosystems, National Parks, and whitebark pine (Pinus albicaulis) *are discussed. Ecosystem management in and around parks involves four elements: (1) expression of desired condition; (2) definition of boundaries; (3) management strategies; and (4) determination of effectiveness. Numerous factors have contributed to the complexity of environmental issues and the requirements for management accountability in National Parks during recent decades. Whitebark pine and western parks possess the potential for a mutually beneficial relationship with the species serving as an environmental barometer and the parks providing a foundation for conservation.*

INTRODUCTION

Mankind has always sought knowledge about the environment and applied it in a fruitful fashion to the ultimate of ecological imperatives—maintaining a livelihood. Historical motivation for the acquisition of new information was likely quite simple and directed almost entirely toward the exploitation of natural resources. More recently, conservation of those same supporting resources has emerged as a critical issue on a worldwide scale. And for the same reasons that drove exploitative behavior over the eons of history—sustaining a future for the human species.

Nearly the entire breadth of the conservation movement has occurred during the current century. Momentum has accelerated during recent decades when numerous Federal and State laws have been enacted to assure appropriate protection and management of natural resources. These laws reflect the conscience of a public concerned about the quality of life and its supporting environment. Extinctions have helped heighten an awareness of biological diversity and the role that individual species play in ecosystem integrity. Mammals have received a predominant share of scientific attention, but there is growing interest in other contributors to the trophic fabric of ecosystems. Whitebark pine (*Pinus albicaulis*) is taking its place on a growing list of plant species for which there are now legitimate reasons for gathering and evaluating new knowledge.

This paper discusses various relationships between ecosystems, National Parks, and whitebark pine. The unique attributes of the species suggest that it plays an important ecosystem role in the mountainous parks of the Western United States. At the same time, the parks will likely play an increasingly important role in management of the species as the global environment changes in future decades.

ECOSYSTEMS AND PARKS

In 1987, a group of managers, scientists, and planners gathered at Pack Forest, WA, to discuss and develop ecosystem management concepts for parks and wilderness. The published results of the workshop provide a rationale for ecosystem management and suggest means by which the concept might be implemented (Johnson and Agee 1988). Managing in an atmosphere of uncertainty was of special concern to the participants and a four-step process was recommended for addressing ecosystem goals for nature reserves.

Step one proposed that the desired condition for the ecosystem be expressed in terms of specific goals and measurable targets. Since past management has focused on protection as the principal means of conserving natural integrity, this element adds a new dimension to future strategies for most natural sanctuaries. Most certainly, the scientific process enters the management picture, but beyond that, the question of congruity between science and philosophy will likely emerge as a dilemma for many areas. In this sense, humans become an integral part of natural systems in terms of both their intellectual direction and their ecological impacts. Significant organizational changes will be required to add management to the essential foundation of protection for parks and wilderness.

Step two is a recommendation that ecosystem boundaries be defined using primary components for guidance. This goal is not only reachable but has been implemented in several settings using information from field studies of large mammals. For example, movements of grizzly bears (*Ursus arctos*) have helped define an ecosystem that includes a large area surrounding Yellowstone National Park (Craighead 1980). At the same time, reality points

---

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

C. J. Martinka is Chief Scientist, K. A. Keating is Conservation Biologist and C. H. Key is Geographer, Glacier National Park, West Glacier, MT 59936.

to the difficulties associated with using components such as migratory birds, continental airsheds, or river systems to define boundaries. Systems of sanctuaries are likely to be an important approach to solving the ecosystem boundary issue on continental or global scales.

Step three moves into the arena of management and recommends the development of strategies to achieve goals that transcend political boundaries. There is little doubt that the focus of this task on the human element will cause it to be the most difficult of the four that were presented. Many, if not most, natural resources tend to be shared by a number of adjacent managing agencies, but goals for species or communities are frequently in conflict. At least a part of the problem has been a rather pervasive attitude that ecosystem elements cannot be managed to satisfy more than one goal. Thus a sanctuary manager may not accept harvest of migratory ungulates as consistent with an objective of maintaining natural relationships with dependent carnivores. Rigorous application of scientific process and knowledge may help move this recommendation toward success.

Finally, the fourth step urges that programs to assess the effectiveness of management in meeting stated goals be implemented. Comprehensive inventories of natural resources to establish baseline ecosystem conditions as well as monitoring systems to assess trends of significant components are critical requirements of this program element. Unfortunately, park and wilderness management have tended to focus on the solution of specific problems; the systematic collection of facts about systems and relationships has typically been relegated to a subordinate role. Current interest in biological diversity, insular population ecology, and landscape management is beginning to alter that tradition in many National Parks. In fact, a knowledge of baseline conditions was thought to be critical to the protection of National Parks within the existing framework of public law (Keiter and Hubert 1987).

This discussion points to the rather obvious fact that ecosystem management in parks is an appropriate strategy for the future but that its implementation requires commitment to a new and complex form of public land administration. With this in mind, it seems essential that a foundation for ecosystem management be constructed in a way that fosters the building of a program in incremental steps. There is every reason to believe that evolution rather than revolution is the most likely pathway to successful land management using ecosystem concepts.

NATIONAL PARK ISSUES

From the National Park perspective, numerous reasonable and legitimate questions might be asked about ecosystem management as envisioned by those gathered at Pack Forest. Perhaps most important are those relating to the feasibility of an intricate new program that carries parks into what is essentially an organizational frontier. Of even greater concern is the almost total absence of factual information from which success for ecosystem management might be predicted. Yet it might also be noted that alternative solutions to the increasing complexity of park conservation have not been proposed, nor are any anticipated in the immediate future.

The recent history of Glacier National Park illustrates a number of changes that have become important elements in the development of a conservation strategy for the park and surrounding lands.

1. The park has become part of an increasingly fragmented natural system in northwestern Montana, a trend that is related primarily to the discovery, development, and use of natural resources. The change is clearly visible from the perspective of high-altitude photography and satellite imagery, but documentation of impacts in terms of ecosystem function remains a rather elusive goal.
2. The protection of rare and endangered species has evolved toward a general public interest in the conservation of biological diversity. In turn, requirements for the inventory of natural resources and monitoring of their status have intensified, especially in view of their demonstrated value in addressing major threats to regional ecosystem integrity.
3. The public has expressed its concern about environmental quality through numerous new laws that address a variety of conservation concerns. The enactment of these statutes has created legal alliances with other agencies that effectively carry park management into the regional setting for issues such as the protection of airsheds, water quality, and endangered species. Even the process of making decisions has been opened to public scrutiny through the National Environmental Policy Act.
4. Rapid advances in collection systems and computer technology have allowed the storage, processing, and retrieval of massive amounts of information about our parks. Using that information has become a challenge that is leading to even more complex programs such as geographic information and database management systems. In turn, continuing education is now a necessity among park staff that must cope with these new demands.
5. The very real prospect of global warming is causing park managers to adjust their thinking about future environments and how anticipated changes in extinction and colonization rates for sensitive species will be addressed. In fact, fundamental philosophies are being questioned by some who now feel that human intervention to assure the attainment of desired conditions will be predominant in the management process.
6. The role of parks is expanding to include scientific values as part of their management strategies (Martinka 1985). These values were recognized in the enabling legislation for many parks, but only recently has the scientific process emerged as an important part of park management programs.

At this point, park science deserves further discussion, since its functional role is both new and dynamic. For example, emphasis is shifting from describing the biology of species to understanding the nature of systems. In turn, park scientists now tend to focus their efforts on regional or even continental study areas rather than confining their activities within ecologically arbitrary park boundaries. And stored information holds unique potential for research with geographic information systems providing the processing tool for design, evaluation, and synthesis of study problems. Each of these changes is significant in terms of the ecology and management of whitebark pine.

WHITEBARK PINE

Whitebark pine is one of thousands of plant species that inhabit numerous National Parks throughout the Western United States. It has not been a species of special concern until recent surveys pointed to locally significant population declines. The combined effects of insect infestations and fungal disease likely promoted the severity of the losses, which are especially visible in subalpine forests. At the same time, survival of this hardy tree as a species has not been seriously questioned.

One benefit of the population decline has been the recognition that whitebark pine possesses attributes that make the species unique in terms of National Park management strategy. It is adapted to the extreme climate and poor soil of high mountains. The species grows slowly, has a long life, and tends to have a patchy distribution, locally and throughout its range. At the same time, seed crops are sufficiently abundant to provide an important food source for birds and animals. These characteristics point to whitebark pine as a possible candidate species for monitoring park ecosystems. A rationale for use of this particular species as a monitor includes the following elements:

1. Its high-altitude ecological niche is likely to be sensitive to habitat changes, especially those induced by atmospheric disturbances such as acid deposition or climatic change.
2. Its patchy distribution provides inherent potential for experimental design and statistical treatment when developing monitoring programs.
3. Trophic relationships to species such as grizzly bears and red squirrels (*Tamaisciurus hudsonicus*) are simple and direct, an attribute that enhances the value of whitebark pine as monitor of ecosystem health.

No one species provides all the elements necessary for a complete environmental monitoring program, but it is likely that whitebark pine would rate high in ranking systems that might be developed in the future.

IMPORTANCE OF PARKS

Discussions to this point have focused on the value of whitebark pine to National Parks. It now seems appropriate to view the reverse relationship—the value of parks to whitebark pine.

First, one can and should value the National Parks for their ability to provide baseline information against which the experiments of exploitative or manipulative management can be compared. This is an inherent value that is currently in its infancy in terms of practical application. However, regional programs to manage natural resources will require comparative baseline information if they are to have a rational basis for assessing the attainment of stated goals.

Second, the parks serve as refuges for whitebark pine and other species as disturbance and change occur on surrounding lands. This is not to suggest the possibility of extinction for whitebark but rather to address the issue of reduced genetic diversity under the various forms of management and environmental stress to which the species is currently subjected. Parks may help conserve that diversity and thereby provide a source of genetic material for restoration of the species over regional landscapes at some point in the future.

Finally, parks may serve as retreats for the distributional changes that are predictable as a result of global climatic change. In this case, suitable habitats are protected along climatic gradients within and adjacent to the current range of the species. Natural or anthropic seed dispersal would carry the species to new habitats as climatic changes occur. This issue is of special interest, since it elevates treatment of a single species to the level of landscape management.

CONCLUSIONS

Whitebark pine is an important subalpine tree in many of the National Parks of the Western United States. The species possesses attributes that contribute to its potential as a monitor of ecological conditions in the parks. At the same time, it appears that parks may play an important role in future conservation of this unique tree. The mutually beneficial relationship between a species, protective sanctuaries, and landscape management is likely to become a common model for the future.

REFERENCES

Craighead, J. J. 1980. A proposed delineation of critical grizzly bear habitat in the Yellowstone region. Bear Biology Association Monograph No. 1: 1-20.

Johnson, D. R.; Agee, J. K. 1988. Introduction to ecosystem management. In: Agee, J. K.; Johnson, D. R., eds. Ecosystem management for parks and wilderness. Seattle, WA: University of Washington Press: 3-14.

Keiter, R. B.; Hubert, W. A. 1987. Legal considerations in challenging external threats to Glacier National Park, Montana, USA. Environmental Management. 11: 121-126.

Martinka, C. J. 1985. New role for science in the National Parks. Transactions of North American Wildlife Natural Resources Conference. 50: 367-373.

A SURVEY OF WHITEBARK PINE MANAGEMENT ON NATIONAL FOREST LANDS

Kent E. Houston
Earle F. Layser

ABSTRACT

Whitebark pine (Pinus albicaulis) *occurs in 25 National Forests in the Western United States. Although this species is of limited commercial value throughout its range, the ecosystems in which it is a major component are highly valued for wildlife, watershed, and esthetics. This paper reviews the results of a questionnaire on past and current management direction regarding* P. albicaulis *on National Forest lands as perceived by 20 Forest Service ecologists, soil scientists, and silviculturists, and discusses how this direction may change to meet future concerns.*

INTRODUCTION

Whitebark pine (*Pinus albicaulis* Engelm.) is a component of high-elevation ecosystems across approximately 25 National Forests in the Northern Rocky Mountains. Although of limited commercial value throughout its range, the ecosystems where it occurs are highly valued for wildlife habitat, watershed, ecological diversity, and esthetics (Arno and Hoff 1989).

Management direction toward whitebark pine on National Forest lands is a function of the harsh climate where these ecosystems are found. High elevations and wilderness designations preclude most intensive management options. These conditions, however, do not negate concerns of land managers as documented in this symposium and in papers by Arno and Hoff (1989), Eggers (1985), and in unpublished Forest Service, U.S. Department of Agriculture, letters (Hamilton 1989; Hann 1989).

While this symposium focuses on whitebark pine, it is important to recognize, as Schmidt (1987) has pointed out, that whitebark pine has ecological counterparts, which occupy similar habitats in North America and Eurasia. European stone pine (*Pinus cembra*), is one such species (see Holtmeier this proceedings). Two North American counterparts are limber pine (*Pinus flexilis* James) and bristlecone pine (*P. aristata* Engelm.); these both occur in National Forests.

The results of a questionnaire on past, present, and future whitebark pine management in National Forests, as perceived by 20 Forest Service ecologists, soil scientists, and silviculturists, are presented and discussed.

QUESTIONNAIRE

To identify Forest Service perceptions, a questionnaire was developed. This questionnaire was mailed, using the Forest Service computer network, to specialists that have worked or are working in whitebark pine ecosystems. Twenty completed surveys were returned representing 25 National Forests. The discrepancy in numbers can be accounted for by zone or regional office responses. Another 10 people responded with short messages or by providing internal memos on the topic. This survey was not intended to be represented as statistically sound. At best, it is subjective, but does give an indication of field personnel concerns. The questions asked and a summary of the responses follow.

QUESTION 1

How would you rate (no or low, moderate or high) the following concerns (past, present, future) about whitebark pine ecosystems? Also rate each for the need for more research.

Table 1 summarizes the results of responses to this question.

Grizzly Habitat

Of foremost interest in the Northern Rocky Mountains is grizzly bear habitat relationships. This concern has given impetus to the study of whitebark pine in National Forests in recent years.

The responses indicated that grizzly bear habitat concerns within whitebark pine ecosystems could be divided between those Forests that express no or low concern and those expressing moderate to high. Naturally, Forests within or close to grizzly habitat show greater interest because of the high food value of whitebark pine seed crops. Conversely, those Forests not within occupied habitat are not as concerned. However, this would change with the possibility of reintroduction and expansion of grizzlies to their historic ranges. Only Forests within occupied grizzly habitat were addressed below.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Kent E. Houston is Forest Soil Scientist, Shoshone National Forest, Cody, WY 82414; Earle F. Layser is Forest Staff Officer for Planning, Public Affairs, and NEPA, Ochoco National Forest, Prineville, OR 97754.

Table 1—Question 1, summary of responses by percentage

Category	Past	Present	Future	Research
Grizzly habitat	[1]50(50)	30(70)	20(80)	20(80)
Regeneration	88(12)	61(39)	34(66)	45(55)
Fire effects	83(17)	55(45)	44(56)	56(44)
Cone production	100(0)	72(28)	50(50)	66(34)
Silviculture concerns	94(6)	72(28)	61(39)	50(50)
Recreation concerns	61(39)	44(56)	17(83)	39(61)
Visual concerns	77(23)	39(61)	34(66)	61(39)
Plant succession	89(11)	61(39)	50(50)	39(61)
Insect and disease	83(17)	83(17)	61(39)	56(44)
Classification	76(24)	65(35)	47(53)	59(41)
Watershed	72(28)	55(45)	34(66)	56(44)
Livestock grazing	78(22)	78(22)	83(17)	89(11)
Nongame	89(11)	78(22)	62(38)	67(33)
Big game	76(24)	64(36)	53(47)	65(35)

[1] Percent of respondents, first number indicates no to low concerns, ( ) indicates moderate to high concerns.

Fifty percent responded that there was moderate to high concern for grizzly habitat in the past and 50 percent said there was at least a low concern. This increased to where 70 percent now have high concerns. In the future, 80 percent envisioned having high to moderate concerns. Research needs were categorized as 20 percent low, 40 percent moderate, and 40 percent high.

Regeneration

Understanding the basic growth requirements for whitebark pine seedlings and how these plant communities are established is an important basis for many management decisions.

Only 12 percent indicated moderate to high concerns about regeneration in the past. This increased to 39 percent for present and 66 percent for future concerns. Fifty-five percent felt research in this area should have a moderate to high priority.

Fire Effects

The Greater Yellowstone fires of 1988 focused the attention of land managers on the consequence of fire in these ecosystems. Fire may have beneficial effects in whitebark pine ecosystems, but what will be the effect of fires of that magnitude on these ecosystems?

The responses show that only 17 percent had moderate to high concerns about fire effects in these ecosystems in the past. This has increased to 45 percent for present and 56 percent for future concerns. Forty-four percent felt there was a moderate to high priority for research in this area.

Cone Production

Cones from whitebark pine are an extremely important wildlife food (Reinhart and Mattson, this proceedings; Tomback and others, this proceedings). Poor seed crop years may affect the whole ecosystem from grizzly to bird and small mammal populations.

The survey indicated interest in cone production in the past was very low; 100 percent of the responses expressed no or low concerns. This changed with research documenting the value of whitebark pine seed crops to wildlife. Twenty-eight percent now feel that cone production is a moderate to high concern. This interest increased to 50 percent when the question about the future was posed. Thirty-four percent felt that there was a moderate to high need for more research in this area.

Silvicultural Concerns

Where whitebark pine communities are adjoining commercial timberland, as in the Shoshone, Bridger-Teton, and Lolo National Forests, there may be opportunities for silvicultural prescriptions to obtain desired habitat conditions and possibly increase the range and cone productivity in specific areas. These practices have been suggested by Eggers (1985, this proceedings) and Hamilton (1989), but would be costly and their practicality may be questionable in inaccessible areas.

Only 6 percent indicated that silvicultural concerns in these ecosystems were of a moderate concern. This increased to 28 percent at present and 39 percent in the future having moderate to high concerns. Fifty percent felt that there was a need for more research in this area.

Recreation and Visuals

High-elevation forests have high recreation and visual values. Commonly, these fragile whitebark pine habitat types are popular areas that receive heavy pressures from hikers, anglers, hunters, campers, and horse traffic. Frequently, these sites are depleted of firewood and soil erosion and compaction problems exist. Rehabilitating these sites is a critical factor in some intensely utilized and visually sensitive areas. Maintaining vegetative diversity and visual integrity is a consideration for any project involving these types.

Thirty-nine percent felt that there were moderate to high concerns regarding recreation in these ecosystems in the past. This increased to 56 percent for the present and 83 percent for the future. Sixty-one percent felt that there were moderate to high needs for further research in these areas.

Twenty-three percent felt that in the past visual quality was a moderate to high concern. This increased to 61 percent for the present and 66 percent for the future. Thirty-nine percent felt research was a moderate to high priority.

Plant Succession

Whitebark pine habitat types moving into late successional stages are being replaced by more shade-tolerant species such as *Abies lasiocarpa* and *Picea engelmannii*. Suppression of fire has allowed the conversion of many of these types (Arno and Hoff 1989; Morgan and Bunting, this proceedings). On the other hand insects, disease, and large fires have affected many acres (Kendall and Arno, this proceedings; Wellner 1989). Natural regeneration on these harsh sites can be a long-term process and it may be several decades before significant cone crops are produced. Research in successional pathways is needed to fully understand what management options are available.

Eighty-nine percent felt that plant succession was not a concern in the past. Thirty-nine percent felt that this was now a moderate to high concern. Fifty percent felt that their future concerns will be moderate to high. Sixty-one percent said that research in this area was a moderate to high priority.

Insect and Disease

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and white pine blister rust (*Cronartium ribicola* Fisch.) have severely affected many whitebark pine ecosystems. Epidemics have diminished some local populations of whitebark pine in northern Idaho and Montana (Arno and Hoff 1989; Kendall and Arno, this proceedings). Certainly, this is affecting cone crops and influencing successional trends over much of the range of whitebark pine. With the potential of white pine blister rust spreading into the Greater Yellowstone ecosystem, interest in this area will increase.

Seventeen percent responded that insect and disease problems were a moderate concern in the past. This remained the same for the present and then increased to 39 percent for future concerns. Forty-four percent felt there was a moderate need for research.

Vegetation Classification

To be able to communicate and compare solutions to resource problems, professionals need to be able to classify the landscape and its associated plant communities and soils. Certainly, this has been illustrated throughout this symposium by people discussing vegetation and ecological classifications. These classifications must be translated into maps of the landscape that allow land managers to assess the extent, productivity, and successional status of vegetation types.

Twenty-four percent felt that classification was a moderate to high concern in the past. This increased to 35 percent as a present concern and 53 percent as a future concern. Forty-one percent said that research was a moderate to high priority in this area.

Watershed

Whitebark pine ecosystems have very high watershed values. These high mountain areas are important for water storage and maintaining flow for downstream uses. Skiers, snowmobilers, and snowshoers also enjoy the heavy snowpack characteristic of these environments.

Only 28 percent had moderate or high concerns for watershed in the past. This increased to 45 percent for present and 66 percent for the future. Forty-four percent felt research had a moderate to high priority.

Livestock Grazing

At the turn of the century, high elevations often were heavily used by sheep. This resulted in deterioration in range by soil compaction and erosion in many instances. Although such sheep grazing is much less prevalent now and hopefully better managed, it still occurs along with some cattle grazing (Hall 1989; Johnson, this proceedings; Wellner 1989; Willard, this proceedings).

Only 22 percent felt that this was a concern in the past. This could be a function of time since this was strongly commented on by two retired Forest Service employees, Chuck Wellner (1989) and Fred Hall (1989). Concerns in this area remained low for present (22 percent), future (17 percent), and research (11 percent).

Nongame and Big Game

Whitebark pine ecosystems are used for summer range by deer, elk, and other wildlife. The role of Clark's nutcracker in seed distribution and significant use of squirrel middens by grizzly bear exemplify how land managers must consider the entire ecosystem when making management decisions.

The survey showed that only 11 percent had moderate or high concerns for nongame in the past. This increased to 22 percent for the present and 38 percent for the future. Thirty-three percent felt that research was a moderate priority.

Twenty-four percent had a moderate concern for big-game habitat in these ecosystems in the past. This increased to 36 percent and 47 percent with moderate and high concerns for the present and future. Thirty-five percent felt that research was a moderate to high priority.

Other Concerns

Other concerns not mentioned in the questionnaire, but brought up in comments, included problems in fuel management, global warming and subsequent species shifts, maintaining biodiversity, and the effects of changing air quality on high-elevation forests.

To summarize responses to the first question, the areas indicated as most important were visual quality, grizzly bear habitat, recreation, watershed, and fire effects. A conclusion drawn from these responses is that what is perceived as important by field people is not necessarily what this symposium has shown to be of critical interest. This is particularly true with respect to insect and disease problems and the importance of nongame species in the dissemination of seed.

QUESTION 2

What, if any, critical information is needed to enable your Forest to improve planning for whitebark pine ecosystems?

Responses indicated that information was needed on successional status and pathways; fire effects; impacts, mitigation, and rehabilitation of disturbed sites; soil-whitebark pine relationships; inventory of status and location of whitebark pine stands; classification in California; knowledge of regeneration techniques; development of whitebark pine resistant to white pine blister rust; and a need to address management of the entire ecosystem.

QUESTION 3

What management direction has your Forest taken in regard to whitebark pine?

A. Active timber management
B. Nonintervention
C. Monitoring
D. Prescribed fire
E. Other

As was expected, none of the respondents was presently doing active timber management within these ecosystems, primarily because these lands are mostly classified as unsuitable for timber production or are within wilderness and are not included in Forest Plan timber bases. However, some activity has occurred—one timber sale in the last 20 years was reported for the Beaverhead National Forest in a whitebark pine habitat type. Other Forests reported sales in adjoining habitat types, in particular, those within the subalpine fir/grouse whortleberry habitat type (whitebark pine phase).

Eighty-two percent reported nonintervention or passive management as the type of direction taken by their Forests.

Thirteen percent responded that their Forest's management direction included monitoring. The Gallatin National Forest was doing "premonitoring" or a basic characterization of these ecosystems. This brings up the important point that one must know what there is and where it is before actual monitoring can take place. Other Forests indicated that whitebark pine types are monitored during insect and disease surveys.

Five percent responded that prescribed fire was part of their management direction. Although not specifically addressed by a question, prescribed natural fire is one of the management prescriptions for many wilderness areas.

QUESTION 4

Do you envision a need to change your Forest's current direction to meet future needs?

Ten Forests responded no change and seven indicated change was needed. Regrettably, how this direction needs to change was not asked. However, change will be dictated by the results of researchers working with resource managers and the accumulation of better knowledge on these ecosystems.

CONCLUSIONS

In the greater scheme of things, little is known about the complex relationships and interactions involved in whitebark pine ecosystems, or of those considered to be ecological counterparts. Only recently have we begun to acquire ecological knowledge on whitebark pine itself. It should be obvious from this symposium that whitebark pine does not exist independently—it is a potentially long-lived part of a complex interdependent system that has evolved amid severe environments.

It is presumptuous to assume that any success with management activities is little more than chance without the knowledge and understanding of relationships within these communities. Worldwide examples of the sensitivity of these high-elevation forests to human activities, given by Holtmeier (this proceedings) in this symposium serve as lessons for our land managers. Therefore, there is a caution—any "active" management undertaken is done with risk of less than success until better information and understanding exist. This symposium has been a step in the right direction of developing some of the necessary understanding and knowledge to better manage these complex environments on National Forest lands.

Until then, "passive" or "nonintervention" management of whitebark pine and its counterpart systems, as indicated by 82 percent of the respondents, makes sense. The exception to this regards recreation management. Here an aggressive "active" approach needs to be undertaken in moderate and high use areas if we are to preserve quality visitor experiences in these visually and ecologically sensitive areas.

One thought that this survey brought out was that all of these management concerns, like the ecosystems they arise from, are interrelated. Management of these high-mountain ecosystems must involve an integrated approach. Resource disciplines will need to work together to achieve positive results. The results of the questionnaire showed a notable difference of opinion within the same or similar disciplines. What would the results have been if an interdisciplinary group had been surveyed? This illustrates the need for better information management and increased communication between the research community and field personnel.

REFERENCES

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Eggers, Douglas E. 1985. Management of whitebark pine as potential grizzly bear habitat. In: Contreras, Glen P.; Evans, Keith E., compilers. Proceedings—Grizzly bear habitat symposium; 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 170-175.

Hall, Fred. 1989. [Personal communication]. February 17. Portland, OR: U.S. Department of Agriculture, Forest Service, retired.

Hamilton, Jerry. 1989. [Personal communication]. February 22. Ogden, UT: U.S. Department of Agriculture, Forest Service, Regional Office.

Hann, Wendel. 1989. Notes from mini-workshop on whitebark pine. Unpublished paper on file at: U.S. Department of Agriculture, Forest Service, Gallatin National Forest, Bozeman, MT.

Schmidt, Wyman C. 1989. Notes from mini-workshop on whitebark pine. Unpublished paper on file at: U.S. Department of Agriculture, Forest Service, Gallatin National Forest, Bozeman, MT.

Wellner, Charles. 1989. [Personal communication]. February 18. Moscow, ID: U.S. Department of Agriculture, Forest Service, retired.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from Anonymous)—The final "pie" showing 45 percent no change (referring to Question 4), does not agree with the aggregate of your "bar" displays (referring to Question 1). Explain. How does this support your questionnaire?

A.—We believe that this contradiction is a result of pragmatism among the respondents. There are many things we do as land managers or specialists that we would like to explore, but they are not always practical with the tight budgets the Forest Service works under. This survey represents valid concerns, but what can be done about these concerns is expressed with some frustration in Question 4.

INFORMATION GAPS AND RESEARCH NEEDS FOR WHITEBARK PINE

Don G. Despain
Richard G. Krebill

ABSTRACT

Whitebark pine (Pinus albicaulis), *an attractive conifer in the upper elevation forests of western mountains, has received little scientific study compared with other conifers prized for their commercial timber properties. Its importance as a food source for grizzly bears* (Ursus arctos) *and other nongame animals and birds is now stimulating considerable interest among specialists in the Rocky Mountains. If managers also take notice, this species will become a prime candidate for increased ecological research. Considerable new information is needed and must be applied if the species is to withstand forest succession and elevated levels of bark beetles hastened by fire prevention, introduction of the devastating white pine blister rust, and potential climatic warming.*

INTRODUCTION

It is easy for researchers to assume that information gaps and research needs are synonymous terms. However, when we look outside our ivory towers we can see that they are not. Most people are not aware of the importance of whitebark pine (*Pinus albicaulis*) in the total ecosystem and many would doubt that this species is worthy of any special consideration. After all, it may be pretty, but it has little direct economic value. Before much consideration will be given to this species, a lot of people must be made aware of its special importance and its possible contributions.

Early in this conference John Mumma said we have barely scratched the surface of the knowledge we need to manage this species. The rest of the symposium bore that out. Just what do we know in relation to what we need to know when we get into a management mode? Steve Arno pointed out that more is known about the whitebark pine in the Intermountain West than in the whole rest of its range. There is a large geographic area where there is an almost total knowledge gap, and there are research opportunities everywhere.

CLIMATIC CHANGE CHALLENGES

Cliff Martinka brought out how rising carbon dioxide levels are going to bring about a climatic change. It may already be with us. Climate has changed in the past on a continuing basis, and we have absolutely no reason to believe that the climate is going to remain static. The rate of this change is subject to some controversy, but there are indications that humans are hastening the process so that changes in the next several decades will occur at a pace previously unknown to whitebark pine.

Regeneration processes may be the first to show the effects of climatic change. Established trees may persist for some time, but when it comes time to replace those trees the site may no longer provide the needs for seedling establishment. Disturbance will eventually come along and eliminate stands. If climatic change means that whitebark pine can no longer get established on that site, are there other sites within range of the seed-dispersing Clark's nutcracker that are suitable for seedling establishment? We may not know enough about the physiological requirements of whitebark pine to successfully replace natural seed dispersal with artificial planting and probably do not have the will to do so. If the climate is warming, as many suspect, there will be very little space for new forests on the tops of mountains above our current subalpine forests where whitebark pine prevails. Kate Kendall indicated that there already are many places where no regeneration takes place. The trees are being killed by bark beetles, fire, or white pine blister rust, but small trees are not becoming established to take their place. Are we seeing the first indication of climatic change or the results of disease or disturbance? Research is needed to determine which is the case.

If the climate that is now in Yellowstone moves northward to Glacier National Park, perhaps the Yellowstone whitebark pine blister rust problem may be solved, but Yellowstone managers will then be faced with another difficult decision if they decide to preserve ecosystems that prevailed when the Park was established, especially if its climate becomes more steppelike. It is extremely expensive, if not impossible, to get trees to grow where the site does not provide all the needs of the species. To begin to assess the problem, we have to learn much more about whitebark pine's environment, where it is and where it is going. We need to know not only the physiological needs of whitebark pine, but also its genetic peculiarities and silvicultural problems.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

Don G. Despain is Research Biologist, U.S. Department of the Interior, National Park Service, Yellowstone National Park, WY 82190; Richard G. Krebill is Assistant Station Director for Research, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Ogden, UT 84401.

ADDITIONAL NEEDS

Although we personally consider whitebark pine's adaptability to climatic change as the most challenging research need that now exists, we came up with a list of additional information gaps and research needs that were mentioned during the symposium and things we thought of on our own. The remainder of this paper is a discussion of that list.

We need a series of permanent plots set up across the elevational and latitudinal range where these plots can act as monitors. They need to be set up for long time periods because we are dealing with a species that has a long life and where changes normally happen slowly. Not only do we need these plots but we need an information storage and retrieval mechanism that will keep these data safe and retrievable for future generations of researchers. We must be able to go back every 5 or 10 years, get access to the previous information for interpretation, and add additional new data. Any individual researcher may only need to access the information once or twice in a whole career; so a desk drawer will not work. We need permanent plots and we need to have long-term, multiuser access to the data.

We need to know the tolerance limits and optima for such factors as soil moisture, soil nutrients, and temperature, and how they relate to climatic factors and to the different growth stages of whitebark pine. It is not enough to know how a tree responds to its environment. We must know how a seedling, a sapling, a young tree, and an old tree respond to the environment. The response to environmental factors is not the same throughout the life of the tree.

What is the role of summer rain as well as spring and fall frosts? It is interesting that Tad Weaver reported that the minimum temperature of both the lower limit and the upper limit are about the same. What does this mean to the plant? Does it mean anything at all? Is this important to whitebark pine or to its competitors?

What are the site requirements of whitebark pine and its associates? We need to extend the kind of work done by Dave Mattson on Mount Washburn to see what the site characteristics are in other parts of the whitebark range. How much sunlight do they need? How much food can they make per packet of sunlight available to them? What is their real shade tolerance? How warm can they get before respiration is greater than photosynthesis? Are there any photoperiodic responses that need consideration, especially if latitudinal movements are to be carried out for management purposes?

We need to know more about tolerance to pollution and tolerance to diseases. What is the genetic variability of the species and local populations in relation to these factors? Are the different stages of growth equally susceptible to fungi and insects?

Is there enough natural resistance to white pine blister rust for natural selection to maintain the species throughout its range? Can resistance be stimulated through tree improvement and more intensive management programs? Can mountain pine beetle mortality be avoided through use of semiochemical repellents such as verbenone?

Our friend from Germany, Dr. Holtmeier, talked about snow-holding capacity of whitebark pine stands. Just what is this capacity and how does it affect the hydrology of the streams of our ecosystems and the safety of the visiting public? This brings up another major information gap. We need to find out what our European counterparts have already discovered about similar species in their countries. Is it time for a review paper or book on the ecology and management of stone pines?

How to determine the factors that control the periodicity of seed production is a frequently mentioned problem needing work. What is the interaction between periodicity of seed production and the seed predator load? How dependent on whitebark pine are the Clark's nutcrackers? How do their populations change in relation to the production of whitebark pine seeds? Do the prevailing theories about minimum viable populations have any application to whitebark pines? We need to amplify and extend the studies on other seed predators reported at this symposium.

We need to know a lot more about the relationship of this species to fire. How do fires burn through these stands, and how fast do they return to the burned area? Are the seeds already in the stand in caches safely below the depth of the lethal temperatures?

BROADER QUESTIONS

These are all very practical questions, but sometimes important research questions seem to be quite impractical, although they are not.

Just where did this species originate? Where did the stone pines in general originate? What are their migration routes? Maybe there is no immediate practical application for answers to these questions, but we may find some piece of information that is vitally important that we had not thought of before. Or perhaps other questions will arise from the knowledge gained that will be crucial for future management of whitebark pine.

What are the DNA relationships among members of the stone pine group? This gets into microbiology and microchemistry. The answers will be helpful in knowing how these taxa are related and how much information can be transferred from studies of other stone pines.

How can we differentiate between young limber pine (*Pinus flexilis*) and whitebark pine? Can some difference be found in the pollens of the two species that will allow us to separate them in the pollen records? This information will be needed before we can successfully look into the migration of the species in past times and be able to better predict speed of future migration. This involves interaction with the nutcrackers and is important relative to climatic change.

What is the mechanism guarding against hybridization? Apparently none of the stone pines hybridize with any others. Similar as they are morphologically, they do not mix genetically. What are the barriers to gene flow and can we use these barriers to our advantage? Or can we break down or bypass these barriers to our advantage? Can barriers be transferred to other species that we may want to keep genetically pure?

Are there ecotypes, and do these ecotypes have the genetic barriers against each other as indicated by the studies of the three different populations in California? What would be the advantages and disadvantages of such barriers? The answers to these questions may be the difference between success and failure in any management scheme that involves transplanting from one region to another.

Do we have any estimate of the number of seeds cached in unsuitable places? A single clump of whitebark pine grows in a meadow. Is that the only cache, or were seeds cached all over the meadow and that is the only place that could successfully produce full-grown whitebark pine?

So far we have mainly discussed the information needs of a single species, whitebark pine, and yet its fate is intimately intertwined with the ecology and behavior of its associates. Especially, we need to know a lot more about the Clark's nutcracker, which is so important to regeneration of whitebark pine.

Little is known about how far nutcrackers carry their seeds, what kind of sites they select, and whether they can be counted on to carry the seeds to those sites that will become whitebark pine sites under new climatic conditions. What are the competitive relationships between whitebark pine and other tree species with which it grows? How does it interact with the herbaceous members of its community?

We need improved landscape level successional models to better understand the complex parameters affecting whitebark pine ecosystems. Future planning and operational decisions will soon be made in a Geographic Information System (GIS) context, so it is timely to move whitebark pine into the computer age. This will require additional research, development of models and systems, and careful testing and improvement.

Finally, a field of research that was not represented at this symposium needs mention. We heard from no archeologists or anthropologists. The pine seeds are an important food source for bear and the bear was brother to the Native Americans. We know pinyons and limber pine were used extensively by earlier cultures.

Did aboriginal populations in this area use whitebark pine seeds? They certainly have more food value than many of the grasses they used for food.

ON WITH THE QUEST

To sum up, this has been a good symposium. Much research has been reported, and exciting discussions were generated. One mark of good research is that it asks more questions than it answers. Such has been the case here. As we go on in our quest for more answers about whitebark pine many, many more questions will surface. Along the way let us keep in mind the knowledge gaps that exist in the minds of the managers, the public, and the decision makers and make sure there is easy access to all the information generated by research.

WHITEBARK PINE SYMPOSIUM HIGHLIGHTS

R. G. Krebill

ABSTRACT

A highly significant step was taken in the assembly of a broad cross section of land managers, scientists, and other experts in this first formal symposium devoted to the whitebark pine ecosystem. Information sharing among the many experts, on and off the agenda, increased our understanding and appreciation of whitebark pine ecology, and should lead to improved research and management of this unique and important high-mountain resource.

THE ECOSYSTEM

The whitebark pine ecosystem has long occupied the northern mountains of the Western United States and Canada. Occurring in the harsh environment near the upper timberline, the ecosystem has amazing natural resilience. The pollen record in south Yellowstone indicates a waxing and waning in inverse synchrony with glacial advances and retreats of the past 100,000 or more years. Besides changes in climate and churning of substrate by frosts and glaciers, whitebark pine forests have evolved under such influences as heavy winter snow cover, violent wind, avalanches, bark beetles, and wildfire. With natural disturbance, whitebark pine has a slight advantage over competing tree species to maintain dominance in the upper elevations of many of the high western mountains.

Whitebark pine is estimated to be present in about 8 percent of the total forests of the National Forest System, and is more prevalent at higher elevations in the northern Rocky Mountains, where for instance, it is a significant component of about 18 percent of Yellowstone National Park. The whitebark pine ecosystem is especially prized for its natural beauty and recreation potential, its importance as wildlife habitat, its value in protecting high-mountain watersheds, and for its biodiversity and intriguing natural processes.

MANY CONCERNS

But is this precious whitebark pine resource imperiled by increasing human influence in high-mountain ecosystems? A little more than 100 years ago, prospecting brought an influx of people into many of our mountain areas. Direct losses of whitebark ecosystems to soil movement were minimal, but as indicated for the Butte vicinity, harvesting of its trees for fuelwood, charcoal, and mine timbers was heavy over fairly broad areas. The high mountains were soon seen as a valuable source of forage, and uncontrolled grazing for a few decades led to serious impacts on meadow and understory vegetation, from which many sites have still not fully recovered in spite of several decades of improved range management.

Even more serious is the threat by white pine blister rust, which was inadvertently introduced early in this century. Unfortunately, whitebark pine is perhaps its most susceptible host and many stands in northwestern Montana, northern Idaho, and British Columbia have already been nearly eliminated. Unlike the situation with mountain pine beetle, whitebark pine had not coevolved with the blister rust pathogen. If that is not enough cause for concern, we also have learned that effective fire control in the current century is allowing forest succession to favor subalpine fir and Engelmann spruce on many sites formerly dominated by whitebark pine.

It is also somewhat disturbing to compare our past century of impact on high-mountain whitebark pine with the more subtle but enduring impacts of wood gathering and conversion of stone pine forests for grazing in Eurasia. In comparison, our North American whitebark pine forests hardly appear impacted, but as we learned in this symposium, they are. And we have only been at it for about a century; the Eurasian mountain forests have accumulated the impacts of many millenia of use. Let us not forget the potential for subtle effects to accumulate into major changes over long periods of time, and give adequate weight to time in our cumulative effects analyses.

Recent concern was also expressed over the increased recreation use in our high-mountain forests over the last few decades, and particularly the exploitation of scarce wood for campfires. Is this different than what was done by many of our ancestors in Eurasia? Other concerns were voiced during the symposium over the ever increasing numbers of roads, transmission lines, electronic sites, and resorts placed in high-mountain areas. Concern also was expressed about the potential for human activity to produce harmful air pollution, and to hasten global climate change to the detriment of high-mountain forests.

Paper presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

R. G. Krebill is Assistant Station Director for Research, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Ogden, UT 84401.

UNDERSTANDING IS KEY

On the positive side, interest in whitebark pine ecosystems has risen dramatically in the 1980's, in part inspired by the surprising finding that whitebark pine seeds are important to the vitality of grizzly bear populations in the Yellowstone area. With this interest have come several studies into the ecology of whitebark pine that have greatly raised our level of understanding of the functioning of whitebark pine ecosystems and the strong reliance of many of its species upon one another. Understanding these relations is a key ingredient to prescribing management that will perpetuate these vulnerable high-mountain forest ecosystems.

Some of this symposium's information highlights to me were:

- The strong evidence that whitebark pine almost totally relies on the Clark's nutcracker for natural regeneration through the bird's seed caching behavior. With an ability to carry up to 150 seeds in its throat pouch, and to disseminate seed up to 15 to 20 km, it is little wonder that this tree has persisted through the millenia in spite of disruptions as severe as glacial activity and major fires.
- The classic interdependence of numerous species in whitebark pine ecosystems. Especially interesting are the relations of bird to tree to red squirrel to bear, and the importance of whitebark pine ecosystems as seasonal range for elk and other wildlife, the importance of these areas as a source for water for fish and other downstream users, and the interactions of mountain pine beetle in both lodgepole and whitebark pine forests.
- The report that whitebark pine seeds have been documented as bear food for at least 15 years.
- The recent research findings clarifying the requirements for whitebark pine seed germination and seedling establishment.
- The wide range of soils and geological formations upon which whitebark ecosystems prevail.
- The capability of whitebark pine to extend itself through layering.
- The use of shape of trees near timberline to quantify mean wind speeds and snow depths.
- The finding that whitebark pine often dominates in upper slope areas that are a little warmer than lower slopes where fir and spruce prevail.
- The importance of fire in maintaining seral whitebark pine forests.
- The evidence of widespread loss of whitebark pine to white pine blister rust in the Northern Rocky Mountains.
- The recent development of a predictive process model for whitebark pine forests.

Thanks to a dedicated group of scientists, specialists, and generalists, a mild revolution obviously has been under way to improve our understanding of whitebark pine ecosystems.

Those who remained for the postsymposium field trip to see whitebark pine firsthand were in luck (fig. 1). As they arrived at Big Sky, the clouds dissipated and the party was treated to the bright splendor of the high mountains at their best. Many of the ecological marvels discussed during the symposium were close at hand for group and individual interpretation. All in all, the field trip was a most fitting climax to an outstanding symposium.

Figure 1—Professor Tad Weaver (right) in his natural habitat, surrounded by interested "students" in a whitebark pine forest during the symposium field trip.

SYMPOSIUM CRITIQUE

My critique of the symposium is that the arrangements, hospitality, and orchestration of the program were superb; the agenda provided exceptionally good coverage of an impressive range of topics; the quality of presentations was variable but always interesting; illustrations were excellent but often used to excess (in part representing the photographic appeal of the whitebark pine resource); and the depth of scientific inquiry was generally shallow, indicating a need for much additional research.

Although it is clear that we do not know all there is to know, surely we are now much better equipped to successfully manage this outstanding high-mountain resource. The best part of the symposium was its many participants who represented a broad range of expertise and interests, yet were always so free to enter into discussion and share ideas.

Comments on the highlights of the symposium were solicited from all participants. Following are excerpts from their comments, slightly edited to follow the phrase, "The highlights of the symposium were . . . "

(from Richard Baker) " . . . the diversity of papers presented, and learning more about the whitebark pine ecosystem and about the ecology of whitebark pine."

(from Ray Brown) " . . . learning the MSU plans to organize a High-Elevation Studies Program, a super, vitally important idea; learning so much about the basic biology and its application to management of the whitebark pine life-zone; and meeting so many vital, intelligent young people (and some old ones) who are so interested in improving our understanding of high-elevation ecosystems."

(from David Charlet) " . . . meeting and speaking with researchers from diverse fields connected with the common theme of high-altitude ecology; the presentations, allowing me to feel very informed on the current state of knowledge; the dissipation of the feeling of isolation in my concerns, perceptions, and research . . . coupled with a renewed hope that we can coordinate our efforts and make a genuine impact reversing the destructive path of the past; and the feeling of being taken care of in fine style by the coordinators of this symposium."

(from Jim Chew) " . . . any presentation that actually had some quantification to it, as many were no more than nice slides and generalizations."

(from Richard Clark) " . . . description of whitebark ecosystem baselines; overview of some theories of management; a look at this ecosystem as a unit of the wilderness system; and the emphasis on the whitebark ecosystem as a unique system with value."

(from Doug Eggers) " . . . the opportunity to hear about what others have observed and documented concerning whitebark pine; the items that helped in my understanding and perspective; for example, the observations on grazing, especially heavy grazing in past years and its effects on today's whitebark pine forests."

(from Phil Farnes) " . . . meeting people having knowledge or doing research in whitebark ecosystems, and the good descriptions of the various components of whitebark pine ecosystems."

(from Sam Gilbert) " . . . the significant increase in interest in whitebark pine ecosystems in the past few years; the encouraging knowledge that we have acquired on the subject; and the excellent visual aids."

(from Ken Gibson) " . . . bringing together of the amount of knowledge on whitebark pine ecosystems; the focus on knowledge gaps; seeing that research is going on, and has been for some time; and the awareness of the uniqueness of whitebark pine ecosystems and the need for special management for these ecosystems."

(from Harvey Good) " . . . the Clark's nutcracker relationship with whitebark pine, the red squirrel ties to grizzly bear and whitebark pine, the genetic aspects of whitebark pine, and the allozyme relationships within strains of *Pinus albicaulis* and other pines."

(from Ron Hamilton) " . . . the assemblage of participants in general; the diversity of the people participating and the good contacts made for future reference; the holistic perspective of presentations; and the somewhat overlooked need to better understand ties between adjacent ecosystems (for example, mountain pine beetle/lodgepole pine/whitebark pine interactions), so that we can improve future management."

(from Harry Hutchins) " . . . animal interactions and the world perspective of the stone pines, especially the unique and interesting perspectives of Jack Ives and Herr Holtmeier."

(from Fredrich-Karl Holtmeier) " . . . the symposium in total—the many different aspects under which the whitebark pine ecosystems have been considered; the papers dealing with the mutual relationships between whitebark pine and animals, and the useful information from all papers presented. It has been an interesting and successful meeting; congratulations and thanks to all who were involved in its preparation and organization."

(from Peter Kolb) " . . . the diversity of subjects covered and the qualifications of most of the speakers."

(from Jack Ives) " . . . the realization of the intricate network—birds, animals, insects, man, fire—involved in whitebark pine ecosystems."

(from James Jacobs) " . . . information gained from climate data and lack of available weather stations; stand dynamics including relations between densities, circumference, basal area, and age; and animal/plant interrelationships."

(from Kate Kendall) " . . . the focus of attention on this resource, which it is to be hoped, will translate into more management concern; the updating of ongoing work in a range of disciplines, and the opportunity to air my concern about declines in whitebark pine to an appropriate audience."

SEEING WHITEBARK PINE IN A NORTHERN ROCKY MOUNTAIN LANDSCAPE: NOTES FOR A FIELD TRIP

T. Weaver

ABSTRACT

The changing role of whitebark pine (Pinus albicaulis) *along an altitudinal gradient typical of the Northern Rocky Mountains (USA) can be seen from the gondolas at the "Big Sky" resort near Bozeman, MT. Whitebark pine appears mostly as seedlings in the lowest zone (7,500 to 8,500 ft), becomes increasingly important in the canopy between 8,400 and 8,900 ft, assumes climax dominance in the woodland zone (8,900 to 9,300 ft), and maintains that dominance to treeline. On this gradient the mature tree's growth form changes from tall-lyrate, to shorter-spherical, to krummholz. The tree is seral in the lowest zones; frequent fires exclude it from canopies in the lowest zone, while low fire frequency gives it subclimax status higher (8,400 to 8,900 ft) in the zone dominated by subalpine fir* (Abies lasiocarpa) *at climax. Above 8,900 ft, whitebark dominates woodlands (formed, probably, when subalpine fir is excluded by cold) and krummholz (due, probably, to winter desiccation). Mountain pine beetles* (Dendroctonus ponderosae) *have killed much of the lodgepole* (P. contorta) *and whitebark pine in the area, and whitebark groves tend to be ringed with dead trees because the especially vigorous trees at grove edges are most susceptible. Cirque bowls on Lone Mountain demonstrate an inverted timberline at which conifers disappear downward, probably due to spring frosts.*

INTRODUCTION

The "Big Sky" a popular resort 50 mi south of Bozeman, MT, is an excellent site for an introduction to whitebark pine (*Pinus albicaulis*) in its Northern Rocky Mountain setting. One sees, there, altitudinal zones demonstrating all its major roles: in a relatively low-altitude band the tree is seral to subalpine fir (*Abies lasiocarpa*), in a middle band whitebark dominates woodlands, and in a higher band it forms krummholz. And the whitebark zone is accessible on a year-round basis—thanks to paved roads leading to the resort and gondolas that traverse the forest zone during both winter and summer seasons (phone 406-995-4211 for information).

This note summarizes observations made by participants in a whitebark pine symposium (March 31, 1989) and can guide professionals visiting the area at later dates. Its three sections describe the study area, vegetation phenomena best seen from the gondola, and landscape phenomena best seen from a road connecting the tops of the north (#1) and south (#2) gondolas. Readers guiding themselves through the area with these notes can use the gondola pylon altitudes (table 1) for orientation. They can find more detailed discussion of most phenomena discussed here in chapters of this proceedings on whitebark pine forests, cited here by author.

PREVIEW OF THE STUDY AREA

The "Big Sky" gondolas rise from 7,500 to 9,200 ft, and chairlifts proceed to 9,800 ft. As they rise, both gondolas cross a gradient in which the soils become rockier, the climate becomes cooler, stand-replacing fires become more infrequent, and a lodgepole pine-subalpine fir (*Pinus contorta-Abies lasiocarpa*) forest mosaic is replaced in turn by open woodlands of whitebark pine and a mosaic of krummholz and alpine grassland.

Geology

Lone Mountain is a conical peak (11,166 ft) built from clay-rich sedimentary beds of the quaternary. The peak dominates its landscape because, while the unconsolidated sediments around it have eroded away, its mass was baked to slate and supported by andesitic intrusions. The quaternary deposits are underlain by mesozoic and paleozoic sediments and precambrian metamorphics exposed at the edges of the Jack Creek/West Fork/Porcupine syncline to the north and south (Tysdal and others 1986).

Substrate

The trees at highest altitude grow on bedrock outcrops, while grassy areas between the spurs occupy substrates deposited by gravity (colluvium), glaciers (till), and water (alluvium). Lower on the slopes (under the gondolas), substrates are less often bedrock and more often glacial or alluvial (Hansen-Bristow and others, this proceedings).

Climate

Showers of more than 0.01 inch fall on about half of the winter days and a third of the summer days. Amounts

---

Presented at the Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource, Bozeman, MT, March 29-31, 1989.

T. Weaver is Plant Ecologist, Department of Biology, Montana State University, Bozeman, MT 59717.

Table 1—Distribution of current forest types, climax forest types, and environmental types under the "Big Sky" gondolas

Altitude	Current vegetation[1]	Climax vegetation[2]	South gondola	North gondola
Ft			*Pylon #*	*Pylon #*
9,200	WB/whortleberry	WB/whortleberry	lift top	
9,000	WB/whortleberry	WB/whortleberry		lift top
8,900	WB/whortleberry	WB/whortleberry	25	21
8,400-8,900	SAF, WB, LPP, wb[3]	SAF/whortleberry		
8,400	LPP/whortleberry	SAF/whortleberry	17	15
7,500	LPP/whortleberry	SAF/whortleberry	base of lift	base of lift

[1] Plants mentioned here are whitebark pine (WB, *Pinus albicaulis*), lodgepole pine (LPP, *Pinus contorta*), subalpine fir (SAF, *Abies lasiocarpa*), and grouse whortleberry (wb, *Vaccinium scoparium*).

[2] Forest environmental types are classified and described by Daubenmire and Daubenmire (1968) and Pfister and others (1977). They are named for the climax vegetation that occupies them. The name consists of the name of the dominant overstory tree, a slash, and the dominant understory plant. The current vegetation of a site of one environmental type can be climax or seral.

[3] While low-altitude subalpine fir sites are dominated by lodgepole, absence of fire in the highest subalpine fir sites allows species representing later seral stages to grow into the overstory.

deposited are likely similar all along the gondola transect, with an average of 3 inches per month in the winter and less than an inch per month in the summer. Average maximum temperatures in the woodland zone just below timberline are probably 20 to 25 °F in January and 65 to 70 °F in July. Average minimum temperatures in the woodland zone are likely 5 to 10 °F in January and 40 °F in July (Weaver, this proceedings).

Fire

Despite similar start frequencies, fire is relatively frequent at the altitude of the gondola base (because it spreads easily in an undissected landscape) and relatively rare in the ridged province at the altitude of the gondola top.

Climax Vegetation and Environmental Types

If it were climax—undisturbed for hundreds of years—the vegetation beneath the gondolas would range from subalpine fir forests (from the gondola base through the current canopy transition zone, 7,500 to 8,500 ft), to a whitebark pine woodland (8,900 to 9,200 ft) at the top (table 1). Near the gondola top (8,900 to 9,300 ft) climax vegetation alternates between whitebark pine woodland and meadow with the forest occupying bedrock ridge sites and the meadow occupying colluvial-alluvial valley sites as well as the south-facing slopes of Lone Mountain. From chairlifts above the gondolas one sees that a mosaic of krummholz and "alpine grassland" occupies stable areas on ridges, while cliffs and excessively drained talus intervene. Ecologists use climax vegetation as an indicator of environmental type (Daubenmire and Daubenmire 1968; Pfister and others 1977).

Seral Vegetation

Because fire is relatively frequent at the altitude of the gondola base, trees that invade after fire (lodgepole pine) often replace climax trees (subalpine fir) there. In contrast, fire is relatively rare in the ridged province at altitudes near the gondola top so the forests there are subclimax and open woodlands are near climax.

OBSERVING THE FOREST ZONE FROM THE GONDOLAS

The gondolas traverse two environmental zones occupied by three vegetation types. Most of the vegetation of the subalpine fir zone (7,500 to 8,900 ft) is seral. The whitebark woodlands (8,900 to 9,300 ft) are near climax. Within a few hundred feet above the gondola tops krummholz dominates the arboreal vegetation. The following paragraphs point out details best seen from the south gondola (#2).

The ski runs are very early seral with bare ground being invaded, below 8,950 ft, by lodgepole pine and, especially on north slopes and cold draw bottoms, Engelmann spruce (*Picea engelmannii*). While whitebark seedlings are common in forests all along the transect, there are essentially none in the ski runs.

In the lowest zone (7,500 to 8,400 ft) most current overstories are dominated by lodgepole pine, which colonized after fires of different dates.

1. Patches containing young (thinner) lodgepoles indicate recent fire, while those containing older (thicker) trees indicate more ancient fires. Lodgepole is recognizable by 2-inch needles in bundles of two and numerous compact, closed cones. While both subalpine fir and whitebark pine seedlings appear in the understory, fires of the past have removed the stands before they could occupy the overstory.
2. The oldest—longest unburned—patches occupy narrower valleys and steep north-facing slopes; their overstories contain subalpine fir, spruce, and old lodgepole pines. The subalpine firs have very pointed tops, the spruce have broader tops often with open cones, and both have flat needles less than 1 inch long.
3. If you look at distant slopes, especially from the bottom and top of the gondola, you will see patches with different textures: the finest textures are young stands, coarser textures indicate older stands, and the coarsest and most ragged-looking stands approach the climax condition.

4. If fire were excluded from this zone, forests in the area would be dominated by subalpine fir in the overstory and grouse whortleberry (*Vaccinium scoparium*) in the understory.

The middle zone (8,400 to 8,900 ft) is covered by relatively old subclimax forests because fires have been much less frequent in it.

1. Pines and pointed-topped subalpine fir are common in the overstory. Broader-topped spruce are relatively uncommon, except in draws.
2. At the lower edge of the middle zone the overstory pine is lodgepole. At the top edge, the overstory pine is whitebark. The two pines can be distinguished by their cones: lodgepoles bear many small, closed cones, while whitebarks bear a few 2- to 4-inch cones in the summer—or, in winter, no cones. While one usually associates the "lyrate" form with whitebark, the branches of some lodgepoles growing in this part of the gradient also fan upward, both here and in other areas.
3. The seral nature of the middle-altitude pines is seen from the fact that, while subalpine fir and spruce continue to thrive in the older stands of this zone, the pines are dying, and were doing so even prior to the recent bark-beetle epidemic.

Higher forests (8,900 ft to timberline) are dominated by whitebark pine.

1. Whitebark pine is climax here, apparently because the physical environment excludes trees that outcompete it in the two lower zones (Arno and Weaver, this proceedings).
2. While the whitebark pines were usually single stemmed in lower forests, many are either multistemmed or clumped here. This clumping derives, in part, from the fact that most were planted by Clark's nutcracker (*Nucifraga columbiana*), a bird which caches the seeds in groups of 1 to 30 for later use (Lanner, this proceedings; Tomback, this proceedings) and is secondarily increased by the tree's tendency to branch at its base (Weaver and Jacobs, this proceedings). I speculate that the increase in clumping is also due to the decrease in competition from closed forests to open woodlands.
3. The shallow structural roots of whitebark pine can be seen on overturned stumps and in cuts along the road between the tops of gondolas #1 and #2.
4. The white bark of the pine has a reddish tinge in winter. Does anthocyanin protect the bark chlorophyll, as it does the chlorophyll in many spring leaves?
5. Nonforest vegetation above 8,900 ft consists of alpine grassland and tundra interfingering characteristically with the subalpine forest (Arno and Weaver, this proceedings).

OBSERVING "BIG SKY" LANDSCAPE ECOLOGY

From the road between the tops of gondolas #1 and #2, one can review the position of whitebark pine forests in a landscape typical of the Northern Rocky Mountains.

Erosion bares steep rock at high altitude and deposition rounds lower slopes and levels valley bottoms. The top of the north gondola (#1) lies at the base of one of the most spectacular glacial cirques in the area. In the bottom of the cirque, just above the top of the north gondola, is a rock glacier, an actively moving mass of rock and ice which models the glacier that originally filled the bowl. The buildings at the base of the gondolas are built on till deposited by the large glacier, which flowed from the cirque during the pleistocene.

The vegetation zones in the high-mountain landscape can be conceived of as more-or-less horizontal zones, including, from the top down:

1. An upper forest-free zone dominated by rock outcrops, talus slopes, and grassy tundra.
2. A zone in which forests are interspersed with nonforests. Whitebark pine forests occupy the rocky ridges. The ridges provide a stable, relatively fire-free site suitable for pine growth. The valleys between may be cleared by avalanches or cold air draining into them from above.
3. The whitebark woodland zone begins in the ridge and valley zone and may extend slightly below it (approximately 8,800 ft and above).
4. The zone in which whitebark pine is codominant with subalpine fir late in succession is detectable from its uneven "ragged" look. The existence of this zone also depends on a low fire frequency attributable to the valley-ridge structure in the landscape (approximately 8,400 to 8,900 ft).
5. Below 8,400 ft the valley broadens so that the spread of fire is less inhibited by the valley-ridge structure. As a result, one sees coarse-grained patches of relatively old trees that burned long ago interspersed with fine-grained patches of young trees on sites that were more recently burned.
6. At successively lower altitudes below the gondola base (7,500 ft), one sees zones of Douglas-fir (*Pseudotsuga menziesii*) and grass-shrubland never occupied by whitebark pine.

Changes in substrate may also affect whitebark distribution. While the whitebark trees near timberline on Lone Mountain are growing on slates, many sandstones, and most of the precambrian metamorphics, whitebark pine avoids limestone in our area (Weaver and Dale 1974) and is generally replaced on limestone outcrops by limber pine (*Pinus flexilis*), subalpine fir, or Douglas-fir.

Many of the pines seen from the gondola are dead. Most of the dead trees were killed by the pine bark beetle (*Dendroctonus ponderosae*) (Bartos and Gibson, this proceedings).

1. A survey of the valley below demonstrates the breadth of this attack.
2. While many of the trees with a phloem layer thick enough to support the beetle (larger diameter trees) are dead, thinner trees often escape beetle attack. I point to two resultant phenomena:
    a. Elimination of lodgepole (thick trees) from the overstory probably favors whitebark pine (thin trees) in the understory and may allow whitebark pine to dominate sites that would otherwise have succeeded more rapidly to subalpine fir.

b. Due to lesser competition, trees at the edge of groves are larger than those in the center. As a result they have thicker phloem, are more readily attacked by the bark beetle, and die. I attribute the fringe of dead trees around the grove north of the north gondola (#1) to this phenomenon.

Near timberline, trees are absent from interridge areas because of avalanches or frost damage due to cold-air drainage. I offer the meadow in the lower cirque bowl (just above the top of the north gondola) as an example of exclusion of trees by cold-air drainage. Three points favor this hypothesis:

1. Cold air is known to pond in such depressions.
2. Conifers are known to "frost deharden" in spring, so heavy frost might eliminate them; such damage was observed on 3- to 5-year-old seedlings in the spring of 1988. Frost resistance apparently declines from whitebark pine > spruce > fir ≥ lodgepole pine.
3. The cold-air pond is ringed by bands of progressively older trees. Due to every-year frosts, no trees exist on the pond bottom (meadow center). A band of small trees (1 m high and buried by snow in winter) occupy a "shoreline" that hasn't experienced killing frost in 10 years or so, but these are likely to be killed eventually. A higher "shoreline" represents the "highest water" (= deepest ponding) that has occurred in 20 to 40 years; the tops of these trees may have emerged from the cold-air pond and, if so, they may grow crowns with normal tops and frost-pruned bottoms. The largest (mostly beetle-killed) trees occupy an area that is always above the cold-air pond's surface.

Most alternate hypotheses put forward to explain the distribution of trees in this bowl can be dismissed:

1. Avalanche damage seems unlikely, because existing trees show no evidence of snow movement and because alluvial-aeolian soil in the basin bottom lacks avalanche-borne rocks.
2. While colder air ponds in the basin in winter than in the spring, trees are adequately hardened against frost in winter (Tranquillini 1979).
3. Though it is in a depression, most if not all of the meadow site is too well-drained to allow water drowning.
4. Absence of flagging on existing trees discounts the possibility of wind-induced desiccation damage.

REFERENCES

Daubenmire, R.; Daubenmire, J. B. 1968. Forest vegetation of eastern Washington and northern Idaho. Tech. Bull. 60. Pullman, WA: Washington Agricultural Experiment Station. 104 p.

Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Tranquillini, W. 1979. Physiological ecology of alpine timberline. Berlin: Springer-Verlag. 137 p.

Tysdal, R.; Marvin, R.; DeWitt, E. 1986. Late Cretaceous stratigraphy, deformation, and intrusion of the Madison Range of southwest Montana. Geological Society of America Bulletin. 97: 859-868.

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. American Midland Naturalist. 92: 222-230.

POSTER PAPERS

Synopses of 14 Posters Shown at the Symposium

POSTFIRE VEGETATIVE RESPONSE IN A WHITEBARK PINE COMMUNITY, BOB MARSHALL WILDERNESS, MONTANA

Maria Ash and Richard J. Lasko

On June 28, 1985, lightning ignited three small fires on the ridge just west of Charlotte Peak in the Bob Marshall Wilderness, MT. These three fires were managed collectively as the Charlotte Peak Prescribed Fire and were part of a program to restore fire to the Bob Marshall Ecosystem. The Charlotte Peak fire burned nearly 5,400 acres before it was extinguished by heavy rains in late July and early August.

A field study was initiated in the summer of 1986 for the purpose of measuring vegetative response to fire in several different community types. A plot in a whitebark pine (*Pinus albicaulis*) community type was located near the point of ignition, just below the main ridgeline west of Charlotte Peak (Plot 114).

The criteria for placing this plot were that the preburn community was a mature stand dominated by *Pinus albicaulis* and was completely consumed by fire. The plot was permanently marked and has been remeasured annually since the fire (1986-1988). The study site is located at an elevation of 7,320 ft with an easterly aspect on a 40 percent slope. The Montana Forest Habitat Type most closely resembles *Abies lasiocarpa / Luzula hitchcockii / Vaccinium scoparium*, though postfire determination is difficult. The preburn stand was approximately 195 years old with a mixed *Pinus albicaulis* and *Abies lasiocarpa* overstory.

METHODS

Plot 114 was sampled using Ecodata Classification Sampling Methods. Species' frequencies and canopy coverages were measured within 25 microplots on a 10th-acre macroplot. Ground cover and production by life form was also measured. Tree and shrub densities were measured by age class. Other data were also taken for each species, including canopy coverage by age/size class, distribution, phenology, height, and hedging class.

RESULTS

It was observed that, even though a stand-replacing fire occurred, fire severity was low due to (1) low mineral soil (1 to 5 percent) and high litter and duff (85 to 95 percent) ground coverages, and (2) the high number of species that resprouted, including *Xerophyllum tenax*, which has a rhizome highly susceptible to severe fires. This low fire severity influenced the types of species that returned. In plot 114, 53 percent of the species found after the fire resprouted from surviving roots (table 1). Six percent were onsite (residual) colonizers, plants which germinated from seeds that were in existence either in the ground or in tree crowns before the fire. Thirty-five percent were offsite colonizers, species which germinated from seeds that were brought to the plot by either animals or wind. Six percent were of unknown origin.

One of the more notable offsite colonizers was *Pinus albicaulis*. Since *Pinus albicaulis* has an indehiscent cone, it is probable that seedlings were established from Clark's nutcracker seed caching. This most likely occurred in 1987, since it was not until the third year (1988) that any conifer seedlings were noted (densities in 1986, 1987, and 1988 were 0, 0, and 264 seedlings per acre, respectively). It appears that cone crop production was poor in 1985 and 1986 but good enough in 1987 to provide enough seeds to explain the 1988 surge in *Pinus albicaulis* seedlings. This was also true for *Abies lasiocarpa*, but since its seed dispersal mechanism is by wind from the nearest unburned area it appeared in much lower densities.

Two other species of particular significance are *Epilobium angustifolium* and *Carex rossii*. *Epilobium angustifolium*'s seeds are windblown onto the site after the fire, subsequently providing vegetative and litter cover. *Carex rossii* usually does not occur in the prefire stand vegetatively, but does in the form of a residual seed in the ground awaiting fire to create the proper germination conditions.

Canopy cover and vegetative production showed significant increases each year (figs. 1 and 2, respectively); however, nested rooted frequency (fig. 3) did not change significantly. This is primarily due to the fact that the plants with the highest coverages and densities were resprouts, therefore not increasing in numbers of plants, only in size in later years. Most of the plants present in postburn years 1 through 3 became established in year 1 with very little colonization occurring in subsequent years. Only four new species with very little cover were recorded after year 1: *Tragopogon dubius*, *Epilobium watsonii*, *Abies lasiocarpa*, and *Pinus albicaulis*. Three species displayed a sporadic occurrence pattern, occurring in one year and not the next. This is probably due to the inability to locate every single plant on the 10th-acre plot each year. These species were *Senecio triangularis*, *Pyrola secunda*, and *Viola orbiculata*.

Maria Ash is Biological Technician and Richard J. Lasko is Resource Assistant, Spotted Bear Ranger District, Flathead National Forest, Forest Service, U.S. Department of Agriculture, Hungry Horse, MT 59919.

Table 1—Survival strategies for plant species occurring on plot 114

Onsite colonizer	Offsite colonizer	Resprout	Unknown origin
Carex rossii	*Abies lasiocarpa*	*Menziesia ferruginea*	*Viola orbiculata*
	Pinus albicaulis	*Vaccinium globulare*	
	Epilobium angustifolium	*Vaccinium scoparium*	
	Epilobium watsonii	*Luzula hitchcockii*	
	Hieracium albiflorum	*Arnica latifolia*	
	Tragopogon dubius	*Pedicularis racemosa*	
		Pyrola secunda	
		Senecio triangularis	
		Xerophyllum tenax	

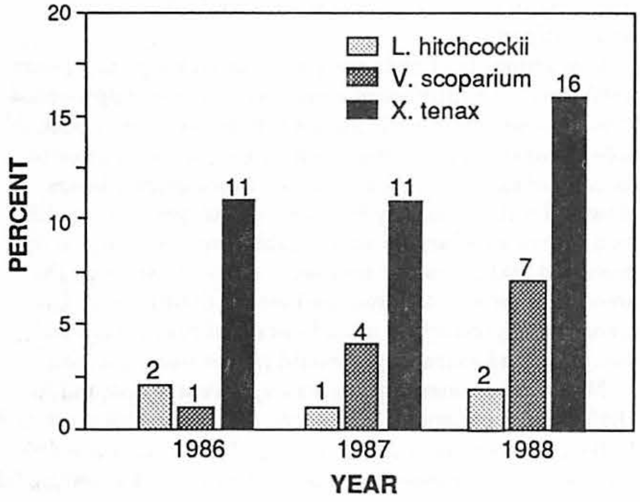


Figure 1—Canopy cover for *Luzula hitchcockii, Vaccinium scoparium*, and *Xerophyllum tenax* on plot 114 from 1986 to 1988.

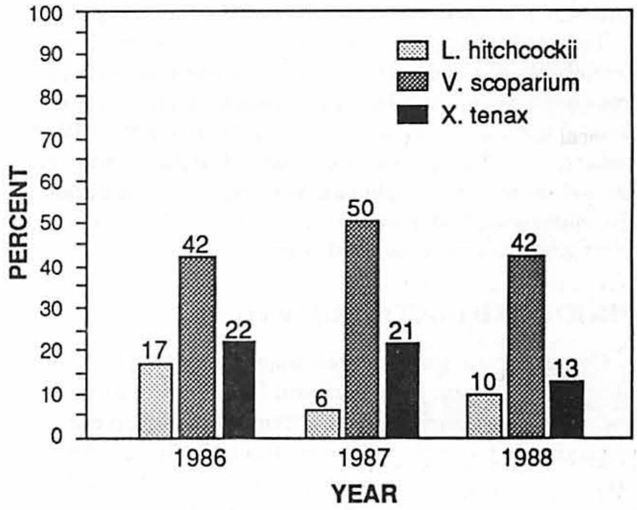


Figure 3—Nested rooted frequency for *Luzula hitchcockii, Vaccinium scoparium*, and *Xerophyllum tenax* on plot 114 from 1986 to 1988.

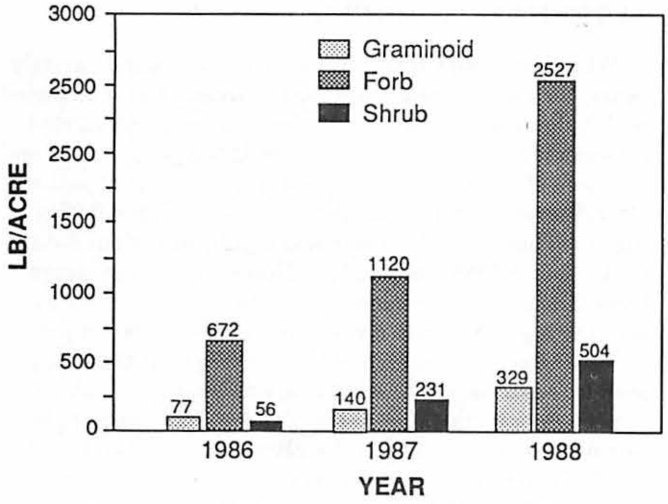


Figure 2—Total production for *Luzula hitchcockii, Vaccinium scoparium*, and *Xerophyllum tenax* on plot 114 from 1986 to 1988.

RELATIONSHIPS BETWEEN WHITEBARK PINE CONE PRODUCTION AND FALL GRIZZLY BEAR MOVEMENTS

Bonnie M. Blanchard

Whitebark pine (*Pinus albicaulis*) nuts are an important and preferred food for Yellowstone grizzly bears (*Ursus arctos horribilis*). Bears will consume these nuts to the near exclusion of other food items when they are available in sufficient quantity. High fat content of the nuts can supply the calories needed to accumulate critical fat reserves during fall in preparation for hibernation. In years of exceptional production, nuts will also be consumed in the spring and summer of the following year.

To monitor annual cone production and subsequent availability of nuts to grizzly bears, 90-m transects of 10 trees each were established in whitebark pine stands throughout the study area: nine in 1980, eight in 1987, and two in 1988. Cones were counted in July and early August before appreciable harvesting by red squirrels (*Tamiasciurus hudsonicus*) and Clark's nutcrackers (*Nucifraga columbiana*) had begun.

PRODUCTION-CONSUMPTION

Generally a significant relationship existed between cone production on transects and frequency of nuts in scats deposited during fall (September to November) when the scat sample was more than 15 (fig. 1). An exception was 1987 when the transects failed to reflect actual cone availability for two primary reasons. Cones matured approximately 2 weeks earlier than normal, probably due to favorable spring weather conditions; and transects were on the average read later than was ideal. Also, production was spotty that year and apparently poorest in xeric, pure to nearly pure whitebark pine stands. The majority of transects were in those types of stands, and cones were often noted on trees outside transects. This prompted the establishment of additional transects in mesic, mixed species stands previously unmonitored.

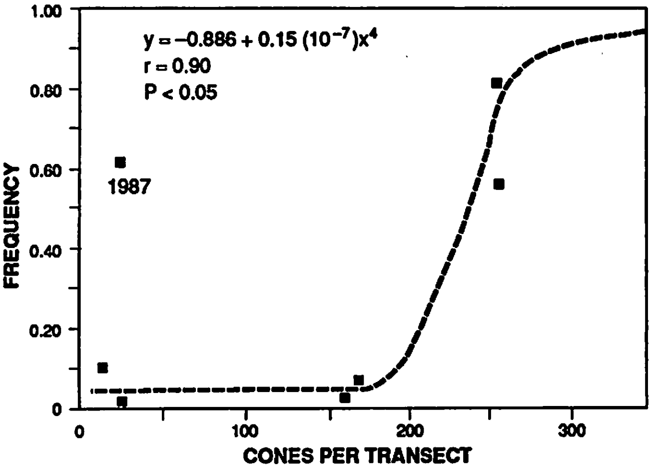


Figure 1—Relationship between mean number of cones per transect and frequency of whitebark pine nuts in fall grizzly scats.

Low amounts of nuts were consumed by grizzly bears until the mean number of cones per transect approached 200. Red squirrels and Clark's nutcrackers were probably able to consume nuts produced up to that level prior to caching of excess cones and nuts. Since grizzly bears obtained nuts primarily by raiding squirrel caches, this food source was largely unavailable until production approached 200 cones per transect. Above that level, the amount of pine nuts consumed would theoretically increase with production until bears had maximized consumption and extra cones would not be used that fall.

Maximized consumption was apparently reached in 1985 when frequency of nuts was 0.81 in all fall scats and 1.00 in October scats alone ($n = 9$). Maximum cone production on one transect was 625. A main diet item the following spring and summer was whitebark pine nuts—those remaining in caches from the fall of 1985. Frequency of nuts in scats increased from 0.06 in May ($n = 32$) to 0.29 in July ($n = 154$), compared to the 1979 to 1987 average frequency of 0.17 in May and 0.19 in July.

ALTERNATE SOURCES

When whitebark pine nuts were unavailable to grizzly bears, they sought alternate food sources, often associated with human activities. A significant correlation existed between mean number of cones produced per transect and numbers of grizzly bears trapped in management actions after August 1 for 1980 to 1986 ($r^2 = -0.815, p < 0.05$) (fig. 2). This correlation was less significant when data for 1987 and 1988 were added. However, data collected those 2 years were not comparable to the 1980-1986 data set. During 1987, cone production on transects did not reflect the actual production level throughout the study area for reasons discussed above, and bears were able to consume appreciable amounts of nuts. Poor cone production during 1988 was offset by alternate food items made available to bears as a direct result of the 1988 Yellowstone wildfires. Grizzly bears seeking alternate food items associated with human activities during August were drawn into burns seeking ungulate carcasses, and only one management action was recorded after October 1, 1988.

Bonnie M. Blanchard is Research Wildlife Biologist, Interagency Grizzly Bear Study Team, Department of the Interior, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717.

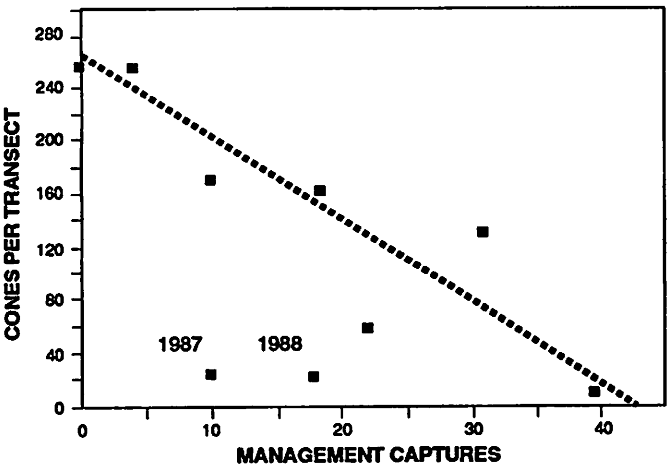


Figure 2—Relationship between mean number of cones per transect and number of management captures of grizzlies after August 1.

When cone production was low and management actions high, mortalities of female grizzly bears were also high ($r^2 = -0.691$, $p < 0.05$). This correlation was not significant when male mortalities were added. Females were possibly displaced by more-dominant males from a preferred but scarce food supply.

Whitebark pine nuts are the most important fall food of Yellowstone grizzlies, and availability of nuts influences annual feeding strategies and movement patterns. During years of low availability, numbers of grizzly/human encounters are greater, resulting management actions more numerous, and mortalities of female grizzly bears higher.

THE FIRE EFFECTS INFORMATION SYSTEM: AN AID TO WILDLAND FIRE MANAGEMENT

Anne F. Bradley

The Fire Effects Information System (FEIS), a "new generation" knowledge management tool, is designed to store and provide easy user access to state-of-the-knowledge information on the effects of fire and general ecology of plant species and communities. System software was developed in a cooperative effort between the University of Montana Computer Science Department and the Fire Effects Research Unit of the Forest Service's Intermountain Research Station.

Information is stored as text in the FEIS knowledge base and can be viewed as paragraphs on a screen by the user. The system is menu-driven and requires only minimal experience with a computer to operate. The information is organized and accessed by categories. Information on plant species, plant communities, and wildlife species is available. As an example of the organizational structure, plant species categories that may be viewed are:

Taxonomic Information
Species Name
Abbreviation
Synonyms
Common Name
Taxonomy
Life Form
References

Species Distribution and Occurrence
General Distribution
BLM Physiographic Regions
Kuchler Plant Associations
SAF Cover Types
Habitat Types and Plant Communities
References

Botanical and Ecological Characteristics
General Botanical Characteristics
Raunkaier Life Form
Regenerative Process
Site Characteristics
Successional Status
Seasonal Development
References

Species Value and Use
Wood Products Value
Importance to Livestock and Wildlife
Palatability
Food Value
Cover Value
Value for Rehabilitation of Disturbed Sites

Anne F. Bradley is Ecologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Intermountain Fire Sciences Laboratory, Missoula, MT 59807.

Other Uses and Values
Management Considerations
References

Plant Adaptations to Fire
General Adaptations to Fire
Lyon-Stickney Fire Survival Strategy
References

Fire Effects
Fire Effects on Plant
Discussion and Qualification of Fire Effect
Plant Response to Fire
Discussion and Qualification of Plant Response
References

Fire Case Studies
Case Name
References
Season/Severity Classification
Study Location
Preburn Vegetative Community
Target Species Phenological State
Site Description
Fire Description
Fire Effect on Target Species
Fire Management Implications

Using a computerized system simplifies information updating. It also permits wider access to and greater consistency in information transferred from researchers to managers. When implemented, the system will be accessible to anyone with computer-to-computer communication capabilities.

FEIS has the potential to "capture" good information that may not be published in the established literature. Good local studies and rules of thumb used by experienced managers in their use of fire can quickly be made accessible to a broad audience once the information is included in the system.

The system's flexibility, logical organization, and ability to handle large amounts of complex information are the result of applying artificial intelligence programming techniques. FEIS contains information on over 240 plant species, including whitebark pine, limber pine, and other species that occur in high-elevation environments. Current plans are to increase the number of coniferous forest plants and communities represented in the system so that information available on high-elevation Rocky Mountain species should expand rapidly in the near future.

During early development of the program, the prototype system was demonstrated at several dozen field locations in Arizona, Idaho, Nevada, Oregon, South Dakota, and Utah. The participants listed the following potential uses of FEIS:

- prescribed fire plans
- fire rehabilitation plans
- escaped fire analysis
- land use plans
- exotic species control plans
- environmental assessments and impact statements
- vegetation management plans (range, wildlife habitat, and silvicultural prescriptions)
- training programs
- research facilitation

The prototype system is now being tested by managers in the Forest Service, Bureau of Land Management, and the National Park Service. Full implementation is expected within the next 2 to 3 years.

WHITEBARK PINE AND CUMULATIVE EFFECTS MODELING FOR THE YELLOWSTONE GRIZZLY BEAR

Bev Dixon

The Endangered Species Act mandates that a biological assessment be performed for any land uses or management activities that may have an impact on any listed species. Part of the biological assessment involves an analysis of the cumulative effects of existing and proposed activities upon a species or its habitat. In order to facilitate this process in grizzly bear habitat, a computerized cumulative effects assessment model was developed by an interagency modeling team for the Greater Yellowstone Ecosystem in 1984.

The basis for this computer model is a series of digitized maps and overlays. The base maps represent the vegetative makeup of an area. Homogenous vegetation types are delineated on aerial photos and the resulting polygons are transferred to 7.5-minute orthophoto quads. Field crews examine a sample of approximately 25 percent of the delineated aerial photos, assigning habitat and cover type codes to forested components and generic five-digit vegetation codes to nonforested components. Data collected by these crews are used as the basis for extrapolating vegetation codes to unsampled areas. Feedsite, scat, and radio relocation data gathered by the Interagency Grizzly Bear Study Team were analyzed to calculate the

---

Bev Dixon is Cartographic Technician, Gallatin National Forest, Forest Service, U.S. Department of Agriculture, P. O. Box 130, Bozeman, MT 59771.

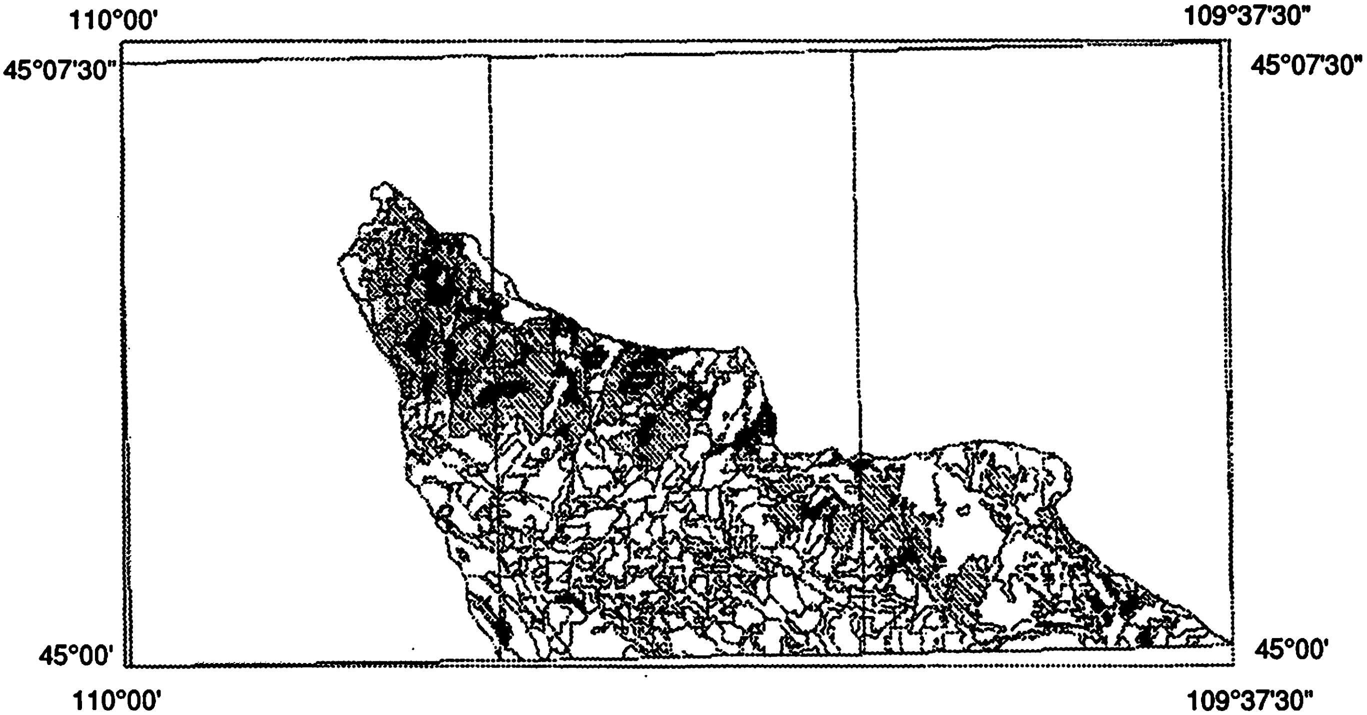


Figure 1—The geographic area represented here includes the northernmost portion (that portion that falls within the Gallatin National Forest boundary) of the Crandall/Sunlight Bear Management Unit of the Greater Yellowstone Ecosystem for grizzly bears. The border of the computer-generated vegetation maps represents the collective boundaries of three 7.5-minute USGS topographic quads: Alpine SW, Alpine SE, and Cooke City SW. The internal boundary represents the Bear Management Unit boundary. Polygons within the Bear Management Unit boundary represent homogenous units of vegetation. Polygons mapped as forested with substantial amounts of whitebark pine are shaded with a solid pattern. Polygons shaded with a cross-hatch pattern represent vegetation components mapped as mosaics of whitebark pine intermingled with other forest or nonforest types.

relative value to bears of the various vegetation components found throughout the Greater Yellowstone Ecosystem.

HABITAT VALUES

While vegetal structure is a critical element in grizzly bear habitat in terms of food and cover, animal food sources are also important as a source of protein for the bears. Therefore, areas of animal concentrations, such as ungulate winter ranges, are also mapped and this information is overlayed onto the vegetation base maps. The animal food sources generally increase the value of those vegetation polygons in which they occur.

Just as animal food sources increase the value of grizzly bear habitat, human activities typically tend to decrease the value of an area to the bears. Thus, sources of human activities, such as roads, trails, campgrounds, and picnic areas, are mapped and overlayed onto the habitat maps. Human activities vary in the degree to which they disturb bears based on the nature of the activity. For example, motorized activities are more disruptive to bears than nonmotorized activities. Occurrences of human activities in high-quality grizzly bear habitat tend not only to displace bears to lower quality areas, but also pose a degree of mortality risk to bears that remain in the area. All of these factors are considered in the cumulative effects assessment conducted as part of a biological assessment. This process is facilitated by the computerized cumulative effects model (CEM).

Whitebark pine (*Pinus albicaulis*) has been proven to provide an important food source to grizzly bears in the Greater Yellowstone Ecosystem. As such, whitebark pine is mapped to various successional stages in the vegetation component mapping process. In the manual "Forest Habitat Types of Montana," Pfister and others describe three specific habitat types containing whitebark pine. These types are: *Abies lasiocarpa-Pinus albicaulis / Vaccinium scoparium* (subalpine fir-whitebark pine/grouse whortleberry), *Pinus albicaulis-Abies lasiocarpa* (whitebark pine-subalpine fir), and *Pinus albicaulis* (whitebark pine) habitat types. Cover types used in the mapping process range in successional stages from recently burned whitebark pine stands (cover type 50—WBP) to stands of mature to overmature whitebark pine (cover type 54—WB). These habitat and cover types are combined to indicate occurrences of whitebark pine on the vegetation base maps.

USE OF MOSS

A Geographic Information System known as "MOSS" (Map Overlay and Statistical System) is currently used with the Greater Yellowstone Ecosystem cumulative effects model for visual display purposes. MOSS is used to display or "plot" the digitized vegetation base maps for viewing either on the terminal screen or printed out in hardcopy. MOSS commands also allow the user to select specific subjects or features on a map and highlight or shade these items to indicate their location on the map. Furthermore, queries can be made to obtain specific information pertaining to selected items within an analysis area, such as number of acres or linear miles, frequency of occurrence, percent of total acres, and other pertinent information.

For purposes of this synopsis, data collected from habitat component mapping for cumulative effects modeling on the Gallatin National Forest, along with MOSS, were used to locate and display potential sources of whitebark pine. Figure 1 provides a visual example of how this process can be used to delineate whitebark pine habitats in a specific management unit. This is another tool that helps increase the effectiveness of management practices on the ground.

CONTAINERIZED WHITEBARK PINE NURSERY PRODUCTION IN THE FOREST SERVICE NORTHERN REGION

Kent Eggleston and Joseph Meyer

The National Forests north of Yellowstone National Park are increasing their efforts in providing whitebark pine seedlings for wildlife habitat and reforestation enhancements. The Coeur d'Alene Nursery has been working with the Gallatin National Forest since 1985 by processing whitebark cones into clean seed and producing containerized seedlings for their outplanting program. Unlike other species produced at the nursery for the Forest Service Northern Region's reforestation programs, whitebark pine has presented several unique cultural and biological challenges.

SEED PROCESSING ACTIVITIES

The Coeur d'Alene Nursery has only recently begun to receive requests for whitebark pine seedlings and we have little experience in handling the cones, seeds, and seedlings (table 1). However, we have started work with whitebark pine and this synopsis is intended to show what we are doing.

Extracting seed from whitebark pine cones is more difficult than it is for other conifers and generally requires hand cleaning to assure seed removal. The seed tends to cling to the cone bracts, making machine (mechanical) cleaning difficult.

Stratification methods need to be refined for whitebark pine. Our records show that this species requires stratification procedures similar to western white pine. Germination is relatively poor. Our best results have been achieved by soaking one-half lb or smaller quantities in mesh bags for 48 hours in cold, running water. Following the soak, each mesh bag is placed inside a polyethylene bag to prevent drying, and the seed is put in the stratification room at 34 to 36 °F for 100+ days.

The Nursery is investigating several stratification methods and seed treatments to improve germination percentage and uniformity. The current treatment being tried is stratifying seed in containers. This method exposes a greater amount of the individual seedcoat surface area to the stratification environment. Another stratification procedure that could be investigated is the combination of warm temperatures prior to the normal cold environments. Both of these treatments have improved western white pine germination and may do likewise with whitebark pine.

SEEDLING PRODUCTION

Whitebark pine seedlings grow slowly compared to other conifers in the Northern Rocky Mountains. The Coeur d'Alene Nursery currently grows 4- to 6-inch seedlings in 3 to 4 months under normal greenhouse culture (table 2). Whitebark pine takes 6 to 8 months to reach those height standards. In order to reach height requirements, whitebark seed is currently sown two crop cycles prior to field planting. This allows the seedlings to be grown for one season inside a greenhouse, then allowed to set a terminal bud, then cold stored, and later grown for a second full season in the shelterhouse to reach adequate height before field planting.

The Nursery has just completed installing a new high-pressure sodium light photoperiod system in our Propagation House. This system enables photoperiod to be extended. This extended photoperiod increases the growing

---

Kent Eggleston is Horticulturist and Joseph Meyer is Forest Nurseryman, Northern Region, Forest Service, U.S. Department of Agriculture, Coeur d'Alene Nursery, Coeur d'Alene, ID 83814.

Table 1—Some specifics of whitebark pine seed received to date at the Coeur d'Alene Nursery

Year collected	Lot number	Date collected	Number bushel	Pounds	Yield (lb/bu)	Seeds/lb	Germination percent
1985	6410	8/17/85	5	13.80	2.76	4,400	2
1987[1]	6653	8/20/87	3	4.50	1.50	3,670	50
1987[2]	6654	8/20/87	1	.07			

[1] Seed for container-planting, fall 1990 in the Gallatin National Forest.
[2] Not enough seed to get testing information.

Table 2—Some specifics of current whitebark pine seedling production at the Coeur d'Alene Nursery

National Forest	District	Lot number	Container size	Number of seedlings requested	Elevation	Planting schedule	Habitat type
					Feet		
Gallatin	Hebgen Lake	6410	Supercel	12,000	8,600	Fall 90	ABLA PIAL/VASC
Gallatin	Gardiner	6410	Pinecell	2,000	8,600	Fall 88	ABLA PIAL/VASC

period from normal daylight period to 18 hours. In a preliminary test, whitebark pine sown under the longer photoperiod increased terminal bud length, but shoot height was little affected by the artificially generated longer daylengths. Apparently, we will still need the second growing season to get enough height development.

Another cultural method to be tested is to sow in April and grow until September of that same year before hardening off the seedlings for the next spring field planting. In the past, under intermittent light, this crop schedule produced premature budset. However, with the new extended photoperiod light system, continued stem elongation may be achieved.

VERTICAL DISTRIBUTION OF EPIPHYTIC LICHENS ON THREE TREE SPECIES IN YELLOWSTONE NATIONAL PARK

Sharon Eversman, Carol Johnson, and Dan Gustafson

Observations throughout Yellowstone National Park had indicated that lichen growth on trees is sparse, with less growth on trunks than on branches. A windstorm in July 1984 blew down thousands of trees in the *Pinus contorta-Vaccinium scoparium* vegetation type between Norris Junction and Canyon Village in Yellowstone National Park. We took advantage of the situation to investigate epiphytic growth on three tree species—lodgepole pine, whitebark pine, and subalpine fir. The location of the windthrow was near the Virginia Cascades road at an elevation of about 2,920 m (Wyoming, Park County, latitude 44°42' N, longitude 111°40'W).

SAMPLING

It was very difficult to locate five trees each of whitebark pine and subalpine fir among the extensive numbers of lodgepole pine. When the whitebark pine and subalpine fir with accessible trunks were found, 1-m increments were marked from the base of the trunk to the tips.

Sharon Eversman is Associate Professor, Carol Johnson is Instructor, and Dan Gustafson is Graduate Student, Biology Department, Montana State University, Bozeman, MT 59717.

Five trees of each species were sampled. Each circumference was divided into four "plots," roughly corresponding to north, south, east, and west exposures when the tree was standing. However, because some trees appeared to have twisted during their fall, the possible direction factor was eliminated during data analysis. Each circumference thus had four sampling plots except where the tree was flat against the ground or another tree at that sampling plot. Based on annual rings visible in nearby sawed trunks, the ages of the lodgepole and whitebark pines were estimated from 95 to 200 years, and the subalpine firs were 50 to 150 years old. Heights of the sampled lodgepole pine were 13.7 to 22.7 m (16 to 29 cm d.b.h.); whitebark pines were 8.1 to 14.0 m tall with d.b.h. of 10 to 20 cm; subalpine firs were 8.1 to 18.4 m with d.b.h. of 13 to 42 cm.

Pieces of outer bark from the three trees (six 350- to 400-mg samples) were soaked in distilled water for 30 minutes, blotted for 10 seconds, then air dried. Their weights were determined every hour for 4 hours to determine drying times of the different kinds of bark. The pH levels were determined by soaking slivers of outer bark (five 1-g samples per species) in 30 mL distilled water for 1 hour, then determining the pH of the water. Bark samples were taken 1.5 m above ground level.

FINDINGS

Most of the lichen species were tiny tufts of fruticose species and crustose forms; there were no bryophytes. Lichen growth was greatest at the base (mostly due to one species, *Parmeliopsis ambigua*) and above 2 m in height.

Seven lichen species grew on whitebark pine. They were, in order of frequency: *Lecanora piniperda, Bryoria lanestris, Parmeliopsis ambigua, Letharia vulpina, Letharia columbiana, Melanelia exasperatula,* and *Usnea fulvoreagens*. Lichens were contained in 59.8 percent of the 224 sampling plots on whitebark pine.

Lodgepole pine had only five lichen species on the trunks: *Parmeliopsis ambigua, Lecanora piniperda, Letharia vulpina, Letharia columbiana,* and *Bryoria lanestris*. Lichen growth was contained in 4 percent of the 360 sampled plots on lodgepole pine.

Subalpine fir had twelve lichen species on the trunks. All the species growing on whitebark and lodgepole pines also grew on subalpine fir. The five additional species on this tree were ones more usually associated with Douglas-fir or deciduous trees: *Xanthoria fallax, Physcia adscendens, Hypogymnia austerodes, Tuckermannopsis pinastri,* and *Parmelia sulcata*. Of 268 sampling plots on subalpine fir, 74.3 percent had lichen growth.

There were no differences in drying times of the three kinds of bark. The average pH of water medium after soaking bark was 4.94 for subalpine fir, 4.03 for whitebark pine, and 3.78 for lodgepole pine.

We concluded that subalpine fir had the most lichen growth because of the smooth nature of the bark, the highest pH, and most protected trunk bark. Whitebark pine had more lichen growth than lodgepole pine, perhaps because of the slightly less scaly bark and higher pH of whitebark pine compared with lodgepole pine.

INVENTORY, MONITORING, AND ANALYSIS OF WHITEBARK PINE ECOSYSTEMS USING THE ECODATA AND ECOPAC SYSTEM

Wendel J. Hann and Mark Jensen

ECODATA consists of a set of standardized sampling methods and data entry programs used in describing vegetation and site variables in the Northern Region of the Forest Service. Sampling methods range from rapid qualitative assessments of plant canopy cover to quantitative, replicated, statistical designs. The basic sampling methods of ECODATA describe site characteristics (such as soils, topography, and disturbance history), and general vegetation characteristics (such as species cover, age, size class, and height). Optional methods include techniques for assessing line intercept cover, nested rooted frequency, microplot cover, phenology, forage use, fuels, fire history, and riparian characteristics.

ECOPAC is an acronym for a series of menu-driven computer programs used in the analysis of ECODATA. Such programs allow the user to generate simple reports, conduct statistical analysis, display resource value ratings, and develop resource response predictions from ECODATA. Programs contained in ECOPAC include: Utility (used to scan for errors, produce reports, and analyze community types), Value (used to predict diversity, succession, forage value, fuels, fire behavior and effects, climate, and wildlife habitat suitability), Ecostat (used for

---

Wendel J. Hann is Ecosystem Manager and Mark Jensen is Ecosystem Analysis/RNA Coordinator, Ecosystem Management Group, Northern Region, Forest Service, U.S. Department of Agriculture, Box 7669, Missoula, MT 59807.

cluster analysis, ordination, descriminant regression, and statistical analysis), and Ecolink (used to summarize plot data into polygon interpretations and link soil and water data bases with vegetation data bases).

In this presentation, various applications of ECODATA and ECOPAC were shown utilizing data collected from the whitebark pine ecosystem. Discussion of the need for standardized sampling and analysis of ecosystem variables also was presented.

ARTIFICIAL REFORESTATION OF WHITEBARK PINE

Richard L. Kracht and Ward W. McCaughey

With increased recognition of whitebark pine's importance in the management of wildlife habitat, watersheds, and recreation, it has become necessary to consider it in reforestation projects to help meet varied resource objectives. An administrative study was designed to evaluate standard reforestation techniques for effectiveness in regenerating whitebark pine. This study identifies climatic and site effects that appear to be important in survival and growth of whitebark pine seedlings.

METHODS

This study is located on the Gardiner Ranger District of the Gallatin National Forest 5.5 air miles east of Gardiner, MT. The planting site is on a 15-acre clearcut abutting a 50-acre clearcut called the Palmer Coop timber sale.

Whitebark pine cones were handpicked from trees adjacent to the planting site during late summer of 1985. Collections occurred during a short time period after the cones were mature and seed ripe, but just prior to harvesting of seed by Clark's nutcrackers and squirrels.

Seeds were extracted and cleaned at the Forest Service nursery in Coeur d'Alene, ID, according to standard nursery techniques. These techniques extracted approximately 50 percent of the seed, but the remainder of the seed required hand cleaning to remove it from the cones.

Seed germination tests indicated low germination of about 5 percent. However, other studies indicate that these tests may not have accurately indicated what the germinability was for this lot of whitebark pine seed. It is also possible that the cones were collected prematurely.

Seeds were cold stratified in the spring of 1986. One pound of seed per nylon mesh bag was soaked in running tap water for 48 hours and placed in cold storage between 34 to 36 °F for 100 days. The seed was then planted in the greenhouse in pine cell containers. Due to slow germination and slow initial growth, it was necessary to hold seedlings for a second growing season at the nursery to obtain enough seedlings of adequate size for planting.

The containerized seedlings were planted on the study site the fall of 1987 using standard reforestation practices: hand planting bars, selecting appropriate microsites, scarifying an 18-inch-square area to mineral soil, and providing natural shade. We staked and numbered 300 trees which were laid out in six parallel rows of 50 each. The seedlings were planted on a northeast aspect with planting sites distributed in a swale, up a side slope of 15 percent, across a bench (a ridge configuration), and down a gentle side slope of 9 percent. Survival counts were made during the spring and fall of 1988 and spring of 1989. We measured and recorded tree height to the nearest 0.5 cm and stem basal diameter to the nearest 0.01 cm during the fall of 1988, 1 year after outplanting.

RESULTS

Survival of whitebark pine seedlings has been good, with an 89 percent survival rate over the first 2 years. Overall survival was 97 percent for the initial overwinter period from the fall of 1987 to spring of 1988. Through the 1988 growing season, a record dry year, survival dropped to 91 percent. Seedling survival was 89 percent after the second overwinter period.

Seedling survival varied slightly in relation to topographic position. Survival was 100 percent on bench sites, 95 percent on 9 and 15 percent slopes, and only 80 percent in swales (fig. 1).

First-year growth of whitebark pine seedlings varied considerably by topographic position for height increment and slightly for basal diameter increment. First-year height increment averaged 1.8 cm for all seedlings—2.7 cm in swales, 1.9 on 9 percent slopes, 1.4 on benches, and 1.3 cm on 15 percent slopes (fig. 2). Basal diameter increment averaged 0.0497 cm in swales, 0.0475 and 0.0473 on 9 and 15 percent slopes, respectively, and 0.0447 cm on benches (fig. 3).

Richard L. Kracht is Forest Silviculturist, Gallatin National Forest, Forest Service, U.S. Department of Agriculture, Bozeman, MT 59771; Ward W. McCaughey is Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Forestry Sciences Laboratory, Bozeman, MT 59717.

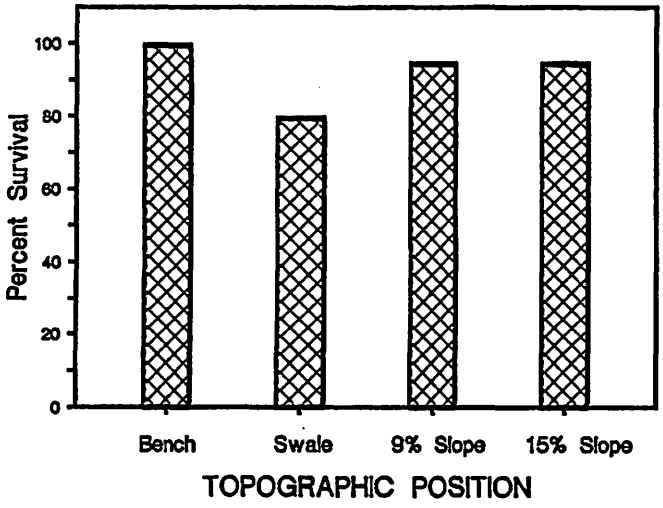


Figure 1—First-year survival of whitebark pine seedlings by topographic position.

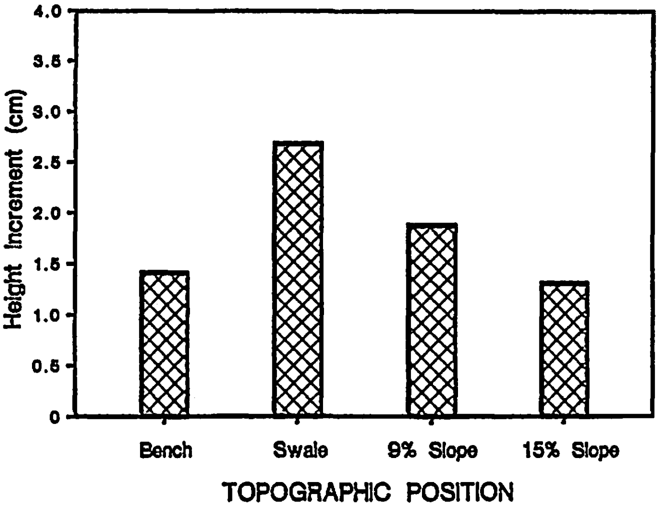


Figure 2—First-year height increment of whitebark pine seedlings by topographic position.

DISCUSSION

These preliminary results indicate that artificial reforestation of whitebark pine using standard operational techniques can succeed. These results are comparable with those of the National Forest System's reforestation program.

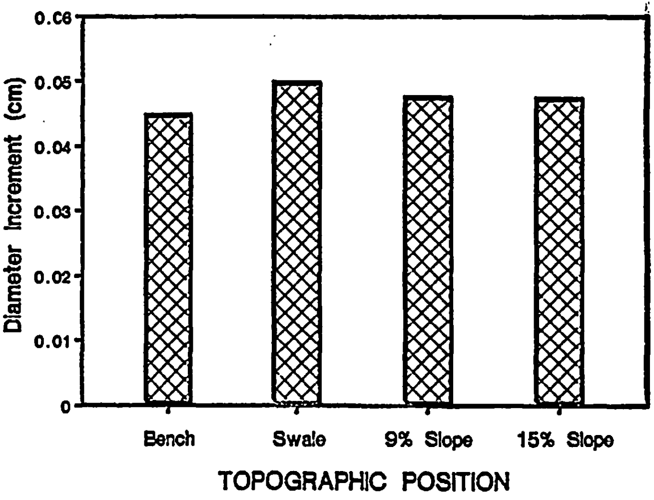


Figure 3—First-year increment of stem basal diameter of whitebark pine seedlings by topographic position.

Whitebark seedlings may be influenced by topographic location both in survival and in height and diameter growth. Although preliminary, it appears that the moister and possibly cooler (frost pocket) conditions in the swale have resulted in slightly lower survival but have enhanced growth of surviving seedlings. Further monitoring of this administrative study should yield more definitive results.

This study has helped to pinpoint further work that will be needed to ensure a cost-effective operational planting program with whitebark pine. This is:

1. Development of seed collection zones.
2. Development of field procedures for determining when seed is mature.
3. Development of seed extraction and cleaning equipment.
4. Development of seed-stratification procedures.
5. Development of optimum growth regimes for nurseries.
6. Recognition of optimum growing sites for highest survival and growth.

To our knowledge, this is the first operational planting of whitebark pine seedlings. A second plantation has recently been established on the Rocky Mountain Ranger District near Choteau, MT. However, survival and growth measurements have not been taken yet. Hopefully these studies will lead to better management of these high-mountain forests.

MORPHOLOGICAL DIFFERENCES BETWEEN WIND-DISPERSED AND BIRD-DISPERSED PINES OF SUBGENUS *STROBUS*

Ronald M. Lanner

Two thirds of the world's Haploxylon (= subgenus *Strobus*) pines have nutlike seeds that cannot be dispersed by wind because: (a) seed wings are absent (these include *Pinus koraiensis, cembra, pumila, sibirica, albicaulis,* some *flexilis,* some *strobiformis, armandii, cembroides, edulis, monophylla, johannis, remota, juarezensis, culminicola, maximartinezii, pinceana, nelsonii, discolor*); (b) their seed wings are ineffective (some *flexilis,* some *strobiformis,* some *ayacahuite,* some *parviflora*); or (c) their seed wings stick to the cone-scale surface (some *parviflora, gerardiana, bungeana*).

Therefore, only a minority of the *Strobus* pines have the wind-dispersible seeds thought to be typical of the Pinaceae: (*aristata, balfouriana, longaeva, strobus, monticola, lambertiana,* most *ayacahuite, peuce, griffithii, dalatensis, morrisonicola, wangii, fenzeliana*).

The seeds of several of these non-wind-dispersible species are known to be dispersed and stored in the soil by birds of family Corvidae who use them as a food source. In North America, studies of pinyon pines (*edulis* and *monophylla*) have shown them to be dispersed and cached on a large scale by pinyon jays, and on a lesser scale by Steller's and scrub jays. These pines as well as *albicaulis, flexilis,* and *strobiformis* are dispersed and cached also by Clark's nutcracker. Several pines in Europe and Asia (*cembra, pumila, sibirica*) have been shown to have their seeds harvested and cached by the widespread Eurasian nutcracker. In all of these pine-Corvid systems, seeds stored in the soil in mast years exceed the birds' winter food requirements and become available for germination. In at least one species (*albicaulis*) there is no other regenerative method, and the tree depends on the bird for survival.

The "bird pines" differ from the conventional, or archetypical *Strobus* pines ("wind pines") in numerous morphological traits. The characteristics of bird pines facilitate seed harvest by Corvids, or survivability of seeds adapted to Corvid dispersal. I argue that these traits have arisen through natural selection exerted by the Corvids; and that it is this selection pressure that has led to the speciation of the bird pines from the older, more conservative wind pines.

TRAIT DIFFERENCES

For example, consider crown form. "Wind pines," such as *strobus, monticola, griffithii,* and *peuce,* are typically monopodial, seldom forked, and horizontally branched. The result is that they have relatively few cone-bearing branches, many of their cones are concealed by layers of foliage, and most of their cones are not readily visible to flying birds (poor display) or even birds perched on the crown. For these reasons, "wind pines" are not especially attractive to Corvids.

On the other hand, "bird pines," like *flexilis, albicaulis,* and the pinyons, are sympodial, frequently forked, and have numerous vertically oriented branches. This results in many cone-bearing branches, and cones that are well displayed to flying birds or to birds perched on the crown. In this way, "bird pines" attract Corvids.

These groups of pines also differ in their cone attachment. Among the "wind pines," branches are usually horizontal. Cones have long peduncles, are pendent, and are loosely attached to the branch. This causes both branches and cones to be unstable in a wind. Corvids must hang upside down to harvest seeds from open cones, a harvest process that is physically difficult and demanding of energy.

"Bird pines" on the other hand, have vertical or upswept cone-bearing branches. The cones are sessile and rigidly attached to the branch. Therefore, branches and cones provide stable perches for birds harvesting the seeds, and Corvids can remain upright when harvesting seed, making the harvesting process easy and less demanding of energy.

One consequence of bearing cones on upswept limbs is the need for heat diffusion within the cones. Cones exposed to the sun endanger their developing seeds, and must diffuse heat to prevent seed proteins from being denatured. In the "wind pines," the cones are shaded by the horizontal branches of the whorls above. Little heat is accumulated, so the cone scales can be thin. But the "bird pines" have cones that are exposed to the sun. Perhaps the thickened cone-scale apophyses that typify the pinyons, *albicaulis, gerardiana,* and some other bird pines have evolved as heat-diffusion masses.

RETENTION DIFFERENCES

Seed retention in cones is a characteristic of many of the "bird pines." Among the "wind pines," the cones open when they dry in the autumn; then the seeds fall out and fly on the wind. The "bird pines" show far more variability. In the subsection *Cembrae,* for example, cones remain closed or open only a little, and the seeds remain inside the cone. In subsection Cembroides (pinyon pines), the cones open, but the seeds are retained by spermoderm "flanges" on the upper cone-scale surface. In some other species (*parviflora, bungeana, gerardiana*) the seed wing sticks to the cone scale, temporarily immobilizing seed.

Among the *Cembrae* (*sibirica, cembra, pumila, albicaulis, koraiensis*) all species have cone scales lacking the coarse-fiber tracheids found in other pine cones. Therefore, they do not open by the differential shrinkage of

---

Ronald M. Lanner is Professor, Department of Forest Resources, Utah State University, Logan, UT 84322.

drying tissues, as do other pine cones; and they are easily broken off by nutcrackers seeking the seeds inside. When *Cembrae* cone-scales are broken off, the seeds remain held in the core of the cone, thus facilitating the nutcracker's harvest.

Among the *Cembrae, cembra, koraiensis,* and *sibirica* seeds have a prominently marked hilum that is displayed when the scale is broken off. Does this serve as a "target" for the nutcrackers? The studies necessary to answer this and many other fascinating questions have not yet been done.

MONTANA'S NATIVE PLANT SOCIETY

Jan Nixon and Anne F. Bradley

New in the State within the last 2 years, the Montana Native Plant Society (MNPS) is an organization devoted to learning more about the plants native to this State and region. Our membership ranges from professionals working in a plant-related field or academic areas to individuals who are simply interested in learning more about the flora of their area on a nontechnical level.

The purpose of the Montana Native Plant Society is: "The preservation, conservation, and study of the native plants and plant communities of Montana and the education of the public to the values of the native flora and its habitat." The society provides a forum for information exchange between scientists, educators, horticulturists, and interested lay people throughout the State of Montana.

MNPS puts on field trips throughout the year and local chapters meet monthly, offering programs on a wide range of plant-related topics. Other projects we are involved in include:

- a knapweed-suppression project at the Kirk Hill Nature Trail south of Bozeman, in cooperation with Museum of the Rockies;
- development of a data base detailing plant communities and species identified on field trips and outings;
- seed collecting in the Logan Pass area of Glacier National Park for revegetation efforts of some of the heavily impacted areas around the Visitor Center there;
- active involvement with the Montana Natural Heritage Program in searching for previously unknown populations of plant species of special concern to that program.

Anyone who would like to learn more about the native vegetation of Montana for scientific or commercial purposes, or for the sake of pure enjoyment, is encouraged to join. MNPS welcomes your interest and involvement with us as we increase our knowledge of the State's flora, its habitats, and importance. For more information contact either of the authors or Montana Native Plant Society, c/o Department of Biological Sciences, University of Montana, Missoula, MT 59812.

Jan Nixon is Newsletter Editor, Montana Native Plant Society, P. O. Box 992, Bozeman, MT 59771-0992; Anne F. Bradley is Botanist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Intermountain Fire Sciences Laboratory, P. O. Box 8089, Missoula, MT 59807.

WIND AND SNOW DAMAGE EFFECTS AFTER THINNING IMMATURE SUBALPINE FORESTS

Jack A. Schmidt

Whitebark pine and lodgepole pine are common associates in many subalpine forests of the Mountain West. This combination occurs at the lower elevational limits of whitebark pine and upper limits of lodgepole pine. Where they merge, densely stocked stands are common and whitebark pine assumes a tall, slender growth form similar to lodgepole pine.

Overstocking often limits the resource values in this zone, and thinning is frequently used to open up the stand for increased light and moisture for reserve trees. This management action can alter wind and snow patterns, subjecting the reserve trees to stresses seldom encountered in densely stocked stands. This study, although aimed primarily at evaluating lodgepole pine, provides insights on the effects of wind and snow in thinned stands where whitebark pine may be a component in these high-elevation forests.

Jack A. Schmidt is Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Forestry Sciences Laboratory, P.O. Box 8089, Missoula, MT 59807.

WHITEBARK PINE—A SUBALPINE SPECIES NEEDING SILVICULTURAL ATTENTION

Wyman C. Schmidt and Ward W. McCaughey

Whitebark pine is a conifer that occupies high-elevation areas of the Mountain West, providing some of the most picturesque "krummholz" forest scenes in America. Snow, ice, and wind sculpture trees in these forests—the forests reciprocate by protecting the soils and watersheds that support them. They also provide food and cover for many species of wildlife, particularly America's large carnivore—the grizzly bear.

Whitebark pine occurs in both mixed and nearly pure stands but will often be succeeded by the more shade-tolerant subalpine fir if fire does not intervene. This gradual change in species composition can have positive or negative effects depending upon the objectives of forest managers. Managers need more information about seed production and dispersal, germination requirements, seedling survival and growth, succession, insect and disease relationships, and interactions with other physical and biological factors. Many of these items are addressed in this "Whitebark Pine Symposium." Some of the things we do know about whitebark pine are:

SEED DISPERSAL

Clark's nutcrackers are considered the main dispersal agent of whitebark pine and likely responsible, inadvertently, for most of the natural regeneration of whitebark pine. Nutcrackers extract whitebark pine seeds from cones in late summer, store up to 100 seeds in their sublingual pouch, and fly considerable distances to store them for later consumption. From one to several seeds are deposited in each of a number of caches in loose soil or duff at a depth of 2 to 4 cm. About half of these seeds are never recovered by the nutcracker and can germinate, often ending up as a clump of germinants.

SEEDLINGS

Whitebark seeds need at least 30 to 60 days of cold-moist conditions before they will germinate. Whitebark seedling growth is slow compared to its other conifer counterparts and this slow growth, particularly at the higher elevations, persists throughout its life.

SQUIRRELS

Red squirrels cut substantial portions of the whitebark cone crop during August and September and cache them in middens for winter food supplies. Although usually much smaller, middens may contain up to 3,000 whitebark pine cones. Middens are a natural attractant and

---

Wyman C. Schmidt is Project Leader and Research Silviculturist and Ward W. McCaughey is Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717.

the whitebark pine seeds an important food source for both grizzly and black bear.

Pure stands of whitebark pine do not readily support red squirrel populations because cone crop failures of whitebark pine in some years leave them without a ready food supply. As a result, squirrel populations fare much better in mixed species stands because cone crop failures of the various species seldom totally coincide, leaving at least some food supply for the resident squirrels.

GRIZZLY BEAR

Grizzly bears frequent high-elevation forests in the Northern Rocky Mountains in search of food and cover. Whitebark pine forests, particularly in the Yellowstone ecosystem, provide both of these important components for this endangered species. Bears feed heavily in both spring and fall on whitebark pine seeds from cones cached by red squirrels. Studies by the Interagency Grizzly Bear Team show that whitebark pine seeds provide over half of the average dietary fat consumed by a grizzly bear over its lifetime in the Yellowstone ecosystem. Survival of grizzly cubs is usually higher in years following good cone crops of whitebark pine.

SILVICULTURE

National Park or Wilderness designation precludes the use of most silvicultural practices, but over much of the range of whitebark pine silviculturists are ultimately responsible for designing and implementing those practices needed to meet management objectives. To do this effectively silviculturists must have adequate information on cone and seed production and how this process can be regulated and predicted, must know the seedbed and other environmental requirements such as shade, moisture, and temperature for seed germination and seedling survival of the various combinations of species in these high-elevation forests, must know how to use prescribed fire effectively, must know how to successfully plant whitebark pine and its associates, and must know how seedlings develop and how immature stands can be cultured to help meet management objectives. All of the above must take into consideration insects such as the mountain pine beetle, cone and seed insects, and diseases such as blister rust.

The days of "healthy neglect" of these forests are likely coming to an end because the results of near-complete fire exclusion are becoming increasingly apparent and the impacts of insects and disease are increasing. All of this becomes more complicated when the possibility of long-term global warming is taken into account. Global warming may reduce the width of that high-elevation zone where the rigorous climate enables whitebark pine, and its high-elevation associated species, to compete successfully with the more mesic species immediately below. Whitebark pine could essentially be "pushed off the top of the mountain" by those tree species better adapted to warmer conditions. Thus, there are many challenges ahead in these forests that have seen little attention by silviculturists.

SUMMARY

Whitebark pine forests merit the increased attention of managers and researchers throughout the Mountain West. The importance of these forests for wildlife, watershed, esthetic, timber, and associated resource values is being increasingly recognized. Information already available on the basic ecology of these forests helps illustrate the complex interactions of mammals, birds, and other biological and physical phenomena—it also points out the need for much more information. The emerging importance of these forests will hopefully prompt accelerated research that helps fill knowledge gaps about these subalpine forest ecosystems and ultimately show how they can best be managed. These subalpine forests truly need increased silvicultural attention.

AUTECOLOGY OF WHITEBARK PINE: CLUSTER AND MICROSITE CHARACTERISTICS

Sharren K. Sund, Diana Tomback, and Lyn Hoffmann

In 1961, over 11,000 ha of subalpine forest were destroyed in the Sleeping Child Burn (Sapphire Range, Bitterroot National Forest, western Montana). Our 1987 study of whitebark pine (*Pinus albicaulis*) regeneration in the burn produced data on tree clusters and microsite characteristics. Three parallel series of plots (total number of plots = 63) were sampled along a 3.5-km, east-west ridge from the whitebark pine seed source in the adjacent forest to the northern center of the burn. Each plot series represented a different aspect: north, south, or ridge (west).

Sharren K. Sund is Research Associate, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523; Diana Tomback is Associate Professor, Department of Biology, University of Colorado at Denver, Denver, CO 80204; Lyn Hoffmann is Graduate Student, Department of Range Science, Colorado State University, Fort Collins, CO 80523.

Analyses of tree cluster sizes (number of individual trees/site) showed whitebark pine clusters on the south plot series to be significantly smaller than clusters on north or ridge plot series. Cluster sizes ranged from one to eight trees; as cluster size increased, percentage of clusters in each size category decreased. In virtually all clusters no tree stems were fused at the base, indicating that each member of a cluster appeared to be a distinct individual. Ages of individual trees within a cluster were the same or similar, usually differing by only 1 or 2 years, but in no case more than 4 years. Age ranges were nearly identical for the three plot series, but trees on the north series had a slightly lower mean.

Frequencies of plant species growing near whitebark pine clusters indicated similarities between aspects, with ridge microsites intermediate between north and south. Three plant species (*Vaccinium scoparium, Carex rossii,* and *Polytrichum*) accounted for the majority of microsite occurrences. Distinct differences were noted between whitebark pine microsite vegetation and characteristic plot series vegetation. "Objects" ranging from small wood pieces to rocks and standing snags were found on 80 percent of whitebark pine microsites.

EFFECTS OF TRAMPLING ON THE UNDERSTORIES OF WHITEBARK PINE FORESTS

T. Weaver and D. Dale

Pinus albicaulis understories are often a low carpet of *Vaccinium scoparium* or graminoids. In 1973 the impact of hikers, motorcycles, and horse trampling on such vegetation was compared experimentally by periodically measuring the depth, width, vegetational cover, and soil bulk density of trails traversed by each trampler (Weaver and Dale 1978). On level ground, damage increased from hiker to cycle to horse, apparently in proportion to the pressures applied. Going up a 25 percent slope, damage increased from hiker to horse to cycle, probably because the cycle tended to "spin out." Going down a 25 percent slope, damage increased from cycle to hiker to horse, probably because hikers and horses tend to "dig their heels in" rather than rolling. Adaptations leading to trampling resistance include flexibility, prostrate life form, and a life cycle completed out of the trampling season (Dale and Weaver 1974; Weaver and others, this proceedings).

Recovery from trampling damage is more rapid in meadow than forest vegetation. The experimentally trampled areas in meadow vegetation were quickly revegetated and almost impossible to distinguish from untrampled areas after 5 years (Weaver and others 1979). Despite lack of subsequent trampling, trampled areas in the *Pinus albicaulis-Vaccinium scoparium* forest were easily distinguished after 5 years (Weaver and others 1979). After 15 years, forest areas traversed 1,000 times on both level and sloping sites still have markedly higher soil bulk densities than less trampled areas and a lack of understory plant growth. One thousand traverse trails are clearly visible, 500 traverse trails are generally visible, and 100 traverse trails are very faint. Trampling effects may persist under forest conditions both because of greater soil stability (for example, less annelid, gopher, and frost churning) and because of overstory competition for resources (light, water, and nutrients) needed for understory plant recovery.

REFERENCES

Dale, D.; Weaver, T. 1974. Trampling effects on vegetation of the trail corridors of northern Rocky Mountain forests. Journal of Applied Ecology. 11: 767-772.

Weaver, T.; Dale, D. 1978. Trampling effects of hikers, motorcycles and horses in meadows and forests. Journal of Applied Ecology. 15: 451-457.

Weaver, T.; Hartley, E.; Dale, D. 1979. The relation of trail condition to use, vegetation, user, slope, season, and time. In: Ittner, R., ed. Recreational impact of wildlands. No. R-6-001-1979. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.

T. Weaver is Plant Ecologist, Department of Biology, Montana State University, Bozeman, MT 59717; D. Dale is Head, Department of Forestry, Salish-Kootenai College, Pablo, MT 59855.

REFERENCE GUIDE TO WHITEBARK PINE

Ward W. McCaughey
T. Weaver

The purpose of this guide is to provide an easy access to literature about whitebark pine (*Pinus albicaulis*) for those managers and researchers who are concerned with this species. Because of the uniqueness of the species and the lack of concentrated research programs in the past, documents about whitebark pine are found in a wide variety of places, including some rather obscure sources. We assembled this guide to help those needing access to whitebark pine information.

This document references all the literature we could find specific to whitebark pine. Biological Abstracts from 1927 to 1988 was our primary source of references; therefore, bioabstract index numbers are provided to give the user easy access to the author's own annotation. Other papers listed in Forestry Abstracts and Agricola were added. The papers included in this symposium proceedings are not listed here.

Anon. 1946. Report on American big trees. American Forestry Association.

Anon. 1951. Canadian woods (their properties and uses). Ottawa, ON: Forestry Branch, Forest Products Division. 367 p.

Anon. 1961. Native trees of Canada. Bull. 61. Ottawa, ON: Canada Department of Forestry. 291 p.

Achuff, P. L. 1989. Old-growth forests of the Canadian Rocky Mountain National Parks. Natural Areas Journal. 9(1): 12-26.

Agee, J. K.; Kertis, J. 1987. Forest types of the North Cascades National Park Service complex, Washington USA. Canadian Journal of Botany. 65(7): 1520-1530. [84086059]

American Forestry Association. 1986. National register of big trees. American Forests. 92(4): 21-52.

Amman, G. D. 1982. Characteristics of mountain pine beetles reared in four pine hosts. Environmental Entomology. 11(3): 590-593. [75017520]

Anderson, A. B.; Rifer, K.; Wong, A. 1969. Monoterpenes, fatty, and resin acids of *Pinus edulis* and *Pinus albicaulis*. Phytochemistry. 8(10): 1999-2001. [51039962]

Angove, K.; Bancroft, B. 1983. A guide to some common plants of the southern interior of British Columbia. Land Manage. Handb. 7. Victoria, BC: British Columbia Ministry of Forests. 225 p.

Armstrong, J. K.; Williams, K.; Huenneke, L. F.; Mooney, H. A. 1988. Topographic position effects on growth depression of California Sierra Nevada pines during the 1982-83 El Nino. Arctic and Alpine Research. 20(3): 352-357. [85101211]

Arno, S. F. 1966. Interpreting the timberline: an aid to help park naturalists to acquaint visitors with the subalpine-alpine ecotone of western North America. Missoula, MT: University of Montana. 206 p. Thesis.

Arno, S. F. 1970. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Missoula, MT: University of Montana. 264 p. Dissertation.

Arno, S. F. 1976. The historical role of fire on the Bitterroot National Forest. Res. Pap. INT-187. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 29 p.

Arno, S. F. 1980. Forest fire history in the Northern Rockies. Journal of Forestry. 78: 460-465.

Arno, S. F. 1981. [Unpublished observations]. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Fire Sciences Laboratory.

Arno, S. 1986. Whitebark pine cone crops—a diminishing source of wildlife food? Western Journal of Applied Forestry. 1(3): 92-94.

Arno, S. F.; Habeck, J. R. 1972. Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. Ecological Monographs. 42: 417-450.

Arno, S. F.; Hammerly, R. 1984. Timberline—mountain and arctic forest frontiers. Seattle, WA: The Mountaineers. 304 p.

Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Arno, S. F.; Petersen, T. D. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. Res. Pap. INT-301. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 8 p.

Ayres, H. B. 1900a. The Flathead Forest reserve. U.S. Geological Survey, 20th Annual Report. V: 245-316.

Ayres, H. B. 1900b. Lewis and Clark Forest reserve, Montana. U.S. Geological Survey, 21st Annual Report. V: 27-80.

Axelrod, D. I. 1986. Cenozoic history of some western American pines. Annals of the Missouri Botanical Gardens. 73(3): 565-641. [32114083]

Ward W. McCaughey is Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Bozeman, MT 59717. T. Weaver is Plant Ecologist, Department of Biology, Montana State University, Bozeman, MT 59717.

Bagnell, C. R., Jr. 1975. Species distinction among pollen grains of *Abies, Picea,* and *Pinus* in the Rocky Mountain area (a scanning electron microscope study). Review of Palaeobotany and Palynology. 19(3): 203-220. [61059061]

Baig, M. N. 1972. Ecology of timberline vegetation in the Rocky Mountains of Alberta. Calgary, AB: University of Calgary. 446 p. Dissertation.

Bailey, D. K. 1975. *Pinus albicaulis*. Curtis's Botanical Magazine. 180(111): 140-147.

Bailey, H. E.; Bailey, V. L. 1941. Forests and trees of the western national parks. Conserv. Bull. 6. Washington, DC: U.S. Department of the Interior. 129 p.

Baker, B. H.; Amman, G. D.; Trostle, G. C. 1971. Does the mountain pine beetle change hosts in mixed lodgepole and whitebark pine stands? Res. Note INT-151. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 1-7. [08052097]

Baker, F. S. 1944. Mountain climates of the western United States. Ecological Monographs. 14(2): 233-254.

Baker, F. S. 1949. A revised tolerance table. Journal of Forestry. 47(3): 179-182.

Baker, R. G. 1970. Pollen sequence from late quaternary sediments in Yellowstone Park. Science. 168(3938): 1449-1450. [52003869]

Baker, R. G. 1976. Late quaternary vegetation history of the Yellowstone Lake basin, Wyoming. Prof. Pap. 729-E. U.S. Geological Survey.

Baker, R. G. 1981. Interglacial and interstadial environments in Yellowstone National Park. In: Mahaney, W. C., ed. Quaternary paleoclimate. Norwich, England: Geo Books: 361-375.

Baker, R. G. 1983. Holocene vegetational history of the Western United States. In: Wright, H. E., Jr., ed. Late-quaternary environments of the United States. Vol. 2. The Holocene. Minneapolis, MN: University of Minnesota Press: 109-127.

Baker, R. G. 1986. Sangamonian(?) and Wisconsinan paleoenvironments in Yellowstone National Park. Bull. 97. Geological Society of America: 717-736.

Baker, R. G.; Richmond, G. M. 1978. Geology, palynology, and climatic significance of two pre-Pinedale Lake Sediment sequences in and near Yellowstone National Park. Quaternary Research. 10: 226-240.

Baranyay, J. A. 1964. Province of Alberta: forest insect and disease survey: forest disease condition. In: Annual report, Forest Insect and Disease Survey for Entomology and Pathology Branch, Canada: 102-105.

Barnosky, C. W.; Anderson, P. M.; Bartlein, P. J. 1987. The northwestern U.S. during deglaciation; vegetational history and paleoclimatic implications. In: The geology of North America. Vol. K-3. North American and adjacent oceans during the last deglaciation. Boulder, CO: Geological Society of America: 289-321.

Beaudoin, A. B.; King, R. H. [Unpublished manuscript]. Late-quaternary vegetation history of Wilcox Pass, Jasper National Park, Alberta. 31 p.

Bedwell, J. L.; Childs, T. W. 1943. Susceptibility of whitebark pine to blister rust in the Pacific Northwest. Journal of Forestry. 41: 904-912.

Berg, M. J.; Carlson, C. E.; Lounsbury, L. P.; Dooling, O. J. 1975. [Unpublished report]. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, State and Private Forestry. 15 p.

Bingham, R. T. 1972. Taxonomy, crossability, and relative blister rust resistance of 5-needled white pines. In: Biology of rust resistance in forest trees. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture, Forest Service: 271-280.

Blanchard, B. M. 1980. Grizzly bear-timber relationships in the Yellowstone area, 1978-1979. In: Yellowstone grizzly bear investigations. Annual Report 1978-79. U.S. Department of the Interior, National Park Service: 76-84.

Blanchard, B. M. 1983. Grizzly bear-habitat relationships in the Yellowstone area. International Conference on Bear Research and Management. Madison, WI: International Bear Association. 5: 118-123.

Blankenship, J. 1905. Native economic plants of Montana. Bull. 56. Bozeman, MT: Montana Agricultural Experiment Station: 1-388.

Borlaug, N. E. 1971. Moderator's summary: a cereal breeder and ex-forester's evaluation of the progress and problems involved in breeding rust resistant forest trees. In: Biology of rust resistance in forest trees. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture, Forest Service: 615-642.

Bourchier, R. J. 1954. Forest disease survey: prairie provinces, Alberta and Rocky Mountain national parks. In: Annual report, Canadian Department of Agriculture, Science Service, Forest Biology Division, Forest Insect and Disease Survey: 128-135.

Branson, B. A. 1987. Timberline sentinel. American Forests. 93(7): 55-56.

Bratkovich, A. A. 1986. Grizzly bear habitat components associated with past logging practices on the Libby Ranger District, Kootenai National Forest. In: Contreras, G. P.; Evans, K. E., compilers. Proceedings—grizzly bear habitat symposium; 1985 April 30-May 2. Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 180-184.

Brayshaw, T. C. 1965. Comments on field identification of whitebark and limber pines based upon needle resin canals. Journal of Forestry. 63: 705-706.

Bright, Donald E., Jr. 1968. Three new species of *Pityophthorus* from Canada (Coleoptera: Scolytidae). Canadian Entomologist. 100: 604-608.

Britton, N. L.; Shafer, J. A. 1908. North American trees. American Nature Series Group 1. Classification of nature. New York: Henry Holt. 894 p.

Brown, D. H. 1969. Aerial application of antibiotic solutions to whitebark pine infected with *Cronartium ribicola Tuberculina maxima*. Plant Disease Reporter. 53(6): 487-489. [50117414]

Brown, D. H.; Dooling, O. J. 1968. Helicopter application of phytoactin antibiotic to whitebark pine: abstract *Cronartium ribicola*. Phytopathology. 58(8): 1045. [05004143]

Brown, J. K. 1978. Weight and density of crowns of Rocky Mountain conifers. Res. Pap. INT-197. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 56 p. [15023042]

Burns, J. E. 1986. Managing political habitat for grizzly bear recovery. In: Contreras, G. P.; Evans, K. E., compilers. Proceedings—grizzly bear habitat symposium; 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 2-13.

Carlson, C. E. 1978. Noneffectiveness of *Ribes* eradication as a control of white pine blister rust in Yellowstone National Park. For. Insect and Dis. Manage. Rep. 78-18. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 6 p.

Carlson, C. E.; Dewey, J. E. 1971. Environmental pollution by fluorides in Flathead National Forest and Glacier National Park. Missoula, MT: U.S. Department of Agriculture, Forest Service, Division of State and Private Forestry, Forest Insect and Disease Branch. 57 p.

Carr, M. E.; Bagby, M. O.; Roth, W. B. 1986. High oil-producing and polyphenol-producing species of the northwest USA. Journal of American Oil Chemists Society. 63(11): 1460-1464. [83042428]

Childs, T. W.; Bedwell, J. L. 1948. Susceptibility of some white pine species to *Cronartium ribicola* in the Pacific Northwest. Journal of Forestry. 46: 595-599.

Childs, T. W.; Bedwell, J. L.; Englerth, G. H. 1938. Blister rust infection on *Pinus albicaulis* in the Northwest. Plant Disease Reporter. 22(8): 139-140.

Ciesla, W. M.; Furniss, M. M. 1975. Idaho's haunted forest. American Forests. 81(8): 32-35.

Clague, J. J.; Mathewes, R. W. 1989. Early Holocene thermal maximum in western North America: new evidence from Castle Peak, British Columbia. Geology. 17: 277-280.

Clausen, J. 1965. Population studies of alpine and subalpine races of conifers and willows in the California High Sierra Nevada. Evolution. 19(1): 56-68.

Cohen, S.; Miller, D. 1978. The big burn—the Northwest's forest fire of 1910. Missoula, MT: Pictorial Histories Publishing Company. 88 p.

Cole, D. N. 1981. Vegetational changes associated with recreational use and fire suppression in the Eagle Cap Wilderness, Oregon: some management implications. Biological Conservation. 20(4): 247-270.

Cole, D. N. 1982. Vegetation of two drainages in Eagle Cap Wilderness, Wallowa Mountains, Oregon. Res. Pap. INT-288. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 42 p.

Coulter, J. M.; Rose, J. N. 1886. Synopsis of North American pines, based upon leaf-anatomy. Botanical Gazette. 11: 256-262.

Craighead, J. J.; Mitchell, J. A. 1982. Grizzly bear. In: Chapman, J. A.; Feldhamer, G. A., eds. Wild mammals of North America. Baltimore, MD: The Johns Hopkins University Press: 515-556.

Craighead, J. J.; Scaggs, G. B.; Sumner, J. S. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Wildlands Inst. Monogr. 1. Missoula, MT: University of Montana. 279 p.

Crane, M. F.; Fischer, W. C. 1986. Fire ecology of the forest habitat types of central Idaho. Gen. Tech. Rep. INT-218. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 86 p.

Critchfield, W. B. 1986. Hybridization and classification of the white pines (*Pinus* section *Strobus*). Taxonomy. 35(4): 647-656.

Critchfield, W. B.; Allenbaugh, G. A. 1969. The distribution of Pinaceae in and near northern Nevada. Madrono. 20: 12-26.

Critchfield, W. B.; Little, E. L. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.

Dallimore, W.; Jackson, A. B. 1948. A handbook of Coniferae including Ginkgoaceae. 3d ed. London: Edward Arnold and Co. 682 p.

Daubenmire, R. 1953. Nutrient content of leaf litter of trees in the Northern Rocky Mountains. Ecology. 34: 786-793.

Daubenmire, R.; Daubenmire, J. B. 1968. Forest vegetation of eastern Washington and northern Idaho. Tech. Bull. 60. Pullman, WA: Washington Agriculture Experiment Station. 104 p.

Davidson, A. T. 1966. White pine blister rust in British Columbia. In: Proceedings, third western white pine blister rust conference. Mimeo. Portland, OR: 9-22.

Day, R. J. 1965. The development and structure of the Rocky Mountain forest. Unpublished Mimeo 65-A-3. Ottawa, ON: Canada Department of Forestry. 19 p.

Day, R. J. 1967. Whitebark pine in the Rocky Mountains of Alberta. Forestry Chronicle. 43: 278-282.

Deitschman, G. H. 1973. Mapping of habitat types throughout a national forest. Gen. Tech. Rep. INT-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 1-14. [10065405]

del Moral, R. 1979. High elevation vegetation of the Enchantment Lakes Basin, Washington. Canadian Journal of Botany. 57(10): 1111-1130.

Despain, D. G. 1983. Nonpyrogenous climax lodgepole pine communities in Yellowstone National Park. Ecology. 64(2): 231-234.

Despain, D. G. 1986. Habitat type and cover type as a base for grizzly bear habitat mapping and evaluation. In: Contreras, G. P.; Evans, K. E., compilers. Proceedings—grizzly bear habitat symposium; 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 230-233.

Detwiler, S. B. 1933. General aspects of the white pine situation. Journal of Forestry. 31: 514-521.

Dimitrov, E. T.; Pazarov, E. 1979. Mathematical models for the dependence of the available wood in a tree trunk on the height of a tree in some local experimental tables for tall tree species. [Bulgarian]. Gorskostop Nauka. 16(2): 23-33. [71066279]

Dooling, O. J. 1974. Evolution of pruning to reduce impact of white pine blister rust on selected areas in Yellowstone National Park. 74-19. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, Division of State and Private Forestry. 5 p.

Dunwiddle, P. W. 1977. Recent tree invasion of subalpine meadows in the Wind River Mountains, Wyoming. Arctic and Alpine Research. 9(4): 393-399.

Eggers, D. E. 1986. Management of whitebark pine as potential grizzly bear habitat. In: Contreras, G. P.; Evans, K. E., compilers. Proceedings—grizzly bear habitat symposium; 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 170-175.

Elias, T. S. 1987. The complete trees of North America. New York: Gramercy Publishing Company. 948 p.

Engelmann, G. 1863. *Pinus albicaulis* Engelm. Transactions of the Academy of St. Louis. 2: 209.

Engelmann, G.; Sargent, Parry. 1882. Notes on western conifers. Botanical Gazette. 7: 4-5.

Ericson, J. E. 1964. Field identification of whitebark and limber pines based on needle resin canals. Journal of Forestry. 62: 576-577.

Ericson, J. E. 1964. Identification of *Pinus flexilis* James and *Pinus albicaulis* Engelm. Proceedings, Montana Academy of Science. 24: 7-10.

Evenden, J. C. 1933. Host selection in relation to the control of bark beetles. Coeur d'Alene, ID: U.S. Department of Agriculture, Entomology, Forest Insect Lab.; unpublished report. 13 p.

Evenden, J. C.; Bedard, W. D.; Struble, G. R. 1943. The mountain pine beetle, an important enemy of western pines. Circ. 664. Washington, DC: U.S. Department of Agriculture. 25 p.

Eversman, S. 1985. Distribution of epiphytic lichens on three species in Yellowstone National Park. In: Annual meeting of the botanical society of America; 1985 August 11-15; Gainesville, FL. American Journal of Botany. 72(6): 793. [29107552]

Eyre, F. H. ed. 1980. Forest cover types of the United States and Canada. Washington, DC: Society of American Foresters. 148 p.

Finley, R. B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. Misc. Publ. 51. In: Contributions in mammalogy. Lawrence, KS: University of Kansas, Museum of Natural History: 233-274.

Fischer, W. C.; Clayton, B. D. 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. Gen. Tech. Rep. INT-141. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 83 p.

Fisher, R. M.; Myres, M. T. 1980. A review of factors influencing extralimital occurrences of Clark's nutcracker *Nucifraga columbiana* in Canada. Canadian Field-Naturalist. 94(1): 43-51. [70021891]

Forcella, F. 1977. Flora, chorology, biomass and productivity of the *Pinus albicaulis-Vaccinium scoparium* association. Bozeman, MT: Montana State University. 99 p. Thesis.

Forcella, F. 1978. Flora and chorology of the *Pinus albicaulis-Vaccinium scoparium* association. Madrono. 25: 139-150. [67021012]

Forcella, F.; Weaver, T. 1980. Food production in the *Pinus albicaulis-Vaccinium scoparium* association. Proceedings, Montana Academy of Sciences. 39: 73-80.

Forcella, F.; Weaver, T. 1977. Biomass and productivity of the subalpine *Pinus albicaulis-Vaccinium scoparium* association in Montana. Vegetatio. 33: 95-106. [65020165]

Franklin, J. F.; Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 417 p.

Funk, A. 1985. Foliar fungi of western trees. Victoria, BC: Canadian Forestry Service, Pacific Forest Research Centre. 159 p.

Furnier, G. R.; Knowles, P.; Aleksiuk, M. A.; Dancik, B. P. 1986. Inheritance and linkage of allozymes in seed tissue of whitebark pine *Pinus albicaulis*. Canadian Journal of Genetics and Cytology. 28(4): 601-604. [82102338]

Furnier, G. R.; Knowles, P.; Clyde, M. A.; Dancik, B. P. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution. 41(3): 607-612. [84046257]

Furniss, R. L.; Carolin, V. M. 1977. Western forest insects. Misc. Publ. 1339. Washington, DC: U.S. Department of Agriculture, Forest Service. 654 p.

Gennett, J. A.; Baker, R. G. 1986. A late quaternary pollen sequence from Blacktail Pond, Yellowstone National Park, Wyoming USA. Palynology. 10(0): 61-72. [84038771]

Ghouse, A. K. M. 1973. Variation in transfusion tissue in pines. Bulletin of the Torrey Botanical Club. 100(3): 151-152. [57035802]

Gifford, D. J. 1988. An electrophoretic analysis of the seed proteins from *Pinus monticola* and eight other species of pine. Canadian Journal of Botany. 66(9): 1808-1812.

Giuntoli, M.; Mewaldt, L. R. 1978. Stomach contents of Clark's nutcracker in western Montana. Auk. 95: 595-598.

Goward, T. 1985. *Ahtiana*-new genus in the Parmeliaceae. Bryologist. 88(4): 367-371. [83021077]

Graber, D. M.; White, M. 1983. Black bear food habits in Yosemite National Park. International Conference on Bear Research and Management. 5: 1-10.

Griffin, J. B.; Critchfield, W. B. 1972. The distribution of forest trees in California. Res. Pap. PSW-82. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 114 p.

Grinnell, J.; Storer, T. I. 1924. Animal life in the Yosemite. Berkeley, CA: University of California Press. 752 p.

Gruell, G. E. 1980. Fire's influence on wildlife habitat on the Bridger-Teton National Forest, Wyoming. Volume 1—photographic record and analysis. Res. Pap. INT-235. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 207 p.

Gynn, J. C.; Chapman, C. M. 1948. Blister rust control, Glacier National Park, 1948. In: White pine blister rust control in the Northwest Region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control: 80-85.

Gynn, J. C.; Chapman, C. M. 1949. Spread of white pine blister rust. In: White pine blister rust control in the Northwest Region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control: 87-88.

Gynn, J. C.; Chapman, C. M. 1950. Blister rust control, Yellowstone National Park, 1950. In: White pine blister rust control in the Northwest Region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control: 92-94.

Gynn, J. C.; Chapman, C. M. 1951. Blister rust control, Mount Rainier National Park, 1951. In: White pine blister rust control in the Northwest Region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control: 64-66.

Gynn, J. C.; Chapman, C. M. 1951. Blister rust control, Yellowstone National Park, 1951. In: White pine blister rust control in the Northwest Region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control: 70-73.

Gynn, J. C.; Chapman, C. M. 1951. Spread of white pine blister rust, scouting in Montana, Wyoming, Idaho, Colorado, 1951. In: White pine blister rust control in the Northwest Region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control: 15-16.

Gynn, J. C.; Chapman, C. M. 1952. Blister rust control, Glacier National Park, 1952. In: White pine blister rust control in the Northwest Region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control: 57-60.

Gynn, J. C.; Chapman, C. M. 1952. Blister rust control, Mount Rainier National Park, 1952. In: White pine blister rust control in the Northwest Region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control: 54-56.

Gynn, J. C.; Chapman, C. M. 1954. White pine blister rust control, national parks. Annual Report. White pine blister rust control. Missoula, MT: U.S. Department of Agriculture, Forest Service, Region One: 41-53.

Habeck, J. R. 1969. A gradient analysis of a timberline zone at Logan Pass, Glacier Park, Montana. Northwest Science. 43: 65-73.

Hagle, S. K.; Tunnock, S.; Gibson, K. E.; Gilligan, C. J. 1987. Field guide to diseases and insect pests of Idaho and Montana forests. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, State and Private Forestry. 123 p.

Hahn, G. G. 1931. Pathological and mycological notes on fungi observed on white pine. In: Proceedings, 17th annual blister rust conference; 1931 October 29-31; Lakeville, CT: 49-51.

Hahn, G. G.; Ayers, T. T. 1934. *Dasyscyphae* on conifers in North America. III. *Dasyscypha pini*. Mycologia. 26: 479-502.

Hall, J. P. 1977. Survival and growth of exotic *Pinus* species in central Newfoundland ten years after planting. Inf. Rep. N-X-154. Newfoundland Forest Research Centre, Canada. 12 p.

Halverson, C. H. 1985. Influence of vertebrates on conifer seed production. In: Shearer, Raymond C., compiler. Proceedings—conifer tree seed in the Inland Mountain West Symposium. 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 201-222.

Hammon, F. M. 1983. Food habits of black bears in the Greys River drainage, Wyoming. Laramie, WY: University of Wyoming and Wyoming Game and Fish Department. 50 p.

Harlow, W. M. 1931. The identification of the pines of the United States, native and introduced by needle structure. Tech. Pub. 32. Syracuse, NY: New York State College of Forestry. 21 p.

Harlow, W. M.; Harrar, E. S. 1958. Textbook of dendrology. New York: McGraw-Hill. 555 p.

Harlow, W. M.; Harrar, E. S.; White, F. M. 1979. Textbook of dendrology. 6th ed. New York: McGraw-Hill. 510 p.

Harvey, A. E.; Graham, S. O.; Becker, L. D.; Brown, D. H. 1966. Translocation and persistance of the antibiotic phytoactin in *Pinus albicaulis*. Phytopathology. 62: 148.

Harvey, A. E.; Grasham, J. L. 1970. Susceptibility of cultured tissues from *Pinus albicaulis*, *Pinus flexilis*, and *Pseudotsuga menziesii* to invasion by *Cronartium ribicola*. Phytopathology. 60(11): 1534. [07015150]

Hawksworth, F. G.; Wiens, D. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). Agric. Handb. 401. Washington, DC: U.S. Department of Agriculture, Forest Service. 234 p.

Helgath, S. F. 1975. Trail deterioration in the Selway-Bitterroot Wilderness. Res. Note INT-193. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 15 p.

Heller, H. C. 1971. Altitudinal zonation of chipmunks (*Eutamias*): interspecific aggression. Ecology. 52(2): 312-319.

Hendrickson, W. H.; Lotan, J. E. 1971. Identification of whitebark and limber pines based on needle resin ducts. Journal of Forestry. 69(9): 584. [08012290]

Hepting, George H. 1971. Diseases of forest and shade trees of the United States. Agric. Handb. 386. Washington, DC: U.S. Department of Agriculture, Forest Service: 288-290.

Hicks, L. L. 1985. Multiple-use on western private industrial timberlands. In: Sabol, K., ed. Transactions of the fiftieth American wildlife and natural resources conference: taking stock: resource management in the 50th year; 1985 March 15-20; Washington, DC. Wildlife Management Institute: 211-214. [30074706]

Hillis, M. 1986. Enhancing grizzly bear habitat through timber harvesting. In: Contreras, G. P.; Evans, K. E., compilers. Proceedings—grizzly bear habitat symposium; 1985 April 30-May 2; Missoula, MT. Gen. Tech.

Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 176-179.

Hiratsuka, Y.; Funk, A. 1976. Additional records of *Gremmeniella abietina* in western Canada. Plant Disease Reporter. 60(7): 631.

Hiratsuka, Y.; Maruyama, P. J. 1976. *Castilleja miniata*, a new alternate host of *Cronartium ribicola*. Plant Disease Reporter. 60(3): 241. [62016479]

Hitchcock, C. L.; Cronquist, A.; Ownbey, M.; Thompson, J. W. 1969. Vascular plants of the Pacific Northwest. Part 1. Seattle, WA: University of Washington Press. 914 p.

Hobbs, S. D.; Partridge, A. D. 1979. Wood decays, root rots, and stand composition along an elevation gradient. Forest Science. 25(1): 31-42.

Hoff, R. J. 1980. [Personal files regarding blister rust resistance of whitebark pine]. U.S. Department of Agriculture, Forest Service, Forestry Sciences Laboratory, Moscow, ID.

Hoff, R. J.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology. 10: 307-316. [71012685]

Hoff, R. J.; McDonald, G. I. 1977. Differential susceptibility of 19 white pine species to woolly aphid *Pineus coloradensis*. Res. Note INT-225. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 6 p. [14011004]

Holland, S. S. 1964. Landforms of British Columbia—a physiographic outline. Bull. 48. Victoria, BC: British Columbia Department of Mine and Petroleum Resources. 138 p.

Holland, W. D.; Coen, G. M., eds. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol. 1: Summary. Publ. M-83-2. Vol. 2: Soil and vegetation resources. Publ. SS-82-44. Alberta Institute of Pedology.

Holmes, G. D.; Kuszewicz, G. 1958. The storage of seed of temperate forest tree species. Part II. Forestry Abstracts. 19: 455-476.

Holzer, Kurt. 1975. Genetics of *Pinus cembra*. Annales Forestales. 6(5): 139-158.

Hopkins, W. E. 1979. Plant associations of the Fremont National Forest. Publ. Ecol. 79-004. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 106 p.

Hottes, F. C. 1958. A new species of *Essigella* from Oregon (Aphidae). Proceedings; Biology Society, Washington. 71: 155-156. [35605]

Hunt, R. S. 1981. Pine needle casts and blights in the Pacific Region. For. Pest Leafl. 43. Victoria, BC: Canadian Forestry Service, Pacific Forest Research Centre. 7 p.

Hunt, R. S.; Ziller, W. G. 1978. Host-genus keys to the Hypodermataceae of conifer leaves. Mycotaxon. 6: 481-496.

Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201. [75079057]

Jackson, M. T.; Faller, A. 1973. Structural analysis and dynamics of the plant communities of Wizard Island, Crater Lake National Park. Ecological Monographs. 43: 441-461. [57036499]

Jacobs, J. 1989. Temperature and light effects on seedling performance of *Pinus albicaulis*. Bozeman, MT: Montana State University. 39 p. Thesis.

Johnson, L. 1981. [Unpublished observation]. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwestern Region.

Jonkel, C. J. 1967. The ecology, population dynamics, and management of the black bear in the spruce-fir forests of northwestern Montana. Vancouver, BC: University of British Columbia. 170 p. Dissertation.

Jonkel, C. J.; Cowan, I. M. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27. 55 p.

Kalgutkar, R. M. 1973. Observations on identification of *Pinus albicaulis* Engelm. and *Pinus flexilis* James based on needle resin canals. Canadian Journal of Forest Research. 3(4): 580-582. [57053286]

Kalgutkar, R. M.; Bird, C. D. 1969. Lichens found on *Larix lyallii* and *Pinus albicaulis* in southwestern Alberta, Canada. Canadian Journal of Botany. 47(5): 627-648. [51016293]

Kasper, J. B.; Szabo, T. 1970. The physical and mechanical properties of whitebark pine. Forestry Chronicle. 46: 315-316. [52013876]

Keane, R. E.; Arno, S. F.; Brown, J. K. 1989. FIRESUM—an ecological process model for fire succession in western conifer forests. Gen. Tech. Rep. INT-266. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 76 p.

Keane, R. E.; Arno, S. F.; Brown, J. K.; Tomback, D. F. [In preparation]. Modeling stand dynamics in whitebark pine forests. [Manuscript submitted to Ecological Modelling].

Kearney, M. S.; Luckman, B. H. 1983. Postglacial vegetation history of Tonquin Pass, British Columbia. Canadian Journal of Earth Sciences. 20: 776-786.

Keenan, F. J.; Glavicic, M. R.; Swindle, P. W.; Cooper, P. A. 1970. Mechanical properties of whitebark pine. Forestry Chronicle. 46(4): 322-325. [52013885]

Kellogg, R. M.; Rowe, S.; Koeppen, R. C.; Miller, R. B. 1982. Identification of the wood of the soft pines of western North America. IAWA Bulletin. 3(2): 95-101. [75023914]

Kendall, K. C. 1980a. Bear-squirrel-pine nut interaction: 1978-1979. In: Yellowstone grizzly bear investigations. Annual Report 1978-79. Bozeman, MT: U.S. Department of the Interior, National Park Service: 51-60.

Kendall, K. C. 1980b. Food habits of Yellowstone grizzly bears: 1978-1979. In: Yellowstone grizzly bear investigations. Annual Report 1978-79. Bozeman, MT: U.S. Department of the Interior, National Park Service: 24-34.

Kendall, K. C. 1981. Bear use of pine nuts. Bozeman, MT: Montana State University. 27 p. Thesis.

Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. International Conference on Bear Research and Management. Madison, WI: International Bears Association. 5: 166-173.

Kilgore, B. N. 1971. The role of fire in managing red fir forests. In: Transactions of the 36th North American Wildland and Natural Resources Conference; Symposium. Washington, DC: Wildlife Management Institute: 405-416. [08019271]

Klikoff, L. G. 1965. Microenvironmental influence on vegetational pattern near timberline in the central Sierra Nevada. Ecological Monographs. 35(2): 187-211.

Klock, G. O.; Helvey, J. D. 1976. Soil water trends following wildfire on the Entiat Experimental Forest. Proceedings: Tall Timbers Fire Ecology Conference. 15: 193-200. [13045746]

Knight, R. R.; Basile, J.; Greer, K.; Judd, S.; Oldenburg, L.; Roop, L. 1977. Yellowstone grizzly bear investigations. Annual report of the interagency study team, 1977. Bozeman, MT: U.S. Department of the Interior, National Park Service. 107 p.

Knight, R. R.; Blanchard, B. M. 1982. Yellowstone grizzly bear investigations. Report of the interagency study team, 1982. Bozeman, MT: U.S. Department of the Interior, National Park Service. 45 p.

Knight, R. R.; Blanchard, B. M.; Kendall, K. C. 1980. Yellowstone grizzly bear investigations. Report of the interagency study team, 1980. Bozeman, MT: U.S. Department of the Interior, National Park Service. 55 p.

Knight, R. R.; Blanchard, B. M.; Kendall, K. C. 1981. Yellowstone grizzly bear investigations. Report of the interagency study team, 1981. Bozeman, MT: U.S. Department of the Interior, National Park Service. 70 p.

Knight, R. R.; Blanchard, B. M.; Kendall, K. C.; Oldenburg, L., eds. 1980. Yellowstone grizzly bear investigations. Report of the interagency study team, 1978 and 1979. Bozeman, MT: U.S. Department of the Interior, National Park Service. 91 p.

Knight, R. R.; Blanchard, B. M.; Mattson, D. J. 1984. Yellowstone grizzly bear investigations. Report of the interagency study team, 1983 and 1984. Bozeman, MT: U.S. Department of the Interior, National Park Service. 82 p.

Knight, R. R.; Blanchard, B. M.; Mattson, D. J. 1985. Yellowstone grizzly bear investigations. Report of the interagency study team, 1985. Bozeman, MT: U.S. Department of the Interior, National Park Service. 58 p.

Knight, R. R.; Blanchard, B. M.; Mattson, D. J. 1986. Yellowstone grizzly bear investigations. Report of the interagency study team, 1986. Bozeman, MT: U.S. Department of the Interior, National Park Service. 82 p.

Knight, R. R.; Blanchard, B. M.; Mattson, D. J. 1987. Yellowstone grizzly bear investigations. Report of the interagency study team, 1987. Bozeman, MT: U.S. Department of the Interior, National Park Service. 80 p.

Knutson, D. M.; Tinnin, R. O. 1981. *Arceuthobium cyanocarpum* (limber pine dwarf mistletoe) in Oregon. Plant Disease. 65(5): 445. [72069355]

Krajina, V. J. 1965. Ecology of western North America. Vol. 1. Vancouver, BC: University of British Columbia. 112 p.

Krajina, V. J. 1969. Ecology of forest trees in British Columbia. In: Ecology of western North America. Vol. 2, No. 1. Vancouver, BC: University of British Columbia. 147 p.

Krajina, V. J.; Klinka, K.; Worrall, J. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Victoria, BC: Faculty of Forestry, University of British Columbia. 131 p.

Krebill, Richard G. 1986. Whitebark pine and the 4 B's: blister rust, bark beetles, burning, and bears. In: Proceedings, 34th Annual Western International Forest Disease Work Conference; 1986 September 9-12; Juneau, AK. 31 p.

Krugman, S. L.; Jenkinson, J. L. 1974. *Pinus* L. Pine. In: Schopmeyer, C. S., ed. Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture, Forest Service: 598-638.

Kuprianova, L. A.; Litvintseva, M. V. 1974. The group *cembra* of the genus *Pinus,* its volume and relationships according to palynological data. Bot. ZH (Leningr). 59(5): 630-644. [60047544]

Lachmund, H. G. 1926. Western blister rust investigations, 1926. In: Proceedings, western white pine blister rust conference. Mimeo. Portland, OR: 12-19.

Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: Sixth North American forest biology workshop proceedings; 1980 August; Edmonton, AB. Edmonton, AB: University of Alberta: 14-48.

Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research. 12(2): 391-402. [75017230]

Lanner, R. M. 1985. Made for each other: Clark's nutcracker and whitebark pine. California Academy of Sciences. 38(3): 31-35.

Lanner, R. M. 1988. Dependence of Great Basin bristlecone pine on Clark's nutcracker for regeneration at high elevations. Arctic and Alpine Research. 20(3): 358-362.

Lanner, R. M.; Vander Wall, S. B. 1980. Dispersal of limber pine seed by Clark's nutcracker. Journal of Forestry. 78(10): 637-639.

Layser, E. 1980. Flora of Pend Oreille County, Washington. Pullman, WA: Washington State University, Cooperative Extension. 144 p.

Leadem, C. L. 1985. Seed dormancy in three *Pinus* species of the Inland Mountain West. In: Shearer, R. C., compiler. Proceedings—conifer tree seed in the Inland Mountain West; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 117-124.

Leiberg, J. B. 1897. General report on a botanical survey of the Coeur d'Alene Mountains in Idaho during the summer of 1895. U.S. National Museum Contribution. Washington, DC: U.S. National Herbarium. 5: 5-85.

Leiberg, J. B. 1900a. Range and Ashland Forest reserves and adjacent regions. U.S. Geological survey 21st Annual Report. V: 219-498.

Leiberg, J. B. 1900b. Sandpoint quadrangle, Idaho. U.S. Geological survey 21st Annual Report. V: 583-595.

Leiberg, J. B. 1904a. Forest conditions in the Absaroka Division of the Yellowstone Forest Reserve, Montana, and the Livingston and Big Timber quadrangles. U.S. Geological Survey Professional Paper 29. 148 p.

Leiberg, J. B. 1904b. Forest conditions in the Little Belt Mountains Forest Reserve, Montana, and the Little Belt Mountains quadrangle. U.S. Geological Survey Professional Paper 30. 75 p.

Lepper, M. G. 1974. *Pinus flexilis* James and its environmental relationships. Davis, CA: University of California. 197 p. Dissertation.

Lindstedt, Gosta. 1950. Constituents of pine heartwood. XXIII. Isolation of dehydropinosylvin monomethyl ether from the heartwood of *Pinus albicaulis* Engelm. Acta Chemica Scandinavica. 4(8): 1246-1249. [29166]

Linhart, Y. B.; Tomback, D. F. 1985. Seed dispersal by nutcrackers *Nucifraga columbiana* causes multi-trunk growth form in pines. Oecologia (Berl.). 67(1): 107-110. [81002392]

Little, E. L., Jr. 1971. Atlas of United States trees—volume 1. Conifers and important hardwoods. Misc. Publ. 1146. Washington, DC: U.S. Department of Agriculture, Forest Service. 9 p. + maps.

Little, E. L., Jr.; Critchfield, W. B. 1969. Subdivisions of the genus *Pinus* (pines). Misc. Publ. 1144. Washington, DC: U.S. Department of Agriculture, Forest Service. 51 p.

Litvintseva, M. V. 1974. Characteristics of needle parenchymal cell structure in species of the group *cembra* genus *Pinus*. Bot. ZH (Leningr). 59(10): 1501-1505. [60012517]

Lohman, M. L.; Cash, E. K. 1940. *Atropellis* species from pine cankers in the United States. Journal of the Washington Academy of Science. 30: 255-262.

Loope, L. L.; Gruell, G. E. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. Quaternary Research. 3: 425-443.

Luckman, B. H.; Jozsa, L. A.; Murphy, P. J. 1984. Living seven-hundred-year-old *Picea engelmannii* and *Pinus albicaulis* in the Canadian Rockies. Arctic and Alpine Research. 16(4): 419-422. [79066523]

Luckman, B. H.; Kearney, M. S. 1986. Reconstruction of Holocene changes in alpine vegetation and climate in the Miligne Range, Jasper National Park, Alberta. Quaternary Research. 26: 244-261.

Lueck, D. 1980. Ecology of *Pinus albicaulis* on Bachelor Butte, Oregon. Corvallis, OR: Oregon State University. 90 p. Thesis.

Mace, R. D.; Jonkel, C. J. 1986. Local food habits of the grizzly bear in Montana. International Conference on Bear Research and Management; Grand Canyon, AZ: 6: 105-110.

Mack, R. N. 1971. Pollen size variation in some western North American pines as related to fossil pollen identification. Northwest Science. 45(4): 257-269. [53062224]

Mack, R. N.; Bryant, V. M., Jr.; Pell, W. 1978. Modern forest pollen spectra from eastern Washington and northern Idaho. Botanical Gazette. 139(2): 249-255. [66072551]

Mack, R. N.; Rutter, N. W.; Bryant, V. M, Jr.; Valastro, S. 1978. Reexamination of postglacial vegetation history in northern Idaho: Hager Pond, Bonner County. Quaternary Research. 10(2): 241-255. [67036774]

Malouf, C. 1969. The coniferous forests and their uses in the Northern Rocky Mountains through 9,000 years of prehistory. In: Coniferous forests of the Northern Rocky Mountains: Proceedings; 1968. Missoula, MT: University of Montana, Center for Natural Resources: 271-280.

Marcum, C. L. 1979. Summer-fall food habits and forage preferences of a Western Montana elk herd. In: Boyce, M. S.; Hayden-Wing, L. D., eds. North American elk: ecology, behavior, and management. Laramie, WY: University of Wyoming: 54-62.

Martinson, A. H.; Basko, W. J. 1988. Soil survey of the Flathead National Forest area, Montana [draft]. Kalispell, MT: U.S. Department of Agriculture, Forest Service.

Mathewes, R. W. 1988. Higher postglacial alpine timberlines in the eastern coast ranges of British Columbia. Botany British Columbia Working Group Newsletter. 3: 5. Abstract.

Mathewes, R. W.; Clague, J. J. 1989. Early Holocene thermal maximum: new evidence from Castle Peak, British Columbia. Ottawa, ON: Canadian Committee on Climatic Fluctuations and Man. Abstract.

Mathiasen, R. L.; Hawksworth, F. G. 1988. Dwarf mistletoes on western white pine and whitebark pine in northern California and southern Oregon. Forest Science. 34(2): 429-440. [86073913]

Mattson, D. J.; Reinhart, D. P. 1987. Grizzly bear, red squirrels, and whitebark pine: third year progress report. In: Yellowstone grizzly bear investigations. Report of the Interagency Study Team, 1987. Bozeman, MT: U.S. Department of the Interior, National Park Service: 36-45.

McAvoy, B. 1931. Ecological survey of the Bella Coola region. Botanical Gazette. 92: 141-171.

McCambridge, W. F.; Trostle, G. C. 1970. The mountain pine beetle. For. Pest Leafl. 2. Washington, DC: U.S. Department of Agriculture, Forest Service. 6 p.

McCaughey, W. W.; Schmidt, W. C.; Shearer, R. C. 1986. Seed-dispersal characteristics of conifers in the Inland Mountain West. In: Shearer, Raymond C., compiler. Proceedings—conifer tree seed in the Inland Mountain West; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 50-62.

McGregor, M. D.; Cole, D. M., eds. 1985. Integrating management strategies for the mountain pine beetle with multiple-resource management of lodgepole pine forests. Gen. Tech. Rep. INT-174. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 68 p.

McHugh, P. 1974. A numerical taxonomic study of some North American *Pinus* spp. Proceedings; Indiana Academy of Science. 83: 397. [11076223]

McKey, D. 1975. The ecology of coevolved seed dispersal systems. In: Gilbert, L. E.; Raven, P. H., eds. Coevolution of animals and plants. Austin, TX: University of Texas Press. 28 p.

Mealey, S. P. 1975. The natural food habits of free ranging grizzly bears in Yellowstone Park, 1973-1974. Bozeman, MT: Montana State University. 85 p. Thesis.

Mealey, S. P. 1980. The natural food habits of grizzly bears in Yellowstone National Park 1973-1974. In: International conference of bear research and management; Kalispell, MT. Madison, WI: International Bear Association: 4: 281-292.

Mehringer, P. J., Jr. 1985. Late-quaternary pollen records from the interior Pacific Northwest and Northern Great Basin of the United States. In: Bryant, V. M., Jr.; Holloway, R. G., eds. Pollen records of late-quaternary North American sediments. Dallas, TX: American Association of Stratigraphic Palynologists Foundation: 167-189.

Mehringer, P. F., Jr.; Arno, S.; Petersen, K. 1977. Postglacial history of Lost Trail Pass Bog, Bitterroot Mountains, Montana. Arctic and Alpine Research. 9(4): 345-368. [65066491]

Mielke, J. L. 1936. Dates of production of the different spore stages of *Cronartium ribicola* in the Pacific Northwest. Phytopathology. 25: 1104-1108.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species—a literature review. Gen. Tech. Rep. PNW-87. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 72 p.

Mirov, N. T. 1946. Viability of pine seed after prolonged cold storage. Journal of Forestry. 44(3): 193-195.

Mirov, N. T. 1961. Composition of gum turpentines of pine. Tech. Bull. 1239. Washington, DC: U.S. Department of Agriculture, Forest Service. 158 p.

Mirov, N. T. 1967. The genus *Pinus*. New York: The Ronald Press. 602 p.

Moeur, M. 1981. Crown width and foliage weight of Northern Rocky Mountain conifers. Res. Pap. INT-283. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 14 p.

Moss, E. H. 1959. The flora of Alberta. Toronto, ON: University of Toronto Press. 546 p.

Muir, N. 1977. Whitebark pine (*Pinus albicaulis*) fir gardens. Gardeners Chronicle/Horticulture Trade Journal. 182(15): 33.

Nance, N. W. 1939. Diseases of plants in the U.S. in 1938. Plant Disease Reporter Supplement. 119: 119-289.

Ogilvie, R. T. 1969. Vegetation zonation in the Rocky Mountains of Alberta, Canada. In: The XI International Botanical Congress and the International Wood Chemistry Symposium; Seattle, WA: 162. [05082001]

Parker, D. L. 1973. Trends of mountain pine beetle outbreaks in mixed stands of preferred hosts. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region, Timber Management, Forest Insect and Disease Prevention and Control; Office Report. 8 p.

Pencic, M. 1986. Current problems in the agricultural research in Yugoslavia. Savrem Poljopr. 34(1/2): 5-16. [42428]

Peterson, D. L.; Arbaugh, M. J.; Lardner, M. A. Leaf area of lodgepole pine and whitebark pine in a subalpine Sierra Nevada forest. Canadian Journal of Forest Research. 19(3): 401-403.

Pfister, R. D.; Kovalchik, B. L.; Arno, S.; Presby, R. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p. [13089165]

Picton, H. D. 1978. Climate and reproduction of grizzly bears in Yellowstone National Park. Nature. 274(5674): 888-889.

Picton, H. D.; Mattson, D. M.; Blanchard, B. M.; Knight, R. R. 1986. Climate, carrying capacity, and the Yellowstone grizzly bear. In: Contreras, G. P.; Evans, K. E., compilers. Proceedings—grizzly bear habitat symposium; 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 129-135.

Pitel, J. A. 1981. Improved germination of whitebark pine (*Pinus albicaulis* Engelm.) seeds. Chalk River, ON: Canadian Forestry Service, Petawawa National Forestry Institute; unpublished report. 5 p.

Pitel, J. A.; Wang, B. S. P. 1980. A preliminary study of dormancy in *Pinus albicaulis* seeds. Bi-Monthly Research Notes. 36(1): 4-5. [19035209]

Plesnik, P. 1973. Some problems of the timberline in the Rocky Mountains compared with central Europe. Arctic and Alpine Research. 5(3 Pt. 2): A77-A84. [10060435]

Pojar, J. 1978. Vegetation of ecological reserve proposal No. 306, Nanika Lake. Victoria, BC: Ministry of Environment, Ecological Reserves Unit; unpublished paper.

Putnam, H. N. 1928. Scouting for blister rust in Washington, 1928. In: Blister rust work in the far West. Spokane, WA: Spokane Branch Office, Blister Rust Control: 119-203.

Reasoner, M. A.; Hickman, M. [In press]. Late quaternary environmental change in the Lake O'Hara region, Yoho National Park, British Columbia. Palaeogeography, Palaeoclimatology, Palaeoecology.

Reed, R. M. 1976. Coniferous forest habitat types of the Wind River Mountains, Wyoming. American Midland Naturalist. 95(1): 159-173.

Rehder, A. 1940. Manual of cultivated trees and shrubs hardy in North America. 2d ed. New York: The Macmillan Co. 996 p.

Reynolds, F. 1990. Whitebark pine ecosystems: the threats and the challenge. Forestry Research West. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, [Rocky Mountain Forest and Range Experiment Station]; January: 5-9.

Ritchie, J. C. 1987. Postglacial vegetation of Canada. Cambridge, England: Cambridge University Press. 178 p.

Romme, W. H. 1979. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Laramie, WY: University of Wyoming. 115 p. Dissertation.

Root, G. A. 1936. B. scouting for blister rust in Oregon and California, 1936. In: Blister rust work in the far West. Spokane, WA: Spokane Branch Office, Blister Rust Control: 229-239.

Rundel, B. W.; Parsons, D. J.; Gordon, D. T. 1977. Montane and subalpine vegetation of the Sierra and Cascade Ranges. In: Barbour, Michael G.; Major, Jack, eds. Terrestrial vegetation of California. New York: John Wiley and Sons: 559-600.

Rydburg, P. A. 1905. Studies on the Rocky Mountain flora-XV. Torrey Botanical Club, New York Bulletin. 32: 597-610.

Rydburg, P. A. 1922. Flora of the Rocky Mountains and adjacent plains. New York: P. A. Rydburg. 1143 p.

Sargent, C. S. 1905. Manual of the trees of North America. Boston and New York: Houghton Mifflin. 826 p.

Schallenberger, A.; Jonkel, C. J. 1980. Rocky Mountain East Front grizzly studies, 1979. Annual report. Border Grizzly Project Special Rep. No. 39. Missoula, MT: University of Montana. 207 p.

Schmidt, W. C.; Lotan, J. E. 1980. Phenology of common forest flora of the Northern Rockies—1928-1937. Res. Pap. INT-259. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 20 p.

Schubert, G. H. 1954. Viability of various coniferous seeds after cold storage. Journal of Forestry. 52: 446-447.

Shaw, G. R. 1914. The genus *Pinus*. Arnold Arboretum Publ. 5. Boston: Houghton Mifflin.

Silen, R. R.; Woike, L. R. 1959. The Wind River Arboretum from 1912 to 1956. Res. Pap. 33. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 50 p.

Slater, J. 1978. Pinatae distribution in the state of Washington. In: Occas. Pap. 51. Tacoma, WA: University of Puget Sound: Museum of Natural History. 694-709. [67039425]

Smerlis, E. 1973. Pathogenicity tests of some discomycetes occurring on conifers. Canadian Journal of Forest Research. 3: 7-16.

Smith, Richard S., Jr. 1972. Needle casts of high-altitude white pines in California. Plant Disease Reporter. 56: 102-103. [54016257]

Snethen, K. L. 1980. Whitebark pine (*Pinus albicaulis*) invasion of a subalpine meadow. Logan, UT: Utah State University. Thesis.

Soegaard, B. F. 1972. Relative blister rust resistance of native and introduced white pine species in Europe. In: Biology of rust resistance in forest trees. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture, Forest Service: 233-239. [08056186]

Sowell, J. B.; Koutnik, D. L.; Lansing, A. J. 1982. Cuticular transpiration of whitebark pine (*Pinus albicaulis*) within a Sierra Nevadan timberline ecotone, U.S.A. Arctic and Alpine Research. 14(2): 97-103. [74086116]

Spaulding, P. 1923. Foreign studies of white pine blister rust. Phytopathology. 13: 45.

Spaulding, P. 1925. A partial explanation of the relative susceptibility of the white pines to the white pine blister rust. Phytopathology. 15: 591-597.

Staley, J. M. 1964. A survey of coniferous foliage diseases (other than rusts) in Colorado. Plant Disease Reporter. 48: 562-563.

Steele, R.; Cooper, S. V.; Ondov, D. M.; Roberts, D. W.; Pfister, R. D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.

Steele, R.; Pfister, R. D.; Ryker, R. A.; Kittams, J. A. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 138 p.

Steinhoff, R. J. 1972. White pines of western North America and Central America. In: Biology of rust resistance in forest trees. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture: 215-232. [08056185]

Stephan, B. R. 1985. Resistance of five-needled pines to blister rust. Zur Blasenrostresisten von fünfnadeligen Kiefernarten Allgemeine Forstzeitschrift No. 28: 695-697.

Sudworth, G. B. 1908. Forest trees of the Pacific slope. Washington, DC: U.S. Department of Agriculture, Forest Service. 455 p.

Sudworth, G. B. 1967. Forest trees of the Pacific slope. New York: Dover Publications. 455 p.

Sund, S. K. 1988. Post-fire regeneration of *Pinus albicaulis* in western Montana: patterns of occurrence and site characteristics. Denver, CO: University of Colorado. 63 p. Thesis.

Sutherland, J. R. 1987. *Sirococcus* blight. In: Sutherland, J. R.; Miller, T.; Quinard, R. S. Cone and seed diseases of North American conifers. North American Forestry Commission Publ. No. 1. Washington, DC: U.S. Department of Agriculture, Forest Service, International Forestry Staff: 34-41.

Swanson, H. E. 1949. Blister rust control on national parks. In: White pine blister rust control in the Northwest Region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control: 13-14.

Swanson, H. E. 1949. Blister rust control in the Northwest Region. In: White pine blister rust control in the Northwest Region. Spokane, WA: U.S. Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control: 1-6.

Thomas, G. P.; Bourchier, R. J.; Lowman, A. A. 1960. Rust diseases. In: Annual Report for Insect and Disease Survey for 1959. Province of Alberta: Canadian Department of Agriculture, Forest Service, Forest Biology, Forest Disease Survey: 90-91.

Thompson, L. S. 1977. Dwarf shrew *Sorex nanus* in north central Montana. Journal of Mammalogy. 58(2): 248-250. [13079007]

Thompson, L. S.; Kuijt, J. 1976. Montane and subalpine plants of the Sweetgrass Hills, Montana, and their relationship to early post-glacial environments of the Northern Great Plains. Canadian Field-Naturalist. 90(4): 432-448. [63056036]

Tisch, E. L. 1969. Seasonal food habits of the black bear in the Whitefish Range of northwestern Montana. Missoula, MT: University of Montana. 108 p. Unpublished M.S. thesis.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird. 16(1977): 123-160. [67001821]

Tomback, D. F. 1980. How nutcrackers find their seed stores. The Condor. 82: 10-19.

Tomback, D. F. 1981. Notes on cones and vertebrate-mediated seed dispersal of *Pinus albicaulis* (Pinaceae). Notes and News. Madrono. 28(2): 91-94.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51(2): 451-467. [75009352]

Tomback, D. F. 1983. Nutcrackers and pines: coevolution or coadaptation? In: Nitecki, M. H., ed. Coevolution. Chicago and London: University of Chicago Press: 179-223.

Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madrono. 33(2): 100-110.

Tomback, D. F. 1989. The broken circle: fire, birds and whitebark pine. In: Walsh, Tom, compiler and ed. Wilderness and wildfire. Misc. Publ. 50. Missoula, MT: University of Montana, School of Forestry, Montana Forest and Range Experiment Station: 14-17.

Tomback, D. F. [In press]. Nutcracker-pine mutualisms: multi-trunk trees and seed size. In: Ouellet, H., ed. Acta XIX Congressus Ornithologici Internationalis.

Tomback, D. F.; Kramer, K. A. 1980. Limber pine seed harvest by Clark's nutcracker *Nucifraga columbiana* in the Sierra-Nevada USA. Timing and foraging behavior. Condor. 82(4): 467-468. [21024147]

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. New York: Springer-Verlag. 137 p.

Trappe, J. M. 1962. Fungus associates of ectotrophic mycorrhizae. Botanical Review. 28: 538-606.

U.S. Department of Agriculture, Forest Service, Region One, Division of State and Private Forestry. 1957. White pine blister rust control calendar year 1957. White pine blister rust control annual report, Missoula, MT: 1-36.

U.S. Department of Agriculture, Forest Service, Region One, Division of State and Private Forestry. 1958. White pine blister rust control calendar year 1958. White pine blister rust control annual report, Missoula, MT: 1-38.

U.S. Department of Agriculture, Forest Service, Region One, Division of State and Private Forestry. 1960. White pine blister rust control calendar year 1960. White pine blister rust control annual report, Missoula, MT: 1-60.

U.S. Department of Agriculture, Forest Service, Region One, Division of State and Private Forestry. 1965. White pine blister rust control calendar year 1965. White pine blister rust control annual report, Missoula, MT: 1-77.

Vander Wall, S. B. 1982. An experimental analysis of cache recovery in Clark's nutcracker. Animal Behavior. 30: 84-94.

Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. Ecological Monographs. 47: 89-111.

Vander Wall, S. B.; Hutchins, H. E. 1983. Dependence of Clark's nutcracker, *Nucifraga columbiana*, on conifer seeds during postfledging period. Canadian Field-Naturalist. 97(2): 208-214. [77089669]

Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. American Midland Naturalist. 92: 222-230. [58054325]

Weaver, T.; Dale, D. 1978. Trampling effects of hikers, motorcycles and horses in meadows and forests. Journal of Applied Ecology. 15(2): 451-457. [67060062]

Weaver, T.; Dale, D.; Hartley, E. 1979. The relationship of trail condition to use, vegetation, user, slope, season, and times. In: Ittner, R.; Potter, D.; Agee, J.; Anschell, S., compilers. Recreation impact on wildlands. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 341 p.

Weaver, T.; Forcella, F. 1977. Biomass of 50 conifer forests and nutrient exports associated with their harvest. Great Basin Naturalist. 37(3): 395-401. [66045645]

Weaver, T.; Forcella, F. 1986. Cone production in *Pinus albicaulis* forests. In: Shearer, R. C., compiler. Proceedings—conifer tree seed in the Inland Mountain West; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 68-76.

Weir, G. H. 1977. Scanning electron microscope studies of late quaternary fossil pollen from northern Idaho and Washington. Palynology. 1: 177. [16035588]

Weir, G. H.; Thurston, E. L. 1977. Scanning electron microscope identification of fossil Pinaceae pollen to species by surface morphology. Palynology. 1: 157-165. [16035552]

Wheeler, D. W.; Sawyer, J. O. 1982. Natural revegetation of exploration trenches in the Stillwater Complex of the Beartooth Mountains, Montana. In: Reclamation in mountainous areas. Guelph, ON: Canadian Land Reclamation Association: 119-138.

Whipple, S. A.; Dix, R. L. 1979. Age structure and successional dynamics of a Colorado subalpine forest. American Midland Naturalist. 101(1): 142-158.

Yole, D.; Lewis, T.; Inselberg, A.; Pojar, J.; Holmes, D. 1989. A field guide for identification and interpretation of the Engelmann spruce-subalpine fir zone in the Prince Rupert Forest Region, British Columbia. Land Manage. Handb. 17. Victoria, BC: British Columbia Ministry of Forests. 83 p.

☆U.S. GOVERNMENT PRINTING OFFICE: 1990-773-039/21002

Schmidt, Wyman C.; McDonald, Kathy J., compilers. 1990. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 386 p.

Includes 52 papers and 14 poster synopses that present current knowledge about ecosystems where whitebark pine and associated flora and fauna predominate. This was the first symposium to explore the ecology and management of these ecosystems, which are becoming increasingly important.

KEYWORDS: *Pinus albicaulis*, stone pines, Clark's nutcracker, climate, autecology, community types, succession, fire influences, seed germination, establishment, stems, chemistry, insects, diseases, berries, history, grizzly bears, deer, red squirrels, seed dispersal, hydrology, recreation, genetics, silviculture

INTERMOUNTAIN RESEARCH STATION

The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

The Intermountain Research Station territory includes Montana, Idaho, Utah, Nevada, and western Wyoming. Eighty-five percent of the lands in the Station area, about 231 million acres, are classified as forest or rangeland. They include grasslands, deserts, shrublands, alpine areas, and forests. They provide fiber for forest industries, minerals and fossil fuels for energy and industrial development, water for domestic and industrial consumption, forage for livestock and wildlife, and recreation opportunities for millions of visitors.

Several Station units conduct research in additional western States, or have missions that are national or international in scope.

Station laboratories are located in:

Boise, Idaho

Bozeman, Montana (in cooperation with Montana State University)

Logan, Utah (in cooperation with Utah State University)

Missoula, Montana (in cooperation with the University of Montana)

Moscow, Idaho (in cooperation with the University of Idaho)

Ogden, Utah

Provo, Utah (in cooperation with Brigham Young University)

Reno, Nevada (in cooperation with the University of Nevada)