

## Chapter 17

# Strategies for Managing Whitebark Pine in the Presence of White Pine Blister Rust

Raymond J. Hoff, Dennis E. Ferguson, GERAL I. McDONALD,  
and Robert E. Keane

Whitebark pine (*Pinus albicaulis*) is one of many North American white pine species (*Pinus* subgenus *Strobus*) susceptible to the fungal disease white pine blister rust (*Cronartium ribicola*) (Chapter 10). Blister rust has caused severe mortality (often reaching nearly 100 percent) in many stands of whitebark pine north of 45° latitude in western North America. The rust is slowly moving south through the range of whitebark pine and other white pine species (Chapters 10 and 11).

In whitebark pine, the rust typically kills the upper, cone-bearing branches long before the tree dies, thus reducing or ending seed production and, consequently, future regeneration. Whitebark pine is a keystone species that increases biodiversity in the subalpine zone in a multitude of ways, especially by providing seeds as a wildlife food source (Chapters 1 and 12). The loss of whitebark pine will lower the environmental carrying capacity for many forest animals as well as alter forest composition and distribution in the upper elevations.

One of the few options to reverse severe losses of whitebark pine to blister rust is to increase the level of genetic resistance. Previous efforts to increase blister rust resistance in western white pine (*Pinus monticola*) provide some guidance for the process. This chapter presents information on the presence of resistance in whitebark pine to white pine blister rust. We will use this knowledge, together with knowledge about the ecology of whitebark pine and the blister rust fungus, to propose integrated rust management strategies for restoring whitebark pine communities.

## Blister Rust Susceptibility in Whitebark Pine

White pine blister rust entered North America from Europe early in the twentieth century at two locations (Chapter 10). One entry point was through New York State before 1906, when several million three-year-old seedlings of eastern white pine (*Pinus strobus*) were imported from nurseries in Europe and outplanted at many forest sites (Spaulding 1911). Only 1 to 3 percent of these seedlings were infected with blister rust; nonetheless, the infection quickly took hold in the native stands of eastern white pine (Chapter 10).

The second entry point was Vancouver, British Columbia, Canada, in 1910, when a few hundred seedlings of eastern white pine were imported from a nursery in France and were planted at Point Grey near Vancouver. However, blister rust in the West was not observed until September 1921, when it was discovered on European black currant (*Ribes nigrum*), one of the many species of the genus *Ribes* that are obligate alternate hosts in the life cycle of blister rust (Mielke 1943; Chapter 10). A hurried survey completed before winter arrived revealed infection on European black currant and a few exotic white pines throughout the lower Fraser River Valley of British Columbia. Surveys in 1922 showed that many native western white pine trees in western British Columbia were infected, and infection of European black currant was observed in western Washington.

The first infected whitebark pine was discovered in 1922 in the arboretum of the University of British Columbia, Vancouver (Bedwell and Childs 1943). In 1926, the rust was discovered on native whitebark pine near the Birkenhead River in the Coast Range of British Columbia, 160 kilometers north of Vancouver (Lachmund 1926). There, whitebark pine occurred in association with western white pine, and Lachmund (1928) observed that whitebark pine appeared to be seven to ten times more susceptible to blister rust than was western white pine.

To further determine the relative susceptibility of western white pine and whitebark pine to blister rust, Bedwell and Childs (1943) established study plots of young whitebark and western white pine in natural and nursery settings. The nursery plot was in the same general area where Lachmund (1928) made his observations, but the natural stands were located in Washington, Oregon, and Idaho. In the natural stands, where blister rust had been present for about ten years, infection level for western white pine ranged from 0 to 70 percent, averaging 28 percent, with 0.06 cankers per 1,000 needles. Whitebark pine infection ranged from 59 percent to 100 percent, averaging 83 percent, with 1.22 cankers per 1,000 needles. In the nursery test, the number of cankers per 1,000 needles for western white pine was 0.18, and for whitebark pine 1.42. Percent infection for the nursery test was not given. These results certainly confirmed Lachmund's (1928) observation.

Furthermore, Bedwell and Childs (1943) observed that whitebark pine trees were dying faster than western white pine because of extremely high numbers of branch cankers. They concluded that the greater susceptibility of whitebark pine was due in part to the longer retention time of needles (5.3 years for whitebark versus 3.8 years for western white pine) and to the higher susceptibility of current year's needles. Estimation of the absolute infection rate (see Chapter 10 for definition of  $r$ ) from published data (Bedwell and Childs 1943) indicates

that whitebark pine was 4.8 times more susceptible than western white pine west of the crest of the Cascade Mountains, but was 72.5 times more susceptible east of the Cascade crest. If whitebark pine is several times more susceptible than western white pine—as estimated by Lachmund (1926), Bedwell and Childs (1943), and McDonald and Hoff (Chapter 10)—the survival of this species appears bleak. However, recent data indicate that western white pine and whitebark pine may have about equal susceptibility when density of *Ribes* plants per hectare are equal (Tomback et al. 1995; Chapter 10). Although the relative susceptibility of these two species is still unclear, it is clear that they are both very susceptible to blister rust.

A large amount of data collected by foresters, pathologists, and geneticists paint a bleak picture for whitebark pine (Chapter 11). The data confirm high levels of mortality by blister rust on many sites north of 45°N latitude and an increasing level of infection south of that line. But, there is hope that human intervention can help save whitebark pine and restore these ecosystems.

### Blister Rust Resistance

It is unusual to find 100 percent mortality from blister rust in stands of either whitebark or western white pine (Hoff et al. 1994; Chapters 10 and 11). In areas where blister rust has infected and killed most of the whitebark and western white pine, often one or more trees have no visible cankers, which indicates the possibility of genetically controlled resistance to the rust. Bingham (1983) estimated that 1 in 10,000 western white pine trees was canker-free in high-infection areas. Then, too, even the surviving but cankered trees may have genes for resistance to blister rust. In western white pine, the number of resistant trees becomes apparent in blister rust-infected stands with an increasing level of mortality (Hoff et al. 1976). On average, the most susceptible trees die first. The last to die, if indeed they die, would be the most resistant. Alternatively, because of nonrandom distribution of spores and/or infection microclimate, blister rust epidemics may not achieve 100 percent rust incidence (Chapter 10). Therefore, healthy trees may be “escapes” rather than phenotypically resistant.

### Tests for Resistance: Western White Pine

Methods for determining the level of resistance in western white pine were worked out by Bingham et al. (1960) and later modified by Hoff and McDonald (1980). Recently, a new breeding and seed orchard plan has been prepared by Mahalovich and Eramian (2000). Methods for determining resistance levels are reviewed by McDonald and Hoff (Chapter 10), and since they are germane to the determination of resistance in whitebark pine, they will be briefly described.

Breeding for resistance in western white pine started in 1950 (Bingham 1983; Chapter 10). The first major objective was to determine if the few rust-free western white pines, growing among neighbors supporting hundreds of cankers, had heritable rust resistance. Seeds were collected from canker-free trees, called candidates, which were cross-bred with other candidates. Bing-

ham's tests included candidates from the inland range of western white pine, that is, eastern Washington, northern Idaho, and western Montana. Seeds of the first four progeny tests in 1952 to 1955 were sown, grown, and inoculated with blister rust in a nursery near Spokane, Washington. The next tests in 1960 to 1970 were completed in Moscow, Idaho. Two-year-old seedlings were inoculated by suspending blister rust-infected *Ribes* leaves over them in the fall. Experimental control was established by using seeds from infected trees (called “comparison trees”) located in the same stands that contained the candidates. The 1952 to 1955 progeny tests were divided into three units and outplanted at three different forest sites. The 1960 to 1970 tests remained in Moscow for the duration of the tests.

The first data tallied were the presence and the number of blister rust needle spots on the secondary needles. The needle spots were easily visible by June, 9 months after inoculation. The second data tallied were the presence of blister rust needle spots, cankers, and/or bark reactions (easily visible bark lesions caused by the seedling attempting to kill the rust) 12 months after inoculation. The third, fourth, and fifth data tallied were for cankers and/or bark reactions and mortality due to blister rust 24, 36, and 48 months after inoculation.

The 1952 progeny test showed that blister rust resistance in western white pine was inherited. Seedlings from the candidates were 17.9 percent canker-free, whereas the comparison or control trees were 5.3 percent canker free. The data also indicated the existence of additional underlying resistance mechanisms.

Additional information from the western white pine tests changed the way we view blister rust resistance; seedlings from surviving, cankered trees in high-mortality stands also have resistance. This insight came from comparing the level of resistance of the seedlings from the comparison trees in the early 1950s, when the level of mortality of the parental stands ranged from 0 to about 15 percent, to the level of resistance of seedlings from comparison trees in the early 1960s, when the level of mortality of parental stands had increased to 80 to 90 percent. About 5.3 percent of the seedlings from the comparison trees for the 1952 to 1955 progeny tests showed blister rust resistance (Bingham et al. 1960), but for the 1964 progeny tests, it was 22.8 percent. Most important, the resistance in the candidate trees increased to 39.3 percent (Hoff et al. 1976). The higher resistance of the candidate trees is due, in part, to the fact that four of the twelve pollen parents used in the breeding design had already been selected (in the 1952 progeny test) for high resistance. It is also probable that better candidates had been selected. Future selection of candidate trees was relaxed to include trees with cankers, depending on the level of stand mortality from blister rust (Mahalovich and Eramian 2000). This exemplifies the high resiliency of western white pine, probably the result of its high within-stand genetic variation (Rehfeldt et al. 1984). In just one generation of selection by blister rust, resistance has already achieved a useful level.

One of the cankered seedlings in the 1954 progeny test illustrates the longevity of infected trees that must have some resistance to blister rust. This exceptional tree was artificially inoculated in 1956 and had a canker by 1958. In 1981 the tree was 14.7 meters tall and was 90 percent girdled by blister rust (Hoff 1984). The tree died in 1991, having lived with a very large canker for

33 years. The average height for trees in this same plot in 1981 was 14.3 meters for cankered trees (12 trees remained) and 14.2 meters for canker-free trees (14 trees remained). Most of the 953 trees planted at this site had died within a few years after inoculation, and most of the canker-free trees were moved to an arboretum near Moscow, Idaho, by 1965.

### Tests for Resistance: Whitebark Pine

Methodology developed to determine the level of resistance in western white pine was used for two whitebark pine tests. The purpose of the first test was to compare the levels of resistance to blister rust among nineteen white pine species (subsections *Cembrae* and *Strobi*) from Asia, Europe, and North America. In spring 1970, seeds were sown in pots arranged in randomized blocks (replications). Two-year-old seedlings were inoculated with blister rust and inspected annually for 3 years (Hoff et al. 1980). In prior tests when seeds of whitebark pine were collected from the general population, whitebark pine was ranked as the most susceptible to blister rust among white pine species (Bingham 1972). But in the 1970 test, the seeds of whitebark pine came from trees with no visible cankers in high-mortality stands (>90 percent by blister rust), and the seeds of western white pine came from a mix of resistant candidates. The level of canker-free seedlings of whitebark pine ranked fourth at 46 percent. To our surprise, western white pine ranked fifth with 36 percent canker-free seedlings, which showed less resistance than whitebark pine.

The second resistance test for whitebark pine was established in 1989 by R. J. Hoff (unpublished data). The purpose of this test was to relate the level of resistance to blister rust in whitebark pine to varying levels of mortality caused by blister rust. Seeds from three high-mortality stands (>90 percent), three moderate-mortality stands (40–60 percent), and three low-mortality stands (<10 percent) were included in the test. Three years after inoculation, 44.4 percent of the seedlings from the high-mortality stands were canker-free, 11.9 percent from moderate-mortality stands, and 0.9% from low-mortality stands (Table 17-1). These results together suggest that surviving whitebark pine trees from high-mortality stands possess usable levels of heritable resistance.

Table 17-1. Rust resistance of whitebark pine (*Pinus albicaulis*) seedlings three years after inoculation with white pine blister rust (*Cronartium ribicola*). The seedlings were grown from parent stands having three levels of mortality caused by blister rust.

Parent Stand Mortality	Number of Seedlings	Spots Per Meter of Needles	Percent Not Cankered	NUMBER OF SEEDLINGS BY RESISTANCE MECHANISM		
				Needle Shed	Short Shoot	Bark Reaction
> 90%	304	8.0	44.4	50	47	38
40–60%	134	10.2	11.9	4	7	5
<10%	226	5.4	0.9	1	0	1

### Resistance Mechanisms

Many mechanisms of resistance have been observed and measured in western white pine (Table 17-2). Mahalovich and Eramian (2000) have included most of these mechanisms in their western white pine–blister rust breeding and seed orchard plans. At this time, tests of resistance of whitebark pine to blister rust have not been detailed enough to determine whether all the resistance mechanisms in western white pine are present. However, three main resistance mechanisms have been observed in whitebark pine:

1. Needle shed—characterized by the premature shedding of the needles that have rust infections, that is, needle spots.
2. Short-shoot—seedlings with this mechanism have needle spots, but when the fungus grows down the needle, it dies as it enters the short shoot. The short shoot is the small, stemlike appendage at the base of the needles that holds the five needles of a fascicle together.
3. Bark reaction—here the fungus can grow into the stem, but it soon dies after being walled off by special cortex cells in the bark, which becomes visible on the surface of the stem as lesions.

In one test of whitebark pine, needle shed was the most common resistance mechanism observed (Hoff et al. 1980). Although this trait also occurred in all

Table 17-2. Defense mechanisms against white pine blister rust (*Cronartium ribicola*) observed in western white pine (*Pinus monticola*).

Defense Symptom	Possible Inheritance
Resistance in secondary needles to a yellow-spot forming race.	Recessive gene
Resistance in secondary needles to a red-spot forming race.	Dominant gene
Resistance in secondary needles to yellow-green-island spot forming race.	Dominant gene
Resistance in secondary needles to red-green-island spot forming race.	Dominant gene
Resistance in secondary needles that prevents spot formation.	Unknown
Reduced frequency of secondary needle infections.	Nondominant gene
Slow fungus growth in secondary needles.	Polygenic
Premature shedding of infected secondary needles	Recessive gene
Fungicidal reaction in the short-shoot.	Recessive gene
Fungicidal reaction in the stem.	Polygenic
Slow fungus growth in the stem.	Polygenic
Tolerance.	Polygenic

other pines showing resistance, it was highest in frequency in whitebark pine. The short-shoot and bark reactions that were the most prevalent resistance mechanisms in the other pines occurred only at a moderate level in whitebark pine. In a 1989 test (R. J. Hoff, unpublished data), the three main resistance mechanisms were about equal in number (Table 17-1).

There are other noteworthy observations from the whitebark pine resistance tests (Hoff et al. 1980; R. J. Hoff, unpublished data). First, some seedlings had huge cankers but did not die until the fourth year after inoculation. Second, cankers in some seedlings grew very slowly, so that these seedlings were still alive five years after inoculation. These observations are signs of two additional resistance mechanisms—"tolerance" and "slow canker growth." If we could breed for these and other resistance mechanisms, the resulting new variety of whitebark pine should provide the level of resistance needed to maintain itself in the presence of blister rust.

McDonald and Dekker-Robertson (1998) and McDonald and Hoff (Chapter 10) argue that all resistance mechanisms thus far observed in Idaho western white pine and whitebark pine fall into the category of horizontal resistance, so-called because when a variety of pine is tested against several different races of the rust, the histograms for proportion infected are equal, although they can vary from near 0 to 1 (Zadoks 1972). This terminology comes from agriculture (Van der Plank 1968; Simmonds 1991), where horizontal resistance factors are usually controlled by minor genes that can be overcome by more aggressive races of rust, although this may take a long time. Mortality typically remains low. Horizontal resistance contrasts sharply with vertical resistance, because when a vertically resistant variety is tested against various races of the rust, the histograms for proportion infected are either 1 or 0. Vertical resistance is nearly always controlled by major dominant genes and is usually (almost invariably) overcome by new races of rust, often within five years or so, rendering the varieties completely susceptible. Mortality is rapid. For example, a dominant gene for resistance to blister rust was found in sugar pine (*Pinus lambertiana*) (Kinloch et al. 1970), but it was soon overcome by a new race of blister rust (Kinloch and Comstock 1981; Chapter 10).

## Management Strategies

It appears that whitebark pine may have stable horizontal resistance to blister rust. The next step is to use one or more strategies to incorporate the resistance genes into future generations of whitebark pine. The discussion that follows provides ideas for managing whitebark pine in restoration efforts. Appropriate management actions will depend on factors such as site conditions, history of blister rust infection, potential for insect outbreaks, landscape considerations, and landowner objectives. Most of these management activities are doubly beneficial because they can increase rust resistance while restoring whitebark pine communities.

## Seed Collection

Whitebark pine seeds must be collected for gene conservation, planting, and for use in any rust-resistance breeding program. Protection of maturing cones is a

major consideration because of seed losses to pine squirrels (*Tamiasciurus* spp.) and Clark's nutcrackers (*Nucifraga columbiana*). Squirrels and nutcrackers can harvest every cone and seed from whitebark pine trees, especially in stands where cone crops are reduced by blister rust. The best strategy is to collect cones whenever there is a good seed crop, and harvest cones from many stands so they can be stored and used when needed. Details of cone and seed collection are summarized by Burr et al. (Chapter 16).

Blister rust-resistance levels in seeds will be higher if cones are collected only from remnant trees that have no cankers, because they probably have the highest resistance in the stand (although some of these isolated trees could be escapes rather than resistant [Chapter 10]). These remnant trees are probably widely scattered and would definitely require the use of wire mesh bags to protect maturing cones from squirrels and nutcrackers. Because of the expected higher levels of resistance, this alternative may be worth the effort.

A better alternative, in terms of levels of resistance, would be to collect pollen from many canker-free or lightly cankered trees (i.e., trees that are apparently rust resistant found in stands having more than 90 percent rust-caused mortality) and artificially pollinate other canker-free or lightly cankered trees. This would require that pollination bags be placed over the strobili (female cones) before they become receptive, artificially pollinating them, removing the pollination bag, and using wire mesh bags to protect developing cones. Each tree would need to be climbed five times to complete the process. Whereas this is a good procedure for research purposes, the process is expensive and probably not very practical.

## Seed Transfer

Most plant species vary genetically across environmental gradients. If plant material (seedlings, pollen, seeds, or clones) is transported too far, there is danger of plants being maladapted to their new environment. Plans to transfer whitebark pine seeds or seedlings from one site to another must avoid making transfers that are genetically maladapted. That is, we must know if there are genetic differences within whitebark pine from one stand to another, or from one mountain range to another, that control adaptive traits. If there are no differences, plant materials could be transferred throughout the range of whitebark pine. If there are differences, where do we draw the boundaries between populations within species?

Several researchers have evaluated genetic variation among populations of whitebark pine using allozymes (Jorgenson and Hamrick 1997; Bruederle et al. 1998; Chapter 8). So far, the results indicate that most of the variation is within populations and that the variation among populations is small and not limiting. More useful are tests that relate survival traits—such as growth, frost hardiness, drought hardiness, and pest resistance—with various aspects of the environment such as latitude, longitude, elevation, and habitat. Whereas the Rocky Mountain Research Station has initiated seed transfer studies for whitebark pine (Chapter 15), we cannot wait for conclusions, which are some years off, and instead must consider alternatives based on what we now know.

Recent summaries and reworking of genetic data indicate that more liberal seed transfer guidelines can be established, because conifers in general have

high amounts of genetic variation (see also Chapter 15). Genetic variation among populations is nearly always detected, but genetic variation within populations is nearly always greater (Hamrick et al. 1994; Rehfeldt 1994; Mitton 1995; Bruederle et al. 1998). The degree of differentiation among conifer populations has turned out to be quite variable. For example, significant genetic differences occur over short elevational gradients among populations of interior Douglas-fir (*Pseudotsuga menziesii*) (Rehfeldt 1989), lodgepole pine (*Pinus contorta*) (Rehfeldt 1988), ponderosa pine (*Pinus ponderosa*) (Rehfeldt 1991), and western larch (*Larix occidentalis*) (Rehfeldt 1982), but not among populations of western white pine (Rehfeldt et al. 1984). Genetic variation within populations of most western conifers is so high that, even if many of the seedlings are not adapted to the site, there will be seedlings within the mix that are adapted. Conversely, some of the seedlings from an on-site population will not be adapted to that specific site.

Another argument for liberal seed transfer guidelines is the short growing season at high elevations. Frost-free periods decrease by ninety days for every 1,000 meters in elevation gain (Baker 1944). For several conifers, increasing elevation increases the size of population differentiation intervals. For example, for Douglas-fir below 1,000 meters elevation, the population boundary is 200 meters; between 1,000 meters and 1,525 meters, it is 350 meters; and above 2,000, meters differentiation is not detected (Rehfeldt 1989). The conclusion for high-elevation Douglas-fir is that either genetic variability has been exhausted (Douglas-fir is genetically homogeneous at high elevations) or the environment is homogeneously severe (the frost-free period is very short, less than twenty days at timberline) and much further decrease in the growing season would end the range of Douglas-fir.

Recent research results for lodgepole pine show that populations within this species grow in suboptimal environments because adjacent populations of lodgepole pine outcompete them for space (Rehfeldt et al. 1999). The amount of space supplanted depends upon the breadth of lodgepole pine's fundamental niche (Hutchinson 1958). Therefore, if survival and growth are the desired traits for seed transfer, the populations with the fastest growth coupled with adequate survival traits would be selected. On the other hand, if survival is the only trait that is selected, the area where populations would be adapted is much broader. We think that the populations of whitebark pine are not strongly differentiated because selection has been mainly for survival and seed production.

Four main factors support broad transfer rules for whitebark pine. First, the environment over the range of whitebark pine is so uniformly severe that the genetic structure among populations, even populations separated by long distances, will likely be similar. The species is restricted at its upper elevations by the most severe climatic conditions and at the lower elevations by competition from other tree species (Chapter 3). Second, many whitebark pine germinants survive the hot, dry conditions resulting from a site that has been burned. Third, whitebark pine trees can tolerate summer frost that would kill or severely damage other tree species (Chapters 1 and 3). Fourth, whitebark pine seeds are bird-dispersed. Gene flow of bird-dispersed seeds is faster and farther than that of wind-dispersed seed; Clark's nutcrackers have been observed

transporting pine seeds up to 22 kilometers and 12 kilometers or farther for whitebark pine specifically (Tomback and Linhart 1990; Bruederle et al. 1998; Chapter 5). Seeds dispersed by wind for species such as western white pine and Douglas-fir travel only 100 meters or so, depending upon wind speed (Wright 1976). Estimated gene flow or populations of limber pine (*Pinus flexilis*), a bird-dispersed pine, separated by 1,700 meters, averaged 11.1 migrants (genes) per generation (Schuster et al. 1989). The gene pools of bird-dispersed seed, even at long distances, are more likely to be mixed than are gene pools of wind-dispersed seed.

Therefore, we propose relatively broad transfer rules for whitebark pine with certain limitations (USDA Forest Service 1999; Mahalovich and Hoff 2000). The most important limit is to restrict transfers with respect to blister rust mortality. First, transfer should be only among high-mortality stands or from high mortality to moderate or low mortality, and never from low to high mortality. Second, transfer should only be within those sites for which whitebark pine restoration is possible or needed, that is, no need to consider krummholz environments. We may be able to grow whitebark pine at low elevations with protection from insects or disease and with periodic cleaning and weeding. This would be useful in speeding up growth and seed production.

We propose the following transfer rules: In the inland mountains of the United States and Canada, land managers should transfer whitebark pine plant material (seed, seedlings, pollen, or clones) no farther than 80 kilometers from the point of origin (USDA Forest Service 1999; Mahalovich and Hoff 2000). At this time we propose no restrictions on elevation transfer.

## Gene Conservation

There are a number of important reasons to consider gene conservation as an integral part of managing whitebark pine. If whitebark pine populations became locally extinct or severely depleted, there should be alternative ways to reestablish populations. Establishment of seed banks should be strongly considered. Whitebark pine seeds can be collected from several different regions and stored in freezers, following recommendations from Burr et al. (Chapter 16). However, fresh seeds have higher germination success than stored seeds; in fact, seeds stored in freezers lose viability over time (McCaughey 1994; Chapter 16).

Establishment of gene banks is also important. Seedlings from various whitebark pine sites could be planted in low fire- or rust-hazard areas. Then, genetically adapted seeds, pollen, or clones are available to reforest sites. An advantage of gene banks over stored seeds is that genetic material can be produced indefinitely from gene banks.

Another management treatment to consider is protecting individual whitebark pines that are apparently resistant to blister rust. Many of these existing trees are in danger of being crowded out by succession to more shade-tolerant Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in the Inland Northwest. Wildfires are also a threat. Individual trees can be protected by thinning back encroaching competition and moving the debris away

from trees. Reduced competition should allow whitebark pine to live longer with less stress, grow faster, have fuller crowns, and produce larger cone crops.

Protection of whitebark pine forests from wildfire and mountain pine beetle (*Dendroctonus ponderosae*) epidemics that originate in lower-elevation forests requires a landscape perspective. Both wildfire and beetles can sweep upward and kill the few remaining rust-resistant whitebark pine. Therefore, management of whitebark pine forests needs to be considered at the landscape level (see Chapter 14).

### Openings in the Forest Canopy

Historically, periodic wildfires in the interior northwestern United States and southwestern Canada helped maintain whitebark pine communities by creating openings in the forest canopy and returning successional advanced communities to earlier seral stages, where whitebark pine was an important component (Chapter 4). Clark's nutcrackers cache seeds in newly created openings, and caches that are not later retrieved for food by nutcrackers germinate and establish whitebark pine seedlings (Hutchins and Lanner 1982; Tomback 1982; Chapter 5). Openings must be large enough to allow enough sunlight to reach the forest floor, so that whitebark pine germinants can survive and grow.

Fire exclusion practices in the twentieth century have drastically reduced both the number of fires and the area burned, resulting in replacement of whitebark pine with shade-tolerant conifers (Chapters 1, 4, and 9). Today, we need to use fire as a restoration tool (see also Chapter 18).

Restoration may be accomplished through controlled prescribed burns, although wildfires could also become controlled burns, especially in national parks and wilderness areas. However, the use of fire in whitebark pine communities has limitations because of abruptly changing weather, scattered fuels, and short growing seasons (Chapter 18). In addition, increasing human populations near forested lands and undesirable smoke pollution may place limits on the use of fire (Chapter 1). The advantage of fire in whitebark pine communities is that it removes competing trees and shrubs at a reasonable cost (Keane et al. 1989; Chapter 18); the risk is that rust-resistant trees will be inadvertently killed. Rare whitebark pine trees that remain free of blister rust should be protected.

An alternative to fire is to create openings in the forest canopy, primarily by harvesting trees. Results obtained by manual, silvicultural methods are more precise than fire, but are more costly and may require access for equipment. Proceeds from harvesting can pay for treatments in some situations. Openings created by harvesting, whether burned or not, are used by nutcrackers for caching whitebark pine seeds (Chapter 5).

### Natural Regeneration

The easiest and least costly method to increase the proportion of rust-resistant genes in whitebark pine populations would be to apply a seedtree silvicultural system that utilizes apparently rust-resistant whitebark pine trees as the seed source. Clark's nutcrackers cache seeds in openings, effectively "planting" a

new stand of whitebark pine seedlings (Tomback 1982; Chapter 5). Natural selection will favor the survival of rust-resistant trees for both seed-bearing trees and their progeny. The process is initiated by selecting sites that have high mortality caused by blister rust, because the seeds of surviving trees would likely contain rust-resistant genes. Site preparation can reduce competition and attract nutcrackers.

A major consideration with natural regeneration is inbreeding depression. In most conifers, perhaps all, trees that are crossed with themselves or close relatives produce seedlings that grow slower, are less hardy, and often exhibit lethal genes (Wright 1976). Stands of whitebark pine that have only a few trees left will produce a high number of selfed seedlings. These trees will likely be slow growing with even less competitive ability than seedlings from outcrossed trees.

### Planting Seedlings and Tending Regeneration

Sites that do not have enough surviving whitebark pine to provide an adequate seed supply should be planted with nursery-grown seedlings (see Chapter 16). Planting may be a good choice where an increased certainty of regeneration establishment is desired, new stands need to be established quickly, local populations have gone extinct, whitebark pine populations are so small that inbreeding depression is a strong possibility, or rust-resistant seedlings need to be established in areas not yet heavily impacted by blister rust. Planting sites must be open enough for adequate sunlight to reach the forest floor, which means it may be necessary to create openings in the forest canopy.

Seedlings should be grown from seeds collected in stands having high mortality (>90%) caused by blister rust, because the surviving trees may have some resistance to the rust. About twice the number of seedlings needed to meet management objectives should be planted, because many trees will be killed by blister rust (depending on the local rust hazard) and other causes. Planted seedlings should be large (e.g., three years old), since they have higher survival rates than planted smaller/younger trees. Good root development of planted whitebark pine is important. Natural whitebark pine regeneration quickly puts down a taproot to aid in survival in hot, dry conditions that kill other conifer seedlings (Chapter 6).

Competing vegetation—mostly spruce, subalpine fir, and lodgepole pine, but also large shrubs or other vegetation—should be removed if open planting sites cannot be found. Although there is little doubt that fire would enhance survival and growth on most sites, successful planting may be achieved without fire once openings in the forest canopy are created.

The need to monitor and manage whitebark pine continues after seedlings become established. Young stands may be overly dense and need thinning. Whitebark pine should not be thinned, because blister rust will kill nonresistant trees. Caution should be used in thinning competing conifer species and shrubs, because open areas allow establishment and growth of *Ribes*, the obligate alternate host of blister rust. Below 80 to 90 percent full sunlight, the number of *Ribes* shrubs decreases rapidly (McDonald et al. 1981), so trade-offs must be considered between keeping high stand densities that shade out *Ribes*

shrubs and keeping low stand densities that help survival and growth of whitebark pine. Thinning alone is not a desirable option for western white pine, because it can increase the amount of cankering (Hungerford et al. 1982).

A management technique developed for western white pine may be useful for whitebark pine as well. Pruning lower live branches on western white pine regeneration helped reduce infections and mortality from blister rust (Schwandt et al. 1994; Barth 1994; Hunt 1998). All lower branches can be pruned as a preventative measure, or infected branches can be pruned before blister rust reaches the main stem. If rust hazard is too high, pruning will not provide any benefit. A management model designed to assist in making decisions about pruning western white pine is under development (G. I. McDonald, in preparation), and this model could be adapted for whitebark pine.

### Ribes Management

Management of local *Ribes* populations can increase the survival of whitebark pine. Research on western white pine shows that high rates of infection are associated with trees close to *Ribes* shrubs. The number of cankers on western white pine usually drops to negligible amounts if pines are 300 meters or more from a *Ribes* shrub (Chapter 10). Although blister rust spores can travel farther to infect pines, reducing *Ribes* populations should lower the local blister-rust hazard level (Chapter 10). Thinning of overly dense stands becomes a viable option if *Ribes* populations are also reduced. *Ribes* management has diminished the blister rust hazard in the northeastern United States (Ostrowsky et al. 1988; Martin 1944), even though it was not deemed successful under western conditions (Toko et al. 1967; Chapter 10).

### Chemical Control of Blister Rust

In the 1950s and 1960s, actidione and phytoactin appeared to be promising chemicals for controlling blister rust, but they were not effective enough, and this part of the blister rust control program was terminated in 1966 (Chapter 10). Recently, two new chemicals proved effective against blister rust infection over a short time period (Johnson et al. 1992). Three-year-old sugar pine seedlings were treated with foliar sprays of triadimefon and benodanil and inoculated with blister rust three weeks later. After six months, the seedlings were inoculated again, and this time only triadimefon was effective. Berube (1996) inoculated eastern white pine seedlings with blister rust two weeks after foliar spray treatment with triadimefon. He found that only 3.8 percent of the treated seedlings but 70.8 percent of the untreated seedlings developed blister rust symptoms. Kelly and Williams (1985) used triadimenol, and a compound closely related to triadimefon, as a dressing on loblolly pine (*Pinus taeda*) seeds, and then inoculated the seedlings with fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*). They found that both compounds were effective in decreasing fusiform infection for up to thirty-six days and that triadimefon was the most effective of the two chemicals.

Slow-release fertilizer plugs containing triadimefon have been produced, and studies are underway by G. I. McDonald to see how much, and for how

long, these protect against blister rust. A slow-release fertilizer plug impregnated with triadimefon would be useful both for protecting seedlings and for imparting faster growth to planted whitebark pine seedlings.

### Establishing a Rust-Resistance Breeding Program

The most complex and costly approach to increasing blister rust resistance in whitebark pine is to conduct a traditional breeding program (Wright 1976). This approach, patterned after the western white pine breeding program (Bingham 1983; Mahalovich and Eramian 2000), would provide the highest gain in resistance. A variety of resistance-gene mechanisms that may not occur together in nature for many years could be packaged into individual trees. Trees that appear to have high resistance, good growth, and good seed production would be selected and cross-bred. The seedlings would be artificially inoculated, and the best families and individuals within families selected and grown in seed orchards. Seed orchards are usually planted on the best growing sites, often good agricultural land. For most conifers, large amounts of seeds are produced in fifteen to twenty years. For whitebark pine, it may take thirty to forty years or more to produce comparable amounts of seeds.

Recently, seed orchards have been moved into greenhouses. This provides opportunities to accelerate growth and stimulate pollen and seed production. Consequently, several conifers have been made to produce seed within five to seven years. While five to seven years seems too optimistic for whitebark pine, perhaps the number of years to seed production could be greatly reduced.

### Integrated Management

Conifer populations at risk for disease, like those of whitebark pine, can be managed more efficiently by integrating information from a variety of sources, including what is known as hazard assessment. Hazard assessment involves estimation of risk stand by stand or over other geographic scales. Some preliminary attempts at an integrated management approach (Ostrowsky et al. 1988; Geils et al. 1999) were not completely successful. A fully integrated approach should include principles of comparative epidemiology, computer modeling, satellite imagery, and GIS. One key to successful deployment of resistance genes in whitebark pine is matching levels of resistance to degree of hazard (McDonald 1979).

Hazard in higher-elevation forests varies across the landscape. Hoff (unpublished data) sampled nineteen stands of whitebark regeneration for rust incidence and classified stands as moist or dry (see also below). Three of the seven stands classed as dry were rust-free after about twenty years' exposure to blister rust. A recent survey of blister rust in 100 whitebark pine communities in southern Idaho, Utah, and western Wyoming determined that 41 percent of the stands surveyed were rust-free (Smith and Hoffman 1998, 2000). Possible explanations for rust-free stands are lack of humidity and few to no *Ribes* shrubs (Chapter 10). Mapping of *Ribes* hazard could facilitate the management of whitebark pine.

Van der Plank (1963), in his theoretical treatment of diseases, emphasizes

that any control measure that reduces absolute infection rate, including horizontal resistance, is additive for “simple interest” diseases such as blister rust (also see Chapter 10). So horizontal resistance to blister rust in whitebark pine, *Ribes* eradication, pruning of cankers, or reduction of incidence by chemicals should be additive in their effects. Thus, blister rust impact expected under various combinations of blister rust hazard and mix of controls can be predicted.

How much success can we expect? The variable  $r$  in models describing disease spread refers to absolute infection rate in incidence/year (Chapter 10). The average  $r$ -value of twelve stands of susceptible whitebark pine was 0.176 (Chapter 10). There was one extremely high-hazard stand (0.691), four high-hazard stands (0.253, 0.221, 0.212, 0.281), four showing moderate hazard (0.124, 0.124, 0.08, 0.089), and three with low hazard (0.018, 0.013, 0.007). The extreme-, high-, and moderate-hazard stands were located in relatively moist environments, whereas the three low-hazard stands were located in more dry environments.

Whitebark pine mostly grows in three types of ecological communities: seral, climax, and tree-line (krummholz form) (Arno and Hoff 1989). Seral whitebark trees are found on sites moist enough to support subalpine fir and/or mountain hemlock (*Tsuga mertensiana*) (Cooper et al. 1991). Climax communities are found on drier, harsher sites, generally south of 47° N latitude (Arno and Hoff 1989). This distribution leads to a natural grouping of whitebark stands into moist (seral) and dry (climax) classes. A series of nineteen plots were established in whitebark pine regeneration (fifteen to twenty-five years old) in 1992 to survey blister rust damage (R. J. Hoff, unpublished data). We classified twelve of these plots as “moist” and seven as “dry” on the basis of their plant associations, and then computed infection rate  $r$  (Chapter 10). The average  $r$ -value for the seven dry stands was 0.007 and for the twelve moist stands 0.046, indicating that moister aspects and areas are a hazard to whitebark pine.

An outplanting of western white pine in a high-rust-hazard area gives us insight to possibilities for resistance. This plantation contained susceptible, resistant first-generation, and resistant second-generation western white pine (Chapter 10). The number of *Ribes* shrubs was 3,700 per hectare. After six years, blister rust incidence had reached nearly 100 percent in susceptible trees. Absolute infection rate ( $r$ ) for this susceptible lot was 0.504. The infection rate for the first generation of rust-resistant western white pine was three times less, and for the second generation, six times less (McDonald and Dekker-Robertson 1998). After twelve years of exposure, all susceptible trees were dead, and at twenty-six years almost 100 percent of the resistant first generation and 93 percent of the resistant second generation were infected. Mortality from blister rust after twenty-six years for the first generation was 78 percent, and for the second generation 56 percent. So, even at this high-hazard site, many of these western white pine trees will likely survive to maturity. The resistance from high-mortality stands of whitebark pine (Table 17-1) is comparable to the resistance of the first generation of rust-resistant western white pine, and should reduce the  $r$ -value by three times and second generation by six times. Blister rust-resistant populations of whitebark pine should be outplanted at extreme hazard sites to verify their  $r$ -values.

Over a half-billion *Ribes* plants have been removed from thousands of hectares in North American white pine forests (Chapter 10). Because of the high cost versus effectiveness, the *Ribes* eradication program was stopped in 1966 (Chapter 10). *Ribes* eradication in eastern white pine forests of Maine has been more successful. Ostrofsky et al. (1988) evaluated a *Ribes* eradication program after seventy years of effort in Maine. The average absolute infection rate ( $r$ -value) for no *Ribes* eradication was 0.091. For stands with *Ribes* eradication, the average  $r$ -value was 0.038. Therefore, trees were becoming infected at a rate 2.5 times less for treated than for untreated stands. Other studies with similar results in eastern white pine were reported by Martin (1944) and Robbins et al. (1988). Removal of *Ribes* shrubs in whitebark pine stands should reduce the  $r$ -value by 2.5 times.

In order to estimate mortality rates, the ratio of the number of dead trees to number of infected trees ( $i$ ), was computed for the “moist” and “dry” whitebark pine stands (R. J. Hoff, unpublished data). A higher  $i$ -value means more mortality relative to infection. This ratio was also computed for young western white pine stands (McDonald 1982). Results for  $i$  were whitebark-dry = 0.22, whitebark-moist = 0.25, and western white pine = 0.31. The  $i$  ratio could vary considerably with interaction among wave years, tree age, and any other factors that would influence relative rust growth rate. Nevertheless,  $i$  facilitates comparisons of predicted performance, so we will use a conservative value of 0.35. Absolute infection rate ( $r$  in Equation 1, Chapter 10) was multiplied by  $i$  to predict blister rust mortality. The multipliers we used to adjust absolute infection rate  $r$  for the effects of first-generation resistance and removal of *Ribes* shrubs are 0.333 and 0.4, respectively. Then, mortality due to blister rust was estimated by multiplying  $r$ , adjusted or not, by the incidence-mortality ratio, 0.35.

Comparisons of predicted performance are then computed for low ( $r < 0.05$ ), moderate ( $r = 0.05$  to 0.2), high ( $r = 0.2$  to 0.4), and extreme ( $r > 0.5$ ) hazard sites. The whitebark pine stand at Sawtell Peak (see Chapter 10) represents a low-hazard site. Computed and actual values after forty years of exposure were absolute infection rate,  $r = 0.018$ ; actual incidence at time  $t$ ,  $y = 0.51$ ; actual mortality = 0.24, and predicted mortality = 0.22. If selected rust-resistant whitebark pine trees from high-mortality stands (Table 17-1) were planted (absolute infection rate,  $r$  reduced by 0.33) at Sawtell Peak, the expectation is  $r = 0.006$ , with actual incidence of infection at time  $t$ ,  $y = 0.26$ , and mortality = 0.1 after fifty years. The manager could probably live with this amount of impact. Adding *Ribes* control would give  $r = 0.007$ , then  $y = 0.30$  and mortality = 0.12.

A stand at Mt. Brundage, located in central Idaho, can serve as the moderate hazard example. Here,  $r$  was 0.123, so after fifty years,  $y = 1.00$  and mortality = 0.88. This level of unacceptable damage would be reduced to only 0.87 infection and 0.51 mortality by planting resistant seedlings. The addition of *Ribes* management would lead to a combined effect of 0.56 and 0.25, respectively, which is within acceptable limits. Our high-hazard example is based on a stand ( $r = 0.253$ ) located in the Olympic Mountains of Washington (see Chapter 10). After fifty years, mortality under these high-hazard conditions would be about 0.98. Application of the combination of first-generation resist-



ance and *Ribes* management would decrease mortality to 0.45. *Ribes* management and second-generation resistance should reduce damage to an acceptable level of 0.26 in fifty years.

Our extreme-hazard stand is Wasco County 2, located on the southeastern flank of Mt. Hood in Oregon (see Chapter 10). Application of second-generation resistance would result in 0.87 mortality after fifty years. Adding *Ribes* management reduces this mortality to a relatively high 0.55. Management in extreme hazard situations will probably require the development of chemical controls and/or advanced generation populations of resistant whitebark pine.

The efficacy of *Ribes* eradication also depends on the source of inoculum. If inoculum is produced locally (within 300 meters), eradication would be successful at lowering the infection rate. If the inoculum comes from off-site (>1 km), for example from lower elevations where *Ribes* is mixed with western white pine stands, then eradication would be less feasible. We do not currently have technology that will reliably identify sources of inoculum. There are stands, however, where the inoculum is definitely local. The forests below are too dry, do not contain *Ribes*, or there are no white pines present.

### Concluding Comments

There is sufficient research to show that natural resistance in whitebark pine to white pine blister rust exists, and it is passed to the next generation. Several resistance mechanisms have been documented, and these mechanisms are likely to be stable (horizontal resistance). We can use knowledge gained from the western white pine breeding program to package multiple resistance mechanisms to provide even more stability.

Several approaches will assist restoration efforts through integrated management. They include seed collection, seed transfer, gene conservation, use of fire, planting, natural regeneration, tending of regenerated stands, blister rust hazard mapping, *Ribes* management, chemical control of blister rust infection, and development of a blister rust-resistance breeding program with its supporting field outplantings. We must also keep in mind that all five-needled white pines behave in a similar fashion regarding blister rust. This means that most of the cost of developing integrated management tools can be spread over all the species. Most approaches that help restore whitebark pine can also be used to increase the level of rust resistance in future generations. These approaches are additive, in that each will increase the level of surviving trees.

We need to develop and implement strategies that will restore whitebark pine ecosystems as quickly as possible. The need is urgent, because the major ongoing threats to whitebark pine—blister rust, mountain pine needle, and secondary succession to shade-tolerant species—continue to decrease the size of whitebark pine populations. Delays in implementing management are actually a decision to accept even greater declines in whitebark pine populations.

Humans are responsible for the introduction of white pine blister rust to North America, which has dramatically reduced populations of five-needled white pines, including whitebark pine. We have accelerated the succession of whitebark pine ecosystems to shade-tolerant conifers through fire suppression activities. The good news is that we can help reverse declines in whitebark pine

populations and restore whitebark pine ecosystems. Whitebark pine is going through an extreme evolutionary bottleneck at present; the species and the ecosystems it occupies can benefit greatly from our assistance.

### Acknowledgment

We thank Eugene Van Arsdel, Texas A & M University, for reviewing an earlier draft of this chapter.

### LITERATURE CITED

- Arno, S. F., and R. J. Hoff. 1989. Silvics of whitebark pine (*Pinus albicaulis*). USDA Forest Service, Intermountain Research Station, General Technical Report INT-253, Ogden, Utah.
- Baker, F. S. 1944. Mountain climates of the western United States. Ecological Monographs 14:223–254.
- Barth, R. S. 1994. Pruning and excising white pine on the Wallace Ranger District as a blister rust control measure. Pages 333–334 in D. M. Baumgartner, J. E. Lotan, and J. R. Tonn, editors. Proceedings, Interior cedar-hemlock-white pine forests: Ecology and management. Cooperative Extension, Washington State University, Pullman, Washington.
- Bedwell, J. L., and T. W. Childs. 1943. Susceptibility of whitebark pine to blister rust in the Pacific Northwest. Journal of Forestry 41:904–912.
- Berube, J. A. 1996. Use of triadimefon to control white pine blister rust. Forestry Chronicle 72:637–638.
- Bingham, R. T. 1972. Taxonomy, crossability, and relative blister rust resistance of 5-needle white pines. Pages 271–280 in R. T. Bingham, R. J. Hoff, and G. I. McDonald, editors. Biology of rust resistance in forest trees: Proceedings of a NATO-IUFRO advanced study institute. USDA Forest Service, Miscellaneous Publication 1221, Washington, D.C.
- . 1983. Blister rust resistant western white pine for the Inland Empire: The story of the first 25 years of the research and development program. USDA Forest Service, Intermountain Research Station, General Technical Report INT-146, Ogden, Utah.
- Bingham, R. T., A. E. Squillace, and J. W. Wright. 1960. Breeding blister rust resistant western white pine. II. First results of progeny tests including preliminary estimates of heritability and rate of improvement. Silvae Genetica 9:33–41.
- Bruederle, L. P., D. F. Tomback, K. K. Kelly, and R. C. Hardwick. 1998. Population genetic structure in bird-dispersed pine, *Pinus albicaulis* (Pinaceae). Canadian Journal of Botany 76:83–90.
- Cooper, S. V., K. E. Neiman, and D. W. Roberts. 1991. Forest habitat types of northern Idaho: A second approximation. USDA Forest Service, Intermountain Research Station, General Technical Report INT-236, Ogden, Utah.
- Geils, B. W., D. A. Conklin, and E. P. Van Arsdel. 1999. A preliminary hazard model of white pine blister rust for the Sacramento Ranger District, Lincoln National Forest. USDA Forest Service, Rocky Mountain Research Station, Research Note RMRS-RN6, Fort Collins, Colorado.
- Hamrick, J. L., A. F. Schnabel, and P. V. Wells. 1994. Distribution of genetic diversity among populations of Great Basin conifers. Pages 147–161 in K. T. Harper, L. L. St. Clair, K. H. Thorne, and W. M. Hess, editors. Natural history of the Colorado Plateau and Great Basin. University of Colorado Press, Boulder.
- Hoff, R. J. 1984. Resistance to *Cronartium ribicola* in *Pinus monticola*: Higher survival of infected trees. USDA Forest Service, Intermountain Research Station, Research Note INT-343, Ogden, Utah.

- Hoff, R. J., and G. I. McDonald. 1980. Improving rust resistant strains of inland western white pine. USDA Forest Service, Intermountain Research Station, Research Paper INT-245, Ogden, Utah.
- Hoff, R. J., G. I. McDonald, and R. T. Bingham. 1976. Mass selection for blister rust resistance: A method for natural regeneration of western white pine. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Note INT-202, Ogden, Utah.
- Hoff, R. J., R. T. Bingham, and G. I. McDonald. 1980. Relative blister rust resistance of white pines. *European Journal of Forest Pathology* 10:307-316.
- Hoff, R. J., S. K. Hagle, and R. G. Krebill. 1994. Genetic consequences and research challenges of blister rust in whitebark pine forests. Pages 118-128 in W. C. Schmidt and F.-K. Holtmeier, compilers. *Proceedings—International workshop on subalpine stone pines and their environment: The status of our knowledge*. USDA Forest Service, Intermountain Research Station, General Technical Report INT-306, Ogden, Utah.
- Hungerford, R. D., R. E. Williams, and M. A. Marsden. 1982. Thinning and pruning western white pine: A potential for reducing mortality due to blister rust. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Note INT-322, Ogden, Utah.
- Hunt, R. S. 1998. Pruning western white pine in British Columbia to reduce white pine blister rust losses: 10-year results. *Western Journal of Applied Forestry* 13:60-63.
- Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia* 55:192-201.
- Hutchinson, G. E. 1958. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* 22:415-427.
- Johnson, D. R., B. B. Kinloch Jr., and A. H. McCain. 1992. Triadimefon controls white pine blister rust on sugar pine in a greenhouse test. *Tree Planters Notes* 43:7-10.
- Jorgenson, S. M., and J. L. Hamrick. 1997. Biogeography and population genetics of whitebark pine, *Pinus albicaulis*. *Canadian Journal of Forest Research* 27:1574-1585.
- Keane, R. E., S. F. Arno, and J. K. Brown. 1989. FIRESUM—An ecological process model for fire succession in western conifer forests. USDA Forest Service, Intermountain Research Station, General Technical Report INT-266, Ogden, Utah.
- Kelley, W. D., and J. C. Williams. 1985. Effects of triadimefon and triadimenol as seed dressings on incidence of fusiform rust on loblolly pine seedlings. *Plant Disease* 69:147-148.
- Kinloch, B. B., and M. Comstock. 1981. Race of *Cronartium ribicola* virulent to major gene resistance in sugar pine. *Plant Disease* 65:604-605.
- Kinloch, B. B., G. K. Parks, and C. W. Fowler. 1970. White pine blister rust: Simply inherited resistance in sugar pine. *Science* 167:193-195.
- Lachmund, H. G. 1926. Western blister rust investigations, 1926. Pages 19-23 in *Report of Proceedings, Western white pine blister rust conference*, Portland, Oregon.
- . 1928. Investigative work, 1928. Pages 12-19 in *Report of Proceedings, Western white pine blister rust conference*, Portland, Oregon.
- Mahalovich, M. F., and A. Eramian. 2000. Breeding, seed orchard, and restoration plan for the development of blister rust resistant white pine for the northern Rockies. USDA Forest Service, Northern Region and Inland Empire Tree Improvement Cooperative, Missoula, Montana.
- Mahalovich, M. F., and R. J. Hoff. 2000. Whitebark pine operational cone collection instructions and seed transfer guidelines. *Nutcracker Notes* 11:10-13. <http://www.mesc.usgs.gov/glacier/nutnotes.htm>
- Martin, J. F. 1944. *Ribes* eradication effectively controls white pine blister rust. *Journal of Forestry* 42:255-260.
- McCaughey, W. W. 1994. The regeneration process of whitebark pine. Pages 179-187 in W. C. Schmidt and F.-K. Holtmeier, compilers. *Proceedings—International workshop on subalpine stone pines and their environment: The status of our knowledge*. USDA Forest Service, Intermountain Research Station, General Technical Report INT-306, Ogden, Utah.
- McDonald, G. I. 1979. Resistance of western white pine to blister rust: A foundation for integrated control. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Note INT-252, Ogden, Utah.
- . 1982. Resistance-hazard alignment: A blister rust management philosophy. Pages 355-277 in D. Miller, compiler. *Proceedings: Breeding insect and disease resistant forest trees*. USDA Forest Service, Timber Management Staff, Washington, D.C.
- McDonald, G. I., and D. L. Dekker-Robertson. 1998. Long-term differential expression of blister rust resistance in western white pine. Pages 285-295 in R. Jalhaner, editor. *Proceedings of first IUFRO rusts of forest trees*, Saariselka, Finland. Finnish Forest Research Institute, Research Papers 712.
- McDonald, G. I., R. J. Hoff, and W. R. Wykoff. 1981. Computer simulation of white pine blister rust epidemics: 1. Model formulation. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper INT-258, Ogden, Utah.
- Mielke, J. L. 1943. White pine blister rust in western North America. *Bulletin* 52, School of Forestry, Yale University, New Haven, Connecticut.
- Mitton, J. B. 1995. Genetics and the physiological ecology of conifers. Pages 1-36 in W. K. Smith and T. M. Hinckley, editors. *Ecophysiology of coniferous forests*. Academic Press, New York.
- Ostrofsky, W. D., T. Rumpf, D. Struble, and R. Bradbury. 1988. Incidence of white pine blister rust in Maine after 70 years of a *Ribes* eradication program. *Plant Disease* 72:967-970.
- Rehfeldt, G. E. 1982. Differentiation of *Larix occidentalis* populations from the northern Rocky Mountains. *Silvae Genetica* 31:13-19.
- . 1988. Ecological genetics of *Pinus contorta* from the Rocky Mountains (U.S.A.): A synthesis. *Forest Ecology and Management* 28:203-215.
- . 1989. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*): A synthesis. *Silvae Genetica* 37:131-135.
- . 1991. Models of genetic variation for *Pinus ponderosa* in the Inland Northwest (U.S.A.). *Canadian Journal of Forest Research* 21:1491-1500.
- . 1994. Evolutionary genetics, the biological species, and the ecology of the interior cedar-hemlock forests. Pages 91-100 in D. M. Baumgartner, J. E. Lotan, and J. R. Tonn, editors. *Proceedings, Interior cedar-hemlock-white pine forests: Ecology and management*. Cooperative Extension, Washington State University, Pullman, Washington.
- Rehfeldt, G. E., R. J. Hoff, and R. J. Steinhoff. 1984. Geographic patterns of genetic variation in *Pinus monticola*. *Botanical Gazette* 145:229-239.
- Rehfeldt, G. E., C. C. Ying, D. L. Spittlehouse, and D. A. Hamilton Jr. 1999. Genetic responses to climate for *Pinus contorta*: Niche breadth, climate change and reforestation. *Ecological Monographs* 69:375-407.
- Robbins, K., W. A. Jackson, and R. E. McRoberts. 1988. White pine blister rust in the eastern upper peninsula of Michigan. *Northern Journal of Applied Forestry* 5:263-264.
- Schuster, W. S., D. L. Alles, and J. B. Mitton. 1989. Gene flow in limber pine: Evidence from pollination phenology and genetic differentiation along an elevational transect. *American Journal of Botany* 76:1395-1403.
- Schwandt, J. W., M. A. Marsden, and G. I. McDonald. 1994. Pruning and thinning effects on white pine survival and volume in northern Idaho. Pages 167-172 in D. M. Baumgartner, J. E. Lotan, and J. R. Tonn, editors. *Proceedings, Interior cedar-hem-*

- lock-white pine forests: Ecology and management. Cooperative Extension, Washington State University, Pullman, Washington.
- Simmonds, N. W. 1991. Genetics of horizontal resistance to diseases of crops. *Biological Review* 66:189–241.
- Smith, J. P., and J. T. Hoffman. 1998. Status of white pine blister rust in Intermountain Region white pines. USDA Forest Service, Intermountain Region, State and Private Forestry, Forest Health Protection Report No. R4-98-02, Ogden, Utah.
- . 2000. Status of white pine blister rust in the Intermountain West. *Western North American Naturalist* 60:165–179.
- Spaulding, P. C. 1911. The blister rust of white pine. USDA Bulletin Number 206. Washington, D.C.
- Toko, H. V., D. A. Graham, C. E. Carlson, and D. E. Ketchum. 1967. Effects of past *Ribes* eradication on controlling white pine blister rust in northern Idaho. *Phytopathology* 57:1010.
- 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., and Y. B. Linhart. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology* 4:185–219.
- Tomback, D. F., J. K. Clary, J. Koehler, R. J. Hoff, and S. F. Arno. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: The Sundance burn of northern Idaho (U.S.A.). *Conservation Biology* 9:654–664.
- USDA Forest Service. 1999. Transfer rules. Chapter 4 in *Seed handbook*. Draft Forest Service Handbook 2409.26f (Regions 1–4), Missoula, Montana.
- Van der Plank, J. E. 1963. *Plant disease—Epidemics and control*. Academic Press, New York.
- . 1968. *Disease resistance in plants*. Academic Press, New York.
- Wright, J. 1976. *Introduction to forest genetics*. Academic Press, New York.
- Zadoks, J. C. 1972. Reflections on disease resistance in annual crops. Pages 43–63 in R. T. Bingham, R. J. Hoff, and G. I. McDonald, editors. *Biology of rust resistance in forest trees: Proceedings of a NATO-IUFRO advanced study institute*. USDA Forest Service, Miscellaneous Publication 1221, Washington, D.C.