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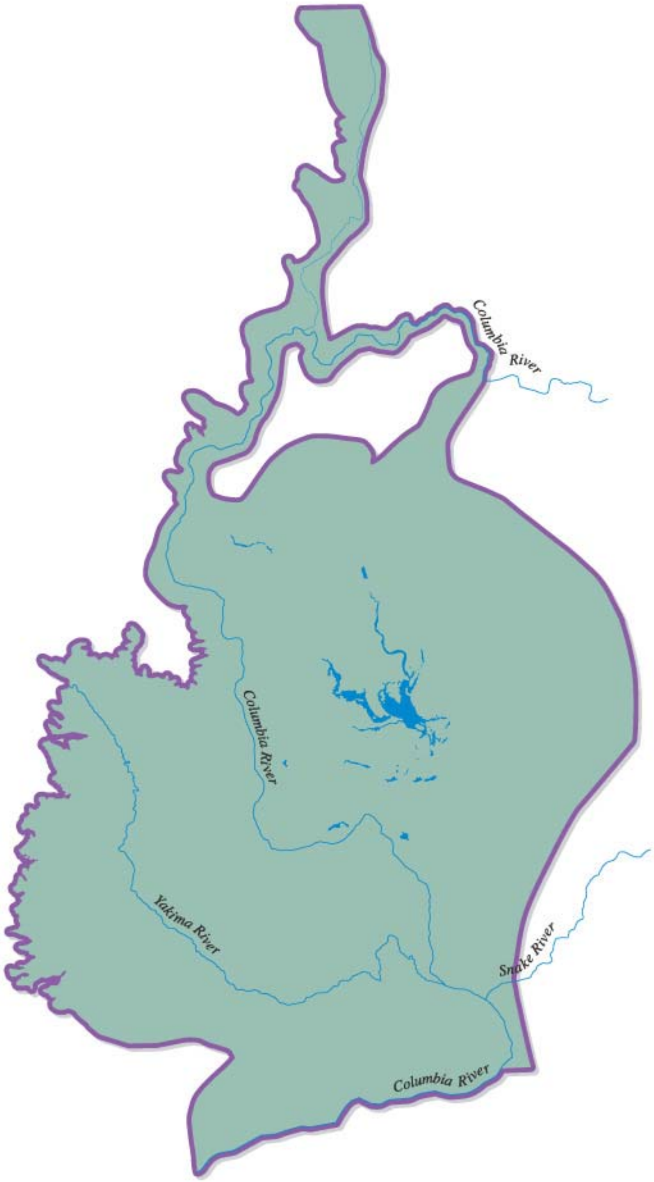
Big Sagebrush: A Sea Fragmented into Lakes, Ponds, and Puddles

Bruce L. Welch



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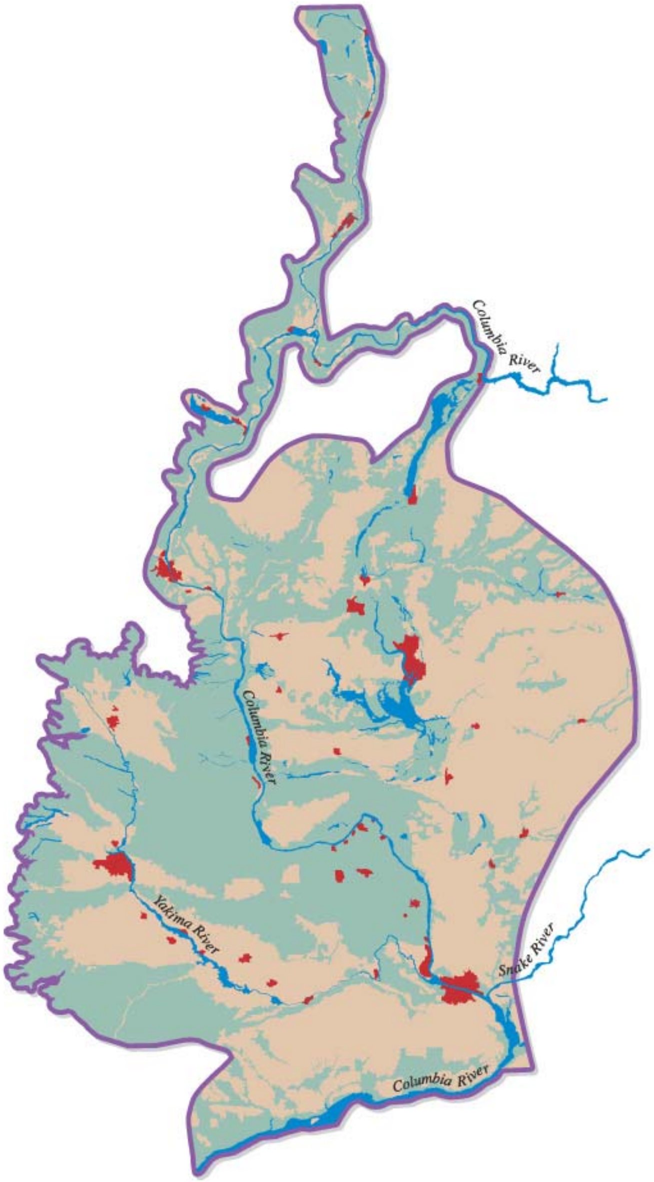

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Washington after settlement

Abstract

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Pioneers traveling along the Oregon Trail from western Nebraska, through Wyoming and southern Idaho and into eastern Oregon, referred to their travel as an 800 mile journey through a sea of sagebrush, mainly big sagebrush (*Artemisia tridentata*). Today approximately 50 percent of the sagebrush sea has given way to agriculture, cities and towns, and other human developments. What remains is further fragmented by range management practices, creeping expansion of woodlands, alien weed species, and the historic view that big sagebrush is a worthless plant. Two ideas are promoted in this report: (1) big sagebrush is a nursing mother to a host of organisms that range from microscopic fungi to large mammals, and (2) many range management practices applied to big sagebrush ecosystems are not science based.

Keywords: *Artemisia tridentata*, distribution, canopy cover relationships, fire interval, nutritive value

The Author

Bruce L. Welch is a plant physiologist with the Rocky Mountain Research Station in Provo, UT. He earned a B.S. degree from Utah State University in 1965 and an M.S. in 1969 and Ph.D. in 1974 from the University of Idaho. He has been a Forest Service scientist since 1977.

Pesticide Precautionary Statement

Big Sagebrush: A Sea Fragmented into Lakes, Ponds, and Puddles

Bruce L. Welch

Preface

Ode to Sagebrush

What an amazing plant; the sage, so many faces has it.
The most versatile of our shrubs. High value must be placed upon it.
So many creatures large and small get winter food source from it.
The pungent leaves forever fresh when others are dormant beside it.
Break the wind and catch the snow, the ground is safe around it.
What a conservationist this plant! Why don't more people know it?
Caretaker of the soil, protecting dormant seeds beneath it.
So the desert can once more bloom when conditions are right for it.
And summer too receives a share of favors coming through it.
The shade, the cover, and nests that birds have built within it.
Insect galls on the limbs and burrows dug below it.
What a vast variety of life, find home and solace in it.
Paintbrush, so beautiful and fine, could not survive without it.
Pushing down roots to attached below, nourishment coming of it.
In fall it blooms and beauty gives to all the land about it.
The autumn days delight the air. Smell the aromas that cause it!
How often I have heard the phrase: "It's just sagebrush,
let's remove it."
So naive these people are to fasten that opinion to it.
I once thought of sage as drab before I really knew it.
Now I view it in another light, and attach much beauty to it.

Dave Hanks, Biology Teacher—Burley High School, Idaho; reprinted from the Idaho Wildlife, March/April 1985, page 16

The above poem by a Burley High School biology teacher shows an incredible amount of insight into the ecology and value of big sagebrush (*Artemisia tridentata*). This general technical report supports the ecological principles and value of big sagebrush as expressed in the poem. Over 1,600 scientific and nonscientific articles concerning big sagebrush have been reviewed; many are cited within these pages.

The subject matter covered in this general technical report can be obtained by scanning the table of contents and need not be repeated here.

After studying the big sagebrush ecosystem for 30 years, I have come to three conclusions:

1. Much misinformation concerning the value and ecology of big sagebrush exists in the land management community.
2. The perceived shortcomings of big sagebrush are a result of livestock grazing.
3. Big sagebrush is a nursing mother to a host of organisms ranging from microscopic to large mammals.

I hope that those who read this general technical report will come to the conclusion that big sagebrush is a valuable plant species worth preserving. I am, Bruce L. Welch.

Acknowledgments

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Dedication

Whatever honor there may be in this publication, I wish to dedicate it to the following: Drs. Alan A. Beetle, Rexford F. Daubenmire, Howard R. Leach, and Arthur D. Smith—all pioneers in big sagebrush research.

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Chapter I

Getting Acquainted With Big Sagebrush

This chapter describes the distribution, life expectancy, morphology, soils, and taxonomy of big sagebrush (*Artemisia tridentata*). Perhaps the most important question addressed in this chapter is: How much of the big sagebrush ecosystem remains?

Distribution

The distribution or range of big sagebrush depends on climate and has fluctuated for the past 30 millennia. In general, big sagebrush favors areas that receive the majority of their precipitation in winter months and the least in summer months (Cook and Irwin 1992; Smith 1940; Whitlock and Bartlein 1993).

Climate

Climate is the prevailing weather condition of temperature, barometric pressure, humidity, precipitation, sunshine, cloudiness, and wind throughout the course of many years. The driving force is the sun. It is the uneven heating of Earth—greater solar heating of the tropic regions than the polar regions—that stirs the atmosphere into motion on an intraplanetary scale and creates Earth's major wind systems. It is this wind system, interacting with Earth's surface topography and bodies of water that bring cold, warm, moist, or dry air to a given region. The global wind system is in constant motion as it pumps tropical warm air toward the poles while moving cooler air back toward the tropics. All the time the wind system is being twisted by Earth's rotation into vast rivers of air with an eastwardly direction, interacting with oceans and continents, climbing mountain ranges and sinking into lowlands, but forever on the move. This relentless stirring of the atmosphere creates contrasting weather patterns as the wind system circumnavigates Earth. Repeated over a course of many years, climate is formed from these contrasting weather patterns. Still, these patterns can be interrupted by variations in the output of the Sun; eruptions of volcanoes that spread ash in the upper atmosphere and in effect reduce the heating of the planet; the uplifting of mountains and plateaus, which intercept moisture and create rain shadows, discordances between air, oceans, and polar ice or the lack there of; and the gravitational tug of other celestial bodies that slightly reshapes Earth's orbit (eccentricity), the tilt of its axis (obliquity), and the time of year when the Earth-Sun distance is maximum or minimum (precession). All of these may redistribute the heating of Earth and cause great changes in the climate of a given region (Schoonmaker and Foster 1991).

For most of the past 100 millennia, the climatic conditions throughout the range of big sagebrush were dominated by the Wisconsin glacial epoch of the Quaternary period, which ended about 8,000 years ago (Antevs 1948).

In fact, the whole Quaternary period comprising the past 1.6 to 2.0 million years has been a period characterized by alternating wet and cool and dry and warm climates (Schoonmaker and Foster 1991). During this period some 24 glacial events have been identified, making the Quaternary period a colder period as compared to the warmer Tertiary period (Schoonmaker and Foster 1991). Glacial stages during the Quaternary period have lasted from 50,000 to 100,000 years. These glacial events result in slow formation of large ice sheets in the high latitudes in an "oscillatory" fashion and end with a rapid melting of the ice sheets, followed by a warming interglacial interlude of some 10,000 to 20,000 years (Schoonmaker and Foster 1991). It is believed that this alternation between glacial and interglacial interludes is caused by the cyclical alteration of Earth's orbit around the Sun (Schoonmaker and Foster 1991). This alteration of Earth's orbit comprises three components: eccentricity, obliquity, and precession. All three are themselves cyclic. Eccentricity, which is the degree that Earth's orbit varies from a perfect circle about the Sun, varies from 0 to 6 percent on a 100,000-year cycle and affects the distance between Earth and Sun (Schoonmaker and Foster 1991). Obliquity refers to the tilt of Earth on its axis; this varies from 22 to 24.5 degrees on a 41,000-year cycle and affects the latitudinal heating of the planet (Schoonmaker and Foster 1991). Precession, or time of year when maximum or minimum distance between Earth and Sun occurs, varies about 10 percent on a 22,000-year cycle and affects seasonality (Schoonmaker and Foster 1991). It is the interplay of these three cycles that determines the specific climatic conditions of a given region and the general climatic conditions of the entire planet. Based on orbital geometry, a cooling trend is predicted in the next few thousands years (Schoonmaker and Foster 1991).

Modern weather patterns are described by Antevs (1948). In the Western Hemisphere, the modern winter weather patterns are characterized by formation of ice and snow throughout all of the northern land (Canada). This in turn reflects a large amount of solar radiation back into space and creates a large cold air mass. It is this contrast of temperature and pressure over the frozen north and open oceans and snow-free and ice-free land that results in the development of anticyclonic pressure (high pressure) that sends waves of cold polar air moving southward. This cold air collides with warm moisture riding on the westerlies that are generated from the subtropical high pressure zones located at about 30° latitude. When these air masses are large enough, semipermanent lows, the Aleutian Low and the Iceland Low, develop resulting in contemporary winter weather patterns. With the tilting of Earth's axis, which warms the northern land and thus melts ice and snow, less solar energy is reflected back into space. In turn, a semipermanent low pressure zone is established over the continent, the Aleutian Low is reduced, and a high pressure zone is formed over the Pacific Ocean at about 40° latitude. This high pressure causes the near rainless summers that occur in the big sagebrush ecosystem or deserts of the Western United States.

The huge unyielding ice sheets created during the Wisconsin Glacial Epoch resulted in the permanency of the Aleutian Low pressure field throughout the summer in spite of rising summer temperatures. This forced the summer subtropical high pressure field of the Pacific to form further south, perhaps below 30° latitude, thus creating a pluvial period for the Western United States as storm tracts move across the region throughout the entire year. This contrasts to weather patterns of the present interglacial interlude of cold, moist winters and dry, hot summers.

Big sagebrush, like other plant species, has over the past 20 or 30 millennia adjusted its distribution as climatic conditions changed, expanding during favorable periods and contracting during unfavorable times (Antevs 1948; Schoonmaker and Foster 1991). This expansion and contraction of plant species distribution can be monitored over time by studying fossil plant parts such as pollen, seeds, leaves, and twigs contained in lake muds, bogs, peats, and in drier climates, woodrat (*Neotoma* sp.) middens (Schoonmaker and Foster 1991).

Woodrat Middens

Woodrat middens are somewhat analogous to sanitary landfills of humans minus the sanitary part. Middens are piles of accumulated organic (plant and animal) and inorganic materials gathered by woodrats and deposited near and within their dens (Dial and Czaplewski 1990; Finley 1990). Dial and Czaplewski's (1990, p. 47) description:

> The midden portion of a modern woodrat den was considered to be those materials accumulated by the woodrat, including unused plant clipping, woodrat feces, and faunal materials (bones and insects). Often the materials were in the process of being coated with or cemented together by rat urine (i.e., they comprised the animal's habitual "toilet" area), but only small portions were consolidated and indurated with urine.

Other materials such as leaves, pollen, and sand may be deposited in the middens by means other than woodrat activities (wind; Finley 1990).

Van Devender and King (1971) studied the plant macrofossils preserved in woodrat middens in the Artillery Mountains of southern Mohave County, AZ. They reported finding what they considered to be

18,000-year-old big sagebrush leaves occurring in what is today a Sonoran Desert community. Pollen analysis of these middens showed the presence of *Artemisia* pollen from 10,000 to more than 30,000 years ago or B.P. (Before Present). Because *Artemisia* pollen is not distinguishable at the species level, the authors believe that the pollen found in the various middens was big sagebrush pollen (Cawker 1983). A modern analogue (big sagebrush) presently grows north and west of the Artillery Mountains in association with pinyon and juniper (Jameson and others 1962; Van Devender and King 1971). Van Devender and King (1971) concluded that from 10,000 to more than 30,000 years B.P., the Artillery Mountains supported a pinyon/juniper woodland with abundant big sagebrush, but as the climate became warmer and drier, sometime after 10,000 years B.P., this plant community could not survive and yielded to the Sonoran Desert vegetation of today. Cole (1985) presents evidence that big sagebrush has been present in the Grand Canyon region of northern Arizona for the past 24,000 years.

Unlike the Van Devender and King (1971) report, Nowak and others (1994a) found evidence of the presence of big sagebrush in the Painted Hills in the Virginia Mountains of northwestern Nevada, from 30,000 year B.P. to the present. Their study site was located about 4.75 miles west of Pyramid Lake, a remnant of the pluvial Lake Lahontan. Present vegetative cover consisted mainly of Utah juniper (*Juniperus osteosperma*), big sagebrush, shadscale (*Atriplex confertifolia*), and various bunchgrasses. They, too, sampled woodrat middens and identified plant macrofossils found in the various midden samples. Some of the fossils they were able to identify as big sagebrush, but a number of others were listed as being *Artemisia* sp. However, Nowak and others (1994a, p. 583) believed that many of the fossils listed as *Artemisia* sp. were likely big sagebrush because "*A. tridentata* is the dominant species for our locale and was the only species identified in the fossil record." An interesting point of the Nowak and others (1994a) study is the occurrence of big sagebrush throughout the fossil record, in spite of large changes in local and regional climatic conditions.

Two possible explanations may account for big sagebrush longevity at this site: first, the site may have been a refugium for big sagebrush (that is, an area of relatively unaltered climate not totally reflecting the continental climatic changes that occur during glacial and interglacial periods). Or, second, big sagebrush may have possessed a high degree of genetic variability. Nowak and others (1994a, p. 588) favor the latter:

> Plants of the sagebrush steppe of the northern Great Basin appear to possess a high degree of genetic variability within a species, which allows these species to tolerate a high degree of climatic variation. Evidence for a high degree of genetic diversity within a variety of modern Great Basin shrub species comes from modern plant ecology studies conducted by the [USDA Forest Service] Shrub Laboratory and by other scientists.

The genetic richness of big sagebrush is discussed in chapter V. They further found a trend from a higher proportion of herbaceous species to a higher proportion of shrubby species as the climate became warmer and drier from the Pleistocene epoch to the current Holocene epoch.

Nowak and others (1994b) found big sagebrush macrofossils occurring in woodrat middens sampled at 11 sites in western Nevada and east-central California near the Nevada-California border. All macrofossils were at least 1,000 years old and many older. Big sagebrush is present in the modern vegetation at all sites except one (Hot Springs Mountains).

About 250 miles east of the Lahontan Basin and within the vicinity of the Bonneville Basin, the story of big sagebrush macrofossils in woodrat middens is similar. Rhode and Madsen (1995), studying plant macrofossils from 15 woodrat middens scattered throughout the vicinity of the Bonneville Basin, found evidence of big sagebrush at all 10 locations. Age of these middens varied from 9,000 to 14,000 years B.P. and varied in elevation from 4,840 to 6,600 feet. Abundance of big sagebrush among the middens varied from rare to dominant. The authors concluded that cold montane steppe, dominated most likely by big sagebrush, covered most of the western Bonneville Basin some 13,000 years ago. After this time and until for a relatively brief period 10,800 years ago, Rhode and Madsen (1995) suggest that limber pine (*Pinus flexilis*) woodlands expanded into the region and then retreated upslope because of drier climatic conditions that followed. Big sagebrush, however, persisted in spite of climatic changes (wetter) and the expanding limber pine woodland, and remained there during the drying period and decline of the limber pine woodland, even to the present day

Thompson (1990), using midden evidence, argued that 34,000 years B.P. big sagebrush in the eastern Great Basin (northern Snake Range of Nevada) commonly grew with bristlecone pine (*Pinus longaeva*) and currant (*Ribes* sp., not identified); at 18,000 years B.P. big sagebrush grew with bristlecone pine, currant, prostrate juniper (*Juniperus communis*), Engelmann spruce (*Picea engelmannii*), and Rocky Mountain juniper (*Juniperus scopulorum*); at 7,000 years B.P. it grew with bristlecone pine, prostrate juniper, limber pine, Rocky Mountain juniper, and Rocky Mountain maple (*Acer glabrum*); and by 2,000 years B.P. all these species, except big sagebrush, were absent in woodrat midden fossil records. He concluded, based on the studies he reviewed, that during the late Pleistocene epoch, sagebrush (most likely big) maintained its modern geographic ranges. It is suggested in Thompson (1990) that much of the historical woodlands, montane, and subalpine vegetation of the Great Basin was an overlay of a continuous matrix (mostly) of big sagebrush habitat. Tausch (1999, p. 15) makes a similar statement for today:

> With the full perspective of Holocene history, plant species found in the understory of today's woodlands, and in the majority of locations, have generally existed in a variety of shrub and grass-dominated communities for far longer periods of time than they have in tree-dominated communities. Because tree-dominated woodlands have been much more temporary or transitory, it is the nontree-dominated communities that are the matrix within which are imbedded pockets of woodlands of various successional stages.

Mehringer and Wigand (1990) studied the macrofossils (leaves, stems, seeds, buds) and microfossils (pollen) of woodrat middens located in the Diamond Craters area of southeastern Oregon. Ages of their middens range from 800 to 4,000 years B.P. All 24 woodrat middens examined showed a dominance of juniper and *Artemisia* in both the macrofossil and microfossil spectrum. There is a high probability that the dominant *Artemisia* was big sagebrush. Big sagebrush is the dominant shrub of present day vegetation. Mehringer and Wigand (1990, p. 309) described their findings: "Pollen from the interiors of twelve middens from Diamond Craters corresponds to the macrofossils in their monotonous predominance of juniper and sagebrush pollen."

Koehler and Anderson (1995) were able to construct a 31,000-year-old vegetative history-pollen spectrum for the Alabama Hills of Owens Valley, CA, from woodrat middens. The presence of big sagebrush was continuous throughout the 31,000-year period in spite of the disappearance of juniper 5,000 years ago; the decline started about 17,000 years ago with the waxing and waning of other species. The big sagebrush pollen profile is the least variable of 13 pollen profiles studied.

So, what have we learned from the study of woodrat middens? That big sagebrush persisted throughout the Great Basin, central Oregon, and east-central California for thousands of continuous years and on some sites for more than 30,000 years. Big sagebrush in humanistic terms is a long-term survivor.

Pollen Spectrum From Lakes, Bogs, and Peats

Pollen records from lake muds, bogs, and peats furnish still more evidence that big sagebrush is a long-term survivor not only in the Great Basin and central Oregon but at other Western United States locations. *Artemisia* pollen cannot be identified as to species. This section cites studies whose *Artemisia* pollen spectrum would have a high probability that some, if not most, of the pollen was derived from big sagebrush.

Five fossil pollen studies have been conducted in and around Yellowstone National Park (Baker and Richmond 1978; Waddington and Wright 1974; Whitlock 1993; Whitlock and Bartlein 1993; Whitlock and others 1995). While the five studies' emphases were concentrated on the reaction of tree species to changes in climate, all reported significant amounts of *Artemisia* fossil pollen throughout their various constructed pollen spectrums from 14,000 to 70,000 years B.P. to the present. Based on modern analogues, of the presence of big sagebrush throughout the region, some if not most of the *Artemisia* pollen found were probably produced by big sagebrush plants (Beetle and Johnson 1982). The percentage of *Artemisia* pollen in the pollen spectra peaked about 14,000 years B.P. and has persisted continuously at a lower level to the present, in spite of changes in climatic conditions and changes through time in tree species composition at the various study sites. In other words, tree species came and went as climatic changes occurred, but big sagebrush still persisted. Moving the scene to the southeast to the Wind River Mountain Range of Wyoming and increasing the elevation to 10,100 feet, we see the same story—a 12,000-year pollen spectrum history showing the persistence of big sagebrush (Fall and others 1995).

Madsen and Currey (1979) describe four glaciation periods during the past 26,000 years in Little Cottonwood and Bell Canyons in Utah's Wasatch Mountains. The earliest of the four (Dry Creek till) reached the mouth of Little Cottonwood Canyon some 26,000 years ago and then receded for a time until about 19,000 years ago. A second glacier (Bells Canyon till) formed and pushed its way down to the mouth of the canyon; it too receded. Then about 12,300 years B.P., several glaciers (Hogum Fork till) were formed and pushed their way to mid-canyon and then receded. Again about 7,500 years ago, a fourth glacier (Devils Castle till) was formed and pushed its way a small distance from where it was formed (Devils Castle area), and it also receded. During these 26,000 years the climatic conditions varied among four possibilities: cool/wet, cool/dry, warm/dry, and warm/wet. Still the pollen spectrum of this area demonstrated the persistence of big sagebrush throughout the period of climatic changes. Madsen and Currey (1979, p. 264), concerning the finding of their fossil pollen study, stated:

> Together these pollen types suggest a dominance of alpine meadows on moist canyon bottoms, a sagebrush-dominated community on ridge sides and knolls, and a large community of alder, birch, and willow along stream sides. Plant communities of this type are presently found at elevations of 2,650 to 2,900 m in the canyon and apparently existed at lower elevations several times during the Holocene.

In the Chuska Mountains of northwestern New Mexico, big sagebrush has persisted in the fossil pollen record for about 50,000 years (Wright and others 1973).

After observing evidence for the presence of big sagebrush pollen throughout three pollen diagrams from southern British Columbia, Cawker (1983, p. 1126) concluded:

> The increasing dominance of grasslands after 1890 by *Artemisia tridentata* and other woody shrubs has often been attributed to overgrazing by domestic livestock, but pollen data indicate that shrub populations were substantial in presettlement times, and that the recent "invasion" represents a recovery from anomalously low population levels during the middle 19th century.

Wigand (1987, p. 427) presents similar data from central Oregon for the past 6,000 years and concluded: "Since the mid-1800s man and changing climate have encouraged sagebrush reexpansion."

Big sagebrush pollen was found to be continuously present in a fossil pollen spectrum from the Dome Creek (3,165 m) area of northwestern Colorado (Feiler and others 1997). The period covered from 10,600 years ago to 120 years ago, during which the pollen profiles of several species were not continuous (Feiler and others 1997). Even though the study site is in a subalpine zone, Feiler and others (1997, p. 54) noted that *Artemisia* steppe, dominated by big sagebrush, "occurs at least as high as 3,050 m on portions of the drier, south-facing side of the drainage."

In southeastern Oregon, a big sagebrush pollen profile was continuous from 2,000 years ago to the present (Mehringer and Wigand 1990). This is in agreement with the woodrat middens analysis covering a period of 800 to 4,000 years B.P. cited earlier in this section. Other areas where big sagebrush pollen profiles are reported as being continuous for thousands of years are: Great Salt Lake, Utah; Swan and Grays Lakes, Idaho; and Sheep Mountain Bog, Montana (Beiswenger 1991; Bright 1966; Mehringer 1985).

What have we learned from all these macrofossil and microfossil studies? Beetle and Johnson (1982) noted that big "sagebrush is where sagebrush was"; only now, "was" can be defined in terms of tens of thousands of years (Bright 1966; Johnson 1986). The converse of this statement is not necessarily true; there are areas where big sagebrush was during earlier climatic regimes but has given way to other vegetative types, such as Sonoran Desert vegetation of the Artillery Mountains of Arizona (Van Devender and King 1971) and coniferous forests of northeastern Washington and northern Idaho (Mehringer 1985).

Historic Accounts of Big Sagebrush

Lewis and Clark described what was probably big sagebrush on April 14, 1805, near the mouth of the Little Knife River, ND (Coues 1965). Another possibility would be plains silver sagebrush (*A. cana*). On August 5, 1805, Captain Lewis encountered areas having little grass but covered with "southernwood" or big sagebrush as they traveled through the Jefferson River region of Montana (Coues 1965). They often sighted sage grouse (*Centrocercus urophasianus*) as they traveled through the upper parts of the Missouri River basin and the plains of the Columbia River (Coues 1965). The presence of sage grouse is a good indicator of vast, dense stands of big sagebrush (see chapter II).

Douglas (1914), as he described it, conducted "botanising" trips into an area ranging from Fort Vancouver on the Columbia River to the Blue Mountain of southeastern Washington, to Kettle Falls on the Columbia River of northeastern Washington, during the years of 1824 to 1827. He collected numerous samples of *Artemisia*; most were probably big sagebrush, along the Columbia River of central Washington. Douglas (1914, p. 180) noted numerous sightings of sage grouse and stated that they "are seen abundantly...seen in large flocks...by no means a rare bird. Raised two large flocks near the Grand Coulee and had to content myself with a sight of them, having no gun." He also noted sage grouse in central Washington and defined their range from the Cascade Range in the west to the Great Dividing Range in the east. All sightings of sage grouse hint at the presence of vast, dense stands of big sagebrush covering central Washington.

Traveling through Nebraska, Townsend (1834) encountered an *Artemisia* on May 25, 1833, that was either big sagebrush or plains silver sagebrush (*A. cana*). His description more closely resembles big sagebrush; the soil it was growing in (poor and sandy) would tend to support big sagebrush. Nonetheless, the sagebrush was thick with little grass. West of Laramie's fork on the North Platte (Fort Laramie in 1846), Townsend (1834, p. 183) on June 7, 1833, describes the country:

> The country has now become more level, but the prairie is barren and inhospitable looking to the last degree. The twisted, aromatic wormwood covers and extracts the strength from the burnt and arid soil. The grass is dry and brown, and our horses are suffering extremely for want of food. Occasionally, however, a spot of lovely green appears, and here we allow our poor jaded friends to halt, and roam without their riders, and their satisfaction and pleasure is expressed by many a joyous neigh, and many a heart-felt roll upon the verdant sward.

The aromatic wormwood spoken of is big sagebrush.

On the Sandy River plains, Townsend (1834, p.188) noted large herds of buffalo grazing on the short and dry grass and observed: "Domestic cattle would certainly starve here, and yet the bison exists, and even becomes fat; a striking instance of the wonderful adaptation of Providence." In spite of the presence of buffalo, Townsend still noted that their poor horses had to fast as before because there was nothing to eat. He further noted on June 17, 1833, that some of their horses ate the tops of big sagebrush "with which the plain is strewed." From the Green River, through Ham's Fork and on to the Bear River on July 6 to 8, 1833, Townsend made many sightings of sage grouse, "but on the plain, nothing flourishes but the everlasting wormwood, or sage as it is here called." After spending some time, perhaps a day or two, at White-Clay Pits on the Bear River (Soda Springs, ID), his party left on July 10 and in doing so observed (Townsend 1834, p. 202):

> Soon after we left, we crossed one of the high and stony hills by which our late camp is surrounded; then making a gentle descent, we came to a beautiful and very fertile plain. This, however, very different from the general face of the country; in a short time, after passing over the rich prairie, the same dry aridity and depauperation prevailed, which is almost universal west of the mountains.

From here the Townsend party moved on to Fort Hall, ID, and noted, upon crossing the Snake River on August 6, a wide sandy plain thickly covered with wormwood or big sagebrush and that their hunters had killed a few sage grouse. From Fort Hall, the Townsend party moved in a northwest direction to the Lost River country of Idaho and then on to Fort Boise. Most travelers from Fort Hall would travel along the Snake River to Fort Boise, but the Townsend party went along the least traveled route. Traveling for about 4 days in the Lost River country of Idaho, Townsend said it was, "covered by the eternal sage bushes." From the Lost River country of Idaho to the Blue Mountains of Oregon, big sagebrush and sage grouse would be their almost constant companions.

Wislizenus (1839), although not the naturalist that Townsend was, also traveled the same course to Fort Hall and noted the abundance of big sagebrush from Nebraska to the Blue Mountains of Oregon. In 1849 Major Osborne Cross and George Gibbs traveled the same route and noted much big sagebrush (Settle 1940, p. 107–108), adding:

> June 29. Our road today passed over a dreary and uninteresting route—more so than any since leaving Fort Laramie. The hills are not so high as you approach the Platte but [are] entirely barren. Nothing was to be seen but the artemisia or wild sage, which is extremely uninteresting, having neither beauty nor usefulness to recommend it and its odor [is] by no means pleasant. We were destined to travel a very long distance where this shrub was constantly to be seen in greater quantity than had been already met with. It may be truly said that we had just entered it, as it was not very [plentiful] or large, compared with what we afterwards met with on the route. There must be something in the composition of the earth particularly adapted to its growth, for whenever the grass was scarce we invariably found it in great quantities. I have traveled for days before reaching the Columbia River where nothing could be seen on the highlands and plains but the artemisia, which for miles looked as if the whole country had been cleared of all other vegetation to make room for it.

In 1843 and 1844, Fremont (1845), a trained naturalist, reported to the Congress of the United States much the same observations of big sagebrush abundance from Nebraska to Fort Hall, ID, as did the Townsend report of 10 years earlier (Townsend 1834). But in addition to the Townsend report, Fremont traveled down the Bear River through Cache Valley to the Great Salt Lake and to Fort Hall, and from Fort Hall, along the Snake River, whereas Townsend moved northwest from Fort Hall to the Lost Rivers country and then west to Fort Boise. Both naturalists traveled to the Blue Mountains of Oregon. Fremont's journey took him down the Columbia River to the Dalles and from there to Pyramid Lake through central California, southern Nevada and Utah, and north-central Utah. During this long trek, Fremont recorded the domination of big sagebrush in Nebraska, Wyoming, Idaho, Oregon, Washington, Nevada, California, and Utah. While traveling to Fort Hall, ID, on September 16, 1843, Fremont (1845, p. 161) made an astute observation concerning big sagebrush: "This plant loves a dry, sandy soil, and cannot grow in the good bottoms where it is rich and moist, but on every little eminence, where water does not rest long, it maintains absolute possession."

Gruell (1986, p. 3) also quoted this statement of Fremont and concluded: "By inference, Fremont's statement suggests that grasses commonly occupied deep soils. Because sagebrush was capable of growing on these sites, there is reason to believe that it was excluded by fire." The key words of the Fremont's statement are "bottoms," "moist," and "water does not rest long." The bottoms spoken of are valley bottoms with a river or creek flowing through it and the zone impacted by the river's water commonly known as riparian zones or the rising of water table by the flow of ground water from mountain slopes into valley bottoms. These zones can be narrow like a small creek running through a big sagebrush stand or large like the Bear River flowing through Cache Valley, UT. "Moist" and "water does not rest long" refer to the fact that big sagebrush cannot survive long in water-saturated soils.

There is a physiological and pathological explanation for Fremont's astute observation. The oxygen requirement for big sagebrush root development, growth, and survival is high. During periods of high soil-water content, plants become stressed, enabling soil-borne plant pathogens to enter the root system, killing the roots of established plants, in the case of flooding, or killing the roots of seedlings, whose seeds fell into a riparian zone or area of high water table (Caldwell 1979; Lunt and others 1973; Nelson and Krebill 1981; USSCS 1950). In fact, Ganskopp (1986) suggests flooding or water spreading as a technique to control Wyoming big sagebrush. Sturges (1989, p. 1035) noted: "[Mountain big] sagebrush on the downwind side of the [snow] fence was eliminated by the third growing season, apparently because of the longer time the soil was saturated."

So the exclusion of big sagebrush spoken by Gruell (1986) probably was not by fire (see Daubenmire 1970 section on aborigines, grazing, and fire; also Welch and Criddle 2003) but rather by the physiological and pathological characteristics or limitations of big sagebrush itself. In many Great Basin valleys, such as Cache and Malad Valleys, high water tables and springtime flooding favor the creation of grassy areas, and grass dominates over big sagebrush (Thatcher 1959). Fire was noted twice by Townsend and Fremont in the portions of their reports that I read (Fremont 1845; Townsend 1834). Two fires were noted in the coniferous forests of the Blue Mountains of Oregon and the remaining two in grasslands.

In addition to high a water table, Woodward and others (1984) suggest that root cation-exchange capacities may also play a role in the differential distribution of big sagebrush and grasses (33.53 versus 14.77 me/100 g).

Stansbury (1852), under orders to survey the Great Salt Lake of Utah and its valley, corroborates the earlier reports of Townsend and Fremont concerning the abundance and dominance of big sagebrush from Fort Laramie to Fort Hall and from Fort Hall to the Great Salt Lake. While surveying the Great Salt Lake, Stansbury (1852) referred to the presence of big sagebrush many times:

> April 12, 1850, "cooking was furnished by the wild sage";
>
> April 30, "the camp pitched in a thicket of grease-wood and artemisia";
>
> May 1, "in wandering among the artemisia";
>
> May 10, "here we found that we had still half a mile farther to go to reach the nearest artemisia-bushes, which have now become our sole dependency for fire wood gave shelter to shoals of gnats";
>
> May 13, "we found, to our dismay, that an extensive flat of sand still lay between us and the line of grass and bushes where alone we could obtain fuel for cooking. Over this, the camp was carried upon weary shoulders, and pitched among some artemisia";
>
> At this same location Stansbury noted: "The place had long been a resort for the few Indians that occasionally pass through this inhospitable region. Remains of old lodges constructed of sage-bush, beds of the same...";
>
> May 16, another entry about using big sagebrush for cooking;
>
> May 28, the vegetation was the ever-recurring artemisia, bunch-grass, and a few scattering dwarf cedars no more than 10 feet high; and the accounts of encounters with big sagebrush continued.

Watson (1871, p. 27) observed this about big sagebrush in the Great Basin:

> Sometimes mingled with them, but wholly free from alkaline preferences and beyond their range usurping entire predominance is the everlasting sagebrush, the *Artemisia tridentata*. This is by far the most prevalent of all species, covering valleys and foothills in broad stretches farther than the eye can reach, the growth never so dense as to seriously obstruct the way but very uniform over large surfaces, very rarely reaching the saddle-height of a mule and ordinarily but half that altitude.

Wakefield (1936, p. 14) who studied the private diaries of explorers and pioneers, historical government reports of geological explorations, and other records, concerning the plant communities of Salt Lake and Utah Valleys, concluded: "The evidence seems to show that there was originally a much larger proportion of grasses on the bench lands than sagebrush or oak." Of interest about his article is the vegetative description of Utah Valley. Along the eastern side much grass and little big sagebrush grow; but on the west side, "They say the wild sage is very plentiful." By the year 2000, little big sagebrush was present on the foothills along the eastern side of Utah Valley, as viewed from the United States Forest Service, Shrub Sciences Laboratory. Big sagebrush can be found in varying degrees on some sites on the east side such as above Pleasant Grove, UT, but for the most part big sagebrush is not dominant until southwest of Spanish Fork, UT. However, Tanner (1940, p. 48) quoted historic evidence of a mixture of "bunch grass and sage-brush that covered much of the land around American Fork," and Emma Evans Stratton stated in her diary published in the Orem-Geneva Times July 16, 1997: "There [were] about 15 families on the bench between Lindon and the river bridge. There were no fences and no roads, just sagebrush as far as the eyes could see. If we wanted to go to the canyon or visit a neighbor, we just cut through the sagebrush and made our roads..." On the west side of Utah Valley, the story is quite different. Big sagebrush dominates the foothills along the entire length of the valley and is lacking only on ground being farmed or where fire has destroyed it. As Stewart (1941, p. 364) pointed out: "Thus, the soils in the heart of the sagebrush zone have been found the most suitable of all Great Basin soils for cultivated agriculture." Thus, based on the historic evidence presented by Wakefield (1936), big sagebrush is currently found where big sagebrush was in the past in Utah Valley (Johnson 1986).

Johnson (1986) conducted a fascinating photographic study of "sagebrush over time." He selected 20 landscape photographs taken by William H. Jackson in Wyoming, Utah, and Idaho during the 1870s while Jackson was a member of Hayden's survey company, and Johnson returned to these landscapes and took current (1974 though1985) photographs from the same photopoints. Comparing Jackson's photographs with the modern photographs over 100 years later, Johnson (1986, p. 223) concluded that "there has been no major shift in sagebrush distribution as a result of use," and "the appearance of the landscape today is a fair indication of its appearance in presettlement times."

Young and others (1979) noted that the use of historical records can be used to justify any preconceived ideas of presettlement vegetation and added (p. 2): "Good sources for quotations from most of the journals written during the contact period are Stewart (1941), who emphasized the abundance of grass under pristine conditions, and Vale (1975) who concluded the opposite and stressed shrub dominance." I have read and studied both the Stewart (1941) and the Vale (1975) reports and conclude that they are not contradictory, but that the problem may stem from either a superficial analysis of the Stewart (1941) report or bias against big sagebrush.

Here is my analysis of the Stewart (1941) report. First, Stewart limited his report to the State of Utah, whereas Vale (1975) was referring to the northern Intermountain West. Second, Stewart reviewed historical records that were concerned with finding suitable sites for the establishment of permanent settlements in the mid-1800s for members of the Church of Jesus Christ of Latter-day Saints (LDS), commonly referred to as "Mormons." Brigham Young, then president of the LDS church, sent parties out to search for sites where settlements could be established, so resulting records highlighted soils, water, and availability of timber and native grasses on promising sites. Stewart (1941, p. 366) described one such search party: "In 1849 an exploring party crossed what is now Cedar Valley and over the Oquirrh Mountains in search of a tract of land on which to pasture livestock." The exploring party crossed over a whole valley and did not find a tract of land on which to pasture livestock because Cedar Valley was not a valley of abundant grass. Yet, a few years later the United States Army would establish a camp in this same valley, concluding that there was enough grass for transitory army purposes. The Stewart (1941, p. 366) report continues: searching on, the exploring party "found a grass-covered spot" (note the use of the word spot, not grass-covered valley) "with timber, water, and moderately good soil" in what is today Tooele Valley. If the historical records Stewart was reading are describing abundance of grass under pristine conditions, why the searching? As I read the Stewart (1941) report, it became quite obvious that the exploring parties had to travel great distances between areas of abundant grass that could support settlements. Stewart's (1941, p. 364) description of settlement sites used the shrub word "sagebrush" many times and stated, "Nearly all of them lie almost in the heart of the sagebrush zone" (not grass zone). Also, as cited earlier, most of the farmlands near these settlements were taken out of big sagebrush. Stewart (1941, p. 364) further observed: "Where the soils and the moisture supply was somewhat more favorable than ordinary, as along stream courses, the wheatgrasses and giant ryegrasses predominated." Vale (1975, p. 32) made a similar statement: "Stands of grass apparently were usually confined to wet valley bottoms, moist canyons, and mountain slopes, with more extensive areas in eastern Oregon near the Cascade Range. The major area was apparently covered by thick stands of brush." That the historical records cited in the Stewart (1941) report gave greater emphasis to the occurrence of grass is evidence that finding tracts of land producing an abundance of grass was a rare find, which is in accord with the conclusions of the Vale (1975) report.

In summary, what do the macro-micro fossil record and historical records tell us about the distribution of big sagebrush? First, that big sagebrush has been present in the Intermountain region and parts of the Great Plains for tens of thousands of years, and that it was established in northeastern Washington and northern Idaho before the present day coniferous forests were established; it was present in northwestern Arizona before giving way to the present day Sonoran Desert; it was present before the establishment of some of the pinyon/juniper woodlands; and some woodlands are continuing to expand into present day big sagebrush habitat. Some of the fossil records parallel the historical records. Lewis and Clark found it in North Dakota and across Montana and Washington in 1805. Douglas (1914) strengthens the testimony of Lewis and Clark concerning the presence of big sagebrush in the State of Washington in 1824. A number of individuals (Townsend, Wislizenus, Cross and Gibbs, Fremont, and Stansbury) established the presence of big sagebrush in what now are the States of Nebraska, Wyoming, Idaho, Utah, Oregon, Nevada, Washington, and California during the early and mid-1800s. All confirming that, in the words of Beetle and Johnson (1982), big sagebrush is where big sagebrush was.

Modern Distribution

Modern distribution of big sagebrush is illustrated in figure 1.1 (McArthur 1983; McArthur and Plummer 1978). This distribution map of McArthur and Plummer (1978) supports both the fossil and the historical records concerning the occurrence of big sagebrush. Big sagebrush grows in the following States: North and South Dakota, Nebraska, Montana, Wyoming, Colorado, New Mexico, Idaho, Utah, Arizona, Washington, Oregon, Nevada, and California. Also, big sagebrush stands can be found in northern Baja of Mexico and southern British Columbia.

The distribution of big sagebrush in the northern Great Plains is illustrated in figure 1.2 and is summarized by Johnson (1979, p. 47): "In all areas, except Wyoming and parts of Montana, big sagebrush exhibits the attributes of a plant at the outer reaches of its range—disjunct populations and concentration on sites

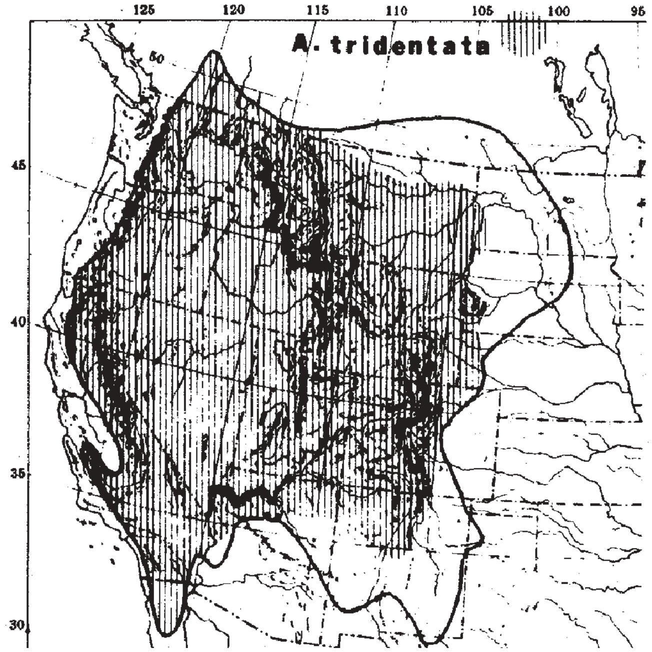

Figure 1.1—A regional distribution map of big sagebrush (*Artemisia tridentata*) by McArthur and Plummer (1978). The solid line delimits the subgenus Tridentatae (big sagebrush and its close relatives).

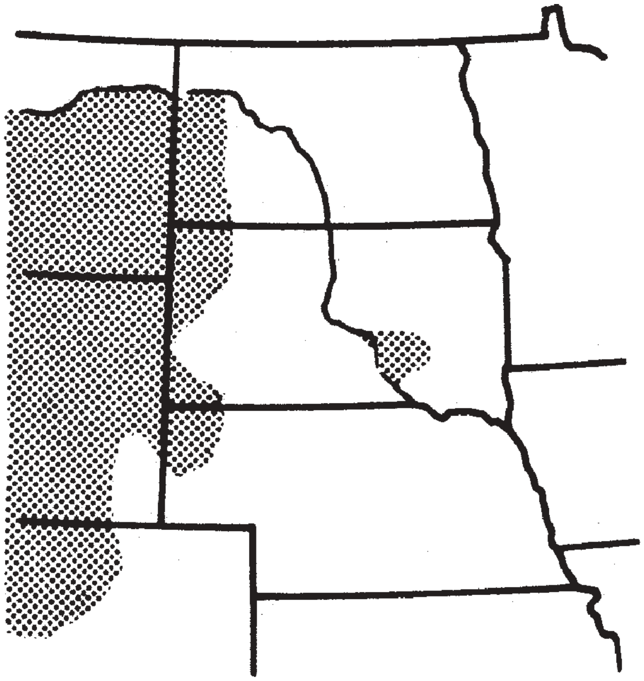

Figure 1.2—Regional map of the distribution of big sagebrush (*Artemisia tridentata)* in the northern Great Plains by Johnson (1979).

with favorable soil and moisture conditions." Hazlett and Hoffman (1975), studying the pattern of plant distribution on sites dominated by big sagebrush in the south unit of the Theodore Roosevelt National Memorial Park in western North Dakota, describe big sagebrush as occurring sparsely over the entire area but dominate (29 percent canopy cover) stands on flat benches or terraces above the Little Missouri River and its tributaries.

The distribution of big sagebrush for the Montana is illustrated in figure 1.3. Morris and others (1976) found big sagebrush to be widely distributed throughout the State and occurring over a wide range of elevations and soils. The most common subspecies of big sagebrush is Wyoming big sagebrush, particular in eastern Montana where the stands are discontinuous, but the transition zones between grasslands and big sagebrush stands can be large; thus Wyoming big sagebrush and the other subspecies can occupy areas greater than what is shown in figure 1.3 but at much lower densities. Basin and mountain big sagebrush are concentrated, for the most part, in southwestern Montana. Payne (1973) published a vegetative map of Montana based on work in the early 1940s. While his map agrees to general distribution of big sagebrush of the Morris and others (1976) map, the latter map appears to have more area delineated as big sagebrush. Both maps outline greater areas of big sagebrush in Montana than regional vegetative maps published by Bailey (1980); Küchler (1970); West (1983a, 1988, 1996); and perhaps Aldous (1924). Possible reasons for variation among vegetative maps for the same area will be discussed later in this section. The distribution of big sagebrush on highly localized vegetative maps is presented by Brown (1971) for southeastern Montana and by Patten (1963) for the Madison mountain range of southwestern Montana.

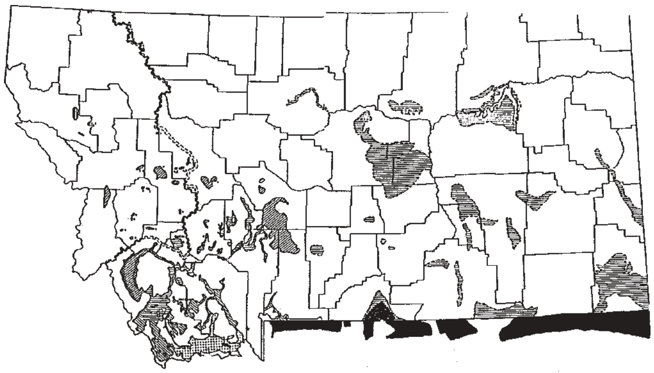

Figure 1.3—A distribution map of big sagebrush (*Artemisia tridentata*) for the state of Montana by Morris and others (1976).

Distribution of big sagebrush within Wyoming is shown in figure 1.4 (Beetle and Johnson 1982). Figure 1.4 is a representation of the distribution of all three subspecies of big sagebrush or combination of the maps printed on pages 38, 42, 46, and 50 of the Beetle and Johnson (1982) publication. Big sagebrush covers nearly the entire State of Wyoming, ranging from 5,000 to 10,500 feet elevation, and grows on a variety of soils. As with Montana, the same regional maps show less area of big sagebrush distribution in Wyoming than the Beetle and Johnson (1982) map. Highly localized vegetative maps and vegetative descriptions of northwest Wyoming have been published by Beetle (1961); Loope and Gruell (1973); McArthur and others (1995); and Sabinske and Knight (1978).

Figure 1.5 represents the distribution of big sagebrush in Idaho (Tisdale and others 1969). While the authors did not distinguish between the various species of sagebrush—such as black sagebrush (*Artemisia nova*), low sagebrush (*A. arbuscula*), three-tip sagebrush (*A. tripartita*), and silver sagebrush (*A. cana*)— big sagebrush dominates well over two-thirds of the sagebrush region of Idaho. Most of the sagebrush region of Idaho lies within a large arc-shaped area called the Snake River Plain of southern Idaho. This plain is some 360 miles long and 50 to 80 miles wide and varies in elevation from 2,300 to 6,600 feet (Tisdale and others 1969). Other areas in southern Idaho that support significant stands of big sagebrush include the Owyhee plateau southwest of the Snake River Plain, the extension of the Basin and Range Province east of the Owyhee plateau, the Middle Rocky Mountain Province bordering the east side of the Snake River Plain, and Little and Big Lost Rivers and Birch Creek, which extend big sagebrush stands into central Idaho (Hironaka and others 1983). Winward and Tisdale (1977) published a map of big sagebrush by subspecies distribution that lacks many of the details of the Tisdale and others (1969) map, but it gives a general idea where these subspecies can be found. Three research reports contain big sagebrush distribution maps for the Idaho National Engineering and Environmental Laboratory in southeastern Idaho (Anderson and others 1996; Atwood 1970; Harniss and West 1973), and Piemeisel (1932) produced a distribution map of big sagebrush for an area of the Snake River Plain called the Salmon River Tract in 1929.

Figure 1.4—A distribution map of big sagebrush (*Artemisia tridentata*) for the state of Wyoming by Beetle and Johnson (1982). This map is a composite of four maps found on pages 38, 42, 46, and 50 of the Beetle and Johnson (1982) publication.

Figure 1.5—A distribution map of big sagebrush (*Artemisia tridentata*) for the state of Idaho by Tisdale and others (1969). The authors did not distinguish between the various species of sagebrush, such as black sagebrush—*Artemisia nova,* low sagebrush—*A. arbuscula,* three-tip sagebrush—*A. tripartita,* and silver sagebrush—*A. cana*. Big sagebrush dominates well over two-thirds of the sagebrush region of Idaho.

I have been unable to locate a big sagebrush distribution map for Oregon; however, regional maps published by a number of researchers outline in general terms where big sagebrush occurs (Beetle 1960; Stoms and others 1998; West 1983a, 1988, 1996). Big sagebrush covers most of the southeastern quarter of Oregon and extends north, essentially following the John Day River through the center of the State, to the Columbia River.

The geographic range of big sagebrush for Washington is illustrated in figure 1.6 (Daubenmire 1970). Big sagebrush habitat is in central Washington starting a few miles east of the confluence of the Snake and

Columbia Rivers, west to the Cascade Range, and north along the Columbia and Okanogan Rivers to British Columbia, Canada. Thus, big sagebrush distribution forms a nearly continuous belt from eastern Montana through Wyoming, Idaho, Oregon, Washington, and ending in southern British Columbia.

Big sagebrush distribution maps have been published for the States of California, Nevada, Utah, Colorado, Arizona, and New Mexico. These are listed in table 1.1

The amount of big sagebrush outlined on a distribution map can vary greatly among reports for a given area. For example, Atwood (1970) delineates greater

Figure 1.6—A distribution map of big sagebrush (*Artemisia tridentata*) for the state of Washington before settlement days by Daubenmire (1970).

Table 1.1—Articles containing big sagebrush distribution maps or vegetative descriptions for the big sagebrush States of Arizona, California, Colorado, Idaho, New Mexico, Nevada, Utah, and the Western United States.

Arizona
- Hodgkinson 1989
- Merkle 1952
- Merkle 1962
- Shreve 1942b

California
- Chabot and Billings 1972
- Heller 1911
- Klyver 1931
- Sampson and Jespersen 1963

Colorado
- Baker and Kennedy 1985
- Johnson 1941
- Robbins 1910

Idaho
- Bright 1966
- Rosentreter and Kelsey 1991
- Winward and Tisdale 1977

Nevada
- Billings 1945

New Mexico
- Wright and others 1973

Utah
- Christensen 1963
- Christensen and Hutchinson 1965
- Cottam 1929
- Fautin 1946
- Kearney and others 1914
- Shantz and Piemeisel 1940
- Stoddart 1941
- Walker and others 1996

Regional
- Bailey 1896
- Beetle 1960
- Branson and others 1967
- Everett 1985
- McArthur 1994
- McArthur and Ott 1996
- Plummer 1974
- Shreve 1942a
- Shultz 1986b
- Tueller and others 1979
- Ward 1953
- West 1983b
- West and others 1998
- Young and others 1990a

amounts of grass habitat on the Idaho National Engineering and Environmental Laboratory than does Harniss and West (1973). Morris and others (1976) classify significantly greater areas of Montana as big sagebrush habitat than does Küchler (1970). Comparing the distribution of big sagebrush along the northern border of Wyoming (fig. 1.4; Beetle and Johnson 1982) to the southern border of Montana (fig. 1.3; Morris and others 1976) gives the impression that much of the big sagebrush of Wyoming stopped at the Wyoming-Montana line, especially in the northeastern and northwestern corners of Wyoming (see black blocks south of the Wyoming-Montana line, fig. 1.3). Plant populations do not recognize State boundaries and the differences seen (big sagebrush occupying 73 percent of the Wyoming-Montana line according to Beetle and Johnson 1982, but 32 percent according to Morris and others 1976), are due to a multitude of reasons including: definition of what constitutes big sagebrush habitat (modicum or dominant), whether the workers are mapping present day, or potential, or historic vegetation; or personal bias against big sagebrush. So it is little wonder that estimates of the number of acres in big sagebrush habitat varies greatly among authorities: 96.5 million to 270 million acres for all species of woody sagebrush with big sagebrush as the principal sagebrush (Bailey 1980; Beetle 1960; McArthur and Ott 1996; Tisdale and others 1969).

Has Big Sagebrush Invaded Grasslands?

It has become conventional wisdom that since Euro-American settlement, big sagebrush has extended its distribution and that much of present day big sagebrush dominated habitat is the end result of overgrazing (Christensen and Hutchinson 1965; Cook 1963; Cottam and Stewart 1940; Gruell 1986; Loope and Gruell 1973; Morris and others 1976; Reitz and Morris 1939; Stoddart 1941; Stoddart and others 1975; Weaver and Alberston 1956). Stoddart and others (1975, p. 34) stated: "Great uncertainty exists as to exact original extent of the bunchgrasses since, with overgrazing, sagebrush has invaded the intermountain grasslands from the south. Some ecologists hold that much of southern Idaho, eastern Washington, eastern Oregon, western Montana, and large areas of northern Nevada and Utah are climax grassland." Cook (1963, p. 190) said: "It has invaded millions of acres of deteriorated foothill range in the intermountain area."

However, Tisdale and others (1969), studying historical records and undisturbed or ungrazed sites, concluded that the geographic distribution of woody species of sagebrush is the same today as in presettlement times. Daubenmire (1970, p. 83) noted: "In Washington, there is no evidence to support claims that *Artemisia tridentata* and *Opuntia polycantha* have increased their ranges since the advent of white man. In fact, the range of *Artemisia tridentata* may have been reduced by promiscuous burning during the early period of settlement in Washington." Hironaka (1979, p. 29) agrees and further noted: "The numerous species and subspecies of *Artemisia* that occur in relatively monospecific stands indicate that they are well adapted to the habitats they presently occupy—strong evidence that adaptation was established well before the advent of livestock grazing in the west."

There is another biological factor that supports the proposition that big sagebrush has not invaded grasslands; this one deals with the manner in which achenes or seeds are dispersed. Pendleton and others (1989) classified the dispersal mechanism of big sagebrush as microwind, meaning that the achenes lack any type of structure that would allow them to float or travel any great distances in wind currents (see also Young 1983). Chambers (2000) noted that seeds lacking appendages but with small surface areas, such as with big sagebrush, do not experience significant horizontal movement. Several workers have estimated maximum distance of achene dispersal of less than 100 feet from the mother big sagebrush plant (Astroth and Frischknecht 1984; Daubenmire 1975; Frischknecht 1979; Johnson and Payne 1968; Walton and others 1986; Wambolt and others 1989; Welch 2000, unpublished data on file at the Shrub Sciences Laboratory, Provo, UT; Young and others 1990b). If it takes from 2 to 4 years for a big sagebrush plant to reach maturity, then big sagebrush would spread from 25 to 50 feet per year, or in other words, it would take big sagebrush about 105 to 211 years to spread 1 mile. In the case of the Snake River Plain of southern Idaho, which varies from 50 to 80 miles wide, it would take big sagebrush some 5,250 to 16,880 years to distribute itself across the entire plain— that is going from south to north; this is in accordance with Stoddart and others (1975) earlier statements concerning sagebrush invasion from the south.

Biological factors and historical and fossil records do not support the contentions that big sagebrush invaded grasslands of the West. The only exceptions are highly localized, wet areas where high water tables had previously excluded big sagebrush but, through draining, created an environment where big sagebrush could grow (Cottam 1929; Cottam and Stewart 1940). Beetle and Johnson (1982, p. 6) put it in these simple terms: "sagebrush is where sagebrush was."

Relationship Between Grazing and Big Sagebrush Canopy Cover

It has been a biological principle, or axiom, that due to overgrazing, big sagebrush has increased in density, or as I would term it, in canopy cover (McArthur and others 1995). Miller and others (1994, p. 115) state it best:

> In the early to mid 1800s much of the sagebrush steppe was probably composed of open stands of shrubs with a strong component of long-lived perennial grasses and forbs in the understory. Shrub canopy cover probably ranged between 5-10% in the drier Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) communities (Cooper 1953; Young et al. 1976; Winward 1991), to 10-20% on the more mesic sites, occupied by mountain big sagebrush (Tisdale et al. 1965; Winward 1991).

Speaking of the present, they noted "Wyoming big sagebrush cover has increased from less than 10% to 20%, and mountain big sagebrush cover from less than 20% to 30 and 40% (Winward 1991)" due to overgrazing. Although, Frischknecht and Harris (1973) reported that fall grazing by sheep decreased the size of big sagebrush plants and greatly reduced the production of flower stalks. This would reduce, not increase the canopy cover of big sagebrush on a given site.

When I began writing of this report I did not envision challenging this concept, especially after reading and studying Tisdale and others (1965) report on their vegetative analysis of the ungrazed Carey kipuka (located 14 miles east of Carey, ID). (A kipuka is an area of older land or soil surrounded by later lava flows.) They reported big sagebrush canopy cover of 13 percent, although in their photograph of the kipuka (their fig. 2), the canopy cover of big sagebrush appears to be a little more than 13 percent. It wasn't until I read and studied the Passey and Hugie (1963a) report, particularly the photograph of their study site, which was a kipuka located some 20 miles southwest of Aberdeen, ID, that I felt perhaps this concept might not be valid. It is clear from the photograph that big sagebrush canopy cover exceeded, at this ungrazed kipuka, the 20 percent upper limit proposed by Miller and others (1994), Baxter (1996), and Winward (1991).

I believe this principle, then, is invalid based on three reasons: first, what do the animals that coevolved with big sagebrush suggest to us concerning canopy cover; second, what are the big sagebrush canopy cover values found in undisturbed relicts such as kipukas; and third, what is the quality of the science that is used to support this principle (Welch and Criddle 2003)?

Numerous studies (see Peterson 1995 and chapter II for a review) show animals of big sagebrush prefer living in big sagebrush canopy cover far above the 20 percent upper limit (Baxter 1996; Miller and others 1994; Winward 1991). In fact, Rasmussen and Griner (1938) noted that the highest sage grouse nesting success in Strawberry Valley of central Utah occurred in mountain big sagebrush stands having 50 percent canopy cover. They estimated that some 270 acres of big sagebrush habitat was in the 50 percent canopy cover class. Ellis and others (1989) reported male sage grouse loafing in areas with 31 percent big sagebrush canopy cover. In addition, Katzner and Parker (1997) reported that areas of high pygmy rabbit (*Brachylagus idahoenesis*) activity occurred in basin big sagebrush stands having 51.1 percent canopy cover, and areas of medium activity occurred in Wyoming big sagebrush stands of 42.7 percent canopy cover.

Still, other sagebrush obligates such as sage thrasher (*Oreoscoptes montanus*), Brewer's sparrow (*Spizella breweri breweri*), and sage sparrow (*Amphispiza belli*) prefer big sagebrush canopy cover of 20 to 36 percent, which is much higher than the 20 percent maximum cover of the axiom (Best 1972; Feist 1968; Grinnell and others 1930; Knick and Rotenberry 1995; Petersen and Best 1986, 1991; Reynolds and Trost 1980, 1981; Rich 1985; Winter and Best 1985). For sagebrush species other than big sagebrush, Walcheck (1970) reported that a population of Brewer's sparrows were living in an area of silver sagebrush having a canopy cover of 53 percent. Petersen and Best (1985), studying nest site selection of sage sparrows, found that these birds nested where (probably Wyoming) big sagebrush canopy cover was 23 percent in the vicinity of nests. Further, they noted that all nests were situated in big sagebrush plants and that large, living shrubs were strongly preferred. Rotenberry (1980) found greater numbers of sage sparrow and western meadowlark (*Sturnella neglecta*) on sites where (probably Wyoming) big sagebrush canopy covers ranged from 25 to 30 percent than on sites with big sagebrush canopy cover of 0 to1 percent and 5 to10 percent. Short (1984) reported that shrub canopy, mostly big sagebrush, had to exceed 30 percent in order to achieve a habitat suitability index of one for Brewer's sparrows. Also, Best (1972) and Feist (1968) found greater numbers of Brewer's sparrow and sage thrashers in stands of (probably Wyoming) big sagebrush with canopy cover at 36 percent than at 21 percent.

Big sagebrush canopy cover measured on undisturbed relicts and kipukas does not support the axiom that big sagebrush canopy cover increased due to overgrazing. Daubenmire (1970, p. 1) reported that big sagebrush canopy cover varied on his "virgin or near virgin vegetation" study sites from 5 to 38 percent. The technique used by Daubenmire (1970) tended to underestimate shrub canopy cover by 3 to 5 percentage points according to an analysis by Floyd and Anderson (1987). Baker and Kennedy (1985) reported that canopy cover of Wyoming big sagebrush remnant stands varied from 8 to 20 percent.

I have measured, using the line intercept method (300 feet), the canopy cover of big sagebrush in four ungrazed kipukas and found that canopy cover ranged from 14 to 34 percent (see chapter IV for details), or in other words, from 66 to 86 percent of the area's surface was occupied by something else other than big sagebrush. Basin big sagebrush was the dominant big sagebrush in two of the kipukas, one about 20 miles west of Idaho Falls, ID, and the other about 14 miles east of Carey, ID. On the first kipuka, big sagebrush canopy cover was 14, 16, and 23 percent for the three 300-foot line intercept transects. These measurements would support the axiom for mountain big sagebrush but not for Wyoming big sagebrush (big sagebrush on this kipuka was basin). A high percentage of the big sagebrush plants had been killed by defoliators, thus reducing live canopy cover to the values given. Big sagebrush canopy cover values were based on live canopy cover intercepted. Had I included, as the USDA Forest Service Handbook recommends (Goodrich and Huber 2001; USDA Forest Service 1993), portions of dead stems, the canopy cover values would have been higher. Along the transects there were numerous big sagebrush seedlings, enough to replace the dead and near dead big sagebrush plants, to the point of a full recovery of canopy cover well above what I measured. Big sagebrush canopy cover values measured on the Carey, ID, kipuka were 26, 30, and 34 percent. There were no signs of defoliators at work. The differences between my measurements and those of Tisdale and others (1965) are difficult to explain; perhaps they took their measurements in areas heavily dominated with threetip sagebrush, which occurs on the east side of the kipuka. My measurements were taken in the center of the kipuka.

For the two kipuka dominated by Wyoming big sagebrush west of American Falls, ID, Wyoming big sagebrush canopy cover values were 14, 23, and 28 percent and 20, 24, and 31 percent. The work done by Daubenmire (1970), Baker and Kennedy (1985), and me (kipuka measurements June 2000) apparently does not support the idea that mountain big sagebrush does not naturally exceed 20 percent canopy cover and Wyoming big sagebrush, 10 percent.

According to West (1999, p. 16), concerning kipukas or relicts: “These relicts are not completely reliable as reference conditions because they are incomplete ecosystems.” I believe they are the best reference areas available. West was a coauthor of Miller and others (1994) report that cites Tisdale and others (1965) to support their assertion that big sagebrush canopy does not naturally exceed 10 or 20 percent. Tisdale and others (1965) collected their data from the Carey kipuka.

For the kipukas I visited, there seemed to be the usual complement of birds, small mammals, reptiles, insects, spiders, lichens, shrubs, grasses, forbs, and biological crusts. On one kipuka I observed deer tracks. For the kipuka that Passey and Hugie (1963b, p. 114) studied, they noted: “Deer and antelope occasionally cross the kipuka and there is evidence of a small rodent population.” Because these kipukas are surrounded by lava flows, the fire return intervals are probably much longer than for nearby big sagebrush stands outside the kipukas. Even though kipukas are small, they represent the best references of pristine big sagebrush stands.

Holechek and Stephenson (1983) found that big sagebrush canopy cover was higher inside the exclosure on their upland study site and higher on the outside of their exclosure on their lowland site. This means that grazing decreased big sagebrush canopy cover outside of the exclosure in the upland site and increased it for the lowland site. Eckeret and Spencer (1986) also reported inconsistences concerning big sagebrush cover response to grazing. Pearson (1965), studying vegetative production in grazed and ungrazed plant communities, found that big sagebrush canopy cover in the ungrazed area was 34 percent and perennial grasses 39 percent compared to 11 percent big sagebrush canopy cover in the grazed area with 22 percent perennial grass cover. Similarly, Anderson and Holte (1981) reported that for an area in southeastern Idaho protected from grazing for more than 25 years, big sagebrush canopy cover increased from15 to 23 percent with an increase in grass cover from 0.28 to 5.8 percent. Wambolt and Watts (1996, p. 148) noted that: “heavy stocking rates reduce sagebrush cover primarily through mechanical damage, but some browsing was observed”; and they added that: “The exclusion of grazing for 30 years had no effect on [Wyoming big] sagebrush canopy [13.5 percent] in untreated plots.” Yet in their treated plots, Wyoming big sagebrush canopy cover increased over time to canopy cover values of 19 percent (plowed and seeded), 17 percent (chemical spray), 14 percent (rotocut), and 11 percent (burn) in the absence of grazing. Muscha and others (2004, p. 181) observed: “Our data demonstrate shrub cover will not always increase where stock are excluded at a greater rate then with livestock present. It is clear that the release of grazing pressure does not decrease shrub canopy; in some cases it may allow shrub canopy to increase [5 out of 9 increase; 2 out of 9 decrease; 2 out of 9 stayed the same]”. Lusby (1970) noted for all sites, including the big sagebrush site, a decrease in shrub overstory as a result of livestock grazing. Last, Johnston (2003) listed three data sets that would in his own words “deny the axiom.” These studies show that grazing may or may not increase big sagebrush canopy cover, or in other words, no general relationship exists between grazing and big sagebrush canopy cover.

Peterson (1995) noted greater big sagebrush cover inside of an exclosure than outside due to heavy wild ungulate grazing. Wambolt and Sherwood (1999) found an average of three times as much big sagebrush canopy cover inside exclosures at 19 sites across the northern Yellowstone winter range as outside. Wild ungulate grazing decreases big sagebrush canopy cover.

The following articles are often cited to support the range management axiom that big sagebrush canopy cover increased above natural levels due to overgrazing: Blaisdell (1949); Blaisdell and others (1982); Clark (1981); Cooper (1953); Hanson and Stoddart (1940); Laycock (1978); Pickford (1932); Robertson (1947;) Stoddart (1941); Tisdale and others (1965); Winward (1991); Wright and Wright (1948); Young (1943); and Young and others (1976). These reports can be classified, in my opinion, into two classes: those based on opinion or experience and those that are data based but with questionable applicability. An example of the first is Laycock's (1978, p. 232) statement: "Overgrazing has resulted in dense stands of sagebrush with little herbaceous understory in many areas." This statement is not supported by citations, or data, but is given as a statement of principle. There may well be little herbaceous understory, but invoking overgrazing as a cause of dense stands of sagebrush is not supported. Other citations that fall into the statements of faith are: Blaisdell and others (1982); Clark (1981); Stoddart (1941); Winward (1991); and Young and others (1976). The remaining articles or citations contain scientific data but I question their applicability. One study (Young 1943) was conducted on non-big sagebrush sites within the Palouse grassland of eastern Washington and northern Idaho; another one was concerned with the impact of grazing on the root system of grasses (Hanson and Stoddart 1940). Two were studies concerned with competition between big sagebrush and grasses (Blaisdell 1949; Robertson 1947); another study (Pickford 1932) used ocular estimates. One study was conducted in the transition zones between shrublands and grasslands of Montana (Wright and Wright 1948). Cooper (1953) expressed his data in percent composition, which would vary according to amount of grasses and forbs removed by grazing or reduced by drought; and I discussed the two remaining studies (Daubenmire 1970; Tisdale and others 1965) earlier.

How Much of the Big Sagebrush Ecosystem is Left?

Euro-American settlers soon discovered that the presence of "big" big sagebrush was a good indicator of soils that were well suited for agricultural pursuits (Clements 1920; Fireman and Hayward 1952; Poulson 1946; Thatcher 1959). The result was that the big sagebrush ecosystem has been shrinking since the first Euro-Americans decided to settle in big sagebrush country. Upon arriving, the first task was to clear big sagebrush to make room for gardens, building sites, fields, orchards, corrals, and so on. Then later, the building of reservoirs, highways, towns, cities, and the practice of range management contributed to the shrinking of big sagebrush ecosystem.

Now an alien annual grass, cheatgrass (*Bromus tectorum*)—a dry, prickly grass—has invaded the big sagebrush ecosystem and has increased fire frequency about 12 to 22 times (Whisenant 1990), resulting in an ecosystem changed to the point that some believe the system is endangered. Knick's (1999) article on this subject—"Requiem for a Sagebrush Ecosystem?"—shares my concerns over the practice of fuels management, developed in the forestry systems, being applied in big sagebrush ecosystems (Winward 1984, 1991). He estimates that about 30 percent of the big sagebrush ecosystem is left in the Snake River Birds of Prey National Conservation Area of southwestern Idaho, and what is left is highly fragmented (also see Knick and Rotenberry 1997).

For the State of Washington, Dobler (1994) estimated that 41 percent of the original shrub-steppe remains, or in other words, 59 percent has been converted to agriculture, development, or water storage. I estimated that 48 percent of the big sagebrush habitat in Washington remains, as determined by superimposing Daubenmire's (1970) vegetation zones map onto the land cover map for the State of Washington developed by Cassidy (1997). Each proportional area (sagebrush habitat, agricultural lands, cities, towns, water storage, and so on) was determined by cutting it from the maps and weighing each area within the former big sagebrush habitat. From these figures, I calculated that 48 percent of the big sagebrush remained.

Effects before and after Euro-Americans on big sagebrush ecosystems in the State of Washington are illustrated in figures 1.6 before, and 1.7 after; note the great amount of fragmentation. Of course, only the most productive big sagebrush sites (deep soils and highly fertile) were developed for agricultural use, leaving big sagebrush growing on less fertile and shallow soils, steep unusable hillside, or suitable sites not yet developed. The largest areas of big sagebrush stands in Washington are the Hanford Reservation (infested with cheatgrass) and the Yakima Firing Range (Cassidy 1997; Welch's personal observation in June of 2000).

Life Expectancy

Pool (1908) described the big sagebrush he studied at Fort Garland, CO, as being 50 years old. For the Escalante Valley near Milford, UT, Shantz and Piemeisel (1940) found 45-year-old big sagebrush plants in a big sagebrush-greasewood community. Lommasson (1948), studying succession in a big sagebrush stand growing on the Beaverhead National

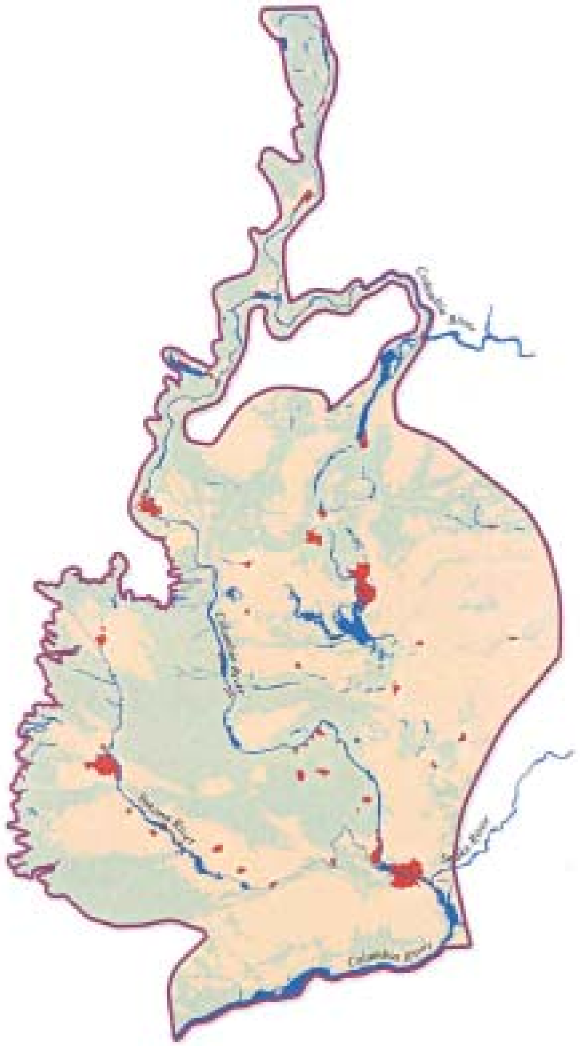

Figure 1.7—A distribution map of big sagebrush (*Artemisia tridentata*) for the state of Washington after settlement days by Cassidy (1997).

Forest in southwestern Montana, noted the average age of big sagebrush plants was 61 years. Ferguson and Humphrey (1959, p. 3) stated: "This study has shown that [big] sagebrush produces a growth ring that is sensitive to changes in annual precipitation and sometimes reaches an age of slightly more than 200 years." In a series of studies by Passey and Hugie (1962, 1963a,b) conducted on relicts and ungrazed kipukas of eastern and southern Idaho, northern Utah, and northeastern Nevada, they found that the age of big sagebrush plants varied from 27 to 120 years. Ferguson (1964), in an extensive study that included 700 samples from areas of northwestern New Mexico, northeastern Arizona, the San Bernardino and Panamint Mountains of California, and White mountains of California and Nevada, found that the age of big sagebrush plants varied from 22 to 216 years. Schneegas and Nord (1967) estimated the age of a large big sagebrush plant found in the White Mountain of eastern California to be 50 to 60 years old. Fowler and Helvey (1974) found, on their study site in the Columbia River Basin of Washington, the maximum age of big sagebrush plants is less than 100 years. Wambolt and Hoffman (2001) reported that mountain big sagebrush plants growing in southwestern Montana ranged in age from 5 to 109 years. Perryman and others (2001) reported, for their study, a maximum age of 81 years for mountain big sagebrush, 75 years for Wyoming big sagebrush, and 55 years for basin big sagebrush. Daubenmire (1975) reported maximum age of big sagebrush plants in Washington to be 95 years. Thus it appears, in humanistic terms, big sagebrush is a long-lived plant but shorter lived when compared to some plant species.

Morphology and Anatomy

Three classic studies have described the general morphological and anatomical characteristics of big sagebrush (Diettert 1938; Pool 1908; Ward 1953). Of these three, perhaps Diettert (1938) is the most comprehensive and will be referenced extensively in this section. Gross morphological characteristics of the three subspecies of big sagebrush will be given in the taxonomy section of this chapter.

Inflorescence Versus Vegetative Branches

Branches or shoots of big sagebrush are of two types—vegetative and reproductive, or inflorescence—which not only appear different externally but also internally (Diettert 1938; Ward 1953). Growth of vegetative branches starts in early spring and stops in early summer, whereas inflorescences start in late spring and terminate growth in late summer (Miller and others 1986). Vegetative branches are perennial in nature, whereas inflorescences are annual; in other words, their growth is determinate in nature and they die upon maturation of fruits or achenes. Leaves of vegetative branches are all tridentate or multiple lobes, but only the lower leaves of inflorescences are tridentate; the upper and majority of leaves are entire or nonlobed (plate I, fig. 3). All inflorescences shed their leaves before maturity, whereas vegetative branches retain about a third of their leaves throughout late summer, fall, and winter (Miller and Shultz 1987). Both kinds of branches are covered by thick layers of trichomes or hairs (plate X), the removal of which reveals that both are distinctly striated. Structure of trichomes will be discussed later in the leaf section. Inflorescences develop large, loose to dense panicles, with sessile heads containing from three to seven flower heads or clusters (plate I, fig. 3). Internally, inflorescences differ from vegetative branches by the presence of chlorenchyma beneath the epidermis, by earlier and more extensive development of fibers in both the xylem and pericycle, and by becoming more slender and less rigid than the vegetative branches. But as the inflorescences reach maturity they become harder due to the production of sclerenchyma tissue.

Floral Development

Flower heads or clusters are ovoid to campanulate in shape and are small, being 3.0 to 4.5 mm by 2.0 to 3.5 mm at maturity (plate I, fig. 1 and 2). Diettert (1938) reported two types of involucral bracts for big sagebrush flower heads: the outer shorter, orbicular-ovate varying in number from four to nine, and the much longer, elliptic-spathulate inner involucral bracts numbering six to nine (plate I, fig. 1 and 2). The first flower part to differentiate is the corolla, followed by the stamens, and then the pistil (plate I, fig. 4 through 10). Pappus, a tuftlike appendage of the achene, is lacking; also lacking is any evidence of a calyx (plate I, fig. 11, 12, and 14). However, Daubenmire (1975), citing a Ph.D. degree dissertation, describes the presence of a calyx tube that “breaks away from the rest of the corolla.” Daubenmire’s (1975) use of “calyx tube” is probably incorrect. The term “corolla tube” instead would have been better. During the early development of the corolla “tube,” the lobes or tips curve inward and their marginal cells become papillated, interlock, and fused, thus sealing the flowers until forced open by enlarging stamens (plate I, fig. 11 through 14). Development of pollen and embryo sac of big sagebrush is typical of dicotyledonpus plants; for details the reader is referred to Diettert (1938).

Embryo, Seed Development, and Anatomy

After double fertilization, the zygote increases in size and then divides transversely resulting in a large basal cell (b) and a smaller apical cell (a), and at the same time first division of the primary endosperm nucleus occurs (plate V, fig. 60 and 61). Continued development of the embryo is described by Diettert (1938, p. 9):

> The next division is also transverse, the basal cell dividing to form a somewhat flattened middle cell (plate V.62-m). The vertical division of the apical cell occurs at approximately the same time (plate V.63), and further divisions of these cells give rise to the cotyledons and plumule (plate V.64-71). The basal cell (b) may divide transversely before the middle cell (m) divides vertically (plate V.65), or the order of the divisions of these two cells may be reversed (plate V.66). The divisions of the middle cell (m) ultimately produce in part the hypocotyledonary portion of the embryo and the basal cell (b) completes this region and forms the suspensor (plate V.67-71). The latter never consists of more than two or three cells which remain small and soon disappear (plate V.71, 74).

During this period, the cells of the endosperm are dividing forming a multicellular endosperm that for a time is far in advance of the embryo, but eventually the embryo enlarges to the point that, in a nearly mature seed, the endosperm forms a thin layer around the entire embryo (plate V, fig. 72 through 75). The point where the mature achene separates from the rest of the corolla tube is smooth as pictured in plate V, figure 75. However, Daubenmire (1975) describes this area as containing a small bur-like structure. In all of the seed lots of big sagebrush that I have inspected, I have never observed any structure that I would call a small bur attached to or part of achenes.

Leaf Anatomy and Development

Leaves in big sagebrush start out as a series of periclinal divisions within the second and third layers of the tunica (plate VI, fig. 76), which leads to development of a papillate protuberance near the shoot apex (plate VI, fig. 77), the leaf primordium. This differentiates into a five-layered structure (plate VI, fig. 77 through 80a), of which the outer layers differentiate into upper and lower epidermis with the next two layers developing into palisade tissue and the central layer into veins and spongy mesophyll. Some epidermal cells start to differentiate early in the development of leaves into trichomes (plate VI, fig. 78). During the early differentiation of big sagebrush leaves, a greater rate of cellular division occurs on the abaxial side than adaxial side of the margins of the developing leaf; thus, the margins turn inward giving the structure a U-shaped appearance in cross section (plate VI, fig. 85). Plate VII, figures 87 through 90; plate VIII, figures 91and 92; and plate IX, figures 93 through 98 illustrate the development of veins, spongy mesophyll, palisade layers, intercellular spaces, and epidermal layers.

Plate X, figures 99 through 119 represent the development of trichomes on big sagebrush leaves. Trichomes of big sagebrush are of two types, glandular (plate X, fig. 99) and nonglandular (plate X, fig. 109), and are distinguishable from each other at an early stage of differentiation (plate X, fig.100 and 111) with the glandular trichomes somewhat in advance of the nonglandular trichomes. Both are derived from epidermal cells (Pool 1908). Diettert (1938, p. 24) describes the development of glandular trichomes:

> Development of the glandular hairs begins with an anticlinal division of a slightly protruding epidermal cell (plate X.101). This division always occurs in the direction parallel to the transverse plane of the leaf. Following this first division the two daughter cells elongate and enlarge considerably and divide periclinally. The two protruding cells then undergo a

> series of periclinal divisions, giving rise to eight cells (plate X.102 through 105, 99). The mature trichomes, without exception, are composed of ten cells, including the two basal cells (plate X.99).

The differentiation of nonglandular T, or cover trichomes (Pool 1908), from epidermal cells is in striking contrast to that of glandular trichomes. First of all, the beginning is recognizable by the elongation and protrusion of a single epidermal cell (plate X, fig. 111 through 113), which divides periclinally, producing an apical cell that does not divide but begins to elongate laterally in two directions in the longitudinal plane of the leaf; hence, forming a T-shaped structure (plate X, fig. 114 through 119). The base cell divides periclinally a number of times to form the stalk of the T (plate X, fig. 116 through 119, and 109 and 110). Diettert (1938, p. 25) observed, "The numerous nonglandular trichomes with stalks of various lengths and with long intertwining apical cells form a dense hairy covering approximately 200 microns thick over the entire surface of the leaf (plate X, fig 119)."

Mature leaves of big sagebrush are usually tridentate. Considerable variability does occur on a single plant from entire or nonlobed to some with as many as eight or more lobes (plate IX, fig. 98; Marchand and others 1966). They are more or less wedge-shaped, tapering gradually from the wide tip to the narrow petiole-like base, which broadens out a little near the point of attachment. Big sagebrush leaves are spirally arranged on the stem with a 2/5 divergence (Diettert 1938; Ward 1953). Diettert (1938, p. 19) noted: "The internodes are often so short that the leaves form dense, rosette-like clusters at the stem tips, a feature especially evident in plants living in less favorable places." He is probably describing leaves of Wyoming big sagebrush. He further observed that leaves produced in the early summer (Marchand and others 1966; plate IX, fig. 98 j, l, n) are larger than those produced later in the summer; or in other words, leaf development in big sagebrush is dimorphic, that is two kinds of leaves (ephemeral and persistent) are produced during the coarse of the growing season (Branson and others 1976; Daubenmire 1975; Link and others 1995; Marchand and others 1966; McDonough and others 1975; Miller and others 1983, 1986; Miller and Shultz 1987; Ward 1953).

Big sagebrush plants start the growing season (early spring) with just persistent leaves that were formed during the pervious growing season; however, early in the current growing season large ephemeral leaves develop (Miller and Shultz 1987). After the first crop of ephemeral leaves have matured, a second crop of smaller ephemeral leaves and persistent leaves start to develop in the axes of the mature ephemeral leaves producing what is termed a short shoot. There are, at this point, actually four kinds of leaves: first, the persistent leaves that overwintered; second, large mature ephemeral leaves; third, secondary ephemeral leaves developing on short shoots; and fourth, a current crop of persistent leaves also developing on short shoots. Ephemeral leaves on inflorescences are not born on short shoots.

Miller and Shultz (1987) noted that persistent leaves live a total of 12 to 13 months. Miller and Shultz (1987, p. 228) described the longevity of big sagebrush leaves: "At the onset of drought, both the previous season perennial and large, early-developing ephemeral leaves begin to senesce. Later-developing ephemerals, including nonlobed leaves, persist during the initial phase of leaf fall, senescing in late summer and fall. By November only the current crop of perennial leaves persists." They estimated that big sagebrush maintained 33 percent of their leaves in the winter. Branson and others (1976) estimated less than 20 percent.

Anatomy of mature big sagebrush leaves is unilateral and consists of upper and lower epidermal layers, an adaxial and abaxial palisade, and a central region of spongy mesophyll and veins (plate IX, fig. 93). The two epidermis layers are similar in structure with many cells differentiating into trichomes, which provide a dense covering over the leaves and give big sagebrush its silvery appearance (Pool 1908; Shultz 1986a). Stomata are evenly distributed over both epidermal layers and are somewhat raised (plates VIII, fig. 91a; IX, fig. 96; Pool 1908). Cuticle covering over the epidermal cells is, as compared to other plants species, thin. Maximum cuticle thickness occurs in the region of the midrib and larger veins, which are less densely covered with trichomes (Diettert 1938).

Stem Anatomy and Development

Two distinguishing characteristics of big sagebrush stems and branches are the evergreen foliage and the absence of winter buds. The difference between vegetative and inflorescence stems has been discussed earlier.

Vegetative stems are conspicuously eccentric in shape (Ferguson and Humphrey 1959). This eccentricity is caused by three factors: (1) the death of inflorescences that results in the formation of numerous depressions (plate XVI, fig. 145 a, b, c); (2) the destruction of the cambium when exposed through the removal of protective bark tissues (plate XVI, fig. 145 d, e, f); and (3) the uneven growth of the annual rings themselves, which can vary from a few hundred microns to several millimeters in thickness within a given growth ring (plate XVI, fig. 145). In spite of stem eccentricity, a number of workers have used width of big sagebrush annual growth rings as predictors of past precipitation and, perhaps, herbage production (Ferguson and Humphrey 1959; Fowler and Helvey 1974; McGinnies 1967).

Bark of mature stems is soft, stringy-like material that is easily removed or peeled off in narrow strips due to the intermixing of cork and sclerenchyma tissues with weak, thin-walled phloem cells. Removal of the bark exposes the cambium and results in its death; normally this is localized along the stems and does not result in the death of the entire plant.

Big sagebrush produces two kinds or types of stems or shoots: long shoots and short shoots (Bilbrough and Richards 1991). Because leader long shoots grow longer than lateral long shoots, big sagebrush has a linear, excurrent growth form. Vegetative growth starts in early spring from terminal and lateral soft buds. Current season long shoots produce ephemeral leaves that die in mid to late summer. Short shoots arise sylleptically from axillary soft buds and produce persistent or overwintering leaves that die the following spring (Bilbrough and Richards 1991; Miller and Shultz 1987). Inflorescences are produced from short shoots, terminal soft buds at the distal end of 1-year-old long shoots; therefore, browsing of current year, long shoots will reduce seed production (Bilbrough and Richards 1991; Rodriguez and Welch 1989; Wagstaff and Welch 1990, 1991). However, this allows inflorescences to be elevated, which enhances wind pollination. One-year-old leader long shoots produce more new long shoots and inflorescences than 1-year-old lateral long shoots, making big sagebrush less tolerant of browsing than many other shrub species (Bilbrough and Richards 1991; Wandera and others 1992).

Big sagebrush produces a diffuse porous wood whose vessels in the spring wood are more numerous but smaller in diameter than the vessels in the summer wood (plate XVIII, fig. 152 and 153). Both spring and summer vessels, lateral walls contain numerous pits. Fibers in summer wood are more numerous and thicker walled than spring wood (Fowler and Helvey 1974). Fowler and Helvey (1974) noted that summer wood is denser, contains more cells per unit of surface than spring wood, and is darker in color than spring wood. Diettert (1938, p. 38) noted: "The maturation of the vessels is rapid, while the development of the fibers is much slower, many of them not reaching maturity until the following year." For this reason the latest annual ring has a lighter appearance and stains less densely than the older rings (plate XVI, fig. 145).

Characteristic of big sagebrush and other sagebrush species stems is the annual development of interxylary cork layers, some two to 18 cells thick, between new annual growth ring and last year's growth ring (plates XVI, fig. 146 and 147; and XVIII. fig. 154 and 155; Dale 1968). A single layer of cells, the interxylary cork cambium, develops between the new annual growth ring and last year's growth ring (plate XX, fig. 160 and 161). This cambium starts to divide and give rise to a multiple cellular layer (plate XX, fig. 162) that remains undifferentiated until early summer when the innermost layers begin to mature and suberize. This maturation and suberization continues in a centrifugal direction until midsummer when all cells in the layer have become suberized and dead (plate XX, fig. 163). To complete the sealing of new wood from old wood, rays are too suberized from the innermost ray cells outward (plate XVIII, fig. 155). The observations of Diettert (1938) were extended by Moss (1940). Moss (1940, p. 764) noted, "The cork extends into the base of the current year's stem, forming there a dome-shaped or somewhat bulbous barrier of considerable thickness and enclosing a core of closely compacted, contorted, thick-walled cells." Moss (1940) found that the interxylary cork extended into the root system of big sagebrush to a distance of 6 to 8 cm from the base of lateral roots. Possible biological functions of the interxylary cork layer are strengthening stem bases, protection against desiccation, protection against pathogenic organisms, and protection against deleterious effect associated with the annual dying of inflorescences (Diettert 1938; Moss 1940). Moss (1940, p. 765), on the function of this layer noted: "Thus, interxylary cork may account in large part for the persistence of the sagebrush in arid regions."

Root Morphology

Robertson and others (1972) described big sagebrush as a phreatophyte, that is, a deep-rooted plant that can meets some of its water needs from the water table or from a layer of soil just above the water table. In soils without restricting layers, root depths for basin big sagebrush have been recorded as deep as 10 to 15 feet (Daubenmire 1975; Kearney and others 1914). For mountain and Wyoming big sagebrush, depths from 5 to 8 feet have been reported (Daddy and others 1988; Manning and Groeneveld 1990; Reynolds and Fraley 1989; Sturges 1977, 1979; Welch 1997). The tap root of individual big sagebrush plants are not necessarily the deepest. Often, the deepest roots are branches (lateral roots) of the tap root (Manning and Groeneveld 1990; Sturges 1977). Not only does big sagebrush produce a deep root system, but just under the soil surface lateral roots branch off the tap root forming a vast root network; the majority of the root system occurs just 12 inches under the soil surface (Daddy and others 1988; Dobrowolski and others 1990; Flanagan and others 1992; Manning and Groeneveld 1990; Sturges 1979). These shallow roots not only absorb water that accumulates in the upper soil layers during winter and spring, but can also make use of infrequent moisture from summer convective storms (Donovan and Ehleringer 1994). Some of these lateral roots extend out from mature plants a distance of 3 to 5 feet before growing deeper into the soil profile (Dobrowolski and others 1990; Reynolds and Fraley 1989; Sturges 1977; Welch 1997). Abbott and others

(1991) found that rooting depth of big sagebrush was more dependent on soil moisture than soil disturbance. Tabler (1964) found that root depth in mountain big sagebrush was deeper on the drier ridge and west-exposure sites as compared to the moister valley bottom and east-exposure sites. Thus, big sagebrush develops a two-tiered root system of dense root network at the soil surface and a deep system with tap root or extending laterals; the diffuse root system of big sagebrush is much greater than the taproot system (Caldwell and Fernandez 1975; Tabler 1964).

Root growth begins in the early spring a few days before shoot or stem growth and continues through the late fall (Caldwell 1979; Caldwell and Fernandez 1975; Eissenstat and Caldwell 1988; Fernandez and Caldwell 1975; Robertson 1943; Sturges 1979). Caldwell and Fernandez (1975) observed that individual root elements may undergo growth and development for only 2 weeks or less, but the entire root system is active for most of the year.

Through experimentation with a radioactive isotope of iodine, Daubenmire (1975) reported that the isotope absorbed by one section of the root system was found only in one discrete section of the crown. Thus, it appears that individual components of the root systems are linked to specific sections of the crown. This supports earlier findings of Cook and Stoddart (1960) who observed that twigs clipped on half of a big sagebrush plant resulted in the death of the root system on the same half. Lunt and others (1973) found that the oxygen requirement of big sagebrush roots is unusually high, 0.50 mg $^{cm-2}$ min^{-1} to sustain a 50 percent maximum root growth rate. This compares to 0.30 for many economic plant species and for bur-sage (*Franseria dumosa*) (Lunt and others 1973).

Soils of Big Sagebrush

Big sagebrush grows on a variety of soils throughout its range. This is illustrated in table 1.2, which lists the

Table 1.2—Soils of big sagebrush according to order, suborder, great group, and subgroup[a].

Order	Suborder	Great group	Subgroup
Alfisols	Boralfs	Cryoboralfs	Mollic Cryoboralfs
			Ochreptic Cryoboralfs
			Typic Cryoboralfs
Aridisols	Argids	Durargids	Haplic Durargids
			Haploxerollic Durargids
			Xerollic Durargids
		Haplargids	Borollic Haplargids
			Lithic Xerollic Haplargids
			Typic Haplargids
			Ustollic Haplargids
			Xerollic Haplargids
		Natrargids	Haplic Natragids
			Xerollic Natrargids
	Orthids	Calciorthids	Xerollic Calciorthids
		Camborthids	Borollic Camborthid
			Duric Camborthids
			Lithic Camborthids
			Lithic Xerollic Camborthids
			Typic Camborthids
			Ustollic Camborthids
			Xerollic Camborthids
		Durorthids	Entic Durorthids
			Haploxerollic Durorthids
			Xerollic Durorthids
		Paleorthids	Xerollic Paleorthids
Entisols	Fluvents	Torrifluvents	Ustic Torrifluvents
			Xeric Torrifluvents
			Xerollic Torrifluvents
		Xerofluvents	Typic Xerofluvents
	Psamments	Torripsamments	Typic Torripsamments
	Orthents	Torriorthents	Lithic Torriorthents
			Typic Torriorthents

(con.)

Table 1.2 (Con.)

Order	Suborder	Great group	Subgroup
			Xeric Torriorthents
		Xerorthents	Typic Xerorthents
	Psamments	Xeropsamments	Typic Xeropsamment
Inceptisols	Aquepts	Vitrandepts	Typic Vitrandepts
Mollisols	Borolls	Cryoborolls	Argic Cryoborolls
			Argic Lithic Cryoborolls
			Argic Pachic Cryoborolls
			Calcic Cryoborolls
			Cumulic Cryoborolls
			Duric Cryoborolls
			Lithic Cryoborolls
			Pachic Cryoborolls
			Typic Cryoborolls
	Rendolls	Rendolls	Lithic Cryic Rendolls
	Xerolls	Argixerolls	Aridic Argixerolls
			Aridic Calcic Argixerolls
			Calcic Argixerolls
			Calcic Pachic Argixerolls
			Duric Argixerolls
			Lithic Argixerolls
			Pachic Argixerolls
			Typic Argixerolls
		Calcixerolls	Aridic Calcixerolls
			Typic Calcixerolls
		Durixerolls	Aridic Durixerolls
			Orthidic Durixerolls
		Haploxerolls	Aridic Haploxerolls
			Calcic Haploxerolls
			Calcic Pachic Haploxerolls
			Calciorthidic Haploxerolls
			Cumulic Haploxerolls
			Entic Haploxerolls
			Lithic Haploxerolls
			Natric Haploxerolls
			Pachic Haploxerolls
			Typic Haploxerolls
		Natrixerolls	Typic Natrixerolls
		Palexerolls	Aridic Palexerolls
			Pachic Palexerolls
			Petrocalcic Palexerolls
			Typic Palexerolls

[a] References used to construct this table: Acker (1992); Barker and McKell (1983); Blackburn and others (1968, 1969b); Charley and West (1975); Daubenmire (1970); Doescher and others (1986); Fisser (1986); Jensen (1989b, 1990); Jensen and others (1990); Lentz and Simonson (1987b); Miller and others (1986); Passey and others (1982); Swanson and Buckhouse (1986); Swanson and others (1986); Thorp (1931); Tueller and Eckert (1987); Weltz and others (1992).

soils of big sagebrush according to order, suborder, great group, and subgroup. Big sagebrush has been found growing on the following five orders: Alfisols, Aridisols, Entisols, Inceptisols, and Mollisols. Within these five soil orders, big sagebrush was reported as growing on 11 soil suborders, 23 great groups, and 72 subgroups (table 1.2). Big sagebrush can be found growing on all 12 soil textural classes—clay, silty clay, silty clay loam, silt loam, silt, clay loam, loam, sandy clay, sandy clay loam, sandy loam, loamy sand, and sand—but it is most often found on a loam or sandy loam soil (Blackburn and others 1968, 1969a; Daubenmire 1970; Fairchild and Brotherson 1980; Lentz and Simonson 1987a,b; Mueggler and Stewart 1980; Passey and others 1982; Shown and others 1972; Thatcher 1959).

Chemical properties of big sagebrush soils are highly variable among soil horizons of a given site and among sites, as shown in table 1.3. For example, the percentages of organic carbon for A, B, and C horizons for a given site were: A 2.70, B 0.71, and C 0.39. A horizon among sites varied from 0.62 to 4.14 (table 1.3). Soil pH of big sagebrush soils also varied among soil horizons within a given site and among sites (table 1.4); big sagebrush grows in soils varying in pH from 5.9 to 10.0 but is usually found growing in soil nearly neutral, that is, a pH of 7.

Annual precipitation falling on big sagebrush soils varies from 5 to 58 inches (Barker and McKell 1983; Blackburn and others, 1968, 1969a,b; Blackburn and Skau 1974; Blank and others 1992; Fisser 1986; Goodrich and others 1999; Jameson and others 1962; Mason and others 1967; Mueggler and Stewart 1980; Passey and Hugie 1963a; Passey and others 1982; Shown and others 1972; Tisdale and others 1965; Van Ryswyk and others 1966). Moisture infiltration rates of big sagebrush soils varied from 0.47 to 4.05 inches per hour (Balliette and others 1986; Blackburn 1975; Blackburn and others 1990; Blackburn and Skau 1974; Branson and others 1967; Gifford 1972; Swanson and Buckhouse 1986). Balliette and others (1986) found infiltration rates under big sagebrush canopy to be higher than the interspaces. Eldridge and Rosentreter (2004, p. 81) stated: “In our study, infiltration under the shrubs was two to six times greater than infiltration in the interspaces.”

Regardless of the taxonomical and textural classification, chemical properties, pH, annual precipitation, or infiltration rate of big sagebrush soils, all soils supporting big sagebrush have two characteristics in

Table 1.3—Soil chemistry[a] of big sagebrush soils.

Horizons	OC	N	P	K	Na	Ca	Mg	CEC	$CaCO_3$	1/3 atmos.	References
A	2.8	0.25	64.0	2.5				20.8		30.5	Barker and McKell 1983[b]
A	1.10	.11	6.8	.5				7.2		17.6	
A	2.09	.17		1.09	.30	26.9	3.96	20.5	3.40	20.4	Passey and others 1982[c]
B	.99	.10		1.23				18.5	8.30	19.1	
C	.58	.07		.61				11.5	28.80	17.6	
A	2.70	.25		3.52	.32			33.1	.85	32.8	
B	.71	.14		1.01	1.07			34.1	21.90	39.4	
C	.39			.37	9.05			40.0	50.70	43.2	
A	1.02	.10		.88	.36			14.8	22.90	18.3	
C	.33	.07		.94	1.99			11.6	35.6	22.4	
A	1.96	.18		2.9	.10	18.2	3.30	24.1			
B	.90	.10		2.0	.10	22.2	3.60	26.7			
C	.62	.07		.6	.30			21.8			
A	1.92	.15		2.60	.10	12.1	5.10	19.6			
B	.31	.05		.68	1.55	16.7		27.8			
C	.15			.55	2.40			30.4			
A	1.80	.15		2.13	.10	13.9	3.40	18.2			
B	.60	.07		1.20	.10	13.6	3.90	17.1			
C	.40	.06		.80	.20			15.7			
A	1.39	.11		1.50	.20	11.5	4.35	17.7			
B	.65	.07		.60	.20	12.7	5.6	18.2			
C	.22			.50		19.0	6.83	12.2			
A	.62										Blank and others 1992
B	.33										
A	1.39	.02									Charley and West 1975
A?	2.15	.10									Doescher and others 1984
A	4.14	.19		1.25	.10	13.65	3.99	21.5			Jensen 1989a
B	2.45			1.05	.10	13.64	6.06	20.95			
A&B	2.23			.64	.25	15.90	3.08	19.9		15.6	Marchand 1973
A	1.12			1.20	.20	8.40	2.80	13.0			Van Ryswyk and others 1966
B	.71			1.00	.20	9.00	2.80	12.8			
C	.22			.70	.20	12.70	4.00	6.6			

[a] OC = organic carbon %; N = nitrogen %; P = phosphorus ppm; K = potassium me/100g; Na = sodium me/100g; Ca = calcium me/100g; Mg = magnisum me/100g; CEC = cation exchange capacity me/100g; $CaCO_3$; 1/3atmos = percent of moisture at 1/3 atmosphere.

[b] Values are extremes (highs and lows) for the study.

[c] Values are means of horizons per site.

Table 1.4—pH of big sagebrush soils.

Soil horizons					
A	B	C	Subspecies	Reference	State
7.1				Blackburn and others 1968	Nevada
7.4					
7.7	7.5				
7.5					
7.3	7.5				
6.9				Blackburn and others 1969a	Nevada
7.6					
7.0					
6.6	7.2				
7.0	7.4				
6.9	7.0				
6.6	6.6			Blackburn and others 1969b	Nevada
6.7	6.8				
7.0	6.7				
6.4	6.6				
6.3	6.4				
7.2					
7.7				Charley and West 1975	Utah
7.7					
6.9	6.8		Mountain	Cottrell and Bonham 1992	Colordao
6.8	6.5		Mountain		
8.2	8.1		Basin		
8.1	8.2		Basin		
8.2	8.3		Wyoming		
7.7	8.2		Wyoming		
6.7	8.0		Basin	Daubenmire 1970[a]	Washington
6.7	7.7		Basin		
6.5	7.2		Basin		
6.4	7.1		Basin		
6.2	7.0		Basin		
6.9	8.0		Basin		
6.7	6.9		Basin		
6.3	6.9		Basin		
7.1	7.9		Basin		
6.1	7.5		Basin		
6.6	7.4		Basin		
6.5	6.3		Basin		
6.4	7.7		Basin		
7.2	7.7		Basin		
6.8	7.3		Basin		
6.7	7.3		Basin		
6.6	7.7		Basin		
6.8	7.2		Basin		
7.2	7.3		Basin		
6.9	7.1		Basin		
6.8	7.9		Basin		
6.7	7.9		Basin		
6.2	7.0		Basin		
6.5	6.8		Basin		
6.6	7.2		Basin		
7.9	7.9		Basin		
6.9	7.2		Basin		
6.6	7.1		Basin		
7.3	7.7		Basin		
5.9	6.6		Basin		
6.2	7.6		Basin		
6.4	6.8		Basin		
6.5	6.6	6.7	Mountain	Doescher and others 1984	Oregon
6.7	6.6	6.6	Mountain		

(con.)

Table 1.4 (Con.)

Soil horizons					
A	B	C	Subspecies	Reference	State
6.5	7.1	7.3	Basin		
6.9	7.3	7.5	Basin		
7.0	7.4	7.5	Wyoming		
7.0	7.2	7.2	Wyoming		
7.1				Fairchild and Brotherson 1980	Arizona
7.3					
7.9	8.3		Basin	Fisser 1986	Wyoming
7.8	7.9		Basin		
8.1	8.5		Basin		
7.1	7.4		Wyoming		
7.6	7.5		Wyoming		
7.5				Hazlett and Hoffman 1975	North Dakota
8.2					
7.7					
7.7	7.2		Wyoming	Jensen 1990	Nevada
7.0	6.6		Basin		
6.4	6.2		Basin		
7.0	7.4		Mountain		
6.2	6.3		Mountain		
6.4	6.6		Mountain		
7.0	7.2		Mountain		
6.4	6.5		Mountain		
7.1			Mountain	Lentz and Simonson 1987a	Oregon
7.4			Wyoming		
7.3			Wyoming		
6.7				Marchand 1973	California
7.6					
7.5	7.6	7.8	Basin	Passey and others 1982	Idaho, Utah
7.4	7.5	8.3	Basin		
6.6	7.1	8.3	Basin		
6.8	7.5	8.0	Basin		
6.6	7.6	8.0	Basin		
6.4	7.6	8.3	Basin		
7.4		7.9	Basin		
7.1	7.6	8.3	Wyoming		
7.3	7.5	8.2	Wyoming		
6.8	6.7	8.7	Wyoming		
6.6	6.9	7.9	Wyoming		
7.0	7.3	8.1	Wyoming		
7.0	7.7	8.5	Wyoming		
7.3		7.6	Wyoming		
7.8				Pearson 1965	Idaho
7.8					
7.8	9.1	10.0		Rickard 1964	Washington
6.0	6.5		Mountain	Robertson and others 1966	Colorado
8.2	8.1			Robocker 1958	Nevada
6.9	7.3		Wyoming	Van Ryswyk and others 1966	British Columbia
7.2	7.4	7.6	Wyoming		
7.3	7.8	8.2			
7.9			Basin	Wang and others 1998	Utah
7.0			Basin-Mountain hybrid		
7.7			Basin-Mountain hybrid		
7.3			Basin-Mountain hybrid		
6.9			Mountain		
6.9			Basin		
6.7			Basin-Mountain hybrid		
7.0			Basin-Mountain hybrid		
7.0			Basin-Mountain hybrid		

Means A = 7.0; B = 7.3; C = 7.9
Range A = 5.9-8.2; B = 6.3-9.1; C = 6.6-10.0

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[a] Daubenmire (1970) did not recognize Wyoming big sagebrush at the time his report was published, but McArthur and Sanderson (1999) found many of the stands to be Wyoming big sagebrush.

common: they are well drained, and they contain low concentrations of salts (Thatcher 1959).

Big Sagebrush Taxonomy and Origin

McArthur (1979) notes that the word or name *Artemisia* was derived from an early word meaning or referring to Mother Nature, and from Artemis who was the Greek goddess of wild animals, the hunt, plants, chastity, and childbirth. Nuttall (1841, p. 398) was the first to describe and give big sagebrush its scientific name, *Artemisia tridentata*. His description:

> canescently tomentose; leaves cuneate, three-toothed at the summit, upper ones entire and obtuse; flowers paniculate; capitulum sessile, ovate and tomentose, small; inner sepals scariose, linear-oblong. Hab. Plains of the Oregon, and Lewis' River. A low, but rather stout shrub, white with a close tomentum. Leaves rather more than an inch long, about two lines wide, more or less deeply three-toothed, sometime entire, the upper ones always so. Panicle much branched, the flowers small. (I have not seen them in a perfect state, and therefore class this species by its apparent affinity with the last.) Somewhat allied to *A. chinensis*.

Later Torrey and Gray (1843, p. 418) added to the description of big sagebrush: "densely silvery-canescent; those of the flower-branchlets often linear and entire; heads obovoid, spicate-glomerate, disposed in dense compound panicles, 5-6 flowered; exterior scales of the involucre canescent, the inner scarious." They also produced the first classification scheme that included big sagebrush. Later this was revised by Rydberg (1916), then by Hall and Clements (1923), followed by Beetle (1959, 1960), Beetle and Young (1965), Brunner (1972), Goodrich and others (1985), McArthur (1979), McArthur and others (1979), Ward (1960), and Winward and Tisdale (1977). Many of these classification schemes are compared in a paper by McArthur (1979).

The taxonomy of big sagebrush is as follows (Beetle 1959, 1960; Beetle and Young 1965; McArthur 1979, 1983; Tisdale and Hironaka 1981; Raven and others 1999):

- Kingdom: Plantae
- Phylum: Anthophyta
- Class: Eudicots
- Order: Asteraceae
- Tribe: Anthemidea
- Genus: *Artemisia*
- Subgenus: Tridentatae
- Species: *tridentate*
- Subspecies: *tridentata* (basin big sagebrush), *wyomingensis* (Wyoming big sagebrush), *vaseyana* (mountain big sagebrush).

Some authorities have divided subspecies *A. t.* ssp. *vaseyana* into two forms or subspecies depending on the authority being quoted. One form is called subalpine big sagebrush (*Artemisia tridentata* ssp. *spiciformis* [McArthur and Goodrich 1986] or *A. t.* ssp. *vaseyana* f. *spiciformis* [Beetle and Johnson 1982]), which in this treatise is treated as an atypical high-elevation (9,300 to 10,600 feet) mountain big sagebrush; also, Goodrich and others (1985) describe a variety of mountain big sagebrush (*A. t.* ssp. *vaseyana* var. *pauciflora*). A second form is referred to as "X" big sagebrush by Winward and Tisdale (1977), as xeric big sagebrush by Rosentreter and Kelsey (1991), but I treat it as an atypical low-elevation (2,500 to 5,000 feet) mountain big sagebrush, and is described as a subspecies of big sagebrush (*A. t.* ssp. *xericensis*) by Hironaka and others (1983). McArthur and Sanderson (1999) note that it is cytologically distinctive. Also, subspecies basin big sagebrush is divided by some authorities into forms or varieties, the typical form, *f. tridentata* and *f. parishii* (Beetle 1959; Hall and Clements 1923).

The dichotomous key (side bar on this page) by McArthur and others (1979) describes the characteristics that separate the woody sagebrush from other plants and distinguishes subspecies of big sagebrush (bold type leads to big sagebrush).

Other workers have constructed dichotomous keys also as an aid in identifying subspecies of big sagebrush (Beetle 1960; Beetle and Johnson 1982; Blaisdell and others 1982; Brunner 1972; Winward 1980; Winward and Tisdale 1977). Blaisdell and others (1982) have compared some of these keys.

In general, mountain big sagebrush grows at higher, cooler, and moister elevations (4,500 to 11,000 feet) than basin or Wyoming big sagebrush; basin big sagebrush grows lower at warmer and dryer elevations (2,500 to 7,000 feet) than mountain big sagebrush; and Wyoming big sagebrush is found at the hottest and driest elevations (2,500 to 7,000 feet) of the big sagebrush subspecies (Beetle and Johnson 1982; Bonham and others 1991; Frisina and Wambolt 2004; Hodgkinson 1989; Johnson 1987; McArthur 1979; Mahalovich and McArthur 2004; McDonough and Harniss 1975; Winward 1983; Winward and Tisdale 1977). Monsen and McArthur (1985) and Goodrich and others (1999) reported average annual precipitation for mountain big sagebrush stands to be about 17 inches, 14 inches for basin big sagebrush, and 11 inches for Wyoming big sagebrush. Tisdale and Hironaka (1981) noted that stands dominated by Wyoming big sagebrush were the first to became water deficient (mid-July), basin big sagebrush stands were second (late July to early August), and mountain big sagebrush stands were the last to become water deficient (September). Barker and McKell (1983), studying the habitat characteristics of contiguous populations of basin and Wyoming big sagebrush, found that

1a. Head with both ray and disc flowers; pappus of several to many scales.

1b. Heads with only disc flowers or if ray flowers present then pappus of capillary bristles or lacking.

  3a. Pappus of capillary bristles, at least in part.

  3b. Pappus lacking…*Artemisia* (sagebrush).

    26a. Heads with both ray (marginal) flowers and disc flowers; plants subshrubs or shrubs.

    26b. Heads with disc flowers only; plants shrubs.

      30a. Plants up to 5 dm high.

      30b. Plants usually over 5 dm high (42b provide most exceptions to 5 dm height).

        36a. Leaves silvery-canescent, linear to linear-oblanceolate, mostly entire (occasionally with a few irregular teeth), or leaves deeply divided into three of more linear or linear-oblanceolate lobes.

        36b. Leaves not silvery-canescent, narrowly lanceolate to broadly cuneate or fan-shaped, typically 3-tooth or lobed (upper leaves may be entire).

          40a. Plants low-growing, flat-topped shrubs up to 8 dm high; leaves somewhat viscid; heads occurring singly or occasionally up to three arranged in short interrupted spike or raceme like inflorescences; heads large with up to 20 disc flowers each; occurs in high mountainous areas of central Colorado, western Wyoming, Utah, central Sierras of California, and Carson Range of Nevada.

          40b. Plants ranging from dwarf to tall, arborescent forms up to 4.5 m; leaves not viscid; inflorescences of numerous heads arranged into leafy panicles; heads smaller with three to eight disc flowers; most widespread and common shrub of Western North America. *Artemisia tridentata* (big sagebrush).

            41a. Plants uneven-topped shrubs with flowering stalks arising throughout the crown; leaves narrowly lanceolate to cuneate; odor of crushed leaves pungent

              42a. Mature plants often arborescent (with single trunk-like main stem), usually from 1 to 2 m but in some forms up to 4.5 m high; leaves narrowly lanceolate with margins not curving outward; average persistent 5.6 times its width; blooming starts in late August or September; odor strongly pungent; normally occurs below 2,100 m in dry, deep, well-drained soils on plains, valleys, and foothills. *A. tridentata* ssp. *tridentata* (basin big sagebrush).

              42b. Mature plants with several main branches usually less than 1 m high; leaves narrowly cuneate to cuneate with margins curved outward; average persistent leaf length is 3.1 time its width; blooming starts in late July or August, odor pungent; occurs on dry, shallow, gravelly soil from 1,500 to 2,100 m. *A. tridentata* ssp. *wyomingensis* (Wyoming big sagebrush).

            41b. Plants usually even-topped shrubs with flower stalks arising from the upper crown portions; leaves broadly cuneate to spatulate; average persistent leaf length is 4.0 time its width; blooming may begin in July; odor slightly pungent to pleasantly mint-like; occurs from 1,400 to 3,000 m in deep, well-drained soils...*A. tridentata* ssp. *vaseyana* (mountain big sagebrush).

basin big sagebrush grew in wetter and more fertile habitats, having a deeper soil than Wyoming big sagebrush. In addition, the vegetative tissue of basin big sagebrush contained great amounts of nitrogen, magnesium, phosphorus, potassium, iron, and zinc. Soil water content at 1/3 atmosphere was higher for sites supporting basin big sagebrush.

Shumar and Anderson (1986) found that basin and Wyoming big sagebrush distributions were closely associated with soil texture. Basin big sagebrush was supported by sandy soils and Wyoming big sagebrush by silty textured soils. Barker and McKell (1983) found in northeastern Utah and southwestern Wyoming that Wyoming big sagebrush grew mainly on Aridisols and basin big sagebrush on Entisols. Swanson and others (1986) found in eastern Oregon that Wyoming big sagebrush often grew on Aridisols soils, mountain big sagebrush on Mollisols at higher elevations, and basin big sagebrush on deeper soils of either order of soils. Jensen (1989a, 1990) noted that all three subspecies of big sagebrush grew on Mollisols soils of northeast Nevada. Cottrell and Bonham (1992), in a study conducted in the Piceance Basin of Colorado, noted big sagebrush subspecies distribution was related to soil moisture, temperature, soil depth, and parent material. Here, basin big sagebrush tends to occupy deep, sandy soils, whereas mountain big sagebrush occurred at cool, moist, higher elevations, and Wyoming big sagebrush tends to be on shallow, silty soils where moisture stress is greater.

Because of the moisture gradient among the three subspecies of big sagebrush, understory or associated plant species differ among subspecies with Wyoming big sagebrush representing the dry side (xeric), mountain big sagebrush the wet side (mesic), and basin big sagebrush in between. Winward (1983) pointed out that fewer perennial forbs grow in association with Wyoming big sagebrush than with the other two subspecies. Grasses associated with Wyoming big sagebrush include bluebunch wheatgrass (*Agropyron spicatum*), needle-and-thread (*Stipa comata*), squirreltail (*Sitanion hystrix*), and Salina wildrye (*Elymus salina*). Winward (1983, p.16) stated, “Some Wyoming big sagebrush sites may have about 25 percent bare ground even under natural conditions.” On mountain big sagebrush sites, many species of forbs, grasses, and nonsagebrush shrubs are present (Winward 1983). Winward (1983, p.16) described the associated vegetation of mountain big sagebrush: “It is not uncommon to find 40 plant species associated with this sagebrush.” Grasses associated with mountain big sagebrush include bluebunch wheatgrass, Idaho fescue (*Festuca idahoensis*), needle-and-thread, junegrass (*Koeleria cristata*), mountain brome (*Bromus carinatus*), basin wildrye (*Elymus cinereus*), and slender wheatgrass (*Agropyron trachycaulum*) (Winward 1983). At higher elevations, dense stands of mountain big sagebrush (subalpine big sagebrush) often support gophers (*Thomomys* ssp.) (Winward 1983). As stated earlier, basin big sagebrush sites are in between the dryness of Wyoming and the wetness of mountain big sagebrush. Forbs are more prevalent than in Wyoming big sagebrush, and grasses of Wyoming big sagebrush are also present in basin big sagebrush along with basin wildrye (Winward 1983).

Chromatographic (both paper and thin-layer) analysis of ethanol extractions of big sagebrush leaf samples led to the development of a simple field technique that can be used as an aid in identifying or separating subspecies of big sagebrush (Hanks and others 1973; Holbo and Mozingo 1965; Young 1965a,b; Young and Asplund 1963, 1964). After chromatographic development, compounds were localized by exposing the wet chromatogram in a dark environment to long wave ultraviolet light (3,660 angstroms), which revealed the color and position of the various diagnostic spots. Taylor and others (1964) exposed moist seeds of mountain and basin big sagebrush to ultraviolet light and observed that mountain big sagebrush seed fluoresced and basin big sagebrush seeds did not. Young (1965a) found that exposing the extracting bottle (2 grams of vegetative leaf tissues to 10 ml ethanol) and noting the color of the fluorescent would give a preliminary classification of big sagebrush subspecies. Mountain big sagebrush extraction bottles contained a light blue fluorescent, and basin big sagebrush red. Wyoming big sagebrush was undescribed at that time (Beetle and Young 1965). Refinements were made to the technique and applied to dried leaves from the field or from herbarium specimens (Winward and Tisdale 1969). Later, Stevens and McArthur (1974) substituted water for ethanol and were able to separate all three subspecies as follows: mountain was intense blue, Wyoming was light blue, and basin was pale blue to colorless. Since then, this technique has been applied to spectrophotometry of both alcohol and water extractions as a means of identifying subspecies of big sagebrush and putative hybrids among subspecies (McArthur and others 1988; Shumar and others 1982; Spomer and Henderson 1988). Kelsey and others (1976) discuss the usefulness of sesquiterpene lactones and thin-layer chromatography as an aid in identifying subspecies of big sagebrush.

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Explanation of Plate I (Diettert 1938)

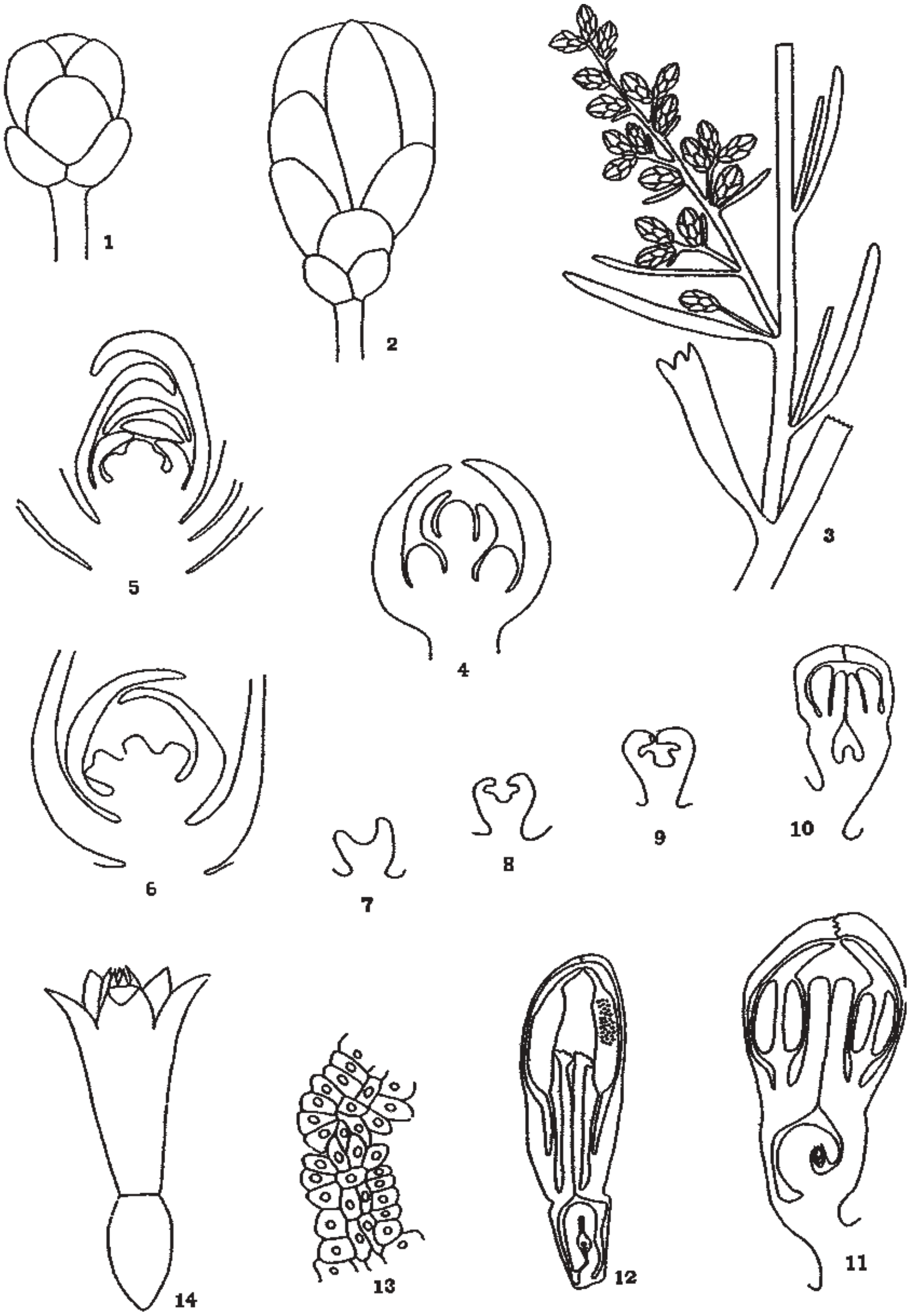


PLATE I

Figure 1—Young flower head. X13. Section of a head at this stage of development is shown in Fig.6.
Figure 2—Older head, just prior to opening. X13.
Figure 3—Portion of flowering branch, showing the arrangement of heads. X11/2.
Figure 4—Section of tip of young flowering branch, showing beginning of heads. X50.
Figure 5—Section of young flowering bud, showing initiation of flowers. X50.
Figure 6-10—Early stages in the development of flowers. X50.
Figure 11—Section of young flower, showing relation of parts at megaspore mother cell stage. X50.
Figure 12—Section of flower just prior to anthesis. X16.
Figure 13—Section of a portion of two corolla lobes, showing interlocking of marginal cells. X245.
Figure 14—A single flower just after anthesis. X15.

Explanation of Plate V (Diettert 1938)

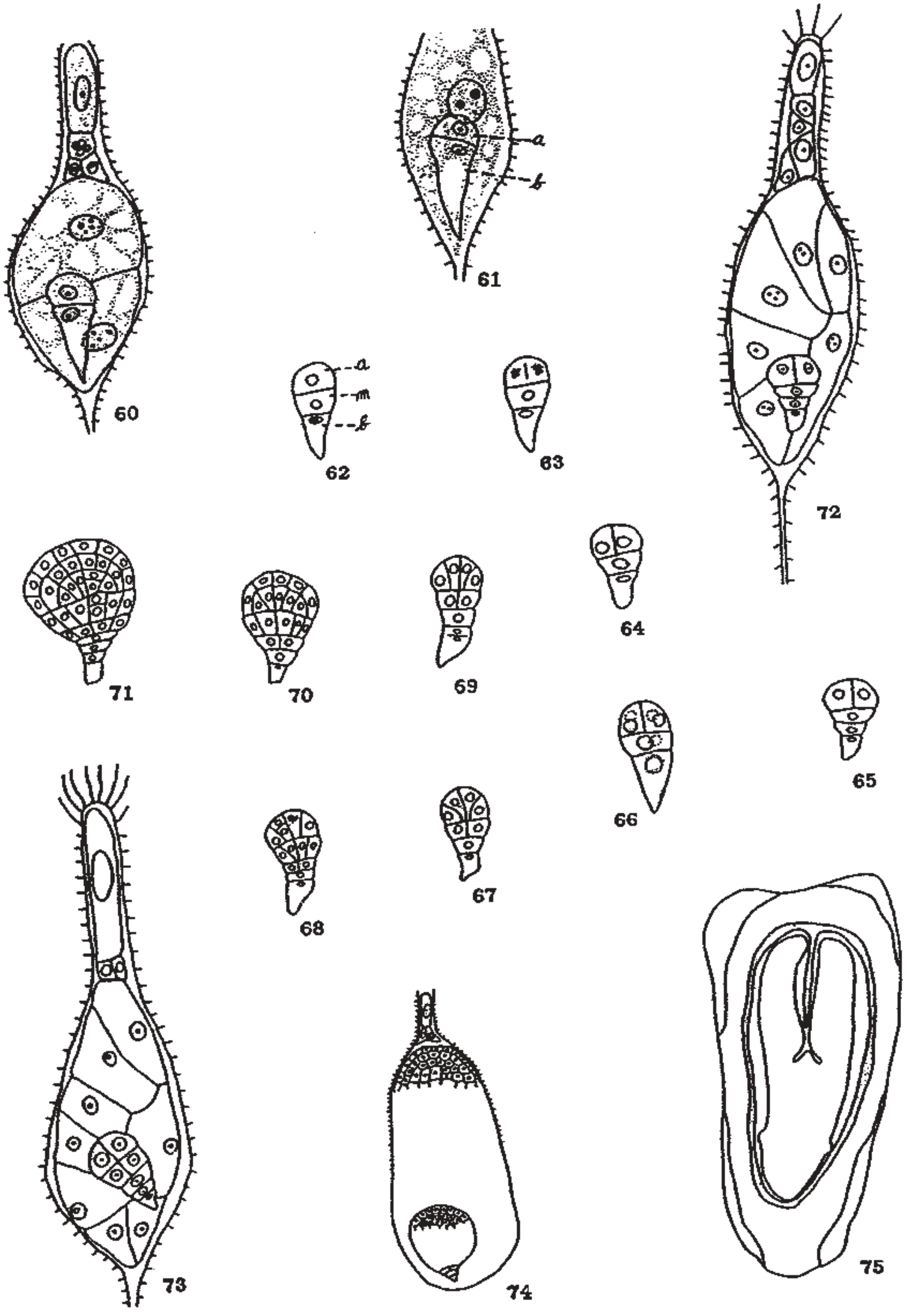


Plate V

Figure 60—Embryo sac with 2-celled embryo and 2-celled endosperm. X165.
Figure 61—Embryo sac with a 2-celled embryo and an undivided primary endosperm cell. X165.
Figure 62-71—Successive stages in the development of the embryo. X165.
Figure 72-73—Embryo sacs with young embryos and endosperm. Note enlargement of chalazal antipodal cell in Fig. 73. X165.
Figure 74—Embryo sac with embryo and endosperm. Note the persisting antipodals. X50.
Figure 75—Nearly mature seed. Endosperm shown by dotted region. X35.

Explanation of Plate VI (Diettert 1938)

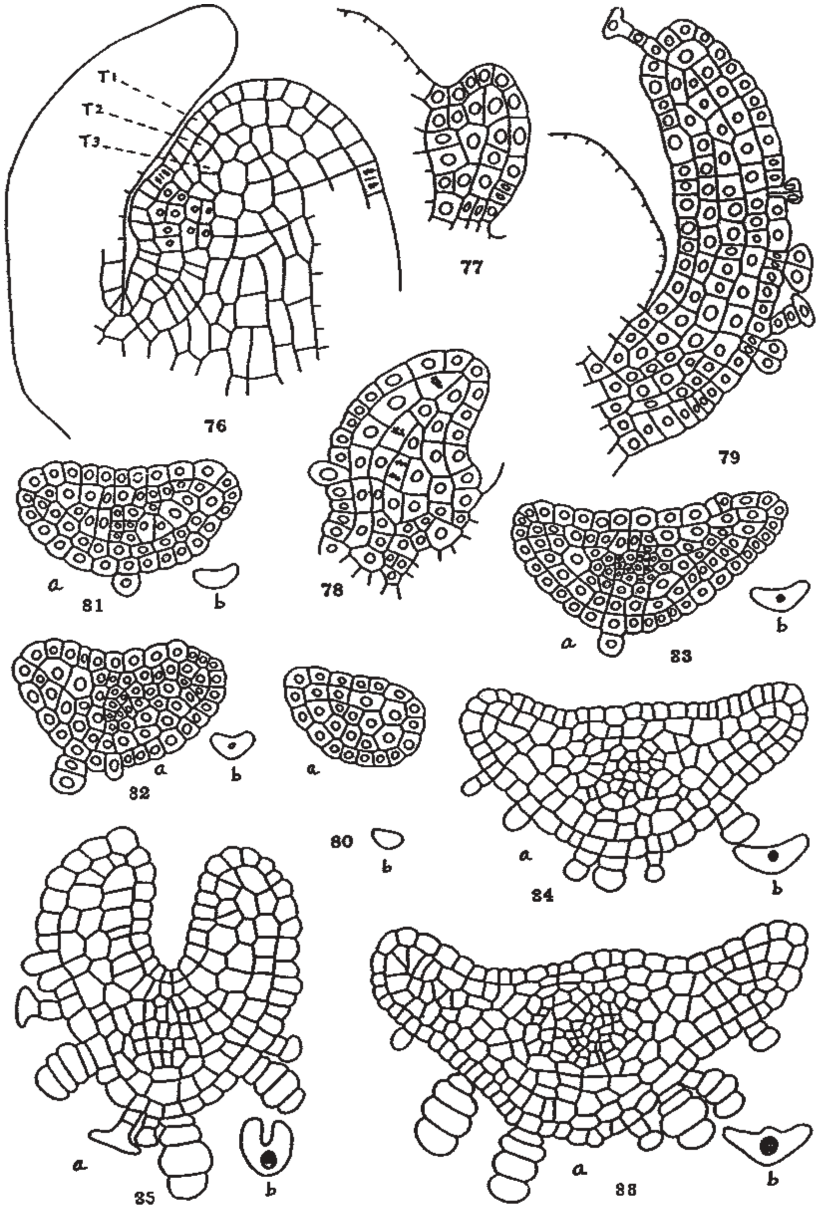


PLATE VI

Figure 76-79—Longitudinal sections of foliar primordia. X245.
Figure 76—Section through stem tip, showing initiation of leaf primordium by periclinal divisions of the second and third layers of the tunica (T_2 and T_3).
Figure 77—Primordium emerging as a papillate protuberance.
Figure 78—Primordium about 80 microns high. Note beginning of trichome on abaxial side.
Figure 79—Primordium 175 microns long. Note development trichomes on abaxial side.
Figure 80-86—Transverse sections of foliar primordia. Drawings showing cellular arrangement (a) x245; outline drawings (b) x50; shaded area in outline drawings indicates region of the midrib.
Figure 80—Primordium 50-60 microns high, 30 microns from base.
Figure 81—Primordium 75-100 microns high, 40 microns from base.
Figure 82—Primordium 120 microns high, 40 microns from base.
Figure 83—Primordium 170 microns high, 60 microns from base.
Figure 84—Primordium 275 microns long, 60 microns from base.
Figure 85—Primordium 360 microns long, 200 microns from base. Note development of trichomes.
Figure 86—Primordium 475 microns long, 120 microns from base.

Explanation of Plate VII (Diettert 1938)

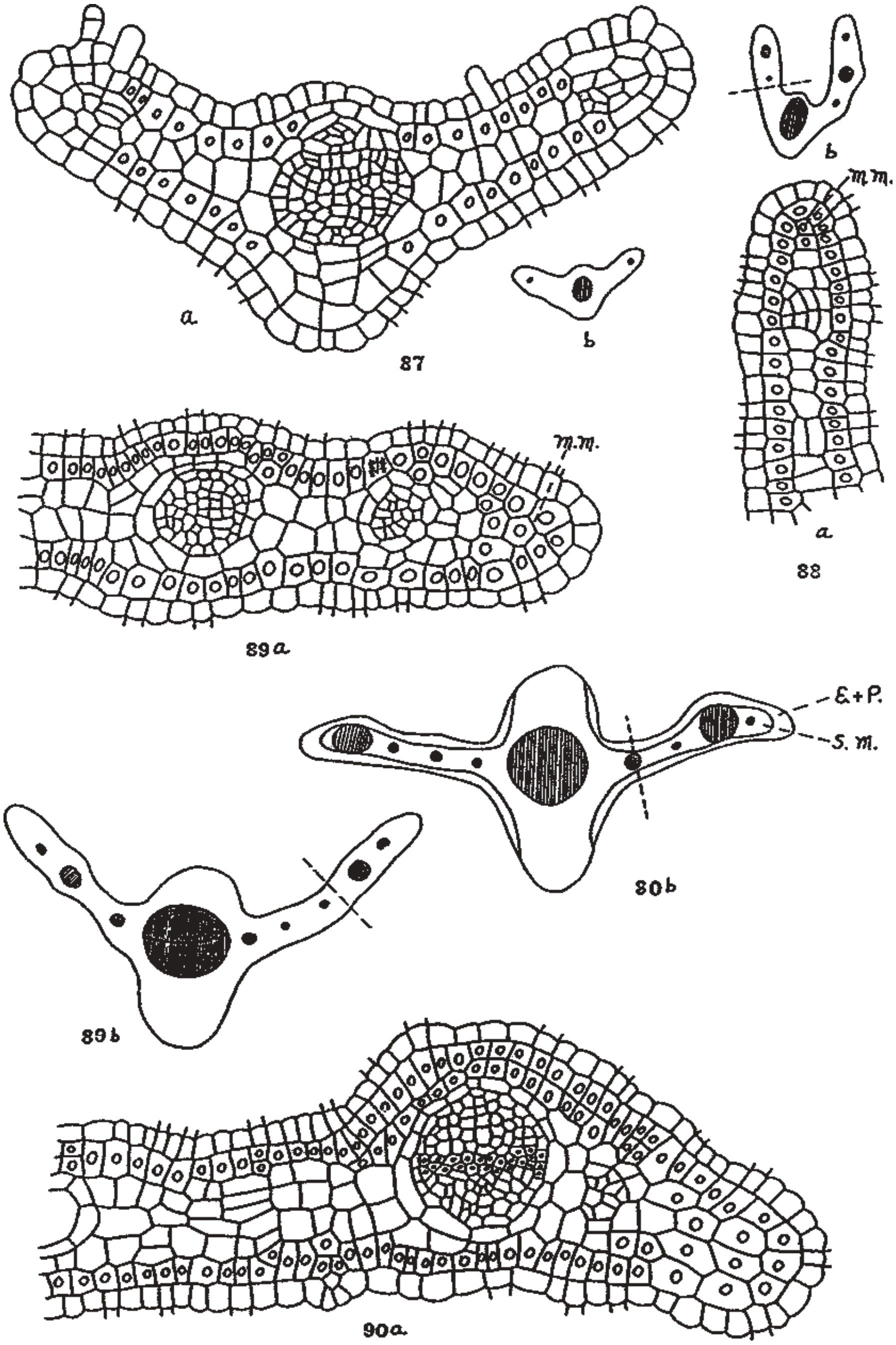


PLATE VII

Figure 87-90—Transverse sections of young leaves: (a) portion of leaf showing cellular arrangement. Nuclei shown in outline only in cells of palisade layers. X245. (b) outline of entire leaf from which (a) was taken. Shaded areas indicate the veins. Portion to right of broken line shown in (a). X50.

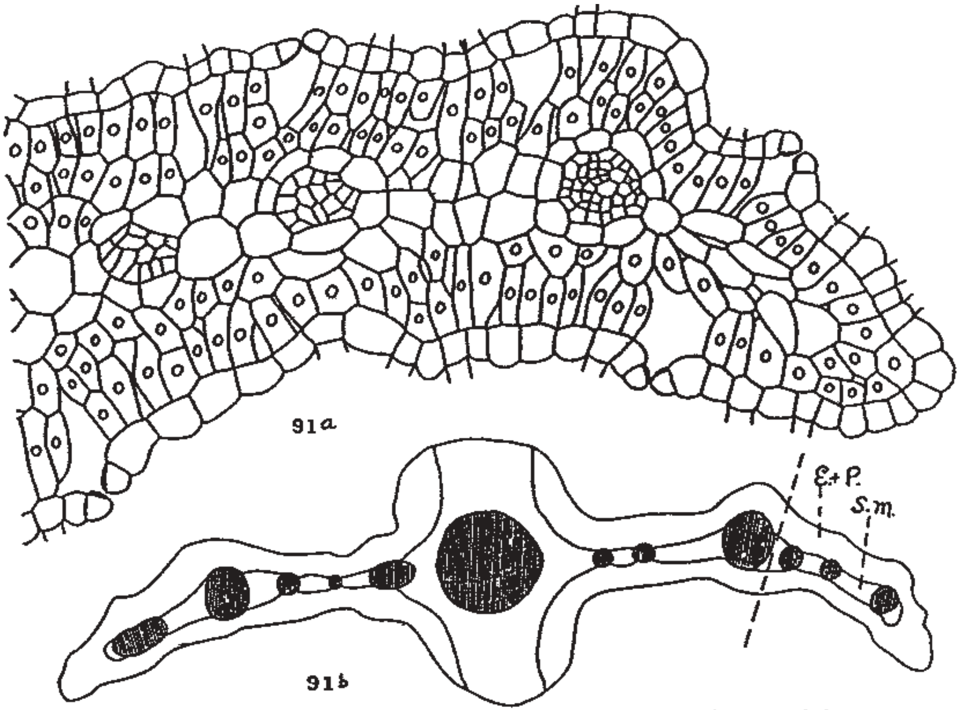
Figure 87—Young leaf 1000-1200 microns long, 300 microns from base. Note beginning of the two major lateral veins. Trichomes on adaxial side just beginning to develop; trichomes on a abaxial side not shown.

Figure 88—Young leaf 1.5 mm. long, about .8 mm. from base.

Figure 89—Young leaf 3-5 mm. long. Note marginal meristem (M.M.)

Figure 90—Young leaf 1.5-2 cm. long, about 7 mm. from base. Note mature vessels in largest vein. (b) E. + P. includes the epidermal and palisade layers; S. M., the spongy mesophyll and veins.

Explanation of Plate VIII (Diettert 1938)



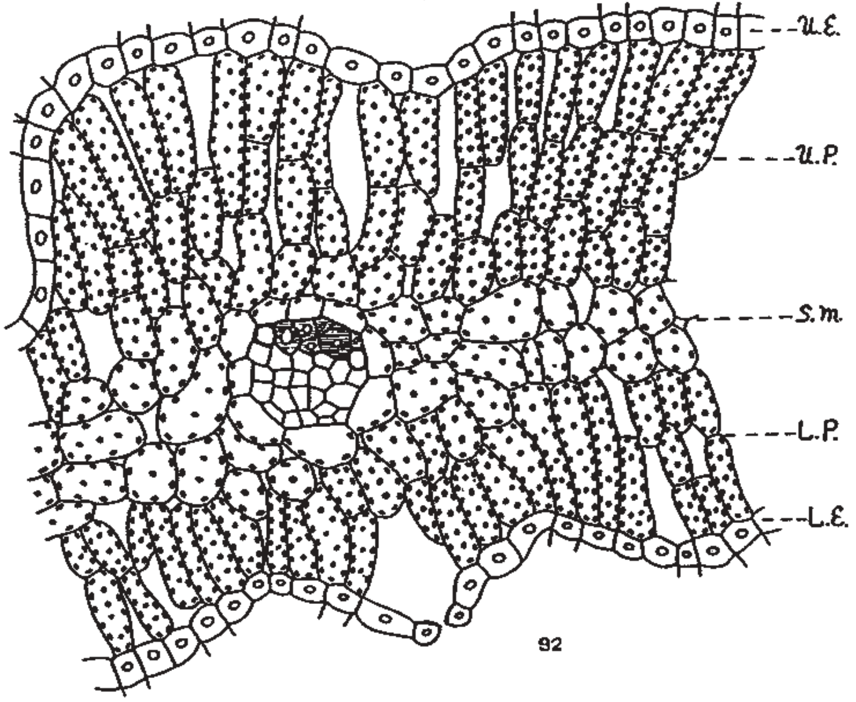
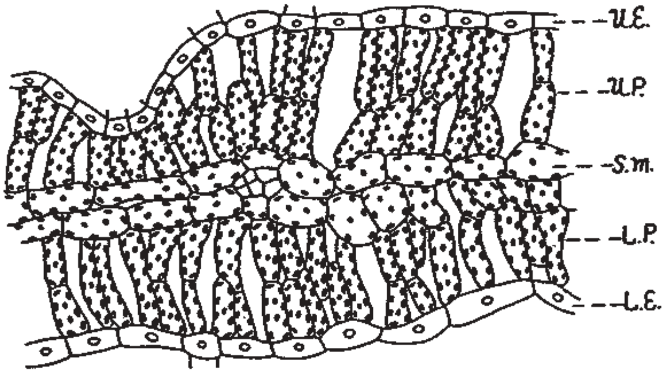


PLATE VIII

Figure 91—(a) Transverse section of portion of leaf, approximately 2.5 cm. long, 1.2 cm. above base and about 3 mm. below forking of midrib. Shortly after the cessation of cell division and the beginning of cell enlargement. X245. (b) Outline of entire section of leaf at the same level. Portion to right of broken line shown in (a). E. + P., epidermal and palisade layers; S. M. spongy mesophyll and veins. Veins indicated by shaded area. X50.

Figure 92—Transverse section of portion of mature leaf. U.E., upper epidermis; U.P., upper palisade; S.M., spongy mesophyll and veins; L.P., lower palisade, L.E., lower epidermis. Note the fibers (shaded) associated with vessels. X245.

Explanation of Plate IX (Diettert 1938)



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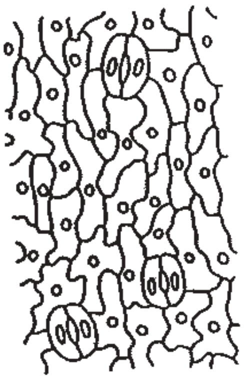

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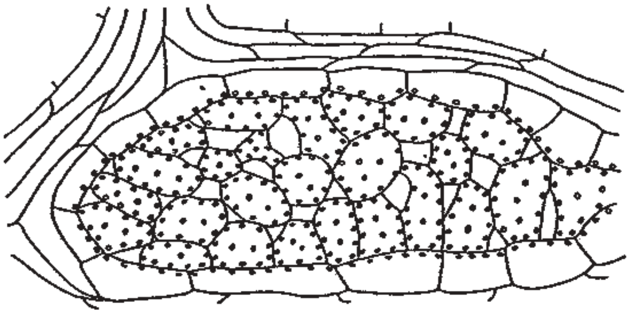

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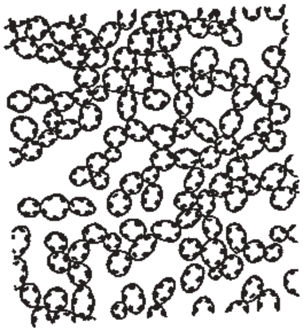

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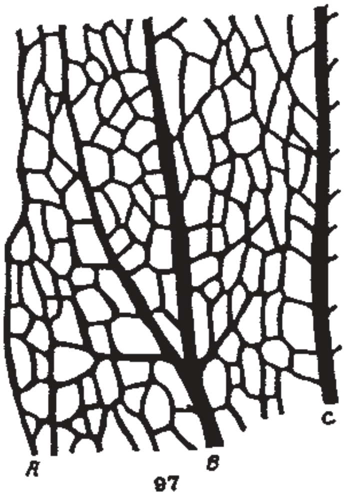

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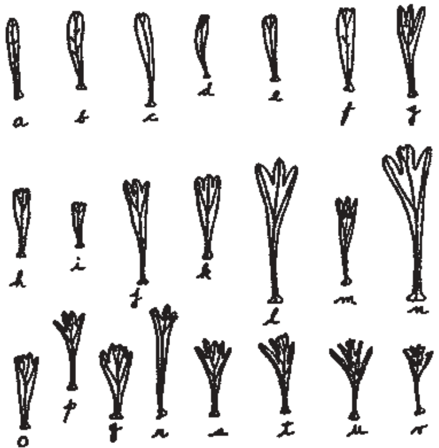

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PLATE IX

Figure 93—Longitudinal section of portion of mature leaf. Legend same as in Fig. 92. Note that the spongy mesophyll is aerated from both side through the palisade layers. X165.
Figure 94—Paradermal section through the spongy mesophyll zone. Note the small spaces in this region. X165.
Figure 95—Paradermal section through the palisade layer. X165.
Figure 96—Portion of epidermal layer. X165.
Figure 97—Vascular system of portion of a leaf just below the lobes. Reconstructed from a series of paradermal sections. A, marginal vein; B, major vein leading into a marginal lobe; C, major vein leading into the central lobe. X11.
Figure 98—Mature leaves, showing variations in size and form and the major veins. X1/3.

Explanation of Plate X (Diettert 1938)

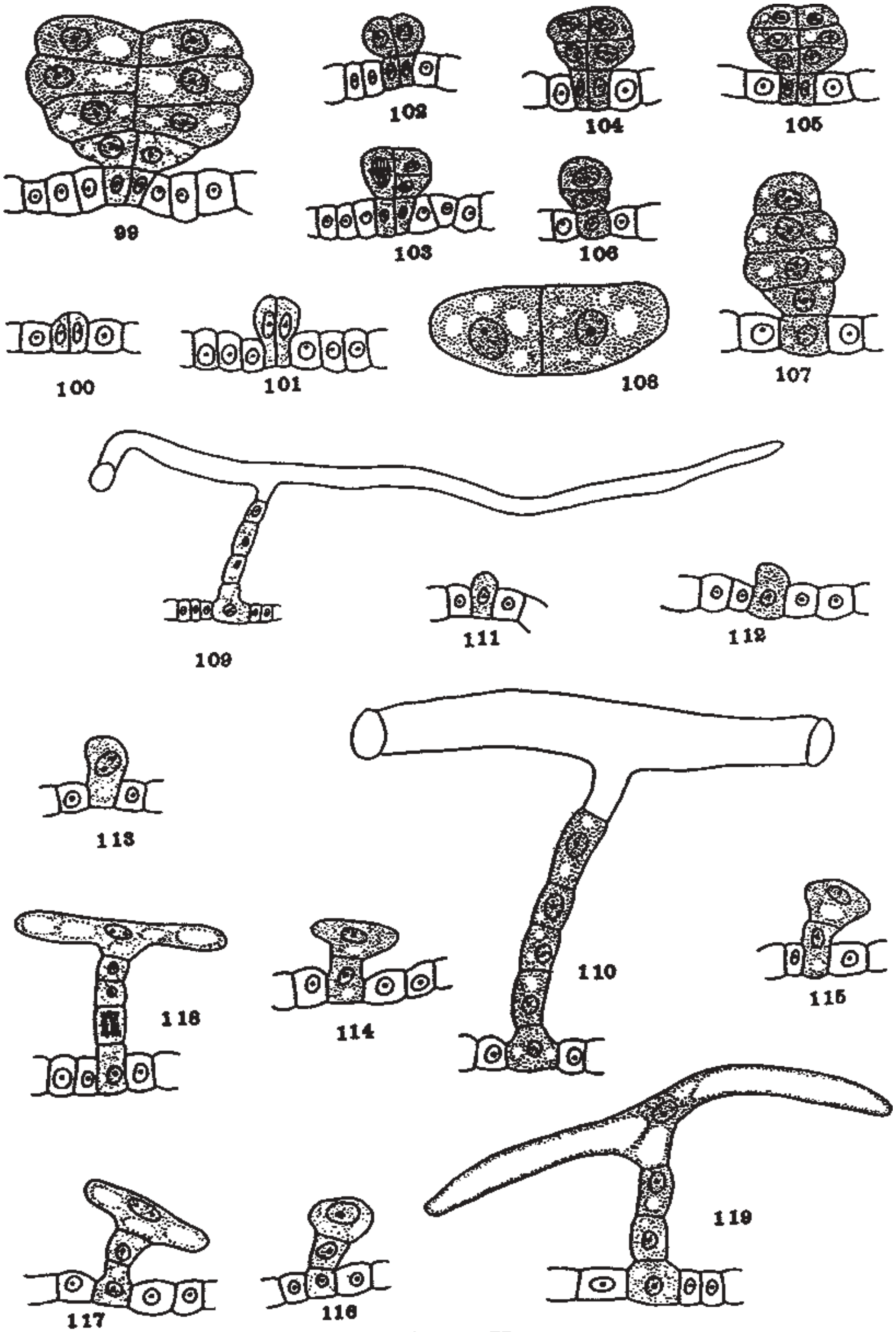
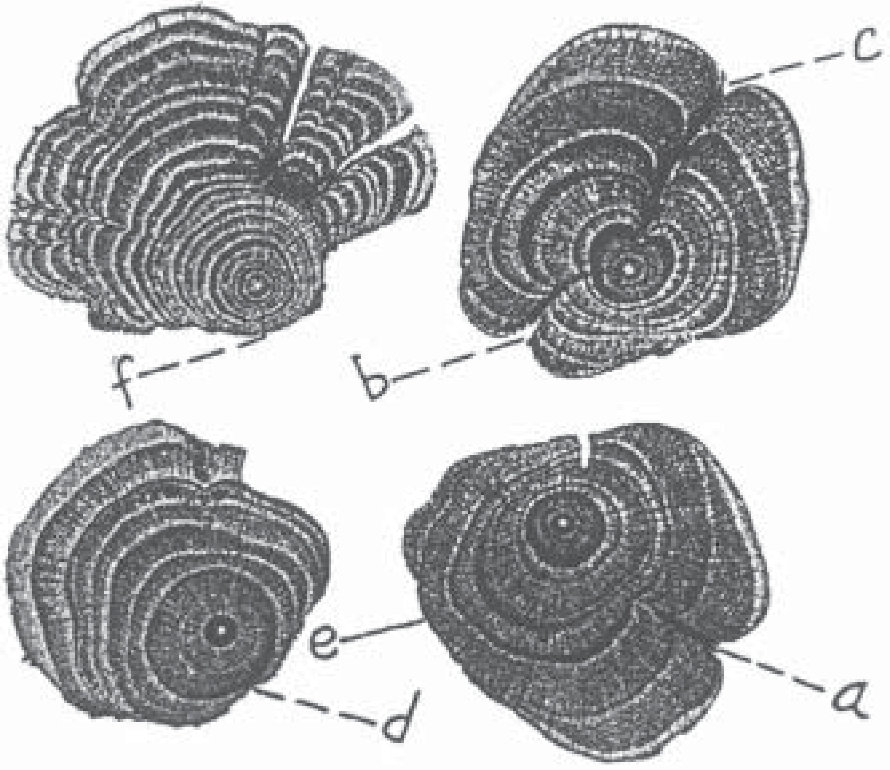


PLATE X

Figure 99—Mature glandular trichome. X365.
Figure 100-105—Successive stages in development of the glandular trichomes. X365.
Figure 106-107—Glandular trichomes as seen in transverse section of the leaf, corresponding to Figs. 104 and 99, respectively. X365.
Figure 108—Two cells of a mature glandular trichome as seen in paradermal section of the leaf. X365.
Figure 109—Mature cover trichome showing entire half of apical cell. X165.
Figure 110—Portion of a mature cover trichome. X365
Figure 111-119—Successive stages in development of the cover trichomes. X365.

Explanation of Plate XVI (Diettert 1938)



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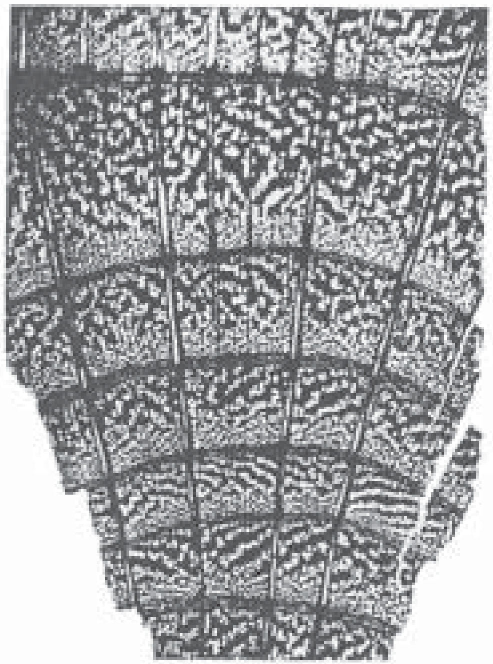

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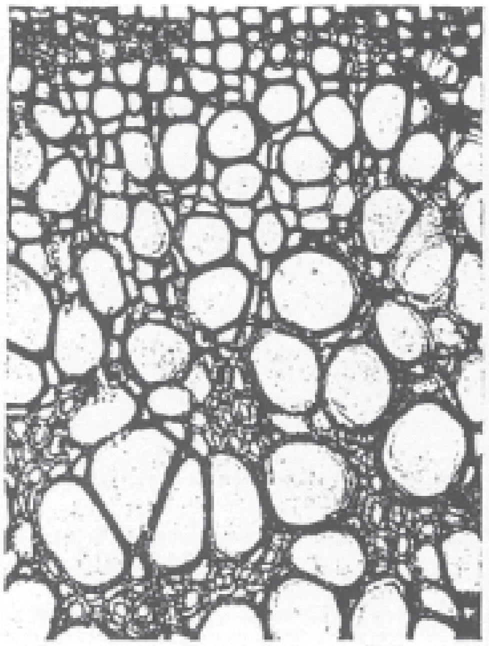
Figure 145—Transverse sections of older stems. Note the eccentricity; a, b, c—caused by death of flowing branches; d, e, f–caused by the death of cambium. Natural size.

Figure 146, 147—Portions of transverse sections of older stems. Note layers of interxylary cork between the annual wood rings. Fig. 146, X10; Fig. 147, X12.

Explanation of Plate XVIII (Diettert 1938)



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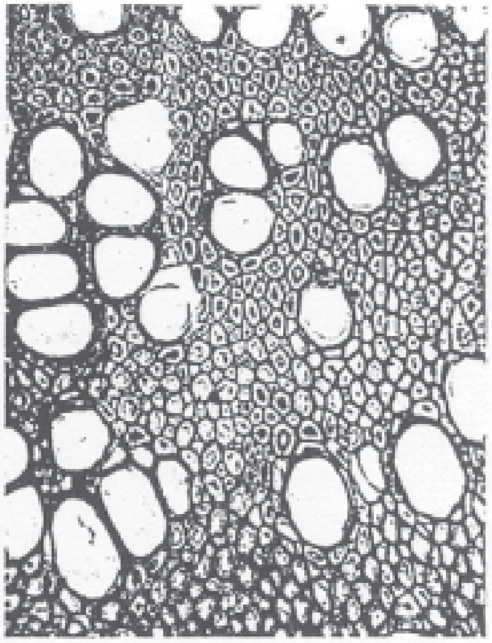

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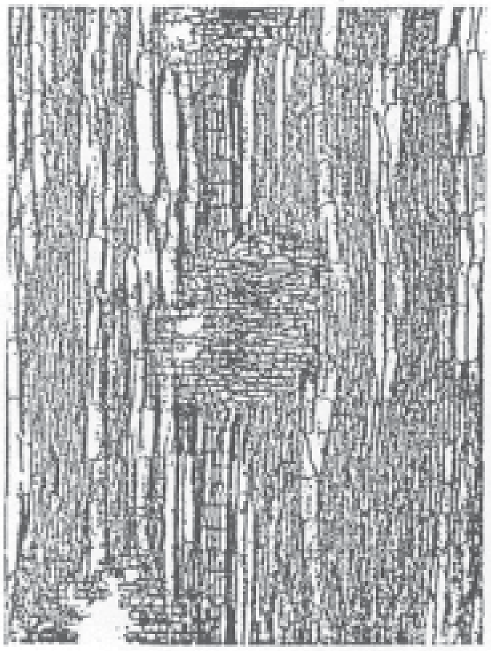

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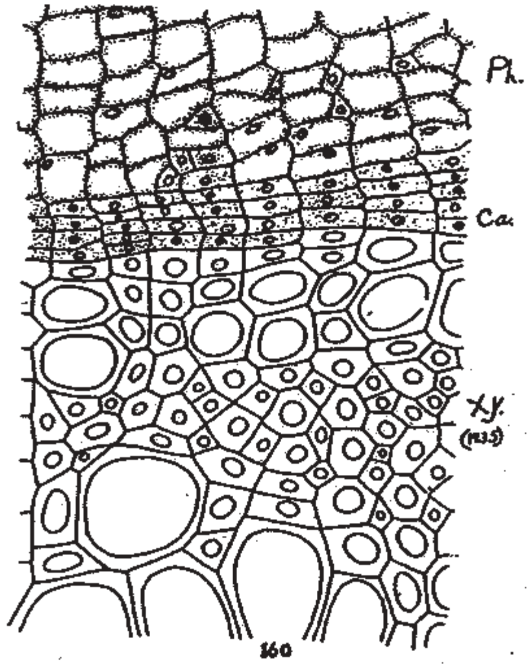
Figure 152, 153—Transverse sections of early and late wood, respectively. X180.
Figure 154—Radial section of an older stem. Note the interxylary cork layer between the two wood rings. X45.
Figure 155—Tangential section of a stem, showing portions of the two latest wood rings. Note the interxylary cork (c) between the two rings; also the progressive suberization of the rays in the latest ring. X27.

Explanation of Plate XX (Diettert 1938)



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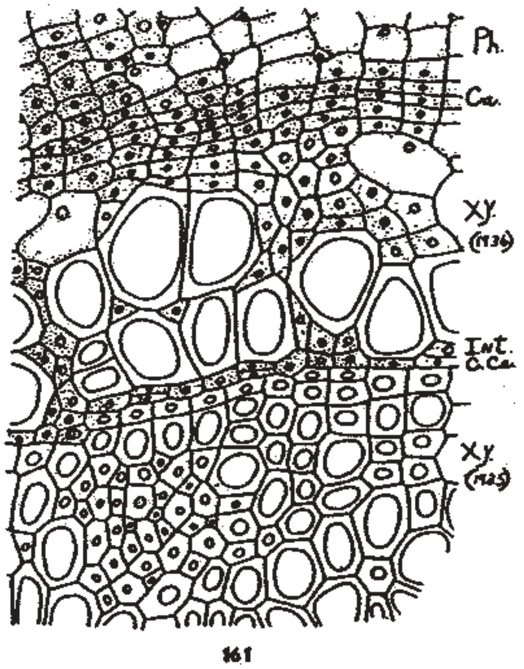

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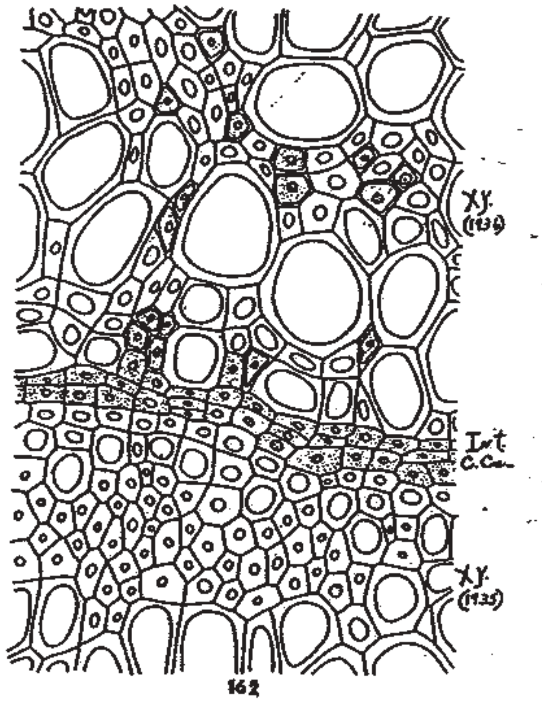

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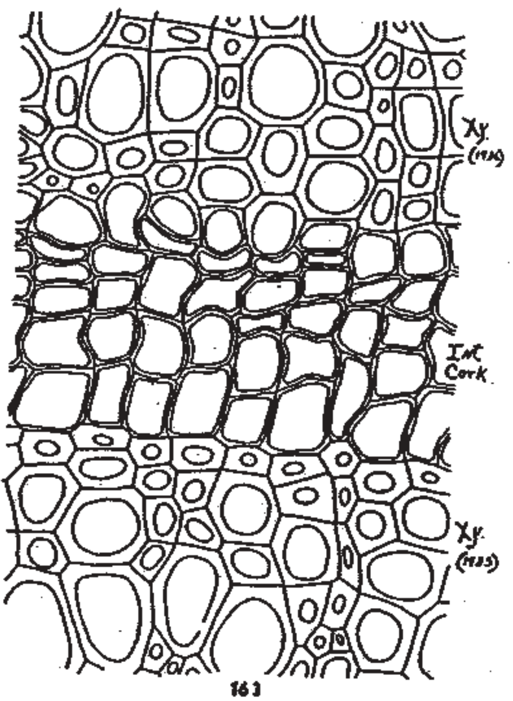

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Figure 160—Transverse section of stem, collected September 29, 1935. Ph.–phloem; Ca–cambium; Xy.–xylem; X365.
Figure 161—Transverse section of stem, collected April 13, 1936. New wood ring about 65 microns wide at this stage. Ph.–phloem; Ca.–cambium; Xy.–xylem; Int. C. Ca.–interxylary cork cambium. X365.
Figure 162—Transverse section of stem, collected May 12, 1936. New wood ring about 330 microns wide at this stage. Only a portion of the new ring is shown in the drawing. X365.
Figure 163—Transverse section of stem, collected August 1, 1936. Xy.–xylem; Int. Cork–interxylary cork. X365.

Notes

Chapter II

Birds, Mammals, and Reptiles Associated With Big Sagebrush

This chapter deals with birds, mammals, and reptiles associated with the three main subspecies of big sagebrush: basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*); Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*). (Fungi, insects, mites, spiders, scorpions, lichens, and so forth are discussed in chapter III.) Birds, mammals, and reptiles associations vary from obligate to facultative. "Obligate associations" are those associations necessary for the animal to complete its life cycle. "Facultative associations" are those associations that vary from being largely dependent on big sagebrush, say for 80 percent of the time, to infrequent use of big sagebrush, perhaps 20 percent of the time.

Birds

A number of bird species have an obligate relationship with big sagebrush. These include sage grouse (*Centrocercus urophasianus*), sage thrasher (*Oreoscoptes montanus*), sage sparrow (*Amphispiza belli*), Brewer's sparrow (*Spizella breweri*), and perhaps the green-tailed towhee (*Pipilo chlorurus*), and they will be discussed below (Braun and others 1976; McEwen and DeWeese 1987). Studying the number of birds and bird species along a Great Basin elevational gradient near and in the Great Basin National Park of east-central Nevada, Medin and others (2000) observed: "Both total number of individual birds and bird species appeared to reach highest values in study plots with a substantial component of mountain big sagebrush."

Obligate Bird Species

Sage Grouse—Sage grouse populations have reached a historical low throughout their entire range (Autenrieth 1986; Beck and others 2003; Connelly and Braun 1997).

Malmsbury (1996) and Braun (1995) reported that sage grouse were once present in as many as 27 counties in Colorado, but are now common in only five to seven. In Oregon, Crawford and Lutz (1985) estimated that sage grouse habitat has decreased by nearly 50 percent and that the abundance of sage grouse within the existing range has declined by about 60 percent. There is concern that sage grouse could be extirpated from the State.

Sage grouse populations are similarly affected in Idaho. The Magic Valley Region of south-central Idaho at one time had 279 active strutting grounds; now only 50 are active—a reduction of 82 percent (Mattise 1995). This region is typical of the entire State. Idaho is one of several States which form the core of sage grouse habitat in the United States. Biologists from Wyoming and Montana are reporting declines in sage grouse populations as well (Connelly and Braun 1997; Western States Sage Grouse Technical Committee 1995).

Utah sage grouse populations are declining in 19 counties, stable in two, and increasing in one (Beck and others 2003; Western States Sage Grouse Technical Committee 1995). Sage grouse occupy only 50 percent of their former range. Today populations are about half or less of those in the mid-1800s, and for some populations only 10 percent of late 1930s populations (Welch and others 1990).

A petition was submitted to the United States Fish and Wildlife Service in May 1999 to list sage grouse as endangered in the State of Washington (Connelly 1999).

Sage grouse—spiny-tailed pheasant—often known locally as sage hen or sage chicken, is the largest grouse native to North America. This species was discovered by 19th century explorers Lewis and Clark above the headwaters of the Missouri River and on the plains of the Columbia River. They named it the "cock of the plains" (Rasmussen and Griner 1938). Sage grouse are gallinaceous birds, meaning they possess specialized stomach or gizzard. However, their gizzard is thin walled and unsuited for digesting seeds (Autenrieth 1986). Sage grouse are a mottled, brownish-gray in color (fig. 2.1) with slight sexual differences during the nonbreeding periods. However, mature males average about 6 pounds but can weigh as much as 7 pounds (Girard 1937; Patterson 1952; Roberson 1986). Females weigh about half as much as males.

Figure 2.1—A sage grouse hen watching over her brood (photo by Bruce L. Welch).

No other North American game bird is as inextricably dependent upon one plant species as sage grouse is on big sagebrush (*Artemisia tridentata* Nutt.) and its near relatives (Peterson 1995; Roberson 1986). They have an obligate relationship with big sagebrush. Rasmussen and Griner (1938) observed close agreement between the original range of sage grouse and the distribution of big sagebrush; also compare Beetle's (1960) distribution map of big sagebrush with Patterson's (1952) sage grouse range map. Patterson (1952) observed that the birds showed no signs of adjusting to the eradication of big sagebrush; also see Braun and others (1977), Dalke and others (1963), and Roberson (1986). Sage grouse use big sagebrush for food and numerous cover requirements including escaping, roosting, loafing, brooding, and nesting (Girard 1937). They are seldom found far from these plants (Peterson 1971).

The dependence of sage grouse on big sagebrush is illustrated by the food preferences of the bird. From October to April, big sagebrush leaves and short shoots make up from 90 to 100 percent of the sage grouse diet (Braun and others 1977; Grinnell and others 1930; Patterson 1952; Roberson 1986; Rogers 1964; Wallestad 1975a; Wallestad and others 1975). Thus, during 7 months, or 58 percent of the year, sage grouse eat nearly pure diets of big sagebrush.

During spring and summer when other foods are available, adult sage grouse still consume large quantities of big sagebrush. Patterson (1952) reported, in a Wyoming study, that it was only during the summer that big sagebrush made up less than 80 percent of the sage grouse diet. He found that big sagebrush comprised 87 percent of the spring diet and 45 percent of the summer diet of adult sage grouse. Rasmussen and Griner (1938) found that big sagebrush comprised 88 percent of the spring diet and 49 percent of the summer diet of adult sage grouse in the Strawberry Valley of Utah. In Montana, Martin (1970) reported that big sagebrush made up 34 percent of the summer diet of adult sage grouse. Also in Montana, Wallestad and others (1975) indicated that big sagebrush comprised 84 percent of the spring diet and 8 percent of the summer diet of adult sage grouse. In Idaho, Gates and Eng (1983) found that big sagebrush comprised 77 percent of the spring/summer diet of adult sage grouse. Leach and Hensley (1954) and Leach and Browing (1958) found that the late summer diet of California sage grouse was 42 percent big sagebrush. Rogers (1964) reported that big sagebrush comprised 60 to 100 percent of the spring diet and 12 to 70 percent of the summer diet of Colorado sage grouse.

Diet of juvenile sage grouse differs from that of adults (Drut and others 1994; Klebenow and Gray 1968; Peterson 1970; Rasmussen and Griner 1938). Sage grouse do not start life eating large quantities of big sagebrush but do eat large amounts of forbs and insects during the first 3 or 4 months of life at a season when those sources are at peak availability. Rasmussen and Griner (1938) compared the diet of adult and juvenile sage grouse over the course of a 3-year study. They found that the juvenile diet in June was still a significant 25 percent big sagebrush, along with 27 percent forbs and 48 percent insects, while the adult diet consisted of 95 percent big sagebrush, 4 percent forbs, and 1 percent insects. The consumption of insects on the part of adults never exceeded 5 percent even though insects were obviously present for the juveniles to eat. In August, adult diets contained high amounts of goldenrod at 57 percent and just 1 percent for juveniles, while their consumption of big sagebrush was 30 percent and 36 percent, respectively. Obviously, the adults and juveniles during June, July, and probably August were utilizing different food resources. At 3 to 4 months of age the juvenile diet becomes similar to the adult diet (Drut and others 1994; Klebenow and Gray 1968; Peterson 1970; Rasmussen and Griner 1938).

During the growing season, forbs can boost nutritive levels in the diet of adult sage grouse. Barnett and Crawford (1994) in an Oregon study reported that forbs during the March 4 to April 8 period contained higher amounts of crude protein, calcium, and phosphorus than did big sagebrush. They suggested that consumption of these forbs could improve the nutritional status of the hens prior to laying and should, by inference, increase reproductive success. From their dietary studies, big sagebrush accounted for 52.4 percent of the dry matter intake while forbs made up 47.4 percent. Thus, forbs should be encouraged whenever possible but not at the expense of big sagebrush; forbs offer little to zero cover. Forb production is more precipitation sensitive than big sagebrush, and in some years the forb production could be nil. Some years, snow cover or cold weather could delay growth or emergence of forbs, which could make them not available soon enough to have any nutritional benefit for egg-laying hens.

Sage grouse have preferences for certain subspecies of big sagebrush. Welch and others (1991) conducted a study to determine sage grouse preference for three subspecies and nine accessions of big sagebrush. The subspecies were mountain big sagebrush, Wyoming big sagebrush, and basin big sagebrush. Results of the Welch and others (1991) study, by order of preference, were mountain big sagebrush, Wyoming big sagebrush, and basin big sagebrush (see fig. 2.2). They observed differential preferences for accessions within a subspecies (fig. 2.3). Despite the preference displayed by sage grouse, the significance to their well being is questionable through a preference ranking alone. Welch and others (1991) noted that when the forage of a preferred subspecies or accession was exhausted, the birds readily ate less preferred subspecies or accessions that generally met or exceeded the nutritional value of the preferred taxa. However, Remington and Braun (1985) provided evidence that Wyoming big sagebrush was preferred over mountain big sagebrush and alkali sagebrush (*A. longiloba*), but their study is not definitive because the sagebrushes grew in different environments.

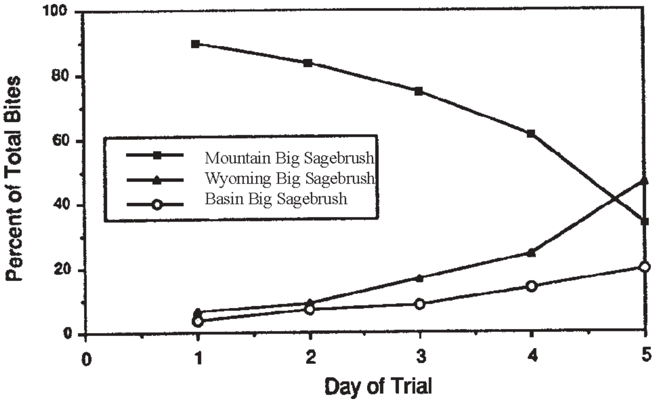

Figure 2.2—The percentage of total sage grouse bites per subspecies of big sagebrush per day of trial. The 3 subspecies of big sagebrush are mountain, basin, and Wyoming (after Welch and others 1991).

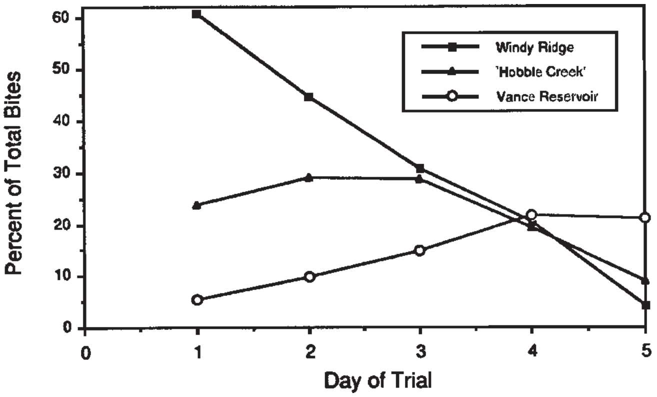

Figure 2.3—The percentage of total sage grouse bites per accession within the mountain big sagebrush group per day (after Welch and others 1991).

Sage grouse eat a variety of sagebrush taxa, but to a lesser extent than big sagebrush. These other sagebrush taxa are alkali sagebrush (*A. longiloba*), black sagebrush (*A. nova*), low sagebrush (*A. arbuscula*), and a half-shrub fringed sagebrush (*A. frigida*) (Barnett and Crawford 1994; Patterson 1952; Rasmussen and Griner 1938; Remington and Braun 1985; Rogers 1964; Wallestad and others 1975).

The importance of big sagebrush in the life history of sage grouse is further illustrated in the bird's preference for cover and the selection of nesting sites (Autenrieth 1986; Braun and others 1977; Connelly and others 1991; Hulet and others 1986; Patterson 1952; Rasmussen and Griner 1938; Roberson 1986; Wallestad 1975a; Wallestad and Pyrah 1974). Sage grouse hens usually nest under big sagebrush plants. Patterson (1952) found in Wyoming that 92 percent of 300 nests were under big sagebrush. Similar results were found in Montana (Wallestad and Pyrah 1974) and Idaho (Klebenow 1969) where 100 percent of the nests were located under big sagebrush plants. Rasmussen and Griner (1938) in Utah reported that 66 percent of the nests were located under big sagebrush and 33 percent under silver sagebrush (*A. cana*). Hulet and others (1986) found on the U.S. Sheep Experiment Station, near Dubois, ID, that 52 percent of 30 nests were under big sagebrush, 17 percent under antelope bitterbrush (*Purshia tridentata*), 14 percent under tall three-tip sagebrush (*Artemisia tripartita*), 10 percent under dead sagebrush, and 7 percent under Russian thistle (*Salsola iberica*). Nest predation for the Hulet and others (1986) study at 37 percent was higher than that reported for the Rasmussen and Griner (1938) study at 26 percent and higher still than the reported nesting failure of 24 percent due to all causes in the Wallestad and Pyrah (1974) study. Connelly and others (1991) in the same region of Idaho found that 79 percent of 84 nests were under big sagebrush plants and that nesting success was higher for nests under big sagebrush (53 percent) than for nests under non-big sagebrush plants (22 percent). The non-big sagebrush plants were rabbitbrush (*Chrysothamnus* spp.), snowberry (*Symphoricarpos oreophilus*), and antelope bitterbrush.

Hens select nesting sites beneath big sagebrush plants that have a relatively large canopy cover and are relatively tall (Braun and others 1977; Roberson 1986). Autenrieth (1986) observed that big sagebrush plants with an umbrella effect were usually selected by the hen. He attributed this selection to improved survival of the hen and improved nest success due to protective camouflaging. Autenrieth (1986, p. 766) concluded: "The importance of big sagebrush cover for nesting cannot be overestimated." Because sage grouse hens show strong fidelity for specific nesting areas, these areas need to be identified and conserved (Fisher and others 1993).

Most studies indicate that the majority of nests are under the tallest plants and in the densest canopy cover. In a Utah study, Rasmussen and Griner (1938) reported that areas with less than 15 percent big sagebrush cover and less than 18 inches (45 cm) tall were rarely chosen for nesting and gave a low nesting success. They noted (p. 862) "an exceptional dense growth of mature sage (50 percent cover and 18 or more inches tall) had revegetated the area and provided a very desirable nesting cover as indicated by the fact that nesting success was highest in this type during both years." Patterson (1952) reported similar results in a Wyoming study. Hulet and others (1986) found in an Idaho study that the canopy cover of big sagebrush 11 feet^2 surrounding nests was 49 percent versus 17 percent 100 feet^2 surrounding the nests; or in other words, the hens were choosing small denser stands of big sagebrush within an 100 feet^2 area in which to build their nests. Big sagebrush plant height for 11 feet^2 surrounding nests was 18 inches versus 9 inches for 100 feet^2 (9.3 m^2) surrounding nests. Again, with plant height held constant, a Montana study by Wallestad and Pyrah (1974) found that successful nests were in stands having a higher big sagebrush canopy cover (27 percent) than unsuccessful nests (20 percent). In Oregon, Gregg and others (1994) reported similar results. They found that shrub canopy cover (Wyoming big sagebrush comprised 87 percent of the shrub cover) at nonpredaceous nests was greater at 41 percent than for predaceous nests where the shrub cover was 29 percent. Gregg and others (1994) also found that the cover of grass was greater at the nonpredaceous nest sites, an observation also made by others (Autenrieth 1986; Beck and Mitchell 2000; Rasmussen and Griner 1938; Roberson 1986). For Washington, Sveum and other (1998) found that nesting sites contained Wyoming big sagebrush canopy cover values of 51 and 59 percent versus 6 and 7 percent Wyoming big sagebrush canopy cover for random sites. Canopy cover of Wyoming big sagebrush for nesting area was 20 and 18 percent compared to random sites of 7 and 7 percent. Bunnell and others (2004) reported that Strawberry Valley (central Utah) sage grouse hens nested in mountain big sagebrush stands having a canopy cover of 25 percent.

These 12 reports conducted in seven Western States indicate the following about nesting habitats of sage grouse. First, sage grouse hens selected big sagebrush plants over other species of wildland plants including other species of shrubs. Secondarily, the preferred canopy cover ranges between 20 and less than 50 percent, and sage grouse prefer plants that are at least 18 inches in height with a good understory of grasses and forbs. More importantly, nest success was greatest at sites with these characteristics. Nesting densities varied from one nest per 7 to 15 acres (Patterson 1950; Patterson 1952; Rasmussen and Griner 1938).

Basically the "Guidelines for Maintenance of Sage Grouse Habitats" of Braun and others (1977) remains valid for nesting habitat.

Connelly and others (2000) in their guidelines placed big sagebrush canopy cover for nesting habitat at 15 to 25 percent. Why the lower minium value of 15 percent is not clear. The vast majority of studies cited by them reported much higher canopy cover values. Autenrieth (1986, p.765) found: "Big-sage canopy per tenth acre surrounding the nest bush ranged from 23.4 to 38.1 percent for five study areas." Connelly and others (2000) values perhaps better represent minimum than maximum cover values. They do describe minimum cover values for grasses (15 percent or more and minimum height of 7 inches) and for forbs (10 percent or more and minimum height of 7 inches). What are not clear are what portion of the grass cover should be under or adjacent to big sagebrush plants and what portion in the interspaces among the big sagebrush plants. Two statements within the Connelly and others (2000) report seem to be in conflict. These are (p. 970): "However, grouse nesting under sagebrush experience greater nest success (53%) than those nesting under other plant species (22%)"; and (p. 971): "Grass height at nests under non-sagebrush plants was greater ($p<0.01$) than that associated with nests under sagebrush, further suggesting that grass height is an important component for nesting sage grouse." Value of grass in the nesting habitat of sage grouse was expressed by Rasmussen and Griner (1938, p. 864): "The presence of grasses and weeds interspersed with the sagebrush made a more successful nesting type than sage of equal density without the understory."

But these needs of nesting habitat are often at conflict with grazing interests. For example, Baxter (1996, p. 60) in his article "Improving rangeland health by thinning dense sagebrush stands with tebuthiuron (Spike 20P)," states: "when big sagebrush cover reaches 12 to 15 percent, the understory production of other plants decreases as canopy cover increases" (also see Phillips 1972). Their recommendation would thin big sagebrush stands before enough canopy cover developed to support preferred sage grouse nesting habitat.

Needs of sage grouse broods differ from that of nesting habitat, although big sagebrush remains an important component. It is the food requirement of the chicks that is the driving force behind the search for brooding habitat. Insects and forbs are important in the diet of chicks during the first 12 weeks or so of life, after which their diet is almost the same as adults (Drut and others 1994; Fisher and others 1996; Patterson 1952; Peterson 1970; Pyle and Crawford 1996; Rasmussen and Griner 1938).

Martin (1970) found in a 3-year study conducted in Montana that big sagebrush canopy cover for brooding habitat was 19 percent (18 percent for a study conducted in Idaho; Musil and others 1994). However, Martin (1970) noted that young broods (less than 6 weeks old) selected habitats with a big sagebrush canopy cover of 14 percent. He observed that by August and September broods and brood groups were located on areas comparable to summering adults, having a big sagebrush canopy cover of about 25 percent. This 25 percent big sagebrush canopy cover for summering adult sage grouse was also recorded by Gregg and others (1993) in Oregon. Similar results were reported from another Montana study conducted by Wallestad (1971). He found broods occupying big sagebrush habitats that had canopy cover of 14 percent for June, 12 percent for July, 10 percent for August, and 21 percent for September. Dunn and Braun (1986) in Colorado found broods occupying big sagebrush habitats that had a mean canopy cover of 24 percent from July to September. In another Montana study, Peterson (1970) noted that the canopy cover of big sagebrush varied in brooding habitat from 1 to 20 percent. Wallestad (1975a) found that 90 percent of broods studied in central Montana were in areas where big sagebrush canopy cover varied from 0 to 25 percent. In both of these Montana studies, feeding sites with low cover were never far from higher density big sagebrush escape areas. Wallestad (1975a, p. 33) observed:

> During the summer less than 15 percent of the observations occurred in dense (25 percent and greater canopy coverage) sagebrush until October, when 40 percent of the birds were observed using sagebrush of this density. During August and September, approximately 65 percent of all grouse observations were recorded in bottomland types (alfalfa fields and greasewood bottoms). ...The time of shift from ranges dominated by sagebrush to bottomland types was dictated by the condition of vegetation as influenced by moisture conditions in any given year. The first killing frost of the season usually occurred any time after September 1. With the frost, many forbs were destroyed, forcing sage grouse to turn to sagebrush for food. Jorgensen (personal communication 1973) reported moisture content of sagebrush leaves increased with fall rains. The increased moisture content may make sagebrush more palatable than during summer. Many years the shift occurred just prior to the hunting season, baffling hunters who consistently hunted alfalfa fields.

From the available research, the ideal brooding habitat would consist of big sagebrush with a canopy cover of some 25 percent with a small creek running through it. The riparian zone about 50 feet wide would reduce the big sagebrush canopy cover to 0 and provide the needed forbs for the chicks to eat with the adjacent big sagebrush cover providing shading, loafing, escape, food, and a source of insects. This situation would be similar to a strip spraying project described by Autenrieth (1969). During the wet years of the study, broods used sprayed strips more than leave strips, but during dry years leave strips were used more than the sprayed. Ranchers in Idaho also noted changes in brood movements between wet and dry years—during wet years they saw fewer broods in their fields that reflected good forb production in the big sagebrush stands (Autenrieth 1986).

Brooding habitat, as important as it is, occupies only a small percentage (perhaps 20 percent) of the total habitat needs of sage grouse. Connelly and others (2000) suggest 40 percent. Therefore, claims that large big sagebrush control projects are going to improve brooding habitat must be subject to careful examination to see if the desire is to help sage grouse or improve grass availability (Fisher and others 1996). Following and citing the guidelines published by Braun and others (1977) and the recommendations of Autenrieth (1986) will avoid the outdated but often used concept that sage grouse habitats will be improved by killing big sagebrush, when the facts clearly show just the opposite results (Peterson 1995).

Summering, broodless hens and males select big sagebrush stands with canopy cover ranging from 20 to 35 percent and some as high as 50 percent (Autenrieth 1986; Braun and others 1977; Ellis and others 1989; Martin 1970; Patterson 1952; Roberson 1986; Wallestad 1975a; Wallestad and Schladweiler 1974; Welch's personal observations; see chapter I). Connelly and others (2000, p. 980) in their guidelines, however, note: "Generally, 10-20% canopy cover of sagebrush and $\leq$ 25% total shrub cover will provide adequate habitat for sage grouse during summer." Based on the values cited in other studies and personal observations, their big sagebrush canopy cover value lower than 20 percent does not appear to be adequate.

The quantity and quality of big sagebrush is important even on strutting grounds (called "leks") where the mating rituals are performed. Characteristics of strutting grounds vary greatly. They may be bare openings in big sagebrush, gravel pits, plowed fields, wheat stubble, salt licks, remote air strips, temporary sheep camps, paved roads, bare exposed ridges, knolls, small buttes, and dry lake beds (Connelly and others 1981; Roberson 1986; Welch and others 1990). Strutting grounds are not distinctive except that they are surrounded by big sagebrush. Sagebrush plants surrounding the strutting grounds are of critical importance. These plants are used as escape cover for females coming into the strutting ground. They provide food and loafing areas for males. The height and canopy cover values are similar to the characteristics of sites selected by summering broodless hens and males.

Sage grouse winter habitats are, like other sage grouse habitats, strongly traditional. As with nesting habitat, summering broodless hen habitat, and male habitat, the birds select wintering areas having greater than 20 percent canopy cover (Autenrieth 1986; Braun and others 1977; Eng and Schladweiler 1972; Wallestad 1975a). Connelly and others (2000) suggest 10 to 30 percent. Slope and aspect also play a strong role in determining winter sage grouse range. Autenrieth (1986) found that sage grouse selected areas of less than 15 percent slope and liked southwest exposures. Hupp and Braun (1989) found feeding activity occurred in drainages and on slopes having south or west aspect. They recommended that sagebrush be maintained on these areas.

Big sagebrush control projects can have serious negative impacts on sage grouse (Benson and others 1991; Braun and others 1977; Carr 1968; Fischer and others 1996; Klebenow 1970; Kufeld 1968; Martin 1970; Peterson 1995; Swenson and others 1987; Wallestad 1975b). If big sagebrush control is undertaken in areas supporting sage grouse, the guidelines published by Braun and others (1977) or the method outlined by Autenrieth (1969) will likely result in minimizing the impact. These recommendations have been summarized by Autenrieth (1986) and are reproduced here:

1. The State wildlife agencies should be notified, by means of an environmental assessment, of each specific proposal to control vegetation a minimum of 2 years in advance of treatment.
2. No control work will be considered where sagebrush cover is less than 20 percent or on steep (20 percent or more gradient) upper slopes with skeletal soils where big sagebrush is a foot tall or less.
3. The breeding complex (leks and nesting) areas will be defined as all lands within a 2-mile radius of an occupied lek. (Connelly and others [1988] and Wakkinen and others [1992] believe this area needs to expanded beyond 2 miles.) In areas with poor-quality nesting habitat, the radius may well exceed 2 miles. Control of vegetation will not be undertaken within the breeding complex or on nesting and brood areas. On-site investigations by land management and State wildlife agency personnel will be essential to determine inviolate areas. Areas to be protected from treatment will be clearly defined on maps.
4. No control will be attempted in any areas known to have supported important wintering concentrations of sage grouse within the past 10 years. No control will be attempted along streams, meadows, or secondary drainages, both dry and intermittent. A strip of living sage no less than 400 yards wide will be retained along the edges of meadows and drainages. On-site inspections by land management and wildlife agency personnel will be made to assess the desirability of increasing or decreasing the width of untreated strips in specific areas.
5. When sagebrush control is found to be unavoidable in sage grouse habitat, all treatment measurements should be applied in irregular patterns using topography and other ecological considerations to minimize adverse effects on the sage grouse resource. Width in treated and untreated areas can vary for the convenience of application techniques except that

treated areas should be no wider than 100 yards and untreated areas will be at least as wide as treated areas. The untreated areas should not be treated until food and cover plants in the treated areas attain a composition comparable to that of the untreated areas.

6. Where possible, spraying should be done with a helicopter or ground equipment. No spraying should be done when wind velocity exceeds 5 miles per hour.

7. Whenever possible, complete kill or removal of sagebrush in treated areas should be avoided. Partial kill or removal of sagebrush may enhance the area for livestock, prevent loss of all snow cover in winter, and allow for some use of the disturbed area by sage grouse.

Sage Thrasher, Brewer's Sparrow, Sage Sparrow—The sage thrasher, Brewer's sparrow, and sage sparrow are also considered big sagebrush obligate species (Belthoff and others 1998; Reynolds and Trost 1981). Their habitat requirements are similar to those of nesting sage grouse—big sagebrush canopy cover from 20 to 36 percent (Best 1972; Braun and others 1976; Feist 1968; Grinnell and others 1930; Knick and Rotenberry 1995; Petersen and Best 1986, 1991; Reynolds and Trost 1980b, 1981; Rich 1985; Winter and Best 1985). Walcheck (1970) reported a population of Brewer's sparrows living in an area of silver sagebrush (*A. cana*) having a canopy cover of 53 percent. Dobler (1994, p. 149) stated in his study that "sagebrush cover density was positively related to occurrence for seven birds, including sage thrasher, sage sparrow, and Brewer's sparrow," but reported a lower canopy cover of about 11 percent as being optimum. However, his study area never exceeded 20 percent big sagebrush canopy cover. McAdoo and others (1989) showed greater numbers of sage and Brewer's sparrows, and sage thrashers occurring in areas having the highest canopy cover of big sagebrush, but the cover values of their study areas did not exceed 21 percent. Petersen and Best (1985) studied nest site selection of sage sparrows in Idaho and reported that these birds nested where Wyoming big sagebrush cover was at 23 percent in the vicinity of nests and 26 percent in the general study area. Further, they noted that all nests were situated in big sagebrush plants and that large, living shrubs were strongly preferred. Petersen and Best (1991) reported that Wyoming big sagebrush canopy cover near sage thrasher's nests was 23 percent. Rotenberry (1980) found greater numbers of sage sparrow and western meadow lark (*Sturnella neglecta*) on sites with big sagebrush canopy covers ranging from 25 to 30 percent than for sites with big sagebrush canopy cover of 0 to 1 percent and 5 to 10 percent.

Sage thrashers place their nests either directly under big sagebrush plants or in big sagebrush plants, whereas sage and Brewer's sparrows place their nests in big sagebrush plants (fig. 2.4 and 2.5; Best 1972; Booth 1952; Petersen and Best 1985, 1986, 1991; Reynolds 1981; Rich 1978a,b, 1980; Schroeder and Strurges 1975; Winter and Best 1985). Only Walcheck (1970) observed Brewer's sparrows nesting in a shrub other than big sagebrush, that being silver sagebrush.

The diets of these three big sagebrush obligates have received limited study. Ryser (1985) indicates that these species feed on insects, spiders, and seeds (see chapter III for more details concerning insects and

Figure 2.4—Brewer's sparrow nest in foliage of big sagebrush (photo by Montana Fish, Wildlife and Parks Department).

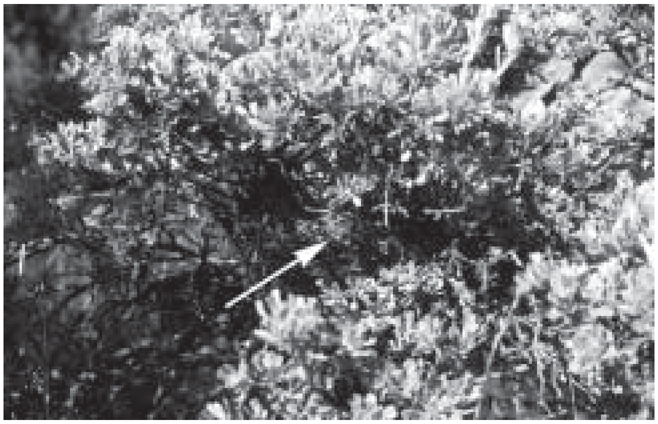

Figure 2.5—Sage sparrow nest hidden (see arrow) in the foliage of mountain big sagebrush (photo by Bruce L. Welch).

spiders that are supported by big sagebrush). Petersen and Best (1986) found that the diet of sage and Brewer's sparrow nestlings was entirely of insects and spiders from early June to late July. For mature Brewer's sparrows, Best (1972) reported that insects and spiders were 71 to 81 percent of the June to July items found in gizzards while seeds made up 8 to 17 percent.

Effects of big sagebrush control are predictably bad for these three species of birds (Castrale 1982; Knick and Rotenberry 1995; Reynolds and Trost 1980a,b, 1981). Schroeder and Sturges (1975) found that Brewer's sparrows' use of sprayed big sagebrush stands was 67 percent lower the first year after treatment and 99 percent lower for the second year, than on unsprayed stands. After the third year of treatment, no nests were found in the sprayed areas. Similarly, Best (1972) noted a 54 percent reduction in the use of first-year sprayed stands of big sagebrush by Brewer's sparrows. Best (1972) found that 15 percent of the nests were placed in dead big sagebrush plants, 13 percent in what he termed partially dead (25 to 95 percent dead), and 72 percent in live plants. Best's (1972) study was conducted in an area that had denser populations of Brewer's sparrows at 42 birds per 100 acres versus 24 birds for the Schroeder and Sturges (1975) study, perhaps forcing a small percentage of the birds to nest in dead plants. Further, Schroeder and Sturges (1975) noted that spraying in 100-foot strips was less damaging on Brewer's sparrows than whole plot control. Not addressed by either study was whether or not the increased edge effect from strip spraying increased nested parasitism (Rich 1978a) by brown-headed cowbirds (*Molothrus ater*) and/or nest predation.

Finally, Best (1972) found that Brewer's sparrows consumed fewer insects and spiders on controlled (sprayed with 2,4-D) stands of big sagebrush than on noncontrolled stands. Fischer and others (1996) noted fewer insects in treated big sagebrush stands than in untreated stands.

A study conducted by Reynolds and Trost (1981) compared the populations of nesting and nonnesting birds among grazed and ungrazed sites dominated either by big sagebrush or crested wheatgrass (*Agropyron desertorum*). They found that sheep grazing did not alter the density or diversity of nesting bird populations. Density and diversity of birds were greater for big sagebrush habitat than for the crested wheatgrass planting. Big sagebrush canopy cover ranged from 17 to 25 percent. Similarly, Bradford and others (1998, p. 13) found that sites converted from big sagebrush to crested wheatgrass "showed significantly reduced species richness, reduced % shrub obligate species, increased dominance, and increased relative abundance of horned larks."

Welch (2002) conducted flushing bird counts between June 11 and 23 and between the hours of 6: 00 a.m. and noon on burned big sagebrush sites dominated by perennial grasses and on unburned big sagebrush sites. Thirteen paired sites (burned and unburned) were used in the study. Two pairs were in Oregon, four in Idaho, three in Utah, two in Wyoming, and two in Montana. Subspecies of big sagebrush represented in the study were Wyoming big sagebrush—five sites, mountain big sagebrush—four sites, and basin big sagebrush—four sites. Selected pairs had to meet the following criteria: length of bird flushing transect 1 mile, buffer width 300 feet between the two pairs, burned sites dominated by perennial grasses, and at least 20 percent canopy cover of big sagebrush on unburned sites. Mean number of bird species found on burned big sagebrush sites was 2.23 and on unburned big sagebrush sites 7.54. Mean total number of birds found on burned big sagebrush sites dominated by perennial grasses was 7.62, and for unburned big sagebrush sites 37.38.

Petersen and Best (1987, p. 328), studying the effect of prescribed burning of big sagebrush on nongame bird, reported: "moderate, incomplete burns are not detrimental to nongame bird populations nor to important components of sage and Brewer's sparrow breeding biology." Their study was conducted on a 13-acre plot of which 45 percent (5.85) acres was burned, which is much smaller than the hundreds of acres burned reported in the previous study.

Facultative Bird Species

Birds having a facultative association with big sagebrush are listed in table 2.1. For the most part, these birds do not require as heavy a canopy cover of big sagebrush as do the obligate species.

One facultative association I found interesting was the consumption of big sagebrush seed by dark-eyed juncos (*Junco hyemalis*), horned larks (*Eremophila alpestris*), and white-crowned sparrows (*Zonotrichia leucophrys*). I first observed dark-eyed juncos pecking at mountain big sagebrush inflorescences near Paul Bunyan's Woodpile, about 35 miles northeast of Delta, UT (Welch 1999). They were eating mountain big sagebrush seeds, which constituted about 70 percent of their diet (Welch 1999). During this initial observation period, I noticed small footprints around many of the mountain big sagebrush plants and trails going from one plant to another (fig. 2.6). This situation is similar to a sage grouse wintering range, except in miniature. In addition, seeds and seed bracts were found on the snow surface. Birds were walking around pecking in those areas, presumably picking up seeds that had fallen. I have watched dark-eyed juncos eating sagebrush seeds at 36 big sagebrush sites from Fort Hall Indian Reservation, ID; in the north; south to Salina, UT; Lynndyl, UT, in the west; and east to Helper, UT. In addition, I have observed the eating of

Table 2.1—Birds having a facultative association with big sagebrush (Booth 1952; Braun and others 1976; Dumas 1950; Giesen 1997; Grinnell and others 1930; Linsdale 1938; McEwen and DeWeese 1987; Medin 1990, 1992; Medin and others 2000; Rasmussen 1941; Reynolds 1979b; Rich 2001; Ryser 1985; Unknown 1950; Welch 1999, 2002). Common and scientific names are given as listed in the various cited articles; some repetition.

Common name	Scientific name
American crow	*Corvus brachyrhynchos*
American kestrel	*Falco sparverius*
American pipit	*Anthus spinoletta rubescens*
American robin	*Turdus migratorius*
American rough-legged hawk	*Buteo lagopus sanctijohannis*
Ash-throated flycatcher	*Myiarchus cinerascen*
Barn swallow	*Hirundo rustica*
Black-billed magpie	*Pica pica hudsonia*
Black-headed grosbeak	*Pheucticus melanocephalus*
Black-throated gray warbler	*Dendroica nigrescens*
Black-throated sparrow	*Amphispiza bilineata deserticola*
Blue-gray gnatcatcher	*Polioptila caerulea*
Blue grouse	*Dendragapus obscurus*
Brewer’s blackbird	*Euphagus cyanocephalus*
Broad-tailed hummingbird	*Selasphorus platycerus platycerus*
Brown-headed cowbird	*Molothrus ater*
Burrowing owl	*Athene cunicularia*
Bushtit	*Psaltriparus minimus plumbeus*
California linnet	*Carpodacus mexicanus frontalis*
California quail	*Callipepla californica*
California shrike	*Lanius ludovicianus gambeli*
Calliope hummingbrid	*Stellula calliope*
Canyon wren	*Catherpes mexicanus*
Cassin’s finch	*Carpodacus cassinii*
Chipping sparrow	*Spizella passerina*
Chukar	*Alectoris chukar*
Clark’s nutcracker	*Nucifraga columbiana*
Cliff swallow	*Hirundo pyrrhonota*
Columbian sharp-tailed grouse	*Tympanuchus phasianellus columbianus*
Common nighthawk	*Chordeiles minor*
Common poorwill	*Phalaenoptilus nuttallii*
Common raven	*Corvus corax*
Common redpoll	*Acanthis linaria linaria*
Cooper’s hawk	*Accipiter cooperii*
Dark-eyed junco	*Junco hyemalis*
Evening grosbeak	*Coccothraustes vespertinus*
Ferruginous hawk	*Buteo regalis*
Gray flycatcher	*Empidonax griseus*
Golden eagle	*Aquila chrysaetos canadensis*
Great horned owl	*Bubo virginianus*
Green-tailed towhee	*Chlorura chlorura*
Hermit thrush	*Catharus guttatus*
Horned lark	*Eremophila alpestris*
House finch	*Carpodacus mexicanus*
House wren	*Troglodytes aedon parkmanii*
Lark bunting	*Calamospiza melanocorys*
Lark sparrow	*Chondestes grammacus*
Lazuli bunting	*Passerina amoena*
Loggerhead shrike	*Lanius ludovicianus*
Long-eared owl	*Asio otus*
Marsh hawk	*Circus hudsonius*
MacGillivray’s warbler	*Oporornis tolmiei*
Mountain bluebird	*Sialia currucoides*
Mountain chickadee	*Parus gambeli*

(con.)

Table 2.1 (Con.)

Common name	Scientific name
Mountain quail	*Oreortyx pictus*
Montana junco	*Junco oregonus montanus*
Mourning dove	*Zenaida macroura*
Northern harrier	*Circus cyaneus*
Northern mockingbird	*Mimus polyglottos*
Northern shrike (Northwestern)	*Lanius borealis invictus*
Nuttall poor-will	*Phalaenoptilus nuttalli nuttalli*
Olive-sided flycatcher	*Contopus borealis*
Pacific nighthawk	*Chordeiles minor hesperis*
Pinyon jay	*Cyanocephalus cyanocephalus*
Prairie falcon	*Falco mexicanus*
Red-tailed hawk	*Buteo borealis calurus*
Ring-necked pheasant	*Phasianus colchicus*
Rock wren	*Salpinctes obsoletus*
Rough-winged swallow	*Riparia riparia*
Scaled quail	*Callipepla squamata*
Say's phoebe	*Sayornis saya saya*
Sharp-tailed grouse	*Pedioecetes phasianellus*
Short-eared owl	*Asio flammeus flammeus*
Sparrow hawk (American kestrel)	*Falco sparverius*
Spotted towhee	*Pipilo maculatus*
Swainson hawk	*Buteo swainsoni*
Turkey vulture	*Cathartes aura septentrionalis*
Vesper sparrow	*Pooecetes gramineus confinis*
Violet-green swallow	*Tachycineta thalassina lepida*
Virginia warblers	*Vermivora virginiae*
Western bluebird	*Sialia mexicana occidentalis*
Western burrowing owl	*Specotyto cunicularia hypugaea*
Western crow	*Corvus brachyrhynchos hesperis*
Western flycatcher	*Empidonax difficilis*
Western kingbird	*Tyrannus verticalis*
Western lark sparrow	*Chondestes grammacus strigatus*
Western meadowlark	*Sturnella neglecta*
Western mockingbird	*Mimus polygottos leucopterus*
Western savannah sparrow	*Passerculus sandwichensis alaudinus*
White-crown sparrow (Gambel sparrow)	*Zonotrichia leucophrys*
White-throated swift	*Aeronautes saxatalis saxatalis*

Figure 2.6—Footprints (arrow) of dark-eyed juncos feeding on big sagebrush seeds in the snow (photo by Bruce L. Welch).

big sagebrush seeds by horned larks (seven big sagebrush sites) and white crown sparrows (fig. 2.7; 11 big sagebrush sites).

Consumption of seeds occurred from early December to late February. In May 1992, dark-eyed juncos were observed flying in and out of an open shed that was being used to dry big sagebrush inflorescences that had been collected the previous winter. Inside the shed, the birds were scratching and pecking around, among, and through the inflorescences. A pile of big sagebrush seeds (about 50 g) was placed near the layers of drying inflorescences. In less than a day, the entire pile was consumed by the birds, thus proving that they will consume big sagebrush seeds at a time other than winter. The importance of big sagebrush seeds in the yearly diet of these birds is unknown. Probably more important than the absolute amount eaten is the timing when the birds are eating the seeds. After fresh snow, big sagebrush seed may be the only food available to these birds (fig. 2.8). Nutritive value of big sagebrush seeds collected near the Paul Bunyan's Woodpile is given in chapter IV.

While conducting a pygmy rabbit (*Sylvilagus idahoensis* or *Brachylagus idahoensis*) survey just west of Utah Lake, I observed over the course of the survey—March 10 to 26, 2003—three distinct flocks of 5 to 10 red-winged blackbirds (*Agelaius phoeniceus*) in the big sagebrush stand. They were feeding on a bounteous supply of insect larvae. What was most curious to me was the fact they were not feeding on the same insect larvae present in a patch of grass located closer to the lake. Apparently, the big sagebrush plants were providing security cover for the birds.

Figure 2.7—White-crown sparrow feeding on basin big sagebrush seeds. Arrow pointing to bird feeding on seeds. All three birds were observed eating basin big sagebrush seeds (photo by Bruce L. Welch).

Figure 2.8—Dark-eyed junco feeding on Wyoming big sagebrush seeds (photo by Bruce L. Welch).

Mammals

Small Mammals

Pygmy Rabbit—Pygmy rabbits (*Sylvilagus idahoensis* or *Brachylagus idahoensis*) are the sage grouse of the mammalian world in that they have an obligate relationship with big sagebrush (Green and Flinders 1980b; Janson 2002; Lyman 1991; Peterson 1995). As the name implies, they are the smallest of North American rabbits. They are endemic to the Great Basin and adjacent Intermountain areas of the Western United States (Campbell and others 1982; Green and Flinders 1980b; Janson 2002; Weiss and Verts 1984). They typically associate with dense stands of big sagebrush where the soils are deep and excavatable (Borell and Ellis 1934; Campbell and others 1982; Gabler and others 2001; Gates and Eng 1983; Green and Flinders 1980a; Grinnell and others 1930; Janson 2002; Orr 1940; Pritchett and others 1987; Severaid 1950; Weiss and Verts 1984). Where vegetative habitat needs are met, pygmy rabbits dig relatively shallow burrows with two or more entrances (Janson 2002). With sufficient big sagebrush cover, soil characteristics such as depth and ease of digging are determining factors in the distribution of these rabbits and not the presence of specific subspecies of big sagebrush (Weiss and Verts 1984).

Early workers (Borell and Ellis 1934; Grinnell and others 1930; Orr 1940; Severaid 1950) found the rabbits in the tallest and densest big sagebrush or heaviest patches of big sagebrush available. Severaid (1950, p. 3) observed: "These rabbits stay constantly under brush canopy and will not run if one walks through their domain." They are elusive rabbits. Campbell and others (1982, p. 100) stated: "Our observations at both sites showed *B. idahoensis* primarily confined to dense stands of big sagebrush growing in deep soils of drainages and hollows." Pygmy rabbits occupy stands of big sagebrush having canopy cover ranging from 16 to 46 percent—similar to the needs of sage grouse (Dobler and Dixon 1990; Gates and Eng 1983; Green and Flinders 1980b; Weiss and Verts 1984). Katzner and Parker (1997) found that wintering areas of highest pygmy rabbit use were in basin big sagebrush stands having a canopy cover of 51.1 percent, compared to areas of medium use of 42.7 percent canopy cover, and to areas of low use of 38.6 percent.

Big sagebrush is also a prime food source (Orr 1940). Green and Flinders (1980b) reported that pygmy rabbits consume big sagebrush and possibly three-tip sagebrush year round. They found that 51 percent of the summer diet was sagebrush, and this increased to 99 percent in the winter. Gates and Eng (1983) noted that the amount of big sagebrush in the diet of pygmy rabbits for July, August, September, November, and December was 30, 9, 52, 89, and 91 percent, respectively. In feeding trials of captive animals, White and others (1982) reported that the rabbits showed no significant preference for one subspecies of big sagebrush over another.

Sagebrush Vole—Another mammal that is considered a big sagebrush obligate by most researchers is the sagebrush vole (*Lagurus curtatus*; Carroll and Genoways 1980; Larrison and Johnson 1973; Marshall 1985; McEwen and DeWeese 1987; Rickard 1960), although Maser and Strickler (1978) found a population inhabiting a grassy area in southeastern Oregon. Sagebrush voles are normally found in "heavy sagebrush" and locate their burrows beneath stumps of the largest big sagebrush plants (Borell and Ellis 1934). Oldemeyer and Allen-Johnson (1988) suggest big sagebrush canopy cover in sagebrush voles' habitat was 52 to 55 percent. Sagebrush voles feed upon the leaves of big sagebrush, which may also serve as a source of water, especially in late summer and early autumn, when forbs and grasses are desiccated (Borell and Ellis 1934; James and Booth 1954; Parmenter and others 1987).

Populations of sagebrush voles are dynamic. At times they may be abundant and then suddenly disappear (Moore 1943). They do not accept baits readily, which could result in low estimates of populations (Johnson and others 1948). Unlike other species of voles, sagebrush voles appear not to damage big sagebrush plants (Frischknecht and Baker 1972; Mueggler 1967; Parmenter and others 1987). The long-tailed vole (*Microtus longicaudus*), mountain vole (*M. montanus*), and meadow vole (*M. pennsylvanicus*) can cause extensive damage and death (10 to 84 percent kill) to big sagebrush plants over areas of 50 to 1,200 acres (Frischknecht and Baker 1972; Mueggler 1967; Parmenter and others 1987).

While conducting a survey (April 2004) for the presence of pygmy rabbits south and east of Deer Creek Reservoir in central Utah, I noted girdling of big sagebrush plants by small rodents (most likely long-tailed voles-*Microtus longicaudus*). There were several occasions where a big sagebrush plant was girdled but an adjacent nonsagebrush woody shrub showed no signs of being girdled. It was clear that the small rodents preferred girdling big sagebrush over the following shrub species: antelope bitterbrush (*Purshia tridentata*), choke cherry (*Prunus virginiana*), Gambel oak (*Quercus gambelii*), rubber rabbitbrush (*Chrysothamnus nauseosus*), and serviceberry (*Amelanchier utahensis*). Differential preference was more than likely due to the ease of peeling big sagebrush bark as compared to the other shrub species.

Other Small Mammals—Parmenter and others (1987) observed that deer mouse (*Peromyscus maniculatus*) nests were made almost entirely from strips of big sagebrush bark. Borell and Ellis (1934), Grinnell and others (1930), and Linsdale (1938) also reported that the bushy-tailed wood rat (*Neotoma cinerea*) uses big sagebrush bark as well as other materials in nest construction. James and Booth (1954), Johnson and others (1948), Moore (1943), and Mullican and Keller (1986, 1987) have reported that sagebrush voles made extensive use of big sagebrush bark for nesting material.

Small mammals having a facultative association with big sagebrush are listed in table 2.2 (Welch and Criddle 2003; fig. 2.9). The table lists about 79 species, of which the inclusion of pikas came as a surprise. My literature search resulted in two references where pikas were either feeding on big sagebrush or making "hay" out of big sagebrush. Severaid (1950, p. 4) noted: "The pikas lives in the rock talus of the abandoned mine dumps and feeds on the *Artemisia* wherein dwells the pigmy rabbit." Linsdale (1938, p. 196) observed the following concerning pikas: "At 2 places, at least, there were accumulation of freshly cut green branches of brushes such as surrounded the rock slides. At 1 place were seen branches of *Artemisia, Chrysothamnus, Symphoricarpos, Ribes,* and an herbaceous plant."

Table 2.3 lists effects of big sagebrush control treatments on individual species of small mammals. Of the 25 species listed, only four showed positive response to

Table 2.2—Mammals having a facultative association with big sagebrush (Allred 1973; Borell and Ellis 1934; Clary and Medin 1993; Doering and Keller 1998; Gray 1943; Kirkland and others 1997; Knick and Dyer 1997; Larrison and Johnson 1973; Linsdale 1938; Longland 1995; McAdoo and Young 1980; McEwen and DeWeese 1987; McGee 1982; O'Farrell 1974; Oldemeyer and Allen-Johnson 1988; Orr 1940; Ports and George 1990; Ports and McAdoo 1986; Priday and Luce 1999; Reynolds 1979b, 1980; Rickard 1960; Root and others 2001; Scheffer 1941, Severaid 1950; Sherwin and others 2000; Smith and Urness 1984; West 1983a; Williams 1984; Yensen and others 1989). Common and scientific names are given as listed in the various cited articles; some repetition.

Common name	Scientific name
Antelope ground squirrel	*Citellus leucurus leucurus*
Badger	*Taxidea taxus taxus*
Big brown bat	*Eptesicus fuscus*
Bison	*Bison bison*
Black hills cottontail	*Sylvilagus nuttallii grangeri*
Black-tailed jackrabbit	*Lepus californicus deserticola*
Bobcat	*Felis rufus*
Boreal redback vole	*Clethrionomys gapperi*
Bushy-tailed woodrat	*Neotoma cinerea cinerea*
California little brown bat	*Myotis californicus californicus*
Canyon mouse	*Peromyscus crinitus crinitus*
Chisel-toothed kangaroo rat	*Dipodomys microps*
Columbian kangaroo rat	*Dipodomys ordii columbianus*
Cottontail rabbit	*Syvilagus nuttalii grangeri*
Coyote	*Canis latrans lestes*
Dark kangaroo mouse	*Microdipodops megacephalus*
Deer mouse	*Peromyscus maniculatus*
Desert cottontail	*Sylvilagus audubonii*
Desert harvest mouse	*Reithrodontomys megalotis megalotis*
Desert shrew	*Notiosorex crawfordi*
Desert woodrat	*Neotoma lepida*
Dwarf shrew	*Sorex nanus*
Elk	*Cervus elaphus*
Fisher pocket gopher	*Thomomys quadratus fisheri*
Gaspe shrew	*Sorex lyelli*
Golden-mantled squirrel	*Spermophilus lateralis* *Callosperophilus lateralis*
Gray fox	*Urocyon cinereoargenteus*
Great Basin kangaroo rat	*Dipodomys microps*
Great Basin pocket mouse	*Perognathus parvus olivaceus*[a]
Harvest mouse	*Reithrodontomys megalotis megalotis*
Inyo chipmunk	*Eutamias quadrivittatus*
Kit fox	*Vulpes macrotis*
Least chipmunk	*Eutamias minimus* *Tamias minimus*
Little pocket mouse	*Perognathus longimembris*
Long-eared myotis	*Myotis evotis*
Long-legged myotis	*Myotis volans*
Longtail pocket mouse	*Perognathus formosus*
Longtail vole	*Microtus longicaudus*
Longtail weasel	*Mustela frenata*
Malheur shrew	*Sorex preblei*
Masked shrew	*Sorex cinerus*
Merriam's kangaroo rat	*Dipodomys merriami*
Merriam's shrew	*Sorex merriami*
Montane shrew	*Sorex monticolus*
Mountain vole	*Microtus montanus*
Mule deer	*Odocoileus hemionus*
Nevada ground squirrel	*Citellus elegans nevadensis*
Northern grasshopper mouse	*Onychomys leucogaster*
Northern pocket gopher	*Thomomys talpoides*

(con.)

Table 2.2 (Con)

Common name	Scientific name
Ord kangaroo rat	*Dipodomys ordii*
Oregon ground squirrel	*Citellus oregonus*
Pallid big brown bat	*Eptesicus fuscus pallidus*
Panamint kangaroo rat	*Dipodomys panamintinus*
Pika	*Ochotona schisticeps* *Ochotona princeps*
Pinyon mouse	*Peromyscus truei*
Paiute ground squirrel	*Citellus townsendi mollis*
Porcupine	*Erethizon dorsatum*
Pronghorn	*Antilocapra americana*
Red fox	*Vulpes vulpes*
Richardson's ground squirrel	*Spermophilus richardsonii*
Sagebrush chipmunk	*Eutamias minimus pictus*
Sagebrush ground squirrel	*Spermophilus townsendii artemisiae*
Short-tailed grasshopper mouse	*Onychomys leucogaster brevicaudus*
Shorttail weasel	*Mustela erminea*
Sonoran white-footed mouse	*Peromyscus maniculatus sonoriensis*
Shrew	*Sorex monticolus*
Southern grasshopper mouse	*Onychomys torridus*
Spotted bat	*Euderma maculatum*
Striped skunk	*Mephitis mephitis*
Thirteen-lined ground squirrel	*Spermophilus tridecemlineatus*
Townsend's big-eared bat	*Corynorhinus townsendii*
Townsend's ground squirrel	*Spermophilus townsendii*
Uinta ground squirrel	*Spermophilus armatus*
Uinta pocket mouse	*Perognathus parvus idahoensis*
Vagrant shrew	*Sorex vagrans*
Wasatch chipmunk	*Eutamias minimus consorbrinus*
Washington ground squirrel	*Spermophilus washingtoni*
Western cottontail	*Sylvilagus nuttallii grangeri*
Western harvest mouse	*Reithrodontomys megalotis*
Western jumping mouse	*Zapus princeps*
Western spotted skunk	*Spilogale gracilis*
White-foot mouse	*Peromyscus maniculatus sonoriensis*
White-tailed antelope ground squirrel	*Ammospermophilus leucurus*
White-tailed jackrabbit	*Lepus townsendii townsendii*
White-tailed prairie dog	*Cynomys leucurus*
Wyoming pocket mouse	*Perognathus fasciatus*
Yellow-haired porcupine	*Erethizon epixanthum epixanthum*
Yuma myotis	*Myotis yumanensis*

[a] McEwen and DeWeese (1987) listed this species as an obligate of big sagebrush.

Figure 2.9—Cottontail living in Wyoming big sagebrush (photo Bruce L. Welch).

Table 2.3–Effects of big sagebrush control treatments on individual species of small mammals. A minus sign means the control treatment had a negative effect; a plus sign means the treatment had a positive effect.

Species	Effects of control	Reference
Badger holes	–	Ritchie and others 1994
Taxidea taxus		
Black-tailed jackrabbit	–	Reynolds and Trost 1980b
Lepus californicus	–	Nydegger and Smith 1986
Boreal redback vole	–	McGee 1982
Clethrionomys gapperi		
Bushytail woodrat	–	Reynolds and Trost 1980b
Neotoma cinerea		
Chisel-toothed kangaroo rat[a]	–	Larrison and Johnson 1973[b]
Dipodomys microps		
Deer mouse	–	Reynolds 1980
Peromyscus maniculatus	–	Smith and Urness 1984[b]
	+	Longland 1994
	+	McGee 1982
	–	Larrison and Johnson 1973[b]
	–	Rickard 1960[c]
	–	Koehler and Anderson 1991
	–	Reynolds and Trost 1980b
Desert kangaroo rat	+	Longland 1995
Dipodomys deserti	+	Longland 1994
Golden-mantled squirrel	–	Longland 1994
Spemophilus lateralis		
Great Basin pocket mouse	–	Reynolds 1980
Perognathus parvus	–	Smith and Urness 1984[b]
	–	Longland 1994
	–	Rickard 1960[c]
Lagomorph pellets	–	Ritchie and others 1994
Least chipmunk	–	Reynolds 1980
Eutamias minimus	–	Smith and Urness 1984[b]
	–	McGee 1982
	–	Larrison and Johnson 1973[b]
	–	Reynolds and Trost 1980b
Longtail weasel	–	McGee 1982
Mustela frenata	–	Reynolds and Trost 1980b
Little pocket mouse	+	Longland 1995
Perognathus longimembris	+	Longland 1994
Merriam’s kangaroo rat	–	Longland 1995
Dipodomys merriami	–	Longland 1994
Mountain cottontail	–	Reynolds and Trost 1980b
Sylvilagus nuttalli		
Mountain vole	–	McGee 1982
Microtus montanus	+	Koehler and Anderson 1991
Northern grasshopper mouse	–	Reynolds 1980
Onychomys leucogaster	–	Reynolds and Trost 1980b
Northern pocket gopher	–	McGee 1982
Thomomys talpoides		
Ord kangaroo rat	+	Longland 1995
Dipodomys ordii	+	Longland 1994
	–	Larrison and Johnson 1973[b]
	+	Koehler and Anderson 1991
	–	Reynolds and Trost 1980b
Panamint kangaroo rat	+	Longland 1995
Dipodomys panamintinus	+	Longland 1994
Pinyon mouse	–	Smith and Urness 1984[b]
Peromyscus truei		
Sagebrush vole	–	Reynolds 1980
Lagurus curtatus	–	Smith and Urness 1984[b]
	–	Rickard 1960[c]
Townsend’s ground squirrel	–	Nydegger and Smith 1986
Spermophilus townsendii	–	Reynolds 1980
Uinta ground squirrel	+	McGee 1982
Spermophilus armatus		
Vagrant shrew	–	McGee 1982
Sorex vagrans		
Western harvest mouse	+	Reynolds 1980
Reithrodontomys megalotis	+	Smith and Urness 1984[b]
	–	Longland 1994
	+	Larrison and Johnson 1973[b]
	–	Rickard 1960[c]
Western jumping mouse	–	McGee 1982
Zapus princeps		
White-tailed antelope ground squirrel	–	Longland 1995
Ammospermophilus leucurus	–	Longland 1994

[a] Known as the Great Basin kangaroo rat in some of the literature.
[b] I use only the crested wheatgrass and sagebrush values in this table.
[c] Study was a comparison between big sagebrush/Agropyron and Agropyron/Poa vegetation type and not a control versus noncontrol treatment.

control of big sagebrush, four species were mixed (that is, some studies showed a positive response, while other studies showed a negative response), and 17 species showed a negative response to the controlling of big sagebrush. Reynolds and Trost (1980b, p. 122) stated: "Crested wheatgrass plantings, regardless of sheep use, supported fewer nesting bird species and a lower density of birds, mammals, and reptiles than did areas dominated by [big] sagebrush." Clary and Medin (1993) reported similar observations. Longland and Bateman (2002) observed that small mammal species richness was greatest in undisturbed big sagebrush, intermediate in big sagebrush islands, and lowest in burned big sagebrush habitats. This lack of a positive response to big sagebrush control for so many species is interesting when one considers that big sagebrush comprises for the most part little of the diet of these animals (table 2.4). It appears that big sagebrush's main function for many small mammals is cover (Longland 1991; McAdoo and others 1987). Food items are then furnished by the understory species of grasses, forbs, and insects.

So what would be the optimal big sagebrush canopy cover for most small mammals? This likely varies by species, but studies generally support at least 20 percent or more, which is greater than the 15 percent or less advocated by Baxter (1996). Listed in table 2.5 are big sagebrush canopy cover percentages for various studies conducted on small mammals occurring in big sagebrush ecosystem. Canopy cover ranged from 0 to 68 percent.

The Allred (1973) study, of special interest, describes the ecological distribution and relative abundance of small mammals in 12 plant communities varying in big sagebrush canopy cover from 0 to 68 percent. The plant community with 68 percent big sagebrush canopy cover had a relative abundance index of 34 with six species living in the community (deer mouse, Ord kangaroo rat, *Dipodomys ordi*; Great Basin pocket mouse, *Perognathus parvus*; northern

Table 2.4—Small mammals reported as consumers of big sagebrush. Common and scientific names are given as listed in the various cited articles; some repetition.

Species			
Common name	**Scientific names**	**Diet**	**Reference**
		Percent	
Black-tailed jackrabbit	*Lepus californicus*	?	Severaid 1950
		?	McAdoo and Young 1980
Black-tailed hare		10	Uresk 1978
Black-tailed jackrabbit		1–8	MacCracken and Hansen 1984
		6–21	Fagerstone and others 1980
		?	McKeever and Hubbard 1960
		8	Gates and Eng 1983
Chisel-toothed kangaroo rat	*Dipodomys microps*	5	Johnson 1961
Deer mouse	*Peromyscus maniculatus*	?	Parmenter and others 1987
Least chipmunk	*Eutamias minimus*	2	Johnson 1961
Long-tailed vole	*Microtus longicaudus*	?	Parmenter and others 1987
Ord's kangaroo rat	*Dipodomys ordi*	3	Johnson 1961
Pika	*Ochotona princeps*	?	Severaid 1950
Pika	*Ochotona schisticeps*	?	Linsdale 1938
Pygmy rabbit	*Sylvilagus idahoensis*	?	Severaid 1950
Brachylagus idahoensis		51–99	Green and Flinders 1980a b
Sagebrush vole	*Lagurus curtatus*	?	Rickard 1960
		?	Parmenter and others 1987
Lemmiscus curtatus		1	Mullican and Keller 1986
Townsend's ground squirrel	*Spermophilus idahoensis*	?	Rogers and Gano 1980
	Citellus townsendi	2	M. Johnson 1977
		?	Rickart 1987
		?	Davis 1939
		?	Maser 1974
Western cottontail	*Sylvilagus nuttallii*	?	Severaid 1950
Nuttall cottontail		3–4	MacCracken and Hansen 1984
Western harvest mouse	*Reithrodontomys megalotis*	12	Johnson 1961
White-tailed jackrabbit	*Lepus townsendi*	?	Severaid 1950
		?	McAdoo and Young 1980

Table 2.5—Percentage of canopy cover of big sagebrush for various small mammal habitats. Common and scientific names are given as listed in the various cited articles; some repetitions.

Species			
Common name	**Scientific names**	**Canopy**	**Reference**
		Percent	
Black-tailed hare	*Lepus californicus*	9, 33	Uresk 1978
Boreal redback vole	*Clethrionomys gapperi*	48–50	McGee 1982
Deer mouse	*Peromyscus maniculatus*	16–23	Nichols and others 1975
		0–68	Allred 1973
		52–55	Oldemeyer and Allen-Johnson 1988[a]
		48–50	McGee 1982
		29	Mullican and Keller 1986
Golden-mantled squirrel	*Spermophilus townsendii*	52–55	Oldemeyer and Allen-Johnson 1988[a]
Great Basin pocket mouse	*Perognathus parvus*	16–23	Nichols and others 1975
		0–68	Allred 1973
		52–55	Oldemeyer and Allen-Johnson 1988[a]
	Tamias minimus	29	Mullican and Keller1986
Least chipmunk	*Eutamias minimus*	16–23	Nichols and others 1975
		0–68	Allred 1973
		52–55	Oldemeyer and Allen-Johnson 1988[a]
		48–50	McGee 1982
		29	Mullican and Keller 1986
Long-tailed weasel	*Mustela frenata*	48–50	McGee 1982
Merriam's shrew	*Sorex merriami*	0–30	Allred 1973
		29	Mullican and Keller 1986
Mountain vole	*Microtus montanus*	48–50	McGee 1982
		29	Mullican and Keller 1986
Northern grasshopper mouse	*Onychomys leucogaster*	0–68	Allred 1973
		29	Mullican and Keller 1986
Northern pocket gopher	*Thomomys talpoides*	48–50	McGee 1982
Ord kangaroo rat	*Dipodomys ordii*	0–68	Allred 1973
		29	Mullican and Keller 1986
Pygmy rabbit	*Brachylagus idahoensis*	19	Green and Flinders 1980a,b
	Sylvilagus idahoensis	16–33	Weiss and Verts 1984
		39–51	Katzner and Parker 1997
Sagebrush vole	*Lagurus curtatus*	52–55	Oldemeyer and Allen-Johnson 1988[a]
	Lemmiscus curtatus	29	Mullican and Keller 1986
Townsend's ground squirrel	*Spermophilus townsendii*	0–50	Allred 1973
		52–55	Oldemeyer and Allen-Johnson 1988[a]
		29	Mullican and Keller 1986
Uinta ground squirrel	*Spermophilus armatus*	48–50	McGee 1982
Vagrant shrew	*Sorex vagrans*	48–50	McGee 1982
Western harvest mouse	*Reithrodontomys megalotis*	16–23	Nichols and others 1975
		0–68	Allred 1973
		29	Mullican and Keller 1986
Western jumping mouse	*Zapus princeps*	48–50	McGee 1982

[a] Not able to differentiate between the cover contributed by big sagebrush and other shrubs.

grasshopper mouse, *Onychomys leucogaster*; least chipmunk, *Eutamias minimus*; western harvest mouse, *Reithrodontomys megalotis*). This relative abundance index ranked second to last, with only the *Juniperus* site at 0 percent big sagebrush canopy cover lower at 11. For sites having 0 percent big sagebrush canopy cover and high amounts of grasses and forbs, the relative abundance index was 140 for the *Elymus*-forb site with seven species, and 160 for the *Oryzopsis-Stipa* site with four species. These compare to the four highest sites: (1) *Artemisia-Chrysothamnus*-grass site at 218 with seven species and 50 percent canopy cover of big sagebrush; (2) *Chrysothamnus-Tetradymia-Artemisia* site at 219 with six species and 20 percent canopy cover of big sagebrush; (3) *Chrysothamnus-Artemisia* site at 269 with eight species and 30 percent canopy cover of big sagebrush; and (4) *Chrysothamnus-Artemisia*-grass site at 346 with nine species and 24 percent canopy cover of big sagebrush. From this study, canopy cover of big sagebrush that appears to support the greatest number of species is between 20 and 50 percent.

McGee (1982) compared small mammal population response to burned and unburned big sagebrush habitat. The unburned big sagebrush habitat had a canopy cover of 49 percent. Deer mouse and Uinta ground squirrel (*Spermphilus armatus*) were the only species out of nine to show a positive response to fall burning of big sagebrush. Other studies that lend support to the Allred (1973) and McGee (1982) studies are Nichols and others (1975); Oldemeyer and Allen-Johnson (1988); and Smith and Urness (1984). From these studies it appears that big sagebrush canopy cover favoring small mammals ranges from 20 to 50 percent.

Such consideration for sagebrush does not exclude the importance of understory plants (grasses and forbs) and insects that supply the food for most of the small mammals of the big sagebrush ecosystem (Koehler and Anderson 1991; Smith and Urness 1984).

Large Mammals

Pronghorn—Pronghorn (*Antilocapra americana*) is a facultative associate of big sagebrush (fig. 2.10; Mace 1956; Peterson 1995; Welch and Criddle 2003; Yoakum 1986). This native antelope occupies vegetative types ranging from shortgrass prairie to shrub-steppe to salt-desert shrublands. Yoakum and others (1996) estimate that 68 percent of the pronghorns inhabit grassland and 32 percent shrubland. Sundstrom and others (1973) reported that 51 percent of pronghorns in Wyoming inhabited a combination of sagebrush steppe, saltbush-greasewood, and wheatgrass-needlegrass shrubsteppe, while 49 percent inhabited grama-needlegrass-wheatgrass, wheatgrass-needlegrass, and grama-buffalo grass ranges. The significance in these values is that Wyoming has probably the largest expanse of unaltered big sagebrush habitat (Sundstrom and others 1973) in North America and by far the largest number of pronghorns—58 percent of the world's population (Sundstrom and others 1973; Yoakum and others 1996). In fact, Wyoming and Montana account for about 73 percent of all the pronghorn in the world (Yoakum and others 1996). A study conducted in central Montana by Bayless (1969) found the distribution of pronghorn to be 55 percent on shrublands, 31 percent on grasslands, and 13 percent on cropland during the summer. He found the winter distribution to be 93 percent on shrublands, 5 percent on grasslands, and 2 percent on croplands. These values are supported by the observations of Pyrah and Schlatterer (1968) as reported by Sundstrom and others (1973, p.17): "They reported that the sagebrush-grassland type received the greatest use, both in summer and winter." Sundstrom and others (1973) reported that 69 percent of the pronghorns in southeastern Montana were found on sagebrush-grassland type.

Figure 2.10—Pronghorn—Flaming Gorge Reservoir, Utah—that consumes large quantities of Wyoming big sagebrush year round (photo by Bruce L. Welch).

Regardless of the division of pronghorns among grasslands, shrublands, and other vegetative types, when pronghorns are on grasslands, they search the habitat for shrubs and forbs to eat (table 2.6). Shrubs dominate the diet year long with forbs being heavily used during spring and matching shrubs in summer (Pyrah 1987). On the other hand, grasses are used sparingly throughout the year (Pyrah 1987; Smith and Beale 1980).

Several studies show that two species of shrubs, Wyoming big sagebrush and silver sagebrush, are associated with higher reproductive levels of pronghorn than that of grasslands. Martinka (1967, p. 159) reported the following for north-central Montana:

> Winter mortality of pronghorn antelopes was studied near Glasgow, Montana, in April 1965. A minimum loss of 500 pronghorns was associated with severe weather and occurred primarily on foothill grassland along the Milk River. Comparisons of rumen samples with feeding site examinations found that starvation occurred while animals were restricted to the grassland vegetative type. Among pronghorns in the Glasgow herd, fawn production was 39-55 fawns per 100 does as compared to a normal 90-110. On the Malta winter range in the adjacent county to the west where sagebrush was abundant, available, and heavily utilized, losses were minor and fawn production normal.

Sundstrom and others (1973, p. 34), citing a variety of reports and letters, stated:

> As the pronghorn populations radiate farther from the primary ranges of these two sagebrush species, the average number of fawns per 100 does decreased significantly. In western South Dakota where the foregoing two plant species are abundant, fawn: doe ratios

Table 2.6—Food habits of pronghorn (*Antilocapra americana*). Data expressed as a percentage of diet.

Season	Shrubs	Forbs	Grasses	Reference
		- - - - - - - - - - *Percent* - - - - - - - - - -		
Winter	75	24	1	Bayless 1969
Spring	78	00	22	Bayless 1969
Winter	59	31	6	Martinka 1967
Spring	80	18	2	Smith and Beale 1980
Summer	63	36	1	Smith and Beale 1980
Fall	96	3	1	Smith and Beale 1980
?	66	31	3	Einarsen 1948
Fall	69	18	1[a]	Einarsen 1948
Summer	63	26	0[a]	Einarsen 1948
Spring	66	33	1	Mason 1952
Summer	48	52	0	Mason 1952
Fall	72	28	0	Mason 1952
Fall	66	12	20[a]	Mitchell and Smoliak 1971
Winter	53	21	26	Mitchell and Smoliak 1971
Summer	47	43	1	Johnson 1979[b]
Winter	77	1	2	Johnson 1979[b]
Spring	25	51	20[a]	Hoover and others 1959
Summer	22	66	1[a]	Hoover and others 1959
Fall	72	22	1[a]	Hoover and others 1959
Winter	54	26	5[a]	Hoover and others 1959
Spring	63	35	2	Ferrel and Leach 1952
Fall	47	52	1	Ferrel and Leach 1952
Winter	96	2	2	Ferrel and Leach 1952
Fall	87	6	7	Couey 1946
Spring	58	42	0	Smith and Malechek 1974[c]
Summer	55	45	0	Smith and Malechek 1974[c]
Fall	70	28	2	Smith and Malechek 1974[c]
Spring	76	23	1	Smith and Malechek 1974[d]
Summer	75	25	0	Smith and Malechek 1974[d]
Fall	77	30	0	Smith and Malechek 1974[d]
Yearly	76	23	1	Gates and Eng 1983
Spring	37	47	16	McInnis and Vavra 1987
Summer	15	79	6	McInnis and Vavra 1987
Fall	56	31	13	McInnis and Vavra 1987
Winter	60	21	19	McInnis and Vavra 1987
Spring	64	34	2	Ferrel and Leach 1950
Summer	47	50	1[a]	Ferrel and Leach 1950
Yearly	88	11	1	Olsen and Hansen 1977
Spring	76-91	—	—	Ngugi and others 1992
Summer	80-90	—	—	Ngugi and others 1992
Fall	80-90	—	—	Ngugi and others 1992
Spring	11	11	78	Dirschl 1963[e]
Summer	40	55	5	Dirschl 1963[e]
Fall	55	42	1[a]	Dirschl 1963[e]
Winter	85	7	1[a]	Dirschl 1963[e]
Spring	66	26	8	Dirschl 1963[f]
Summer	45	52	1[a]	Dirschl 1963[f]
Fall	87	12	1	Dirschl 1963[f]
Winter	83	8	0[a]	Dirschl 1963[f]
Year long	71	22	7	Yoakum 1983
Year long	63	34	3	Sundstrom and others 1973

[a] If values do not sum to 100, percentages for agricultural crops or unknowns were not included in this table.

[b] Data from this study were expressed as relative densities (percent) of plant fragments in feces.

[c] Values from Awapa Plateau.

[d] Values from Desert Experimental Range.

[e] Values from Cypress Hills.

[f] Values from Matador.

> were approximately 100: 100. Along the Missouri River in the same state, Wyoming big sagebrush and silver sagebrush are much less abundant; there, average fawn: doe ratios were 50: 100. In Montana, well within the primary range of Wyoming big sagebrush and silver sagebrush, the average fawn: doe ratio was 90: 100. Yet, when some of these same antelope were transplanted from Montana to Kansas, where there were no large, woody sagebrush species, and general environmental conditions were different, reproduction decreased within a few years to 52 fawns per 100 does.

They reported similar results for the Sand Hills of Nebraska, Idaho, and New Mexico. These reports contrast with the view of Yoakum and others (1996), which is that pronghorn are more productive on grasslands than shrublands.

Martin and others (1951) described big sagebrush as an outstanding pronghorn food that is eaten throughout the year. The amount of big sagebrush in the diet of pronghorn varies, with the most occurring during the winter and spring and lesser amounts in the fall and lowest in the summer months. Details are given in table 2.7.

Smith and others (1965) fed six pronghorn, cafeteria style (free choice), 16 species of shrubs that occur commonly on desert ranges of Utah. Big sagebrush was the number one diet item and made up 55 percent of the diet. Black sagebrush was second at 21 percent of the diet.

Last, Autenrieth and Fichter (1975) point out the importance of big sagebrush as cover for parturient does and for fawns in the Pahsimeroi drainage of Idaho. Pyrah (1987) records similar observations for Yellow Water Triangle area of Montana.

Mule Deer—The mule deer (*Odocoileus hemionus*) is a facultative associate of big sagebrush, which provides food (fig. 2.11), cover during fawning, and cover for fawns (fig. 2.12) and adults (Martin and others 1951; Peterson 1995; Robinette 1972; Welch and Criddle 2003). The utilization of the current year's growth of big sagebrush varies (Anderson and others 1972; Elderkin and others 1986; Grimm 1939; Hoskins and Dalke 1955; Van Dersal 1938; Wambolt 2001; Wood and others 1995). In fact, mule deer use on big sagebrush can be so heavy that extensive damage and death to the big sagebrush plants can occur (Gysel 1960; McArthur and others 1988; Smith 1949; Wambolt 1996; Wambolt and Sherwood 1999). McArthur and others (1988) reported 11 times more death on browsed plants than nonbrowsed plants (fig. 2.13). Julander (1937) ranked big sagebrush palatability to mule deer in the top third of 148 plants. He ranked 99 plants species less palatable than big sagebrush, 10 plant species as the same, and 39 plants species as having greater palatability than big sagebrush. What then is the value of big sagebrush to mule deer?

Dietz and Yeager (1959, p. 151) pose two questions in their attempt to assess the role of sagebrush in the management of mule deer winter range (see Urness 1986): "Is sagebrush, specifically big sagebrush, an important mule deer feed? Do deer feed on sage by preference or through necessity?"

The answer to the first question is yes. Reynolds (1960) referred to big sagebrush, along with five other shrub species, as one of the staples in the diet of Utah mule deer. In the State of Oregon, big sagebrush is considered the main source of food for mule deer (Mace 1957). For California, Longhurst and others (1952, p. 41) stated: "The other group includes abundant species of inferior palatability, such as big sage

Table 2.7—Amount of big sagebrush (*Artemisia tridentata*) in the diet of pronghorn (*Antilocapra americana*).

Season	Big sagebrush	Reference
	Percent	
Spring	18–35	Smith and Beale 1980
Summer	2–10	Smith and Beale 1980
Winter	55	Smith and Beale 1980
Cafeteria	63	Smith and Beale 1980
Spring	76	Ngugi and others 1992[a]
Spring	91	Ngugi and others 1992[b]
Spring	41	Hall 1963
Summer	36	Hall 1963
Winter	95	Hall 1963
Summer	12	Gates and Eng 1983
Fall	96	Gates and Eng 1983
Spring	37	McInnis and Vavra 1987
Summer	15	McInnis and Vavra 1987
Fall	55	McInnis and Vavra 1987
Winter	57	McInnis and Vavra 1987
Spring	41	Ferrel and Leach 1950
Summer	35	Ferrel and Leach 1950
Spring	95	Olsen and Hansen 1977
Summer	42	Olsen and Hansen 1977
Fall	77	Olsen and Hansen 1977
Winter	95	Olsen and Hansen 1977
Spring	30	Bayless 1969
Winter	51	Bayless 1969
Spring	6–85	Smith and Malechek 1974
Summer	0–5	Smith and Malechek 1974
Spring	41	Ferrel and Leach 1952
Fall	35	Ferrel and Leach 1952
Winter	95	Ferrel and Leach 1952
Summer	27	Johnson 1979[c]
Winter	65	Johnson 1979[c]
Fall	51	Couey 1946[d]
Winter	49	Singer and Renkin 1995
Yearly	28	Einarsen 1948
	60-90	Marshall 1985

[a] Mountain big sagebrush community.

[b] Wyoming big sagebrush community.

[c] Percent not by volume but by relative densities of plant fragments in feces.

[d] Did not distinguish between big sagebrush (*Artemisia tridentata*) and silver sagebrush (*A. cana*).

Figure 2.11—Mule deer feeding on big sagebrush (photo by Bruce L. Welch).

Figure 2.12—Big sagebrush providing cover for mule deer fawns (photo by Thomas M. Holland).

Figure 2.13—Fenceline contrast where heavy mule deer browsing killed mountain big sagebrush plants (photo by E. Durant McArthur).

(*Artemisia tridentata*) and California juniper (*Juniperus californica*). Despite the fact that these may be 'second choice' foods, they furnish a large part of the diet of deer in eastern California." Studying the food habits of mule deer in Wyoming, Goodwin (1975, p. 1) concluded that "the most important diet species were big sagebrush, antelope bitterbrush, and true mountain mahogany." A Nevada food habit study conducted by Papez (1976) found that big sagebrush and mountain mahogany were the most preferred species on mule deer winter range (see Lesperance and others 1970). Studying the preference and digestibility of big sagebrush and black sagebrush, Wambolt and others (1987), Personius and others (1987), Wambolt (1996), and Wambolt and Sherwood (1999) found that big sagebrush is an important component in the diet of mule deer. In their summary publication of 99 studies concerning the foods of the Rocky Mountain mule deer, Kufeld and others (1973) reported heavy use of big sagebrush in winter and spring with moderate use in fall and light use in the summer. Heavy use was defined as 20 percent or more in the diet; moderate—between 5 and less than 20 percent; and light—between 1 and less than 5 percent. Singer and Renkin (1995) suggest that the 66 percent decline in mule deer of the Northern Yellowstone Winter Range may be due to declining Wyoming big sagebrush stands. Thus, it appears that the use of big sagebrush by mule deer is a widespread phenomenon throughout the Western United States.

In general, use peaks in the winter, with less use occurring in the fall and spring and least in the summer (table 2.8). Scanning the data given in table 2.8 shows that the variation from one study to another is impressive. One possible explanation for such variability is the amount of differential preference that mule deer have for various subspecies and populations within subspecies of big sagebrush (Hanks and others 1971; Scholl and others 1977; Wambolt 1995, 1996; Welch and McArthur 1981, 1986; Welch and others 1983). A detailed discussion of wintering mule deer and other animal species preference for subspecies and populations within subspecies of big sagebrush is given in chapter V.

Do deer feed on sage by preference or through necessity? Studying the food habits of the Great Basin deer herds of California, Leach (1956) noted a switch in the fall diet from bitterbrush to big sagebrush, adding that light utilization of bitterbrush during winter and spring was not necessarily due to lack of bitterbrush. From his report (p. 279): "Had a March sample of deer been collected, it might have revealed a possible low utilization of bitterbrush, as in April. This was found to occur on all the other deer ranges reported in the study and could not always be attributed to the unavailability of bitterbrush forage." Lassen and others (1952, p. 217) also noted a winter shift from bitterbrush to big sagebrush even when bitterbrush was still available and further observed that "bitterbrush seems to have a period of low palatability in February, March and April." Welch and Andrus (1977, p. 4), studying the use and value of rose hips for wintering mule deer, observed: "Vasey big sagebrush showed signs of being heavily browsed by deer. It was clear that deer preferred rose hips and sagebrush as browse. Black chokecherry and antelope bitterbrush were not heavily browsed for another month." As the senior author of that report, I had expected or believed, based on my knowledge of untested remarks in the older literature, that big sagebrush was a food of last resort. I was surprised that, in spite of the large amount of available bitterbrush, the deer chose to eat rose hips and big sagebrush. I made similar observations, during the winter of 1997 to 1998 (an open winter), in shrubs gardens planted at the Point of the Mountain south of Salt Lake City, UT. In those gardens wintering deer ate rose hips and big sagebrush before feeding on bitterbrush and other shrub species. During open winters, I have noted heavy utilization of big sagebrush at Gordon Creek (near Helper, UT), Hobble Creek (near Springville, UT), Ironton Mountain (near Provo, UT), White River (near Meeker, CO), and Piceance Basin of Colorado. In addition, Welch and Wagstaff (1992), who compared by paired plants 'Hobble Creek' mountain big sagebrush to bitterbrush as a winter forage for mule deer, found that wintering mule deer preferred 'Hobble Creek' mountain big sagebrush over bitterbrush.

After reviewing the literature, Peterson (1984, p. 75) of the Montana Fish, Wildlife, and Park Department stated:

> In summary, the literature clearly provides a basis of fact that sagebrush is a nutritional, digestible, and desirable forage source for mule deer as well as for other wild ungulates. The premise that sagebrush is detrimental to deer if it makes up the majority of that animal's diet is unfounded. Animal condition (fat reserves) upon entering the winter season are a critical factor in determining overwinter survival. However, winter ranges with forage plants high in nutritional quality that will maintain animals or lessen the drain on their fat reserves are important. Big sagebrush, being a common component of many of our winter ranges, has been shown to be capable of providing this important winter sustenance.

The nutritive values of big sagebrush are discussed in chapter IV.

Elk—Elk (*Cervus canadensis*) is a facultative associate of big sagebrush, which provides food and cover during calving, and cover for fawns and adults (Booth 1947; Hansen and Clark 1977; Hansen and Reid 1975; Johnson 1951; Kufeld 1973; Peterson 1995; Reid 1942; Smith 1960; Wambolt 1995, 1996, 1998; Wambolt and McNeal 1987). Wambolt (1998) found that elk wintering on the Northern Yellowstone Winter Range preferred habitats dominated by big sagebrush (fig. 2.14) and

Table 2.8—Percent of big sagebrush (*Artemisia tridentata*) in the diet of mule deer (*Odocoileus hemionus*).

Spring	Summer	Fall	Winter	References
- - - - - - - - - - - - - *Percent* - - - - - - - - - - - - - -				
4–64	Trace	0–10	12–81	Leach 1956[a]
			52	Wambolt 1995[b]
			40–49	Papez 1976[c]
34–44		4-12	27–65	Bissell and Strong 1955[c]
8–40	0–9	1	12–69	Tueller 1979[d]
			16	MacCracken and Hansen 1981[b]
		18		Lucich and Hansen 1981[b]
.1–13			13–37	Willms and McLean 1978[e]
4			4	Kasworm and others 1984[b]
			26	Willms and others 1979
	3			Hubbard and Hansen 1976[b]
			3–21	Hansen and Dearden 1975[b]
46		23	44	Hansen and Reid 1975[b]
			2–33	Carpenter and others 1979[e]
			19	Hall 1963
			4–45	Julander 1952[c]
12	7	17	40	Richens 1967[e]
7–43		Trace-17	39–70	Lassen and others 1952[b]
			52	Wambolt 1996[b]
3–14		3	8–53	Urness 1986
0–8			64	Smith and Julander 1953
18–28	23	28	20–33	Goodwin 1975[b]
16	1	6	25	Wilkins 1957[c]
			27–56	Hilken and Vavra 1981[b]
3		3	8–53	Austin and Urness 1983[e]
48	15	2–5	16–25	Rosenstock and others 1989[b]
	0		Trace-63	Julander 1955
25				Austin and others 1983[e]
			37	Smith 1952
			23	Singer and Renkin 1995
26	0	15	37–51	Mustard 1958
			41	Hansen and others 1977
			10–63	Riggs and others 1990
3	0		1–39	Pederson and Welch 1982
0–64	0–23	0–45	Trace-81	All studies

[a] Percentage of big sagebrush in the diet based on rumen volume; study conducted on four deer herds and for 8 years.

[b] Percentage of big sagebrush in the diet was determined by fecal microhistological techniques.

[c] Percentage of big sagebrush in the diet was determined by rumen volume.

[d] Percentage of big sagebrush in the diet was determined by rumen volume; study conducted on six deer herds and for 9 years.

[e] Percentage of big sagebrush in the diet was determined by percent of bites.

Figure 2.14—Big sagebrush providing feed for elk (photo by Carl L. Wambolt).

that excessive consumption of big sagebrush has caused big sagebrush stands to decline. He reported that mean big sagebrush canopy cover inside 36- and 41-year old elk exclosures was 20 percent but only 7 percent outside. Even after 36 or 41 years, Wambolt (1998) felt that big sagebrush recovery inside of the exclosures is not complete. This concern about elk's excessive browsing on big sagebrush was voiced more than 70 years ago but has been largely ignored even today (Rush 1932; Wright and Thompson 1935).

The utilization of big sagebrush by elk may have a nutritional basis (Wambolt and Sherwood 1999). During fall and winter, protein content of grasses does not meet the protein requirement of elk; thus, Wambolt and others (1997) reasoned that elk consumed big sagebrush as a means of raising dietary protein (nutritive value of big sagebrush is discussed in chapter IV). Kufeld (1973) ranked it as a valuable winter and fall food (5 to 20 percent of the diet; Kufeld and others 1973). Murie (1951, p. 223) states:

> Elk are fond of the matured seed stalks, which project above the snow, and the animals have been seen going from bush to bush, consistently picking them off. Although *A. tridentata* may be considered a valuable food resource at a time when other sources fail, it should not be relied on as an indicator of food shortage. The degree of use is important in judging range depletion because elk have been known to eat sagebrush leaves in fall and early winter, at least as early as November 14, when other forage was plentiful.

Big sagebrush is used as calving ground and cover for calves (fig. 2.15). Johnson (1951) reported that 42 percent of newborn calves were found in big sagebrush, 33 percent in timber, and 25 percent on the edge of big sagebrush and timber. However, 77 percent of all calves were found in big sagebrush compared to 11 percent in timber and 4.5 percent on the edge of timber and big sagebrush. Ward (1973) did not agree with the findings of Johnson (1951). In his report, "Sagebrush control with herbicide has little effect on elk calving behavior," he stated in the abstract that "elk did not change their calving behavior or feeding habits on a site where 96.7 percent of the big sagebrush (*Artemisia tridentata*) cover had been killed with 2 pounds acid equivalent of 2,4-D herbicide." Unfortunately, no calving data were provided. His data showed that spraying had no effects on feeding and presence of calves and adults on the sprayed or unsprayed areas in the summer.

Figure 2.15—Elk, 7 in all, using big sagebrush as cover (photo by Carl L. Wambolt).

Rocky Mountain Bighorn Sheep—The Rocky Mountain bighorn sheep (*Ovis canadensis*) is another facultative associate of big sagebrush. Studying the winter food habits of two herds of Rocky Mountain bighorn sheep, Keating and others (1985) reported that 25 percent of the winter diet was big sagebrush, which was the number one item in their diet. The second herd's diet was 6 percent big sagebrush, which ranked fifth in their diet. Big sagebrush on the second herd's range was nil because of overuse by wintering elk (Wambolt 1998). On winter ranges where big sagebrush canopy cover was 0.5 and 0.2 percent, Kasworm and others (1984) reported Rocky Mountain bighorn sheep diets contained 1.9 to 2.3 percent big sagebrush with deer and elk, on the same sites, also consuming big sagebrush. Martin and others (1951) ranked big sagebrush high as a winter food for Rocky Mountain bighorn sheep.

Desert Bighorn—The desert bighorn (*Ovis canadensis nelsoni*) is another facultative associate of big sagebrush and uses big sagebrush, in a limited way, as a forage plant (Barrett 1964; Bradley 1965; Browning and Monson 1981; Dunnaway 1972; McQuivey 1978; Yoakum 1964, 1966). Amount of big sagebrush in the diet of desert bighorns varied from 0 to 24 percent (Barrett 1964; Bradley 1965; Dunnaway 1972; Yoakum 1964, 1966). McQuivey (1978) and Browning and Monson (1981) listed big sagebrush on certain sites among the most preferred shrubs. There was no mention of big sagebrush cover value in the habitats of desert bighorn.

Domestic Sheep—The use of big sagebrush by domestic sheep has been known for a long time. Concerning domestic sheep, Nelson (1898, p. 25) stated:

> The amount of sagebrush consumed in the desert is simply amazing. Sheepmen and herdmen say that for sheep a straight sagebrush diet at certain times seems to 'meet a long felt want.' Whole bands will leave all other forage and browse sagebrush for a day or two at a time, after which they will not touch it again for some days, or even weeks. This is especially true for the common sagebrush (*Artemisia tridentata* Nutt.).

Studying sheep utilization of big sagebrush accessions, Welch and others (1987) reported that wintering sheep consumed big sagebrush, despite the fact the sheep had continuous access to high quality alfalfa hay and 0.28 kg of rolled barley per head per day. Also, Burritt and others (2000, p. 91), studying the influence of early life experiences and macronutrients on the intake of mountain big sagebrush by sheep found: "when sagebrush comprised 20 percent of an alfalfa/barley ration, lambs ate the sagebrush ration readily even when a nutritious alternative was offered indicating the flavor of sagebrush did not prevent lambs from feeding."

Sampson (1924), using the term "black sage" for big sagebrush, described big sagebrush as not as palatable as some of the other sagebrushes but is relied upon as a "filler" for cattle, sheep, and goats on winter and autumn range. He pointed out that big sagebrush can be a straight ration for sheep on winter range when more palatable low-growing forage is covered with snow. On small experimental paddocks of crested wheatgrass used for tests of lambing, Springfield (1960) reported heavily utilization (80 percent) of big sagebrush by pregnant ewes in early May. Snowder and others (2001), studying the diet of free-grazing Rambouillet sheep in Idaho, found that mountain big sagebrush comprised 22 percent of the September diet and 32 percent of the October diet. Research conducted by Frischknecht and Harris (1973) suggests, due to the amount of big sagebrush eaten by sheep, that sheep could be used as a biological control agent to control big sagebrush in crested wheatgrass plantings. Their data showed that fall grazing by sheep decreased the size of big sagebrush plants and greatly reduced the production of flower stalks, thus lowering the number of seeds available for establishing more plants in the seedling.

General Comments—Hoffman and Wambolt (1996) reported that reductions in seed and vegetative production of big sagebrush plants in Yellowstone National Park was due to excessive browsing by elk in large numbers. The reduction of inflorescences due to excessive browsing is a morphological problem and not an energy or carbon assimilation problem (Evans and Black 1993; Rodriguez and Welch 1989). Inflorescences arise from axils of the leaves of the vegetative shoots. Therefore, browsing removes the primordial cells that give rise to inflorescences (Diettert 1938). High populations of mule deer can, also, damage big sagebrush stands (McArthur and others 1988; Rodriguez and Welch 1989; Smith 1949; Wambolt 1998; Wambolt and Sherwood 1999).

K. Johnson (1977) observed:

> The sheer abundance of big sagebrush makes it difficult to overestimate its importance. It provides high-quality food for both livestock and wildlife, although the volatile oils tend to make it unpalatable and may interfere with digestion and nutrition [see chapter IV for a detail discussion of volatile oils, digestion, and palatability]. The volatile oils vary with subspecies, areas, seasons and sometimes individual plants. But for general Wyoming conditions, big sagebrush, particularly a dwarf form, provides important winter forage for sheep, antelope and deer, especially as part of a mixed diet.
>
> The larger growth forms provide protective cover, a ready source of fuel, and a landscaping ornamental. There has been wide use of the plant in folk medicine as a tonic, antiseptic and tea. Where big sagebrush attains undesirable concentrations, it may be readily controlled by fire and irrigation, or by mechanical and herbicidal treatments, to increase forage production [these items are covered in chapter VII]. Conversely, it can be very useful in restoring depleted big game range. So in the overall view, big sagebrush may be said to be an extremely hard working, if unglamorous, pillar of the plant community—sometimes loved, sometimes hated, always important.

Reptiles

Unlike mammals and birds, reptiles do not have a species that is known to have an obligate relationship with big sagebrush—all are facultative associates of big sagebrush. A list is given in table 2.9.

Even though many of these species can be found in vegetative types other than big sagebrush, their populations may be higher in big sagebrush habitats than other vegetative types. Diller and Wallace (1996), for example, reported capturing more western rattlesnakes (*Crotalus viridis*) and gopher snakes (*Pituophis melanoleucus*) in big sagebrush communities than in winterfat (*Ceratoides lanata*), shadscale (*Atriplex confertifolia*), greasewood, and grassland communities. Studying the response of native vertebrate populations to crested wheatgrass plantings, Reynolds and Trost (1980b) (also see Reynolds 1979a) noted greater numbers of short-horned lizards (*Phrynosoma douglassii*), sagebrush lizards (*Sceloporus graciosus*), and gopher snakes in big sagebrush than in crested wheatgrass plantings.

The importance of big sagebrush in the lives of birds, mammals, and reptiles is masterfully illustrated by a study conducted by Reynolds and Trost (1980a, p. 666). Their conclusion was simple and to the point: "Converting native sagebrush rangeland to a crested wheatgrass monoculture has a negative effect on native wildlife populations."

Table 2.9—Reptiles and amphibians having a facultative association with big sagebrush (Anderson and others 1987; Baxter and Stone 1980; Cox and Tanner 1995; Grinnell and others 1930; Hammerson 1982; Linder and Fichter 1977; McEwen and DeWeese 1987; Merriam and Stejneger 1891; Nussbaum and others 1983; St. John 1980; Tanner 1999; West 1983a,b; Young and Evans 1980). Common and scientific names are given as listed in the various cited articles; some repetition.

Common names	Scientific name
Brown-shouldered uta	*Uta stansburiana stansburiana*
Bullsnake	*Pituophis melanoleucus* *Pituophis catenifer*
Collared lizard	*Crotaphytus collaris baileyi*
Desert horned lizard (horned toad)	*Phrynosoma platyrhinos*
Desert night snake	*Hypsiglena torquata deserticola*
Desert spiny lizard	*Sceloporus magister*
Desert striped whipsnake	*Masticophis taeniatus*
Eastern short-horned lizard	*Phrynosoma douglassi brevirostre*
Gopher snake	*Pituophis melanoleucus* *Pituophis catenifer deserticola*
Great Basin gopher snake	*Pituophis melanoleucus deserticola*
Great Basin skink	*Eumeces skilitonianus utahensis*
Great Basin spadefoot toad	*Scaphiopus intermontanus*
Great Basin rattlesnake	*Crotalus viridis lutosus*
Great Basin whiptail	*Cnemidophorus tigris*
Leopard lizard	*Crotaphytus wislizeni*
Longnose leopard lizard	*Gambelia wislizenii*
Long-nosed snake	*Rhinocheilus lecontei*
Long-toed salamander	*Ambystoma macrodactylum*
Many-lined skink	*Eumeces multivirgatus*
Mesa Verde night snake	*Hypsiglena torquata loreala*
Midget faded rattlesnake	*Crotalus viridis concolor*
Milk snake	*Lampropeltis triangulum*
Mormon racer	
New Mexico spadefoot	*Scaphiopus multiplicatus*
Night snake	*Hypsiglena torquata*
Northern alligator lizard	*Gerrhonotus coeruleus*
Northern plateau lizard	*Sceloporus undulatus elongatus*
Northern sagebrush lizard	*Sceloporus graciosus graciosus*[a]
Northern tree lizard	*Urosaurus ornata wrighti*
Pacific blue-bellied lizard	*Sceloporus occidentalis occidentalis*
Pale milk snake	*Lampropeltis triangulum*
Plains spadefoot toad	*Scaphiopus bombifrons*
Plateau striped whiptail	*Cnemidophorus velox*
Prairie rattlesnake	*Crotalus viridis*
Pygmy horned lizard	*Phrynosoma douglassi douglassi*
Racer	*Coluber constrictor*
Red racer	*Masticophis flagellum piceus*
Sagebrush lizard	*Sceloporus graciosus*[a]
Side-blotched lizard	*Uta stansburiana*
Short-horned lizard	*Phrynosoma douglassi*
Striped racer	*Coluber taeniatus taeniatus*
Striped whipsnake	*Masticophis taeniatus*
Tiger salamander	*Ambystoma tigrinum*
Tree lizard	*Urosaurus ornatus*
Wandering garter snake	*Thamnophis elegans vagrans*
Western blackhead snake	*Tantilla planiceps*
Western fence lizard	*Sceloporus occidentalis*
Western longnose snake	*Rhinocheilus lecontei lecontei*
Western rattlesnake (rattlesnake)	*Crotalus viridis* *Crotalus lucifer*
Western spadefoot toad	*Scaphiopus hammondii*
Western skink	*Eumeces skiltonianus*

(con.)

Table 2.9 (Con.)

Common names	Scientific name
Western terrestrial garter snake	*Thamnophis elegans*
Western toad	*Bufo boreas*
Western whiptail	*Cnemidophorus tigris*
Western yellow-bellied racer	*Coluber constrictor mormon*
Whip-tail lizard	*Cnemidophorus tessellatus tessellatus*
Woodhouse's toad	*Bufo woodhousei*
Yellow-bellied racer	*Coluber constrictor*

[a] McEwen and DeWeese (1987) lists the sagebrush lizard as a possible obligate of big sagebrush.

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Notes

Chapter III

Other Foragers and Winter Damage on Big Sagebrush

This chapter describes organisms that, although they receive little attention, feed on big sagebrush or consume organisms that feed on big sagebrush. The fungi (diseases), insects, spiders, scorpions, lichens, and parasitic plants that live in, on, and around big sagebrush plants are discussed. Some have obligate relationships with big sagebrush, others a facultative relationship. Obligate associations are those associations necessary for the organism to complete its life cycle. Facultative associations vary from associating with big sagebrush 80 percent of the time to infrequent use of big sagebrush, perhaps 20 percent of the time. Also included is a section dealing with nonparasitic diseases of big sagebrush.

Diseases of Big Sagebrush

A diseased big sagebrush plant is a plant having a parasitic or nonparasitic condition that interferes with normal development. Parasitic agents of plant disease are called pathogens and include bacteria, fungi, nematodes, viruses, mycoplasmas, viroids, and parasitic plants. Three factors, known as the "disease triangle," must be present for a parasitic disease to develop: a susceptible host (in this case, the big sagebrush plant), a pathogen (a rust fungus), and proper environment (free water, correct temperature, and so forth).

Nonparasitic agents of plant disease are nonliving agents in the environment such as unfavorable water relationships (lack or excess), mineral deficiencies, mineral excesses, toxic substances in the soil or atmosphere, low or high temperatures, or mechanical damage that prevent the normal development of a plant.

Nonparasitic Diseases

Extensive winter injury of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*, see chapter I for a discussion on subspecies of big sagebrush) occurred in the Western United States during the winter of 1976 to1977 (Nelson and Tiernan 1983). Winter injury can result from either an unusual temperature event or winter drought. In the case of an unusual temperature event, an unusual cold wave, usually in the fall and prior to dormancy, can result in freeze injury to plants. An unusual warm spell, usually in late winter, which will stimulate growth activity, followed with a return to winter cold, can result in freeze injury. Winter drought can cause lethal dehydration of plant tissues resulting from continued transpiration and inadequate water absorption by the root system. Abnormally low snow depth may allow the soil and root systems to freeze, thus preventing the replacement of water loss in the aboveground plant parts. Also, a lack of insulating snow cover, accompanied with severe cold temperatures and drying winds, can cause water loss through freeze drying or sublimation.

Most of the winter injury that occurred during the winter of 1976 to1977 in Idaho, Utah, Nevada, Wyoming, and Colorado was above 6,000 feet (1,800 m); however, damage to mountain big sagebrush was reported from California and Oregon at elevations below 6,000 feet. Nelson and Tiernan (1983, p. 3) stated: "Virtually all large plants of mountain big sagebrush were killed on the high plateau areas we surveyed on Idaho's Sawtooth National Forest and Utah's Uinta and Manti-LaSal National Forests [fig. 3.1]. Even in the most severe kill areas, however, some young plants up to 12 inches (30 cm) high were not affected." Hanson and others (1982) and Nelson and Tiernan (1983) observed that partial killing of mature plants was common and that the most severe killing of mountain big sagebrush took place in areas normally having the deepest covering of snow, but killing was less or even lacking in areas that normally have thinner snow cover. Hanson and others (1982, p. 145) observed:

> Mountain big sagebrush plants that are not normally covered by snow seem to have evolved a dormancy condition that enables them to withstand winter-induced physiologic droughts. However, mountain big sagebrush plants that have evolved in an environment where snow cover normally prevents the soils from freezing and provides a protective plant cover that reduces transpiration demand are apparently not acclimated to long periods of winter-induced physiologic drought.

Nelson and Tiernan (1983) found that winter injury on mountain big sagebrush occurred in the following Western States: California, Colorado, Idaho, Montana, Nevada, Oregon, Utah, and Wyoming. They and Hanson and others (1982) described the probable cause of the widespread winter injury to mountain big sagebrush as either freezing or winter desiccation or both. During the November through February period, precipitation was extremely low, about 31 percent of normal, resulting in thin snow cover. Likely, soils were frozen and soil moisture unusually low. November's above-normal temperatures and December's below-normal temperature could have resulted in mountain big sagebrush tissues being susceptible to damage by freezing. Walser and others (1990) showed that properly hardened-off big sagebrush short shoots and stems can tolerate temperatures as low as –50°C; however, subject to 6 days of warm temperatures (20 °C), these same plants would freeze kill at –20 °C. February's above-normal temperatures may have broken winter dormancy, resulting in an increased in the transpiration rate during a

Figure 3.1—Extensive mountain big sagebrush mortality on the high Cassia Plateau of southern Idaho, Sawtooth National Forest (photo by David L. Nelson).

period of low soil moisture, or frozen soil. Either could cause lethal desiccation of aboveground parts. In March the temperatures fell below normal and again could have, for the second time, caused freezing damage to the mountain big sagebrush plants.

Nelson and Tiernan (1983, p.15) stated: "The extensive kill of big sagebrush over large areas represents a significant natural vegetational change. These areas will eventually return to [mountain big] sagebrush, however, because some young plants survived and seeding will occur from plants in surrounding areas."

Parasitic Diseases

In 1973, Sturges and Nelson (1986) discovered a snowmold disease caused by a fungus on mountain big sagebrush in south-central Wyoming (fig. 3.2 and 3.3). This disease has caused extensive death in areas of heavy snowpacks in Colorado, Utah, and Wyoming (fig. 3.2). This disease is just the opposite from the winter injury just described. Winter injury is caused by the lack of snow cover; with snowmold the cause is too much snow. This unknown snowmold fungus was

Figure 3.2—Big sagebrush plants partially and some entirely killed by a snowmold fungus (photo by David L. Nelson).

Figure 3.3—A dense, web-like mycelium covers the snowmold infected portion of a big sagebrush plant after snowmelt (photo by David L. Nelson).

not found on Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*) or black sagebrush (*A. nova*), taxa that occupy sites with typically little snow cover.

Can the occurrence of snowmold be related to snow depth and not to genetic differences among the two subspecies and black sagebrush? Yes, as Sturges and Nelson (1986) found in their study that when the snow cover was less than 16 inches, snowmold infected 2 percent of the plants, but when snow cover exceeded 47 inches, percentage of infected plants increased to 93 percent. This disease reduces the canopy cover or kills mountain big sagebrush plants in areas of deeper snow accumulation.

In another study, Nelson and Sturges (1986) were able to infect, under laboratory conditions, plants of basin big sagebrush (*A. tridentata* ssp. *tridentata*), Wyoming big sagebrush, and black sagebrush with the snowmold fungus, giving more proof that snow depth is more important than genetic makeup of the host sagebrush (fig. 3.4). Morphology, ultrastructure, and etiology of the snowmold fungus is given in Hess and others (1985) and Nelson and Sturges (1986).

Five rust fungi have been reported to induce rust diseases on big sagebrush: *Puccinia atrofusca, P. cnici-oleracei, P. similis, P. tanaceti,* and *Uromyces oblongisporus* (Arthur and Cummins 1962; Cooke and Shaw 1952; Cummins 1975; Weber and others 2001; Welch and Nelson 1995). The most studied of these has been black stem rust caused by *Puccinia tanaceti* (Welch and Nelson 1995). This disease is referred to as "black stem rust" because of the conspicuous and characteristic "blackening" of infloresecent stems resulting from dense sporulation of the black telial sori (fruiting structures) (fig. 3.5). Arthur and Cummins (1962) noted that this rust fungus occurs on 35 species of *Artemisia* in North America. On big sagebrush, *P. tanaceti* has been collected in all 11 conterminous Western States except Arizona. It is an autoecious obligate parasite; that is, all spore stages (pycnial, aecial, uredinial, telial) occur on one host. Usually, infection levels of this disease are low and require some hand searching through vegetative and inflorescent shoots to locate the widely scattered telial sori, but occasionally (perhaps 1 out of 10 or 15 years), heavy infections build to the point where signs (coalescing of individual telial sori together into large black bodies) of the disease can be seen 2 or 3 feet away from an infected big sagebrush plant (fig. 3.6).

With heavy infection, during mid to late summer, Welch and Nelson (1995) observed, in a seed increase garden of 'Hobble Creek' mountain big sagebrush (Welch and others 1986), that both ephemeral and

Figure 3.5—Nature of the black stem rust on big sagebrush. The black circular structures are the telial sori of the rust fungus; magnification 10x (photo by David L. Nelson).

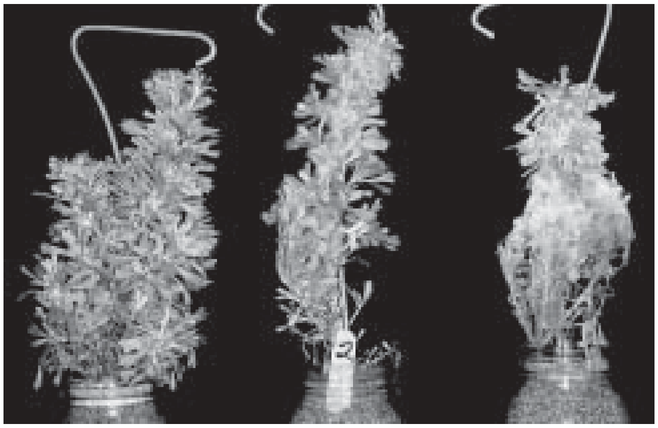

Figure 3.4—Sagebrush plants infected with snowmold under laboratory conditions. Plant on left not inoculated (photo by David L. Nelson).

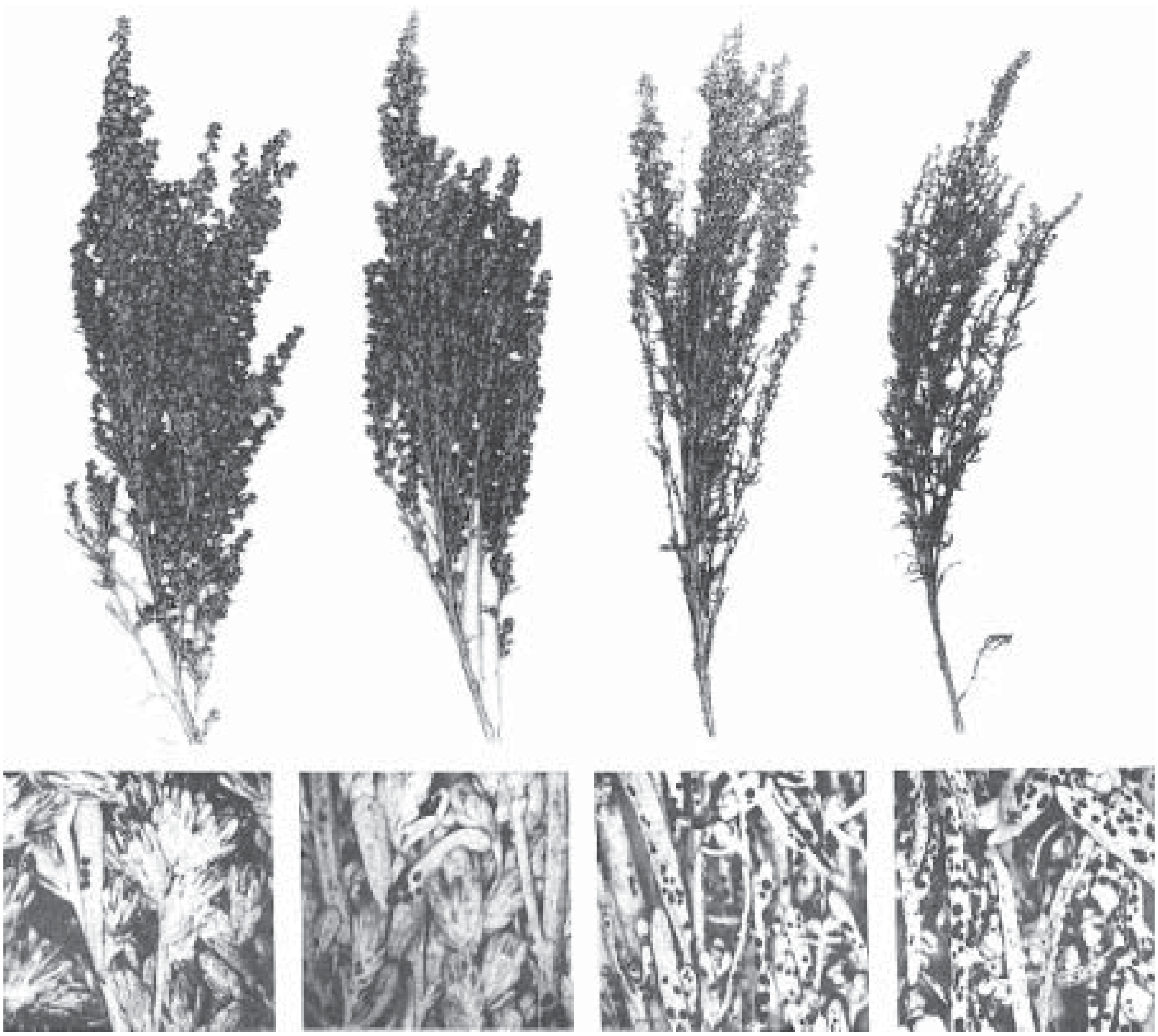

Figure 3.6—Illustration of different fungus infection intensity. Inflorescent shoots (left to right) with corresponding enlargement below showing intensity level of telial sori on leaves, stems, and florets. (One-third actual size of inflorescent shoots, 2x magnification of telial sori, photos by David L. Nelson.)

persistent leaves had begun to defoliate. Defoliation became severe, especially on vegetative shoots, and continued through fall and winter. There was a noticeable stunting of inflorescent shoots and an inhibition of floret development. Only a few of the late-forming florets on the tip of inflorescent shoots eventually flowered. A comparison among inflorescent shoots, with different levels of infection, is illustrated in figure 3.6. At heavy infection levels, seed production was reduced by 63 to 91 percent (Welch and Nelson 1995). Decreased photosynthetic capacity of plants by defoliation, stunting of inflorescent shoots, and inhibition of floret development is likely the main cause of reduced seed productivity.

Nelson and Krebill (1981) described a big sagebrush wilt disease occurring in uniform shrub testing gardens (fig. 3.7). The pathogen or pathogens of this disease have not been identified. Nelson and Krebill (1981, p. 185) described the disease development: "First symptoms of the disease usually occurred in late fall or early spring as wilted leaves and shoot tips. By midsummer, portions or entire plants collapsed and died." They noted that a prominent bluish green vascular discoloration was associated with some but not all dying plants and sometimes with nonwilted plants. This discoloration can be symptomatic of the *Verticillium*-induced disease of woody plants. Nelson and Krebill (1981, p. 185) further observed that

Figure 3.7—Wilt disease symptoms on big sagebrush plant growing on a uniform shrub testing garden. Note wilted leaves and shoots tips (photo by David L. Nelson).

“portions of the root systems of some wilt-diseased plants were necrotic, but death of plants did not seem to be associated with earlier advanced root rot or decay.” For portions of dead crown, they found that the corresponding portion of the root system was also dead.

Fungi—Weber and others (2001) have compiled a list of pathogenic and nonpathogenic fungi species, 31 in all, that have been collected from big sagebrush (table 3.1).

Insects and Other Arthropods of Big Sagebrush

Even for the casual observer of big sagebrush, the number of insects and other arthropods associated with this species of plant is impressive and truly deserves the name “mother sage.” Many insects feed directly on big sagebrush, and some feed on the insects that feed on the plant. The story of the insects and other arthropods of big sagebrush is a fascinating lesson in ecosystem association.

Aphids and Other Parasites

Aphids are a large group of soft bodied insects somewhat pear-shaped, $^{3}/_{16}$ to $^{5}/_{16}$ of an inch long, with a pair of cornicles (tubes or small “horns”) near the posterior end of the abdomen (fig. 3.8). When at rest, wings when present are held horizontal (Borror and White 1970). Aphids are usually found in large numbers feeding on stems, leaves, and inflorescences and may cause curling or wilting of the plant. Some are vectors of plant diseases (Borror and White 1970).

Table 3.1—Pathogenic and nonpathogenic fungi collected from big sagebrush (Weber and others 2001).

Alternaria tenuis
Camarosporium compositarum
Cucurbitaria obducens
Diplodina tridentatae
Discomycete sp.
Epicoccum nigrum
Fusarium sp.
Glyphium corrugatum
Godronia montanensis
Guepiniopsis buccina
Guepiniopsis torta
Heliocybe sulcata
Heterobasidion annosum
Leptosphaeria artemisiae
Leptosphaeria preandina
Leptosphaeria tumefaciens
Odontotrema oregonense
Phoma terrestris
Phyllosticta raui
Puccinia absinthii
Puccinia atrofusca
Puccinia cnici-oleracei
Puccinia similis
Puccinia tanaceti
Pyrenopeziza artemisiae
Stigmina sycina
Syncarpella tumefaciens
Teichospora obducens
Teichospora sp.
Typhula sp.
Uromyces oblongisporus

Their life cycle is complex, involving bisexual and parthenogenetic (without fertilization) generations, winged and wingless forms, and with some species alternating food plants sometime during their life cycle. Aphids overwinter as eggs, which in the spring hatch as wingless females that give rise to still more wingless females. After two or more generations, winged females are produced that usually migrate to a different food plant. In turn, these winged migrant females reproduce parthenogenetically wingless females, and later winged females are again produced that migrate back to the original food plant to produce a generation of males and females that mate, and the females lay overwintering eggs (Borror and White 1970).

Some species of ants form close associations with aphids. They collect aphid eggs and overwinter them in their nests, later transporting the eggs to feed plants in the spring where the ants care and tend the

Figure 3.8—A potpourri of aphids feeding on big sagebrush (photos by Bruce L. Welch).

aphid during the season and even transport aphids to new feed plants. Ants will defend aphid pasture plants on big sagebrush against defoliating insects (Arnott 1957).

Our knowledge of aphids and big sagebrush comes mainly from the life work of George F. Knowlton. Following is a list of his publications concerning species of aphids collected on big sagebrush: Knowlton (1929a,b, 1935a,b, 1946a,b, 1947, 1948, 1983), Knowlton and Allen (1938, 1940); Knowlton and Smith (1936a,b,c, 1937).

Knowlton's (1983) summary publication on the aphids of Utah notes there are more than 550 species in the State of which 47 were collected from big sagebrush, making it the host champion out of 259 plant species listed (table 3.2). Mean number of aphid species per plant species was three. Rubber rabbitbrush (*Chrysothamnus nauseosus*) was second with 22 species. Knowlton (1983, p. 2) observed: "Some plants,

Table 3.2—Species of aphids collected from big sagebrush (*Artemisia tridentata*) (Gillette and Palmer 1928, 1933; Knowlton 1983).

Anuraphis hermistonii
Anuraphis oregonensis
Aphis artemisicola
Capitophorus heterohirsutus
Epameibaphis atricornis
Epameibaphis frigidae
Epameibaphis utahensis
Flabellomicrosiphum knowltoni
Flabellomicrosiphum tridentatae
Hyperomyzus accidentalist
Macrosiphoniella frigidicola
Macrosiphum longipes
Microsiphoniella acophorum
Microsiphoniella artemisiae
Microsiphoniella oregonensis
Obtusicauda albicornus
Obtusicauda anomella
Obtusicauda artemisicola
Obtusicauda artemisiphila
Obtusicauda cefsmithi
Obtusicauda coweni
Obtusicauda essigi
Obtusicauda filifoliae
Obtusicauda flavila
Obtusicauda frigidae
Obtusicauda jonesi
Obtusicauda zerohypsi
Obtusicauda zerothermum
Pleotrichophorus decampus
Pleotrichophorus glandulosa
Pleotrichophorus heterohirsutus
Pleotrichophorus infrequens
Pleotrichophorus longipes
Pleotrichophorus pseudoglandulosus
Pleotrichophorus pullus
Pleotrichophorus quadritrichus
Pleotrichophorus quadritrichus ssp. *pallidus*
Pleotrichophorus spatulavillus
Pleotrichophorus wasatchii
Pleotrichophorus zoomontonus
Pseudoepameibaphis essigi
Pseudoepameibaphis glauca
Pseudoepameibaphis tridentatae
Pseudoepameibaphis xenotrichis
Pseudoepameibaphis zavillus
Zyxaphis canae
Zyxaphis filifoliae
Zyxaphis hermistonii
Zyxaphis infrequens
Zyxaphis minutissima
Zyxaphis oregonensis
Zyxaphis utahensis

such as the common sagebrush (*Artemisia* spp.) host a great number of aphid species, nearly all of which feed only on this genus of plants." Gillette and Palmer (1928, 1933) describe five more species of aphids collected from big sagebrush not included in the Knowlton (1983) report, bringing the total to 52 (table 3.2).

Messina and others (1996) used two species of aphids (*Obtusicauda coweni* and *O. filifoliae*), as well as other insect species, to evaluate four genetic hypotheses concerning herbivore attack (preference or palatability) on hybrids and parental lines between two subspecies of big sagebrush, basin and mountain. The four hypotheses were: dominance, additivity, elevated hybrid susceptibility (that is, the degree of feeding on the plant—the higher the feeding the greater the susceptibility), and elevated hybrid resistance. The test was to compare the responses of the insects to the parents and hybrids, and by inference, which of the four hypotheses best explain the observations. *O. filifoliae* did not discriminate among hosts or did not show differential preference for parents or hybrids; however, *O. coweni* seem to like the basin big sagebrush parent and the hybrid better than the mountain big sagebrush. Messina and others (1996, p. 513) concluded: "Although we eliminated several confounding factors, our results agree with the conclusion from natural hybrid zones that insect responses to hybrid plants are likely to be idiosyncratic; even congeneric species did not respond similarly to hybrid and parental plants." Thus, clarity is still lacking as to what factors contribute to palatability or the lack thereof (see chapter IV for details).

Pike and others (1997) conducted an extensive survey across eastern Washington on big sagebrush for parasitic Hymenoptera that parasitize the various species of aphids. All insects collected were members of the Braconidae family, a large and widely distributed group whose larvae are parasites of a great variety of insects including aphids on big sagebrush. From this survey, Pike and others (1997) identified 10 species parasitizing a number of big sagebrush aphid species just from the eastern Washington region (table 3.3).

Where big sagebrush is the keystone species, one could describe the location as a miniecosystem. First, there are the aphids feeding directly on big sagebrush with 10 or more species of parasitic Hymenoptera feeding on the aphids, and an unknown number of ladybird beetle species (fig. 3.9) feeding on both aphids and their parasites, plus an unknown number of ant species pasturing their honeydew-producing "cows," aphids, on big sagebrush. All this is based on one plant species and aphids that feed on it; this constitutes a relatively rich diversity of life (52 species of aphids, 10 species of parasitic Hymenoptera, an unknown number of ladybird beetle species, and aphid-attending ants).

Table 3.3—Parasitic Hymenoptera that parasitize aphids feeding on big sagebrush (*Artemisia tridentata*) (Pike and others 1997).

Parasitic Hymenoptera	**Aphid parasitized**
Binodoxys clydesmithi	*Obtusicauda artemisicola*
	Obtusicauda coweni
	Zyxaphis sp.
Binodoxys coruscanigrans	*Obtusicauda coweni*
Ephedrus californicus	*Obtusicauda coweni*
	Obtusicauda sp.
Lysaphidus adelocarinus	*Epameibaphis atricornis*
	Flabellomicrosiphum knowltoni
	Flabellomicrosiphum tridentatae
	Flabellomicrosiphum sp.
	Microsiphoniella acophorum
	Microsiphoniella sp.
	Obtusicauda artemisicola
	Obtusicauda filifoliae
	Obtusicauda sp.
	Pleotrichophorus sp.
	Pseudoepameibaphis essigi
	Pseudoepameibaphis glauca
	Pseudoepameibaphis tridentatae
	Zyxaphis sp.
Lysaphidus ramithyrus	*Pleotrichophorus* sp.
	Zyxaphis sp.
Lysiphlebus utahensis	*Obtusicauda artemisicola*
	Obtusicauda coweni
	Obtusicauda filifoliae
Praon artemisaphis	*Flabellomicrosiphum knowltoni*
	Obtusicauda coweni
	Obtusicauda sp.
	Pleotrichophorus sp.
Praon artemisicola	*Epameibaphis atricornis*
	Flabellomicrosiphum knowltoni
	Flabellomicrosiphum sp.
	Obtusicauda filifoliae
	Pleotrichophorus sp.
	Pseudoepameibaphis tridentatae
Trioxys artemisiarum	*Macrosiphoniella ludovicianae*
Trioxys bonnevillensis	*Epameibaphis atricornis*
	Epameibaphis sp.
	Epameibaphis utahensis
	Flabellomicrosiphum knowltoni
	Flabellomicrosiphum tridentatae
	Flabellomicrosiphum sp.
	Microsiphoniella acophorum
	Microsiphoniella sp.
	Obtusicauda artemisiae
	Obtusicauda artemisiphila
	Obtusicauda filifoliae
	Obtusicauda sp.
	Pleotrichophorus sp.
	Pseudoepameibaphis essigi
	Pseudoepameibaphis tridentatae
	Zyxaphis canae

Figure 3.9—Ladybird beetles hunting for aphids and other insects on big sagebrush (photos by Bruce L. Welch).

Beetles

Beetles, which form the largest order of insects (Coleoptera), feed on all sorts of plant and animal materials (Borror and White 1970). At least 23 species are known to be associated with big sagebrush, most of which feed directly on this plant (table 3.4; fig. 3.10).

Barr and Penrose (1969) noted that two beetle species (*Crossidius ater* and *Prionus* (*Homaesthesis*) *integer*) were found in the roots of big sagebrush. Barr and Penrose (1969, p. 92–93) observed of *P. integer*: "On one occasion larvae were found damaging newly planted bean seeds in a field near Burley, Cassia County, and in another instance, cutting underground stems of potato plants in a field near American Falls, Power County. In both cases the fields had been recently cleared for cultivation." Tilden and Mansfield (1944) found that the beetle *Coenonycha bowlesi* occurred only on the tips of big sagebrush plants, and their mating and feeding activities were strictly nocturnal.

Table 3.4—Beetles associated with big sagebrush (*Artemisia tridentata*) (Banham 1962; Barr and Penrose 1969; Blake 1931; Furniss and Barr 1975; Graham and others 2001; Halford and others 1973; Massey and Pierce 1960; Pringle 1960; Rickard 1970; Rogers and Rickard 1975; Tilden and Mansfield 1944).

Calosoma luxatum
Coenonycha bowlesi
Coniontis setosa
Crossidius ater
Dichelonyx sp.
Eleodes hispilabris
Eleodes sp.
Eusattus muricatus
Exema conspersa
Lyctus sp.
Mecas bicallosa
Monoxia grisea
Monoxia sp.
Octinodes sp.
Pelecyphorus densicollis
Philolithus densicollis
Prionus (*Homaesthesis*) *integer*
Stenomorpha puncticollis
Sternechus sp.
Trirhabda attenuata
Trirhabda confusa
Trirhabda nitidicollis
Trirhabda pilosa

Figure 3.10—Beetles feeding on big sagebrush (photos by Bruce L. Welch).

A survey of two species of darkling beetles (*Philolithus densicollis* and *Stenomorpha puncticollis*) in big sagebrush and greasewood (*Sarcobatus vermiculatus*) showed higher number of beetles in the big sagebrush habitat than in the greasewood habitat (Rickard and Havefield 1965; Rogers and Rickard 1975), although greasewood contained higher numbers of *Stenomorpha puncticollis*. The 1973 survey found fewer numbers of the two beetles in both habitats compared to the 1963 survey.

The beetle species that has received the greatest amount of study and attention is *Trirhabda pilosa* because of its ability, during heavy infestations, to kill big sagebrush (Anonymous 1956; Arnott 1957; Banham 1961; Furniss and Carolin 1977; Haws and others 1990; Pringle 1960). Haws and others (1990, p. 137) noted that land managers often asked, “Where can I get some of these bugs?” This species is an obligate insect on big sagebrush (Anonymous 1956; Pringle 1960). Its life history has been described by a number of workers (Anonymous 1956; Arnott 1957; Banham 1961; Pringle 1960). *T. pilosa* overwinter as an egg laid under bark or in duff at the base of big sagebrush plants. Eggs hatch in late spring, and larvae crawl up the main trunks and move out to the tips of branches where they feed on the epidermis of big sagebrush leaves and pass through several stages. Mature larvae are about a half inch long and metallic blue. In early July, mature larvae move down the host plants into duff at the base of the plant to pupate. After 1 to 2 weeks, adult beetles, shiny green, emerge and move up the host plant to feed on leaves, buds, and tender twigs. Pringle (1960) found rigid host specificity. In his study, adult beetles starved to death when placed on four other sagebrush species common to his study area as well as on rabbitbrush and goldenrod.

Amount of big sagebrush killed by infestations of this insect varied from a few acres to a few thousand acres (Banham 1961; Pringle 1960). Pringle (1960, p. 139) observed:

> In the spring of 1955, visual observations showed that 90 percent of the sagebrush over the original two-acre patch was dead. It was most interesting that the shrubs used by ants as aphid pasture were not damaged to any degree and hence survived to stand out like flags. In some cases the ants died out and plants protected in this manner were utilized and killed in the following season by hatching larvae.

Defoliator

An important pest of big sagebrush is a defoliator, a single insect species of moth (*Aroga websteri*) that damages to varying degrees vast acres of big sagebrush habitat over widespread areas in California, Idaho, Montana, Nevada, Oregon, Utah, and Washington (Anonymous 1963; Furniss and Carolin 1977; Gates 1964; Hall 1963, 1965; Hsiao 1986).

The sagebrush defoliator, also known as webworm, is a small gray moth with a wing span of $^9/_{16}$ to $^5/_8$ inch that has black markings on the front wings. Eggs are white, and mature larvae have a brown head with a creamy white body and a row of black spots on either side of the abdomen (Hall 1965). This insect produces just a single generation per year and overwinters in the egg stage as a fully developed embryo (Hsiao 1986).

Hsiao (1986) described the sagebrush defoliator’s life history. Eggs are laid under the bark and hatch into larvae during early spring. The larvae feed on sagebrush foliage, starting with young leaves near the end of short shoot, and they construct web tubes from the main webbing sites as they grow. Feeding is done at night, and then the larvae return to the main webbing site where they remain inside the protective cover of the webbing site during the day. This continues until they reach the five instar stage, then pupation starts. Pupation occurs among leaves and stems (Hall 1965) and adults emerge. The adults are also nocturnal, like the larvae, and start laying eggs in late July to early August. Most of the eggs enter an embryonic diapause.

Hsiao (1986, p. 195) described the effects of the sagebrush defoliator:

> In general, an increase in the number of defoliators was associated with a decrease in the number of flower stalks (the reproductive tissue of the plant). The number of flower stalks was also positively correlated with the weight of the plants, and may reflect the plant’s age and reproductive potential. Foliage production also decreased as the number of defoliators increased.

Of course, mortality of branches and whole plants increased with increasing numbers of the insect.

As with all other living organisms, *Aroga websteri* comes with its own set of parasites, predators, and diseases (Furniss and Barr 1975; Hall 1963,1965; Hsiao 1986). During his study, Hsiao (1986) found 10 species of insect parasites, one insect predator, and one disease-causing organism attacking the sagebrush defoliator. These and certain abiotic agents influence the size of the sagebrush defoliator populations. Hsiao (1986, p. 196) felt that abiotic factors were the most important: “Weather affects the defoliator population through the insect’s host plants. Hot, dry periods cause water stress on the sagebrush plants and reduce moisture in the foliage, thus reducing foliage acceptability to the defoliator larvae, especially during their prime feeding period.” High moisture years favor outbreaks.

Other species of *Artemisia* are attacked by the sagebrush defoliator, but as Hsiao (1986) noted, big sagebrush and three-tipped sagebrush (*Artemisia tripartita*) are the most important natural hosts and serve as another example of big sagebrush playing a key role in another insect life cycle.

Another moth species, a leaf miner (*Bucculatrix tridenticola*), can also cause heavy defoliation of big sagebrush, as can perhaps still another moth, *B. seorsa* (Hall 1963, 1965). To date, three species of moths are known to feed on big sagebrush, which in turn have 10 insect parasite species, one insect predator, and a disease organism.

Crickets, Grasshoppers, and Katydids

Interestingly, big sagebrush tops the menu for Mormon crickets (*Anabrus simplex*; fig. 3.11). According to a study conducted northeast of Dinosaur, CO, by Redak and others (1992), the diet of Mormon crickets was 51 percent big sagebrush, 23 percent forbs, 7 percent grasses, 6 percent arthropods, and small amounts of moss, fungi, and seeds. Even with removal of 75 percent of the big sagebrush plants, Mormon crickets still chose to eat large amounts of big sagebrush. Redak and others (1992, p. 100) concluded: "Despite the reputation of Mormon cricket as a rangeland pest, we found little evidence that this insect significantly affects understory vegetative biomass or production of palatable forages. Likewise, Swain (1944) rarely found severe damage to forage in heavily cricket-infested sites in Nevada." They questioned the need for aerial spray control programs for Mormon crickets, and suggested that crickets may actually make a net "improvement" to range condition by removing some of the big sagebrush overstory.

During a Mormon cricket outbreak in 1999 in an area about 1 mile southeast of the Juab-Tooele County line in Utah on U.S. Highway 6, I observed tens of thousands of the crickets marching along the highway headed in a southeasterly direction. The mean number of crickets on big sagebrush plants was five. Rarely did I observe crickets on the Utah juniper (*Juniperus osteosperma*) plants that were interspersed among the big sagebrush plants. Occasionally I found patches of some 15 to 20 big sagebrush plants where all leaves had been consumed by Mormon crickets along with portions of stems and bark, but most big sagebrush plants were only little consumed. Forbs were more heavily utilized than were grasses but neither to excess.

Some species of grasshoppers also consume large quantities of big sagebrush, even to the point of killing big sagebrush plants (table 3.5; fig. 3.12) (Allred 1941; Graham and others 1995; Sheldon and Rogers 1978).

Table 3.5—Grasshopper species that eat big sagebrush (Anonymous 1992; Hewitt and others 1974; Isely 1944; Johnson and Lincoln 1990, 1991; Scharff 1954; Sheldon and Rogers 1978).

Ageneotettix deorum
Ageneotettix elliotti
Apote notabilis
Aulocara elliotti
Conozoa wallula
Melanoplus cinereus
Melanoplus differentialis
Melanoplus mexicanus mexicanus
Melanoplus sanguinipes
Melanoplus yarrowii
Oedaleonotus enigma
Trimerotropis caeruleipennis

Figure 3.11—Mormon cricket feeding on big sagebrush (photos by Bruce L. Welch).

Figure 3.12—Grasshopper feeding on big sagebrush (photo by Bruce L. Welch).

Sheldon and Rogers (1978), studying the food habits of eight species of grasshoppers, found that seven of the eight consumed some big sagebrush, but *Melanoplus cinereus* was the champion big sagebrush eater (61 percent of its diet). Sheldon and Roger (1978) reported the amount of big sagebrush in the diet of other species of grasshoppers as 47 percent for *Oedaleonotus enigma,* 18 percent for *Apote notabilis*, 12 percent for *Melanoplus yarrowii,* 6 percent for *Trimerotropis caeruleipennis,* 4 percent for *Ageneotettxi deorum*, 1 percent for *Conozoa wallula*, and 0 percent for *Hesperotettix viridis*. Sheldon and Rogers (1978, p. 89–90) further observed:

> The combined results for all grasshopper species ... show that the diet frequency of 41% for big sagebrush is more than twice that of any other vascular plant. These results correct the statement by Daubenmire (1975) that the foliage of big sagebrush is not eaten by grasshoppers. He states that grasshoppers "congregate on big sagebrush at night, roosting on the canopy." We confirmed this and also found that during the heat of the day many species of grasshoppers sit on big sagebrush to avoid the high temperatures of exposed soil surface areas.

Allred (1941) noted that *Melanoplus mexicanus* readily fed on big sagebrush over large areas in eastern Montana, even when grasses were available. Table 3.5 lists the grasshopper species, 12 in all, that eat various amounts of big sagebrush. Graham and others (1995) reported in test gardens that grasshoppers (species unknown) browsed more on hybrid big sagebrush plants than on the parental lines of mountain and basin big sagebrush. Scoggan and Brusven (1973), studying the grasshopper-plant community associations in Idaho, found that 24 species of grasshoppers were associated with big sagebrush.

Fielding and Brusven (1992) found that two agricultural pest grasshoppers (*Aulocara elliotti* and *Melanoplus sanguinipes*) population densities were lower on big sagebrush sites than on crested wheatgrass and cheatgrass sites; or in other words, range or biodiversity improvement projects may stimulate or support the buildup of grasshopper pests. Based on these observations these two workers expanded their observations.

Fielding and Brusven (1994), conducted a study to determine effects of habitat degradation and shrub loss due to range improvement (seedling of crested wheatgrass, *Agropyron cristatum*) and fire frequency associated with the invasion of cheatgrass (*Bromus tectorum*) on grasshopper density and species richness. They selected five vegetation types within a small geographic area to factor out effects of local weather patterns. Three of the vegetative types were dominated by big sagebrush (probably Wyoming big sagebrush subdominated by bluebunch wheatgrass, *Agropyron spicatum*, or crested wheatgrass, or cheatgrass), one dominated by crested wheatgrass, and one dominated by cheatgrass/medusahead wildrye (*Taeniantherum asperum*). Fielding and Brusven (1994, p.162) reported: "Grasshopper density was lowest and species diversity was highest in vegetation types with shrub cover. Annual grasslands had the highest grasshopper densities and the lowest species diversity, and were dominated by generalist species with wide diet breadths." A comparison of the density of grasshopper and species richness of the big sagebrush/crested wheatgrass vegetation type to the crested wheatgrass/cheatgrass type showed only a difference in the amount of big sagebrush. The range improvement or crested wheatgrass sites were found to have a higher density of grasshoppers (1.18 versus 0.68) with a lower richness of species (six versus nine) but contained twice the percentage of the pest grasshopper *Melanoplus sanguinipes*. This particular species of grasshopper will migrate from wildland to irrigated cropland where it becomes a major problem. Fielding and Brusven (1994, p. 165) concluded that "these results indicate that areas with shrub cover and an understory of perennial grasses will have lower overall grasshopper densities with a lower proportion of pest species." Given these study results, one could ask if the cost of combating insect pest problems due to the killing of big sagebrush should be added to the cost of range improvement programs.

Fielding and Brusven's (1994) work is supported by an early report by Scoggan and Brusven (1973). They also found that grasshopper density was greater after big sagebrush control, and species richness less. Hewitt and Onsager (1988) also noted an increase in the density of *Melanoplus sanguinipes* with the removal of big sagebrush.

Long horned katydids and green grasshoppers also feed on big sagebrush. Tinkham's (1944) study on the shield-back katydids of the North American deserts reported finding 10 species of this group peculiar to big sagebrush as a host plant, and two other species were also found on big sagebrush and other plants species, for a total of 12 (table 3.6).

Cicadas

Cicadas are large insects 1 to 2 inches in length, nonjumping, and the males usually have a sound-producing organ at base of the ventral side of the abdomen (Borror and White 1970). After mating (early summer) adult females use their sharp ovipositor to form slits in the bark of woody plants where eggs are deposited and hatch in a few days (Hugie and Passey 1963). Hatchlings, called nymphs, drop to the ground and burrow into the soil where they stay for 2 to 6 years feeding on the roots of plants, after which they emerge as adults to mate and lay eggs for the next generation (Hugie and Passey 1963). Sugden (1940) found seven species of cicadas living in an association with big

Table 3.6—Shield-back katydids using big sagebrush as a host (feed) plant (Tinkham 1944).

Aglaothorax segnis
Ateloplus hesperus
Idiostatus elegans
Idiostatus hendersoni
Idiostatus inermis
Idiostatus inyo
Idiostatus magnificus
Idiostatus nevadensis
Idiostatus variegatus
Neduba carinata
Plagiostira albontata
Plagiostira gillettei

Table 3.7—Thrips species collected from big sagebrush (Bailey and Knowlton 1949; Knowlton and Thomas 1933; Tingey and others 1972).

Anaphothrips obscurus
Anaphothrips tricolor
Aptinothrips rufus
Frankliniella minuta
Frankliniella moultoni
Frankliniella occidentalis
Frankliniella tritici
Frankliniella sp. unknown
Frankliniella sp. unknown
Leptothrips mali
Leptothrips sp.
Odontothrips loti
Rhopalandrothrips corni
Sericothrips sp. unknown
Sericothrips sp. unknown
Thrips tabaci

sagebrush: *Neoplatypedia constricta*, *Platypedia putnami lutea*, *Okanagana fumipennis*, *O. luteobasalis*, *O. striatipes*, *O. vanduzeei*, and *O. utahensis*. Damage to plants by root feeding cicada nymphs is unknown, but their effects on soil genesis can be substantial (Hugie and Passey 1963).

Thrips

Thrips are small, slender insects $^1/_{64}$ to $^3/_{16}$ inch in length with four hairy wings (Tingey and others 1972). Mouthparts are rasping-sucking and thus obtain food by sucking out the contents of plant cells or other insects and mites (Borror and White 1970). Damage to plants is confined to localized killing of cells and perhaps to developing seeds. Sixteen thrips species have been collected from big sagebrush (table 3.7). Some are obligates.

Gall Inducers

Felt (1916) is the earliest work that I could find concerning insects inducing galls on big sagebrush. He described three species of midges, small flylike insects that resemble a mosquito, that were hatched from galls, and which presumably induced gall formation. These three species were *Diarthronomyia artemisiae*, *D. occidentalis*, and *Rhopalomyia ampullaria*. To this list, Felt (1940) added the following gall-inducing midges: *Rhopalomyia navasi*, *R. tridentatae*, *Trypetid* (fly), and *Cecidomyia* sp. Each species induces a gall that is unique in shape, size, placement, texture, color, and pubescence, so much so that a dichotomous key was constructed as an aid in species identification (fig. 3.13). Later, Jones and others (1983) described 26 species of midges that induce galls on big sagebrush in Idaho. Table 3.8 lists 32 species of midges that induce

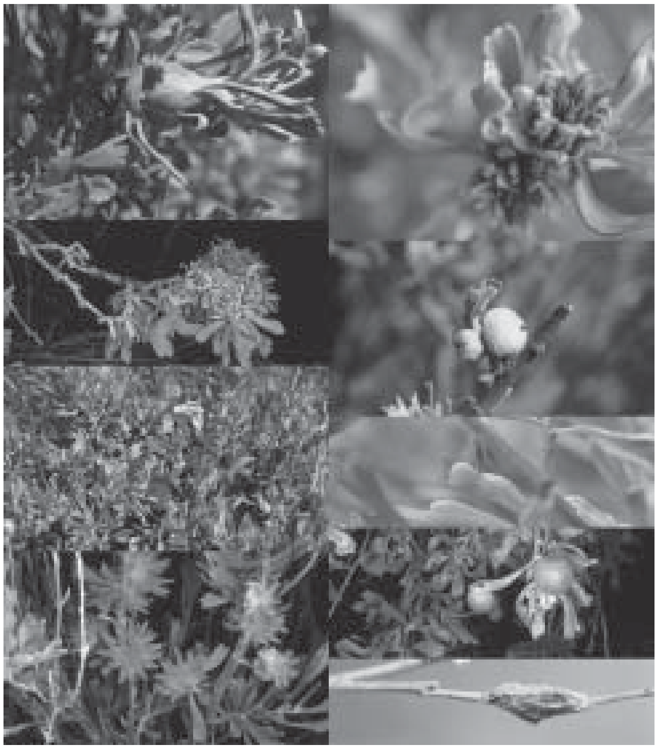

Figure 3.13—Various insect galls growing on big sagebrush except lower right corner which was induced by a fungus (photos by Bruce L. Welch)

Table 3.8—Midges that induce galls on big sagebrush (Felt 1916, 1940; Jones and others 1983).

Cecidomyia spp.
Diarthronomyia artemisiae
Diarthronomyia occidentalis
Rhopalomyia ampullaria
Rhopalomyia anthoides
Rhopalomyia brevibulla
Rhopalomyia calvipomum
Rhopalomyia conica
Rhopalomyia cramboides
Rhopalomyia culmata
Rhopalomyia florella
Rhopalomyia gossypina
Rhopalomyia hirtibulla
Rhopalomyia hirticaulis
Rhopalomyia hirtipomum
Rhopalomyia lignea
Rhopalomyia lignitubus
Rhopalomyia mammilla
Rhopalomyia medusa
Rhopalomyia medusirrasa
Rhopalomyia navasi
Rhopalomyia nucula
Rhopalomyia obovata
Rhopalomyia pomum
Rhopalomyia rugosa
Rhopalomyia sp.
Rhopalomyia sp. near *lignea*
Rhopalomyia tridentatae
Rhopalomyia tubulus
Rhopalomyia tumidibulla
Rhopalomyia tumidicaulis
Trypetid sp.

gall formation on big sagebrush. In addition to galls induced by midges, Foote and Blanc (1963) and Fronk and others (1964) described several species of fruit flies that also induce gall formation on big sagebrush: *Asphondylia* sp., *Aciurina maculata*, *Eutreta diana*, *E. oregona*, *Neotephritis finalis*, *Orellia undosa*, *Oxyna palpalis*, *O. utahensis*, and *Trupanea nigricornis*. Emlen (1992) described an additional gall-inducing fruit fly, *Eutreta diana*. In all, 42 species of insects are known to induce galls on big sagebrush.

But the story does not stop with these 42 insect species. Fronk and others (1964) found two species of parasitic Hymenoptera, *Tetrastichus* sp. and *Dacnusa* sp., that are parasitoids on some of these gall-inducing insects. Jones and others (1983) described an additional 11 insects that are associated with these gall-inducing midges. Some were parasites on larva, pupa, and adults, and others were nonharmful associates. These 11 species were: *Apion sordidum*, *Encyrtidae* sp., *Eupelmidae* sp., *Platygaster utahensis*, *Platygaster* sp., *Pogonomyrmex owyheei*, *Pteromalinae* sp., *Reduviolus alternatus*, *Synopeas* sp., *Torymus aeneoscapus*, and *Torymus koebelei*. Emlen (1992), studying a high-altitude population of *Eutreta diana*, found two more parasitic Hymenoptera species parasitizing this gall inducer (*Torymus citripes* and *Zatropis* sp.). So great was the parasitism that only 2 percent of the galls contained live larvae. Still, two more parasitic Hymenoptera species reared from insect galls on big sagebrush were described by Santiago-Blay (1989) (*Eurytoma* sp. and *Sympiesis* sp.). A study by Goeden (1990) described three more Hymenoptera parasitic species on the gall former *Eutreta diana*—*Eupelmus* sp., *Pteromalus* sp., *Rileya* sp. Goeden (2002) described *Oxyna palpalis* (Coquillett, Dipters: Tephritidae) as a facultative predator of *Rhopaloymyia florella* making a total of 21 species. Goeden (1990) found two species that were described as gall miners, *Apion* sp. (Coleoptera: Apionidae) and *Liriomyza* (Diptera: Agromyzidae). Goeden (1990, p. 31) described an avian predator: "However, the more common predators of *E. diana* larvae and puparia were birds, which were especially active at the Mormon Rocks study site, where many galls bore open holes pecked by social, insectivorous bushtits, *Psaltriparus* sp." I observed mountain chickadees (*Parus gambeli*) preying on insect larvae inside of mountain big sagebrush galls on April 2002 at the Great Basin National Park.

Fronk and others (1964, p. 575) stated, "It is well known that some insects use galls as places to overwinter." They described the following insect species as possible hibernators in galls of big sagebrush: *Coleophora* sp., *Thiodia* or *Eucosma* sp., *Bucculatrix* sp. (all Lepidotera), *Brachyrhinus ovatus* (a Coleoptera), Miridae genus, and Nabidae *Nabis* sp. (last two are nymphs, Hemiptera). In summary: 42 insect species have been described as inducing gall formation on big sagebrush, 20 insect species as parasitizing the gall or gall inducers, six species that use galls on big sagebrush as a hibernacula, and two bird species that eat the larvae inside of galls. This is an interesting ecosystem with big sagebrush as the keystone plant species.

Ants

In a big sagebrush community near Twin Falls, ID, Cole (1933) found seven species of ants (*Formica fusca*, *F. fusca neorufibarbis*, *F. pallide-fulva*, *F. rufa obscuripes*, *F. sanguinea subnuda*, *F. subpolita*, and *Pogonomyrmex occidentalis*) that were associated with big sagebrush (fig. 3.14). Sneva (1979) listed one more species occurring in the big sagebrush type, *P. owyheei*; Blom and others (1991) listed one more, *P. salinus*;

Figure 3.14—An ant attending aphids on big sagebrush (photos by Bruce L. Welch).

and Graham and others (2001) listed one more, *Formica dakotensis*. Both Furniss and Barr (1975) and Cole (1933) reported higher colony densities in big sagebrush than for other vegetative types. Allred and Cole (1971, p. 238), in their study of ants of the National Reaction Testing Station near Idaho Falls, ID, observed: "Ants representing the greatest number of species were found in the *Artemisia-Chrysothamnus*-grass and *Artemisia* associations, and fewest were found in the *Juniperus*, *Chenopodium-Eurotia*, and *Oryzopsis-Stipa* associations." The *Artemisia* of their study was big sagebrush. Allred and Cole (1971) captured 15 species of ants living in association with big sagebrush; 12 of those were species not listed by workers cited earlier in this chapter: *Camponotus vicinus*, *Formica haemorrhoidalis*, *F. manni*, *F. montana*, *F. neogagates*, *F. obtusopilosa*, *F. oreas*, *Lasius crypticus*, *Monomorium minimum*, *Mymica lobicornis*, *Myrmecocystus mojave*, and *Tapinoma sessile*. So, 23 species of ants are found living in association with big sagebrush. Furniss and Barr (1975) noted that these ant species defoliate numerous annual and perennial plants, particularly in the immediate area surrounding their mounts, and they also can defoliate big sagebrush. Ants protecting their aphids pasturing big sagebrush plants have been discussed in the aphid section (fig. 3.14). Heikkinen (1999) found that the presence of the western thatching ant (*Formica obscuripes*) reduces the number of spiders found on big sagebrush plants.

Other insect species reported as associating with big sagebrush include: *Apterona crenulella* (Furniss and Barr 1975), *Clastoptera atrapicata* (Hamilton 1977), *Hippodamia apicaulis* (Graham and others (2001), *Lygus hesperus* (Scott 1977), *Lygus robustus* (Knight 1921), *Orthezia artemisiae* (Furniss and Barr 1975), and *Cercopeus artemisiae* (Graham and others 1995).

- In summary, the following numbers of insect species have been found on or in big sagebrush: 52 aphids and 10 parasites
- 23 beetles
- 3 moths
- 1 Mormon cricket
- 12 grasshoppers
- 12 katydids
- 7 cicadas
- 16 thrips
- 42 gall inducers and 21 parasites
- 2 gall miners
- 6 gall hibernators
- 23 ants
- 7 miscellaneous

Total: 237 insect species are associated with big sagebrush (fig. 3.15). This explains the large number of insect-eating birds, mammals, and reptiles all living within the big sagebrush ecosystem (see chapter II).

Spiders

Spiders are predaceous Arachnida having four pairs of legs but lacking antennae or wings, with a body composed of two parts attached by a narrow stalk—cephalothorax and abdomen (fig. 3.16) (Borror and White 1970). They feed on insects and other small animals by paralyzing them through injection of venom

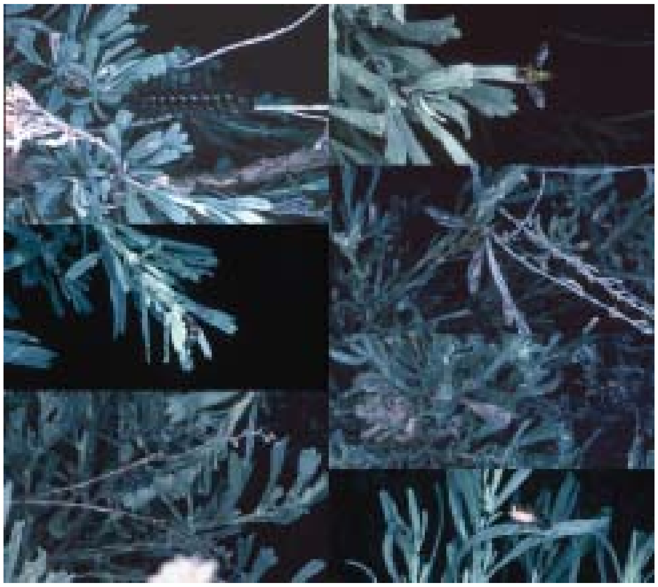

Figure 3.15—A potpourri of insects on big sagebrush (photo by Bruce L. Welch).

Figure 3.16—A potpourri of spiders on big sagebrush (photos by Bruce L. Welch).

from ducts through the fangs leading from the poison glands.

Studies conducted by Abraham (1983), Allred (1969), Ehmann (1994), and Hatley and Macmahon (1980) found 72 spider species in or on big sagebrush plants (table 3.9). Spiders spread from big sagebrush plant to big sagebrush plant by two dispersal modes: long-distance, passive, aerial dispersal called ballooning (here, the spider climbs onto a branch and releases silk into the wind until the wind lifts the spider off its perch and it floats to a new area) and local, active, ground dispersal (Ehmann 1994; Hatley and Macmahon 1980). Allred (1969, p. 108), studying the spiders of the National Reactor Testing Station in Idaho, observed: "The greatest variety of species was found in study area 10 where the vegetation analysis was 68% *Artemisia*, 7% *Opuntia*, 7% mixed grasses, and 5% miscellaneous forbs. The fewest numbers of species were found in study areas 7 and 11, typified predominantly by *Chrysothamnus* plants." Hatley and Macmahon

Table 3.9—Spider species associated with big sagebrush listed by guild (Abraham 1983; Allred 1969; Ehmann 1994; Hatley and Macmahon 1980).

Jumpers
Metaphidippus aeneolus
Oxyopes scalaris
Phidippus johnsoni
Sassacus papenhoei
Synageles idahoanus
Tutelina similis
Trappers
Dictyna idahoana
Dipoena nigra
Dipoena tibialis
Euryopis sp.
Hyposinga singaeformis
Metepeira foxi
Theridion neomexicanum
Theridion petraeum
Ambushers
Coriarachne sp.
Misumenops sp.
Xysticus cuncator
Xysticus gulosus
Xysticus montanensis
Pursuers
Anyphaena pacifica
Chiracanthium inclusum
Ebo sp.
Philodromus histrio
Additional species from Allred (1969)
Ceratinella acerea
Ceratinella parma
Circurina new species
Dictyna coloradensis
Drassyllus mannellus
Enophognatha wyuta
Gnaphosa
Haplodrassus eunus
Schizocosa avida
Tarentula kochi
Zelotes pullatus
Xysticus knowltoni
Xysticus nigromaculatus
Additional species from Abraham (1983)
Aculepeira verae
Alopecosa kochi
Araneus gemma
Araniella displicata
Argiope trifasciata
Dictyna completa
Ebo evansae
Enoplognatha ovata
Erigone dentosa
Euryopis scriptipes
Herpyllus sp.
Latrodectus hesperus
Meioneta sp. 1
Meioneta sp. 2
Meioneta sp. 3
Metaphidippus verecundus
Metaphidippus sp.
Micaria sp.
Misumenops asperatus
Misumenops lepidus
Neoscona arabesca
Pardosa wyuta
Pellenes hirsutus
Phidippus octopunctatus
Philodromus californicus
Philodromus rufus
Philodromus satullus
Philodromus speciosus
Spirembolus mundus
Steatoda americana
Synagales sp. nov.
Tetragnatha laboriosa
Thanatus formicinus
Tibellus chamberlini
Tibellus oblongus
Zelotes subterraneus

(1980) reported greater numbers of spiders and greater diversity of spider species on big sagebrush plants having greater foliar density. Abraham (1983) reported similar results. With the large numbers of insects associated with big sagebrush, it is not surprising that a large number of spider species are there to prey on this large food base (Welch and Criddle 2003).

Scorpions

Scorpions are also predaceous Arachnida, large, with pincers and a long segmented abdomen that usually curves upward and ends in a stinger at the tip. They are largely nocturnal and feed chiefly on insects and spiders. Allred (1973) found the scorpion species *Paruroctonus boreus* in big sagebrush and two other shrub communities in Idaho. He noted a strong correlation between scorpion number and the abundance of ants and spiders. Ideal scorpion habitat was described as having bare ground cover of less than 15 percent, at least 5 percent grass cover, and 60 percent or more broad-leaf shrubs cover (big sagebrush, rabbitbrush, *Chrysothamnus* sp., horsebrush, *Tetradymia*).

Wiens and others (1991), studying the interrelationships between leaf-tissue secondary chemistry, avian predation, and the abundance and diversity of arthropods occurring on big sagebrush in central Oregon, collected 168 arthropod species from big sagebrush. I have listed 309 in this chapter.

Lichens

Lichens, composed of a fungus partner and either a population of unicellular or filament algal or cyanobacterial cells, are found growing on the bark of mature big sagebrush plants (fig. 3.17). Rosentreter (1990) reported finding 24 species (table 3.10) growing on the trunk of big sagebrush. Some species were found on all three subspecies of big sagebrush, others on just one or two. He described 21 species growing on basin big sagebrush, 17 on Wyoming big sagebrush, and nine on mountain big sagebrush. Rosentreter (1990) found that the key factors influencing the amount of lichen cover on big sagebrush were: canopy density (open more light), shrub growth rate (slower),

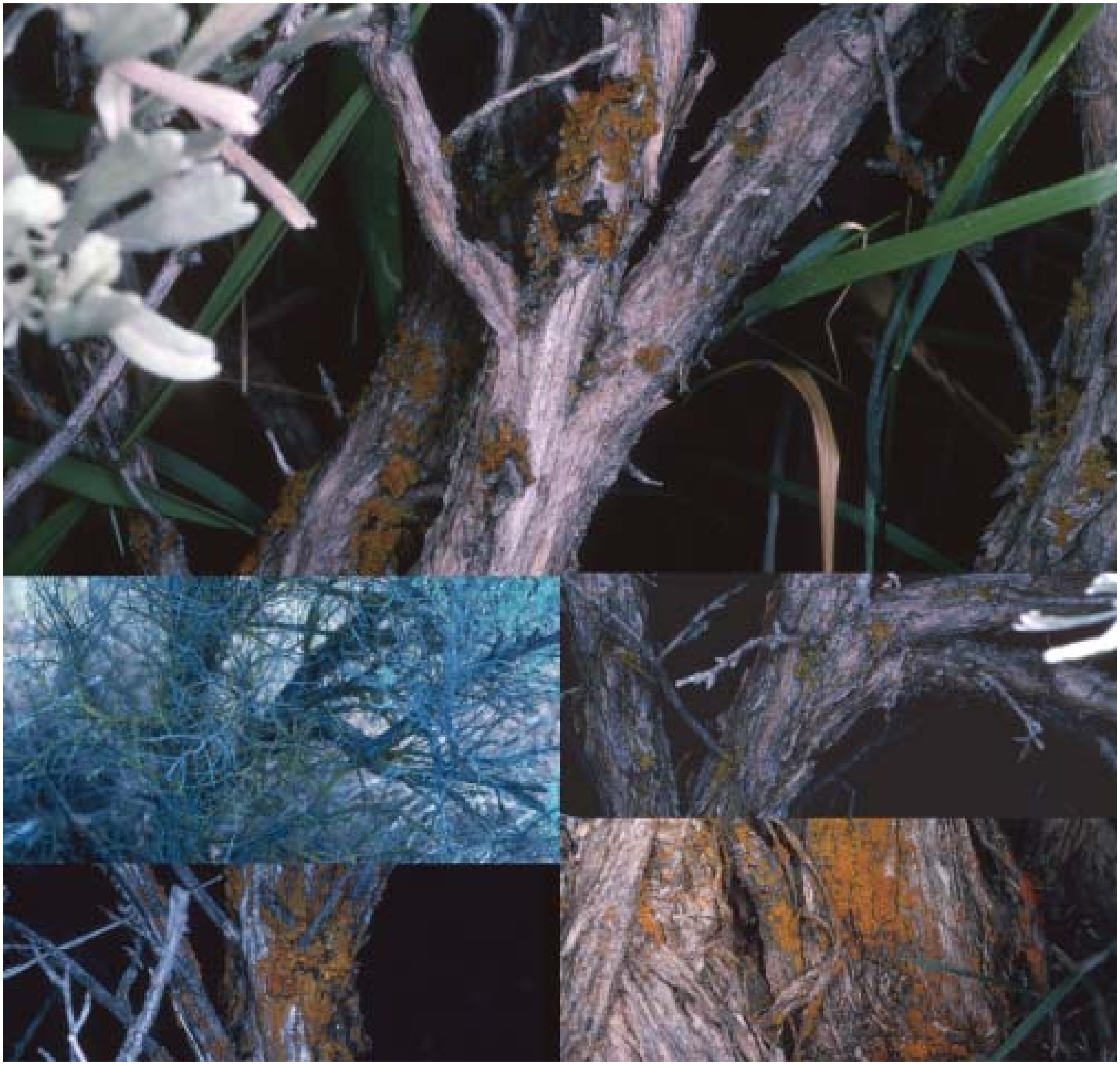

Figure 3.17—Lichens growing on mature big sagebrush plants (photos by Bruce L. Welch)

Table 3.10—Lichen species associated with big sagebrush (Rosentreter 1990).

Buellia punctata
Caloplaca fraudans
Candelaria concolor
Candelariella rosulans
Candelariella vitellina
Hypogymnia physodes
Lecanora cf. *varia*
Lecanora sp.
Lecidea plebeja
Lepraria neglecta
Letharia vulpina
Melanelia exasperatula
Melanelia incolorata
Physcia dimidiata
Physcia sp.
Physconia detersa
Physconia grisea
Physconia muscigena
Rinodina sp.
Usnea sp.
Xanthoria candelaria
Xanthoria fallax
Xanthoria polycarpa
Xanthoria sorediata

Figure 3.18—Desert paintbrush—*Castilleja chromosa*—parasitizing mountain big sagebrush (photo by Bruce L. Welch).

bark stability (less sloughing), and pH. Daubenmire (1970) collected 11 species of lichens growing on the stems of big sagebrush in Washington.

Parasitic Plants

Paintbrushes

Paintbrushes, *Castilleja*, are flowering facultative root hemiparastic plants that add a splash of color throughout the big sagebrush ecosystem (Taylor 1992; fig. 3.18). About 16 species are known to use big sagebrush as a host plant (Cronquist and others 1984; Goodrich and Neese 1986; Hitchcock and others 1959; table 3.11). From the big sagebrush host, paintbrushes receive water, solubles, and organic compounds (Ducharme and Ehleringer 1996; Hansen 1979; see chapter IV). These paintbrushes are perennials with woody, well-branched root systems and herbaceous aboveground stems. Their flowers are small and nonshowy but bloom among several colorful bract-like leaves that vary in colors of yellows, reds, oranges, and purples (Taylor 1992).

Matthies (1997) using greenhouse techniques found that *Castilleja chromosa* (desert paintbrush) grew larger in the presence of a host than alone and that it grew larger with alfalfa as the host plant than with a grass host. I have observed in the field that desert paintbrush plants growing within 48 inches of big sagebrush plants seem taller than those growing more than 48 inches from the center of big sagebrush plants. I collected data, height of desert paintbrush plants, and distance from the center of big sagebrush host plants, from West Mountain located about 14 miles southwest of Provo, UT (table 3.12). I found that there was a significant drop in desert paintbrush plant

Table 3.11—Paintbrushes (*Castilleja*) associated with big sagebrush (Cronquist and others 1984; Goodrich and Neese 1986; Hitchcock and others 1959).

Castilleja angustifolia
Castilleja applegatei
Castilleja aquariensis
Castilleja chromosa
Castilleja cusickii
Castilleja dissitiflora
Castilleja flava
Castilleja linariifolia
Castilleja miniata
Castilleja pallescens
Castilleja pilosa
Castilleja oresbia
Castilleja rustica
Castilleja scabrida
Castilleja thompsonii
Castilleja xanthotricha

Table 3.12—The relationship between height of desert paintbrush (*Castilleja chromosa*) plants and distance from the center of big sagebrush (*Artemisia tridentata*) host plant. Break point or distance from center of big sagebrush where height of desert paintbrush was significantly decreased occurred at 47 inches. This was determined by a piecewise linear regression model (Neter and others 1989).

From center of big sagebrush plant	Height of desert paintbrush
- - - - - - - - - - - - *Inches*	- - - - - - - - - - - -
2	31
3	14, 22, 24
4	23
5	24
6	18, 21
7	29
8	23
9	21
10	24, 25 19, 19,
11	28, 23
12	15
13	20
14	26
15	15
16	15, 24
18	14, 17
19	19, 13, 15
20	18
21	35
23	18, 16
25	18
27	16
28	15
30	14
36	18
37	11
38	10, 6
39	8, 5
40	10
42	8
44	5, 8
45	12, 5
47	8
48	5, 5, 6, 9
49	6, 6
50	5
51	4, 9
52	7
54	6, 7
55	8
56	9
57	9
59	8
60	5
62	7
64	9, 8
65	7
70	6
72	5
74	7
77	8
79	6, 7

heights that were growing farther than 47 inches from the center of big sagebrush host plants.

Owl-Clovers

Owl-clovers (*Orthocarpus*) are facultative root hemiparasites but unlike paintbrushes are smaller and are annuals. They are not as colorful as the paintbrushes but their bract-like leaves do vary in color—yellows, violets, purples, and reds. Seven species have been identified as using big sagebrush as host plants: *Orthocarpus barbatus*, *O. copelandii*, *O. hispidus*, *O. luteus*, *O. purpureo-albus*, *O. tenuifoliun*, and *O. tolmiei* (Cronquist and others 1984; Ducharme and Ehleringer 1996; Goodrich and Neese 1986; Taylor 1992).

Other Parasitic Plants

A number of other facultative root parasites may use big sagebrush as host plants. These include: Bird's beaks—*Cordylanthus capitatus*, *C. kingii*, *C. parviflorus*, *C. ramosus*, *C. wrightii*; and Broomrapes—*Orobanche corymbosa*, *O. fasciculata*, *O. ludoviciana* (Cronquist and others 1984; Goodrich and Neese 1986). A large number of flowering root parasites may receive nourishment from big sagebrush. Counting all the organisms listed in this chapter that receive some, and in many cases all, of their sustenance from big sagebrush, the title "mother sagebrush" seems appropriate.

Sego Lilies in a Stand of Wyoming Big Sagebrush

During a pygmy rabbit (*Brachylagus idahoensis*) survey (June 2003) south of the Painted Rocks area (about 6 miles due east of the Yuba State Park) of central Utah, I observed that the vast majority of sego lily (*Calochortus nuttallii*) plants were growing under the canopy cover of Wyoming big sagebrush. I conducted a half mile long by about 15 feet wide belt transect and noted the location, either under the canopy of a Wyoming big sagebrush plant or outside the canopy, of each sego lily plant encountered. I encountered 482 sego lily plants. A total of 81 percent (391) of the sego lily plants were growing under the canopy cover of Wyoming big sagebrush plants with 19 percent (91) growing outside the canopy. The sego lily plants growing under the canopy cover of Wyoming big sagebrush appeared to be taller and to produce more flower heads per plant (fig. 3.19).

Figure 3.19—Photographs showing sego lily (*Calochortus nuttallii*) plants and perennial grass plants growing under the protective cover of living and dead Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) plants. It was found that 94 percent of the perennial grass cover on this site was under the protective cover of Wyoming big sagebrush plants. Cattle were allowed to grazed this site, in spite, of the general lack of grasses and forbs in the interspaces between Wyoming big sagebrush plants and the continuation of a five year drought (photo by Bruce L. Welch).

To test the above hypothesis, sego lily plants growing in the interspaces between Wyoming big sagebrush plants were paired (24) with sego lily plants growing within 10 feet under the canopy cover. Measurements taken were height (inches) and number of flower heads per plant. Paired data sets, height and flower number per plant, were statistically compared using paired T-test at the 5 percent probability level (Hintze 1992). Results from the 24 pairs showed that the sego lily growing in the interspaces were significantly shorter (5.34 ± 1.26-range 3.75 to 8.0 inches) than those growing under the canopy cover (16.93 ± 3.33-range 11.5 to 24.5 inches). Number of flower heads was significantly less for those growing in the interspaces (1.29 ± 0.46-range 1 to 2) than those growing under the canopy cover (1.96 ± 0.36-range 1 to 2). This would indicate that sego lily plants growing under the canopy cover of Wyoming big sagebrush were more vigorous and achieved a higher reproductive potential than those growing in the interspaces between Wyoming big sagebrush plants.

Four possible reasons explain these observations. First, the nutrient content of soil is higher under the big sagebrush plants (see chapter IV for details); second, favorable surface water relationships last longer under the canopy cover (see chapter IV); third, hydraulic lift of water by big sagebrush supplies more water to the sego lily plants growing under the canopy (see chapter IV); and fourth, the canopy cover protects the sego lily plants from grazing livestock.

During the study time, the general area was suffering from a combination of abusive grazing practices and a continuing 5 year drought. A 300-foot line intercept vegetative analysis was conducted to determine the cover values of big sagebrush, bare ground, grass, and percent of grass under the big sagebrush plants. The line transect started at a point located at N 39° 20.625; W 111° 57.428 and went northeast for 300 feet. Results were: Wyoming big sagebrush canopy cover 28 percent, bare ground 43 percent, and grass cover 9 percent with 94 percent of the grass occurring under the protective cover of the Wyoming big sagebrush plants (fig. 3.19). Livestock were being allowed to graze this area at the time this study was conducted (June 2003).

I found the same relationship between sego lily and Wyoming big sagebrush at two other sites. (I used the same statistical/experimental design as with the first site; paired T-test of 24 pairs; Hintze 1992). One site was at the Gordon Creek Management Area Near Helper, UT, at N 39° 39.566'; W 110° 55.091'. Here 71 percent of the sego lily plants were found under the canopy cover of Wyoming big sagebrush plants. Canopy cover of Wyoming big sagebrush was 14 percent. Sego lily plants growing under the canopy cover were significantly taller at 13.90 ± 3.0 inches, range 9.25 to 21.0 inches. Those growing in the interspaces between Wyoming big sagebrush plants were significantly shorter at 5.7 ± 1.3 inches, range 3.0 to 7.5 inches. Sego lily plants growing under the canopy cover of Wyoming big sagebrush produced significantly more flower heads—2.5 ± 0.7 versus 1.4 ± 0.50 for those growing in the interspaces between Wyoming big sagebrush plants.

The second site (not recently grazed) was about 5.5 miles west of Lehi, UT, at N 40° 22.736'; W 111° 59.211'. (I used the same statistical/experimental design as with the first site; paired T-test of 24 pairs; Hintze 1992). Here 64 percent of the sego lily were growing under the canopy cover of Wyoming big sagebrush. Canopy cover of Wyoming big sagebrush was 21 percent. Sego lily plants growing under Wyoming big sagebrush were significantly taller at 10.9 ± 2.9 inches, range 6.75 to 19.5. Sego lily plants growing in the interspaces of Wyoming big sagebrush were significantly shorter at 5.4 ± 0.9 inches, range 3.75 to 6.5. Number of flower heads per plant was significantly greater for the sego lily growing under the canopy cover of Wyoming big sagebrush at 1.6 ± 0.5 versus 1.0 ± 0.2 for plants growing in the interspaces.

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Notes

Chapter IV

Big Sagebrush Chemistry and Water Relations

Nutritive Value

All animals are driven to find the right kinds of food and enough of it (Van Dersal 1938). The survival and activities of animals depend on food supply. As discussed in chapters II and III, many animals use big sagebrush directly as a food—sometimes their only food; thus the nutritive value of big sagebrush is of major importance to the animals eating it (Welch 1989).

Two morphological characteristics set big sagebrush and other shrubs apart from grasses and forbs: a deep and extensive root system and a rigid and tall stature. A deep, extensive root system allows big sagebrush to draw water from a greater volume of soil than can grasses and forbs. This makes big sagebrush a more dependable forage source during both seasonal and extended drought (Medin and Anderson 1979). Medin and Anderson (1979, p. 16) stated: "Observed declines in 1962–1964 yields of true mountain mahogany and antelope bitterbrush were associated with marked decreases in annual precipitation. Concurrent stable yields of big sagebrush suggest less susceptibility to drought or to its secondary effects; hence, it is a more reliable forage source." A taller and rigid stature makes big sagebrush more available for consumption during periods of deep snow (Welch 1989).

To appreciate the nutritive value of big sagebrush, we need knowledge of the nutrient requirements of animals and how these requirements are expressed. The nutritive value of any plant should be measured in terms of the plant's ability to supply the nutrients needed to meet the physiological requirements of the consuming animal. The quantity of nutrients needed by animals varies according to species, age, size, and activity (Welch 1989). Qualitatively, nutrient needs of animals can be placed into five classes: dry matter intake, energy-producing compounds, protein, minerals, and vitamins (Welch 1989).

Dry Matter

Intake of dry matter by animals varies according to species, weight, and activity of the animal. Greatest consumption of dry matter, as a proportion of live weight, occurs with lactation, followed by growth, gestation, and maintenance (Welch 1989). The amount of dry matter consumed is considerably important to land managers calculating carrying capacity. Dry matter requirements are expressed as pounds consumed per day per animal. Dry matter intake of selected animals is given in table 4.1.

Energy-Producing Compounds

Energy-producing compounds are the single largest class of nutrients needed by animals (Welch 1989). Energy is needed to drive the various physiological processes of the body and to provide movement and heat. Energy can be derived from a variety of compounds, including sugars, fats, pectin, starch, and protein, and in the case of ruminants and other animals with fermentation digestion systems, indirectly from cellulose and hemicellulose.

The energy needs of animals are expressed in several forms such as total digestible nutrient (TDN) and metabolizable energy. TDN requirements of animals are expressed as kilograms per animal per day or as a percentage of the diet. Metabolizable energy requirements of animals are expressed as megacalories per day or as megacalories per kilogram of dry matter.

Energy needs of animals vary according to weight and activity of the animal. Larger animals require more kilograms of TDN per day for a given activity than do smaller animals. A lactating female requires more kilograms of TDN per day than a nonlactating female of similar weight. On a constant weight basis, lactation requires more energy than any other activity. In descending order of energy needs, lactation is followed by fattening, growth, gestation, and maintenance. Unfortunately, the TDN content or amount of metabolizable energy is unknown for many forages. Table 4.1 expresses the energy requirements of animals in terms of *in vitro* digestibility. Maintenance requirement was set at 50 percent *in vitro* digestibility with all other activities adjusted accordingly (Welch 1989).

Protein

Animal protein makes up a large chemically related but physiologically diverse group of compounds. Protein is the major organic compound of the organs and soft tissues of the body and in other structures including hemoglobin, cyctochromes, and membranes. Enzymes are another functionally important group of protein compounds.

Because proteins are involved in so many bodily functions, the animal body needs a liberal and continuous supply. As with energy, the protein requirements of an animal vary according to species, weight, and activity (table 4.1). For ruminants and other animals that have fermentation-type digestive systems (horses, rabbits, burros, and so forth), the quality of the protein is not important—only the quantity. The protein requirement of an animal is expressed as grams per day of digestible protein or as a percentage of digestible protein in the diet. Protein requirement may also be expressed as grams per day of crude or total protein or as a percentage of crude or total protein in the diet. As with energy, the greater the weight of the animal, the higher are the protein needs, assuming that body activity is held constant. On a constant weight basis, lactation requires more protein than any other activity. In descending order of protein needs, lactation is followed by fattening, growth, gestation, and maintenance (Welch 1989).

Minerals

Fifteen elements are essential for the health of animals, and seven are considered major: sodium, chlorine, calcium, phosphorus, magnesium, potassium, and sulfur. The remaining eight are classified as trace elements: iodine, iron, copper, molybdenum, cobalt, manganese, zinc, and selenium. These essential mineral elements constitute the major components of bones and teeth, maintain osmotic relations and acid-base equilibrium, play an important role in regulating enzymatic systems and muscular contraction, and are constituents of most organic compounds. They are also important in energy transfer (Welch 1989).

Under most conditions, calcium and phosphorus are the mineral elements of major concern. Animal needs for calcium and phosphorus are expressed as grams per day per animal or as a percentage of the diet (table 4.1). Larger animals under similar body activity need greater amounts of calcium and phosphorus than do smaller animals. With size held constant, lactating animals require the most calcium and phosphorus, followed by growth, fattening, gestation, and maintenance.

Vitamins

Vitamins are organic compounds that the body needs in relatively small amounts. Vitamins are unrelated chemically but function as metabolic regulators. For animals capable of supporting microbial fermentation, only vitamin A is of major concern. Vitamin A combines with a specific protein of the eye to produce visual purple, which aids night vision. In addition to visual purple, vitamin A plays an important role in normal development of bones, in the normal power of disease resistance, and in maintaining healthy epithelium tissues. Vitamin A is manufactured in the liver from the plant precursor, carotene. Therefore, the vitamin A requirement is expressed in terms of carotene as either milligrams per animal per day or milligrams per kilogram of dry matter (table 4.1). With size

Table 4.1—Nutritive requirements of selected animals (after Welch 1989).Animal weights are in pounds.

	Dry matter[a]	*In vitro* digestion[b]	Crude protein	Calcium	Phosphorus	Carotene[c]
	lb	- - - - - - - - - - - - - - - *Percent of dry matter*	- - - - - - - - - - - - - - -			*mg/kg*
Sheep						
Maintenance						
110	2.2	50	8.9	0.30	0.28	1.9
132	2.4	50	8.9	.28	.26	2.0
154	2.6	50	8.9	.27	.25	2.2
176	2.9	50	8.9	.25	.24	2.3
Last 6 weeks of gestation						
110	3.7	53	9.3	.24	.23	3.6
132	4.2	53	9.3	.23	.22	3.9
154	4.6	53	9.3	.21	.20	4.2
176	4.8	53	9.3	.21	.20	4.5
Lactation						
110	3.7	60	11.0	.52	.37	2.6
132	4.2	60	11.0	.50	.36	2.9
154	4.6	60	11.0	.48	.34	3.1
176	6.6	60	11.0	.48	.34	3.3
Growth						
66	2.7	56	10.0	.45	.25	1.5
88	3.1	56	9.5	.44	.24	1.8
110	3.3	56	9.5	.42	.23	2.1
132	3.3	56	9.5	.43	.24	2.5
Cattle						
Maintenance						
881	13.4	50	5.9	.18	.18	4.1
1,102	15.9	50	5.9	.18	.18	4.1
1,323	18.3	50	5.9	.18	.18	4.1
Gestation						
881	16.5	50	5.9	.18	.18	4.1
1,102	19.0	50	5.9	.18	.18	4.1
1,323	21.4	50	5.9	.18	.18	4.1
Lactation						
881	23.8	53	9.2	.42	.38	5.7
1,102	26.0	53	9.2	.39	.36	5.7
1,323	28.4	53	9.2	.36	.34	5.7
Growth						
661	19.4	57	10.2	.31	.26	3.2
881	24.3	57	10.2	.21	.21	3.2
1,323	26.5	56	8.8	.18	.18	3.2
Horses						
Maintenance	16.4	50	8.5	.30	.20	2.4
Gestation	16.4	53	11.0	.50	.35	5.0
Lactation	21.5	56	14.0	.50	.35	4.1
Growth	13.2	58	16.0	.70	.50	2.9
Work						
Light	—	53	8.5	.30	.20	2.4
Moderate	—	57	8.5	.30	.20	2.4
Intense	—	58	8.5	.30	.20	2.4
Deer						
Maintenance	2.2	50	7.5	.30	.25	—
Gestation	2.5	53	9.0	.30	.25	—
Lactation	3.0	60	10.0	.48	.48	—
Growth	—	56	16.0	.38	.27	—
Small mammals (rabbits, squirrels, foxes)						
Maintenance	—	—	22.0	.30	.30	8.7
Gestation	—	—	38.0	.40	.40	8.7
Lactation	—	—	46.0	.60	.60	8.7
Growth	—	—	35.0	.40	.40	8.7
Birds (grouse, pheasant, quail, turkey)						
Maintenance	—	—	12.0	.50	.25	5.9
Breeding	—	—	14.0	2.25	.35	5.9
Growth	—	—	20.0	.75	.38	5.9

[a] Dry matter intake is expressed as pounds per day per head.

[b] Energy is expressed as a percentage of dry matter digested by in vitro means.Unfortunately, the total digestible nutrients content or amount of metabolizable energy is unknown for many wildland forages.More information is expressed as in vitro digestibility.Maintenance was set at 50 percent in vitro digestibility, with other activities adjusted accordingly.

[c] Carotene is expressed as mg/kg of dry matter.

held constant, a lactating animal requires the most carotene, followed by fattening, growth, gestation, and maintenance (Welch 1989).

Factors Affecting Nutritive Content of Big Sagebrush

Three factors affect the nutritive content of big sagebrush: season, genetics, and environment. Nutritive content is usually highest during the spring months and from there declines gradually, reaching a low level in the winter (Tueller 1979). This decline is illustrated in table 4.2. Peak crude protein content occurred during the spring at 15.0 percent for big sagebrush, 13.4 for antelope bitterbrush, and 21.3 for unknown Nevada grass. Crude protein levels were lowest during the winter at 10.5 percent for big sagebrush, 7.5 for antelope bitterbrush, and 2.7 for unknown Nevada grass, with summer and fall levels intermediate. It is apparent that plant genetics play a role in the amount of crude protein levels in the dry matter of plant tissues. Again, an inspection of table 4.2 reveals that big sagebrush, as a species, is genetically programmed to contain higher winter levels of crude protein than antelope bitterbrush, and antelope bitterbrush contains higher winter levels of crude protein than the unknown grass. Some populations of big sagebrush contain higher winter levels of crude protein than others; more on this in chapter V (Welch and McArthur 1979). Elderkin and others (1986) found that irrigated and fertilized big sagebrush plants contained higher levels of crude protein and were more heavily utilized by wintering mule deer than plants not irrigated, and irrigated but not fertilized (also see Williams 1972). Bayoumi and Smith (1976) found that spring applications of nitrogen significantly increased the percent of crude protein in the forage of big sagebrush and that elk used nitrogen-fertilized plants more heavily than the unfertilized plants. These two studies demonstrate that environmental factors such as soil fertility also play a role in determining the amount of nutrients within the tissues of big sagebrush.

Wambolt (2004) studied the effects of plant age on the crude protein content of current year leaves and stems for three subspecies of big sagebrush. He noted that young plants of mountain and basin big sagebrush did not contain higher levels of crude protein than mature plants. He did detect a statistically higher amount of crude protein in young Wyoming big sagebrush plants of 1.2 percentage points (11.25 percent versus 12.45) over mature Wyoming big sagebrush plants. His conclusions (Wambolt 2004) were: “I conclude that there is no meaningful difference for herbivores in crude protein levels between the age classes of the 3 big sagebrush subspecies. The additional 1.2% crude protein for young Wyoming big sagebrush would result in a increase of 0.6% digestible protein (Striby et al. 1987). It would be a rare circumstance when that level would be significant for wintering ungulates.”

Value of Specific Nutrients in Big Sagebrush

The nutritive values of big sagebrush are given in tables 4.3, 4.4, 4.5, and 4.6. Each table represents a different nutrient: *in vitro* digestion (table 4.3), crude protein (4.4), calcium (4.5), and phosphorus (4.6). The values expressed in the tables are from a number of independent researchers. Where more than one value was given in a study for a given season (spring, summer, fall, and winter), a mean was calculated and listed as the value for the study. Only studies using current year’s growth of leaves and stems were quoted in the tables, because most animals eat both leaves and stems, with birds and insects as exceptions (personal observations by the author). Data for *in vitro* digestion, crude protein, calcium, and phosphorus were expressed on a dry-matter basis.

The data given in the tables demonstrate the relative stable nutrient content across seasons. For example, calculating seasonal means among the various studies for *in vitro* digestibility reveals *in vitro* digestion ranged from 54 percent (winter), to 59 percent (spring and fall). All of these values are above the

Table 4.2—Seasonal variation of crude protein for big sagebrush (*Artemisia tridentata*), antelope bitterbrush (*Purshia tridentata*), and an unknown Nevada grass (after Tueller 1979).

Month/year	Big sagebrush	Antelope bitterbrush	Grass
	Percent of crude protein		
June 1968	11.8	13.4	13.4
July 1968	12.7	12.8	7.8
September 1968	11.8	9.7	9.6
December 1968	10.5	7.5	2.7
March 1969	14.0	9.9	3.4
May 1969	15.0	11.3	21.3

Table 4.3—In vitro digestibility of big sagebrush (*Artemisia tridentata*) dry matter by seasons as reported by various studies.

Spring	Summer	Fall	Winter	References
- - - - Percent of dry matter digested - - - -				
			50	Elderkin and others 1986[a]
	61			Fajemisin and others 1996
			50	Kufeld and others 1981[a]
	53		47	Krysl and others 1984
			55	Welch and Pederson 1981[a]
45	44	50	45	Hickman 1975
			51	Wambolt and others 1987[a]
			62	Urness and others 1977
57			51	Striby and others 1987[a]
65		63	61	Urness and others 1983[a]
58			50	Wambolt and others 1985[a]
			53	Welch and Wagstaff1992
			53	Ward 1971[a]
			59	Nunez-Hernandez and others 1989
68	67	65	67	Pederson and Welch 1982[a]
59	56	59	54	Mean of all studies
45-68	44–67	50–65	45–67	Range for all studies

[a] Study mean of several values.

maintenance and gestation requirements of most animals but do not meet the lactation needs (tables 4.1 and 4.3). Crude protein levels of big sagebrush are also fairly stable across seasons with means varying from 11.4 percent for summer and winter to 11.9 percent for spring and 12.1 percent for fall (table 4.4). Big sagebrush contains enough protein to meet the maintenance, gestation, growth, and lactation requirements of sheep and cattle year round; maintenance and gestation of horses; maintenance, gestation, and lactation of deer; and maintenance of birds (tables 4.1 and 4.4). Winter crude protein content levels of big sagebrush seeds could meet the breeding and growing requirements of birds (tables 4.1 and 4.3). Calcium levels vary more seasonally than the other nutrients, reaching a high of 0.72 percent in the spring followed by a low level of 0.55 percent in the winter with summer and fall levels intermediate (table 4.5). Only the calcium requirements of breeding birds, growing birds, and lactating small mammals are not met by the winter level of calcium in big sagebrush (tables 4.1 and 4.5). Phosphorus levels of big sagebrush current year's growth peaks in the spring and summer at 0.30 to 0.31 percent and declines in the fall to 0.25 percent and reaches a low level at 0.20 percent in winter (table 4.6). At the spring and summer levels, big sagebrush could meet the phosphorus needs for maintenance, gestation, and growth of sheep, cattle, and deer; and maintenance of horses and birds (tables 4.1 and 4.6).

How do nutritive values of big sagebrush compare to other wildland forage plants? Tables 4.7 and 4.8 give the answer. Table 4.7 compares the spring *in vitro* digestibility, crude protein, phosphorus, and carotene levels of a number of wildland plants including shrubs, forbs, and grasses. As a spring forage plant, big sagebrush nutritive value ranks low among the plant species listed; many are more digestible and contain higher levels of crude protein, phosphorus, and carotene (table 4.7). It is in the winter when big sagebrush nutritive value reigns supreme (table 4.8). Winter current year's growth of big sagebrush is more digestible than all 22 forage plant species listed; its crude protein levels are second only to crested wheatgrass fall regrowth; phosphorus levels are also second only to crested wheatgrass fall regrowth; and it ranks third in carotene. It is a very nutritious winter forage that a number of wildlife species and domestic sheep feed upon (see chapter II for more details).

Not all big sagebrush subspecies and populations or accessions within subspecies are equal in digestibility, levels of crude protein, levels of monoterpenoids, productivity, and preference (see chapter V for more details). This wealth of variation among big sagebrush subspecies and populations within subspecies helps explain some of the differences that occurred among the various studies conducted on big sagebrush.

For some species of animals such as domestic sheep, big sagebrush is not a food that they can readily switch to without a period of slow adjustment. I learned growing up on a dairy farm that when spring came, cows were allowed on the green pasture—switching from dry lot to green pastures—for an hour or two for the first 3 days, then increased to 3 or 4 hours for the next 3 days, and then increased to 6 hours for 3 more

Table 4.4—Crude protein content of big sagebrush (*Artemisia tridentata*) dry matter by seasons as reported by various studies.

Spring	Summer	Fall	Winter	References
- - - - - - - *Percent of dry matter* - - - - - - - -				
			10.5	Welch and Wagstaff 1992
16		14	14	Urness and others 1983[a]
	10.4		9.1	Krysl and others 1984
8.9			10.0	Williams 1972[a]
			13.4	Elderkin and others 1986[a]
		13		Bayoumi and Smith 1976[a]
			12.4	Welch and McArthur 1979[a]
13.4	13.6	9.8	10.6	Tueller 1979[a]
			11.6	Bissell and others 1955[a]
			11.0	Smith 1950
			9.4	Cook and others 1954[a]
			10.1	Dietz and others 1962a[a]
		11.2		Kinney and Sugihara 1943
			11.2	Chemists and Botanist 1906
		17.5		Tiedemann and others 1984
	8.5			Fajemisin and others 1996
			11.9	Nunez-Hernandez and others 1989
			10.1	Kufeld and others 1981
	12.3		11.2	Dietz and others 1962b[a]
			12.3	Welch 1981
	12.0			Pederson and Harper 1979
19.9	13.0	13.5	14.4	Dietz and others 1959
10.5	10.2	10.7	9.7	Bissell and Strong 1955[a]
		7.3		Otsyina and others 1982[a]
			11.7	Goebel and Cook 1960[a]
			10.6	Esplin and others 1937
			11.7	Cook and others 1951[a]
11.9	11.4	12.1	11.4	Mean of all studies
8.9–16.0	8.5–13.6	7.3–17.5	9.1–14.4	Range for all studies
			31.1	Kelrick and MacMahon 1985[b]
			28.8	Welch 1999[b]

[a] Study mean of several values.
[b] Crude protein content of seeds only.

Table 4.5—Calcium content of big sagebrush dry matter by seasons as reported by various studies.

Spring	Summer	Fall	Winter	References
- - - - - - - *Percent of dry matter* - - - - - - - -				
			0.25	Cook and others 1951[a]
	0.60		.46	Krysl and others 1984
			.24	Elderkin and others 1986[a]
		0.66	.68	Cook and others 1954[a]
			.71	Esplin and others 1937
			.72	Goebel and Cook 1960
0.87	.81	.80	.77	Dietz and others 1959
	.49			Pederson and Harper 1979
	.68		.64	Dietz and others 1962b
.56	.54	.48	.48	Medin and Anderson 1979
.72	.62	.65	.54	Mean of all studies
0.56–0.87	0.49–0.81	0.48–0.80	0.24–0.77	Range for all studies

[a] Study mean of several values.

Table 4.6—Phosphorus content of big sagebrush dry matter by seasons as reported by various studies.

Spring	Summer	Fall	Winter	References
- - - - - - - Percent of dry matter - - - - - - - -				
0.25	0.29	0.20	0.18	Medin and Anderson 1979
	.37		.25	Dietz and others 1962b[a]
	.20			Pederson and Harper 1979
.39	.33	.27	.28	Dietz and others 1959
			.23	Goebel and Cook 1960[a]
			.23	Esplin and others 1937
			.18	Welch and Wagstaff 1992
		.21	.15	Cook and others 1954[a]
.27	.41	.30	.22	Tueller 1979[a]
			.08	Elderkin and others 1986[a]
	.26		.15	Krysl and others 1984
			.24	Cook and others 1951
.30	.31	.25	.20	Mean of all studies
0.25–0.39	0.20–0.43	0.20–0.30	0.08–0.28	Range for all studies
			.55	Welch 1999[b]

[a] Study mean of several values.
[b] Big sagebrush seed only.

Table 4.7—Spring nutritive values of selected wildland plants (after Welch 1989).

Species	In vitro digestibility	Crude protein	Phosphorus	Carotene
	- - - - - - - Percent of dry matter	*- - - - - - -*		*mg/kg*
Shrubs				
Antelope bitterbrush	49.1	12.4	0.19	—
Big sagebrush	58.1	12.6	.25	—
Common winterfat	—	21.0	—	—
Curlleaf mountain mahogany	—	9.9	—	—
Fourwing saltbush	—	14.1	—	—
Low rabbitbrush	—	22.6	.46	—
Rubber rabbitbrush	—	20.7	.45	—
Utah juniper	49.0	6.2	.15	—
Forbs				
Alfalfa	86.8	28.5	.37	372.0
American vetch	71.3	21.2	—	—
Arrowleaf balsamroot	—	28.8	.43	—
Gooseberryleaf globemallow	69.7	19.7	—	—
Oneflower helianthella	—	20.0	.40	—
Small burnet	—	17.4	—	—
Grasses				
Bluebunch wheatgrass	60.6	17.0	.30	414.0
Bottlebrush squirreltail	72.3	18.5	.24	—
Crested wheatgrass	73.6	23.7	.36	452.0
Fairway wheatgrass	72.6	11.3	—	—
Idaho fescue	—	14.0	.30	92.0
Indian ricegrass	76.1	15.9	—	—
Intermediate wheatgrass	74.3	8.2	—	—
Needle-and-thread grass	64.4	12.0	.18	—
Reed canarygrass	—	16.2	.40	—
Sandberg bluegrass	62.2	17.3	.33	—
Sand dropseed grass	—	15.1	.25	—
Smooth brome	—	23.5	.47	493.0
Western wheatgrass	77.2	17.6	.45	185.0

Table 4.8—Winter nutritive values of selected wildland plants (after Welch 1989)[a].

Species	In vitro digestibility	Crude protein	Phosphorus	Carotene
	- - - - - - - *Percent of dry matter* - - - - - - -			*mg/kg*
Shrubs				
Antelope bitterbrush	23.5	7.6	0.14	—
Big sagebrush	57.8	11.7	.18	8.0
Black sagebrush	53.7	9.9	.18	8.0
Common winterfat	43.5	10.0	.11	16.8
Curlleaf mountain mahogany	49.1	10.1	—	—
Fourwing saltbush	38.3	8.9	—	3.1
Gambel oak	26.6	5.3	—	—
Low rabbitbrush	36.0	5.9	.15	—
Rubber rabbitbrush	44.4	7.8	.14	—
True mountain mahogany	26.5	7.8	.13	—
Utah juniper	44.1	6.6	.18	—
Forbs				
Arrowleaf balsamroot	—	3.6	.06	—
Oneflower helianthella	—	2.8	.17	—
Small burnet	—	6.6	—	—
Grasses				
Bluebunch wheatgrass	45.2	3.2	.05	.2
Bottlebrush squirreltail	42.0	4.3	.07	1.1
Crested wheatgrass	43.7	3.5	.07	.2
Crested wheatgrass (fall regrowth)	50.6	15.0	.39	432.0
Galleta	48.2	4.6	.08	.4
Idaho fesuce	46.1	3.8	.08	—
Indian ricegrass	50.5	3.1	.06	.4
Needle-and-thread grass	46.6	3.7	.07	.4
Reed canarygrass	—	7.8	.14	—
Sandberg bluegrass	—	4.2	—	—
Sand dropseed grass	53.2	4.1	.07	.5
Smooth brome	47.0	4.1	.12	—
Western wheatgrass	50.2	3.8	.07	.2

[a] Data are expressed as a percentage of dry matter, except carotene, which is expressed as mg/kg of dry matter.

days, and so on, thus slowing switching the diet from alfalfa hay to green grass and alfalfa. This switching took place over the course of 10 to14 days. If the switch was made too quickly, the cow's milk production would drop. Johnson and others (1976, p. 278) illustrate this same principle for big sagebrush when it is force fed to domestic sheep:

> Big sagebrush (*Artemisia tridentata*) fed to sheep by stomach pump to study its abortifacient properties during the 2nd trimester of pregnancy produced no reproductive difficulties. However, big sagebrush was lethal when 3/4 lb was fed by this method daily for 1, 2, or 3 days. Sagebrush fed 1/4 lb daily and slowly increased to 3/4 lb daily was not toxic. These findings confirm many general reports of suspected sagebrush toxicity and indicate the need for caution in moving sheep rapidly onto big sagebrush areas.

The preference rating of the big sagebrush used in the Johnson and others (1976) study is unknown. Higher preferred foods are more readily eaten. It is often speculated that secondary metabolites produced by big sagebrush are toxic to livestock; however, as Johnson and others (1976, p. 278) point out: "authoritative evidence of toxicity is scarce."

Secondary Metabolites

Secondary metabolites are organic compounds that have no obvious role in the growth and development of plants but may serve some significant ecological function or functions, such as essential or volatile oils that give plants their distinctive odors and flavors, warding off plant pathogens, deterring herbivory, attracting pollinators, and so forth. Secondary metabolites can be classified into five large groups: terpenes, phenolics, saponins, various glycosides or glucosides, and alkaloids (Hopkins 1999). Raven and others (1992, p. 553) observed:

> Certain groups of angiosperms have evolved various secondary products, or secondary metabolites such as alkaloids, which protect them from most foraging herbivores. However, certain herbivores (normally those with narrow feeding habits) are able to feed on those plants and are regularly found associated with them. Potential competitors are excluded from the same plants because of their inability to handle the toxins.

In the next section, I will discuss monoterpenoids, sesquiterpenoids, and certain phenolic compounds produced by big sagebrush and their ecological significance.

Monoterpenoids

Chemistry and Production—Monoterpenoids are the major constituents of essential or volatile oils in big sagebrush and are synthesized by way of the mevalonic acid pathway by "head-to-tail" linkage of two isoprene units (Buttkus and Bose 1977; Buttkus and others 1977; Charlwood and Charlwood 1991; Hopkins 1999; Kelsey and others 1983; Kinney and others 1941; Nagy and Regelin 1977; Powell 1970; Sneva and others 1983). These monoterpenoids are 10 carbon units of esters, ethers, aldehydes, alcohols, ketones; some are known as irregular monoterpenes (Boyd and Epstein 1976; Buttkus and others1977; Kinney and others 1941; Powell 1970; Shaw and others 1975). Monoterpenoids are synthesized by epidermal secretory cells of leaves (glandular trichomes) and are stored in an extracellular cavity surrounded by cuticle of the epidermis (Hopkins 1999; Kelsey 1982; Slone and Kelsey 1985). Over 1,000 monoterpenoids, many from higher plants, have been isolated and identified (Charlwood and Charlwood 1991).

The monoterpenoids of big sagebrush are a mixture of various esters, ethers, aldehydes, alcohols, and ketones. Thus far, 33 individual monoterpenoids have been isolated and identified from the tissues of big sagebrush (table 4.9). (The reader should not infer that a given big sagebrush plant population within subspecies or subspecies will contain all monoterpenoids listed.) Various studies have reported that individual monoterpenoids isolated from big sagebrush plants varied from seven to 17, making the composition of monoterpenoids in big sagebrush tissue among the most complex in the plant kingdom (Buttkus and others 1977; Kelsey and others 1983; Kinney and others 1941; McArthur and others 1988; Scholl and others 1977; Weaver and others 1995; Welch and others 1989). Weaver and others (1995), studying the chemical composition of volatiles extracted from four plant species—mountain big sagebrush, wild bergamot (*Monarda fistulosa*), arrowleaf balsamroot (*Balsamorhiza sagittata*), and sticky geranium (*Geranium viscoissimum*)—isolated 11 monoterpenoids from big sagebrush, eight from wild bergamot, and none from arrowleaf balsamroot and sticky geranium.

Monoterpenoid levels of big sagebrush differ not only from a qualitative but also from a quantitative point among sites or different environmental factors, seasons, and subspecies and populations within subspecies. Sneva and others (1983, p. 143), studying the

Table 4.9—Monoterpenoids isolated from the tissues of big sagebrush (Buttkus and others 1977; Kelsey and others 1978, 1983; Kinney and others 1941; McArthur and others 1988; Shaw and others 1975; Weaver and others 1995; Weber and others 1994; Welch and others 1989).The reader should not infer that a given big sagebrush plant, population within subspecies, or subspecies will contain all monoterpenoids listed.

Artemisia acetate
Artemisia alcohol
Artemisia ketone
Artemisol
Artemiseole
Arthole
Borneol
Camphene
Camphor
Carene
Carvacrol
1,8-Cineole
Cymene
Fenchone
Frenchyl alcohol
Menthol
Methyl santolinate
Myrcene
Ocimene
Ocimeone
Phellandrene
α-Pinene
β-Pinene
Sabinene
Santolina expoxide
Santolina triene
Terpinene
Terpinen-4-ol
Terpineol
α-Thujone
β-Thujone
Thujyl alcohol
Yomogi alcohol

effects of nitrogen fertilization on the essential oil production of Wyoming and mountain big sagebrush, observed: “No significant effects were found due to large variation in oil levels between plants within a fertilizer treatment. A tendency for lower oil concentration in fertilized mountain and Wyoming big sagebrush was evident, whereas levels of oil in low sagebrush were almost nil, regardless of treatment.” Kelsey (1986a) reported similar results for the production of crude terpenoids. Powell (1970) reported, based on a study of 39 plots with a wide range of vegetative, physiographic, and soil factors, that volatile oil content of big sagebrush was positively and significantly correlated with effective rooting depth, phosphate in the A horizon, nitrogen in the 6- to 12-inch layer of soil, clay content in the upper 6 inches of soil, and big sagebrush plant size. Each of these factors reflects an increase in oil content with an increase in the favorableness of growing conditions for big sagebrush. Factors that seem to reduce oil content were clay content in the effective rooting depth, potassium, and magnesium in the A horizon, and favorable water relationships. However, there may be a problem with the Powell (1970) study. In all likelihood, he was working with different subspecies of big sagebrush; thus, genetic factors were not kept constant throughout the 39 study plots, which would in turn confound the results. The effects of environmental factors on big sagebrush monoterpenoid production are therefore most likely confounded by subspecific variation.

Seasonal concentration of monoterpenoids in big sagebrush leaf and stem tissues varies independently of genetic and environmental factors. Kelsey and others (1982) noted that monoterpenoid levels were lowest during the spring and increased through the summer until reaching peak levels in the fall (September) and then decreased to intermediate levels in the winter. A study conducted by Cedarleaf and others (1983) agrees with the general trend of the Kelsey and others (1982) study, but peak monoterpenoid levels occurred in the summer months of July and August. The Kelsey and others (1982) study did not sample big sagebrush tissues in July or August. Both studies noted differences in the levels of monoterpenoids for subspecies and populations within subspecies.

Welch and McArthur (1981) offer the strongest proof that the production of monoterpenoids is under strong genetic control. They studied the variation of monoterpenoid content among subspecies and populations within subspecies of big sagebrush plants grown in a common or uniform garden; or in others words, with environmental factors held constant. They reported significant differences among subspecies and populations.

The Monoterpenoid Controversy—Monoterpenoids have bacteriostatic and bactericidal properties (Nagy and Regelin 1977; Nicholas 1973). Microbiologists have investigated these compounds in determining their usefulness as prophylactic agents. With the discovery of antibiotics, the interest in using monoterpenoids to prevent or ward off bacterial infections died. Because of the antimicrobial nature of monoterpenoids, researchers in the 1960s and 1970s and even to the 1990s became concerned about the possible adverse effects monoterpenoid-producing plants such as big sagebrush might have on ruminant and fecal microorganisms’ cellulolytic digestive abilities (Dietz and Nagy 1976; Hobbs and others 1986; Nagy 1979; Nagy and others 1964; Nagy and Tengerdy 1967, 1968; Ngugi and others 1995; Wallmo and others 1977; Wallmo and Regelin 1981). Dietz and Nagy (1976) suggested that the “theoretical” decline of mule deer in the Western United States was due principally to undue dependence on big sagebrush, juniper (*Juniperus* ssp.), pine (*Pinus* ssp.), and other species that contain high levels of monoterpenoids. They labeled monoterpenoids as toxic materials. Further, Nagy (1979) reported that during a 30-day winter grazing trial, deer experienced considerable weight loss and some became ill at the peak of big sagebrush consumption. Carpenter and others (1979) found, however, during a 30-day winter grazing trial with six mule deer, that at the peak of big sagebrush consumption, three deer were gaining weight and two deer were maintaining their weight. The sixth deer lost weight throughout the entire study. Wallmo and others (1977), embracing the *in vitro* evidence that big sagebrush monoterpenoids are toxic to rumen microorganisms, describe an inescapable nutritional dilemma that faces wintering mule deer. The dilemma centers on the need of wintering mule deer to extract 7 percent crude protein from forages with an average crude protein content of 5 percent. To increase protein intake, deer would need to consume more of the highly lignified browse twigs or more big sagebrush along with its toxic monoterpenoids, thereby lowering total digestibility. To increase digestibility, deer would need to eat more grass, which in turn would lower protein intake.

These ideas about the adverse effects of big sagebrush monoterpenoids on digestion do not agree with the *in vitro* digestibility data reported in table 4.8 that big sagebrush is among the most digestible winter forage listed (Welch and others 1982). Wallmo and others (1977), however, pointed out that the preparatory techniques used could have caused large losses of monoterpenoids from the big sagebrush samples, thus introducing bias. The *in vitro* digestion trials conducted by Welch and Pederson (1981) were designed to overcome the loss of monoterpenoids during the preparatory step. They did this by grinding the samples in liquid nitrogen with a steel motorized mortar and pestle. The results of their study showed that big sagebrush is a highly digestible browse (also see supporting studies by Striby and others 1987; Wambolt and others 1985, 1987).

Additional evidence that a high level of big sagebrush in the diet of mule deer does not adversely affect digestion comes from a study conducted by Tueller (1979). He reported that the diet of mule deer wintering in the Fox Mountain area of Nevada was 69 percent big sagebrush, whereas the diet of the White Rock herd was 28 percent. While the amount of big sagebrush in the diet of the deer from the two areas differed by a factor of 2.5, the percentage of tail fat (an indicator of body condition) was almost the same for the two deer herds: Fox Mountain 32.4 percent and White Rock 29.1 percent. It should be noted that 69 percent big sagebrush in the diet of the Fox Mountain deer herd is 2.3 to 4.6 times the level considered safe by some workers (Nagy and others 1964; Wallmo and others 1977; Wallmo and Regelin 1981).

The conflict between the digestion data of table 4.8 and the reports of Striby and others (1987), Tueller (1979), Wambolt and others (1985, 1987), and Welch and Pederson (1981), on one side, and the studies of Ngugi and others (1995), Nagy and others (1964), Wallmo and others (1977), and Wallmo and Regelin (1981) on the other side, can be explained. Two options seem apparent: (1) microorganisms can adapt to the presence of monoterpenoids, or (2) the host animal can reduce concentration of monoterpenoids in the rumen below levels toxic to the microorganisms (Welch 1983, 1993). Nagy and Tengerdy (1968, p. 441) observed:

> Rumen microorganisms of wild and captive deer were subjected to increasing amounts of volatile oils. The oils had a marked antibacterial effect on the rumen bacteria when the concentration reached approximately 16 *u*liter of oil per 10 ml of rumen fluid nutrient broth. The gross reactions of rumen bacteria obtained from wild, as well as captive, deer to the volatile oils seemed to be of the same magnitude; thus no adaptation by the bacteria to the oils was apparent.

The data presented in table 1 of the Nagy and Tengerdy (1968) study do not support their conclusion. The rumen inoculum exposed to big sagebrush monoterpenoids, that is wild deer, showed signs of being more tolerant of the presence of monoterpenoids than the rumen inoculum not exposed, that is the tame deer. For instance, at an oil (monoterpenoid) concentration of 18 *u*l per 10 ml of culture medium, the wild deer inoculum contained 6.67×10^8 bacterial survivors per ml of culture medium compared to 5.77×10^4 for the tame deer inoculum. In other words, the deer consuming big sagebrush (wild deer) had 11,715 times more bacterial survivors per ml of culture medium than did tame deer that did not consume big sagebrush. This is strong evidence of adaptation. However, Pederson and Welch (1982) reported that inocula from mule deer not previously exposed to big sagebrush or any other monoterpenoid-producing plant species digested all test forages, including big sagebrush, equally as well as inoculum from deer that had been exposed to big sagebrush monoterpenoids. They concluded that rumen microorganisms do not have to adjust to the presence of the monoterpenoids.

During *in vitro* digestion trials conducted by Welch and Pederson (1981), they wanted to know what was happening to the monoterpenoids during the digestibility trial. Therefore, they modified the digestibility trial by adding three digestive tubes that contained only buffer. To these tubes, they added specific amounts of pinene and camphor, and after the first incubation period the solutions in the tubes were extracted with absolute ether. Gas chromotography was used to detect any changes in the monoterpenoid content. None of the pinene was recovered; all was lost from the tubes, and 17.3 percent of the camphor was lost. A white condensate had formed a ring around the neck of the tubes. Each ring was located about 70 mm above the surface of the digestion solution; the condensate was identified as camphor. The force that drove these compounds out of the digestion solution was heat. Apparently, 38.5 °C, which is close to the normal body temperature of mule deer, is sufficient to volatilize the monoterpenoids. From this observation, Welch and Pederson (1981) hypothesized that monoterpenoid levels could be greatly reduced in the rumen in three ways: (1) through mastication and rumination, (2) volatilization by body heat and eructation, and (3) possible absorption through the rumen wall and excretion through the kidneys.

This hypothesis was tested by Cluff and others (1982) with wild mule deer and by White and others (1982) with pygmy rabbits (*Brachylagus idahoensis*). They found monoterpenoid levels in the rumens of mule deer or the stomachs of pygmy rabbits were only 20 to 23 percent of expected levels. This large loss of monoterpenoids from ingested forage has been observed in other species including sage grouse (*Centrocercus urophasianus*), greater glider (*Petauroides volans*), and brushtail possum (*Trichosurus vulpecula*) (Foley and others 1987; Welch and others 1989). This large loss of monoterpenoids resolves the conflict between *in vitro* evidence that big sagebrush monoterpenoids inhibit rumen microorganisms and digestive trials that show that big sagebrush is a highly digestible winter forage.

A study concerning the influence of crude terpenoid on *in vitro* digestion among taxa of big sagebrush and black sagebrush by Striby and others (1987) deserves special attention. Crude terpenoid is defined as the compounds that are extracted from the glandular trichomes of leaves using batch extraction for 5 minutes in chloroform. This would remove not only the monoterpenoid but also other terpenoids, waxes, and other chloroform soluble compounds. Striby and others

(1987) found that intact big sagebrush tissues that are not extracted with chloroform were a highly digested food. But digestibility could be increased 12.3 percent by removing the crude terpenoid faction from big sagebrush. Unfortunately, the authors were not able to determine if the increase was due to the removal of monoterpenoids, or other kinds of terpenoids, or waxes, and so forth. They did note that the taxon with the highest crude terpenoid content was also the same taxon with the highest intact digestibility. This data, again, suggest little negative impact of any terpenoids on digestion of big sagebrush tissues.

During digestibility trials, Smith (1950) noted that deer showed definite aversion to individual big sagebrush plants. This preference of mule deer for certain subspecies, populations within subspecies, and individual plants has been observed in the field by a number of researchers (Hanks and others 1971; McArthur and others 1979; Scholl and others 1977; Sheehy and Winward 1981; Stevens and McArthur 1974; Wambolt 1996, 2001; Wambolt and others 1987; Welch and others 1981; Willms and others 1979).

Nagy and Tengerdy (1968) and Dietz and Nagy (1976) hypothesized that black sagebrush (*Artemisia nova*) is preferred over big sagebrush by mule deer because black sagebrush contains lower concentrations of monoterpenoids than does big sagebrush. Observations made by Smith (1950) and Sheehy and Winward (1981), however, showed that mule deer preferred big sagebrush over black sagebrush even though monoterpenoid content of black sagebrush was lower than big sagebrush. Mule deer preference for populations of black sagebrush grown on a uniform garden that is grown under similar environmental conditions varied, and the levels of monoterpenoids also varied (Behan and Welch 1985; Scholl and others 1977; Welch and others 1983). Behan and Welch (1985) pointed out that a population of black sagebrush from Pine Valley Ridge, UT, was preferred by wintering mule deer over six other populations, but monoterpenoid content was not related to preference. In an earlier study conducted on the same uniform garden, Welch and others (1983) reported the percentage of current year's growth consumed by mule deer for a population of big sagebrush collected from the mouth of Hobble Creek Canyon near Springville, UT, was 83 percent or almost the same use as the Pine Valley Ridge at 82.7 percent (Behan and Welch 1985). While the use of the two taxa was the same, the monoterpenoid concentration was not. Total monoterpenoid content for the Hobble Creek big sagebrush population was 2.21 percent of dry matter, and concentration for the black sagebrush was 0.63 percent of dry matter; or in other words, Hobble Creek big sagebrush contained 3.5 times more monoterpenoids than did the black sagebrush, but both were equally used.

Welch and Wagstaff (1992, p.140) observed that "'Hobble Creek' mountain big sagebrush, a monoterpenoid producing shrub, was preferred by wintering mule deer over a non-monoterpenoid shrub antelope bitterbrush." In addition, Welch and Andrus (1977, p. 5), who were studying the value of rose hips as a winter food for mule deer, noted: "Mule deer prefer rose hips over black chokecherry and antelope bitterbrush but not Vasey big sagebrush." Leach (1956, p. 279), studying food habits of the Great Basin deer herds of California, found that the high use of big sagebrush "could not always be attributed to the unavailability of bitterbrush forage," or in other words, deer in his study consumed big sagebrush by choice.

Remington and Braun (1985) concluded from their study that subspecies Wyoming big sagebrush was preferred by wintering sage grouse over subspecies mountain big sagebrush. Remington and Braun (1985, p. 1055) stated: "Mountain big sagebrush (ATV) is common in drawbottoms and on east facing slopes where snow accumulates. Wyoming big sagebrush (ATW) is common on drier sites including ridge tops and benches or in alkaline areas in association with black greasewood (*Sarcobatus vermiculatus*) and alkali sagebrush (AL)."

Is there a problem with equal access (Welch and others 1991)? Are mountain big sagebrush plants growing in drawbottoms as accessible to wintering sage grouse as Wyoming big sagebrush plants growing on ridgetops, benches, and so forth? If not, then utilization and chemical comparisons between subspecies would be biased toward accessibility and bird behavior and not preference. Comparisons within subspecies were meaningful. Remington and Braun (1985) found that browsed, unbrowsed, and random Wyoming big sagebrush samples of leaves differ in the amount of crude protein and that sage grouse seem to select plants with leaves containing higher crude protein levels but similar levels of monoterpenoids. For mountain big sagebrush, sage grouse also selected plants with higher concentrations of crude protein but containing lesser amounts of three of 15 monoterpenoids. Again, we have some evidence that monoterpenoids do not influence preference for browsing on big sagebrush and some evidence that monoterpenoids do influence preference; however, the choice the sage grouse were making was among monoterpenoid-producing big sagebrush plants and not monoterpenoid plants versus nonmonoterpenoid plants.

Personius and others (1987, p. 87) studying the influence of crude terpenoid on mule deer preference for sagebrush concluded:

> Determining the importance of sagebrush epidermal chemicals as mediators of herbivory requires further

> investigation. There are numerous variables. Little information is available on chemical potencies and threshold levels for individual compounds. Carefully controlled feeding trials are necessary to clearly evaluate the effects of specific sagebrush chemicals on the feeding behavior of mule deer and other herbivores.

However, Kelsey (1986b, p. 385) claims: "Epidermal chemicals of sagebrush appear to function as a defense against herbivores." He also noted that defoliation of sagebrush plants failed to produce higher concentrations of these defense chemicals as a means of providing additional protection, like described by Bryant (1981) for snowshoe hare. Later, Bryant and others (1992, p. 18), concerning the protection of plants by secondary metabolites, noted: "Herbivory by mammals also affects the chemical defenses of woody plants. In some cases browsing results in increased defense and in others decreased defense." The role of secondary metabolites in determining preference of animals for subspecies, populations within subspecies, and individuals within populations of big sagebrush appears to create more controversy than enlightenment.

Weber and others (1994, p. 689) noted: "Several studies have shown that high levels or composition of monoterpenoids reduce rumen microbial activity of browsing species and affect palatability of *A. tridentata* (Longhurst *et al*., 1969; Personius *et al*., 1987; Bray *et al*., 1991)." This statement needs special comment. What does "several studies" mean? Do high levels mean levels normally found in big sagebrush tissues? They cited three references to support their statement, but only one (Longhurst and others 1969) was concerned with digestibility. The Personius and others (1987) and Bray and others (1991) studies, contradictory in nature, were concerned with preference and monoterpenoids. Effects or lack thereof of monoterpenoids on digestion has been discussed in the previous section. Personius and others (1987) clearly show that wintering mule deer preferred mountain big sagebrush over all other sagebrush taxa studied (see their table 1). Mountain big sagebrush contained greater concentrations of 1,8-cineole, a monoterpenoid, than the other taxa by a factor ranging from 3.4 to 27.5 (see their table 2). 1,8-cineole in this case could be called a preference "attractant." But Bray and others (1991) found 1,8-cineole to be the strongest preference "deterrence" of all the compounds tested. McLean and others (2001, p. 1078) observed: "most mammalian herbivores ingest large concentrations of many PSMs (plant secondary metabolites) that do not appear to have major effects on their choices of foods." These last three references do not lend much support to the statement of Weber and others (1994).

Methyl Jasmonate

Methyl jasmonate—a volatile substance from big sagebrush and other plants and a common perfume ingredient—has the ability to induce antiinsect compounds called "proteinase inhibitors" in other plant species. Farmer and Ryan (1990) demonstrated that when big sagebrush leaves and stems are incubated with tomato plants, proteinase inhibitors are induced in tomato plants. These inhibitors interfere with the normal metabolism of protein inside the insect, resulting in growth irregularities and death (Chen 1990). Farmer and Ryan (1990, p. 7713) maintained that their study demonstrated "interplant communication can occur from leaves of one species to leaves on another species to activate the expression of defensive genes." Karban and others (2000) and Karban (2001) reported that wild tobacco (*Nicotiana attenuata*) plants became more resistant to herbivores when near clipped big sagebrush plants. The basis of this resistance appears to be an increase in the activity of polyphenol oxidase in the tobacco plants.

Sesquiterpenoids

Sesquiterpenoids are 15 carbon unit compounds that form the largest class of terpenoids and commonly occur with the monoterpenoids in essential oils but in lower concentrations (Bramley 1997). They, like the monoterpenoids, are manufactured in glandular trichomes (Kelsey 1982). Thousands of these compounds have been isolated and identified and more than 100 sesquiterpenoids skeletons are known. They form acyclic, monocyclic, bicyclic, and tricyclic molecules with a variety of functional groups. These compounds are responsible for a number of biological, ecological, and pharmacological activities including antimicrobial properties, growth regulators, insect hormones, insect pheromones, phytoalexins, antioxidants, organoleptic properties, antitumour, antiinflammatories, antihyperlipidemic properties, antiulcer, expectorant, sedative, analgesic properties, allelopathy, antifeedant, and so forth (Bramley 1997). Sesquiterpenoid lactones are the largest group of sesquiterpenoids; over 3,000 naturally occurring compounds are known. They have been studied in terms of chemotaxonomy and for delineation of phylogenetic relationships among closely related plant groups.

Sesquiterpenoid lactones have received some attention as an aide in understanding the phylogenetic relationships among the various groups of big sagebrush and other sagebrushes (Bhadane and others 1975; Geissman and others 1967; Irwin and others 1969; Kelsey and others 1973; Shafizadeh and Bhadane 1973; Shafizadeh and others 1971). To date 24 sesquiterpenoid lactones have been isolated and identified from big sagebrush (table 4.10; Kelsey and Shafizadeh 1979). The biological and ecological significance of these compounds of big sagebrush has not been determined. However, Kelsey and Shafizadeh (1979) concluded that the chemical data from

Table 4.10—Sesquiterpenoids isolated from the tissues of big sagebrush (Bhadane and others 1975;Geissman and others 1967; Irwin and others 1969; Kelsey and others 1973; Kelsey and Shafizadeh 1979; Shafizadeh and Bhadane 1973; Shafizadeh and others 1971).The reader should not infer that a given big sagebrush plant, population within subspecies, or subspecies will contain all sesquiterpenoids listed.

Arbusculin-A
Arbusculin-B
Arbusculin-C
Artevasin
Badgerin
Deacetoxymatricarin
Deacetyllaurenobiolide
Deacetylmatricarin
Dehydroleucodin
Dentatin-A
Dentatin-B
Isophotosantonic lactone
Parishin-A
Parishin-B
Parishin-C
Ridentin
Rothin-A
Rothin-B
Spiciformin
Tatridin -A
Tatridin-B
Tatridin-C
W-A
W-B

sesquiterpenoid lactones studies suggest that big sagebrush developed from a North American ancestral line rather than Old World lines.

Phenolic Compounds

The basic structural unit of phenolic compounds is an aromatic ring (a ring of six carbons with three double bonds) to which a hydroxyl group is attached (—OH). From this simple structure a large and chemically diverse family of chemicals arises that are universally present in plants and in all plant parts. Raven and others (1999, p. 34) observed: "Although they represent the most studied of secondary metabolites, the function of many phenolic compounds is still unknown." They range from simple phenolic acids to large and complex polymers such as tannins and lignin; also included in this family of compounds are flavonoids and coumarins. All are products via the shikimic acid pathway.

Table 4.11 lists 13 to14 (the exact number is uncertain because of potential spelling differences among studies for possibly the same compounds) coumarins and 10 flavonoids that have been isolated and identified. The biological and ecological significance of these substances has not been established. They were used in an attempt to understand the phylogenetic relationship among closely related groups of sagebrush.

Allelopathy

Allelopathy is chemical warfare among plants, among animals, and even between plants and microorganisms, or other such relationships. Originally, the term allelopathy encompassed all inhibitory and stimulatory

Table 4.11—Coumarins and flavonoids isolated from the tissues of big sagebrush (Brown and others 1975; Rodriguez and others 1972; Shafizadeh and Melnikoff 1970; Tamma and others 1985; Wilt and Miller 1992; Wilt and others 1992).The reader should not infer that a given big sagebrush plant, population within subspecies, or subspecies will contain all coumarins or flavonoids listed.

Coumarins
  Aesculetin
  Aesculin
  Artelin
  Cichoriin
  Esculetin
  Esculin
  Isoscopoletin
  Methylaesculin[a]
  Methylesculin[a]
  Scoparon
  Scoparone
  Scopoletin
  Skimmin
  Umbelliferone
Flavonoids
  Apigenin-7-0-glucoside
  Axillarin
  Cupafolin
  Eupafolin
  Kaempferol
  Luteolin
  Luteolin-7-glucoside
  Penduletin
  Quercetagetin
  Quercetin

[a] Question as to whether these compounds are different or difference in spelling for the same compound.

interactions, but the term was derived from the Greek words allelon (each other) and pathos (to suffer) and should mean injurious effects of one on another (Friedman 1995; Kelsey and Everett 1995). Many plant-derived chemicals phytochemicals stimulate plant growth and development at low levels, but are inhibitors at high levels (Friedman 1995; Kelsey and Everett 1995). As with Kelsey and Everett (1995), I will restrict the term allelopathy in this presentation to inhibitory effects.

The reader needs a clear understanding of the difference between allelopathic relationships among plants living together, and competitive relationships. Kelsey and Everett (1995, p.481) explain the difference:

> When two or more species live together they may interfere with each other. This interference can have positive, negative, or neutral effect on the fitness of each species. Competition occurs when there is a limited resource, or resources, in an environment where species are interacting. The result is negative interference because the interacting species will be less successful in the presence of a competitor than they would have been if growing alone in the limiting environment.
>
> Allelopathy differs from competition in its mode of action and its effect on species interactions. Allelopathy functions through the addition of phytochemicals to the environment by one of the interacting species, thereby resulting in the inhibition of its neighbor sharing the habitat simultaneously or sequentially (Fuerst and Putnam 1983). In this situation, the fitness of the phytochemical donor species remains unchanged relative to its growth alone, whereas the recipient species, suffering from growth inhibition, will be less successful because of the reduced fitness or negative interference.

Most allelopathy research has been conducted under controlled or semicontrolled environments of the laboratory or greenhouse (Friedman 1995). To determine the allelopathic effects of a plant, germinating seeds are exposed to whole plant, specific plant parts (seeds, shoots, roots, and so forth), plant extracts, or to a specific phytochemical produced by the "aggressive" species (Friedman 1995). Plant species showing an allelopathic reaction under laboratory (Rychert and Skujins 1974) or greenhouse environments to phytochemicals (terpenoids, phenolics) of big sagebrush are listed in table 4.12. Not included in the listing are blue-green algae-lichen crusts (Rychert and Skujins 1974).

Rychert and Skujins (1974), using laboratory techniques, found that aqueous extracts from big sagebrush leaves inhibit nitrogen fixation or acetylene reduction of the blue-green algae (now called cyanobacteria) lichen crusts, thus providing evidence of possibly allelopathic effects. Kelsey and Everett (1995) suggest that litter of big sagebrush may have the same inhibitory effects.

Yet five reports claim that soil nitrogen levels under big sagebrush plants are higher than in the interspace between plants (Charley 1977; Charley and West 1975, 1977; Fairchild and Brotherson 1980; Wikeem and Pitt 1982). Charley and West (1977) reported total and nitrate nitrogen levels under big sagebrush canopy to be significantly higher—almost twice that of the interspaces. If the secondary metabolites of big sagebrush are inhibiting nitrogen fixation, how does one explain the results of these five studies? Perhaps Kelsey and Everett (1995, p. 482) offer a clue: "Because of the experimental difficulties and the complexity of biotic and abiotic factors influencing natural interactions, not all ecologists and biologists are convinced that allelopathy is a significant ecological phenomena in natural environments." Inderjit and Weston (2000) agree.

Hoffman and Hazlett (1977, p. 137) observed: "In our experiments the germination of *Parietaria pensylvanica*, *Euphorbia podperae*, *Hedeoma hispida*, and *Achillea millefolium* was inhibited by litter extracts of *Artemisia tridentata*. Yet, in the field, these same species are most abundant directly under or very near *A. tridentata* shrubs." Further Hoffman and Hazlett (1977, p. 137) stated: "It is important to point out that most plant-plant interactions are not simple one factor interactions. A plant is influenced by a multiplicity of environmental factors." Krannitz and Caldwell (1995, p. 166), studying root growth responses of two grass species when their roots came into contact with mountain big sagebrush roots, observed: "Contrary to expectations, when roots of any test species contacted, or were in the vicinity of, *Artemisia* roots, their growth rate was not significantly affected." This "contrary to expectations" statement demonstrates the long held belief that big sagebrush possess allelopathic powers over other range plants.

To counter this preconceived idea, I add my personal observations. In 1989, I established a big sagebrush seed increase garden at the Point of the Mountain just west of the Utah State Prison and south of Salt Lake City. For 5 years I kept this garden nearly weed free until 1994 when general weed control was no longer practiced; however, weeds under the canopy of the big sagebrush plants were removed by use of needle nose pliers. During spring of 1999, a list of species was generated that had germinated in the fall of 1998 or spring of 1999 under the canopy of established big sagebrush plants. Seedlings of species so found were: big sagebrush, cheatgrass (*Bromus tectorum*), common mallow (*Malva neglecta*), dalmatian toadflax (*Linaria genistifolia*), Kentucky bluegrass (*Poa pratensis*), needle-and-thread grass (*Stipa comata*), prickly lettuce (*Lactuca serriola*), puncturevine (*Tribulus terrestris*), rubber rabbitbrush (*Chrysothamnus nauseosus*), red root pigweed (*Amaranthus retroflexus*), Russian thistle (*Salsola pestifer*), rye (*Secale cereale*), tumble mustard (*Sisymbrium altissimum*), flixweed (*Descurainia sophis*), western

Table 4.12—Species showing allelopathic effects under laboratory or green house conditions to big sagebrush chemicals (Groves and Anderson 1981; Hoffman and Hazlett 1977; Kelsey and others 1978; Klarich and Weaver 1973; McCahon and others 1973; Reid and others 1963; Schlatterer and Tisdale 1969; Weaver and Klarich 1977; Wilkie and Reid 1964).

Common name	Scientific name
Alfalfa	*Medicago sativa*
Barley	*Hordeum vulgare*
Bean	*Phaseolus vulgaris*
Bottlebrush squirreltail grass	*Sitanion hystrix*
Bluebunch wheatgrass	*Agropyron spicatum*
Canada bluegrass	*Poa compressa*
Creeping juniper	*Juniperus horizontalis*
Crested wheatgrass	*Agropyron desertorum*
Corn	*Zea mays*
Cucumber	*Cucumis sativus*
Douglas-fir	*Pseudotsuga menziesii*
—	*Echinacea pallida*
Englemann spruce	*Picea engelmannii*
—	*Euphorbia podperae*
Fairway wheatgrass	*Agropyron cristatum*
Field pennycress	*Thlaspi arvense*
—	*Hedeoma hispida*
Giant wild rye	*Elymus cinereus*
Idaho fescue	*Festuca idahoensis*
Indian ricegrass	*Oryzopsis hymenoides*
Ironplant goldenweed	*Haplopappus spinulosus*
Limber pine	*Pinus flexilis*
Lodgepole pine	*Pinus contorta*
Mountain big sagebrush	*Artemisia tridentata* spp. *vaseyana*
Pennsylvania pellitory	*Parieteria pennsylvanica*
Ponderosa pine	*Pinus ponderosa*
Prairie sandgrass	*Calamovilfa longifolia*
Oat	*Avena sativa*
Radish	*Raphanus sativus*
Rocky Mountain juniper	*Juniperus scopulorum*
Rubber rabbitbrush	*Chrysothamnus nauseosus*
Slender wheatgrass	*Agropyron trachycaulum*
Silver sage	*Artemisia cana*
Smooth brome	*Bromus inermis*
Subalpine fir	*Abies lasiocarpa*
Sunflower	*Helianthus annuus*
Thickspike wheatgrass	*Agropyron dasystachyum*
Thurber needlegrass	*Stipa thurberiana*
Western yarrow	*Achillea millefolium*
Western wheatgrass	*Agropyron smithii*
Wheat	*Triticum aestivum*
White spruce	*Picea glauca*
Wooly plantain	*Plantago patagonica*

salsify (*Tragopogon dubius*), and yellow sweetclover (*Melilotus officinalis*). All these species had germinated under the canopy of 9-year-old big sagebrush plants whose litter had not been disturbed for at least 4 years. These personal observations do not support the contention that big sagebrush is an agent of allelopathy.

In 1990, I established a garden of mixed species at the Point of the Mountain. Species planted were antelope bitterbrush (*Purshia tridentata*), black sagebrush, big sagebrush, firecracker penstemon (*Penstemon eatonii*), Gambel oak (*Quercus gambelii*), Indian ricegrass (*Oryzopsis hymenoides*), scarlet globemallow (*Sphaeralcea coccinea*), and rubber rabbitbrush. This garden was also kept weed free by means of a hoe, except under the developing canopy of the big sagebrush plants. Here weed control was achieved by hand pulling small weed plants with needle nose pliers, thus minimizing disturbance to the buildup of litter under the big sagebrush plants. At the beginning of the 10th growing season a list of plant species that had germinated under the big sagebrush canopy during the spring of 1999 was made. Species found included those listed for the 1989 garden, but additional species were found: firecracker penstemon, desert paintbrush (*Castilleja chromosa*), and Indian ricegrass (fig. 4.1). Again, these personal observations do not support the contention that big sagebrush is an agent of allelopathy.

In addition to these garden observations, I have found in the field the seedlings of bigtooth maple (*Acer grandidentatum*), box elder (*Acer negundo*), singleleaf pinyon pine (*Pinus monophylla*), and Utah juniper (*Juniperus osteosperma*) growing under the canopy of mature big sagebrush plants.

Diettert (1938, p. 5) observed: “Not only is [big sagebrush] of direct value as a forage crop but in many places it provides shelter for tender and perhaps more useful plants.” Drivas and Everett (1987, 1988), Callaway and others (1996), and Chambers (2001) describe the use of big sagebrush as nurse plants for singleaf pinyon (*Pinus monophylla*) seedlings, Patten (1969) for lodgepole pine (*Pinus contorta*), and Schultz and others (1996) for curlleaf mountain mahogany (*Cercocarpus ledifolius*). Also in the field, I have noticed at various locations that the only grasses and forbs present on a site were to be found under the canopy of big sagebrush plants (also see Weaver and Albertson 1956). Figure 4.2 illustrates this point. This photograph was taken at the Benmore Experimental Range just south of Vernon, UT, where pastures of crested wheatgrass were established to determine how much grazing pressure the grass could tolerate. The increase in bare ground in the picture was due to grazing, not to increasing big sagebrush canopy as hypothesized by Baxter (1996).

Blaisdell (1953, p. 1) observed: “Even when livestock force their way into heavy [big] sagebrush stands, they are often unable to reach more than half of the palatable grasses and forbs.” In other words, big sagebrush canopy form a protective barrier (Costello 1944; Weaver and Albertson 1956). How then, can big sagebrush be both a protector of grasses and forbs and an agent of allelopathy?

Daubenmire (1975, p. 31) states: “Field observations in Washington indicate that not only is there no allelopathic influence from the species of *Artemisia*, but that it has a beneficial effect on other plants.” Wight and others (1992) describe a “beneficial effect on other plants” as being in the area of water conservation (Chambers 2001) and extending water near the soil surface by 2 weeks versus interspaces between plants. They noted that big sagebrush canopies reduce

Figure 4.1—Four plant species (firecracker penstemon, *Penstemon eatonii*; Indian ricegrass, *Oryzopsis hymenoides*; common mallow, *Malva neglecta;* tumble mustard, *Sisymbrium altissimun*) germinated under the litter and canopy of a mature big sagebrush (*Artemisia tridentata*) plant (photo by Bruce L. Welch).

Figure 4.2—A site where the only grass present is under the protective canopy of mature big sagebrush (*Artemisia tridentata*) plants (photo by Bruce L. Welch).

solar radiation and prolong the period favorable for seedling establishment for perhaps as long as 28 days (also see Chambers 2001; Pierson and Wight 1991; for favorable soil temperatures under big sagebrush).

Hazlett and Hoffman (1975) studied the pattern of plant species placement in relation to big sagebrush distribution in western North Dakota. Their study site was dominated by big sagebrush, which had a cover value of 29 percent. They counted the number of established plants found in three concentric zones under and beyond the individual big sagebrush plant canopies. The number of established plants in the inner zone (zone 1), which is directly beneath the canopies, greatly exceeded the number of plants (most forbs—18 species) of the two outer most zones (3,145 for zone 1; 1,845 for zone 2; and 325 plants for zone 3). However, they felt that grass cover was greater in the outer zone. Eckeret and others (1986) reported similar results.

Even experts such as Kelsey and Everett (1995, p. 518) have questions: “Can volatile terpenes adsorbed on soil particles the previous summer and fall, or leached during the winter, remain at toxic levels until spring germination? Does sagebrush litter, in spring, have sufficient concentrations of toxins to interfere with growth? What happens to the large quantities of sesquiterpene lactones in the foliage of sagebrush? Are they ever inhibitory?” Evidence suggests that allelopathy of big sagebrush is more myth than fact (Caldwell 1979; Daubenmire 1975; Peterson 1995).

Issue of Bare Ground Cover and Grass Cover

There is an untested hypothesis that states: the surface roots of big sagebrush roots in the interspaces among big sagebrush plants have the capacity to capture water and nutrients to the point that they starve out associated herbaceous plant species. Because of this untested hypothesis and the alleged allelopathic properties of big sagebrush, some workers claim that when big sagebrush canopy cover exceeds 15 percent (12 to 20 percent), bare ground cover will increase while grass production and/or cover will decrease (Baxter 1996; Winward 1991). Let us examine this issue.

Big Sagebrush Cover Versus Bare Ground Cover

The relationship between big sagebrush canopy cover and the percent of bare ground can be seen in table 4.13. Data in this table were collected during the 1998 Utah big game range trend studies and published by the Utah Department of Natural Resources, Division of Wildlife Resources (Davis and others 1999). I chose only those study sites where big sagebrush canopy cover exceeded all other shrub species present on the sites. Subspecies of big sagebrush present on a given site is listed in the table. Percent of big sagebrush canopy cover ranged from 3 to 24 percent. In 12 of the 26 sites selected, cover exceeded the recommended limits set by Baxter (1996). Correlation coefficient for this data set was $r = -0.2592$, and coefficient of determination was $R^2 = 0.07$. Neither value is significant. Calculating r and R^2 for the 12 sites where big sagebrush canopy cover was 15 percent or greater, r was + 0.02 with $R^2 = 0.0003$; or, in other words, there is no significant relationship between big sagebrush canopy cover and bare ground. Other studies present data containing big sagebrush canopy cover and bare ground, which show the relationship between these two variables to be nonexistent or extremely weak (Burke and others 1989; Richardson and others 1986; Tiedeman and others 1987).

On extended field trips in 2000 and 2001, I collected data concerning the relationship of big sagebrush canopy cover and perennial grass and bare soil cover in the States of Idaho, Oregon, Washington, and Wyoming (Welch and Criddle 2003). This data set is shown in table 4.14. I use the 300-foot line intercept method for determining percent of cover for big sagebrush, perennial grass, and bare soil. The relationship between big sagebrush cover and bare soil was significant but weakly related in the negative direction, $r = -0.5045$; $r^2 = 0.2546$. The negative relationship means

Table 4.13—Relation of percent of big sagebrush cover to percentage of bare ground on 26 Utah big game range trends study sites (data and pages are from Davis and others 1999).

Pages	Subspecies[a]	Percent big sagebrush cover	Percent of bare ground
7–8	M	16	8
50–51	M	19	12
62–63	W	18	22
71–72	M	4	10
79–80	W	11	7
87–88	W	17	14
96–97	W	14	18
113–114	W	15	12
119-120	M	15	21
128–129	M	24	6
137–138	W	3	29
143–144	W	16	13
152–153	W	9	18
167–168	W	9	8
177–178	W	7	44
187–188	W	12	33
193–194	W	13	21
249–250	M	15	7
263–264	M	9	19
274–275	W	12	18
294–295	M	14	4
313–314	W	14	20
335–336	M	20	29
371–372	W	9	13
379–380	W	17	4
386–387	W	18	20

[a] M = mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*); W = Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*).

that as big sagebrush cover increases, bare soil would tend to decrease. Other factors, such as precipitation, grazing history, soil properties, and community species composition have a greater influence on the amount of bare soil than does big sagebrush canopy cover (Daddy and others 1988; Richardson and others 1986).

Branson and Miller (1981), studying the vegetative changes over 17 years in the Willow Creek basin near Glasgow, MT, found that in spite of a significant increase in big sagebrush canopy cover (23 to 30 percent), bare soil decreased significantly (from 40 to 30 percent). They attributed these increases to higher precipitation and better grazing management. Mueggler and Stewart (1980) reported that four big sagebrush habitat types had big sagebrush canopy cover of 18,, 22, 21, and 24 percent, and bare soil cover of 11, 4, 3, and 1 percent, respectively. These bare soil cover values compare to grass habitat types of 24, 9, 14, 7, 18, 9, 12, 12, 5, 5, 1, 1 percent, and so forth (Mueggler and Stewart 1980). Also, Mueggler and Harris (1969) found that bare soil in grasslands of central Idaho varied from 1 to 52 percent with grass communities dominated by bluebunch wheatgrass (*Agropyron spicatum*) having greater percentages (22 percent) of bare soils than communities dominated by Idaho fescue (*Festuca idahoensis*) (6 percent) (see Fosberg and Hironaka 1964; Mueggler and Stewart 1980; Tueller and Eckert 1987 for more data). In addition, Lusby (1970, p. 258), studying grazed and ungrazed watersheds, found "marked increase in bare ground soil and rock on all grazed watersheds, accompanied by a decrease in shrub overstory." Factors other than big sagebrush canopy cover are involved in determining the amount of bare soil in a given area such as: precipitation, associated or understory species, grazing history, and soil properties (Welch and Criddle 2003).

I have, on a number of occasions, found sites in Utah, Idaho, Wyoming, Oregon, Nevada, Colorado, and Washington where big sagebrush cover has exceeded

Table 4.14—Relation of big sagebrush cover to percent cover of perennial grass and bare ground based on Welch’s Y2K and Y2K+1 big sagebrush odyssey through the States of Idaho, Oregon, Utah, Washington, and Wyoming. Data on file at the Shrub Sciences Laboratory, 735 N 500 E, Provo, UT. Data were based on 300-foot line transects. Data for the first 12 transects were collected on ungrazed kipukas in southern Idaho. The three transects per kipuka were continuous.

Location and transect	Big sagebrush cover	Perennial grass cover	Bare ground
N43° 31.346'			
W112° 28.475' —1	14	56	11
Same —2	16	31	17
Same —3	23	43	12
N43° 19.306'			
W113° 38.257' —4	34	58	11
Same —5	30	58	14
Same —6	26	43	21
N42° 52.776'			
W113° 08.665' —7	28	41	5
Same —8	14	29	3
Same —9	23	31	4
N42° 52.478'			
W113° 07.547'—10	20	45	2
Same —11	24	42	1
Same —12	31	45	2
N43° 26.159'			
W112° 46.013'—13	0	43	41
Same —14	20	38	21
N43° 28.815'			
W112° 5.296' —15	0	44	44
N42° 36.726'			
W113° 14.964'—16	8	10	1
N42° 31.036'			
W113° 19.869'—17	5	51	6
N42° 18.861'			
W115° 49.612'—18	21	16	38
N42° 2.963'			
W115° 51.353'—19	26	33	11
N43° 19.778'			
W116° 57.576'—20	19	47	1
N43° 19.716'			
W116° 57.414'—21	3	20	21
N42° 54.357’N			
W117° 16.888'—22	14	31	37
N42° 54.424'			
W117° 17.027'—23	13	54	19
?N			
?W —24	31	12	41
N42° 52.202'			
W117° 57.389'—25	28	5	2
N43° 11.557'			
W118° 21.096’WW—26	41	38	5
N41° 46.191'			
W111° 09.274'—27	41	71	4
N41° 53.901'			
W109° 21.165—28	22	42	15
N43° 12.303'[a]			
W107° 55.298'—29	24	31	20
N43°12.303'[a]			
W107° 55.298'—30	5	46	24
N44° 07.187'			
W107° 15.592'—31	38	67	3
N44° 08.807'			
W107° 11.830'—32	50	59	.4
N42° 25.887'[b]			
W111° 08.002—33	29	72	3

[a] Both line transects share the same starting point. Transect 29 was from south to north, whereas, transect 30 was from north to south.

[b] Based on a 1500-foot transect moving to the southeast; forb cover was also determined at 28 percent.

the recommended cover of 15 percent (12 to 20 percent; Baxter 1996; Winward 1991) and noted lush growth of grasses and forbs. Figures 4.3 and 4.4 illustrate such a site. On this site in Utah, the mountain big sagebrush cover was 32 percent, and the mountain big sagebrush plants were about 42 years of age with just 5 percent bare ground and a well-developed understory of grasses and forbs.

Big Sagebrush Cover Versus Perennial Grass Cover

Daubenmire (1970, p.13) describes the lack of a relationship between big sagebrush coverage and the coverage of perennial grasses:

> One might question whether the stands with more *Artemisia* also have less of the perennial forage grasses and more of the annuals favored by grazing...But when the stands are listed in order of the coverage of *Artemisia*..., there is neither positive correlation with the grazing increasers, nor negative correlation with the preferred forage species.

R^2 and r values for his table 3 were 0.0004 and 0.0208, respectively; or in other words, no relationship existed between big sagebrush canopy cover and perennial native grass cover (also see Baker and Kennedy 1985; Doescher and others 1986; Richardson and others 1986).

Calculated r and R^2 values between big sagebrush canopy cover and perennial grass cover for my data set in table 4.14 were not significant at +0.2130 and 0.0454, respectively. Mean big sagebrush canopy cover for this data set was 21.8 percent (range 0 to 50 percent) and for perennial grass cover 41.0 percent (range 5 to 72 percent). Highest perennial grass cover values were found in big sagebrush stands having above average canopy cover of 29 percent (transect 33-grass cover = 72 percent), 41 percent (transect 27-grass cover = 71 percent), and 38 percent (transect 31-grass cover = 67 percent). This data set does not support the contention that big sagebrush canopy cover above 15 percent decreases perennial grass cover (Welch and Criddle 2003).

Tart's (1996) report contained 29 data sets, his plant community composition, comparing mountain big sagebrush canopy cover with perennial grass and forb cover. These comparisons are listed in table 4.15 along with means, standard deviations, range, correlation coefficients, and coefficients of determination. Lowess statistical analysis was also performed on this data set (Chamber 1983). Results from both statistical procedures were in agreement. A quick glance through table 4.15 clearly shows no relationship between mountain big sagebrush canopy cover and perennial grass cover and between mountain big sagebrush canopy cover and perennial forb cover. Mean canopy of mountain big sagebrush was 28.03 percent, which is well above

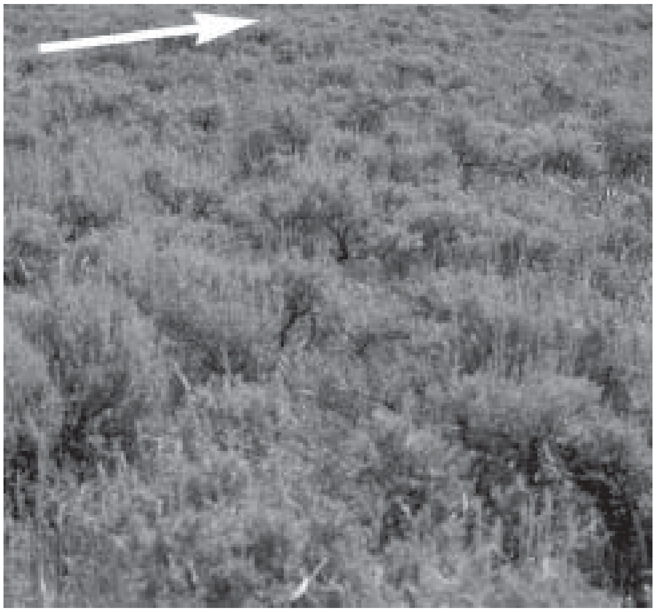

Figure 4.3—General view of an area having an abundance of grasses and forbs in spite of a 32 percent canopy cover of big sagebrush. Bare ground was 5 percent. The arrow points to an orange tagged mature big sagebrush plant that was cut down to provide a close-up view of the area that is presented in figure 4.4 (photo by Bruce L. Welch).

Figure 4.4—See figure 4.3 caption (photo by Bruce L. Welch).

Table 4.15—Relationship of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) canopy cover to perennial grass cover and perennial forb cover and to number of grass and forb species and to total number of plant species. Data and page numbers refer to Tart (1996). His plant communities tables.

Page number	Mountain sagebrush cover (%)	Grass cover (%)[a]	Forbs cover (%)[b]	Total number of plant species[c]
26	21	52 (11)[a]	17 (18)[b]	44[c]
	26	43 (10)	13 (18)	42
	17	38 (10)	22 (18)	44
31	21	48 (11)	27 (25)	45
	24	47 (11)	31 (25)	46
	23	36 (11)	35 (26)	47
37	30	55 (13)	20 (16)	35
	31	51 (9)	24 (18)	33
	22	22 (10)	19 (19)	36
42	31	61 (10)	25 (24)	46
	46	58 (10)	35 (25)	46
	34	40 (10)	33 (25)	47
47	22	79 (13)	27 (19)	39
	34	69 (16)	46 (19)	43
	17	41 (16)	47 (19)	43
52	27	67 (11)	22 (16)	33
	24	54 (11)	22 (13)	36
57	29	63 (14)	26 (19)	44
	30	49 (12)	34 (21)	43
	30	72 (14)	40 (21)	47
62	28	53 (9)	48 (19)	33
	31	57 (11)	79 (23)	39
	30	52 (11)	60 (23)	41
67	37	55 (8)	11 (17)	29
	34	53 (14)	29 (19)	40
	30	40 (12)	31 (21)	39
72	30	70 (9)	58 (21)	38
	26	40 (8)	67 (21)	36
	26	30 (8)	41 (16)	29
Mean	27.97	51.59	34.10	
S. D.	±6.15	±13.02	±16.32	
Range	17-46	22-79	11-79	

[a] Number of grass species.
[b] Number of forb species.
[c] Number of total plants species.
r = 0.3289; R^2 = 0.1082 (mountain big sagebrush canopy cover versus perennial grass cover) not significant.
r = 0.1092; R^2 = 0.0119 (mountain big sagebrush canopy cover versus perennial forbs cover) not significant.
r = –0.0966; R^2 = 0.0093 (mountain big sagebrush canopy cover versus number of grass species) not significant.
r = 0.1933; R^2 = 0.0374 (mountain big sagebrush canopy cover versus number of forb species) not significant.
r = –0.0738; R^2 = 0.0054 (mountain big sagebrush canopy cover versus total number of plant species) not significant.

the 12 to 15 percent limits set by Baxter (1996) or 12 to 20 percent limits set by Winward (1991). Mean cover of perennial grass was at 51.59 percent, and cover of perennial forbs was at 34.10 percent. These values demonstrate that on 26 of these sites there was an abundance of big sagebrush (20 percent or more), perennial grass (50 percent or more), and perennial forbs (15 percent or more).

Tart's (1996) data showed that plant communities of mountain big sagebrush with the highest canopy cover at 46 percent had grass and forb cover above the study averages; conversely, plant communities of mountain big sagebrush with the lowest canopy cover at 17 percent had below average grass and forb cover. This report does not support the contention that mountain big sagebrush canopy cover above 20 percent suppresses grass and forbs species cover or species numbers.

In addition, statistical analyses (both correlation and lowess analyses) conducted on Tart's (1996) seral stages data, found that total shrub canopy cover (dominated by big sagebrush) was positive but weakly related to graminoids cover; meaning as total shrub canopy cover increased, graminoids cover tended to increase too (table 4.16). Total shrub canopy cover (dominated by big sagebrush) was not significantly related to forb cover (table 4.16). A significant negative relationship was detected between total shrub canopy cover (dominated by big sagebrush) and bare soil; meaning as total shrub canopy cover increased, the amount of bare soil tended to decrease (table 4.16). The two data sets from Tart (1996; tables 4.15, 4.16) do not support his often repeated statement (Tart 1996, p. 27, 32, 38, 43, 48, 58, 63, 69, 73): "If sagebrush canopy cover exceeds 20 percent for a long period of time, the density, cover, and biomass of herbaceous

Table 4.16—Relationship of total shrub canopy cover to cover of graminoids[a], forbs[b], and bare soil[c]. Big sagebrush (*Artemisia tridentata*) was the dominant shrub for all plant associations described. Data obtained from the reort of Tart (1996), his seral stages.

Page number	Total shrub (%)	Total graminoids cover (%)	Total forbs cover (%)	Bare soil
25	29	37	12	13
	33	28	8	18
	20	26	16	16
32	28	41	16	8
	23	33	14	16
	21	14	17	22
36	38	45	17	9
	35	35	14	14
	17	20	15	25
43	29	53	16	7
	30	44	25	7
	26	25	18	21
46	31	48	23	7
	40	43	32	8
	25	22	29	17
51	27	57	17	10
	25	53	18	3
58	29	53	18	6
	30	40	24	5
	26	37	22	13
63	28	48	33	6
	32	44	41	13
	29	37	39	6
68	45	50	10	1
	26	43	18	11
	30	29	23	9
73	25	57	30	7
	26	39	35	9
	26	32	25	8
	—	—	—	—
Mean	28.6	39.1	21.6	10.9
S.D.	±5.81	±11.36	±8.52	±5.83
Range	17-45	14-57	8-41	1-25

[a] $r = +0.4404$; $R^2 = 0.1940$ (total shrub canopy cover-dominated by big sagebrush versus graminoids cover) weakly related in a positive direction; meaning as total shrub canopy cover increased, graminoids cover also increased.

[b] $r = –0.0257$; $R^2 = 0.0007$ (total shrub canopy cover-dominated by big sagebrush versus forb cover) ns.

[c] $r = –0.5445$; $R^2 = 0.2964$ (total shrub canopy cover-dominated by big sagebrush versus bare soil) significantly related in a negative direction; meaning as total shrub canopy cover increased, bare soil decreased.

species will be reduced through shading and competition for moisture." One possible explanation could be the positive effect of canopy shading on soil moisture.

Pearson (1965), studying vegetative production in grazed and ungrazed plant communities, found that big sagebrush canopy cover in the ungrazed area was 34 percent and perennial grasses 41 percent, compared to 11 percent big sagebrush cover in the grazed area with 22 percent perennial grass cover. Similarly, Anderson and Holte (1981) reported that, for an area in southeastern Idaho protected from grazing for 25 years, Wyoming big sagebrush canopy cover increased from 15 to 22 percent with an increase in grass cover from 0.28 to 5.6 percent. This work has been extended to more than 45 years by Anderson and Inouye (2001) who found that the maximum canopy cover of Wyoming big sagebrush (20 percent) and maximum cover of perennial grasses (6.2 percent) occurred in 1975 (their figure 4), and both have declined from these maxima. McLean and Tisdale (1972) found that from 1959 to 1968 in their West Mara exclosure that cover of perennial grasses increased in spite of a constant big sagebrush canopy cover at 31 to 34 percent. This was also true for the grazed area next to the exclosure. Another interesting data set comes from the study of Doescher and others (1984) where they selected two types of sites—those having high big sagebrush canopy cover and low grass cover, and those having low big sagebrush canopy cover and high grass cover. The calculated r and R^2 values were not significant, but what was most interesting is that for both types of sites, the study plot with the greatest big sagebrush canopy cover for either site type also contained the greatest grass cover for that site type (26.0 versus 8.2 percent, and 20 versus 27.5 percent). Smith (1969) reported a big sagebrush canopy cover at his Soldier Creek site of 24 percent, but it produced 750 pounds per acre of grass versus his Buck Creek site of 14 percent big sagebrush canopy cover that produced only 230 pounds per acre of grass. West and York (2002; their fig. 3 and 4) found that burned and ungrazed exclosures contained higher cover of perennial grasses than burned grazed macroplots 17 out of 19 years. Unburned and grazed (their fig. 5) macroplots had cover of perennial grasses greater than burned grazed macroplots 10 out of 19 years. Yorks and others (1992, p. 569) reported increasing big sagebrush canopy cover and increasing grass cover together over 56 years and noted, "Some of the observed shifts of dominance/diversity are contrary to widely accepted expectations in the literature."

Wambolt and others (2001) studying the recovery rate of big sagebrush after burning give 26 data points concerning big sagebrush cover and perennial grass cover in their tables 2 and 5. Big sagebrush cover ranged from 0.00 to 28.3 percent and grass cover ranged from 16.3 to 61.7 percent. Correlation coefficient (r) and coefficient of determination (R^2) were not significant. Determining r and R^2 for big sagebrush stands having higher than 15 percent cover with grass cover yielded nonsignificant values. Wambolt and others (2001, p. 243) concluded: "Managers considering prescribed burning of big sagebrush communities should be aware that herbaceous plant responses may be minimal while shrub values will likely be lost for many years. The loss of the dominant shrubs in any ecosystem will affect many other organisms and severely impact species that have an obligate habit with the shrubs." Branson and Miller (1981) studying the vegetative changes over 17 years in the Willow Creek basin near Glasgow, MT, found that in spite of a significant increase in big sagebrush canopy cover (23 to 30 percent), grass cover also increased significantly (3 to 41 percent). Peterson (1995, p. 12) has reported similar observations in Montana and concluded, "In fact, well-developed grass and forb understories are commonly associated with big sagebrush stands on ranges that have proper grazing management practices."

Nitrogen Metabolism

For higher plants, such as big sagebrush, nitrogen is the fourth most abundant nutrient element in dry matter. For big sagebrush, the leaves contain 58 percent of the nitrogen in aboveground parts with 1-year-old shoots containing 10 percent and old stems 32 percent, so the leaves are the main source of nitrogen (Bilbrough and Richards 1993). Nitrogen is an important structural component of many primary and secondary compounds such as proteins, nucleic acids, hormones, chlorophyll, alkaloids, polyamines, and so forth. Nitrogen appears in several inorganic forms in nature including gaseous (N_2), nitrite (NO_2^-), nitrate (NO_3^-), ammonia (NH_3), and nitrogen oxides (NO and N_2O). The most abundant form is gaseous nitrogen in the atmosphere, but higher plants such as big sagebrush are unable to convert gaseous nitrogen into a physiologically useable form. Big sagebrush must depend on prokaryotic organisms, living in the soil, to convert atmospheric nitrogen into useful forms of nitrogen (nitrates and ammonia). These are then absorbed from the soil, but the supply is limited. Plants not only compete among themselves for limited supplies of nitrates and ammonia but are also pitted against soil microorganisms. Thus, in arid and semiarid settings, soil nitrogen availability is second only to soil moisture availability as a limiting factor for plant growth (James and Jurinak 1978; O'Brien 1978; Wallace and others 1978; West and Klemmedson 1978).

For big sagebrush, as well as other dominant arid and semiarid shrub species, nitrogen accumulates toward the soil surface and under the shrub canopy, resulting in “islands of fertility” across the landscape (Chambers 2001; Charley and West 1975, 1977; Doescher and others 1984; Fairchild and Brotherson 1980; Halvorson and others 1994; Wikeem and Pitt 1982). Charley and West (1975), reporting on a percent of dry-weight basis, noted that total nitrogen content of surface soil under big sagebrush plants was 0.233 percent compared to interspace content of 0.151 percent. It was suggested that concentrating of nitrogen under big sagebrush canopy was closely related to the decline of nitrogen levels in the interspaces. Charley and West (1975) suggested that three factors may be operating in concert to account for the accumulation: first, enhanced fixation by free-living microorganisms in or under litter; second, animal activity; and third, canopy capture of wind-transported solids. Further, they reported that nitrogen levels were significantly higher under big sagebrush canopy than under grass (*Agropyron desertorum*) and other shrub communities.

Charley and West (1977, p. 357), studying nitrogen mineralization activity of surface soil under big sagebrush canopies and interspaces, found “mineralization of N proceeded at a greater rate in soils beneath shrub canopies than in soils from interspace areas between shrubs.” They concluded that this mineralization process increased nitrogen availability and in turn “water-use efficiency of the vegetation.” In addition, Charley and West (1977) reported total nitrogen under big sagebrush canopy cover exceeded that in interspace by a factor of 1.85 (296 versus 160 *u*g $g^{-1)}$ and that this value was among the highest for the eight communities studied. Fairchild and Brotherson (1980) found that nitrogen levels under big sagebrush canopy were greater by a factor of 1.67 than levels between big sagebrush plants (559.6 versus 335.0 parts per million). Not only were nitrogen levels higher under big sagebrush canopies but the soils were significantly deeper under canopies than in areas between big sagebrush plants (45.2 versus 37.8 cm). Studies conducted in British Columbia by Wikeem and Pitt (1982), in Oregon by Doescher and others (1984), and in Wyoming by Burke (1989) further support the findings of the previous studies cited in this section.

A few studies have been conducted to measure the response of big sagebrush to supplemental nitrogen fertilization. Results varied among studies. Greenhouse studies conducted by Wallace and others (1978) showed that big sagebrush plants respond to nitrogen fertilizer by increases in both dry matter production and nitrogen foliage content. Toft and others (1989), using field plants, found that additional nitrogen increased the photosynthetic rate of Wyoming big sagebrush plants. Miller and others (1991b), studying the effects of nitrogen amendments on a Wyoming big sagebrush site, found that additional nitrogen increased biomass production of Wyoming big sagebrush. Elderkin and others (1986), studying effects of nitrogen/phosphorus fertilization and irrigation on big sagebrush, found that irrigated-fertilized plants were significantly more productive, preferred by wintering mule deer, and contained higher levels of crude protein, phosphorus, and monoterpenoids than irrigated and control plants. Elderkin and others (1986, p. 144) stated: “Overall, our investigation indicated that big sagebrush was a good winter deer browse and that production, utilization, and nutritive value could be enhanced by irrigation and the addition of a nitrogen-phosphorus fertilizer.” Bayoumi and Smith (1976) found that spring applications of nitrogen significantly increased the percent of crude protein in forage of big sagebrush and that nitrogen-fertilized plants were used more heavily by elk than unfertilized plants. Doescher and others (1990) observed that both nitrate and ammonium treatments significantly increased leaf nitrogen content, mean maximum length of ephemeral leaves, number of ephemeral leaves per terminal shoot, and current year’s vegetative stem length of big sagebrush plants over control plants. Doescher and others (1990, p. 9) concluded: “This study suggests *A. tridentata* ssp. *wyomingensis* would opportunistically take advantage of increased availability of soil nitrogen. The ability of this species to respond positively to increased soil nitrogen may enhance its competitiveness over associated perennial species.” However, Booth and others (1990) discovered that, in a nonlimiting environment, both top growth and growth rate of Wyoming big sagebrush are under genetic control that appears to be size limiting. In contrast to previous reports, Carpenter and West (1987) noted no response of mountain big sagebrush to small annual additions of nitrogen fertilizer. Sneva (1978) noted that nitrogen and sulfur fertilizers increase big sagebrush establishment in wet years but not for dry years.

BassiriRad and Caldwell (1992) conducted a study to determine how drought and recovery from drought affects nitrate uptake in big sagebrush. Drought conditions were created in greenhouse-reared big sagebrush seedlings by reducing water allotments to one-third of the well-watered seedlings (controls). This water deprivation lasted for 24 days after which the water-stressed seedlings received the full water allotment of the well-water seedlings. Uptake of nitrate in water-deprived plants was reduced by 40 percent, and this reduction lasted 4 days after receiving full water allotment, but after 4 days nitrate uptake of previously stressed plants was equal to the well-watered seedlings. They found that water deprivation changed the distribution patterns of newly acquired nitrates. Water-stressed seedlings allocated a greater proportion of newly acquired nitrates to the roots than the well-watered plants (also see Dina and others 1973). This continued 4 days after receiving full water allotment. After 14 days, the allocated pattern of nitrate was the same for the two groups of seedlings. Based on root relative growth rate of water-stressed seedlings (rate was one-fourth of control during drought and three times greater than control, 4 days after the drought), lack of osmotic adjustment, a loss of turgor, and equal rate of nitrate uptake after drought, BassiriRad and Caldwell (1992, p. 493) concluded: "The pattern of NO_3^- uptake upon rewatering was apparently more closely associated with root uptake capacity" than root growth. Dina and Klikoff (1973) found that water-stressed big sagebrush moved nitrogen out of leaves and into stems and roots; however, total level of nitrogen in the entire plant remained the same. These shifts are evidence of adaptation for conservation of nitrogen during periods of water stress, and the nitrogen pool stored in the stems may be shifted again to the leaves once water stress is relieved.

Phosphorus Metabolism

The primary source of phosphorus is not the atmosphere, as is the case for nitrogen, but is the Earth's crust. Weathering of rocks and decomposition by fungi and bacteria in the soil of organic phosphorus creates three forms of polyprotic phosphoric acid (H_3PO_4)—monovalent, divalent, and trivalent. The exact form of phosphoric acid that is most prevalent in a soil is dependent on soil pH. In soils having a pH of 6.8 and lower, the prevailing form of phosphorous is the monovalent orthophosphate. This anion is readily absorbed by plants' roots. The divalent form of phosphorous is most prevalent in soil having a pH between 6.8 to 7.2 and is not as readily absorbed by plant roots. For soil having a pH above 7.2 or alkaline soils, the trivalent form of phosphorous is most abundant. Unfortunately, trivalent phosphorous is unavailable to plants. In neutral pH soils, phosphorus can form complexes with aluminum and iron that render the phosphorous insoluble, while in basic soils it forms insoluble complexes with calcium and magnesium. Insoluble phosphorous is released slowly into the soil solution. Phosphorous is almost immobile in soils and plant roots, and with their associated mycorrhizae, must be within a few millimeters of phosphorous in order for uptake to occur. Phosphorous is limited in highly calcarious soils. However, mycorrhizal associations enhance the uptake of phosphorous, thus helping to supply this important nutrient in the quantity need (Hopkins 1999).

Phosphorous, as phosphate esters, plays an important role in energy transport at the photosynthesis and intermediary metabolism levels. In addition, microorganisms that are involved in nitrogen fixation require some phosphorous, and limiting supplies may interfere with nitrogen fixation. Phosphate esters are found in the structure of a number of molecules—adenosine triphosphate (ATP), adenosine diphosphate (ADP), a host of phosphorylated sugars and organic acid, nucleotide, phospholipids, several coenzymes, and many more (Hopkins 1999).

Mack (1977), studying the production of litter and mineral return to soil of big sagebrush, reported that annual return of available phosphorous was 127.2 kg/ha—this in spite of mass withdrawal of phosphorous from senescent leaves into the plant prior to leaf fall. Mack (1977, p. 196) further observed:

> Certainly the total amount of ash elements returned via *Artemisia* litter is small compared to the amounts in the soil nutrient sink. However, *Artemisia* may play an important role in the community by increasing the effective zone in the solum from which these nutrients are regularly recycled to the soil surface. This cycle is important particularly for relatively shallow-rooted associates. Such benefit should be considered in evaluating the wholesale eradication of the shrub to increase rangeland.

It appears that phosphorous accumulates under the canopy of big sagebrush similar to the accumulation of nitrogen. Fairchild and Brotherson (1980) and Chambers (2001) reported significantly higher concentrations of phosphorous under the canopy of big sagebrush than in adjacent areas. In an Oregon study, Doescher and others (1984) found higher soil surface levels of phosphorous under the canopies of big sagebrush than in interspace and grass influenced soils. Charley and West (1975) reported significantly higher levels of soil surface organic phosphorous under big sagebrush canopies than in interspaces, equal levels of bicarbonate-phosphorous at both locations, and greater amounts of total phosphorous in the interspaces than under canopies.

Because of phosphorous immobility in soil and the presence of two radio-active isotopes, ^{32}P and ^{33}P, workers have been able to design experiments to measure the competitiveness for this element of plants growing together (Black and others 1994; Caldwell and others 1985, 1991a). Caldwell and others (1985) describe a method for determining the relative competitiveness of big sagebrush, and a native grass associate, bluebunch wheatgrass (*Agropyron spicatum*), and an exotic grass from Eurasia, crested-wheatgrass (*A. desertorum*). The first stage of the experiment was to establish a garden; in this case, three species were transplanted in an evenly spaced matrix (0.5 m). Each big sagebrush plant was surrounded by four plugs of grasses, two of each grass species on opposite sides. The transplants were allowed to grow for at least 6 years to ensure thorough intermingling of root systems. Next, small holes were created by the use of steel rods halfway between the big sagebrush plants and the grass plants, and then isotopes ^{32}P and ^{33}P were injected into the 30-cm-deep holes. Using this dual-isotope technique, Caldwell and others (1985, p. 229) found that the uptakes of phosphorous between the two species of grasses were very different: “Of the total phosphorus-32 and -33 absorbed by *Artemisia*, 86 percent was from the interspace shared with *Agropyron spicatum* and only 14 percent from that shared with *Agropyron desertorum*.” They concluded that the exotic grass species was better able to compete with big sagebrush for phosphorus than the native grass (Black and others 1994; Jackson and Caldwell 1989; Jackson and others 1990). Under shading, the exotic grass species outcompeted big sagebrush for nitrogen and phosphorus (Cui and Caldwell 1997). However, the Caldwell group, in another study (Caldwell and others 1987), found that defoliating neighboring grass plants increased phosphorus uptake by big sagebrush sixfold over the uptake of unperturbed neighbors. Caldwell and others (1987, p. 616) concluded: “The rapid shift in resource acquisition demonstrated in these experiments not only indicates immediate resource competition, but also shows how quickly the balance of competition might change in the event of herbivory.” Further, they stated (p. 616): “We do not, however, feel that P is the only, nor necessarily the pivotal, resource in the competitive balance of these plants.” West and others (1984) also noted that exotic crested wheatgrass stands removed more phosphorus from the soil than native stands of big sagebrush and voiced concerns that such export could lead to long-term declines in productivity.

Van Auken and others (1992), studying the uptake of phosphorus by seedlings of big sagebrush, crested wheatgrass, and bluebunch wheatgrass grown in pots, with interspecies competition and without, found that juvenile big sagebrush plant uptake of phosphorous was four to five times greater than crested wheatgrass and seven to eight times greater than bluebunch wheatgrass. These observations again show the competitiveness of crested wheatgrass, an exotic species, to absorb phosphorus more readily than the native grass bluebunch wheatgrass.

Billings (1950) described isolated stands of Sierran conifers, mainly *Pinus ponderosa* and *P. jeffreyi*, growing in the midst of big sagebrush vegetation. The open woodland communities were growing on soils derived from hydrothermally altered andesite. For the most part, these two plant communities did not mix, and the Sierran conifer communities were growing on sites dryer than normal. When Sierran conifers and big sagebrush were grown in soil from the Sierran sites, growth of the conifers was 72 to 90 percent of the growth of plants grown in unaltered andesite—10 percent for big sagebrush (Delucia and others 1989). This retarding of growth was attributed to low phosphorus levels and lower pH values, which were more severely expressed in big sagebrush than in Sierran conifers (Delucia and others 1989; Gallardo and Schlesinger 1996; Schlesinger and others 1989).

Trace Elements

During the mid-1970s to the early 1980s, some research was conducted on trace element content of big sagebrush. This was done to determine whether or not big sagebrush could be used to monitor the level of fine particles, trace metals, and other contaminants being released by mining and electrical general operations and other activities of man. Natural variations due to season and region for trace elements have been established and baseline levels established. The reader is referred to the following publications for details: Connor and others (1976); Gough and Erdman (1980, 1983); Rickard and Garland (1983); Rickard and Van Scoyoc (1984); Severson and Gough (1976).

Photosynthesis and Carbohydrate Metabolism

Photosynthesis

In spite of the discovery of bacterial chemosynthesis-based ecosystems in dark, deep oceanic trenches, photosynthesis by green plants and other organisms is still the foundation of life on this planet. Photosynthetic organisms are able to convert light energy into chemical energy and reduce carbon dioxide into one of two organic acids, either a three-carbon acid (3-phosphoglycerate) or four-carbon acid (oxaloacetate). The first stable product of big sagebrush photosynthetic process is 3-phosphoglycerate; thus big sagebrush is classified as a C_3 plant as opposed to a C_4 plant or CAM plant.

In C_3 plants, photosynthetic reactions are divided into two major groups: energy-transduction reactions and carbon-fixation reactions. During the energy transduction reactions, light energy is captured by photosynthetic pigments chlorophylls, carotenoid, and phycobilins, and used to split water molecules in the production of adenosine triphosphate (ATP) from adenosine diphosphate (ADP) and nicotinamide adenine dinucleotide, reduced (NADH) from nicotinamide adenine dinucleotide, oxidized (NAD^+). These two molecules (ATP and NADH) then furnish the fuel needed to drive the carbon-fixation reactions, commonly called the Calvin cycle, into the basic building unit of all organic compounds (3-phospoglycerate). The carbon dioxide used in the Calvin cycle diffuses from the atmosphere into the leaves through stomata.

When C_3 plants are exposed to hot, dry conditions, stomata close to conserve water and thus cut off the supple of carbon dioxide to the leaves. Oxygen, a byproduct of water splitting, accumulates, and a series of reactions takes place called photorespiration. The results of photorespiration are the consumption of oxygen and the production of carbon dioxide, an "undoing of photosynthesis" so to speak, a wasteful process that yields neither ATP nor NADH. Photorespiration should not be confused with mitochondrion respiration of the Krebs cycle, sometimes called "dark respiration."

The photosynthetic rate of big sagebrush varies seasonally and daily within season (Caldwell 1979; DePuit 1979; DePuit and Caldwell 1973, 1975a; Mooney and others 1966; Moore 1977; Pearson 1975). Seasonally, DePuit and Caldwell (1973) reported highest photosynthetic output in late May and early June when temperatures and soil moisture were most favorable, and photosynthesis declined to minimum output in August when soil moisture was also at a minimum. Pearson (1975) observed higher photosynthetic rates in July than in June. He attributed this to the occurrence of heavy rains in late June and early July, which replenished soil moisture. During mid summer drought, Mooney and others (1966) noted a marked reduction in the growth of big sagebrush but a return to a higher growth level after rain had recharged the soil in early August. DePuit and Caldwell (1975a), studying the photosynthetic rates of irrigated and nonirrigated big sagebrush at varying temperatures (5 to 40 °C), found that irrigation stimulated photosynthesis at all temperatures (also see Toft and others 1989). Big sagebrush is an evergreen, and there is evidence that some photosynthesis takes place year around (Pearson 1975; Smith and others 2002).

Daily patterns of photosynthetic rate vary with season. During the spring and early summer when temperatures are not excessive and soil moisture readily available, photosynthetic rates are lowest at sunrise and sunset and peak at about midday (Caldwell 1979; DePuit and Caldwell 1973). As the growing season advances and temperatures become warmer and soil moisture is less available, peak photosynthetic rates occur at midmorning, and by midday photorespiration has overwhelmed photosynthesis, and net carbon fixation becomes negative and remains so for rest of the day. Photorespiration increase is due to stomata closure and buildup of oxygen levels inside leaves of the big sagebrush plants. However, Pearson (1975, p.15) noted in his study for midsummer:

> All six plants tended to follow the same photosynthesis pattern with the highest rates occurring in midmorning and late afternoon. Rates of photosynthesis were low before sun up and for an hour or two after sun up before reaching the morning peak, and then dropped again following the peak. During the hottest part of the day, when presumably the roots could not absorb water fast enough to make up transpiration losses unless the stomates were closed, the photosynthetic rates generally became negative, indicating that respiration was continuing but that gross photosynthesis had essentially ceased. In the late afternoon, photosynthesis became positive.

Pearson (1975) goes on to suggest that stomata close tightly enough to allow water to accumulate in the photosynthetic tissue to the point that the stomata again open, allowing carbon dioxide to diffuse in, thus allowing the resumption of photosynthesis and a net gain of carbon.

The optimum temperature for photosynthesis in big sagebrush appears to be about 20 ^{0}C (DePuit and Caldwell 1973, 1975a,b; greenhouse studies of Mooney and others 1966 and West and Mooney 1972). However, optimum temperature for photosynthesis in big sagebrush varies according to the environment it has been exposed to (Mooney and West 1964). For instance, Mooney and others (1966) were able to shift the optimum temperature for a high-elevation (10,150 feet) population of big sagebrush from 10 to 20 °C. They noted that the greenhouse big sagebrush plants grown at Los Angeles had higher photosynthetic rates at all test temperatures than field plants tested at different times through out the growing season. West and Mooney (1972) collected uniform-sized seedlings of big sagebrush from a lower (2,400 m) elevation site and a higher (3,090 m) elevation site. The seedlings were transplanted into pots, reared in a greenhouse for 6 months, and then maintained in field autoirrigators at the two elevations for 2 months; after which the photosynthetic rates of the seedlings were determined for various temperatures. At the higher site, seedlings had an optimum photosynthetic temperature of 15 °C compared to the seedlings collected at the lower site of 20 °C. At the lower site, the two sets of seedlings showed a shift in optimum photosynthetic temperature of 5 °C, higher elevation seedlings 20 °C, and the lower elevation seedlings 25 °C. Regardless of site, seedlings from the higher site, or cooler site, did better at the cooler temperature, and the seedlings from the lower site, or warmer site, did better at the warmer temperatures. These sets of data suggest a genetic as well as an acclimation component in determining optimum photosynthetic temperature. Caldwell (1979, p. 79), after reviewing the West and Mooney (1972) study, stated, "Therefore, although *Artemisia tridentata* exhibited a notable acclimation potential, its successful widespread distribution must be attributed to genetic differentiation within the species."

Growth in big sagebrush is a two-phase process: first vegetative growth and second reproductive growth (Miller and others 1983). Vegetative growth occurs during spring and early summer when temperatures and water supplies are usually optimum. Reproductive growth starts in early summer and reaches maximum growth during late summer with florets fully developed by late summer to early fall (DePuit and Caldwell 1973; Evans and others 1991). Flowering occurs during early to mid fall with fruit development commencing almost simultaneously with flowering (DePuit and Caldwell 1973). Thus, reproductive growth occurs when water supplies and temperatures are not particularly favorable; in fact, during this period, big sagebrush plants have started shedding ephemeral leaves from vegetative shoots, and neighboring plant species are largely dormant (Miller and others 1983). Evans and Black (1993) found, through the use of a carbon isotope, that vegetative fixed carbon does not transfer to reproductive structures. Further, they found that inflorescences of big sagebrush do generate positive net photosynthesis at a time when the whole plant is in a water conservation mode; that is, leaf abscission is occurring and stomata are exerting control over water loss. Evans and Black (1993, p. 1524) noted: "Vegetative and reproductive modules both responded to the limited availability of water and increased evaporative demand by abscising leaves and decreasing stomatal conductance. Reproductive modules, however, consistently had higher transpiration rates." They reported that supplemental watering stimulated inflorescences growth but not vegetative growth (also see Evans and others 1991). Evans and others (1991, p. 676) stated:

> Expanding inflorescences during summer may enhance competitive ability because biomass can be allocated solely toward vegetative growth during spring, increasing the capacity of *Artemisia tridentata* to acquire resources when they are most abundant. Conversely, inflorescences that are photosynthetically self-sufficient can better respond to favorable soil moisture or intermittent precipitation during summer, because photosynthesis can be increased without investing resources into further vegetative growth.

A study conducted by DePuit and Caldwell (1975b) determined that net photosynthesis of green stems of big sagebrush was low. They concluded that big sagebrush, which maintains a large amount of leaves during dry periods, would be less dependent on carbon fixation by stem tissues during such periods, whereas plants species that shed many, if not all, of their leaves during drought may depend more on stem photosynthesis for supplying the energy needed for tissue maintenance.

Frank and others (1986) studied the relationship of big sagebrush subspecies (basin, mountain, Wyoming) growth rates with rates of photosynthesis, transpiration, and ^{13}C. They found that basin big sagebrush growth rate was significantly higher than mountain and Wyoming big sagebrush. Frank and others (1986, p. 335) noted: "Subspecies of big sagebrush that exhibit rapid growth also show high rates of photosynthesis (reflected in less isotopic fractionation) and high rates of transpiration."

Ducharme and Ehleringer (1996) measured the photosynthetic rate, ^{13}C, and heterotrophy of *Castilleja linariifolia*, a facultative root hemiparasite of big sagebrush. They calculated that 40 percent of the *C. linariifolia* leaf carbon was derived from its big sagebrush host. Also, Hansen (1979) described the movement of reducing sugars from parasitized big sagebrush plants to a parasite desert paintbrush (*Castilleja chromosa*).

Carbohydrate Metabolism

Closely related to photosynthesis is carbohydrate metabolism. Unlike other plant species, seasonal trends (increases and decreases in concentration of nonstructural carbohydrates such as starch, sugars, and so forth) were lacking for crown and root tissues of big sagebrush (Coyne and Cook 1970; Garrison 1972). But twigs of big sagebrush showed a pronounced seasonal trend starting off high in the spring, reaching lowest levels in the summer, and building back in the fall (Coyne and Cook 1970). Twigs contained significantly higher concentrations of nonstructural carbohydrates than entire crowns or root systems. What is unusual about big sagebrush is the high concentration of nonstructural carbohydrates in the spring. Most plant species are using carbohydrate reserves at this time of year to support new growth, thus carbohydrates are at their seasonally lowest level. It appears that the overwintering leaves of big sagebrush can more than support the needs of nonstructural carbohydrates for new spring growth. Bilbrough and Richards (1993) found that over 45 percent of the nonstructural carbohydrates of twigs were stored in the leaves, 42 percent in older shoots, and 13 percent in 1-year-old long shoots. Coyne and Cook (1970, p. 439) pointed out: "In big sagebrush, twigs are apparently an important site of reserve storage. This would appear to be an efficient adaptation provided the twigs are not removed by grazing. If grazed, much of the stored carbohydrates could be directly removed by the animals." In fact, Trlica and Cook (1971) found that removing 90 percent of the twig's tissues in either spring, summer, or fall resulted in reduced fall concentrations of nonstructural carbohydrates in crowns and roots tissues as compared to nondefoliated plants. Wandera and others (1992) reported killing of mountain big sagebrush plants when removing 90 percent of the previous year's growth either in the winter or spring. Heavy grazing during the spring is most detrimental to big sagebrush (Bilbrough and Richards 1993; Cook and Child 1971; Cook and Stoddart 1963; Pearson 1964). Also, heavy winter and spring grazing reduces the number of fall flowering stocks, but this may be due more to the removal of flowering buds located at the distal end of long shoots than loss of carbohydrates (Bilbrough and Richards 1993; Rodriguez and Welch 1989). Cook and Stoddart (1960, p. 15) observed: "It was found that clipping all of the current year's growth from one side of the plant during late winter or early spring caused death of that one-half of the plant after three years of treatment; whereas clipping one-half of all the current year's growth over the entire plant reduced vigor of the entire plant substantially, but only small isolated twigs or branches were killed." Or in other words, carbohydrates and perhaps other compounds are not translocated from one side of big sagebrush plants to the other side.

Dina and Klikoff (1973), studying the effects of moisture stress on carbohydrate concentrations in big sagebrush, found that starch levels were not affected, but sugar concentrations increased significantly in leaves, stems, and roots of water-stressed plants. This increase in sugar levels may provide some protection to RNA-DNA complex, enzymes, and other cellular organelles during periods of high water stress—an adaptive mechanism.

Water Relationships

Knowledge of the morphology of big sagebrush root system and leaf production and leaf shed is essential to understanding its water relationships. Robertson and others (1972) describe big sagebrush as a phreatophyte that is a deep-rooted plant that can meet some of its water needs from the water table or from a layer of soil just above the water table. In soils without restricting layers, root depths for basin big sagebrush (many of Daubenmire's [1975] basin big sagebrush stands are probable Wyoming big sagebrush stands; McArthur and Sanderson 1999) have been recorded as deep as 10 feet (3 m) (Daubenmire 1975). For mountain and Wyoming big sagebrush, depths from 5 to 8 feet (1.5 to 2.5 m) have been reported (Daddy and others 1988; Manning and Groeneveld 1990; Sturges 1977b, 1979; Welch 1997). The tap root of individual big sagebrush plants is not necessarily the deepest. Often, the deepest roots are branches off of the tap root (Manning and Groeneveld 1990; Sturges 1977b). Not only does big sagebrush produce a deep root system, but just under the soil surface lateral roots branch off the tap root forming a vast root network; the majority of the root system occurs just 12 inches (30.48 cm) under the soil surface and under the canopy of big sagebrush plants (Daddy and others 1988; Flanagan and others 1992; Leffler and others 2004; Manning and Groeneveld 1990; Sturges 1977b, 1979). These shallow roots not only absorb water that accumulates in the upper soil layers during winter and spring but can also make use of infrequent moisture from summer convective storms (Donovan and Ehleringer 1994; Leffler and others 2004). Some of these lateral roots extend out from mature plants a distance of 3 to 5 feet (1 to1.53 m) before growing deeper into the soil profile (Sturges 1977b; Welch 1997). Thus, big sagebrush develops a two-tiered root system of dense root network at the soil surface and a deep system with tap root or extending laterals. Root growth begins in the early spring a few days before shoot or stem growth and continues through the late fall (Fernandez and Caldwell 1975; Robertson 1943; Sturges 1979).

Leaf development in big sagebrush is dimorphic, that is, two kinds of leaves—ephemeral and persistent—are produced during the coarse of the growing season (Branson and others 1976; Daubenmire 1975; Link and others 1995; Miller and others 1983, 1986; Miller and Shultz 1987). Diettert (1938) noted the two types of leaves and the timing of their development but did not differentiate them by name. Big sagebrush plants start the growing season in early spring with just persistent leaves that were formed during the pervious growing season; however, early in the current growing season large ephemeral leaves develop (Miller and Shultz 1987). After the first crop of ephemeral leaves have matured, a second crop of smaller ephemeral leaves and persistent leaves start to develop in the axes of the mature ephemeral leaves producing what is termed a short shoot. There are, at this point, actually four kinds of leaves: (1) the persistent leaves that overwintered, (2) large mature ephemeral leaves, (3) ephemeral leaves developing on short shoots, and (4) current crop of persistent leaves also developing on short shoots. Ephemeral leaves on inflorescences are not borne on short shoots. Miller and Shultz (1987) noted that persistent leaves live a total of 12 to 13 months. Miller and Shultz (1987, p. 228) described the longevity of big sagebrush leaves: "At the onset of drought, both the previous season perennial and large, early-developing ephemeral leaves begin to senesce. Later developing ephemerals, including nonlobed leaves, persist during the initial phase of leaf fall, senescing in late summer and fall. By November only the current crop of perennial leaves persists." They estimated that big sagebrush maintained 33 percent of their leaves in the winter. Branson and others (1976) estimated greater than 20 percent.

Water relations, whether plant or soil, are expressed in terms of water potential. The guiding principle is that water moves from a region of higher water potential to a region of lesser water potential. Water potential is expressed in bars for early literature or in megapascals for later literature. Both units are expressed as negative values; the less negative the higher the water potential or the more negative the lower water potential. In other terms, water moves from a region of higher water concentration to a region of lower water concentration.

Water use pattern of big sagebrush and soil moisture patterns have been described by a number of workers (Anderson and others 1987; Branson and others 1976; Branson and Shown 1975; Campbell and Harris 1977; Carpenter and West 1989; Donovan and Ehleringer 1994; Kolb and Sperry 1999; Link and others 1995; Matzner and Richards 1996; McArthur and others 1998; Miller and others 1983, 1986; Rawls and others 1973; Shumar and Anderson 1986; Sturges 1977b, 1980). Comparisons of water relationships among subspecies of big sagebrush are discussed in chapter V on big sagebrush genetics (Kolb and Sperry 1999; McArthur and others 1998; Miller and others 1983, 1986; Shumar and Anderson 1986).

In general, the water use pattern of big sagebrush begins in the late winter or early spring where water potentials of plants (–1.3MPa) and soil (–0.03 MPa) are at their maximum (Miller and others 1986). Of course, climatic conditions or wet or dry years would have a major influence on these maximum water potentials (Anderson and others 1987; Campbell and Harris 1977; Miller and others 1986). During this time of maximum water potential, roots expand and the first and largest set of ephemeral leaves develop (Miller and Shultz 1987). As the growing season progresses, the first set of ephemeral leaves matures, and the short shoots with their second but smaller set of ephemeral leaves and set of persistent leaves develop, and roots continue to grow (Miller and others 1986). Drought, however, can severely limit the production of leaves (Rickard and Warren 1981). Water demands at this time are mostly supplied from the top 10 inches of the soil near the trunk of the plant, but as the season progresses, soil water potential becomes less, and water is absorbed by the big sagebrush plant in an outward and downward direction (Sturges 1977a). By early summer, with plants' water potential about –3.0 MPa and soil water potential below –0.20 MPa, vegetative growth is terminated and reproductive growth—inflorescences—starts (Miller and others 1986; Shumar and Anderson 1986). As the seasonal drought of midsummer approaches, first and second sets of ephemeral leaves and last year's persistent leaves start to senesce, followed soon by leaf abscission. Miller and others (1986) estimated that 53 percent of total leaf biomass is lost during the midsummer drought. But in spite of hot temperatures, low soil water, and low internal plant water potentials (–5.0 MPa), inflorescences keep on growing and maturing, and by late fall-early winter become leafless, dried out—senescent—with mature seeds (Daubenmire 1975; Evans and others 1992).

How does big sagebrush support reproductive growth or growth of inflorescences during the driest part of the year? First, water is conserved by terminating vegetative growth, reducing leaf biomass more than 50 percent, and reducing stomata conductance. Second, the growth and maintenance of a deep root system is able to extract available water deep in the soil profile when available water has been exhausted in the upper portion of soil profile (Rickard 1985). Last, big sagebrush has the ability to decrease osmotic potential, thus maintaining turgor pressure above 0 MPa (Evans and others 1992). Evans and others (1992) concluded that this decrease is not due to osmotic adjustment (accumulation of solutes in big sagebrush cells). They found that leaf water volumes decreased by 75 percent, which would in effect concentrate, in a passive manner, solutes within the leaves. This, coupled with elastic cell walls (Evans and others 1992), would maintain turgor pressures above 0 Mpa. They noted the accumulation of proline (a free amino acid) and cyclitol (a sugar alcohol) in leaves; both compounds would help to maintain turgor pressure and protect enzymes of water-stressed cells. All these factors taken together allow big sagebrush to tolerate drought while actively supporting inflorescence growth. However, another factor called hydraulic lift may play a role in the support of growing inflorescences and drought tolerance.

Hydraulic Lift

Roots often pass through dry soil to soil that contains more water, and drier soil's water potential can be more negative than root water potential; this sets up the possibility of water movement out of roots and into soil (Richards and others 1987). Richards and Caldwell (1987), studying the daily fluctuation of soil water potential of the upper layers of soil (35, 50, and 80 cm) beneath the canopy of big sagebrush, found that soil water potential was greater at night and less during the day. When they suppressed transpiration, soil water potential of the upper soil layers increased steadily, both day and night, throughout the 3-day experiment. They concluded from their soil water potential data and experimental results that "at night water absorbed from moist soil by deeper roots is transported to and lost from roots into drier upper soil layers." They termed this phenomenon "hydraulic lift."

Additional evidence for hydraulic lift comes from a study by Caldwell and Richards (1989) who treated big sagebrush roots at depths of about 4 feet (1.2 m) with deuterated water and found deuterated water appearing in the stem water of neighboring grass plants. Not only did this experiment support the hydraulic lift hypothesis but also raised the possibility of parasitism of water stored in the upper soil layers by neighboring plant roots. Later, Ryel and others (2002) reported that parasitism of water from hydraulic lift could increase transpiration of non big sagebrush plants by 20.5 percent.

Caldwell (1990) noted, concerning the ecological implication of hydraulic lift:

> Several benefits of hydraulic lift have been suggested, including maintenance of active fine roots in the upper drier soil layers and facilitation of nutrient uptake in these layers (Richards & Caldwell, 1987; Caldwell et al. 1991). It has been demonstrated that hydraulic lift can improve the effectiveness of water uptake by the sparse deep root system by allowing the plant to temporarily store water in the upper soil layers at night. Thus, the deep roots can continue to absorb water 24 hours per day and thereby increase their effectiveness. The evidence supporting this concept was an appreciable reduction (25 to 50 percent) of transpiration on days following circumvention of hydraulic lift by nighttime illumination (Caldwell & Richards, 1989). Despite the advantages of hydraulic lift, if water is released into the soil in the proximity of neighboring plant roots, some of this moisture might be forfeited to water parasitism by neighbors.

In addition, water from hydraulic lift should prolong the activity of soil microorganisms, especially those of the rhizoshphere, which in turn should aid nutrient uptake in the upper soil zone where nutrients are more concentrated (Caldwell and others 1991b; Matzner and Richards 1996).

Big Sagebrush Water Potentials Compared to Other Plant Species

Comparisons of big sagebrush water potentials to other plant species are given in table 4.17. Values sharing the same author or authors and year are comparable. For example, the Dina and others (1973) report shows that big sagebrush experiences the least plant water potential (–70.3 bars) or greater water stress than the other plant species studied. But in the Branson and others (1976) report, six out of 10 species studied experienced less plant water potential (–79 to –103 bars) or greater water stress than big sagebrush. Everett and others (1977, p. 274) noted, "Water potentials of big sagebrush and shadscale were significantly (0.5) lower than those of rabbitbrush or galleta grass in the same community." Big sagebrush, unlike a number of plant species, does not undergo osmotic adjustment to maintain turgor pressure with drying soils but adjusts through the reduction of cellular water and cell wall elasticity and the accumulation of proline and cyclitol (Evans and others 1992).

Like other plants, big sagebrush intercepts rainfall and snowfall. Hull (1972, p. 65) found that "sagebrush intercepts both rain and snow, and that both evaporate from the plant surface without getting to the soil. Thus, an overlooked and undesirable feature of big sagebrush is that it prevents rain and snow from replenishing the soil moisture and thus reduces yields of associated grasses." Would not grass, forb, and nonsagebrush shrubs also intercept rainfall and snowfall and "prevent replenishing soil moisture" to some degree? Hull (1972) noted that wheatgrass growing in the open had an average root depth of 60 inches compared to 39 inches when growing with sagebrush. West and Gifford (1976) estimated that for an entire big sagebrush community the amount of total annual rainfall, excluding snowfall, intercepted by the plants to be 4 percent.

Hutchison (1965) compared snow accumulation and disappearance in big sagebrush and grass study plots. He found more snow accumulation, hence more water, in the big sagebrush plots than in the grass-covered plots (also see Sturges 1977a, 1979). During snowmelt, the grass plots formed a continuous layer of ice, which prevented some of the meltwater from entering the soil beneath the grass plots, resulting in earlier peak flows and incomplete soil moisture recharge. A continuous layer of ice did not form on the big sagebrush plots, thus meltwater would have a better chance of recharging soil moisture.

Gifford and Busby (1974) noted in their study that water infiltration rates for big sagebrush sites that were disturbed by plowing or grazing were lower than undisturbed sites, resulting in greater sediment production on disturbed sites than the undisturbed big sagebrush site. Lusby (1979) noted just the opposite in his study.

Ryel and others (2003) compared the pattern of water movement into soils following rain events, between basin big sagebrush plots and bared soil plots. They (p. 757) observed: "Rainwater was moved rapidly downward shortly after the rain event and continued over a period of a few days. For rainwater reaching a 0.3-1.5 m depth, the portion redistributed by roots was estimated to range from 100% for small rainfall events (<8 mm) to 74% for a 36 mm event." This process is termed hydraulic redistribution. They found that during the fall-spring soil recharge period, 67 percent of all water movement downward below 0.1 m was by the root system and 87 percent below 0.3 m level.

Anderson and others (1987) conducted a study to determine the ability of monocultural stands of crested wheatgrass (*Agropyron desertorum*), giant wildrye (*Leymus cinereus*), streambank wheatgrass (*Elymus lancealatus*), Wyoming big sagebrush, and natural big sagebrush steppe vegetation to deplete water from a clay-loam soil. The problem they were investigating was the intrusion of water into the zone where hazardous materials were buried. Their objectives were to determine the water use pattern of different vegetative cover and select which cover would best prevent the intrusion of water into hazardous waste zones. They concluded that for their study site at the Idaho National Engineering Laboratory Field Station a monocultural stand of any of three perennial grasses or Wyoming big sagebrush would prevent intrusion of water into hazardous waste zone of soil 1.4 m deep and that the native community would also prevent intrusion.

Table 4.17—Comparisons of plant water potentials of big sagebrush to other plant species.Data expressed as megapascals (Mpa) or bars.Bars can be coverted to Mpa by multiplying bars by 10^5Pa.Values sharing the same author or authors and year are comparable.

Species	Plant water potential	Source
Antelope bitterbrush (*Purshia tridentata*)		
	–5.5 to –45.5 bars	Dina and others 1973
Big sagebrush (*Artemisia tridentata*)		
	–8.3 to –70.3 bars	Dina and others 1973
	–0.95 to –2.99 Mpa	Drivas and Everett 1987
	–0.80 to –2.10 Mpa	Evans and Ehleringer 1994
	–1.10 to 1.70 Mpa	Romo and Haferkamp 1988
	–2.00 to –3.00 Mpa	Drivas and Everett 1988
	–5.00 Mpa	Delucia and Heckathorn 1989
	–2.00 to –3.30 Mpa	Link and others 1995
	–4.00 to –4.50 Mpa	Romo and Haferkamp 1989
	–20 to –66 bars	Branson and others 1976
	–55 to –60 bars	Branson and others 1967
Bigtooth maple (*Acer grandidentatum*)		
	–4.5 to –33.1 bars	Dina and others 1973
Creeping barberry (*Berberis repens*)		
	–9.0 to –35.7 bars	Dina and others 1973
Gambel oak (*Quercus gambelii*)		
	–9.7 to –45.5 bars	Dina and others 1973
Greasewood (*Sarcobatus vermiculatus*)		
	–29 to –64 bars	Branson and others 1976
	–52 to –70 bars	Branson and others 1967
	–3.50 to –3.80 Mpa	Romo and Haferkamp 1989
Green rabbitbrush (*Chrysothamnus greenei*)		
	–29 to –85 bars	Branson and others 1976
Horsebrush (*Tetradymia spinosa*)		
	–28 to –50 bars	Branson and others 1976
Mat saltbush (*Atriplex corrugata*)		
	–32 to –96 bars	Branson and others 1976
Nuttall saltbush (*Atriplex nuttallii*)		
	–32 to –103 bars	Branson and others 1976
	–83 to –94 bars	Branson and others 1967
Pinyon pine (*Pinus edulis*)		
	–0.80 to –2.10 Mpa	Evans and Ehleringer 1994
Ponderosa pine (*Pinus ponderosa*)		
	–2.50 Mpa	Delucia and Heckathorn 1989
Prostrate kochia (*Kochia prostrata*)		
	–1.30 to –2.10 Mpa	Romo and Haferkamp 1988
Rubber rabbitbrush (*Chrysothamnus nauseosus*)		
	–0.70 to –0.70 Mpa	Evans and Ehleringer 1994
	–20 to –41 bars	Branson and others 1976
Shadscale (*Atriplex confertifolia*)		
	–23 to –94 bars	Branson and others 1976
Singleleaf pinyon (*Pinus monophylla*)		
	–1.10 to –2.02 Mpa	Drivas and Everett 1987
	–1.50 to –2.50 Mpa	Drivas and Everett 1988
Silver sagebrush (*Artemisia cana*)		
	–42 bars	Branson and others 1967
Spiny hopsage (*Grayia spinosa*)		
	–2.00 to –6.20 Mpa	Link and others 1995
	–32 to –79 bars	Branson and others 1976
Utah juniper (*Juniperus osteosperma*)		
	–0.80 to –2.80 Mpa	Evans and Ehleringer 1994
Water birch (*Betula occidentalis*)		
	–3.8 to –22.3 bars	Dina and others 1973
Winterfat (*Eurotia lanata*)		
	–31 to –91 bars	Branson and others 1976

Global Warming

Concerns over possible warming of the Earth's atmosphere, due to rising levels of atmospheric CO_2 and other greenhouse gases from burning of fossil fuels and other human activities, has stimulated research on effects of global warming on big sagebrush (Harte and Shaw 1995; Johnson and Lincoln 1990, 1991; Loik and Harte 1996; Miller and others 1991a; Perfors and others 2003; Shaw and others 2000). Although dry-wet cycles and cooling-warming cycles are not new, the consensus among the cited authors is that big sagebrush would be favored by global warming. Miller and others (1991a) point out that big sagebrush, like other plants, reduces its biomass output during a drought but has the ability to recover quickly. Miller and others (1991a, p. 8) predict: "If an accelerated warming trend does occur in the Great Basin (Global Warming), accompanied with a decrease in precipitation, we can expect, based on past events, an increase in dominance of woody plants, a decrease in total plant cover and an increase in soil erosion." Medin and Anderson (1979) noted that during drought big sagebrush was a more dependable forage for mule deer than other species studied. Studying the effects of heated plots across a soil moisture gradient, Harte and Shaw (1995) found that big sagebrush biomass increases in the drier habits and an enhancement of big sagebrush seedling establishment in the heated plots. They suggested that global warming would change the dominant vegetation of a meadow habitat toward big sagebrush. Perfors and others (2003) observed: "Our findings suggest that global climate change [warming] will result in increased growth and range expansion of sagebrush near northern or high-elevation range boundaries in the Western United States."

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Notes

Chapter V

Big Sagebrush Genetics

This chapter covers chromosome number, polyploid level, hybridization, variability of a host of characteristics (chromatographic profiles, monoterpenoids, digestibility, preference, protein, biomass, germination) selection, and breeding of big sagebrush.

Chromosome Number

For eukaryotic organisms such as big sagebrush, the chromosomes are the structures within the nucleus that carry the genes. Chromosomes are the chemical blueprint of life. Each chromosome is made up of a long linear deoxyribonucleic acid molecule (DNA) and appears as threads or contracted rods of chromatin during mitosis and meiosis. DNA is composed of four units called nucleotides; and each nucleotide is in turn made up of three molecules—phosphate, deoxyribose sugar, and one of four nitrogenous bases (thymine, cytosine, adenine, and guanine). The pairing of the nitrogenous bases among the four types of nucleotides—adenine-thymine, guanine-cytosine—is responsible for the double helix configuration of DNA molecule, its replication, and its ability to carry genes or segments that encode ribonucleic acid (RNA) molecules, which in turn are responsible for protein synthesis necessary for the orderly development and well-being of organisms (Fairbanks and Andersen 1999; Raven and others 1999; Solbrig 1972).

The continuity of life is a major function of chromosomes. This is achieved by self-replication of the DNA molecules during the interphase of mitosis and meiosis and separation of whole chromosomes into daughter cells or passing of these replicates from parent to offspring as gametes (Fairbanks and Andersen 1999; Raven and others 1999; Solbrig 1972).

Orientation of homologous chromosomes on the spindle equator during metaphase I of meiosis I with respect to paternal- versus maternal-derived chromosomes is random, or in other words, nonhomologous chromosomes sort independently into the two daughter cells. This results in a large number of chromosomal combinations that can be calculated from the formula 2^n, where n equals the haploid chromosome number. For example, if an organism's haploid chromosome number is 9, the chromosomal combinations for the gametes would be 512. Chromosomal recombination to form gametes is an important source of variability or genetic recombination within a species but is not the only source. During prophase I of meiosis I, when homologous chromosomes are paired, nonsister chromatids can exchange segments in a process referred to as "crossing over." This is yet an additional source of an organism's variability or genetic recombination

(Fairbanks and Andersen 1999; Raven and others 1999; Solbrig 1972). Mutations and changes in ploidy are other sources of genetic recombination.

The haploid chromosome number “n”—due to presence of two ploidy levels, “x” is the proper term—of big sagebrush has been intensively studied (Barker and McKell 1986; Diettert 1938; Kelsey and others 1975; McArthur 1989; McArthur and others 1979, 1981; McArthur and Sanderson 1999; McArthur and Welch 1982; Sanderson and others 1989; Stahevitch and Wojtas 1988; Taylor and Brockman 1966; Taylor and others 1964; Ward 1953). The results of all these studies agree that the base number of chromosomes for big sagebrush is 9 (n = x = 9; fig. 5.1). Two levels of ploidy have been reported among the three common subspecies of big sagebrush—diploid and tetraploid 2n = 2x = 18 (fig. 5.2) and 2n = 4x = 36 (fig. 5.3) (Barker and McKell 1986; Diettert 1938; Kelsey and others 1975; McArthur and others 1979, 1981; McArthur and Sanderson 1999; Sanderson and others 1989; Stahevitch and Wojtas 1988; Taylor and Brockman 1966; Taylor and others 1964; Ward 1953).

Polyploidy

“Polyploidy” is the term used to describe species that have three or more complete chromosome sets in somatic cells (Fairbanks and Andersen 1999; McArthur 1989). Polyploidy is the driving force in the evolutionary development of many species of flowering plants. It has been estimated that from 47 to over 70 percent of flowering plants are polyploid (Raven and others 1999). For big sagebrush, tetraploidy is the highest common level of ploidy known to date, although higher levels are known but rare (McArthur and others 1979; McArthur and Sanderson 1999). Tetraploid zygotes can be produced by the union of two unreduced gametes from diploid plants. Also, tetraploids can be produced by a process called endoploidy. Here a somatic cell of a diploid plant replicates its chromosomes but fails to go through cytokinesis and in turn replicate its chromosomes a second time. Next, division is finished by cytokinesis. The resultant daughter cells

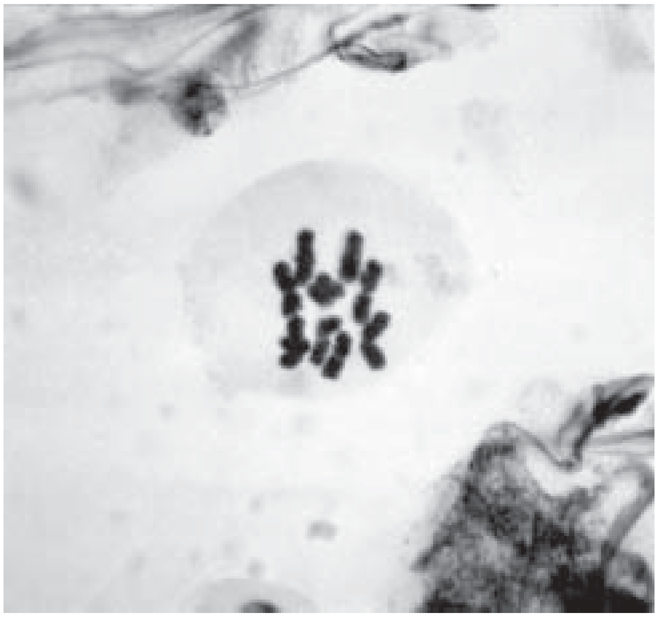

Figure 5.1—Big sagebrush chromosomes (meiosis, metaphase I) haploid n = x = 9 (photo by E. Durant McArthur).

Figure 5.2—Big sagebrush chromosomes (mitosis, metaphase) diploid 2n = 2x = 18 (photo by E. Durant McArthur).

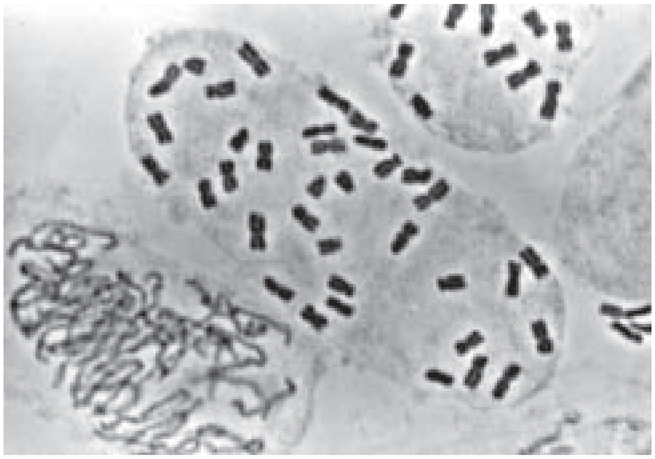

Figure 5.3—Big sagebrush chromosomes (mitosis, metaphase) tetraploid 2n = 4x = 36 (photo by E. Durant McArthur).

have two complete sets of chromosomes. Continued mitotic division by these daughter cells could produce a sector of plant tissues that would be entirely composed of tetraploid cells. If this sector developed into flowers, gametes produced from such flowers would be diploids, and self-fertilization would produce tetraploid seeds (Fairbanks and Andersen 1999).

All three subspecies of big sagebrush (*Artemisia tridentata* ssp. *tridentata*—basin big sagebrush, *A. t.* ssp. *vasyana*—mountain big sagebrush, and *A. t.* ssp. *wyomingensis*—Wyoming big sagebrush) contain polyploid populations (McArthur and Sanderson 1999). Wyoming big sagebrush appears to be uniformly tetraploid (4x = 36), that is, all populations examined to date were tetraploids (Barker and McKell 1986; McArthur and others 1979, 1981; McArthur and Sanderson 1999; Sanderson and others 1989). Basin and mountain big sagebrush are of mixed ploidy levels having both diploid and tetraploid populations (McArthur and Sanderson 1999). McArthur and Sanderson (1999, p. 1767) stated about 75 percent of the basin big sagebrush populations studied were diploid; however, tetraploid "populations are scattered throughout the range with notable pockets in north-central Washington extending into south-central British Columbia and in southern California." For mountain big sagebrush, about 70 percent of the populations studied are diploid with tetraploids scattered throughout its range, although McArthur and Sanderson (1999, p1767) noted "4x populations have not been discovered in the Colorado Rockies or south-central British Columbia."

Knowing the chromosome number of a species is important from two points of view: chromosome number can give an indication of breeding or hybridization compatibility, and it can indicate the degree of genetic recombination potential. For example, a cross between a diploid and a tetraploid would produce a sterile triploid. Odd ploidy level plants are sterile because it is not possible during meiosis to divide an odd number of chromosome sets equally into complete euploid sets, or in other words, cannot produce balance gametes from an odd number of chromosomes (Fairbanks and Andersen 1999). The number of genetic recombination increases from 512 for diploids plants such as big sagebrush that have a chromosome set of 9, to 262,144 for tetraploids plants with a chromosome set of 18. Tetraploids should express greater genetic diversity and perhaps greater adaptation. However, the expected variation is damped by polyploid chromosome segregation (McArthur 1989).

McArthur and others (1981, 1998b) give strong evidences that big sagebrush is autopolyploid as opposed to allopolyploid. Autopolyploid plants are derived from the same ancestral diploid species, whereas allopolyploid plants are derived from different ancestral diploid species. Tetraploids plants derived from the process of autopolyploidy should be morphologically similar to the diploid plants. Also, their chromosomes morphology or karyotype should be similar. Tetraploid plants derived from allopolyploidy would look different (Fairbanks and Andersen 1999). McArthur and others (1981, p.589) cite the following evidence for autopolyploidy in big sagebrush: "morphologically indistinguishable 2x and 4x plants, a few mixed ploidy populations, consistent formation of IVs in 4x PMCs, a relatively uniform 2x karyotype, which is twice the 2x one."

Ward (1953) observed that tetraploid big sagebrush plants were limited to the poorer, rockier soils and were smaller, slower growing plants than the diploid big sagebrush plants. Recently, Barker and McKell (1983), McArthur and Sanderson (1999), and Sanderson and others (1989) have noted that diploids of basin and mountain big sagebrush do grow faster and are generally larger plants, and they grow in wetter habitats than the tetraploids of Wyoming big sagebrush (more on this in a later section of this chapter). However, there is some evidence that tetraploids of basin big sagebrush are smaller plants than diploids and are more readily eaten by domestic sheep (*Ovis aries*) (McArthur and Welch 1982; Welch and others 1987).

Kelsey and others (1975) studied chromosome numbers of mountain big sagebrush as related to three sesquiterpene lactone races. These three races were: Hot Spring, which produced five sesquiterpene lactones (arbusculin-A,-B,-C; rothin-A, -B; high-elevation, which produced two (artevasin, dehydroleucodin); and low-elevation, which produced three (arbusculin - A, -B, -C). Kelsey and others (1975, p. 209) concluded that "there appears to be no correlation between chromosome numbers and sesquiterpene lactone races." They did present data that demonstrated the exchange of genetic material among sesquiterpene lactone races and that this exchange is mainly restricted to narrow zones of sympatry.

Hybridization

Ward (1953, p. 170) in his study of basin and mountain big sagebrush stated, "It should be pointed out that we have been comparing here only the extremes and that all degrees of intermediacy may be found." This observation of intermediacy is a hint that subspecies of big sagebrush can hybridize, although at this time, only two subspecies of big sagebrush were recognized—basin and mountain. Later, Beetle (1960) found what he believed were natural crosses between basin and mountain big sagebrush. Hanks and others (1973) reported chromatographic evidences of natural hybridization occurring between mountain and basin big sagebrush and between these two subspecies of big sagebrush and other *Artemisia* species. McArthur and others (1979) describe big sagebrush as a highly polymorphic, wind-pollinated species, with numerous ecotypes and biotypes that readily cross both intraspecifically and interspecifically. However, they felt their hybridizing data were more suggestive than definitive.

A more definitive way of identifying hybrids between basin and mountain big sagebrush was discovered by Taylor and others (1964). They found that seeds of mountain big sagebrush, when soaked in water, would fluoresce brightly when exposed to long-wave ultraviolet light, and seeds of basin big sagebrush do not fluoresce or do so only slightly. Others have extended this observation to crushed leaves soaked in water, methanol, or ethanol (Stevens and McArthur 1974; Winward and Tisdale 1969; Young 1965). The molecules responsible for this fluoresce have been identified as coumarins (Brown and others 1975; Shafizadeh and Melnikoff 1970) (for more information see chapter IV). However, soaking crushed leaves in methanol or ethanol resulted in blue fluoresce for mountain big sagebrush and red or brownish red for basin big sagebrush (Winward and Tisdale 1969; Young 1965). Regardless of the solvent used, the technique of crushing two or three leaves in water or alcohol and exposing the mixture to long-wave ultraviolet light provides a genetic marker to separate mountain and basin big sagebrush or to identify hybrids between the two (fig. 5.4).

Noller and McArthur (1986) were the first to use the fluoresce test to identify hybrids resulting from artificial hybridization between basin and mountain big sagebrush. They crossed an accession of basin big sagebrush from Dove Creek, CO, with an accession of mountain big sagebrush from Hobble Creek, UT (near Springville). Dove Creek was used as the maternal line and Hobble Creek was the paternal line. Seeds were collected from the maternal line. Because the maternal line does not contain coumarin compounds that fluoresce under ultraviolet light, seedlings that do are the result of hybridization between Hobble Creek and Dove Creek accessions. Hybridization was accomplished by collecting pollen from onsite Hobble Creek mountain big sagebrush plants and transferring this pollen to white pollination bags attached to Dove Creek plants prior to flower opening. The maternal line was established several years ago in a uniform garden located at Ephraim, UT, about 56 miles south of the Hobble Creek site. Seedlings from the maternal line with the highest fluorescence were selected for a mass selection garden.

From this mass selection garden, McArthur and others (1988) reported several lines of evidences that seedlings collected from the maternal line were intermediates between paternal and maternal parents (tables 5.1 and 5.2). Coumarin content of hybrids as measured by percent transmittance—that is the higher the transmittance the lower the concentration of coumarins—were intermediate of the parental lines, 69 versus 54 and 86 percent (table 5.1). Methacrolein content of hybrids was also intermediate of the parental lines as well as camphor, camphene, 1,8 cineole, b-thujone, unknown monoterpenoid labeled as unknown 1, and total monoterpenoids (table 5.2). All these measurements are evidence that the seedlings selected from the maternal line were hybrids and verified that hybridization between basin and mountain big sagebrush could be achieved through artificial means.

From this same study, McArthur and others (1988) recorded evidence of natural hybridization between a stand of basin and mountain big sagebrush located in Diamond Fork Canyon, Utah County, UT, about 11 miles southeast of Spanish Fork. There, mountain big

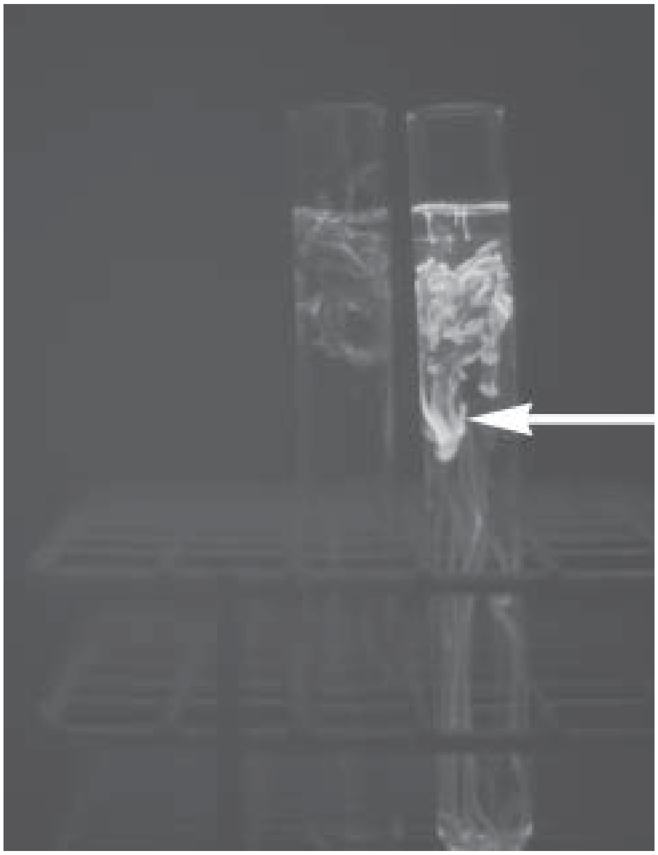

Figure. 5.4—Fluorescing of coumarin compounds leaching from crushed leaves of mountain big sagebrush into water exposed to long-wave ultraviolet light. Test tube on left contains crushed leaves of basin big sagebrush that does not leach coumarin compounds (photo by Bruce L. Welch).

Table 5.1—Amount of fluorescence produced by maternal and paternal lines of big sagebrush and their putative hybrid. The maternal line was an accession of basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) collected from Dove Creek, CO, and the paternal line was an accession of mountain big sagebrush (*A. t.* ssp. *vaseyana*) collected at the mouth of Hobble Creek Canyon near Springville, UT. Data are expressed in terms of percentage of transmittance, or in other words, the greater the fluorescence the less light that will pass through the sample and the lower the transmittance. Data from McArthur and others (1988).

	Percentage of transmittance[1]
Dove Creek maternal line	85.6 ± 1.3[a]
Putative hybrid	69.1 ±.9[b]
Hobble Creek paternal line	54.0 ± 6.3[c]

[1] Means and standard error of the means. Values sharing the same superscripts are not significantly different at the (p <.01) Student-Newman- Keuls means comparison test.

sagebrush grows on a bench and basin big sagebrush near the canyon floor or valley bottom. Separating these two subspecies is a narrow zone or a 250-foot hillside that supports a population of big sagebrush that appears to be an intermediate between the two subspecies. As with artificial hybridization, these natural hybrids were intermediate, for the same chemical characteristics described earlier, of mountain and basin big sagebrush (also see Byrd and others 1999).

Narrow hybrid zones between mountain and basin big sagebrush have been studied at three additional sites: Orem, UT; Salt Creek Canyon east of Nephi, UT; and Clear Creek Canyon west of Richfield, UT (Freeman and others 1991; Wang and others 1998). All three zones were reported as producing stable hybrids that expressed intermediate characteristics of the parental subspecies (Freeman and others 1995; Wang and others 1998).

Graham and others (1995, p. 709) noted, "Stable hybrid zones are inconsistent with the classical theory of speciation." The classical theory of speciation holds that when two populations come into contact, they

Table 5.2—Monoterpenoid profiles of the maternal and paternal lines in the production of a hybrid line. The maternal line was an accession of basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) collected from Dove Creek, CO, and the paternal line was an accession of mountain big sagebrush (*A. t.* ssp. *vaseyana*) collected at the mouth of Hobble Creek Canyon near Springville, UT. Individual monoterpenoids data are expressed in relative terms to the total monoterpenoid content, which is a percentage of the total. Total percent of monoterpenoids are expressed on a dry-weight basis. Data from McArthur and others (1988).

Monoterpenoids	**Dove Creek**	**Putative hybrid**	**'Hobble Creek'**
Methacrolein[a]	9.0 ± 1.1[b]	4.2 ± .5	—
a-pinene	—	0.7 ± .2	1.9 ± 10.8
Camphene	—	1.4 ± .4	6.1 ± 1.5
1,8 cineole	—	2.1 ± .7	16.0 ± 4.7
Unknown 1	27.0 ± 4.6	18.6 ± 2.7	—
Unknown 2	1.1 ± .6	Trace	—
b-thujone	56.2 ± 3.8	25.5 ± 3.8	4.7 ± 2.5
Unknown 4[c]	2.2 ± .9	21.4 ± 3.5	—
Camphor	2.2 ± 1.1	22.8 ± 2.7	59.2 ± 7.1
Unknown 5	—	—	4.7 ± 2.6
Unknown 6	2.2 ± 1.1	2.8 ± .6	4.0 ± 2.9
Unknown 7	—	1.4 ± .3	4.1 ± 2.5
Total percent dry weight	0.91 ± .07	1.47 ± 1.0	2.15 ± .17

[a] Not a monoterpenoid.

[b] Means and standard error.

[c] Unknown 3 is listed in table 7 of the McArthur and others (1988) report but is not pertinent to the above data set.

either remain reproductively isolated, or the populations fuse into one (Graham and others 1995). If, indeed, these zones of hybridization form a stable hybrid and are not an artifact of short-term observations, then the factor responsible for hybrid zone stabilization is either endogenous or exogenous in nature (Wang and others 1997).

Wang and others (1997, p. 95) explain these two possibilities. First, endogenous factors: "The ecologically neutral dynamic equilibrium model postulates that hybridization disrupts coadapted gene complexes, causing developmental and physiological problems that reduce the fitness of hybrids. Thus, in this model, selection results solely from internal genetic factors and hence is endogenous." Second, exogenous factors: "In contrast, the ecologically dependent bounded hybrid superiority model assumes that the selection stabilizing hybrid zones is due to genotype by environment interactions, and occurs because of environmental heterogeneity. Specifically, this model assumes that hybrids should be more fit than their parental taxa within the hybrid zones, and less fit outside the hybrid zones."

To test the hybrid superiority model, Wang and others (1997) conducted reciprocal transplant experiments. They found that hybrids were more fit in the hybrid zone gardens than in either parental garden, and paternal taxon were more fit in their respective gardens than either the hybrids or alien parent. These observations support the hybrid superiority model. Earlier, a study conducted by Graham and others (1995) found that overall fitness of hybrids in terms of stand density and recruitment, flower, seed production, germination, and herbivore load were equal to, and in some cases superior to, parents. Wang and others (1997, p. 101) simply stated, "Our results do not agree with the predictions of the dynamic equilibrium hypothesis, which specifically predicts that heterozygotes for genes distinguishing two hybridizing taxa should have lower fitness than either parent." McArthur and others (1998a) measured respiration and water potential profiles of two parents and hybrids. Even though the three habits differed from one another, hybrid plants' respiratory and water potentials profiles were intermediate of the parent's profiles, or in other words, the study showed no decreases in adaptation within the hybrid plants. In the ninth study of narrow hybrid zones between mountain and basin big sagebrush, Wang and others (1999, p. 1099) observed, "The concentrations of elements in the leaves of site-indigenous sagebrush and the biological absorption coefficients differed significantly between the subspecies and between either parental taxon and hybrids." Smith and others (2002) reported metabolic difference among populations and subspecies of big sagebrush from a narrow hybrid zone. These differences were expressed in reciprocal transplanted gardens, thus supporting the fitness of the hybrids in adapting to the uniqueness of the hybrid zone.

Not only are the parents and hybrid different chemically and morphologically, but the habitats they occupy are also different or unique (Wang and others 1998). Wang and others (1998) measured certain soil properties within parental and hybrid zones. Properties measured were soil thickness, pH, and the concentration of a number of soil elements. Some of their data appear in table 5.3. They found that soil thickness, pH, and levels of certain elements differ among the three sites. Wang and others (1998, p. 139) concluded: "The hybrid zone soil is not just a simple blend of the two parental habitat soils. Rather, it possesses novel characteristics found in neither parental habitat and is more variable than the parental habitat soils." McArthur and others (1988) reported similar results in an earlier study (also see Miglia and others 2004). These observations support the hybrid superiority model. Further support comes from the work of Freeman and others (1999) and Freeman and others (2001), who measured the floristic and vegetative composition of parental sites and hybrid zones in Clear Creek Canyon near Richfield, UT. Freeman and others (1999, p. 487) found that:

> …the species composition, proportions of annual plants, perennial forbs and grasses, shrubs, rock, litter, bare ground and total vegetative cover differ among the parental sites and hybrid zone. Canonical correspondence analysis and ordination showed that the two big sagebrush subspecies and their hybrids are each associated with different groups of species, and occupy edaphically distinct habitats.

Table 5.3—Soil properties—soil thickness (cm), pH, elemental concentration (mg/kg dry weight)—of a basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) site, a mountain big sagebrush (*A. t.* ssp. *vaseyana*) site, and their narrow hybrid zone. Data from Wang and others (1998)[1].

Soil properties	Basin[2]	Hybrid	Mountain
Soil thickness	37^{a}	23^{b}	18^{c}
pH	7.9^{a}	7.7^{a}	6.9^{b}
Ca	$3{,}918^{ab}$	$5{,}309^{c}$	$4{,}602^{bc}$
K	319^{a}	$1{,}474^{c}$	687^{ab}
Mg	158^{a}	216^{ab}	528^{c}
Ba	20^{a}	43^{bc}	49^{bc}
Fe	18^{ab}	13^{b}	20^{ab}
Mo	7^{a}	8^{a}	15^{b}
Na	4^{a}	18^{bc}	12^{c}
Se	8^{a}	4^{ab}	3^{b}
Zn	5^{ab}	2^{b}	1^{b}
Cu	3^{a}	3^{a}	3^{a}

[1] Not all data are given.

[2] Means within rows with different superscripts are significantly different from each other ($p < .05$).

Autopolyploidy and a wind-pollination breeding system that allow gene flow within and among populations of big sagebrush gave this species the necessary variability to dominate much of Western North America before the onslaught of Euro-American settlers and the invasion by cheatgrass (*Bromus tectorum*) and other alien weed species. This breeding system has also allowed big sagebrush to develop into at least three subspecies that occupy different habitats. Stanton and others (2002, p. 579) suggest: "differentiation within the *Tridentatae* is the result of strong ecotypic selection over a background of widespread hybridization." Another possible source of genetic variability is gene mutation, but this has not been studied in big sagebrush. The following section covers the variability for a number of traits and the breeding and selection schemes that could give rise to superior forms of big sagebrush.

Variability

Preference

During in vivo digestibility trials, Smith (1950) noted that mule deer (*Odocoileus hemionus hemionus*) showed definite aversion to individual big sagebrush plants. This is the first evidence of differential preference of an animal for big sagebrush. Since that time, a number of researchers have made similar observations for a variety of animals: mule deer (Hanks and others 1971; Personius and others 1987; Sheehy and Winward 1981; Smith 1959; Wambolt 1995, 1996; Welch and McArthur 1986b; Welch and others 1981,1983; White and Welch 1981); elk (*Cervus elaphus nelsoni*) (Wambolt 1995, 1996); cattle (*Bos bovine*) (Hanks and others 1971); domestic sheep (Sheehy and Winward 1981; Welch and others 1987); pygmy rabbits (*Brachylagus idahoensis*) (White and others 1982); and sage grouse (*Centrocercus urophasianus*) (Remington and Braun 1985; Welch and others 1988, 1991).

Table 5.4—Effects of subspecies, site, and year on preference of wintering mule deer (*Odocoileus hemionus hemionus*) for accessions of big sagebrush (*Artemisia tridentata*). Data expressed as percent of current year's vegetative growth eaten (3 years, 630 plants, three uniform gardens). Data from Welch and McArthur (1986a).

Preference for subspecies		
Basin[1]	**Wyoming**	**Mountain**
32.6^{a2}	**35.3^{b}**	**44.1^{c}**
Effects due to site		
Salt Creek	Gordon Creek	Springville
30.4^{a1}	35.0^{b}	50.2^{c}
Effects due to years		
1980	1981	1982
31.6^{a1}	41.7^{b}	42.4^{b}

[1] Basin = *Artemisia tridentata* ssp. *tridentata;* Wyoming = *A. t.* ssp. *wyomingensis*; mountain = *A. t.* ssp. *vaseyana*.

[2] Means within rows sharing the same superscript are not significantly different at the 5 percent level.

A study conducted by Welch and McArthur (1986b) illustrates the variability of wintering mule deer preference for accessions and subspecies of big sagebrush. In this study, 21 accessions of big sagebrush were established on three uniform gardens on three mule deer winter ranges. Ten accessions were collected from different populations of mountain big sagebrush, seven for basin big sagebrush and four for Wyoming big sagebrush. Each accession was represented by 10 plants, and all 210 plants were planted at random on a 7- by 7-foot grid. Results of the Welch and McArthur (1986b) 3-year study are given in tables 5.4 and 5.5. All plants, accessions, and subspecies received some mule deer use. Wintering mule deer significantly preferred mountain big sagebrush over Wyoming big sagebrush, and Wyoming over basin big sagebrush (table 5.4). More big sagebrush was consumed at the Springville site than at the Salt Creek site, and more was consumed at the Salt Creek site than at the Gordon Creek site (table 5.4). For some reason, more big sagebrush was consumed in 1981 and 1982 than in 1980. On an accessional basis, Welch and McArthur (1986b, p. 284) observed (table 5.5):

> Wintering mule deer significantly preferred the Hobble Creek accession over the other 20 accessions across all sites and years. Overall use of the Hobble Creek accession was 57.5 percent. Use of Hobble Creek big sagebrush varies significantly among sites. At the Salt Creek site, the Hobble Creek accession received 47.4 percent use, 52.0 percent use at Gordon Creek, and 73.0 percent use at Springville. The consistency of ranking for preference of the Hobble Creek accession was not present for the other accessions and further strengthens our contention that Hobble Creek is the most preferred.

Wambolt (1996) concluded after a 10-year study that wintering elk and mule deer preferred mountain big sagebrush over Wyoming big sagebrush, basin big sagebrush, and black sagebrush (*A. nova*). Wambolt (1996, p. 499) further observed:

> Wyoming big sagebrush (*A. t. ssp. wyomingensis* Beetle and Young) was narrowly preferred (38.6%) over basin big sagebrush (*A. t.* Nutt. ssp. *tridentata*) (30.3%). Black sagebrush (*A. t. nova* Nels.) was least preferred (17.0%). Differences in preference among taxa were smallest during the severest winter when more elk were present thereby increasing total sagebrush utilization. Mule deer diets averaged 52% sagebrush over the study. Many sagebrush plants were damaged and even killed by heavy browsing during the study.

Table 5.5—Preference of wintering mule deer (*Odocoileus hemionus hemionus*) for accessions of big sagebrush (*Artemisia tridentata*) grown in three uniform gardens. Data expressed as a percent of current year's vegetative growth eaten. Data points for gardens represent a 3-year mean (Welch and McArthur 1986a).

	Garden			
Accession[1]	**Gordon Creek**	**Salt Creek**	**Springville**	**Mean**[2]
	Percent			
Evanston (b)	25.2	18.1	41.6	28.3^{a}
Trough Springs (w)	17.5	30.9	41.9	30.1^{ab}
Dove Creek (b)	26.3	31.3	35.1	30.9^{abc}
Clear Creek Canyon (b)	31.5	19.7	42.7	31.3^{abcd}
Loa (b)	25.0	18.5	51.3	31.6^{abcd}
Kaibab (w)	30.9	27.2	42.4	33.5^{abcd}
Dog Valley (b)	28.6	23.6	49.1	33.8^{abcde}
Brush Creek (b)	35.2	24.6	47.2	35.7^{abcde}
Wingate Mesa (b)	32.5	33.9	42.8	36.4^{abcdef}
Milford (w)	34.5	29.0	47.4	37.1^{bcdefg}
Clear Creek Canyon (m)	34.4	25.6	55.1	38.4^{bcdefg}
Benmore (m)	40.1	39.3	38.4	39.3^{bcdefg}
Pinto Canyon (m)	36.8	27.8	56.2	40.3^{cdefg}
Evanston (w)	31.1	43.8	46.3	40.4^{defg}
Durkee Springs (m)	36.3	27.7	58.1	40.7^{defg}
Salina Canyon (m)	40.5	29.4	55.2	41.7^{efg}
Sardine Canyon (m)	45.8	29.9	58.0	44.6^{fg}
Indian Peaks (m)	40.9	40.9	55.0	45.6^{fg}
Petty Bishop's Log (m)	46.4	33.8	57.7	46.0^{g}
Colton (m)	43.1	37.9	60.1	47.0^{g}
Hobble Creek (m)	52.0	47.4	73.0	57.5^{h}

[1] (b) = basin big sagebrush (*Artemisia t.* ssp. *tridentata*); (m) = mountain big sagebrush (*A. t.* ssp. *vaseyana*); (w) = Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*).

[2] Means sharing the same superscript are not significantly different at the 5 percent level.

Hanks and others (1971) studied the chromatographic profile and preference of 100 populations of big sagebrush. They described four chromatographic profiles within mountain big sagebrush and two within basin big sagebrush. Cattle grazing in the Jackson Mountains in northwestern Nevada preferred mountain big sagebrush over basin big sagebrush. Cattle utilized more than 60 percent of the current year's growth of mountain big sagebrush but utilized less than 15 percent of basin big sagebrush current year's growth.

Welch and others (1987), using the same three gardens as described in the wintering mule deer preference study of Welch and McArthur (1986b), studied the utilization of big sagebrush by wintering domestic sheep. Five range-experienced domestic sheep were allowed to graze in the three gardens while having continuous access to high quality alfalfa hay and 0.28 kg of rolled barley per head per day; thus, feeding on big sagebrush was out of choice, not out of hunger. Results of their experiment are given in table 5.6. Accessions that were most heavily used were Kaibab, Colton, Trough Springs, Wingate Mesa, Milford, Brush Creek, and Hobble Creek; three Wyoming, two basin, and two mountain big sagebrushes. Welch and others (1987, p.113) noted that "the sheep tend to remove significant (60 to 70%) amounts of current growth from the more preferred accessions before removing even small (15%) amounts of less preferred accessions." Repeated grazing of an area may result in the loss of preferred plants (Rodriguez and Welch 1989; Wagstaff and Welch 1991).

Pygmy rabbits, an obligate of big sagebrush, showed no preference for either mountain or basin big sagebrush; instead, preference was expressed at the accession or population level (White and others 1982). An accession called Hobble Creek II was among the most preferred.

Welch and others (1991) conducted an experiment to determine sage grouse preference for mountain, Wyoming, and basin big sagebrush and for accessions within subspecies. This study was carried out by placing captured sage grouse in a cage supporting different subspecies and accessions within subspecies

Table 5.6—Variation in the utilization of 21 big sagebrush (*Artemisia tridentata*) accessions by wintering domestic sheep. Plants grown in three uniform gardens. Data expressed as percentage of current year's growth eaten. Data from Welch and others (1987).

Accession[1]	Garden			
	Gordon Creek	**Salt Creek**	**Springville**	**Mean[2]**
	Percent			
Kaibab (w)	100.0	97.8	97.1	98.3[a]
Colton (m)	93.5	96.0	87.5	92.3[a]
Trough Springs (w)	96.8	85.5	91.0	91.1[a]
Wingate Mesa (b)	78.8	88.5	90.5	85.9[ab]
Milford (w)	76.8	84.5	86.7	82.7[ab]
Brush Creek (b)	82.5	83.5	79.0	81.7[ab]
Hobble Creek (m)	79.6	84.1	78.0	80.6[ab]
Pinto Canyon (m)	78.4	70.5	81.2	76.6[b]
Sardine Canyon (m)	61.3	59.6	53.5	58.1[c]
Petty Bishops Log (m)	42.2	48.9	55.3	48.3[c]
Evanston (w)	46.3	33.8	52.5	44.2[cd]
Indian Peaks (m)	35.1	45.9	38.3	39.8[cde]
Clear Creek Canyon (m)	18.7	24.6	21.6	21.6[de]
Benmore (m)	11.1	18.5	20.6	16.7[de]
Durkee Springs (m)	12.3	21.4	14.7	16.1[ef]
Salina Canyon (m)	9.9	12.3	10.4	10.9[f]
Dog Valley (b)	.0	5.2	8.1	4.4[f]
Clear Creek Canyon (b)	.0	3.9	1.7	1.9[f]
Evanston (b)	.0	1.5	.0	.5[f]
Loa (b)	.0	.0	.0	.0[f]
Dove Creek (b)	.0	.0	.0	.0[f]

[1] (b) = basin big sagebrush (*Artemisia t.* ssp. *tridentata*); (m) = mountain big sagebrush (*A. t.* ssp. *vaseyana*); (w) = Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*).

[2] Means sharing the same superscript are not significantly different at the 5 percent level.

of big sagebrush. Number of bites per subspecies and accessions within subspecies were recorded on video tapes. Results, by order of preference, were mountain, Wyoming, and basin big sagebrush. On an accessional basis, Windy Ridge, a mountain big sagebrush, was preferred over all accessions. The Hobble Creek accession, also a mountain big sagebrush, was the second most preferred accession. The Windy Ridge accession was collected from the Strawberry Valley area of north-central Utah, about 225 km north by northeast of the sage grouse capture site about 4 miles west of Loa, UT. Welch and others (1991) had observed birds in this area eating this accession for a number of years. The 'Hobble Creek' accession was a released accession of mountain big sagebrush for use on wintering mule deer and domestic sheep ranges (Welch and others 1986a). 'Hobble Creek' was collected about 209 km north of the sage grouse capture site. Sage grouse are not present in the collection area; thus, sage grouse use for this accession was unknown. The third and last accession representing mountain big sagebrush was Vance Reservoir. This accession was collected near the capture site of the sage grouse used in the Welch and others (1991) study. They had observed sage grouse use of this accession for several years prior to their study. If predisposing factors were playing a role in determining sage grouse preference, then Vance Reservoir would have been favored. The same could have been said for the Loa accession of Wyoming big sagebrush and the Elise accession of basin big sagebrush, but none of these accessions collected near the capture site were among the most preferred accessions. Therefore, previous exposure did not play an important role in determining sage grouse preference.

In summary, Welch and others (1991, p. 464) stated:

> Sage grouse under the conditions of this study showed definite preference for mountain big sagebrush and for certain accessions within this subspecies. However, when leaves and buds of the preferred plants became limited, the birds shifted to lesser liked plants. This shift was not noticeable until after analysis of the video tapes. We concluded that the birds, while expressing preference, are capable of shifting their eating habits.

Remington and Braun (1985) reported that wintering sage grouse in their study preferred Wyoming big sagebrush over mountain big sagebrush. There were significant differences in the ways the two studies were carried out. The plants of the Welch and others (1991) study were planted at random in a common garden, meaning the birds had equal access to all accessions and subspecies. A cage was built over the garden to maintain the sage grouse. The Remington and Braun (1985) study was conducted in the field where the subspecies grow in different habits, such as the bottom of draws, which may influence the movement of the birds; if so, their perceived preferential use could be due to uneven bird distribution. Mountain big sagebrush does not normally grow where Wyoming big sagebrush does, so preference may become more of an academic issue than a real issue with sage grouse, because as Welch and others (1991) observed, the birds are capable of shifting from preferred big sagebrush plants to lesser preferred big sagebrush plants without any perceived problems.

Data by Graham and others (2001, table 4) show that gall-forming insects preferred mountain big sagebrush over basin big sagebrush. For example, the gall formed by *Rhopalomyia ampullaria*, a midge, induced 31.2 galls per cubic meter on basin big sagebrush growing on its native sites verus 5,610 on mountain big sagebrush growing on its native site. Four species of gall-inducing insects were found forming galls on basin big sagebrush, whereas, seven gall-inducing insects were forming galls on mountain big sagebrush. Only the fruitfly, *Eutreta diana*, formed more galls on basin big sagebrush (2.73 per cubic meter) than on mountain big sagebrush (0.835 per cubic meter). Welch and McArthur (1981) and McArthur and others (1988) showed that mountain big sagebrush contained higher concentrations of monoterpenoids than basin big sagebrush. Still Graham and others (2001, p. 245) state: “The major herbivore deterrents used by *Artemisia* are terpenes.” How the authors square their statement with the fact that a host of organisms feed directly on big sagebrush and that mountain big sagebrush contains higher concentrations of terpenes is not known (chapters II and III).

Because a number of preference studies were conducted on uniform or common gardens, or in other words, environmental factors that could influence preference were kept constant, any differences in preference would be due to differences in the genetic makeup of the accessions and or subspecies (Scholl and others 1977; Welch and McArthur 1986b; Welch and others 1981, 1983, 1987, 1991,1992a). The heritability of preference is unknown in big sagebrush.

Digestibility

Digestibility is an important characteristic of forage plants such as big sagebrush. Welch and Pederson (1981) studied winter in vitro digestibility by mule deer inoculum of accessions and subspecies of big sagebrush. Results of their research are given in table 5.7. In a uniform garden, where environmental factors were held constant, basin big sagebrush was more digestible than mountain and Wyoming big sagebrush. On an accession level, some accessions were more highly digested than others. In a companion study, Welch and others (1992a) studied the winter in vitro digestibility of 13 accessions of Wyoming big sagebrush grown on three uniform gardens. Results of their study are given in table 5.8. Overall, these studies demonstrated that big sagebrush is a highly digestible forage for wintering mule deer and that digestibility is under genetic control.

Table 5.7—Winter *in vitro* digestibility among accessions and subspecies of big sagebrush (*Artemisia tridentata*) grown in a uniform garden. Data expressed as percent of digestible dry matter. Data from Welch and Pederson (1981).

Subspecies of big sagebrush		Accessions of big sagetrush	
Subspecies	Percent digested[1]	Accessions[2]	Percent digested[1]
Basin	62.1[a]	Clear Creek (b)	64.8[a]
Mountain	53.2[b]	Dove Creek (b)	64.6[a]
Wyoming	51.4[b]	Loa (b)	57.0[b]
		Indian Peaks (m)	55.8[b]
		Benmore (m)	55.2[b]
		Kaibad (w)	54.9[b]
		Milford (w)	54.6[b]
		Sardine Canyon (m)	48.7[bc]
		Trough Springs (w)	44.6[c]

[1] Values sharing the same letter superscript in a column are not significantly different at the 5 percent level.

[2] (b) = basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*); (m) = mountain big sagebrush (*A. t.* ssp. *vaseyana*); (w) = Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*).

Table 5.8—Winter in vitro digestibility of 13 accessions of Wyoming big sagebrush (*Artemisia tridentata* ssp. w*yomingensis*). Data from three uniform gardens were pooled. Data expressed as the percentage of dry matter digested. Data from Welch and others (1992a).

Accessions	Percent digested^{1}
Arco	56.6^{a}
Squaw Butte	55.1^{ab}
South Fredonia	53.7^{ab}
Warren	53.7^{abc}
Gordon Creek	52.8^{bcd}
Oasis	51.7^{bcd}
Brown’s Park	50.8^{cde}
Rush Valley	50.8^{cde}
Glenns Ferry	50.5^{cde}
Loa	50.4^{de}
North Kemmerer	50.1^{de}
Daniel	47.8^{e}
Dinosaur	47.7^{e}

[1] Means sharing the same superscript are not significantly different at the 5 percent level.

Table 5.9—Winter crude protein content of current year’s vegetative growth among accessions of big sagebrush (*Artemisia tridentata*) grown in a uniform garden. Data expressed on a dry-matter basis. Data from Welch and McArthur (1979b) and Welch (1983).

Accessions^{1}	Percent of crude protein^{2}
Dove Creek (b)	16.0^{a}
Clear Creek Canyon (b)	15.3^{ab}
Evanston (b)	15.2^{b}
Dog Valley (b)	14.5^{bc}
Loa (b)	14.5^{bc}
Big Brush Creek (b)	13.1^{bcd}
Evanston (w)	12.9^{cd}
Wingate Mesa (b)	12.8^{de}
Colton (m)	12.0^{def}
Kaibab (w)	11.9^{def}
Clear Creek Canyon (m)	11.7^{def}
Salina Canyon (m)	11.7^{def}
Alton (m)	11.3^{efg}
Milford (w)	11.2^{efg}
Petty Bishop’s Log (m)	11.2^{efg}
Indian Peaks (m)	11.2^{efg}
Trough Springs (w)	11.0^{fg}
Pinto Canyon (m)	11.0^{fg}
Sardine Canyon (m)	10.5^{fg}
Durkee Springs (m)	10.0^{a}
Benmore (m)	10.0^{g}

[1] (b) = basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*); (m) = mountain big sagebrush (*A. t.* ssp. *vaseyana*); (w) = Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*).

[2] Means sharing the same superscript are not significantly different at the 5 percent level.

Table 5.10—Winter crude protein content of three subspecies of big sagebrush—basin, mountain, and Wyoming—2-year summary. Plants grown in a uniform garden; percentages expressed on a dry matter basis. Data from Welch and McArthur (1979b) and Welch (1983).

Subspecies^{1}	Percent of crude protein^{2}
Basin	14.5^{a}
Wyoming	11.8^{b}
Mountain	11.1^{b}

[1] Basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*); mountain big sagebrush (*A. t.* ssp. *vaseyana*); Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*).

[2] Means sharing the same superscript are not significantly different at the 95 percent level.

Crude Protein

Winter crude protein content of dry matter is also an important characteristic of forage plants. Welch and McArthur (1979b) reported that some accessions grown under uniform conditions contained significantly higher levels of crude protein than others (table 5.9). Thus, crude protein of big sagebrush is under genetic control. They further noted that basin big sagebrush (table 5.10), the least preferred by wintering mule deer, contained higher levels of crude protein than mountain or Wyoming big sagebrush (table 5.11). They suggested that a high crude protein accession might be hybridized with a highly preferred accession, resulting in a superior form of big sagebrush. Welch and others (1992a) noted that accessions grown within a subspecies, such as Wyoming big sagebrush, varied significantly in amount of winter crude protein. In general, big sagebrush contains higher levels of winter crude protein than most winter forages (see chapter IV for more details).

Monoterpenoids

The postulated adverse effects that big sagebrushs’ monoterpenoids might have on mule deer digestion and preference were proven later to be erroneous (Welch and others 1982; Welch and Pederson 1981)

Table 5.11—Winter crude protein of 13 accessions of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*). Data from three uniform gardens were pooled. Data expressed as the percentage of dry matter. Data from Welch and others (1992a).

Accessions	Percent of crude protein[1]
Daniel	13.9^{a}
North Kemmerer	13.5^{ab}
Squaw Butte	13.1^{ab}
Arco	13.1^{ab}
Oasis	12.8^{bc}
Rush Valley	12.5^{bc}
Gordon Creek	11.9^{cd}
Warren	11.9^{cd}
Dinosaur	11.9^{cd}
Glenns Ferry	11.8^{d}
Brown's Park	11.7^{de}
Loa	11.3^{de}
South Fredonia	10.8^{e}

[1] Means sharing the same letter superscript are not significantly different at the 5 percent level.

(see chapter IV for details). So studies were conducted to measure the amount of variability among accessions and subspecies of big sagebrush grown in uniform gardens for monoterpenoid concentration. The idea was to locate accessions or subspecies having low concentrations of monoterpenoids that might be used in a breeding and selection program to improve the nutritive value of big sagebrush. Welch and McArthur (1981) found that the midwinter monoterpenoid (volatile or essential oils) concentration of big sagebrush was under genetic control, although there is a strong seasonal factor (Cedarleaf and others 1983). This conclusion was based on the results of their study, which showed that mountain big sagebrush contained significantly higher concentrations of monoterpenoids than basin and Wyoming big sagebrush growing in a uniform garden (table 5.12). In addition, certain accessions of big sagebrush contained significantly lower concentrations of monoterpenoids than others. Total monoterpenoids, expressed on a percentage of dry-matter basis, varied from 0.93 to 2.95 percent among 20 big sagebrush accessions grown in a uniform garden (Welch and McArthur 1981) (table 5.13). Welch and McArthur (1981, p. 380) concluded: "If monoterpenoids interfere with digestion or have a negative impact on palatability, breeding and selection schemes can be developed to capitalize on the significant variation that exists among accessions of *A. tridentata*."

The inheritance of monoterpenoids and other hydrocarbons in big sagebrush has received limited study. Inheritance of monoterpenoids involving a cross between basin big sagebrush (Dove Creek accession) and mountain big sagebrush ('Hobble Creek' accession) by McArthur and others (1988) is illustrated in table 5.2. As explained in an earlier section, the F_1 hybrid's monoterpenoid profile was, in general, intermediate between the two parents. These observations have been extended to F_2 hybrids by Weber and others (1994). They compared the number of volatile compounds detected by capillary gas chromatography from parental lines with the number of volatile compounds produced by the F_2 hybrids. Capillary gas chromatography detected 25 compounds, some of which were monoterpenoids, from the Dove Creek parent, 18 from the 'Hobble Creek' parent, and 22, 27, and 37 from the F_2 hybrids. Weber and others (1994) explained that such results would be expected from the principles of genetic recombination. In comparing Dove Creek to 'Hobble Creek' there were 37 compounds, 19 common to both, 17 unique to Dove Creek, and one unique to 'Hobble Creek'. The number of compounds between Dove Creek and F_2 hybrids was 43, 27 common to both,

Table 5.12—Winter total and individual monoterpenoid concentrations of three subspecies of big sagebrush (*Artemisia tridentata*) grown in a uniform garden. Data expressed as the percentage of dry matter. Data from Welch and McArthur (1981).

	Monoterpenoids[1]								
Subspecies[2]	a-pinene	Camphene	1,8 cineol	a-thujone	b-thujone	d-camphor	Terpineol	Unknowns	Totals
					Percent				
Mountain	0.02^{a}	0.04^{ab}	0.10^{b}	0.27^{b}	0.47^{b}	0.35^{a}	0.19^{b}	0.73	2.20^{b}
Basin	$.02^{a}$	$.03^{a}$	$.02^{a}$	$.09^{a}$	$.41^{b}$	$.31^{a}$	$.02^{a}$	.44	1.40^{a}
Wyoming	$.08^{b}$	$.08^{b}$	$.04^{ab}$	$.04^{a}$	$.01^{a}$	$.58^{b}$	$.01^{a}$	.19	1.07^{a}

[1] Values of total and individual monoterpenoid levels among the subspecies sharing the same superscript are not significantly different at the 5 percent level.

[2] Mountain = *Artemisia tridentata* ssp. *vaseyana;* basin = *A. t.* ssp. *tridentata;* Wyoming = *A. t.* ssp. *wyomingensis*.

Table 5.13—Winter total and individual monoterpenoids concentrations among 20 accessions of big sagebrush (*Artemisia tridentata*) grown in an uniform garden. Data expressed as the percentage of dry matter basis. Data from Welch and McArthur (1981).

	Monoterpenoids[1]								
Subspecies[2]	**a-pinene**	**Camphene**	**1,8 cineol**	**a-thujone**	**b-thujone**	**d-camphor**	**Terpineol**	**Unknowns**	**Totals**
Kaibab (w)	0.11^{d}	0.11^{c}	0.02^{a}	0.00^{a}	0.00^{a}	0.63^{cd}	0.01^{a}	0.05	0.93^{a}
Clear Creek (b)	$.00^{a}$	$.00^{a}$	$.02^{a}$	$.05^{b}$	$.31^{b}$	$.24^{bc}$	$.01^{a}$	.32	$.95^{a}$
Milford (w)	$.05^{c}$	$.03^{abc}$	$.01^{a}$	$.13^{cd}$	$.04^{a}$	$.22^{bc}$	$.00^{a}$	.33	$.99^{a}$
Wingate (b)	$.04^{c}$	$.08^{bc}$	$.01^{a}$	$.02^{a}$	$.02^{a}$	$.71^{cd}$	$.02^{a}$	.07	1.01^{a}
Big Brush (b)	$.02^{bc}$	$.08^{bc}$	$.04^{ab}$	$.00^{a}$	$.06^{a}$	$.42^{bc}$	$.02^{a}$	.38	1.02^{a}
Colton (m)	$.01^{b}$	$.01^{ab}$	$.01^{a}$	$.02^{ab}$	$.48^{bc}$	$.15^{b}$	$.00^{a}$	.34	1.02^{a}
Trough Springs (w)	$.09^{d}$	$.09^{bc}$	$.08^{bc}$	$.00^{a}$	$.00^{a}$	$.89^{d}$	.02	.24	1.41^{ab}
Dog Valley (b)	$.02^{bc}$	$.02^{abc}$	$.01^{a}$	$.24^{d}$	$.33^{b}$	$.26^{bc}$	$.03^{a}$	.60	1.51^{ab}
Pinto Canyon (m)	$.04^{c}$	$.08^{bc}$	$.06^{b}$	$.04^{b}$	$.01^{a}$	$.54^{cd}$	$.37^{b}$	.29	1.63^{ab}
Evanston (b)	$.01^{b}$	$.00^{a}$	$.00^{a}$	$.09^{bc}$	$.89^{d}$	$.13^{b}$	$.01^{a}$	0.53	1.66^{ab}
Dove Creek (b)	$.00^{a}$	$.00^{a}$	$.02^{a}$	$.07^{bc}$	$.71^{bc}$	$.13^{b}$	$.00^{a}$	.77	1.70^{bc}
Indian Peaks (m)	$.00^{a}$	$.04^{abc}$	$.12^{c}$	$.03^{ab}$	$.02^{a}$	$.31^{bc}$	$.01^{a}$	1.19	1.72^{bc}
Sardine (m)	$.02^{bc}$	$.11^{c}$	$.06^{b}$	$.25^{d}$	$.58^{c}$	$.62^{cd}$	$.05^{ab}$	.05	1.74^{bc}
Clear Creek (m)	$.00^{a}$	$.00^{a}$	$.09^{c}$	$.00^{a}$	$.75^{cd}$	$.00^{a}$	$.18^{ab}$	.80	1.82^{bcd}
Loa (b)	$.01^{b}$	$.03^{abc}$	$.09^{c}$	$.13^{cd}$	$.55^{c}$	$.28^{bc}$	$.05^{ab}$	.76	1.91^{cd}
Alton (m)	$.04^{c}$	$.07^{bc}$	$.11^{c}$	$.01^{a}$	$.29^{b}$	$.58^{cd}$	$.19^{ab}$	.69	2.03^{cd}
Petty Bishop (m)	$.00^{a}$	$.00^{a}$	$.01^{a}$	$.74^{e}$	$.60^{c}$	$.00^{a}$	$.33^{b}$	0.88	2.58^{d}
Salina (m)	$.00^{a}$	$.00^{a}$	$.02^{a}$	$.63^{c}$	$.47^{bc}$	$.00^{a}$	$.31^{b}$	1.12	2.60^{d}
Benmore (m)	$.00^{a}$	$.00^{a}$	$.09^{c}$	$.96^{f}$	$.49^{bc}$	$.05^{ab}$	$.32^{b}$	.90	2.89^{d}
Durkee Sp. (m)	$.05^{c}$	$.08^{bc}$	$.41^{d}$	$.00^{a}$	$.85^{d}$	1.20^{d}	$.16^{ab}$	.12	2.95^{d}

[1] Values of total and individual monoterpenoid levels among accessions sharing the same superscript are not significantly different at the 5 percent level.

[2] (m) = mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*); (b) = basin big sagebrush (*A. t.* ssp. *tridentata*); (w) = Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*).

eight unique to Dove Creek, and eight unique to F_2 hybrids. For the 'Hobble Creek' and F_2 hybrids comparison, there were 35 compounds, 20 common to both, none unique to 'Hobble Creek', and 15 unique to the F_2 hybrids. When they subjected their data set to cluster analysis, parents and F_2 hybrids clustered separately from one another. Weber and others (1994, p. 696) concluded with this statement: "Of particular interest in the current study is the reduced amount of the bitter methacrolein in some of the F_2s. Lowering methacrolein in hybrid selections while maintaining the desirable biomass, palatability, and protein values of one or the other parental species in those hybrid lines gives promise to the possibility of selection for *A. tridentata* for particular rangeland purposes."

Growth

Mature plant height in big sagebrush is highly variable. Pool (1908), in an extensive study of big sagebrush in Colorado, found that big sagebrush plants ranged in height from 18 inches to 8 feet. A big sagebrush plant 10 feet tall was reported by Beetle (1962) in the Wind River Valley of Wyoming and a plant about 13 feet tall at Dutch Creek in Rio Blanco County, CO. Schneegas and Nord (1967) described a monarch big sagebrush plant at 14 feet 8 inches high in the White Mountains of eastern California. Pase (1956) found a big sagebrush 15 feet 7 inches tall east of Kanab, UT. In his checklist of native and naturalized trees of the United States, Little (1953) described big sagebrush as a small tree that can be as high as 12 to 20 feet, thus earning its namesake among sagebrushes as big sagebrush. In general, basin big sagebrush is the tallest of the three subspecies of big sagebrush (Beetle 1960, 1962) with Wyoming the shortest and mountain intermediate (McArthur and Welch 1982) (table 5.14).

McArthur and Welch (1982) found that the fastest growing and largest plants were diploid, 2n = 18, and the slowest and smallest plants were tetraploid, 2n = 36. McArthur and Welch (1982, p. 396) concluded, "Comparison of three accessions' performances at two uniform gardens and their native sites indicated that growth parameters, while subject to environmental influences, are under genetic control." These observations are illustrated in table 5.15. Barker and others (1983) and Barker and McKell (1983) support the findings of McArthur and Welch (1982).

Table 5.14—Subspecies mean annual vegetative leader lengths of big sagebrush (*Artemisia tridentata*) plants grown for 5 years in three uniform gardens. Data expressed as centimeters of current year's growth. Data from Welch and McArthur (1986a).

Subspecies[1]	Length[2]
	cm
Wyoming	17.3[a]
Mountain	20.4[b]
Basin	29.6[c]

[1] Wyoming = *Artemisia tridentata* ssp. *wyomingensis*; mountain = *A. t.* ssp. *vaseyana*; basin = *A. t.* ssp. *tridentata.*

[2] Means sharing the same superscript are not significantly different at the 5 percent level.

Table 5.15—Mean vegetative leader lengths of 21 accessions of big sagebrush (*Artemisia tridentata*) plants growth on two uniform gardens for 5 years. Data expressed as centimeters of current year's growth. Data from Welch and McArthur (1986a).

Accession[1]	Length[2]
	cm
Petty Bishop's Log (m)	15.3[a]
Trough Creek (w)	15.5[a]
Evanston (w)	15.8[a]
Big Brush Springs (b)	16.7[ab]
Colton (m)	17.2[ab]
Milford (w)	17.2[ab]
Benmore (m)	18.8[bc]
Clear Creek Canyon (m)	20.1[cd]
Sardine Canyon (m)	20.2[cd]
Durkee Springs (m)	20.6[cde]
Kaibab (w)	20.7[cde]
Wingate Mesa (b)	20.9[cde]
Indian Peaks (m)	22.4[def]
Salina Canyon (m)	23.0[ef]
Hobble Creek (m)	23.1[ef]
Pinto Canyon (m)	23.2[f]
Clear Creek Canyon (b)	30.8[g]
Evanston (b)	30.9[g]
Dog Valley (b)	33.0[h]
Loa (b)	33.1[h]
Dove Creek (b)	41.4[i]

[1] (m) = mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*); (w) = Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*); (b) = basin big sagebrush (*A. t.* ssp. *tridentata*).

[2] Means sharing the same superscript are not significantly different at the 5 percent level.

Davis and Stevens (1986) also studied the vegetative growth rate of subspecies and accessions within subspecies grown in uniform gardens. However, their experimental design differs from the pervious studies in that they measured growth in terms of grams of dry matter per centimeter of leader length as compared to length of vegetative leader or current year's growth. They were unable to demonstrate a statistical difference among subspecies, but their data did show a trend that favored mountain big sagebrush (0.346 g/cm) over basin (0.303 g/cm) and basin over Wyoming (0.293 g/cm). When their values (grams of dry matter per centimeter of leader length) for the three subspecies of big sagebrush are combined or multiplied with the values for vegetative leader length (table 5.14), basin big sagebrush was 9.00 g per leader length, which exceeded mountain at 7.06 g, which in turn exceeded Wyoming at 5.07 g. Still valid are the observations by previous workers that in general basin big sagebrush is a larger subspecies than mountain, and mountain is larger than Wyoming (Barker and McKell 1983; Barker and others 1983; McArthur and Welch 1982; Welch and McArthur 1986a).

The influence of genetics on growth rates among subspecies and accessions of big sagebrush is illustrated in a greenhouse study conducted by Booth and others (1990). They were able to grow big sagebrush plants representing three subspecies that were, in turn, represented by four or five accessions in a nonlimiting environment for 25 weeks. Results of this study are shown in figure 5.5. Three points are apparent: (1) over an extended period and in a nonlimiting environment, the rate of seedling growth in Wyoming big sagebrush approached zero and was less than that of seedlings of basin and mountain big sagebrush; (2) basin and mountain big sagebrush continued to have nonnegligible growth rates even at the end of the 25-week growing period; and (3) Wyoming big sagebrush reached its point of maximum growth rate approximately 2 weeks earlier than did the other two subspecies. Because this study was conducted in a nonlimiting environment, they concluded that genetic factors, not environmental factors, were responsible for limiting seedling growth of Wyoming big sagebrush. It would appear that evolutionary pressures, mainly dryness and shallow soils, resulted in the development of genetic control for smallness in Wyoming big sagebrush plants. Smallness would allow Wyoming big sagebrush to survive on xeric sites, where basin and mountain big sagebrush cannot.

Results of the Booth and others (1990) study disagree with the report of Harniss and McDonough (1975). They were unable in a 10-week study to differentiate the rate of growth of seedlings among the three subspecies.

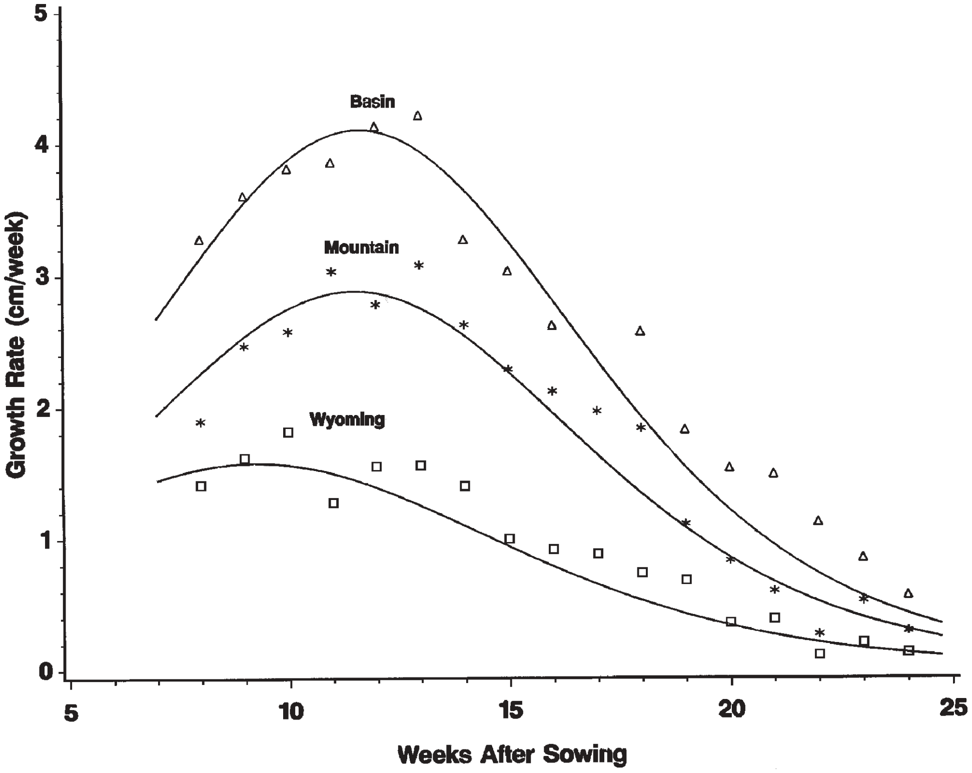

Figure 5.5—The growth rate of seedlings of three subspecies of big sagebrush (*Artemisia tridentata*) in a non-limiting water environment (after Booth and others 1990).

In a companion study to that of Booth and others (1990), Welch and Jacobson (1988) reported that for the first 10 days after germination the rate of root growth of Wyoming big sagebrush significantly exceeded that of basin and mountain big sagebrush. Part of this faster root growth was attributed to a faster germination rate for Wyoming big sagebrush. At 20 and 30 days, the rate of root growth of Wyoming and basin big sagebrush was not significantly different, but both significantly exceeded mountain big sagebrush. At 40 days, the rate of root growth of basin big sagebrush significantly exceeded that of Wyoming, which, in turn, exceeded mountain. At 174 days, basin (926 mm) and Wyoming (876 mm) big sagebrush root lengths were significantly longer than mountain (680 mm), but were not different from each other.

Thus, it appears that Wyoming big sagebrush has evolved to achieve maximum aboveground growth rate early in the growing season but limits the amount of aboveground growth. Limiting aboveground growth would allow the plant to assign energy to rapid root growth and development, characteristics that are important for surviving a xeric site. There appears to be exploitable genetic variability among subspecies and accessions within subspecies for growth that may be incorporated in a selection and breeding program aimed at combining rapid growth with other desirable characteristics. However, rapid growth cannot be supported by all environments that big sagebrush live in.

Germination

There appear to be genetic factors involved in the expression of germination patterns among subspecies and accessions within subspecies. Meyer and Monsen (1992) found that mountain big sagebrush contained a higher percentage of dormant seeds that germinated slower than basin and Wyoming big sagebrush seeds. McDonough and Harniss (1974) noted lower mean percent germination for mountain big sagebrush as compared to basin and Wyoming big sagebrush and that stratification increased seed germination for all accessions of mountain big sagebrush and for some accessions of basin and Wyoming big sagebrush. Young and others (1991) found differences in germination profiles among accessions of big sagebrush. Meyer and Monsen (1992, p. 87) were able to relate some of these germination profile differences to environmental differences: “Collections from severe winter sites required up to 113 days to germinate to 50% at 1° C, while collections from mild winter sites required as few as 6 days.” Details on germination patterns among big sagebrush subspecies and accessions within subspecies are given in chapter VI.

Summary

An alternate title for this section on variability could be “Not All Big Sagebrush Are Created Equal.” Due to the large variability expressed among subspecies and accessions within subspecies of big sagebrush for preference, digestibility, crude protein, monoterpenoids, growth or biomass production, and germination, it is apparent that big sagebrush has a rich, variable germplasm. A rich, variable germplasm is the foundation on which successful selection and breeding programs are based. In the next section, I will discuss the feasibility of improving big sagebrush through selection and breeding (Welch and McArthur 1979a).

Selection and Breeding

Voigt (1975, p. 42) stated in the Improved Range Plants Symposium, “Species that are aggressive, productive, and persistent are the ones most likely to benefit from increased forage quality and possibly from increased palatability.” Perhaps few Western native range plants are more aggressive, productive, and persistent than big sagebrush. Big sagebrush contains a rich array of characters (McArthur 1981). This genetic diversity provides the opportunity for finding (selection) or building (breeding) superior big sagebrush germplasms and cultivars that could better meet the needs of land managers (Plummer 1972; Welch and others 1986b). Success of a big sagebrush improvement program depends on the degree that improved big sagebrush germplasms and cultivars meet specific management needs (Plummer 1972; Welch 1994). A precise description of management needs is therefore basic. These needs vary but fall into three general categories: soil stabilization, animal habitat, and esthetics (Blaisdell 1972). For soil stabilization, evaluation criteria would include: rooting characteristics such as depth, distribution, and soil binding ability; potential resistance to disease and insect problems; ease of establishment such as direct seeding, site preparation, competitiveness, and seedling vigor; palatability (for some needs, unpalatable big sagebrush may be desirable); longevity; and adaptation to the environmental conditions detailed in the description of management needs. Animal habitat needs include forage and cover. Forage must meet the nutritional requirements of target animals (Welch and McArthur 1990). These requirements are digestibility, minerals, vitamins, protein, and biomass production (see chapter IV for more details). Cover requirements of target animals include thermal, escape, nesting, and breeding. Evaluation criteria for cover include not only basic survival characteristics, but also form (height, spread) and compatibility with other plant species.

The heart of a big sagebrush selection and breeding program is the performance of subspecies and accessions in uniform gardens. Uniform gardens standardize the environmental effect on character expression, and any differences are due to genetic differences that may be exploitable (McArthur and others 1985). Exploitable variability for a host of important characteristics has been discussed in the previous section (tables 5.4 through 5.15).

Selection

A need that has been worked on for some years is to raise the nutritive level of forage plants on critical big game winter ranges (Blaisdell 1972). Because of its superior winter nutritive content (see chapter IV for details) big sagebrush became the leading candidate to meet this need. “No matter how abundant or how nutritious a plant may be, it has no value as fodder unless animals eat it” (Everist 1972). The search for palatable forms of big sagebrush that could be used on big game winter ranges began in the late 1960s with the establishment of uniform gardens at Gordon Creek near Helper, UT, and at the Snow Field Station at Ephraim, UT (Hanks and others 1971; Plummer and others 1968). This search resulted in the release, through the Utah Crop Improvement Association, of a named selection of mountain big sagebrush collected at the mouth of the Hobble Creek Canyon east of Springville, UT, named ‘Hobble Creek’ (Welch and others 1986a).

‘Hobble Creek’ Mountain Big Sagebrush

‘Hobble Creek’ mountain big sagebrush was released for use on mule deer and domestic sheep winter ranges, sage grouse habitat, and restoration projects (McArthur 1988; Welch 1992, 1993; Welch and others 1986a). Of the 186 big sagebrush accessions tested in Utah, ‘Hobble Creek’ was the most preferred by wintering mule deer (Welch and others 1986a) (table 5.5). In studies conducted in Colorado, Idaho, Oregon, and Washington, winter mule deer preferred ‘Hobble Creek’ over native big sagebrush (Welch 1993; Welch and others 1986a, 1992b). It was also preferred by winter mule deer over an unknown selection of antelope bitterbrush (*Purshia tridentata*) (Welch and Wagstaff 1992). Wintering domestic sheep, on the other hand, ranked ‘Hobble Creek’ high but not as most preferred (Welch and others 1987) (table 5.6). Similar results were obtained for sage grouse (Welch and others 1991). In Utah and Oregon, pronghorn antelope ate a high percent of the current year's growth of 'Hobble Creek' plants (Welch and others 1992b).

Winter crude protein content of 'Hobble Creek' big sagebrush is 11 percent of dry matter, which is well above the maintenance requirement of 7 to 8.9 percent. This ranks high among winter forages, in general, but as a big sagebrush its winter crude protein level is below the average of those tested in table 5.9. Winter phosphorus content of 'Hobble Creek' is 0.21 percent of dry matter, which, like crude protein, ranks high for a winter forage but somewhat average for a big sagebrush. Winter in vitro digestibility of 'Hobble Creeks' dry matter is 52.6 percent, just below the average of big sagebrush accessions tested in table 5.7.

'Hobble Creek' big sagebrush productivity, expressed as length of vegetative leader growth, was exceeded only by five accessions of basin big sagebrush tested (table 5.14). 'Hobble Creek' productivity, expressed as grams per centimeter of vegetative stem, ranked third out of 20 accessions tested (Davis and Stevens 1986).

'Hobble Creek' big sagebrush can be grown or established on sites with the following physical characteristics:

1. Mean annual precipitation of 14 or more inches.
2. Deep, well-drained soils with an effective rooting depth of at least 4 feet.
3. Soil no finer than clay loam (40 percent clay or less). On sites with heavy clay soils, 'Hobble Creek' appears to be predisposed to root rot and vascular wilt type pathogens.
4. Soil pH between 6.6 and 8.6.
5. Growing season of 90 days or more.

Because of shallow soils and lower precipitation, trying to establish Hobble Creek on Wyoming big sagebrush sites is not recommended.

'Hobble Creek', like other types of big sagebrush, can be established on suitable sites by direct seeding onto properly prepared seedbeds and by transplanting bareroot or containerized stock (see chapter VI for details).

Gordon Creek Wyoming Big Sagebrush

For dryer habitats, 10 to 13 inches of precipitation per year, uniform gardens of Wyoming big sagebrush were established on three mule deer winter ranges in Springville, UT, Glenns Ferry, ID, and Taylor Flats in Brown's Park, UT, about 12 mile east of Dutch John (Welch and others 1992a). Thirteen accessions were collected from geographically distinct sites in the States of Utah, Idaho, Arizona, Oregon, Colorado, Montana, and Wyoming (Welch and others 1992a). Each accession was evaluated in terms of current year's growth of vegetative leaders, winter mule deer preference, winter crude protein, phosphorus content, and in vitro digestibility.

Based mainly on the preference measurements, an accession of Wyoming big sagebrush collected from the Gordon Creek area near Helper, UT, was chosen as a superior tested germplasm of Wyoming big sagebrush (Welch and others 1992a). While not as preferred as 'Hobble Creek' big sagebrush, wintering mule deer utilized a significantly higher percentage of its current year's vegetative growth as compared to the remaining Wyoming big sagebrushes (Welch and others 1992a). Sage grouse also will eat it (Welch and others 1991). Its nutritive value ranked in the middle of the accessions tested for crude protein at 11.9 percent of dry matter, in vitro digestibility at 52.8 percent, and phosphorus at 0.21 percent (tables 5.8 and 5.11) (Welch and others 1992a). While these nutritive values exceed most winter forages, as a big sagebrush, they are about average (Welch 1989).

Gordon Creek Wyoming big sagebrush germplasm appears to be widely adapted and can be grown on sites with the following physical characteristics:

1. Mean annual precipitation of 10 to 13 inches.
2. Deep to shallow, well-drained soils.
3. Clay content to 55 percent.
4. Soil pH between 6.6 and 8.8.
5. Growing season of at least 80 days.

Breeding

Pendleton and others (1989) described the breeding system of big sagebrush as wind-pollinated, perfect flower producing a dry fruit called an achene that is 2 to 3 mm in diameter (also see McArthur 1984, 1989). McArthur (1984) observed that self-pollination is possible, but outcrossing leads to a higher production of viable achenes or seeds and greater population variability. Pendleton and others (1989) classified the dispersal of big sagebrush achene as microwind, meaning that the achenes are dispersed by wind because they are light and small but lack any special structures that would enhance floating or moving with the wind.

Not all superior characteristics are expressed in a single accession or subspecies of big sagebrush (see tables 5.5 through 5.15). For example, 'Hobble Creek', an accession of mountain big sagebrush, is most preferred by wintering mule deer, but Dove Creek, an accession of basin big sagebrush, is more digestible, contains higher amounts of crude protein, and produces greater vegetative leader growth or biomass. In addition, both 'Hobble Creek' and Dove Creek are diploids and have compatible chromosome numbers (McArthur and others 1981; McArthur and Sanderson 1999). Therefore, a superior form of big sagebrush could be achieved if the nutritive characteristics of Dove Creek could be combined with the high preference of 'Hobble Creek'.

Hybridization between 'Hobble Creek' and Dove Creek has been described in a previous section. Resultant hybrids are for the most part intermediates of the two parental lines. However, hybrid growth performance is subject to environmental x genotype interaction; F_2 plants grew at intermediate rates (fig. 5.6; McArthur, unpublished data) at the Upper Colorado Environmental Plant Center at Meeker, CO, but demonstrated equal growth rates to parental plants at Green Canyon, near Logan, UT (Messin and others 2002). Unfortunately, hybrids have not been evaluated either for nutritive characteristics or for their environmental adaptation. Leaf shape of the hybrid is broadly cuneate, like that of the paternal line—'Hobble Creek' (fig. 5.6).

An accession of Wyoming big sagebrush, a tetraploid, has been successfully hybridized with silver sagebrush (*Artemisia cana*; McArthur and others 1998b; McArthur and Sanderson 1999). The idea behind this cross is to combine the widespread adaptability of Wyoming big sagebrush with the root-sprouting fire-tolerance ability of silver sagebrush as a means of maintaining woody species on areas exposed to frequent fires due to the presence of cheatgrass (*Bromus tectorum)* and other alien annual weeds.

Figure 5.6—Maternal (Dove Creek—basin big sagebrush—*Artemisia tridentata* ssp. *tridentata*–large photo left) and paternal('Hobble Creek'—mountain big sagebrush—*A. t.* ssp. *vaseyana*–bottom right photo) used to produce F_2 hybrid (top right photo). All three plants are shown growing in a uniform garden (photos by E. Durant McArthur).

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Notes

Chapter VI

Putting Big Sagebrush Back Into Its Ecosystem

This chapter covers the principles of establishing big sagebrush stands in areas where they have been destroyed; the production, harvesting, cleaning, and storage of big sagebrush seeds; and seed dispersal.

Establishment

Big sagebrush can be established on suitable sites by direct seeding, by transplanting bareroot or containerized stock, or by a technique termed “mother plant.” Descriptions of these techniques follow (McArthur and others 1974; Plummer and others 1968; Welch and others 1986, 1992).

Direct Seeding

Direct seeding is the most practical method of establishing big sagebrush on areas larger than 10 acres. The first step in establishing a big sagebrush stand is obtaining high-quality, certified (source-identified and pathogen-free) seed. Chapter I noted that the three major subspecies of big sagebrush discussed in this work grow on vastly different sites or habitats. Wyoming big sagebrush occupies the driest and hottest big sagebrush habitats, whereas mountain big sagebrush occupies the wettest and coolest habitats, with basin somewhat intermediate between the two. Therefore, the first job in any attempt to reestablish big sagebrush is to determine what subspecies of big sagebrush the prospective site supported. Mountain big sagebrush will do poorly on the dry and hot Wyoming big sagebrush sites and, conversely, Wyoming big sagebrush will do poorly on mountain big sagebrush sites.

Selection of Seed Source

Several studies show that seeds of the different big sagebrush subspecies germinate differently. McDonough and Harniss (1974a), studying the germination rate of seed collected from the three subspecies of big sagebrush, noted that basin big sagebrush germination percentages were significantly higher than those of Wyoming and mountain big sagebrush, and Wyoming was significantly higher than mountain big sagebrush under the conditions of their experiment. Evans and Young (1986) studying germination profiles for five populations of big sagebrush reported higher germination percentages for seeds of basinbig sagebrush compared to mountain big sagebrush (also see Young and others 1991). Unfortunately, there was no indication that ungerminated seeds were checked for viability; thus, the differences noted among subspecies may be due to the presence of dormant seeds that may require additional treatments to break dormancy. In fact, stratification of mountain big sagebrush seeds for 30 days increased their germination percentage well above those of basin and Wyoming big sagebrush (McDonough and Harniss 1974a). McDonough and Harniss (1974b), characterizing seed dormancy of mountain big sagebrush, found that removal of pericarp from achenes stimulated germination to 95 percent; in addition, the germination rate, that is the number of days to reach one-half of final percentage germination, was reduced to 1 day as compared to 8 to 12 days for other treatments. McDonough and Harniss (1974, p. 19) concluded: "Under natural conditions, the combined effects of winter stratification on the promotion of growth of the embryo and erosion of the pericarp by weathering and by the action of soil micro-organisms probably insure prompt and nearly complete germination by the time of snowmelt in spring." The point is that mountain, basin, and Wyoming big sagebrush all evolved under different environmental conditions and do not grow well or compete well in the others' environment.

Meyer conducted several experiments in the early 1990s (Meyer 1990; Meyer and Monsen 1990, 1991, 1992; Meyer and others 1990) that compared the germination rate of big sagebrush subspecies and sources or populations within subspecies from sites varying in winter severity. She defined germination rate as the number of days to reach 50 percent of final germination and severity of winter as the mean January temperature. Her results showed a strong negative relationship between mean January temperature and germination rate and percent of dormant seeds. That is, the warmer the mean January temperature, the fewer days needed to reach 50 percent of final germination, and a smaller percent of the seeds were dormant. Those subspecies and sources or populations within subspecies from the severest winter sites required the greatest number of days to reach 50 percent germination at 1 °C and, in the case of mountain big sagebrush, exhibited the greatest percentage of dormant seeds. These relationships for mountain big sagebrush are illustrated in table 6.1. For all subspecies and sources or populations of big sagebrush studied, the number of days to 50 percent varied from 16 to 113. She also noted that basin and Wyoming big sagebrush seeds were essentially nondormant compared to mountain big sagebrush.

Allen and Meyer (1998, p. 183) explained the significance of Meyer's work:

> Population from severe winter sites, where the major risk to seedlings is frost, tend to have long chilling requirements or to germinate very slowly at low temperatures. Populations from warmer sites, where the major risk is drought, are non-dormant and germinate very rapidly under these same conditions. Seed populations from intermediate sites exhibit variation in dormancy levels, both among and within plants, which spreads germination across a considerable time period.

Therefore, it is important to determine not only what subspecies of big sagebrush a prospective rehabilitation site supported or would support but also whether the site represents a severe, intermediate, or warmer winter site and to obtain big sagebrush seed that match these criteria (Meyer and Monsen 1993).

Because the inflorescences of big sagebrush are indeterminate, achene or seed quality varies with temperature, moisture, and time; therefore, all seedlots must be checked for viability of achenes or seeds (see plate V, fig. 75, of chapter I). Achenes harvested too early will not be filled and will show signs of shrinkage. Proper cleaning should remove most, if not all, of these shriveled nonviable achenes. Bai and others (1996) found that heavier Wyoming big sagebrush seeds exhibited higher germination and germination rates (also see Senft 1996). Viability tests by tetrazolium chloride (Weber and Wiesner 1980) should be at least 80 percent. Once an adapted and viable seed source has been collected or selected, the next task in restoring big sagebrush is seedbed preparation.

Seedbed Preparation

Seedbed preparation has two basic goals: firming the soil and reducing competing vegetation (Blaisdell 1949; Meyer 1994; Plummer and others 1968; Shaw and Monsen 1990). Because of the small size of big sagebrush seeds and limited energy reserves, seeds must germinate near or on the surface of the soil (Jacobson and Welch 1987). If big sagebrush seeds are planted or buried too deep in the soil, they could run out of energy before emergence. In the case of populations requiring light for germination, buried seed may not receive the necessary quantity of light needed for germination (McDonough and Harniss 1974b; Meyer and others 1990; Shaw and Monsen 1990; Weldon and others 1959). However, Meyer and others (1990) showed that the light requirement is almost completely relieved with stratification for 2 weeks at 1 °C. Shaw and Monsen (1990) suggested delaying planting in fall/winter until after a rainstorm, which firms soil surfaces. The use of a cultipacker or land-imprinting implement can also help to firm loose soil surfaces and prevent soil sloughing and burying big sagebrush seeds too deep.

Young and Martens (1991) noted that big sagebrush seeds germinating on the surface of the seedbed must satisfy two important conditions: first, uptake of moisture from the soil surface must be faster than it is lost to the atmosphere, and second, seedling radicle must grow into the soil and begin absorbing water as soon as possible. Young and Martens (1991, p. 438) also observed that "achenes of big sagebrush are not truly mucilaginous, but the achene coat becomes gelatinous when imbibed, which may aid moisture relations." During a microphotographic study of big sagebrush radicles and hypocotyls emergence, Young and Martens (1991) observed the development and rapid growth of hypocotyl hairs during the early phases of germination. These hairs form a dense ring around the lower region of the hypocotyl and the radicle emerges through this ring. They believe that the hairs attach the germinating seedling to the surface of the soil, thus aiding the radicle to penetrate into the soil. Mucilage-like substance was found among the hairs, which probably help cement the hairs to soil particles. Young and Martens (1991, p. 438) further observed: "In most studies, dislodging the seedling and breaking the contact of the hypocotyl hairs to the substrate reduced seedling survival and increased the number of surviving seedlings with abnormal geotropism." Chambers (2000) noted that seeds lacking appendages and with small surface areas, such as big sagebrush, do not experience significant horizontal movement. Thus, it appears that big sagebrush has evolved certain germination processes that allow it to cope with the rigors of a surface environment.

Competition can be reduced by using three basic methods: fire, herbicide, or mechanical cultivation (Boltz 1994; Fisser 1981; Plummer and others 1968). Fires are the least costly and are effective in reducing competition, but fires are nondiscriminating; that is, tree, shrub, and forb species are all killed or thinned, and highly intense fires can remove needed litter, reduce water infiltration, increase erosion, decrease available moisture, and create an unstable seedbed (Monsen and McArthur 1985). Herbicides, on the other hand, are expensive but effective and can be selected to kill all types of vegetation or certain segments such as dicots (woody and other broadleaf plants) or monocots (grasses) without the negative effects of high-intensity fires. Mechanical cultivation

Table 6.1—Comparison of 24 mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) populations as to severity of winter (as defined by mean January temperature) percent of dormant seed, and germination rate at 1 °C (defined by number of days to 50 percent of final germination) (after Meyer and Monsen 1992).

Location	State	Mean January temperature	Percent dormant seed	Germination rate
		°C		*Days*
Kemmerer	WY	–8.9	45	107
Nebo Overlook	UT	–8.9	30	103
Huntsville	UT	–8.3	13	90
Scow's Hollow	UT	–8.3	58	112
Daniel	WY	–8.3	27	113
Reynolds Creek	ID	–7.8	58	108
Maple Canyon	UT	–7.8	60	110
Mirror Lake Road	UT	–6.7	36	100
Park City	UT	–6.1	31	98
Thorn Creek Junction	ID	–6.1	1	50
Hailstone Junction	UT	–5.6	9	88
Squaw Butte	OR	–4.4	3	54
Lucky Peak	ID	–3.9	8	54
Wheeler Guard Station	CA	–3.3	0	60
Lee Vining	CA	–3.3	3	41
Hiko	NV	–2.8	0	26
Pine Valley	UT	–2.2	0	52
Bootleg Campground	CA	–2.2	0	40
Nephi	UT	–1.7	0	45
Gardinerville	NV	–1.1	0	34
Browse Offramp	UT	–0.2	0	44
Upper Kyle Canyon	NV	1.1	0	32
Lower Kyle Canyon	NV	2.6	0	16
Utah Hill	UT	2.8	0	30

is also expensive but can be a selective or broad spectrum in the killing or thinning of competitive vegetation (see chapter VII for more details concerning fire, herbicides, and mechanical cultivation) (Boltz 1994; Plummer and others 1968).

Planting

After seedbed preparation, the next step is planting. The best time to plant big sagebrush seed is in the late fall (late November early December), about the same time that the seeds are naturally dispersing (Deitschman 1974; Ferguson and Frischknecht 1981; Fisser 1981; Meyer and Monsen 1990; Rosentreter and Jorgensen 1986; Shaw and Monsen 1990; Stidham and others 1980; Van Epps and McKell 1977; Vories 1981; Welch and others 1986, 1992; Young and Evans 1986). Klott and Ketchum (1991) demonstrated that big sagebrush can be seeded successfully on a burned site by broadcasting the seeds onto snow that is 4 to 8 inches deep. Payne (1957) found that big sagebrush seeds sown in greenhouse flats in January and placed out of doors under snow cover germinated 2 days after snowmelt (April 12), and he concluded (p. 42): "This early germination was considerably ahead of the germination of other plants which may be a factor accounting for the dominance of big sagebrush in certain areas." Planting after February is extremely risky, particularly on the drier Wyoming big sagebrush sites and for ecotypes of mountain big sagebrush that require long stratification periods.

Jacobson and Welch (1987) conducted a greenhouse study to determine the optimal planting depth for big sagebrush seeds. Their results showed that the optimal planting depth is 0.2 inch or less (table 6.2). These results are in general agreement with the recommendations of other workers (Deitschman 1974; Fisser 1981; Kelsey 1986; Meyer 1994; Rosentreter and Jorgensen 1986; Shaw and Monsen 1990; Vories 1981). Apparently, frost heaving or expansion and contraction of the soil surface due to wetting and drying is enough to cover surface-sown big sagebrush seeds sufficiently for germination and establishment. Young and others (1990) found that big sagebrush seeds placed on the soil surface may be buried by a process called winnowing.

Table 6.2—Optimal planting depth for mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) stratified and unstratified seeds. Data are expressed as a mean and standard deviation per depth for five pots containing 15 seeds per pot (after Jacobson and Welch 1987).

	Seed treatment	
Depth	Stratified seeds germinated[1]	Unstratified seeds germinated[1]
Surface	9.6 ± 1.02^a	7.0 ± 0.89^a
0.07 inch	9.8 ± 0.81^a	5.4 ± 3.01^a
0.2 inch	9.0 ± 0.89^a	6.6 ± 1.10^a
0.4 inch	0.0 ± 0.00^b	1.8 ± 1.17^b
0.6 inch	0.0 ± 0.00^b	0.4 ± 0.80^b

[1] Means sharing the same superscript within a seed treatment are not significantly different at the 5 percent level.

Big sagebrush seeds can be planted with any planter that will deposit the seeds on the surface of a firm seedbed. These include aerial seeders, cyclone seeders, dribblers, and drills that have been adjusted to drop the seeds into furrows onto the soil surface without covering them (Welch and others 1986, 1992). When using a drill to plant big sagebrush with other species, Richardson and others (1986) and Rosentreter and Jorgensen (1986) recommend that the big sagebrush seeds be placed in separate compartments of the drill, and these compartments adjusted to place the seeds on the surface of the seedbed. This lessens intrarow competition between big sagebrush seedlings and seedlings of other species. To prevent clogging of the drill tube, much of the trash usually associated with big sagebrush seed will need to be removed. Preparation or planting methods that create a loose, sloughing seedbed must be avoided. Thus, under certain situations the use of drills must be avoided (Meyer 1994).

The amount of big sagebrush seed to plant on a per-acre basis has not been well studied. Recommendations vary from 0.065 to 1.33 pounds of pure live seed per acre (Boltz 1994; Cotts and others 1991; Plummer and others 1968; Meyer 1994; Quinney and others 1996; Richardson and others 1986; Rosentreter and Jorgensen 1986; Shaw and Monsen 1990; Skousen and others 1989; Welch and others 1986, 1992). Richardson and others (1986) measured the influence of varying seeding rates of grasses-forbs, shrubs, and mountain big sagebrush, and the effects of grazing on the establishment of mountain big sagebrush on mine disturbances. The results of their research are given, in part, in table 6.3. Protected plots yielded a greater number of mountain big sagebrush plants, and treatments containing zero amounts of grass and forb seeds also resulted in the greatest number of mountain big sagebrush plants. A seeding rate of 14.96 pounds per acre of pure live seed (pls) of grass and forbs, with 5.95 pounds pls of shrubs of which 0.42 pounds pls was mountain big sagebrush, yield one mountain big sagebrush plant for about each 10 feet^2. These workers used a Brillion grass-seeder to plant the various mixtures (also see Richardson and Trussell 1981). This seeder has two sets of cultipacker type rollers, and the seeds are metered out between the front and rear sets of rollers, which firms the seedbed but probably buries

Table 6.3—Number of established mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) plants per acre per seeding rate treatment and for grazed and protected sites (after Richardson and others 1986). Seeding rate treatments are expressed as pounds of pure live seeds planted per acre.

Seeding rate			Mountain big sagebrush plants	
Grass-forb	**Shrub**	**Big sagebrush**	**Grazed**	**Protected**
9.87	1.18	0.08	54	81
14.96	1.18	.08	37	0
41.62	1.18	.08	46	0
14.96	5.95	.42	3,538	4,530
.00	1.18	.08	no data	2,207
.00	13.41	.95	1,742	7,663
.00	14.91	1.06	2,439	5,343

some of the mountain big sagebrush too deep. Therefore, a greater quantity of seeds may be required to achieve the same number or density of plants compared to a broadcast type of planter, which would not create a firm seedbed, so establishment could be lower and seed requirement greater.

Vicklund and others (2004) studied the influence of grass seeding rates on Wyoming big sagebrush plant density on mine spoils. They (Vicklund and others 2004, p. 42) noted: "Sagebrush seedling density after three growing seasons was not significantly different among grass seeding rates..., although, sagebrush seedling density within the 14 kg PLS per ha [12.474 lbs per acre] grass seeding rate was less than half that observed at the lower grass seeding rates." Grass seeding rates above 4 kg PLS/ha (3.564 lbs PLS/a) did have a significant negative impact on canopy volume of Wyoming sagebrush seedlings. On completion of their study, Vicklund and others (2004), recommended the following seeding rate: 2 kg PLS per ha (1.782 lb/acre) of Wyoming big sagebrush and 4 kg PLS per ha (3.564 lb/acre) of grasses.

Interseeding

Van Epps and McKell (1977) have established big sagebrush by direct seeding in stands of native and introduced perennial grasses by a technique known as interseeding (also Shaw and Monsen 1990; Stevens 1994). The steps are basically the same as those outlined earlier in the planting section, except the whole area or plant community is not altered; only strips or spots are treated with herbicides or by mechanical means such as pitters, scalpers, rototillers, or plows to reduce competition and firm the seedbed (Pendery and Provenza 1987; Shaw and Monsen 1990). Van Epps and McKell (1977) noted that scalps should be at least 24 inches wide for native perennial grasses and greater (40 inches) for the more aggressive grass species such as crested wheatgrass (*Agropyron cristatum*).

Owens and Norton (1992) studied the survival of basin big sagebrush seedlings in ungrazed pastures and in pastures with protected and unprotected seedlings that were spring grazed by cattle and sheep. They found that unprotected seedlings in grazed pastures suffered the greatest mortality due mainly to the trampling effects of the grazing animals. Owens and Norton (1990) reported that small (less than 50 cm^2 crown area) juvenile basin big sagebrush plants suffered the greatest mortality due to livestock grazing. Larger plants suffered much less. However, Austin and Urness (1995) found that horse grazing in spring benefited big sagebrush seedling survival and seedling recruitment. All three of these studies were conducted on sites having mature big sagebrush plants already present; protection of newly seeded sites of big sagebrush for 2 to 3 years seems the prudent thing to do.

Transplanting Bareroot and Containerized Stock

Because of the expense, the usefulness of transplanting bareroot or containerized stock is limited to small, critical areas such as seed-increase gardens, demonstration plots, and roadsides (Everett 1980; Shaw 1981; Shaw and Monsen 1990). The same principles of source selection (subspecies and types of winters) must be adhered to as outlined in the direct seeding section. Planting stock should be from 4 to 8 inches tall with a well-developed root system that completely binds the growing medium together, and overwintered in a nonheated nursery bed or lathhouse

(Ferguson and Frischknecht 1981). Methods outlined by Nelson (1984) should be followed to produce disease-free stock. Actual transplanting of properly hardened planting stock can occur as soon as the frost has left the soil and the soil is tillable (Ferguson and Frischknecht 1981). Early spring transplanting of properly hardened (this takes 3 to 6 weeks) planting stock is highly recommended (Shaw 1981; Shaw and Monsen 1990). Advantages of early spring planting include: (1) maximum soil moisture, (2) minimal frost heaving, (3) transplants still dormant, (4) temperatures low, and (5) high probability of spring storms (Stevens 1994). However, summer transplanting of containerized stock can be successful if the transplants receive adequate irrigation during the first growing season. Fall planting of bareroot or containerized stock is not recommended because of the danger of frost heaving and the lack of dependable soil moisture. Nonhardened, containerized planting stock, such as containerized stock grown in greenhouses during the winter, needs to receive a couple of water stress treatments before being planted out (Welch and others 1986).

For each transplant, an area of 0.5 to 1 foot^2 needs to be cleared, one time only, of all grass, forb, and shrub competition (Pendery and Provenza 1987). The key to proper competition reduction is the mixing of the soil and the killing of tops, roots, stolons, and rhizomes. This can be done with hand shovels, posthole diggers, or similar tools. Holes must be at the proper depth to allow the roots to be straight, and the root collar placed at ground level except for containerized stock (Stevens 1994). The growing medium of containerized stock should be covered by 0.5 inch of native soil to prevent wicking of moisture into the atmosphere by the growing medium and thus drying out the transplant (Shaw and Monsen 1990; Welch and others 1986). Soil must be packed firmly around the transplant to eliminate air pockets (Stevens 1994). To enhance survival, a basin about 0.5 foot in diameter with the transplant at the bottom, 1 to 3 inches deep, could be constructed (Ferguson and Frischknecht 1981). The basin would serve as a water catchment or be filled with water during dry periods. Shaw and Monsen (1990) suggest the use of mulching material, furrowing, snow harvesting, and other water harvesting techniques as a means of enhancing seedling survival (also see Senft 1996). Using polyacrylamide as a soil amendment was found to be ineffective in aiding the establishment, growth, or seed production of big sagebrush transplants (Al-Rowaily and West 1994).

Care must be exercised during the planting process to avoid excessive drying of exposed roots of both bareroot and containerized stock (Stevens 1994). Roots need to be kept damp and cool at all times. Stevens (1994, p. 303) emphasized that “mishandling most commonly occurs just before placing the transplant in the soil. Transplants must be moved rapidly from the protected holding area into the soil to minimize root exposure.”

When using scalper equipment to reduce competition, Stevens (1994) makes two recommendations: first, scalping should be perpendicular to direction of prevailing winter storms (this will harvest snow along the scalp), and second, scalping depth should be deep enough to reduce competition but not so deep as to remove the most fertile portion of the soil. Stevens (1994) further noted that a tractor-mounted reinforced tree planter works well in combination with a scalper to plant both bareroot and containerized stock of big sagebrush. Ferguson and Frischknecht (1981) suggest that the scalp should be at least 36 inches wide (also see Van Epps and McKell 1977). Where possible, the transplants should be protected from heavy grazing for two or three growing seasons (Austin and others 1994; Shaw and Monsen 1990; Stevens 1994; Welch and others 1986). Pendery and Provenza (1987, p. 514) suggest, however, that “it is probably more important to reduce interspecific competition than to modify grazing practices when planting shrubs in a crested wheatgrass stand.” First-year survival rates should be about 80 percent or higher, assuming normal precipitation (Evans and Young 1990; Shaw and Monsen 1990; Welch and others 1986).

A cautionary note: Welch (1997) compared the seed production of big sagebrush plants established from containerized seedlings to plants established by direct seeding. He found that seed-derived plants produced more seeds, larger top growth, deeper roots, lateral roots nearer the soil surface, heavier root systems, and a lower death rate than containerized-derived plants. Therefore, bareroot or containerized-derived big sagebrush plants may not perform as well as seed-derived big sagebrush plants.

Areas heavily infested (688 plants per square meter) (Young and others 1976) with exotic annual grasses such as cheatgrass (*Bromus tectorum*) will limit, if not outright eliminate, natural recruitment of big sagebrush; or in other words, these areas have crossed over thresholds that resulted in the domination of cheatgrass and will not allow the natural recovery of big sagebrush without human intervention (Young and Longland 1996). Young and Evans (1989) found in their study, occurring over 4 years and five sites, that emerged seedlings of big sagebrush failed to establish themselves on cheatgrass-dominated sites. Wagstaff and Welch (1990) also reported failure of big sagebrush recruitment on mule deer winter ranges whose understory was dominated by cheatgrass and where mature big sagebrush plants were heavily browsed by deer.

Heavy browsing on big sagebrush plants will reduce the number of seed stocks (Rodriguez and Welch 1989). Wagstaff and Welch (1991) found that recruitment could occur if the competition from cheatgrass was reduced around remnant maternal plants by tillage after the fall greenup of cheatgrass. Recruitment could also be enhanced by protecting mature plants from heavy mule deer browsing (see table 6.4 for details). This experiment shows that big sagebrush can be established on sites dominated by cheatgrass, as on any other site, when competition has been reduced per instructions outlined in previous sections. However, the catch is in maintaining the stand once establishment has been achieved. Cheatgrass domination is quickly reestablished, along with its frequent fire cycle, far too frequently for big sagebrush stand maintenance (Whisenant 1990).

For big sagebrush stand maintenance, cheatgrass cover must be reduced to the point where it cannot carry fire. This will undoubtedly require repeated treatments, starting with burning infested sites before seed dispersal (table 6.5). Even then, some of the seeds or caryopses survive (table 6.6) and if left unchecked can eventually dominate the site again (Hassan and West 1986; Monsen and McArthur 1985; Young and others 1976). Surviving cheatgrass caryopses can be eliminated through deep burial where soil conditions would permit the use of a plow or other tillage equipment such as a disk-chain (Boltz 1994) that would bury the caryopses at least 1 inch deep. Repeated burning with a propane field flamer may further reduce the number of surviving cheatgrass caryopses (Boltz 1994). An alternative or additional method would be to allow surviving caryopses to germinate and then use a grass herbicide to kill the seedlings, keeping in mind that the herbicide would also kill other grass species but leave woody species and broadleaf forbs unaffected. A sequence of events

Table 6.4—Number of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) seedlings counted around mature plants. Treatments were no tillage, early fall tillage before cheatgrass greenup (*Bromus tectorum*), and late tillage after cheatgrass greenup (after Wagstaff and Welch 1990).

	Sites			
Treatment	**Pleasant Grove**	**Hobble Creek**	**Diamond Fork**	**Total**
No tillage				
Number of mature plants	32	34	18	84
Seedlings	0	0	0	0
Early tillage				
Number of mature plants	—	40	18	58
Seedlings	—	0	0	0
Late tillage				
Number of mature plants	64	28	—	92
Seedlings	164	557	—	721

Table 6.5—Number of cheatgrass (*Bromus tectorum*) seedlings per square meter from burned and unburned big sagebrush communities (after Young and others 1976).

	Seedling density		
Site	**Burned**	**Unburned**	**Percent reduction**
7	560	5,400	90
8	320	4,800	93
9	46	3,300	99
10	1,100	6,400	86
11	860	5,100	83
12	470	8,600	94

Table 6.6—Survival of cheatgrass (*Bromus tectorum*) caryopsis after a burn. Data expressed as means and standard deviations of caryopsis per square foot (after Monsen and McArthur 1985).

Treatments	Date of burn	Number of caryopsis
Highway 6 Juab County, UT	June 1984	
Burned		1,131 ± 713
Unburned		2,669 ± 2,124
Desert Mountain, Juab County, UT	July 1984	
Burned		502 ± 366
Unburned		2,746 ± 1,976
Yuba Lake, Juab County, UT	August 1984	
Burned		186 ± 179
Unburned		2,895 ± 2,433

for cheatgrass control could be: (1) fire, (2) seedbed preparation, (3) fall planting of broadleaf forbs and shrubs, (4) spring treatment with grass herbicide, (5) repeat step 4 when needed, (6) fall planting of native perennial grass species, and (7) the use of specific biological control agents, such as head smut, when available (Meyer and others 1999).

Mother Plant Technique

Plummer and others (1968, p. 85) observed: "Since wildlings and seedlings are transplanted easily, big sagebrush can be used widely for stabilizing gullies and eroding spots on hillsides. Such transplants reproduce and spread easily from seed within a 3- to 7-year period." Thus, the mother plant technique is a combination of transplanting and natural seed dispersal (Shumar and Anderson 1987; Wagstaff and Welch 1990; Welch and others 1986). This technique could be used after a fire or some other process that has destroyed native sagebrush stands. "Mother plants" are planted as containerized, bareroot, or wildlings on a grid (50 by 50 feet or greater) or established by hand-broadcasting seed to produce "source islands" throughout a site (Quinney and others 1996). The direction of spread from the mother plants would be dependent on prevailing fall and winter winds (Wambolt and others 1989). Energy is then directed toward the establishment, maintenance, growth, and protection of the mother plants on an individual plant basis. This may include fertilization, irrigation, fencing, and so forth. Once the mother plants are producing seeds, mechanical or chemical means, if needed, can be used to reduce competition either in strips or spots as an aid in stand thickening.

Wagstaff and Welch (1990) described success in using the mother plant technique to rejuvenate mountain big sagebrush stands on mule deer winter ranges heavily infested with cheatgrass by using onsite plants as a seed source. The onsite plants were protected from heavy browsing and by controlling cheatgrass around the mother plants (fig. 6.1).

Seed Production

Reproductive Growth

Reproductive or inflorescence growth starts in late spring to early summer and reaches its maximum rate during late summer with florets fully developed by late summer to early fall (DePuit and Caldwell 1973; Evans and others 1991; Fisser 1986; Sauer and Uresk 1976). Flowering or pollination occurs during late summer to mid-fall with fruit development commencing almost simultaneously with flowering and achenes

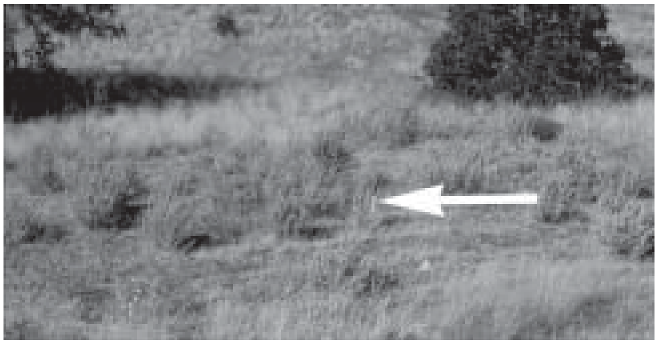

Figure 6.1—A mother plant—white tag—of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana)* surrounded by her offspring after protection from excessive browsing by wintering mule deer. Grass competition—mainly cheatgrass (*Bromus tectorum*)—was reduced through tillage after fall green-up. Photograph taken 3 years after treatment (photo by Bruce L. Welch).

(dry single-seeded fruit) (Meyer 1994) maturing during midfall to midwinter (DePuit and Caldwell1973; Everett and others 1980; Fisser 1986; Pitt and Wikeem 1990; Sauer and Uresk 1976). Thus, reproductive growth occurs when water supplies and temperatures are not particularly favorable; in fact, during this period, big sagebrush plants have started shedding ephemeral leaves from vegetative shoots and neighboring plant species are largely dormant (Miller and others 1983). Evans and Black (1993) found, through the use of carbon isotopes, that vegetative fixed carbon does not transfer to reproductive structures. Further, they found that inflorescences of big sagebrush generate positive net photosynthesis at a time when the whole plant is in a water conservation mode, that is, leaf abscission is occurring and stomata are exerting control over water loss. Evans and Black (1993, p. 1524) further noted that: "Vegetative and reproductive modules both responded to the limited availability of water and increased evaporative demand by abscising leaves and decreasing stomatal conductance. Reproductive modules, however, consistently had higher transpiration rates." They reported that supplemental watering stimulated inflorescence, but not vegetative growth (also see Carpenter and West 1988; Evans and others 1991). Evans and others (1991, p. 676) stated:

> Expanding inflorescences during summer may enhance competitive ability because biomass can be allocated solely toward vegetative growth during spring, increasing the capacity of *Artemisia tridentata* to acquire resources when they are most abundant. Conversely, inflorescences that are photosynthetically self-sufficient can better respond to favorable soil moisture or intermittent precipitation during summer, because photosynthesis can be increased without investing resources into further vegetative growth.

Inflorescences are produced from short shoots' terminal soft buds at the distal end of 1-year-old long shoots (see chapter I for a detailed discussion of inflorescence morphology) (Bilbrough and Richards 1991; Hoffman and Wambolt 1996). This allows inflorescences to be elevated, enhancing wind pollination and wind dispersal of achenes (McArthur and others 1988; Pendleton and others 1989). One-year-old leader, long shoots produce more new long shoots and inflorescences than 1-year-old lateral, long shoots, making big sagebrush less tolerant of browsing than other shrub species (Bilbrough and Richards 1991; Wambolt and Hoffman 2004). Therefore, browsing of current year long shoots will reduce seed production (Booth and others 2003; Rodriguez and Welch 1989; Wagstaff and Welch 1990, 1991).

Seed Dispersal

The small mature achenes or seeds are wind dispersed from midfall to midwinter; however, big sagebrush achenes lack special structures that would aid in long distance dispersal, 100 feet being maximum (Everett and others 1980; Meyer 1994; Pendleton and others 1989; Pitt and Wikeem 1990; Sauer and Uresk 1976; Welch 1999; Welch and others 1990; Young and Evans 1989). Most achenes are dispersed within 3 or 4 feet from the mother plant, and achenes are not dispersed evenly but are heavily influenced by wind direction. Assuming that it takes 2 to 4 years (Young and others 1989) for a big sagebrush plant to reach maturity, it would take about 105 to 211 years for big sagebrush to spread 1 mile across a large grass seeding or burn. Surviving plants would serve as a seed source that could speed the recovery of big sagebrush from a burn or some other disturbance (Frischknecht and Bleak 1957; Johnson and Payne 1968; Marlette and Anderson 1986).

Blaisdell (1953) speculates that big sagebrush seeds can be dispersed with the wind across snow. There are a number of problems with this: first, snow and especially crusted snow is not a smooth surface, and seeds of big sagebrush do settle into small pits, cracks, and other surface irregularities where winds cannot move them; second, the dark-colored seeds absorb solar energy and melt deeply into the snow pack (Welch 1999); and third, the seeds can be quickly buried into the snow through a process known as winnowing (Young and others 1990).

Evidences for persistence of big sagebrush seeds in soil seed banks are contradictory. Hassan and West (1986) and Mueggler (1956) found a small fraction of viable seeds in the soil seed bank samples after a burn; Young and Evans (1989) did not (see Meyer 1994). At any rate, the recovery of big sagebrush from fires or grass seedings is slow but can be speeded up through artificial seeding as described earlier.

Seed Increase Gardens

A single mountain big sagebrush plant growing on a seed increase garden can produce more than 500,000 achenes per year (Meyer 1994; Welch, and others 1990). Production from native stands of big sagebrush can range from 0 achenes or seeds per acre to about 20 million seeds per acre (Young and others 1989). Achene or seed production, however, can be influenced by a number of factors: genetic potential expressed at the subspecies and populations level, site differences, years (wet versus dry), intra- and interspecific competition, diseases, insects, excessive browsing, and plant age (Booth and others 2004; Carpenter and West 1988; Hoffman and Wambolt 1996; Meyer 1994; Rodriguez and Welch 1989; Wagstaff and Welch 1991; Welch 1997; Welch and Nelson 1995; Young and others 1989).

To obtain the necessary volume of big sagebrush seeds for seeding onto a large disturbance where just a limited number of remnant plants exist, seed production gardens may be needed. For populations of big sagebrush possessing desirable characteristics, seed production gardens may also be needed (Meyer 1994; Welch and others 1986, 1992).

Garden sites should be chosen that have deep, well-drained soils, low salt, a pH near neutral, and the possibility of supplementing natural rainfall with irrigation water during a drought or when growing subspecies of big sagebrush that may require more water than that provided by normal precipitation. Clean cultivation will help to conserve moisture for the production of seeds. For most populations and subspecies, planting on a 7- by 7-foot grid will provide enough space for cultivation, harvesting, and other operations. However, some larger basin big sagebrush populations may require a 10- by-10-foot grid.

As pointed out earlier, Welch (1997) compared the seed production of big sagebrush plants established from containerized seedlings to plants established by direct seeding. Welch (1997) found that seed-derived plants produced more seeds, larger top growth, deeper roots, lateral roots nearer the soil surface, heavier root systems, and a lower death rate than container-derived plants (table 6.7). Therefore, bareroot or container-derived big sagebrush plants may not perform as well as seed-derived big sagebrush plants. Also, seed increase gardens must be protected from browsing ungulates because browsing will reduce the number of seed stalks and overall plant vigor (Rodriguez and Welch 1989; Wambolt and Sherwood 1999).

Table 6.7—Comparisons of 1993 to 1995 seed production years and vegetative measurements of Gordon Creek Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) plants established from direct seeding and from containerized stock. Data are expressed as means ± standard deviations of grams of pure live seed (after Welch 1997).

	Seed[1]	Containerized[1]
Seed production		
1993 (g)	39 ± 16^{a}	25 ± 17^{b}
1994 (g)	34 ± 17^{a}	9 ± 6^{b}
1995 (g)	64 ± 23^{a}	33 ± 10^{b}
Vegetative measurements		
Aboveground biomass (g)	2,080 ± 306^{a}	1,531 ± 472^{b}
Root mass (g)	946 ± 99^{a}	679 ± 201^{b}
Root depth (cm)	231 ± 11^{a}	191 ± 27^{b}
Depth to first root (mm)	38 ± 14^{a}	71 ± 20^{b}
Death rate (%)	0	13

[1] Row means with the same superscripts are not significantly different ($p \leq 0.05$) paired t-tests.

Big sagebrush seed increase gardens can be established by hand placing five to 10 seeds on a firm soil surface and then carefully pressing the seeds into the soil by stepping on them with a smooth-soled shoe. Yields from these gardens should range from 40 to 70 pounds of pure live seed per acre in 2 to 3 years (Welch and others 1990).

As a cautionary note, care must be exercised when collecting big sagebrush seeds to be used in the establishment of seed increase gardens. Hild and others (1999) studied characteristics of seedlings derived from maternal Wyoming big sagebrush plants occupying upslope, core, and downslope positions. They found that these seedlings differed significantly in a number of key growth characteristics. Sampling across ecotones may not be desirable (see chapter V for more details).

Harvesting and Cleaning Big Sagebrush Seed

Harvesting—Nearly all big sagebrush seed sold have been collected from wildland stands (Meyer 1994). It is important that the stand location be clearly noted so that seeding sites may be matched to the characteristics of the collection site as noted earlier.

Seeds are usually harvested by beating the inflorescences with a wooden paddle or tennis racket, which detaches the achenes or seeds from the seed heads and drives them into canvas hoppers or other containers (Deitschman 1974; Plummer and others 1968; Shaw and Monsen 1990; Wasser 1982). Achenes cannot be detached from the seed heads with tennis rackets or wooden paddles until they have reached the proper degree of maturity, or dryness. Thus, potential collection sites must be checked several times to ensure readiness, which can vary from the first of October to the end of December, depending on subspecies, population, weather conditions, and so forth (Payne 1957). If collections are attempted too soon, achenes are not harvestable; if too late, some of the achenes have shattered. Under certain circumstances, it may be necessary to harvest before the achenes are mature enough to detach them from the seedheads. In this case, entire inflorescences may be removed or clipped. When this is done care must be exercised to avoid the buildup of heat and humdity within inflorescence storage piles. When the immature embryos are tan color, inflorescences may be clipped without shrinkage or damage to unripened achenes. It is extremely important to dry all material collected to less than 9 percent moisture as quickly as possible, regardless of harvesting technique (Welch and others 1996). Drying big sagebrush seed during the cold, wet weather of the harvesting period creates special challenges for commercial suppliers that can only be solved by the use of forced-air driers (Welch and others 1996).

Big sagebrush achenes can tolerate temperatures up to 140 °F (Payne 1957; Welch 1996). After proper drying, the next step is cleaning.

Seed Cleaning—The first step in cleaning of big sagebrush achenes or seeds is to pass the harvested mixture of inflorescences, achenes, seed bracts, small twigs, leaves, and so forth through a debearder. Welch (1995) and Booth and others (1996a,b) reported that passing achenes or seeds through a debearder does not damage the achenes or lower seed germination or viability. This is illustrated in table 6.8. It is clear from the data presented in this table that seed viability was not adversely affected even with two passes through the debearder; however, when the exit door was tied in such a manner as to force harvested material through a small opening, then and only then was seed viability reduced (Welch 1995). Passing harvested materials through a debearder not only aids in the thrashing of seeds or achenes from the seedheads but also breaks fine stems and other trash into small pieces that can be readily removed by most commercial fanning-screening seed cleaners. A single pass of harvested material through a debearder is enough (Welch 1995).

Welch (1995) reported that purity of 50 percent or greater could be achieved by using a two-screened Crippen model XV-242-LH seed cleaner with air lift. He equipped the cleaner with a 14 by 14 mesh screen in the top screen position and a 36 by 36 mesh screen in the bottom position and adjusted the air lift to maximum without picking up fully ripen achenes or seeds. After four passes through this cleaner purities ranged from 51 to 59 percent. This cleaning procedure is illustrated in figure 6.2. Use of a gravity table or

Table 6.8—Effects of debearder on big sagebrush seed viability. Data expressed as a percent of live seeds (after Welch 1995).

	Percent of viable seeds[1]
Experiment 1 (Wyoming big sagebrush)	
Before debearder	93.3 ± 1.79^{a}
After first debearder pass	93.0 ± 1.87^{a}
After second debearder pass and cleaning	93.0 ± 0.71^{a}
Experiment 2 (mountain big sagebrush)	
Before debearder	87.8 ± 3.11^{a}
After first debearder pass	89.0 ± 3.74^{a}
After second debearder pass and cleaning[2]	40.8 ± 8.26^{b}

[1] Means and standard deviations sharing the same superscripts in columns of the same experiment are not significantly different ($p < 0.05$).

[2] This experiment was conducted in the same manner as experiment 1, except when the mixture of seeds, achenes, and so forth, were passed through the debearder the second time the exit door was tied so the material could exit only a small opening (about 10 percent of the usual opening). Materials that passed through the debearder a second time were warm to the touch. This treatment exposed the seeds to the maximum harshness of the debearder.

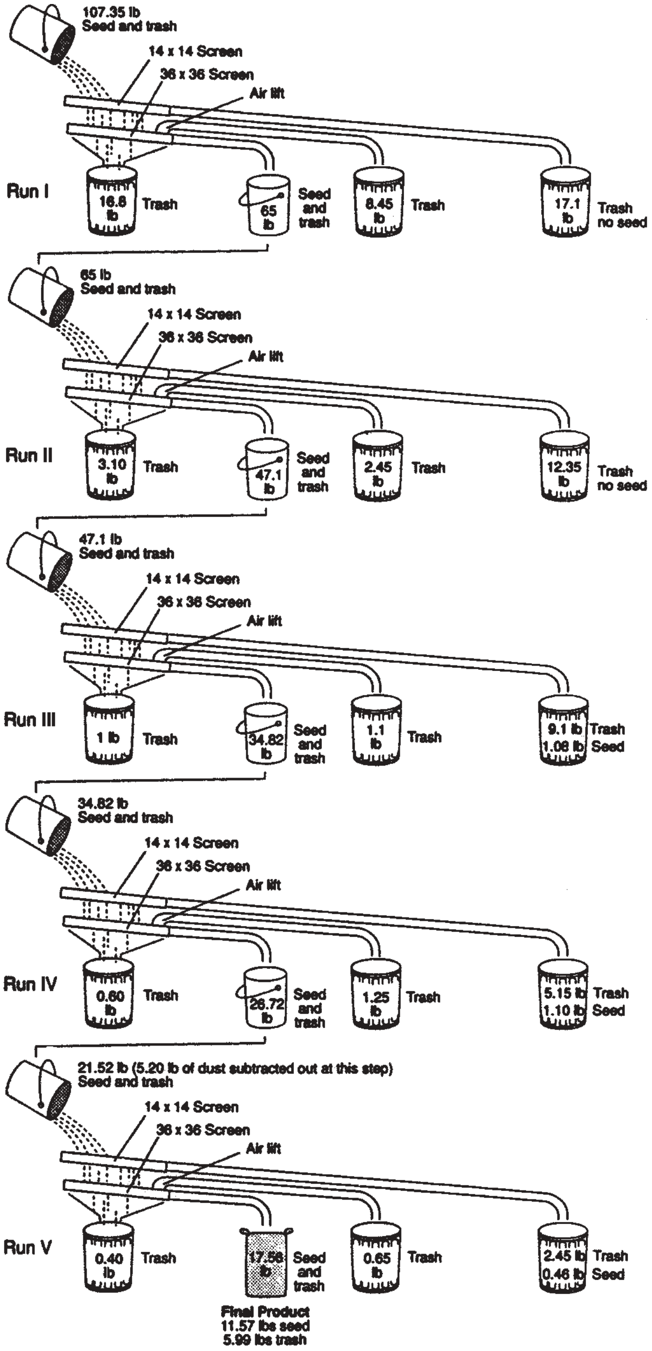

Figure 6.2—A flow chart outlining the movement of a big sagebrush seed lot, weighing 107.35 lbs, through an air/screen seed cleaner. Before cleaning, the seed lot was passed once through a debearder. Trash was separated from seeds by being carried over a 14-by-14 mesh screen, being air lifted from the seed, passing through a 36-by-36 mesh screen, or being lost as flying dust. The final product was obtained by running the material carried off the 36-by-36 mesh screen five time through the seed cleaner. Final product had a purity of 65.9 percent and a seed viability of 93 percent (after Welch 1995).

other equipment can increase purity to 80 percent or greater (Welch 1995)—purities greater than published standards of 8 to 12 percent (Stevens and Meyer 1990). Purities greater than the standard of 8 to 12 percent save money well beyond the extra cost of cleaning the seed lots (Welch 1995) by reducing the amount of material that needs to be handled, stored, and shipped. For example, 1,000 pounds of pure live big sagebrush seed at 50 percent purity and 80 percent seed viability would weigh 2,500 pounds compared to 10,417 pounds for the same weight of pure live seed at 12 percent purity and 80 percent viability. Welch (1995) estimated a savings of at least $1,176 in shipping, storage, and handling costs at the higher purity with a sizable reduction in the amount of dust produced when handling the seed sacks. Also, less material would be required to pass through planting equipment when seeding at higher purities.

Seed Storage

After seed cleaning, storing the seed under proper conditions is absolutely critical to be able to maintain high levels of viability (75 percent) and for many years (at least 9 years) (Welch and others 1996). Humidity is the enemy of stored seeds (Welch 1996) (table 6.9). Welch (1996) concluded that big sagebrush seeds should not be stored in environments with humidities over 40 percent.

Welch and others (1996) studied the effects of storing big sagebrush seeds at constant humidity (20 percent) but in three environments: cool, constant temperature (refrigerator 50 °F); room temperature (58 to 76 °F); and a nonheated warehouse (–18 to 112 °F). They found a significant drop in seed viability occurred first in the seed lots stored in the nonheated warehouse and then in seeds stored at room temperatures (table 6.10). Seed viability stored in a cool environment dropped the least. Even in the nonheated warehouse, high seed viability (75 percent or more) was maintained for 6 years; and 7 years for seed stored at room temperature; and 9 years for seeds stored at a constant cool temperature of the refrigerator (table 6.10). These storage years of high seed viability compare to the reports of Hull (1973), Stevens and others (1981), and Stevens and Jorgensen (1994) of 2 and 3 years.

The keys to storing big sagebrush seeds at high levels of viability beyond 3 years are: drying to a minimum of 9 percent, reducing seed moisture as soon as possible after harvesting, and storing in a dry environment with less than 40 percent humidity and with low constant temperature. Bewley and Black (1985) noted that seed moisture content greater than 30 percent would cause nondormant seed to germinate in storage and that moisture contents between 18 to 30 percent caused rotting of seeds by microorganisms. They further explained that seeds stored at 18 to 20 percent will respire but seeds stored below 8 to 9 percent moisture will not respire and will not be attacked by insects. Haws and others (1996) found that 6 to 45 percent of big sagebrush seeds from 26 seed lots examined were damaged by insects, perhaps due to storing big sagebrush at a high moisture content. Bewley and Black (1985, p. 392) stated: "below 4-5% moisture content seeds are immune from attack by insects and storage fungi, but they may deteriorate faster than those maintained at a slightly higher moisture content. The activities of seed storage fungi are ultimately more influenced by the RH (relative humidity) of the inter-seed atmosphere than by the moisture content of the seeds themselves."

Table 6.9—Viability of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) seed stored at different humidities and for various lengths of time. Data expressed as means and standard deviations of the percent of live seed as determined by tetrazolium staining method. Three replications per humidity-time cell; 300 seeds tested per replication. Starting (0 days) viabilities were compared to the various humidities and times by unpaired, upper-tailed T-test (p = 0.05) (after Welch 1996).

	Percent humidity							
Days	**0[1]**	**Open[2]**	**32**	**45**	**56**	**66**	**86**	**100**
	Viability[3] (percent)							
0	90 ± 0.8[a]	91 ± 1.4[a]	92 ± 0.9[a]	91 ± 1.3[a]	92 ± 1.6[a]	91 ± 0.5[a]	91 ± 2.2[a]	92 ± 0.0[a]
60	90 ± 0.5[a]	91 ± 2.2[a]	91 ± 2.5[a]	93 ± 2.5[a]	64 ± 0.5[b]	6 ± 1.7[b]	0	0
120	86 ± 2.5[a]	91 ± 2.7[a]	91 ± 3.7[a]	92 ± 1.6[a]	57 ± 5.8[b]	0	0	0
180	86 ± 2.3[a]	89 ± 1.7[a]	90 ± 1.7[a]	90 ± 2.5[a]	51 ± 1.9[b]	0	0	0
240	90 ± 0.4[a]	91 ± 2.6[a]	92 ± 1.3[a]	88 ± 2.6[a]	54 ± 3.4[b]	0	0	0
300	90 ± 0.0[a]	89 ± 0.8[a]	89 ± 2.6[a]	86 ± 3.7[a]	24 ± 3.7[b]	0	0	0
360	92 ± 2.1[a]	93 ± 2.8[a]	93 ± 1.9[a]	89 ± 1.2[a]	0	0	0	0

[1] Zero humidity = seeds stored over regenerated anhydrous calcium sulfate.

[2] Open = seeds stored in open containers in a growth chamber (humidity about 26 percent).

[3] Values in columns with an [a] are not significantly different from the starting (0 days) seed viability. Those with a [b] or 0 are significantly different from the starting (0 days) seed viability.

Table 6.10—Big sagebrush seed viability under three storage environments with humidity held constant at 20 percent. Cool storage was in a refrigerator 50 °F with little temperature fluctuation. Room storage was in a heated and air-conditioned room with temperature fluctuation about 18 °F. Warehouse storage was in a nonheated warehouse where temperatures fluctuated about 130 °F. Data are expressed as means and standard deviations of the percent of live seed (after Welch and others 1996)

Year	Cool[1]	Room[1]	Warehouse[1]
1986	96.7 ± 1.5^{a}	96.3 ± 1.2^{a}	96.0 ± 1.6^{a}
1987	$97.2^{n} \pm 1.4^{a}$	$95.5^{n} \pm 2.2^{a}$	$97.8^{n} \pm 1.1^{a}$
1988	$96.2^{n} \pm 2.0^{a}$	$96.3^{n} \pm 1.8^{a}$	87.3 ± 4.8[2]
1989	$96.3^{n} \pm 1.6^{a}$	$96.0^{n} \pm 1.9^{a}$	$95.7^{n} \pm 1.7^{a}$
1990	$95.7^{n} \pm 2.0^{a}$	$95.2^{n} \pm 1.8^{a}$	$93.5^{n} \pm 1.9^{a}$
1991	$96.5^{n} \pm 1.9^{a}$	$95.1^{n} \pm 2.3^{a}$	$91.9^{s} \pm 4.2^{b}$
1992	$95.2^{n} \pm 2.2^{a}$	$94.6^{n} \pm 1.9^{a}$	$89.3^{s} \pm 4.7^{b}$
1993	$95.5^{n} \pm 2.1^{a}$	$81.2^{s} \pm 16.3^{b}$	$71.8^{s} \pm 12.3^{c}$
1994	$93.8^{s} \pm 2.1^{a}$	$70.2^{s} \pm 17.2^{b}$	$51.0^{s} \pm 17.5^{c}$
1995	$92.1^{s} \pm 3.3^{a}$	$53.8^{s} \pm 20.2^{b}$	$25.9^{s} \pm 14.5^{c}$

[1] Means in rows sharing the same superscripts are not significantly different at the 5 percent level.Means in columns with an ^{n} are not significantly different at the 5 percent level from the 1986 seed viability. Those with an ^{s} are significantly different.

[2] An anomaly in the data set, cause unknown.

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Chapter VII

Consequences of Controlling Big Sagebrush

Reflecting on a previous publication of mine (Welch 2002, p. 6), I noted that: "I have never liked the term controlling big sagebrush because it infers that big sagebrush is out of control. Who has the ecological insight to determine when big sagebrush is out of control?" In this chapter, I explore the ecological and political issues of managing big sagebrush and what has happened ecologically when there have been efforts to control the species.

A brief look at attitudes toward big sagebrush found in the literature sets the stage. Welch (1999) pointed out that for the six range management textbooks he read (Heady 1975; Heady and Child 1994; Holechek and others 1989; Stoddart and others 1975; Vallentine 1989, 1990), 68 percent of the comments made concerning big sagebrush he considered negative, including: "unpalatable to livestock," "high levels of volatile oils," "invader," "undesirable," "reduces the production of better plants," "causes rumen disorders," "uses up water," "woody," "noxious," "poisonous," "low value," "little used," "control," "eradicate," "convert," "suppress grasses," and so on. Only 9 percent of the comments on big sagebrush were positive, including: "provide mule deer (*Odocoileus hemionus hemionus*), pronghorn antelope (*Antilocapra americana*), and domestic sheep (*Ovis aries*) with winter feed," "food for jack rabbits (*Lepus californicus*)," "food for sage grouse (*Centrocercus urophasianus*)," and "nesting sites for Brewer's sparrow (*Spizella breweri*)."

Such contrasting views continue today, and the negative attitudes are used to justify the killing of big sagebrush. However, Peterson (1995, p. 38) concluded: "Removing sagebrush in an effort to improve forage for livestock does not automatically equate to benefits for wildlife." And Fischer and others (1996) noted that their research findings did not support the idea that killing big sagebrush through the use of fire enhanced sage grouse brood-rearing habitat.

Upon Euro-American settlement of the Western United States, the rationale for destroying big sagebrush was directly related to enhancing the livestock industry, or as Vallentine (1989, p. 1) states: "Range improvements are special treatments, developments, and structures used to improve range forage resources or to facilitate their use by grazing animals. Range seeding, control of undesirable range plants [big sagebrush being one], applying fertilizer, and pitting, furrowing, and waterspreading are direct means of developing and improving range forage resources.” Further, Vallentine (1989, p. 58) lists big sagebrush as one of the individual problem plants. West and Hassan (1985, p. 131) stated: “If fire destroys a large fraction of the undesirable brush and is relatively undamaging to the desired herbaceous species, then a landscape that is better for livestock production and water shed may be created.” However, many wildlife species depend on big sagebrush including sage grouse, Brewer’s sparrows, sage sparrows (*Amphispiza belli*), sage thrashers (*Oreoscoptes montanus*), pygmy rabbits (*Brachylagus idahoensis*), sagebrush vole (*Lagurus curtatus*), 52 species of aphids, and so on (see chapters II and III).

There are some signs that a different philosophy and policy are emerging. For example, the USDI Idaho Bureau of Land Management lifted its ban on the planting of big sagebrush in the mid-1980s and today is purchasing tens of thousands of pounds of big sagebrush seed to be used on fire rehabilitation projects. Also, the USDI Utah Bureau of Land Management is encouraging higher big sagebrush production on critical mule deer winter range by allowing heavy livestock grazing (Wambolt and Watts 1996). And there is this statement of Heady and Child (1994, p.301), authors of a range management textbook: “The word ‘undesirable’ is difficult to eliminate from a discussion of vegetational modification because a plant may be both desirable and undesirable depending upon the use to be made of it. One example, *Artemisia* ssp. in thick stands are generally undesirable for livestock but furnish food and cover for wildlife species.”

Negative Impacts of Big Sagebrush Control

Daubenmire (1970) listed six concerns he has with big sagebrush control. These six concerns are discussed here, with additional observations by other researchers.

First concern is that increase in grass production is not a long-lived phenomenon and could be the effect of dead big sagebrush roots supplying a greater quantity of nutrients—that is a “green-manure effect.” Daubenmire points out that fire itself stimulates grass production. Thilenius and Brown (1974) observed: “On three summer cattle ranges in the Bighorn increased herbage production after sagebrush control with 2,4-D was a relatively short-lived phenomenon. Declines in production and in the proportion of graminoids in the herbage did not appear to be related to reinvasion of sagebrush as this was minimal on all three sites even after 10 to 11 years.” Also, Clary and others (1985) reported no significant increase in the production of perennial grasses in spite of a significant reduction in shrub production (mainly mountain big sagebrush, killed by tebuthiuron treatments) of some 73 to 99 percent.

The second concern is that, by its physical presence alone, big sagebrush protects grass from total destruction, and elimination of big sagebrush could lead to the total destruction of grass during periods of overgrazing such as during a drought. Pechanec and Stewart (1944a, p. 1) observed: “Even when they [livestock] force their way into the shrubby growth, half the palatable grasses and weeds beneath the sagebrush are likely to be unavailable to them.”

The third concern is about fertility of the earth. Due to the deep-rooted nature of basin and mountain big sagebrush (*Artemisia tridentata* ssp. *tridentata* and *vaseyana*) and in some locations Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*), islands of fertility are formed across the land by extracting minerals far deeper in the soil profile than grasses or forbs can. Sagebrushes’ constant removal could easily affect soil fertility and grass production itself.

Fourth, controlling big sagebrush can destroy wildlife habitat of birds, small mammals, reptiles, insects, spiders, and so forth, that depends upon big sagebrush.

Fifth, some big sagebrush controlling projects use herbicidal sprays that kill nontarget plant species such as broadleaf forbs.

And sixth, big sagebrush helps to promote the uniform accumulation of snow, deeper depth of snow, delays its melting, and retards the development of ice sheets, thus benefitting deep soil water storage (also see Hutchison 1965).

Daubenmire (1970, p. 79) summarized:

> The more diversified the biota of an area, the more completely the environmental resources are being used, and the better the community is buffered against disease and weather hazards. Simplification of shrub-steppe vegetation by removing a major component that contributes a distinctive life-form and phenology, and is necessary for other species to remain in the community, cannot fail to have significant consequences.

One of these consequences is expressed by Nelle and others (2000, p. 586): “No benefits for sage grouse occurred as a result of burning sage grouse nesting and brood-rearing habitats. Burning created a long-term negative impact on nesting habitat because sagebrush required over 20 years of postburn growth for percent canopy cover to become sufficient for nesting.” (Also see the following supporting articles by Benson and others 1991; Connelly and others 2000; Fischer and others 1996.) Further, Kochert and others (1999) noted that the burning of big sagebrush had a negative effect on golden eagles (*Aquila chrysaetos*) in southwestern Idaho.

Pechanec and others (1965) noted that plant species such as rabbitbrush (*Chrysothamnus* spp.), horsebrush

(*Tetradymia* ssp.), cheatgrass (*Bromus tectorum*), and halogeton (*Halogeton glomeratus*) may increase sharply after big sagebrush control. They caution (p. 4): "Care must be taken in sagebrush control work to avoid exchanging one problem for a more difficult one."

Figure 7.1 illustrates this possibility, where just west of Trout Creek located in the Strawberry Valley of central Utah, land managers conducted a prescribed burn during the fall of 1999. In the fall of 2000, following the 1999 fall burn, I constructed a belt transect 400 feet by 2 feet starting at the photo point of figure 7.1. Half the transect was in the burn area and half in the mountain big sagebrush stand. Canopy cover of mountain big sagebrush exceeded 30 percent. Within this transect, I counted, in the burned proportion, 37 (36 in 2003) musk thistle plants, all at the rosette stage of development (fig. 7.2), meaning that the plants had established themselves during the spring of 2000 and would bolt and flower the following summer of 2001. In the mountain big sagebrush stand, I counted two (five in 2003) small rosette plants. The burn had the undesirable effect of increasing the distribution and abundance of a noxious weed.

Figure 7.1—A view (north to south) along a 400 ft by 2 ft belt transect from a prescribed fire (fall 1999) of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) into unburned mountain big sagebrush having a canopy cover greater than 30 percent. The prescribed fire was located just west of Trout Creek in the Strawberry Valley of central Utah. Two hundred feet of the transect was in the burned area and the remaining 200 feet was in the unburned area. The burned portion of the transect contain 37 plants in 2000 and 36 in 2003 of the noxious weed musk thistle (*Carduus nutans*) and unburned area 2 small plants in 2000 and 5 in 2003 (photo by Bruce L. Welch fall 2000).

Figure 7.2—A closeup view in the burned area of figure 7.1 showing at least 7 plants of musk thistle (*Carduus nutans*) and a few blacken stump of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*); (photo by Bruce L. Welch fall 2000).

Does Killing, Thinning, or Controlling Big Sagebrush Increase Grass Production?

Kissinger and Hurd (1953) and Hedrick and others (1966) studied the improvement of perennial grass production by killing big sagebrush. I interpreted their findings as comparing grazed-out big sagebrush plots, to treated plots, with treated plots showing a substantial gain in perennial grass production—some two or threefold or more increase. The conclusions from these and many like studies were that big sagebrush suppresses perennial grass production. Yet, the possible contribution of poor grazing practices in suppressing perennial grass production has not been factored out. A comparison between treated big sagebrush plots and nongrazed big sagebrush plots would help to ascribe how much of the observed perennial suppression was due to the presence of big sagebrush and how much was due to poor grazing practices.

Do we have data available to allow for such a comparison. Yes, to a limited degree. In table 7.1, I have listed the results of 29 studies that were conducted to determine the amount of perennial grass production that was achieved by killing big sagebrush by various means, on varying sites, and for varying lengths of times after treatment. Some of the studies involved seeding perennial grasses (mostly nonnative) and forbs after the treatments, and others did not. Table 7.2 displays the production of perennial grasses on ungrazed kipukas and relicts from the study of Passey and others (1982). Data in both tables are based on pounds of air-dried perennial grass forage per acre. The yearly means (1, 2 to 3, 4 to 5, 6 or more years after treatment) for the 29 studies were 283, 421, 609, and 438 pounds. The range for these studies was 42 to 1,805. These values compare fairly close with the overall mean of 455 and range of 90 to 1,169 for the Passey and others (1982) study of ungrazed kipukas and relicts (also see, Passey and Hugie 1963; Pechanec and Stewart 1949). These data support the proposition

Table 7.1—Production of perennial grass on big sagebrush (*Artemisia tridentata*) controlled plots. Data expressed as pounds per acre of air-dried grass. Perennial grass production was grouped according to number of years after treatment 1, 2 to 3, 4 to 5, and 6 years or more.

		Perennial grass production					
Study	**Treatments**	**1**	**2–3**	**4–5**	**6+**	**Study range**	**Big sagebrush subspecies**
lb/acre							
Baxter 1996	Teb				495	—	—
Olson and others 1996	Teb				725	582–819	—
Halstvedt and others 1996	Teb				536	368–750	—
Kay and Street 1961	24D				970	90–970	—
Miller and others 1980	24D		267	550	—	—	Mountain
			615	579	—	—	Mountain
Clary and others 1985	Teb	218	524	—	—	135–885	Mountain
Sturges 1986	24D	281	426	347	—	261–521	Mountain
Wambolt and Payne 1986	Burn	206	240	382	379	93–672	Wyoming
	24D	162	550	428	289	157–664	Wyoming
Plow	144	255	365	200	74–540	Wyoming	
Rotocut	145	331	333	200	88–567	Wyoming	
Murray 1988	Teb	—	331	493	—	160–605	Mountain
Thilenius and Brown 1974	24D	—	—	—	267	174–359	—
Evans and Young 1975	24D	276	503	508	—	339–677	—
	24D+Picl	588	913	1274	—	588–1381	—
Robertson 1969	24D	143	450	1163	—	143–1163	—
		291	429	798	—	291–798	—
Johnson 1969	24D	—	253	187	255	182–294	—
Tabler 1968	24D	310	400	800	410	—	—
Hedrick and others 1966	24D	375	343	743	358	300–910	—
Rotobeat	388	405	643	276	285–725	—	
Peek and others 1979	Burn	85	215	—	—	—	Wyoming
West and Hassan 1985	Burn	80	259	—	—	—	Wyoming
Alley 1956	24D	—	—	—	—	769–1347	—
Schumaker and Han. 1977	24D	—	259	—	—	—	Wyoming
Grubbed	—	308	—	—	—	Wyoming	
	24D	—	411	—	—	400–473	Mountain
Grubbed	—	412	—	—	400	–424	Mountain
Tueller and Evans 1969	24D	—	325	461	517	110–910	—
Picoram	—	308	971	510	250–1805	—	
Olson and others 1994	Teb	—	—	—	724	582–819	—
Miller 1957	24D	—	780	—	—	—	—
Kissinger and Hurd 1953	245T	—	530	—	—	460–590	—
Hyder and Sneva 1956	245T	501	324	—	—	—	—
Grubbed	474	333	—	—	—	—	
McDaniel and others 1991	24D	442[a]	338[a]	—	554[a]	327–554[a]	Wyoming
Metsulfuron	510[a]	716[a]	—	558[a]		315–1185[a]	Wyoming
McDaniel and others 1992	Teb	—	678[1]	540[a]	492[a]	42–1344[a]	Wyoming
Raper and others 1985	Burn	192	—	—	—	144–240	Mountain
Blaisdell 1953	Burn	—	—	—	305	290–321	Mountain
	Burn	—	—	367	—	365–369	Wyoming
Harniss and Murray 1973	Burn	139	448	—	254	—	Wyoming
Means		283	421	609	438	(42–1805)	—

[a] Values based on total herbaceous standing crop.

Table 7.2—Production of perennial grasses, forbs, and total herbage on ungrazed kipukas and relict areas as determined by Passey and others (1982). Data expressed as pounds of air dried forage per acre and represents a 10-year mean, with arithmetic range in parentheses per exhibit or stand.

Exhibit or stand	Big sagebrush subspecies	10-year mean grasses lbs/acre	10-year mean forbs lbs/acre	10-year mean herbage
3A	Basin	563 (301–901)	131 (79–206)	694
4A	Basin	544 (245–781)	120 (42–211)	664
6A	Wyoming	160 (90–300)	92 (13–246)	252
8A	Basin	790 (435–1149)	212 (100–504)	1002
9A	Basin	453 (168–764)	181 (45–331)	634
10A	Basin	672 (347–1169)	166 (37–337)	838
11A	Wyoming	390 (225–713)	172 (51–289)	562
12A	Wyoming	369 (195–553)	205 (58–398)	574
13A	Wyoming	426 (266–632)	80 (5–173)	506
14A	Wyoming	299 (152–424)	65 (15–164)	364
15A	Basin	665 (362–1033)	100 (28–189)	765
16A	Wyoming	439 (271–612)	296 (175–463)	735
17A	Wyoming	307 (171–420)	138 (54–223)	445
18A	Wyoming	316 (208–480)	200 (122–290)	516
19A	Wyoming	426 (288–732)	180 (53–304)	606
Means	Basin	616 (168–1169)	152 (28–504)	767
Wyoming	348 (90–732)	159 (5–463)	507	
Overall	455 (90–1169)	156 (5–504)	611	

that ungrazed or undisturbed big sagebrush sites produce about the same amount of perennial grasses as treated sites where the big sagebrush has been destroyed. Big sagebrush canopy cover of the kipukas ranged from 14 to 34 percent (table 4.14; see chapter IV for a discussion concerning big sagebrush canopy cover and grass production).

Peterson (1995, p. 34) has suggested that: "Sagebrush is a product of the range, range condition is not a product of sagebrush." Differences in perennial grass production in big sagebrush stands have less to do with shrub cover than it has with soils, moisture (wet or dry years), grass species, and especially grazing history differences (Peterson 1995; Pechanec and others 1937; Pechanec and Stewart 1949; Piemeisel 1945). Johnston (2003) observed: "CCOV (canopy cover of big sagebrush) is not significantly correlated (at ∝ = 0.05 or 0.01) with either graminoid cover, forb cover, or bare soil cover." Thilenius and Brown (1974) observed: "On three summer cattle ranges in the Bighorn increased herbage production after sagebrush control with 2,4-D was a relatively short-lived phenomenon. Declines in production and in the proportion of graminoids in the herbage did not appear to be related to reinvasion of sagebrush as this was minimal on all three sites even after 10 to 11 years." Sneva's (1972) figure 2 shows a close relationship between herbage production and precipitation. In fact r and R^2 values are high at +0.9649 and 0.9311, respectively. Passey and Hugie (1963) noted on an ungrazed kipuka dramatic difference in the yield of perennial grasses and forbs on different soils within the kipuka. The Brunt silt loam soil yields 227 pounds of herbage per acre compared to 524 pounds of herbage per acre of the Newdale silt loam soil. Precipitation was slightly below average during the study period. So, it appears that the recurrence of perennial grass after big sagebrush control may be a reestablishment of potential grass production, without big sagebrush.

The Harniss and Murray (1973) report is often cited by those trying to justify the use of fire to improve grass production in the big sagebrush ecosystem. If you read and study just the figures or graphs in their report, it appears fairly obvious that burning big sagebrush increases grass yield substantially. Their figures or graphs are constructed based on four data points of vegetation production for the years 1937, 1939, 1948, and1966, all of which are related back to the so-called base year of 1936 or 100 percent. I do not believe that four data points representing 30 years of vegetative growth constitute an adequate sampling size, nor is expressing the data in relative terms of the 1936 year or 100 percent appropriate because weather conditions vary greatly among years. In fact, Pechanec and Stewart (1949, p. 23) noted: "Records from these range pastures and from detailed plot studies showed that not until 1937 had perennial bunchgrasses fully recovered from the effects of the 1934 drought." My interpretation of their (Harniss and Murray 1973) table 1 suggests an interesting contradiction to their figures. While their figures may portray accurately the relationship of grass production of 1936 to the other 4 years, I do not think they accurately represent the effects of burning or the killing of big sagebrush on grass production. Their table 1 shows that half of the data points of the unburned plots (1937 and 1966) produced more grass than burned plots, yet big sagebrush production was substantially lower in the burned plots that produced less grass. It should be pointed out that during 1966, precipitation was 75 percent of the long-term average (NOAA 1966) and that they cannot separate the alleged negative effects of big sagebrush on grass production from the negative effects due to drought. Also, there is a high probability that Harniss and Murray (1973) misidentified the big sagebrush in the study area; 11 inches of annual precipitation is more characteristic of Wyoming big sagebrush than mountain big sagebrush (Blaisdell 1953; see chapter I for details).

Peterson and Flowers (1984, p. 7) used a simulation model to predict the effects of fire on range production (grasses and forbs) in a number of ecosystems. One model was for the sagebrush ecosystem. They state: "The information used to simulate the effects of fire on sagebrush range is derived from long-term studies on sagebrush-grass range in Idaho (Blaisdell 1953, Harniss and Murray 1973, Mueggler and Blaisdell 1958) and Oregon (Hedrick and others 1966, Sneva 1972)." However, two of these five studies used for their model development were not burns. Both Oregon studies used 2,4-D to kill big sagebrush. The relationship between burning big sagebrush stands and spraying with 2,4-D is unknown.

In their model, Peterson and Flowers (1984) chose a prefire production level of 280 pounds of grasses and forbs per acre and a gain of 800 pounds of grasses and forbs per acre until sagebrush allegedly establishes dominance and reduces herbaceous production to the prefire level. In my opinion, there are a number of erroneous assumptions that the authors made in developing their model. First, the 280 pounds per acre of grasses and forbs probably reflects the production of degraded big sagebrush stands. If they had used the study average of Passey and others (1982) conducted in ungrazed big sagebrush stands, the prefire production level would have been 611 pounds of grasses and forbs per acre instead of the 280 pounds. Second, study average production of grasses and forbs for the five studies cited were: Blaisdell (1953), 507 pounds per acre for his Fremont County site and 512 pounds per acre for his Clark County site; Harniss and Murrary (1973), 534 pounds per acre for 1939, and 508 pounds per acre for 1948; Mueggler and Blaisdell (1958), 602 pounds per acre; Hedrick and others (1966), 438 pounds per acre; and Sneva (1972), about 681 pounds per acre. The Peterson and Flowers (1984) postfire production of 800 pounds per acre seems much too high (the average of the studies cited above is 540 pounds per acre). Third, the authors did not build into their model the effects of precipitation on grass and forb production. Holecheck and others (1989, p. 21) state: "Precipitation is the most important single factor determining the type and productivity of vegetation in an area." This relationship is illustrated in the Sneva (1972) citation. In fact r and R^2 values are high at +0.9649 and 0.9311, respectively. If the authors (Peterson and Flowers 1984) had analyzed grass and forb yield for the years 1963 to 1969, where Sneva (1972) claimed that big sagebrush was reestablishing itself on the sprayed plots to the years 1954 to 1962, they would have discovered that the mean yields under the influence of big sagebrush was 680 pounds per acre as compared to 672 pounds per acre with reduced big sagebrush.

A common practice before a prescribed fire is to rest the proposed treatment area from livestock grazing for a year or two, to allow the buildup of fine fuels (grasses and forbs); or in other words, grasses and forbs increase in pounds per acre and/or cover without prekilling big sagebrush (Bunting and others 1987). This could be considered as range improvement without killing big sagebrush.

Peek and others (1979), in their table 3, show no significant increase in grass production 1, 2, and 3 years after a burn on Wyoming big sagebrush winter range. Similar results occurred in the study conducted by Raper and others (1985) 1 year after a burn in mountain big sagebrush. West and Hassan's (1985) report in their table 2 shows that perennial grass production decreased after wildfire. Blaisdell (1953) found no significant increase in total perennial grass production due to burning, 15 years after the burn, on his Fremont County site but did detect a significant increase in total perennial grass production due to burning, 12 years after the burn, on his Clark County site. Out of 12 data points, four sites and 3 years, Cook and others (1994) found that perennial grass yields were higher on burned sites versus unburned sites six times for 50 percent. Wambolt and others (2001, p. 243) studying 13 burned sites versus paired unburned sites in Montana noted: "Total perennial grass canopy coverage was not different ($P< 0.05$) between treatments over the 13 sites. Managers considering prescribed burning of big sagebrush communities should be aware that herbaceous plant responses may be minimal while shrub values will likely be lost for many years." Even where overall grass production has shown an increase, certain important species for wildlife and livestock (Idaho fescue, *Festuca idahoensis*) are frequently reduced (Peterson 1995).

Several studies showed that total vegetative production—that is, pounds of air-dried forage for all classes of plants—is reduced with big sagebrush control (Blaisdell 1953; Britton and Sneva 1983; Harniss and Murray 1973; Mueggler and Blaisdell 1958; Murray 1988; Pechanec and Stewart 1944a,b; Schumaker and Hanson 1977; Sturges 1986; Tabler 1968). Sites with big sagebrush are not only more productive, but the big sagebrush itself is important for the entire vegetative community by providing protection for understory plants, storing more snow, improving soil conditions at greater depth through root decay, and recycling deep soil moisture and nutrients (Peterson 1995; see also chapter IV).

There are natural abiotic and biotic forces at work in all big sagebrush stands that affect shrub density and age structure over time. See previous chapters for discussion of most of these natural agents, such as Aroga moth (*Aroga websteri*), leaf beetles (*Trirhabde pilosa*), snow mold, wilt diseases, voles, mule deer, and so forth (Austin and Urness 1998; Ganskopp 1986; Gates 1964; Hall 1963; McArthur and others 1988; Mueggler 1967; Nelson and Krebill 1981; Nelson and Sturges 1986; Partlow and others 2004; Pringle 1960; Smith 1949; Sturges 1989; Wambolt and Hoffman 2004). These agents act to create interspaces within the big sagebrush stand where new seedlings can be established, thus resulting, if given enough time, in a multiage stand that contains more diversity.

Does Killing, Thinning, or Controlling Big Sagebrush Increase Biodiversity?

Olson and Whitson (2002, p. 146) observe: "Late successional, dense *Artemisia tridentata* (big sagebrush) stands restrict associated plant species production, resulting in a monotypic, shrub-dominated community that threatens biodiversity preservation and ecosystem function." This statement raises three issues: (1) dense stands of big sagebrush reduce yields of associated plant species, meaning grasses and forbs; (2) dense stands reduce biodiversity; and (3) big sagebrush is a highly competitive, dominating, suppressive plant species.

The effect of big sagebrush canopy cover on grass production has been addressed in an earlier section of this chapter and also in the big sagebrush canopy cover versus bare ground cover and perennial grass cover section in chapter IV. The second and third issues listed above will be addressed here.

Olson and others (1994) reported that in their big sagebrush control plots, the number of plant species increased by three to four species over untreated big sagebrush plots. However, they did not name the plant species and their origins, so we do not know if they were desirable or undesirable species. Other questions arise. Are their comparisons between overgrazed big sagebrush sites versus treated sites proper, or should the comparisons be between undisturbed or never grazed by livestock big sagebrush sites versus treated sites?

Should the measurement of biodiversity be determined only on number of plant species present or on total number of species of all life forms? Killing of big sagebrush certainly reduces the frequency and perhaps the number of lichen species in a treated area, thus resulting in a loss of biodiversity. In chapters II and III of this manuscript we see that a host of organisms feed directly and indirectly on big sagebrush, including large and small mammals, birds, insects, fungi, parasitic vascular plants, and so forth—definitely an expression of biodiversity.

I calculated correlation coefficients and coefficients of determination for the data (plant community composition) published in Tart (1996), including data between canopy cover of mountain big sagebrush and number of perennial grass species, number of forb species, and total number of plants (table 4.15). No significant relationships were detected. In the Tart (1996, p. 42) study is found a description of a mountain big sagebrush community with a canopy cover of 46 percent with 48 species of grasses and forbs; this compares to a description of a mountain big sagebrush community with a canopy cover of 17 percent with 33 species of grasses and forbs (his p. 26). On his page 74 is a description of a mountain big sagebrush community with a canopy cover of 17 percent with 35 species of grasses and forbs.

The Goodrich and Huber (2001) study also demonstrates a lack of relationship between big sagebrush canopy cover and number of grass and forb species:

> 31-4-exclosure 32.4 percent big sagebrush canopy cover-41-grasses & forbs-46-total plants,
>
> 32-66-grazed 16.4 percent big sagebrush canopy cover-38-grasses & forbs-41-total plants,
>
> 32-67-grazed 15.1 percent big sagebrush canopy cover-44-grasses & forbs-47-total plants,
>
> 31-35A-grazed 5.0 percent big sagebrush canopy cover-43-grasses & forbs-46-total plants,
>
> 32-78-grazed and burned 0.2 percent big sagebrush canopy cover-42- grasses & forbs-46 total plants.

Perryman and others (2002, p. 419) studying the response of vegetation to prescribed fire in Dinosaur National Monument, Utah, found: " Mean number of [plant] species on combined control and burn areas were 17 and 18, respectively." Only one comparison out of 20 showed a significant increase in number of plant species for the burned site versus the unburned site. Tiedeman and others (1987) and Baker and Kennedy (1985) reported similar results. It appears highly unlikely that dense big sagebrush canopy cover suppresses or reduces biodiversity.

Big sagebrush is the mother of biodiversity. It is what supports life in Bailey's (1896, p. 359) description: "One never recovers from his surprise that there should be so much life where apparently there is so little to support it."

Is Big Sagebrush a Highly Competitive, Dominating, Suppressive Species?

Winward (1991, p. 5) answers this question:

> Mountain and basin big sagebrush sites in best condition have cover values between 15-20 percent. Those numerous sites that support cover values in the 30-40 percent category have a much restricted herbaceous production and are essentially closed to recruitment of new herbaceous seedlings. Some type of shrub removal process will be needed before understory forbs and grasses can regain their natural prominence in these communities.

He also states that Wyoming big sagebrush stands with canopy cover over 15 percent would, also, have "a much restricted herbaceous production."

During the 1940s and 1950s the range management community recognized that the canopy cover of big sagebrush provided a protective barrier for grasses and forbs from excessive livestock grazing (Pechanec and Stewart 1949). Big sagebrush forms such an effective protective cover for grasses and forbs that Pechanec and Stewart (1944a) estimated that 50 percent of the palatable grasses and forbs under big sagebrush is unavailable to grazing livestock. This is illustrated in figure 4.2.

There is an untested hypothesis proposed by some in the range management community that states: the surface roots of big sagebrush roots in the interspaces among big sagebrush plants have the capacity to capture water and nutrients to the point that they starve out associated herbaceous plant species. Data within Tart's (1996) report refutes this hypothesis (see table 4.15, chapter IV, and the previous section). Stands of mountain big sagebrush with the highest canopy cover at 46 percent had grass and forb cover above the study averages (Tart 1996, p. 42). Conversely, stands of mountain big sagebrush with the lowest canopy cover at 17 percent (p. 26) had below average grass and forb cover. Also, this hypothesis ignores a number of ecological facts concerning the interactions of big sagebrush with its associated herbaceous plant species.

This untested hypothesis brings up the question: If big sagebrush roots are so competitive, why is it that in grazed-out big sagebrush stands, the only place grasses and forbs can be found is under the protective cover of big sagebrush plants (fig. 4.2)? Daddy and others (1988) found that the greatest root concentration is under the canopy cover of big sagebrush. Why do the roots of big sagebrush not starve out grasses and forbs under its canopy?

Four scientific articles show that when grazing is eliminated or reduced, grass cover increases in spite of high or increasing big sagebrush canopy cover. McLean and Tisdale (1972), studying the time it requires for land to recover from overgrazing, found inside their West Mara (British Colombia) plot that perennial grass cover increased from 51 to 67 percent in 9 years with (probably mountain) big sagebrush canopy cover of 31 to 34 percent. Outside, big sagebrush canopy cover was 38 percent, and the cover of perennial grass increased from 35 to 51 percent. Branson and Miller (1981) found that after 17 years of improved grazing management canopy cover of (probably Wyoming) big sagebrush increased from 23 to 30 percent, and grass cover increased from 3 to 41 percent. Three other study sites showed similar trends: below hill top—big sagebrush canopy cover increased from 15.1 to 30.7 percent, perennial grass cover increased from 2.8 to 33.3 percent; big sagebrush-big sagebrush canopy cover increased from 12.6 to 39.3 percent, perennial grass cover increased from 1 to 27.9 percent; and sagebrush strip-big sagebrush canopy cover increased from 31.9 to 36.6 percent, perennial grass cover increased from 10.1 to 36.3 percent. Pearson (1965) found big sagebrush canopy cover inside of an 11-year-old exclosure to be 34 percent with 39 percent cover of perennial grasses. Outside his exclosure, canopy cover of big sagebrush was 11 percent with a perennial grass cover of 22 percent. Anderson and Holte (1981) reported big sagebrush canopy cover increased with more than 25 years of protection from grazing from 15 to 23 percent with perennial grass cover increasing from 0.28 to 5.8 percent. What I found interesting about this study was that perennial grasses showed any signs of recovery after starting at a cover value of less than three-tenths of a percent. Also, of interest is Daddy and others (1988) citation of the Anderson and Holte (1981) study. Daddy and others (1988, p. 415) stated: "Anderson and Holte (1981) reported that canopy cover of big sagebrush increased 54% with little change in cover of understory grasses after 28 years of complete protection from grazing in southern Idaho." They expressed the increase of big sagebrush canopy cover as a percentage, and changed the terms for expressing grass cover increase as "little change." Percentage increase in grass cover was 2,071 percent (from 0.28 percent to 5.8 percent). These studies showed that as canopy cover of big sagebrush increased, perennial grass cover also increased.

Richards and Caldwell (1987) found that big sagebrush has the capacity to draw water from deep, moist soil layers and at night redistribute water into the drier upper layers of the soil. Here nonbig sagebrush plants may parasitize this water (Caldwell and Richards 1989). They termed this phenomenon hydraulic lift. Caldwell and others (1991) listed the following advantages for hydraulic lift as prolonging the activities of fine roots, mycorrhizae, and nutrient uptake in drying soils. Ryel and others (2002) listed another advantage, a delay in the development of xylem embolisms. They estimated that as much as 20 percent of the water used by nonbig sagebrush plants can come from hydraulic lift on a given day.

A number of studies show that big sagebrush is a soil builder (Chambers 2001; Charley and West 1975, 1977; Doescher and others 1984; Fairchild and Brotherson 1980). The nutrient content—such as nitrogen, phosphorus, potassium, calcium, and so forth—directly under the canopy of big sagebrush is higher than the nutrient content in the interspaces. For nitrogen, Charley and West (1975) suggested that three factors may be operating in concert to account for the accumulation: first, enhanced fixation by free-living microorganisms in or under litter; second, animal activity; and third, canopy-capture of wind-transported solids. Mack (1977) describes a fourth factor, that of absorbing minerals deeper in the soil and depositing them on the soil surface as litter. As a result big sagebrush creates islands of fertility that can be utilized by other plant species. Krannitz and Caldwell (1995, p. 166) note: "Contrary to expectations, when roots of any test species contacted, or were in the vicinity of, *Artemisia* roots, their growth rate was not significantly affected."

Finally, from the allelopathic section (chapter IV), Daubenmire (1975, p. 31) states: "Field observations in Washington indicate that not only is there no allelopathic influence from the species of *Artemisia*, but that it has a beneficial effect on other plants." Wight and others (1992) describe one of these "beneficial effects on other plants" as water conservation (also see Chambers 2001) and extending water near the soil surface by 2 weeks versus interspaces between plants. They noted that big sagebrush canopies reduce solar radiation and prolong the period favorable for seedling establishment for perhaps as long as 28 days (also see Pierson and Wight 1991 and Chambers 2001 for favorable soil temperatures under big sagebrush).

Recovery of Big Sagebrush After Fire and Fire Interval

Recovery After Fire

The length of fire interval in the big sagebrush ecosystem remains an active debate. Mueggler (1976, p. 6) stated: "Judging from the reports of early explorers, these fires were not frequent enough to alter the vegetation in favor of more fire-enduring grasses." Winward (1991, p. 4) argued for a short interval of 10 to 40 years but acknowledges "…that I perhaps could not back-up if I were asked for specific figures." Winward (1984, p. 3) states: "Normally sagebrush survives fires through rapid regeneration of seedlings and in this sense it may be called fire tolerant."

How rapid can fire-intolerant big sagebrush reestablish itself after a fire? Winward (1984, p. 3) says: "In most cases it is well on its return to the site 5-10 years after a burn. Normally enough sagebrush seed remains in the soil surface for rapid recolonization." None of 13 mountain and Wyoming big sagebrush burned sites studied by Wambolt and others (2001) support Winward's (1984) statement. Hanson (1929) noted that grasses were dominant over (probably mountain) big sagebrush 5 to 10 years after a fire. Pechanec and Stewart (1944b, p 13) stated the following concerning the recovery of big sagebrush after a burn: "Eleven years after burning almost no sagebrush has reoccupied the area." Blaisdell (1950), studying what was probably a mountain big sagebrush stand, noted some reestablishment 15 years after a fire. Blaisdell (1953) found little reestablishment of what was probably a Wyoming big sagebrush stand 12 years after a fire. Harniss and Murray (1973) noted that full big sagebrush recovery had not occurred even after 30 years. Bunting and others (1987, p. 4) set mountain big sagebrush recovery at 15 to 20 years and observed that "Wyoming big sagebrush will establish readily from seed if seed is available. Slow growth, however, reduces the rate at which it recovers compared to other big sagebrush subspecies." Eichhorn and Watts (1984, p. 32) reported: "burning removed big sagebrush (*Artemisia tridentata wyomingensis*) from the site and it has not reinvaded after 14 years." Wambolt and Payne (1986) reported that 18 years after a fire, Wyoming big sagebrush canopy cover was only 16 percent of control and significantly below other control methods. Fraas and others (1992) found little recovery of mountain big sagebrush on an 8-year-old burn. Wambolt and others (1999), studying the production of three subspecies of big sagebrush 19 years after a fire on the northern Yellowstone winter range, found that "recoveries of burned compared to unburned

Wyoming, mountain, and basin big sagebrushes were…0.1, 1.4 and 11% for production of winter forage, respectively." They further studied seven other burn sites of mountain big sagebrush on the northern Yellowstone winter range and found no significant recovery of mountain big sagebrush 9 and 13 years after prescribed burning. West and Yorks (2002, p. 175) noted after 19 years: "*Artemisia* [Wyoming big sagebrush] has been slow to reestablish at our burned locations." Humphrey (1984), studying the patterns and mechanisms of plant succession after fire in the big sagebrush habitat, found a pronounced delay of some 18 to 32 years in the establishment of big sagebrush. He attributed this delay to big sagebrush dependency on the dispersal of its propagules, achenes, or seeds. Seed dispersal of big sagebrush as explained in chapter VI could take some 105 to 211 years to spread 1 mile (Chambers 2000; Noste and Bushey 1987).

However, Mueggler (1956, p. 1) on probably a Wyoming big sagebrush site noted: "Establishment of thick stands of big sagebrush (*Artemisia tridentata*) seedlings the year following planned burning of sagebrush-grass range sometimes occurs despite all known precautions." The key word in his statement is "sometimes." Unfortunately, workers such as Burhardt and Tisdale (1976, p. 478) have changed the word "sometime" to "generally," which gives the misleading impression that most burned big sagebrush stands can regenerate quickly; or in the case of Winward (1984, p. 3) most of the time as would be inferred by his statement that big sagebrush is well on its return 5 to 10 years after a fire.

Somewhat supportive of the Mueggler (1956) study is the data set I collected from a recent fire near Provo, UT. In August 1999, a wildfire swept across the northern half of West Mountain located about 7 miles southwest of Provo. The fire killed all big sagebrush plants in its path. The big sagebrush population on the study site seemed to be a mixture of mountain big sagebrush and a Wyoming big sagebrush introgressed by mountain big sagebrush (McArthur and Sanderson, personal communication). Prior to the fire, summer 1997, I established two line intercepts to determine big sagebrush canopy cover. The area where these two line intercepts had been established were burned.

GPS coordinates (elevation 5,000 feet in a 14 to 16 inch precipitation zone) for the start of the first line intercept was N 40° 07.357; W 111° 48.997 and went 1,500 feet due west. The intercept was divided into five 300 foot sections. Canopy cover of big sagebrush was 31.6 ± 4.45 percent. In spring of 2004, canopy cover was 0 percent. During the spring 2004, I established six 1-acre plots along the intercept and counted the number of big sagebrush plants growing within the boundaries of each plot. The 1-acre plots were established south and north of the intercept for a total of eight plots. The closest seed source for big sagebrush was 0.4 mile away; therefore, all big sagebrush plants counted in the 1 acre plots were from residual seed surviving the fire. Production of seed stalks were noted 5 years after the fire in autumn 2004. Results on a per plot bases were: 0, 0, 0, 2, 3, 14, 21, 47 big sagebrush seedlings.

GPS coordinates (elevation 6,000 feet in a 14 to 16 inch precipitation zone) from the start of the second line intercept was N 40° 06.815; W 111° 49.214 and went 900 feet due south. Canopy cover of big sagebrush was 32.4 ± 4.9 percent. In spring 2004, canopy cover was 0.05 percent. Five 1-acre plots were established along the intercept as described above. Results on a per plots bases were 1, 1, 3, 11, 121 seedlings.

The above data set suggests that in some cases big sagebrush can give the appearance of being well on its return 5 to 10 years after a fire but in most cases it is not. All this on the same fire. I define, some cases or sometimes, as being an event that occurs with a frequency of 20 percent or less. Plots that would give appearance of rapid recovery of big sagebrush after the 1999 West Mountain Fire contained 47 and 121, 4-year-old big sagebrush plants derived from residual seeds surviving the fire, or 15.4 percent of the plots showing signs of a possible rapid recovery. I intrepret this data set not to support Winward's (1984, p. 3) statement: "In most cases…"

In addition to the scientific articles previously cited, I have measured the reestablishment of mountain big sagebrush on an approximately 360 acre, 14-year-old burn known as the Grandine Fire located some 3 miles northeast of Stone, ID (Klott and Ketchum 1991). I established a point at N 42° 01.545'; W 112° 38.283'; 300 feet from the western edge of the Grandine Fire and constructed a line running due east into the burned area for 3,300 feet (the line could have been continued for an additional 3,000 feet or more) and used this line to determine percent canopy cover of mountain big sagebrush and sprouting shrubs such as rabbitbrush (*Chryothamnus* ssp.), snakeweed (*Gutierrezia* ssp.), and horsebrush (*Tetradymia* spp.). Mountain big sagebrush canopy cover for the unburned area—the first 300 feet—was 30 percent and 4 percent for the sprouting shrubs. For the first 300 feet into the burned area, mountain big sagebrush canopy cover was 3 percent and 2 percent for the sprouting shrubs. Three percent mountain big sagebrush canopy cover continued to 600 feet and from 600 feet to the 3,300-foot point; that is, for 2,400 feet my line did not intercept a single big sagebrush plant. Sprouting shrubs canopy cover varied over the same distance from 8 to 26 percent. The rate of mountain big sagebrush reestablishment on this burn from the west to the east was about 42 feet per year. Reestablishment from the east to the west and from the north to the south was essentially nil, and the reestablishment rate from the south to the north was half of that of the west to the east. Based on these measurements, recovery of big sagebrush on the burn would take some 71 years just to reach the 3,300-foot point and would not include the time needed for full canopy recover. There were widely scattered mountain big sagebrush plants throughout most of the burn site that would help to reduce the 71-year recovery rate, but they too are subject to 42 feet per year spread in an easterly direction and even shorter distance in a northerly direction. These scattered plants were probably derived from soil-borne seeds that survived the burn.

Fire Interval

In an often-cited article by Winward (1991, p. 4), he, in reference to the big sagebrush ecosystem, states: "These ecosystems, which have developed with an historical 10-40 year fire interval, were dependent on this periodic removal or thinning of sagebrush crowns to maintain their balanced understories." However, a 31-year study of a mature big sagebrush stand in the Gravelly Mountains in Montana demonstrated the ability of a big sagebrush ecosystem to maintain itself without the occurrence of fire (Lommasson 1948). Others estimate a much longer fire interval.

Houston (1973) estimated the fire interval in what he termed "bunchgrass steppes" of northern Yellowstone National Park winter range to be from 53 to 96 years. Feeling that modern humans have influenced the fire interval through fire suppression activities, he adjusted the interval by subtracting 80 years from the ages of living trees and came up with adjusted fire intervals of 32 to 70 years in the big sagebrush steppes of northern Yellowstone National Park. I believe that Houston (1973) was overly optimistic in his estimate on how soon modern humans could significantly suppress fires. This ability may not have occurred until the 1950s (see "Fire Statistics-Average number of fires and acres burned by decade" on http://www.nifc.gov/stats/wildlandfirestats.html-Wildland). Even Houston's (1973) adjusted fire interval of 32 to 70 years exceeds the interval suggested by Winward (1991). Wright and Bailey (1982, p.159) suggested fire interval of 50 years "based on the vigorous response of horsebrush (*Tetradymia canescens*) to fire and the 30-plus years that are needed for it to decline to a low level after a fire in eastern Idaho." They further observed (p. 160): "If fires occurred every 20 to 25 years, as Houston [1973] implies, many sagebrush-grass communities in eastern Idaho could be dominated by horsebrush and rabbitbrush (*Chrysothamnus* ssp.)." (Also see Young and Evans 1978b and Britton 1979.) For Wyoming big sagebrush ecosystems, Wright and Bailey (1982) suggested a fire interval as long as 100 years. Whisenant (1990, p. 4) stated: "Prior to the arrival of white settlers, fire intervals in the sagebrush (*Artemisia*)-steppe probably varied between 60 and 110 years," and that due to the presence of cheatgrass (*Bromus tectorum*), on what was big sagebrush steppe, these areas can burn at intervals of less than 5 years, resulting in a total loss of big sagebrush.

Winward (1984) suggests that mountain big sagebrush, which usually grows at higher elevations, has a burn cycle of 20 to 30 years. This is based on higher vegetative productivity of the mountain big sagebrush sites, or in other words, higher fine fuel accumulation and higher frequency of lightning strikes, which he believes results in a shorter fire cycle as compared to basin and Wyoming big sagebrush sites that produce less fine fuels and experience fewer lightning strikes. However, I believe that the greater accumulation of biomass and higher number of lightning strikes on mountain big sagebrush sites could be offset somewhat by lower temperatures and higher humidity that occur on these sites.

Arno and Gruell (1983) found that the fire interval prior to 1910, at ecotones between mountain big sagebrush ecosystems and forest ecosystems, ranged from 35 to 40 years (also see Gruell 1983). Miller and Rose (1999) suggest a fire interval of 12 to 15 years based on fire scars found on ponderosa pine (*Pinus ponderosa*). Neither Arno and Gruell (1983) nor Miller and Rose (1999) have linked fire scarring of trees to fire interval in mountain big sagebrush communities. On the ridge just west of Brown Lake in the Great Basin National Park, I have found basal fire scarring of limber pine (*P. flexilis*) and Engelmann spruce (*Picea engelmannii*) growing on talus that is not capable of carrying ground fires. These scars were caused by lighting strikes. Perhaps fire scarring due to ground fires can be identified from scars due to lighting strikes.

Soil characteristics of the ponderosa pine clusters used in the Miller and Rose (1999) study may be dramatically different from those of the adjacent mountain big sagebrush stands (Billings 1950; Delucia and others 1989; Gallardo and Schlesinger 1996; Schlesinger and others 1989). If so, what effects these differences might have on fire intervals on either plant community were not addressed. Also, Miller and Rose's (1999) sampling method was not done in a randomized manner; they chose only trees bearing fire scars. In fact, they (Miller and Rose 1999, p. 553) stated: "In clusters I and IV, trees with the maximum number of fire scars visible on the surface were selected for sampling." Would this tend to overestimate number of fires for a given period? Baker and Ehle (2001, p. 1205) state: "Inadequate sampling and targeting multiple-scarred trees and high scarred densities bias mean FI toward shorter intervals." They suggest mean fire interval for ponderosa pine may be 22 to 308 years.

The Miller and Rose (1999) report does present data that show a major fire event occurring at a 50-year or more cycle. These major fire events could have burned over a significant amount of mountain big sagebrush area. A fire interval of greater than 50 years is probably compatible with maintaining a mountain big sagebrush community (Lommasson 1948).

There are 10 biological and ecological characteristics of mountain or any other big sagebrush that do not support the idea that this big sagebrush evolved in an environment of frequent fires: (1) a life expectancy of 70+ years (Daubenmire 1975; Ferguson 1964; Fowler and Helvey 1974; Passey and Hugie 1963); (2) highly flammable bark (the stringy bark makes excellent fire starting material); (3) production of highly flammable essential oils (Buttkus and Bose 1977; Cedarleaf and others 1983; Charlwood and Charlwood 1991; Kelsey 1986; Kinney and others 1941; Powell 1970); (4) a low-growth form that is susceptible to crown fires (Beetle 1960; McArthur and others 1979); (5) nonsprouting (Peterson 1995; West and Hassan 1985; Wright and others 1979); (6) seed dispersal occurs in late fall or early winter long after the fire season has ended (Beetle 1960; Young and Evans 1989); (7) lack of a strong seed bank in the soil (Beetle 1960; Meyer 1990, 1994; Young and Evans 1989), although sometimes big sagebrush can express a strong seed bank (Mueggler 1956); (8) seed has no anatomical fire resistance structures or adaptations, that is, it has no thick seed coat (Diettert 1938); (9) seeds must lie on the soil surface, which exposes them to higher temperatures than seeds that are deeper in the soil (Hassan and West 1986; Jacobson and Welch 1987); and (10) seeds lack any adaptations for long-distance dispersal, hence, mountain big sagebrush lack the ability for rapid reestablishment (Astroth and Frischnecht 1984; Chambers 2000; Frischknecht 1979; Johnson and Payne 1968; Walton and others 1986; Wambolt and others 1989; Young and Evans 1989).

Effects of Fire on the Big Sagebrush Ecosystem

Effect of Fire on Soil Chemistry

The effects of fire on soil-surface (0 to 5 cm) chemistry have been studied by a number of workers (Acker 1992; Blank and others 1994a, 1995; Britton and Ralphs 1979; Daubenmire 1968; Hobbs and Schimel 1984; Mueggler 1976; Nimir and Payne 1978; Young 1983b). In general, these effects on burned sites are increases in the amounts of phosphorus, potassium, calcium, magnesium, micronutrients, and an increase in soil pH, and decreases in the amounts of sulfur and total nitrogen. It seems after a fire that nitrogen lost through volatilization is more than replaced by an increased output of nitrifying bacteria and increased nitrogen mineralization; thus, more nitrogen is available to the plants for at least a couple of years after the fire. Part of this increase in nitrogen comes from the green manure effect of dead big sagebrush and other species roots mentioned earlier by Daubenmire (1970). Acker (1992) detected no change in soil organic matter as a result of fire, but his sampling depth of 10 cm may have been too deep to measure changes that may have occurred at the surface. Blank and others (1995), however, found organic carbon to be significantly lower on soil surfaces of burned sites than unburned sites. They further found the following soil surface attributes to be significantly lower on burned sites: cation exchange capacity, cooper, zinc, and nitrate nitrogen. Attributes that were significantly higher on burned sites were: iron, sulfate, acetate, formate, and water drop penetration time or wettability of the soil.

Water Repellency

Water repellency induced by the burning of big sagebrush litter was studied by Salih and others (1973). They found that water repellency did not occur until temperatures reached about 704 to 760 °C, and above 982 °C there was no repellency at all. Blank and others (1995) also described a decrease in moisture infiltration due to water-induced repellecy as a result of burning big sagebrush. Water repellency can also be induced by burning litter of plant species other than big sagebrush (DeByle 1973; de Jonge and others 1999; Everett and others 1995; Robichaud and Hungerford 2000). Blank and others (1994b, p. 220) noted in their study concerned with the production of the organic acid from four different soil litters (big sagebrush, squirreltail [*Elymnus hystrix*], cheatgrass, and medusahead [*Taeniatherum caputmedusae* ssp. *Asperum*]): "The lack of variation in levels of certain organic acids among the soil-litters, however, suggest they were synthesized via pyrolysis of the soil humic fraction, rather than originating from the plant litter itself."

Other Fire Effects

In addition, fires can change the soil fabric of seedbeds in the following five ways: (1) caused the compaction of mineral grains through loss of organic detritus, (2) carbonized plant litter to a depth of approximately 5 cm, (3) caused the loss of fluoresecent compounds in sagebrush litter, (4) coated mineral particles with organic compounds, and (5) cleaved micaceous minerals (Blank and others 1995). Wicklow-Howard (1989) presents data suggesting that vesicular-arbuscular mycorrhizae fungi require 2 years to recover from the effects of fire. The overall effects of these changes on plant reestablishment on burned sites are not fully understood.

Islands of fertility occur under the canopy of big sagebrush plants (see chapter IV for details). According to work done by Halvorson and others (1997), these islands are detectable 9 years after a fire. In general, their unburned sites were significantly higher in most of the soil variables measured, and differences were greatest near the location of a big sagebrush plant or charred stump. They further noted (p. 287): "In contrast, burned soil was not distinguishable from unburned soil at distances greater than 50 cm away from a live *A. tridentata* axis or a charred stump indicating that soil patterns were most affected by removal of the plant and not by the fire." Soil factors that showed significantly higher levels, 9 years after a fire, closer to charred stumps, were: total organic carbon, total nitrogen, water soluble carbon, electrical conductivity, and soil microbial biomass carbon. Therefore, it is apparent that big sagebrush plants build soil fertility while alive, and these islands of fertility remain for years after their death.

There is some evidence that, for a few years after a fire, crude protein levels of grasses and forbs are higher on burned sites than unburned sites (Bunting 1989; Cook and others 1994; Hobbs and Spowart 1984). It should be noted, however, that any increases in crude protein levels are generally negated by late summer and fall when green foliage becomes desiccated and dormant (Peterson 1995).

Removing Big Sagebrush

Big sagebrush can be killed or thinned by a variety of techniques that can be classified into three basic categories: prescribed burning, chemical, and mechanical (Alley 1965; Pechanec and others 1954, 1965; Vallentine 1989). An additional method involves flooding (Ganskopp 1986; Pechanec and others 1954; Vallentine 1989).

Prescribed Burning

Guidelines for burning of big sagebrush have been published by Bunting and others (1987) and cover season of the year, size of fire, rest and deferment, prescription development, and safety.

Season of the Year—Cool season grasses such as bluebunch wheatgrass (*Agropyron spicatum*) are damaged the least by fall burns, and warm season grasses such as blue grama (*Bouteloua gracilis*) are damaged the least by spring burns. In the northern portion of the big sagebrush range no warm season grasses are present, thus eliminating the conflict between spring and fall burning. Bunting and others (1987, p. 9) stated: "In our experience, the perennial herbaceous species are most resistant if they are burned when completely dormant. In much of the Great Basin, spring fires are frequently not feasible due to the abundant moisture in late winter and spring." Late winter burning may often be feasible in eastern Idaho and western Montana. Caution should be taken when there has been sufficient late summer or early fall precipitation to cause fall green-up, because under these conditions, fire mortality of grasses can be much higher than burning during periods of complete dormancy.

Fall burning is the most common time to burn in the northern Great Basin, but due to possible fall green-up, managers also consider late summer burning when perennial grasses are dormant. This maximizes the number of burning days, and the drier conditions allow the carrying of fire with lower fuel loads and larger fire size. Also, due to drier conditions, late summer fires have a greater risk of fire escape. Spring burnings, due to high moisture and compacted fuels, are usually smaller and leave more unburned patches. Neuenschwander (1980) describes a method for burning in the winter that requires no fire control or mopup and burns only small patches.

Size of Fire—Bunting and others (1987, p. 15) point out: "Consideration should also be given to the amount of area that can be burned in a single burning period (normally 4 to 6 hours). In continuous fuels this limits the maximum size to about 500 to 2,000 acres when hand firing, and 1,000 to 3,500 acres when aerial ignition is used. Of course, where natural fire breaks do not occur, fire lines will have to be constructed to restrict fires to the desired size."

Rest and Deferment—The common plan for burning a given site is to rest the site from grazing to allow the buildup of fine fuels that are needed (600 to 700 pounds per acre) (Wright and others 1979) to carry the fire through the big sagebrush stand, or in other words, no pretreatment is needed to reduce big sagebrush canopy cover to increase grass yields to the point that grass would be able to carry a fire. After the burn, rest is recommended for at least 1 year and preferably 2 years.

Prescription Development—Bunting and others (1987) list weather factors for a prescribed big sagebrush burn: (1) relative humidity 15 to 35 percent; (2) temperature 60 to 85 °F; and (3) midflame wind 4 to15 miles per hour. Of these three factors, the most important is windspeed, which influences flame lengths and rate of spread. Bunting and others (1987, p. 16) noted: "When the relative humidity is greater than 30 percent, the temperature is less than 60 °F, and the midflame windspeed is less than 4 mi/h, it is unlikely that fire will spread satisfactorily unless fine fuels exceed 600 lb/acre." They further observed (p. 16): "When the relative humidity is less than 15 percent and the temperature is greater than 85 °F, fire control becomes more difficult. Windspeeds greater than 15 mi/h not only create fire control problems but also limit the effectiveness of fire within the burn area. At high windspeeds, the lateral spread of the fire is limited, and long narrow stringers of burned areas result." Slope does influence the rate of spread. A 30 percent slope will increase the rate of spread of a fire by a factor of two to three times over the same conditions on level ground, and 50 percent slope by a factor of four to seven times. Slopes increase the effective reach of a fire and lower the need of fuel loads and windspeed.

Safety—Bunting and others (1987, p. 17) warn: "Burning under hotter and drier conditions increases the risk of escape and the need for suppression forces." The fire crew needs to be briefed as to the overall plan and each individual's assignment. Personnel in charge of holding firelines need to be aware of critical points along the fire perimeter. The contingency plan in case of fire escape must be outlined. Location of water sources should be identified for all engine operators. Finally, escape routes for all personnel must be clearly identified.

Other factors that need to be discussed include: communication, what to do in case of changing weather conditions, and self-generating fire winds. Publications concerning fire behavior and modeling in big sagebrush ecosystems are available (Brown 1982; Frandsen 1983; Sapsis and Kauffman 1991).

Chemical Control

The literature on chemical control of big sagebrush is voluminous, as will be seen in this section.

Nine chemicals have been used to kill big sagebrush:

- 2,4-D [(2, 4-dichlorophenoxy) acetic acid]
- 2,4,5-T [(2,4,5-trichlorophenoxy) acetic acid]
- dicamba (2-methoxy-3,6-dichlorobenozic acid)
- tebuthiuron (N-[5-(1,1-dimethylethyl)-1,3, 4 thiadiazol-2-yl]-N, N'-dimethylurea)
- clopyralid (3, 6-dichloro-2-pyridinecarboxylic acid monoethanolamine salt)
- picloram (4-amino-3,5,6-trichloropicolinic acid)
- karbutilate [tert-butylcarbamic acid ester with 3(m-hyroxyphenyl)-1, 1-dimethylurea]
- metsulfuron [2-[[[[(4-methoxy-6- methyl-1,3,5-triazin-2yl) amino]carbonyl]amino]sulfonyl] benzoic acid]
- fluroxypyr

(Baxter 1996; Cornelius and Graham 1951; Evans and others 1983; Pechanec and others 1954; Whisenant 1986; Whitson and Nix 1989; Young and Evans 1978a).

The first three are synthetic auxins (Hopkins 1999) and are more resistant to oxidative enzymes than natural auxins. At low concentration they behave like auxins, that is, control or regulate plant cell growth and stem elongation, and can be used to enhance rooting of cuttings, development of seedless fruit, setting of fruit, and so forth. But at higher concentrations they kill broadleaf plants without harming grasses and other nonbroadleaf plants (Hamner and Tukey 1944; Hopkins 1999; Young 1983a). The herbicide 2,4,5-T has been banned by many jurisdictions because of high concentrations of dioxin, a highly carcinogenic substance; therefore, I will not discuss its uses any further in this publication (Hopkins 1999).

2,4-D is perhaps the most widely used herbicide for the control of big sagebrush. Its use as an herbicide was first proposed in 1941 in the form of a personnel communication by Kraus, as referenced by Hamner and Tukey (1944). The first successful uses of 2,4-D to kill big sagebrush were reported by Cornelius and Graham (1951) and Hull and Vaughn (1951). This started an avalanche of reports and studies that continued into the mid-1980s.

2,4-D can be manufactured as three esters: butyl, isopropyl, and ethyl (Hyder and others 1958a). Hyder and others (1958a) tested the different formulations and concluded that the isopropyl form was not as effective against big sagebrush as the butyl and ethyl esters. They suggested that 1.5 ai (active ingredient) pounds per acre emulsified in water would kill in excess of 75 percent of the big sagebrush plants. Alley and Bohmont (1958) recommended 2 ai pounds per acre of butyl ester mixed in oil. Cook (1963, p. 194), studying the effectiveness of a mixture of equal parts isopropyl and butyl esters of 2,4-D in water at 1.5, 2.0, and 3.0 ai pounds per acre applied on three dates (about May 15, May 30, and June 15), found that "when growing conditions were favorable, all three rates gave satisfactory results; when growing conditions were unfavorable none of the rates gave satisfactory control." Cook (1963) showed that the two May dates were usually more effective in killing big sagebrush than the June date in work performed in Utah. The difference between satisfactory and unsatisfactory results seems to lie with temperatures and percentage of soil moisture—maximum temperatures above 70 °F and minimum temperatures above 40 °F with soil moisture above 12 percent on the day of treatment, or in others words, during periods of favorable growing conditions. For California, Cornelius and Graham (1958) found best control of big sagebrush occurred using butyl ester of 2,4-D at a rate of 2 ai pounds per acre during active big sagebrush growth that usually occurs from late May to mid-June. Hyder (1953, 1954), Hyder and others (1956, 1962), and Hyder and Sneva (1955) reported similar results in Oregon. Cornelius and Graham (1958) further noted that the spray must be distributed to all the leaves of a plant for a total kill. Hormay and others (1962, p. 326) confirmed the effective distribution: "More often than not the unsprayed portion continued to live, indicating the chemical was not translocated in amounts enough to affect growth of the unsprayed portion."

Bartolome and Heady (1978), studying the rate of big sagebrush establishment after plowing and spraying with 2,4-D, found that "reinvasion begins immediately after treatment." Unlike a burn in which fire kills all big sagebrush plants in its path (Cluff and others 1983), spraying big sagebrush with 2,4-D kills some plants totally, others partly, and a few are totally missed, all at random. These partial killed and total escaped plants can recover quickly and become a seed source, which results in a quicker recovery of big sagebrush under these kinds of treatment than with fire.

This point is illustrated by Wambolt and Payne (1986) who compared four methods of Wyoming big sagebrush control. Wyoming big sagebrush recovered faster from plowing, rotocutting, and spraying with 2,4-D than when burned. Weldon and others (1958, p. 303) noted: "Rangeland on which 75 per cent or more of the sagebrush has been chemically controlled may be expected to remain relatively free from sagebrush seedlings for at least a 4-year period after chemical treatments." Gardner (1961) estimated the life of 2, 4-D spraying projects to be about 12 years, Johnson (1969) estimated less than 14 years, and Thilenius and Brown (1974) estimated 3 to 4 years. Thilenius and Brown (1974, p. 224) observed: "On three summer cattle ranges in the Bighorn, increased herbage production after sagebrush control with 2, 4-D was a relatively short-lived phenomenon. Declines in production and in the proportion of graminoids in the herbage did not appear to be related to reinvasion of sagebrush as this was minimal on all three sites even after 10 to 11 years."

In additional to killing big sagebrush when spraying with 2,4-D, this method can and does kill other broadleaf plants such as forbs, thus reducing the productivity of these valuable plants (Anderson 1969a; Blaisdell and Mueggler 1956; Miller and others 1980; Schumaker and Hanson 1977; Tabler 1968; Wilbert 1963). As a result of reduced biomass production of shrubs and forbs on 2,4-D sprayed big sagebrush ecosystems, a reduction also occurs in total biomass production of the treated site (Schumaker and Hanson 1977; Sturges 1986, 1994; Tabler 1968).

Often after spraying big sagebrush ecosystems with 2,4-D, grass production is increased two or threefold or more when compared to unsprayed areas (Alley 1956; Cornelius and Graham 1951; Hull and others 1952; McDaniel and others 1991; Miller and others1980; Sturges 1986, 1994; Tabler 1968; Wilbert 1963). Some of the workers seemed to be comparing treated sites with untreated sites, the latter appearing, in their photos, to be heavily overgrazed. This issue was discussed earlier (Evans and Young 1975; Hedrick and others 1966; Hull and others 1952; Hyder and Sneva 1956; Johnson 1969) (tables 7.1 and 7.2). Hull and Klomp (1974) noted in their study that to obtain the two- or threefold increase in grass production that nearly 100 percent of the big sagebrush needed to be killed, which would be devastating to the obligates of big sagebrush and would result in an overwhelming reduction in the biodiversity of the treated sites (Welch 2002; Welch and Criddle 2003; see chapters II and III for more details).

The effects of spraying mountain big sagebrush sites with 2,4-D on soils have been studied by Burke and others (1987, p. 1337), whose results or conclusions are somewhat confusing in that they claim that "Essentially, control of big sagebrush, in the absence of grazing, has no effect on site fertility." This conflicts with their earlier statement (p. 1337) that "undershrub net N mineralization rates were higher under shrubs in the sagebrush vegetation than under former shrubs in the grass vegetation," and that in the grass vegetation, N mineralization rates were similar under former shrub sites versus former interspace sites among shrubs. Nitrogen is the most limiting of all the plant mineral nutrients in arid and semiarid soils; therefore, decreases in nitrogen mineralization due to the loss of big sagebrush would greatly affect soil fertility.

Tebuthiuron is a nonselective herbicide that is surface broadcast onto soil where it moves with water into the rooting zone of plants and is absorbed by plant roots. Once absorbed, tebuthiuron is translocated to stems and leaves where it inhibits photosynthesis. Klauzer and Arnold (1975) were among the first to demonstrate the ability of tebuthiuron to kill big sagebrush on native wildlands. Due to its nonselective properties, tebuthiuron not only reduced the productivity of big sagebrush but also herbaceous productivity at all application rates—0.22 to 3.57 ai pounds per acre (Britton and Sneva (1981, 1983). Clary and others (1985), working in a mountain big sagebrush site, found no significant increases in grass or forb production 3 years after using tebuthiuron at the rates of 0.53 to 2.41 ai pounds per acre, even though big sagebrush production was dramatically reduced. Whitson and Alley (1984) reported similar results. Marion and others (1986, p. 123) also reported satisfactory control of big sagebrush using tebuthiuron at levels from 0.25 to 1.50 ai pounds per acre and observed: "Sandberg bluegrass reduction due to the herbicide was not significant at any rate tested." Whitson and others (1988) reported, 7 years after treatment with tebuthiuron (0.27 to 0.98 ai pounds per acre), a significant increase of cheatgrass on one site and a significant increase of western wheatgrass on the other site.

Not all perennial grasses showed an increase. Murray (1988) reported no significant increase in grass production 2 and 3 years after treating a mountain big sagebrush site with tebuthiuron (0.11 to 0.35 ai pounds per acre) but found a significant increase in grass production the fourth year. Forb production was unaffected by the treatment, while big sagebrush production was greatly reduced at all levels of tebuthiuron and for all 3 years. Wachocki and others (2001) reported no significant increase in understory vegetation due to treating mountain big sagebrush sites with tebuthiuron. McDaniel and others (1992), however, reported significant increases in understory vegetation due to treating primary Wyoming big sagebrush sites with tebuthiuron. They found a few big sagebrush seedlings 8 to 10 years after tebuthiuron treatments were applied, suggesting a long big sagebrush recovery period.

Tebuthiuron appears to be an effective herbicide against big sagebrush, but because of its nonselective characteristic it may harm nontarget plants such as grasses and forbs.

Other chemicals that can control big sagebrush but have received limited study are dicamba, clopyralid, picloram, karbutilate, metsulfuron, and fluroxypyr (McDaniel and others 1991; Whisenant 1986, 1987; Whitson and Nix 1989; Young and Evans 1978a).

More information on this topic can be found in the literature listed in table 7.3.

Table 7.3—Literature not cited in text on controlling big sagebrush with herbicides.

Anderson 1969b
Hyder and Sneva 1962
Hyder and others 1958b
Johnson and others 1980
Johnson 1964
Johnson 1958
Kay and Street 1961
Kituku and others 1993
Lord and Sanderson 1962
Mangan and Autenrieth 1985
Robertson and Cords 1956
Schroeder and Sturges 1980
Sneva and Hyder 1966

Mechanical Control

Mechanical control techniques involve uprooting, shredding of aerial parts, crushing, or trampling of big sagebrush plants that result in the death of a high percentage of the plants. Names of mechanical control techniques reflect the type of equipment used: plowing/disking, disk-chaining, root plowing, anchor chaining, railing, harrowing, and rotobeating (Davis 1983; Parker 1979; Pechanec and others 1954, 1965; Plummer and others 1968; Sampson and Schultz 1957; Vallentine 1989). The first three techniques not only destroy big sagebrush but also the herbaceous vegetation to such a degree that seeding after treatment is required. Any control method conducted near or after big sagebrush seed have matured (mid-October and on) will help to speed up the recovery of big sagebrush and reduce the amount of big sagebrush seeds needed to seed after treatment (Bleak and Miller 1955; Johnson and Payne 1968).

Plowing/Disking—Several kinds of equipment are used in this method of big sagebrush control: standard disk, wheatland diskplow, brushland diskplow, and the offset disk. The standard disk and wheatland diskplow are too light to hold up under the rigors of wildland tillage. The brushland plow and heavier versions of the offset disk are built strong enough to avoid excessive breakage (Vallentine 1989). The brushland diskplow is a heavy duty plow where each disk pair is connected by a common shaft and bearing assembly to a single spring-loaded arm, which allows a given pair of disks to ride over obstructions, such as rocks, or to move down into small holes without interfering with the workings of other disk sets. Plowing near or after big sagebrush seed have matured (mid-October) will help to speed the recovery of big sagebrush and reduce the amount of big sagebrush seeds needed to seed after treatment. Sprouting shrubs are not killed by brushland plowing.

Disk-Chain—The disk-chain represents the combination of two pieces of equipment: an anchor chain and a disk. It was developed in Australia during the early 1960s by welding large disks 22 inches in diameter and 0.75 inch thick to alternate links of an anchor chain about 100 feet long that was pulled diagonally by two crawler tractors. This implement works like a disk plow but with the flexibility and lower cost of an anchor chain. In addition to the diagonal pulling configuration, a triangular configuration has been developed that is pulled by a single crawler tractor. The base of the triangle is a flexible, packer-rolling brace attached to the two trailing ends of the disk chains. The packer-rolling brace aids in seedbed preparation by firming the treated soil. Broadcast seeders can be attached above the implement or the treated area can be seeded aerially. The disk chain is ineffective against sprouting shrubs.

Root Plow—This implement is constructed by attaching a wedge shaped blade to two sturdy upright shanks usually mounted behind a crawler tractor. Riser fins are welded on top of the blade to aid in cutting rhizomes and heaving roots and crowns toward the surface of the soil. The root plow is not useful in rocky or uneven soil.

Anchor Chain—The anchor chain is probably the most used implement for the control of big sagebrush. It consists of an anchor chain usually 200 to 500 feet long dragged in a U-shape behind two crawler tractors traveling parallel to each other. Vallentine (1989) recommended a chain length to swath width ratio of 2:1 to 3:1. For a 300-foot chain, the swath width should be from 100 to 175 feet for effective control of big sagebrush. Also, higher speeds give a higher kill rate. The weight of chain links varies from 40 to 90 pounds. Heavier chains kill greater numbers of big sagebrush plants but also cause greater damage to nontarget plant species. The anchor chain is ineffective against sprouting shrubs. Plummer and others (1968, p. 25) noted: "Chaining efficiently thins and opens dense stands of big sagebrush, and it covers seed well. This allows establishment of perennial herbs or permits development of suppressed understory herbs, yet retains sufficient big sagebrush for use as a satisfactory browse component." Chaining allows litter to remain on the soil surface, thus providing a protective layer for both soil and seedlings.

Railer—A railer is constructed of a heavy railroad rail, H-beam, or channel iron attached to a rigid A-frame with the apex being the pulling point. The rail is dragged over the big sagebrush resulting in uprooting and breaking off mature big sagebrush plants with little adverse effect on most grasses and forbs and young big sagebrush plants. The railer is ineffective against sprouting shrubs.

Pipe Harrow—A pipe harrow is built by welding spikes in a spiral pattern to a 4-inch steel pipe. Several such pipes are attached to a spreader bar by means of individual swivels, which allow the pipe to rotate as debris comes in contact with the harrow. It is then self-cleaning and usable on rocky sites. It is effective in thinning big sagebrush stands but does some damage to perennial grasses and forbs. Enough soil is disturbed to effectively cover broadcast seeds. This implement is ineffective against sprouting shrubs.

Rotobeater—Rotobeaters are simply heavy duty rotary mowers with single or double blades. They are effective on mature big sagebrush plants but ineffective on seedlings and young plants under 12 inches high and on sprouting shrubs. Perennial grasses and forbs are not damaged when rotobeaters are properly adjusted to cut about 3 inches above the soil surface.

Combining Burning and Mechanical Control Techniques

On the Curlew National Grasslands a combination of techniques is used to control bulbous bluegrass (*Poa bulbosa*) and mountain big sagebrush. These techniques consist of fall burning and deep plowing, summer fallowing (disking), fall planting of dry land wheat, harvesting, and then planting exotic forbs and grasses with a rangeland drill.

In May 2001 I visited one such treatment site (800+ acres) called the North Hess-Haws field, 9 years after treatment. Here a 1,500-foot line intercept vegetive analysis was conducted to determine the cover of bulbous bluegrass. The line started at N 42° 12.887'; W 112° 34.929 in the southern half of the field and went west. Cover of bulbous bluegrass ranged on a per 100-foot basis from 10 to 48 percent for an overall cover of 22 percent. Bulbous bluegrass cover in the north half of the field appeared to be doubled that of the 1,500-foot line intercept of the south half. So controlling bulbous blue grass appears to be questionable at best.

But control of mountain big sagebrush was extremely effective; that is, the number of mountain big sagebrush plants on the 800+ acres of treated land was nearly zero. However, there were a few small sites (islands) that escaped treatment. The young mountain big sagebrush plant that had established itself the farthest into the treated area was 217 feet east of a stand of mountain big sagebrush. Meaning that in 9 years mountain big sagebrush was advancing at a maximum rate of 24 feet per year, or in other words, it would take mountain big sagebrush about 220 years to reoccupy the 1-mile-wide treated site.

One effect of this type of control method is a reduction in the number of birds and in the number of species of birds that used the treated area as compared to nontreated big sagebrush (Welch 2002). I conducted a 1-mile-long bird census in the treated area and in the adjacent big sagebrush stand (east of treated site; see Welch 2002 for study details and for information on other areas). The starting point for the treated site was: N 42° 12.709'; W 112° 35.066' and went north (Welch 2002, transect 5, Idaho, Holbrook). A total of 10 birds of three species were spotted (Welch 2002). The starting point for the big sagebrush stand was: N 42° 13.510'; W 112° 34.795' and went south (Welch 2002, transect 6). A total of 44 birds of 11 species were spotted (Welch 2002).

More information concerning the various methods to control big sagebrush can be found in Vallentine (1989).

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