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**Intermountain
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Ogden, UT 84401**

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March 1986

Proceedings—Symposium on the Biology of *Artemisia* and *Chrysothamnus*

Provo, Utah, July 9-13, 1984



Proceedings of the Third Annual Wildland Shrub Symposium



Sponsored by the Shrub Research Consortium

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Proceedings—Symposium on the Biology of *Artemisia* and *Chrysothamnus*

Provo, Utah, July 9-13, 1984

Compilers:

E. DURANT MCARTHUR, Supervisory Research Geneticist, Intermountain Research Station, Provo, Utah

BRUCE L. WELCH, Principal Plant Physiologist, Intermountain Research Station, Provo, Utah

Symposium Host:

Brigham Young University, Provo, Utah

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Ogden, Utah 84401

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SYMPOSIUM WELCOME

Bruce N. Smith
Dean, College of Biology and Agriculture
Brigham Young University

On behalf of Brigham Young University, the Shrub Sciences Laboratory of the Intermountain Research Station (USDA Forest Service), and the Shrub Research Consortium, I bid you welcome to this symposium.

I invite you to visit any of the university laboratories, greenhouses, gardens, or libraries. The herbarium is located in the M. L. Bean Museum, which you are most welcome to visit.

The Shrub Sciences Laboratory will also welcome visitors, I am sure. Many people representing diverse interests and a variety of organizations are met together here. We expect an exciting symposium.

As those who went on the field trip are aware, we are pleased to be located in shrub heaven. Artemisia and Chrysothamnus really like it here so this should be a good setting in which to discuss them.

Part of our commitment to the Shrub Consortium is our intent to establish at Brigham Young University a center of excellence in shrub research. We have on our faculty several people working on aspects of wildland shrubs. A key to our future is the Shrub Sciences Laboratory of the Intermountain Research Station of the USDA Forest Service. A long-term cooperative agreement between the Forest Service and BYU has placed the facility on our campus and made the Shrub Lab professionals adjunct faculty members at BYU. Durant McArthur, our able program chairman, is a good example of the caliber of people involved.

As you will see in these proceedings, the work has barely begun. There is much to be done. We need active cooperation with scientists from around the world. We must coordinate our research efforts. In that spirit we welcome you most heartily to this conference. May your week be a most profitable one.

INTRODUCTION: ARTEMISIA AND CHRYSOTHAMNUS

E. Durant McArthur and Bruce L. Welch

These proceedings are the third in a series on the biology and management of western wildland shrubs. Earlier accounts provide information on bitterbrush (Purshia), cliffrose (Cowania), and related rosaceous species and on Atriplex and related chenopods (Tiedemann and Johnson 1983; Tiedemann and others 1984). Proceedings of the fourth symposium are in preparation. That symposium dealt with plant/animal interactions with an emphasis on woody plants and mammalian herbivores. All four proceedings have been or will be published by the Intermountain Research Station. Various institutions have cosponsored the symposia. The Shrub Research Consortium (see the inside front cover of these proceedings) now has the continuing role of sponsoring periodic symposia and workshops on shrub biology and management.

These proceedings include contributions in the general areas of distribution, systematics, and genetics; revegetation and plant control; animal relationships; ecological relationships; entomology and pathology; and physiology for the genera Artemisia and Chrysothamnus. The genera Artemisia and Chrysothamnus provide interesting contrasts and parallels. Both are members of the family Asteraceae (Compositae) and both are important members of the vast shrublands of the Intermountain West (Küchler 1964; McArthur 1984). The 54 papers in these proceedings substantially review and expand the knowledge base for these two genera. Modern interest in their taxonomy and management owes its foundation to the seminal work of Hall and Clements, especially as embodied by their treatise of 1923 (Hall and Clements 1923).

Artemisia (wormwood, southernwood, tarragon, mugwort, wormseed, sagebrush, and others) is a widespread, mainly temperate and northern genus (Grieve 1931; Good 1974; McArthur 1984). Artemisia belongs to the tribe Anthemideae (Heywood and Humphries 1977). It is composed of some 400 species divided into four subgenera (Artemisia, Dracunculus, Seriphidium, and Tridentatae) based mostly on floral, but also on chemical and distributional characteristics. Although some other Artemisia species are important--for example, sandsage (A. filifolia), budsage (A. spinescens), fringed sage (A. frigida), Louisiana sagewort (A. ludoviciana), tarragon (A. dracunculus), and California sage (A. californicia)-- big sagebrush (A. tridentata) and its close relatives (subgenus Tridentatae) are the Artemisia landscape dominants of western North America (McArthur and Plummer 1978; McArthur 1984). Tridentatae includes approximately 20 taxa (McArthur and others 1981; Shultz these proceedings). In addition to the biological and management information presented in these proceedings we recommend consulting these publications for entry into the literature and further information:

Hall and Clements 1923
Plummer and others 1955, 1968
Beetle 1960
Johnson 1977, 1979, 1983
Plummer 1977
McArthur and Plummer 1978
McArthur and others 1979
Utah State University 1979
Welch and McArthur 1979
Winward 1980
Harniss and others 1981
Tisdale and Hironaka 1981
Blaisdell and others 1982
Johnson and Fisser 1984

Chrysothamnus (rabbitbrush) is a genus of some 20 shrub species endemic to western North America. Chrysothamnus belongs to the tribe Astereae (Anderson 1970; McArthur and others 1978). It is similar to subgenus Tridentatae, the sagebrushes, in that both groups occupy the same general geographic area. Often species of both groups are to be found in the same plant communities. Both groups of plants also share the characteristic that some of their members are considered useful forage by range managers and other members are sometimes the object of eradication to improve quality of range livestock forage (Hall and Clements 1923; Hanks and others 1975; Keller 1979; McArthur and others 1979; and papers in these proceedings). Both genera are characterized by plants with a rich array of secondary metabolites (Herz 1977; Heywood and others 1977; Heywood and Humphries 1977). The classes of these metabolites in the two groups are quite different. For example, Artemisia is rich in sesquiterpene lactones and Chrysothamnus (C. nauseosus) is rich in rubber. They differ in distribution. Artemisia has a wide extra-North American distribution, Chrysothamnus is restricted to western North America.

E. Durant McArthur is Supervisory Research Geneticist and Bruce L. Welch is Principal Plant Physiologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT.

Both genera have species that dominate landscapes but that characteristic is much more common in Artemisia. Often landscapes dominated by Chrysothamnus species have been disturbed. Some Chrysothamnus species are rapid invaders of disturbed plant communities. Both sagebrush (Tridentatae) and rabbitbrush include large species complexes that tend to overshadow other members of their respective groups. For sagebrush, the most important species complex is big sagebrush (A. tridentata); that role is assumed by rubber rabbitbrush (C. nauseosus) in rabbitbrush.

More and more, subspecific taxonomic designations are used for these and other species complexes in the two groups (Tridentatae, Chrysothamnus). We support this trend and believe and hope that it will continue. Nevertheless, taxonomic determinations are not always easy, even for experts. We believe both groups have clusters of taxa that are actively speciating and that some intermediate forms are difficult to pidgeonhole taxonomically.

For information in addition to that presented in these proceedings on the taxonomy and management of Chrysothamnus and for entry into the literature we recommend that the following references be consulted:

Hall 1919
Hall and Clements 1923
Anderson 1966, 1970
Plummer and others 1968
Hanks and others 1975
Plummer 1977
McArthur and others 1978, 1979

ACKNOWLEDGMENTS

As compilers of this symposium proceedings we thank all members of the Shrub Research Consortium for their efforts in making the symposium a success. We especially thank session chairs; R. H. Abernethy, J. R. Goodin, M. R. Haferkamp, N. V. Hancock, and R. G. Kelsey; and field trip leaders A. H. Winward and L. C. Anderson. Brigham Young University Conferences and Workshops were excellent symposium hosts. Several other individuals also gave extra effort to ensure the success of the symposium and quality of the proceedings. In this regard we note especially M. Collins, S. Goodrich, R. L. Powell, C. Shuler, and R. Stevens.

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Section 1. Field Trip

FIELD TOUR--THE BIOLOGY OF ARTEMISIA AND CHRYSOTHAMNUS

Alma H. Winward and Loran C. Anderson

In conjunction with the wildland shrub symposium, "The Biology of Artemisia and Chrysothamnus," a 2-day field tour was conducted in central Utah. This tour was designed to allow interested participants an opportunity to see several of the sagebrush (Artemisia) and rabbitbrush (Chrysothamnus) taxa in their natural settings. We attempted to describe important taxonomic and ecological characteristics associated with each taxon of these two genera at each stop.

The field trip began July 9, 1984, at Provo, UT. We traveled southward through the central Utah communities of Springville and Huntington to Richfield (overnight), then northward through Fillmore, Nephi, and back to Provo with various stops between at selected populations of sagebrush and rabbitbrush. We were able to observe over 20 species and subspecies of these two important western genera.

MONDAY - JULY 9, 1984

Stop #1. Springville Nursery

At this first stop we observed several accessions of big sagebrush species and subspecies growing in a common garden. The garden is maintained through a cooperative effort between the U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Shrub Sciences Laboratory, and the Utah Division of Wildlife Resources. We also were able to observe results of selective use by mule deer that were allowed into the garden area the preceding winter and spring.

Stop #2. Thistle Slide Area

This was a general-interest stop to allow participants an opportunity to view effects of the massive slide. This slide deposited millions of tons of earth into the Spanish Fork Canyon forming the temporary Thistle Lake. The group was able to observe the awesome scenes remaining after the lake was lowered.

Stop #3. Milburn Junction

We stopped just east of Highway 89 on the road to Milburn at an Artemisia tridentata ssp. tridentata site. Not many acres of ssp. tridentata remain in this portion of the State since most have been put into agricultural production. Subspecies tridentata grows on deep, well-drained soils and, aside from a few special accessions, is generally more valuable for its cover values than foraging aspects. Since this subspecies can be confused with other big sagebrush subspecies, we took time to demonstrate useful characteristics used to differentiate it. The persistent leaves are long and narrow compared to the shorter and belled lobes of ssp. wyomingensis. Also ssp. wyomingensis generally has deep-lobed ephemeral leaves. Subspecies tridentata is differentiated from ssp. vaseyana based on shrub shape and the relative length of the vegetative versus the flower stalks. Subspecies tridentata has vegetative stalks more than half as long as the adjacent flower stalk while ssp. vaseyana has vegetative stalks less than half the length of the nearest flower stalk. Subspecies vaseyana also fluoresces a bright creamish-blue color under long-wave ultraviolet light when soaked in water or alcohol. The other two subspecies have no or very little fluorescence.

Several kinds of rabbitbrush were seen at this site. Mountain low rabbitbrush (C. nauseosus ssp. lanceolatus) was frequent among the sagebrush. Two subspecies of C. nauseosus were present: ssp. consimilis and ssp. hololeucus. Although they have different "preferred" ecological sites, they obviously can grow together. Threadleaf rubber rabbitbrush (ssp. consimilis) has generally narrower leaves than ssp. hololeucus and usually occurs in somewhat saline soils. Subspecies hololeucus grows in better drained soils of the Great Basin and in the mountains of central Utah. It is often confused with ssp. albicaulis which grows more in Idaho and the Pacific Coast States. Both of these taxa have hairy white stems (tomentose) but differ in floral characteristics. Other rabbitbrushes seen here were C. vaseyi (near the northern limit of its range) and C. parry ssp. attenuatus.

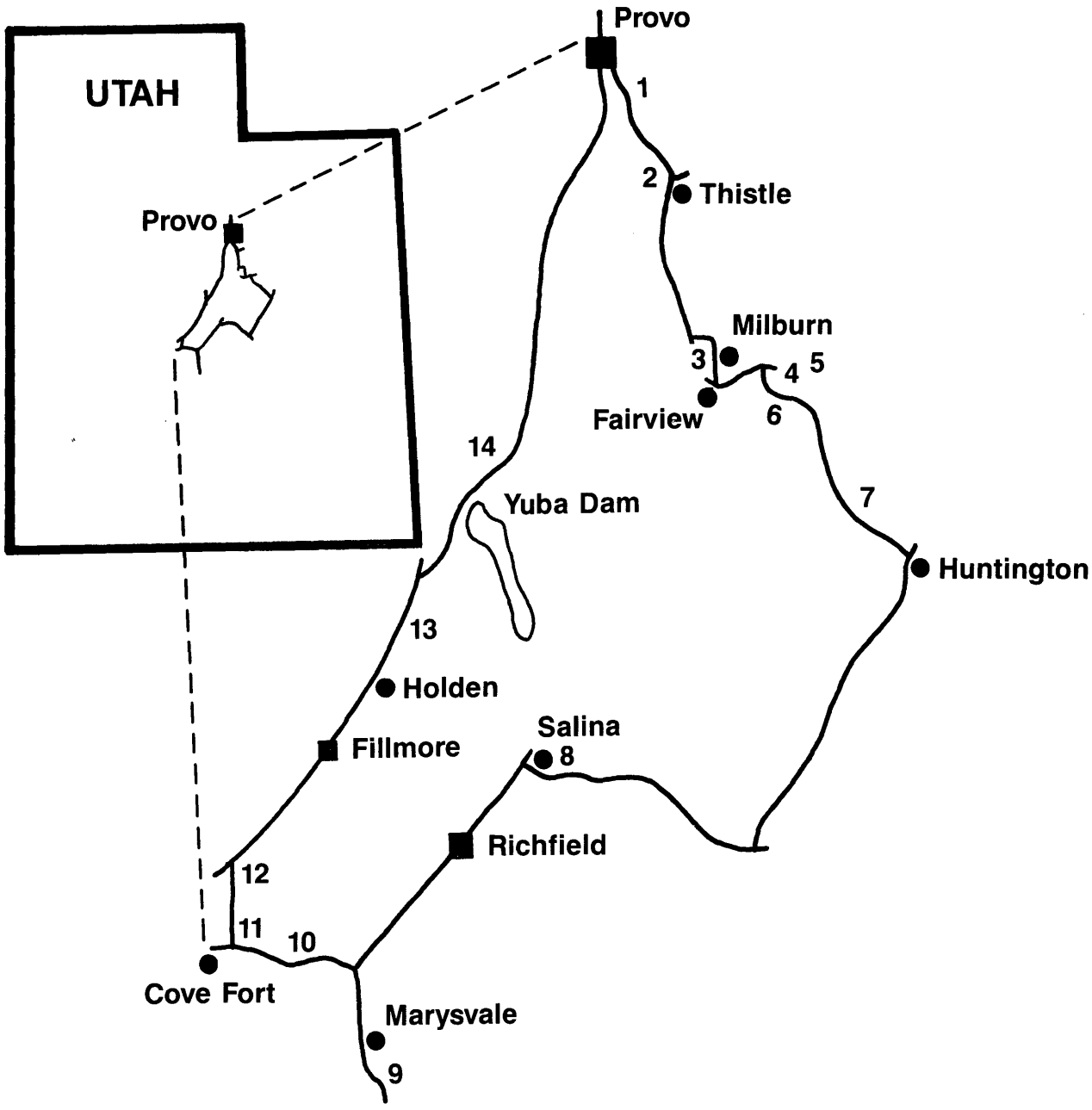
This paper is an invited account of the July 9-10 field trip conducted during the symposium, Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984. It is adapted for do-it-yourself visits.

Alma H. Winward is Regional Ecologist, U.S. Department of Agriculture, Forest Service, Intermountain Region, Ogden, UT.

Loran C. Anderson is Professor of Biological Sciences and Curator of the Herbarium, Florida State University, Tallahassee, FL.

FIELD TOUR
BIOLOGY OF ARTEMISIA AND CHRYSOTHAMNUS

Stops 1-8, July 9, 1984
Stops 9-14, July 10, 1984



Stop #4. Fairview Canyon Summit (1)

Vegetation at this stop was dominated by A. tridentata ssp. vaseyana. This subspecies is common in the mountainous areas of most western States. It is found on well-drained, moderately deep soils, as is ssp. tridentata, but is restricted to the cooler, more moist mountain climates. This particular stand demonstrated the flat-topped growth form common in ssp. vaseyana. We pointed out the diversity of associated species and general high production capabilities of this site. We also discussed potential high cover and density values often found associated with poor condition vaseyana sites. Unlike ssp. tridentata and wyomingensis, ssp. vaseyana seeds stored in the surface soils tend to be stimulated by fire. We discussed implications of this for management of these sites.

At this site, C. viscidiflorus ssp. lanceolatus is diploid (2n = 18); those seen at Stop #3 were tetraploid (2n = 36). Chromosomal races of this subspecies are generally separated altitudinally.

A mountain form of C. nauseosus (ssp. salicifolius) is found only in northern Utah and occurs sporadically here on the Wasatch Plateau. At our lunch stop just below Fairview Summit, we saw a specimen of this wide-leaved taxon (salicifolius means willow-leaved). The plant was not yet in full bloom; most C. nauseosus bloom a few to several weeks later than C. viscidiflorus when they occur together.

Stop #5. Fairview Canyon Summit (2)

Closely associated with Stop #4 were stringers or islands of A. cana ssp. viscidula. This subspecies is adapted to areas where moisture in the soil profile persists into the summer months. During spring these sites may be super saturated or even flooded. Subspecies viscidula is able to persist in these seasonally wet situations while subspecies of A. tridentata would drown out. Subspecies viscidula sites support a high diversity of grass and forb species and often produce 1,780 lb/ac (2 000+ kg/ha) of dry weight vegetation. We discussed the importance of separating ephemeral from persistent leaves on this taxon since ephemerals may or may not be lobed while persistent leaves are nonlobed. We also observed here the herbaceous A. ludoviciana ssp. incompta which is a common plant at higher elevations of the Wasatch Plateau.

Stop #6.

At the highest point of our tour, approaching 9,000-feet (2 743-m) elevation, we encountered two unique sagebrush taxa. One has characteristics similar to ssp. vaseyana encountered at Stop #4 except for larger seed heads with six or more seeds per head. Previously this taxon has been referred to as A. tridentata ssp. vaseyana forma spiciformis. However, workers at the Shrub Sciences Laboratory recently have determined from the type specimen collected in Washington State that this taxon is the originally named "vaseyana". There is a proposal to name this ssp. vaseyana var. vaseyana, and the variant described at Stop #4 as ssp. vaseyana var. pauciflorus (meaning few flowered). This effort would keep both variations as vaseyana with distinction available at the variety level since they do have genetic and environmental differences.

The other type of sagebrush at this stop is common at higher elevations in northeastern Utah, southeastern Idaho, southwestern Wyoming, and northwestern Colorado. It has large seed heads with more than six flowers per head, has large, sharp-pointed and deeply divided leaves, and has the unique distinction of being the only member of the A. tridentata group that is able to resprout. It has been erroneously referred to as A. rothrockii or A. cana. The type specimen of this variant is from Colorado and has been named "spiciformis." This taxon is in the process of being named A. tridentata ssp. spiciformis. It is differentiated from other tridentata taxa by its resprouting characteristic and several morphological differences that will be described in a forthcoming article from the Intermountain Research Station. It can be best separated from A. rothrockii, a Sierran species, by geographic distribution as well as such morphological features as shrub height and leaf pubescence.

Stop #7.

As we proceeded down Huntington Canyon, we stopped at approximately the 5,700 foot (1 737-m) level and observed several additional Artemisia and Chrysothamnus taxa. Artemisia nova, a low-growing, often bright green leaved shrub is well adapted to this relatively droughty site. It is known from most western States and occurs in two color phases: green, as found here, and gray. The green color phase is readily separated from other sagebrush by color, stickiness, and smell. The gray phase is more difficult to differentiate, especially from A. arbuscula. Stickiness of crushed leaves and smell help, but often a hand lens observation of leaf pubescence is required. Artemisia nova has obvious resin glands visible on leaf surfaces and a matted, tangled, or mashed type of pubescence, while A. arbuscula has glands almost camouflaged by a soft, singular, fluffy pubescence. Also A. arbuscula often can be separated by its bright bluish fluorescence in alcohol or water.

We also observed plants of A. bigelovii at this stop. This species has a more southern distribution and is common in the southwestern States. It is one of our most drought-resistant sagebrushes. It is most easily separated from other sagebrush taxa in the Great Basin by presence of a few ray flowers. With experience, it may also be distinguished by presence of relatively sharp-pointed leaf lobes and its low, many branched growth form.

Two relatively large rabbitbrushes were found in the wetter sites along the highway. Flax-leaved or spreading rabbitbrush (C. linifolius) has broad, smooth dark green leaves and is the only species in the genus that regularly forms large colonies by underground rootstocks (soboliferous). Some specimens of this species seen in southern Utah were 12-feet (3.7-m) tall. Green rubber rabbitbrush (C. nauseosus ssp. graveolens) looks much like ssp. consimilis seen at Stop #3 but is somewhat more robust, has wider leaves, and occurs generally more to the east of ssp. consimilis (central Utah to Colorado and the Dakotas).

A third low-growing rabbitbrush was on the drier, rocky slopes with A. nova; this was C. viscidiflorus ssp. puberulus. Abundant short, fine hairs give a dull cast to its foliage. Its major range is the Great Basin, and this site is near the eastern limit of the subspecies.

Stop #8.

Our last stop of the day was at the mouth of the canyon just east of Salina. Here we observed differential insect preference for two subspecies of Chrysothamnus nauseosus. Gall forms on ssp. consimilis can be described as cottony, whereas those on ssp. hololeucus are smooth and hard--the callus form.

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Stop #9. Marysvale/Piute Area

As we proceeded south out of Richfield, beyond the Big Rock Candy Mountain we encountered extensive "flats" of A. tridentata ssp. wyomingensis. This is the most drought-resistant member of A. tridentata and occurs on sites that sharply contrast those of A. tridentata ssp. spiciformis and other big sagebrush taxa observed the first day. Precipitation here is 8-11 inches (20-28 cm) annually with long, hot summer periods. Potential biomass is normally 400-800 lb/ac (448-896 kg/ha) at best and, on this site, was mostly in sagebrush. Most understory species have been lost as a result of past management activities. Subspecies wyomingensis sites have natural low diversity of associated species and are difficult to revegetate with herbaceous species except for Agropyron cristatum or similar drought-resistant grasses. We discussed the problems associated with restoring these sites due to their droughty nature and the availability of seed from native species and/or adaptability of introduced species. We presently have many acres of ssp. wyomingensis in a similar poor ecological condition and with low species diversity. We reinforced our taxonomic separation of this subspecies from others seen the first day (see Stop #3).

The frequently seen C. nauseosus ssp. hololeucus (white rubber rabbitbrush) was found along the edge of the ssp. wyomingensis flats, and C. greenei was found sporadically in the flats. Chrysothamnus greenei looks much like C. viscidiflorus but has pointed involucral bracts in the flower heads; it often occurs in nearly pure stands with Ceratoides (Eurotia) lanata in the basins of western Utah and adjacent Nevada.

Stop #10. Clear Creek Pass

At the top of Clear Creek Pass, enroute to the Cove Fort area, we stopped to collect samples of A. tridentata ssp. vaseyana ("pauciflorus") for comparison with sagebrush at the next stop (Stop #11). Here, too, we observed Artemisia dracunculus, an herbaceous species with long, narrow, entire, bright green leaves. This is the tarragon of the herbalist. We also observed several subspecies of Chrysothamnus, particularly C. parryi ssp. attenuatus and C. viscidiflorus ssp. viscidiflorus.

Stop #11. Cove Fort (1)

As we descended into the valley surrounding Cove Fort, we stopped to observe the large stands of sagebrush and rabbitbrush along the bench areas. An initial glance at the sagebrush and the ecological setting indicated a ssp. wyomingensis site. However, closer observations showed this to be a unique variation of ssp. vaseyana. We have encountered this variant in several locations in Nevada, Utah, and southern Idaho. It occurs at or just below the pinyon/juniper belt. It often has a cuneate, bell-shaped leaf like ssp. wyomingensis but has slightly longer flowering stalks and fluoresces bluish under alcohol and water as does ssp. vaseyana. At its upper range it blends into ssp. vaseyana at about the oakbrush zone. Although it is not yet a recognized separate taxon, it is important that land managers separate it from ssp. wyomingensis. Unlike ssp. wyomingensis, sites supporting this variant have higher potential for natural diversity and management opportunities. Seedings may include bitterbrush (Purshia tridentata), alfalfa (Medicago sativa), Lewis flax (Linum lewisii), intermediate wheatgrass (Agropyron tricophorum), and other species suited to ssp. vaseyana but not ssp. wyomingensis sites.

We took time to fluoresce a few leaves of this sagebrush to demonstrate its close relationship to ssp. vaseyana.

Two subspecies of C. viscidiflorus grow together here. The smaller plants of ssp. puberulus were abundant, and the larger, greener plants of ssp. viscidiflorus were more restricted on the slightly more favorable sites (depressions with more moisture and deeper soils). Low-growing forms of ssp. viscidiflorus have been called ssp. pumilus, and very narrow-leaved forms have been called ssp. stenophyllus. Experimental studies have shown that both are just environmental variants and should not be separated from ssp. viscidiflorus. We saw C. vaseyi again; it looks somewhat like C. viscidiflorus but is easily distinguished

because it lacks hairs on the seeds that characterize most other rabbitbrush taxa we have seen on the tour.

Horsebrush (Tetradymia canescens) was examined also; it is sometimes confused with C. nauseosus, but Tetradymia has only four bracts in the flower heads rather than several in layers as in rabbitbrushes.

Stop #12. Cove Fort (2)

Approximately 1 mile north of Cove Fort we stopped to again observe the droughty variant of ssp. vaseyana just seen at Stop #11. We dug a soil pit to get a feeling for its site relationships compared to other big sagebrush taxa.

Stop #13.

After lunch at Fillmore, we traveled to an area just north of Holden administered by the Utah Division of Wildlife Resources. Here we observed a successful planting of pubescent wheatgrass onto a site previously occupied by the droughty vaseyana observed around Cove Fort. We also were able to see interplantings of sagebrush, rabbitbrush (mostly ssp. hololeucus), and other shrubby species established into the pubescent wheatgrass for wildlife forage and diversity.

Stop #14.

Our final stop of the tour was just northeast of the dam on Yuba Lake. Here we observed islands of A. nova on appropriate sites and a few small stands of A. pygmaea. Artemisia pygmaea is a dark green cushionlike shrub easily identified from other sagebrush by its pinnatified leaves (3-11 lobes). Thus far, this species is found only in the States of Utah, Nevada, and Arizona. It occurs on special sites believed to be strongly calcareous. More needs to be known about this species since it appears limited to a few special sites.

On the drier, rocky sites with A. pygmaea, we observed what looked like a somewhat "anemic" C. nauseosus ssp. consimilis. It was ssp. leiospermus which is distinguished from ssp. consimilis in having glabrous seeds (no hairs below the pappus hairs on the end of the seed). We saw yet another subspecies of C. nauseosus (ssp. turbinatus) beside the road. Unfortunately there wasn't much of it, and it was heavily galled which made characterization difficult. It prefers sandier sites in southwestern Utah but also occurs sporadically east of the Wasatch Plateau.

We returned to Provo at approximately 5:00 p.m. via Nephi.

SPECIES AND SUBSPECIES OBSERVED ON THE FIELD TOUR TO ARTEMISIA AND CHRYSOTHAMNUS SITES IN CENTRAL UTAH

ARTEMISIA (SAGEBRUSH)

A. bigelovii (Bigelow sagebrush)
A. cana
  ssp. viscidula (mountain silver sagebrush)
A. dracunculus (tarragon)
A. ludoviciana
  ssp. incompta (mountain Louisiana sagewort)
A. nova (black sagebrush)
A. pygmaea (pygmy sagebrush)
A. tridentata
  ssp. tridentata (basin big sagebrush)
  ssp. vaseyana (mountain big sagebrush)
  ssp. wyomingensis (Wyoming big sagebrush)
  ssp. spiciformis (subalpine big sagebrush)

CHRYSOTHAMNUS (RABBITBRUSH)

C. linifolius (spreading rabbitbrush)
C. nauseosus
  ssp. consimilis (threadleaf rubber rabbitbrush)
  ssp. graveolens (green rubber rabbitbrush)
  ssp. hololeucus (white rubber rabbitbrush)
  ssp. leiospermus (smoothseed rubber rabbitbrush)
  ssp. salicifolius (mountain rubber rabbitbrush)
  ssp. turbinatus (sand rubber rabbitbrush)
C. parryi
  ssp. attenuatus (thinleaf Parry rabbitbrush)
C. vaseyi (Vasey rabbitbrush)
C. viscidiflorus
  ssp. lanceolatus (mountain low rabbitbrush)
  ssp. puberulus (hairy low rabbitbrush)
  ssp. viscidiflorus (stickyleaf low rabbitbrush)

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UTAH GEOLOGY AND BOTANY

Stanley L. Welsh

ABSTRACT: This paper is a result of an invited lecture on the field trip of the Biology of Artemisia and Chrysothamnus symposium. In it Dr. Welsh traces his beginnings as a geobotanist to an assignment at Dinosaur National Monument. Some relationships between plant distributions and geology in Utah are described.

The view at my front was one of awe and splendor. Parallel ridges of varicolored rock extended east along the southern flank of the Split Mountain anticline in Dinosaur National Monument. Steeply plunging rock formed hogbacks and cuestas. Between the ridges, minor drainages occurred along the strike of the formations, paralleling the strata awhile before plunging at right-angles through the tilted, more resistant layers of rock. The backdrop of Split Mountain stood as a grand phenomenon, with the Green River flowing through, instead of around, the anticline.

This was my introduction as a practical field botanist to the technicolor geology of eastern Utah. Before my eyes was a whole new world, one where the aridity of the land produced a naked or nearly naked landscape. Its geology could be viewed without hindrance of an obscuring mantle of vegetation. Yet, vegetation was present in the picture. Portions of the geological setting were obscured, but not enough to prevent even a novice from detecting the differences in strata, their color, texture, and composition. Salts coated the margins of seeps and the few tiny streams flowing across the formations in the vicinity indicating the presence of water-soluble materials. The salts had not been leached away by water and now appeared like eternal snow. But the landscape, carved as it was into a badlands topography, gave evidence of the action of water as a principal erosive element.

Geomorphological features within my view had been carved by the combined effects of water, wind, heat, and cooling. The water had not been placed gently on the land, but came, as it still does, in feast-or-famine amounts. When the rains come, the water strikes the naked or nearly naked slopes, the surface is soon saturated, and then the water runs overland, cutting the substrate and carrying it away down the great river system of the Green-Colorado. Rills become gullies and these become canyons downward along the headcutting system. The water reads the underlying substrata and follows the paths of least resistance. The shape of sequential and resequential tributaries thus formed is controlled by the hardness of the rocks. Wind and alternating heat and cold serve to pry loose fragments of stone and alluvium from previous erosive cycles; water then adjusts them into the most stable contours possible. No particle of material is allowed to remain constantly free. Even the most resistant stone is removed grain by grain and redeposited again, usually following a series of moves, into other stone at some other place.

The scene east of the Dinosaur Quarry was marked by sandstone ridges alternating with softer mudstone or siltstone and shale valleys. The summits of the parallel ridges were approximately the same elevation, about a mile above sea level in the vicinity of the quarry, but increased gradually up the slope of the anticline toward the heights of Split Mountain. Even in the lower reaches, where one would expect the amount of precipitation to be approximately equal from year to year, and where vegetation should reflect that amount with some degree of uniformity, the plants from stratum to stratum were not the same. The vegetative cover, thin though it was, reflected the underlying geology. Each of fourteen formations, from Mancos Shale to Weber Sandstone (Cretaceous to Pennsylvanian), supported vegetation that differed in subtle ways from that on adjacent formations. The salt-desert shrub and annual-dominated plant communities of the Mancos Shale gave way abruptly at the margin of the Frontier Formation, with its widely spaced juniper and Utah serviceberry. That thin covering of shrub species changed again at the margin of the acidic Mowry Shale, which is marked with parallel rows of Eriogonum corymbosum and E. lonchophyllum var. saurinum. The basic Morrison, Carmel, and Moenkopi supported clumps of a milkvetch of great beauty, Astragalus saurinus, an endemic to those and similar formations in the immediate area. Growing on the Entrada Formation was the newly described grass milkvetch, Astragalus chloodes, another narrow endemic of sandstones of the Uinta Basin.

On each of the formations, the basic community type changed abruptly where the alluvium obscured the underlying geology, insulating the vegetation from the peculiarities of the individual formations. The plants were displaying the different chemical and physical makeup of the formations and of the alluvium derived from them.

Thus began my association with geology and botany. The appellation "geobotanist" has been applied to me, especially by my Russian colleagues.

Research dealing with the ecology of higher plants of Dinosaur National Monument involved learning the stratigraphy of the region. Fortunately for me there

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Stanley L. Welsh is Professor and Curator of the Herbarium, Department of Botany and Range Science, Brigham Young University, Provo, UT.

were in Vernal, UT, two eminently qualified geologists who were more than happy to aid this novice. G. E. (Ernest) and B. R. (Billie) Untermann were in charge of the State museum in Vernal. This remarkable husband-and-wife team had spent their lives in the area learning about its geology, and had in preparation a field guide to the geology of the Uinta Mountains and vicinity (Untermann and Untermann 1954). They gave me a manuscript copy and instructed me in features of geological strata. With that information I went again to Dinosaur, to view the unmatched scenes. Soon my footprints marked each of the formations as I collected plants. The sequence of strata became a part of my memory, and it is to that type series of formations that I compare all geology of the State. A side benefit was, of course, the friendship that grew between the Untermanns and me. Much later, after both had died, I named a species of daisy Erigeron untermannii (Welsh 1983) in honor of that amazing couple. The studies at Dinosaur led to completion of a thesis on the vegetation of Dinosaur National Monument (Welsh 1957).

Following completion of my doctoral degree in 1960, I returned to Utah where I began what has developed into a lifetime of wandering through the geology of the State in search of plants, a study aided by geologists at Brigham Young University, especially by Dr. Keith Rigby and Dr. Lehi Hintze.

Utah is huge and its geology diverse. Classification of the stratigraphy of the State has been under way for a long time. There are hundreds of named formations, with some further divided into members or other subunits (Hintze 1972). To know all of them requires a lifetime of concerted effort, which I have not made. However, there are some natural divisions that make the task of understanding Utah's geology easier. The State is divided into two portions by an overthrust belt that runs from northern to southwestern Utah. West of the eastern margin of that overthrust zone, the geological formations are gray in color, with minor exceptions, and the rocks are old, consisting mainly of limestone and dolomites, but with some major quartzites. They range in age from Precambrian to Pennsylvanian, marked here and there with younger sequences derived mainly from the products of erosion, or by igneous deposits.

The mountain ranges of the Great Basin belong to that western section. These mountains are the bases of still older mountains that arose in Paleozoic times and were worn away in the Mesozoic. The products of erosion were carried to the east where they were deposited in a shallow sea. Mancos Shale is a product of such deposition. The worn mountains were faulted, uplifted, and thrust to new heights in a landlocked basin, and are now hip-deep in their own detritus. The great bajadas and fans of the Great Basin have no counterpart in the Colorado Basin. The Great Basin is a region of accumulation of detritus and alluvium; the Colorado Basin is one of excavation. The difference can be noted easily by discerning the location of aggregate-quarrying operations. Gravel can be taken from lacustrine or fluvial deposits almost anywhere in the valleys of the Great Basin, but in the Colorado Basin the gravels are taken mainly from ridge crests where ancient pedimental deposits are hung between entrenched drainages.

The faulted gray geology of western Utah is interesting mainly to those who are color blind and to those who find challenging the subtle differences in texture and color, or are encoding fossils of that geology. Even where the stratigraphy is subtle, and it is difficult for geologists to detect the differences, some plant species occur with remarkable consistency on strata or portions of strata that appear to be the same to the untrained. Sevy Dolomite is such a formation. It is exposed in western Millard and Beaver counties, and supports a unique vegetation consisting of peculiar buckwheats, catseyes, globe mallow, and cacti.

Many of the strata are buried beneath the accumulated debris of the mountains themselves. Most low-elevation geology involves alluvium and other valley fill. While some of the alluvium approaches the character of the formations from which it is derived, most does not. Changes in particle size and mixing with other parentally derived material dictate differences in water and mineral relations. Vegetation on the bajadas, alluvial fans, and valley floors consists of different community types than that on the mountains proper, where the original strata are exposed to the plants directly. The species might be the same, in large or small part, but the community structure is different.

Comparable elevations in the Colorado Basin do not bear the vast expanses of alluvium, and the vegetation grows directly on the exposed geological strata. The peculiarities of those strata are reflected directly by the plants growing on them. The exposed geological strata of the Colorado Basin result in a large number of habitats not available in western Utah. Plants respond to the habitats available by developing ecotypes that can survive on the peculiar substrates, often without significant competition from other plants. Many low-elevation endemics occur in the Colorado Basin, but the Great Basin does not have endemics in the same proportion at lower elevations, even discounting the preexistence of Lake Bonneville.

In order for the geological substrates to be controlling, in Utah at least, the area must be xeric. Desiccation is apparently a necessity for ultimate expression of edaphic control of vegetation; that desiccation can be actual or physiological. There are areas in the State where fine-textured substrates occur at high elevations. At those elevations, the surface layers of the formations are treated to greater precipitation and leaching of some of the soluble salts. Plants that do grow form a compact vegetative cover. Organic material accumulates and soil formation results. The soil acts to insulate the plants from the parent material. Edaphic control by the parental substrate becomes less important and other features become controlling. Plants that occupy the developed soils tend not to be specialists; they are broadly distributed. Diversity tends to be low.

However, even at high to very high elevations there are xeric sites, despite the occurrence of increased

precipitation. Xeric sites are geomorphologically controlled. Plateau margins, cliff faces, and other steep sites, where water is shed easily and where exposure is such that energy per unit area is high, are examples of xeric sites at high elevations. The substrate there is controlling also, and other peculiar habitats are present. Endemic plant taxa grow on them also. Note the occurrence of Silene petersonii on the margins of the Flagstaff Limestone of the Wasatch Plateau, and the Pink and White Limestone Members of the Wasatch Formation on the Sevier and Paunsagunt plateaus. Other plants with similar distribution include: Astragalus montii, Eriogonum aretioides, Cryptantha ochroleuca, Eriogonum panguicense, Lomatium minimum, Lesquerella rubicundula, Penstemon bracteatus, Townsendia montana, and Cymopterus minimus.

The geologic strata discussed previously are mainly sedimentary. Igneous geology is important over much of the State, however. Both intrusive and extrusive materials are present in such places as Marysvale, where igneous deposits up to 30,000 ft (9 150 m) thick cover a shield-shaped area more than 50 mi (80 km) wide, the laccolithic mountains of the Henry's, La Sal's, and Abajo's, and the basalt flows near Panguitch Lake, Black Rock, and St. George. The igneous deposits are diverse in type, form, texture, and composition. Some of them are further complicated by chemical or thermal modification. Big Rock Candy Mountain, Monroe Hot Springs, and the Tushar Mountains consist at least in part of thermally modified rocks. There are examples of plant species endemic to many of the peculiar igneous substrata. The high-elevation portions of the Tushar Mountains contain half a dozen examples of endemic species including Astragalus perianus, Castilleja parvula, Lesquerella wardii, Draba sobolifera, Gilia tridactyla, Penstemon tusharensis, and Penstemon parvus.

Thus, the search for peculiar plants in Utah is correlated with the location of peculiar geological strata. The fine-textured formations, the limestones, shales, siltstones, and mudstones, which I lump under the inclusive term "garp," contain most of the endemic species. The Moenkopi, Chinle, Carmel, Entrada, Mancos Shale (including Tropic Shale), Uinta, and Duchesne River formations are examples of strata with fine-textured substrates. Each of these supports one or more peculiar species of plant with some special genetic structure.

Walter P. Cottam is reported to have said of the Mancos Shale, where he camped one night, that there were only four plant species growing on the formation and that he didn't know three-fourths of the flora. One should not expect to walk onto Mancos Shale and immediately begin collecting new and undescribed species. Rare plants do not exist in high numbers; neither do they occupy the entire formation. The plants grow as small populations scattered here and there on the stratum, often restricted to some minor subunit or chemically differing portion. Water relations are poor and soluble salts are high. Presence of gypsum and selenium often complicates plant growth. The combination of high salt concentrations (up to 30,000 ppm), gypsum, selenium, colloids, and other substances tends to restrict plants to those species that can tolerate the poor qualities. Those that can grow there are not subjected to much competition from other plant species.

Sandstones and other coarsely textured strata also support peculiar plant species, but the reasons are less obvious. The Cedar Mesa Sandstone, a member of the Cutler Group of formations, bears the distinctive Astragalus monumentalis, but the White Rim Sandstone, a member of that same group but borne stratigraphically above the Cedar Mesa, does not support that species. Rather, on the White Rim there occurs a similar, but wholly distinct taxon, Astragalus desperatus, a generalist on many formations.

Much work remains to be done. The State contains some 84,000 mi^2 (218 000 km^2) of land. Perhaps a quarter of that area is sufficiently well-known botanically and geologically to require little additional study, but we have lifetimes of work left to do.

Those who would understand the flora of any region must view the geological basis carefully. The plants are often better stratigraphers than are the geologists, as sheep are the ultimate botanists. Thus, I recommend that those who study plants should study geology also, and don't forget about the sheep.

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HABITAT TYPE, RANGE SITE, AND COMMUNITY TYPE

M. Hironaka

ABSTRACT: Placement of habitat type, range site, and community type in a hierarchy forms a framework for an ecologically based information storage-retrieval system for land management. The community type classification concept needs to be revised to associate community types to respective habitat types.

CLASSIFICATION BASED ON VEGETATION

Today, three land classification schemes based on vegetation are used by land management agencies. Researchers use these classifications to describe the setting of their study areas and to project applications of their findings to areas of similar capabilities.

Habitat type is the most recent of the classification schemes (Daubenmire 1952). It is an ecological classification and is based on climax vegetation. By definition the habitat type is the aggregate land area that presently supports, or until recently supported, and presumably is again capable of supporting the same climax vegetation (Daubenmire 1968). Thus, the habitat type is the land area that has the same effective environment as is evidenced by its present or recent support of the same climax vegetation. From a mapping viewpoint, all land that supports or supported the same specific climax vegetation is of the same habitat type. Different habitat types occur because the effective environment is different and in turn supports or supported different climax vegetation. From a land management viewpoint, lands within the same habitat type have similar potential because of similar effective environment.

Range site classification was introduced earlier than the habitat type classification by about 3 years. The former was introduced by Dyksterhuis (1949) of the U.S. Department of Agriculture, Soil Conservation Service. Range site classification is an ecological classification based on climax vegetation, also. In addition, it is based on site productivity and/or species composition uniformity due to site differences within a climax vegetation (Dyksterhuis 1949; Shiflet 1973). In some mapping instances, a range site may be delineated on the basis of a nonecological interpretation, such as extremely rocky or extremely steep, which may have important management implications (Shiftlet 1973; USDA 1976). In recent years, the term "ecological site" has been used in place of range site (Anderson 1983).

The third unit of classification is the community type (Mueller-Dombois and Ellenberg 1974; Shimwell 1976). It is an ecological classification based on current vegetation and is not specific as to its successional status (Whittaker 1975; Shimwell 1976; Youngblood and Mueggler 1981). Thus, community type classification is able to handle disturbed communities, of which we have so many.

The three classification schemes have been used in classifying and delineating (mapping) our sagebrush ranges singularly. At times, overlays of two of the three classification schemes have been used, but rarely has the information contained in the overlays of all three systems been used simultaneously.

IMPORTANCE OF PLANT SPECIES IDENTIFICATION

Identification of dominant and prominent species has been basic in the development of the three classification schemes. Without the recognition of subspecies of Artemisia tridentata, development of accurate land classification schemes would be difficult, if not impossible. This taxon is the dominant shrub species occupying vastly different kinds of effective environments. It is the dominant species in areas that receive 8 to 20 inches (200 to 500 mm) of annual precipitation, spans an elevational gradient from 600 ft to more than 10,000 ft (180 to 3 300 m) and occurs on all major nonforest soils in the Intermountain Region.

The recognition of ecologically meaningful subspecies in Artemisia tridentata by Beetle (1959, 1960) and Beetle and Young (1965) permitted the development of the habitat type classification of the sagebrush region (Hironaka and others 1983). The subspecies wyomingensis, vaseyana, and tridentata are excellent diagnostic taxa because of their consistent relation to climate and soil conditions.

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M. Hironaka is Professor of Range Resources, Range Resources Dept., University of Idaho, Moscow, ID.

RANGE SITE CLASSIFICATION PRIOR TO 1965

One might wonder how the range site classification, as perceived by Dyksterhuis (1949, 1958), was workable in the sagebrush region prior to the recognition of subspecies in Artemisia tridentata. Prior to 1965, it was to a large extent by chance that range sites coincided with the distribution of the yet-to-be-recognized subspecies. A separation of range sites was arbitrarily established at the 12-inch (300 mm) isohyet (average annual precipitation) which coincided fairly near the division in the distribution of subspecies wyomingensis and subspecies vaseyana. The highly productive range sites on deep soils agreed with the occurrence of subspecies tridentata. The division of range regions into physiographic provinces (USDA 1976) helped further in stratifying sites and effective environments. Range site, as mentioned earlier, is based on the climax vegetation as is habitat type. Within a climax vegetation, there is variation in productivity due to soil differences. Range site stratifies the different productivity levels within a climax vegetation, with each level constituting a different range site. In reality, the range site is a subdivision within a habitat type, based on productivity or uniformity in species composition (Hironaka and others 1983).

CLASSIFICATION CONTROVERSY

Recently, one hears that habitat type and range site are the same, or there is no need for both classification schemes in range management (Dyksterhuis 1983). One also hears that habitat type classification should be restricted to forest vegetation and should not be used in classification of rangelands, or habitat type is based on climax vegetation whereas range site classification is based on soils. All of these statements are incorrect; habitat type and range site are not the same (Hironaka and others 1983). Habitat type classification can be used for forest and rangeland (Daubenmire 1952; Daubenmire 1973; Mueggler and Stewart 1980; Hironaka and others 1983). Both classifications are based on climax vegetation, and both are associated with unique sets of soils, with particular reference to the soil series and soil series phase level of soil classification (Hironaka and others 1983). So what is the controversy? From a philosophic viewpoint, Dyksterhuis (1958, 1983) states that the range site concept is based on the premise that climax vegetation is a continuum, whereas habitat type as defined by Daubenmire (1968, 1978) views climax vegetation as being composed of discrete communities. Other than the difference in philosophic viewpoint on whether climax communities are discrete or form continua, the two approaches to classification are basically the same. Whether one accepts the continuum or the discrete community concept (Curtis 1958; Whittaker 1960; Daubenmire 1978), the classification units remain unchanged, so I cannot see how one classification scheme or the other is invalidated.

IMPORTANT DIFFERENCES

Although the basic floristic composition of habitat type and range site of the climax vegetation is similar, the species composition and site productivity within the bounds of a range site is more homogeneous than that of a habitat type. The range site is a homogeneous subdivision of a habitat type based on uniformity of productivity or species composition. The uniformity of effective environment is evidenced by greater similarity of soils with than between range sites (Heerwagen and Aandahl 1961). The range site is comparable to habitat type phase (Pfister and others 1977; Hironaka and others 1983).

Community type classification is generally used without reference to climax or potential natural vegetation and often gives the impression that it is wholly different and independent of the other two classification schemes. In reality, community types are related to range sites and habitat types, but not uniquely.

A UNIFYING SCHEME

Proper interpretation and use of these classification schemes can provide the wherewithal to do something monumental for land management. Unifying and incorporating the three schemes into a simple hierarchical scheme can be the basis for a sound information storage-retrieval system for land management. Prior to the introduction of habitat type classification, there was no basis by which range sites could be ecologically aggregated. As initially conceived, each range site was an independent unit with no relation to other range sites. The habitat type permits the grouping of range sites with the same basic climax vegetation, but differing productivities because of soil differences. The soils associated with specific range sites are in turn associated with specific habitat types. Thus, each range site is associated with a unique set of soils. The same is the case with each habitat type.

INFORMATION STORAGE-RETRIEVAL SYSTEM

If the community types that occur in each range site and habitat type are identified and their responses to management are documented, the information could be stored and provide a library of information for later retrieval. Prior to habitat type classification, there was no ecological basis by which range sites could be aggregrated. True, range sites could be grouped as to precipitation zone, land form, topographic position, and other site features, but with no reference to vegetation, potential or otherwise. As originally developed, range site classification was not a part of a hierarchical system, but one of independent units. Habitat type classification permits range sites with the same basic climax vegetation, but different productivity levels, to be grouped together. With this information,

productivity levels within habitat type can be identified. In addition, if the associated community types are identified and characterized, there would be available much information concerning any landscape that had been classified. The boundaries of habitat type and range site remain permanent for all practical purposes. The only changing unit is the community type as the vegetation undergoes changes because of secondary succession, retrogression, or drastic vegetational alteration without excessive change in site potential. As information is documented for a particular community type, it is filed and cataloged by habitat type and range site for later retrieval.

Each land management district can have available an inventory of habitat types, their associated range sites and community types as well as soils and other site and management implication information. This would enable recall of any community type in relation to specific range sites and habitat types and have available much pertinent land management information based on the first-hand experiences of many land managers. For the first time, a means would be available by which this type of information could be filed and retrieved so that each succeeding land manager could build on what was learned by his predecessors on comparable landscapes rather than rely on his own experiences. As new experiences and information are gained, they are added to the library of information.

This becomes the ultimate use of the three classifications. Each by itself has limited value, but when the three schemes are viewed as members of a larger system, it enables the development of a comprehensive information storage-retrieval system on an ecological base for land management. All three classification schemes are needed to classify our rangelands. They are not duplications; each provides different kinds of information about the land and the vegetation it supports or supported. No one scheme is better than the other. All are needed for the wise management of our rangelands.

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In: McArthur, E. Durant; Welch, Bruce L., compilers. Proceedings--symposium on the biology of Artemisia and Chrysothamnus; 1984 July 9-13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 398 p.

Section 2. Genetics, Systematics, and Synecology

TAXONOMIC AND GEOGRAPHIC LIMITS OF ARTEMISIA SUBGENUS TRIDENTATAE (BEETLE) MCARTHUR (ASTERACEAE: ANTHEMIDEAE)

Leila M. Shultz

ABSTRACT: Illustrations, distribution maps, and ecological notes are presented as an aid to identification of sagebrush. An historical background outlines some of the nomenclatural development of the complex leading to the current classification of taxa presented here.

HISTORICAL BACKGROUND

Rydberg (1916) considered members of Tridentatae as three sections within the subgenus Seriphidium. These sections were Tridentatae (11 species), Rigidae (1 species), and Pygmaeae (1 species).

In the most conservative treatment of the group, Hall and Clements (1923) recognized only five species, with seven subspecies, in the section Seriphidium. Following the division of the genus into four sections by Besser (1829), Hall and Clements considered Artemisia bigelovii as a member of section Abrotanum that was transitional to section Seriphidium. They also included Artemisia palmeri in section Seriphidium.

In a cytogenetic study of the species, Ward (1953) recognized eight species and 11 subspecies in the western North American Seriphidia. Ward included A. palmeri A. Gray as a member of section Seriphidium, and A. bigelovii A. Gray as a member of the Abrotanae. Beetle (1960) preferred to treat the complex as the section Tridentatae and questioned the relationship to European members of the section Seriphidium.

McArthur (McArthur and others 1981) elevated section Tridentatae to subgeneric status, adding a fifth subgenus to Artemisia. I have adopted this subgeneric classification, differing from McArthur only in the transfer of A. bigelovii and A. palmeri to the subgenus Artemisia which is the old section Abrotanae (Shultz 1983). I consider the inclusion of A. pygmaea the only enigmatic consideration in circumscribing the Tridentatae as a natural, monophyletic group.

Paper presented as an invited postscript to the symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

Leila Shultz is Associate Professor and Curator of the Herbarium, Utah State University, Logan, UT.

DISCUSSION

The specific and intraspecific taxonomy of sagebrush remains controversial. Considering the complexity of the group, this situation is unlikely to change. The complex is in a dynamic state of expansive evolution and hybridization among species and subspecies is common. The precise definition of species, therefore, becomes obscured and rests in part on individual evolutionary philosophy. Controversy exists primarily at the intraspecific level in the division of subspecies and varieties.

Morphological entities display a remarkable fidelity to certain habitats and hybridization among populations occurs primarily at the interface of these habitats. Thus, in an evolutionary sense, we can see morphological specializations and adaptations along environmental gradients. For the most part, there is consensus among field workers in the Intermountain region concerning identification of the basic groups and the ecological integrity of different types of sagebrush. However, one may become easily confused in making identifications because of the great morphological similarity of the groups. The illustrations, distribution maps, and ecological notes in this paper are offered as a simplified means to identification of the species and subspecies of sagebrush.

Dots on the maps represent several thousand collections that I have examined and verified at the herbaria of the institutions listed below. Populations that have not been documented in collections are not included, and certainly, these maps may stimulate the report of important records. I welcome all correspondence. A complete file of specimen citations is maintained at the Intermountain Herbarium. I am grateful to the curators at the following institutions who have graciously permitted access to all files:

Brigham Young University
California Academy of Sciences
University of California at Berkeley
Colorado State University
University of Colorado
University of Idaho*
Gray Herbarium at Harvard*
Missouri Botanical Garden
New York Botanical Garden*
Oregon State University*
Rancho Santa Ana Botanical Garden
Smithsonian Institution (U.S. Natl. Herbarium)*

University of Utah
Utah State University (Intermountain Herbarium)
Washington State University*
University of Washington*
University of Wyoming (Rocky Mountain Herbarium)*

*Asterisks indicate collections in which sagebrush collections were only partially examined and recorded.

SPECIES AND SUBSPECIES OF ARTEMISIA SUBGENUS TRIDENTATAE, WITH ECOLOGICAL NOTES

1. (a) Artemisia arbuscula Nutt. ssp. arbuscula, Trans. Am. Phil. Soc. 2(7): 398. 1884. Occurs on rocky, shallow soils, such as rock ridges and other sites swept free of snow by winds, in the mountains. The leaves on the flowering stem are lobed, as are other subspecies of Artemisia arbuscula.

   (b) A. arbuscula Nutt. ssp. longiloba (Osterh.) L. Shultz, ined. Occurs on fine-textured clay basins in the valley and mountains. Morphologically, this subspecies is very similar to typical arbuscula although it is reproductively isolated by blooming time. This is the only taxon that blooms in late spring and early summer rather than late summer to fall.

   (c) A. arbuscula Nutt. ssp. thermopola Beetle, Rhodora 61:83. 1959. Habitat as for subspecies arbuscula. Varies morphologically in having more finely divided leaves, and being restricted to areas adjacent to those occupied by A. tripartita, with which A. arbuscula may have hybridized to form the subspecies thermopola.

2. (a) Artemisia cana Pursh ssp. cana, Fl. Amer.: 521. 1814. Occupies sandy soils of prairies and along streams, in valleys east of the Continental Divide.

   (b) A. cana Pursh ssp. bolanderi (A. Gray) Ward, Contr. Dud. Herb. 4(8):192. 1953. Found primarily in the Sierra Nevada Mountains of California, barely entering Oregon and Nevada. Similar to A. cana ssp. viscidula, from which it varies in its dense tomentum on the stem. Occurs along streams and in snow catchment basins, on granitic soils.

   (c) A. cana Pursh. ssp. viscidula (Osterh.) Beetle, Rhodora 61:84. 1959. Habitat of moist meadows and snow-catchment basins in mountains east of the Sierra Nevadas, usually on limestone-derived soils. I include A. argillosa Beetle with this subspecies.

3. Artemisia nova A. Nels., Bull. Torr. Club 27:274. 1900. Found in desert valleys and mountain slopes (south and west exposures), on shallow lithosols overlying bedrock.

4. Artemisia pygmaea A. Gray, Proc. Am. Acad. 21:413. 1886. Restricted to shale-barrens at low elevations within the Great Basin of Nevada and Utah and Uinta Basin of Utah and Colorado (first collection in Colorado reported by Shultz [1983]).

5. Artemisia rigida (Nutt.) A. Gray, Proc. Am. Acad. 19:49. 1883. Grows on basalt scablands of the Columbia Basin of eastern Washington, Oregon, and extreme western Idaho.

6. Artemisia rothrockii A. Gray, Bot. Calif. 1:618. 1876. Endemic to California in the southern Sierra Nevada and San Bernardino Mountains where it is found in high elevation silt basins and on rocky slopes. I consider collections from the Intermountain region previously referred to as A. rothrockii as A. X spiciformis.

7. Artemisia X spiciformis Osterh, Bull. Torr. Club 27:507. 1900. The "X" designates this taxon as a hybrid. Because the populations are stable and apparently reproducing (see McArthur and Goodrich, this proceedings), it is worthy of formal taxonomic status. A. spiciformis is often considered a subalpine form of Vasey sagebrush, although I consider it to be a hybrid of A. cana ssp. viscidula and A. tridentata ssp. vaseyana at most sites. In Colorado, at the type locality of A. spiciformis, A. arbuscula may be a putative parent. Because of the need for experimental work with this taxon and the uncertain nature of hybridity, I leave this taxon with the name previously published by Osterhout rather than use the subspecies designation proposed by Goodrich and others (1985). The illustration shows leaf and floral features which are obviously intermediate between subspecies A. cana ssp. viscidula and A. tridentata ssp. vaseyana.

8. (a) Artemisia tridentata Nutt. ssp. tridentata, Trans. Am. Phil. Soc. 2(7):398. 1841. This is the common big sagebrush of valleys and foothills. It occurs in deep, well-drained sandy or gravelly soils.

   (b) A. tridentata Nutt. ssp. parishii (A. Gray) Hall & Clements, Carn. Inst. Wash. Publ. 326:137. 1923. This taxon is distinguished by its hairy achenes and usually drooping flower branches. It is restricted to the coastal ranges and cismontane region of California.

(c) A. tridentata Nutt. ssp. vaseyana (Rydb.) Beetle, Rhodora 61:83. 1959. Vasey sagebrush is the most common and abundant sagebrush in the West. It is often the dominant shrub on mountain slopes and occurs throughout the Rocky Mountains and Intermountain West, from low benches into the alpine zone, usually on rocky soils. Its wide ecological diversity is reflected in a sometimes bewildering array of morphological forms.

(d) A. tridentata Nutt. ssp. wyomingensis Beetle & Young, Rhodora 67:405. 1965. Wyoming sagebrush may be the most difficult to recognize of the various subspecies. The short, narrow flower clusters and "twiggy" appearance are characteristic of tetraploid populations. Polyploidy apparently contributes to the ability of this plant to colonize drier sites than those occupied by A. tridentata ssp. tridentata.

9. (a) Artemisia tripartita Rydb. ssp. tripartita, Mem. N.Y. Bot. Gard. 1:432. 1900. Occurs on deep, well-developed loam soils, in valleys, primarily on the fertile volcanic soils of Idaho. Much of this area has been plowed for farmland, which accounts for what may seem to be a spotty distribution.

(b) A. tripartita Rydb. ssp. rupicola Beetle, Rhodora 61:60. 1959. Differs from typical tripartita in having a dwarfed growth form and preference for drier habitat. Occurs on shallow, rocky soils east of the Continental Divide, usually on barren knolls surrounded by well-developed grasslands.

ACKNOWLEDGMENTS

I am grateful to Steven Cannon for carefully executed illustrations and to Mary Bybee and Bryan Hammond for their help in preparing distribution maps. I also thank Drs. Durant McArthur and Al Winward, Prof. Arthur Holmgren and Sherel Goodrich who have provided many stimulating conversations on sagebrush taxonomy.

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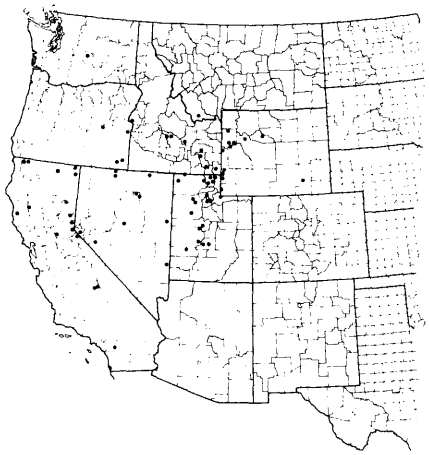
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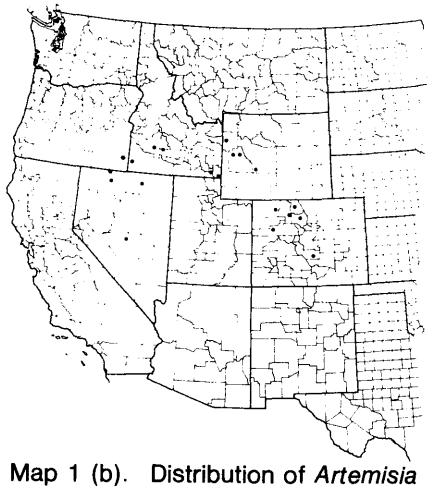
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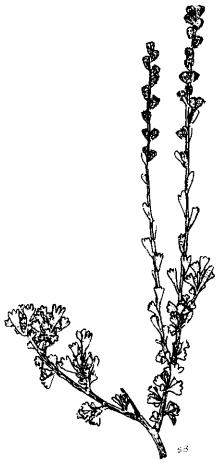
Map 1 (a). Distribution of *Artemisia arbuscula* ssp. *arbuscula*.



Artemisia arbuscula ssp. *arbuscula*



Map 1 (b). Distribution of *Artemisia arbuscula* ssp. *longiloba.*



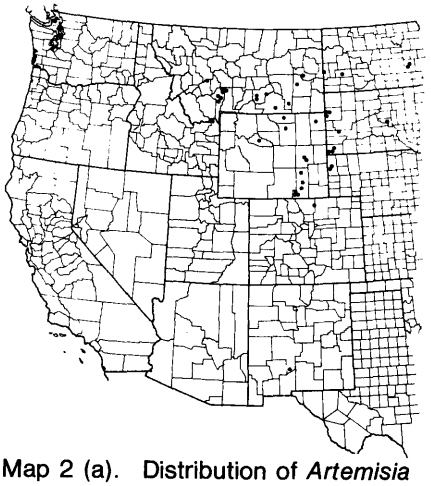
Artemisia arbuscula ssp: *longiloba*



Map 1 (c). Distribution of *Artemisia arbuscula* ssp. *thermopola.*



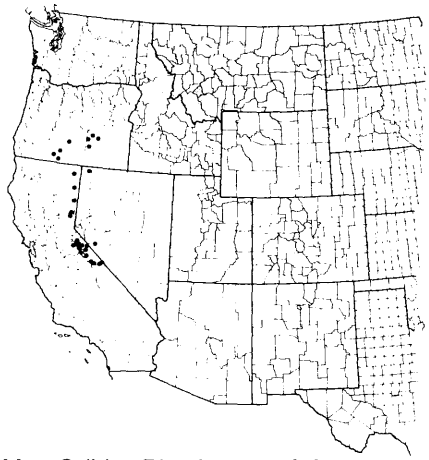
Artemisia arbuscula ssp. *thermopola*



Map 2 (a). Distribution of *Artemisia cana* ssp. *cana.*



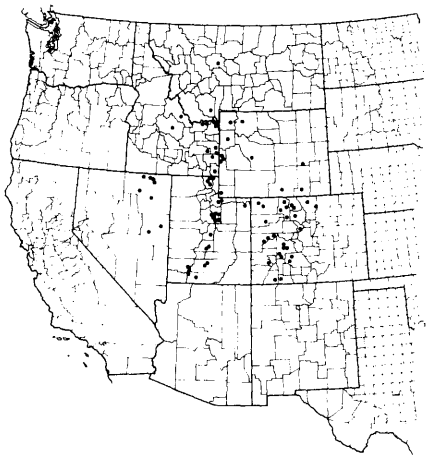
Artemisia cana ssp. *cana*



Map 2 (b). Distribution of *Artemisia cana* ssp. *bolanderi.*



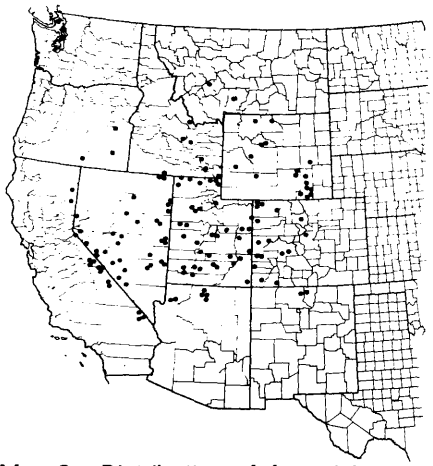
Artemisia cana ssp. *bolanderi*



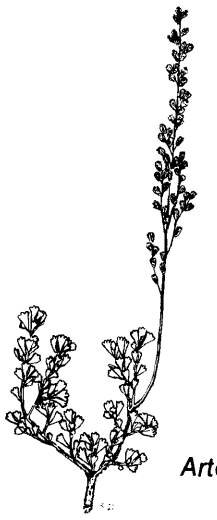
Map 2 (c). Distribution of *Artemisia cana* ssp. *viscidula.*



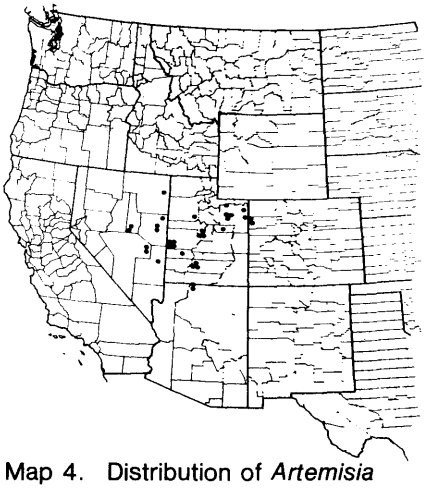
Artemisia cana ssp. *viscidula*



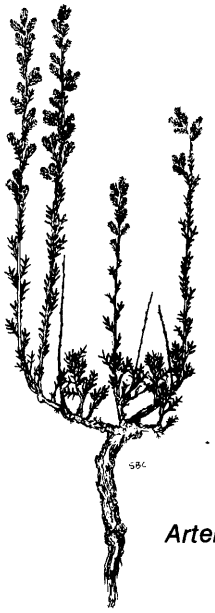
Map 3. Distribution of *Artemisia nova.*



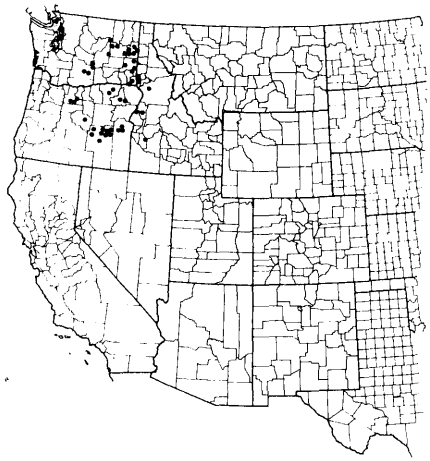
Artemisia nova



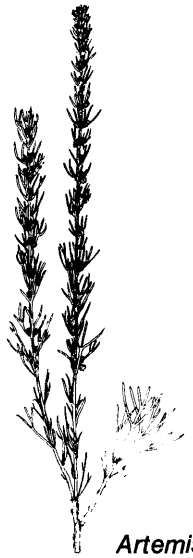
Map 4. Distribution of *Artemisia pygmaea.*



Artemisia pygmaea



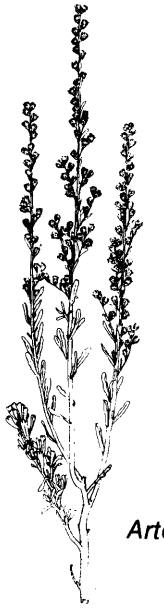
Map 5. Distribution of *Artemisia rigida.*



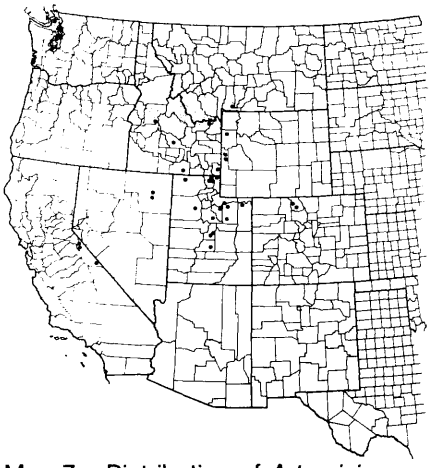
Artemisia rigida



Map 6. Distribution of *Artemisia rothrockii.*



Artemisia rothrockii



Map 7. Distribution of *Artemisia* X *spiciformis*.



Artemisia x *spiciformis*



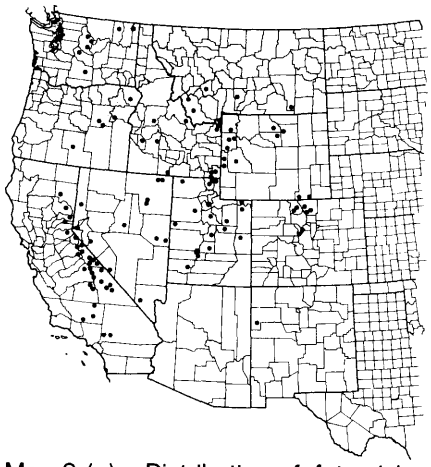
Map 8 (a). Distribution of *Artemisia tridentata* ssp. *tridentata*.



Artemisia tridentata ssp. *tridentata*



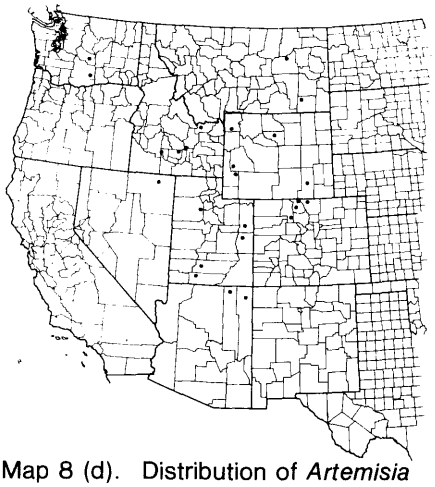
Map 8 (b). Distribution of *Artemisia tridentata* ssp. *parishii*.



Map 8 (c). Distribution of *Artemisia tridentata* ssp. *vaseyana.*



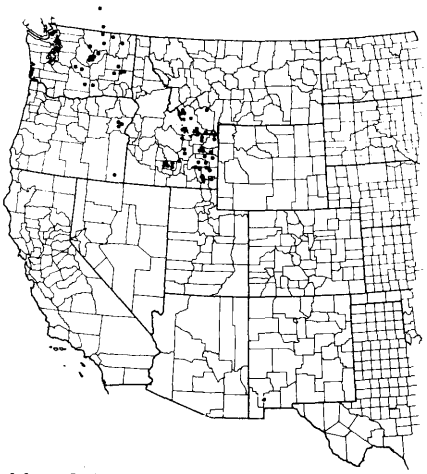
Artemisia tridentata ssp. *vaseyana*



Map 8 (d). Distribution of *Artemisia tridentata* ssp. *wyomingensis.*



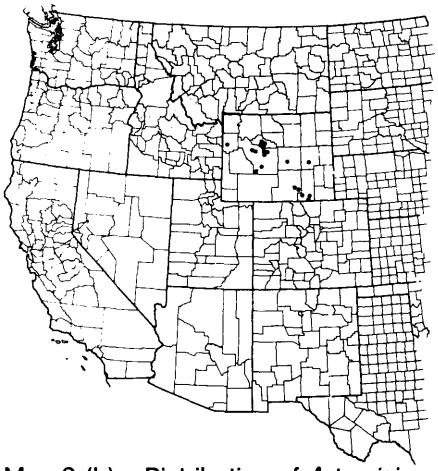
Artemisia tridentata ssp. *wyomingensis*



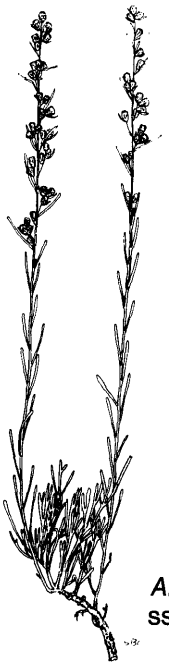
Map 9 (a). Distribution of *Artemisia tripartita* ssp. *tripartita.*



Artemisia tripartita ssp. *tripartita*



Map 9 (b). Distribution of *Artemisia tripartita* ssp. *rupicola*.



Artemisia tripartita ssp. *rupicola*

In: McArthur, E. Durant; Welch, Bruce L., compilers. Proceedings--symposium on the biology of Artemisia and Chrysothamnus; 1984 July 9-13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 398 p.

AN OVERVIEW OF THE GENUS CHRYSOTHAMNUS (ASTERACEAE)

Loran C. Anderson

ABSTRACT: The genus Chrysothamnus contains five sections, 16 species, and 41 subspecies. General comments, keys to the species and subspecies, and an atlas of distributional maps are given.

INTRODUCTION

Chrysothamnus (commonly known as rabbitbrush) is a widespread genus over much of western North America. Some species are sub-dominants in sagebrush desert and desert grassland; others are truly montane. This overview is provided now in anticipation of my upcoming monograph, which will include much more detail. The early nomenclatural history of the genus was summarized by Hall and Clements (1923). They recognized four sections, 12 species, and 40 subspecies.

Subsequent work has resulted in additional resolution of the taxonomy. For example, C. pyramidatus was transferred to Haplopappus (Blake 1926) and finally to Baccharis (Rzedowski 1972). Chrysothamnus gramineus was reclassified as a Petradoria (Anderson 1963). New species include C. eremobius, C. molestus, and C. spathulatus (Anderson 1964, 1983). Chrysothamnus linifolius and C. humilis are recognized as distinct species again. One fossil species, C. pulchelloides, has been recorded for the genus (Anderson 1980c). In addition, several new subspecies have been described (Anderson 1978, 1980a, 1980b, 1981, 1984), and sectional composition within the genus has been modified.

The transfer of C. gramineus to Petradoria (as P. discoidea) was made with the knowledge available at that time. With the recent discovery of C. eremobius (Anderson 1983), it is apparent that C. gramineus should be retained in Chrysothamnus. A new section of the genus is formally described to accommodate the species C. eremobius and C. gramineus (type species of the section).

Chrysothamnus Gramini L. C. Anderson, sect. nov.

Caules recti annui e caudice lignoso crescentes; folia plana, rigida, chartaceae, manifeste venosa, plusminusve persistentia.

Sectional composition in Chrysothamnus is now perceived as follows:

Section Chrysothamnus
- C. albidus (Jones ex Gray) Greene
- C. greenei (Gray) Greene
- C. humilis Greene
- C. linifolius Greene
- C. spathulatus L. C. Anderson
- C. viscidiflorus (Hook.) Nutt.

Section Gramini
- C. eremobius L. C. Anderson
- C. gramineus Hall

Section Nauseosi
- C. parryi (Gray) Greene
- C. nauseosus (Pallas) Britt.

Section Pulchelli
- C. depressus Nutt.
- C. molestus (Blake) L. C. Anderson
- C. pulchellus (Gray) Greene
- C. vaseyi (Gray) Greene

Section Punctati
- C. paniculatus (Gray) Hall
- C. teretifolius (Dur. & Hilg.) Hall & Clem.

Characteristics of the sections are given in the key to the species. Presumed phylogenetic relationships of taxa within and among sections are given in Anderson and Fisher (1970) and Anderson (1983). Figure numbers precede taxon name in right-hand column.

Paper presented at the Symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

Loran C. Anderson is Professor and Curator of the Herbarium, Florida State University, Tallahassee, FL.

KEY TO THE SPECIES

1. Stems tomentose, hairs often densely compacted (Section Nauseosi)

   2. Phyllaries attenuate, weakly keeled, rather membranous; inflorescences mostly racemose; heads 5-20 flowered . . . . . C. parryi (12 ssp.)

   2. Phyllaries obtuse to acute, if attenuate then strongly keeled, chartaceous; inflorescences mostly cymose; heads usually 5 flowered . . . . . C. nauseosus (22 ssp.)

1. Stems glabrous, puberulent, or resinous-punctate, never tomentose

3. Stems and leaves resinous-punctate; corollas yellow (Section Punctati)

4. Involucres 6-8 mm long, turbinate; phyllaries weakly aligned vertically . . 19. C. paniculatus

4. Involucres 7.6-9.5 mm long, cylindric; phyllaries strongly aligned vertically with swollen tips . . . . . 26. C. teretifolius

3. Stems not resinous-punctate, if leaves resinous-punctate then corollas white

5. Upright stems annual; leaves flat, rigid, strongly veined, more or less persistent (Section Gramini)

6. Involucres 11-17.5 mm long; phyllaries not keeled; achenes glabrous . . 3. C. gramineus

6. Involucres 6.5-9 mm long; phyllaries keeled; achenes pubescent . . . . . 3. C. eremobius

5. Upright stems perennial; leaves often twisted, not rigid, strongly veined if persistent

7. Achenes glabrous with few glands just below pappus or few hairs along ridges (Section Pulchelli)

8. Corollas less than 9 mm long, surpassing the pappus

9. Involucres 5-7 mm long; phyllaries weakly aligned and keeled . . . 27. C. vaseyi

9. Involucres 10-13 mm long; phyllaries strongly aligned and keeled

10. Leaves less than 2 mm wide, densely glandular-hispid . . . . . 6. C. molestus

10. Leaves more than 2 mm wide, hispid or glabrous, rarely sparsely glandular . . . . . 2. C. depressus

8. Corollas mostly over 9 mm long but surpassed by abundant pappus . . . C. pulchellus (2 ssp.)

7. Achenes densely pubescent, rarely sparsely so in C. humilis and C. spathulatus but then achenes not ridged (Section Chrysothamnus)

11. Corollas white; leaves resinous punctate . . . . . 1. C. albidus

11. Corollas yellow; leaves more or less resinous, never punctate

12. Heads often overtopped by leaves; flowers 2-3(4); style branches included or barely surpassing corolla lobes, appendages long . . 5. C. humulis

12. Heads not overtopped by leaves; flowers 3 or more; styles long exserted beyond spreading corolla lobes

13. Style appendages long (40-70% of style branch); leaves lanceolate or spatulate, never twisted; shrubs over 7 dm tall

14. Involucres less than 6 mm long, turbinate; leaves lanceolate; plants soboliferous; achenes densely pubescent . . . . . 6. C. linifolius

14. Involucres over 6 mm long, cylindric; leaves spatulate; plants never soboliferous; achenes sparsely pubescent . 26. C. spathulatus

13. Style appendages short (30-45% of style branch); leaves linear to oblong-lanceolate, frequently twisted or involute

15. Phyllaries acuminate-cuspidate; leaves 1-2 mm wide . . . 4. C. greenei

15. Phyllaries obtuse or acute; leaves 1-10 mm wide . . . . C. viscidiflorus (5 ssp.)

The species are fairly well defined, but a few of them have considerable intraspecific variability, which has resulted in differing taxonomic treatments as seen in table 1.

Table 1.--The complex taxa of Chrysothamnus

Species	Total names as species	Subspecies number (Hall and Clements 1923)	Subspecies number (Anderson this paper)
C. nauseosus	62	20	22
C. parryi	15	10	12
C. viscidiflorus	25	9	5

KEY TO THE SUBSPECIES

Chrysothamnus nauseosus

1. Involucres pubescent to tomentose, rarely nearly glabrous; stems mostly whitish with tomentum; leaves mostly dark green or grayish-white ("gray group")

   2. Achenes glabrous, at least on lower half

      3. Achenes with tuft of hairs just below pappus; phyllaries sparsely villous as well as tomentose . . . . . 18. ssp. washoensis

      3. Achenes totally glabrous; phyllaries tomentose to nearly glabrous

         4. Leaves linear; corollas over 9 mm long

            5. Pappus about equal to corolla in length; style appendages longer than stigmatic portion . . . . . 9. ssp. bigelovii

            5. Pappus much shorter than corolla; style appendages shorter than stigmatic portion . . . . . 17. ssp. texensis

         4. Leaves narrowly oblanceolate; corollas less than 9 mm long . . . . . 17. ssp. psilocarpus

   2. Achenes densely pubescent

      6. Leaves 3-10 mm wide; phyllaries mostly obtuse . . . . . 17. ssp. salicifolius

      6. Leaves 1-3 mm wide; phyllaries various, usually acute

         7. Outer phyllaries densely tomentose, inner ones glabrous

            8. Plants mostly 1-2 dm tall; corolla lobes 1-2.5 mm long

               9. Involucres 8-9 mm long; corolla lobes 1.6-2.5 mm long . . . . 15. ssp. nanus

               9. Involucres 11-13 mm long; corolla lobes 1-1.5 mm long . . . . 18. ssp. uintahensis

            8. Plants over 3 dm tall; corolla lobes 0.5-1 mm long . . . . . 14. ssp. latisquameus

         7. All phyllaries tomentose, sometimes sparsely so

            10. Involucres 7-10(11) mm tall

               11. Corolla lobes 1-2 mm long; style appendages longer than stigmatic portions

                  12. Corollas 6-8.5 mm long; involucres 7-9.5 mm long; shrubs mostly 2-6 dm tall . . . . . 16. ssp. nauseosus

                  12. Corollas (8)9-11 mm long; involucres mostly 9-11 mm long; shrubs 4-15 dm tall (lower in some alpine forms) . . . . 7. ssp. albicaulis

11. Corolla lobes 0.5-1 mm long; style appendages shorter than stigmatic portions . . . . . 12. ssp. hololeucus

10. Involucres 11-13 mm long

13. Corolla lobes 1.7-2.3 mm long, glabrous . . . . . 8. ssp. bernardinus

13. Corolla lobes 0.5-1 mm long, villous . . . . . 18. ssp. turbinatus

1. Involucres glabrous, outer phyllaries sometimes ciliate or scurfy; stems greenish, tomentum more compacted; leaves usually greenish-yellow or absent ("green group")

14. Achenes glabrous

15. Outer phyllaries scurfy tomentulose, obtuse; inner ones glabrous, weakly keeled; stems yellowish-green . . . . . 16. ssp. nitidus

15. Outer phyllaries glabrous, obtuse to acute, keeled; stems brownish to grayish-green

16. Involucres 7.5-10.5 mm long; stems often leafless . . . . . 14. ssp. leiospermus

16. Involucres 12-16 mm long; stems very leafy . . . . . 13. ssp. iridis

14. Achenes pubescent

17. Involucres over 15 mm long; phyllaries strongly keeled and cuspidate 8. ssp. arenarius

17. Involucres less than 15 mm long; phyllaries not cuspidate

18. Leaves 1-3 mm wide, 1-5-nerved

19. Involucres 11-13 mm long; corolla lobes 1.7-2.3 mm long . . . 8. ssp. bernardinus

19. Involucres 6.7-9.5 mm long; corolla lobes 0.6-1.5 mm long . . 11. ssp. graveolens

18. Leaves 1 mm wide or less, 1-nerved

20. Phyllaries abruptly pointed, recurved . . . . . 9. ssp. ceruminosus

20. Phyllaries acute, erect

21. Involucres 7-8 mm long; stems usually leafy; corolla lobes glabrous (achenes sometimes glabrous in Idaho) . . . . . 10. ssp. consimilis

21. Involucres 9-10 mm tall, phyllaries strongly ranked; stems often leafless

22. Corolla lobes glabrous . . . . . 15. ssp. mohavensis

22. Corolla lobes villous (sometimes sparsely so) . . . . 13. ssp. junceus

Chrysothamnus parryi

1. Flowers mostly 8-20 per head or leaves over 5 mm wide (never with stalked glands)

2. Shrubs over 3 dm tall; leaves mostly over 3 cm long

3. Flowers 8-20 per head; leaves 2-3 mm wide . . . . . 24. ssp. parryi

3. Flowers 5-7 per head; leaves 5-14 mm wide . . . . . 22. ssp. latior

2. Shrubs 1-2 dm tall; leaves mostly less than 3 cm long

4. Leaves 2-3.5 cm long, overtopping the inflorescence; corollas 9-10 mm long . . . . . 23. ssp. montanus

4. Leaves 1-1.5 mm long, not overtopping inflorescence; corollas 10-12 mm long . . . . . 22. ssp. imulus

1. Flowers mostly 5-7 per head; leaves 1-3 mm wide (flowers up to 10 per head and leaves to 4 mm wide in ssp. asper, then leaves with stalked glands)

   5. Leaves oblanceolate, with short stalked glands; corollas up to 9 mm long . 20. ssp. asper

   5. Leaves linear to oblanceolate, without stalked glands

      6. Inflorescences reduced to 1-2 heads, each with 8-11(13) phyllaries; corollas 8-9 mm long . . . . . 22. ssp. monocephalus

      6. Inflorescences with many heads; corollas mostly over 9 mm long

         7. Inflorescences lax and elongated; involucres 12.5-15 mm long with 9-13 straight, narrow phyllaries . . . . . 24. ssp. vulcanicus

         7. Inflorescences more compact; involucres shorter or with more phyllaries, often broader, spreading or recurved

            8. Upper leaves overtopping inflorescence; corollas pale yellow, mostly 8-10 mm long

               9. Inflorescences somewhat elongate, sparsely leafy; involucres 10-12 mm long; corolla lobes 1-1.5 mm long . . . . . 24. ssp. salmonensis

               9. Inflorescences compact, very leafy; involucres 11.5-16 mm long; corolla lobes 1.5-1.7 mm long . . . . . 21. ssp. howardii

            8. Upper leaves shorter than inflorescence; corollas often over 10 mm long

               10. Corollas pale yellow, tubes abruptly dilated; corolla lobes 0.7-1 mm long, lanceolate . . . . . 20. ssp. affinis

               10. Corollas clear yellow, tubes gradually flaring; corolla lobes 1.5-2 mm long, relatively broader

                  11. Phyllaries mostly straight tipped; involucres 11-15 mm long . . . . . 21. ssp. attenuatus

                  11. Phyllaries with recurved tips; involucres 14-19 mm long . 23. ssp. nevadensis

Chrysothamnus pulchellus

1. Shrubs 8-12 dm tall; leaves glabrous or puberulent, margins entire; corollas 11-13 mm long . . . . . 25. ssp. pulchellus

1. Shrubs 0.5-5(7) dm tall; leaves with scabrous-ciliolate margins, otherwise glabrous; corollas 7-12 mm long . . . . . 25. ssp. baileyi

Chrysothamnus viscidiflorus

1. Leaves planate, glabrous; corollas 3.5-4(4.5) mm long . . . . . 30. ssp. planifolius

1. Leaves more or less twisted or pubescent or corollas longer

   2. Upper stems, frequently leaves, hairy

      3. Stems and leaves finely puberulent; leaves 1-2(4) mm wide . . . . . 30. ssp. puberulus

      3. Stems hispid near inflorescence; leaves over 2 mm wide, hirsute or glabrous . . . . . 29. ssp. lanceolatus

   2. Stems glabrous; leaves often with ciliate margins, otherwise glabrous

      4. Leaves $\pm$ 1 mm wide; flowers 3-4(5) per head; involucres somewhat turbinate . . . . . 28. ssp. axillaris

      4. Leaves 1-10 mm wide; if 1 mm then flowers 4 or more per head and involucres narrowly cylindric . . . . . 31. ssp. viscidiflorus

NAMES EXCLUDED FROM THE KEYS

Chrysothamnus nauseosus ssp. glareosus (Jones) Hall & Clem.: taxon described as having glabrous achenes and flowers a half inch long, from Marysvale, UT. No specimens have been located in the herbaria or in the field.

Chrysothamnus nauseosus ssp. viscosus Keck: taxon described as differing somewhat from ssp. hololeucus. Type collection is an intergeneric hybrid between ssp. hololeucus and Haplopappus cuneatus.

Chrysothamnus parryi ssp. bolanderi (Gray) Hall & Clem.: known only from type locality. It is an intergeneric hybrid between C. nauseosus ssp. albicaulis and Haplopappus marconema.

NOMENCLATURAL INFORMATION AND TRIVIA

Figure

1. C. albidus (Jones ex Gray) Greene. The only white-flowered and most resinous species in the genus. Its geographical range is extensive, but it is not particularly abundant anywhere.

2. C. depressus Nutt. Somewhat variable species with stouter forms in Nevada and California, but there are no correlated patterns of variability worthy of taxonomic recognition.

3. C. eremobius L. C. Anderson. This very distinctive species was only recently discovered and described. Vegetatively it looks somewhat like Petradoria pumila.

3. C. gramineus Hall. This species was transferred to Petradoria by me several years ago based on then current data. Morphology of C. eremobius warrants returning this species to Chrysothamnus.

4. C. greenei (Gray) Greene. The species is very closely related to C. viscidiflorus. Narrow-leaved forms have been called ssp. filifolius, but leaf width varies under garden culture. I choose not to recognize the subspecies. It could be recognized at the varietal level.

5. C. humilis Greene. The earliest blooming species in the genus, it is sometimes confused with C. viscidiflorus ssp. puberulus, from which it can be distinguished by its coarser vesture in addition to the key characters and more cryptic anatomical features.

6. C. linifolius Greene. The only species in the genus that is soboliferous, it also has some unique anatomy--clearly distinct from C. viscidiflorus.

6. C. molestus (Blake) L. C. Anderson. This rare species is distinctive in the genus with its glandular-hispid foliage.

C. nauseosus (Pallas) Britt. The most complex and wide-ranging species in the genus. I have merged some of the subspecies of Hall and Clements but have also described new ones. Names of varieties within the more complex subspecies will be given in the upcoming monograph for those who wish further details of interrelationships. Twenty-two subspecies are currently recognized; they are sometimes subdivided as the "gray group" and the "green group" based on density of tomentum of stems and leaves. That categorization is not very good because individual plants of ssp. bernardinus fit one group or the other, and considerable variation in tomentum density can occur within a given population in several subspecies.

7. ssp. albicaulis (Nutt.) Hall & Clem. Includes the names californicus, macrophyllus, and speciosus. Perhaps the most variable ssp. in C. nauseosus, it intergrades somewhat with ssp. consimilis, nauseosus, and especially hololeucus where their ranges overlap.

8. ssp. arenarius L. C. Anderson. Very distinctive with heads up to 20 mm long and phyllaries strongly keeled. Recently found in Mesa Co., CO (new to that state), but not shown on map.

8. ssp. bernardinus (Hall) Hall & Clem. Very close to ssp. albicaulis.

9. ssp. bigelovii (Gray) Hall & Clem. Very distinctive, but rarely mistaken for C. parryi spp. howardii.

9. ssp. cerminosus (Dur. & Hilg.) Hall & Clem. Looks like a ssp. consimilis or mohavensis but with prominently recurved phyllary tips.

10. ssp. consimilis (Greene) Hall & Clem. Includes names artus, oreophilus, petrophilus (a form with glabrous achenes), pinifolius, and viridulus. Several of these are worthy of varietal status within the subspecies.

11. ssp. graveolens (Nutt.) Piper. Includes names confinis, falcatus, glabrata, and nivecaulis. Intergrades with ssp. hololeucus in eastern Utah to give plants with white stems but glabrous involucres.

12. ssp. hololeucus (Gray) Hall & Clem. Includes the names gnaphalodes and zionis. Largely sympatric with ssp. consimilis, but intergradations between the two have not been observed.

13. ssp. iridis L. C. Anderson. Known from only two locations on barren gypsiferous shale.

13. ssp. junceus (Greene) Hall & Clem. Distinctive with fastigiate rushlike branches. Recently found in Mesa Co., CO (new for state), but not shown on map.

14. ssp. latisquameus (Gray) Hall & Clem. Very distinctive in southern part of range, but intergrades with ssp. graveolens in north-central New Mexico.

14. ssp. leiospermus (Gray) Hall & Clem. Includes names abbreviatus and oliganthus. Intergrades with ssp. mohavensis in Clark Co., NV.

15. ssp. mohavensis (Green) Hall & Clem. Includes name occidentalis. Closely related to ssp. consimilis.

15. ssp. nanus (Cronq.) Keck. Local, montane variant close to ssp. albicaulis.

16. ssp. nauseosus. Includes the names frigidus, pallidus, plattensis, pulcherrimus, and wyomingensis. A variable subspecies that seemingly intergrades only with ssp. albicaulis.

16. ssp. nitidus L. C. Anderson. A few pubescent-achened plants found in some populations. Distinctive with its yellowish-green stems (chartreuse) and very pleasant odor.

17. ssp. psilocarpus (Blake) L. C. Anderson. Very local glabrous-achened subspecies.

17. ssp. salicifolius (Rydb.) Hall & Clem. Distinctive with wide leaves; close to ssp. albicaulis but seems to mix a little with ssp. graveolens near Soldier Summit, UT.

17. ssp. texensis L. C. Anderson. Endemic to Guadalupe Mtns. of New Mexico and Texas with unusually short pappus.

18. ssp. turbinatus (Jones) Hall & Clem. Rarely has glabrous achenes but then distinct from ssp. bigelovii in villous corolla lobes and involucral features.

18. ssp. uintahensis L. C. Anderson. Apparently a local, stabilized hybrid involving C. parryi.

18. ssp. washoensis L. C. Anderson. Close to ssp. albicaulis but unique with white villous hairs distally on otherwise glabrous achenes.

19. C. paniculatus (Gray) Hall. Often easily identified by black bands on stems from insect or fungal attack.

C. parryi (Gray) Greene. Variation hardly accounted for with just trinomials; 11 subspecies:

20. ssp. affinis (Nels.) L. C. Anderson. Close to ssp. attenuatus, but involucres more stramineous.

20. ssp. asper (Greene) Hall & Clem. Distinctive with stalked glands but stalks sometimes fairly short.

21. ssp. attenuatus (Jones) Hall & Clem. Intermediate in range and morphology between ssp. howardii and ssp. nevadensis.

21. ssp. howardii (Parry) Hall & Clem. Includes name collinus. Geographically variable in plant height.

22. ssp. imulus Hall & Clem. Very local, perhaps only an extreme form of ssp. asper.

22. ssp. latior Hall & Clem. Distinctive with broadly oblanceolate leaves, looks like certain Haplopappus.

22. ssp. monocephalus (Nels. & Kenn.) Hall & Clem. High alpine form probably derived from ssp. nevadensis.

23. ssp. montanus L. C. Anderson. Known only from type locality and remote from near relatives.

23. ssp. nevadensis (Gray) Hall & Clem. Variable in stature and leaf size.

24. ssp. parryi. Wide ranging, hybridizes with C. nauseosus only at its range limits in Nevada and Wyoming.

24. ssp. salmonensis L. C. Anderson. Plants look much like C. nauseosus ssp. consimilis, but possibly derived from ssp. attenuatus.

24. ssp. vulcanicus (Greene) Hall & Clem. Plant form suggests some influence from C. nauseosus ssp. albicaulis.

C. pulchellus (Gray) Greene. Distinctive desert species with prominently angled achenes; 2 subspecies:

25. ssp. baileyi (Woot. & Standl.) Hall & Clem. Wide ranging, somewhat variable in involucral features.

25. ssp. pulchellus. Includes name elatior, which was applied to puberulent form (which grows intermixed with standard subspecies).

26. C. spathulatus L. C. Anderson. Only species in genus that rarely has a few ray flowers, but only in two geographically peripheral populations.

26. C. teretifolius (Dur. & Hilg.) Hall & Clem. Sometimes confused with C. paniculatus, this grows mostly on rocky slopes, whereas paniculatus grows in sandy washes.

27. C. vaseyi (Gray) Greene. Includes name bakeri. Looks somewhat like C. viscidiflorus but more closely related to C. depressus.

C. viscidiflorus (Hook.) Nutt. Most wide ranging and complex after C. nauseosus; five subspecies:

28. ssp. axillaris (Keck) L. C. Anderson. Confused with stenophyllus form of ssp. viscidiflorus but distinct.

29. ssp. lanceolatus (Nutt.) Hall & Clem. Includes names elegans, glaucus, latus, and spathulata; intergrades extensively with ssp. viscidiflorus.

30. ssp. planifolius L. C. Anderson. Local form with small heads and flat leaves.

30. ssp. puberulus (D. C. Eat.) Hall & Clem. Often with ssp. viscidiflorus but not intergrading.

31. ssp. viscidiflorus. Includes names latifolius, pumilus, stenophyllus, tortifolius, and varus. The combination C. v. ssp. viscidiflorus var. stenophyllus has already been made (Anderson 1980b); others will be made in upcoming monograph.

RANGE MAPS

The maps that follow (figures 1-31) depict the natural distribution of each taxon. More precise dot maps will be provided in the upcoming monograph. Ranges were determined from extensive field observations and from study of over 24,000 herbarium specimens.

ACKNOWLEDGMENT

This work has been supported by a series of grants from the National Science Foundation, the most recent being DEB-8021776.

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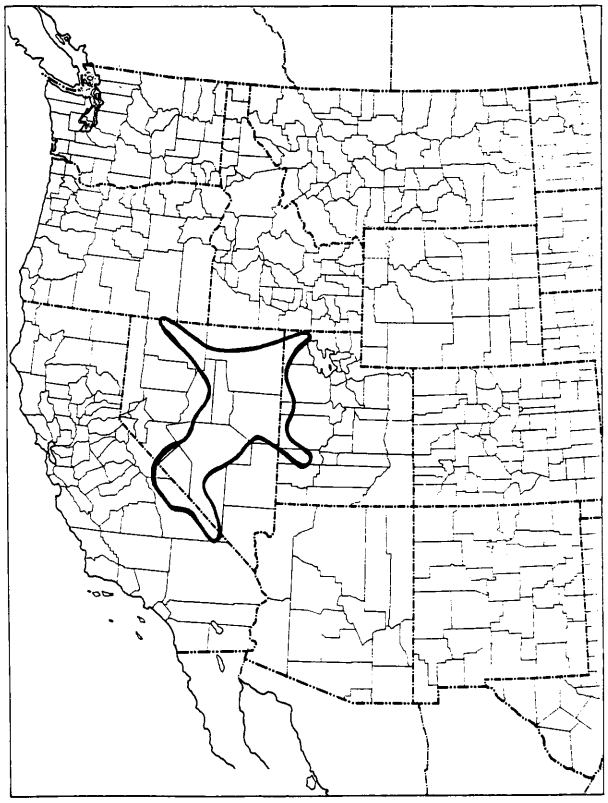


Figure 1.--Range of Chrysothamnus albidus.

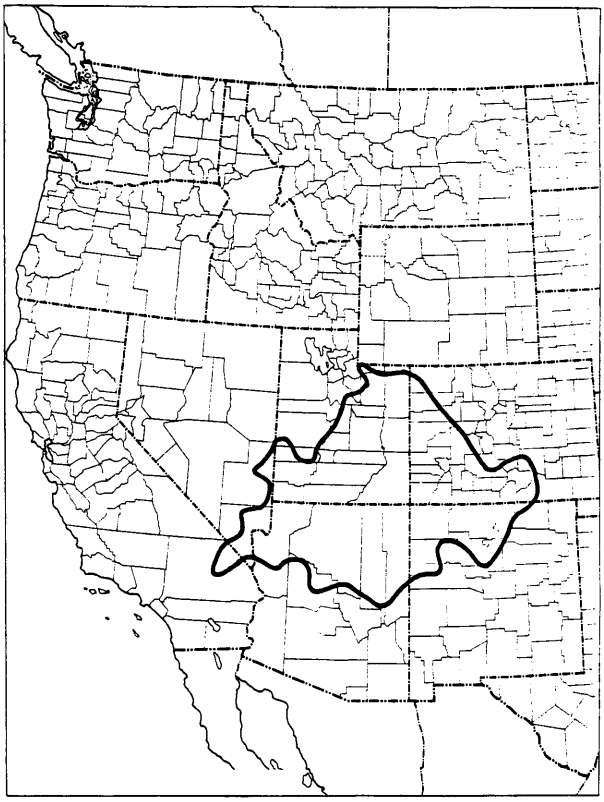


Figure 2.--Range of Chrysothamnus depressus.

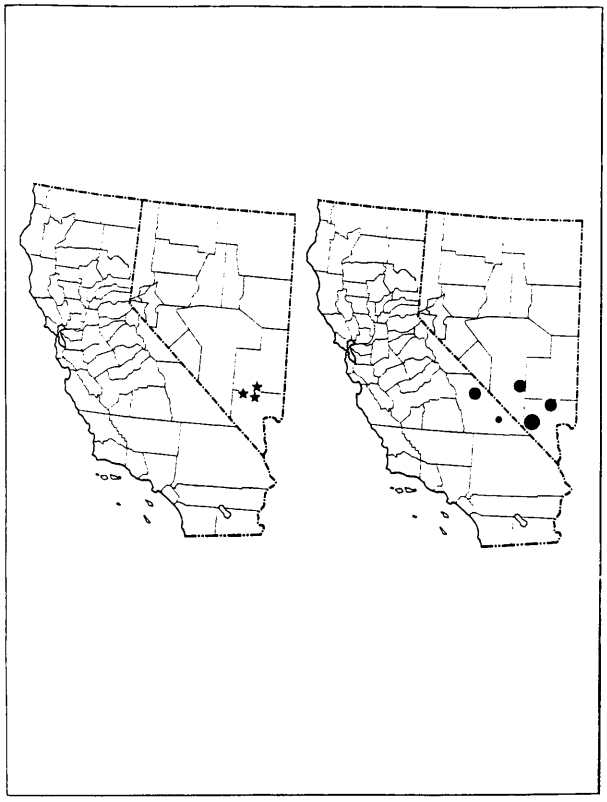


Figure 3.--Range of Chrysothamnus eremobius (stars); range of C. gramineus (dots).

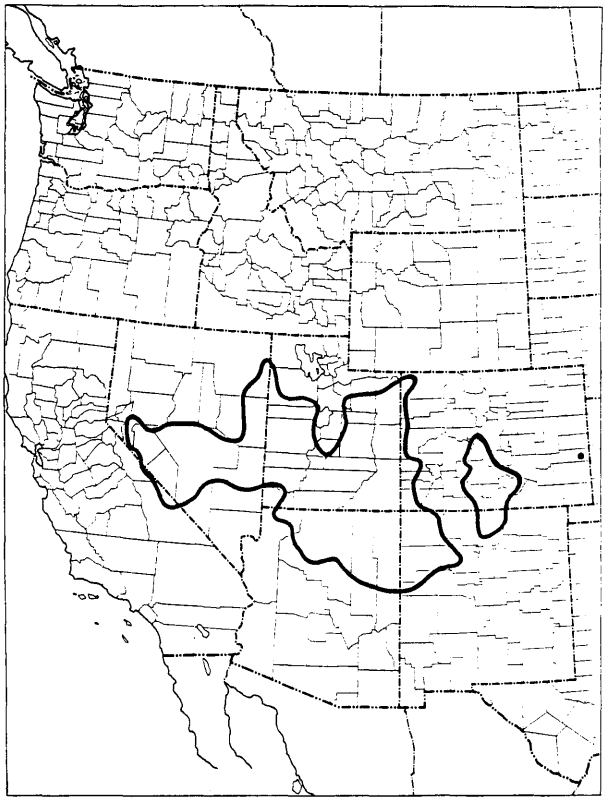


Figure 4.--Range of Chrysothamnus greenei.

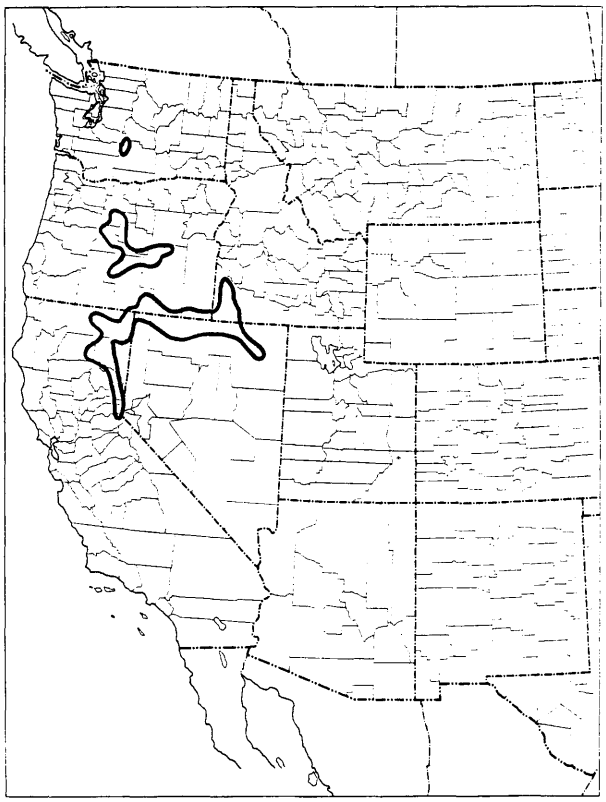


Figure 5.--Range of Chrysothamnus humilis.

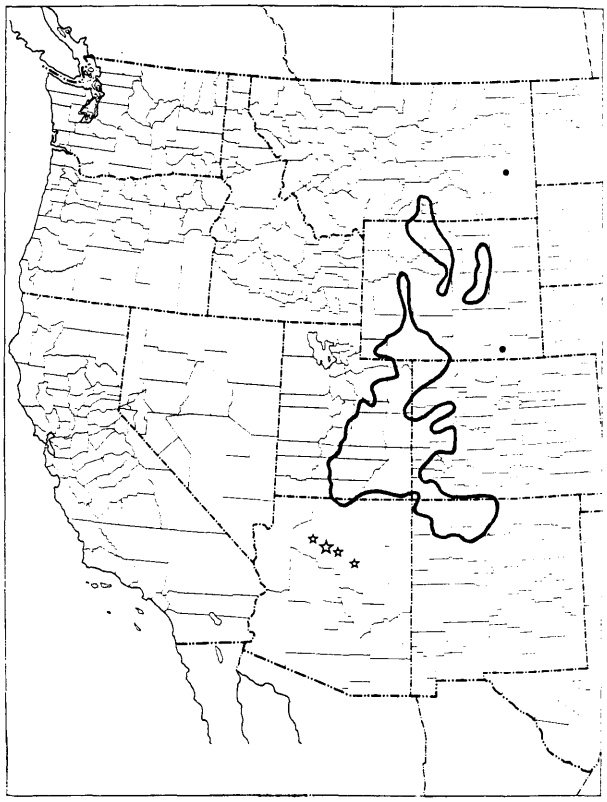


Figure 6.--Range of Chrysothamnus linifolius (dots and loops); range of C. molestus (stars).

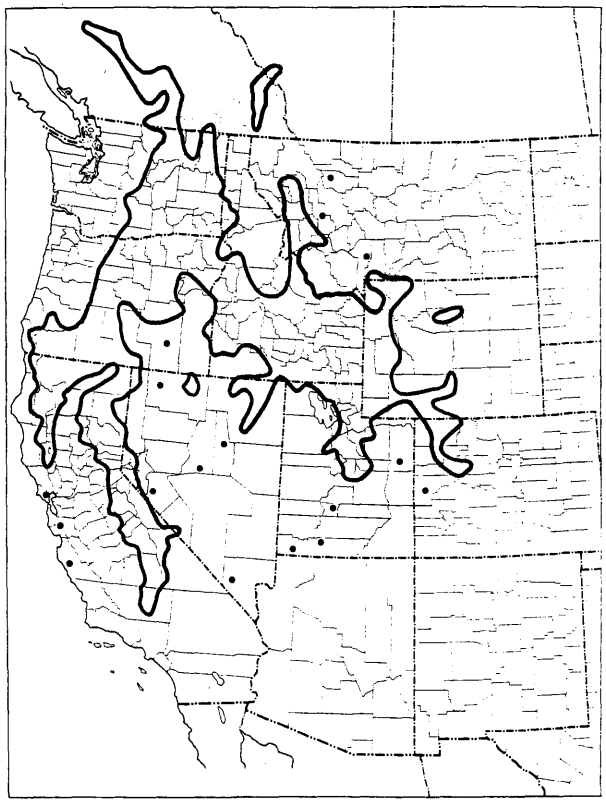


Figure 7.--Range of Chrysothamnus nauseosus ssp. albicaulis.

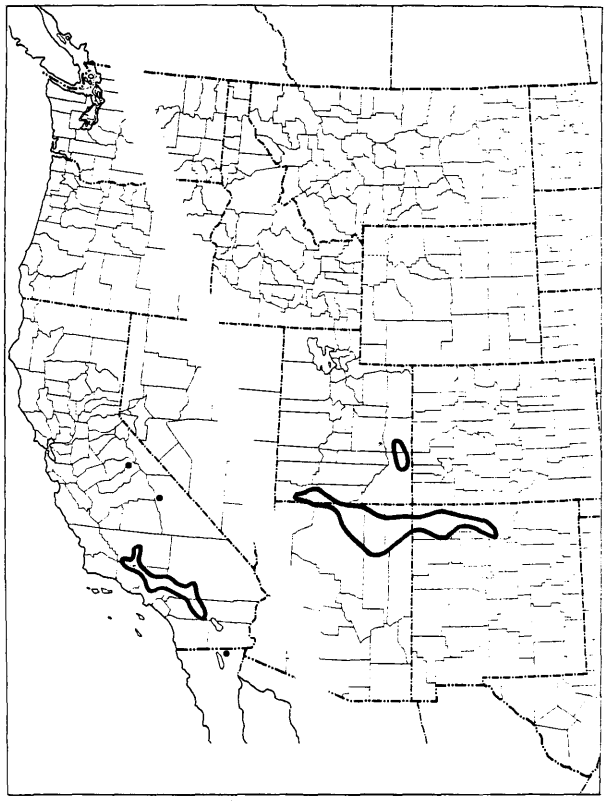


Figure 8.--Range of Chrysothamnus nauseosus ssp. arenarius (right map); range of C.n. ssp. bernardinus (left map).

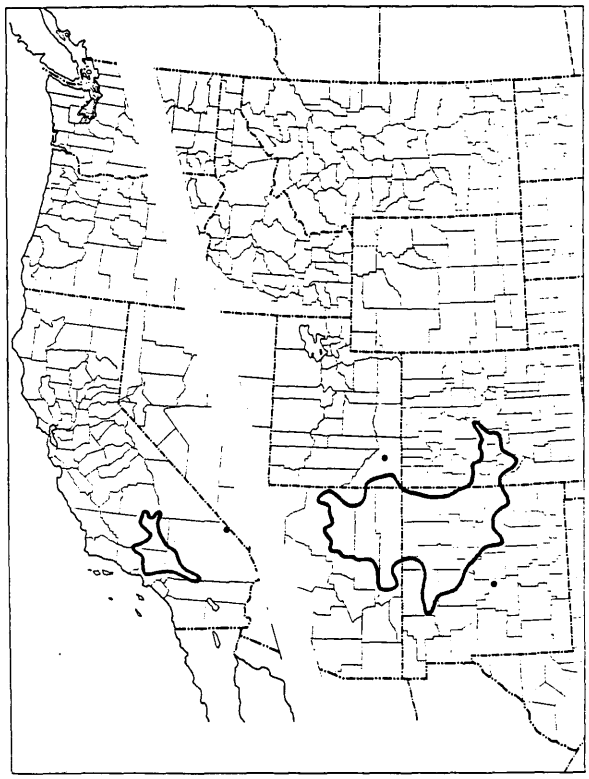


Figure 9.--Range of Chrysothamnus nauseosus ssp. bigelovii (right map); range of C.n. ssp. ceruminosus (left map).

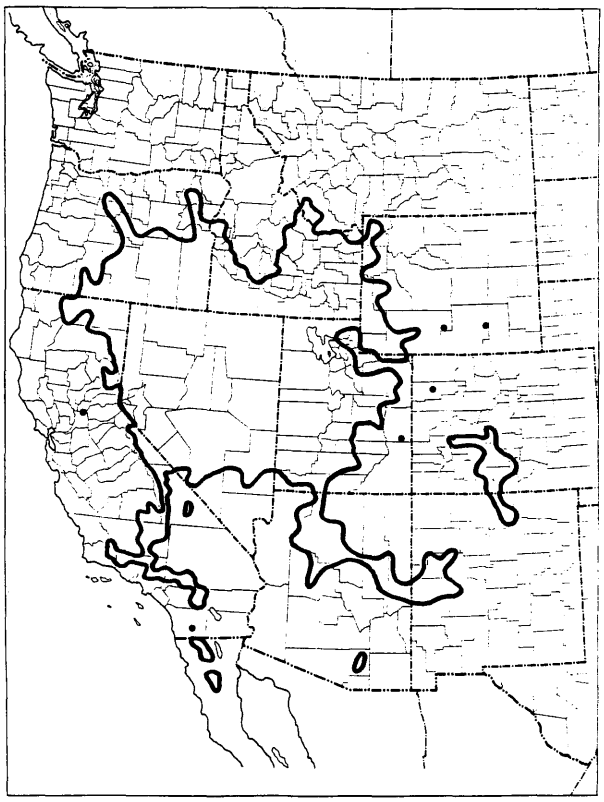


Figure 10.--Range of Chrysothamnus nauseosus ssp. consimilis.

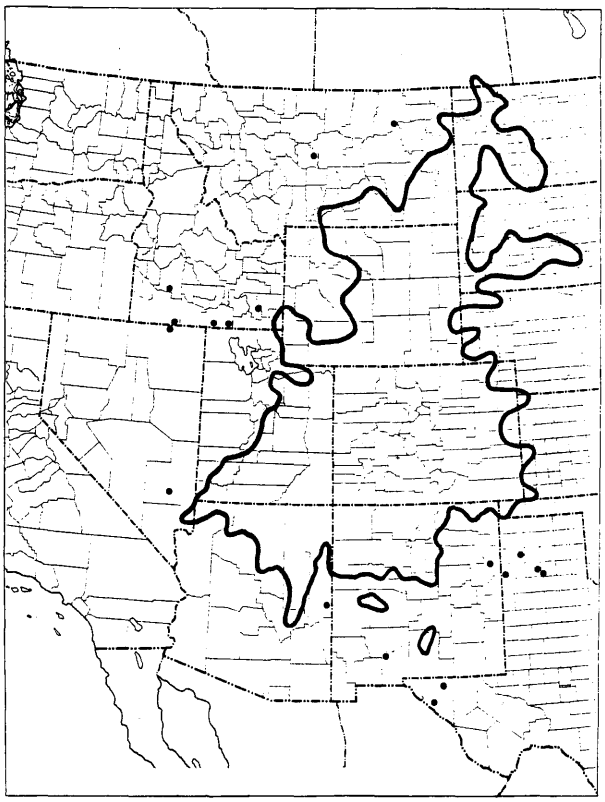


Figure 11.--Range of Chrysothamnus nauseosus ssp. graveolens.

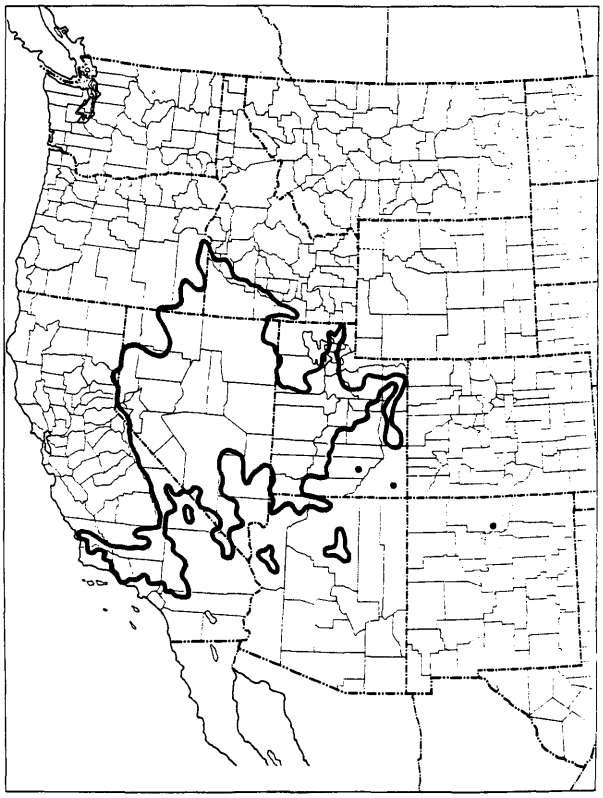


Figure 12.--Range of Chrysothamnus nauseosus ssp. hololeucus.

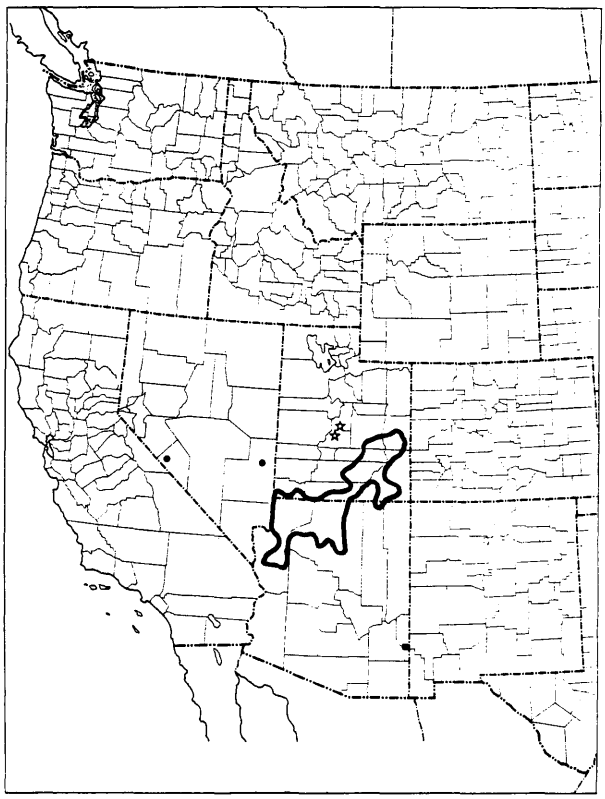


Figure 13.--Range of Chrysothamnus nauseosus ssp. iridis (stars); range of C.n. ssp. junceus (dots and loop).

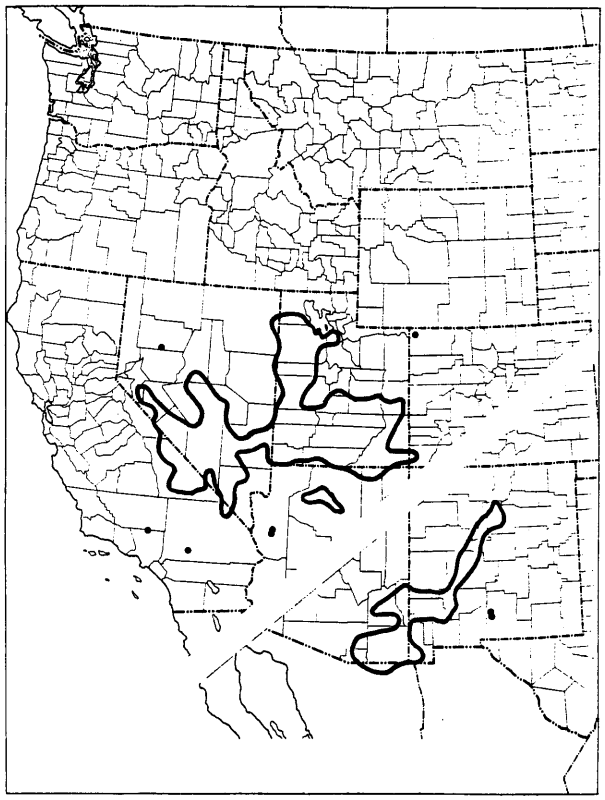


Figure 14.--Range of Chrysothamnus nauseosus ssp. latisquameus (lower right); range of C.n. ssp. leiospermus (upper left).

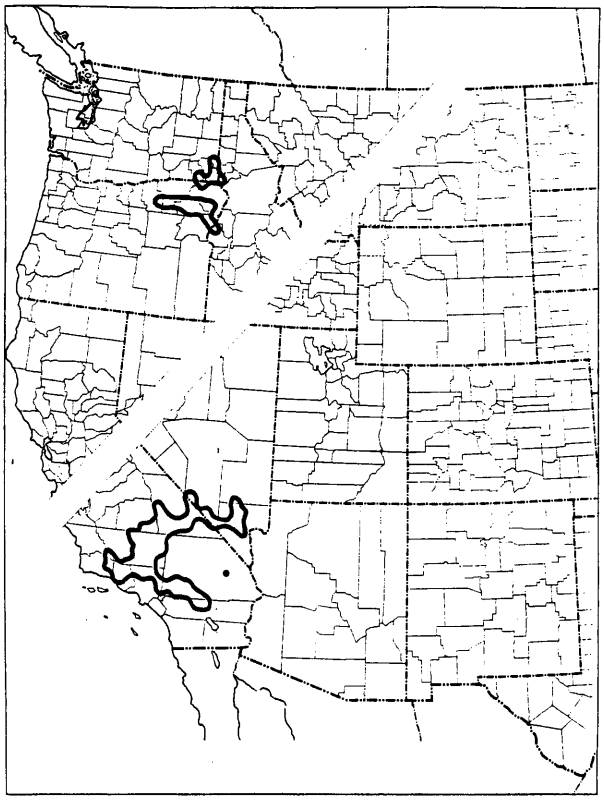


Figure 15.--Range of Chrysothamnus nauseosus ssp. mohavensis (lower map); range of C.n. ssp. nanus (upper map).

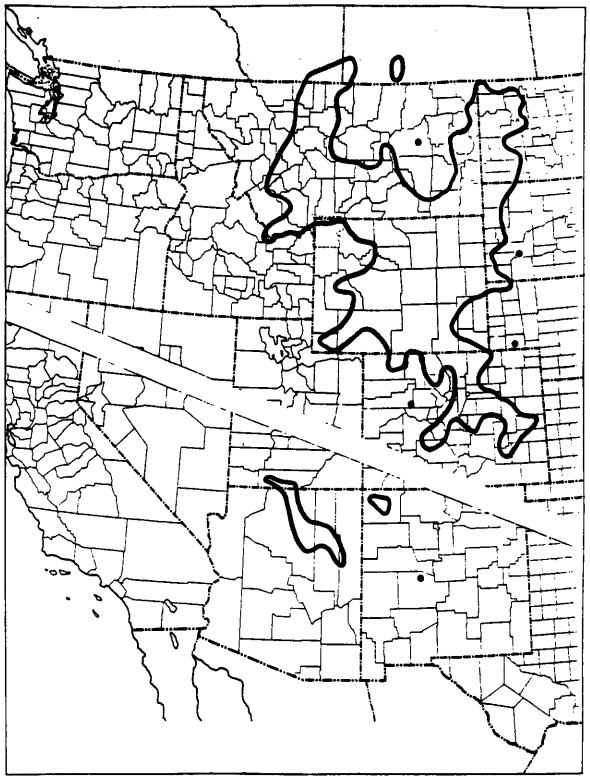


Figure 16.--Range of Chrysothamnus nauseosus ssp. nauseosus (upper right); range of C.n. ssp. nitidus (lower left).

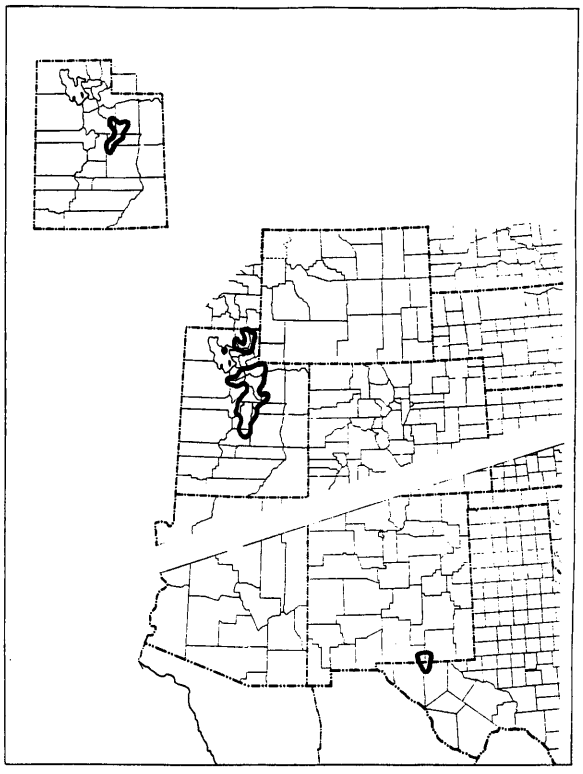


Figure 17.--Range of Chrysothamnus nauseosus ssp. psilocarpus (upper left); range of C.n. ssp. salicifolius (middle map); range of C.n. ssp. texensis (lower map).

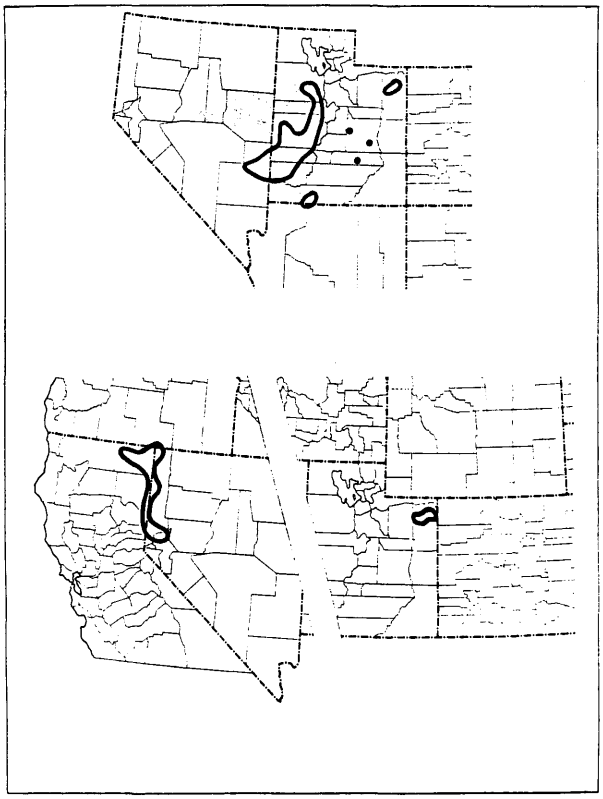


Figure 18.--Range of Chrysothamnus nauseosus ssp. turbinatus (upper map); range of C.n. ssp. uintahensis (lower right); range of C.n. ssp. washoensis (lower left).

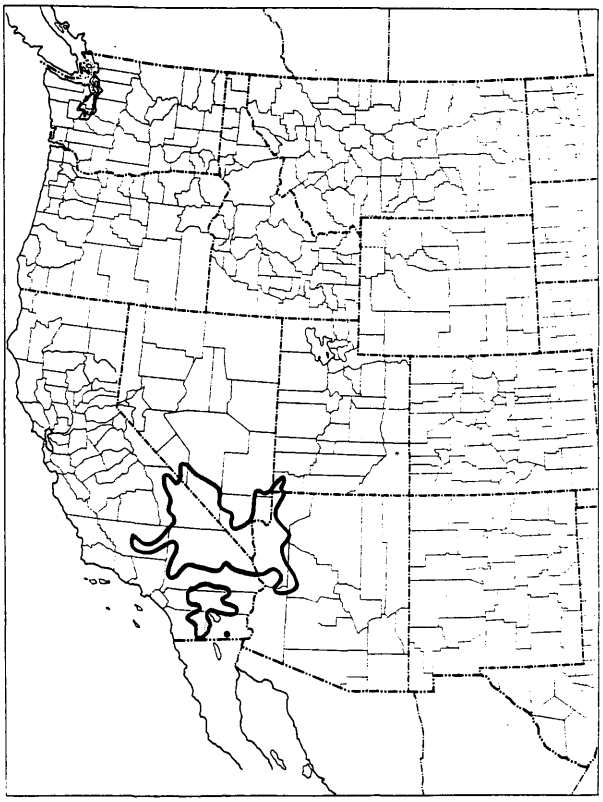


Figure 19.--Range of Chrysothamnus paniculatus.

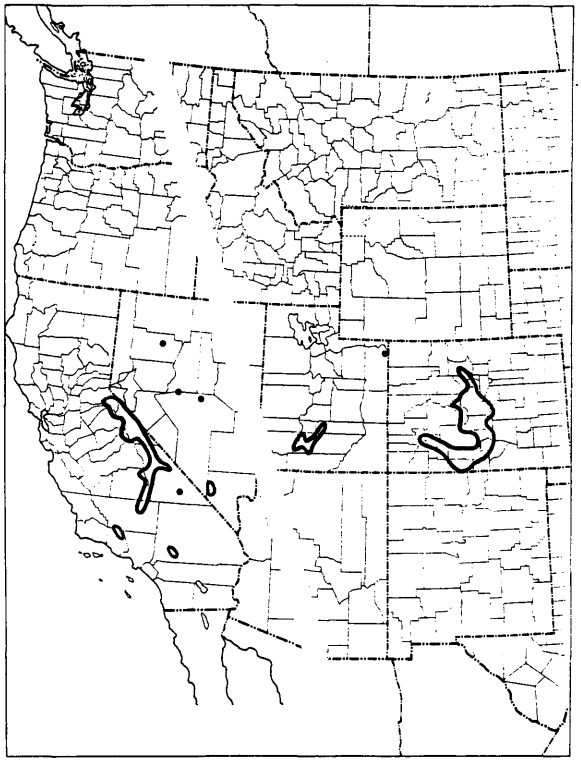


Figure 20.--Range of Chrysothamnus parryi ssp. affinis (right map); range of C.p. ssp. asper (left map).

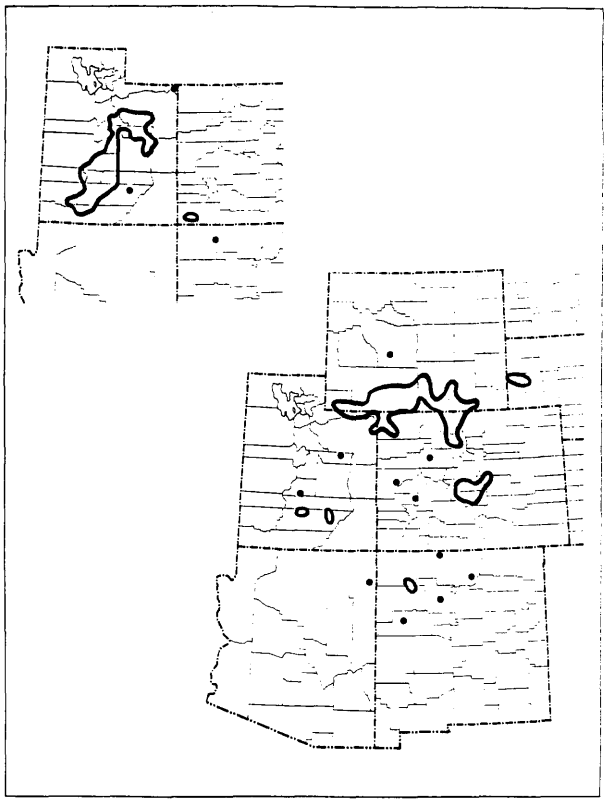


Figure 21.--Range of Chrysothamnus parryi ssp. attenuatus (upper left map); range of C.p. ssp. howardii (lower right map).

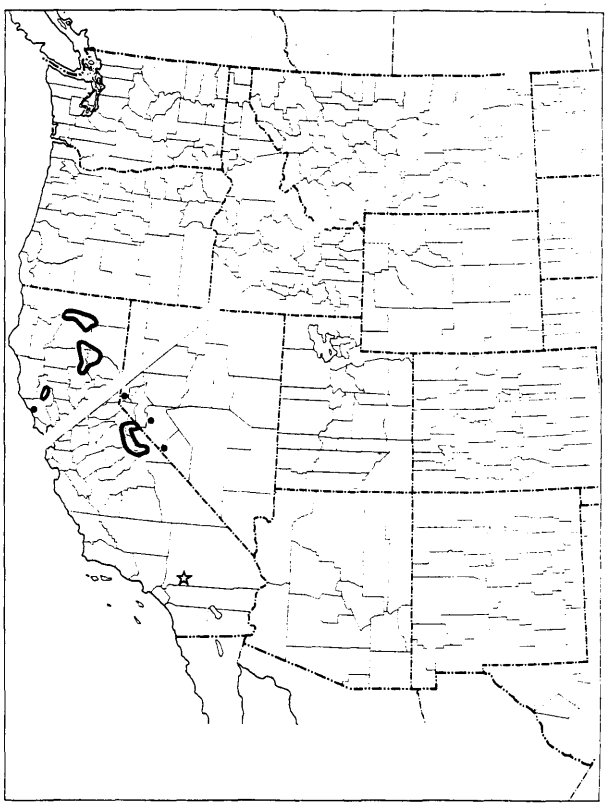


Figure 22.--Range of Chrysothamnus parryi ssp. imulus (star, lower map); range of C.p. ssp. latior (upper map); range of C.p. ssp. monocephalus (dots and loop, lower map).

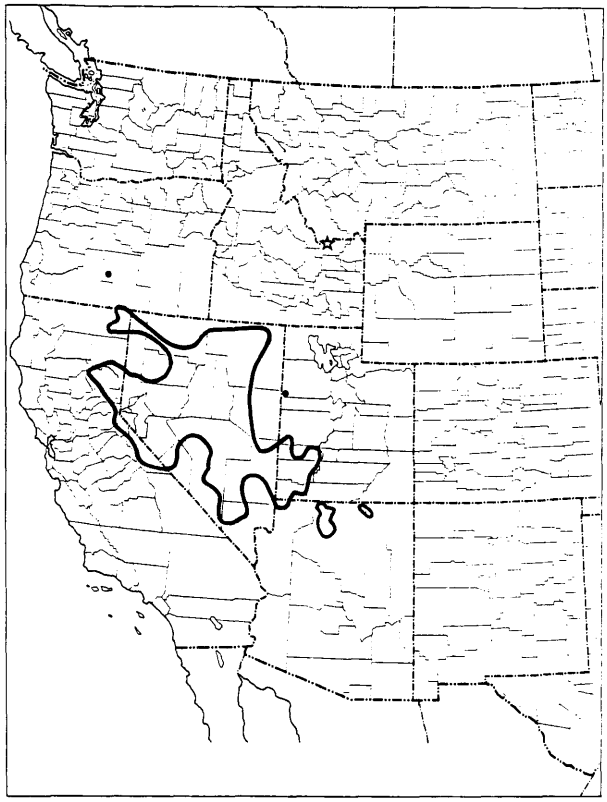


Figure 23.--Range of Chrysothamnus parryi ssp. montanus (star); range of C.p. ssp. nevadensis (dots and loops).

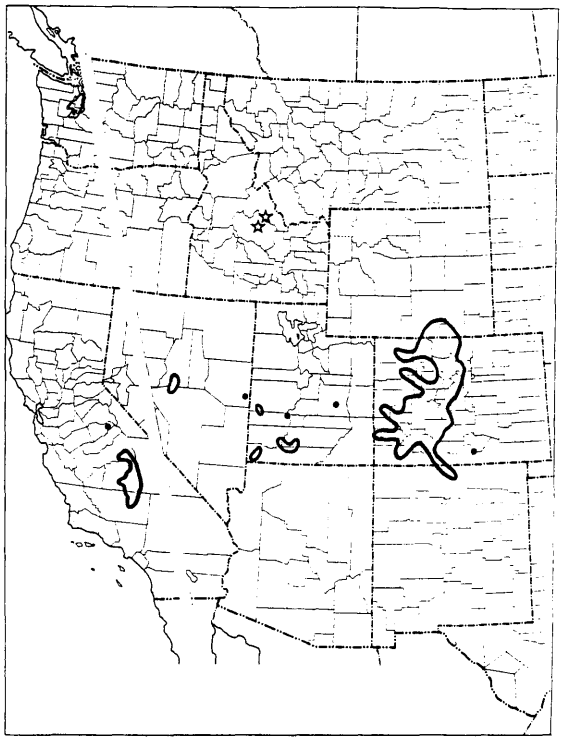


Figure 24.--Range of Chrysothamnus parryi ssp. parryi (dots and loops, right map); range of C.p. ssp. salmonensis (stars, right map); range of C.p. ssp. vulcanicus (left map).

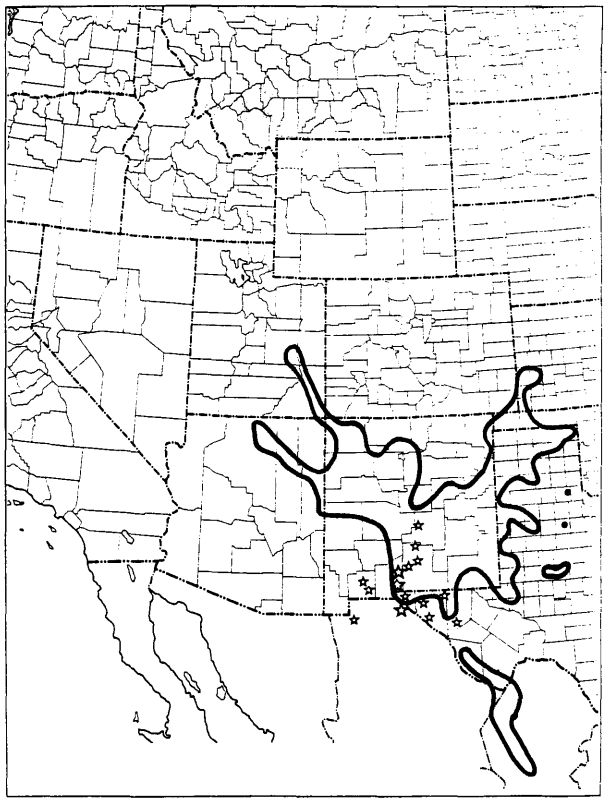


Figure 25.--Range of Chrysothamnus pulchellus ssp. baileyi (dots and loops); range of C.p. ssp. pulchellus (stars).

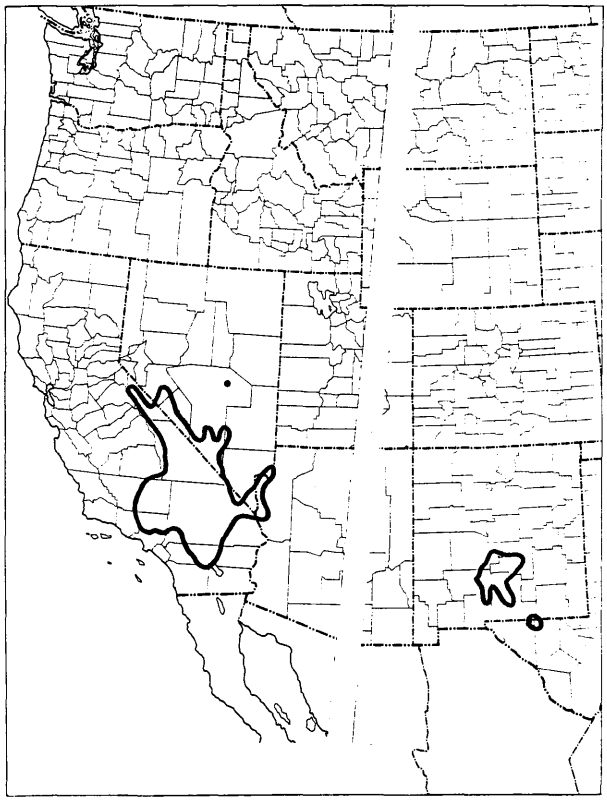


Figure 26.--Range of Chrysothamnus spathulatus (right map); range of C. teretifolius (left map).

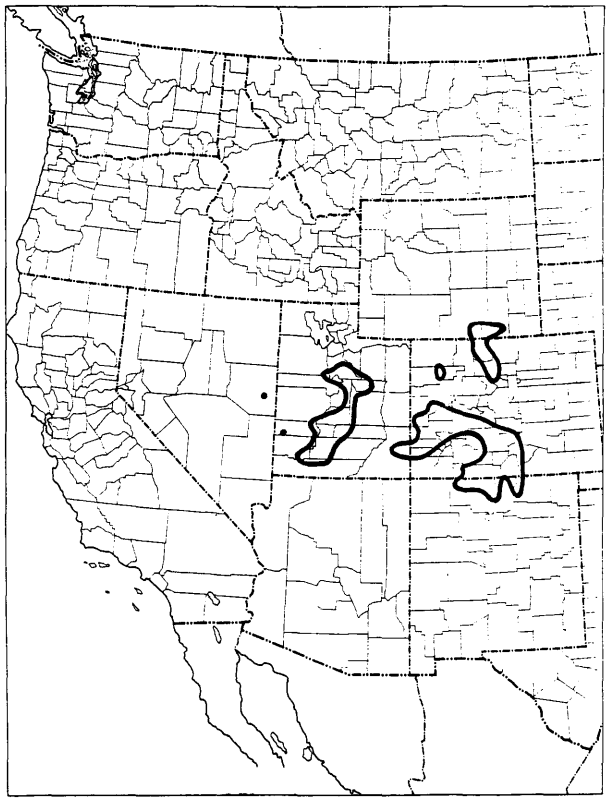


Figure 27.--Range of Chrysothamnus vaseyi.

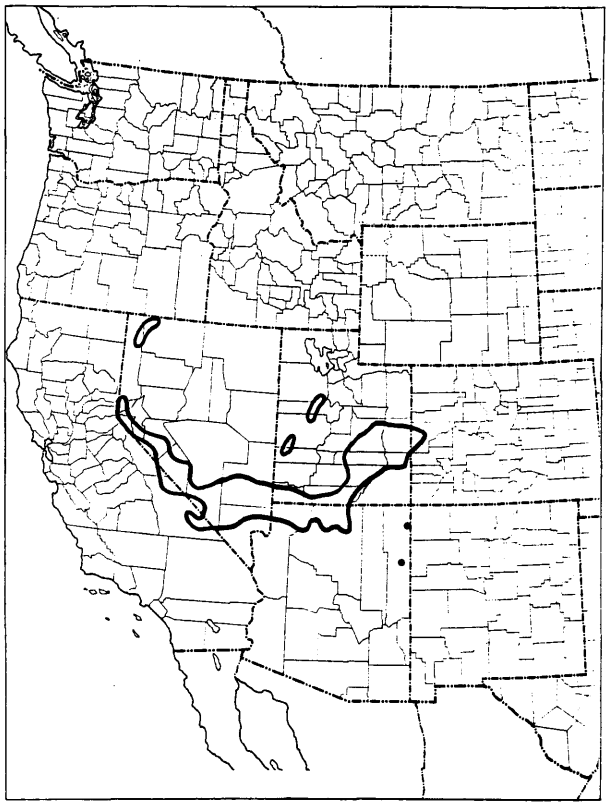


Figure 28.--Range of Chrysothamnus viscidiflorus ssp. axillaris.

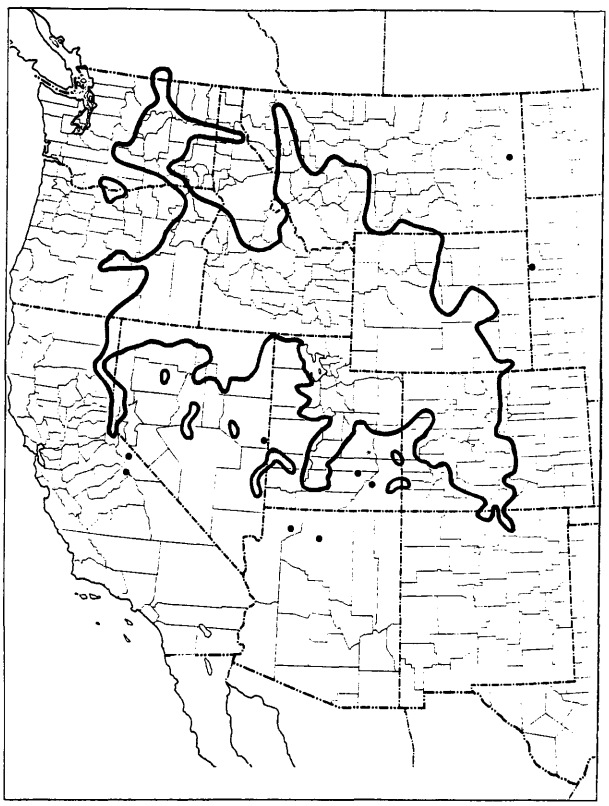


Figure 29.--Range of Chrysothamnus viscidiflorus ssp. lanceolatus.

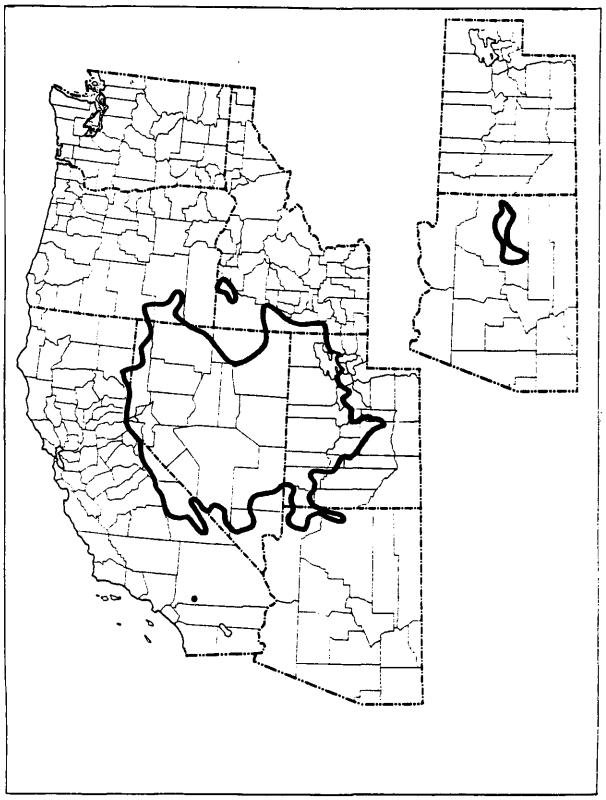


Figure 30.--Range of Chrysothamnus viscidiflorus ssp. planifolius (upper right map); range of C.v. ssp. puberulus (lower left map).

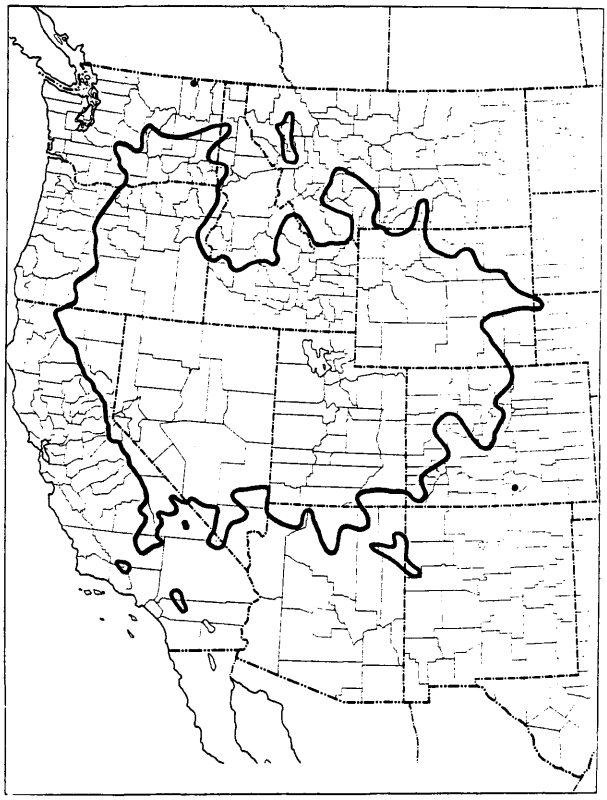


Figure 31.--Range of Chrysothamnus viscidiflorus ssp. viscidiflorus.

FRINGED SAGEBRUSH (ARTEMISIA FRIGIDA)--A NEGLECTED FORAGE SPECIES OF WESTERN RANGES

Allen Y. Cooperrider and James A. Bailey

ABSTRACT: Fringed sagebrush (Artemisia frigida) is widely distributed on western rangelands. While some consider it a pest species, many others consider it a valuable forage species. Data on food habits and forage preference of four wild ungulates on common range in southern Colorado suggest that it is preferred forage during all seasons except summer. The species spreads and reseeds itself well and has high resistance to grazing at the population level. Artemisia frigida has potential for use in grazing systems and in reseeding and rehabilitation. Range managers should be cautious about attempting to control or eradicate fringed sagebrush.

INTRODUCTION

Fringed sagebrush (Artemisia frigida) is one of the least understood shrubs and half-shrubs of the genus Artemisia in North America. In spite of increasing evidence of its great potential as a forage plant for livestock and big game, it continues to be studied very little. The species is so enigmatic that it seems to defy most traditional classifications. It is considered a forb by some researchers (Currie and others 1977) and a shrub by others (Dietz 1972). It is considered a pest species by some (Alley 1972), yet others report it to be a highly valuable forage species in areas as widely separated as Texas (Vines 1960), Montana (Spang 1954), and Mongolia (Anisimova and Ojun 1974). Furthermore, it seems to have physiological characteristics typical of both cool season and warm season plants (Williams and Markley 1973). Finally, although it is considered an increaser, invader, or indicator of overgrazing by many (Vines 1960; Sabo and others 1979), individual plants are quite susceptible to heavy grazing (Trlica and others 1977). In fact, populations of the species decrease or remain stable under certain grazing treatments (Jones 1965; Smith 1967).

This paper will review literature of the ecology, forage value, and response to grazing of fringed sagebrush, and suggest some explanations for the seemingly contradictory evidence in the literature. We will also discuss management and research implications of these explanations.

Paper presented at the Symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

Allen Y. Cooperrider is a wildlife biologist with the U.S. Department of the Interior, Bureau of Land Management, Denver, CO. James A. Bailey is a Professor of Wildlife Biology with the Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO.

ECOLOGY

Distribution

Fringed sagebrush is probably one of the most widely distributed and abundant species of its genus, with a range that extends from Mexico northward through most of the western United States and Canada into Alaska and from there to Siberia, Northern Asia, and Europe (Dayton 1937).

Habitat Sites

Fringed sagebrush is a common plant of the high plains along the eastern slope of the Rocky Mountains from Alberta and Saskatchewan south to northern New Mexico. It also occurs in the low semidesert valleys, mesas, and mountains of the Rocky Mountain and intermountain regions up to elevations of over 9,000 ft. (3 000 m) (Dayton 1937).

In the intermountain region, the species is dominant in dense stands along shallow depressions that collect moisture and floodwaters from summer rains. However, it also grows in lower density on slopes, foothills, and mountainsides intermixed with a variety of grasses, forbs, and shrubs (Dayton 1937).

The species occupies a fairly wide variety of sites, but grows most typically in full sunlight on dry, porous, coarse, gravelly, sandy, or shallow loam soils (Dayton 1937).

Growth and Reproduction

Growth of fringed sagebrush is not particularly rapid and it is not therefore considered an outstanding forage producer in terms of volume per plant. It typically does not grow over 24 inches (60 cm) high. Furthermore, grazing of individual plants results in decreased height growth (Trlica and others 1977; Savchenko 1973). This response is advantageous under moderate and heavy grazing pressure and thus, like other low-growing species such as blue grama (Bouteloua gracilis), fringed sagebrush has a selective advantage under heavy grazing pressure when growing in mixtures with taller grasses and forbs. The low growth form also

results in many plants being covered with snow and thus unavailable on winter ranges where taller shrubs are subjected to heavy browsing pressure from wild and domestic ungulates.

The most outstanding feature of fringed sagebrush is its tremendous reproductive potential. The species produces an abundance of very small seeds and can also multiply from rootstocks (Dayton 1937). Fringed sagebrush produces over 4 million seeds per pound, far in excess of most other rangeland plants (Plummer and others 1968). Early germination tests indicated that fringed sagebrush germinated poorly at first, but viability of seed increased for several years (Wilson 1931). Recent tests, however, have shown that high germination can be achieved under a wide range of temperatures, but that germination is affected greatly by water stress (Sabo and others 1979). In summary, fringed sagebrush appears to produce a large amount of seed that can germinate well under optimum conditions yet can also remain viable in the soil for many years until favorable conditions are present.

FORAGE VALUE

Evidence is strong that fringed sagebrush is one of the better shrubs on western ranges in terms of forage value. The evidence comes from several sources: food habits and forage preference of animals, nutritional analyses, and in vitro and in vivo digestion trails.

Wildlife

Many studies report fringed sagebrush is a major component of seasonal diets of wildlife species. Using fecal analysis, Bailey and Cooperrider (1982) found that fringed sagebrush was the single most important species in the winter diet of bighorn sheep (Ovis canadensis), pronghorn antelope (Antilocapra americana), mule deer (Odocoileus hemionus), and elk (Cervus canadensis), and was also important in the spring and fall diets for these same four species on Trickle Mountain in southern Colorado (table 1). This information supports previous observations on the value of fringed sagebrush to wild ungulates.

Blood (1967) and Sugden (1961), using feeding site examinations as well as rumen analyses, reported that fringed sagebrush made up 35 to 63 percent of the winter diet of California bighorn sheep in British Columbia and that it was actively sought out by bighorn sheep in midwinter. Todd (1972) noted that fringed sagebrush was one of the most common species in the diet of Rocky Mountain bighorn sheep.

Hoefs and Cowan (1979) report that fringed sagebrush was the second most abundant species in the annual diet of Dall sheep (Ovis dalli), the most abundant from December through April. They further state that most researchers agree that whenever fringed sagebrush is an important component in the vegetation cover of a sheep range, it is also an important forage species.

Table 1.--Percentage of fringed sagebrush (Artemisia frigida) in the diets of wild ungulates on common range on Trickle Mountain, CO, as determined by fecal analysis (Bailey and Cooperrider 1982)[1]

Season	Bighorn sheep	Pronghorn antelope	Mule deer	Elk
Winter	55	68	35	48
Spring	22	43	30	14
Summer	4	26	tr	5
Fall	20	24	11	7

[1]The fecal analysis technique is designed to determine food habits at the genus level; however, fringed sagebrush can be distinguished from other species in the genus. It was the only Artemisia species found in any great abundance on Trickle Mountain. Slide readers reported that virtually all of the sagebrush in winter fecal samples were fringed sagebrush. However, small amounts of other sagebrush species were found in fecal samples at other times of the year and are included in the percentages above.

Fringed sage, along with other sages (Artemisia spp.), has also been reported as a common species in diets of pronghorn antelope. More importantly, there is evidence that it is a preferred species, i.e., its consumption is disproportionate to its composition on the range (table 2). Mitchell (1980) reports substantial

Table 2.--Pronghorn antelope preference indices for fringed sagebrush in a rabbitbrush community in Saguache County, CO (derived from data in Bear and others 1973)

Season	Percentage of fringed sage in diet (D)	Percentage of fringed sage on range (R)	Preference Index (D/R)
April-June	37	2	18.5
July-September	3	3	1.0
October-March	23	4	5.8

use of fringed sagebrush and suggests that "the role and importance of Artemisia tridentata in the diet of pronghorns south of latitude 49°N. is assumed by A. cana and A. frigida in the annual diets of pronghorns in Alberta."

Similarly, fringed sage has been reported as a common species in the spring diet of mule deer in northern Colorado (Lucich 1977). Using fecal analysis he found that fringed sagebrush made up 64 percent of the diet in April, 16 percent in May, and then dropped sharply to less than 2 percent from June through September (table 3). Sugden (1961) reported that mule deer diet contained 63 percent fringed sagebrush on a range in British Columbia. Currie and others (1977) reported that tame mule deer selected 13 percent fringed sagebrush in April, 2 percent in May, 7 percent in June, and less than 1 percent from July through August on the Manitou Experimental Forest in central Colorado.

Thus, several major wild ungulate species in North America make considerable use of fringed sagebrush on ranges where it is present. Furthermore, evidence suggests that they actively seek the species. Bison (Bison bison) diets have been reported to contain over 20 percent of the species in March on heavily grazed shortgrass range in northern Colorado (Peden 1976). Mountain goats (Oreamnos americana) not only eat large quantities of it, but also appear to prefer it in winter where it is available (Adams 1981). The other major ungulates in North America, moose (Alces americana), caribou (Rangifer tarandus), white-tailed deer (Odocoileus virginiana), and muskox (Ovibos moschatus), probably do not make much use of it because their geographic distribution and habitat preferences are such that they do not occupy ranges where it is abundant.

Livestock

Studies also show that fringed sagebrush is highly palatable and nutritious for livestock. Dayton (1937) reported that the forage value of the species is highest in the Southwest where it rates fairly good in palatability for cattle and very good for sheep and goats, especially during the winter and spring. It is highly prized as sheep feed during the lambing season. He also reported that the species is considered practically worthless on the cattle ranges of the northern plains and prairies except during the late fall and winter. On the other hand, Macoun (1877), in early explorations of the Northwest, reported that fringed sagebrush was important winter feed for cattle throughout upper British Columbia and the dry Northwest, and that local stockmen often preferred it to

Table 3.--Percentage of fringed sagebrush in the diet of various North American wild and domestic ungulates by month and/or season

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Source
Cattle					20	23	0	4	9	--	9		Malechek (1966)
Cattle						2	1	5					Vavra and others (1977)
Domestic sheep		----60---											Spang (1954)
Bighorn sheep	-------55-------			-------22------			--------4--------			-------20--------			Bailey and Cooperrider (1982)
Pronghorn antelope	-------68-------			-------43------			-------26--------			-------24--------			Bailey and Cooperrider (1982)
Pronghorn antelope	-------23-------			-------37------			--------3--------			-------23--------			Bear and others (1973)
Mule deer	-------35-------			-------30------			--------tr-------			-------11--------			Bailey and Cooperrider (1982)
Mule deer					34	1	tr	tr	tr				Lucich (1977)
Elk	-------48-------			-------14------			--------5--------			--------7--------			Bailey and Cooperrider (1982)

cured grass or hay because it maintained livestock in "sleek and fat" condition even in the dead of winter.

More recent food habit studies tend to confirm the value of fringed sagebrush to livestock. Spang (1954) reported that the average diet of domestic sheep on a spring foothill range in Montana was 60 percent fringed sage in February and March on an area where the species was estimated to comprise less than 1 percent of the plant cover. Similarly, Malechek (1966) noted that the diet of cattle grazing native ponderosa pine/bunchgrass ranges on the Manitou Experimental Forest in Colorado consisted of up to 20 percent fringed sagebrush. Cattle diets on these ranges, however, contained less than 3 percent fringed sagebrush for the period from June through mid-August; the percentage rose to about 10 percent through December (table 3). In 1974 and 1975, Currie and others (1977) grazed the same areas with tame mule deer and found that they ate less fringed sagebrush than cattle although the seasonal pattern was similar (table 3). The techniques used may partly account for the lower utilization by mule deer. There is evidence that tame animals may select less fringed sagebrush. Schwartz and Nagy (1976) found that tame pronghorn ate significantly less fringed sagebrush than wild pronghorn from the same area. Vavra and others (1977) reported that esophageally fistulated cattle had a very low preference for fringed sagebrush during summer (table 3).

In summary, fringed sagebrush is not only important to wild ungulates, but also is a preferred species for domestic sheep and possibly even cattle during spring and fall. Evidence of the value of such forage for either wild or domestic ungulates does not appear to be an artifact of the technique used to estimate food habits; data are reported from studies using fecal analyses, rumen analyses, fistulated animals, feeding site examinations, range sampling, and tame animal observations.

Unfortunately, no comprehensive studies of nutritional value have been made. Proximate analyses of the species show that it has relatively high levels of crude protein (table 4). In fact, Anisimova and Ojun (1974) indicate it is one of the best protein sources for domestic sheep on Mongolian pasture lands, exceeding the major grass species of the region. However, numerous studies have shown that volatile oils in browse species, particularly conifers and members of the genus Artemisia, can reduce both palatability and digestibility of plants, making such analyses of limited value (Nagy and others 1964; Longhurst and others 1968). However, see Welch (1983) for a discussion that minimizes the importance of volatile oils in the digestive processes of animals that eat big sagebrush. Nutritional analyses that utilize in vivo or in vitro digestibility are better measures in that they can integrate such factors and thus provide a measure of how much actual energy or nutrients an animal can receive from the forage.

Table 4.--Proximate analysis of fringed sagebrush (from Anisimova and Ojun 1974)

Month/stage	Ash	CP	EE	CF	NFE
		Percent			
June: vegetative	17.4	21.3	2.4	24.6	34.3
July: floral shoots forming	7.4	11.9	3.2	32.3	45.2
September: full bloom	8.7	10.1	3.6	35.7	41.9
October: dormant	7.7	8.8	4.9	39.0	39.6

The few studies using such techniques suggest that fringed sagebrush is high in dry matter digestibility (DMD), digestible energy (DE), and digestible protein (DP). Dietz (1972) reported that DMD was 59.5 percent, which was higher than six other shrub species. Values for DE and DP reported by Taylor (1972) and Cook and others (1977) are somewhat inconsistent, but tend to be higher than those for other forages. Cook and others (1977) reported DE values for fringed sagebrush ranging from 2275 kcal/kg for winter to 3473 kcal/kg for spring. By comparison, the same authors report DE values for alfalfa ranging from 2336 kcal/kg in summer to 4312 kcal/kg in spring.

The overall evidence from food habits, preference indices, and nutritional analyses is that fringed sagebrush is a highly palatable, digestible, and nutritious forage that is preferred by many domestic and wild species during all seasons except summer.

RESPONSE TO GRAZING

The response of fringed sagebrush to grazing will be considered in terms of individual plant response and then in terms of population response.

Individual Plants

Trlica and others (1977) studied the effects of defoliation on individual fringed sagebrush plants by clipping 90 percent of the current annual growth during four phenological stages: quiescence (November 5-20), early growth (April 15-20), rapid growth (June 1-10), and near maturity (August 1-15) on the Central Plains Experimental Range in northern Colorado. All treatments resulted in significant reductions in seed stalk length, live crown coverage, and

herbage yield even after a minimum of 14 months of rest (table 5). Clipping was most detrimental during rapid growth (June).

Buwai and Trlica (1977) studied the effects of multiple defoliation of fringed sagebrush on the same area by clipping individual plants at two different intensities (60 and 90 percent of current annual growth removed) and at three phenological stages: quiescence (late October), rapid growth or flowers developing (early June), and near maturity (early August). All treatments resulted in reduction in live crown cover, plant height, live crown diameter, plant vigor, and herbage yield.

The limited evidence available suggests that individual plants are quite sensitive to grazing pressure and quite slow to recover.

Plant Populations

Sarvis (1923), Dayton (1937), and Klipple and Costello (1960) all reported that fringed sagebrush is considered an indicator of overgrazing on the northern Great Plains and in the northwestern United States and British Columbia. However, there is contradictory evidence from other areas and studies. Sarvis (1941), working on the northern Great Plains, reported that the species increased greatly during the first 10 years of heavy grazing but diminished in the next 15 years. After 25 years, density was similar to that on lightly grazed ranges. Demarchi and others (1968) noted that on the Bull River bighorn sheep winter range in British Columbia fringed sagebrush made up 8 percent of the cover of plant species on ranges with low accessibility to cattle whereas it was found in only trace amounts where accessibility was high. Jones (1965), on the other hand, reported that fringed sagebrush decreased significantly under winter elk grazing, but appeared to increase under summer cattle grazing. Johnson (1956) studied pastures that had been grazed from 1941 to 1950 on the Manitou Experimental Forest in southern Colorado at heavy, moderate, and light intensities, as well as not grazed. Grazing occurred from June 1 to October 31 each year. He noted that the percentage composition, number of plants per plot, and forage yield of fringed sagebrush increased, as grazing increased from light to heavy. However, all three measures were higher under no grazing than under light or moderate grazing. In one of the best documented, long-term studies of grazing impacts on ranges with sagebrush, Smith (1967) analyzed 18 years of data from the Manitou Experimental Forest, including some reported previously by Johnson (1956). He found that neither percentage cover nor percentage composition of fringed sagebrush was significantly affected by summer cattle grazing.

Perhaps the most enlightening study of fringed sagebrush is that of Savchenko (1973) who measured the age structure as well as the percentage of cover on areas subject to varying levels of grazing pressure from domestic sheep. His data indicate that increased grazing pressure resulted in an increased number of individual plants of fringed sagebrush, accompanied by a shift in the population structure to young plants rather than middle-aged or older ones (table 6). The maximum total cover as well as percentage of fringed sagebrush occurred at intermediate levels of grazing.

Table 5.--Average seedstalk length, live crown cover, and herbage yield for plants of fringed sagebrush subjected to a single defoliation. Measurements made in the fall after defoliated plants had received 14 to 26 months of rest (from Trlica and others 1977)

Phenological stage when defoliated	Seedstalk length	Livecrown cover	Herbage yield
	cm	percent	g/plant
Control	22	74	4.8
Quiescence	7	15	1.8
Early growth	5	9	1.0
Rapid growth	3	3	0.7
Near maturity	4	12	1.5

Whereas individual fringed sagebrush plants are quite sensitive to grazing pressure, populations are not. The study conducted by Savchenko (1973) suggests that under increased grazing pressure, populations of fringed sagebrush respond by producing more young plants.

DISCUSSION

The enigmatic character of fringed sagebrush may be examined by considering how it fits into the traditional dichotomy of decreaser versus increaser or invader species. In simplified form, decreasers are plants characterized by high palatability, limited ability to spread or reseed, and limited resistance to heavy selective grazing. Increasers, on the other hand, are less palatable, spread easily either by seed or vegetatively, and have a higher resistance to grazing. Invaders may be considered an extreme category of increasers. We will discuss each of these characteristics in relation to fringed sagebrush.

Table 6.--Age structure and percentage cover of fringed sagebrush populations on pastures subject to different intensities of grazing (from Savchenko 1973)

	Intensity of Grazing				
	Light	Moderate	Strong	Very Strong	Semi-denudation
Number of plants per plot by age class					
Young	4	8	13	20	79
Middle-aged	18	43	51	38	1
Old	18	9	8	18	1
Total	40	60	72	76	81
Percentage cover of fringed sagebrush	25	45	40	35	27
Total cover (all species)	40	60	60	50	30

Palatability

The evidence is strong that fringed sagebrush is a highly palatable, nutritious, and preferred shrub on most parts of its range during all seasons except summer for wild ungulates and domestic sheep. However, it is frequently stated that it is unpalatable and of little value to cattle in the Northwest and northern Great Plains.

Two hypotheses can be used to explain the apparent difference in forage value from region to region. First, the traditional explanation is that there is significant ecotypic or subspecific variation in the species with regard to palatability. Considering the great variation within big sagebrush (A. tridentata) that has been documented in the last 20 years (McArthur and Plummer 1978; McArthur 1979), and the substantial variation in palatability between big sagebrush subspecies, this theory deserves further investigation.

There is a second explanation, however, that does not require hypothesizing geographic or taxonomic variation. This is that fringed sagebrush is highly palatable relative to other forages during all seasons except summer, and that the evidence for lack of palatability is based on experience with summer cattle grazing. When one compares the percentage of fringed sagebrush in the diets of cattle reported by Vavra and others (1977) and Malechek (1966) with those of other wild and domestic ungulates (table 3), the pattern is not that different; cattle food habit data are simply not available for many ranges with fringed sagebrush for seasons other than summer.

Both theories are useful in that they can be easily tested. A systematic study of geographic variation in palatability, preference, and nutritional value of fringed sagebrush, combined with a taxonomic study, could determine the degree to which subspecific or ecotypic variation is responsible for any measurable geographic variation in forage quality. Similarly, year-round studies of food habits and forage preferences of cattle and sheep on fringed sagebrush ranges could determine the value of the species to livestock at times other than summer.

In any case, fringed sagebrush appears to be highly palatable at most times of year to most animal species, and in this respect is a typical decreaser species.

Establishment

Fringed sagebrush has a high ability to spread, reseed itself, and/or invade new areas. There is no evidence to contradict the assertion that the species may rapidly invade or increase on ranges heavily grazed by cattle in summer. The wide ecological amplitude of the species combined with its tremendous seed production and prolonged seed viability make it a formidable competitor on areas that have been opened up by

grazing or other disturbance. There is little question that fringed sagebrush behaves like an increaser or even an invader species.

Resistance to Grazing

At least some populations of fringed sagebrush appear able to remain stable or increase under heavy grazing pressure. On the other hand, individual plants are quite susceptible to heavy defoliation. The explanation appears to be in the population response shown by Savchenko (1973). The evolutionary "strategy" of fringed sagebrush appears to be to produce large amounts of viable seed rather than to develop resistance to grazing. Moderate to heavy grazing thus has the effect of shifting the age structure of the population to younger age classes without necessarily reducing the density of plants or the total cover. This type of density dependent increase in reproductive success has been reported and studied in many animal populations and is the basis for many wildlife management practices. Such a response has not been as well documented or studied in plant populations, and population dynamics approaches are not commonly utilized in range management in North America.

It is interesting to speculate as to the degree to which such a reproductive strategy is tied to seasonal unpalatability. Given that seedling establishment is a critical time period in the life history, one could predict that there would be tremendous selection for factors that would make seedlings unpalatable during their first few months; this selection pressure would be highest in plant species with a high reproductive rate. The role of volatile oils in reducing palatability and digestibility of plants has already been mentioned. Nagy (1966) noted that there were seasonal changes in volatile oil content of fringed sagebrush as well as big sagebrush and black sagebrush (A. nova), with the highest content in August and the lowest in April. A pattern like this would have the advantage of providing increased protection from grazing during the critical times when seed production is occurring, and when seedling establishment is at a peak.

In any case, the relative unpalatability of fringed sagebrush in summer confers a great advantage under a pattern of summer grazing by livestock and may explain the apparent inconsistencies in the literature. For example, the increase of fringed sagebrush under summer cattle grazing and decrease under winter elk grazing as reported by Jones (1965) could be explained by unpalatability during summer even in the absence of variation in preferences among animal species.

The overall pattern then is that fringed sagebrush is a species with high palatability (except during summer), good ability to spread and reseed, and high resistance to grazing at the population level. Such a species defies classification as either an increaser or decreaser, but seems to have the best characteristics of each. These properties make it a highly desirable species to have on the range except where summer forage is the primary factor limiting production of wildlife and/or livestock. On many western ranges, however, production of wildlife and livestock is primarily limited by the availability of quality forage at other times of year. Thus, fringed sagebrush may prove to be a far more valuable forage than is now recognized. It seems desirable to conduct research to test some of the conjectures of this paper and to develop optimal grazing systems for ranges with fringed sagebrush for the benefit of both livestock and wildlife. The species would also appear to be a likely candidate for reseeding in many areas, although Plummer and others (1968) do not give it a particularly good overall rating for reseeding suitability for Utah.

The evidence presented here also suggests that range managers should be cautious about embarking on programs aimed at eradicating the species, as proposed by Alley (1972). First, control may be difficult due to the high rate of seed production and prolonged viability of seed. Second, drastic reduction in the density of the species may be quite detrimental to wild ungulates in an area if they are relying on fringed sagebrush for fall, winter, or spring forage. Third, if field managers increased spring or fall livestock grazing, there may be opportunities for utilizing rather than eradicating the resource. Finally, if range managers determine that eradication or reduction of fringed sagebrush is desirable, they should consider whether it might be easier and cheaper to do so through the use of sheep, goats, or other ungulate species through fall and/or winter grazing rather than embarking on an expensive program of herbicide application and/or mechanical control followed by reseeding.

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ARTEMISIA TRIDENTATA SSP. SPICIFORMIS: DISTRIBUTION AND TAXONOMIC PLACEMENT

E. Durant McArthur and Sherel K. Goodrich

ABSTRACT: Subalpine big sagebrush (Artemisia tridentata ssp. spiciformis) is widely distributed and occurs in large uniform stands in several areas. It is probably a stabilized hybrid from A. tridentata ssp. vaseyana and A. cana ssp. viscidula parental stock. Several large populations (up to 750 acres [about 300 ha] in size) are mapped.

INTRODUCTION

Subalpine big sagebrush (Artemisia tridentata Nutt. ssp. spiciformis [Osterhout] Goodrich & McArthur) is found in mountains of central and north-central Colorado, west-central Wyoming, southeastern Idaho, and central and north-central Utah (fig. 1). In Utah these plants have been referred to as A. rothrockii A. Gray. Both Ward (1953) and Shultz (1983) maintained that A. rothrockii is restricted to California. The Utah materials are clearly referable to the type specimen of A. spiciformis which taxon was named and described by Osterhout (1900) from materials collected in North Park, CO.

In the original description of A. spiciformis, Osterhout (1900) described the plants as having the heads of A. cana Pursh and the leaves of A. tridentata. To this comparison we add: with the sprouting feature and the small, multistemmed habit of A. cana ssp. viscidula, but forming communities on upland montane, well-drained sites; sites similar to those occupied by A. tridentata ssp. vaseyana (Rydb.) Beetle.

Beetle (1959) made the combination Artemisia tridentata ssp. vaseyana forma spiciformis. However, with the head size, sprouting feature, and growth form of A. cana, we feel the plants are too closely aligned with A. cana, or at least too different from A. tridentata ssp. vaseyana to be considered a form of that taxon. In addition, the size of the heads and number of flowers per head are more like those of A. cana than something intermediate between A. cana and A. tridentata. We feel that plants of A. tridentata ssp. spiciformis exhibit a unique set of features and represent a distinct taxon that is more sharply defined than several other sagebrush taxa.

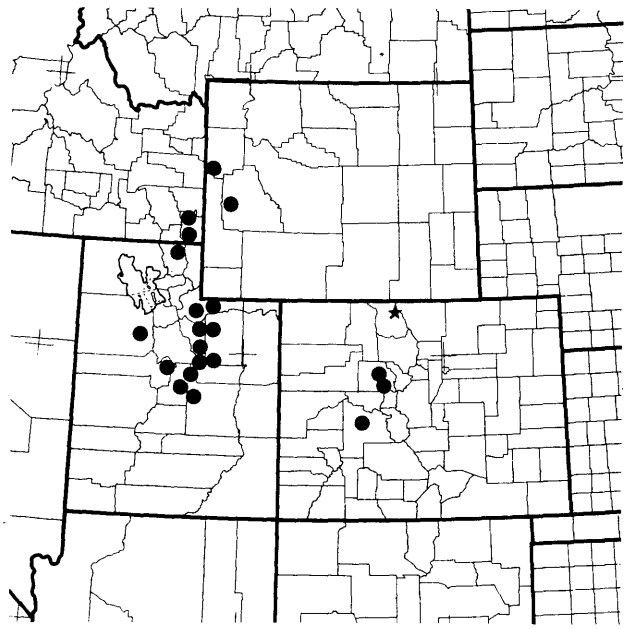


Figure 1.--Dot map distribution of populations of subalpine big sagebrush (A. tridentata ssp. spiciformis). Locations are from Goodrich and others (1985). Star is type location.

Teeth or lobes on persistent leaves are the most obvious and about the only morphological features by which A. cana and A. tridentata are distinguished in taxonomic works. Based on this feature and the habitat, we have placed A. spiciformis as a subspecies of A. tridentata (Goodrich and others 1985).

Implications of a hybrid origin (involving A. cana and A. tridentata) are strong. However, we feel these plants represent a taxon as distinctive as many other Artemisia taxa. Other recognized Artemisia taxa are also thought to be of hybrid

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E. Durant McArthur is Supervisory Research Geneticist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT. Sherel Goodrich is Range Conservationist, Ashley National Forest, Forest Service, U.S. Department of Agriculture, Vernal, UT.

origin. For example, A. tridentata ssp. wyomingensis has been suggested to have been derived from A. tridentata ssp. vaseyana x A. tridentata ssp. tridentata or A. tridentata ssp. x A. nova (Beetle and Young 1965; McArthur 1983); A. rothrockii (in the narrow California sense) has been suggested to have been derived from A. arbuscula x A. tridentata (Ward 1953.)

The purpose of this paper is to supplement our formal recognition of A. tridentata ssp. spiciformis (Goodrich and others 1985) by documenting the occurrence of large uniform populations of this taxon. And, to locate the A. tridentata ssp. vaseyana and A. cana ssp. viscidula plants nearest each population. One concept of the taxon is that of an incidental hybrid of limited significance (Shultz 1983).

POPULATIONS OF SUBALPINE SAGEBRUSH

The subspecies occurs in the mountains of several western states (fig. 1). The populations listed in table 1 are free of one or both putative parents. Each population is mapped (fig. 2). We believe the size and the number of these large populations are compelling evidence that the plants are self sustaining and the taxon valid.

There are other populations that bear on the question of the independence of the taxon. A population, probably less than 5 acres (2 ha) in size, on the Stansbury Mountains, Tooele County, UT (Tye 1259, BRY)[1] is adjacent to populations of A. tridentata ssp. vaseyana but is separated by nearly 50 miles (80 km) from the nearest known population of A. cana.

Other smaller populations of subalpine sagebrush include some in Colorado on the Eagle River near Minturn (Osterhout 3370 and 3384, RM; McArthur 1428 and 1431, SSLP) and at North Park--the type location (Osterhout 2011 and 2255, RM; McArthur 1434, SSLP). Although these populations are smaller, they are, nevertheless, composed of distinctive ssp. spiciformis plants. Plants in these Colorado populations are adjacent to A. tridentata ssp. vaseyana plants, but further removed from A. cana ssp. viscidula plants. The ssp. spiciformis plants in these locations showed no visible evidence of introgression with either putative parent.

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Table 1.--Some large Utah populations of subalpine big sagebrush (A. tridentata ssp. spiciformis)

Population	Approximate size[1]	Elevation[1]	Approximate distance from populations of: A. cana ssp. viscidula	Approximate distance from populations of: A. tridentata ssp. vaseyana
	Acres	Feet		
Wolf Creek Summit[2], Wasatch Co.	750	9,300	2 miles[1]	Adjacent to
Whitney, Summit Co.	550	9,300	Near at the lower end but wholly free for the length of the population (ca. 3 miles)	Adjacent to the lower end but free for 2 miles at the upper end.
Mansfield Meadows[3], Summit Co.	135	10,500	1 mile	1 mile
Bald Mountain Summit Co.	25	10,600	2 miles	2 miles
Olsen Bench[3], Sanpete Co.	500	10,400	4 miles	1 mile

[1]Conversions: acre = 0.405 ha; ft = 0.305 m, mi = 1.61 km.
[2]Isolated from A. cana by conifer and aspen forest.
[3]Isolated from both A. cana and A. tridentata ssp. vaseyana by conifer forest.

[1]Collection number and herbarium of deposit. Herbaria abbreviations: BRY = Brigham Young University, RM = University of Wyoming, SSLP = Shrub Sciences Laboratory.

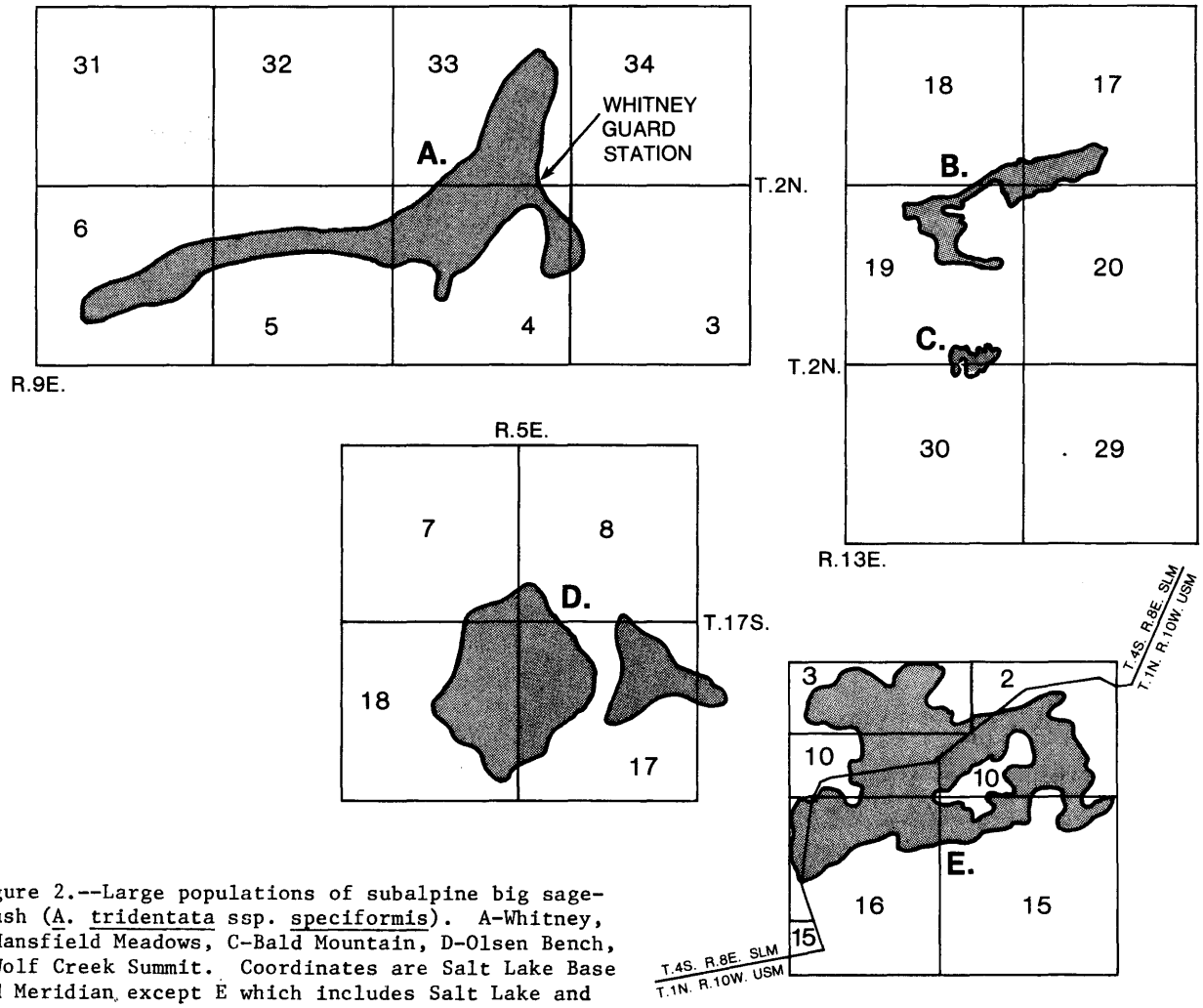


Figure 2.--Large populations of subalpine big sagebrush (A. tridentata ssp. speciformis). A-Whitney, B-Mansfield Meadows, C-Bald Mountain, D-Olsen Bench, E-Wolf Creek Summit. Coordinates are Salt Lake Base and Meridian, except E which includes Salt Lake and Uintah meridians. Map D is adapted from Ellison (1954). All other maps are original. Authors visited all populations.

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HABITAT RELATIONSHIPS OF SANDSAGE (ARTEMISIA FILIFOLIA) IN SOUTHERN UTAH

Lars L. Rasmussen and Jack D. Brotherson

ABSTRACT: Ten populations of sandsage in Washington County, UT, were paired with 10 adjacent populations for comparison studies of vegetation and soil nutrient components. Perennial grasses and forbs were much more abundant in the sandsage communities than in the adjacent desert types, although species diversity was lower. Several species were common to both types. With the exception of copper, soil nutrients were significantly lower on the sandsage sites. Indications are that sandsage has adapted to habitats of low fertility. This did not appear to affect the nutrient quality of sandsage as its nutrient content was found to be comparable to other shrubs.

INTRODUCTION

Sandsage (Artemisia filifolia Torr.) is likely the most widespread shrub species occurring on sand dunes and sandhills (McArthur and others 1979) in the southern Black Hills of South Dakota, Wyoming, Colorado, Nebraska, Kansas, Texas, Utah, Arizona, and Nevada (McKean 1976). Despite its widespread distribution, little research has been published concerning this species. Recent research has concerned landscape potential and propagation (Tipton and McWilliams 1976 and 1977), physiology (Hoehne and others 1968; Torrance and Steelink 1974), eradication (McIllvain and Armstrong 1963; Scifres and Polk 1974), and faunal associates (Cannon and Knopf 1981; Miller and Kevan 1979).

There is a lack of information concerning the ecology of sandsage. The purpose of this study is to describe the habitat and ecological relationships of selected sandsage populations in comparison to adjacent vegetation types in southern Utah.

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Lars L. Rasmussen is Range Conservationist, Ellensburg Field Office, U.S. Department of Agriculture, Soil Conservation Service, Ellensburg, WA; Jack D. Brotherson is Professor of Botany and Range Science, Brigham Young University, Provo, UT.

STUDY AREA

Sandsage communities in Washington County (fig. 1) are generally associated with deep sand deposits. These deposits are formed by the weathering of Navajo, and possibly Kayenta, sandstone formations.

Sandsage is the dominant overstory component within its community. The understory is composed primarily of annuals with a few sand-loving perennial forbs and grasses. Adjacent vegetative communities vary, but they are predominantly blackbrush stands associated with shallow coarse soils (Callison 1983).

The climate of the study area is characterized by mild winters and hot summers. Average annual temperatures range from 58° to 66 °F (14° to 19° C) with a frost-free period of 190 to 205 days. Most precipitation occurs in the form of rain and averages 8 to 10 inches (200 to 275 mm) annually. Precipitation falls primarily as gentle showers in winter and early spring, and as intense thunderstorms during July and August (Mortensen and others 1977).

METHODS

Ten populations of sandsage in Washington County, UT, were selected for study in June and July of 1984. Sites were selected that represented a cross section of conditions within the sandsage populations in the county. Sandsage sites were paired with sites in adjacent vegetation zones to help define the habitat requirements of sandsage.

Thirty-three (1-m^2) quadrats were stratified across each site in three 36-yard (33-m) parallel transects. Each quadrat was divided in fourths creating 132 quadrats per site. Total living cover was estimated in each quadrat. Frequency data from the quadrats were collected for exposed rock, bare soil, litter, cryptogams, trees, shrubs, perennial grass, annual grass, perennial forbs, annual forbs, and individual plant species.

Three soil samples were taken along each transect line at 33-foot (10-m) intervals from the top 8 inches (20 cm) of soil and later combined for laboratory analyses. This depth is considered adequate based on Ludwig's results

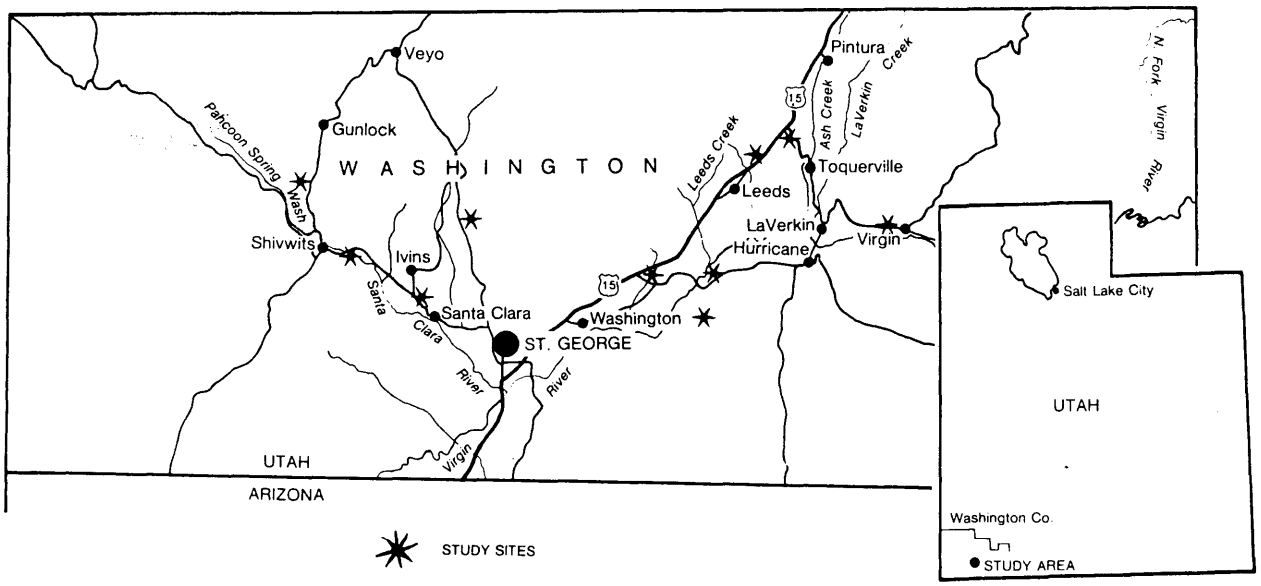


Figure 1.--Map of study site locations in Washington County, UT.

(1969) which show that the surface decimeter of soil yields 80 percent of the information useful in correlating plant response with concentrations of essential mineral nutrients in the soil. Supporting these results, Holmgren and Brewster (1972) show that greater than 50 percent of the fine roots of plants in desert communities are found in the top 6 inches (15 cm) of the soil profile.

Soil samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, cation exchange capacity, mineral composition, and organic matter. Soil pH was determined with a glass electrode pH meter. Soluble salts were determined with a Beckman electrical conductivity bridge. Exchangeable calcium, magnesium, potassium, and sodium were extracted with DTPA (diethylene triamine-penta-acetic acid (Lindsay and Norvell 1969). A Perkin Elmer Model 403 atomic absorption spectrophotometer was used to determine individual ion concentrations (Isaac and Kerber 1971). Phosphorus was extracted with sodium bicarbonate (Olsen and others 1954). Organic matter was estimated from total carbon using methods described by Allison (1965).

Cluster analysis based on Ruzicka's (1958) similarity index was used to group sandsage and adjacent communities. Individual species were also clustered on niche overlap values related to their geographical distribution patterns (Cowell and Futuyma 1971). Means and standard deviations were computed for all biotic and abiotic variables measured. Prevalent species were selected from frequency values using a procedure described by Warner and Harper (1972). Diversity indices were computed using the Shannon-Weaver index (Shannon and Weaver 1949). Interspecific association patterns were computed using Cole's (1949) index.

RESULTS AND DISCUSSION

Sandsage in southern Utah occupies aeolean deposits of sandy soil formed primarily by weathering of Navajo sandstone. There were several differences in edaphic factors in the sandsage and adjacent communities (table 1). Exposed rock and soil gravel levels were significantly higher on the adjacent sites. The sandsage soils had significantly less clay and organic matter than the adjacent site soils. With the exception of copper, nutrients were also less abundant in soils occupied by sandsage. The lower soil fertility of the sandsage habitat also resulted in a significantly lower cation exchange capacity. Tisdale and Nelson (1975) stated that soils with greater amounts of clay and organic matter generally have higher exchange capacities than more sandy soils. We found that where cation exchange capacities were low, percent clay and percent organic matter were also low. These results may indicate that sandsage is adapted to less fertile soils than are the species of adjacent communities. Possible explanations for sandsage survival in such areas include reduced mineral requirements for growth, increased ion exchange capacity of the root system, or the ability of sandsage to concentrate nutrients in its tissues to acceptable levels for growth.

Our data (table 2) indicate that sandsage accumulates mineral nutrients well above levels found in the soils in which it grows. Concentration ratios (plant/soil) ranged from a low of 5:9 for sodium to 484.2 for potassium. The high concentration ratios for potassium (484.2) and phosphorus (342.5) are not well understood. When the mineral content of sandsage tissue was compared with the mineral content of several other desert shrubs, the values were equivalent

Table 1.--Means ($\bar{x}$) and standard deviations (SD) for soil factors and significance levels for the difference of the means observed in sandsage and adjacent communities in Washington County, UT. Significance levels were computed using the Student's t-statistic

Soil factor	Sandsage		Adjacent	
	X	SD	X	SD
Bare soil %	94.0	4.9	80.8	27.2
Exposed rock %	5.5	8.0	53.0	31.0
Sand %	86.1	16.5	78.3	8.94
Silt %	7.7	16.4	11.47	0.58
Clay % ***[1]	4.12	1.09	9.73	5.42
Organic Matter % **	0.152	0.102	.305	0.138
pH	7.59	0.33	7.71	0.26
Soluble salts (ppm)	0.551	0.620	0.71	0.68
CEC (meq/100g) ***	4.76	3.61	10.13	4.17
Calcium (ppm) *	1128	1595	4720	7140
Magnesium (ppm) *	58.2	34.1	204	163
Sodium (ppm)	8.00	3.47	8.85	3.48
Potassium (ppm)	49.9	18.5	168.4	84.6
Iron (ppm)	9.16	9.14	12.5	11.6
Manganese (ppm)	4.55	3.2	8.24	8.11
Zinc (ppm)	0.433	0.220	0.377	0.194
Copper (ppm) **	0.195	0.580	0.0672	0.414
Phosphorus (ppm)	7.598	0.328	7.712	0.263

[1]Significance levels: * = 0.1; ** = 0.01; *** = 0.005.

Table 2.--Means and standard deviations (SD) for mineral nutrient concentrations in sandsage soils and sandsage tissue along with ratios of plant to soil concentrations

Nutrient	Mean soil concentrations	Mean plant concentrations	Plant/soil ratios
Calcium (ppm)	1128.00	7971.00	7.06
SD	±1595.00	±995.00	
Magnesium (ppm)	58.20	1874.00	32.19
SD	±34.10	±221.10	
Sodium (ppm)	8.00	47.70	5.96
SD	±3.50	5.85	
Potassium (ppm)	49.90	24,160.00	484.16
SD	±18.50	3,052.90	
Iron (ppm)	9.20	92.60	10.06
SD	±9.10	±29.80	
Manganese (ppm)	4.60	30.43	6.61
SD	±3.20	±9.55	
Zinc (ppm)	.43	23.80	55.34
SD	±.22	±3.37	
Copper (ppm)	.20	11.65	58.25
SD	±.58	±2.78	
Phosphorus (ppm)	7.60	2603.00	342.5
SD	±.33	±236.59	
Nitrogen (%)	.17	2.38	13.94
SD	±.07	±0.28	

(Fairchild and Brotherson 1980) and therefore would support the hypothesis that sandsage (in Washington County, at least) is adapted to soils of lowered fertility.

Forty-eight species were encountered in the sandsage communities, while 72 species were encountered in the adjacent communities. The large number of species on the adjacent sites was due to the variability in community types found adjacent to the sandsage communities. Of the 72 species, 18 were considered prevalents in the sandsage type and 19 were considered prevalents in the adjacent areas (table 4). A total of 40 species occurred in both sandsage and adjacent community types; this accounts for the relatively large diversity values (table 3). Though the species diversity measurements were high, the differences between the two vegetation types were not significant.

Vegetation differences between sandsage and adjacent communities are shown in table 4. Shrub frequency was significantly higher in the adjacent communities. Perennial grasses and forbs occurred with significantly greater frequency ($p < 0.025$) within the sandsage community type. Cryptogams had higher frequencies in the adjacent communities as did annual grasses and total cover. Annual forbs showed no differences. Davis and Bonham (1979) reported related findings that sandsage canopy afforded protection to needle-and-threadgrass (Stipa comata) thus increasing its frequency on some sites.

Cluster analysis (fig. 2) was used to group study sites of similar vegetation type. Seven of the 10 sandsage communities clustered together with similarity indices ranging from 27 to 62 percent. Two of the three remaining



Figure 2.--Cluster dendogram of sandsage and adjacent communities.

sandsage communities were associated with a group of four adjacent sites. This association resulted from a large number of understory species occurring in both sandsage and adjacent communities.

The final sandsage community did not cluster with the other groups and had a similarity of 17 percent to the previously described clusters. The relatively low association level of this stand with the other sandsage sites was due to the increased frequency on this site of burweed (Ambrosia acanthicarpa) and threadleaf eriastrum (Eriastrum sparsiflorum). Extreme fluctuation in abundance of annual species from site to site is common in desert ecosystems and in our case, is considered responsible for the three sandsage sites not clustering with the sandsage group.

To explore species interactions, clusters on niche overlap were done for all species found in both types. Two groups in this cluster were of particular interest with respect to the sandsage community. Sandsage clustered tightly with four perennial understory species: Indian ricegrass (Oryzopsis hymenoides), sand dropseed (Sporobolus cryptandrus), sand verbena (Abronia villosa), and California croton (Croton californicus). These species are all highly adapted to sandy habitats. Though sandsage was strongly associated with this perennial herbaceous understory, its overlap with the most prevalent annual species in the community was only 9 percent. These annuals include red brome (Bromus rubens), cutleaf filarea (Erodium cicutarium), cheatgrass (Bromus tectorum), cryptantha (Cryptantha spp.), and six-weeks fescue (Vulpia octoflora). Two understory shrub species, little rabbitbrush (Chrysothamnus viscidiflorus) and snakeweed (Gutierrezia sarothrae) were tightly clustered with these annuals. Other groups were defined but were mainly associated with the adjacent community types.

To define these relationships more precisely, we employed the use of Cole's (1949) index of interspecific association (fig. 3; table 5). Two groups of species were apparent from the analysis. Both groups contain a mixture of perennial and annual species. Each group contains species which show positive affinities for species within that group and negative relationships (table 5) for the species found in the opposite group. The two groups are bridged by a single species of Cryptantha which had the highest percent frequency values of any species in the study. Such high frequency (48.3 percent) indicates that this species was very widespread across the study sites.

The analysis has shown the existence of two groups of understory species and indicates that these species are doing quite different things with respect to the sand pocket environments of sandsage in Washington County. The underlying reasons for the groupings are unknown, but they may be due to differences in microhabitat preferences or competitive relationships existent among the species themselves. Further study at this point is warranted.

Table 3.--Prevalent species occurring in sandsage and adjacent communities in Washington County, UT. Values represent average percent frequency

Species	Sandsage $\bar{X}$	Adjacent $\bar{X}$
Ambrosia acanthocarpa	6.0	0.2
Artemisia filifolia	42.4	Ø
Artemisia tridentata	Ø	4.9
Astragalus nuttalianus	Ø	8.8
Atriplex canescens	*T	5.4
Brickellia spp.	4.7	1.2
Bromus rubens**	25.9	57.3
Bromus tectorum**	47.0	32.9
Chrysothamnus viscidiflorus	2.5	12.6
Coleogyne ramosissimum	Ø	22.0
Croton californicus	3.9	Ø
Cryptantha** spp.	48.3	22.3
Eriogonum spp.	4.6	0.4
Eriogonum enflatum	Ø	7.4
Eriophylum wallecii**	10.2	11.7
Erodium cicutarium**	16.6	13.7
Gilia inconspicuum	1.0	10.6
Hilaria jamesii	3.8	5.8
Larrea tridentata	Ø	3.9
Lupinus alpestrus	6.8	Ø
Oenothera pallida	4.2	0.3
Oryzopsis hymenoides	14.2	2.1
Phacilia rotundifolia	Ø	5.8
Plantago insularis	1.8	5.2
Prunus fasiculatus	3.3	0.2
Psorothamnus fremontii	4.7	1.2
Schismis barbatus	1.4	8.9
Sporobolus cryptandrus	16.9	0.9
Vulpia octoflora**	33.1	41.4
Gutierrezia sarothrae	4.7	16.7

*T = trace
** = Prevalent species in both sandsage and adjacent communities.

Table 4.--Means ($\bar{x}$) and standard deviations (SD) for vegetation factors and significance levels for the difference of the means observed in sandsage and adjacent communities in Washington County, UT. Significance levels were computed using the Student's t-statistic

Site factor	Sandsage		Adjacent	
	X	SD	X	SD
Total cover	24.2	6.93	31.8	11.42
Litter	89.7	8.81	86.7	27.90
Cryptograms	48.8	33.20	60.0	34.50
Shrubs***[1]	52.1	5.56	68.5	15.80
Perennial grass**	33.7	24.20	10.8	9.81
Annual grass	66.2	31.20	77.5	27.20
Perennial forbs*	19.2	22.50	3.9	4.34
Annual forbs	71.8	26.70	69.3	36.60
Diversity				
Shannon-Weaver's index	3.3	0.38	3.2	0.47
MacArthur's index	7.7	1.77	7.5	2.35

[1]Significance levels: * = 0.025; ** = 0.01; *** = 0.005.

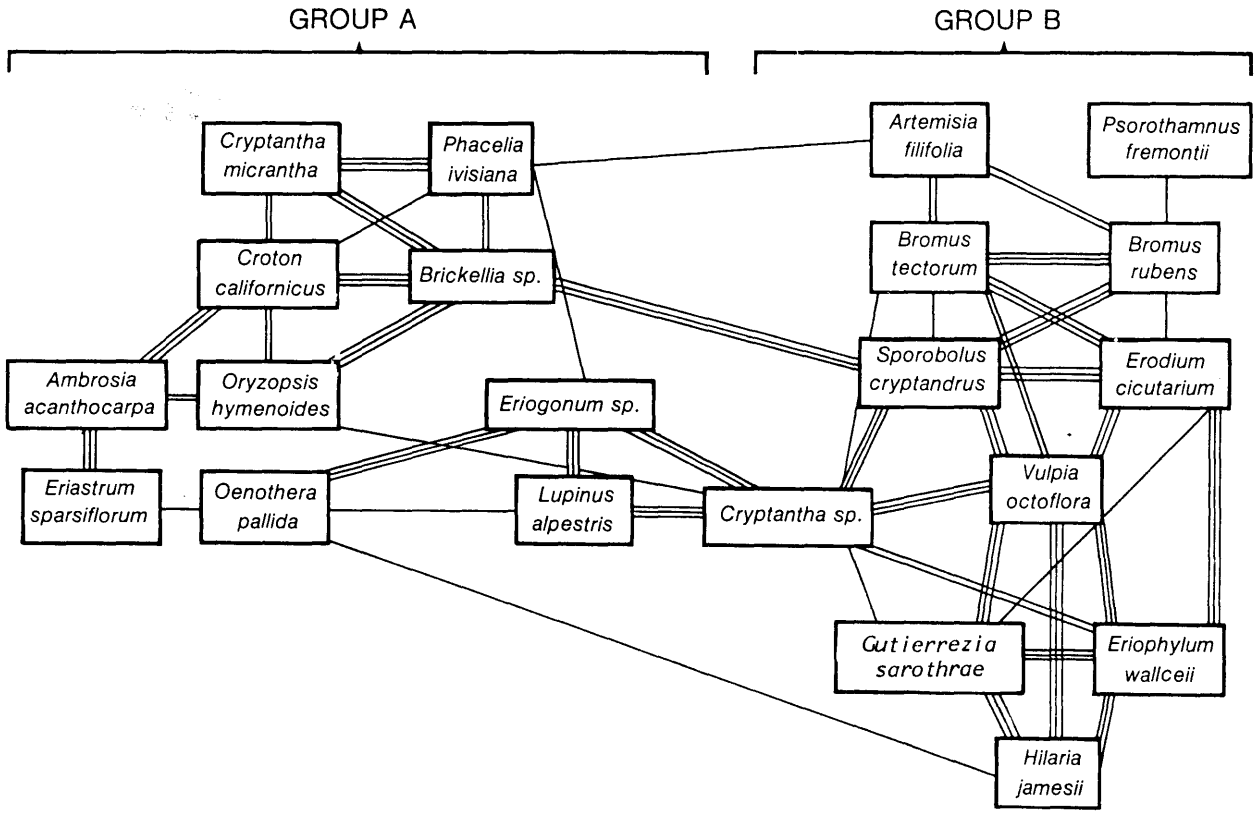


Figure 3.--Cluster diagram of positive interspecific associations between plant species occurring in the sandsage communities on Washington County, UT. Cluster is based on Cole's index of interspecific association and relates to species geographical distribution. The more lines between species, the more significant the association.

Table 5.--Results of Cole's index analyses with respect to the interspecific association patterns of species growing in the sandsage communities of Washington County, UT. Significance levels of the chi-square values are as follows: 0.05 = $p \leq 3.85$; 0.01 = $p \leq 6.64$; and 0.001 = $p \leq 11.21$

	Positive associations				Negative associations			
Species	Species	x^2	Coef.	SD	Species	x^2	Coef.	SD
				GROUP A				
Ambrosia acanthocarpa	Croton californicus	11.5	0.203	0.060	Bromus tectorum	36.3	0.752	0.125
	Eriastrum sparsiflorum	65.1	0.491	0.060	Cryptantha spp.	18.5	0.695	0.161
	Oenothera pallida	6.1	0.139	0.057	Erodium cicutarium	10.5	1.000	0.308
	Oryzopsis hymenoides	8.6	0.361	0.123	Sporobolus cryptandrus	8.3	0.704	0.244
					Vulpia octoflora	19.5	0.852	0.193
					Gutierrezia sarothrae	5.5	1.000	0.427
Brickellia sp.	Croton californicus	30.5	0.319	0.058	Bromus rubens	4.2	0.380	0.185
	Cryptantha micrantha	46.2	0.493	0.073	Bromus tectorum	10.7	0.394	0.121
	Oryzopsis hymenoides	14.1	0.446	0.119	Cryptantha spp.	7.4	0.425	0.156
	Phacelia iviciana	9.6	0.147	0.047	Erodium cicutarium	4.2	0.610	0.297
	Sporobolus cryptandrus	16.2	0.460	0.114	Eriastrum sparsiflorum	4.7	1.000	0.459
					Eriophyllum wallecii	6.0	1.000	0.407
					Vulpia octoflora	4.0	0.375	0.187
					Gutierrezia sarothrae	5.9	1.000	0.412
Croton californicus	Cryptantha micrantha	10.9	0.239	0.073	Cryptantha spp.	7.4	0.425	0.156
	Oryzopsis hymenoides	6.7	0.308	0.119	Erodium cicutarium	6.2	0.740	0.298
	Phacelia iviciana	5.8	0.114	0.047	Eriophyllum wallecii	6.0	1.000	0.407
					Vulpia octoflora	9.8	0.583	0.186
Cryptahntha micrantha	Phacelia iviciana	13.4	0.138	0.038	Cryptantha spp.	65.2	1.000	0.124
					Eriastrum sparsiflorum	7.5	1.000	0.365
					Eriogonum spp.	4.4	1.000	0.476
					Eriophyllum wallecii	9.5	1.000	0.324
					Hileria jamesii	4.6	1.000	0.465
					Lupinus alpestris	7.5	1.000	0.365
Eriastrum sparsiflorum	Oenothera pallida	4.8	0.118	0.054				
Eriogonum spp.	Lupinus alpestris	176.7	1.000	0.075	Oryzopsis hymenoides	6.6	0.723	0.291
	Oenothera pallida	8.7	0.206	0.070	Sporobolus cryptandrus	7.8	0.854	0.302
	Phacelia iviciana	4.1	0.123	0.060				
Lupinus alpestris	Oenothers pallida	4.8	0.118	0.054	Oryzopsis hymenoides	8.7	0.657	0.223
					Sporobolus cryptandrus	12.5	0.819	0.232
					Gutierrezia sarothrae	6.1	1.000	0.406
Oenothera pallida					Sporobolus cryptandrus	10.2	0.796	0.249
Oryzopsis hymenoides					Vulpia octoflora	7.2	0.244	0.091
Phacelia iviciana					Vulpia octoflora	7.0	0.602	0.228
				GROUP B				
Artemisia filifolia	Bromus rubens	7.7	0.102	0.037				
	Bromus tectorum	10.9	0.187	0.057				
	Phacelia iviciana	5.0	0.027	0.012				
Bromus rubens	Bromus tectorum	11.9	0.307	0.089	Cryptantha micrantha	18.2	0.629	0.147
	Erodium cicutarium	6.4	0.091	0.036	Oenothera pallida	5.8	0.470	0.195
	Psorothamnus fremontii	5.6	0.043	0.018	Phacelia iviciana	7.2	0.605	0.226
	Sporobolus cryptandrus	11.8	0.156	0.045				
Bromus tectorum	Cryptantha spp.	6.2	0.112	0.045	Croton californicus	6.2	0.301	0.121
	Erodium cicutarium	25.1	0.117	0.023	Eriogonum spp.	7.2	0.413	0.154
	Sporobolus cryptandrus	5.8	0.071	0.029	Eriastrum sparsiflorum	14.9	0.457	0.119
	Vulpia octoflora	9.8	0.117	0.037	Lupinus alpestris	12.1	0.412	0.119
					Oenothera pallida	4.9	0.282	0.127
					Phacelia iviciana	7.3	0.398	0.147
Cryptantha spp.	Eriogonum spp.	9.9	0.047	0.015	Eriastrum sparsiflorum	8.6	0.340	0.153
	Erophyllum wallecii	10.8	0.073	0.022	Phacelia iviciana	7.1	0.505	0.189
	Lupinus alpestris	8.7	0.058	0.019	Psorothamnus fremontii	6.1	0.482	0.195
	Oryzopsis hymenoides	4.5	0.084	0.040				
	Sporobolus cryptandrus	7.9	0.107	0.038				
	Vulpia octoflora	12.2	0.169	0.048				
	Gutierrezia sarothrae	6.2	0.054	0.022				
Eriophyllum wallecii	Hileria jamesii	57.9	0.306	0.040	Lupinus alpestris	6.2	1.000	0.400
	Sporobolus cryptandrus	8.6	0.293	0.099	Oryzopsis hymenoides	5.1	0.455	0.197
	Vulpia octoflora	63.0	1.000	0.126	Phacelia iviciana	4.1	1.000	0.497
	Gutierrezia sarothrae	41.3	0.366	0.057	Psorothamnus fremontii	3.9	1.000	0.509
Erodium cicutarium	Eriophyllum wallecii	19.4	0.186	0.042	Eriogonum spp.	6.9	1.000	0.381
	Sporobolus cryptandrus	41.5	0.470	0.073	Lupinus alpestris	11.7	1.000	0.293
	Vulpia octoflora	49.0	0.645	0.092	Oenothera pallida	5.2	0.714	0.314
	Gutierrezia sarothrae	4.7	0.091	0.042	Psorothamnus fremontii	7.2	1.000	0.372
Hileria jamesii	Oenothera pallida	12.6	0.242	0.068	Sporobolus cryptandrus	6.0	0.722	0.295
	Vulpia octoflora	30.6	1.000	0.181				
	Gutierrezia sarothrae	20.3	0.368	0.082				
Psorothamnus fremontii					Vulpia octoflora	4.2	0.480	0.233
Sporobolus cryptandrus	Vulpia octoflora	12.4	0.257	0.073				
Vulpia octoflora	Gutierrezia sarothrae	26.2	0.133	0.026				

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ARTEMISIA REPRODUCTIVE STRATEGIES: A REVIEW WITH EMPHASIS ON PLAINS SILVER SAGEBRUSH

Todd P. Walton, Richard S. White, and Carl L. Wambolt

ABSTRACT: Plains silver sagebrush (Artemisia cana Pursh ssp. cana) is a little-studied but important ecological dominant over much of the Missouri Plateau and peripheral zones east of the Continental Divide. Understanding the taxon's ecology and reproductive characteristics can be furthered by understanding related species. Knowledge of otner Artemisia species and bits of specific silver sagebrush information provide a basis for research hypotheses needed for additional research of this species.

INTRODUCTION

The geographic range and ecological relationships of silver sagebrush (Artemisia cana Pursh) merit intensive research attention. However, this has not occurred. While big sagebrush (Artemisia tridentata Nutt.) has been studied extensively in recent years, biological information dealing with silver sagebrush is very limited. The western states rely heavily on range and pasture forage for their livestock industry. Therefore, appreciation of silver sagebrush communities and their implications for management is important.

Several adaptive features operate within the North American endemic Subgenus Tridentatae of the Genus Artemisia L. that have resulted in its extensive distribution and persistence in a variety of habitats. Features such as the ability to carry on photosynthesis at low temperatures, the ability to germinate over a wide range of temperatures, an extensive root system, and prominent secondary metabolic compounds may confer a competitive advantage for sagebrush (DePuit and Caldwell 1973; Caldwell 1978).

Two genetically different groups in the subgenus Tridentatae can be recognized. One group resprouts after disturbance (A. tripartita Rydb., A. cana Pursh, and A. rigida [Nutt.] Gray), while the other group does not (A. tridentata Nutt., A. arbuscula Nutt., A. longiloba [Osterh.] Beetle, A. nova A. Nels., A. bigelovii Gray, and A. pygmaea Gray).

Evidence indicates that all species and subspecies of Tridentatae can be given the status of topographic and edaphic climax dominants. As such, each defines a different niche. Many of the factors which influence the distribution patterns of sagebrush function through soil development combined with climatic or environmental characteristics (Hazlett and Hoffman 1975; Winward 1980; Froeming 1981). Several species such as silver and big sagebrush have achieved sufficiently wide distribution and have differentiation so as to have developed subspecific taxa. Big sagebrush is more widespread and has received the most research attention. Silver sagebrush is second in distribution but is not nearly so well researched.

SILVER SAGEBRUSH TAXONOMY

The silver sagebrush complex is composed of three subspecies with allopatric distribution (fig. 1) and characteristic ecological niches (Beetle 1977). Subspecies are separated morphologically on the basis of leaf width, sesquiterpene lactone content, and geography (Morris and others 1976).

Mountain silver sagebrush (A. cana Pursh ssp. viscidula [Osterh.]) is typified by greenish, linear leaves. It occurs on streambanks, meadows, and depressions generally at higher elevations. It is often found in close association with conifers in the Rocky Mountain region. Bolander silver sagebrush (A. cana Pursh ssp. bolanderi [Gray] Ward) has linear, canescent leaves and grows on poorly drained soils in central Oregon and eastern California. Plains silver sagebrush (A. cana Pursh ssp. cana) is an erect, canescent, freely branching shrub up to 5 feet (1.5 m) in height with large linear leaves. This taxon is found growing on well-watered, deep soils throughout the Northern Great Plains, especially along streambottoms and drainageways, in sparse to dense stands. Wyoming big sagebrush (A. tridentata Nutt. ssp. wyomingensis Beetle & Young) is the only other major shrubby sagebrush in the Northern Great Plains (Beetle 1977; Johnson 1978; Tisdale and Hironaka 1981).

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Todd P. Walton is Research Assistant, Animal & Range Sciences Department, Montana State University, Bozeman. Richard S. White is Research Plant Physiologist, U.S. Department of Agriculture, Agricultural Research Service, Fort Keogh Livestock and Range Research Station, Miles City, MT. Carl L. Wambolt is Associate Professor of Range Science, Animal & Range Sciences Department, Montana State University, Bozeman.

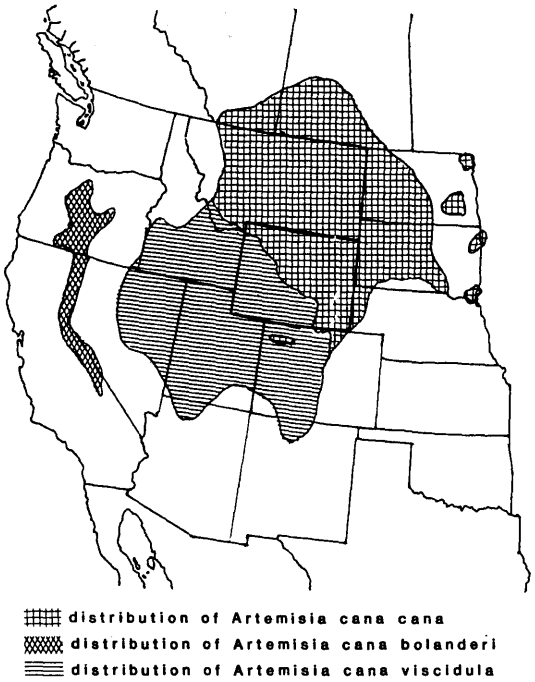


Figure 1.--Distribution of three subspecies of silver sagebrush in western North America (Harvey 1981).

DISTRIBUTION OF PLAINS SILVER SAGEBRUSH

Silver sagebrush occupies an estimated 34 million acres (14 million ha) in the 11 western United States (Beetle 1960). In Montana there are about 19.3 million acres (7.8 million ha) of big sagebrush and 12.8 million acres (5.2 million ha) of silver sagebrush, while in Wyoming there are 23.0 and 7.0 million acres (9.3 and 2.9 million ha) respectively.

Plains silver sagebrush occurs east of the Continental Divide (except for the Yampa River Valley, CO) in Wyoming and Montana north to southern Alberta and Saskatchewan and east to central North and South Dakota and northwest Nebraska. Several disjunct populations occur in the eastern Dakotas (Harvey 1981).

Plains silver sagebrush was first collected by Lewis and Clark on the bluffs of the Missouri River (Nuttall 1841). Typical habitats include loamy to sandy, well-drained upland soils and alluvial flats and terraces of valley bottoms. It is further distinguished as growing in dense or open stands along streams and valleys that are subject to erosion, flooding, and deposition. Hence, stratification and heterogeneity are conspicuous in the alluvial profiles (Thatcher 1959; Hazlett and Hoffman 1975; Johnson 1978). Thatcher (1959) noted that of the four sagebrush species he studied, only plains silver sagebrush grew on soils influenced by high water tables. Johnson (1978) reported that silver sagebrush and western wheatgrass (Agropyron smithii Rydb.) thrived together in areas of frequent flooding.

SOIL RELATIONSHIPS

Soil characteristics have been examined to evaluate their relationship to sagebrush distribution. Silver sagebrush prefers well-drained, alluvial, coarse-textured soils in bottomlands. Detailed soil and vegetation relationships in silver sagebrush communities have been reported. Lower levels of P, K, N, organic matter and cation exchange capacity were reported in soils where silver sagebrush dominated than in adjacent soils where big sagebrush was most abundant (Hazlett and Hoffman 1975). This was probably due to more mature soil development in the big sagebrush community. Cunningham (1971) reported that moderate to high levels of extractable magnesium in the 12- to 24-inch (31 to 61 cm) layer were important to the presence and success of silver sagebrush. This was associated with imperfect soil drainage and a shallow root system. Optimum habitat seemed to include a moist upper 6 inches (15 cm) of soil along with coarse materials in the soil profile.

Although similar research has not been done with silver sagebrush, Sturges (1977) states that water-use zones shift outward and downward in the soil from big sagebrush plants as the growing season advances. Sturges (1977) and Caldwell (1978) both characterize big sagebrush as having a prominent, deep taproot with sufficient lateral spread and root density to capture summer precipitation. Deeper roots allow utilization of deeper water reserves.

FACTORS AFFECTING REPRODUCTION BY SEED

Allelopathy

Allelopathy has been extensively reviewed in the literature on Artemisia. This work has shown that allelopathy is prominent in Artemisia species throughout the world, and much foreign research focuses on it.

Allelopathic substances from Artemisia roots and leaves are universally thought to decrease respiration or inhibit germination of grass seeds (Chirca and Fabian 1973; Friedman and others 1977; Hoffman and Hazlett 1977; Weaver and Klarich 1977; Groves and Anderson 1981; Hussain and Khanum 1982). In India, Melkania and others (1982) attributed the allelopathic potential of Artemisia vulgaria L. to certain hydrophilic metabolites. In Japan, Numata and others (1975) found a biologically active agent (caffeic acid) in the roots of mugwort (Artemisia princeps Pampan.). Inhibition of grass germination has been the most commonly reported response, but in some cases stimulation of growth has been recorded (Hoffman and Hazlett 1977; Weaver and Klarich 1977; Chirca and Fabian 1973). Hale (1982) noted that leachates from A. vulgaris L. also increased growth of the fungus Pythium myriotylum. Harvey

(1981) observed autopathy in some sagebrush species in Montana, including plains silver sagebrush.

Seed Dispersal

One of the primary features of any reproductive strategy is the number of propagules that are produced and dispersed. In this respect, efficiency of seed dispersal by wind and reproductive capacity are associated. Sagebrush species are generally low in dispersal efficiency but high in seed production capacity (Bostock and Benton 1979). Seed dispersal is one of the most important factors promoting gene flow in plant populations. Dispersal is one way that plants can keep their descendants separated in space, and it provides each new plant with its own site where it has greater potential to compete with other plants (van der Pijl 1982). Dispersal strategy is complex and represents a compromise among conflicting demands. Consequently, in some species establishment might be more important than dispersal for achieving reproductive success. In most plant species, including sagebrush, dispersal seems to be incidental, especially during storms, and is not based on any special morphological structure.

Dispersal can play a critical role in determining population size. Because seeds of most plants are dispersed close to the parent, seed density falls off steeply as distance from the parent increases (Harper 1977; Cook 1980). This is the case with sagebrush (Beetle 1960; Friedman and Orshan 1975; Harvey 1981; Tisdale and Hironaka 1981; Walton 1984).

Seed dispersal in arid communities is described as falling into two classes (Mott 1979): (1) widespread dispersal, often of large numbers of seeds, enabling exploitation of a number of potential sites, and (2) utilization of a favorable habitat facilitated by minimal movement of seed from the parent plant. Under desert conditions, this second strategy is thought to improve the chances of seedling establishment since adjacent sites have already proved suitable for growth and development of parent plants (Friedman and Orshan 1975). Although dispersal is important, only a few dispersal patterns are noted by Cook (1980) as being published. In one such study, the patterns of achene dispersal, seedling emergence, appearance of cotyledons, and seedling mortality of A. herba-alba Asso were related to distance from the parent plant. Eighty-five percent of the achenes of this species fell under the existing shrub canopy.

Sagebrush seed dispersal can be by animals, water, or wind (Tisdale and Hironaka 1981). However, the relative importance of each agent can vary. Although rodents play an active role in seed dispersal of many herbaceous species, no sagebrush seed was reportedly dispersed by rodents in Nevada (LaTourette and others 1971). However, Harvey (1981) believes that long-distance dispersal by silver sagebrush is probably due to mucilaginous seeds attaching to animals. Beetle (1960) declares that water is undoubtedly an important dispersal agent, but anemochory (wind dispersal) is more representative of Asteraceae (Compositae) and seems to be of greatest importance (Harper 1977; Bostock and Benton 1979; Evans and Young 1982). Seedlings of basin big sagebrush have been found up to 33 meters from the nearest possible source plant. Since sagebrush seeds have limited morphological mechanisms for distant wind-borne dispersal, the range of the plant is probably extended in contiguous bands around the periphery of established stands (Daubenmire 1975). Walton (1984) found that most seed was dispersed close to, or under, individual silver sagebrush plants. However, in at least one case, the largest proportion of seed was dispersed at 9.8 feet (3 m). In this instance, seed was evenly dispersed from the seed-bearing plant out to 9.8 feet (3 m), and there was no rapid decrease in dispersed seed until that distance was reached. Seed numbers then dropped off sharply.

Achenes of certain Artemisia species, including silver sagebrush, develop a transparent gelatinous envelope around the seed upon contact with water (Clor and others 1974; Harvey 1981; van der Pijl 1982). This seems an important method for attaching to soil particles, thereby enhancing germination potential by protecting the delicate embryo from dessication and mechanical injury (Clor and others 1974; van der Pijl 1982). The mucilaginous seed coat has also been regarded as a dispersal agent, and in general, the drier the climate the more mucilaginous coating is present (Harvey 1981; van der Pijl 1982).

Phenological development in sagebrush results in most seed being shed during late fall and winter, although a few remain attached throughout the winter (Beetle 1960; Harvey 1981; Tisdale and Hironaka 1981). After the inflourescence reaches a seed-ripe condition, most viable seed is dispersed during the first 7 days. However, aborted florets and half-filled seeds are commonly dispersed over the following 2 to 4 weeks (Goodwin 1956). Tisdale and Hironaka (1981) have stated that up to 300,000 achenes per plant can be produced in big sagebrush, but Harvey (1981) reported a maximum production of only 54,000 achenes in silver sagebrush.

Germination Factors

Interest in germination characteristics of sagebrush is twofold. First, efforts to use sagebrush to provide forage or cover for livestock, wildlife, and erosion control depend upon this knowledge. Second, there is often a desire to reduce stand density in areas where plants become too abundant and compete with other forage plants (Pechanec and others 1965; McArthur and others 1974; Harvey 1981).

The combination of habitat conditions that favor seedling establishment has been referred to as a safe site (Harper 1977; Cook 1980). In this environment, the water, nutrient resources, and stimuli immediately surrounding a seed determine whether it will germinate (Harper 1977). Germination in a specific seedbed is also controlled by inherent characteristics of seeds, or in some

cases, through modification of the physical environment by the seed itself (Evans and Young 1982). Heterogeneity in the microenvironment and the extreme subtlety of germination requirements can determine the number and variety of seedlings that are recruited into the plant population from the seedbank. High-density stress can adversely affect seedling success. Another important element, herbivory, tends to diversify range plant communities. Herbivory within the local microenvironment influences seedling establishment and subsequent growth of plants, and therefore initiates regeneration cycles on a small scale.

One aspect of sagebrush communities is that very few Artemisia seeds germinate and survive beyond the first year (Evenari and others 1971; Hazlett and Hoffman 1975; Cook 1980; Harvey 1981), despite high annual seed production. Several factors contribute to this phenomenon including: soil matric potential with its effect on wetted contact between seed and soil (Collis-George and Hector 1966), early death of seedlings (Eddleman 1979), seasonal climatic conditions and plant age (Nosova 1973; Evans and Young 1982), and soil moisture relationships and litter (Beetle 1960).

Achenes of sagebrush in general do not exhibit specific germination requirements. Therefore, they are usually considered nondormant (McDonough and Harniss 1975; Caldwell 1978) and do not persist for long periods in the soil (Young and Evans 1975). However, if seeds are subjected to ideal laboratory conditions, germination can be as high as 90 percent (Harvey 1981). Important factors to examine, with respect to germination requirements, include cold treatments (stratification), temperature, light, water stress, and maturity of the seed.

Stratification.--Stratification has been defined as a cold treatment which breaks seed dormancy. It is important in many species. Bewley and Black (1982) state that it is most beneficial if seeds are hydrated. The amount of prechilling needed to enhance germination is quite variable among species and can range from a few days to several months (Young and Evans 1979; Bewley and Black 1982). It can also be unnecessary. Stidham and others (1980) state that most shrubs require prechilling to achieve maximum germination, and they identified big sagebrush in this category without regard to subspecies. Krueger and Shaner (1982) reported that prostrate spurge (Euphorbia supina Raf.) increased germination by 70-80 percent with stratification, but Krasikova (1978) showed that seeds of annual composites (Artemisia vulgaris L. included) were not affected by stratification. Because seeds of sagebrush species have been classified as nondormant, it might be hypothesized that such seeds would not benefit from prechilling. The only exception to this speculation has been mountain big sagebrush (McDonough and Harniss 1974; McDonough and Harniss 1975; Caldwell 1978). Stratification can also affect germination responses to environmental variables. In arrowleaf balsamroot (Balsamorhiza sagittata [Pursh] Nutt.), stratification lowered the optimum temperature for germination (Young and Evans 1979). In a similar fashion, prechilling significantly lessened the effect of water stress on germination of mountain big sagebrush seeds (McDonough and Harniss 1975). In plains silver sagebrush, stratification had no effect on germination success, probably due to seed not being dormant and therefore not requiring the dormancy-breaking cold treatment (Walton 1984).

Temperature.--The effects of temperature on seed germination have been studied extensively in many species. Temperature regimes are frequently involved in seasonal control of dormancy especially in response to interactions with light. An optimum temperature becomes apparent when seeds are germinated over a wide range. In addition, most seeds germinate better under constant rather than fluctuating temperature regimes (Bewley and Black 1982; Evans and Young 1982). Bewley and Black (1982) also note that rate of germination is of great value in characterizing seed responses to temperature, although there is often considerable variability due to genetic differences. This genetic heterogeneity is demonstrated through subpopulations of seed from a plant population. These subpopulations germinate under different temperature regimes and germination rates change with these temperatures. All subspecies of big sagebrush are noted to speed up germination from 2 to 18 days with increasing temperatures (McDonough and Harniss 1975). Sagebrush and other Artemisia seeds germinate over a wide range of temperatures, but optimum temperatures are usually well-defined (Weldon and others 1959; Clor and others 1974; Caldwell 1978; Krasikova 1978; Sabo and others 1979; Wilson 1982). In silver sagebrush, Harvey (1981) stated that the optimum seems to be about 57 ^{o}F (14 ^{o}C). However, Walton (1984) reported that higher temperatures of 68 ^{o}F (20 ^{o}C) were generally more favorable for germination when other factors such as osmotic potential and light regime were examined concomitantly.

Light.--Light can influence seed germination of Artemisia, depending on the species and associated environmental factors. Fringed sagewort (Artemisia frigida Willd.) germination required light, but this could be circumvented by treating seed with gibberillic acid (Wilson 1982). Sabo and others (1979) asserted that light had no effect on germination of either fringed sagewort or big sagebrush seed. However, evidence to the contrary has been presented that states that light increased germination by as much as three times in big sagebrush (Weldon and others 1959). The germination response that has been observed in other species clearly demonstrates that light could play a role in the germination of silver sagebrush. This has been confirmed by Walton (1984).

Osmotic potential.--The specific effects of osmotic potential on silver sagebrush are little known. However, big sagebrush responded to more negative osmotic potential with less total germination, but this was ameliorated by light (Weldon and others 1959). In contrast, Sabo and others (1979) reported little effect of osmotic potential until 10 atm (1.0 MPa) was reached. Fringed sagewort was much more sensitive than big sagebrush and showed initial responses at 2 atm

(0.2 MPa). Walton (1984) found germination percentages and rates dropped off steeply under the influence of more negative osmotic potentials, and no germination was observed below -7.5 bars (-0.75 MPa).

Maturity of seed.--Maturity of seed does have an effect on plains silver sagebrush germination with higher values being observed in later seed collections (Walton 1984). Clor and others (1974) reported that Artemisia herba-alba reacted this way, and both prostrate spurge and prostrate kochia (Kochia prostrata [L.] Schrad.) showed higher germination percentages when seed was collected later (Waller and others 1980; Krueger and Shaner 1982).

PLANT ESTABLISHMENT

After seeds have germinated, reproductive success depends ultimately upon successful emergence from the soil, survival as a young seedling, and growth to maturity as a seed producer. Although Hickman (1979) pointed out that at least 95 percent of all plant mortality occurs within the first year, seedling demography has not received extensive research attention. In addition, a priori logic is sometimes used to conclude that most, if not all, seedlings will reach reproductive maturity if they can survive the first growing season. In Artemisia species, little is known about seedling dynamics.

Although sagebrush seed production is high, very few seedlings emerge and survive. Walton (1984) found that only 1.2 percent of field-planted silver sagebrush seeds emerged, but only 11 percent of these seedlings survived the first growing season. This can be attributed to the amount of competitive vegetation, litter, adverse environmental factors such as water stress and depth of burial, and allelopathy (autopathy) (Johnson and Payne 1968; Evenari and others 1971; Friedman and Orshan 1975; Eddleman 1979; Cook 1980; Harvey 1981; Evans and Young 1982; Wilson 1982). Depth of seed burial also influences emergence. The maximum depth from which sagebrush seed will emerge has been estimated at 0.2 inches (5 mm) by Harvey (1981). Burial at 0.08 inches (2 mm) was considered an optimum depth for plains silver sagebrush. However, Walton (1984) reported that more seeds planted at 0.2 inches (5 mm) produced seedlings in the field than at depths of 0 and 0.6 inches (0 and 15 mm). In addition, mortality was least for those emerging from 0.6 (15 mm). Years that are favorable for seedling establishment can occur at irregular intervals. The primary controlling factor is soil moisture (Johnson and Payne 1968; Gordon and Wright 1981).

Growth characteristics of sagebrush seedlings seem to be primarily subject to genetic control although environmental influences also contribute to seedling response. Among big sagebrush accessions and subspecies, growth parameters showed significant differences in each measure. Height, crown, length of leaders, and annual yield were among the parameters differing between accessions and subspecies (McArthur and Welch 1982).

VEGETATIVE (ASEXUAL) REPRODUCTION

Vegetative reproduction in Artemisia has been examined, but few in-depth studies have been completed. Bostock and Benton (1979) studied five perennial composites with varying degrees of lateral extension and growth. They subsequently related seed and vegetative reproduction strategies. Seed was generally more important than vegetative capacity. However, Artemisia vulgaris L. perennates only by vegetatively produced propagules, and it has rhizome growth measured at 11.8 inches (30 cm) per year.

Went (1979) contends that survival of perennial desert plants depends mainly upon vegetative reproduction, and seeds are only a secondary method of reproduction that becomes important when summer rains allow abundant germination. Contradictory evidence has been presented in a study by Young and Evans (1972). They examined green rabbitbrush which was long thought to invade sites by root sprouting. They discovered that it relied heavily on seed dispersal to establish new plants. Apparently either mechanism can be successful.

There are special problems that vegetative reproduction presents for the field and experimental ecologist. Abrahamson (1980) stated that vegetative reproduction is more similar to growth than to reproduction with confusion coming from using animals as models. He stated further that vegetative reproduction is a distinct and well-defined phenomenon.

Clonal reproduction is common in forest herbs, aquatic plants, and at higher altitudes and latitudes where ecosystems are often influenced by fire, climatic, and other disturbances (Abrahamson 1980; Legere and Payette 1981). A clone can be defined as the aggregate of individual organisms descended by asexual reproduction from a single sexually-produced individual (Barnes 1966). Plants in such diverse genera as Ophioglossum, Pteridium, Populus, Equisetum, Carex, Rhus, Cornus, Prunus, and Artemisia form clones by initiating shoots from underground parts. Clonal growth is much more prevalent in many species than sexual reproduction, in spite of the fact that there may be a large and viable seedbank in the soil (Evenari and others 1971; Hazlett and Hoffman 1975; Cook 1980; Harvey 1981; Lovett-Doust 1981). Silver sagebrush stem cuttings may root within 8 weeks when collected at the leaf growth phenological stage (Everett and others 1978). Walton (1984) discovered that, in nearly every instance, plains silver sagebrush showed some degree of rhizomatous growth, even among small seedlings.

Soil texture influences what reproductive strategy is favored. Higher clay content usually favors vegetative reproduction. Increasing litter decreased the success of vegetative reproduction, while increased environmental severity accentuated it (Abrahamson 1980).

CONCLUSION

As shown in this review, specific information on the reproductive strategies of plains silver sagebrush is lacking. However, the bits of specific information available coupled with knowledge of other members of the genus Artemisia provide a basis for formulating research hypotheses to further investigate this important, but relatively ignored, taxon.

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ECOLOGICAL ADAPTATION AND GRAZING RESPONSE OF BUDSAGE (ARTEMISIA SPINESCENS) IN SOUTHWESTERN UTAH

Benjamin W. Wood and Jack D. Brotherson

ABSTRACT: Several Artemisia spinescens sites representing different plant communities and different grazing histories were studied to investigate physical adaptations and the influence of grazing on this species. Summer dormancy and root growth patterns indicate methods of adaptation. Grazing records show that late winter grazing could be very detrimental to A. spinescens growth and survival.

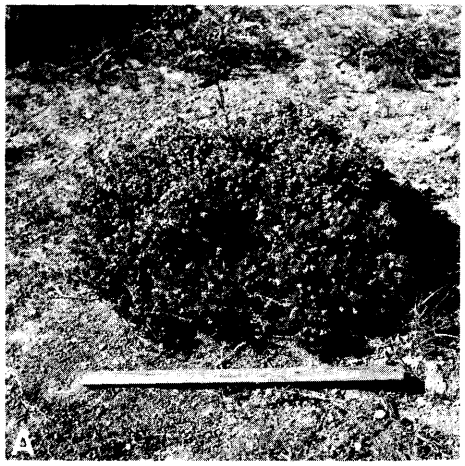
INTRODUCTION

Budsage (Artemisia spinescens D. C. Eaton) is one of the more common perennial shrubs growing on the semiarid valley bottoms and benches of the Great Basin of the western United States (fig. 1). This species was first described as Picrothanmus desertorum by Nuttall (1841). In 1871, D. C. Eaton placed this plant in Artemisia because the flowers are reduced and have a tendency toward fusion of the style-branches of the disk flowers. Budsage is well set off as a species by its spinescent habit and consistent characteristics in the involucre and floral parts. The harsh environment where it grows has undoubtedly helped to stabilize the species so that variants do not occur or are at least unknown. Budsage is not known to hybridize with any other species.

Unlike most of the woody species of the genus, budsage is deciduous. The leaves normally fall off the plant by midsummer. Budsage is easily recognized in all seasons of the year. It is one of the first shrubs to become green in early spring (fig. 2A) and has a gray-green foliate. During the summer and winter (fig. 2B), it can



Figure 1.--Geographical range of A. spinescens.



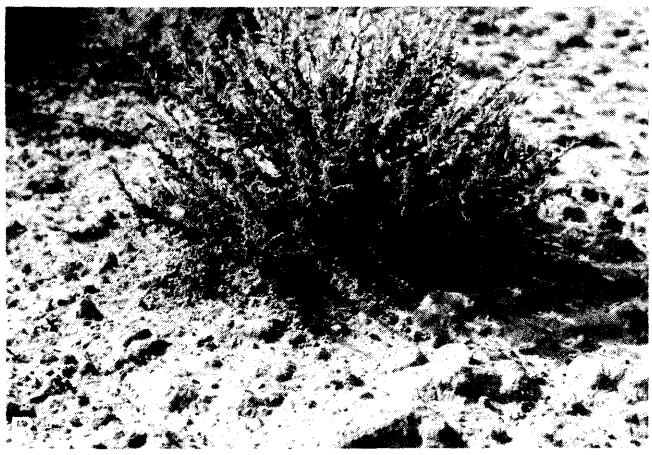


Figure 2.--Habit of A. spinescens during the spring (A), summer and winter (B) seasons. Rule in "2A" is 20 inches (50.8 cm) long. Plant in "B" is 15 inches (38.1 cm) in diameter.

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Benjamin W. Wood and Jack D. Brotherson are Associate Professor and Professor, respectively, Botany and Range Science Department, Brigham Young University, Provo, UT.

be recognized by its spiny habit and absence of leaves. This shrub is also pungently aromatic.

When the plant first shows signs of breaking dormancy, but before the buds elongate, the bark can be easily removed from last season's growth by pulling action. It is at this time that budsage becomes palatable to sheep. This condition is referred to by sheepmen as "slipping". Budsage is one of the most palatable forage species on sheep winter range during the late winter and early spring (Hutchings 1954: Dayton 1931). This relatively short period of time (generally February and March) closely coincides with the period of slipping. Such early availability is important on sheep range because budsage adds high quality nutrition to sheep diets at or about the time of lambing (table 1). Although most winter forage plants are borderline to decidedly deficient in digestible protein, phosphorus, and metabolizable energy (Cook and others 1954), budsage has especially high calcium, magnesium, and phosphorus content (Millar 1958). Its protein content is also high.

After the new twigs have elongated somewhat, its palatability drops because the content of volatile oils increases (Cook and others 1954) and because other plants such as grasses and winterfat (Ceratoides lanata) become green. Cattle and horses seldom utilize budsage, possibly because of its aromatic oil content.

Wild game such as mule deer (Odocoileus heminonus) and pronghorn antelope (Antilocapra americana) utilize this species during the spring while it is green and succulent. Mountain sheep (Ovis canadensis) eat it in the summer when it is dry (Gullion 1964).

Black-tailed jackrabbits (Lepus californicus) and small rodents generally eat only the leaves, smaller branches and twigs. However, black-tailed jackrabbits may occasionally prune back a whole plant. Harper and others (1958) reported that Chucker partridge (Alectoris graeca) eat the flower heads and leaves.

Hall and Clements (1923) reported there is some evidence that calves have been poisoned by eating the green foliage. They also noted that the pollen of budsage is a cause of hay fever.

Table 1.--Summary of forage values of Artemisia spinescens under average range conditions[1] of the Great Basin (Cook and Harris 1950; Cook and others 1954; Cook and Harris 1968)

			Protein					Energy				
	Cellulose	TN	Digestible	Consumed	Total	Carotene	Ca	P	Gross	Metabolizable	Eaten	Digestible
	(%)	(%)	(%)	(%)	(%)	(mg/lb)	(%)	(%)	(cal/lb)		(cal)	(cal)
Optimum intake:												
Artemisia spinescens 3.30 lbs/day - oven-dried (under range conditions for a 130-lb ewe)			2.60	0.09	4.3-5.4			0.09	1587-1693	577	1904	
Average intake:			4.70			7.20		0.12		614		
Browse species 3.5-3.6 lbs/day - oven-dried (under range conditions for a 130-lb ewe)												
A. spinescens:												
Green, spring growth	18.1	50.6			9.79	10.20	0.97	0.09	1923			1160
In saltbush communities			13.70				1.32	0.33		911		
In sagebrush communities			13.70					0.33		911		
Heavily grazed (70% utilization) 4.20 lbs/day - oven-dried			13.70		17.30	10.80		0.33		911		
Digestion coefficient	58.1				79.10				60.3			

[1] Average range conditions:

	Production	Utilization	Floral composition of diet	Species composition
Artemisia spinescens	1 lb/acre	53%	7%	1 to 5%
Browse species	255 lb/acre	24%	83%	74%

This study of budsage's ecological life history was undertaken to determine how it has adapted to the rather harsh environment of southwest Utah and bordering Nevada and to investigate the influence of sheep grazing upon its survival and reproduction.

STUDY AREA AND METHOD

This study was conducted from 1963 to 1965 in western Millard County, UT, and adjacent White Pine County, NV (fig. 3). Specific study sites were located at seven locations where budsage grows in Pine, Antelope, Snake, and Hamlin Valleys. Most of the sites in Pine Valley were on the Desert Experimental Range (DER) which is maintained by the U.S. Department of Agriculture, Forest Service, Intermountain Research Station. Those in the other valleys are on land managed by the U.S. Department of the Interior Bureau of Land Management. The study sites were selected as being representative of the different communities in which budsage occurs. They also represent different grazing histories and treatments of winter sheep range (table 2).

Climate

The precipitation of the area is not evenly distributed throughout the year. During April, May, July, August, and October, the area receives about 57 percent of the total precipitation; during July and August it receives almost as much as the other three months combined. The area receives the least amount of moisture in January and December.

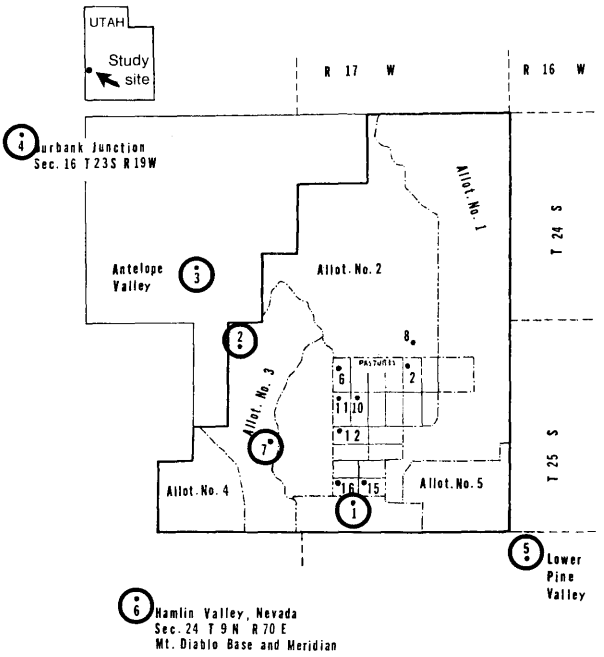


Figure 3.--Location of study sites. Circled numbers indicate study sites and correspond to site numbers used in text.

Drought is not uncommon to the desert; great fluctuations in annual and monthly precipitation are characteristic. During a 30-year period for which climatological data have been recorded at the Desert Experimental Range (DER), the area has, at least once, received no measurable precipitation during each month.

The summers are warm, and midday temperatures are usually above 90 °F (32 °C). The winter temperatures vary considerably and sometimes are very cold. The temperature extremes may be from -26 °F (-34 °C) in the winter to about 100 °F (38 °C) in the summer.

The weather during the study period was somewhat unusual because the summers of 1963 and 1965 were some of the wettest recorded at the DER. Summer precipitation was 5.10, 1.38, and 5.03 inches for 1963, 1964, and 1965, respectively. The precipitation in late summer of 1963 and 1965 was sufficient to moisten the root zone of natural seedlings during the last week in August and September, but that of 1964 did not moisten the root zone.

The winds are frequent and may be of rather high velocity. The monthly means are between 4 to 6 miles per hour (6.4 and 9.7 km per hour) with gales reaching 15 to 30 miles per hour (24.1 to 48.3 km per hour) (DER water station records). Scarcely a day passes without some wind. This reduces the intensity of the high summer temperatures, but also increases the rate of evaporation to which the plants and soil are subjected.

Soils

Soil pits were dug and sampled to ascertain the various soil conditions tolerated by budsage. Vest (1962) reported that near Dugway Valley, UT, budsage grows only on clay loams and sandy clay loams. He also indicated budsage showed the narrowest tolerances to changes in soil texture of all the species he studied. However, at the DER and adjacent areas, this species grows in soils ranging from sandy to loam textures, indicating it has a wider tolerance to soil texture than previously reported.

Each soil was sampled by horizons. Analyses were completed using duplicate samples representing the horizons. Averages of the data obtained are reported. The presence and relative amounts of carbonates in the soil were determined by the effervescence caused by 0.1 N hydrochloric acid (Wood 1966).

Soil textural analyses were made by the hydrometer method of Bouyoucos (1951) using sodium silicate as the dispersing agent. The exchangeable bases were determined by leaching 25-gram soil samples with 200 ml of 1 N ammonium acetate and then determining the amount of cations present using a flame spectrophotometer. The amount of each cation present is expressed in milliequivalents per 100 grams of soil.

Table 2.--Grazing history, elevation, exposure, and dominant vegetation of principal study sites. The Hamlin Valley site is according to the Mt. Diablo Base and Meridian; all other sites reckoned from Salt Lake Base and Meridian. Site numbers correspond to numbers used for sites in text

Site number		Elevation (meters)	Slope (%)	Exposure	Dominant vegetation
Ungrazed #1	Ungrazed area of west DER headquarters T25S R17W Sec. 33.	1615	1	NE	A. spinescens, A. confertifolia, C. lanata, Oryzopsis hymenoides, Hilaria jamesii
Grazed #2	Grazed by sheep at specific times in winter and early spring. Unit 3 or DER Allotment 3. T25S R18W Sec. 2.	1768	3	W	Artemisia spinescens, Ceratoides lanata
Grazed #3	Grazed by sheep all winter. Antelope Valley. T24S R18W Sec. 26.	1798	1.5	SW	Atriplex confertifolia, Artemisia spinescens
Grazed #4	Grazed by cattle in winter and early spring. Burbank Junction. T23S R19W Sec. 16.	1652	0	Flat	Sarcobatus vermiculatus, Artemisia spinescens, Atriplex confertifolia
Grazed #5	Grazed by cattle in winter and early spring. Lower Pine Valley T36S R16W Sec. 6.	1567	0	Flat	Atriplex confertifolia, Artemisia spinescens, O. hymenoides, H. jamesii
Grazed #6	Grazed by cattle in winter and early spring. Hamlin Valley. T9N R70E Sec. 24.	1737	2	NW	Artemisia spinescens, Ceratoides lanata
Grazed #7	Grazed by cattle in winter and early spring. Warm Cove. T25S R18W Sec. 24.	2438	3	S	Atriplex confertifolia, Artemisia spinescens

Soil salinity was determined by measuring resistance of a saturated soil paste with a Wheatstone electrical conductivity bridge. Data are expressed in parts per million of soluble salt in the soil. A Beckman glass electrode pH meter was used to determine the hydrogen ion concentration of saturated soil samples.

The parent material of the soils is alluvial in origin, derived principally from Paleozoic sedimentaries. The soil surface between the plants is nearly always covered with an erosion pavement of gravel or rock of uniform size. It is usually dark in contrast to the light gray soil beneath.

The soils that support budsage have markedly less gravel between 20 and 30 inches deep than those supporting other vegetation. This zone of less gravel is also a zone of lime accumulation. The soils of the adjacent shadscale-winterfat (A. confertifolia - C. lanata) type contain less gravel in the upper horizons than surrounding types. These soils were also less saline and deeper than those supporting adjacent winterfat and shadscale communities.

Soil moisture content was studied at four locations and at three depths: 0-5.1 cm, 15.24-20.32 cm, and 25.40-30.5 cm. These depths were chosen because budsage is a relatively shallow-rooted plant. Soil moisture indices were determined using pressure membranes. The moisture content held in the soils at 1/3 and 15 atmospheres of pressure is expressed as a percentage of the oven dry weight of the soil. The soil moisture content was determined using a "speedy" Soil Moisture Tester apparatus that measures moisture by a calcium carbide gas method. The moisture content is expressed as a percentage of the dry weight. The moisture holding capacity of the soils is less than 10 percent in the first 2 feet. Soil moisture increased only after rains in the fall; the summer rains did not generally penetrate more than 5.7-7.6 cm deep, except in washes and outwash areas. In this arid area, essentially all the moisture from light to moderate summer showers may be lost by evaporation within 1 to 3 hours after the storm is over. The desert soils are very dry during the rather long summer period. This is the period which budsage evades by becoming dormant.

Some plants modify the characteristics of the soil in which they grow, especially the rate of water infiltration. For example, moisture infiltrates faster and penetrates deeper into the soil under budsage plants than under Indian ricegrass (O. hymenoides), shadscale, or winterfat. This phenomenon was observed to occur more frequently in sandy soils than those having a silty texture.

Plant Communities

The various plant communities at the sites can be classed into three broad vegetation types, budsage-winterfat, shadscale including winterfat, and shadscale without winterfat.

The shadscale with winterfat type is a mixed shrub community that contains a substantial amount of grasses. Data reported here for this type were from an ungrazed area. Other data from an area grazed moderately by sheep in early or late winter in alternate years indicate the important grass species is sand dropseed (Sporobolus cryptandrus) as opposed to Indian ricegrass and galleta (Hilara jamesii).

The shadscale communities contained very few other perennial species except galleta. Annual species such as Russian thistle (Salsola iberica) and halogeton (Halogeton glomeratus) were abundant. The communities studied were grazed all winter long, and such grazing has probably eliminated any winterfat and perennial grasses that may have been present. These communities are in the valley bottoms rather far from the mountains.

Budsage is not restricted to these community types; it grows in almost every type of desert community that occurs on benches or low-lands of the Cold Desert or Northern Desert Shrub Formation (Shantz 1925) of the Great Basin and to some extent of the Colorado Plateau. It is particularly abundant on plains and high mesas of northern Nevada, usually growing on moderately alkaline soils (Shreve 1942). Budsage is commonly associated with species of the salt-desert or salt-bush formation as defined by Hutchings and Stewart (1953), Harrington (1954), Gates and others (1956), and Bronson (1966); not that defined by Shantz (1925) which was a greasewood formation, although budsage does occur with greasewood (Sarcobatus vermiculatus).

Plant Measurements

At each of five sites, 60 plants were chosen at random and the total number of current year's vegetative twigs and current year's spines on each plant were counted. The spine/vegetative twig ratio was computed from these data in 1964 and 1965. These data were obtained from two DER pastures and an allotment which are moderately grazed in winter, from a BLM range allotment which is heavily grazed all winter long, and from a protected area in one of the above pastures.

Cover estimates were made in 1964 on grazed and protected plots or sites located in four experimental pastures, two grazed at a heavy and two at a light rate of stocking with sheep. These pastures also represent grazing in mid and late winter. The 1964 data were compared with the cover data obtained in 1934 when the pastures were established.

Cover estimates were obtained using the line-intercept method (Canfield 1941) and the line-point method which is a modification of the point-frame method of Levy and Madden (1933). These methods give cover data from which the percentage of bare soil, litter, plant cover, plant composition, and foliage cover were calculated. At each location six 100 foot transects were used.

Percentage of plant composition was calculated by dividing the total sum of the intercepts of each species by the total of all vegetational intercepts at each location times 100.

The percentage cover composition data from four experimental pastures are reported in table 3. Two kinds of composition are reported: the relative amounts of shrubs, forbs, and grasses in the total plant cover, and the relative amounts of different species in the shrub component. Plant counts (density) of budsage and three associated species, (shadscale, winterfat, and Indian ricegrass) were made on the same plots where the cover data were obtained and on plots in two additional pastures. Plant counts were made using 1 m^2 plots at each location and from these data density was calculated. Density was determined by dividing the total number of plants of a species by the total area sampled.

Phenology

Plant growth and development of 32 budsage seedlings growing on an area of past intense disturbance by burrowing rodents were observed and recorded during the summers of 1963 and 1964. The plants were one year old in 1963. One-half of these plants were watered once a week for eight weeks beginning in mid-June of both years before the plants became summer dormant. Several other seedlings in the same area were dug up in September and November of 1963 and April, June, July, and August of 1964 to compare the root systems of watered and nonwatered plants.

Plant growth and development studies of mature budsage plants were made. Plant collections were made in August, September, and November of 1963. Plants were also collected about every two weeks beginning in late February through June of 1964. From these collections data on leaf, stem, flower stalk lengths, and age of flowering were obtained as well as the time of growth.

Table 3.--Percentage cover composition from 40 200-square-foot plots in each enclosure and adjacent grazed acre in four experimental pastures of DER. Light grazing = 49% utilization (10 sheep days per acre). Heavy grazing = 68% utilization (17 sheep days per acre)

	Light grazing								Heavy grazing							
	Midwinter - Pasture 11				Late-winter - Pasture 10				Midwinter - Pasture 12				Late-winter - Pasture 15			
	Enclosure		Grazed		Enclosure		Grazed		Enclosure		Grazed		Enclosure		Grazed	
	1935	1964	1935	1964	1935	1964	1935	1964	1935	1964	1935	1964	1935	1964	1935	1964
Grasses	53.5	43.2	53.8	37.8	52.9	16.9	59.7	46.7	45.0	18.1	25.3	31.7	5.6	5.9	10.9	17.6
Forbs	8.6	5.5	9.9	9.9	3.0	7.0	4.8	6.7	11.0	7.5	1.2	7.5	0.1	1.4	0.5	4.7
Shrubs	37.8	51.3	36.3	52.3	44.1	76.0	35.5	46.6	44.0	74.4	73.5	60.8	94.3	93.7	88.6	77.7
Atremisia spinescens	22.3	48.7	25.7	26.5	41.4	56.6	36.2	8.4	20.2	59.1	22.3	28.8	4.5	35.7	3.8	0.8
Atriplex confertifolia	77.5	48.7	74.1	73.0	56.8	43.2	52.9	88.0	79.7	40.8	74.4	66.2	42.4	10.7	42.3	0.8
Ceratoides lanata	0.1	0.6	--	--	--	--	0.2	0.5	0.1	0.1	3.3	5.0	53.1	53.1	53.9	55.7
Kochia vestita	--	--	--	--	--	--	--	--	--	--	--	--	--	0.3	--	--
Chrysothamnus viscidiflorus stenophyllus	--	--	--	--	--	--	--	--	--	--	--	--	--	0.2	--	--
Ephedra nevadensis	--	2.0	0.2	0.5	1.5	--	10.2	2.6	--	--	--	--	--	--	--	--
Polygala subspinosa	--	--	--	--	0.3	0.2	--	--	--	--	--	--	--	--	--	--
Gutierrezia sarothrae	--	--	--	--	--	--	0.5	0.5	--	--	--	--	--	--	--	--

Root growth was studied by digging small trenches 1 foot wide by 2 feet deep and 3 feet long along one side of a budsage plant. This was done in August, 1963. All of the roots of the plant were removed from the trench. The roots were also removed from the soil taken from the trench by screening it before it was replaced back into the trench.

The trench was dug again in November, 1963, February, 1964, and June, 1964. When the trenches were redug all of the new roots were obtained by screening the soil taken out of the trench. The amount of growth was determined by measuring the total length of new root segments collected. In addition, some other plants were also dug up with the greatest possible care, and the root systems were mapped to scale. Seedling budsage, 2- and 4-year-old budsage specimens, and specimens 4 inches high were excavated and drawn to scale to compare the development of the root system as the plant matured.

Ring counts were made on 25 plants in each of four size classes. The plants were cut at the ground level, because this is usually below the point where the plant is branched. The ring count inspection was confined to the pattern of growth layers between adjacent rays.

RESULTS AND DISCUSSION

Seedling Development

Budsage seedlings have two very small orbiculate dark green cotyledons. The seedlings grew rapidly and in 10 days from planting some seedlings grown in moist sandy soil had some deeply lobed leaves and were 10.2 mm high. The lowest leaves were lobed and the upper ones entire. The roots were 5-7 inches (12.7-17.8 cm) long having several short branchlets. If the soil was allowed to dry out during the first 20-30 days of development, the seedlings died. This was true whether the plants were planted in soil flats or growing naturally. During the first year of growth, the shoot did not grow more than 3/8-7/16 inches (8.5-11 mm) high and the roots grew to 5-8 inches (12.7-20.3 cm) deep.

In 1963 a group of natural seedlings was given supplemental water and a comparable group was not. The former group broke summer dormancy August 28, and the latter group broke summer dormancy 2 weeks later. The total growth displayed by either group was, however, essentially the same when cold weather began in late September; all plants produced one or two twigs bearing leaves up to 5.5 mm long. The following spring, no difference in growth could be detected between the two groups. Before the seedlings became summer dormant, they produced an average of four new lateral twigs and one terminal twig that were 6.3 to 19.0 mm long. These plants became dormant by June 21, 1964.

During the summer of 1964, the seedlings received the same treatments as in 1963. Those that did not receive supplemental water remained dormant throughout the summer. The group that received supplemental water began to break dormancy in mid-July. The only obvious growth was new leaves. However, not all of the young plants produced new leaves, although all produced new root growth. At the end of the summer, the group that was watered had root systems considerably larger than the one that was not watered.

Plant Growth and Development

Budsage broke dormancy by late August of 1963 in response to storms that yielded sufficient moisture to penetrate the soil 25.4 to 30.5 cm. The terminal buds burst and produced small, new leaves; the stems did not elongate. The stems remained very short, mostly within the protecting petiole base of the previous year's leaf in whose axil they were growing, until the following March when elongation occurred. The maximum leaf length produced that fall was 5 mm. From plants that were dug up, it was obvious that the greatest amount of growth in the early fall was in the root system. The tap roots had produced many new branch roots.

Shortly after the plants broke dormancy in late August, the stems began to slip. Sheep grazed budsage from the time they arrived on the winter range in November 1963 through April 1964. Previously, slipping and the grazing period of this species were thought to occur only in late winter or early spring (Cook and others 1954).

The precipitation of the summer of 1964 was not enough to permit breaking of dormancy in budsage as in 1963, and the plants did not slip or become usable browse for sheep until March 1965. But the late summer of 1965 again brought abundant moisture and slipping occurred early in the fall. Once again, as 2 years earlier, budsage was browsed by sheep throughout the following winter.

In the late summer and fall of 1963, storms over the northern portion of the DER yielded enough rain so that the soil was visibly moist from the surface down to 30.5 cm by the first of September. Near the valley bottoms, moisture was visible down to 38.1-45.7 cm deep at the end of November. The maximum depth was 50.8 cm to which the moisture penetrated during the fall and winter before budsage began to elongate in March 1964.

The wetting front of the soil from Site 4 was below 1.2 m throughout the entire summer in both 1963 and 1964. Budsage is sufficiently deeply rooted at this location that the onset of summer dormancy is usually 2 weeks later than that observed at the other study sites.

In most years and on most sites, the annual growth of budsage is completed by the first of June. The terminal and lateral buds generally expand and begin to elongate in late March and early April at the latter part of the slipping period. Bud burst has been recorded as early as February 6 and as late as April 13.

Leaves and flower heads usually begin to turn brown in early June; by the third week of June, both were falling off the plants. All the leaves and flowers were gone by the first week of July, and the annual growing cycle was completed. In years of spring drought, summer dormancy may occur in early June.

Flowering

In general, flower buds begin to elongate two weeks later than vegetative buds. However, in February 1964, some floral buds located just below the terminal buds on the previous season's growth elongated to 6 to 9 mm long.

Budsage usually blooms from the last week of April through the last week of May. It has been found from herbarium specimens that this species has bloomed as early as March 29 at 6000 feet (1829 m) elevation in White Pine County, NV. (Moore m 537, Brigham Young University Herbarium) and March 24 at 2700 feet (1341 m) elevation near Empire City, NV (Jones, June 19, 1882, Intermountain Herbarium, Utah State University).

Flowering may occur when plants are as young as 2 years old. This species, however, ordinarily blooms in the fourth or fifth growing season. This average age of first flowering was determined from a survey by making ring counts of many young plants that had only 1 to 2 flower stalks, and which obviously had not flowered previously because there were no persistent spines on them.

Root Growth and Development

Budsage has a short thick vertical toproot up to 15 cm long, with many small horizontal branches. New root growth in budsage was first observed on plants that broke summer dormancy by late August 1963. The new rootlets were produced from the short taproot and from the larger horizontal branches. The newest roots were very succulent and whitish in color. The more mature new roots were somewhat woody and brown in color.

Table 4 reports the total length of new root growth that occurred in three trenches dug along one side of three plants at site 1. The period of growth was from August 23 to December 1, 1963. Even though this sample is only a part of the roots of the whole plant, it does point out that a considerable amount of root growth will occur when there is adequate later summer moisture.

The new roots produced were found in the top 30.5 cm of soil-- principally at the 15 cm level. One of the plants that was dug up had a new root that was at least 45.75 cm long. It grew across the trench through the disturbed soil in a horizontal direction at 15 cm below the ground surface.

Further examinations in February 1964 and June 1964 indicated that root growth continued at a low slow rate from December 1963 to February 1964 and then the rate increased from February to June. There are no comparable data for June because badgers dug up the plants. Nevertheless, in June water became a limiting factor and root growth ceased that growing season. Most of the roots grew in the top 7.6 to 17.8 cm of soil at both locations.

Table 4.--Amount of new root growth produced (August 23, 1963 to December 1, 1963) by three A. spinescens plants

Plant	Total length of succulent roots		Total length of brown roots		Total	
	inches	cm	inches	cm	inches	cm
A	66.25	168.3	24.50	26.2	90.75	230.5
B	38.50	97.8	--	--	38.50	97.8
C	21.50	54.6	89.00	226.1	110.50	280.7

Occasionally budsage produces adventitious roots. This occurs when the lowest branches are completely covered by soil. Plants growing in the bottomlands produced adventitious roots more often than those growing on benches.

The taproot of seedlings does not grow much deeper than 5 inches (12.7 cm) during the first year (fig. 4), and then lateral branchlets are produced (fig 5). As the plants mature, the taproot becomes much branched (fig. 6). The root systems shown are not complete, but show the relative amount of branching, rather than the total length of growth away from the taproot.

Roots of budsage are commonly found in the top 38.1-50.8 cm of soil and may be as shallow as 2.5-7.6 cm deep. Roots grow out in a horizontal direction as much as 1 m and as deep as 1.1 m.

Horizontal branch roots as long as 2.1 m have been observed. Depth of soil, soil texture (which includes the amount of gravel present), and depths to which moisture penetrates seem to be the primary physical factors that determine the depth of penetration and distribution of the roots of budsage.

The roots of this species are much more branched and more thoroughly interpenetrate the soil than its associated shrub species. Such a highly branched root system allows budsage to take advantage of the limited spring soil moisture supply before the summer drought comes.

Budsage evades summer drought, yet it is able to take advantage of late summer rains and break dormancy. It is well distributed, but its relatively shallow root system is probably the key to adaptation to drought conditions and an

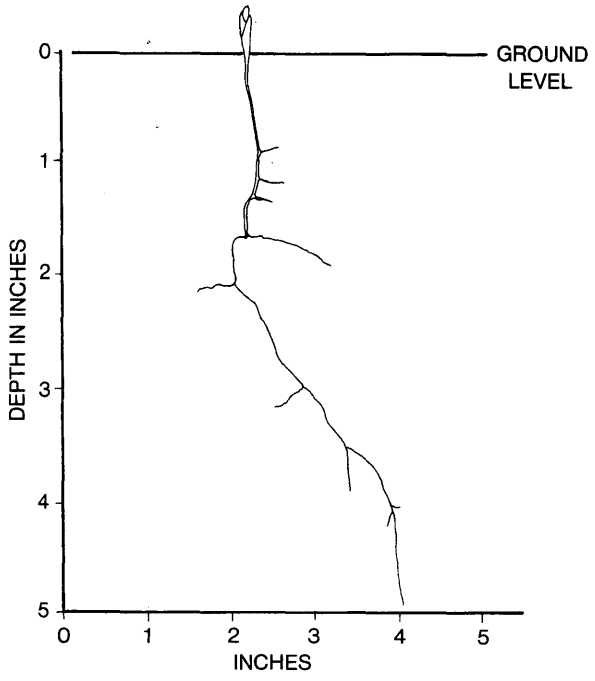


Figure 4.--Artemisia spinescens plant 26 days old. Seed was collected and planted June 11, 1964.

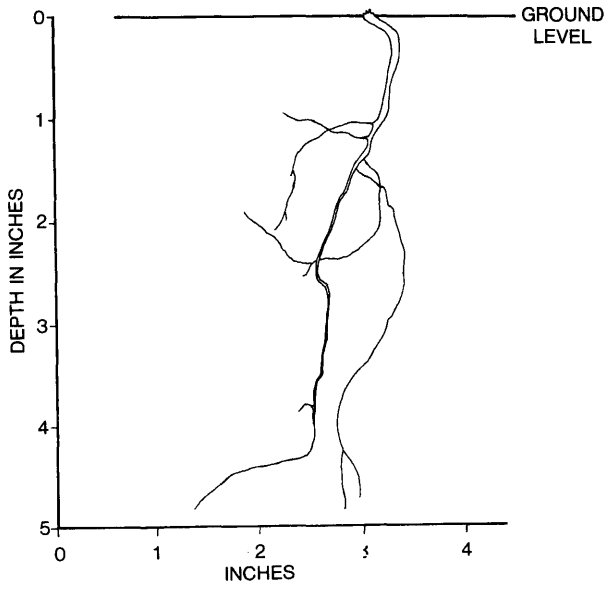


Figure 5.--Root system of a 1-year-old A. spinescens seedling.

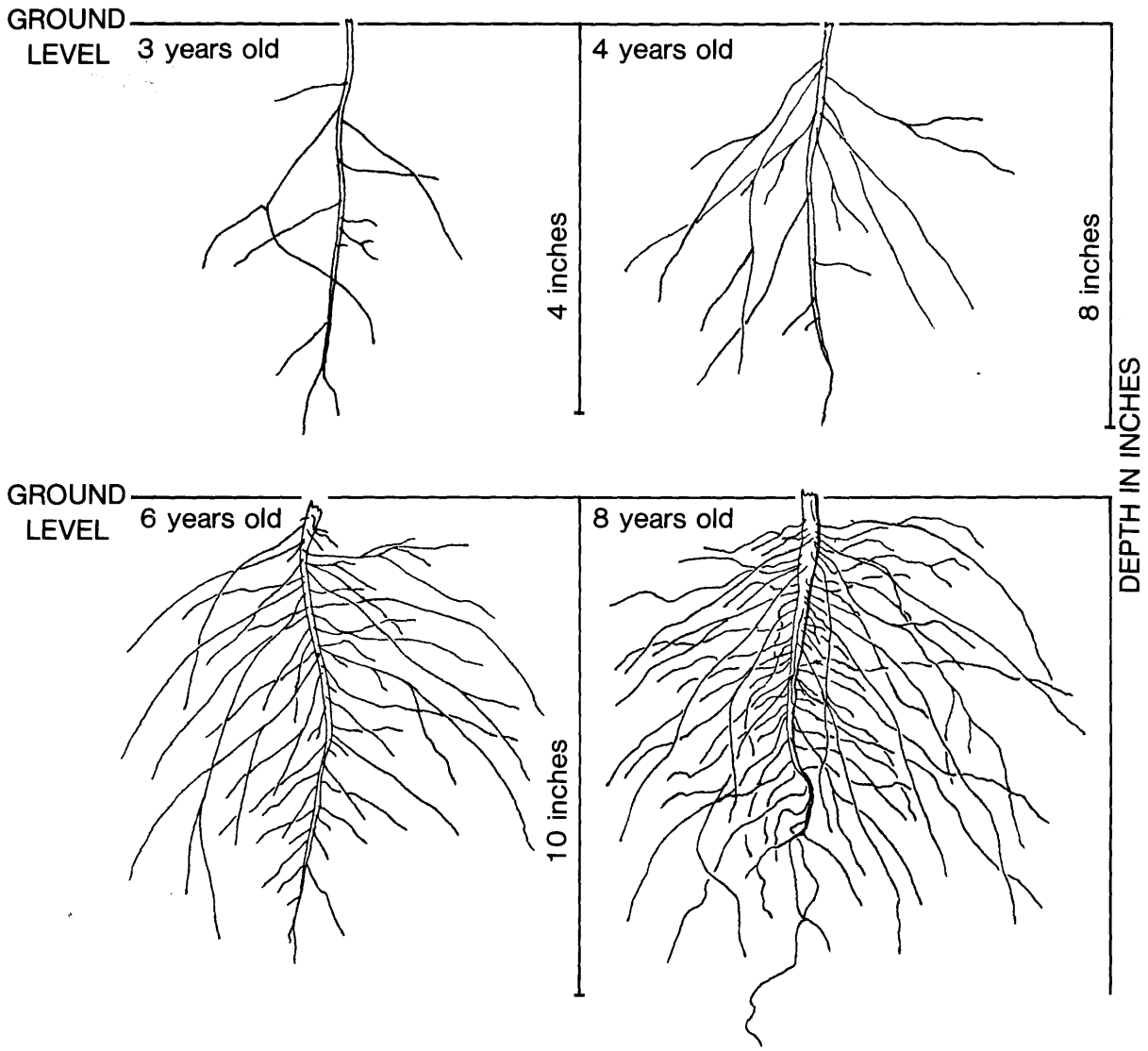


Figure 6.--Development of a much-branched root system on A. spinescens plants. Age was determined by counting annual rings.

ability to break dormancy when adequate moisture is present. Consequently, this species is able to taken advantage of summer moisture, but if moisture does not come, budsage is not seriously affected because it is dormant. If late summer rains do come, it does not put out an expanse of transpiring leaves. Substantial amounts of growth, however, can occur in the root system.

During those months in which growth conditions are suboptimum, only the small leaves and twigs are photosynthetic. Active growth takes place only when there is a more dependable supply of moisture in the spring and when evaporation is low.

Longevity of Budsage

It is difficult to obtain accurate ring counts on budsage because the center of the stem and root has usually rotted or has been eaten by boring insects. A lobing habit multiplies this difficulty of counting rings. In advanced age, the lobes separate and form a decumbent or nearly prostrate collection of stem segments (fig. 7).



Figure 7.--Artemisia spinescens that has separated into three branches.

Stem diameter is not necessarily proportional to age. From field observations it was found that large, rapid growing bushes reach an early maturity.

Plant counts of budsage on eight, 100-ft^2 charting quadrats in each of six experimental pastures of the DER indicated some plants were at least 29 years old. In the protected quadrats, out of 84 plants mapped in 1935 nearly one-fourth were still alive in 1964 (table 5). On the other hand, only 14 percent of the plants on the grazed quadrats were still present in 1964 (table 6).

Other observations on establishment of budsage in plots that contained no plants of this species in 1935 were made in pasture 16 which is grazed moderately in early winter. From 1935 to 1964, budsage became established at the rate of 23 plants per 400 ft^2 (37.2 m^2) in the protected enclosures and 3 plants per 400 ft^2 on the grazed areas. The lower establishment on the grazed plots can probably be attributed to preferential heavy use of individual plants. Effects of grazing on establishment are discussed later in this paper.

Table 5.--Number of A. spinescens plants that had become established since 1936, and were still alive in 1964. Grazing intensity was judged as follows: light = 10 sheep days per acre; moderate = 14 sheep days per acre; heavy = 17 sheep days per acre

	Season of use			
	Midwinter		Late winter	
Grazing intensity	Protected	Grazed	Protected	Grazed
Light	34	2	5	0
Moderate	17	21	2	1
Heavy[1]	26	13	11	0
Totals	77	36	18	1

[1]Number of plants per four 100-ft^2 (9.3-m) charting quadrats; the other data are plants per eight quadrats.

Table 6.--Survival of individual A. spinescens plants from 1935 to 1964. Grazing intensity was judged as follows: light = 10 sheep days per acre; moderate = 14 sheep days per acre; heavy = 17 sheep days per acre

	Protected		Grazed	
Grazing intensity	No. plants present in 1935	No. original plants still present-1964	No. plants present in 1935	No. original plants still present-1964
		Grazed in midwinter		
Light	4	0	12	2
Moderate	8	2	20	4
Heavy	24	3	13	0
Totals	36	5	45	6
Percent survival		13.9		13.3
		Grazed in late winter		
Light	29	8	35	6
Moderate	17	5	22	3
Heavy[1]	2	2	3	0
Totals	48	15	60	9
Percent survival		31.5		15.0

[1]Number of plants per four 100-ft^2 (9.3-m) charting quadrats; the other data are plants per eight quadrats.

Effect of Clipping

At each of six sites, ten 200-ft^2 plots were randomly selected. In August 1963, current annual growth was estimated than clipped on five plots and estimated only on the remaining plots. In August 1964, all plots of the ten were clipped.

All of the plants clipped in 1963 had noticeable dieback on the clipped twigs. These dead areas extended 3 to 13 mm below the part of the stem which had been clipped. At the base of the dieback, from one to five, but ordinarily two, new lateral twigs were produced from latent, lateral buds. Almost all of the clipped plants produced more lateral vegetative twigs than those that were not clipped.

Because the current year's growth was clipped off, most of the buds which would have produced flowers in 1964 were also removed. Consequently, the clipped plants produced very few flowers in 1964. The flowers that were produced on the clipped plants came from flower buds located at the very base of the previous season's growth that were missed in twig removal. No latent reproductive buds were observed on stems older than the current year's growth.

Data regarding the effects of clipping are presented in table 7. In every case there was an increase in the number of twigs per plant from 1963 to 1964. This increase was greater on the clipped plants than on the nonclipped plants. The length of the twigs produced in 1964 was generally longer on the clipped plants. Only at site 7 was the length of the twigs on clipped plants shorter in 1964.

The plants from the protected site showed that the clipping in 1963 stimulated a small increase in herbage yield. The plants on the sites grazed by sheep and cattle had variable response. The data, however, show that the clipped plots produced more vegetative growth than the plots that were not clipped. Wherever there was a decrease, the decrease on the unclipped plots was greater than on the clipped; wherever there was an increase, the increase on the clipped plots was greater than on the unclipped.

One possible reason for this increase, even though the clipping was severe, is that the clipping removed essentially all of the reproductive potential; consequently, the plants were forced to produce only vegetative growth. It is not known how long the plants could withstand such severe clipping or grazing. These and other observations suggest that repeated heavy grazing may kill budsage quite rapidly.

Table 7.--Effect of clipping on A. spinescens. Average precipitation for October 1962 to May 1963 was 3.50 inches; for October 1963 to May 1964, 4.09 inches (Average for October to May period was 3.76 inches)

Sites	Treatment	Average number of twigs per plant		Average twig length (inches)		Productivity Grams/1000 ft^2		Percent change
		1963	1964	1963	1964	1963	1964	1963 to 1964
Protected:								
Ungrazed area	clipped	33.4	124.4	0.5	0.8	120	140	+17
(site 1)	control	30.1	69.5	0.5	0.7	180	87	-52
Grazed by sheep:								
Allotment No. 3	clipped	28.7	57.7	1.0	0.7	60	70	+17
(site 7)	control	22.0	40.5	0.5	1.2	65	60	-8
Allotment No. 2	clipped	19.9	42.6	0.5	0.8	125	172	+38
(site 8)	control	15.3	31.7	0.4	0.8	135	170	+26
Grazed by cattle:								
Burbank Junction	clipped	45.3	79.9	0.4	0.9	316	304	-6
(site 4)	control	38.7	38.9	0.8	0.8	280	172	-39
Lower Pine Valley	clipped	45.2	147.5	0.5	1.5	132	280	+112
(site 5)	control	46.8	78.5	0.7	1.4	175	202	+15
Hamlin Valley	clipped	--	--	--	--	386	380	-2
(site 6)	control	--	--	--	--	375	215	-43

EFFECTS OF GRAZING

Ratio of Spine to Vegetative Twigs

In 1964 and 1965 plants were chosen and their current year's vegetative twigs and current year's spines were counted. A spine/ vegetative twig ratio was then computed. These data were obtained from a protected area, from moderately winter grazed DER pastures and from a heavily winter grazed allotment. Table 8 presents the total number of vegetative twigs and spines counted on the plants and the computed ratios. Even though these data do not represent clearcut interactions between grazing and plant growth because the effects of climate, specifically precipitation, are included, they do indicate that heavy grazing and late winter grazing adversely affect production of vegetative twigs and spines, respectively.

These data also indicate that some grazing in midwinter may actually stimulate growth of twigs, which become spines. This observation is proposed because the number of spines produced in 1964 and 1965 under moderate midwinter grazing did not change.

The apparent difference in the spine/twig ratios of plants under moderate grazing can probably be explained on the basis of herding. Sheep in a pasture tend to be more confined, thus graze preferred species more repeatedly than those in an allotment, which is more like being on open range.

The large decrease in the spine/vegetative twig ratio in the enclosure was probably related to plant vigor. These plants were rather large and symmetrical compared to the grazed plants. The grazed plants had branches with varying lengths and numbers of buds, and therefore had less variation in the spine/twig ratio, except under the heavy grazing regime.

Each year all of the flower buds elongate and few, if any remain latent. When the plants are grazed or clipped, they produce mostly vegetative growth from latent buds on stems older than the current year's growth. Normally fewer flower stalks were observed per plant in areas grazed by sheep than in areas grazed by cattle or in protected areas.

The effects of grazing on plant establishment are reported in Table 5. Plant establishment appeared directly affected by season of grazing but not by the intensity of grazing.

Cover of A. spinescens

On the DER, budsage is present in moderate amounts in most of the plant communities (tables 9 and 10). The period of grazing on this species is shorter, and the amount of herbage it produces is less than that of the associated shrubs. The percentage utilization on budsage is highest during the late winter (Hutchings and Stewart 1953). During February and March, it usually is one of the principal shrubs browsed by sheep. Nevertheless, this species does not

Table 8.--Spine:vegetative ratio of plants under protection and grazed moderately and heavily

Grazing	Vegetative twigs per plant		Spines per plant		Spines:twigs	
	1964	1965	1964	1965	1964	1965
A. Moderate[1]						
Midwinter season						
DER Allotment No. 2, Unit No. 2	22.0	27.6	27.0	32.4	1.23	1.17
DER Pasture 2	27.5	34.5	17.7	18.1	0.64	0.52
Mid - late winter season						
Pasture 6	31.9	48.4	76.0	24.9	2.38	0.51
B. Heavy[2]						
All winter season						
Antelope Valley - BLM Rangeland	25.4	20.7	18.0	9.7	0.71	0.47
C. Protected						
Enclosure in DER Pasture 2	38.3	40.1	87.2	43.9	2.28	1.09

[1]Moderate = 53% utilization of herbage produced the previous summer (14 sheep-days per acre).

[2]Heavy = 68% utilization of herbage produced the previous summer (17 sheep-days per acre).

Table 9.--Cover data for six desert communities. Site No. 5 was evaluated using the line-point method which is a modification of the point-frame method of Levy and Madden (1933). The other communities were evaluated using the line-intercept method (Canfield 1941). Six 100-foot (30.5 m) transects were used at each location "T" = 1% cover

Site factor	Site number 1	2	3	4	5	6
	% cover					
Bare soil	66	81	77	56	74	82
Litter	16	6	8	20	11	--
Vegetation	19	13	15	24	15	18
	% composition					
Artemisia spinescens	9	51	26	28	10	75
Ceratoides lanata	15	49	T	--	T	25
Atriplex confertifolia	13	--	59	8	29	--
Chrysothamnus viscidiflorus ssp. stenophyllus	10	--	--	--	--	T
Sarcobatus vermiculatus	--	--	--	64	--	--
Opuntia sp.	--	--	--	--	T	--
Ephedra nevadensis	--	--	2	--	--	--
Oryzopsis hymenoides	11	--	2	--	5	--
Hilaria jamesii	10	--	--	--	12	--
Sporobolus cryptandrus	--	--	T	--	--	--
Aristida fendleriana	1	--	--	--	--	--
Bromus tectorum	--	--	T	--	--	--
Sphaeralcea glossulariaefolia	T	T	T	--	--	T
Salsola iberica	30	--	--	--	44	--
Aster sp.	1	--	T	--	--	--
Lappula redowski	--	--	T	--	--	--
Halogeton glomerata	T	--	5	T	--	--
Astragalus lentiginosus	--	--	--	--	T	--

Table 10.--Plant density of five desert communities. Values represent numbers of plants per square meter. p = present but not counted

Species	Site number 1	2	3	4	5	6
Artemisia spinescens	2.4	21.6	9.7		1.6	35.2
Ceratoides lanata	5.6	33.9	0.2		0.1	31.5
Atriplex confertifolia	2.8	--	21.6		3.4	--
Chrysothamnus viscidiflorus ssp. stenophyllus	0.9	--	0.1		--	0.3
Opuntia sp.	--	--	--		0.6	--
Tetradymia spinosa	--	--	--		0.1	--
Xanthocephalum sarothoae	--	--	--		3.3	--
Oryzopsis hymenoides	2.3	--	0.5		48.9	--
Hilaria jamesii	17.8	--	--		--	--
Sporobolus cryptandrus	--	--	p		--	--
Aristida fendleriana	0.1	--	0.1		0.2	--
Sphaeralcea glossulariaefolia	--	--	0.8		0.1	--
Salsola iberica	p	--	0.8		14.9	--
Aster sp.	1.3	--	--		--	--
Halogeton glomerata	--	--	p		0.6	--
Astragalus lentiginosus	--	--	--		1.0	--

constitute a large portion of the sheep's diet, because it is usually a minor constituent of the available forage. In most of the communities in which it occurs, budsage is less than 20 percent of the total cover. However, it does constitute an important portion of the forage, especially in years when it breaks dormancy in late summer or fall. As pointed out earlier, in the 1963-64 and 1965-66 grazing seasons, it was grazed through the entire winter season at the DER. Sheep graze the growth of the preceeding season on the erect and easily obtainable twigs and the green foliage as it expands and grows in the early spring. If this species is the only one to begin growth in early spring, it is preferentially grazed and probably grazed rather heavily.

The relative amount of shrubs contributing to the total cover was markedly higher in 1964 than in 1935 in the enclosures and adjacent grazed areas except those which were heavily grazed (table 11). In each of the enclosures, there has been a marked increase in budsage with a simultaneous decrease of shadscale. In pastures 11 and 12, budsage increased from about one-fifth to about one-half of the shrub cover. This represents an actual increase from 8.4 to 44.0 percent of the total plant cover for pastures 11 and 12, respectively. This same trend also occurred in the enclosures of pastures 10 and 15 (Holmgren and Hutchings 1972).

The trends in cover composition of budsage with respect to grazing by sheep indicate that season of grazing is more important than intensity of grazing. This is because this species ordinarily does not slip until late winter, and therefore, is usually not grazed until then. Regardless of grazing intensity in midwinter, its cover composition did not change from 1935 to 1964 (Holmgren and Hutchings 1972). On the other hand, under light grazing in late winter, budsage decreased from 12.9 to 3.9 percent of the total plant cover. Heavy grazing in late winter has almost eliminated this species, while winterfat remained almost constant. Additional evaluations by Holmgren and Hutchings (1972) show winterfat has actually decreased under late winter, heavy grazing. Because of its high palatability, especially in late winter, budsage is one of the first plants to be affected by heavy grazing.

Density of Budsage

The effects of grazing by season on the density of budsage and three associated species are presented in figures 8 and 9. In all of the protected areas, there is a trend of shrubs increasing at the expense of Indian ricegrass. In general, the density of budsage increased or remained essentially the same. Where winterfat was present in large numbers, it decreased in the ungrazed enclosures from 1936 to 1964; where winterfat was present in low numbers, it increased.

Light grazing in midwinter at pasture 11 allowed budsage to increase somewhat, but the increase was not as great as that in the enclosure. Budsage and winterfat decreased and shadscale and Indian ricegrass increased at pasture 2, which is grazed moderately in midwinter. In pasture 12, which is heavily grazing in midwinter, budsage, shadscale, and Indian ricegrass decreased, whereas winterfat increased.

Table 11.--Percentage change of A. spinescens numbers from 1936 to 1964 on protected and grazed plots. Plant counts were made on 80 200-square-foot plots in each treatment at each site. Grazing intensities were judged as follows: light = 10 sheep days per acre; moderate = 14 sheep days per acre; heavy = 17 sheep days per acre

Grazing intensity and season	DER pasture	Protection			Grazed		
		1936	1964	% change	1936	1964	% change
Light:							
Midwinter	11	301	746	+134	335	520	+55
Late winter	10	1007	1007	-11	831	187	-77
Moderate:							
Midwinter	2	254	953	+275	557	277	-52
Late winter	6	775	807	+4	698	161	-77
Heavy:							
Midwinter	12	495	1286	+160	663	677	+0.6
Late winter	15	274	892	+225	396	48	-88

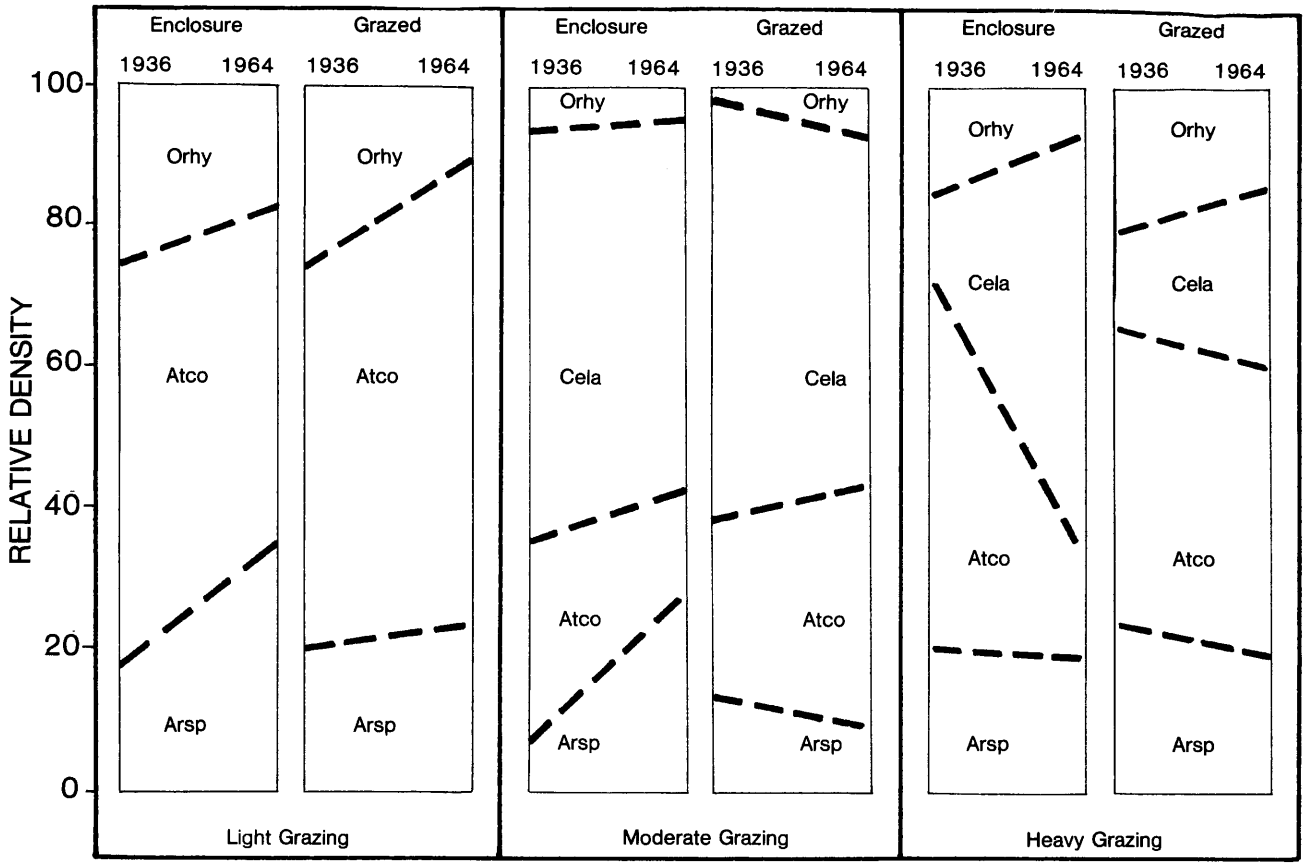


Figure 8.--Effects of midwinter grazing on relative density of A. spinescens, Atco - Atriplex confertifolia, Cela = Ceratoides lanata, and Orhy = Oryzopsis hymenoides.

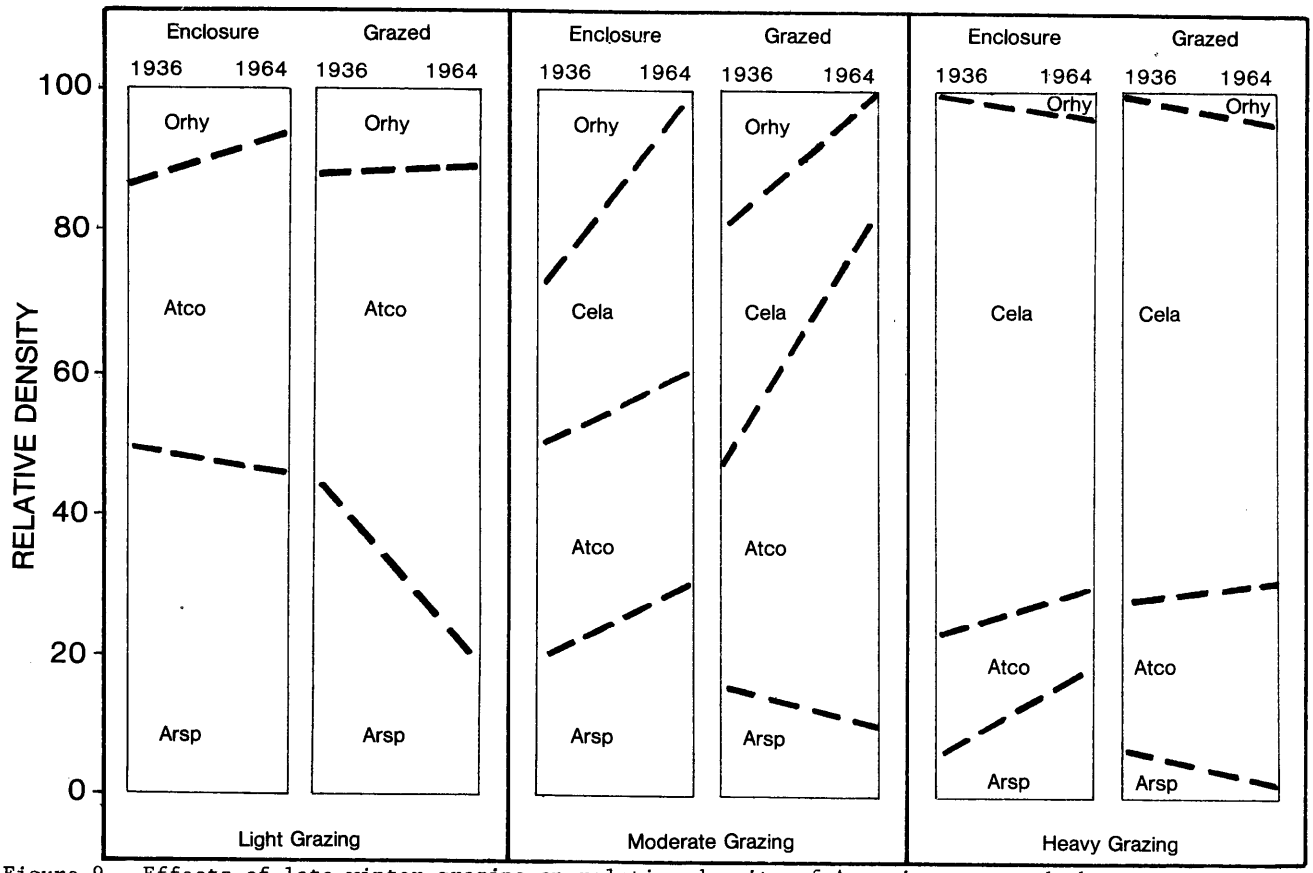


Figure 9.--Effects of late winter grazing on relative density of A. spinescens and three associated perennial species. Arsp = A. spinescens, Atco = Atriplex confertifolia, Cela = Ceratoides lanata, and Orhy = Oryzopsis hymenoides.

Grazing in late winter decreased both budsage and winterfat resulting in a corresponding increase in shadscale. The decrease of budsage under both heavy and moderate grazing was approximately the same, 5 percent. However, pasture 15, the more heavily grazed pasture, had only a small amount of budsage to begin with, and heavy grazing at this site has almost eliminated it. On the other hand, light grazing at pasture 10 has also severely decreased this species. Because pasture 10 is dominated by only two shrub species, budsage is preferentially grazed detrimentally. This is not the case in pastures 6 and 15, even though they are grazed moderately and heavily, respectively, because winterfat is present in those two pastures and it receives some of the grazing pressure budsage would otherwise receive. Shadscale, the least palatable species, increased under any grazing intensity during late winter.

Figures 8 and 9 also show that the grazed acres under all six treatments have deteriorated. In no case is variety of species as good as it was 28 years earlier. The percentage change of the number of budsage plants from 1936 to 1964 is reported in table 11.

The same trends, budsage increasing under protection or light grazing in midwinter and decreasing when grazed in late winter, were also observed on a range allotment of the DER as well as the open range. In these areas, field observations indicate that where budsage is common, it is preferentially and rather heavily grazed in late winter until other plants such as forbs, grasses, and winterfat begin to grow. In order to maintain these areas, sheep must not be allowed to remain too long.

It is generally accepted that change in composition of dominant palatable and unpalatable species is a function of grazing pressure. Norton (1978) studied many of the same plots from which the cover and density data presented here were taken, and after considering all species concluded there is a general lack of difference between survival of grazed and ungrazed populations. Norton (1978) also concluded there are only small differences in the vegetation and its changes under different intensities of use. The above conclusions were based on evaluations comparing grazed and ungrazed populations without pointing out the interactions of season and intensity of grazing that have particular application in the case of budsage.

Figure 10 illustrates a comparison between site 2, which is moderately grazed in midwinter every other year, and the adjacent heavily grazed open range. The stand within the fence is 51 percent budsage and 46 percent winterfat by cover. The stand on the open range is almost 100 percent winterfat. Heavy grazing has essentially eliminated budsage.

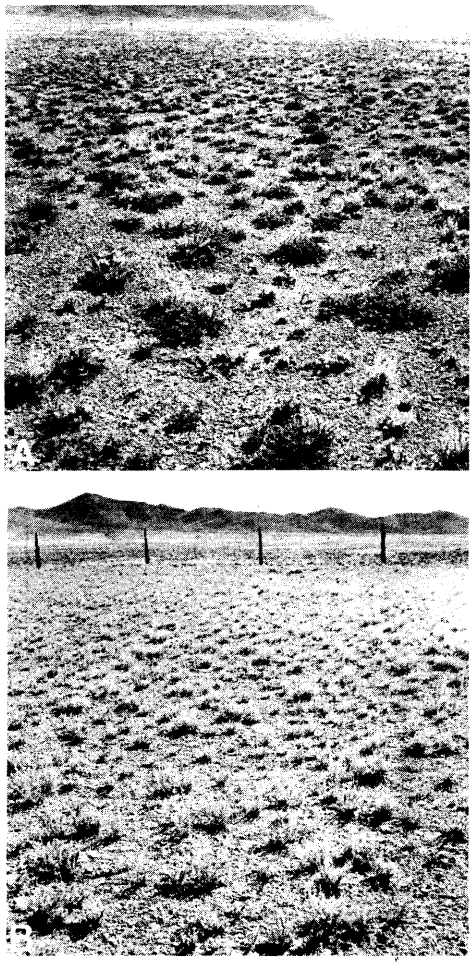


Figure 10.--Comparison of adjacent moderate and heavily grazed areas. Vegetation in the moderately grazed area (A) is an A. spinescens - C. lanata stand; that of the heavily grazed area (B) is almost a pure stand of C. lanata. Photos correspond to site 3 in table 1. The dark plants in photo "A" are A. spinescens and the light ones are C. lanata.

Heavily grazed plants become hedged and grow close to the ground. These plants may never produce flowers at all; consequently, seedlings are rare. The budsage plants in the open range allotments are small hedged plants. In those areas that were not grazed during the 1962-63 grazing season, most of the plants produced only a few flower stalks. However, in 1963, hardly any plants produced even one flower stalk because nearly every twig of the 1963 growing season had been grazed off short enough to remove reproductive buds.

The combination of the effects of grazing and climate tend to produce stands of budsage which are even aged, or that have only two or three age classes. The stands are also generally of the same size and state of vigor. Only in protected areas or in areas having mixed shrubs

and grasses are there plants of all ages, size classes, and different states of vigor. Protected plants are not as bushy as those that are lightly or moderately grazed. Even light grazing was found to break apical dominance allowing more lateral buds to elongate. Consequently, lightly grazed plants tend to be more rounded with the larger branches having more lateral bud development.

ACKNOWLEDGEMENTS

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CYTOGEOGRAPHY OF CHRYSOTHAMNUS VISCIDIFLORUS

Loran C. Anderson

ABSTRACT: Polyploidy in Chrysothamnus (Asteraceae) is restricted to three of the five subspecies of C. viscidiflorus. Comparisons between the diploids and polyploids are made for each subspecies. Geographical and climatological correlations show that polyploids in each case seem to be adapted to warmer, usually drier sites than their diploid counterparts. Ironically, the two subspecies known only as diploids also occur in the warmer, drier parts of the species' range.

INTRODUCTION

Chromosome numbers have been determined for nearly 500 populations representing all taxa of Chrysothamnus. Polyploidy is restricted to C. viscidiflorus (Hook.) Nutt. All other species are basically diploid with x = 9. Rarely, an individual in a diploid population has been shown to be tetraploid, or a few cells in a diploid plant are polyploid.

Chrysothamnus viscidiflorus has five subspecies. The ssp. axillaris (Keck) L.C. Anderson and ssp. planifolius L.C. Anderson are known only as diploids (2x). Subspecies lanceolatus (Nutt.) Hall & Clem. and ssp. puberulus (D.C. Eaton) Hall & Clem. have both 2x and 4x populations, whereas ssp. viscidiflorus has 2x, 3x, 4x, 5x, and 6x plants (the notation 2n, 3n, 4n, etc., is used in the figures). The triploid and pentaploid plants (one each) were atypical in appearance.

The polyploids are mostly autopolyploids (Anderson 1966) although allopolyploids (the term used here in a very narrow sense) derived from ssp. lanceolatus and ssp. viscidiflorus occur sporadically from northern Colorado to northeastern Nevada.

Chrysothamnus viscidiflorus is wide-ranging and has great ecological amplitude. Geographical and climatological data are compared with plant morphology and ploidy levels in an attempt to understand further the biology and taxonomy of the species.

METHODS

Chromosome counts for the 238 samples of ssp. lanceolatus, ssp. puberulus, and ssp. viscidiflorus used in this study have already been recorded (Anderson 1966, 1971; Anderson and others 1974). Measurements of vegetative and floral features were taken as in Anderson (1964).

Altitude and latitude were determined for each collection. Mean annual temperature and mean annual precipitation were obtained mostly from U. S. Weather Bureau documents. Data for more remote collection sites were supplied by state climatologists, but precipitation data for a few collections were not available.

Statistical studies of the plant and environmental data included multivariate analysis and Wilk's Lambda test.

RESULTS

Analysis of Polyploid Subspecies

C. v. ssp. lanceolatus.--This subspecies ranges from southern British Columbia to northern New Mexico. Specimens of diploids used in this study came from latitudes of 38°12'N. to 47°24'N. and occurred from 976 to 11,000 ft (297-3353 m) in elevation. The tetraploids studied had a greater range (36°0'N. to 49°02'N.) and came from 800 to 8,500 ft (243-2590 m) in elevation. Mean latitude and altitude are given for each ploidy level in table 1. Mean annual climatological data are also given.

Table 1.--Means for selected environmental and morphological data for C. v. ssp. lanceolatus. Features that are significantly different (1 percent level) are underscored

Feature	2x	4x
Latitude	41°11'N.	41°58'N.
Altitude (ft)	7,139.3	5,745.5
Annual temperature (°F)	38.01	43.68
Annual precipitation (in)	17.80	13.82
Leaf width (mm)	3.18	3.11
Leaf width/length	0.106	0.111
Involucral length (mm)	6.60	7.43
Corolla length (mm)	5.19	5.56

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Loran C. Anderson is Professor and Curator of the Herbarium, Florida State University, Tallahassee, FL.

Diploids have slightly longer, relatively narrower leaves than tetraploids, but the differences are not significant. The relatively shorter involucres and corollas of the diploids are significantly different when mean lengths are considered (table 1). However, sufficient overlap in size occurs to preclude use of such measurements to determine ploidy level of plants in the field. Other floral features were measured and statistically analyzed for each group but were not sufficiently interesting to record here.

C. v. ssp. puberulus.--This subspecies is largely a plant of the Great Basin. It was probably derived phylogenetically from ssp. lanceolatus. Specimens of diploids used in the study came from latitudes from 36°54'N. to 41°12'N. and from altitudes of 4,200 to 10,000 ft (1280-3048 m). The tetraploids studied have a narrower range in south-central Nevada and adjacent California at 36°30' to 38°06' north latitude; they occurred from 5,200 to 8,100 ft (1585-2467 m) in elevation. Mean latitude and altitude data are given in table 2. In that portion of the subspecies' range where both diploids and tetraploids occur, the tetraploids are at higher elevations. The tetraploids generally receive warmer weather and more precipitation than the diploids, but the differences are not statistically different.

Table 2.--Means for selected environmental and morphological data for C. v. ssp. puberulus. Features that are significantly different (1 percent level) are underscored

Feature	2x	4x
Latitude	38°39'N.	37°10'N.
Altitude (ft)	6,085.9	6,795.6
Annual temperature (°F)	47.42	48.07
Annual precipitation (in)	8.65	9.84
Leaf width (mm)	1.32	1.76
Leaf width/length	0.078	0.119
Involucral length (mm)	5.87	7.10
Corolla length (mm)	5.11	5.25

Diploids have generally shorter, relatively narrower leaves than the tetraploids. The diploids also have shorter involucres, but corolla lengths are not distinctive between the two groups.

C. v. ssp. viscidiflorus.--This subspecies is one of the most widespread taxa in the genus. It ranges from northern Washington, western Montana, and northwestern Nebraska to southern California and northern Arizona. It occurs in a wide variety of habitats, and the few soils that have been tested range in pH from 6.0 to 8.4

Specimens of diploids used in this study came from latitudes from 34°18'N. to 47°19'N. and from altitudes of 850 to 12,800 ft (259-3901 m). Tetraploids occurred, generally, but not exclusively, in more southern latitudes (35°05'N. to 46°18'N) and at altitudes of 960 to 10,300 ft (283-3139 m). In mountains of southern California, the southern limits of the subspecies' range, diploids occur, but in deserts of northern Arizona only tetraploids occur. At any given latitude where both occur, the tetraploids are generally at lower elevations than the diploids (fig. 1). But in northeastern Nevada and in eastern Washington the two ploidy forms can occur in mixed populations.

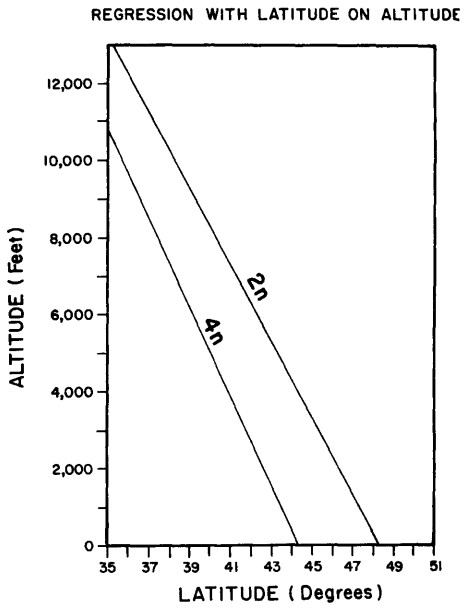


Figure 1.--Geographical relationships of cytotypes of C. v. ssp. viscidiflorus.

The hexaploids of the subspecies occur sporadically from southwestern Utah through south-central Nevada at latitudes of 37°06'N. to 39°12'N. and at elevations from 5,100 to 7,000 ft (1554-2133 m). Mean latitudinal differences among the three ploidy levels are significantly different. An excellent example of altitudinal and climatological zonation among the different ploidy levels is found on the Desert Experimental Range in southwestern Utah (fig. 2). The hexaploids occur in the Pine Valley desert mostly below 7,000 ft (2133 m) in areas that receive about 5.5-11 inches (14-28 cm) precipitation annually. The tetraploids are in the pinyon-juniper zones of the Needle Range and Wah Wah Mountains around 7,500 ft (2286 m) in elevation and receive about 12.5-13.2 inches (32-34 cm) of precipitation annually. Diploids

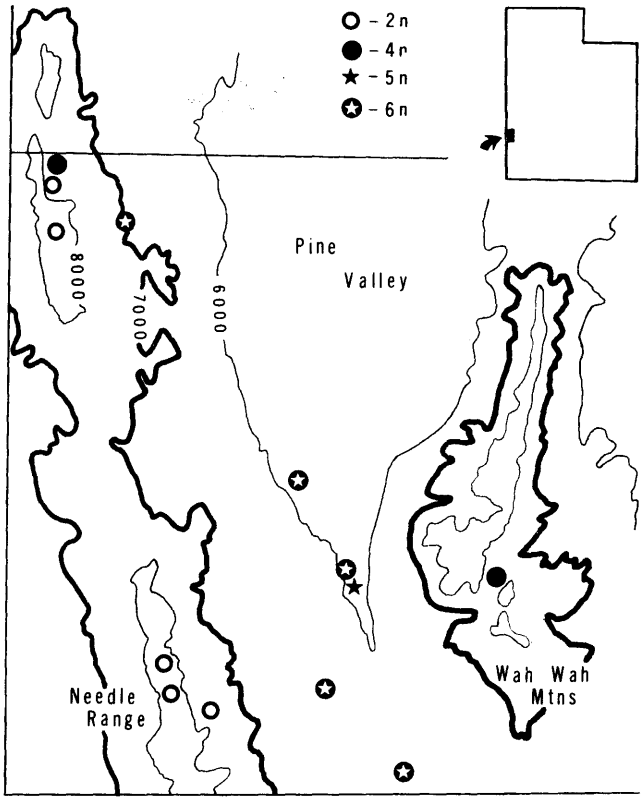


Figure 2.--Elevational distribution of ssp. viscidiflorus cytotypes in southwestern Utah (elevations in feet).

generally occur above 8,000 ft (2438 m) in the Needle Range and receive 15-17.5 inches (38-44 cm of precipitation annually.
Mean climatological data for all samples of this subspecies (table 3) show that diploids occur on the coolest and wettest (highest elevation) sites, whereas the hexaploids occur on the hottest and driest sites, with the tetraploids being intermediate.

The three major ploidy levels in subspecies viscidiflorus (2x, 4x, 6x) are not readily distinguishable in the field based upon morphological characteristics. However, measurements from all samples show that the mean leaf width and mean involucral and corolla lengths are significantly different for the three (table 3). In general, polyploids have increased cell size (Lewis 1980) and may show increased plant size when compared to diploids. The pattern is evident in involucral and corolla lengths--involucres and corollas of tetraploids are longer than those of diploids, and those of hexaploids are longer than those of tetraploids. The trend for increased size is not maintained in foliar features. Although the tetraploids have somewhat wider leaves than the diploids, the hexaploids have the narrowest leaves.

Table 3.--Means for selected environmental and morphological data for C. v. ssp. viscidiflorus. Features that are significantly different (1 percent level) are underscored

Feature	2x	4x	6x
Latitude	40°49'N.	38°53'N.	37°53'N.
Altitude (ft)	6,236.1	6,335.6	6,031.0
Annual temperature (°F)	43.75	46.86	46.45
Annual precip. (in)	13.50	12.31	7.36
Leaf width (mm)	2.42	2.91	2.29
Leaf width/length	0.073	0.078	0.066
Involucral length (mm)	6.58	7.22	8.13
Corolla length (mm)	4.97	5.49	5.67

Ploidy Level Sorting by Environmental Factors

Wilk's Lambda test was applied to the multivariate discriminant analysis of the data to determine the significance of environmental factors in sorting the ploidy levels by environmental factors. For C. v. ssp. lanceolatus, the computer had 80 percent accuracy in correctly sorting the diploids and tetraploids by mean annual temperature alone (2x with low temperatures; 4x with high temperatures).

For C. v. ssp. puberulus, the computer had 81 percent accuracy in sorting by primarily using latitude, then altitude, and then precipitation (2x with high latitude and low altitude and precipitation; 4x with low altitude and high altitude and precipitation).

For C. v. ssp. viscidiflorus, the hexaploids were not considered because of small sample size. The computer had 67 percent accuracy in its discriminating power using latitude and temperature equally (2x with high latitude, low temperature; 4x with low latitude, high temperature).

Ploidy Level Sorting by Morphological Features

Wilk's Lambda test was also used to determine the significance of selected morphological features in sorting ploidy levels. For C. v. ssp. lanceolatus, the computer was not able to sort the different ploidy levels effectively. It showed no significant differences in the morphologies even though the means for floral features were significantly different (table 1).

For C. v. ssp. puberulus, there was strong correlation between morphological features and ploidy level. The computer correctly sorted the

ploidy levels 87 percent of the time using first leaf width, then corolla length, and finally involucral length (table 2).

For C. v. ssp. viscidiflorus, the hexaploids were again omitted because of small sample size. Correlations for the diploids and tetraploids were weak. The computer had 64 percent accuracy in sorting leaf width. Other variables were not significant.

DISCUSSION

Early research on polyploidy suggested that the distribution of polyploids was generally correlated with increases in latitude or altitude. More recent research has failed to confirm those hypotheses (Ehrendorfer 1980). Chrysothamnus analyses certainly do not support those earlier views. Figure 3 gives a schematic summary of the relationships of cytotypes to one another and to geography. Diploids of ssp. lanceolatus and, especially, ssp. viscidiflorus seem generally to occur at higher latitudes or altitudes. Their polyploid derivatives occur at lower latitudes or altitudes. A similar pattern in the same geographical region has been reported for Atriplex confertifolia by Stutz and Sanderson (1983).

In figure 3, the dotted lines show tetraploids derived from crossing between ssp. lanceolatus and ssp. viscidiflorus. The dashed line suggests that the Great Basin ssp. puberulus may have been derived from the Rocky Mountain ssp. lanceolatus. The exception to the general trend

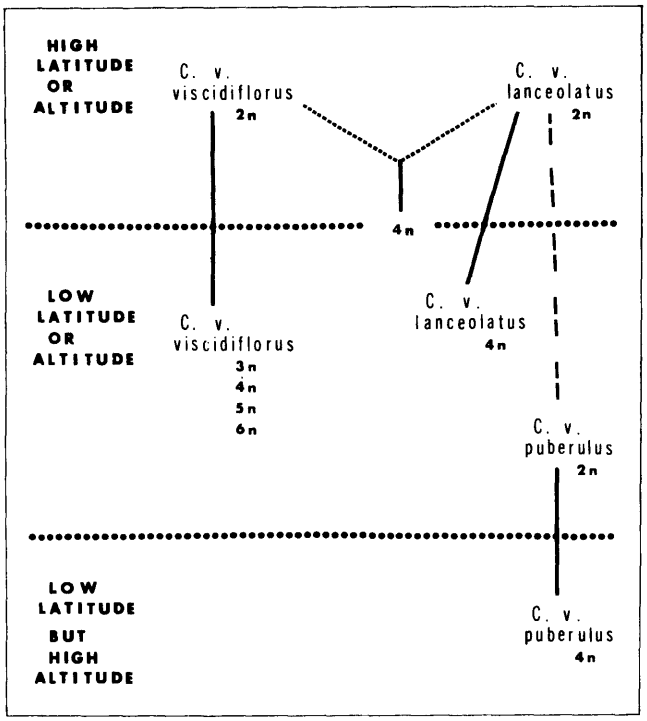


Figure 3.--Cytotype relationships in the polyploid subspecies of C. viscidiflorus.

in cytogeography in the species involves ssp. puberulus wherein the tetraploids occur at lower latitudes but at higher elevations.

Most of the lower latitudes of the Great Basin are those areas anciently covered by Lake Bonneville and Lake Lahontan. These areas represent the newer (and drier) habitats, and they are the sites largely inhabited by the polyploids of Chrysothamnus.

In an earlier study (Anderson and Fisher 1970), a numerical index of phylogenetic specialization was obtained for each taxon of Chrysothamnus based upon floral anatomy. Subspecies viscidiflorus with an index of 6.4 on a scale of 1 to 10 is thought to be the least specialized subspecies of C. viscidiflorus. The phylogenetic indicators may be applied to the data presented here. Subspecies puberulus is thought to be derived from ssp. lanceolatus. Diploid puberulus has a higher index (7.9) of specialization (i.e., is more advanced) than ssp. lanceolatus (7.6). The polyploids are clearly derived from the diploids in each subspecies. In each of the three subspecies, the tetraploids have slightly higher indexes than their diploid counterparts, which reinforces the presumed reliability of the floral indicators of specialization. Floral anatomy of hexaploids was not studied.

The preferential occurrence of polyploids of the three subspecies in the warmer, generally drier parts of the range of C. viscidiflorus is well documented here, but adaptation to those areas via polyploidy is not the only way. The ssp. axillaris and ssp. planifolius, which are known only as diploids, occur in the same warm, dry areas. Based on floral anatomy, the former has a relatively high index of specialization (8.0), but ssp. planifolius has an index of 7.3. Considering the entire genus, the diploid C. paniculatus occurs in the hottest, driest parts of the genus's range, and that species has the highest index of specialization in the genus, 9.3.

ACKNOWLEDGMENTS

Ralph C. Holmgren is thanked for providing seed for chromosome counts and climatological data from the Desert Experimental Range. Nick Gotelli helped with statistical analyses. This work has been supported by a series of grants from the National Science Foundation, the most recent being DEB-8021776.

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SYMPATRIC SUBSPECIES IN CHRYSOTHAMNUS NAUSEOSUS

Loran C. Anderson

ABSTRACT: Chrysothamnus nauseosus (Asteraceae) is the most complex species in the genus. The 22 recognized subspecies are variously allopatric, parapatric, or sympatric. Tendencies for inbreeding enhance the sympatricity. Some sympatric units represent distant members of a ring of races but are interconnected through a series of other subspecies. Others appear to be reproductively isolated over much of their sympatric ranges, but the isolation breaks down at the edge of one of the subspecies' geographical and ecological range limit.

INTRODUCTION

In western America, C. nauseosus is the most widespread species in the genus and the most complex taxonomically. Hall recognized 22 varieties of C. nauseosus in 1919, and he noted the difficulty in assigning specific or varietal rank to all of the forms with the following:

> Nothing can be more certain than that these forty-two attempts to recognize species and varieties do not by any means exhaust the resources of the group. Every autumnal excursion into a new district brings to light one or more forms not previously described. The only limits set to the number of new species or varieties which might be set up lie in one's ability to visit all parts of the field during the flowering period and the failure or disinclination to recognize minute variations.

In 1923, Hall and Clements recognized 20 subspecies. Now 22 subspecies are recognized, although not the same entities listed by Hall in 1919 (Anderson overview paper, this proceedings).

The complexity in C. nauseosus prompted Feddema (in Voss 1981) to propose:

> The overwhelming need for simplicity and stability in nomenclatural practice by non-botanical scientists and land managers must be considered. We would be reluctant to invite a proliferation of names in such complex genera as Artemisia and Chrysothamnus which are of such practical importance in the Western United States.

Simplicity and stability in nomenclature can only truly be obtained in such a difficult species complex when the taxonomy most closely approaches the major patterns of variation that are present.

Diversity in C. nauseosus is apparently due to a nearly optimal combination of outbreeding and inbreeding (Anderson 1966, 1973). There are no indications of apomixis in the species (Anderson 1970). Several subspecies are generalists with fairly wide ecological amplitudes, but some subspecies are more narrowly adapted in habitat and range.

The need for so many names in C. nauseosus can be understood, in part, through an examination of distributional patterns. Many subspecies maintain their identities despite overlapping ranges because of their tendency toward inbreeding. The terms allopatric and sympatric are commonly used to describe spatial relationships between populations or taxa. In allopatry the taxa live in different areas; they may be disjunct or contiguous (in the latter case they are often termed parapatric). Sympatric taxa live in the same territory. Grant (1981) subdivides sympatry into neighboring sympatry, wherein taxa live in different niches in the same general habitat, and biotic sympatry, where taxa live in the same niches.

Tendencies for inbreeding in subspecies of C. nauseosus make it difficult to assess the degree to which they can interbreed (Anderson 1973, McArthur and others 1978). Therefore, introgression between taxa is inferred here based upon extensive field observations and herbarium studies coupled with reduced pollen fertilities in certain specimens. Distributional patterns in and interrelationships among the more widely distributed subspecies are discussed below.

OBSERVATIONS

Map 1. Subspecies albicaulis and Subspecies nauseosus

The subspecies are parapatric. Their morphologies are distinct, but the taxa intergrade

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Loran C. Anderson is Professor and Curator of the Herbarium, Florida State University, Tallahassee, FL.

freely through their narrow zone of contact in western Montana and Wyoming. Such a distributional pattern fits that of classical subspecies.

Map 2. Subspecies albicaulis and Subspecies hololeucus

The subspecies are largely allopatric, but their ranges are adjacent in the Owens Valley of California and overlap in southwestern Idaho and central Utah. They are separate morphologically except in Utah where intergradation is evident. It should be noted that not all Utah specimens represent intergradants. Subspecies albicaulis occurs in the higher mountains and ssp. hololeucus occupies the basins. The two intergrade at the lower elevations in the mountains of Utah, but not in Idaho or in Owens Valley. Populations in the Spring Mountains of southern Nevada and Clark Mountain of adjacent California represent intergradants of these two subspecies.

Map 3. Subspecies albicaulis and Subspecies consimilis

The subspecies are neighboringly sympatric without observable introgression in many parts of their ranges; ssp. albicaulis is more montane and ssp. consimilis more in the valleys. On the Snake River plains of southern Idaho, the two are biotically sympatric, and there they intergrade extensively.

There is considerable variability within each subspecies. The Idaho phase of ssp. consimilis has been called oreophilus; the predominant phase in California has been called viridulus. The populations in Baja California are morphologically similar to the Nevada forms of ssp. consimilis even though the California forms are closer geographically.

Map 4. Subspecies consimilis and Subspecies hololeucus

The taxa are sympatric over most of their ranges. In the Great Basin, ssp. consimilis prefers the lower sites that are more saline, whereas ssp. hololeucus likes the better-drained, less saline sites. The two occasionally are found side by side and show no signs of intergradation. If C. nauseosus were represented only by ssp. consimilis and ssp. hololeucus, the two would be recognized at the species level.

Map 5. Subspecies consimilis and Subspecies graveolens

The subspecies are closely related morphologically. They are largely allopatric, but they have a greater degree of range overlap than is found between ssp. albicaulis and ssp. nauseosus (map 1). These subspecies (map 5) do intergrade but to a much smaller degree than ssp. albicaulis and ssp. nauseosus do. Intergradations between ssp. consimilis and ssp. graveolens are seen in southwestern Wyoming, south central Utah, and western New Mexico. They remain distinct in northern Arizona. Populations of ssp. consimilis in the San Luis Valley of Colorado are disjunct from their western counterparts but seemingly do not intergrade with ssp. graveolens.

Map 6. Subspecies graveolens and Subspecies hololeucus

The subspecies are mostly allopatric but share mutual range over a portion of Utah and extreme northwestern Arizona. The subspecies are considered rather widely separated taxonomically. They do not intergrade in their common ranges from central Utah to northwestern Arizona. In eastern Utah and adjacent Colorado, introgression is evident where many plants with the general aspect of ssp. graveolens have woolly-white stems like ssp. hololeucus. The names falcatus and nivecaulis have been applied to specimens with these introgressed characteristics. I include them under ssp. graveolens because their total morphology is closer to that than to ssp. hololeucus.

Map 7. Subspecies graveolens and Subspecies nauseosus

The subspecies are sympatric over approximately half of their respective ranges from western North Dakota to central Colorado. They are frequently biotically sympatric and show little or no intergradation.

Map 8. Subspecies bigelovii, Subspecies leiospermus, and Subspecies mohavensis

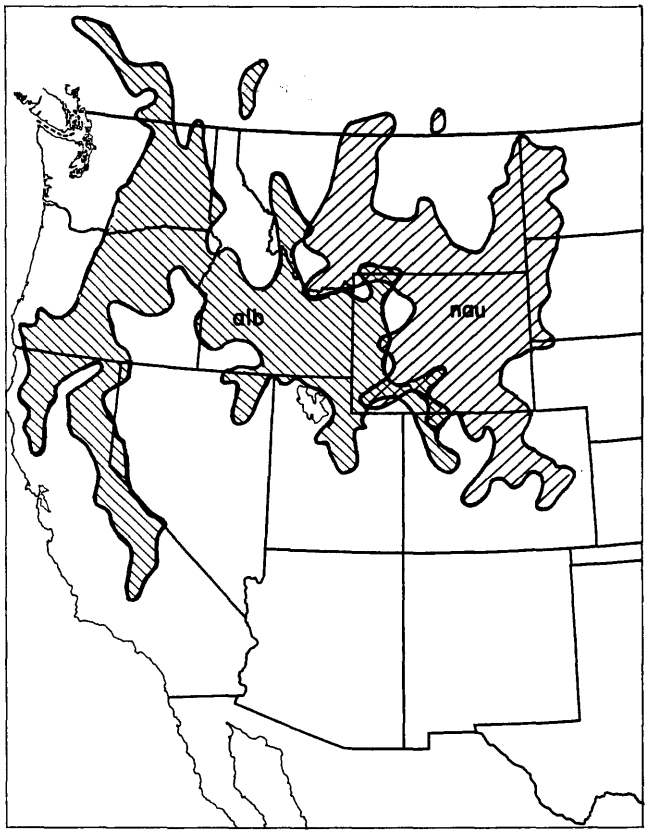
This set of subspecies will serve as final examples for geographical relationships in C. nauseosus although many others could be included. The three have strongly distinguishing morphologies when compared one to another, yet there is limited intergradation in portions of their joint ranges.

Specimens of ssp. bigelovii and ssp. leiospermus are rarely mistaken for one another because they are so distinctive. In extreme southeastern Utah where their ranges overlap, however, specimens that are intermediate between these subspecies are frequently found.

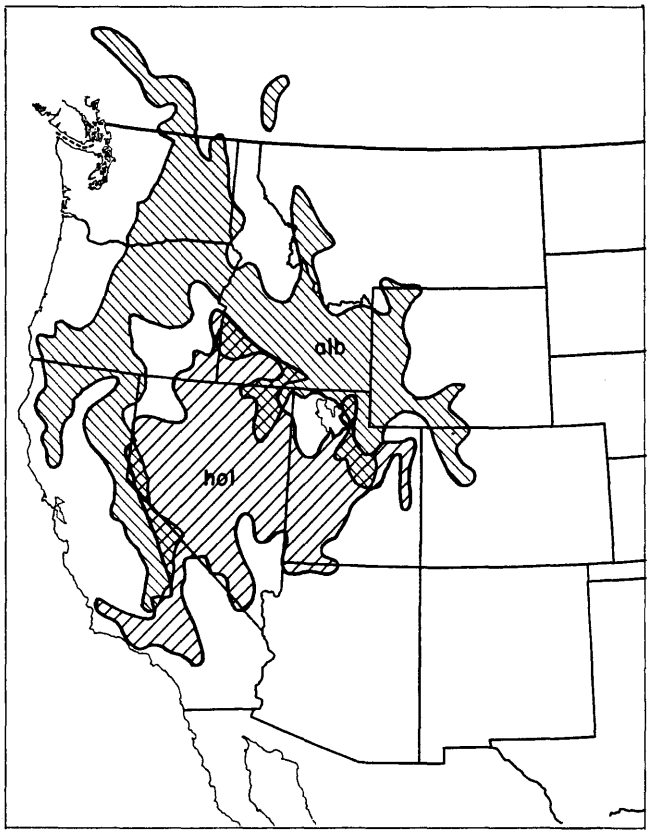
Subspecies leiospermus and ssp. mohavensis maintain their integrity in their range overlap in California, but in the Spring and Pine Valley Mountains of Clark County, Nevada, introgression between the two is evident. Here, some plants that look like ssp. mohavensis have shorter involucres than usual and have glabrous achenes. Also, some plants that look mostly like ssp. leiospermus have slightly longer involucres and very sparse pubescence on their achenes.

DISCUSSION

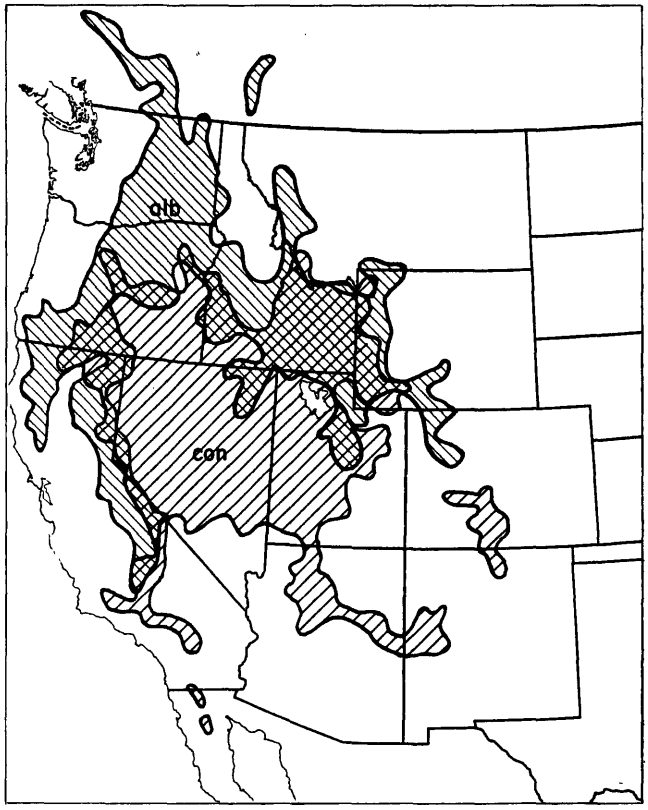
Hall (1919) identified two series within C. nauseosus: the gray forms and the green forms.



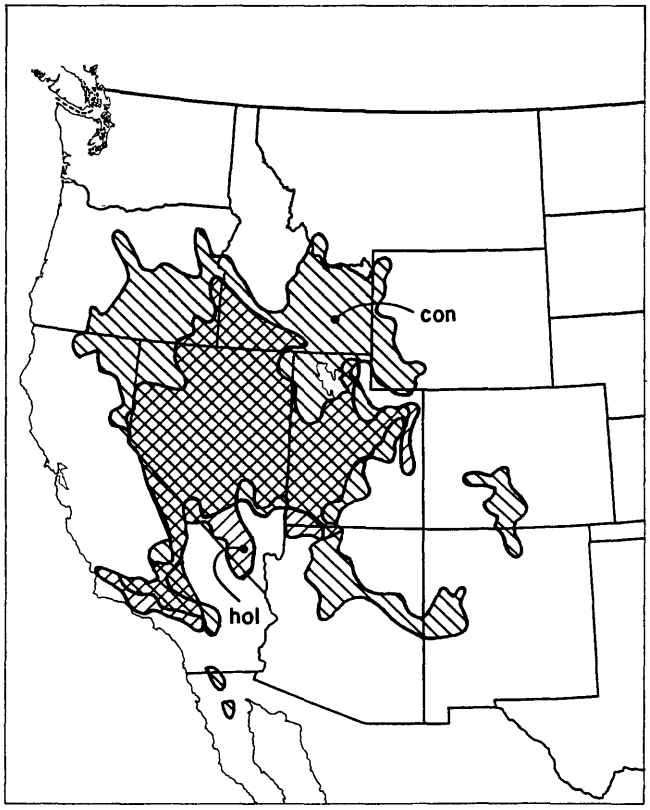
Map 1.--Ranges of ssp. albicaulis (alb) and ssp. nauseosus (nau) in western United States and Canada.



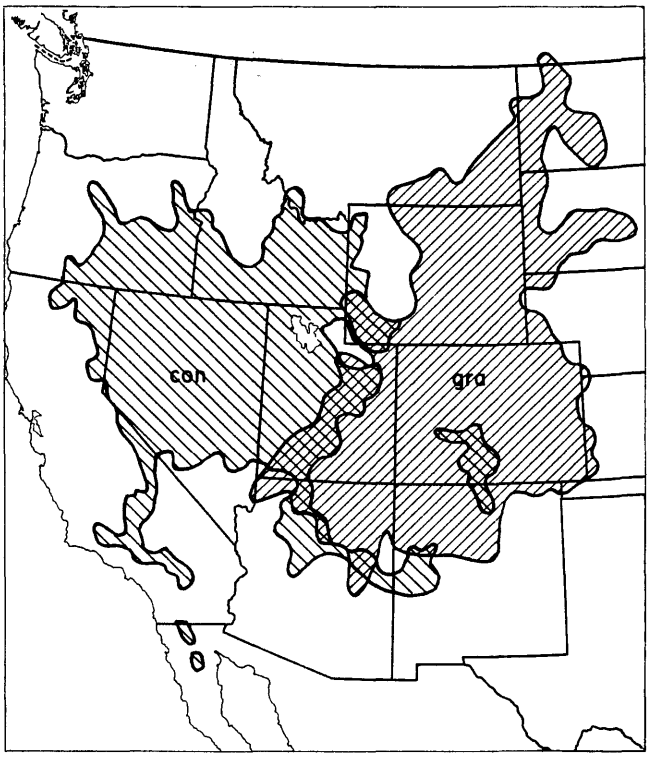
Map 2.--Ranges of ssp. albicaulis (alb) and ssp. hololeucus (hol).



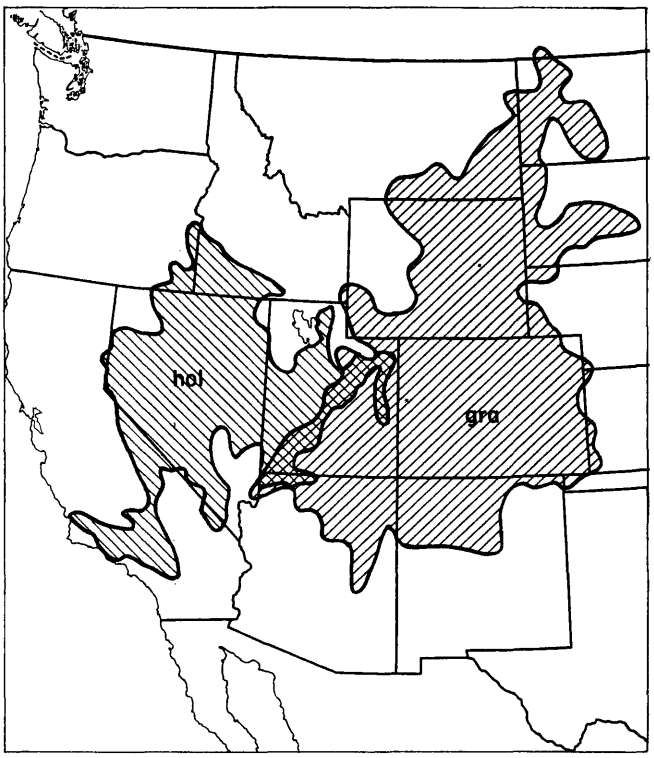
Map 3.--Ranges of ssp. albicaulis (alb) and ssp. consimilis (con).



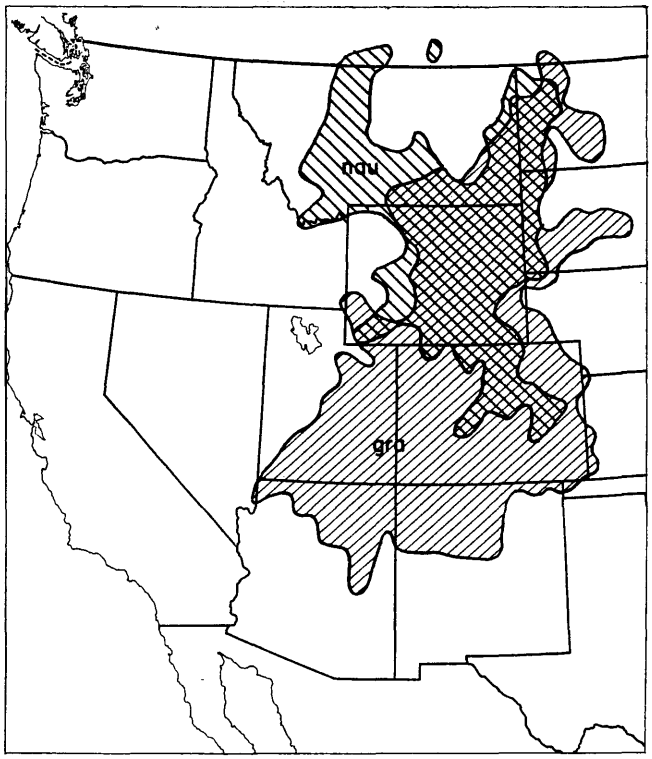
Map 4.--Ranges of ssp. consimilis (con) and ssp. hololeucus (hol).



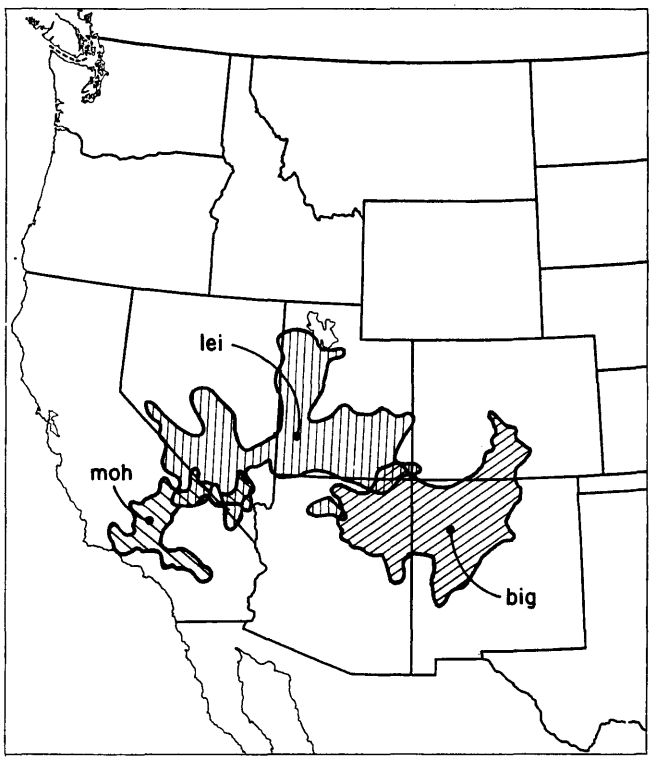
Map 5.--Ranges of ssp. consimilis (con) and ssp. graveolens (gra).



Map 6.--Ranges of ssp. graveolens (gra) and ssp. hololeucus (hol).



Map. 7.--Ranges of ssp. graveolens (gra) and ssp. nauseosus (nau).



Map 8.--Ranges of ssp. bigelovii (big), ssp. leiospermus (lei), and ssp. mohavensis (moh).

The gray forms have tomentulose involucres and gray to whitish foliage and stems (and include ssp. albicaulis, bigelovii, hololeucus, and nauseosus as discussed here). The green forms have glabrous involucres and greenish leaves and stems (like ssp. consimilis, graveolens, leiospermus, and mohavensis). Most observations here tend to support the recognition of the two series. Subspecies albicaulis intergrades fairly frequently with ssp. hololeucus and nauseosus (all of the gray group), whereas intergroup associations such as those of ssp. consimilis with hololeucus and ssp. graveolens with nauseosus show very limited or no intergradation. The distinctness of the two color series is weakened with cross-group intergradations such as those of ssp. albicaulis with consimilis, ssp. bigelovii with leiospermus, and ssp. hololeucus with graveolens.

Introgression between subspecies of C. nauseosus is variable relative to distribution patterns of the taxa involved. In some, such as ssp. albicaulis and ssp. nauseosus, the taxa are allopatric (parapatric) and intergrade rather frequently along their contact zone. Other cases show different degrees of sympatry with limited to frequent intergradation. Usually the intergradation does not occur throughout the mutually occupied area but is limited to a portion of the joint range. This phenomenon is most pronounced in the case of ssp. hololeucus and ssp. graveolens (map 6), where exchange occurs only at the eastern range limit of ssp. hcloleucus. Apparently some breakdown of internal genetic barriers accompanies the general stressing that must occur in those geographically peripheral populations; the two subspecies do not intergrade in other parts of their mutual range. Finally, there are cases in which taxa can be extensively sympatric but seemingly fail to introgress (maps 4 and 7).

Figure 1 illustrates levels of presumed gene exchange among the major subspecies discussed here. Addition of other subspecies to figure 1 would result in a reticulate maze. For example, ssp. mohavensis hybridizes with ssp. hololeucus (Anderson 1973) and intergrades with ssp. albicaulis and ssp. consimilis to some degree as well as with ssp. leiospermus (map 8). A few specimens from southern California appear to have mixed characteristics of ssp. bernardinus, consimilis, hololeucus, and mohavensis.

Some of the variation in C. nauseosus could be described as an overlapping ring of races: ssp. nauseosus mixes (genetically) with ssp. albicaulis, which mixes with ssp. consimilis, which in turn mixes to some degree with ssp. graveolens. But ssp. graveolens, which occurs with ssp. nauseosus, does not mix with it (fig. 1). Also, ssp. consimilis and ssp. hololeucus do not intergrade, but they have a common associate (ssp. albicaulis) with which each of them does intergrade. I believe ssp. hololeucus is a Great Basin derivative of ssp. albicaulis and ssp. consimilis is a Great Basin derivative of ssp. graveolens. These two Great Basin

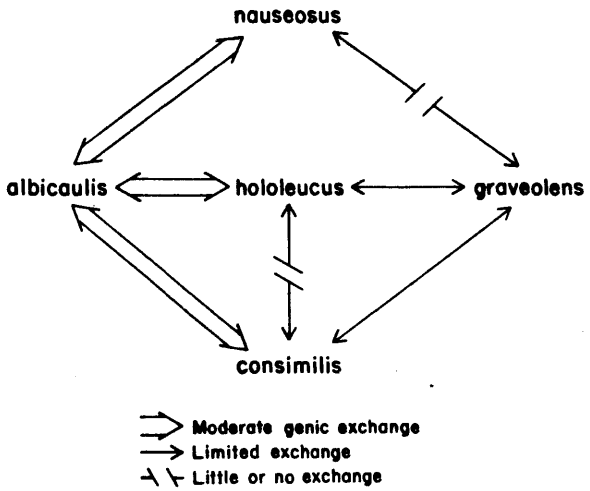


Figure 1.--Relationships among selected subspecies of C. nauseosus (parapatric or sympatric); those not connected by continuous or broken arrows are allopatric and do not intergrade.

subspecies are at a level of divergence that enables them to behave like sympatric species. Most of the subspecies discussed here are at intermediate levels of divergence and reproductive isolation; such populations are often referred to as semispecies (Grant 1981).

It should be remembered that all subspecies of C. nauseosus are relatively well defined and often coexist with little or no gene exchange. Instances of hybridization and intergradation are discussed here to help understand the interrelationships within this species complex and should not be given inordinate emphasis. Continued sympatricity with only limited gene exchange may allow greater development of internal isolating mechanisms and eventual sympatric speciation. Loss of connecting links in the ring of races would lead to speciation as well.

ACKNOWLEDGMENT

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ESTABLISHMENT AND INITIAL RESULTS FROM A SAGEBRUSH (*ARTEMISIA TRIDENTATA*) MASS SELECTION GARDEN

Gary L. Noller and E. Durant McArthur

ABSTRACT: This study was undertaken to combine characteristics of two promising sagebrush accessions. One accession, *Artemisia tridentata* ssp. *tridentata* from Dove Creek, CO, was chosen because it has high nutritive quality and superior growth rate. The second accession, *A. t.* ssp. *vaseyana* from Hobble Creek, UT, was selected because of its high palatability and vigorous multi-stemmed growth habit. Seedlings were planted in a mass selection garden at Meeker, CO, in 1981, and evaluated yearly.

INTRODUCTION

The study was initiated as a result of a severe mule deer (*Odocoileus hemionus*) die-off in Utah in the early 1950's. A. Perry Plummer assembled a team of Forest Service, U.S. Department of Agriculture, and Utah Division of Wildlife Resources people to study ways of improving deer winter range. Sagebrush became an important object of the study because it was used so heavily, was widely distributed, and establishes rapidly from both transplanting and direct seeding.

A cooperative study was initiated in 1981 between the Intermountain Station's Shrub Sciences Laboratory and the Upper Colorado Environmental Plant Center to establish a mass selection garden at the plant materials center in Meeker, CO.

Distribution and Variability

McArthur and others (1979) indicated that big sagebrush is the most widespread and common shrub of Western North America. Beetle (1960) estimated that it covers approximately 226,374 mi^2 (58 655 000 ha) in 11 western States. Across this wide expanse, Plummer and others (1968) observed that "each geographic area has a distinctive type of big sagebrush" and they differ greatly in preference, growth, seed production, and other characteristics. They (Plummer and others 1968) predicted the possibility of developing improved strains or cultivars for use in revegetation projects.

Paper presented at the Symposium: Biology of *Artemisia* and *Chrysothamnus*, Provo, UT, July 9-13, 1984.

Gary L. Noller is Assistant Manager of the Upper Colorado Environmental Plant Center, Meeker, CO. E. Durant McArthur is Supervisory Research Geneticist and Project Leader, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT.

Importance

Big sagebrush is often the dominant forage in the diet of mule deer during winter in the Rocky Mountains and Great Basin (Leach 1956; Kufeld and others 1973; Tueller 1979; Pederson and Welch 1982). Welch (1983) stated that as a winter food big sagebrush ranks among the highest in digestibility, crude protein, phosphorus, and carotene. Plummer (1974) indicated that big sagebrush is one of the best shrubs available for use in revegetation of depleted winter game ranges in the intermountain area. Plummer and others (1968) pointed out that big sagebrush stands are unexcelled in providing ground cover and forage when grazed properly.

Recent research has pointed out differences among accessions of big sagebrush for preference, growth, winter crude protein content, winter in vitro digestibility, and effects on grass cell wall digestion (Welch and McArthur 1979b; Welch and Pederson 1981; Welch and others 1981; McArthur and Welch 1982; Hobbs and others, these proceedings). No one accession contains all of the important characteristics of highest preference, crude protein, in vitro digestibility, growth, and no effect on grass cell wall digestion. This study is an attempt to combine the superior characteristics into one cultivar of big sagebrush to be used to improve mule deer winter range.

MATERIALS AND METHODS

Plant Collections

One hundred accessions of subspecies of *Artemisia tridentata* were collected by A. Perry Plummer and his colleagues from throughout their range. From these accessions, E. Durant McArthur and Bruce L. Welch selected 21 that showed the most promise and had a range of natural variation for plantings at Gordon Creek, Salt Creek, and Springville--all Utah sites.

From the 21 accessions, McArthur and Welch selected accessions from Hobble Creek, UT, (*Artemisia tridentata* ssp. *vaseyana*--commonly called mountain big sagebrush) and Dove Creek, CO, (*A. t.* ssp. *tridentata*--commonly called basin big sagebrush) for crossing. These offered the best early opportunity for improvement in growth rate, growth form, and palatability characteristics (Welch and McArthur 1979a).

Plant and Site Description

Dove Creek.--The accession from Dove Creek, CO, was selected because it has a high crude protein content (16.0 percent) and good growth rate (Welch and McArthur 1979a). The Dove Creek site is 3.75 miles (6 km) east of Dove Creek, CO. The soil is deep. The elevation is 6,790 ft (2 070 m). Dove Creek plants are generally single to few stemmed and large statured. Leaves are slender or linear and leaders are generally longer than those on the Hobble Creek plants. Dove Creek plants have a strongly pungent aromatic odor.

Hobble Creek.--The accession from Hobble Creek was selected because of its high utilization (84 percent) by mule deer (Welch and McArthur 1979a). The site is located at the western slope of the Wasatch Mountains, approximately 1 mile (1.6 km) up Hobble Creek Canyon (approximately 2 miles from Springville, UT). The elevation is about 4,900 ft (1 470 m). Soils are generally deep, stream-deposited alluvium and shallower rocky hillside materials. The Hobble Creek plants are generally smaller than the Dove Creek plants, with multiple main stems. Leaves are broadly cuneate and have a camphorlike fragrance.

Crossing Procedures

The first crossing of the Dove Creek and Hobble Creek accessions was done in late September 1980. The procedures were developed by E. Durant McArthur and involved using the Dove Creek accession as the mother plants. They were located at the Snow Field Station at Ephraim, UT. Pollen was taken from plants located at the Hobble Creek site. Each pollen sample was a composite of two or three separate bushes. Five different pollen combinations were used. The pollen samples (branches) were introduced into white pollination bags. These bags were put on mother plants just prior to flower opening, so that pollen for pollination was either introduced or produced by the perfect flowers on the mother plants.

Seed Production and Seedling Selection

Seed produced from the crossing procedure was collected in November 1980 and germinated in March 1981. Seedlings were tagged and numbered and promising plants were selected. Putative hybrids were evaluated by means of a spectrophotometric analysis (McArthur and Welch 1983). The procedure was to crush a 10-mg leaf and put it in distilled water. The spectrophotometer measured the amount of coumarin and other water-soluble compounds present. Coumarins are abundant in the Hobble Creek plants but present in only small quantities in Dove Creek plants. The abundance of coumarins in the Hobble Creek plants was considered an important genetic marker. Seedlings with the highest concentrations of coumarins were kept for planting.

Planting

A mass selection garden was planted on July 15, 1981, at the Meeker plant materials center. A total of 90 plants were put in 6 rows. Spacing between plants and rows was 10 ft (3 m). Holes were dug, water was added, and potted plants were inserted and covered.

Meeker Environmental Conditions

Environmental conditions at the Meeker plant center are characterized by 16.19 inches (41.1 cm) of annual precipitation, 6,500 ft (1 981.2 m) elevation, and a 90-day frost-free growing season. Winter temperatures of -20 to -30 °F (-28.9 to -34.4 °C) are not unusual. The planting is located on a clay loam soil.

Data Collection

The mass selection garden is evaluated at least twice per year. Each of the 90 plants is examined. A wildlife use evaluation is recorded in early spring to quantify wildlife use. Wildlife use is rated as none, very light, light, moderate, or heavy. It should be noted that the plant materials center is fenced with a 6.5 ft (2 m) fence. However, deer and elk (Cervus canadensis) do get inside the fence. A second evaluation is made in midsummer. Values are recorded for survival, vigor and uniformity, height and crown growth, seed production, and number of main stems. Height and crown growth are measured in centimeters and represent the tallest and widest growth of each plant. The abundance of flowers is estimated to determine potential seed production. Vigor and uniformity of the plants is estimated and given a numerical value (1=low and 9=high). The number of main stems was counted in 1983. This was done to determine whether the crossed plants were more like the Dove Creek parent, which generally has one or few main stems, or like the Hobble Creek parent with multiple stems.

We also plan to examine other factors. Seed viability will be determined from seed samples taken in November 1983. Winter protein content will be established from stem and leaf samples taken in March 1984. Essential oil analysis will be done by chromatograph to compare these plants with the parent Hobble Creek and Dove Creek plants. This test may also produce a sort of fingerprint of these crossed plants. In addition, it may help determine if the plants were self pollinated. We also plan to examine palatability of these crossed plants. This will probably be done by allowing deer to use plants inside an exclosure.

RESULTS

Survival

Survival through 1983 has been good. All but one of the 90 plants are still alive.

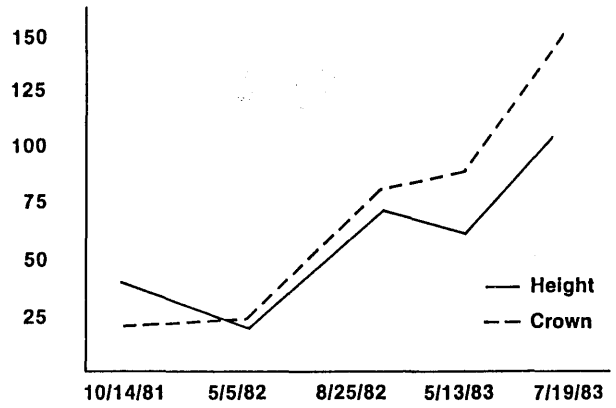


Figure 1.--Plant height and crown width comparisons (cm).

Height and Crown Measurements

The pattern of growth shows that the plants initially had greater height, but with time are now wider than tall (fig. 1). Height decreased from summer to spring readings due to wildlife use and some winter top die-back. Height in 1983 ranged from 29 inches (74 cm) to 50 inches (127 cm) and averaged 40 inches (101.9 cm) (table 1). Crowns in 1983 averaged 55 inches (141.3 cm)

Vigor and Uniformity

The vigor and uniformity rating in 1983 ranged from 5 to 9 and averaged a high 8.2. This indicates the plants were generally vigorous and uniform.

Seed Production

Seed production was first noted in 1982, a little more than a year after planting. In 1982, 66 percent of the plants were flowering. In 1983, all 89 plants were producing seed. The seed production rating averaged 8.4, suggesting high potential seed production (table 1).

Number of Main Stems

The number of main stems in 1983 ranged from 3 to 13 and averaged 6.8 per plant, which points out that the multiple-stem character of Hobble Creek is being expressed.

Table 1.-- Height and crown measurements (cm), vigor and uniformity rating (1=low and 9=high), seed production (1=low and 9=high), and number of main stems in 1983

Characteristic	1983 evaluations (n=49) $\bar{x}$ + se	Range
Height	101.9 ± 1.4	74 - 127
Crown	141.3 ± 2.2	87 - 188
Vigor/uniformity	8.2 ± 0.1	5 - 9
Seed production	8.4 ± 0.2	1 - 9
Number of main stems	6.8 ± 0.2	3 - 13

Wildlife Use

The crossed sagebrush plants were used by mule deer, white-tailed jack rabbits (Lepus townsendii), and sage grouse (Centrocercus urophasianus). Droppings from these animals were noted in the garden.

Animals use the plants at different times of the year. Mule deer used the plants in late summer and fall, then they migrated out of the area. Sage grouse used the plants at about the same time as mule deer. White-tailed jack rabbits used the plants in winter and early spring before green plants were available. In October 1981 (the year of planting) wildlife made very light use of 44 percent of the 90 plants (table 2). By May 1982 (from fall to next spring) 52 percent of the plants had moderate use and 48 percent had light use. In May 1983, 17 percent of the plants had heavy use, 46 percent moderate, and 37 percent had light wildlife use. In May 1984, 13 percent of the plants had moderate use, 31 percent had light use, and 29 percent had very light wildlife use.

Table 2.--Wildlife use by years

Use level	Percent Use Oct 1981	May 1982	May 1983	May 1984
None	56	0	0	27
Very light	44	0	0	29
Light	0	48	37	31
Moderate	0	52	46	13
Heavy	0	0	17	0

FUTURE DIRECTION OF PROJECT

The other factors mentioned will be examined (seed viability, winter protein content, essential oil analysis, and palatability). Based on continued performance of the crossed plants, 20 to 25 of the best performing plants will be allowed to cross-pollinate. Seed will be collected from the cross and 90 to 100 plants will be selected for additional evaluation. A plant release is anticipated within a period of about 5 years.

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SELECTION OF A CULTIVAR OF ARTEMISIA LUDOVICIANA FOR DISTURBED LAND PLANTINGS

Sam E. Stranathan and Stephen B. Monsen

ABSTRACT: The characteristics of Artemisia ludoviciana Nutt. are presented. Comparative evaluations of different accessions and subspecies are discussed with emphasis on the characteristics of the accession 'Summit' recently selected for release. Recommendations pertaining to the culture and use of this selection for planting on disturbed lands are made.

INTRODUCTION

Mining activity, roadway construction, and similar disturbances have created harsh infertile sites throughout a wide topographic area of the western United States. Few plants of any one taxa are capable of growing on such a variety of sites, particularly pioneer species suitable for initial planting (Olsen and Nagle 1965; Thornburg 1982; Rumbaugh 1983; Monsen 1984).

Efforts at the Upper Colorado Environmental Plant Center (Meeker Plant Center) and the U.S. Forest Service, Shrub Sciences Laboratory, have been directed toward the development of plant materials suitable for treating seriously disturbed and erosive sites. Emphasis has been on the selection of herbaceous and woody species adaptable to fresh disturbances that will be effective in stabilizing erosion, that can be easily propagated, and will serve as pioneer species or nurse crops capable of moderating disturbances and facilitating the entry of other desirable species.

Selections of Louisiana sage (Artemisia ludoviciana Nutt.), also called Louisiana sagewort, sagebrush, and cudweed, have been tested for use as conservation plantings at locations in Idaho and Colorado for nearly 15 years (Monsen 1975). Initial tests demonstrated the plant to be highly useful on disturbed sites; however, variations among ecotypes have been encountered (Shaw and Monsen 1983). In addition, different subspecies and closely related species are recognized (Estes 1969). Subspecific distribution and rigorous taxonomic treatment of the A. ludoviciana complex have not been fully completed.

Selections express differences in vegetative stature, growth rates, and rooting habits. The influence of these factors on survival and plant performance has not been documented. In addition, culture requirements essential to establish and propagate plants on wildland disturbances are undefined. Consequently, selections from various plant communities and different sites were assembled in an attempt to develop a genetically superior cultivar suited for wildland uses.

DISTRIBUTION

Artemisia ludoviciana is a widely diverse taxa. Numerous subspecies are described and intergrade in areas of overlapping occurrence. It grows naturally over a wide range of soil conditions with populations existing at elevations over 10,000 ft (3 000 m) to less than 3,000 ft (900 m) throughout western North America (Estes 1969).

Four principal subspecies, described by Harrington (1964), occur in Colorado: A. ludoviciana ssp. ludoviciana, A. ludoviciana ssp. albula, A. ludoviciana ssp. incompta, and A. ludoviciana ssp. mexicana. Plants differ due to the parted or divided condition of the primary leaves and the shape of the panicle. The four subspecies intergrade somewhat, although each occurs in distinct regions. Artemisia ludoviciana ssp. ludoviciana is more abundant and widespread; A. ludoviciana ssp. incompta occupies restricted areas at much higher elevations.

Some subspecies reproduce aggressively by spreading rhizomes while others express weak rhizomes. Most produce seed adequately with flowers that can be self or open pollenated. Alpine subspecies are generally decumbent compared to the upright forms found at lower elevations.

POTENTIAL VALUE

As forage, Louisiana sage is not highly valued, yet it is used by sheep, mule deer, and other game animals and may be seasonally important in their diets (Hermann 1966; McCulloch 1973).

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Sam E. Stranathan is manager of the Upper Colorado Environmental Plant Center, Meeker, CO, on assignment by the Soil Conservation Service. Stephen B. Monsen is principal botanist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, located at Provo, UT.

Some attempts have been made to remove the plant from native grasslands to increase production of more desirable species. Louisiana sage usually occurs in scattered amounts and does not dominate extensive areas. Its presence and composition often fluctuate; frequently it is more prevalent following fire or clearing practices that reduce the dominant species. Plant density may slowly diminish as other species recover. Thus, it does not seriously affect the presence or production of other species.

Louisiana sage frequently exists on exposed ridges and sites free of snow accumulation. Under these conditions, the plant receives select use during fall and winter. When frozen, most of the stems and leaves die back to ground level. The dead material apparently does not cure well, as wintering animals normally consume only green tissue. Some forms produce a large rosette of green leaves that remains until late winter.

Although Louisiana sage has not received much attention as a forage plant, it is recognized as a useful conservation species. Farnsworth and Hammond (1968) discussed possible nodulation and nitrogen fixation by this species. Nodulation has been inconsistent, and it has been difficult to confirm any significant degree of nitrogen fixation. In fact, Wullstein and Harker (1982) could not confirm nodulation or nitrogen fixation.

The plant is known to naturally invade and grow vigorously on mine and roadway disturbances. Plants can also be successfully seeded and will spread readily by root proliferation. The extensive root system, a dense coarse root mass 1 to 4 inches (3 to 10 cm) below the soil surface, significantly reduces erosion. The aboveground biomass contributes to reduced erosion, but seldom reflects the extensive subsurface root mass. Plants are not seriously affected by moderate sedimentation or surface slippage, and actually spread with some soil burial. Louisiana sage encourages other species to invade its stabilized space, serving as a very unrestrictive nurse crop.

The potential conservation features of Louisiana sage may be summarized as follows:

1. Different subspecies and ecotypes occur over a wide range of plant communities, extending from semiarid shrublands to subalpine conditions. Diverse taxa provide extensive genetic materials for plant selection and development.

2. Plants develop considerable variability in vegetative and rooting habits suitable to soil stabilization.

3. Plants express excellent establishment characteristics and can spread quickly on harsh disturbances.

4. Established plants serve as an excellent nurse crop that promotes the invasion of other species.

5. Plants are well-suited to infertile soils and appear to improve soil fertility and tilth.

SELECTIONS UNDER STUDY

In the cooperative testing program of the Shrub Sciences Laboratory and the Meeker Plant Center, 22 accessions of Louisiana sage were selected for advanced evaluation. The plant materials originated from native sites in Idaho, Utah, and Colorado (table 1). Plants were assembled for reclamation uses in the mountain West on

Table 1.--Collection sites of the accessions selected for advanced evaluation studies

Control number	Collection name	Collection site	Elevation (ft)
T40955	Blacks Creek	Ada Co., ID	3,100
T40958	Oakley	Cassia Co., ID	4,600
T40971	Hagerman	Twin Falls Co., ID	2,964
T40952	Leslie	Butte Co., ID	5,500
T40957	Hereford Pasture	Elmore Co., ID	3,690
T40953	Lucky Peak	Boise Co., ID	3,200
T40963	Rocky Bar	Elmore Co., ID	6,350
T40966	Bell Creek	Valley Co., ID	3,156
T40962	Cabarton Road	Boise Co., ID	4,700
T40959	Cascade No. 2	Valley Co., ID	4,500
T40964	Bannock Creek	Boise Co., ID	3,021
T4090	Crouch No. 2	Boise Co., ID	3,021
T21457	Franktown	Douglas, CO	5,800
T40968	Deadwood	Boise Co., ID	5,324
T40970	Ola	Gem Co., ID	2,600
T40969	Meridian	Ada Co., ID	2,800
T40967	Smiths Ferry	Valley Co., ID	4,536
T21474	'Summit'	Bear Lake Co., ID	6,299
T40965	Pine View Reservoir	Rich Co., UT	7,000
T40954	Buckhorn Road	Elmore Co., ID	4,000
T40956	Council No. 1	Adams Co., ID	3,300
T40961	Baumgartner	Elmore Co., ID	4,850

different site conditions: (1) harsh, cold sites at elevations above 4,000 ft (1 230 m) receiving 14 to 30 inches (35 to 76 cm) precipitation; and (2) dry, harsh sites, receiving below 14 inches (35 cm) precipitation and occurring at elevations below 4,000 ft (1 230 m).

Selections were also planted at the Meeker Plant Center under both irrigated and nonirrigated conditions. Study plots were established to evaluate survival, vigor, cold and drought tolerance, spreadability, seed production and harvestability, leaf retention, and biomass production (table 2).

Although field studies have been conducted at various field locations, the principal results and discussion in this paper are for the Meeker Center.

Table 2.--Selected parameters and performance of 22 Louisiana sage accessions transplanted in two projects at the Meeker Plant Center

Accession origin	Control number	Percent 1st year establish.	2nd year spread/cm		Ground cover		Percent winter leaf retention	Fall leaf greenness	Fall green sprout abundance
			Irrig.	Dryland	Irrig.	Dryland			
Blacks Creek	T40955	75	19	15	[1]4	6	90	9	7
Oakley	T40958	100	32	18	3	8	95	9	4
Hagerman	T40971	100	39	35	4	2	95	5	4
Leslie	T40952	43	35	--	3	5	90	9	3
Hereford	T40957	100	28	30	3	5	90	9	3
Lucky Peak	T40953	81	20	--	5	8	80	7	3
Rocky Bar	T40963	100	17	30	7	7	95	7	8
Bell Creek	T40966	88	36	28	5	4	70	9	1
Cabarton	T40962	93	30	25	4	2	20	9	9
Cascade #2	T40959	93	38	30	2	3	70	9	2
Bannock	T40964	100	58	45	2	3	80	9	6
Crouch #2	T40960	93	30	35	4	5	90	9	9
Franktown	T24175	100	40	15	5	6	90	3	7
Deadwood	T40968	81	26	--	6	8	95	9	9
Ola	T40970	100	35	30	5	4	90	7	7
Meridian	T40969	91	28	--	4	3	20	9	5
Smiths Ferry	T40967	100	40	30	3	3	30	9	3
Georgetown Summit	T21474	100	41	25	3	6	90	2	5
Pine View	T40965	100	50	40	4	2	90	9	3
Buckhorn	T40954	88	30	--	5	7	95	9	3
Council #1	T40956	88	40	32	4	4	30	7	5
Baumgartner	T40961	63	25	--	6	5	90	9	4

[1]Values 1 to 9 with 1 being the best.

STATUS OF SELECTIONS

Field plantings of Louisiana sage selections have been maintained for approximately 15 years at different locations. Plantings located above 5,000 ft (1 540 m), approximately six entries, appear promising for conservation use. Selection T21474 from Georgetown, ID, has performed the best, and pending Varietal Review Committee approval, is scheduled for release as 'Summit.'

'Summit' establishes most rapidly from sprigs or transplants. It also establishes moderately well from direct seeding. Results from trial plantings on mines in northwestern Colorado have been impressive. At Silverton, CO, 'Summit' spread 78 inches (200 cm) in a 5-year period after being planted on unstable and steep slopes. Other selections have also demonstrated rapid spreadability, but 'Summit' has been the most robust. Selections acquired from south-central Idaho growing on granitic soils and as an understory with ponderosa pine (Pinus ponderosa) also exhibit excellent rooting habits. Collections identified as Bannock Creek and Cascade No.2 are examples. 'Summit' has been one of only a few selections able to survive and spread at high elevations on disturbed soils. Most collections succumb when planted at elevations over 9,000 ft (2 769 m). Selections are usually well adapted to the elevation from which collected. 'Summit' exhibits a wide range of adaptation to differences in elevation and soils. 'Summit' also grows well on infertile soil, as evidenced by its performance on heavy metal tailing ponds at the Silverton Mine where coarse, sterile sands are subject to wind and water erosion, frost during any month, and an annual precipitation of 18 to 22 inches (46 to 56 cm). Although other selections initially survive when planted at elevations above 5,000 ft (1 540 m), few persist for more than 3 to 5 years. Consequently, spreadability and persistence of 'Summit' have accounted for its acceptance. 'Summit' also grows and spreads well on road disturbances when immediate stability is desired.

Grasses may begin to invade plantings of all selections including 'Summit' within 2 to 5 years. Tree and shrub entry normally proceeds more slowly. As these plants increase, the Louisiana sage decreases. Some invading plants increase dramatically, but recede quickly. Louisiana sage re-emerges to occupy the exposed openings. Seedlings of invading species are observed to establish amid the clumps of Louisiana sage. This response encourages the use of Louisiana sage as a nurse crop to speed up and direct positive succession on poor sites. Studies have not demonstrated that any single selection of Louisiana sage performs better than another as a nurse crop. The aggressive growth habit of 'Summit' has not delayed the invasion of other plants nor appeared to favor certain species.

Since 1982, 'Summit' has been compared with many other excellent-performing selections of Louisiana sage in irrigated and dryland gardens at the Meeker Plant Center. Under agronomic conditions, 'Summit' initiates rhizomes and spreads as rapidly as any comparable type. It has been rated highly for its soil protection

characteristics. In can grow on clays as well as sterile sands. It initiates growth early and is noted for retaining green leaves into the fall (table 2).

Other top-performing lines warranting further comparisons are Pine View, Bannock, Smiths Ferry, Meridian, Council #1, and Hagerman. Hagerman may be best for drier climates at lower elevations. It shows excellent vigor, good early growth, and moderate spread. Pine View has been comparable to 'Summit,' exceeding 'Summit' in vigor and biomass production in garden trials. In the garden trials there are differences in growth habits among accessions and the ease with which other plants invade into the plots. 'Summit' spreads well and is invaded easily.

Very few accessions have illustrated poor winter tolerance. Some, like the Franktown accession, start growing quite slowly in the spring but finish the growing season comparable in biomass and seed production to the top performers. Bannock is a good grower, but lodges early in the fall. Smiths Ferry and Pine View produce an abundance of green sprouts in the fall. Some of the mediocre performers produce an abundance of fall sprouts. Bell Creek is the greatest producer of sprouts in the fall, but has less than the average number of sprouts by spring. Pine View, 'Summit', and Hagerman all do a good job of retaining leaves well into fall, while accessions such as Council #1 lose 70 percent of their leaves by early fall.

SEED PRODUCTION

Field culture of Louisiana sage seed is important for its use in wildland plantings. Selections that can be grown under varied conditions will reduce planting costs and enable expansion of rearing to farms located in different geographical areas.

Seed production studies at the Meeker Plant Center revealed that considerable variability in seed production exists among selections (table 3). A number of selections produce greater amounts of seed than the 'Summit.'

Differences in seed germination have been recorded among accessions when grown at the Meeker location (table 3). Factors that affect seed production and viability are not fully understood. However, inherent differences among accessions and culture treatments, including storage, affect seed quality.

The Meeker Plant Center production fields of 'Summit' were sprigged to establish the plantings, using about 1,100 sprigs (4 bushels) to the acre (0.35 m^3/ha) irrigated. The rows were set on 6-ft (1.8-m) centers and sprigs were set 12 inches (30 cm) apart in the row. Seed fields established from sprigs produced seed by the end of the second growing season. Seed culture techniques have a marked influence upon yields.

'Summit' seed yields have reached 84 pounds cleaned seed per acre (94 kg/ha); however, yields have been reduced by excessive shatter created by loose seed heads damaged by seed head insects identified as immature Psyllids, order of Homoptera, family Psyllidae. The timing of harvest is critical because the seed heads quickly mature and shatter.

Standard combines and cleaning equipment can be used to harvest and process the seed. The seed retains high levels of dormancy and often has a germination value of 30 to 48 percent with a purity over 90 percent. Dormancies have ranged from 30 to 40 percent.

Seed production enhancement studies on 'Summit' have been initiated at the Meeker Plant Center (table 4). These studies evaluate seed production responses to fertilizer levels, fall and spring tillage, chemical and implement stripping, and use of systemic insecticides.

Variability within each plot and between similar treatments indicates soil variability may override treatment response differences. Fall-fertilized plot J produced the most biomass, while its counterpart, plot A, produced less than the 8,548-pound average for all plots, but more than the control. Seed yield data are not available at this time, however, seed yields respond similarly to herbage production. Fall-applied fertilizer treatments were consistently the most productive.

SEEDING RECOMMENDATIONS

Although plantings of Louisiana sage can be accomplished by transplanting, direct seeding is the most practical approach for large projects. Seeds are very small for all selections tested. No single selection appears to establish better by direct seeding. All selections grow rapidly, and thus compete well in mixtures with other herbs. Fall seedings have been most successful. The tiny seed (approximately 3,000,000/lb [6.6 million/kg]) should be seeded at very shallow depths at a rate of one-quarter pound or less per acre (280 g/ha). Seed size and depth of planting create problems when using a standard drilling operation. When seeded in mixtures with seed of other species, Louisiana sage seeds separate rapidly, falling to the bottom of the drill box.

Stands have been successfully established by broadcasting the seed followed with a light harrowing. Drill seeding can be improved by using a commercial sticker that attaches the seed to perlite, which then can be mixed with a bulky seed mix and seeded through the trashy seed box on a drill. This second system allows the seed to be metered and dropped on the surface immediately in front of the press wheels.

Pelletizing the seed helps resolve the seed size problem. In a greenhouse trial in cooperation with Germain's, Inc., 'Summit' seed was coated

Table 3.--Variability of seed production in Louisiana sage accessions in a uniform garden

Accession number	Seed abundance	Seed stock height(cm)	Uniformity	Standability	Harvestability	Uniform maturity	Pounds per/acre	Percent germination
T40959	[2]2.5	93	[2]2.0	[2]3.0	[2]2.5	[2]1.5		
T40962	3.5	58	2	6	4	2.5	320	
T40953	1.5	86	3	1	1	3	1142	[1]77.5
T40971	2	101	2	2	2	2.5	955	51
T40955	3	90	4	4	3.5	3.5		
T40958	2	82	2.5	2	2	3	365	
T40968	3.5	110	1.5	1	2.5	3	152	
T40964	2	108	2	4	3	2.5	296	
T40952	2.5	100	2	4	2.5	2	1032	36.5
T40960	3	88	2	3.5	3	2	572	32.7
T40957	2	104	2.5	4	2.5	3	624	46.5
T40963	4	88	1.5	2.5	3	3		
T21474	2	82	2.5	3.5	3	3		
T40970	3	86	1	1	2	2.5	122	
T40969	1	98	1	1	1	1	441	
T40966	1	85	2	3.5	2.5	1.5	411	
T40956	1.5	109	2	2.5	2	2	1970	37
T40967	3	94	2.5	3.5	2.5	2	638	25.2
T40954	3	52	2	1	2	2	660	21
T21475	2.5	78	3	2	2	2	15	
T40961	3	91	3	3.5	2	2.5		
T40965	2	88	2	1.5	2	2		

[1]Data only for those tested.
[2]Values 1 to 10 with 1 being best.

Table 4.--Initial results of seed enhancement treatments on a 'Summit' Louisiana sage production field

Plot	Treatment	Dry weight per/acre	Uniformity	Seed stalk abundance	Height by percent of plot
A	Fertilize 30-46-0	7295	[1]5	6	15% - 73 cm, 85% - 34 cm
B	Control	6780	5	5	20% - 65 cm, 80% - 40 cm
C	Fertilize 34-0-0	10679	5	5	20% - 70 cm, 80% - 30 cm
D	Spring chisel	5901	6	5	10% - 66 cm, 90% - 30 cm
E	Fertilize 90-30-0	10326	5	4	20% - 67 cm, 80% - 34 cm
F(a)	Spring strip	8601	4	5	70% - 66 cm, 30% - 46 cm
F(b)	Spring Roundup	6214	4	6	80% - 40 cm, 20% - 18 cm
G	Insecticide	9350	3	5	50% - 60 cm, 50% - 32 cm
H	Chisel/24-30-0-21	8308	4	5	40% - 70 cm, 60% - 40 cm
I	Fall chisel	9580	4	5	50% - 68 cm, 50% - 40 cm
J	Fertilize 30-46-0 (Fall)	11003	2	2	30% - 89 cm, 70% - 57 cm
Average		8548			

[1]Values 10 to 10 with 1 being best.

at two different ratio levels, one at 18 to 1 and the other at 26 to 1. By random sample count, the 18 to 1 ratio reduced the number of units per pound from 3,000,000 to 240,000 and the 26 to 1 to 129,000 (530,000 to 285,000/kg). Germination was not reduced by the 18 to 1 coating level; however, the 26 to 1 coating reduced germination by 50 percent.

CONCLUSIONS

Louisiana sage T21474 was selected for release as 'Summit' primarily based on its performance on extremely harsh sites, persistence, ability to reduce erosion rapidly, wide area of adaptation, leaf retention, quality of all green foliage, and apparent outstanding ability to serve as a nurse crop[1]. Studies are currently being conducted to determine methods for seed production and processing. Plantings have demonstrated that Louisiana sage can be used to colonize harsh sites and improve site conditions for other species.

[1]More exhaustive data documenting the performance and release of 'Summit' Louisiana sage is available from the Meeker Plant Center.

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Section 3. Revegetation and Plant Control

HERBICIDE USE IN ARTEMISIA AND CHRYSOTHAMNUS COMMUNITIES:

REDUCING DAMAGE TO NONTARGET SPECIES

Steven G. Whisenant

ABSTRACT: In 1983, a series of experiments was conducted in Utah to compare selectivity and effectiveness of clopyralid, 2,4-D, dicamba, and picloram. Big sagebrush, threadlead rubber rabbitbrush, and stickyleaf low rabbitbrush can be controlled using any of these herbicides. Preliminary results suggest that clopyralid will control rabbitbrush without damaging members of the Rosaceae family.

INTRODUCTION

Sagebrush Ecosystem

Big sagebrush (Artemisia tridentata) occupies a substantial portion of the western United States: over much of Utah, Nevada, southern Idaho, eastern Oregon, western Montana, Wyoming, and Colorado, as well as smaller areas in Washington, California, Arizona, and New Mexico (Tisdale and others 1969). Estimates of the size of the sagebrush ecosystem range from 94 million acres (38 million ha) (USDA Forest Service 1972) to 269 million acres (109 million ha) (Beetle 1960). Either estimate indicates that the sagebrush ecosystem is one of the largest range ecosystems in the United States.

Many important shrubs and herbaceous species are associated with sagebrush (Blaisdell and others 1982). This species diversity is an important aspect of the sagebrush ecosystem. Partially because of this diversity the sagebrush ecosystem is inhabited by a wide variety of mammals and birds. Antelope, mule deer, elk, sage grouse, mourning doves, and chukar partridges are the most important game species (Garrison and others 1977).

The size, accessibility, and productive potential of the sagebrush ecosystem make it an important resource for production of livestock and wildlife, watershed values, and a variety of recreational activities. Unfortunately, much of the sagebrush ecosystem has been degraded by abusive grazing. As a result, the sagebrush ecosystem is still far below its potential production of livestock forage and wildlife habitat (USDA Forest Service 1972).

A primary problem of the sagebrush ecosystem is the increase in density and size of sagebrush and other low-value shrubs, accompanied by the reduction in perennial grasses and forbs. Sagebrush stands frequently become dense enough to reduce forage production and inhibit livestock movement (Blaisdell and others 1982). Because of its long life and ability to compete with perennial herbs for soil-water and nutrients, sagebrush in dense stands is a serious obstacle to range improvement through grazing management or seeding of desirable plant species (Blaisdell 1953).

Depending on its density, size, and inherent palatability, big sagebrush may either be a valuable component of the community or a problem (Blaisdell and others 1982). Big sagebrush in proper mixtures with other shrubs, forbs, and grasses is critical for sage grouse (Klebenow 1969) and antelope (Yoakum 1980) habitat. It is a superior winter forage for mule deer because of its high crude protein content and coefficient of digestion (Welch and McArthur 1979a,b). However, despite its importance, it can become too plentiful at the expense of other desirable plants. Despite the prominence of sagebrush in their diet, antelope do best where the shrub cover is moderate and low in stature (Urness 1979; Yoakum 1980). Sage grouse do not nest in, nor do broods occupy areas of tall, dense sagebrush with little understory (Klebenow 1969). Domestic livestock, particularly sheep, use the more palatable forms of sagebrush but do much better with a greater diversity of food items.

Rabbitbrush

The rabbitbrushes (Chrysothamnus spp.) occupy a wide variety of habitats in western North America. They occur on open plains, valleys, foothills, and mountains from sea level to 10,900 feet (3 300 m) in elevation (Hitchcock and others 1969). At least eight species occur in the intermountain area. Most herbicide control efforts have been directed at two of these species: rubber rabbitbrush (Chrysothamnus nauseosus) and low (green, Douglas) rabbitbrush (Chrysothamnus viscidiflorus).

Rubber rabbitbrush ranges from Saskatchewan and British Columbia south to eastern California,

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Steven G. Whisenant is Assistant Professor of Botany and Range Science, Brigham Young University, Provo. UT.

Baja, and western Texas. It is common on plains, valleys, and foothills. It grows best in openings within the sagebrush, pinyon-juniper (Pinus edulis-Juniperus), and ponderosa pine (Pinus ponderosa) zones on sandy, gravelly, or clayey alkaline soils from 500 to 9,000 feet (150 to 2 750 m) (McArthur and others 1979). Rubber rabbitbrush vigorously invades disturbed sites such as roadcuts and overgrazed rangelands. Destroying big sagebrush with fire or heavy grazing may cause rubber rabbbitbrush to increase and become the dominant vegetation (Evans and others 1973). At least four subspecies of rubber rabbitbrush are found in the intermountain area. Some of these subspecies vary greatly in their value as browse (McArthur and others 1979) while others are sympatric and hybridize.

Low rabbitbrush occurs on dry, open areas and is one of the most widely distributed shrubs on western North American rangelands. It is found between 2,600 and 11,000 feet (790 and 3 300 m) from British Columbia and North Dakota south to New Mexico, Arizona, and California (McArthur and others 1979). Low rabbitbrush is usually associated with sagebrush, snakeweed (Gutierrezia), and other species of rabbitbrush. This species may rapidly increase on overgrazed or otherwise disturbed sites. Following a fire, low rabbitbrush increases by basal sprouts and seedling establishment. Low rabbitbrush continues to dominate for at least 15 years (Young and Evans 1974). Some subspecies adapt well to higher elevations while others do best in lower desert and foothill habitats (Plummer 1977).

Vegetation Management

Restoration of desirable vegetation seldom is obtained solely through improved grazing management or even by eliminating domestic livestock. Improvement of degraded sagebrush communities in a reasonable length of time usually requires practices such as prescribed burning, herbicides, or mechanical control. Biological measures using insects, diseases, or mammals are also possibilities.

Fire is often successfully used for sagebrush management. However, under some circumstances fire may have undesirable results. Many sagebrush communities are difficult to burn except under hazardous burning conditions (Evans and others 1979). If few herbaceous perennial plants are present, the stand becomes more difficult to burn and the chances of increasing undesirable shrubs, such as rabbitbrush or annual grasses, are greatly increased. Some perennial grasses are susceptible to damage or are killed by burning at certain times in the growing season (Wright and Klemmedson 1965).

The use of large anchor chains to uproot sagebrush and rangeland plows to plow sagebrush communities has been extensive. However, the lack of selectivity and high energy costs of many mechanical methods have greatly reduced their use. Chaining may stimulate species, such as rabbitbrush, which resprout from basal buds following disturbance.

Biological methods of sagebrush control using insects and diseases are still in the research phases. Biological control may require the introduction of exotic insects or pathogens, a procedure which requires extreme caution. However, present knowledge indicates some degree of sagebrush control may be possible using sheep (Frischknecht 1979) or goats (Urness and Jensen 1983) as control agents.

Suitability of a particular method depends upon such factors as density, height, and age of the sagebrush stand, associated shrubs, amount and kind of herbaceous vegetation, topography, soils, erosion potential, available equipment, size of area to be treated, planned use of area, economics, and even personal preference. In many situations herbicides have been the chosen method.

Herbicides

Following World War II, the discovery of 2,4-D ((2,4-dichlorophenoxy)acetic acid) as a plant growth regulator led to the development of herbicides for the control of sagebrush (Bovey 1971). This was the first truly selective herbicide used on rangelands since monocots such as grasses were undamaged by 2,4-D. After a few years of widespread use, it became apparent that root-sprouting subdominant shrubs in sagebrush communities were relatively difficult to kill with 2,4-D compared to big sagebrush (Young and others 1981). Low rabbitbrush control required careful timing of 2,4-D for success. Phenological development was later integrated with soil-water content to predict the best 2,4-D application date for low rabbitbrush control (Hyder and others 1958).

Because of the often undesirable effects of 2,4-D on nontarget species, vegetation composition should be carefully considered before treatment. Perennial grasses are seldom damaged and usually increase as a result of reduced competition from sagebrush. Unfortunately, many desirable perennial forbs and shrubs are severely damaged by 2,4-D. This damage should be evaluated relative to the anticipated benefits of the herbicide treatment.

Among the important forbs moderately or severely damaged by 2,4-D are arrowleaf balsamroot (Balsamorhiza sagittata), milkvetch (Astragalus stenophyllus), one flower sunflower (Helianthella uniflora), several lupines (Lupinus spp.), and bluebell (Mertensia oblongifolia) (Blaisdell and others 1982). The loss of forbs has been considered a major problem with the use of herbicides on sage grouse range (Autenrieth 1981).

Carpenter (1974) demonstrated that, under certain conditions, sagebrush can be controlled with 2,4-D without forb damage. Applications of 2,4-D on April 4 (with some snow cover) killed 26

percent of the sagebrush with no forb mortality. Twenty-six percent mortality may be considered a failure for many purposes, but was ideal for thinning sagebrush on sage grouse range. Application of 2,4-D on April 17 killed 63 percent of the sagebrush and 17 percent of the forbs. Later applications were more damaging to forbs. Autenrieth (1981) suggested winter applications of a contact herbicide, such as glyphosate (N-(phosphonomethyl) glycine) be tested, to kill sagebrush without forb damage.

Damage to other shrubs, though often temporary, may be severe. Aboveground portions of snowbrush (Ceanothus velutinus), aspen (Populus tremuloides), chokecherry (Prunus virginiana), and snowberry (Symphoricarpos oreophilus) are easily damaged by 2,4-D. These species resprout vigorously, but production of foliage and seed is greatly reduced for several years (Blaisdell and others 1982). Serviceberry (Amelanchier alnifolia) is severely damaged by 2,4-D and may not resprout. Pechanec and others (1965) found serviceberry to be among the shrubs most susceptible to 2,4-D damage. Resprouting of serviceberry following 2,4-D damage was reported by Mueggler (1966) and Ferguson (1983). Gratkowski (1978) reported that serviceberry sprayed with 2,4-D had not recovered its original vigor after 19 years.

Bitterbrush (Purshia tridentata), an important forage species for both livestock and big game, is somewhat resistant to spraying provided the plants are mature. Young bitterbrush plants are very susceptible to 2,4-D (Hyder and Sneva 1962). Phenological selectivity was successfully demonstrated (Hyder and Sneva 1962) with the use of 2,4-D to control big sagebrush without killing bitterbrush. Big sagebrush plants start growth earlier in the spring than bitterbrush. When 2,4-D applications are carefully keyed to these phenological differences, selectivity can be obtained. Application of 2,4-D between the time of bitterbrush leaf appearance and early fruit development resulted in progressively greater damage. Spraying 2,4-D at any time killed virtually all leaf tissue and current growth of bitterbrush; however, spraying at the time of leaf origin and before the appearance of distinct stem elongation or flowers caused only a small amount of dead tissue on large plants (Hyder and Sneva 1962). Subsequently, dormant buds initiated new growth, and by autumn only slight evidence of injury remained. Hyder and Sneva (1962) summarized by stating that the proper timing for spraying 2,4-D on mixed stands of big sagebrush and bitterbrush on dry sites is indicated by the appearance of (1) new leaves on big sagebrush and bitterbrush and (2) heads on Sandberg bluegrass (Poa sandbergii). Spraying may continue until bitterbrush is in flower.

Chemical properties of herbicides may also provide a means of selectivity. Soil-active herbicides with low water solubility may be used to control shallow-rooted species without damaging deeper-rooted species. This form of selectivity is routinely used in agronomic situations. In rangelands it forms the basis of atrazine (2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine) selectivity between cheatgrass (Bromus tectorum) and the deeper rooted perennial wheatgrasses (Agropyron spp.) This may also be the basis for tebuthiuron's (N-[5-(1,1 dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea) selectivity between sagebrush and bitterbrush. Pelleted formulations of tebuthiuron have been used effectively for big sagebrush (Artemisia tridentata) control (Whitson and Alley 1984). Bitterbrush and serviceberry are relatively unharmed by tebuthiuron rates commonly used for sagebrush control (0.4 to 0.7 lb/ac, 0.44 to 0.75 kg/ha). Rabbitbrush is unaffected by rates of up to 2.0 lb/ac (2.20 kg/ha) tebuthiuron. Increasing precipitation and decreasing amounts of clay and soil organic matter will move these herbicides deeper into the soil profile, thus reducing selectivity.

Selectivity also may be achieved by avoiding or minimizing contact between the herbicide and desirable plants. This type of selectivity is called placement selectivity and may be just as effective as true selectivity (Anderson 1983), but involves no plant-herbicide interaction. This is usually obtained with individual plant treatments involving only the target species. Individual plant treatments are usually labor-intensive but may be economically feasible under certain situations (Ueckert and Whisenant 1982). Pelleted formulations are well suited to individual plant treatments. Picloram (4-amino-3,5,6-trichloropicolinic acid) pellets control both rabbitbrush and sagebrush and tebuthiuron pellets work well on sagebrush.

Clopyralid (3,6 dichloropicolinic acid) is a new selective hormone-like herbicide somewhat similar to the phenoxy herbicides and picloram in activity. It is highly effective against members of the Polygonaceae, Compositae, and Leguminosae families (Herbicide Handbook Committee 1983). In 1983, a series of experiments designed to compare the selective control potential of clopyralid with 2,4-D, dicamba, and picloram were initiated.

MATERIALS AND METHODS

Herbicides were applied with a CO_2-powered backpack sprayer to plots in Wasatch and Garfield Counties, UT on June 18 and July 20, 1983, respectively. Herbicides were applied at a rate of 15 gal/acre (140 L/ha) in water containing 0.5 percent (v/v) surfactant. Treatments were applied to 10 by 100 ft (3 by 30-m) plots replicated three times in randomized complete block designs.

The Wasatch County study area contained mountain big sagebrush (Artemisia tridentata ssp. vaseyana), bitterbrush, and serviceberry. Clopyralid (monoethanol amine salt of 3,6 dichloropicolinic acid) was applied at the rate of 0.25, 0.50, 1.00, and 2.00 lb/acre (0.28, 0.55, 1.12, and 2.24 kg/ha). One treatment of

2.00 lb/acre (2.2 kg/ha) 2,4-D (propylene glycol butyl ether ester of 2,4-D) was applied. Dicamba (3,6-dichloro-o-anisic acid) and picloram (4-amino-3,5,6-trichloropicolinic acid) are not often used for sagebrush control and generally cause more damage to bitterbrush and serviceberry than 2,4-D. For these reasons, neither dicamba nor picloram were used at this study area. Phenology at the time of spraying was as follows: sagebrush, full leaf expansion and 2 inches (10 cm) of new stem growth; bitterbrush, full flower and leaf expansion; and serviceberry, 2 inches (5 cm) of new stem growth. Temperature was 70°F (21°C) and relative humidity was 43 percent during spraying.

The Garfield County study area contained threadleaf rubber rabbitbrush (Chrysothamnus nauseosus ssp. consimilis), stickyleaf low rabbitbrush (Chrysothamnus viscidiflorus ssp. viscidiflorus), and mountain big sagebrush. Treatments consisted of clopyralid at 0.50, 1.00, and 2.00 lb/acre (0.55, 1.12, and 2.24 kg/ha; 2,4-D at 2.2 kg/ha); dicamba (as the dimethylamine salt) at 3.00 and 4.00 lb/acre (3.30 and 4.40 kg/ha); and picloram (as the potassium salt) at 0.25, 0.50, and 0.75 lb/acre (0.28, 0.55, and 0.83 kg/ha). Phenology at the time of spraying was: sagebrush, flowers unopened; threadleaf rubber rabbitbrush, 4-5 inches (10-12 cm) of new stem growth; and stickyleaf low rabbitbrush, 2 inches (5 cm) of new stem growth. Temperature, during spraying was 72°F (22°C) and relative humidity was 65 percent.

In August 1984, the percent foliar reduction was estimated for each species and plot at both locations. Percentage reduction was subjected to arcsine transformation prior to conducting analyses of variance. Mean separations were made at the 5 percent level of significance using Duncan's multiple range test.

RESULTS

Mountain big sagebrush response.--Canopy reductions of at least 90 percent followed clopyralid applications of 1.00 or 2.00 lb/acre (1.1 or 2.2 kg/ha) at both the Garfield County (table 1) and Wasatch County (table 2) locations. At the Wasatch County study area 2.00 lb/acre (2.2 kg/ha) of 2,4-D reduced foliar canopies by 95 percent (table 2). However, at the Garfield County study area 2.00 and 4.00 lb/acre (2.2 and 4.4 kg/ha) of 2,4-D reduced mountain big sagebrush canopies by 40 and 90 percent, respectively (table 1). Canopy reductions of 100 percent resulted from applications of either 3.00 or 4.00 lb/acre (3.3 or 4.4 kg/ha) of dicamba (table 1). At the Garfield County study area picloram applications of 0.25, 0.50, and 0.75 lb/acre (0.28, 0.55, and 0.83 kg/ha) resulted in reductions in mountain big sagebrush canopy of 20, 80, and 100 percent, respectively (table 1).

Threadleaf rubber rabbitbrush response.--Canopy reductions of 75, 100, and 100 percent followed clopyralid applications of 0.50, 1.00, and 2.00 lb/acre (0.55, 1.10, and 2.20 kg/ha) respectively (table 1). Applications of 2.00 and 4.00 lb/acre (2.2 and 4.4 kg/ha) 2,4-D resulted in 40 and 90 percent reductions, respectively in threadleaf rubber rabbitbrush canopy. Both the 3.00 and 4.00 lb/acre (3.3 and 4.4 kg/ha) rates of

Table 1.--Percentage canopy reduction on August 24, 1984, of threadleaf rubber rabbitbrush, stickyleaf low rabbitbrush and mountain big sagebrush following herbicide applications on July 20, 1983, in Garfield County, UT

Treatment		Canopy reduction		
		Mountain	Threadleaf	Stickyleaf
Herbicide	Rate	big sagebrush	rubber rabbitbrush	low rabbitbrush
	Kg/ha	Percent		
2,4-D	2.20	40 c	40 c	35 d
2,4-D	4.40	90 ab	90 ab	90 ab
Dicamba	3.30	100 a	100 a	92 a
Dicamba	4.40	100 a	100 a	95 a
Picloram	.28	20 cd	80 b	75 bc
Picloram	.55	80 b	100 a	85 ab
Picloram	.83	100 a	100 a	100 a
Clopyralid	.55	50 c	75 b	55 c
Clopyralid	1.10	90 ab	100 a	93 a
Clopyralid	2.20	100 a	100 a	100 a
Untreated		10 d	5 d	8 e

[1]Means within a column followed by the same letter are not significantly different ($P \leq 0.05$) according to Duncan's multiple range test.

Table 2.--Percentage canopy reduction on August 23, 1984, of mountain big sagebrush, bitterbrush, and serviceberry following herbicide applications on June 18, 1983, in Wasatch County, UT

Treatment		Canopy reduction		
Herbicide	Rate	Mountain big sagebrush	Bitterbrush	Serviceberry
	Kg/ha	Percent		
2,4-D	2.20	95 a	90 a	100 a
Clopyralid	.28	10 c	10 b	10 b
Clopyralid	.55	80 b	5 bc	10 b
Clopyralid	1.10	90 a	10 b	15 b
Clopyralid	2.20	95 a	15 b	15 b
Untreated		3 c	3 c	5 b

[1] Means within a column followed by the same letter are not significantly different ($P \leq 0.05$) according to Duncan's multiple range test.

dicamba and the 0.50 and 0.75 lb/acre (0.55 and 0.83 kg/ha) rates of picloram resulted in 100 percent canopy reduction (table 1). Only the 0.25 lb/acre (0.28 kg/ha) rate of picloram resulted in less canopy reduction (80 percent).

Stickyleaf low rabbitbrush response.--Canopy reductions of at least 90 percent resulted from applications of dicamba (3.00 and 4.00 lb/acre, 3.3 and 4.4 kg/ha), 2,4-D (4.00 lb/acre, 4.4 kg/ha), picloram (0.50 and 0.75 lb/acre, 0.55 and 0.83 kg/ha), and clopyralid (1.00 and 2.00 lb/acre, 1.10 and 2.2 kg/ha) (table 1). Lower rates of 2,4-D (2.00 lb/acre, 2.20 kg/ha), picloram (0.25 lb/acre, 0.28 kg/ha), and clopyralid (0.50 lb/acre, 0.55 kg/ha) resulted in 40, 80, and 75 percent canopy reductions, respectively.

Bitterbrush response. The 2.00 lb/acre (2.20 kg/ha) application rates of 2,4-D severely reduced canopy coverage (90 percent). Clopyralid applications of 0.25, 0.50, 1.00, and 2.00 lb/acre (0.28, 0.55, 1.10, and 2.20 kg/ha) resulted in bitterbrush canopy reductions of only 10, 5, 10 and 15 percent (table 2).

Serviceberry response. Application of 2.00 lb/acre (2.20 kg/ha) 2,4-D reduced canopies of serviceberry 100 percent (table 2). None of the clopyralid applications resulted in canopy reductions in excess of 15 percent.

DISCUSSION

Several methods of selective big sagebrush control are presently available to resource managers. Exploiting the phenological differences between big sagebrush and bitterbrush can reduce damage to bitterbrush. Using soil-active herbicides with low-water solubility (such as tebuthiuron) can effectively reduce damage to deeper-rooted species. This may be desirable in the case of bitterbrush, or undesirable in the case of rabbitbrush. Selectivity can be expected to increase with increasing clay content and decreasing precipitation. Placement selectivity, using individual plant treatments, may be a viable alternative for small or critical areas.

Mountain big sagebrush, threadleaf rubber rabbitbrush, and stickyleaf low rabbitbrush can be adequately (90 percent) controlled using 2,4-D, dicamba, picloram, or clopyralid. However, results from these studies, though preliminary, suggest that clopyralid can potentially be used to control these members of the Compositae family while causing relatively little damage to members of the Rosaceae family, such as bitterbrush and serviceberry. Both bitterbrush and serviceberry are often damaged severely by 2,4-D applications. These results and data presented by Tueller and Evans (1969) also suggest that low rates of picloram (0.25 to 0.40 lb/acre, 0.28 to 0.44 kg/ha) could be used to control some rabbitbrush species while only thinning the sagebrush.

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RANGE BRUSH CONTROL WITH GRASLAN[R] PELLETS

J. H. Marion, E. I. Hackett, J. W. Burkhardt

ABSTRACT: Graslan[R] Pellets impregnated with either 10 or 20 percent tebuthiuron by weight were applied to plots on two sites. Five rates from 0.25 to 1.50 pounds per acre (1.28 to 1.68 kg/ha) were distributed on site 1, and three rates of 0.75, 1.0, and 1.50 pounds per acre (0.84, 1.12, 1.68 kg/ha) on site 2. A satisfactory reduction of 78.1 and 81.3 percent, respectively, of Artemisia tridentata was obtained. Chrysothamnus nauseosus was not controlled at any of the rates used. The shallow, wide spread of A. tridentata lateral roots allows this species greater exposure to the pellets; therefore, it is more susceptible to herbicide absorption. Application time was found to be noncritical; response to spring and fall treatments was not significantly different.

INTRODUCTION

Big sagebrush (Artemisia tridentata) and rubber rabbitbrush (Chrysothamnus nauseosus) dominate the ranges of northeastern Nevada, reducing the early season carrying capacity for both wildlife and livestock. Thinning of these shrubs is desirable when the dense stands crowd out more palatable grasses and forbs. Thinning is also desirable where the sagebrush is an unpalatable biotype (Welch and others 1981).

Various herbicides have been used to accomplish this thinning, but most require specific conditions to be effective. One herbicide, tebuthiuron in pellet form, appears to be effective in controlling a wide range of shrubs and trees such as whitebrush, spiny hackberry, and Berlandier wolfberry, found on the mixed shrub ranges of south Texas (Scifres and others 1979). Western juniper (Britton and Sneva 1981), sand shinnery oak (Pettit 1979, Jones and Pettit 1984), huisache (Bovey and Meyer 1978), blackjack oak, winged elm (Shroyer and others 1979), and pinyon-juniper (Clary and Goodrich 1983) also have reportedly been effectively controlled.

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J. H. Marion is County Agent and E. I. Hackett is Range Specialist, Cooperative Extension Service; J. W. Burkhardt is Associate Professor of Range Science, all of the University of Nevada, Reno.

The purpose of this study was to evaluate Graslan[R] (tebuthiuron impregnated pellets) as a method of controlling big sagebrush and rubber rabbitbrush.

MATERIALS AND METHODS

Site 1, selected in the spring of 1980, was in the foothills of the Ruby Mountains, NV at an elevation of 6,000 ft (1 800 m). Annual precipitation average was 9 inches (23 cm) on a shallow soil over a clay pan. Site 2, selected a year later, was 18 miles (28 km) to the southeast at 6,700 ft (2 000 m). Annual precipitation was 15 inches (38 cm), mostly snow, on rocky, deep, well-drained soil of a lateral moraine. Sagebrush density was about equal on both sites. Site 1 had over twice as much rabbitbrush as did site 2. Utah juniper (Juniperus osteosperma), spiny hopsage (Grayia spinosa), and horsebrush (Tetradymia spp.) on site 1 were not found on site 2. Antelope bitterbrush (Purshia tridentata) was found only on the higher site 2.

The plot design was a complete randomized block with three parallel, adjacent replications. Site 1 individual plots were 100 x 100 ft (30.5 x 30.5 m) with a 10-ft (3-m) buffer strip between each plot. There were six treatments and one control plot in each replication, for a total of 21 plots on this site, covering 5.8 acres (2.3 ha). Site 2 was also a complete randomized block with three parallel, adjacent replications of 100 x 100 ft plots, but without the buffer strip between plots. Ten plots were required for each replication to accommodate six spring and three fall treatments plus a control plot. This 30-plot site required 7 acres (2.8 ha).

The Graslan[R] pellets supplied by Elanco were 3 mm in diameter and 5 mm long, averaging 8,000 per pound (Graslan technical manual 1983). The pellets were impregnated with either 10 or 20 percent tebuthiuron designated as 10P and 20P. Untreated blank pellets of the same size were also supplied for making up the correct rates. Elanco suggested a rate of 1 pound active tebuthiuron per acre (1.12 kg/ha) as a midpoint for the rate trials on site 1. Therefore, rates of 0.25, 0.50, 0.75, 1.00, and 1.50 pounds per acre (0.28, 0.56, 0.84, 1.12, 1.68 kg/ha) were prepared for site 1 by weighing out the impregnated pellets and diluting each weight with blank pellets to make up a volume filling a

2-pound coffee can. At site 2 the rates for the spring treatment were 0.75, 1.00, and 1.50 pounds per acre (0.84, 1.12, and 1.68 kg/ha), comparing both the 10P and 20P at each rate. The fall treatment used only the 10P for the 0.75 and 1.00 pound rates and 20P for the 1.50 pound rate. Grams of impregnated pellets used on individual plots at the designated rate per acre are tabulated below.

Lbs/Acre Rate	Percentage concentration	
	20	10
0.25	130	--
0.50	260	--
0.75	390	780
1.00	520	1040
1.50	780	1560

The impregnated pellets and blank pellets were mixed thoroughly and applied to the designated plot with a small, hand-operated, cyclone spreader. One-half of the volume was spread traversing the length of the plot, the remainder being applied crosswise by walking a grid of 10-ft (3-m) increments to accommodate the range of the spreader.

The Graslan pellets were applied to site 1 in March 1980. In April 1981, pellets were applied to the six plots designated for spring treatment on site 2, and in November, the remaining three fall plots were treated. No other work was done on either site, except for random observation, until they were read in October 1983.

Tebuthiuron treatment effects were assessed by establishing three parallel line transects 25 ft (7.5 m) apart in each plot. Starting 25 ft into the plot and extending 50 ft (15 m) towards the opposite boundary, a measuring tape was stretched and anchored just above the plants' canopy. Perennial plants falling under this line transect were recorded by species and measured as inches of live or dead plant material intercepted. Live or dead plants of the major species in a 3-ft wide strip paralleling the transect were also recorded. Cover of annual bromegrass (Bromus tectorum) was estimated at point intercepts at 1-ft intervals along the three transects in each plot.

Ten species of plants were recorded and an additional four noted along the 63 transects on site 1, and 90 transects on site 2. For statistical purposes, only four species were recorded consistently enough to analyze. These were big sagebrush, rubber rabbitbrush, Sandberg bluegrass (Poa secunda) and annual bromegrass. A random block analysis of variance was used to test for differences among treatments.

The variance due to treatment (percentage of dead plants) in the treated plots compared to the control plots was applied to the perennial species. Only live annual bromegrass plants were counted; therefore, the plant counts were used instead of percentage dead.

RESULTS AND DISCUSSION

Herbicide treatments produced significant reduction of big sagebrush compared with the control plots, except for the lowest rate applied on site 1 (0.25 pounds). The 0.75 pound rate was the lowest used on site 2 and big sagebrush reduction was significant for all rates, both spring and fall treatments, regardless of the percentage of active material in the pellets. Rabbitbrush was not controlled and few plants were killed at any of the rates on either site (table 1). At least an 80 percent reduction of rabbitbrush on site 1 and 50 percent on site 2 would have been required for the desired range improvement.

Table 1.--Plant survival percentages

Pounds/acre tebuthiuron	ARTR[1]	CHRY3[2]	POSE[3]
Site 1			
0.25	37.5	83.5	99.3
0.50	25.3*	84.0	89.5
0.75	12.8*	78.5	82.3
1.00	23.3*	85.5	64.9
1.50	9.8**	86.4	53.0
Mean	21.9	84.1	79.0
Control	66.4	90.5	98.4
Site 2			
0.75	25.1*	97.3	52.2
1.00	19.8*	94.2	63.3
1.50	11.6*	84.2	44.3
Mean	18.7	91.7	52.7
Control	85.3	99.9	92.5

* Indicates significant reduction at the 5% level.
** Indicates significant reduction at the 1% level.
1 ARTR = Artemisia tridentata
2 CHRY3 = Chrysothamnus spp.
3 POSE = Poa secunda

Sandberg bluegrass reduction due to the herbicide was not significant at any rate tested. Live annual bromegrass plants were significantly less only at the highest rate (1.50 pounds per acre active tebuthiuron).

Antelope bitterbrush, a desirable species for deer winter range, was found only on site 2 and was not reduced by the tebuthiuron treatments. A total of 65 bitterbrush plants were counted along the 90 transects on site 2 and only five of these were dead, one of which was on an untreated control plant.

The application in March 1980 on site 1 was followed by a very dry period and little effect

of the herbicide was seen 6 months later. The fall of 1981 began a period of above normal moisture that continued until the plots were read in October 1983. It was interesting to note that the herbicide remained effective enough through the long, dry spell of 1980 and 1981 to induce a significant sagebrush reduction after moisture finally came in sufficient quantity to move the material into the root zone.

Site 2 treatments in April 1981 occurred while some snow still remained in sheltered areas, and a 6-inch snow came 2 days later. By the time the fall applications were made in November the results of the spring treatments could be easily seen by the dying sagebrush and hit spots in the understory grass and forbs. Sandberg bluegrass, the major understory species, was quite variable across the plot sites. Zero counts were recorded on several of the transects. More bluegrass was found on site 2 where the spring treatment compared the 10P and 20P (10 and 20 percent active tebuthiuron) pellets. It was found that the 10P killed more grass than the 20P, but the reverse was apparent with the sagebrush where the 20P killed slightly more sagebrush at the same rates per acre of tebuthiuron. Sandberg bluegrass sustained a 41 percent loss with the 10P material and 34 percent with the 20P, an average of all rates. The 20P pellets gave 87 percent control of the sagebrush, and the 10P gave 83 percent. This trend followed through on all treatment pairs, but it was not statistically significant due to the variability of the bluegrass stands on the site (fig. 1). Twice the number of 10P pellets were required to equal the same rate of tebuthiuron, therefore, more hits where grass was killed appeared on the 10P plots. The more concentrated 20P pellets provided a higher lethal dose to the roots of the sagebrush.

A fall treatment on site 2 provided essentially the same results as the spring treatments by the time the plots were read in the fall of 1983. All herbicide rates and concentrations, both spring and fall, provided a significant control of the big sagebrush. No control of the rubber rabbitbrush was found at any of the rates,

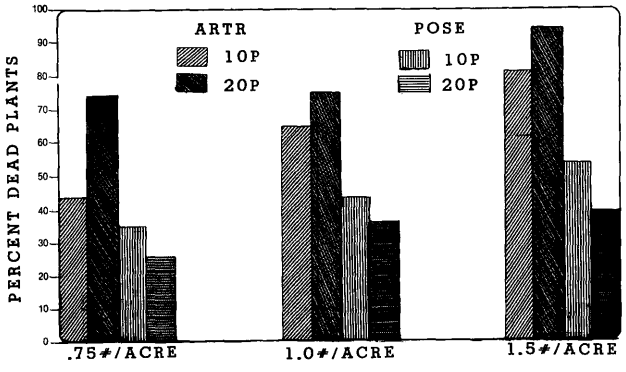


Figure 1.--Lethal effects of tebuthiuron concentrations in Graslan pellets on sagebrush (ARTR) and bluegrass (POSE).

concentration of pellets, or season of treatment. The rooting habit of the sagebrush makes it particularly vulnerable to this herbicide. Its lateral roots spreading profusely just below the surface, well beyond the plant's canopy, provide a large surface area within which the pellets can fall and still reach the plant's zone of active absorption. This rooting habit is well illustrated by Tabler (1964). The excavated sagebrush plant in the foreground of the photo (fig. 2A) shows the horizontal roots that are in the top few inches of the soil profile. Bovey and others (1978) reported that most of the tebuthiuron residue at any given time was found in the upper 15-cm of the soil.

Rubber rabbitbrush has lateral roots angling downward and not extending much beyond the plant's canopy until deep within the soil. The effect of the herbicide is greatly diluted by the soil before reaching the active root zone of the plant. The photo also illustrates the rooting habit of the rubber rabbitbrush (fig. 2B).

These plants were arranged for photographing at approximately the same distance from each other

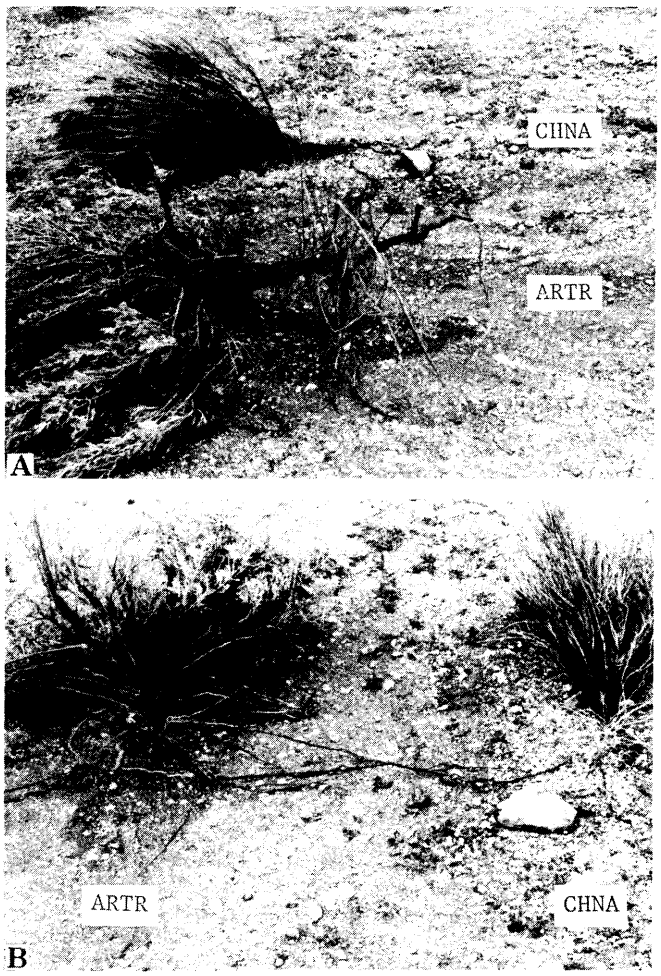


Figure 2.--Differing rooting habits of big sagebrush (ARTR) and rubber rabbitbrush (CHNA).

that they occupied in the soil when growing. The sagebrush roots extended beyond the rabbitbrush plant, but the rabbitbrush roots were not found beyond the plant's own canopy (fig. 2B).

CONCLUSIONS

Graslan is an effective management herbicide for the reduction of A. tridentata. The herbicide was found ineffective in control of rubber rabbitbrush (table 1). The chief advantage of the tebuthiuron-impregnated pellets is that timing of application is not as critical as with foliage spray herbicides. At low concentration (0.5 pounds per acre) most of the grass, forbs, and browse species were preserved. They increase rapidly when sagebrush competition is reduced. The more desirable shrubs such as antelope bitterbrush are not seriously damaged.

Scifres and Mutz (1978) found that although forb production decreased with increasing rates of tebuthiuron, recovery after 3 years was evident. Grass production increased after the first year. Our observations concur with this report.

Tebuthiuron pellets are an excellent management tool for the rancher whose ranges are dominated with big sagebrush. It is effective in thinning sagebrush, allowing the grasses and forbs to increase, thereby providing earlier, longer season, and better balanced forage. There are no secondary effects from the pellets falling in water or from animal waste that includes treated forage. The pellets can be distributed with a minimum of equipment, hand spread from a saddlebag or cyclone seeder as was done on these plots, or by pickup or tractor-mounted spreader. Large acreages can be treated by aerial applications. The pellets can be applied any time that is convenient, except on snow-covered ranges.

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RESPONSE OF AN ALKALI SAGEBRUSH/FESCUE SITE TO RESTORATION TREATMENTS

Stephen B. Monsen and Nancy Shaw

ABSTRACT: The 5-year response of shrubs, broadleaf herbs, and grasses on an alkali sagebrush site to spraying, burning, chaining, disking, and protection from grazing is presented. With the exception of protection from grazing, all treatments reduced shrub density and the vigor of understory species improved. Shrub density and age class did not stabilize within the 5-year period for most treatments. Alkali sagebrush (Artemisia longiloba) plants were susceptible to all treatments. Existing shrubs that were able to survive treatments regrew from new stems not by root sprouting. Recovery of the shrubs and understory plants was aided by unusually high amounts of moisture during years following treatment. Physical alteration of the surface soil by chaining or disking reduced shrub seedling establishment compared to burning or spraying where soils were not disrupted. Perennial bunchgrass and broadleaf forb cover increased slowly after treatment due to low initial density.

INTRODUCTION

Alkali sagebrush (Artemisia longiloba [Osterhout] Beetle) occupies more than 30,000 acres (12 140 ha) of Idaho's Upper Snake River Plain in Blaine and Camas Counties (U.S. Department of the Interior, Bureau of Land Management, Idaho State Office n.d.). Habitat type of these sites has been described by Hironaka and others (1983) as alkali sagebrush/Idaho fescue (Festuca idahoensis Elmer). Stands in good condition support a mixed understory of perennial grasses and annual and perennial forbs, providing valuable forage and cover for sage grouse, antelope, and other wildlife. In this area, alkali sagebrush received light use by cattle and light to moderate sheep use, but deteriorization of understory cover and increases in sagebrush density have resulted from past grazing practices. Although the taxonomic position and site requirements of alkali sagebrush have been studied (Beetle 1960; Tisdale and others 1965; Brunner 1972; Zamora and Tueller 1973; McArthur and others 1979), little research has been conducted on management or manipulation of alkali sagebrush to improve its value for wildlife and livestock.

Alkali sagebrush is distributed over approximately 5,120 mi^2 (1 325 000 ha) from southwestern Montana to northwestern Colorado, along the foothills of the Continental Divide and on scattered sites across southern Idaho and Oregon and northern Utah and Nevada at elevations between 4,500 and 8,000 ft (1 370 to 2 450 m) (USDI Bureau of Land Management and USDA Soil Conservation Service 1976; McArthur and others 1979). It is distinguished from other low sagebrush by its dark green spreading branches to 1.5 ft (4.5 dm) tall, large flowering heads, and early phenology. Flowering heads vary from 0.12 to 0.2 inches (3 to 5 mm) wide, and flowering and fruiting dates are approximately 1 month earlier than for other low sagebrushes (Beetle 1960; McArthur and others 1979; Blaisdell and others 1982).

Edaphic factors limit the distribution of alkali sagebrush. It characteristically grows in small, sharply defined stands on rocky claypan soils with fine-textured surface horizons and strongly developed agrillic B horizons within 1 or 2 ft (0.3 to 0.6m) of the surface (USDI Bureau of Land Management and USDA Soil Conservation Service 1976; Blaisdell and others 1982). Beetle (1960) associated alkali sagebrush with highly alkaline soils. However, Passey and Hugie (1962), Robertson and others (1966), Passey and others (1982), and Tisdale and others (1965) found the pH of alkali sagebrush sites to range from slightly acidic to slightly basic. Therefore, Blaisdell and others (1982) have proposed "early sagebrush" as a more appropriate common name for the species.

Surface soils of alkali sagebrush sites are temporarily saturated in the spring, but soil moisture is rapidly lost through evapotranspiration. Robertson and others (1966) found that soils on an alkali sagebrush site in North Park, CO, limited root penetration and moisture availability. They concluded that only a "low-producing plant community of alkali sagebrush and other shallow-rooted, drought-adapted shrubs, grasses, and forbs are able to survive under these conditions." Adapted species quickly complete their vegetative and reproductive phenologies or, in the case of annuals, their entire life cycle early in the season while soil water is available. Perennial species may respond to fall rains.

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Stephen B. Monsen is a Botanist/Biologist with the Intermountain Research Station, Forest Service, U.S. Department of Agriculture, stationed at Provo, UT. Nancy Shaw is a Botanist with the Intermountain Research Station, Forest Service, U.S. Department of Agriculture, stationed at Boise, ID.

Treatment of alkali sagebrush stands to improve understory herbs yet retain some shrubs requires selective treatment. Hironaka and others (1983) recommended chemical and mechanical methods that could be implemented with a minimal amount of equipment breakage. Eckert and Evans (1968) achieved an average of 96 percent control of alkali and low sagebrush (Artemisia arbuscula Nutt.) in Nevada by spraying with 2,4-D. Dominant climax perennial grasses showed a production response 2 years following treatment with Sandberg bluegrass (Poa sandbergii Vasey) demonstrating the greatest initial response. The most successful treatments were on high potential sites in fair condition. Blaisdell and others (1982) reported that mechanical treatments have been successfully implemented on dwarf sagebrush sites, but recommended treatment of only those areas with the greatest production potential. Prescribed burning has been attempted on alkali sagebrush sites only infrequently; the understory is normally not heavy enough to carry a fire (Blaisdell and others 1982).

The goal of this study was to evaluate and compare control of alkali sagebrush and the response of native understory species on a south-central Idaho site to: (a) spraying with 2,4-D, (b) chaining, (c) disking, (d) burning, and (e) protection from livestock grazing.

STUDY AREA

Macon Flat is an undulating basaltic lava plain located along the southeastern edge of Camas Prairie, Camas County, ID. Elevation ranges from 4,800 to 5,500 ft (1 463 to 1 677 m). Slopes are generally between 0 and 8 percent, but may be as high as 20 percent. Climate is semiarid with cold winters and hot, dry summers. Annual rainfall averages 14.6 inches (36 cm) (table 1) with 89 percent falling between October and June, largely in the form of snow and spring rain. Wide fluctuations in annual percipitation are typical. From 1973 to 1983 total annual precipitation varied from 8.9 to 26.8 inches (23 to 68 cm). Mean annual temperature is 42 °F (5 °C) with average winter lows of -23 °F (-31 °C) and summer highs of 96 °F (35 °C). The frost free season averages 68 days, from June 22 to September 1.

Soils are Magic montmorillonitic frigid Vertic Xerocrepts and Manard fine montmorillonitic frigid Argic Durixerolls derived from basaltic residuum (USDI Bureau of Land Management and USDA Soil Conservation Service 1976). Surface layers are very stony, and there are occasional outcrops of basalt bedrock. Both soils are moderately deep and moderately well drained with low permeability (USDI Bureau of Land Management and USDA Soil Conservation Service 1976; Case 1981). The high shrink-swell capacity and seasonal perched water table that develops on the strongly developed claypan soils restricts rooting depth to 20 to 40 inches (51 to 102 cm).

Productivity is limited by soil conditions and the short growing season. The dominant habitat type of Macon Flat is alkali sagebrush/Idaho fescue. Alkali sagebrush is virtually the only shrub growing on these sites. Bluebunch wheatgrass (Agropyron spicatum) [Pursh] Scribn. & Sm.), Idaho fescue, bottlebrush squirreltail (Sitanion hystrix [Nutt.] J.G. Sm.) and Columbian needlegrass (Stipa columbiana Macoun) are major perennial grasses. Perennial forbs include narrowleaf pussytoes (Antennaria stenophylla Gray), longleaf phlox (Phlox longifolia Nutt.), Hood's phlox (Phlox hoodii Richards.), and Wyeth's eriogonum (Eriogonum heracleoides Nutt.), while littleflower collinsia (Collinsia parviflora Dougl. ex Lindl.) and Brewer's navarretia (Navarretia breweri [Grey] Greene) are common annuals. Isolated patches of basin big sagebrush (Artemisia tridentata Nutt. ssp. tridentata) and antelope bitterbrush (Purshia tridentata [Pursh] DC) occur on ridges or hills with deep, well-drained, loamy soils. Fuzzy sagebrush (Artemisia papposa Blake & Cronq.) inhabits intermittent drainageways (USDI Bureau of Land Management and USDA Soil Conservation Service 1976).

Prior to 1972, the Macon Flat allotment was grazed by cattle and sheep in the spring and early summer and by sheep in the fall. Season of use was restricted and a modified three-pasture rest-rotation system was instituted in 1972. In 1978, cattle grazing was restricted to May 1 to May 22 or May 22 to June 15. Sheep graze the area in the spring and fall with spring grazing confined to the use pastures. From 1972 to 1982 grazing by sheep amounted to 7 to 56 percent of the total use. The Spring Creek pasture, which includes the study exclosure, is in the most depleted condition with about 14 acres (5.7 ha) required per AUM (Boltz n.d.).

METHODS

In 1978, an 80-acre (32.4-ha) tract of the Spring Creek Pasture, Macon Flat allotment was fenced to exclude livestock. Spraying with 2,4-D, chaining, disking, and burning were performed on 300 by 1,000 ft (91.5 by 305 m) plots. A control plot of the same size was established adjacent to treatment plots. One-half of each treated plot was seeded using a rangeland drill. The unseeded portion of each plot was allowed to recover through natural successional changes. This report describes the response of treated areas that were not seeded. Response of the seeded treatments will be presented in a separate publication. The treatments applied included:

Spraying.--The first spraying was completed on June 13, 1979, with a ground spray unit. Two pounds per acre (0.9 kg per ha) of low-volatile 2,4-D ester was applied with water as a carrier. However, by this date the sage had completed most of its vegetative growth and the spray was ineffective. Respraying by helicopter on May 2, 1980, using the same herbicide and application rate was successful.

Table 1.--Weather data for Fairfield, Camas County, ID, during the 1978-83 study period and 10 year averages

Category	Year						Mean
	1978	1979	1980	1981	1982	1983	1973-83
	Inches						
Precipitation							
January 1 - March 31	6.5	5.0	5.9	3.0	7.0	8.9	5.4
April 1 - June 30	2.5	2.0	3.7	5.1	2.9	3.6	2.6
July 1 - September 30	3.7	3.3	2.7	0.4	4.8	3.6	6.0
October 1 - December 31	1.8	4.8	4.5	9.5	3.3	10.7	3.7
Annual	14.6	14.3	16.8	18.0	18.0	26.8	14.6
	°F						
Temperature							
High	96	95	97	95	95	98	96
Low	-20	-27	-23	-12	-32	-40	-23
Average	42	42	42	44	40	41	42
	Days						
Growing season[1]							
32 °F	52	84	69	23	103	20	68
28 °F	93	135	111	24	124	117	98

[1] Number days between last spring and first fall occurrence.

Chaining.--The area was double chained in October 1978, using an 80-lb (36-kg) smooth-link chain drawn by two D-9 Caterpillar tractors.

Disking.--Treatment was completed with a brush-land plow in October 1978. Grass seed was mistakenly seeded over portions of the area to be left unseeded. Presence of the seeded grass was felt to interfere with the recovery of native vegetation. Consequently, this treatment was not included in comparative analysis.

Burning.--Burning was conducted in mid-June 1978, using a thermal brush burner (Davis 1978). The burner heads were held 2.5 to 3 ft (0.8 to 0.9 m) above the shrubs to ignite and burn the plants and understory. Temperatures at the heads ranged from 2,000 to 2,150 °F (1 093 to 1 177 °C). The burner was drawn through the area at about 3 mi/h (0.8 km/h), burning strips approximately 12 to 14 ft (3.6 to 4.3 m) wide. Fires frequently burned about 20 to 30 ft (6 to 9 m) into the surrounding vegetation before burning out.

Control.--No seeding or plant control methods were employed.

Age class structure, percent live crown cover, and density of alkali sagebrush and cover of all grass and forb species, litter, and bare ground were determined prior to treatment. Evaluations were repeated 1 and 5 years following treatment--1979 and 1983. A single evaluation of the sprayed area was completed in 1983, 4 years following treatment. Data were collected in late June or early July.

Ten 50-foot transects were randomly placed in each treatment. Percent live crown, age class, height, and crown measurements were determined for each shrub rooted within a 4.4-ft (1.3-m) belt centered on the transect line. Ten 10.8-ft^2 (1-m^2) circular plots were randomly located along each transect line. Percent cover of all species, bare ground, litter, and rock within each circular plot were estimated ocularly. Permanent photopoints were established and rephotographed at each sampling date. All study plots and transects were permanently marked for future sampling and observation.

RESULTS AND DISCUSSION

Response of Alkali Sagebrush

In 1979, 1 year following treatment, the alkali sagebrush population on the control plots consisted of approximately 74 percent mature, 25 percent decadent and 1 percent immature plants (table 2). By 1983 the total number of alkali sagebrush plants on these plots had increased by nearly 30 percent with a substantial alteration of age structure. Numbers of immature plants and seedlings increased to about 12 percent of the total; this could be attributed to a combination of protection from grazing and weather conditions. All years of the study period received at least normal precipitation while precipitation for 1980 to 1983 was from 15 to 84 percent above average. This might have resulted in high seed production, improved germination and seedling emergence, and greater seedling vigor. Untreated areas supported only a light understory of herbaceous plants at the beginning of the study that apparently was not prohibitive to shrub seedling establishment. A 25 percent increase in numbers of mature plants between 1979 and 1983 may have resulted both from growth of plants recorded as immature at the beginning of the study and recovery of decadent shrubs. Number of decadent shrubs decreased 33 percent between 1979 and 1983.

Table 2.--Mean number of alkali sagebrush plants by age class and treatment at Macon Flat; standard error of mean within parentheses

Age class	Sprayed	Burned	Chained	Control
		No. shrubs/acre		
Seedlings				
1979	-	709(466)a	142(81)ab	0b
1983	0	284	0	203(122)
Immature				
1979	-	729(284)	365(122)	142(61)
1983	689(223)ab	425(142)b	486(203)b	1,479(344)a
Mature				
1979	-	5,977(810)	5,126(1,175)	8,205(973)
1983	486(203)c	3,039(648)b	2,026(608)bc	10,799(1,074)a
Decadent				
1979	-	770(486)	1,783(1,094)	2,674(446)
1983	284(162)b	4,194(871)a	6,058(770)a	1,783(405)b
Total				
1979	-	8,185(1,276)ab	7,415(839)b	11,021(932)a
1983	1,459(142)c	7,942(648)b	8,570(973)b	14,263(1,094)a

[1] Means in the same row followed by the same letter are not significantly different ($P \leq 0.05$).

Shrubs in the decadent category usually support scattered live branches, but a majority of the main branches are dead. Under protection and with favorable weather conditions, some of these plants recover to produce more uniform crowns.

In 1979, one year after treatment, total shrub populations on the burned, chained, and disked plots were reduced by 26, 33, and 65 percent, respectively, compared to the control plot (tables 2 and 3). Reduction in plant numbers on the three treated areas occurred primarily in the numbers of mature and decadent plants. The sprayed area was not sampled at this time as the treatment had recently been applied and its effects could not yet be evaluated.

Although no seedings were reported for the control plots in 1979, there were 709, 180, and 142 per acre (1 752, 445, 351 per ha) on the burned, disked, and chained plots, respectively. The numbers per acre of immature plants recorded in 1979 for the control, burned, disked, and chained sites were 142, 729, 461, and 365, respectively (351, 1 801, 1 139, 902 per ha). The low number of seedlings and immature plants in the control plots is not fully understood but may have been related to the below-normal precipitation during the preceding 12 months. Competition and low seed reserves may also have been involved. Reduction of competition likely contributed to the higher rates of recruitment on the burned, disked, and chained areas. Burning occurred prior to seed dispersal in 1978, but the burn resulted in a very spotty kill. Apparently enough seed ripened on unburned shrubs or remained in the soil to provide a seed source. Seedling establishment may have been enhanced in ash mounds left following combustion of the shrubs as seedlings often appeared in clusters. Although chaining and disking left large patches of ground bare in 1979, the loose soil surface of these areas was not conducive to shrub seedling establishment. In addition, the mechanical treatments may have buried many of the small sagebrush seeds and prevented their germination or emergence. The effects of physical alteration of soil on shrub seedling establishment persisted through 1983.

In 1983 the total number of shrubs remained significantly lower in all treated areas than the control. Total number of shrubs in the sprayed, disked, burned, and chained areas were 10, 32, 56, and 60 percent, respectively, of the control. In 1983, the combined number of seedlings and immature plants in the control area was more than twice as great as in the burned, disked, chained, or sprayed areas (tables 2 and 3). This may have been due to differences in seed production in the treated and control areas or increased competition from rapidly developing understory plants on the treated sites. Precipitation from 1981 to 1983 was well above normal, presumably encouraging establishment of all species on all sites. Between 1979 and 1983 there was a significant shift in numbers of plants from the mature to the decadent category on the disked, burned, and chained areas. The category represented 33, 53, and 71 percent, respectively, of the total populations, compared to 13 percent for the control. This indicates a continued loss of vigor of many plants for several years following treatment. Numbers of plants and age structure

Table 3.--Mean number of alkali sagebrush plants by age class for disk treatment

Age class	Year 1979	1983
	-----No. shrubs/acre-----	
Seedlings	180	20
Immature	461	341
Mature	3,251	2,730
Decadent	0	1,505
Total live plants	3,892	4,596

have not stabilized on the treated sites 4 and 5 years after treatment, and it is still impossible to determine the fate of some mature and decadent plants. Changes in weather conditions following treatment undoubtedly play a major role in ultimate shrub survival and recruitment and corresponding changes in cover and composition of the understory species.

Two factors must be considered when treating to prevent or encourage recovery of alkali sagebrush through natural seedings: (1) surface tillage and (2) competition from associated plants. Treatments that till or bury the small sage seeds can prevent seedling establishment; untilled surfaces are more desirable. Competition reduces seedling establishment.

Few seedlings of alkali sagebrush became established for any treatment except the control during the study period. The number of seedlings and immature plants diminished for most treatments between 1979 and 1983. The resurgence in vigor of herbaceous plants apparently was sufficient to prevent shrub seedlings from becoming established and causing plants weakened by physical treatments to succumb.

Elimination or reduction of alkali sagebrush can be achieved with any of the control methods tested. Spraying provided the greatest reduction in shrub numbers during the first 4 years following treatment. During this same period, shrub density had not stabilized in the burned, disked, or chained plot, and numbers continue to diminish in these areas.

The method used to burn the study plot may not be comparable to a natural or prescribed burn that would likely occur much later in the season. A large number of burned shrubs were able to recover. Plants did not resprout from the base of the crowns, but were able to regrow from the remaining branches and apparently are not as susceptible to physical or physiological damage as the various subspecies of big sagebrush.

Burning can be used to reduce shrub density and is an appropriate technique to use if some shrubs are to be retained. Unless a sufficient understory of herbs is present, burning without seeding may result in a rapid increase of shrub seedlings. However, burning will be difficult to conduct in many alkali sagebrush stands unless understory herbs are present to carry a fire.

After 5 years, total shrub numbers were similar on the burned and chained sites. Although differences were nonsignificant, the number of young plants was lower and decadent plants greater for the chained area. If chaining is employed, removal of shrubs can be regulated using chains with links of different weights and by single or double chaining. Chaining would be particularly effective when plants are dormant and the ground frozen.

Shrub recovery on the disked site was influenced by the presence of seeded grasses. Compared with the 11,021 shrubs per acre (27 233 per ha) on the control plot in 1979, disking reduced shrub numbers in 1983 by 42 percent or 4,596 plants per acre (11 357 per ha) (table 3). Disking was particularly destructive to mature and decadent plants and provided a poor seedbed for alkali sagebrush seedlings.

In all treatments, live but damaged shrubs recovered via regrowth of remaining stems. Basal sprouting or root sprouting did not occur, and shrubs were killed if the main stems were uprooted or cut off. Consequently, treatments are most effective if existing plants are completely killed and live stems are not left to regrow.

Response of Herbaceous Species

In 1983 there were no significant differences in total cover provided by perennial grasses on any of the sites (table 4). On treated sites the native perennial grasses were able to recover through natural resprouting or seeding. Differences between treated and control plots may have been minimized by favorable weather conditions during the preceding 3 years.

Significant differences did exist among treatments in cover provided by several perennial grass species. Bottlebrush squirreltail provided greater cover on all treatments than on the control, but significantly so only on the sprayed plots. Bottlebrush squirreltail is a short-lived perennial that invades open sites quickly. Other perennials do not respond as rapidly but may slowly increase in density. Idaho fescue appears to be more sensitive to damage by mechanical tillage than the other perennial grasses present. In 1983 its cover remained significantly lower on the sprayed and chained areas than on burned or controlled sites.

Most perennial grasses are adapted to specific sites. Bluebunch wheatgrass and Thurber needlegrass (Stipa thurberiana Piper in Scribn.) are more prevalent on the deeper well-drained soils. Idaho fescue, Sandberg bluegrass, and Nevada bluegrass (Poa nevadensis Vasey in Scribn.) are more common on the shallow, rocky soils. Chaining was more damaging to the perennial grasses occurring on shallow soils than deep soils, while burning was generally less effective on shallow sites. Fewer grasses and broadleaf herbs survived disking than any

Table 4.--Percent (standard error of mean in parentheses) at Macon Flat in 1983

Cover type	Spray	Burn	Chain	Control
Annual grasses	0.6(0.2)	0.5(0.5)	0.3(0.2)	0
Perennial grasses	[1]15.7(2.9)	12.0(1.3)	11.7(1.6)	12.2(1.3)
Festuca idahoensis	0.3(0.1)b	3.6(1.1)a	0.4(0.3)b	3.8(1.1)a
Poa nevadensis	0b	1.0(0.4)a	0.1(0.1)ab	0.4(0.1)ab
Poa secunda	3.4(0.4)a	0.3b	2.2(0.6)a	2.8(0.3)a
Sitanion hystrix	9.4(1.5)a	4.4(0.5)b	5.6(1.0)b	3.0(0.6)b
Stipa thurberiana	2.6(1.1)	1.1(0.4)	3.2(0.7)	1.5(0.9)
Agropyron smithii	0.1(0.1)b	1.4(0.7)a	0b	0b
Other grasses	0	0.1(0.1)	0.3(0.2)	0.6(0.4)
Annual forbs	4.0(0.4)ab	3.3(0.4)b	6.1(1.0)a	4.0(0.7)b
Perennial forbs	11.5(1.1)	8.2(1.7)	13.9(1.8)	14.5(2.9)
Allium spp.	0.1b	0.2(0.4)ab	0.6(0.2)a	0.2(0.1)ab
Arenaria aculeata	3.0(0.4)a	0.5(0.3)c	2.4(0.6)ab	1.6(0.6)bc
Antennaria spp.	0	1.3(0.5)	1.0(0.4)	0.9(0.2)
Eriogonum caespitosum	0.1b	1.7(0.6)a	2.8(0.5)a	2.8(0.7)a
Eriogonum spp.	0.4(0.2)	0	0.6(0.4)	0.8(0.2)
Happlopappus nanus	2.0(0.5)	1.4(0.7)	2.4(1.3)	4.5(2.0)
Phlox spp.	2.0(0.3)	1.7(0.8)	1.3(0.3)	2.0(0.3)
Viola beckwithii	0.2(0.1)c	0.5(0.1)b	1.5(0.2)a	0.9(0.2)a
Astragalus spp.	0.8(0.3)a	0.2(0.2)b	0.1(0.1)b	0.1(0.1)b
Other forbs	1.8(0.6)a	0.1(0.1)b	1.1(0.5)ab	0.4(0.2)b
Shrubs	6.5(0.8)c	27.5(2.3)b	23.5(2.0)b	36.6(1.6)a
Total vegetation	38.3(2.8)c	51.5(2.3)b	55.6(2.2)b	67.3(1.4)a
Litter	30.1(3.6)a	20.2(2.0)b	16.8(1.1)bc	14.4(1.9)c
Rock/bare ground	32.9(1.9)	32.9(2.4)	34.9(2.0)	29.0(2.3)

[1] Means in the same row followed by the same letter are not significantly different ($P \leq 0.05$).

other treatment. The heavy disk plowed all surfaces. However, the treatment did not completely eliminate any species.

Cheatgrass brome was the only annual grass to appear on all plots. Following disturbance it did not increase noticeably, providing less than 1 percent cover on all areas in 1983. Consequently, it did not interfere with recovery of native species.

The percent ground cover for native annual broadleaf forbs increased on the disked, and chained treatment, but not on the burned or sprayed treatment. These treatments likely provided better microsite conditions for invasion and establishment. Nearly all species provided very low amounts of cover with the totals for all annual forbs ranging from 3.3 to 6.2 percent on the various treatments.

Cover provided by perennial forbs did not vary significantly among treatments. Nearly all species present in the area occurred in each treatment where microsites permitted, but in low percentages, generally totaling between 0 and 3 percent. Response to treatment is difficult to assess due to the low percentages, but in general no species were lost or increased markedly following treatment (see Blaisdell and others 1982; Eckert and others 1972).

The low density and pattern of distribution of most broadleaf herbs and some grasses must be considered in evaluating the success or usefulness of each treatment. With the exception of bottlebrush squirreltail, few seedlings of the perennial species have yet appeared. Increases in density of most native grasses and broadleaf herbs resulted from enlargement of existing crowns or spread by rooting. The low numbers of new seedlings may be due to a number of factors:

1. Native herbs occurred in low densities prior to treatment, producing only low quantities of seeds. Unless adequate number of understory plants are present at the time of treatment, recovery or improvement occurs very slowly. Few perennial forbs or grasses have invaded many exposed sites in the chained or sprayed areas. New seedlings are not plentiful in any treatment.

2. Many plants require specific site conditions and occupy only restricted areas.

Plants spread slowly among the scattered adapted sites.

3. Some desirable species (bluebunch wheatgrass, Idaho fescue, and most species of Stipa) do not have vigorous seedlings and recovery is often quite slow.

If the recovery is to be based on the response of native herbs, treatments that destroy understory plants should not be used. With the exception of disking, treatments were not very disruptive. Existing plants respond by enlargement of the crowns, rooting, and new seedlings. As existing plants improve in vigor, seeds are produced to repopulate the site. Seedling spread may not occur for a number of years until a seed bank can be rebuilt. Recovery of Idaho fescue was particularly slow on all treatments; plants regrew and reseeded more slowly than most other grasses. Bluebunch wheatgrass plants regrew quickly, but spread very slowly by seedlings. Managers may expect most native perennial grasses to require several years to recover following vegetation treatment. Although the total cover of grasses can be expected to improve for most treatments, some desirable species may not recover for many years. Management should be designed to accommodate this response.

CONCLUSIONS AND RECOMMENDATIONS

Alkali sagebrush sites that support a good component of understory herbs provide excellent livestock forage during the early spring and fall--vital grazing periods. To be cost effective, improvement of the herbaceous understory of depleted sites must result in a substantial increase in herbage production. This has not occurred for any treatment, and seeding following site preparation appears necessary to improve areas that are void or sustain remnant numbers of herbs.

Autenreith (1981) emphasized the need for manipulation practices designed to enhance degraded sagebrush habitats for both livestock and wildlife. He recommended treatments that reduce sagebrush density and increase both grass and forb production for sage grouse habitats. With the exception of protection from grazing, all treatments reduced shrub density, but understory herbs have not recovered sufficiently. Shrub density has recovered from all treatments except spraying, and may prevent further increase of herbs. Autenreith also suggested that treatments resulting in total shrub elimination be restricted to selected patches or strips producing a mosaic of shrub and grasslands. Disking, chaining, and spraying are procedures that can be used to treat specific irregular tracts. Kindschy and others (1982) and Yoakum (1968) described suitable antelope habitat as supporting one-third each of grasses, forbs, and shrubs with a height of 24 inches (61 cm) or less, ground cover of about 50 percent, and production of 500 to 1,000 lb/acre (563 to 1 125 kg/ha). Response of herbaceous understory has not yet achieved these figures. Consequently, extensive treatments of depleted sites are not recommended unless an adequate understory of herbs is present for recovery or artificial seedings is part of the treatment.

The method ultimately used to treat large areas depends on the costs involved, density of understory species, and wildlife and livestock uses. Several major considerations in selecting an appropriate treatment include:

1. Providing protection from livestock grazing without additional treatment may be beneficial, but the community composition, particularly shrub density, would be extremely slow to change. The time required would not be acceptable for most management purposes.

2. Burning can be effective, but only if a sufficient understory is present to carry the fire. A rapid increase in alkali sagebrush could occur unless controlled by competition with understory plants.

3. Spraying is an effective method for killing existing shrubs. It can also be an effective method of controlling shrub reestablishment if the understory is able to respond and provide competition with shrub seedlings. Spraying was no more detrimental to the survival of broadleaf herbs than other treatments. Broadleaf herbs, particularly mat-forming species, recovered surprisingly well.

4. Spraying must be completed early in the season (prior to May 20, at Macon Flat) before alkali sagebrush completes most of its vegetative growth. Spraying early in the season also increases the chance of survival for some broadleaf herbs as the understory plants are not in full production at this time and are not damaged greatly by the herbicide. Spraying can be recommended if an adequate quantity of understory species is present and regulatory measures are satisfied.

5. Chaining effectively reduces shrub density. Heavy chains can be used to remove most plants regardless of age or size. Many dense stands of alkali sagebrush support a preponderance of mature and decadent plants. Chaining in late fall and winter will kill these plants. Chaining is generally less destructive to the understory plants than spraying and would be more useful in retaining some alkali sagebrush. Both methods are adapted to treatments that include seeding.

6. Disking is most frequently employed to treat low and alkali sagebrush. The technique usually kills a high percentage of shrubs and understory herbs. Recovery of the herbs requires a longer period than for other treatments. This practice is acceptable if significant reduction in shrub density is desired to accommodate seeding.

7. Chaining and disking are useful techniques to prepare a seedbed and facilitate artificial seeding. The equipment can be adjusted or modified to enhance site preparation.

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INTERSEEDING SELECTED SHRUBS AND HERBS ON MINE DISTURBANCES IN SOUTHEASTERN IDAHO

Bland Z. Richardson, Stephen B. Monsen, and Diane M. Bowers

ABSTRACT: Mountain big sagebrush, rubber rabbitbrush, and antelope bitterbrush were successfully established from seed in revegetating a mine disturbance in southeastern Idaho. Grazing and competition from seeded herbs were found to significantly decrease shrub density, particularly antelope bitterbrush. Increasing the shrub seeding rate from 4 to 50 lb/acre (5 to 56 kg/ha) resulted in greater numbers of shrubs, but differences varied by species and treatments. Seeding methods and rates are discussed. Recommendations based on the results are made.

INTRODUCTION

Shrubs and herbs are desirable components for revegetation of mined areas. Benefits derived from their use include: enhanced forage yields and ground cover (Medin and Ferguson 1972; Clarke and DePuit 1981; Ferguson and Frischknecht 1981); promotion of ecosystem processes such as accumulation of litter, nutrient cycling, and soil stability (McArthur 1981; McKell and Van Epps 1981); enhanced animal and wildlife habitat; and increased livestock and wildlife forage (Monsen and Christensen 1975; McArthur 1981).

However, few shrubs and herbs are adapted to semiarid mine disturbances and only a small number of these have been evaluated for use in revegetation of those mined areas (Monsen and Richardson 1984). Further, results are often erratic due to a lack of satisfactory planting equipment (Monsen and Shaw 1983). Most equipment that has been used was developed for planting grasses and is not capable of handling trashy seeds or a mixture of different size seeds.

Mountain big sagebrush (Artemisia tridentata ssp. vaseyana), rubber rabbitbrush (Chrysothamnus nauseosus), and antelope bitterbrush (Purshia tridentata) are useful plants for disturbed sites. However, seeds of the first two species are difficult to clean and usually are sold with a high percentage of inert material. Seeds are small and difficult to regulate in most seeding devices. In contrast, seeds of antelope bitterbrush are large, easily cleaned, and seed freely. When they are seeded in a mixture, a carrier is often needed to regulate seeding rates and this is often not satisfactory.

Grazing is an additional factor affecting revegetation success in some areas. Young plants are adversely affected not only by grazing, but also by trampling (Whittaker 1953; Plummer and others 1968). Despite these effects, "...almost no research has been conducted on improved practices for grazing of land reclaimed after mining" (Power 1978).

This study investigated the suitability of seeding mountain big sagebrush at different rates with herbs on a mine disturbance in southeastern Idaho. Specifically, the study had three objectives: (1) to evaluate the capability of the Brillion grass-seeder to plant a mixture of shrubs and herbs; (2) to determine the "best" seeding rate to establish a diverse mixture of shrubs and herbs; and (3) to evaluate the influence of livestock grazing (cattle) on plant establishment and composition.

LOCATION

Studies were established at the Gay Mine, a phosphate mine near Pocatello, ID, at an elevation of 5,600 feet (1 707 m). Situated in the northeastern extremity of the Great Basin Desert, average annual precipitation is approximately 11 inches (28 cm). Vegetation is characterized by Saskatoon serviceberry (Amelanchier alnifolia), mountain big sagebrush, antelope bitterbrush, and rubber rabbitbrush. Aspen (Populus tremuloides) is encountered in small restricted areas. In addition to minerals, principal resources of the area are watershed, game habitat, and livestock forage.

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Bland Z. Richardson is Research Forester, Intermountain Research Station, Forest Service-USDA, Logan, UT; Stephen B. Monsen is Principal Botanist/Biologist, Intermountain Research Station, Forest Service-USDA, Provo, UT; Diane M. Bowers is a doctoral candidate in ecology and presently Lead Research Technician, Intermountain Research Station, Forest Service-USDA, Ogden, UT.

METHODS

The research plantings were established in a large valley fill in which overburden materials had been deposited. Phosphate overburden had been removed from a pit approximately 44 acres (17.8 ha) in size and having an average depth of 250 feet (76.2 m). The total area disturbed as a result of the pit and the overburden backfill was approximately 100 acres (40.5 ha). The study area, approximately 5 acres (2.0 ha) in size, was ripped to a depth of approximately 3 feet (0.92 m), fertilized (16-16-16 at a rate of 580 lb/acre [649.6 kg/ha]), and planted in the fall of 1977. Three separate seed mixtures: (1) combinations of mixed grasses and broadleaf herbs; (2) mixed shrubs; and (3) grass-herb mixture plus shrubs were sown with a Brillion grass-seeder at different seeding rates (table 1) resulting in a total of 10 treatments.

Table 1.--Planting treatments and seeding rates at the Gay Mine

Treatment number	Seeding rate	
	Grass-Herb	Shrubs
	lb/acre	
1	12	
2	18	
3	50	
4	12	4
5	18	4
6	50	4
7	18	20
8		4
9		45
10		50

The Brillion grass-seeder used in this study is more accurately known at the Brillion Turf-Maker. It is designed for accurately seeding grasses and it is an ideal seeder for surface mine rehabilitation work where the spoil material has been previously ripped and harrowed.

The Turf-Maker has two sets of rollers. The front set crushes lumps and forms a firm seedbed. Seeds are metered into the seedbed with a hopper that is mounted between the front and rear sets of rollers. The rear rollers split the shallow ridges formed by the front rollers and firm the soil around the seed thereby ensuring good hydraulic conductivity of the soil with the seed. Using this equipment and various size seed there will always be some of the seed at the proper depth for best germination.

There are two common misconceptions about using the Brillion on rocky soils. One is that it will not plant in rocky materials. The second is that rocks break the rollers, thereby requiring a great deal of time and effort to change the broken rollers. The first complaint is not valid except when the Brillion is misused. The second complaint is sheer misuse and abuse of equipment. Speed is the greatest enemy of the Brillion when used in rocky spoils. The larger the rocks, the slower the seeder must travel. The Brillion used by the authors was purchased in 1972 and has seeded under the most severe rocky conditions and never required any repair. It is not uncommon for the Brillion to seed over spoil materials that have been deep-ripped, harrowed and have rocks six inches to one and one-half feet in diameter.

The grass and shrub species used are listed in tables 2 and 3. Treatments 1, 2, and 3 were planted with the grass-broadleaf herb mixture, but at three different seeding rates (12, 18, 50 lb/acre [13, 20, and 56 kg/ha] respectively) and with no shrubs. Treatments 4, 5, and 6 also were seeded with the grass-broadleaf herb mixture at 12, 18, and 50 lb/acre (13, 20, and 56 kg/ha); shrubs were simultaneously seeded at 4 lb/acre (5 kg/ha) in these three treatments. Treatment 7 was seeded at 18 lb/acre (20 kg/ha) of mixed grass-broadleaf herb and 20 lb/acre (22 kg/ha) of shrubs. Treatments 8, 9, and 10 were seeded with shrubs only at 4, 45, and 50 lb/acre (5, 50, and 56 kg/ha). The percent composition of species seeded in both the grass-broadleaf herb and shrub mixtures remained consistent (tables 2 and 3).

The research area was fenced so that four-fifths of each treatment was protected from cattle grazing, while the other one-fifth was exposed. Annual assessments determined percent ground cover, species density, and production for each treatment in the grazed and protected area. Herbaceous vegetation was sampled using 10 randomly placed 1 by 2 feet (0.33 by 0.66 m) plots in each treatment. Five transects, 5 by 15 feet (4.6 by 13.8 m) were randomly placed in all shrub seeding treatments to record shrub numbers and annual growth features.

RESULTS AND DISCUSSION

Grasses and Broadleaf Herbs

The percent herbaceous ground cover (grasses and broadleaf herbs) for the different grass-broadleaf herb seed mixture treatments recorded in 1984, 7 years after planting, is presented in table 4. The percent ground cover of seeded grass differed little between grazed and protected areas for each treatment. In contrast, the percent ground cover of seeded herbs was distinctly less on grazed areas. Alfalfa (Medicago sativa) was the most prevalent broadleaf herb and received heavy grazing. Consequently, it was more abundant in the protected areas. Further, the protected areas had less bare ground than the grazed areas because the lack of grazing pressure allowed the plants to attain larger size and a greater accumulation of litter.

Increasing the grass-broadleaf herb seeding rates from 12, 18 or 50 lb/acre (13, 20 and 56

kg/ha) did not result in an increase in ground cover for either the grazed or protected treatments (table 4). The lack of any large difference between the three rates 7 years after planting suggests that seeding the area at 12 lb/acre (13 kg/ha) would be suitable unless more total cover is needed the first year for erosion control.

The percent herbaceous ground cover for the grass + shrub seed mixture treatments is listed in table 5. The amount of ground cover for both grasses and broadleaf herbs was greater on the protected treatments. As with the grass seed mixture, somewhat less variability in ground cover occurred among the grazed treatments. The high variability in the amount of ground cover on the

Table 2.--Grasses and broadleaf herbs planted and seeding rates for all treatments

Species seeded	Purity	Germination	PLS[1]	No seeds per lb	Pct of mixture (weight)	Treatments 1	2	3	4	5	6	7
	- - - Percent - - - - -					Pounds pure live seed (PLS) - - - - - Planted per acre - - - - - -						
Grasses												
Agropyron cristatum	95	90	85.5	319,660	15.6	1.60	2.40	6.67	1.60	2.40	6.67	2.40
Agropyron intermedium	96	90	85.5	88,110	26.0	2.67	4.00	11.12	2.67	4.00	11.12	4.00
Agropyron riparian	95	90	85.5	137,830	5.2	.53	.80	2.23	.53	.80	2.23	.80
Agropyron siberian	97	90	87.3	212,855	5.2	.55	.82	2.27	.55	.82	2.27	.82
Agropyron smithii	86	80	68.8	149,210	5.2	.43	.64	1.79	.42	.64	1.79	.64
Bromus inermis	90	85	76.5	105,980	5.2	.48	.72	1.99	.48	.72	1.99	.72
Dactylis glomerata	95	90	85.5	600,000	5.2	.53	.80	2.23	.53	.80	2.23	.80
Festuca idahoensis	95	90	87.3	1,050,000	6.1	.55	.96	2.67	.55	.96	2.67	.96
Festuca ovina duriuscula	96	85	81.6	633,520	10.4	1.02	1.53	4.25	1.02	1.53	4.25	1.53
Psathyrostachys junceus	90	70	63.0	130,760	5.2	.39	.59	1.64	.39	.59	1.64	.59
Broadleaf Herbs												
Linum lewisii	90	85	76.5	278,280	1.3	.12	.18	.50	.12	.18	.54	.18
Medicago sativa	99	82	81.2	213,760	10.4	1.01	1.52	4.22	1.01	1.52	4.22	1.52

[1]PLS=Pure live seed.

Table 3.--Shrubs planted, seed features, and seeding rates for all treatments

Species	Seed features: Purity	Germ.	PLS[1]	No. seed per lb	% seed mixture	Amount seed planted (PLS[1]/AC) --Treatments-- 4 (4 lb) bulk	5 (4 lb) bulk	6 (4 lb) bulk	7 (20 lb) bulk	8 (4 lb) bulk	9 (45 lb) bulk	10 (501b) bulk
Artemisia tridentata	12	80	9.6	2,575,941	0.08	0.08	0.08	0.08	0.42	0.08	0.95	1.06
Chrysothamnus nauseosus	80	78	62.4	693,220	3.0	0.07	0.07	0.07	0.37	0.07	0.84	0.95
Purshia tridentata (Carrier)	95	85	80.7	15,370	32.0 43.0	1.03	1.03	1.03	5.16	1.03	11.62	12.9

[1]PLS=Pure live seed.

Table 4.--Percent ground cover for grass-broadleaf herb seeded treatments, 1984[1]

Cover	Treatment 1 (12 lb/acre)		Treatment 2 (18 lb/acre)		Treatment 3 (50 lb/acre)	
	Grazed	Prot.	Grazed	Prot.	Grazed	Prot.
Seeded grass	33.4	38.4	29.8	21.2	27.8	30.9
Seeded broadleaf herbs	35.2	44.6	26.4	46.0	16.2	32.6
Total liver cover	68.6	83.0	56.2	67.2	44.0	63.5
Bare ground	21.4	5.2	41.6	9.4	34.4	5.8

[1]Totals do not equal 100 percent since litter is not included and storied cover was recorded.

Table 5.--Percent ground cover for grass-broadleaf herb and shrub seed mix treatments, 1984[1]

Cover	Treatment 4 (12/4)[2]		Treatment 5 (18/4)		Treatment 6 (50/4)		Treatment 7 (18/20)	
	Grazed	Prot.	Grazed	Prot.	Grazed	Prot.	Grazed	Prot.
Seeded grass	39.0	35.0	28.2	37.2	21.6	32.3	23.4	39.4
Seeded broadleaf herbs	21.8	37.2	37.0	43.0	36.0	60.6	22.0	35.0
Seeded shrubs	.5	7.8	.3	.1	20.3	47.7	.4	.5
Bare ground	24.6	6.6	18.8	2.2	29.8	2.2	41.6	11.6

[1]Totals do not equal 100 percent since litter is not included and storied cover was recorded.
[2]Grass/shrub seed mix, pounds per acre.

protected treatments was probably due to the aggressive growth of alfalfa.

Where herbs and shrubs were seeded together, the major difference in herbaceous ground cover appeared to be due to grazing, not seeding rate (tables 4 and 5). Comparison of the two tables shows that addition of shrubs to the seed mixture did not alter the amount of herbaceous ground cover. Further, increasing the seeding rates did not change the proportion of the plants seeded.

Shrubs

With protection from grazing a satisfactory number of mountain big sagebrush plants were able to establish when grasses-broadleaf herbs were seeded at the lowest rate (12 lb/acre [13 kg/ha]) and shrubs were seeded at 4 lb/acre (5 kg/ha, table 6. Slightly over 800 plants per acre (1 976/ha) were recorded in the protected area compared to 54 plants (133/ha) in the grazed portion. Physical damage to the seedbed by livestock perhaps accounted for some decrease in numbers between grazed and protected sites. However, even with protection, mountain big sagebrush plants were unable to compete with the herbaceous plants when the grass-broadleaf herb seeding rates were increased to 18 or 50 lb/acre (20 to 56 kg/ha) and the shrubs seeded at 4 lb/acre (5 kg/ha), treatments 4 and 5, (table 6). Apparently the herbaceous plants provided sufficient competition to prevent the initial establishment of this shrub. With grazing a few mountain big sagebrush plants were able to establish with the higher grass-broadleaf herb seeding rates. Grazing appeared to reduce herb density allowing the establishment of a few shrubs.

With protection, rubber rabbitbrush plants were also able to establish when seeded in mixtures with herbs if the grass-broadleaf herb rate was at 12 lb/acre (13 kg/ha) and shrubs at 4 lb/acre (5 kg/ha). The number of rubber rabbitbrush plants decreased as the grass-broadleaf herb mixture seeding rate was increased from 12 lb/acre (13 kg/ha) to 18 and 50 lb/acre (22 and 56 kg/ha); see table 6. With grazing, no rubber rabbitbrush plants occurred regardless of the grass-broadleaf herb seeding rates. Apparently rubber rabbitbrush plants were susceptible to grazing impacts including foraging and trampling.

When the seeding mixture was increased to 18 lb/acre (22 kg/ha) of grass-broadleaf herbs and 20 lb/acre shrubs (22 kg/ha), the numbers of both mountain big sagebrush and rubber rabbitbrush increased dramatically (table 6). Approximately 3,500 and 4,500 mountain big sagebrush plants per acre (8 648 and 11 119/ha) occurred in the grazed and protected site, treatment 7. The increased numbers of mountain big sagebrush plants in the protected site demonstrate the ability of the shrub to survive with herbaceous competition. Rubber rabbitbrush plants were also able to compete with the herbs

Table 6.--Number of shrubs per acre by treatment, 1984

Treatment	Seeding rate (grass/shrub)	Number Plants: Mt. Big sagebrush Grazed	Mt. Big sagebrush Prot.	Rubber rabbitbrush Grazed	Rubber rabbitbrush Prot.	Antelope bitterbrush Grazed	Antelope bitterbrush Prot.
	lb/acre						
4	12/3	54	81	0	116	0	0
5	18/4	37	0	9	37	0	0
6	50/4	46	0	0	28	0	0
7	18/20	3,538	4,530	0	2,091	0	0
8	/4		2,207		2,788	0	1,041
9	/45	1,742	7,663	826	929	0	2,091
10	/50	2,439	5,343	939	1,041	0	5,576

in the protected site. No rubber rabbitbrush plants were able to establish if grazing was permitted.

Antelope bitterbrush plants were unable to establish in any treatment when seeded with understory grasses and broadleaf herbs. Regardless of the seeding rates, antelope bitterbrush was unable to successfully compete with the herbs (table 6).

If shrubs were seeded alone without grasses and broadleaf herbs, a substantial increase in shrub numbers occurred for all species (table 6). However, responses were affected by grazing. The number of mountain big sagebrush plants increased from 213 to 2,207 per acre (526 to 5 433/ha) in the protected area when shrubs were seeded at 4 lb/acre (5 kg/ha) with and without grasses-broadleaf herbs. As the shrub seeding rate increased from 4 to 45 or 50 lb/acre (5 to 50 or 56 kg/ha) the number of mountain big sagebrush plants nearly doubled in both the grazed and protected sites. However, nearly twice as many plants occurred in the protected site as the grazed area.

The number of rubber rabbitbrush plants also increased substantially when shrubs were seeded alone. However, increasing the seeding rate of shrubs did not result in an increase in rubber rabbitbrush density (table 6). Slightly fewer plants appeared in the grazed areas for all seeding rates.

In protected treatments where shrubs were seeded without grasses and broadleaf herbs, antelope bitterbrush was able to establish. A significant increase in numbers of plants occurred as the shrub seeding rate was increased from 4 to 45 or 50 lb/acre (5 to 50 or 56 kg/ha), table 6. Slightly over 1,000 antelope bitterbrush plants per acre occurred in the protected area when shrubs were seeded alone at 4 lb/acre (5 kg/ha). The number increased to over 2,000 plants and 5,500 plants per acre (4 942 and 13 590/ha) as the seeding rates were increased to 45 and 50 lb/acre (50 and 56 kg/ha). No antelope bitterbrush plants established in the grazed area when shrubs were seeded alone at any planting rate.

CONCLUSIONS

This study demonstrated that the Brillion grass-seeder is capable of planting a mixture of different sized seeds. Further, it is able to disperse "trashy" seeds such as sagebrush and rabbitbrush when they are seeded alone or in a mixture of other species.

An adequate shrub cover was obtained for all three species on the protected plot seeded only to shrubs at a rate of 4 lb/acre (5 kg/ha). A satisfactory number of mountain big sagebrush plants were established in both the protected and grazed areas when seeded with herbs at a rate of 18 lb/acre grasses broadleaf herbs, and 20 lb/acre shrubs (20 and 22 kg/ha). Rubber rabbitbrush was also adequately established when seeded at this rate, but only in the protected area. Therefore, the authors recommend a mixture of 0.17 lb/acre (0.19 kg/ha) pure live seed (PLS) sagebrush, 0.15 lb/acre (0.17 kg/ha) PLS rabbitbrush, and 1.0 lb/acre (1.1 kg/ha) PLS bitterbrush (see table 3). These recommendations are minimum rates based upon shrubs being seeded alone and protected from grazing. Mountain big sagebrush and rubber rabbitbrush can be seeded directly with grasses and broadleaf herbs if the herbs are planted at 12 lb/acre (13 kg/ha). The most advantageous seeding rate for both shrubs when planted with grasses and broadleaf herbs was not determined but appeared to be 0.85 lb/acre (0.95 kg/ha) PLS for mountain big sagebrush and 0.75 lb/acre (0.8 kg/ha) PLS for rubber rabbitbrush.

Establishing a mixture of shrubs and herbs can be achieved by seeding the two different groups in separate strips (Richardson and Trussell 1980). Since grasses and broadleaf herbs develop much faster and offer serious competition to the young shrubs, the amount of shrub seeds required can be reduced if this separation is practiced.

Areas seeded to shrubs must be protected from grazing during the period of shrub establishment, particularly if seeded to antelope bitterbrush or rubber rabbitbrush. Damage to young shrubs from cattle trampling may be as important as the impact of foraging.

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IRRIGATION BY MINE DISCHARGE WATER AND FERTILIZATION OF BIG SAGEBRUSH: EFFECTS OF NUTRITIONAL COMPOSITION, PRODUCTION, AND MULE DEER USE

R. L. Elderkin, Jr., D. R. Dietz, B. L. Welch, P. M. Ralphs, and J. K. Czarnecki

ABSTRACT: Field plots of Artemisia tridentata (big sagebrush) were irrigated by mine discharge water, irrigated-fertilized, and left untreated (control). Measurements were taken to determine the effects of treatments on plant productivity, mule deer preference, digestibility, and chemical composition of forage. The irrigated-fertilized plants were significantly more productive, preferred by wintering mule deer, and contained higher levels of crude protein, phosphorus, and monoterpenoids. The use of mine discharge water and fertilization could compensate for loss of mule deer winter range through mining by increasing the productivity and nutritive value of the remaining range.

INTRODUCTION

Big sagebrush (Artemisia tridentata) is one of the most common range plants on mule deer winter range in the Piceance Creek Basin of western Colorado's oil shale region. Sagebrush, along with pinyon (Pinus edulis) and juniper (Juniperus osteosperma), provide most of the vegetation biomass in the Basin. The use of big sagebrush, pinyon, and juniper for cover and food is well documented (Leach 1956; Kufeld and others 1973; Hansen and Dearden 1975; Tueller 1979; Cluff and others 1982; Pederson and Welch 1982). Although mule deer intensively inhabit big sagebrush stands during winter in the Piceance Basin, just how much big sagebrush is consumed by deer and sagebrush nutritional value are not well documented. An opportunity to study sagebrush use and its nutritive value for wintering mule deer came on the Federal Prototype Oil Shale Lease Tract C-b (Cathedral Bluffs Oil Shale Company) during the spring of 1980. In an attempt to dispose of excess mine water, employees of Tract C-b installed a sprinkler irrigation system on a big sagebrush-dominated deer winter range. Several plots within the irrigated area were fertilized with a nitrogen/phosphorus fertilizer to observe vegetative response to irrigation and fertilization.

During the winter of 1980-1981, we observed that mule deer were highly attracted to the irrigated and fertilized plots and were browsing heavily on big sagebrush plants within those plots. Untreated plots were mostly unbrowsed by deer. We also observed, during our fall inspection, significant vegetative response in the treated plots versus the untreated plots. To quantify our observations, we repeated the irrigation and fertilization treatments in the spring of 1981 and took measurements to determine: big sagebrush response to the treatments, wintering mule deer use, and effects of treatments on winter nutritive value of big sagebrush.

MATERIALS AND METHODS

Within a 160-ft radius, irrigated circle created by a "big gun" sprinkler head applying about 220 gallons per minue, two treatment plots (270 by 270 ft [82.3 by 82.3 m]) were located. One plot received irrigation only; the other was irrigated and received 200 pounds of actual nitrogen per acre and 100 pounds of actual phosphorus. Irrigation was accomplished by applying 4.72 inches of mine water in an 18-hour period every 15 days. An untreated plot, the same size as the treated plots, was selected adjacent to the treatment plots and was comparable in aspect, slope, microrelief, vegetation, and soils. Big sagebrush plants were randomly selected for measurement in the three plots. Ten plants were selected in each plot. The 30 plants were tagged in the spring of 1981. Wire cages were placed around the plants after the growing season in October. During this time, each caged plant was paired with a nearby big sagebrush plant of similar height, growth form, and leaf characteristics. These uncaged plants were used to determine mule deer use and productivity. Caged plants were used to furnish the vegetative tissues needed for nutritive analysis.

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R. L. Elderkin is Environmental Scientist (Wildlife), U.S. Department of the Interior, Bureau of Land Management, Oil Shale Project Office, Grand Junction, CO; D. R. Dietz is Fish and Wildlife Biologist, U.S. Department of the Interior, Fish and Wildlife Service, Oil Shale Project Office, Grand Junction, CO; B. L. Welch is Principal Research Plant Physiologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT; P. M. Ralphs is Reclamation Specialist, Cathedral Bluffs Shale Oil Co., Grand Junction, CO; and J. K. Czarnecki is Computer Specialist, U.S. Department of the Interior, Bureau of Land Management, Oil Shale Project Office, Grand Junction, CO.

On the uncaged plants, 20 or more leaders of current annual growth per plant were measured after the end of the growing season, but prior to deer use. These measurements represented productivity (Welch and McArthur, this proceedings). After deer use, the remains of the same leaders were measured again to determine mule deer use. Use was expressed as a percent of current year's growth consumed.

At the time wintering mule deer were browsing on the plants, samples of current year's growth were removed from the caged plants. Samples were divided in half, placed in paper sacks, and frozen on site with dry ice. Vegetative samples were kept separate by individual plant and by treatment class. One half of the samples was used to determine monoterpenoid level and *in vitro* digestion; these were kept frozen until processed. Samples to be used for other chemical analyses were air-dried, ground in a Wiley mill, passed through a 1-mm sieve, and placed in airtight containers.

A steel, motorized mortar and pestle was precooled with liquid nitrogen before grinding the samples for monoterpenoid and *in vitro* digestion. Samples, one at a time, were placed in the mortar and another aliquot of liquid nitrogen was poured over the samples before grinding. After grinding, the samples were placed in plastic bottles fitted with airtight caps and stored at -35° F (-37° C).

Monoterpenoids were extracted in soxhlet extraction apparatus with absolute ethyl ether. For each sample, we placed 10 g of freshly ground tissue in a cellulose soxhlet extraction thimble. A fiberglass plug on top of the sample inside the thimble prevented spillover of tissue during the extraction process. Monoterpenoids were exhaustively extracted over a 6-hour period. The volume of the extract was reduced to about 30 ml by use of reduced pressure. We then added an internal standard carvone (2.5 ug/ul) to each extract and absolute ethyl ether to bring the volume to 50 ml. Extracts were stored in airtight bottles at -35° F (-37° C) until chromatographic analyses.

We conducted chromatographic analyses with a 5830A Hewlett-Packard Flame Ionization, Recording Gas Chromatograph. Monoterpenoids were separated by use of 3-mm by 1.2-m stainless steel column packed with 10 percent carbo-wax 20M on 80/1000 Chromosorb WHP. Temperature programming was used to separate individual monoterpenoids (Welch and McArthur 1981). We identified monoterpenoids by comparing retention times with those of standards. Dry matter content of each sample was determined, and the concentration of individual monoterpenoids was expressed as a percentage of dry matter. Total monoterpenoids are the sum of individual monoterpenoids.

We used the *in vitro* digestion procedure as outlined by Pearson (1970), except 1.0 g of fresh tissue was placed in digestion tubes. Dry matter content was determined for all samples digested. Data were expressed as a percentage of digestible dry matter. Rumen inoculum was collected from a slaughterhouse steer fed alfalfa hay and barley (Welch and others 1983b).

For the air-dried samples, the following chemical measurements were made: oven-dry weight, ash, plant cell wall, hemicellulose, lignin, phosphorus, calcium, crude protein, starch, and sugar (Van Soest 1967; Association of Official Analytical Chemists 1980). Data were expressed on an oven dry-matter basis.

Data were statistically analyzed by random design analysis of variance and one-way heirarchical analysis of variance (Anderson and Bancroft 1952; Steel and Torrie 1960). Means were compared using Duncan's multiple range test ($\alpha = 0.05$).

RESULTS AND DISCUSSION

Productivity, as measured by length of current year's leader growth, was significantly greater for the irrigated-fertilized treatment than for the irrigated and unirrigated treatments. Average growth per leader for irrigated-fertilized was 10.7 cm, irrigated was 3.8 cm, and unirrigated was 2.3 cm. Irrigated-fertilized treatment increased plant growth by a factor of 2.8 over irrigated and 4.7 over unirrigated. What was surprising was that the irrigated treatment did not significantly increase plant growth over the unirrigated treatment. Apparently, soil fertility was a more limiting factor during the study period than soil moisture.

Analysis of variance detected significant ($\alpha = 0.063$) differential use by mule deer among treatments. There was a large intratreatment variation. The mean percentage of utilization for the irrigated-fertilized treatment was 56.1 percent (standard deviation ±19.1 percent). Utilization for irrigated and unirrigated treatments was 42.1 ± 14.2 percent and 29.4 ± 14.6 percent, respectively. Worthy of note is the high standard deviation associated with all treatments. Although sample size was too small to statistically detect significant differences among treatments at a lower or normal alpha ($\alpha = 0.05$) level, the trend favors heavier deer use on the irrigated-fertilized treatment.

It is important to note that while the difference in percentage utilization among treatments is not large, the difference in volume of materials consumed is quite large. Actual mean length of each current year's leader growth eaten is calculated by multiplying the mean leader length of a treatment by the percent utilization. Actual length consumed for the irrigated-fertilized treatment was 6.0 cm (10.7 cm x .561), for the irrigated treatment 1.6 cm (3.8 cm x .421), and for the unirrigated treatment .9 cm (2.3 cm x .394). The deer were consuming 3.8 times more leader length in the irrigated-fertilized plot than the irrigated plot and 6.7 times more than in the unirrigated plot. In the irrigated plot, deer consumed 1.8 times more leader length than in the unirrigated plot.

The results of the chemical analyses, tested statistically by a hierarchical analysis of variance and Duncan's multiple range test, disclosed significant differences among treatments, among plants within treatments, and between samples within plants. The unirrigated, irrigated, and

Table 1.--Chemical composition and digestibility of big sagebrush (Artemisia tridentata) growing on irrigated, irrigated-fertilized, and untreated plots on a Colorado oil shale mine site. Data expressed on a percentage dry matter basis. Both means and standard deviations are given

	Treatments			
	Unirrigated	Irrigated	Irrigated-fertilized	Mean
Plant cell wall	37.1 ± 3.1	35.3 ± 3.6	38.1 ± 3.1	36.8 ± 3.3
Hemicellulose	10.1 ± 2.4	9.8 ± 2.1	10.6 ± 2.5	10.1 ± 2.3
Cellulose	16.0 ± 1.9	15.2 ± 2.5	17.0 ± 2.5	16.7 ± 2.3
Lignin	10.7 ± 1.4[a]	10.9 ± 1.9[a]	10.5 ± 1.3[b]	10.6 ± 1.6
Crude protein	11.8 ± 1.2[a]	12.4 ± 1.2[a]	15.8 ± 0.7[b]	13.4 ± 1.1
Starch	2.9 ± 0.5[a]	2.4 ± 0.3[b]	2.3 ± 0.5[b]	2.5 ± 0.4
Sugar	10.3 ± 2.4	9.7 ± 1.3	9.3 ± 2.2	9.8 ± 2.0
Ash	4.1 ± 0.5	4.5 ± 1.5	3.6 ± 0.4	4.1 ± 1.0
Phosphorus	0.076 ± 0.006[a]	0.087 ± 0.012[b]	0.088 ± 0.009[b]	0.084 ± 0.011
Calcium	0.241 ± 0.030[a]	0.253 ± 0.041[b]	0.221 ± 0.036[a]	0.238 ± 0.36
Digestibility	48.8 ± 3.2	50.8 ± 3.0	50.1 ± 2.9	49.9 ± 3.0

Treatment means sharing the same or no superscript are not significantly different (α= 0.05).

irrigated-fertilized treatments induced significant differences in crude protein (α= 0.001), starch (α= 0.01), phosphorus (α= 0.01), and calcium (α= 0.10) levels (table 1).

The irrigated-fertilized sagebrush plants were higher in protein and phosphorus and lower in starch than the unirrigated and the irrigated plants (table 1). Unirrigated (control) plants had the highest starch content and the lowest crude protein and phosphorus percentages. Irrigated plants were highest in calcium and in between for crude protein, starch, and phosphorus.

Individual plant variability was highly significant for all chemical constituents. The distribution of the variance components determined by hierarchical analysis of variance is shown in table 2 for protein, starch, calcium, and phosphorus-constituents significantly affected by treatment. Crude protein was the only component in which most of the variance was between treatments rather than between plants within a treatment. No replicate sagebrush samples were analyzed for crude protein, thus no information was obtained about within-sample variance.

Both starch and phosphorus had high within-treatment (between plants) variance; accounting for almost half of the total variance while within-treatment variance accounted for less than one-third and between-sample variance accounted for about one-fifth of the total variance. Calcium had a high between-sample variance, accounting for about one-half of the total variance. Only about one-tenth of the total variance for calcium was due to between-treatment variance while over one-third of the total variance was between plants within a treatment (table 2).

The nutritional results indicate that the irrigation-fertilization treatment caused crude protein levels to rise enough above the untreated sagebrush levels to play a major role in attracting mule deer to that plot. The higher phosphorus and lower starch also indicate that big sagebrush, irrigated and fertilized, was probably in the vegetative growth stage longer compared to the more phenologically advanced control plants.

Energy-producing compounds, protein, and phosphorus are nutrients commonly listed as being deficient in

Table 2.--Distribution of variance components for chemical constituents significantly affected by nonirrigation, irrigation, or irrigation-fertilized big sagebrush (Artemisia tridentata) plants on a Colorado oil shale mine site

Chemical constituent	Variance component			
	Between treatments	Within treatments	Between samples[1]	Total variance
	%			
Protein	79.6	20.3	--[2]	100.0
Starch	31.5	46.6	21.9	100.0
Calcium	10.8	38.2	50.9	100.0
Phosphorus	30.5	48.9	20.5	100.0

[1]Variance is between replicated samples of the same plant.
[2]Protein analyses were not replicated on the same plant.

Table 3.--Monoterpenoid composition of big sagebrush (Artemisia tridentata) growing on irrigated, irrgated-fertilized, and nonirrigated plots on a Colorado oil shale mine site. Data expressed on a percent dry matter basis. Both means and standard deviations are given.

Monoterpenoid	Treatment			
	Unirrigated	Irrigated	Irrigated-fertilized	Means
α -pinene	[1]0.03 ± 0.02[a]	0.09 ± 0.06[b]	0.09 ± 0.04[b]	0.07 ± 0.05
Camphene	0.09 ± 0.06[a]	0.15 ± 0.07[b]	0.23 ± 0.14[c]	0.16 ± 0.11
1,8 Cineol	0.15 ± 0.10	0.21 ± 0.12	0.25 ± 0.18	0.20 ± 0.14
β-thujone	0.08 ± 0.04[a]	0.11 ± 0.07[b]	0.13 ± 0.05[b]	0.11 ± 0.06
Camphor	0.55 ± 0.29[a]	0.81 ± 0.38[b]	1.22 ± 0.73[c]	0.86 ± 0.56
Terpineol	0.05 ± 0.06	0.07 ± 0.07	0.04 ± 0.02	0.05 ± 0.05
Fenchyl alcohol	0.05 ± 0.06	0.07 ± 0.06	0.10 ± 0.09	0.07 ± 0.07
[2]5.36 (unknown)	0.16 ± 0.09[a]	0.23 ± 0.23[b]	0.39 ± 0.17[c]	0.26 ± 0.16
8.56 (unknown)	0.34 ± 0.55	0.17 ± 0.25	0.58 ± 0.77	0.36 ± 0.53
12.70 (unknown)	0.28 ± 0.19	0.17 ± 0.10	0.17 ± 0.21	0.20 ± 0.17
Total	1.78[a]	2.08[b]	3.20[c]	

[1]Treatment means sharing the same or no superscript are not significantly different at the 5 percent level.
[2]Numbers are retention times posted on the chromatogram.

Table 4.--Distribution of variance components for monoterpenoids significantly affected by nonirrigation, irrigation, or irrigation-fertilization of big sagebrush (Artemisia tridentata) plants on a Colorado oil shale mine site

Monoterpenoid constituent	Variance component		
	Between treatments	Within treatments	Total variance
		%	
α -pinene	22.4	77.7	100.0
Camphene	14.8	85.2	100.0
B-thujone	19.1	80.9	100.0
Camphor	26.7	74.4	100.0
5.36 (unknown)	32.6	67.4	100.0

the winter diet of mule deer and livestock (Dietz 1965; Halls 1970; Nagy and Wallmo 1972). In vitro digestibility (a measurement of energy-producing compounds) was at the 50 percent level needed for maintenance (Ammann and others 1973). The in vitro digestibility found in this study compares closely to the in vivo digestibility of big sagebrush reported by Dietz and others (1962) for north-central Colorado. Crude protein levels ranged from 11.8 to 15.8 percent, which is somewhat higher than that reported for big sagebrush in north-central Colorado by Dietz and others (1962), in California by Bissell and others (1955), and in Utah by Smith (1957). However, Welch and McArthur (1979b) reported winter crude protein levels in 21 accessions of big sagebrush ranged from 10.0 to 16.0 percent.

Based upon these substantial crude protein levels and the approximately 50 percent dry matter digestibility of big sagebrush, it is believed that digestible protein intake is above the maintenance requirements given by Welch and McArthur (1979a). Mean phosphorus levels ranged from 0.076 to 0.088 percent and are considerably below those recommended for maintenance by various authors (French and others 1955; Ullrey and others 1975; Welch 1983b). However, when big sagebrush is compared nutritionally with other range browse species in the West, it is generally rated good for wintering mule deer (Dietz and others 1962; Welch 1983a).

Analysis of variance detected significant differences both between treatments and within treatments for monoterpenoids (tables 3 and 4). Total monoterpenoids were significantly higher in vegetative tissue collected from big sagebrush plants under the irrigated-fertilized treatment (3.20 percent) than plants under irrigated (2.08 percent), and unirrigated (1.78 percent) treatment. As with browsing, there was considerable plant-to-plant variation. Of the ten individual monoterpenoids found, five were significantly affected by treatment. Irrigated-fertilized plants contained significantly higher levels of camphene, camphor, and 5.36 (unknown monoterpenoid) than plants not irrigated or irrigated only. Irrigated-fertilized and irrigated plants contained significantly higher levels of α-pinene and β-thujone than the unirrigated treatments. For these five monoterpenoids, the variability between treatments ranged from a low of 14.8 percent for camphene to a high of 32.6 for the unknown. Within-treatment (plant-to-plant) variance ranged from a low of 67.4 percent for the unknown to a high of 85.2 percent for camphene (table 4). The results of this study indicate that mule deer selected sagebrush material containing higher levels of monoterpenoids. The role monoterpenoids play in diet selection has been studied by a number of workers (Oh and others 1967; Sheehy 1975; Scholl and others 1977; Radwan and Crouch 1978; Connolly and others 1980; Schwartz and others 1980; Narjisse 1981; White and others 1982; Welch and others 1983a). Some of these have reported that monoterpenoids exert a negative influence on diet selection; others report no effect. The role monoterpenoids play in diet selection is confusing and far from resolved.

CONCLUSIONS AND SUMMARY

Water pumped during mine-dewatering efforts at the Cathedral Bluffs Oil Shale Mine was disposed of through a sprinkler irrigation system onto winter deer range. Mule deer use and chemical composition of big sagebrush was determined for plants receiving the mine-discharge water, mine discharge water along with a nitrogen-phosphorus fertilizer application, and plants in an unirrigated-unfertilized (control) plot.

The irrigated and fertilized sagebrush plants received moderate to heavy deer use during the mid- to late-winter period. Irrigated-only plants received light to moderate use, control plants received almost no use. The results of chemical analyses were tested statistically by analysis of variance using a hierarchical (nested) design. There were significant differences due to treatment for protein, starch, phosphorus, and calcium, but not for ash, plant cell walls, hemicellulose, cellulose, lignin, sugar, and in vitro digestibility. There were, however, significant differences within treatments indicating considerable variability among plants receiving the same treatment. Irrigated-fertilized plants were higher in protein and phosphorus, and lower in calcium and starch. Control plants were highest in starch and lowest in phosphorus and protein. Irrigated-only plants were highest in calcium and between the irrigated-fertilized and control plants in the levels of other nutrients.
The monoterpenoid content of big sagebrush was also determined. There was a significant difference in these oils due to treatment for α-pinene, camphene, β-thujone, camphor, and an unknown monoterpenoid. Within treatment, variance was high for all the monoterpenoids. The irrigated-fertilized plants contained the highest levels of α-pinene, camphene, β-thujone, camphor, and the unknown. The irrigated-only plants were in between in levels of these oils and the control plants contained the least, indicating that these essential oils did not negatively affect sagebrush utilization by mule deer.

Individual plant variability was much greater, in general, for the irrigated and irrigated-fertilized treatments than for the control. Uneven sprinkler and/or fertilizer application may have contributed to the wide variability among individual plants within treatments. Microsite differences, as well as the differential ability of plants to assimilate the fertilizer and mine water, may also have been a factor in the significant individual plant variability for the various chemical constituents. 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.

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ECONOMIC CONSIDERATIONS IN MANAGEMENT OF SAGEBRUSH RANGES

Fred J. Wagstaff

ABSTRACT: Economic factors give managers added information about the effects of various management strategies. In order to make meaningful economic analyses and comparisons of alternative management scenarios, accurate and sufficient physical information covering the fullest range of inputs and outputs possible must be available. Realistic alternatives should be developed and considered to assure that desired goals are being achieved and that scarce resources are being used in the most efficient manner. Deciding which factors are important, and realizing the true cost of taking actions can provide important comparisons before irreversible actions are taken. It is also important to study completed projects to see what impacts actually occurred so that future analyses can be more easily and accurately completed.

INTRODUCTION

Review of the literature and a considerable number of project analyses leads to the conclusion that some sagebrush rangelands can be successfully managed for profit or public benefit exceeding costs (Wagstaff 1983a). To be economically feasible, management must use good treatment techniques, reasonable cost control procedures, and good posttreatment management. With resources becoming scarce relative to demand, the need for efficient management of our sagebrush rangelands is increasing.

Rangelands are managed for the outputs in goods and services they are capable of providing. A good deal of thought is needed to identify and clearly state management goals for a specific unit of rangeland, this being the most crucial step in planning. Any conclusion about whether a project, treatment, or management action is good or bad must compare the results with the goals of management. Much of the difficulty in developing dependable and realistic management plans is due to unclear or contradictory goals (Alston 1972; Rensi 1979). Reasons for managing sagebrush rangelands are numerous and are often difficult to specify in measurable units.

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Fred J. Wagstaff is range economist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT.

There are several economic principles and procedures of analysis which are useful when formulating treatment or management plans (Sneva and Britton 1982; Winward 1983). Every rangeland use has value, costs, and benefits (Randall 1979). A good deal of custom fitting of management and treatment procedures must be done on the basis of specific site characteristics. A given treatment can be applied to different subspecies of sagebrush at a uniform cost, but the productivity can vary quite widely. Only a portion of sagebrush rangelands have the physical characteristics needed for successful and profitable treatment to increase productivity.

Treatments to enhance productivity are done after specific decisions, such as method of treatment, time of treatment, species to be seeded, amount of rest, and the level and kind of posttreatment use, are made. Of all of these, the most important factor is setting management goals and followup actions to achieve those goals.

Using economic factors in decisions would lead to treatment area selection on the basis of the value of net production. The acres having the highest net would be treated first and then so on down the scale. Each acre should yield a net benefit or it should not be treated. The net benefit or degree of economic efficiency associated with treatment of sagebrush ranges is affected most by posttreatment management of grazing (Nielson 1977).

BASIC ECONOMIC CONCEPTS

The concept of benefits and costs is very important. Benefits are the desirable impacts of a project or management action; however, what is considered desirable depends upon the goals of the land manager. For example, a complete brush kill may be perceived as highly desirable for livestock production by a private owner while game managers may feel this would be undesirable.

Costs are negative impacts that can take the form of money costs, resource obligation, opportunities foregone, or damages. The concept of costs is also subject to the goals and values of the land manager. It is important to identify and categorize all impacts of an action so benefits and costs can be compared.

Opportunity cost is the value of the best alternative foregone. If removal of brush

precludes wildlife use of an area, then the net benefits for wildlife not realized become an opportunity cost.

Marginality is a concept that holds that each divisible part of a project should be looked at separately. Applying this concept to rangelands means we should look at an area on the basis of soil type, vegetation, and other indicators of productive potential. When real differences occur in productivity, net benefits will also differ. Treatment costs are often the same regardless of the difference in soil or subspecies of sagebrush. Only those units where benefits exceed costs can be treated or managed economically.

Values

Valuing outputs is a very important concept because feasibility depends directly on those values. Were all outputs traded in markets, a price or unit value could be obtained rather easily. However, many rangeland uses and outputs are of the nonmarket type and setting values is imprecise and difficult. Many things, such as wildlife, scenery, and enjoyment of open spaces, upon which people place a good deal of value, are nonmarket in nature. Problems arise when market and nonmarket outputs are included in an analysis and trade-offs are indicated. Ignoring nonmarket unit values does not make the problem easier (Young 1979; Bartlett 1982).

Distribution

Problems can arise when one group gains benefits and another pays the costs (Wagstaff 1983b). Such problems occur frequently with wildlife where the public gains benefits from wildlife and the private landowner may suffer loss of resources to wildlife use.

Discounting

One other economic concept needs to be mentioned to give a general base for analysis. Discounting is used to make future benefits and costs comparable to present-day values (Nielsen 1977; USDA 1982). Essentially, discounting is applying an expected rate of interest and reducing future value by this amount. The concept rests on the fact that future incomes or expenses are not valued as highly as those occurring at the present.

Future expenses can be met by deposit of an amount lower than the cost with the remainder being interest earned. Likewise a future benefit is reduced in value to account for the opportunity cost of capital (interest which could be earned) and a risk factor.

ECONOMIC FACTORS AS DECISION CRITERIA

Every use connected with rangelands has value, costs, and benefits (Randall 1979). Funding is limiting, however, and many other uses of these funds can be made, so proposed expenditures for treatment or improvement of sagebrush rangelands must be compared to alternative uses (Kerr and Dooley 1982). Private landowners are faced with a dual problem. Borrowing money is expensive, with double-digit interest rates common. Also, capital or equity funds can be invested in the money markets or other low-risk investments and command 10 to 12 percent interest rates. These rates are high when compared to the average rate of return common in ranching enterprises. Most resource agency budgets have been declining, and the short-term outlook is for more reductions. This means a closer look must be taken at the costs and benefits associated with sagebrush rangeland treatment projects and management activities.

ECONOMIC DECISION CRITERIA

There are many criteria that can be used in making rangeland management decisions. Economics is usually just one factor in a decision and can be of major or minor importance. More attention is now being paid to economic factors of public projects due to the high price of capital and increased competition for tax dollars among public programs.

As pointed out by Workman (1981), the use of different criteria may change decisions. A few basic economic measures that are widely used are:

Net Present Worth.--The present value of future benefits minus all costs. The level of net benefits depends on the unit values used for costs and benefits, the time frame, and mostly, the rate of discount.

Rate of Return.--Is the annual rate of return on the investment received as net benefits.

Benefit-Cost Ratio.--The ratio of total benefits/total costs. All benefits and costs should be compared on an equal time frame so discounting is needed. Generally, present values of benefits and costs are used although other techniques can yield identical results.

Payout or Break-Even Period.--The length of time it would take to return the original investment. Only benefits above operation and maintenance costs can be applied to investment recovery. If borrowed funds were used, this would be the period of time required to repay the loan.

Cash Flow Analysis.--Amount of cash expected to be received or paid during a given time interval.

Distribution Analysis.--The incidence of benefits and costs is often quite important. Who pays and who gains should be set forth in an analysis so that questions of equity among individuals or groups can be addressed (Keith 1983; Obermiller 1983). There has been increasing resistance to programs which benefit few persons.

A couple of major points concerning physical characteristics and related economic principles need to be made. Treatment costs and responses are often viewed as linear functions across large changes in project size.

A more reasonable cost function would follow a more classic pattern: reducing costs to a certain size, then increasing cost per unit treated. Production functions could be viewed as essentially linear as long as the same sagebrush subspecies is being treated and the soil, climate, slope, aspect, and other physical features remain constant. The temptation is to treat large areas, thereby reducing unit costs as much as possible. However, this may not be as efficient as treating only the most productive acres (Bartlett and others 1974; D'Aquino 1974). Treatment costs per unit of land may be higher by doing selected areas, but the net difference between costs and benefits can be greater because of the higher production per unit treated.

VALUE OF ADEQUATE PHYSICAL DATA

Without accurate estimates of the physical parameters, economic analysis is of little value. Any errors in the estimates of inputs and outputs will be magnified in an analysis. There is a tendency among analysts to accept estimates by range conservationists as completely accurate. As Clary (1983) pointed out, the need for sampling points to obtain statistically sound estimates is great. In the absence of budgets or manpower to get such estimates, we tend to rely on small sample estimates from a number of projects over a diverse area and time interval. Perhaps analysis should be done with bands of confidence rather than merely giving single point estimates.

Two factors loom large in estimates of production. Climatic variation can dramatically alter production (Sneva and Britton 1983), and management can offset almost all other factors.

The best estimates of input and output data should be used. Extrapolation of data can be very misleading unless adjustments for site differences are made. Disregard of the physical factors can lead to improper treatment or management. This then leads to projects which do not perform well and waste money (Nielsen 1977). Also, costly mistakes can be made that set ecological processes in action that are very difficult and expensive to change.

Whenever possible, numerous projects in close proximity to the proposed area should be studied to determine their degree of success and reasons for success or failure. Close attention needs to be given to basic physical data such as soil, climate, sagebrush subspecies, understory, adapted species for introduction, and associated wildlife species. Disregard for these or other significant factors can cause project failure that can be very expensive both economically and environmentally.

To be most helpful, physical parameters must be of two general types. First, the basic input-output relationships relevant to the site need to be identified. What output levels can be achieved for what level of inputs? A general form of this function is shown in figure 1 where one output from one input is graphically portrayed. Such a physical function can be converted to an economic one by pricing the output and input.

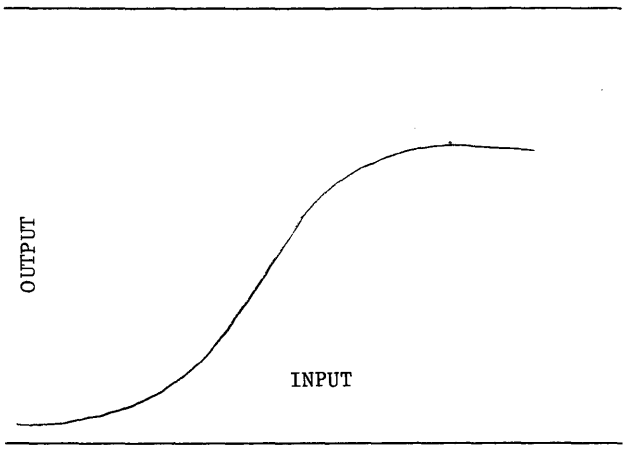


Figure 1.--Conceptual input-output curve.

Figure 2 may show, for example, how forage can be used by two species of grazing animals. At some point of use there will be competition for forage. The more complete the dietary overlap between animal species, the greater competition will be, if other factors are not limiting. For example, a small number of elk may not reduce forage available for cattle on a range where large numbers would. Figure 2 shows an output-output or transformation function. It is so called because it shows the amount of each (or both) species that can be produced using a set amount of forage on a range area.

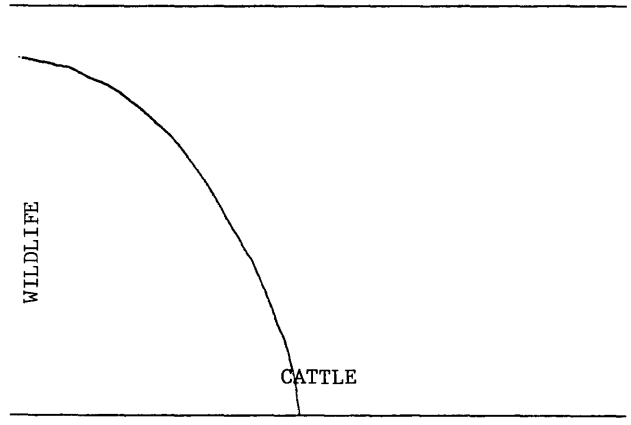


Figure 2.--Output-output or transformation function.

If the value of wildlife and livestock is known, the best or most profitable combination can be determined. The problem is that input-output and tradeoff relationships usually are not well defined, estimates are often not as accurate as they should be, and values for wildlife are not readily determined. Therefore, decisions are made on scanty information. More information about these basic relationships could lead to less costly methods of producing forage.

MAKING AN ECONOMIC ANALYSIS

The major step in making an economic analysis is developing realistic alternatives. There may appear to be only one option, but a closer look usually reveals possible changes. Alternatives should be legally, administratively, and technically feasible. The physical relationships of outputs and inputs for each alternative must be determined and quantified. Selection criteria, goals, or purposes for all alternatives should be specified. This will allow comparison and ranking of the alternatives, and selection of the best option.

Projects and alternatives should be of the size, scale, or intensity that would best meet management goals. If economic criteria are given, weight increments or units of inputs should be added until the additional costs of adding other units are just equal to the benefits expected (marginality concept).

Once benefits and costs are determined by amount and time of occurrence, the process of discounting will adjust them for time differences. The last step is determining the net benefit level for each of the alternatives and making any other economic ranking tests.

Curlew National Grasslands

The data in table 1 are from analyses of development projects on the Curlew National Grasslands in southern Idaho. On the Grasslands, periodic treatment of sagebrush is needed to keep grazing capacities high. There are three main ways of reducing sagebrush once it has dominated a site long enough to reduce understory forage plants beyond a point where natural recovery would be accomplished in a reasonable time. These methods have different costs. The chaining method has a different potential production level. The increased production is valued by determining a value for livestock forage.

In table 1, two values for grazing are shown to reflect the local practice of making winter use of crested wheatgrass seedings. As the data show, winter grazing is considerably more valuable since it substitutes for hay while summer grazing substitutes for other grazing.

The results of summarized analyses show positive percent values less costs except for summer grazing with chaining and broadcasting seed. An expanded analysis summary could include other uses, such as recreation or wildlife, and other methods. The most economic alternative presented in table 1 is burning and drilling seed. Winter use with this method shows the best return per dollar of investment.

DISCUSSION

It is rare that project plans are compared to results. In order to determine which estimates were good, physical success and productivity should be monitored. Many times, post-project grazing use is delayed due to poor treatment techniques or adverse weather. Such delays have a significant financial impact on permittees and project economics.

By looking at completed projects, land managers should be able to make better estimates. Also, probability estimates can be introduced to give confidence bands around the estimated impacts of a new project. Building a data base and confidence in analysis techniques is time consuming and difficult. Much better estimates are needed to significantly upgrade analyses. If sagebrush rangeland projects are to compete successfully for funds, they must be presented in the best possible light. This means counting all benefits and producing reliable and realistic analyses. Also, treatment of all areas in a uniform manner, whether the output is to be used or not, could be eliminated. More selectivity is necessary if rangeland projects are to be competitive with projects of other kinds.

Table 1.--Summary of analysis of sagebrush range improvement, Curlew National Grasslands[1]

Improvement method	AUM/acre			Value of increase/acre		Discounted value		Discounted value-costs	
	Without treatment	With treatment	Increase	Summer	Winter	Summer	Winter	Summer	Winter
Plow and drill	0.1	0.5	0.4	$2.80	$6.00	$24.89	$74.77	$4.89	$44.77
Chain and broadcast	.1	.3	.2	1.40	3.00	17.45	37.39	-2.55	17.39
Burn and drill	.1	.5	.4	2.80	6.00	34.89	74.77	24.89	64.77

[1]Data on file at Shrub Sciences Laboratory, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT.

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Section 4. Animal Relationships

PREY POPULATIONS IN RELATION TO ARTEMISIA VEGETATION TYPES IN SOUTHWESTERN IDAHO

Nicholas C. Nydegger and Graham W. Smith

ABSTRACT: Densities of Townsend ground squirrels and black-tailed jack rabbits are reported for Artemisia and related vegetation types in the Snake River Birds of Prey Study Area. The presence of shrubs is critical to black-tailed jack rabbits and may benefit Townsend ground squirrels. Habitat maintenance is essential to the preservation of the breeding population of birds of prey which utilize black-tailed jack rabbits and Townsend ground squirrels as primary prey species.

INTRODUCTION

Habitat-specific abundances of raptor prey species were investigated within the Snake River Birds of Prey Study Area (BPSA) to aid in the evaluation of critical habitat, to determine the response of prey species to habitat alteration, and to examine predator-prey interrelationships. The BPSA has one of the densest nesting populations of raptors in the world (USDI 1979). More than 600 pairs representing 15 species nest in the area annually.

One of the most important factors contributing to the diversity and density of raptors in the BPSA is the abundance of prey species. Diversity in vegetation or habitat types allows a variety of prey species to exist. Prey species include: lagomorphs, rodents, a variety of other mammals, reptiles, amphibians, insects, other arthropods, and avian prey.

In this paper we address the two most important prey species in the BPSA: the Townsend ground squirrel (Spermophilus townsendii) and the black-tailed jack rabbit (Lepus californicus). The U.S. Department of the Interior, Bureau of Land Management (BLM) Birds of Prey Research Project has shown a significant correlation between prairie falcon (Falco mexicanus) productivity and Townsend ground squirrel abundance. They have also shown a significant correlation between golden eagle (Aquila chrysaetos) productivity and black-tailed jack rabbit abundance (USDI 1979). Plant names follow Welsh and others (1981).

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Nicholas C. Nydegger is a Research Associate, Department of Biological Sciences, University of Idaho, Moscow, ID. Graham W. Smith is a PhD candidate, Department of Fisheries and Wildlife, Utah State University, Logan, UT.

STUDY AREA

The BPSA encompasses about 837,000 acres (339 000 ha) in southwestern Idaho along an 81 mi (130 km) stretch of the Snake River. Canyon walls, numerous buttes, and side canyons provide ideal nesting sites for raptors.

The area ranges from about 2,300 to 3,500 ft (700-1 067 m) in elevation. The topography is flat to rolling with scattered volcanic cones and buttes. Precipitation ranges from 7 to 10 inches (18 to 25 cm) per year with the majority falling from November through March. Vegetation ranges from sagebrush/grassland to salt desert shrub (Sharp and Sanders 1978).

VEGETATION

In 1977 and 1978, the vegetation within the BPSA was mapped. Homogeneous stands of vegetation were identified from 1:31680 scale color aerial photographs. Each vegetation stand was delineated on 7.5' USGS topographic maps. Only stands greater than 40 acres (16.2 ha) were mapped. In 1979, all boundaries between vegetation stands were verified on the ground and refined. The vegetation in each stand was sampled along a 1,312-ft (400-m) transect line. At least one transect was sampled in each vegetation stand. More than one transect was sampled in some large stands. A total of 40 canopy cover estimates, using the technique of Daubenmire (1959), were systematically taken on each transect line. Fifteen 1/300-acre (13.5-m^2) density plots were also systematically sampled on each transect line to assess the density and height of shrubs (Asherin 1973).

Habitat or cover types were identified primarily on the basis of dominant shrub species. We address 10 cover types: big sagebrush (Artemisia tridentata spp. wyomingensis); big sagebrush/winterfat (Ceratoides lanata) mosaics; big sagebrush/shadscale (Atriplex confertifolia) mix; big sagebrush/rabbitbrush (Chrysothamnus sp.);

winterfat, shadscale; shadscale/winterfat mix; rabbitbrush; black greasewood (Sarcobatus vermiculatus); and a grass type. An examination of the mean percentage plant cover (table 1) and the mean shrub density (table 2) for each cover type shows that each type was named for the dominant shrub species present with the exception of bud sagebrush (Artemisia spinescens). Bud sagebrush occurred as a codominant with shadscale throughout the study area and was ignored in naming types. Tables 1 and 2 also reveal that each cover type is indeed a unique plant community.

TOWNSEND GROUND SQUIRRELS

Methods

Townsend ground squirrels were live-trapped annually on five, 2.47-acre (1-ha) study sites from 1975 to 1979. Site 1 was located within a big sagebrush stand, site 2 in a heavily overgrazed stand of winterfat, site 3 in a healthy stand of winterfat, site 4 in an annual grassland (the result of a 1974 range fire), and site 5 in a big sagebrush/winterfat mosaic. Twice weekly from February to June of

Table 1.--Mean percent canopy cover by species for cover types in the Snake River Birds of Prey Study Area

Cover type	Big sagebrush	Big sagebrush/ winterfat	Big sagebrush/ shadscale	Big sagebrush/ rabbitbrush	Winterfat
Artemisia spinescens	0.3	0.2	2.9	0.2	1.1
Artemisia tridentata	11.8	7.2	3.6	7.4	
Atriplex confertifolia			6.0	.5	
Grayia spinosa	.8	1.4	1.2	.6	.4
Ceratoides lanata		11.3	.2	.3	22.2
Chrysothamnus sp.	T[1]			2.9	
Sarcobatus vermiculatus		.3			
Bromus tectorum	6.8	3.4	5.3	6.4	1.9
Vulpia octoflora	1.8	1.7		.1	1.9
Oryzopsis hymenoides	.1			.7	
Poa secunda	2.9	5.7	1.3	1.0	4.2
Sitanion hystrix	1.6	1.4	1.1	.7	.8
Descurainia pinnata	.4	.9	.2	.1	.8
Halogeton glomeratus	T		.3	T	
Salsola iberica	.6	.1	1.2	1.4	.1
Sisymbrium altissimum	.9	.1	.4	1.4	
Bare ground	74.2	69.8	78.3	77.1	67.4

Table 1.--Continued

Cover type	Shadscale	Shadscale/ winterfat	Rabbitbrush	Greasewood	Grass
Artemisia spinescens	3.7	3.8	0.1	0.8	T
Artemisia tridentata				1.8	.1
Atriplex confertifolia	6.7	6.4		1.0	
Grayia spinosa	.6	.4		.7	
Ceratoides lanata	T	9.0			
Chrysothamnus sp.	.2		8.0	.6	.1
Sarcobatus vermiculatus				8.0	
Bromus tectorum	3.4	3.1	6.8	6.7	11.4
Vulpia octoflora			.2	.2	1.0
Oryzopsis hymenoides	.1		.1	.2	.2
Poa secunda	.8	.2	5.4	.5	2.2
Sitanion hystrix	.8	1.2	.2	.4	.7
Descurainia pinnata	.3	.4	.2	.6	.9
Halogeton glomeratus	.2	.1		.9	.1
Salsola iberica	.6	.5	3.0	1.5	3.1
Sisymbrium altissimum	.4		3.8	.6	3.5
Bare ground	80.8	75.9	69.6	74.7	71.2

[1] T=trace (1979 data)

Table 2.--Mean dominant shrub density by cover type in the Snake River Birds of Prey Area

Cover type	Species	Mean density	SE[1]	Height	SE
		N/ha		cm	
Big sagebrush	Artemisia tridentata	5,565.6	354.8	49.1	1.1
Big sagebrush/ winterfat	Artemisia tridentata	3,579.1	571.1	51.1	1.9
	Ceratoides lanata	20,145.4	2,500.4	16.5	.8
Big sagebrush/ shadscale	Artemisia tridentata	1,074.4	293.3	44.9	2.5
	Atriplex confertifolia	3,019.9	722.1	27.6	1.3
	Artemisia spinescens	2,645.6	727.0	15.3	.8
Big sagebrush/ rabbitbrush	Artemisia tridentata	2,744.2	426.4	54.5	2.7
	Chrysothamnus sp.	1,199.2	240.2	36.1	2.0
Winterfat	Ceratoides lanata	34,518.4	3,790.5	18.5	1.2
Shadscale	Atriplex confertifolia	4,171.3	600.2	25.9	1.1
	Artemisia spinescens	3,664.1	623.7	16.2	.8
Shadscale/ winterfat	Atriplex confertifolia	3,132.1	780.6	29.4	1.6
	Artemisia spinescens	3,354.2	1,462.7	13.8	.6
	Ceratoides lanata	13,559.5	3,979.5	23.0	.8
Rabbitbrush	Chrysothamnus sp.	5,596.0	1,729.1	35.27	2.2
Greasewood	Sarcobatus vermiculatus	1,258.8	184.9	71.8	3.6
Grass	None				

[1] Standard error.

each year twenty, 16-by 5-by 5-inch (40-by 13-by 13-cm) live traps were set randomly about specific locations on each grid, baited with apple, and checked three times daily. Squirrels were permanently marked by toe clipping. April population estimates on each grid were obtained using CAPTURE, a computer program for analysis of capture-recapture data (Otis and others 1978).

Due to the time involved in using the trapping technique, it was not possible to live-trap all cover types. To ascertain ground squirrel abundance in all cover types another technique was employed. In 1978 and 1979, ground squirrel burrows were counted on approximately 350 systematically located transects. Each hole-count transect was 17 ft 10 inches (5 m) wide and 1,312 ft (400 m) in length. All active ground squirrel burrows within this strip were tallied by an observer traversing the center line of the transect. Data were stratified by cover type, and the mean number of holes per cover type was calculated. Hole-count transects were also established on each of the five, 1-ha, trapping sites. Regression analysis of the average density (1975-79) and the hole counts on each trapping site showed that ground squirrel density and the number of burrows present were significantly correlated ($r=0.94$, $P=0.002$, fig. 1). Eighty-nine percent of the variation in ground squirrel density was explained by burrow density. By substituting the average hole count for each cover type into the regression equation, densities were determined for each cover type (table 3).

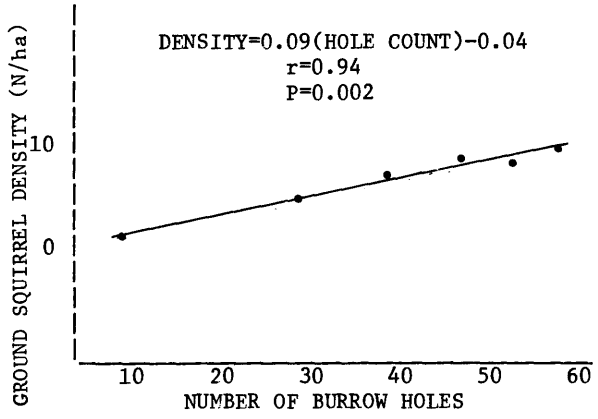


Figure 1.--Townsend ground squirrel hole count regression, trapping grid density on burrow hole counts, Snake River Birds of Prey Study Area.

Results and Discussion

An examination of ground squirrel densities by cover type within the BPSA (table 3) reveals that the big sagebrush/winterfat, winterfat, and grassland types support the largest populations of ground squirrels. These three vegetation types are probably most important to the maintenance of this prey base; however, the wide distribution of ground squirrels in the

other cover types lends importance to them also. Ground squirrel abundance can be related to soils as well as vegetation. The deep soils associated with the big sagebrush and winterfat communities are important to this burrowing rodent.

Table 3.--Townsend ground squirrel density by cover type, Snake River Birds of Prey Study Area

Cover type	Mean number of burrows	Predicted[1] density	SE[2]
		N/ha	
Big sagebrush	19.2	1.72	.84
Big sagebrush/ winterfat	31.6	2.86	.72
Big sagebrush/ rabbitbrush	19.0	1.70	.84
Big sagebrush/ shadscale	20.7	2.96	.72
Winterfat	32.7	1.45	.88
Shadscale	16.2	1.48	.87
Rabbitbrush	18.2	1.63	.85
Greasewood	Insufficient data		
Grass	28.1	2.54	.75

[1] Based on regression of 1975-79 mean trapping grid density on trapping grid hole counts.
[2] Standard error.

Ground squirrels eat green plant material, particularly grasses. Important species are Sandberg's bluegrass (Poa sandbergii), cheatgrass (Bromus tectorum), a variety of forbs, and some shrubs (Johnson 1977; Smith and Johnson in press). The shrub communities containing native perennial grasses and forbs as well as annuals probably support more stable populations in the long term as they are not as severely impacted by annual climatic fluctuations as are annual grasslands. They also offer more diversity in microhabitat than the monoculture of annual grasslands, thus green vegetation is available for a longer period of time.

BLACK-TAILED JACK RABBITS

Methods

Black-tailed jack rabbits were surveyed annually from 1979 to 1981 on 11 spotlighting transects (Flinders and Hansen 1973; Smith and Nydegger in press) running through the major vegetation types within the Study Area. Transects varied from 1 to 32.8 mi (1.6 to 53 km) in length. Transects were surveyed each year beginning in mid-May. Three replicates of each route were completed by early June. Surveys were begun about 10 p.m. when it was dark and were completed before 5 a.m. when it began to get light. One technician drove a pickup truck at 5 to 10 m/h (average 7 m/h, 11 km/h) while another technician spotlighted from the truck bed. Approximately 350 mi (560 km) of transect were surveyed each year. Data were stratified by cover type and analyzed using TRANSECT (Burnham and others 1980), a computer program for analysis of line transect data.

Results and Discussion

Black-tailed jack rabbits were most abundant in the big sagebrush and black greasewood cover types (table 4) and occurred somewhat equally in those other types with some species of tall shrub present. Shrubs provide the cover necessary to protect the jack rabbit, which does not burrow, from predators and environmental extremes. Shrubs also provide food in the winter months. Donoho (1972) found that black-tailed jack rabbit densities were proportional to shrub density in Colorado. Those cover types listed as insufficient line length (table 4) are cover types without adequate transect length in any year. The winterfat and grass cover types (noted as insufficient data in table 4), both had in excess of 20 mi (32 km) of transect length each year. Few rabbits were seen in these types

Table 4.--Mean black-tailed jack rabbit density 1979-81 from spotlight line-transects, Snake River Birds of Prey Study Area

Cover Type	Density[1]	SE[2]
	N/ha	
Big sagebrush	0.81	0.06
Big sagebrush/ winterfat	.24	.07
Big sagebrush/ rabbitbrush	Insufficient line length	
Big sagebrush/ shadscale	.43	.11
Winterfat	Insufficient data	
Shadscale	.42	.08
Shadscale/winterfat	.39	.09
Rabbitbrush	Insufficient line length	
Greasewood	.92	.18
Grass	Insufficient data	

[1] Calculated using program TRANSECT (Burnham and others 1980).
[2] Standard error.

especially within large homogeneous stands away from ecotones. In effect, the winterfat and grassland types do not support black-tailed jack rabbit populations within our study area.

HABITAT ALTERATION

Habitat alteration occurs from three sources within the area; fire, brush removal to enhance forage production and conversion to agriculture. With the withdrawal of the BPSA in 1980 agricultural encroachment has been halted. Conversion of native range to agriculture is detrimental to both black-tailed jack rabbit and Townsend ground squirrel populations through loss of habitat, disturbance, and control programs. Brush removal has not been utilized to any magnitude within the study area, but depending on the technique used, its effects are similar to fire.

The primary cause of habitat alteration within the study area is wildfire. Huge blocks of native rangeland burn each year. Eighty thousand acres (32 400 ha) burned in 1983, 20,000 acres (8 100 ha) in 1982, and 78,000 acres (31 600 ha) in 1981 (USDI unpublished fire records). Along with loss of shrubs, large blocks of land are being invaded by exotic annuals, primarily cheatgrass. These areas then become susceptible to repeated burning (Stewart and Hull 1949). As shrubs are eliminated, these areas become unsuitable to black-tailed jack rabbits and the Townsend ground squirrel becomes more vulnerable to both predation and annual climatic fluctuations. Overall, we see reduced diversity in prey species, reduction in habitat, and ultimately reduced prey productivity within these areas.

The continued existence of the breeding population of birds of prey in this area is dependent on the maintenance of prey populations and ultimately the maintenance of a shrub and grassland mosaic.

We need increased knowledge of habitat use by both predator and prey species to more closely examine the impacts of habitat alteration and rehabilitation efforts. Because the majority of current rehabilitation efforts are targeted at domestic grazing we need to develop rehabilitation techniques that maximize benefits to both wildlife and domestic species.

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SAGE GROUSE-SAGEBRUSH RELATIONSHIPS: A REVIEW

Jay A. Roberson

ABSTRACT: This paper was written to synthesize and suggest management application of sage grouse-big sagebrush research. In the life of sage grouse, big sagebrush and other sagebrush species are most critical for food and cover during winter and breeding-nesting periods. The strutting ground is the hub of year-round activity, but structural components of big sagebrush used for nesting, the proximity or interspersion of nesting, brooding, and male feeding-loafing areas to the strutting ground, and natal fidelity appear to be more important than structural characteristics of the strutting ground itself. Suitable male sage grouse feeding-loafing sites within 0.6 mile (1 km) of the strutting ground are critical for optimum use of the strutting ground. Males use big sagebrush plants that are taller and have greater canopy cover than random plants on the site. Loss of feeding-loafing sites around strutting grounds has resulted in population declines. Sage grouse hens nest almost exclusively under big sagebrush plants that are taller with greater canopy cover than the average.

Big sagebrush control should not be conducted on sage grouse sites where big sagebrush plants are less than 12 inches (30 to 48 cm) tall with less than 20 percent canopy cover. Also big sagebrush control should not be conducted on big sagebrush plants 7 to 30 inches (17.78 to 76.2 cm) tall with 20 to 40 percent canopy cover within 2 mi (4.8 km) of strutting grounds. Tall, dense, robust clumps of big sagebrush at the head of shallow draws and hollows should be protected for nesting habitat. Water developments should be protected, maintained, or constructed within 1 mi (1.6 km) of nesting habitats in zeric zones (less than 10 inches [25 cm] of rainfall).

INTRODUCTION

This report is a survey of literature and, based on that review, some recommendations for research and management. My purpose is to identify critical sage grouse-big sagebrush relationships, recommend management practices to protect habitats, and suggest areas of needed big sagebrush research.

No other North American game bird is so highly specialized and so inextricably dependent upon one plant species as sage grouse (Centrocercus urophasianus) is on big sagebrush (Artemisia tridentata) and its near relatives. Sage grouse has a near obligate relationship with big sagebrush and its close relatives of the subgenus Tridentatae of Artemisia. There is no evidence that sage grouse can adapt to changing vegetation resulting from human land use practices. Schoenberg (1982, p. 76) states that sage grouse select winter, breeding, nesting, and brood-rearing habitats on the basis of suitable structure and probably big sagebrush subspecies composition. It cannot be assumed that grouse will move elsewhere and maintain the same populations present before disturbance of preferred habitats.

A great deal of similarity exists between Beetle's (1960) map of the distribution of big sagebrush and Braun's (1985) unpublished map of sage grouse distribution. Sagebrush is used as food or cover in every season of the year (Girard 1937; Griner 1939; Patterson 1952; Klebenow 1969; Peterson 1970; Wallestad 1971; Eng and Schladweiler 1972).

Big sagebrush habitat types are declining in size. Estimates of big sagebrush lands altered to improve grass productivity range from 4.9 to 24.7 million acres (2 to 10 million ha) (Schneegas 1967; Braun and others 1976) from an original range of 144.9 to 269.9 million acres (58.7 to 109.3 million ha) (Beetle 1960; Sturges 1973).

Eradication of large areas of big sagebrush has been found to be detrimental to sage grouse (Autenrieth and others 1977). Sage grouse harvests in most states and provinces have declined in the last 10 to 15 years. These trends indicate actual population declines since harvest regulations have not changed appreciably and hunter effort has increased (Donoho and Roberson 1985).

Sage grouse are a unique wildlife resource with historical, scientific, and esthetic value deserving careful consideration. They are the largest North American grouse with some adult males reaching 7 lb (3.2 kg). Their reproduction rates are among the lowest of any upland game bird due to their relatively high

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Jay A. Roberson is Upland Game Program Coordinator, Utah Division of Wildlife Resources, Salt Lake City, UT.

rate of nest desertion, especially among yearling hens, delayed age of first breeding, relatively small clutch sizes, and high chick mortality. They differ from other tetraonids in not having a muscular grinding gizzard. Thus, they are generally restricted to soft-tissue foods. Before 1940, and the establishment of ring-necked pheasant (Phasianus colchicus), sage grouse was the most popular and heavily hunted game bird in the western states.

Although numbers are declining, sage grouse remain an important recreational resource. During 1980, an estimated 110,000 sage grouse hunters in western North America harvested 245,000 birds (Donoho and Roberson 1985). Based on a 1972 estimate of $19.45 per hunter trip in Idaho (Autenrieth 1981), sage grouse hunting in the West generates over $2 million to local economies. Additional money is spent on nonconsumptive use.

Conflicts between sage grouse and livestock do not arise from direct competition between the animals, but from competition between their food resources--big sagebrush versus grass. It has been stated but is difficult to prove that big sagebrush ties up soil moisture and nutrients otherwise available to perennial grasses (Sturges 1975). It has been just as difficult to prove sage grouse population declines result from big sagebrush eradication. Obviously, grass production as measured by pounds of air-dry matter per unit area can be doubled or tripled by removal of big sagebrush; however, from an ecological point of view, the grass increase is only temporary and big sagebrush reinvades. It is obviously part of the climax vegetation. Apparently big sagebrush adds species diversity and therefore ecosystem stability, improves transfer efficiency, and leads to a biotic community better buffered against disease and weather (Daubermire 1970; McArthur and Plummer 1978). It also reduces soil erosion by interrupting precipitation and provides for deeper snow accumulation. Daubenmire (1970) raised concerns about attempts to eradicate sagebrush which were again raised by Autenrieth (1981). These concerns were:

1. "There is little evidence to indicate the extent to which the desired grass increase (measured shortly after shrub eradication) is maintained. . . ."

2. "The protection afforded many grass plants by dense clumps of shrubs is the sole reason why any perennial grass remains on much of the depleted ranges. Artemisia elimination opens the way to complete destruction of perennial grass by overuse."

3. "Studies in Washington (Daubenmire 1969) have shown that for more than 4 months in the summer Artemisia tridentata uses only what water has percolated through the soil profile below the reach of grass roots. . . . The question should be raised: to what extent does the removal of this shrub allow some minerals to migrate permanently below the reach of grass roots. . . ."

4. "Removing Artemisia eliminates certain elements of the avifauna. While rearing their young these birds make a heavy drain on insect populations. Increased insects may damage the residual grass."

5. "When Artemisia is removed by herbicidal sprays, certain perennial broadleaved forbs are heavily damaged or eliminated (Hurd 1955, Blaisdell and Mueggler 1956, Mueggler and Blaisdell 1958, Anon. 1968). The loss is generally ignored on the tacit assumption that the unharmed grass, which supplies nearly all the domestic animals' food and which may produce more because competition is lessened, is the only component of economic significance. However, depending on the kind of vegetation and type of animals involved, spray removal of Artemisia may entirely destroy many desirable plant species and allow their replacement by inferior species and forage production may be seriously reduced for a period of several years (Blaisdell and Mueggler 1956). In western Colorado herbicides reduced forb production by 95%, yet these forbs contained more protein than the best of the forage grasses (Anon. 1968). . . ."

6. "In most areas Artemisia promotes the uniform accumulation of snow and delays its melting; both are desirable from the standpoint of range management (Hutchinson 1965). Several of the consequences of Artemisia removal enumerated above involve an important ecologic principle. 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 serious consequences. If herbicides are used to remove Artemisia, other species are also eliminated. Rather than focus interest on just the quantity of grass available and acceptable to one class of domestic animal, those points should be studied broadly."

I agree with Autenrieth and others (1977) who state that simplification of shrub-steppe vegetation by removing a major life form and phenology in order for other species to remain in the community cannot help but have serious consequences. I do not deny that removal of big sagebrush significantly reduces soil moisture loss (Sturges 1973), increases dry matter production by forbs that remain, and makes grass more readily available to livestock (Daubenmire 1970), but it is clear that big sagebrush control is short-lived and treatments must be repeatedly applied to maintain the grass (Harniss and Murray 1973; Thilenius and Brown 1974) and disturbed or treated big sagebrush habitats are vulnerable to overgrazing (Braun and others 1976).

Conflicts also arise from inadequate research. Most studies attempting to analyze the effect of big sagebrush control on sage grouse have been too brief or too limited in scope to identify critical sage grouse seasonal use areas before treatment. Hopefully, new study will fill in the gaps.

Basically, the 1977 "Guidelines for Maintenance of Sage Grouse Habitats" still apply in 1984 (Braun and others 1977). However, there have been some misunderstandings or misapplications of the "Guidelines." Studies of sage grouse life history and habitat requirements have provided information on why sagebrush treatment around strutting grounds is so detrimental to the species. The strutting ground itself is not the critical habitat in need of protection. Rather, it appears that the winter, nesting, and rank escape cover for male feeding-loafing areas close to the strutting ground are critical. I will deal with each of these in this report. Big sagebrush for brood-rearing habitat is of lesser importance and will not be discussed.

WINTER HABITAT

Big sagebrush makes up 95 to 100 percent of the winter diet of sage grouse from October through April. In May, sage grouse shift from a big sagebrush-dominated diet to one dominated by forbs; in September there is an opposite shift from forbs to big sagebrush, triggered by freezing temperatures or snow accumulations (Girard 1937; Griner 1939; Bean 1941; Dargan and others 1942; Patterson 1952:198; Nelson 1955; Klebenow and Gray 1968; Savage 1969; Martin 1970; Peterson 1970; Oakleaf 1971; Wallestad and others 1974). Winter flocks or concentrations shift their winter range in response to snow depth and food availability. The extent of winter movement depends on the severity of the weather, topography, and vegetative cover (Beck 1975). Autenrieth (1981) attributed the initial predictable movements to palatability of big sagebrush, and secondly, to its availability above the snow.

Wintering areas can be identified by topography, structural characteristics, and subspecies of big sagebrush. For sedentary populations, the wintering area is often located within 2 miles (3.2 km) of the strutting ground and nesting area. Sedentary populations are nonmigratory with the total straight-line distance between brood and winter centers generally less than 10 miles (16 km). Sage grouse moving more than 10 miles are considered migratory (Baker 1978:21; Berry and Eng 1985). They appear to prefer large, flat or gentle slopes of less than 15 percent (Eng and Schladweiler 1972; Jarvis 1974; Beck 1977; Autenrieth 1981). Winter-use areas are determined by amount of snow rather than affinity to a particular site.

In wintering areas, sage grouse tend to concentrate on the higher wind-swept ridges and flats where big sagebrush is available (Jarvis 1974). Southern aspects seem preferred (Beck 1977; Autenrieth 1981). There is no difference between vegetation or physical characteristics of winter roosting and feeding-loafing sites (Beck 1977; Eng and Schladweiler 1972). However, researchers have noted sage grouse selecting areas with the greatest canopy cover available. The majority of winter observations were in sagebrush with more than 20 percent canopy coverage. In Idaho, the average height was 22 inches (55.8 cm) and canopy coverage was 28.1 percent (Autenrieth 1981). This was confirmed by Schoenberg (1982) in North Park, CO, who found that the length, width, height, and canopy cover of big sagebrush plants were greater at sage grouse winter feeding-loafing sites than at any of the breeding season feeding-loafing sites.

The species and subspecies of sagebrush that seem to be preferred by grouse in the winter are black sagebrush (A. nova), low sagebrush (A. arbuscula), and certain subspecies of big sagebrush (Crawford 1960; Autenrieth 1981). Remington (1983) found in North Park, CO, that 90 percent of the plants identified as fed-upon were Wyoming big sagebrush (A. t. wyomingensis). Mountain big sagebrush (A. t. vaseyana) and alkali sagebrush (A. longiloba) made up 7 percent and 3 percent, respectively, of the remaining sagebrush plants fed upon.

Nitrogen may be an important factor in food selection. High nitrogen levels may be physiologically critical. Remington (1983) found that Wyoming big sagebrush contained more protein (14.1 percent vs. 10.8 percent) than mountain big sagebrush. There was significant variation in protein content within subspecies. Plants fed upon had higher protein than those not fed upon. Monoterpenoids content did not vary between plants of Wyoming big sagebrush fed upon and not fed upon.

Winter diet quality was high in sage grouse (protein = 15.9 percent, cell contents = 77.8 percent, ADF = 13.7 percent) relative to winter diets of other grouse, resulting in increased fat content over winter. Thus, the normal critical energy period for sage grouse appears to be the breeding-nesting period and not winter. However, there is evidence to indicate that during severe winters sage grouse lose considerable energy reserves which may influence both the duration and intensity of breeding activity.

Because sage grouse do not have a muscular grinding gizzard and select subspecies and plants low in monoterpenoids, they are adapted to avoid the harmful effects of monoterpenoids in sagebrush. Reduced digestibility and a requirement for a high-quality winter diet of big sagebrush are probably consequences.

Winter Habitat Management

Before winter habitat can be properly managed it must first be located. This should occur during moderate-to-heavy snow years. Wintering areas can be located by examining telemetry fixes, topography, or ground and aerial sightings.

After these sites have been located and verified by the presence of snow roosts the following habitat characteristics should be measured: sagebrush species and subspecies composition, plant height, percent of sagebrush cover.

If winter habitat must be disturbed, compatible sagebrush species and subspecies need to be seeded. Genotypes of big sagebrush high in protein (Welch and McArthur 1979), high in digestibility (Welch and Pederson 1981), and low in monoterpenoids (Welch and McArthur 1981) should be used.

The lack of protection of critical winter habitat has resulted in sage grouse population declines. In Montana, Pyrah (1972) found sage grouse winter use declined proportionally to the severity of big sagebrush eradication. Strip-partial kill, block-partial kill, mechanical treatments, and total-kill spray, in that order, were increasingly detrimental to sage grouse. Winter use essentially ceased in the total-kill areas. Critical winter habitats were quite vulnerable to treatment since big sagebrush control historically has been directed toward dense stands on flat to gentle slopes.

Remington (1983) suggests some management techniques for improving critical winter-use areas. These include: (1) fertilize with nitrogen to enhance the quantity and quality of big sagebrush forage (Carpenter 1976; Laycock 1982) and (2) encourage sage grouse use of Wyoming big sagebrush stands normally unavailable due to snow depth by use of snow fences or carbon black (Regelin and Wallmo 1975).

Winter Habitat Research Needs

Research that would be of greatest value in managing sage grouse winter habitat is listed below:

1. Determine the effects of various fertilizer applications, formulas, concentrations, phenology, and sagebrush subspecies on the nutritional content of big sagebrush.

2. Determine the effects of big sagebrush removal by various means on soil erosion, nutrient leaching, and soil water retention.

3. Determine the subspecies of big sagebrush as indicators of ecological sites relative to suitability for treatment by herbicide or prescribed burning.

4. Determine the characteristics of the soil or habitat type of subspecies of big sagebrush.

5. Define the soil type and moisture relationship to nutritional composition and phenology of big sagebrush.

6. Develop through genetic engineering superior big sagebrush cultivars high in protein and low in monoterpenoids.

7. Develop a data base on big sagebrush response to herbicides under varying dosages and environmental conditions, guidelines for data to be taken, and computer storage.

8. Determine the relationship between insect infestations and resistant genotypes of big sagebrush which produce natural phytotoxins or repellents and the effects of these toxins on sage grouse nutrition.

9. Determine the nutritional value of big sagebrush by age class and optimum canopy cover and morphology by age classes.

10. Determine use levels of big sagebrush by deer, antelope, or sage grouse which stimulate (if any) plant growth and vigor.

BREEDING AREAS

A second critical time when big sagebrush quantity and quality is important to sage grouse is during breeding. Strutting grounds vary greatly in topographical or physical features (Rogers 1964). Strutting grounds may be gravel pits, plowed fields, wheat stubble, salt licks, remote air strips, temporary sheep camps, paved roads, bare exposed ridges, knolls, small buttes, bare openings in big sagebrush, and dry lake beds. Sage grouse seem to take advantage of newly disturbed areas. Therefore, strutting grounds are not distinctive except that they are usually surrounded by big sagebrush cover and provide a panoramic view (Autenrieth 1981).

Adult male sage grouse first move to strutting grounds in March (Jenni 1971). Hens arrive later. Males are attracted to hens rather than their mating centers. Hens breed with individual males that are more active than other males. Hens are not attracted to geographic sites themselves. This accounts for the slight movement of grounds from year to year.

The big sagebrush surrounding the strutting grounds is critical! Big sagebrush surrounding strutting ground is used as food, loafing, and escape cover by the males. Male activity is generally restricted to these sites within .6 mile (1 km) of the strutting ground (Wallestad and Schladweiler 1974; Autenrieth 1981; Carr 1967; Rothermaier 1979; Emmons and Braun 1980). Male sage grouse select big sagebrush stands that are taller and have greater canopy coverage than random sites (Ellis and others 1984; Wallestad and Schladweiler 1974; Autenrieth 1981; Schoenberg 1982). Emmons and Braun (1980), Wallestad and Schladweiler (1974), and Autenrieth (1981) reported that 80 percent of all male locations were in big sagebrush cover of 20 to 50 percent. Big sagebrush canopy coverage averaged 30 percent on male feeding-loafing areas in Montana (Eng and Schladweiler 1972) and males were not observed in areas with less than 10 percent canopy coverage. Emmons and Braun (1980) found that cover and height at feeding-loafing areas averaged 28.1 percent and 15 inches (38.3 cm)

respectively. Schoenberg (1982) found that both cover and height were greater in use areas than in randomly chosen areas (33 percent vs. 26 percent and cm vs. 19 cm, respectively). Patterson (1952) found optimum loafing sites were along stream bottoms, ravines, and draws.

Spraying big sagebrush in these male feeding-loafing areas probably resulted in some of the population declines reported by so many researchers. Wallestad (1975) reported that a 31 percent loss of habitat adjacent to a strutting ground coincided with a 63 percent decline of males counted on strutting grounds. Strutting grounds that had averaged 54 males for 13 years dropped to 3 within 2 years after spraying, and after that were totally abandoned. In Idaho, Autenrieth (1969) observed that sprayed strutting grounds continued to be used if the surrounding nesting and brood-rearing habitat was not destroyed. Others (Enyeart 1956; June and Higby 1965) also noted declines resulting from land-use changes.

The preferred solution to this problem is to identify male feeding-loafing use areas and protect them from big sagebrush control. This can be accomplished by radio-marking males and monitoring their movements during the breeding season. The next best alternative is to conduct an appraisal of big sagebrush quantity and quality within a 2-mile (3.2 km) radius of the strutting ground of sedentary (resident) populations. This appraisal could include range site-habitat type, soil type, topography, aspect-slope, and identifying on aerial photographs the locations of seeps, springs, and meadows. Data could be verified by site inspections. This should include identifying subspecies of big sagebrush and the tallest and greatest canopy cover on aerial photographs.

Where protection of strutting grounds is not possible, birds have been transplanted (Ligon 1946; Wing 1951; Patterson 1952) or strutting grounds have been moved (Eng and others 1979; Tate and others 1979). Both actions require extensive habitat appraisals and telemetry studies of seasonal use areas to be successful. However, the latter is more labor intensive and the outcome less sure.

NESTING HABITAT

Big sagebrush also is critically important during the May nesting period. Typically, hens begin nesting within 10 days after breeding. The peak of breeding in Utah varies, but generally occurs sometime in late April. The incubation period is 25 days. The peak of hatch also varies, but occurs about June 5. This corresponds with the start of livestock use on many ranges.

A pressing issue is that sage grouse hens nest almost exclusively under big sagebrush (Schlater 1912). Keller and others (1941) found that 94 percent of located nests were under big sagebrush. Similar results have been found by Girard (1937), Patterson (1952, p. 114), Gill (1965), Gray (1967), and Wallestad and Pyrah (1974). Jarvis (1974) found 48 of 60 nests in south-central Utah were located under big sagebrush.

Hens appear to select nesting sites beneath big sagebrush that has good canopy cover and is relatively tall. Autenrieth (1981, p. 20) 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. "The importance of big sage cover for nesting cannot be over-estimated," he said.

Most studies indicate that the majority of nests are located under the tallest plants available in the area (Keller and others 1941; Patterson 1952:114; Trueblood 1954; Rogers 1964; Gray 1967; Klebenow 1969; Jarvis 1974; Wallestad and Pyrah 1974;). Jarvis (1974) found that hens tended to select sites with big sagebrush for nesting rather than black sagebrush sites. However, Autenrieth (1981) indicated that hens on his five areas selected something less than the greatest height and canopy cover. He believed the height and density of sagebrush in his study areas was greater than those in other study areas, and apparently height and canopy cover were not limiting factors in his areas. Thus, he postulated a threshold level of tolerance for these values.

Most researchers agree that hens nest under sagebrush plants that are taller than plants of average height in the area. Wallestad and Pyrah (1974) found the average height of big sagebrush plants where nests were located was 16 inches (40.4 cm) compared with 9 inches (23.4 cm) in surrounding stands. Similar heights over nests were reported by Patterson (1952) and Klebenow (1969). Patterson (1970) found that the average height of sagebrush at nest sites in Colorado was 21 inches (52.3 cm) while height of the surrounding big sagebrush was 13 inches (32.3 cm). Areas of big sagebrush taller than 35 inches (89 cm) were seldom used. Jarvis (1974) also found that big sagebrush used for nesting averaged 39 percent taller than adjacent shrubs. Autenrieth (1981:17) found that in all cases the nest shrubs were taller than surrounding shrubs, indicating that the hen is selecting a particular shrub. Nest shrubs ranged in height from 22.4 inches to 31.5 inches (57 cm to 80 cm) while shrubs surrounding the nest site ranged from 9.1 inches to 31 inches (23 cm to 79 cm). Basically, figures on optimum sagebrush heights for nesting provided in the "Guideline for Maintenance of Sage Grouse Habitats" (Braun and others 1977) remain valid. Optimum heights are between 6.7 inches (17 cm) and 31.1 inches (79 cm).

Sagebrush canopy cover is an important variable associated with the selection of nest sites. Canopy cover percentages of 20 to 40 are selected as nesting cover (Patterson 1952, p. 114; Klebenow 1969; Martin 1970; Jarvis 1974; Wallestad and Pyrah 1974; Autenrieth 1981).

Recent research by Peterson (1970) in North Park, CO, confirmed these figures, but Schoenberg (1982) studying the same area in 1979-80, found a slightly higher (44 percent) canopy cover for big sagebrush used for nesting. In Idaho, Klebenow (1970) found that nesting ceased on newly sprayed areas with less than 5 percent live big sagebrush canopy cover. Nesting was nearly nonexistent in older sprayed areas with about 5 percent live big sagebrush cover.

Big sagebrush canopy cover is positively correlated with hatching success. Wallestad and Pyrah (1974) found 31 successful nests had greater than average sagebrush cover within 24 inches (61 cm) of the nest and these were located in stands with a higher average canopy cover (27 percent) than unsuccessful nests (20 percent). No nests were found where canopy coverage was less than 15 percent. Jarvis (1974) attributed the significantly higher nest success under big sagebrush compared to black sagebrush on his Utah study area to the greater canopy cover at big sagebrush sites. Although Autenrieth (1981,p.20) found that for 165 nests in Idaho there was no significant difference between the height or canopy cover of the nest shrub on successful versus unsuccessful sites, he suggested this was because sagebrush height and canopy cover were not limiting. His study areas had taller big sagebrush and greater canopy cover than study areas in Montana.

The proximity of nesting to strutting grounds depends upon the proximity of quality and quantity of preferred nesting habitats to the strutting ground (Autenrieth 1981). In migratory populations, the majority of nesting may not occur within 2 miles (3.2 km) of the strutting ground. In fact, some evidence suggests that some hens move as much as 15 to 20 miles (24.1 to 32.2 km) from the strutting ground to nest.

Most viable sage grouse populations are considered sedentary or resident. That is, they move less than a 10-mile (16-km) radius in 1 year. In these populations, it appears that the majority of nesting occurs within 2 miles (3.2 km) of the strutting ground (table 1). Autenrieth (1981) found that when good nesting cover was available near the strutting ground, the nesting radius tended to be less than when cover was sparse and only in clumps. Poor nesting habitats result in longer migrations by the hen to quality nesting sites, which increased the probability of predation and reduced survival.

The proximity of riparian areas may be another important variable determining nest site selection. Some researchers have concluded or implied that readily available water is essential for optimum nesting habitat and that the availability of water influences nest site selection (Griner 1939; Patterson 1950, 1952; Trueblood 1954; Carr 1967). However, Keller and others (1941) indicated in their Colorado study that there was no definite preference for sites close to water. Klebenow (1969) and Wallestad (1975) did not mention free water as a component of optimum nesting habitat in Idaho and Montana. Batterson and Morse (1948) and Nelson (1955) also indicated that nest distribution was not affected by water. Autenrieth (1981) found no relationship between water or meadows and proximity of nests. Jarvis (1974) found almost all of his nests within 1.3 miles (2.1 km) of a lake, reservoir, or pond, but only about one-third were within one-half mile (.8 km) of a water source. Although water may not be a limiting factor on some sage grouse habitat, water developments should be protected, maintained, or constructed within 1 mile of each other on nesting habitats in zeric zones (less than 10 inches [25 cm] annual precipitation).

It appears that species of sagebrush is an important determinant of nest location. A significant positive correlation is indicated in the literature for number of nests located and big sagebrush overstory. Big sagebrush is extremely important for nesting cover (Girard 1937; Keller and others 1941; Patterson 1952; Gill 1965; Gray 1967; Wallestad and Pyrah 1974).

The effect of grazing on nesting habitats is important. Autenrieth (1981, p. 20) found that understory ground cover contributed to a microclimate warmer than air temperature 3 ft

Table 1.--Results of a literature review of the percent of sage grouse nests found within a specified radius of the strutting ground

		Percent of nests located a given distance from the strutting ground							
Location and reference	Sample size	1 mi (1.6 km)	1.5 mi (2.5 km)	2 mi (3.2 km)	3 mi (4.8 km)	4 mi (6.4 km)	5 mi (8.0 km)	6 mi (9.7 km)	8 mi (12.9 km)
Northwest Colorado, Gill (1965)	23	--	--	87	--	--	--	--	--
Southwest Montana, Martin (1970)	5	--	--	80	--	--	--	--	--
Montana, Wallestad and Pyrah (1974)	--	68	--	--	--	--	--	100	--
South Idaho, Autenrieth (1981)	306	28	--	59	73	85	96	97	100
Southwest Wyoming, Berry and Eng (1985)	17	--	53	--	59	--	--	--	--
Southcentral Utah, Jarvis (1974)	62	--	--	66	76-81	--	--	--	--

(1.9 m) above the nest. Nest temperatures dropped less during hen absence where understory was greatest. Sheep grazing from December through May on nesting areas should be regulated to prevent overuse of grasses and forbs.

Topographical features may also be important in nest site selection. Schlatterer (1960) found that sage grouse hens in eastern Idaho showed some preference for islands of big sagebrush on rock outcrops, surrounded by grassy openings. No nests were found on north-facing slopes, and southern slopes seemed to be preferred. Keller and others (1941) found no definite preference for either slope or exposure in North Park, CO, but they observed that the highest nesting success occurred in little draws where the bottoms were covered with low-growing vegetation. Jarvis (1974) made similar observations on his study area in Utah. Optimum nesting habitats were located where numerous dendritically arrayed shallow draws were separated by relatively broad flats (Jarvis 1974). The upper extremities of these small, shallow tributaries having a northerly or easterly aspect seem to be preferred. Nests were frequently located just above the bottom of the drainage or in shallow basins at its head. The majority of the nests were in the more robust vegetation associated with these sites (heavier and higher than the surrounding cover).

Slope appeared to be important. Almost 69 percent of the nest sites were situated on relatively flat sites of 5 percent or less slope. An additional 21 percent were on 5 to 20 percent slopes. Hens avoided steeper slopes.

Unlike Schlatterer's (1960) or Keller and others (1941) findings, Jarvis (1974) found a fairly definite preference for northern aspects. About 35 percent of nests were located on slopes facing north or northeast as opposed to only 14 percent facing south or southeast. Jarvis thought that this was due to the more mesic conditions of northern aspects.

Management recommendations for nesting habitats should include:

1. Give 1-year written advance notice to the appropriate wildlife agency of intent to treat so use can be appraised.

2. Identify nesting habitat by marking-telemetry studies and habitat appraisals and determine what are limiting habitat components.

3. Maintain or protect nesting habitats, especially those nearest breeding complexes.

4. Limit disturbances and sagebrush control programs on nesting areas during April-May-June breeding-nesting periods.

5. Regulate grazing on nesting habitats.

6. When reseeding drilling pads and reclaimed mine sites, include dryland legumes like alfalfa (Medicago spp.), sainfoin (Onobrychis vicaefolia), and vetches (Astragalus spp.) in seed mixes.

7. Do not block-spray, but preferably use ground application in irregular-shaped patterns, avoiding taller denser patches of sagebrush within 2 mi (3.2 km) of strutting ground with irregular margin for maximum edge and diversity. Openings created in uniform habitats of sagebrush should not exceed 50 yd (45.7 m) in diameter with optimum diameter of 5 to 10 yd (4.6 to 9.1 m). Treatment areas should not exceed 40 ac (16 ha). The goal of treatment should be to not reduce sagebrush cover below 20 percent and 3,400 plants per acre. If strip-sprayed, leave strips should be at least twice as wide as kill strips and at right angles to prevailing wind or slope of the land (Braun and others 1976).

8. Do not treat sagebrush on sites where costs exceed expected benefits.

9. Do not treat sagebrush on sites with less than 20 percent canopy cover of sagebrush.

Research that would be of greatest value in managing sage grouse on nesting habitat is listed below:

1. Determine rate of reestablishment of sagebrush after treatment via photo-trend plots and vegetative measurements.

2. Test hypotheses for reasons hens select nest sites and nest success with:
   a. proximity to strutting grounds
   b. proximity to brood habitat
   c. nest site quality-concealment
   d. nest site temperature-microclimate
   e. distance to water
   f. sagebrush characteristics, e.g. canopy volume, canopy cover, height, age by multivariate analysis
   g. ground cover-understory
   h. camouflaging
   i. morphology-age class

3. Assess impact of application rates, phenology, date of application, and herbicide (2,4-D-Tebuthiuron) on live sagebrush canopy cover 1 mo, 1 yr, and 5 yr after treatment; and assess effects on sage grouse reproduction, distribution, and density.

4. Make nest preference studies on subspecies of big sagebrush.

5. Determine minimum viable population for specific population and minimum habitat needed to sustain populations.

6. Determine the relationship between xeric sage grouse habitats and the tendency of sage grouse populations to migrate.

7. Assess the effect of various grazing systems on winter and breeding-loafing habitats.

8. Study the effect of prescribed burns on nesting habitat.

CONCLUSIONS

Big sagebrush is extremely important to sage grouse especially during winter and spring. The protection or maintenance of wintering, breeding (male feeding-loafing areas), and nesting sagebrush habitats is essential for the survival of sage grouse populations. For sedentary populations, protecting these habitats within 2 mi (3.2 km) of the strutting ground is very important. This does not mean that all sagebrush within 2 mi (3.2 km) of all strutting grounds must be protected. The 2-mi (3.2 km) limit set in the 1977 "Guidelines" was not intended to be rigidly substituted for a good habitat reconnaissance and appraisal. One-year lead time is critical if this appraisal is to be adequate and of value.

The 1977 "Guidelines" still apply in 1985 for sedentary populations, but for migratory populations, critical seasons use areas must be identified through marking-telemetry studies.

There is no substitute for an adequate habitat appraisal to identify sacrifice areas where big sagebrush can be treated without significant harm to the sage grouse population. To accurately predict the effects of big sagebrush manipulation on sage grouse populations we need a comprehensive understanding of sage grouse seasonal use areas and which are limiting. This requires lead time, which is a basic professional courtesy extended by the Federal land management agency to the State Wildlife agency. There must be a cooperative spirit and a commitment to get the job done by both types of agencies.

Sage grouse depend on big sagebrush to fulfill their basic requirements. The future of sage grouse depends upon our ability and willingness to maintain sagebrush habitat types. I tend to agree with Pyrah (1966) who wrote 20 years ago that:

> "A continued lack of concern is prevalent in most agencies which are causing the serious shrinkage of sage grouse habitat. They show little regard for sage grouse or other wildlife when its welfare is weighed against the demands of the livestock monoculture being benefitted."

Wildlife biologists in land managing agencies need to take their multiple-use charge in the Federal Land Management and Policy Act more seriously.

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SEASONAL MOVEMENTS AND HABITAT SELECTION OF SAGE GROUSE IN SOUTHERN IDAHO

Brian V. Hulet, Jerran T. Flinders, Jeffrey S. Green, and Robert B. Murray

ABSTRACT: In 1980 and 1981, 31 sage grouse hens were captured at the U.S. Sheep Experiment Station, Dubois, ID, and fitted with radio transmitters to document movement and selection of habitat. Similarities between habitat by months and areas were determined by discriminate analysis. Data were gathered on the effects of predation and weather on nesting and brood production. The sage grouse were found to be migratory. One hen moved at least 106.0 air miles (160.9 air/km) between nesting, summering, and wintering areas, and then in 1981 nested within 82 ft (25 m) of her 1980 nest.

INTRODUCTION

Sage grouse (Centrocercus urophasianus) have developed a migratory or nonmigratory strategy for survival depending on topography, vegetative cover, available water, and winter climatic conditions (Beck 1975). Wallestad (1975) stated that wintering, nesting, and brood habitats for sage grouse in the Yellow Triangle area of Montana were interspersed and required no long seasonal movements by these birds. In contrast, sage grouse in southeastern Idaho travel up to 49.7 mi (80 km) between summer and winter range (Pyrah 1954). Sage grouse that nest near the Red Road (Clark County) site in southeastern Idaho have distinctly different wintering, nesting, and brood rearing areas (Dalke and others 1963), while sage grouse on the Idaho National Engineering Laboratory (INEL) site (Jefferson Co.), also in southeastern Idaho, nest on or near their winter range and then move to summer areas (Connelly and others 1981).

Several good reviews are available that discuss the seasonal importance of big sagebrush to sage grouse (Patterson 1952; Johnsgard 1973; Wallestad and Pyrah 1974; Wallestad 1975; Braun and others 1977). There is good documentation that certain stands of big sagebrush may have too much cover or be too tall or not have enough component interspersion to serve as ideal habitat for sage grouse during specific periods of their yearly cycle (Martin 1970; Peterson 1970; Call 1974).

Seasonal sagebrush cover for sage grouse include the following recommendations: winter, 20 percent (Eng and Schlandweiler 1972; Wallestad 1975); brood, 8.5 to 14 percent (Gill 1965; Klebenow 1969; Martin 1970; Autenreith 1981); nesting, 20 to 40 percent (Patterson 1952; Gray 1967; Klebenow 1969; Wallestad and Pyrah 1974).

Recommendations for management of habitat on sage grouse ranges may differ depending on whether the flock is migratory or nonmigratory. Nonmigratory flocks generally use one area for nesting, brood production, and wintering while migratory flocks use different areas for one or more activities. Proper management of habitat for sage grouse should include consideration of seasonal and functional uses in each area.

In this study, we observed the year-round movements of selected female members of a migratory sage grouse flock in southeastern Idaho. Nesting and summer habitats were measured and comparisons were made in relationship to migration.

STUDY AREA AND METHODS

The study was initiated on the U.S. Sheep Experiment Station (USSES) 5 mi (8 km) north of Dubois, Clark Co., southeastern Idaho. The USSES provides spring-fall grazing for domestic sheep and has an average elevation of 5,657 ft (1 700 m). Twenty-six sage grouse leks were located in 1980 and 1981 on the 40 mi^2 (103.6 km^2) USSES. Major shrub species include big sagebrush (Artemisia tridentata) and three-tip sagebrush (A. tripartita). Tailcup lupine (Lupinus caudatus) and arrowleaf balsamroot (Balsamorhiza sagittata) are two of the prominent forbs. Principal grasses are bluebunch wheatgrass (Agropyron spicatum) and thickspike wheatgrass (A. dasytachyum).

During summer, sage grouse used areas near Kilgore and Humphrey, Clark Co., ID. The Kilgore area, 19 mi (30 km) northeast of the USSES, is

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Brian V. Hulet was Graduate Research Assistant, Department of Botany and Range Science, Brigham Young University, Provo, UT. Jerran T. Flinders is Professor of Wildlife and Range Resources, Brigham Young University, Provo, UT. Jeffrey S. Green is Research Wildlife Biologist, U.S. Sheep Experiment Station, Agricultural Research Service, U.S. Department of Agriculture, Dubois, ID. Robert B. Murray, is Range Scientist, U.S. Sheep Experiment Station, Agricultural Research Service, U.S. Department of Agriculture, Dubois, ID.

typified by cultivated dryland alfalfa-grass hay surrounded by big sagebrush rangelands at an average elevation of 6,400 ft (1 951 m). Water in the dryland farm area is abundant due to a high water table and numerous streams. Humphrey is 21.1 mi (33.8 km) north of the USSES and is vegetated by sparse big sagebrush with much of the area having been sprayed at some time with 2,4-D herbicide. The elevation at Humphrey is about 7,000 ft (2 134 m). Water is always available within short distances. Cattle and sheep graze the Humphrey and Kilgore areas during summer months. Winters are severe with all shrubby vegetation being mostly covered with snow.

Southwestern Clark County and northwestern Jefferson County are used by sage grouse in winter. The area is sagebrush-dominated rangeland interspersed with irrigated, cultivated farmland. Big sagebrush and black sagebrush (A. nova) are the major shrubs with black sagebrush occupying the rocky areas and windswept ridges.

Thirty-one sage grouse hens (including three juveniles) were captured between March 25 and June 5, 1980, and during the same dates in 1981. Each hen was fitted with a 2-oz (57-g) backpack radio transmitter to document movement and selection of habitat. Nine hens were recaptured in late August 1980, and refitted with active transmitters. Two of the nine were again refitted in early spring 1981 so they could be monitored for a complete annual cycle. Hens were captured at night with aid of a spotlight and long-handled net. Instrumented hens were located as often as possible (usually weekly) from the ground during summer. During winter, grouse were located bimonthly from aircraft, followed by ground location, if possible.

In summer, measurements of habitat were taken each time a radioed hen was located. The percentage cover of each plant species (with the exception of grasses which were combined) was estimated in 12 7.8 by 19.7-inch (20- by 50-cm) plots (Daubenmire 1959), three in each cardinal direction, 4.9 ft (1.5 m) apart, using the observation point of the bird as the center reference point for placement of the plots. In addition, the percentage of bare ground, rock, litter, and the height of the tallest shrub of each species in each plot were measured.

Nesting habitat was quantified by measuring the height, width, and length of each woody species in a 100-ft^2 (9.3-m^2) circular plot, with the nest as the center point. Also percentage cover of forbs, grass, and each shrub species was estimated in a 10.8-ft^2 (1-m^2) circular plot around each nest. The height and species of shrub directly above the nest were recorded, as well as the distance from the nest to the lowest canopy above the nest. Statistical analyses were made by using group comparison t-tests or paired t-tests unless otherwise stated (Johnson 1976).

Counts of cocks and hens were taken periodically on each lek (strutting or breeding area) on the USSES throughout the 1980 and 1981 seasons. Counting began one-half hour before sunrise and continued to 1 hr after sunrise (Jenni and Hartzler 1978). Leks were approached via truck. The research counted and classified all observed birds with the aid of 7 x 35 binoculars. Locations of historical leks, as well as numbers of birds per lek, were obtained for 1966 (Klebenow, unpublished data) and 1979-80 (Green, unpublished data).

RESULTS AND DISCUSSION

Movements

In 1980, the instrumented sage grouse hens nested an average of 1.7 mi (2.7 km) from the nearest lek; this was significantly ($P \leq 0.25$) farther than the 0.5 mi (0.8 km) nesting distance in 1981 (table 1). Ten of 15 hens had probably commenced nesting when they were captured in 1981 compared to only three of the 13 in 1980.

Ten of 13 hens in 1980 nested within 1.9 mi (3 km) of the lek nearest to their nest site; however, two hens traveled over 6.2 mi (10 km) before nesting (table 1). These two hens, one a yearling and the other an older adult, nested at elevations of 6,549 ft (1 996 m) and 6,460 ft (1 969 m). These elevations were 869 ft (265 m) and 800 ft (244 m) higher, respectively, than the nearest lek site.

The movements of two hens, 478 and 473, were monitored for over 1 yr (fig. 1, table 1). Hen 478 was periodically located from April 14, 1980, to August 5, 1981; during this period she traveled 106.0 air mi (169.6 km). She moved 20.2 mi (32.2 km) from her nesting area to the Humphrey area for the summer. In the fall, she traveled 47.2 mi (76.5 km) to the wintering area on the INEL site. In the spring, she returned to the USSES and nested within 82 ft (25 m) of her nest from the previous year.

Hen 473 traveled 73 air mi (117 km) from her nest site in 1980 to the 1980-81 wintering area and back to her nest site in 1981, nesting within 820 ft (250 m) of her nest from the previous year.

Following nesting, instrumented female sage grouse used three distinct summer areas (figs. 2 and 3). In 1980 and 1981, eight hens used the Kilgore area, six used the Humphrey area, and eight stayed just north of the USSES. In 1980, adult females moved an average of 16.4 mi (26.2 km) to the summer range from the breeding ground. This distance was significantly greater ($P \leq 0.01$) than the 6.3 mi (10.1 km) traveled by the yearling female sage grouse (table 1). Overall, in 1980 and 1981, the average distance traveled from the nesting area to the summer range was 12.6 mi (20.1 km) and the increase in elevation was 1,464 ft (446.2 m) (fig. 4). Hens left the USSES about June 23 and arrived at their summer ranges usually within a few weeks.

Table 1.--The distance of movement and the elevation of the radio-instrumented sage grouse hens captured at the USSES, Dubois, ID, in 1980 and 1981

Bird number	Lek to nest distance	Nest elevation	Breeding ground to summer range	Summer elevation	Summer range to winter range	Breeding ground to winter range	Yearly distance	Winter elevation
	(miles)	(ft)	(miles)	(ft)	(miles)			(ft)
1980								
465	0.2	5,580						
467	0.1	5,690	18.0	6,390	31.1			5,249
468	3.8	5,920	6.2	6,060	24.1			5,098
469	0.6	5,685	17.6	6,319	33.5			5,049
470	0.8	5,690	11.7	6,260				
471			18.7	6,490				
473	0.5	5,850	19.2	6,400	33.9	20.1	73.2	4,902
475	6.6	6,460	20.9	8,100				
478	0.1	5,690	10.0	6,915	47.3	38.7	106.0	5,000
479	0.5	5,665	12.9	6,370				
480	0.4	5,685	18.8	8,160				
Sub. mean	1.4a[1]	5,971	16.4a	6,745a	34.0	29.4	89.6	5,059
	(2.2 km)	(1 765 m)	(26.2 km)	(2 056 m)	(54.4 km)	(47.1 km)	(143.4 km)	(1 542 m)
466	0.2	5,660	5.0	5,980	31.2			4,850
472	1.4	5,950	5.2	5,980				
474	6.3	6,549						
476			8.8	6,220				
Sub. mean	2.6a	6,053a	6.3b	6,060a	20.6			4,850
	(4.1 km)	(1 845 m)	(10.1 km)	(1,847 m)				
Total mean	1.7a	5,850a	14.1a	6,590a	31.4a	31.2	84.9	5,025
	(2.7 km)	(1 783 m)	(22.5 km)	(2 008 m)	(50.2 km)	(49.9 km)	(135.9 km)	
1981								
465A	0.7	5,560	17.9	7,200				
471A	0.3	5,655	15.3	8.600	13.1			6,250
472A	0.3	5,700	16.7	5,600				
621	0.8	5,620	5.1	5,900	43.8	39.8		4,800
626	0.5	5,660	15.6					
627	1.5	5,840	14.5	6,700				
628	0.7	5,620	4.4	5,980	26.2			5,049
478	0.2	5,680	17.9	6,800				
469A	0.3	5,700	3.5	5,870				
473	0.4	5,869						
473A	0.1	5,680	7.4	6,800				
474A	0.3	5,880	9.7	7,260				
480A	0.4	5,700	2.3	5,751				
624	0.9	5,580						
629	0.2	5,670						
Mean	0.5b	5,660b	10.9b	6,620a	27.7a			5,367
	(0.81 km)	(1 736 m)	(17.4 km)	(2 018 m)	(44.2 km)			(1 636 m)

[1] a and b = the same letter for the sub. mean or total mean in a column indicates no significant difference; different letters denote significant differences ($P \leq 0.05$).

Some birds moved almost continuously through August; others established a relatively small home range. Of those that established home ranges, the largest was 1,762.0 ac (7.1 km^2); the smallest was 22.2 ac (0.09 km^2), and the average was 704.2 ac (2.85 km^2).

Movements from the summer range to the winter range, in 1980 and 1981, are illustrated in figures 3 and 4. The average distance from summer to winter range was 10.1 mi (48.2 km) with a drop in elevation of 1,463.9 ft (446.2 m) (table 1, fig. 4). The greatest distance traveled from the winter area to the breeding grounds was 39.8 mi (63.7 km). Six of nine birds monitored during the winter either died or their radios stopped transmitting. Therefore, they may not have reached their final wintering area.

In 1980, five of seven hens were still at their summer areas on October 31. The other two were at their summer locations on October 4, but had begun to move to their winter areas by October 31. Three of five birds were still at their summer locations on October 23, in 1981. All the instrumented sage grouse moved in a southwesterly direction to wintering areas. Of the nine birds located during winter, five used areas dominated by black sagebrush, usually on exposed ridgetops.

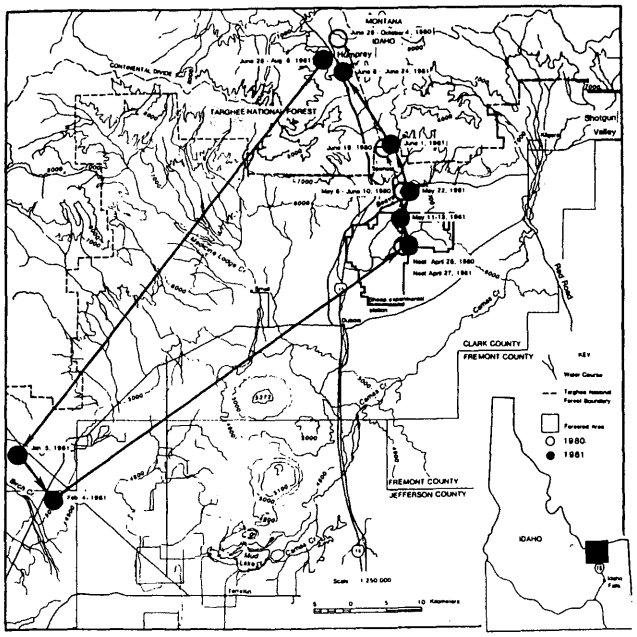


Figure 1.--Movements of hen 478 from April 25, 1980, to June 24, 1981, in Clark and Jefferson Counties, ID (from Hulet 1983).

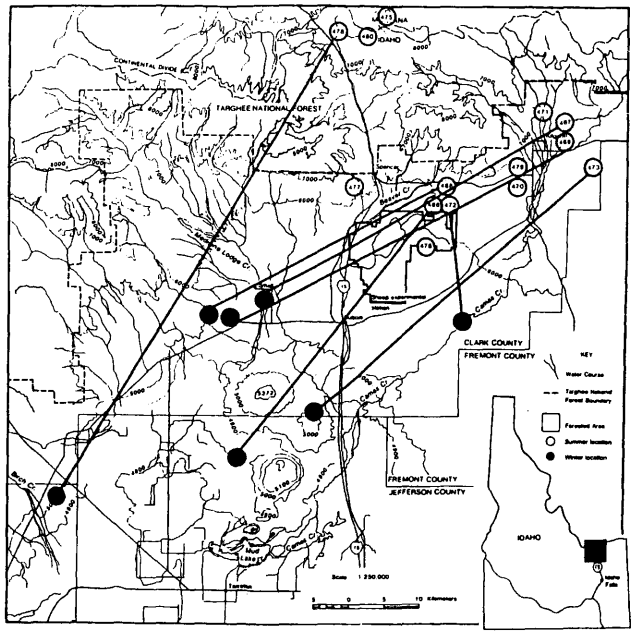


Figure 2.--Summer and winter locations of 14 radio instrumented female sage grouse captured at the USSES, Dubois, ID, 1980 (from Hulet 1983).

Nesting

Average big sagebrush cover in the 100-ft^2 (9.3-m^2) circular plots around the 30 measured nests was 17.2 percent, comprising only 65 percent of the relative cover of the 26.2 percent total shrub cover (table 2). Of the

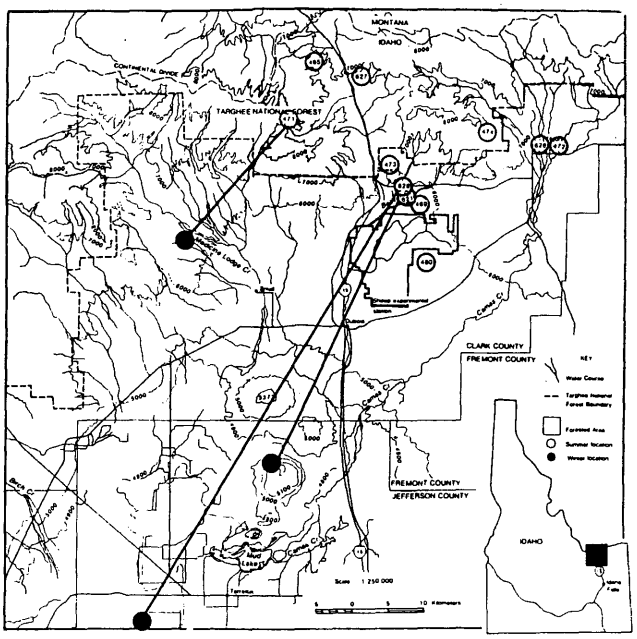


Figure 3.--Summer and winter locations of 11 radio instrumented sage grouse captured at the USSES, Dubois, ID in 1981 (from Hulet 1983).

total 87 percent canopy cover measured in the 10.8-ft^2 (1-m^2) plots around each nest, only 49 percent was big sagebrush, and this represented just 56 percent of the relative cover.

For 30 nests around which habitat measurements were taken, the main shrubs above the nests were big sagebrush (52 percent), three-tip sagebrush (14 percent), antelope bitterbrush (Purshia tridentata) (17 percent), and dead sagebrush (10 percent). Seven percent of the nests had no shrub cover; these were located beneath the canopy of Russian thistle (Salsola iberica). These data differ from what Patterson (1952) found in Wyoming where 92 percent of 300 nests were found beneath the canopy of big sagebrush. Gill (1965) and Wallestad and Pyrah (1974) found, respectively, that 92 percent and 100 percent of nests were under the canopy of big sagebrush. Hen 478 nested under big sagebrush in 1980 and under antelope bitterbrush in 1981, while hen 473 nested under three-tip sagebrush in 1980 and big sagebrush in 1981. These two grouse seemed to have little or no preference for the shrub species whose canopy they nested beneath. The 17.2 percent big sagebrush cover for nests on the USSES was less than the 23.4 to 38.1 percent found by Autenrieth (1981) in southern Idaho. This is probably due to the greater availability of different shrub species suitable for nesting cover on the USSES.

Sage grouse chose to nest beneath the canopy of shrubs that were taller than average for the immediate area. For example, the average shrub height, 18.4 inches (46.7 cm), for all shrubs combined above nests was significantly greater ($P \leq 0.05$) than the 9.8 inch (25.0 cm) average

Table 2.--The percent cover of the shrubby vegetation 10.8 ft^2 (1 m^2) and 100 ft^2 (9.3 m^2) around the nests of radio-instrumented sage grouse captured at the USSES, Dubois, ID, in 1981 and 1981. Included are the height of certain shrubs and percent cover of grass and forbs 10.8 ft^2 (1 m^2) around the nest.

	Percent cover					
	100 ft^2 (9.3 m^2)			10.8 ft^2 (1 m^2)		
Vegetation	1980	1981	Mean	1980	1981	Mean
Amelanchier alnifolia	0.4		0.2			
Artemisia tridentata	14.1	19.2	17.2	35.9	57.0	49.0
Artemisia tridentata (dead)				6.5	9.5	8.5
Artemisia tripartita	3.0	1.1	1.9	22.9	5.3	12.0
Chrysothamnus nauseosus		0.3	T[1]		0.3	0.2
Chrysothamnus viscidiflorus	0.9	0.7	0.8	1.4	0.6	0.9
Purshia tridentata	6.3	2.5	4.0	28.5	9.3	16.6
Rosa woodsii	0.2	T	0.1			
Symphoricarpos oreophilus	0.2		0.1			
Tetradymia canescens	1.8	1.8	1.8		0.4	0.2
Gutierrezia sarothrae	0.1	T	T			
Total shrub cover	27.1	25.7	26.2	95.2	82.0	87.2
Grass cover				12.0	18.5	16.0
Forb cover				15.3	23.7	10.9
Artemisia tridentata						
Height (inches)	9.5	9.2	9.4			
Mean shrub height (inches)	9.8	9.9	9.8			

[1] T = trace.

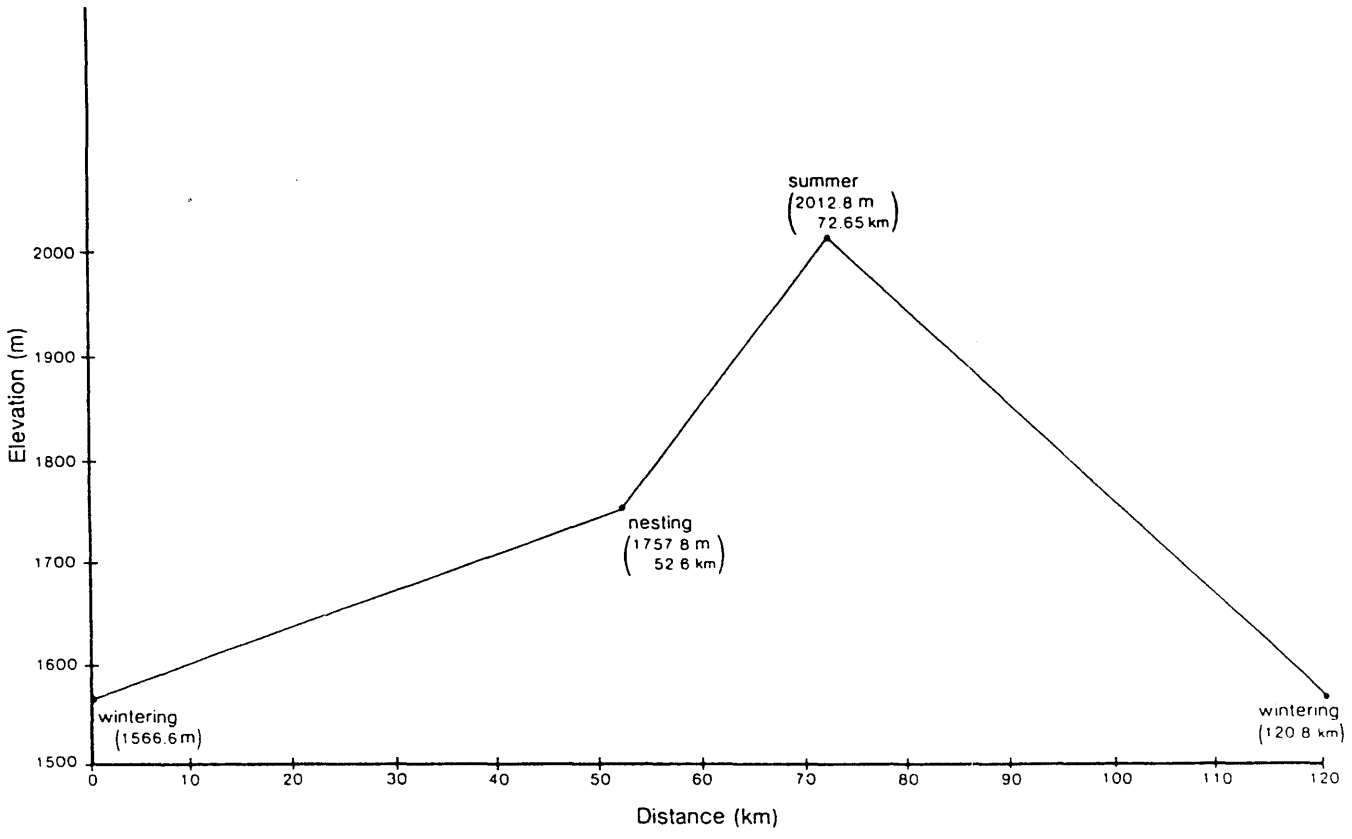


Figure 4.--Comparison of elevation and distance traveled to wintering, nesting, and summering areas of 28 radio-instrumented sage grouse hens captured at the USSES, Dubois, ID, in 1980 and 1981 (from Hulet 1983).

height for shrubs in the 100-ft^2 (9.3-cm^2) circular plots around the nest. Similarly, average height for big sagebrush over nests was 17.6 inches (44.8 cm) compared to the 9.4 inch (23.9 cm) average height of big sagebrush within the 100-ft^2 (9.3-m^2) plot around each nest. Average height of the shrub above the nest, percent cover of grass, forbs, and all shrubs (10.8 ft^2 (1 m^2) around each nest for 1980 and 1981 are detailed in table 2. The percent cover for all shrubs located within the 100-ft^2 (9.3-m^2) plot around the nests in 1980 and 1981 also is listed in table 2.

Predation

Eleven nests were destroyed by predators in 1980 and 1981, with the Uinta ground squirrel (Spermophilus armatus) being responsible for most (7 nests or 64 percent) of the destruction. Three of the four hens that renested had their nests destroyed by predators. In 1981, four successful nest sites were compared vegetatively to five nest sites that had been destroyed by predation (table 3). Within a 100-ft^2 (9.3-m^2) circular plot around each nest, predator-destroyed nests had a

Table 3.--Comparison of shrub characteristics 100 ft^2 (9.3 m^2) and 10.8 ft^2 (1 m^2) around five predated nests and four successful nests in 1981 at the USSES, Dubois, ID

Characteristics	Predated nests n=5	Successful nests n=5
100 ft^2 (9.3 m^2) around nest		
Mean shrub cover (percent)	30.0a[1]	25.8a
Mean shrub height (inches)	9.4a	9.3a
Mean big sagebrush cover	20.6a	17.2a
10.8 ft^2 (1 m^2) around nest		
Mean shrub cover (percent)	92.6a	72.0a ($P \leq 0.10$)
Mean shrub height (inches)	20.9a	11.0b ($P \leq 0.025$)

[1] a and b in the same row denotes significant difference ($P \leq 0.05$).

greater (although not significant) total shrub cover, big sagebrush cover, and total height of all shrubs than nests not destroyed by predators. Within a 10.8-ft^2 (1-m^2) area around the nest, the shrub height was significantly ($P \leq 0.025$) taller and the total shrub cover was greater ($P \leq 0.20$) for those nests destroyed by predators. These data indicate successful nests were located in areas of lower shrub cover and height than those nests destroyed by predators. This contrasts to findings of Wallestad and Pyrah (1974) in Montana where successful nests had significantly ($P \leq 0.005$) greater sagebrush cover within 23.6 inches (60 cm) of the nest and within a 200-ft^2 (9.3-m^2) plot around the nest than those of unsuccessful nests.

Leks

Only two of 12 leks located in 1966 on the USSES were still active in 1981; 14 new leks had been established (fig. 5). This casts doubt on the long-term survival of leks on the USSES.

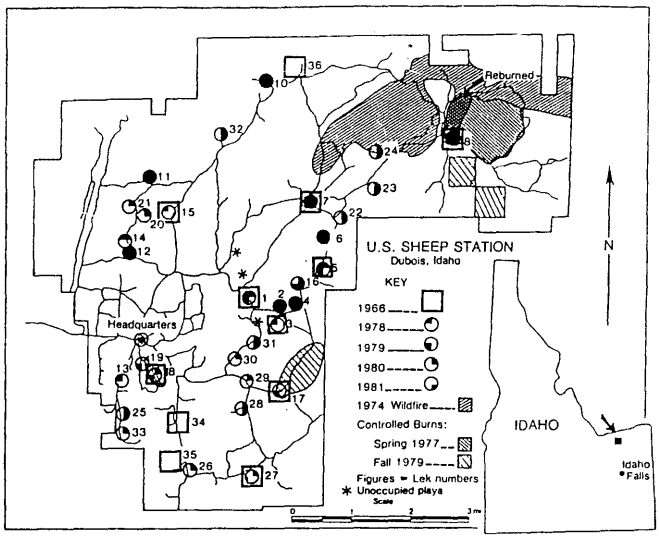


Figure 5.--Locations and dates of active leks in the U.S. Sheep Experiment Station, Dubois, ID, from 1966 to 1981. Location of recent wildfire and prescribed burns and the location of three unoccupied playas are also shown (from Hulet 1983).

Four of the active leks established since 1966 had some relationship with fire (either prescribed or wildfire). A 1,919 ac (777 ha) wildfire in July, 1974, burned approximately 29 percent of the area within a 1.9 mi (3 km) radius of lek site 24. This new lek was established as early as 1971, 1,312 ft (400 m) inside the burn area. In April, 1980, it had the largest concentration of male birds (51), compared to all other leks on the USSES. Lek site 8, burned by a 1,919 ac (777 ha) and a 647 ac (262 ha) wildfire and prescribed burn, respectively, has been active since 1966.

Forty-one percent of the area within a 1.9 mi (3 km) radius around these two leks had been burned. Another lek site was burned in a small prescribed burn in the fall of 1979, but it was still active in the 1980 mating season (15 males, 9 females on March 23). This lek was not used in 1981, probably because the crested wheatgrass (A. cristatum) planted in 1980 was not grazed to allow for after-fire rejuvenation and the 1980 growth of over 15 inches (38 cm) covered the entire lek site in 1981. The final

lek site was abandoned after a prescribed burn in 1979. Since 1966, prescribed burns or wildfires apparently helped create one lek, caused desertion of two, and had no noticeable effect on the other.

Migrations

During the summer months, the instrumented sage grouse hens moved to higher and more moist areas. A five-step discriminate analysis showed we can discriminate between the three summer areas (Kilgore, Humphrey, and northern USSES) with 82.3 percent accuracy (table 4). The discriminate analysis used 79 habitat variables (including plant species) obtained from Daubenmire plots at locations of radio-instrumented grouse during June, July, and August 1981.

Table 4.--Discriminating between the USSES, Humphrey, and Kilgore in southeastern Idaho in 1981. Percent of "grouped" cases correctly classified was 82.3 percent

Actual group	No. of cases	Predicted group membership USSES	Humphrey	Kilgore
USSES	47	45	2	0
		95.7%	4.3%	0.0%
Humphrey	20	6	14	0
		30.0%	70.0%	0.0%
Kilgore	13	6	0	7
		46.2%	0.0%	53.8%

No convergence was obtained when a discriminate analysis was used to compare individual locations of female sage grouse in June, July, and August. However, by combining July and August samples, we could correctly classify samples taken in June versus July and August 96.2 percent of the time. This indicates that vegetation differs greatly from spring to mid- and late-summer. Observed movements of hen sage grouse to new areas in July, after annual forbs mature and dry out, reflect this difference.

Records of the Idaho Fish and Game Department show there are 137 known sage grouse leks in Clark, Lemhi, and Jefferson counties that are within migratory range of sage grouse that nest on the USSES (Autenrieth 1981). Sage grouse that nested on the USSES could thus have nested at one of three other major lek and nesting areas. These three areas are: the INEL site, Medicine Lodge, and the Red Road. Most of the birds that wintered on the north end of the INEL site also nested there and then moved up the Birch Creek drainage during summer (Connelly and others 1981). Birds that nested on the Medicine Lodge drainage generally moved to Snowline, MT, or Humphrey, ID, for the summer (Gray 1967). The sage grouse studied by Dalke and others (1963) nested near the Red Road and moved into the Kilgore and Shotgun Valley area. In comparison, sage grouse on the USSES used wintering areas occupied by all of the above-mentioned groups and part of the summer areas used by grouse from Medicine Lodge and Red Road.

Bird 478 wintered on the INEL site and bypassed perhaps 68 leks and two major breeding sage grouse populations to nest at the USSES. One wonders why she would move 39 mi (62 km) to nest at the USSES when she could have found suitable nesting and breeding areas on the INEL.

DISCUSSION

Further research should be directed toward monitoring movements of hens whose nesting areas have been destroyed to determine how the hens respond when they return the following year. In addition, chicks born to hens with established migratory routes should be monitored to see if the chicks return to the same nesting and summer areas as their mother. Results may help explain how chicks acquire essential migratory traditions and whether there are migratory and nonmigratory birds within the same breeding population.

One of the largest leks on the USSES was established 5 yr after a 1,919 ac (777 ha) wildfire burn in 1974. Although this large lek was created several years after the fire, much nesting habitat near the lek was destroyed for a much longer period of time. Further study should be directed to determining the positive and negative effects of various-sized prescribed burns on breeding and nesting behavior of migratory sage grouse.

After leaving the nesting areas, hen sage grouse seemed less restrictive in selecting summering habitats. For example, big sagebrush cover ranged from 5.0 percent to 17.4 percent in the three areas used by the USSES sage grouse. Discriminate analysis showed that we could distinguish between the three areas 82.3 percent of the time. In summer, sage grouse were found in barley and hay fields as well as in big sagebrush with a canopy cover of 44.4 percent. Hen 474 was found on August 21, 1981, under a Douglas-fir (Pseudotsuga menziesii). Our data indicate the habitat sage grouse utilize during the summer is more variable than that required during the nesting period.

Because the population of sage grouse nesting at the USSES is migratory and uses different habitats during nesting, brooding, and wintering seasons, the USSES should be managed for minimal disruption of essential nesting, breeding, and early brooding activities. Habitat management for wintering sage grouse at the USSES would be of lesser consideration since this is not a major wintering area.

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USE OF ARTEMISIA AND CHRYSOTHAMNUS BY PRONGHORNS

Jim Yoakum

ABSTRACT: Pronghorns use Artemisia and Chrysothamnus for food and cover. The amount of forage these plants provide varies greatly. It is highest in the pronghorn's northern range and much lower in southern rangelands. On some pronghorn ranges, these shrubs provide more feed than any other herbage. They are especially valuable as forage during winter months when snow covers low vegetation. These shrubs also provide critical protective cover for newborn pronghorns. This important pronghorn-shrub relationship requires further study. Management recommendations are provided for maintenance and restoration of these shrubs on pronghorn range in the Great Basin.

INTRODUCTION

Today sagebrush (Artemisia spp.) and rabbitbrush (Chrysothamnus spp.) occur throughout most of the American pronghorn antelope's (Antilocapra americana) occupied habitat (figs. 1, 2, and 3). These shrubs have provided forage and cover for antelope for centuries (Yoakum 1978).

A review of the literature reveals that these shrubs are important sources of food for pronghorns, especially on shrub-grassland steppes (tables 1 and 2). Less use is made on grasslands and deserts.

This paper reviews the importance of sagebrush and rabbitbrush to the pronghorn as forage and protective cover for fawns, and recommends practices for maintaining and enhancing these two shrubs on pronghorn range.

PRONGHORN REQUIREMENTS FOR VEGETATION

The pronghorn's vegetation requirements have been identified for the sagebrush-grasslands of the Great Basin (Yoakum 1978) and the shortgrass prairies (Yoakum 1984). Based on dietary studies and pronghorn densities on preferred rangelands, it became apparent that pronghorn distribution

Table 1.--Estimated percent consumption of sagebrush and other Artemisia spp. in pronghorn dietary studies

Vegetative community and references	Season of use				Total
	Winter	Spr.	Sum.	Fall	Annual
Sagebrush-grasslands					
Hansen 1982	12	38	37	33	29
Koerth and others 1984	16	3	14	20	13
Mason 1952	87	65	32	71	64
Severson 1966	78	ND[1]	30	49	52
Yoakum 1958	83	58	35	54	56
Shortgrass prairies					
Dirschl 1963	10	20	17	85	33
Mitchell and Smoliak 1971	15	7	20	20	15
Schwartz and Nagy 1976	ND	57	23	20	50

[1]ND = no data.

Table 2.--Estimated percent consumption of rabbitbrush in pronghorn dietary studies

Vegetative community and references	Season of use				Total
	Winter	Spr.	Sum.	Fall	Annual
Sagebrush-grasslands					
Hansen 1982	1	2	1	1	1
Koerth and others 1984	-	-	-	-	0
Mason 1952	1	2	-	-	0
Severson 1966	12	ND[1]	30	28	30
Yoakum 1958	-	3	6	-	2
Shortgrass prairies					
Did not occur in any studies					

[1]ND = no data.

and abundance were correlated with the variety and abundance of forbs and shrubs. Such data allow managers to recommend key plant species for grazing plans and seed selections for restoration projects.

Pronghorn habitat requirements are specific to each vegetative community. Optimum pronghorn habitats in the Great Basin shrub-grasslands

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Jim Yoakum is a certified wildlife biologist with U.S. Department of the Interior, Bureau of Land Management stationed at the Department of Range, Wildlife and Forestry, University of Nevada, Reno, NV.

have from 5 to 20 percent of ground cover of shrubs with a mean height of 18 inches (38 cm). On shortgrass prairies, shrub-ground cover is 1 to 5 percent. Shrubs must be available in the right combination with all other biotic factors in order to provide optimum habitat for pronghorns. Too little or too much of any one species may limit pronghorn production or survival. This is especially true for sagebrush. In certain areas of the Great Basin, pronghorns do not occupy areas where sagebrush makes up 60 to 90 percent of the vegetative cover.

FORAGE

Pronghorns are opportunistic herbivores selecting the most palatable and succulent forage available at any given time. Annual diets vary depending on the availability of plants in a specific area. Forbs and shrubs are used predominantly yearlong. Grasses are used very little (Salwasser 1980).

Sagebrush

Without a doubt, sagebrush and other Artemisia species are one of the most important plant groups consumed by pronghorns. This statement can be made for the grasslands of Alberta and Colorado as well as for the shrubland steppes of Oregon and Nevada. Table 1 documents this well, five of eight annual food habit studies list Artemisia as more than 30 percent of total diet. No other plant genus was used as much. Wherever Artemisia was available, it was consumed during all four seasons of the year. The availability of shrubs for forage during severe winters has been directly linked to pronghorn survival (Bayless 1969; Barrett 1982).

Too much or too little of any habitat component can be detrimental to wildlife (Dasmann 1964). This is especially true for shrubs on pronghorn habitat. A shortage of shrubs can increase antelope mortality during winters when snow covers most vegetation and only shrubs protrude to provide forage, and also when there are too few plants for adequate cover for fawns. Too many shrubs, on the other hand, impede rapid escape from predators and compete for moisture and soil nutrients needed to produce other preferred forage species. A plant community containing five to 10 shrub species making up 5 to 20 percent of the ground, provides optimum browse on pronghorn shrubland steppes.

Preferred rangelands in southeastern Oregon commonly have low sagebrush (Artemisia arbuscula) on summer rangelands and black sagebrush (Artemisia nova) on winter rangelands. Areas dominated by big sagebrush (Artemisia tridentata) are less used, probably because of tall growth of the plant. The components of sagebrush communities essential for optimum pronghorn habitat are illustrated in figure 1.

Sundstrom and others (1973) listed the following vegetation criteria for optimum pronghorn habitats on shrub-grassland steppes.

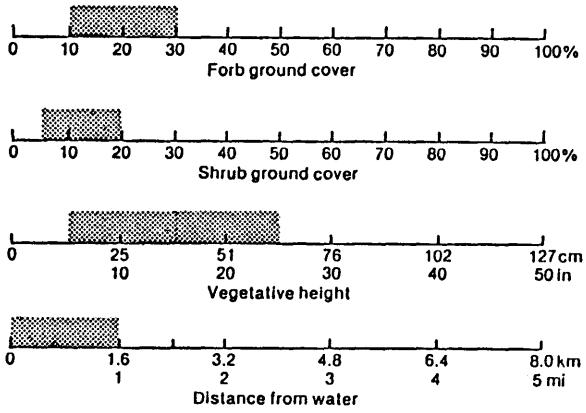


Figure 1.--Components of pronghorn habitat in the sagebrush steppe. Habitat becomes optimum when all components occur together within the bounds marked by bars. (Kindschy and others 1982.)

1. Community to be relatively open (cover less than 40 to 60 percent).

2. Height of shrubs (or other vegetation) not to average more than 18 inches (38 cm).

3. Composition usually consisting of:

   a. 10 to 20 percent sagebrush
   b. 5 to 15 percent other shrubs (including rabbitbrush)
   c. 25 to 35 percent forbs
   d. 40 to 60 percent grasses

4. Preferred species of shrubs for browse are:

   a. Artemisia tridentata (big sagebrush)
   b. A. filifolia (sand sagebrush)
   c. A. frigida (fringed sagebrush)
   d. A. cana (silver sagebrush)
   e. Chrysothamnus viscidiflorus (Douglas rabbitbrush)

In summary, Sundstrom and others (1973) stated that preferred pronghorn habitat in sagebrush-grasslands is characterized by (1) the presence of Wyoming big sagebrush and/or silver sagebrush in combination with other preferred sagebrushes and Douglas rabbitbrush, and (2) the general environmental factors associated with these plant communities. They also stated that antelope density and reproduction appeared to be correlated directly with available amounts of preferred species of sagebrush and associated forbs.

The pronghorn's most northern endemic rangelands are the shortgrass prairies of Alberta and Saskatchewan in Canada. A 6-year study of habitats in Alberta by Barrett (1982) disclosed that wintering antelope herds were largest on rangeland containing silver sagebrush. These key wintering areas, where sagebrush frequently formed more than 75 percent of the diet, were critical to antelope survival.

Deming (1963) provided a provocative perspective of the relationship of sagebrush to pronghorns by stating that the importance of sagebrush in the antelope diet may be due to availability rather than palatability. He further stated that some of the best ranges, with the highest antelope densities, in the past and today, are rolling grasslands, and that sagebrush ranges generally do not produce these highest densities of pronghorns. This has since been substantiated by Yoakum (1978) who documented that two-thirds of the total antelope population occupy grasslands and one-third use shrub-grasslands.

Rabbitbrush

Rabbitbrush is usually considered an undesirable forage plant for livestock; however, it is a highly preferred species for pronghorns (fig. 2).

It should be managed as a needed component on pronghorn rangelands. Table 2 indicates that rabbitbrush comprised more than 1 percent of pronghorn year-long diets on shrub-grasslands. For certain areas, such as the Red Desert in Wyoming, rabbitbrush was consumed slightly more than sagebrush (Severson 1966). Douglas rabbitbrush was preferred over sagebrush during summers and early fall. One reason for less use of rabbitbrush than sagebrush during the winters was that more of the rabbitbrush was covered with snow. According to Severson (1966): "The most important species in the antelope diets were Douglas rabbitbrush and big sagebrush." Rabbitbrush was consumed as soon as it started to grow in the spring and was used extensively until it matured in the fall. It was extremely important, comprising 30 percent of the annual diet (Severson 1966).



Figure 2.--A yearling male pronghorn feeding in a rabbitbrush-grassland community (photo by author).

Fawn Bed Sites Needs

Vegetation characteristics of pronghorn fawn bed sites were documented in Idaho (Autenrieth 1976) and Montana (Pyrah 1974). Both studies identified tall sagebrush habitats as important bed sites for fawns. However, Beale and Smith (1970) in Utah, Barrett (1978) in Alberta, Bodie (1979) in Idaho, and McNay and O'Gara (1982) in Nevada did not reach this conclusion. Beale and Smith (1970) and Bodie (1979) found high predation on fawns in tall shrublands.

Habitat requirements of pronghorn fawns require further study. Tall shrubs may provide important protective cover in some communities, but not in others. For example, shrubs often comprise less than 5 percent of vegetative cover in grasslands, yet grasslands support the highest pronghorn densities in North America (Yoakum 1978). Figure 3 illustrates low sagebrush as cover for pronghorn.



Figure 3.--A neonate pronghorn using low sagebrush as cover (photo by author).

MANAGEMENT RECOMMENDATIONS

A comparison of plant inventory and trend studies relating to the pronghorn's biotic requirements should determine whether an area should be maintained in present condition or enhanced to better meet the pronghorn's requirements for vegetation.

Maintain Habitats in Quality Condition

A cardinal rule of wildlife habitat management is when an environment is in good ecological condition, maintain it in good condition. Following this ecological rule, alone, may not meet all management objectives, such as producing maximum numbers of pronghorns. For example, some sagebrush communities in the Great Basin are 70 percent or more shrub ground cover. If this is the site's natural potential, it will not support a large pronghorn population,

because with this much sagebrush, the site has a low carrying capacity for pronghorn. Management should not expect the site to produce more pronghorns. However, when inventories disclose that a site has the ecological site condition meeting the habitat requirements of pronghorns, then the objective of management should be to protect and maintain the quality of that site. It cannot be emphasized too strongly that where good quality natural habitat exists, management should maintain that habitat quality.

Enhance Habitats in Low Quality Condition

If a rangeland is in good condition, it is producing its natural potential of pronghorns; therefore, manipulation of vegetation cannot be justified as a means to improve conditions for pronghorns. Only on those sites which provide inadequate vegetative conditions, but which provide the right combination of other habitat factors, can manipulation be justified. Pronghorns thrive on rangelands in a subclimax vegetative condition (Kindschy and others 1982). Such conditions can be the result of wildfires caused by lightning, grazing by herbivores, or vegetation manipulation. Optimum pronghorn habitats contain a variety of grasses, forbs, and shrubs. Range improvement projects that provide similar mixed forage classes can best meet pronghorn requirements.

Extensive areas of dominant (more than 30 percent plant composition), tall (exceeding 24 inches [60 cm]) sagebrush and rabbitbrush communities provide low-density rangelands for pronghorns, compared to similar sites with fewer shrubs and more grasses and forbs. These shrublands can be treated to make the vegetal structure more favorable for pronghorns.

Shrub control has been a major practice on western rangeland during the past four decades. Removing sagebrush with large brushland plows was one method used extensively. Chaining, another mechanical shrub control method, does not kill as many shrubs as plowing and is less damaging to native grasses and forbs; therefore, chaining is more favorable for pronghorn rangeland management.

Because sagebrush and rabbitbrush are important to pronghorns, these plants should not be eliminated. Illegal spraying of sagebrush on public lands in Wyoming resulted in an administrative law decision requiring the appellant to replant sagebrush for wildlife (Diamond Ring Ranch, IBLA 73-48, August 17, 1973).

If preferred plant species are scarce, pronghorn habitats can be seeded artificially. Scarcity of favored plants can result from repeated wildfires destroying endemic sagebrush-grassland types (Leopold 1966), and also when mining operations strip off the natural vegetation. Under such circumstances on public lands, the Surface Mining Act of 1977 requires rehabilitation of the site to its original vegetative conditions, including the replanting of sagebrush and rabbitbrush.

Complex mixture seedings (Plummer and others 1968) serve pronghorns best because they reestablish a mixed plant community of grasses, forbs, and shrubs, approximating natural conditions. They meet the vegetation requirements of pronghorns and many other wildlife species more than monotypic seedings.

We have the technology to successfully plant sagebrush and rabbitbrush on western rangelands. Thousands of acres have been successfully planting during the past three decades.

DISCUSSION AND CONCLUSIONS

Today we have a wealth of information about the relationship of pronghorn habitat requirements. Knowledge is sufficient for managers to maintain and enhance rangelands for pronghorns. For the shrub-grassland steppes, this means the retention of endemic sagebrush and rabbitbrush. In many areas, the survival and abundance of antelope are directly related to these two shrub species. Their importance as native species cannot be emphasized too strongly. Pronghorns and many other species of wildlife have been dependent on these shrubs in natural ecosystems for eons.

Manipulation of the environment to meet human needs is the major factor affecting wildlife habitat quality today. It is imperative for the future of wildlife that these needs be compromised on sagebrush-rabbitbrush rangelands.

Sagebrush and rabbitbrush are important forage and cover shrubs directly related to the survival and abundance of pronghorns on shrub-grassland steppes. When these endemic shrubs are eliminated from the natural ecosystem by repetitive fires, mining activities, or planned conversion practices on public lands, it is mandated by Public Laws that these species be reestablished.

Sagebrush and rabbitbrush have existed on western rangelands for centuries; they are a part of the natural vegetative community. Pronghorns and many other native wild animals rely on these shrubs for survival. Today's land ethic dictates that land managers perpetuate these native plants and animals as a part of ecosystems in good natural ecological condition.

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BLACK SAGEBRUSH RESPONSE TO GRAZING IN THE EAST-CENTRAL GREAT BASIN

Warren P. Clary

ABSTRACT: Results from a variety of sites with different sheep or sheep-cattle grazing histories show a rather consistent reduction in black sagebrush cover compared to areas that were not grazed. Low-elevation black sagebrush experienced the greatest cover reduction. Moderate use during midwinter or alternate year use during midwinter appear to be compatible with maintaining black sagebrush cover.

INTRODUCTION

Winter grazing of the low-shrub cold desert ranges by livestock began in the late 19th century soon after settlement of the intermountain West. Grazing at seasons other than winter was possible only in a few places near reliable water. Winter use was possible because the light snowfall provided water for the animals, and snow was rarely deep enough to inhibit animal movement and foraging (Holmgren 1973). The cold desert ranges therefore complemented other ranges in the region which, because of deep winter snows, could be grazed only in the summer.

In the 1880's major herds of sheep arrived in the area and a predominant use of the desert as sheep winter range began. Sheep numbers were highest between 1905 and 1931, then began to decline. During this period the most valuable forage species declined in number and vigor, and inferior species increased, greatly reducing the grazing value of the desert (Stewart and others 1940).

Most of these lands were publicly owned and unmanaged until the passage of the Taylor Grazing Act in 1934. Prior to passage of the Act, concerns about grazing impacts on winter grazing land had led to the initiation of a series of study plots in western Utah and across central and northern Nevada. This consisted of pairs of fenced and unfenced 4-acre (1.6-ha) plots. They were established in 1932 through 1939, roughly at the point that grazing came under some control. The Desert Experimental Range was also established in western Utah during this period (1933) to provide a place for the study of winter livestock grazing (Holmgren 1973).

Black sagebrush (Artemisia nova) is the sagebrush most closely associated with low-shrub cold desert (salt desert shrub) habitats in the Great Basin. It is a small, spreading, aromatic shrub 6 to 18 inches (15 to 45 cm) tall. Black sagebrush is most abundant at elevations from 5,000 to 8,000 ft (1 500 to 2 400 m) on dry, shallow, stony soils often underlain by bedrock or hardpan (Blaisdell and Holmgren 1984). Black sagebrush populations in the east-central Great Basin are highly preferred by sheep (Hutchings and Stewart 1953), pronghorn (Beale and Smith 1970), and, for certain cultivars, by deer (Welch and others 1981).

This study was conducted to determine the response of black sagebrush to sheep and cattle grazing in the east-central Great Basin.

STUDY SITES AND METHODS

Four-Acre Plots

In 1981 and 1982, data were collected from nine pairs of 4-acre (1.6-ha) plots located in Millard County, UT, and White Pine County, NV. The selected plot pairs were limited to those which contained black sagebrush. The paired plots were located approximately 100 yards (91 m) apart. Each plot contained 40 permanent 200-ft^2 (18.6-m^2) subplots. Plant cover by species was determined using the point-observation-plot method (Stewart and Hutchings 1936). Four of the nine plot pairs occurred within the boundaries of the Desert Experimental Range (DER). The grazed member of these pairs received moderate grazing use averaging 2.1 acres (0.8 ha) per sheep month. Grazing use on public land sampled by the remaining five plot pairs is unknown, however, use records for allotments surrounding the DER suggest moderate levels of stocking may have been approached for the last two decades. Earlier use on at least some of these areas was described as heavy (Hutchings and Stewart 1953). Plot pairs were considered to be blocks in a randomized block analysis of variance. Analyses were performed to determine if plant cover of grazed and ungrazed plots differed after 42-50 years, during a period of some control of grazing.

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Warren P. Clary is Supervisory Range Scientist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Boise, ID.

One pair of 2-acre (0.8-ha) plots, containing 20 200-ft^2 (18.6-m^2) subplots each, was also sampled and used in the climatic comparison described later.

Black Sagebrush Corner

In 1981 and 1983 across-the-fence comparisons were made in different locations. These were located along the west side of the Desert Experimental Range (DER) in an area known as Black Sagebrush Corner. The DER side of the fence had received moderate late fall and early winter grazing which averaged 2.1 acres (0.8 ha) per sheep month since 1933. No specific record of grazing use is available for the Bureau of Land Management (BLM) area outside the DER boundary fence, but Hutchings and Stewart (1953) reported that use was heavy and recollections of older sheepherders were that use continued into the spring when forage plants are more easily damaged (Blaisdell and Holmgren 1984). Forty 200-ft^2 (18.6-m^2) plots on each side of the fence were sampled. Plant cover differences were assessed using unpaired t-tests.

Bud Sagebrush Corner

Another area on the west side of the DER known as Bud Sagebrush Corner contained black sagebrush, but only in the bottoms of small ephemeral washes. Another across-the-fence comparison was made on six of these washes. They were sampled using five 200-ft^2 (18.6-m^2) plots on each side of the DER boundary fence. The area on the DER side was grazed every other year in midwinter at a rate of 1.5 acres (0.6 ha) per sheep month. However, the amount of use received by the washes themselves is unknown. Unpublished data from the first 24 years of the grazing comparison suggest that utilization of black sagebrush in the entire Bud Sagebrush Corner grazing unit was not greater than in other grazing units on the DER (Holmgren and Hutchings, unpublished data). The area outside of the fence was grazed annually by the same sheepmen that grazed outside the Black Sagebrush Corner, until 1979, when cattle grazing began outside the Bud Sagebrush Corner. Differences in plant cover within the washes were analyzed by paired t-test using samples within the same wash as members of a pair.

Climatic Scale

A climatic scale for the study sites was computed as the product of elevation (ft) times precipitation (in) divided by 1,000 to reduce the size of the numbers. Relative change in black sagebrush cover on grazed plots in relation to control plots was regressed against this climatic scale. All available data were utilized--the nine 4-acre (1.6-ha) plot pairs, one pair of 2-acre (0.8-ha) plots, and the black sagebrush and bud sagebrush corner locations for which the DER portion of the comparisons was considered the control. Locations used in this study varied from 5,640 ft (1 720 m) to 6,400 ft (1 950 m) in elevation, and from 6.0 in (15 cm) to 8.5 in (22 cm) in annual precipitation received.

RESULTS

Four-Acre Plots

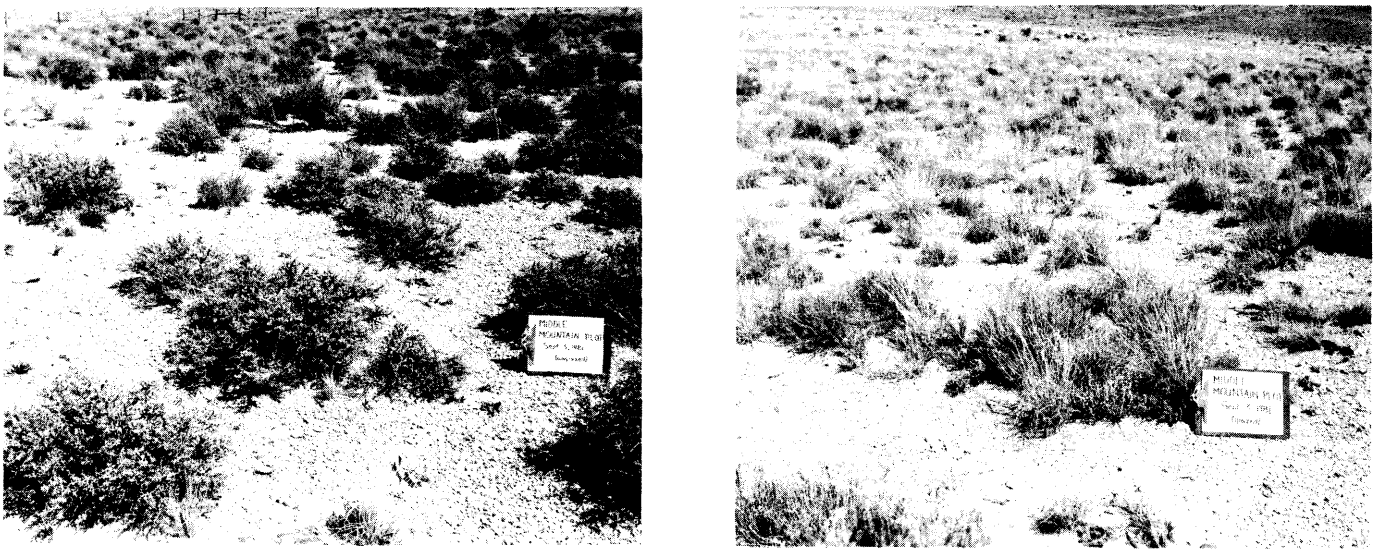
Significant differences had developed in plant cover on grazed and ungrazed plots during the 42-50 years since establishment (table 1). Total plant cover was less on grazed than ungrazed plots ($P<0.10$). This reduction of cover occurred almost entirely within the shrub group. Cover of black sagebrush was strongly depressed ($P<0.01$). Other shrubs as a group showed a moderate increase ($P<0.05$), presumably in response to reduced black sagebrush competition (fig. 1). The most abundant shrubs in this group were shadscale (Atriplex confertifolia), low rabbitbrush (Chrysothamnus viscidiflorus ssp. puberulus), winterfat (Ceratoides lanata), and broom snakeweed (Gutierrezia sarothrae). Forbs showed no significant differences between grazed and ungrazed sites. Grasses were somewhat more abundant on grazed plots ($P<0.10$), probably in response to a reduction in black sagebrush.

Table 1.--Plant cover of grazed and ungrazed black sagebrush sites

Plants	Percent cover		Probability
	Grazed	Ungrazed	
Shrubs	2.56	3.47	<0.05
Black sagebrush	1.36	2.79	<.01
Others	1.20	.68	<.05
Forbs	.09	.19	NS
Grasses	.59	.36	<.10
Total	3.24	4.02	<.10

Black Sagebrush Corner

The comparison here is of moderate (usually December) use on the DER versus heavier use that continued into the critical spring period on BLM land. The two data sets from Black Sagebrush Corner show similarities and differences (tables 2 and 3). Significantly greater amounts of black sagebrush ($P<0.01$, 0.10) and bud sagebrush (Artemisia spinescens) ($P<0.10$, 0.05) occurred on the DER side of the fence. At location 1, total cover ($P<0.01$) and shrub cover ($P<0.01$) were greater on the DER side, but low rabbitbrush ($P<0.01$) and grasses ($P<0.05$) were greater on the BLM side. At location 2, total cover, shrub cover, and low rabbitbrush cover were not different, although winterfat ($P<0.10$) and grasses ($P<0.01$) were greater on the BLM side. One forb, King budbeak (Cordylanthus kingii), was very abundant on the DER side in 1983 ($P<0.05$).



A B

Figure 1.--Black sagebrush dominates the ungrazed plot (A) while grasses and other shrubs dominate the grazed plot (B).

Table 2.--Plant cover at location 1, Black Sagebrush Corner, in 1981

Plants	Percent cover DER	BLM	Probability
Shrubs	6.19	3.24	<0.01
Black sagebrush	5.54	1.92	<.01
Bud sagebrush	.13	.04	<.10
Low rabbitbrush	.15	.98	<.01
Others	.37	.30	NS
Forbs	.08	.48	NS
Grasses	.34	.47	<.05
Total	6.61	4.19	<.01

Table 3.--Plant cover at location 2, Black Sagebrush Corner, in 1983

Plants	Percent cover DER	BLM	Probability
Shrubs	6.67	6.04	NS
Black sagebrush	3.38	2.04	<0.10
Bud sagebrush	.34	.09	<.05
Low rabbitbrush	2.02	2.38	NS
Winterfat	.89	1.40	<.10
Others	.04	.13	NS
Forbs	.66	.23	<.05
King budbeak	.26	.07	<.05
Others	.40	.16	NS
Grasses	1.30	2.30	<.01
Total	8.63	8.57	NS

Bud Sagebrush Corner

This comparison is of grazing every other year in midwinter at a fairly heavy stocking rate (DER) to winter-long grazing each year (BLM). Black sagebrush responded strongly to this difference in grazing regimen by developing and maintaining substantial cover ($P<0.05$) on the DER side, and being almost entirely replaced by rabbitbrushes (low rabbitbrush and shortleaf rubber rabbitbrush [Chrysothamnus nauseosus ssp. leiospermus]) ($P<0.05$) and broom snakeweed ($P<0.05$) on the BLM side (table 4). The near 1:1 replacement of black sagebrush resulted in no differences in total shrub cover or total plant cover between grazing treatments. This area differed from the ones discussed above in that no increase in grasses appeared where a reduction in black sagebrush occurred.

Table 4.--Plant cover in dry washes, Bud Sagebrush Corner

Plants	Percent cover DER	BLM	Probability
Shrubs	3.02	2.88	NS
Black sagebrush	1.50	.06	<0.05
Broom snakeweed	.25	.85	<.05
Rabbitbrush	.67	1.56	<.05
Others	.60	.41	NS
Forbs	.01	.00	<.10
Grasses	.66	.56	NS
Total	3.69	3.44	NS

Relationship to Local Climate

The study areas showed significant differences in average cover of black sagebrush. Closer examination of the individual study locations reveals that the degree of grazing response

varied substantially. The proportional difference in black sagebrush cover was greatest in locations which were at the lower, drier edge of the black sagebrush elevational distribution (fig. 2). At higher elevations within the black sagebrush distribution where annual precipitation was greater, black sagebrush cover changed little under grazed conditions.

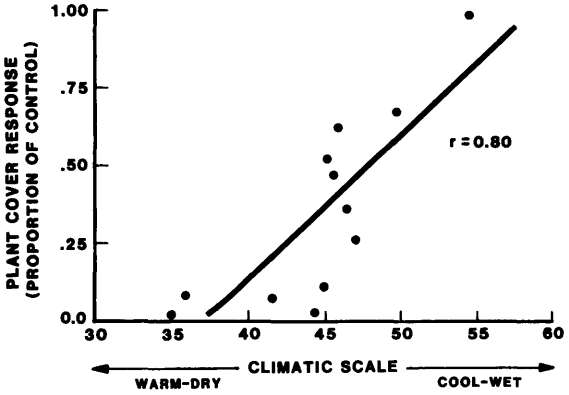


Figure 2.--Black sagebrush response to grazing in relation to climatic variation.

The differences in response may simply be due to the fact that black sagebrush is less tolerant of grazing use in drier, more stressful sites. However, assuming the lower elevation black sagebrush does experience more utilization, a question of interpretation is whether greater use occurs there because black sagebrush is part of a mixed plant composition (Cook and others 1951) or because plants in the more arid sites taste differently. Welch and others (1981) evaluated deer preferences for four accessions of black sagebrush and found utilization in a uniform garden varied from 0 to 60 percent. Behan and Welch (1985) found similar results (0 to 83 percent). This strongly demonstrates that genetically based differences among black sagebrush populations result in taste variation and, hence, preference differences.

Have the preference differences arisen by chance, or as a response to environment? For instance, the relationship shown in figure 2 could be interpreted to suggest drier sites cause an evolutionary selection for populations which are more preferred. In an initial test of this hypothesis, the deer utilization data of Welch and others (1981) were graphed against the approximate climatic conditions of the collection sites. The results of this limited examination were inconclusive. However, no soils data were available, and these should also be investigated as part of the environmental complex under which local plant communities evolve (Powell 1970). Basic differences in monoterpenoids (Welch and McArthur 1981) and other plant constituents potentially affecting preference may occur as an indirect plant population response to environmental pressures associated with different sites. An investigation of the ability of certain sites (climate-soil combinations) to produce more preferred genetic races should prove quite beneficial in the study of variation in natural plant populations.

CONCLUSIONS

These results from widely varying sites with differing grazing histories show that winter livestock grazing (principally sheep), even at stocking rates reduced from early-1900 levels, has had a measurable and often severe effect on black sagebrush. Earlier studies have illustrated that black sagebrush is often grazed more heavily by sheep than most other forage shrubs on winter ranges (Green and others 1951; Cook and Stoddart 1953). In addition, black sagebrush is one of the plants most severely impacted by defoliation (Cook and Child 1971).

Winter grazing by sheep in the lower portions of the black sagebrush elevational distribution must be carefully managed if black sagebrush populations are to be maintained. Limited comparisons among different grazing regimens suggest that moderate grazing use during midwinter or alternate year use are compatible with maintenance of black sagebrush populations.

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EFFECTS OF BIG SAGEBRUSH ON IN VITRO DIGESTION OF GRASS CELL WALL

N. Thompson Hobbs, Bruce L. Welch, and Thomas E. Remington

ABSTRACT: Using nylon bags in digestion tubes, we tested the hypothesis that substances in big sagebrush (Artemisia tridentata) inhibit digestion of grass cell walls. In our first experiment, Colton accessions (A. t. ssp. vaseyana) had no effect on cell wall digestion, but plants from Benmore (A. t. ssp. vaseyana), Wingate, and Loa (A. t. ssp. tridentata) significantly depressed cell wall digestibility. In our second experiment, we found that Loa sagebrush, which had been heated to volatilize its monoterpenoid constituents, as well as untreated Hobble Creek sagebrush (A. t. ssp. vaseyana), had no effect on cell wall digestion. We conclude that some, but not all, accessions exhibit potent antimicrobial action in vitro and surmise that volatile constituents, probably specific monoterpenoids, are responsible for that action when it occurs.

INTRODUCTION

Big sagebrush (Artemisia tridentata) is frequently a dominant constituent of the winter diet of mule deer (Odocoileus hemionus) in the Rocky Mountains and Great Basin (Leach 1956; Kufeld and others 1973; Tueller 1979; Pederson and Welch 1982). Most workers agree that big sagebrush is an important forage for deer, but there is substantial disagreement about its nutritional value. Monoterpenoids in big sagebrush have been shown to inhibit or reduce microbial activity (Oh and others 1967; Nagy and Tengerdy 1968) and to retard in vitro fermentation of cellulose (Nagy and others 1964). However, Welch and Pederson (1981) found monoterpenoids were not correlated with in vitro digestion of big sagebrush. Smith (1950), Bissell and others (1955), and Dietz and others (1962) observed that winter sagebrush was readily digested in vivo.

These conflicting lines of evidence can be reconciled by the following reasoning. Big sagebrush tissue contains a highly lignified, indigestible cell wall surrounding a large and relatively digestible fraction of cell solubles (Kufeld and others 1981). Consequently, digestion of big sagebrush requires little microbial action. It follows that dry matter digestion of sagebrush is largely insensitive to antimicrobial effects of monoterpenoids. In contrast, digestion of mature grass relatively high in cell wall should be dramatically influenced by the presence of antimicrobial substances. Grass cell wall differs chemically from the cell wall of big sagebrush. Grass cell wall contains relatively higher percentages of cellulose and hemicellulose, carbohydrates that can be digested by rumen microbes. The cell wall of big sagebrush contains higher percentages of indigestible lignin that strongly limit cell wall digestion (Kufeld and others 1981; Van Soest 1981); digestion of big sagebrush appears to depend on its solubility, whereas, digestion of mature grass results from microbial action on cell wall.

Mule deer mix grass and big sagebrush in their diets, particularly during the winter and spring (Leach 1956; Kufeld and others 1973; Hobbs and others 1983). The purpose of this study was to test the hypothesis that big sagebrush contains substances that inhibit microbial digestion of grass cell wall.

MATERIALS AND METHODS

We examined effects of big sagebrush vegetative tissue on digestion of mature grass containing high levels of cell wall. Two experiments were conducted for this study. One was a five-by-five factorial design with five replications per cell. The second was a three-by-three factorial design with five replications per cell. Factors included substrate composition and substrate amount.

Experiment One

The grass we used for this experiment was a mature Timothy hay with fiber and protein levels characteristic of senescent grass (table 1). Big sagebrush vegetative tissue was supplied

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N. Thompson Hobbs is Wildlife Researcher, Colorado Division of Wildlife, Fort Collins, CO; Bruce L. Welch is Principal Plant Physiologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT; Thomas E. Remington is Research Associate, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO.

Table 1.--Composition of grass used in in vitro digestions

Constituent	Percentage of dry matter
Neutral detergent fiber	71.3
Acid detergent fiber	43.4
Lignin	4.1
Crude protein	5.2
Dry matter digestibility[1]	45.0
Cell wall digestibility[1]	40.0

[1] In vivo in mule deer, D. L. Baker, unpublished data.

from four accessions of big sagebrush grown in a uniform garden (Colton and Benmore A. t. ssp. vaseyana, Wingate and Loa A. t. ssp. tridentata). The experiment was conducted as follows: two nylon bags were placed inside each digestion tube filled with inoculum and buffer. We designated one bag as the treatment bag, the other as the response bag. In the treatment bag, we placed varying amounts of big sagebrush vegetative tissue (0, 0.2, 0.4, 0.6, 0.8 g of dry matter). Mature grass tissue was placed in the response bag in varying amounts (0.2, 0.4, 0.6, 0.8, 1.0 g dry matter). Treatment and response bags were paired in the digestion tubes so the total dry matter of the pair would equal 1 g. Five combinations of digestion tubes were prepared for each accession of big sagebrush. Big sagebrush vegetative tissues were collected and processed using the procedure described by Welch and McArthur (1981). This procedure preserved the volatile constituents of the big sagebrush tissues. Mature Timothy hay tissues were prepared by ovendrying at 50°C. Grass was ground in a Wiley mill to pass through a ½-mm screen. Rumen inoculum was obtained from a fistulated Holstein cow fed native grass hay similar in composition to the mature grass used in this study. We estimated cell wall disappearance from the response bags gravimetrically using the in vitro digestion procedure of Van Soest and others (1966).

Experiment Two

This experiment was conducted like experiment one, except we used two different types of big sagebrush samples in a three-by-three factorial design. We took a sample of the Loa big sagebrush and ovendried it for 24 hours at 100°C. This was done to drive all of the volatile constituents out of the Loa tissue. The other big sagebrush was a fresh sample of vegetative tissue from another accession we call Hobble Creek (A. t. ssp. vaseyana). Welch and others (1981) have reported that the Hobble Creek accession was preferred by wintering mule deer over 10 other accessions (Welch and McArthur 1985, unpublished data). The reason for including the Hobble Creek accession was to test the hypothesis that highly preferred accessions of big sagebrush do not contain substances that inhibit microbial digestion.

Statistical Analysis

We examined effects of the big sagebrush treatments by using regression analysis with dummy variables (Kleinbaum and Kupper 1978). Cell wall digestion was the dependent variable; treatment amount, the independent. Separate models were fitted for each treatment substrate. All models shared a common origin at treatment amount = 0.0. Differences among model slopes were established with "t" tests.

RESULTS

Results of experiment one showed that constituents in the Wingate, Benmore, and Loa accessions of sagebrush inhibited digestion of grass cell wall (fig. 1). We observed no difference in magnitude of treatment effects among these accessions (P = 0.14). Effects of the Colton accession did not differ from the grass control (P = 0.98). Increasing amounts of Wingate, Benmore, and Loa sagebrush caused steep, linear declines in cell wall digestion. Although increasing amounts of Colton and grass in treatment bags appeared to enhance cell wall digestion of grass in response bags, this apparent enhancement probably resulted from differences in compaction of grass in the response bag at different treatment levels. Consequently, it represents an experimental artifact rather than a real biological influence.

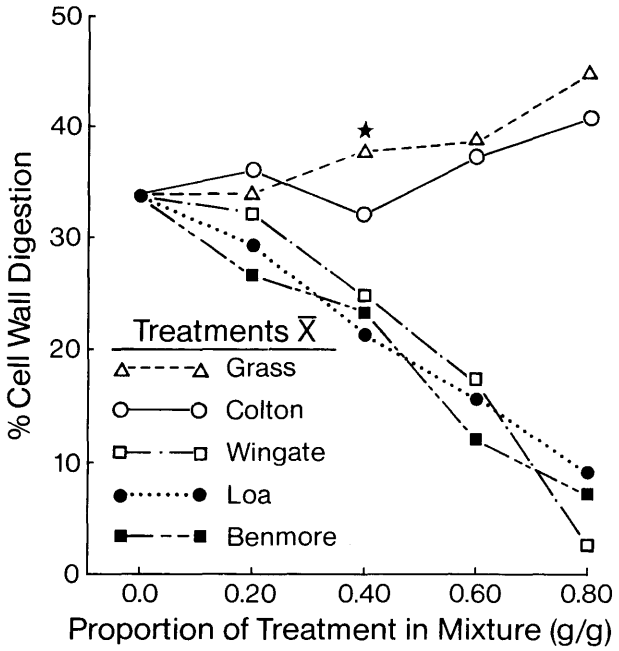


Figure 1.--Effects of sagebrush and a grass control on the in vitro digestion of grass cell wall. Star shows cell wall digestion of loose, unbagged samples. In vivo cell wall digestion of this grass in mule deer = 40.

Results of experiment two showed that removal of the volatile constituents from the sample of Loa big sagebrush removed the substances responsible for the inhibition of grass cell wall digestion detected in experiment one (fig. 2). Fresh Hobble Creek big sagebrush tissue had no effect on the digestion of grass cell wall (fig. 2).

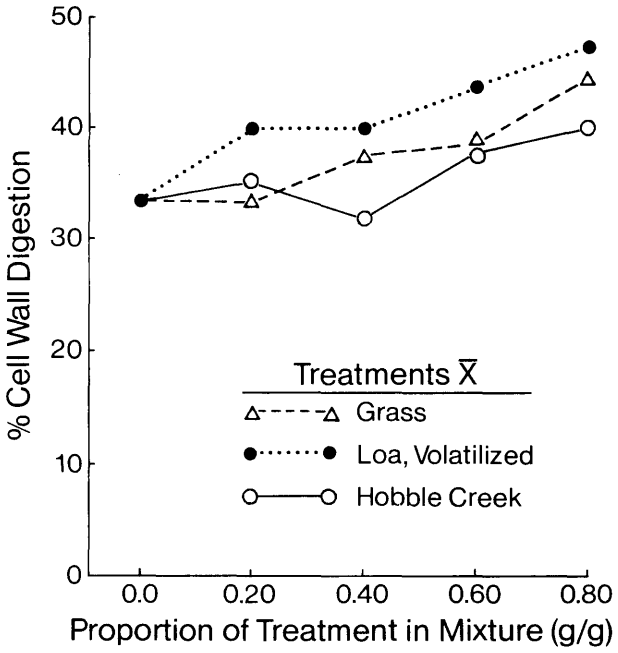


Figure 2.--Effects of Hobble Creek sagebrush, volatilized Loa, and a grass control on the in vitro digestion of grass cell wall.

DISCUSSION

Many workers have observed that herbivores show marked differences in preference among seemingly similar big sagebrush plants (Welch and others 1981; White and others 1982a; Welch and others 1983). Such differences, taken collectively, led Hanks and others (1973) to propose that two types of big sagebrush may exist side by side on western rangelands. One type is frequently eaten, the other frequently avoided.

We demonstrate a nutritional basis for this divergence in herbivore preference for big sagebrush. It appears that substances in some accessions of big sagebrush severely inhibit fiber digestion in ruminant animals. Other accessions have no inhibitory substances. These differences are associated with differences in preference. Mule deer preference for big sagebrush that shows no inhibitory effects (Colton and Hobble Creek accessions) was qualitatively greater than their preference for digestion-inhibiting accessions (Wingate, Benmore, and Loa; Welch and others 1985, unpublished data).

Several factors may mitigate the influence of inhibitory substances. These include the loss of volatile compounds from the rumen and short retention time of big sagebrush in the rumen (Cluff and others 1982; White and others 1982b; Hobbs and others 1983; Baker unpublished data 1984).

We conclude that some, but not all, accessions of big sagebrush contain volatile substances that inhibit cell wall digestion of grasses. These constituents appear to influence mule deer diet selection. Future work will focus on identifying those specific inhibitory constituents.

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Section 5. Entomology and Pathology

BIOLOGY AND DEMOGRAPHY OF THE SAGEBRUSH DEFOLIATOR AND ITS IMPACTS ON BIG SAGEBRUSH

T. H. Hsiao

ABSTRACT: The seasonal history and population dynamics of the sagebrush defoliator (Aroga websteri Clarke) were monitored for 5 years (1971-76) at Curlew Valley, ID. Defoliator infestation at the study site was initially high causing severe defoliation, but declined in subsequent years. High temperature and low precipitation were the major causes of drastic decreases in defoliator populations. Host specificity tests revealed that only certain species belonging to Artemisia subgenus Tridentatae were acceptable as hosts for feeding and oviposition. Severe defoliation could kill or reduce the vigor of big sagebrush. Defoliated plants produced less foliage, had more dead branches, and had a smaller percentage of live branches that produced flower stalks. Defoliator-resistant sagebrushes offer the best management strategy for reducing defoliator infestation.

INTRODUCTION

The sagebrush defoliator (Aroga websteri Clarke [Lepidoptera: Gelechiidae]) is an important pest of sagebrush. It causes varying degrees of defoliation and mortality over widespread areas in Utah, Idaho, Oregon, California, and Nevada (Knowlton 1960; Henry 1961; Hall 1965; Artz 1972; Bechtel 1972). During the 1960's, several studies on the defoliator and its natural enemies were conducted by Hall (1965) in northern California, Gates (1964) in Oregon, and Fillmore (1965) and Henry (1961) in Idaho. This report reviews some of the research findings of the Desert Biome Research Program, Invertebrate Process Studies, between 1971 and 1976 concerning various aspects of biology, population dynamics, and natural mortality factors of the defoliator and its effects on big sagebrush (Artemisia tridentata Nutt.). In view of the lack of research on this important sagebrush insect during the past decade, it is hoped that this report will stimulate interest in the subject.

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T. H. Hsiao is Professor of Entomology, Department of Biology, Utah State University, Logan, UT.

STUDY SITE

Several aspects of the field study were carried out 6 miles north of the Utah-Idaho border at Curlew Valley, a large, arid drainage basin of a former bay of the glacial Lake Bonneville, located at approximately 42 °N. latitude and 113 °W. longitude, and at an elevation of 4900 feet (1 500 m). Annual precipitation varies from 10 inches (25 cm) in the south to 13 inches (33 cm) in the north. Most rainfall occurs in spring and fall; drought conditions predominate in summer months. The valley is generally blanketed with snow in winter. Mean temperature ranges from 71 °F (21 °C) in July to 25 °F (-4 °C) in January. Maximum daily temperatures above 100 °F (38 °C) are frequently recorded from June to August. A minimum temperature of -45 °F (-43 °C) has been recorded in January. The defoliator study was conducted on a 2.5-acre (1-ha) study site near the south border of a 0.77-mi^2 (2-km^2) validation site used by the Desert Biome Program. Twenty-three plant families are found at the study site. Besides Artemisia tridentata, dominant shrubs are two rabbitbrushes, Chrysothamnus viscidiflorus and C. nauseosus. Seasonal undergrowth consists of many species of ephemeral flowers and grasses. The predominant grasses are both introductions, Bromus tectorum and Agropyron cristatum.

SEASONAL HISTORY AND BIOLOGY

Population dynamics of the defoliator were determined by weekly sampling during the spring and summer months. The sampling procedure used between 1971 and 1973 involved 40 randomly selected sagebrush branches that were measured, cut at ground level, weighed, and placed in plastic bags. In the laboratory, the defoliators were hand-sorted and their numbers and stages recorded (Hsiao 1972; Hsiao and Kirkland 1973). Beginning in 1974, the sampling and sorting techniques were improved (Hsiao and Green 1974; Hsiao and Temte 1975). Sixty plant samples were taken on each sampling date. In the laboratory these samples were initially examined for defoliator larvae by hand sorting. The number and instars of the defoliator were recorded. Samples were then placed in Berlese funnels for 3 to 5 days. The insects were collected in 70 percent alcohol, sorted, counted by instar, and added to the totals for each sample. This method increased the numbers of

early instar larvae collected. Population density was expressed as the number of defoliators per kilogram of fresh sagebrush. A Malaise trap was erected in early July near the study plot. The number and sex ratio of moths collected were recorded each week.

Figure 1 summarizes the seasonal variation in defoliator population during 1973-75 (Hsiao and Temte 1976). The defoliator has one generation a year and overwinters in the egg stage as a fully developed embryo (Kirkland 1972). Eggs are normally laid under the bark of sagebrush plants and start to hatch in late March or early April; hatching continues to mid-May. Larvae feed on sagebrush foliage for about 55 days while passing through five instars. The larvae first attack the young leaves near the terminal tips of the plants. As they grow, larvae construct web tubes that extend from the main webbing site to the terminal end of several branches. They feed on the surrounding leaves at night and remain within the protective webbing during the day. Pupation occurs in late June and adult emergence starts in early July. First instar larvae collected from the field and reared at constant temperatures of 86, 80, and 70 °F (30.0, 26.5, and 21.0 °C) became adults after 27-34, 30-35, and 40-50 days, respectively (Hsiao and Kirkland 1973).

Adult activity lasted for 2-2.5 months. Adults were found in the Malaise trap at the begining of July. Numbers peaked in the last week of July and continued at the peak level for about 3 weeks, an indication that the adults live at least this long. Five times as many males as

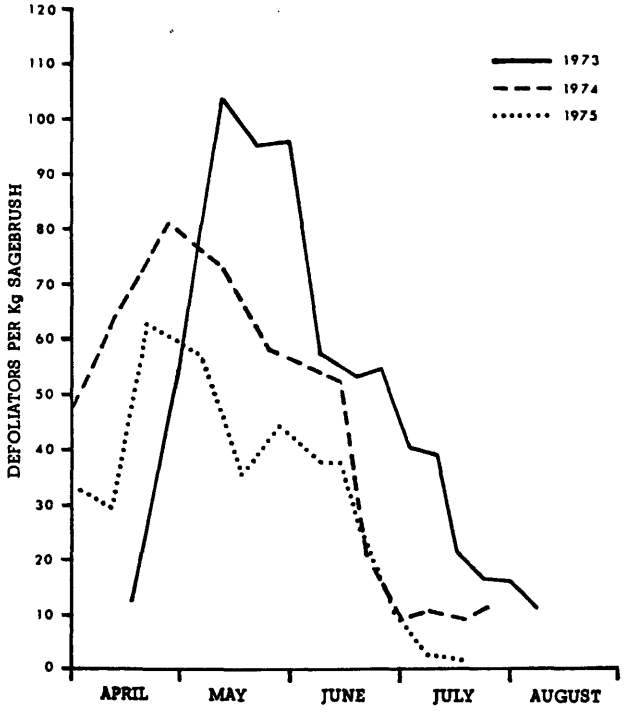


Figure 1.--Comparison of defoliator population densities at Curlew Valley site during 1973, 1974, and 1975.

females were trapped during early emergence (Hsiao and Kirkland 1973). The ratio gradually changed to a sex ratio of 1:1. Adults placed on caged plants became active 2 to 3 hours following dusk; maximum activity occurred between 11 p.m. and 5 a.m. They remained hidden through the diurnal period. Data from sticky traps set at various heights revealed that most moths were captured at a height between 12 and 31.5 inches (30 and 80 cm) above the ground, an indication that they tended to move near the periphery of the sagebrush crown (Hsiao and Kirkland 1973). Females captured in the Malaise trap were gravid. Examination of oocytes in the ovarioles indicated that fecundity was at least 120 eggs per female (Kirkland 1972). Egg laying in the field was noticed in late July and continued into August. Berlese funnel samplings of late-season plants indicated that relatively few larvae hatched between late August and mid-October (Hsiao and Temte 1975). The majority of eggs entered an embryonic diapause.

NATURAL ENEMIES

During the study period, 10 species of parasitoids, one predator, and a Nosema disease were recorded on the sagebrush defoliator (table 1). Four species (Orgilus ferus, Phaeogenes sp., Spilochalcis leptis, and Apanteles cacoeciae) comprised 75 percent or more of the total number of parasitoids in the field population. Fillmore (1965) recovered 18 species of Hymenoptera and one species of Diptera that were parasitoids of the defoliator in southern Idaho. Of Fillmore's parasitoids, seven species are listed in table 1. The other 13 species he found were considered to be rare. Three species (Microdontomerus sp., Meteorus sp., and Microtypus sp.) (listed in table 1) are previously unrecorded parasitoids of the defoliator.

Larvae of the clerid beetle (Phyllobaenus sp.) occasionally fed on the larvae and pupae of the defoliator. The adult stage was never found to attack the defoliator. The microsporidian disease, found in larval and pupal stages in the field and in the laboratory, accounted for less than 5 percent of the mortality in the field (Hsiao and Kirkland 1973).

POPULATION TRENDS AND MAJOR MORTALITY FACTORS

Population trends for the entire study period are illustrated by the mean population density (fig. 2) and the accumulated adults caught in the Malaise trap (fig. 3). The defoliator population initially increased from 1971 to 1972, but gradually declined between 1973 and 1975. Preliminary life tables constructed from 1971 and 1972 field and laboratory data indicated that the fifth larval instar was the "crucial trial" period for the defoliator (Hsiao and Kirkland 1973). High mortality was due to natural enemies and food shortage. Parasitism was considerable in 1971 (51.5 percent), but

Table 1.-- Natural enemies of Aroga websteri at Curlew Valley

Species	Stage attacked	Abundance
Parasitoids		
Braconidae		
Apanteles cacoeciae	Larva	Common
Orgilus ferus	Larva	Common
Meteorus sp.	Larva	Rare
Microtypus sp.	Larva	Rare
Chalcididae		
Spilochalcis leptis	Pupa	Common
Encyrtidae		
Copidosoma bakeri	Larva	Occasional
Ichneumonidae		
Temelucha sp.	Larva	Common
Diadegma sp.	Larva	Occasional
Phaeogenes sp.	Pupa	Common
Torymidae		
Microdontomerus sp.	Pupa	Rare
Predators		
Phyllobaenus sp. (Cleridae)	Larva, pupa	Occasional
Diseases		
Nosema sp. (Microsporidia)	Larva, pupa	Common

declined to less than 10 percent after 1972 (fig. 2). Thus, natural enemies have a relatively minor detrimental impact on the defoliator. A severe infestation of the defoliator was observed in 1972 (Hsiao and Kirkland 1973). Many sagebrushes at the study site and adjacent area were completely defoliated by late June, causing food shortages for the defoliator. Consequently, fewer moths were caught in 1972 than in 1973 (fig. 3), even though more defoliators appeared in field samples in 1972 (fig. 2). The decline of defoliator populations in 1974 and 1975 (fig. 1) is attributable to weather (Temte 1977). Population crashes were noted on June 22, 1974 and on July 7, 1975. The mean maximum temperatures for 2-week periods preceding the crashes were 90 °F (32.2 °C) in 1974, and 83.5 °F (28.6 °C) in 1975. High daily temperature and lack of precipitation dehydrated sagebrush foliage and made it unsuitable for defoliators at a critical period of growth. The low food value of foliage was evident in the small size and high mortality of field-collected pupae (Hsiao and Temte 1975). The population crashes caused corresponding reductions in the number of moths caught during 1974 and 1975 (fig. 3). These data indicate the defoliator population at the Curlew Valley site was influenced mainly by abiotic factors.

HOST SPECIFICITY

The defoliator is a rather restricted feeder. Besides Artemisia tridentata, Henry (1961) reported natural infestations on A. tripartita, A. nova, A. arbuscula, A. cana, and A. longiloba in southern Idaho. Gates (1964) observed positive feeding on A. tridentata, A. arbuscula, A. nova, and A. cana in Oregon. Hall (1965) reared the defoliator on A. tridentata, A. arbuscula, and A. cana in California, and erroneously included rabbitbrush (Chrysothamnus nauseosus) and bitterbrush (Purshia tridentata) as hosts. While most investigators agree that big sagebrush and the species listed above are probably the principal hosts, suitability of other Artemisia species as hosts is unknown. Twenty-three Artemisia species and many varieties of these species are found in the

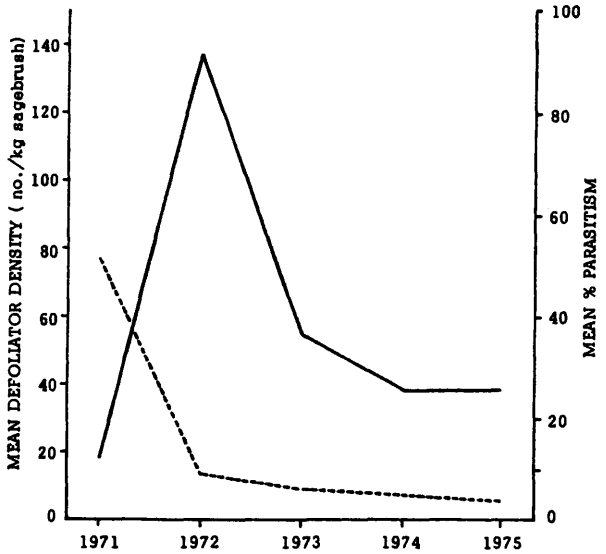


Figure 2.--Five-year population trends of the defoliator (solid line) and its parasitoids (dotted line) at Curlew Valley site.

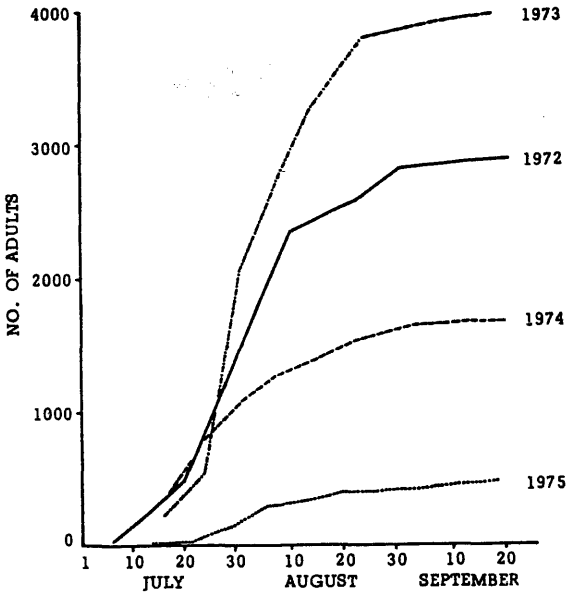


Figure 3.--Cumulative record of defoliator moths captured in a Malaise trap at Curlew Valley site during four seasons.

Intermountain region (Beetle 1960; Holmgren and Reveal 1966; McArthur and others 1979).

Two types of experiments were conducted to determine the host range of the defoliator. Laboratory tests determined the acceptability and suitability of 21 species and varieties of Artemisia and 15 other plant species (Hsiao and Green 1974). Ten field-collected fourth and early fifth instar defoliator larvae were group-reared in plastic cages on individually potted plants or fresh foliage. Foods were changed as needed. There were three to four replicates on each test plant. Percent survival, pupal weight, and rearing duration were criteria of acceptability and suitability. Several Artemisia species were obtained from the U. S. Department of Agriculture, Forest Service, Great Basin Experiment Station in Ephraim, UT. Other plants collected throughout Utah and southern Idaho were established in pots for rearing experiments.

None of the 13 tested Compositae plants outside the genus Artemisia were acceptable to the defoliator: Chrysothamnus viscidiflorus, C. nauseosus, Chaenactis douglasii, Tetradymia canescens, Townsendia scapigera, Senecio canus, Erigeron pumilus, Cirsium undulatum, Tragopogon dubius, Wyethia mulenburgia, Taraxacum officinale, Erigeron sp. (1), Erigeron sp. (2) (Hsiao and Green 1974). Two other plant species, Atriplex confertifolia (Chenopodiaceae) and Purshia tridentata (Rosaceae) were also unacceptable. All of these plants are commonly found in the habitats of Artemisia and can be excluded as potential hosts for the defoliator.

Among Artemisia, no feeding was observed in the following five species: A. abrotanum, A. absinthium, A. dracunculus, A. ludoviciana ssp incompta, and A. ludoviciana ssp ludoviciana. Slight feeding but no growth was found on seven species: A. cana ssp viscidula, A. carruthii, A. filifolia, A. frigida, A. longiloba, A. ludoviciana ssp candicans, and A. rothrockii. Successful rearings were recorded for nine species and varieties (table 2). Pupal weights and adult yields indicated that the six most suitable plants were A. arbuscula, A. bigelovii, A. cana ssp cana, A. tridentata ssp tridentata, A. tridentata ssp wyomingensis, and A. tripartita. The three less suitable plants were A. nova, A. pygmaea, and A. spinescens. With the exception of A. spinescens, all acceptable plants were from the Artemisia subgenus Tridentatae (table 2) (McArthur and others 1981).

Oviposition preferences of the defoliator were tested in three field cages (3.3 by 5 by 6.6 ft; 1 by 1.5 by 2 m) (Hsiao and Green 1974). Each cage contained nine potted plants, one plant from each of eight Artemisia species and a plant from an unrelated Compositae. Newly emerged adults were released in the cages during late July and early August. The potted plants were inspected for defoliator eggs during October. No eggs were found on A. caruthii, A. frigida, A. ludoviciana, and the gum-plant, Grindelia squarrosa. Eggs were recovered from all three caged plants of A. tridentata, from two of three plants of A. spinescens, and from one of three plants of A. arbuscula, A. bigelovii, and A. cana ssp viscidula. With the exception of A. cana ssp viscidula which received one egg, those species subject to oviposition were also accepted by the larvae (table 2). Clearly, oviposition and feeding preferences of the defoliator are correlated with Artemisia species.

Field surveys of the host range of the defoliator were conducted throughout Utah in 1973 (Hsiao and Green 1974) and in southern Idaho in 1974 (Hsiao and Temte 1975). The following six Artemisia plants showed no evidence of defoliator infestation in Utah: A. bigelovii, A. carruthii, A. ludoviciana ssp candicans, A. ludoviciana ssp incompta, A. ludoviciana ssp ludoviciana, and A. pygmaea. However, both A. bigelovii and A. pygmaea were accepted as hosts during laboratory rearing (table 2). Throughout Utah and southern Idaho, A. tridentata and A. tripartita were the most important natural hosts of the defoliator. A. arbuscula was also infested but this species was less abundant and succulent than other species. Defoliator pupae collected from A. arbuscula were consistently smaller than those from favorable hosts (Hsiao and Green 1974).

DEFOLIATOR IMPACTS ON BIG SAGEBRUSH

In 1973, a study was initiated at the Curlew Valley site to assess the long-term effect of the defoliator on sagebrush mortality and

Table 2.--Suitability of Artemisia species for the defoliator
(Fourth and young fifth instar larvae were used in these tests)

Species	No. defoliator	Percent pupated	Mean pupal wt. mg ± S.E.	Percent yield of adult
A. arbuscula[1]	40	57.5	10.8 ± 0.33	30.0
A. bigelovii	40	32.5	8.9 ± 0.33	20.0
A. cana ssp cana	30	30.0	10.2 ± 1.07	16.7
A. nova[1]	30	23.3	7.8 ± 0.75	10.3
A. pygmaea	30	23.3	7.5 ± 0.49	3.3
A. spinescens	30	6.7	7.4 ± 1.90	3.3
A. tridentata ssp tridentata[1]	30	53.3	9.9 ± 0.48	26.7
A. tridentata ssp wyomingensis[1]	30	33.3	8.7 ± 0.84	20.0
A. tripartita[1]	30	23.3	9.6 ± 0.33	16.7

[1] Recorded natural hosts of the defoliator.

productivity. During July, when defoliator feeding ceased, 150 completely defoliated sagebrush plants were tagged at the study site. In September and October these plants were checked to determine size (plant height and diameter) and status of growth (number of live branches per plant, number and size of flower stalks, etc.) The biomass (green and stem weights) of several defoliated plants was determined to assess productivity. A group of healthy sagebrush plants from the study site was evaluated in the same manner to determine the normal level of plant productivity under minimum insect damage. All tagged plants were monitored again in 1974, 1975, and 1976 to determine plant mortality due to defoliation.

A second study conducted at the same site during 1974 and 1975 determined how defoliator infestations affected sagebrush productivity. At the beginning of the field season, about 40 healthy sagebrush plants were treated with an insecticide (Temik in 1974; Dieldrin in 1975) to establish them as defoliator-free controls. In early July of both years, when there was about 50 percent pupation of defoliators, 70 to 100 defoliated plants were tagged and examined to determine levels of defoliator infestation; that is, numbers of feeding and webbing sites and defoliators. The height, crown dimensions, and number of living and dead branches were also recorded for each plant. In October, following the flowering and fall growth periods of the sagebrush, the control plants and the tagged defoliated plants were measured again, cut off at the ground level, and taken to the laboratory where fresh and dry weights of the total plant, foliage, flowers, and woody parts were determined. The number of flower stalks, flower stalk length from basal to terminal flower, and the number of live and dead branches were recorded for each plant. The insecticide-treated control plants indicated normal levels of plant productivity under minimum insect damage.

Table 3 shows how defoliator infestation affected sagebrush productivity. A detailed statistical analysis of these data was presented by Temte (1977). 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 plant, and may reflect the plant's age and reproductive potential. Foliage production also decreased as the number of defoliators increased. This was more apparent in 1975 than in 1974. Because defoliator infestations at the study site were relatively low during both years, the defoliators' overall impact on sagebrush productivity was not as apparent as it would have been at higher infestation levels.

By 1976, long-term effects of the defoliator on sagebrush were noticeable on tagged plants (Hsiao and Temte 1976). Of the 148 sagebrush plants tagged in July 1973, completed records over the four seasons were available on 123 plants. Of these, 82 plants (66.7 percent) survived. Sagebrush mortality was 18.7 percent in 1973 and 13.8 percent in 1974, but was insignificant thereafter as defoliator infestation decreased (figs. 2 and 3). The mean number of live branches per plant decreased by 40 percent in the fall of 1973, 50 percent in 1974, and stabilized at 57 percent in 1975. Only 43 percent of the total branches were alive at the end of the study period, an indication that there were fewer live branches on surviving plants. The number of plants that flowered each year also declined initially and gradually increased in subsequent years. Sagebrush mortality by plant height, presumably reflecting different age groups, is depicted in fig. 4. Mortality was over 50 percent for plants 16-24 inches (41-60 cm) high, about 25 percent for those 32-35 inches (81-90 cm) high, and over 40 percent among plants of 36-55 inches (91-140 cm) high. Thus, small and large plants were more vulnerable to defoliator damage.

Table 3.--Effects of defoliator infestation levels on sagebrush productivity

Level of infestation: No. defoliator per plant	No. plants examined	Mean No. defoliator per kg fresh sagebrush	Mean No. flower stalks per plant	Percent foliage weight	Percent dead branches	Mean plant height	Mean plant weight
						cm	kg
1974							
1-5	29	22.5	15.3	15.6	20.5	51.5	.194
6-10	27	57.5	11.3	14.3	6.5	50.5	.189
11-20	9	84.6	7.1	13.5	13.7	46.1	.251
Control	30	-	15.6	14.7	0.8	62.5	.281
1975							
1-5	35	29.8	14.5	22.2	6.7	49.5	.160
6-10	12	64.6	8.6	18.2	5.0	52.0	.171
11-20	14	82.8	23.1	18.5	7.7	56.3	.249
Control	24	-	63.7	25.6	0	67.3	.479

These data indicate that moderate defoliator infestation decreased sagebrush productivity by reducing the amount of foliage and the number of new flower stalks. Severe defoliator infestation could kill sagebrush branches or entire plants, especially when such an infestation continues for several years.

CONCLUSIONS

Sagebrushes, among the most common and important native plants of the arid Western United States,

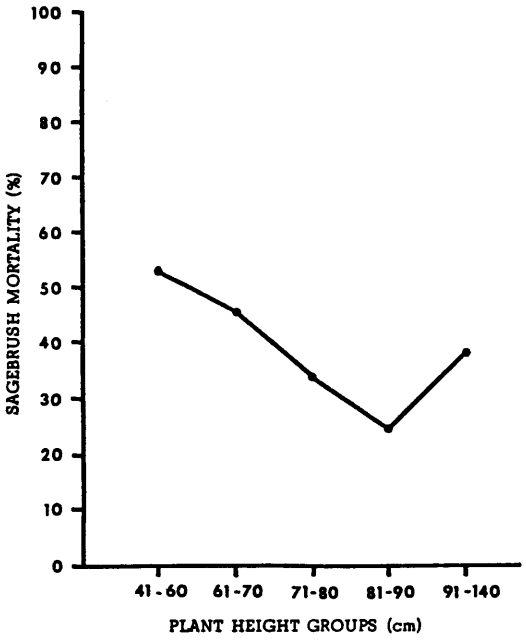


Figure 4.--Size-related mortality in severely defoliated big sagebrushes at Curlew Valley site after a 2-year period.

are found on an estimated 270.3 million acres (109.4 million ha) (Beetle 1960). Approximately 11 percent (6.2 million acres; 2.5 million ha) of Utah is dominated by various species of sagebrush (McArthur and others 1979). Throughout this region, the sagebrush defoliator is considered to be the most important insect pest. The defoliator is a restricted feeder that has evolved to feed on a few Artemisia species of the subgenus Tridentatae, species well-known for possessing a variety of allelochemicals, notably terpenoids and phenolics. Since only 3 of 18 indigenous species of the genus Aroga are known to feed on Artemisia (Busck 1939; Hodges 1974), their adaptation to these food plants is unique. The known host for Aroga rigidae is Artemisia rigida (Clarke 1936) and for A. eldorado is Artemisia vulgaris (Keifer 1936). These two Aroga species are not as common as A. websteri and little is known about their biology. The wide geographic distribution of the sagebrush defoliator in several western states and dramatic increases in infestation levels indicate that the species is well adapted to its environment.

Both abiotic and biotic factors influenced the defoliator population at the Curlew Valley site. The defoliator has high reproductive potential. As a native insect, it also supports a wide range of natural enemies. About 20 species of parasitoids, predators and diseases have been recovered from the defoliator. However, natural enemies are not important in stabilizing the population in most years. Abiotic factors appear to be more 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. These factors caused the population declines

observed in 1974 and 1975. Such density-independent factors have similar effects on the insect's natural enemies, since parasitism had little influence on defoliator numbers during this period. Periodic outbreaks of defoliators reported in several western states are probably due to favorable weather conditions during consecutive years. Monitoring weather conditions may provide a realistic method to predict defoliator population trends.

Several common sagebrushes provide food for the defoliator. Severe defoliator infestation can substantially reduce foliage and kill sagebrush plants. Plant loss due to defoliator infestation is a valid concern in range management. For reasons noted above, it does not appear feasible to manage the defoliator by manipulating its natural enemies. Other than conventional insecticides, the most promising strategy appears to be the selection and breeding of sagebrush varieties or species that are unacceptable to the defoliator. This strategy is feasible because of the high degree of host specificity of the defoliator. Screening for plant resistance to the defoliator may occur in conjunction with current attempts to select sagebrushes superior as animal feed. Failure to consider insect damage in plant breeding programs could result in sagebrushes that are more acceptable to the defoliator.

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RABBITBRUSH (CHRYSOTHAMNUS NAUSEOSUS SSP. CONSIMILIS) MORTALITY ASSOCIATED WITH DEFOLIATION BY A LEAF-FEEDING BEETLE, TRIRHABDA NITIDICOLLIS

Raymond S. Dalen, Reggie A. Fletcher, and Francis A. Winter

ABSTRACT: Defoliation of rabbitbrush (Chrysothamnus nauseosus (Pallas) Britt. ssp. consimilis (Greene) H. & C.) by a leaf-feeding beetle (Trirhabda nitidicollis LeConte (Coleoptera: Chrysomelidae)) on herbicide-treated and untreated plants on 10 paired transects in the Zuni Mountains of New Mexico was monitored from 1978 to 1983. While 2,4-D and picloram treatments were generally ineffective in controlling rabbitbrush, they did not appear to affect leaf beetle defoliation. Plant mortality varied by transect from 7 to 68 percent. Mortality relates well to small plant height and 2 consecutive years of heavy or moderate beetle defoliation. The leaf beetle is partially effective as a natural control for rabbitbrush.

INTRODUCTION

Rabbitbrush (Chrysothamnus nauseosus and C. viscidiflorus) covers 2,822,800 acres (1 142 834 ha) of rangeland in New Mexico in moderate or dense stands (Garrison and McDaniel 1982). Under favorable conditions, C. nauseosus spreads rapidly from light, prolifically produced, wind-disseminated achenes (McArthur and others 1979). Chrysothamnus nauseosus ssp. consimilis is a difficult plant to control and frequently invades the deeper soils adjacent to drainage bottoms at densities that compete with other forage species. In May 1978, a relatively heavy but spotty infestation of larvae of a leaf-feeding beetle (Trirhabda nitidicollis) was observed on rabbitbrush. Massey and Pierce (1960) had reported a relatively heavy infestation of this insect near the survey area in 1957, where large areas of rabbitbrush were killed. They suggested studies were needed to determine the possibility of using the insect as a biological control agent. Andres (1971) suggests there is a potential for the use of native insects in controlling native weeds.

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Raymond S. Dalen is Range Improvement Specialist, U.S. Department of Agriculture, Forest Service, Albuquerque, NM; Reggie A. Fletcher is Regional Botanist, U.S. Department of Agriculture, Forest Service, Albuquerque, NM; Francis A. Winter is Wildlife Biologist, U.S. Department of Agriculture, Forest Service, Cibola National Forest, Albuquerque, NM.

This paper reports the results of observation and demonstration plots established to determine the growth pattern and phenology of rabbitbrush and to monitor the effect of larval leaf beetle defoliation of rabbitbrush on herbicide-treated and untreated plants in west-central New Mexico.

On May 17, 1978, from the leaf beetle larval activity observed, we did not know if foliar-applied herbicides would be effective on insect-defoliated rabbitbrush. We also did not know the effects of combining herbicides with leaf beetle activity or how leaf beetle activity would be affected by herbicides.

LEAF-FEEDING BEETLE PHYSIOLOGY

The leaf beetle occurs from western Montana to New Mexico, westward to southern California (Hogue 1970). The adult beetle is 0.5 to 0.75 inches (13 to 19 mm) long with a yellowish-green stripe in the center and on each side of the elytra. The pronotum is yellow, with three blue-green spots, one located in the center and one on each side (Massey and Pierce 1960).

Hogue (1970) described the leaf beetle life cycle. Emergence from the egg coincides with the development of new leaf growth on the host plant in the spring. The small (1 to 2 mm) shiny, black first instar larvae crawl up the main stem and lateral branches of the host plant to the terminal foliage where feeding begins. Second larval instars are sedentary and feed primarily at the base of new leaf fascicles. By the fourth instar, the large (7 to 12 mm) larvae are very active. Prepupal larvae burrow into the soil at the base of the host plant to a depth of 0.25 to 0.5 inch (6 to 13 mm), where a pupal chamber is formed. The pupal period is approximately 10 days. After emergence, adults feed on the host plants for 6 to 8 days before mating. Fifteen to 20 days after mating, the female deposits her eggs in the soil at the base of the host plant, where they overwinter.

Hogue (1970) did not measure the effects of larvae and adults on host plants, but stated that beetle populations may increase rapidly and defoliate host plants resulting in reduced vigor or death. During the initial stages of an infestation, distribution of the leaf beetle in the rabbitbrush community is uneven. Adults and/or larvae may be present in large numbers on some plants but absent from other plants. At the peak of an infestation, nearly all plants are heavily infested. Massey

and Pierce (1960) observed larval feeding only on rubber rabbitbrush (C. nauseosus), but adults were found feeding on rubber rabbitbrush and big sagebrush (Artemisia tridentata). Utilization by the adults was not heavy enough to cause damage. Hogue (1970) reported host plants of the leaf beetle as two species of rabbitbrush, C. nauseosus and C. viscidiflorus, and Acamptopappus sphaerocephalus.

MATERIAL AND METHODS

The monitoring of leaf beetle defoliation on rabbitbrush was conducted in the Zuni-Bonita Canyon area of the Zuni Mountains located in the Cibola National Forest. The site is about 10 miles (16 km) southwest of Grants, Cibola County, NM. Average elevation is 7,500 ft (2 286 m). Average annual precipitation is 16 inches (40.6 cm), 40 percent of which occurs during the summer period of May-September. Rabbitbrush is the primary overstory in the open canyon bottoms. Elsewhere, ponderosa pine (Pinus ponderosa) dominates all but the most exposed slopes where pinyon pine (Pinus edulis) dominates. The soils are deep, well drained, and high in inherent fertility. They are Typic Argiborolls and Cumulic Haploborolls. The most common grass species are blue grama (Bouteloua gracilis) and western wheatgrass (Agropyron smithii). Livestock grazed the study area from 1978 to 1981, but were not present in 1982 and 1983.

The monitored rabbitbrush plants were located on 10 paired belt transects 4.36 by 100 ft (1.33 by 30.5 m) established on July 10-11, 1978, in rabbitbrush-invaded canyon bottoms. Eight transects were in Zuni Canyon in an area of about 320 acres (129 ha). Two transects were about 2.5 miles (4 km) south in Bonita Canyon. The transects were located in areas subjectively assessed as having light, moderate, and heavy leaf beetle defoliation based on general observations during the May 1978 survey. Light defoliation sites were represented by transects 5, 6, 7, and 8; moderate defoliation sites included transects 3 and 4; moderate to heavy, transects 1 and 2; and heavy defoliation by transects 9 and 10. The classification of light, moderate, and heavy defoliation based on transect means is 0-34, 35-74, and 75-100 percent.

The location of each rabbitbrush plant rooted within the transect was recorded along a center-line reference tape. The transects were measured each July from 1978 to 1983. Each rabbitbrush plant was measured as follows: (1) live crown height (initially measured to the nearest foot (0.3 m), but from 1980 on, small plants 0.5 feet (0.15 m) or less were also recorded); (2) live crown, visually estimated to the nearest 10 percent; (3) live crown defoliated, visually estimated to the nearest 10 percent; and (4) presence or absence of adult beetles.

On July 19, 1978, two 1-acre (0.45-ha) plots in Zuni Canyon that included two transects in lightly defoliated areas were treated with herbicides using a ground sprayer with a 20-ft (6.1-m) spray boom. A mixture of triisopropanoline salts at the rate of 1 lb/acre (1.12 kg/ha) acid equivalent (ae) 2,4-D and 0.25 lb/acre (0.28 kg/ha) ae picloram was applied to the plot that included transect 5, and 2 lb/acre (2.24 kg/ha) ae 2,4-D and 0.5 lb/acre (0.56 kg/ha) ae picloram to the plot that included transect 6, both in 19.5 gal/acre (182 L/ha) of water.

On July 24, 1978, a 5-acre (2.27-ha) plot in Zuni Canyon that included transect 1 was treated with 3 lb/acre (3.36 kg/ha) ae of 2,4-D ester (propylene glycol butyl ether) in 19.25 gal/acre (180 L/ha) of water with the same ground sprayer.

On April 13, 1979, just before bud break, 3 lb/acre (3.36 kg/ha) ae of 2,4-D ester in a diesel oil carrier at 12 gal/acre (112 L/ha) was applied to two sets of 20- by 33-ft (6.1- by 10.1-m) plots each replicated three times. The herbicide was applied using a 5-ft (1.5-m) hand-held spray boom. One set of plots was located near transects 5, 6, 7, and 8 representing light leaf beetle infestation and light defoliation. A second set of plots was located near transects 9 and 10 representing heavy leaf beetle infestation and heavy defoliation. The treated plots, and paired number of untreated plots, were sampled on August 18, 1979, July 8, 1980, July 31, 1981, and August 5, 1983. The same measurements as gathered on the 10 transects were recorded.

Four transects were sampled on October 3, 1979, and six transects on November 5, 1980, to determine the amount of flower development. Flower development on each plant was visually estimated as none, light, moderate, and heavy. Heavy meant that flowers were present over the total plant crown.

Rabbitbrush mortality on the 10 transects is the net percentage accumulated plant loss based on the number of live plants measured in July 1978. Plants recorded as dead occasionally resprouted the following year.

Statistical analysis of the data is limited since the 10 belt transects represent observation plots and were not replicated. The transect mean percentage defoliation is the mean of all the live plants. The standard deviation and variance was calculated and the "t" test was used to determine the significance of the difference in mean percentage defoliation each year on the same transect.

A stepwise logistic regression was used to predict rabbitbrush survival or mortality (Dixson and others 1981). Independent variables were mean percentage defoliation for the two highest consecutive years and mean live plant height the same two years during the period 1978 to 1982. Since two consecutive years of individual plant data were used, survival or mortality was for the period 1980 to 1983. Plants that died in 1979 and new plants were not included. The logistic model is fitted directly to actual values measured for 369 individual plants from the untreated transects.

RESULTS AND DISCUSSION

Transects

The life cycle of the leaf beetle coincides with the growth pattern of rabbitbrush (fig. 1). The heaviest defoliation occurs from larval feeding on rabbitbrush during its slow growth period. After the emergence of adults, the plant may resprout and recover except when the defoliation is heavy enough to result in reduced vigor; this restricts both resprouting and flower development. The timing shown in figure 1 varies slightly with annual climatic conditions.

The larvae fed on all height classes of plants. For example, in 1978, the mean defoliation of plants in the 1-, 2-, and 3-ft height classes was 60, 63, and 57 percent, respectively. Defoliation of plants in the 4- and 5-ft height classes was 46 and 35 percent, but the number of plants sampled was small. This agrees with Massey and Pierce (1960) who reported larvae fed on plants of all ages.

Some leaf beetle defoliation occurred on each transect every year, except on transect 4 in 1982. The overall level of leaf beetle activity based on mean percent defoliation peaked in 1979 on 6 of the 10 transects (table 1). Activity on transect 1 did not peak until 1983, while that on transects 3, 9, and 10 peaked in 1978. The mean percentage defoliation combining all transects was highest in 1979 at 74 percent, but was at its lowest point at 13 percent the next year (table 1). Leaf beetle activity was not uniform throughout the study area. Small areas of heavy defoliation were interspersed with areas of light activity. The mean percentage defoliation on four of the 10 transects was significantly different during each of the 5 years (table 1). Moderate defoliation occurred on at least one transect 5 of the 6 years. Heavy defoliation occurred 3 of the 6 years on at least two transects. No transect was heavily defoliated 2 consecutive years, but four transects had 2 consecutive years of heavy and moderate defoliation. Three other transects were moderately defoliated for 2 consecutive years.

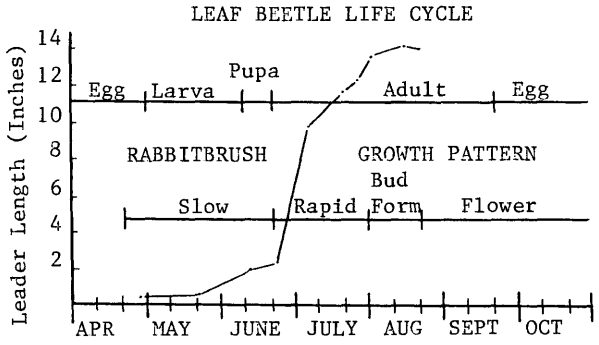


Figure 1.--Life cycle of the leaf beetle and growth pattern and phenology of rabbitbrush. Leader length (inches) 1979.

Table 1.--Mean percentage defoliation of rabbitbrush plants by the leaf beetle, July sample each year, by transect and treatment

Transect	Treatment	1978	1979	1980	1981	1982	1983
		Percent[1]					
1	2,4-D[2]	62	52	34	62*	60	83
2	None	44	96*	8*	27*	14*	59*
3	None	92	8*	47*	71*	2*	6
4	None	28	95*	4*	53*	0*	3*
5	2,4-D+picloram[3]	32	97*	4*	46*	75*	28*
6	2,4-D+picloram[4]	22	92*	23*	39	52	56
7	None	29	56*	21*	22	30	47*
8	None	26	78*	15*	40*	32	47
9	None	82	65*	5*	16*	34*	39
10	None	91	73*	2*	5*	58*	81*
	No treatment mean	63	73	12	29	28	45
	Treatment mean	41	82	18	50	66	50
	Mean	60	74	13	33	35	46

[1]Means with an asterisk are different from the preceding year at the 5 percent level using the t test.

[2]Three lb/acre (3.36 kg/ha) ae 2,4-D PGBE ester, July 24, 1978.

[3]One lb/acre (1.12 kg/ha) 2,4-D ae + 0.25 lb/acre (0.28 kg/ha) picloram ae both triisopropanoline salt.

[4]Two lb/acre (2.24 kg/ha) 2,4-D ae + 0.5 lb/acre (0.56 kg/ha) picloram ae, both triisopropanoline salt.

Untreated transects.--The shifting beetle activity is also evident based on individual plant data. Only two of 417 plants located on the untreated transects were heavily defoliated 3 consecutive years during the study period. A total of 100 plants (24 percent) were heavily defoliated, with 65 of these completely defoliated 2 consecutive years. A total of 247 plants (59 percent) were heavily defoliated at least 1 year.

Sixty-three of the 65 rabbitbrush plants on the untreated transects were completely defoliated in both 1978 and 1979. This was followed by 2 years of light defoliation, allowing the remaining live plants to recover. Of these 63 plants, mortality peaked at 52 percent in 1981, remaining relatively constant through 1983 (fig. 2).

Adult leaf beetle activity appears to be more consistent than larval activity. The frequency of plants with adult leaf beetles varied from 23 to 50 percent during the study period and was about average (37 percent) in 1980, the year with the lowest mean percent defoliation.

Rabbitbrush mortality over the 5-year period by transect is shown in table 2. Mortality of plants on the untreated transects was 51 percent by 1981 and increased slightly to 54 percent by 1983. Natural senescence or loss due to other factors could not be determined or isolated, but the mortality in 1981 is primarily attributed to leaf beetle defoliation in 1978 and 1979. The transects with the highest plant mortality generally had the highest mean percent defoliation during 2 consecutive years and the lowest mean live plant height the same 2 years. One year of heavy defoliation is apparently less effective. The heavy defoliation on transect 4 in 1979, between 2 years of light defoliation, resulted in 29 percent plant loss in 1981 (tables 1 and 2). On transect 10, 2 consecutive years with heavy and moderate defoliation in 1978 and 1979 resulted in 62 percent plant loss in 1981 (tables 1 and 2). The mean live plant height for the 1978-79 period was 1.3 ft (0.4 m) in both transects 4 and 10.

The stepwise logistic regression (Dixson and others 1981) suggests a relationship of rabbitbrush mortality to defoliation and plant height (fig. 3). The percent probability of mortality increases as mean percent defoliation increases over 2 consecutive years and as live plant height decreased the same 2 years. Individual plant data, when used to predict rabbitbrush survival or mortality, are predictable only 60 percent of the time. Also, the regression predicts some mortality for all plant height

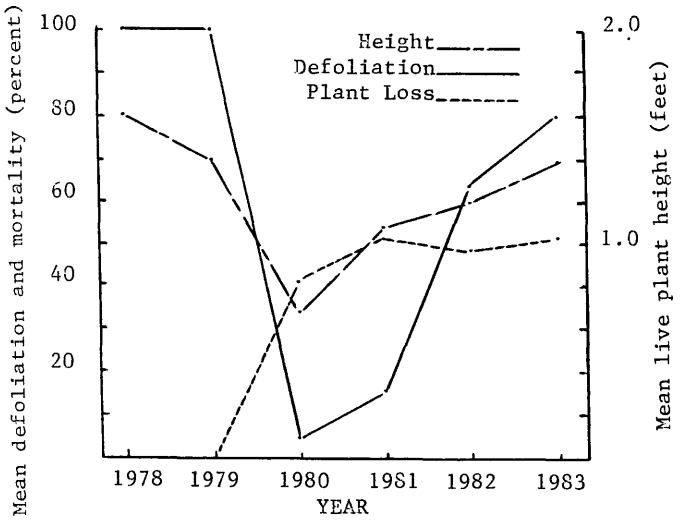


Figure 2.--Yearly mean percentage defoliation, percentage plant mortality, and mean live plant height of 63 rabbitbrush plants on the untreated transects completely defoliated by the leaf beetle in both 1978 and 1979.

Table 2.--Percentage plant mortality 1978 to 1983, using number (N) of live plants 1978 as baseline, rabbitbrush, July samples

Transect	Live Plants, 1978	Year 1978	1979	1980	1981	1982	1983
	N	Percent[2]					
[1]1	29	0	21	31	38	38	45
2	119	0	24	59	67	64	66
3	32	0	0	3	19	31	31
4	35	0	9	9	29	29	34
[1]5	28	0	4	0	0	0	7
[1]6	19	0	5	21	47	47	47
7	23	0	0	0	17	22	13
8	26	0	8	15	19	19	27
9	79	0	14	33	54	51	56
10	103	0	25	52	62	60	68
Untreated	417	0	17	38	51	50	54
Treated	76	0	11	17	26	26	32

[1]Herbicide treated transects, see table 1.

[2]Sixty new plants that came in on the untreated transects and one new plant on the treated transects are not included.

classes with no defoliation, indicating there are additional variables, such as age and plant competition, which were not measured.

Moderate and heavy defoliation appear to reduce plant vigor and flower development. For example, on transect 4 in July 1979, the mean defoliation was 95 percent; only 3 percent of the plants developed flowers that year. In 1980, mean defoliation decreased to 4 percent and 25 percent of the plants developed flowers. On transect 10, which was heavily and moderately defoliated in 1978 and 1979, only 1 percent of the plants developed flowers in 1979. Defoliation was light in 1980, but only 8 percent developed flowers indicating the plants apparently had not recovered. On transect 2, which received moderate, heavy, and light defoliation in 1978, 1979, and 1980, respectively, 47 percent of the plants developed flowers in 1980. Flower development also appeared to be greater with increased mean plant height.

Treated transects.--The general trend in mean percentage defoliation on the treated transects was similar to that on untreated transects (table 1). The shifting beetle activity was also similar. Only three plants were heavily defoliated 3 consecutive years during the study period. A total of 17 plants (22 percent) were heavily defoliated with seven completely

defoliated for 2 consecutive years. A total of 47 plants (62 percent) were heavily defoliated at least 1 year.

Herbicide treatments during July 1978 had no apparent effect on leaf beetle defoliation activity in 1979. Mean defoliation on transect 1 decreased from 62 to 52 percent, but the difference in the means is not significant. On transects 5 and 6, defoliation increased from light to heavy (table 1).

The effectiveness of herbicide treatment alone in controlling rabbitbrush cannot be determined directly. By July 1981, no mortality was recorded on transect 5, but the higher rate of 2,4-D and picloram applied to transect 6 resulted in 47 percent mortality (table 2). The logistic regression equation (fig. 3) indicates that expected plant mortality on transect 6 without herbicide treatment would have been 28 percent. This suggests the herbicide treatment on this transect resulted in more plant mortality than predicted from defoliation alone.

The 2,4-D treatment on transect 1 was not effective in killing rabbitbrush. The 45 percent plant mortality recorded in July 1983 (table 2) is similar to the 45 percent predicted plant loss with defoliation alone using the logistic regression (fig. 3).

The moderate defoliation of plants on transect 1 and light defoliation in 1978 on transects 5 and 6 may have affected herbicide results.

The frequency of plants with adult leaf beetles varied from 55 to 83 percent during the study period and was about average (65 percent) in 1980, the year with the lowest mean percent defoliation.

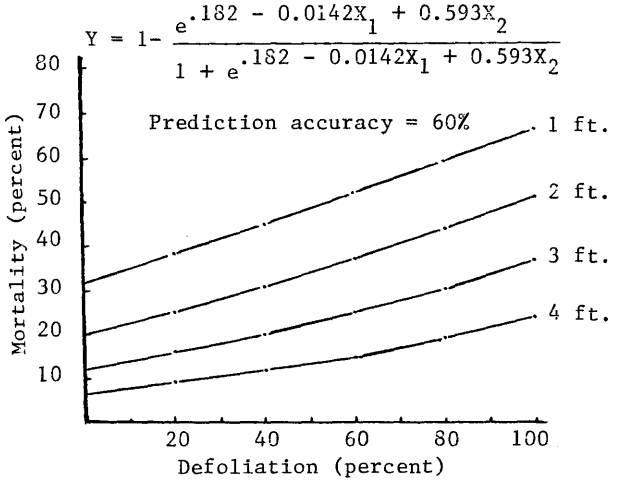


Figure 3.--Probability of percentage mortality (Y) of rabbitbrush 1980-83 from mean percentage defoliation (X_1) over the 2 highest consecutive years and mean live plant height in feet (X_2) the same 2 years during the period 1978-82. Based on 369 individual plants from the untreated transects using stepwise logistic regression.

Table 3.--Mean percentage defoliation by the leaf beetle and percent mortality of rabbitbrush following dormant spray treatment with an ester of 2,4-D in diesel oil, April 13, 1979, on light and heavy defoliation classes at two sites

Defoliation class and treatment		Date Sampled			
		8/17/79	7/08/80	7/31/81	8/05/83
		---------Percent defoliation[1]---			
Light					
Treated		85	15*	14	13
Control		67	31*	35	6*
Heavy					
Treated		100	0*	24*	83*
Control		100	7*	32*	68*
	N[2]	------Percent mortality[2]-----			
Light					
Treated	44	2	9	5	2
Control	32	0	3	6	16
Heavy					
Treated	47	26	66	81	79
Control	46	15	50	67	72

[1]Defoliation means with an asterisk are different from the preceding year at the 5 percent level using the t test.

[2]Plant mortality is based on the number (N) of plants measured 8/17/79 and does not include three new plants which came in.

Dormant Spray Plots

The dormant herbicide treatment did not appear to be effective in killing rabbitbrush at either the light- or heavy-defoliation sites. The percentage plant mortality in 1983 was much higher on the heavy-defoliation site compared to the light-defoliation site, but the treated and control plots at both sites had similar mortality (table 3). The treatment did not seem to inhibit leaf beetle defoliation.

The treated and control plots at the light defoliation site were heavy and moderately defoliated in 1979. This was not expected but was consistent with the heavier defoliation measured on transects 5, 6, 7, and 8 (tables 1 and 3). The heavy-defoliation site was heavily defoliated in 1979, and the trend in 1980, 1981, and 1983, was consistent with the defoliation measured on transects 9 and 10 (tables 1 and 3).

CONCLUSIONS

Results from this preliminary study where defoliation of rabbitbrush was monitored on 10 transects and the dormant spray plots suggest the leaf beetle is at least moderately effective as a natural control of rabbitbrush.

In this study, herbicide treatments did not increase rabbitbrush mortality when coupled with leaf beetle defoliation. Transect 6, where the higher rate of 2,4-D and picloram was applied, may be an exception. However, herbicide treatments did not appear to inhibit leaf beetle defoliation.

Even a moderate reduction of rabbitbrush in dense stands or stabilization of density in light or moderate stands is beneficial. Total elimination of rabbitbrush is not needed. In habitats with scattered plants, this species has little effect on herbaceous species and on some sites it does not suppress grass growth (McArthur and others 1979).

The effects of grass competition on rabbitbrush mortality and reduced seedling establishment were not measured, but observations in 1983 and July 1984 suggest that western wheatgrass is more competitive than blue grama. Further studies should assess the effectiveness of grass competition in conjunction with leaf beetle defoliation.

Research is needed to determine how leaf beetle populations can be modified, introduced, or enhanced, and information is needed on population dynamics, parasitism, and predation. Additional work is also needed on the interaction of leaf beetles and more effective herbicides in reducing rabbitbrush stands.

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SPECIFICITY OF GALLS ON CHRYSOTHAMNUS NAUSEOSUS SUBSPECIES

E. Durant McArthur

ABSTRACT: Several galls of distinctive morphology occur on rubber rabbitbrush (Chrysothamnus nauseosus). "Cotton" and "callus" galls are induced by tephritid flies (Diptera: Tephritidae) of the genus Aciurina. "Mace" and "flower" galls are induced by other insect species. Evidence from several sites in Utah and Arizona over a 10-year period indicates that tephritid taxa ("sibling species") partition the Chrysothamnus resource differently in different areas. Different tephritid taxa cause different gall forms; tephritid populations fluctuate over time, and there is a relationship between gall forms and rubber rabbitbrush taxonomy. Callus galls are found only on the white-stemmed C. nauseosus ssp. albicaulis and ssp. hololeucus at my study sites. Cotton galls are commonly found on the green-stemmed subspecies C. nauseosus ssp. consimilis, turbinatus, and graveolens. Flower and mace galls show less plant and host specificity. Sibling species formation of Aciurina spp. may be facilitated by changes in larval survival and host recognition genes.

INTRODUCTION

In an earlier paper, I and my colleagues made a case for gall form specificity on rubber rabbitbrush (Chrysothamnus nauseosus) subspecies (McArthur and others 1979b). In that paper we demonstrated that specificity of "cotton" and "callus" stem galls occurs at many locations in the central portion of the range of C. nauseosus. However, we acknowledged that in some locations the specificity was lacking. Wangberg (1976, 1978, 1980, 1981) also reported on varying degrees of gall form specificity in Chrysothamnus depending upon gall form and plant distribution. Wangberg's analyses were not confined to the cotton and callus galls, but covered a wide range of gall forms induced by three fruit fly genera (Tephritidae) on several Chrysothamnus species. Wangberg (1976, 1981) and McArthur and others (1979b) suggested that the flies (Aciurina spp.) that induce formation of cotton and callus galls show specificity in areas of fly sympatry and C. nauseosus ssp. sympatry and thus reduce interspecific competition by partitioning a resource.

In this paper, I report additional data on the specificity of gall forms now covering a 10-year period of observation. These data then are used in a plant/insect coevolutionary discussion.

SITES, MATERIAL, AND METHODS

Sites

I made observations of galls on C. nauseosus over a wide portion of the Intermountain area (Sierra Nevada to Rocky Mountains, 36° to 40° N. latitude) from 1975 to 1984. Many of these observations were incidental to other plant and data collection missions. However, I collected quantitative data on gall frequency at several Utah and Arizona sites during the period of study (Arizona: Mohave County, Moccasin. Utah: Iron County near Paragonah; Juab County near Nephi; Sevier County, Big Rock Candy Mountain; Sanpete County, Ephraim Canyon, near Fountain Green; Utah County near Goshen, Provo; Washington County, Gould Wash, near St. George).

Materials

Chrysothamnus nauseosus subspecies and other Chrysothamnus taxa were determined following the keys of Anderson (1973) and McArthur and others (1979a). Chrysothamnus nauseosus subspecific identification at some locations in the earlier report (McArthur and others 1979b) was corrected. The green subspecies at the Goshen Dam Site is ssp. turbinatus. The white subspecies at Paragonah, Fountain Green, and Gould Wash is ssp. hololeucus. Subspecies hololeucus and albicaulis are very similar, differing only in cryptic floral characteristics.

I observed many gall forms as described by Wangberg (1978, 1980, 1981) and Larew and Capizzi (1983). This paper emphasizes callus and cotton galls described and illustrated in McArthur and others (1979a, 1979b).

> Callus gall: more or less glabrous, round to ovoid, 0.3-1.2 cm in diameter, and persistent up to 2 years.

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E. Durant McArthur is supervisory research geneticist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT

Cotton gall: covered with a thick white tomentum, round to ovoid, 0.7-1.4 cm in diameter, and generally not as persistent as the callus gall, although some persist for 2 years; the tomentum not as persistent as the gall body.

Cotton and callus galls are emphasized because they are locally and, I believe, geographically more widespread and abundant than the other galls. In addition, they are visually striking and prominent. Two other galls are also treated in a limited way. These are the "mace" gall of McArthur and others (1979b) and a gall that resembles a flower head gone to seed that I have designated the "flower" gall.

Mace gall: Usually glabrous, round to ovoid, 0.5-1.2 cm in diameter, and covered with small bracts. Persistence past the first year is unknown (see McArthur and others 1979b; Larew and Capizzi 1983).

Flower gall: Round to ovoid, 0.7-1.5 cm in diameter, subtended by several (4-8) more or less glabrous bracts (to 3.0 cm long), but "flower head" portion covered with cottony thick white tomentum. Persistence past the first year is unknown (see Larew and Capizzi 1983).

Emergent flies were collected from sample galls that had been brought into the laboratory and isolated in glass jars covered with cheesecloth. Flies were compared to the descriptions listed in Foote and Blanc (1963). J. K. Wangberg examined some of our fly specimens.

Methods

Gall frequencies were assessed in two ways. In one method, gall frequencies were scored in the manner that we used earlier (McArthur and others 1979b). Galls were counted on terminal 6 inches (15 cm) of a randomly selected branch of each mature shrub (>30 cm or >12 inches tall) on more or less straight line transects through Chrysothamnus populations. In a few cases, when gall frequencies were low, galls from the whole plant were counted. Fifty or more plants for each taxa were scored at each location as the plants occurred on the transects. The second way was to map out populations by scoring all plants for number and type of galls present. This technique was used at the Paragonah site where a ca. 50 by 300-ft (15-m by 275-m) transect was used to sample the populations and at Gould Wash where all plants were sampled along three transects totaling 3,400 ft (1 035 m) in length.

A paired t-test was used to test the significance of gall form frequency differences where two gall types occurred on the same rabbitbrush taxon (Woolf 1968).

RESULTS AND DISCUSSION

Gall Form Specificity

Plant galls may be restricted to a greater or lesser extent to various host plants (Mani 1964; Coulson and Witter 1984). An insect vector often produces a characteristic gall on a certain part of a specific plant. A problem with the specificity of gall forms on C. nauseosus is that species' proliferation of subspecies--some of which are similar and show some intergradation (Hanks and others 1975; Anderson 1984). We raised another possible point of confusion in our earlier paper stating that "another possible explanation for gall-form specificity is that different gall forms are not a response to different fly species, but rather a response to the host plant" (McArthur and others 1979b).

In the earlier paper (McArthur and others 1979b), we presented data from six C. nauseosus populations consisting of uniform subspecies bearing exclusively only cotton or callus galls. In those pure stands only cotton galls were found on ssp. consimilis and ssp. graveolens and only callus galls on ssp. albicaulis. A few other gall forms (e.g., mace galls) were also present. Results from the present study (tables 1 and 2, figs. 1 and 2, and observations) lead me to strengthen some points made in our earlier paper (McArthur and others 1979b) and draw some conclusions.

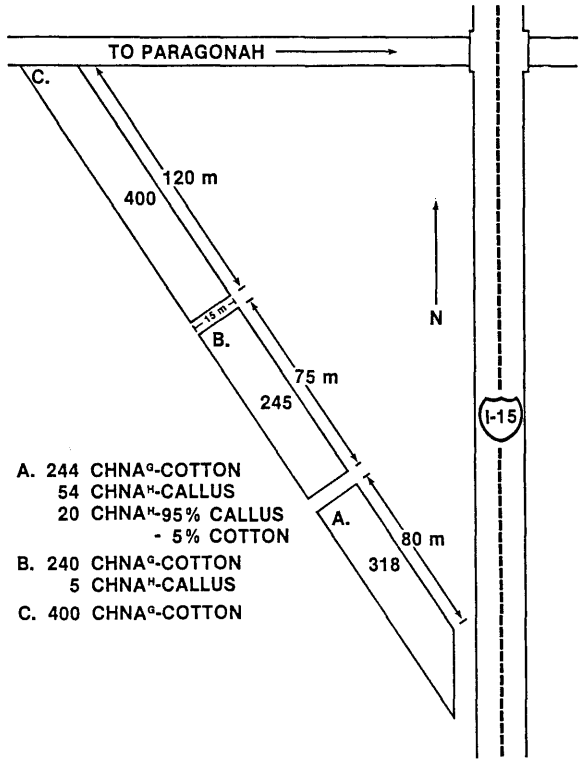


Figure 1.--Map of linear transect through Chrysothamnus nauseosus populations showing ssp. hololeucus (CHNA^{h}) and ssp. graveolens (CHNA^{g}), and gall form distributions near Paragonah, UT; 1980.

Table 1.--Gall frequencies in Chrysothamnus populations, 1984

Collection, location and number, and taxon[2]	Gall type and frequency[1]		
	Callus	Cotton	Mace
Goshen Dam, Utah Co., UT			
$Chna^h$, 1407[3]	0.34 ± 0.13 (0-5)	0	0
$Chna^t$, 1408	0	8.92 ± 0.74 (0-34)	0
Gould Wash, Washington Co., UT			
$Chna^h$, 1526	8.92 ± 0.74 (0-28)	0	Rare[4]
$Chna^g$, 1527	0	3.00 ± 0.32 (0-8)	Rare
Moccasin, Mohave Co., AZ			
$Chna^h$, 1410	0	2.66 ± 0.34 (0-6)	Rare
$Chna^t$, 1409	0	10.42 ± 0.84 (0-24)[5]	0.38 ± 0.15 (0-9)
$Chvi^v$, 1411	0	0	0.62 ± 0.21 (0-2)

[1]See Sites, Materials, and Methods section; values are means ± standard error of the mean and in parentheses extreme range values.
[2]Abbreviations for Chrysothamnus taxa: $Chna^c$ = C. nauseosus ssp. consimilis, $Chna^g$ = C. nauseosus ssp. graveolens, $Chna^h$ = C. nauseosus ssp. hololeucus, $Chna^t$ = C. nauseosus ssp. turbinatus, $Chvi^v$ = C. viscidiflorus ssp. viscidiflorus.
[3]Author's collection number.
[4]Observed in population, but not necessarily on samples.
[5]Cotton and mace frequencies significantly different ($P < 0.01$).

Table 2.--Gall frequencies at the Chrysothamnus nauseosus ssp. consimilis and ssp. hololeucus cline site; Parowan, UT; 1984[1]

Chrysothamnus population structure and collection number	Gall type and frequency[2]			
	Callus	Cotton	Mace	Flower
Uniform $Chna^h$, 1400[3]	4.80 ± 0.58 (0-24)	0	Rare (0-1)	Rare (0-4)
Mixed $Chna^h$, 1401	11.46 ± 1.00[4] (1-38)	0.08 ± 0.03 (0-1)	0.05 ± 0.05 (0-3)	0
$Chna^g$, 1402	0	7.18 ± 0.43[5] (1-16)	0.26 ± 0.10 (0-3)	Rare (0-1)
Uniform $Chna^g$, 1403	0	9.68 ± 0.56[5] (1-19)	0.18 ± 0.12 (0-6)	0

[1]See figure 1 and Sites and Methods Section.
[2]See Sites, Materials, and Methods section. Values are means ± standard error of the mean; numbers in parentheses are range values. Rare infers present in population, but only encountered on one or two samples.
[3]Abbreviations for Chrysothamnus nauseosus ssp.: $Chna^h$ = ssp. hololeucus, $Chna^g$ = ssp. graveolens.
[4]Callus gall frequency significantly different than cotton and mace gall frequencies ($P < 0.01$).
[5]Cotton gall frequency significantly different than mace gall frequency ($P < 0.01$).

First, in pure stands of subspecies within areas of general subspecies sympatry and high gall-former populations, the gall forms maintain a tight correlation to the C. nauseosus subspecies. In much of Utah the cotton gall is found exclusively on the green-stemmed subspecies consimilis, graveolens, and turbinatus and the callus gall exclusively on the white-stemmed subspecies albicaulis and hololeucus. In other areas, where one or the other gall form is absent, a gall will sometimes appear on the nontypical host (McArthur and others 1979b; Wangberg 1981). In this discussion, the rarer stem gall forms (mace, flower, and some illustrated by Wangberg [1978, 1980, 1981] and Larew and Cappizi [1983]) were not considered.

Second, in mixed or interdigitating stands of subspecies where both cotton and callus gall forms occur there is remarkable specificity. Cotton galls occur on the green-stemmed subspecies consimilis, graveolens, and turbinatus and callus galls on the white-stemmed subspecies albicaulis and hololeucus (McArthur and others 1979b; tables 1, 2). At two sites we did rather intensive sampling (figs. 1, 2). At a site in Iron County, UT, we sampled a uniform

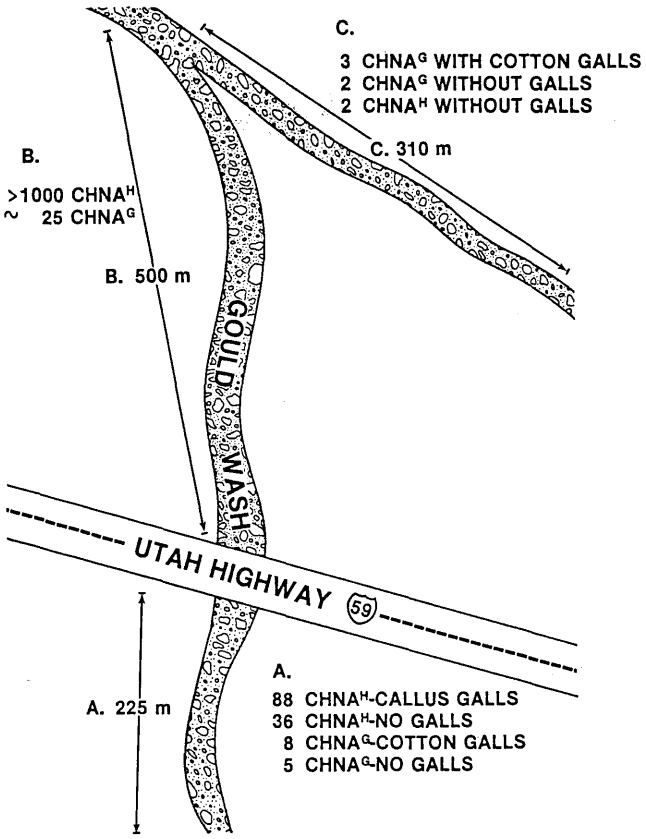


Figure 2.--Map of distribution Chrysothamnus nauseosus subspecies and gall form distributions in Gould Wash, UT, flood plain; 1980. C. nauseosus ssp. hololeucus (CHNA^{h}) in B segment have callus galls at relatively low frequency; C. nauseosus ssp. graveolens (CHNA^{g}) plants there are without galls.

ssp. hololeucus site in an abandoned field on the outskirts of Parowan and a mixed population grading into a pure stand of ssp. graveolens 2.5 mi (4 km) north, just west of Paragonah (table 2). Here the uniform ssp. hololeucus stand possessed callus galls only, and the uniform ssp. graveolens stand had cotton galls only. In the mixed stand, ssp. graveolens had cotton galls only; however, ssp. hololeucus had both kinds, but 97 percent of its sampled galls were callus (table 2).

At the site west of Paragonah, we inventoried 963 plants in 1980 (fig. 1). The results were similar to those given in table 2. Gall occurrence has been particularly heavy at that site. For example, in 1980 a large, 4.9 ft (1.5 m) tall by 6.9 ft (2.1 m) crown ssp. graveolens bush had 1,562 cotton galls and a large ssp. hololeucus, 4.3 ft (1.3 m) tall by 5.6 ft (1.7 m) crown bush had 262 callus galls and one cotton gall. A second intensive sampling was at the U-59 crossing of Gould Wash. At this site, callus galls and cotton galls were only found on ssp. hololeucus and ssp. graveolens, respectively, in 1977 (McArthur and others 1979b), 1980 (fig. 2), and 1984 (table 1).

In mixed stands where a certain gall form is absent, galls of the type present may occur on the nontypical host as in the following three examples: (1) near Big Rock Candy Mountain, UT, in 1984, 50 ssp. hololeucus bore only callus galls (1-50/plant) whereas 40 ssp. consimilis plants bore no galls and 10 had callus galls (1-6/plant); (2) at Moccasin, AZ in 1984 ssp. turbinatus (10.42/branch) and ssp. hololeucus (2.66/branch) both bore cotton galls to the exclusion of callus galls (table 1); (3) in 1977 along U.S. 89 north from Kanab to Long Valley Junction, UT, the white-stemmed ssp. hololeucus and the green-stemmed ssp. turbinatus, graveolens, and consimilis all bore cotton galls only.

Third, morphologies of cotton and callus galls are controlled by the flies, not the plant. Data from the cline site (table 2) are particularly instructive. Here, cotton formers rarely induce galls on the "wrong" plants (ssp. hololeucus). Dodson (personal communication) also observed a low frequency of cotton galls among the numerous callus galls on white-stemmed C. nauseosus in mixed stands of rabbitbrush in New Mexico. Plants with intermediate morphology are few in number, but they often bear both kinds of galls. Rabbitbrush has a generally inbreeding breeding system (Anderson 1980; McArthur 1984).

Fourth, galls can be used, with restrictions, as taxonomic indicators as we suggested earlier (McArthur and others 1979b). Both gall forms need to be present in the same general area. In that case, the gall forms can be used to help differentiate among subspecies groups. If the callus gall is present the specimen is ssp. albicaulis or hololeucus; the cotton gall indicates ssp. turbinatus, graveolens, or consimilis. The cotton gall may also be on albicaulis and hololeucus, but at a much lower frequency than the callus gall. While the two groups (consimilis, graveolens, and turbinatus versus albicaulis and hololeucus) generally have different stem colors, the colors are not always distinct. The galls have the advantage of being present in winter when leaf and flower characteristics are not present for identification purposes (Anderson 1973; McArthur and others 1979a).

Mace and flower galls are not good subspecies indicators (tables 1, 2). Both occur sporadically among the subspecies examined and neither is as common as cotton and callus galls. The mace gall also occurs on C. viscidiflorus (table 1). It may be induced by a widely distributed, if not common, vector. It is found at higher elevations than the other galls, often on the mountain taxon, C. nauseosus ssp. salicifolius, that has not been observed to bear either callus or cotton galls (McArthur and others 1979b).

Change in Gall Frequency

Galls may have different frequencies in space, as in the case of ssp. hololeucus at Gould Wash (8.92 galls/branch) versus ssp. hololeucus at Goshen Dam (0.34 galls/branch), $P < 0.05$ (data from table 1; see also McArthur and others 1979b). Galls also have different frequencies over time. For example, the number of galls in north-central Utah in 1984 was down dramatically from previous years. The stand we sampled in 1977 at Fountain Green then bore 1.0 callus galls/branch on ssp. hololeucus and 0.7 cotton galls/branch on ssp. consimilis (McArthur and others 1979b). At the same site in 1984, I found no callus galls on 300 ssp. hololeucus plants and only five cotton galls on 50 ssp. consimilis plants. I suspect the recent wet weather and cold winters (Richardson and others 1982) decimated the fly vector populations in some local areas.

The Gall Inducers

Galls on Chrysothamnus are abnormal tissue proliferations caused by fly vectors. The cotton and callus galls are caused by Aciurina spp. (Diptera: Tephritidae) (Wangberg 1981). Adult flies lay eggs in midsummer. Larvae appear by August with coincident formation of galls. The galls then serve as the winter home for the larvae which pupate and emerge the next summer. Cotton and callus galls contain one larva per gall.

The flower gall, on the other hand, contains several larvae per gall. The gall I observed is identical to the one illustrated in a photograph by Larew and Capizzi (1983, p. 75). These authors state that this gall is caused by gall midges (Diptera: Cecidomylidae). However, Wangberg (1980) describes a similar gall and one I have also observed--it lacks the cottony center part of the flower head, but includes more bracts. This gall is induced by Procecidochares spp. (Diptera: Tephritidae), undescribed but called Procecidochares spp. B by Wangberg (1980).

The mace gall is illustrated by a line drawing (McArthur and others 1979b) and in a photograph by Larew and Capizzi (1983, p. 74) who, again, state that the gall is induced by gall midges. Dodson (personal communication) confirmed that gall midges do indeed induce the mace gall. My examination of galls indicates that the gall contains two larval chambers. Our attempts to rear flies from this gall have yielded equivocal results. One Aciurina fly and several small wasplike insects that may have been secondary occupants of the gall (Mani 1964) are all that our efforts have netted.

Our data, together with Wangberg's (1980, 1981), show that there are considerable gall forms and gall-former specificity in Chrysothamnus nauseosus. Wangberg (1980) gave Aciurina maculata and A. trixa as the formers for the cotton and callus galls, respectively. However, recent work by Dodson (unpublished) indicates that A. bigeloviae may be a causative agent for the cotton gall. Steyskal (1984) recently revised Aciurina, but it may remain for Dodson's work to unravel the taxonomic difficulty in Aciurina. Aciurina maculata and A. bigeloviae are very similar (Foote and Blanc 1963; and especially Dodson, personal communication). These two species are similar in behavior and morphology (Foote and Blanc 1963; Wangberg 1981). Local sympatric populations of these two species apparently divide the Chrysothamnus nauseosus resource by partitioning green-stemmed (A. maculata) and white-stemmed (A. trixa) rubber rabbitbrushes as minimally overlapping habitats. These fly species choices may also be a clue to the phylogeny of C. nauseosus subspecies.

Similarity of stem tomentum in the two C. nauseosus subspecies groups and the specificity of the two fly species argue for two ancestral lines in C. nauseosus--the green- and white-stemmed groups. In other areas of the two Aciurina species' distribution, they compete for a common resource. I believe that they are in active phases of speciation. Perhaps, the two species are really more than two; sibling species may have developed. Wangberg (1981) gives some evidence for this possibility when he suggests that A. trixa forms four distinct gall types--the common callus and three rarer, sometimes geographically distinct, forms. I have observed that the cotton galls of A. maculata come in apparent different sizes--much larger ones for C. nauseosus ssp. graveolens and ssp. turbinatus than for ssp. consimilis. Might not speciation be going on in A. maculata--the cotton gall former? Determination of differences by fly morphology is extremely difficult. However, Wangberg (1980, 1981) has shown that behavioral differences can be useful. Dodson (personal communication) has recently provided evidence for life history and behavioral differences in sympatric Aciurina gall formers (A. bigeloviae and A. trixa), and demonstrated that isozyme patterns are correlated with morphological and gall-forming traits. Such work needs additional emphasis to solve a set of interesting problems. Aciurina speciation may well gain its impetus, as does the apple maggot fly, Rhagoletis pomonella, another tephritid, by changes in host recognition and in mutation of larval survival genes (Prokopy and Roitberg 1984). Under such a scenario, host specificity changes and consequent sympatric sibling speciation are easily envisioned.

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PHYTOPHAGOUS INSECTS OF GREEN RABBITBRUSH IN SOUTHEASTERN IDAHO

Michael P. Stafford and James B. Johnson

ABSTRACT: Insects associated with green rabbitbrush were surveyed throughout the summers of 1981-82 in southeastern Idaho. Results indicated that a diverse insect fauna is associated with green rabbitbrush and nearly all plant parts are attacked. The impact of these insects on the host has not been well documented and is in need of further study.

INTRODUCTION

Throughout much of southeastern Idaho, vegetation is dominated by big sagebrush (Artemisia tridentata Nutt.). In many of these sagebrush communities the subdominant shrub is green or low rabbitbrush (Chrysothamnus viscidifloris (Hook.) Nutt.). This species is an important component of these communities. The significant increase in green rabbitbrush after a range fire is important in stabilizing the watershed and restoring site productivity. Species of Chrysothamnus have not received much attention from the scientific community relative to many other plant groups. In particular, the insects associated with rabbitbrush have received little attention from range entomologists. Generally the insects go unnoticed and unstudied until a population outbreak occurs, resulting in considerable defoliation of the host plants.

A diverse insect fauna is associated with green rabbitbrush. This fauna is poorly known both taxonomically and biologically. Therefore, in order to gain a better understanding of the insects and their relationship to green rabbitbrush, we conducted an insect survey in the summers of 1981-82. Our work has been supplemented with information provided by Dr. William. F. Barr, Professor of Entomology Emeritus, University of Idaho.

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Michael P. Stafford is a Graduate Assistant and James B. Johnson is an Assistant Professor of Entomology, Department of Plant, Soil, and Entomological Sciences, University of Idaho, Moscow, ID.

METHODS

The majority of our observations and collections came from a 1,500-acre (600-ha) study site located 6 miles (10. km) south of Howe, Butte County, ID, on a portion of the Idaho National Engineering Laboratory. This area is situated on a broad alluvial fan originating at the base of the Lost River Mountains and extending out onto the Upper Snake River Plains. Average elevation is 4,850 feet (1 478 m) and average annual precipitation is 8.7 inches (22 cm). Wyoming big sagebrush (A. tridentata ssp. wyomingensis) is the dominant plant in this area. Green rabbitbrush, however, is interspersed throughout the sagebrush and several large patches of rabbitbrush occur.

We surveyed the insects, using several collecting techniques. Sweeping large amounts of foliage with a standard 15-inch (38-cm) diameter sweep net gave us an indication of the relative abundance of many insect species. The most useful information, however, was provided by close visual observations of the insects on the host. After observing the insects, we either hand-picked them or used an aspirator to remove them from the plant so they could be identified. Plants were also uprooted and examined for root-inhabiting insects. We monitored the seasonal occurrence of these insects by the use of Malaise, windowpane, and pitfall traps.

RESULTS AND DISCUSSION

We have grouped the phytophagous insects into five broad categories: root borers, defoliators, fluid feeders, gall-formers, and flower feeders. Table 1 lists the insect species found to utilize green rabbitbrush as a host. A large number of bees, wasps, and moths visit the nectaries of rabbitbrush; however, we have not included these three groups in this paper.

Root Borers

Two species of beetle larvae bore the root system of green rabbitbrush. The buprestid, Agrilus pubifrons Fisher, is a common inhabitant and causes slight structural damage

to the root structure. Nearly one-half of the plants we examined were previously bored by this species. The boring activity of A. pubifrons seems to have little impact on the host.

Less frequently found, at least in the Howe area, are the larvae of the cerambycid, Crossidius hirtipes allgewahri LeConte. The impact of this species on the host plant varies, evidently depending upon moisture conditions. Although we never observed any plant mortality caused by Crossidius, Barr (1984) observed locally heavy mortality in an area suffering from drought.

Defoliators

A number of insects consume the foliage of green rabbitbrush. All but one species are Coleoptera or Lepidoptera. We observed four species of leaf beetles (Chrysomelidae) feeding on green rabbitbrush. The leaf beetles Pachybrachys caelatus LeConte and Cryptocephalus spurcus LeConte were found feeding on the leaves in late July and August.

Due to their small size and relative scarcity, their feeding seems to have little impact on the host. The five-striped fleabeetle, Disonycha latifrons Schaeffer, is sometimes abundant on rabbitbrush. Larvae were found on the host throughout the summer and adults appeared in late July and August. Although we never observed any noticeable damage to infested plants, Furniss and Barr (1975) reported considerable defoliation in isolated stands. Rarely, we found adult Trirhabda nitidicollis LeConte on green rabbitbrush. These plants, however, were in close proximity to a heavily infested stand of rubber

Table 1.--Phytophagous insects utilizing green rabbitbrush in southeastern Idaho

ROOT BORERS
Coleoptera
- Buprestidae
  - Agrilus pubifrons
- Cerambycidae
  - Crossidius hirtipes allgewahri

DEFOLIATORS
Coleoptera
- Chrysomelidae
  - Pachybrachys caelatus
  - Cryptocephalus spurcus
  - Disonycha latifrons
  - Trirhabda nitidicollis
- Curculionidae
  - Anthonomus spp.
  - 2 undetermined species

Lepidoptera
- Noctuidae
  - 2 undetermined species
- Geometridae
  - undetermined species
- Coleophoridae
  - Coleophora sp.
- Tortricidae
  - Synnoma lynosyrana

Orthoptera
- Acrididae
  - Hesperotettix viridis

GALL-FORMERS[1]
Diptera
- Tephritidae
  - Aciurina ferruginea
  - Aciurina lutea
  - Aciurina spp.
  - 2 undescribed species
  - Procecidochares sp.
  - undescribed species

FLOWER FEEDERS
Coleoptera
- Phalacridae
  - Olibrus rufipes
- Meloidae
  - Lytta vulnerata cooperi
  - Gnathium eremicola
- Buprestidae
  - Agrilus pubifrons
- Cerambycidae
  - Crossidius hirtipes allgewahri

Thysanoptera
- Thripidae
  - Frankliniella occidentalis

FLUID FEEDERS
Hemiptera
- Miridae
  - Lygus desertinus
  - 4 undetermined species
- Lygaeidae
  - Nysius niger
- Rhopalidae
  - Harmostes reflexulus

Homoptera
- Cicadellidae
  - Aceratagalia poudris
  - Ballana hebea ?
  - undetermined species
- Cercopidae
  - Clastroptera sp.
- Aphididae[2]
  - Aphis gregalis
  - Aphis ornata
  - Brachycaudus helichrysi
  - Uroleucon escalanti
  - Durocapillata utahensis
  - Myzus persicae
  - Pleotrichophorus pycnorhysus
  - Pleotrichophorus utensis

[1] From Wangberg (1976).
[2] From Gittins and others (1976).

rabbitbrush (C. nauseosus (Pall.) Britt.). Although Hogue (1970) listed green rabbitbrush as a host for T. nitidicollis, we never observed the larvae on green rabbitbrush, even on rabbitbrush growing adjacent to C. nauseosus infested with Trirhabda. We frequently collected from the foliage two small species of weevils (Curculionidae), both of which are in the genus Anthonomus. Little damage to the plant occurs as a result of their feeding.

Lepidoptera larvae from four families (Noctuidae, Geometridae, Coleophoridae, Tortricidae) utilize green rabbitbrush as a food source. Of these, only the tortricid, Synnoma lynosyrana Walsingham, causes significant defoliation. The developing larvae web leaves and branches together and feed within this webbed mass. Infested plants appear unsightly and less vigorous. Hawkes (1962) reported a reduction in flowering as well.

Although grasshoppers (Acrididae) may occasionally consume rabbitbrush, most species do not utilize it. The species Hesperotettix viridis (Thomas); however, feeds readily on Chrysothamnus and Brusven (1972) reported that in Idaho it is the preferred host.

Fluid Feeders

All above-ground parts of the plant are attacked by fluid-feeding insects in the orders Hemiptera and Homoptera. This group is important because they have the potential to transmit plant diseases. As far as we know, however, no one has investigated insect-transmitted diseases of Chrysothamnus.

Leaf bugs (Miridae) comprise the largest group of Hemiptera feeding on green rabbitbrush. One frequently found species, Lygus desertinus Knight, can be an economically important pest to seed crops in southern Idaho. The false chinch bug, Nysius niger Baker (Lygaeidae), can also be abundant on rabbitbrush. It can be of economic importance on potatoes, but control treatments are rarely needed.

Green rabbitbrush is attractive to several aphid species (Aphididae). Gittins and others (1976) listed eight species that utilize this plant. The impact of these insects on the host depends upon the severity of the infestion. We observed a profuse, flowerlike growth on one plant that was caused by aphids.

A large complex of leafhoppers (Cicadellidae) and one species of spittlebug (Cercopidae) feed on the plant juices also. Early in the summer, leafhoppers are the most abundant group of insects on the plant.

Gall-Formers

Insect-induced galls are frequently found and conspicuous on the plants. Wangberg (1976, 1980, 1981) found that five species of tephritids induced galls on green rabbitbrush in Idaho. In most situations these galls have little apparent impact on the host plant; however, heavily infested plants appear unthrifty and Wangberg (1976) did report some plant mortality.

Flower Feeders

Rabbitbrush flowers are especially attractive to insects. To our knowledge, the impact of this group's feeding activities on seed production and viability has not been documented. Five species of beetles from four families (Phalacridae, Meloidae, Buprestidae, Cerambycidae) consume either pollen or nectar. The meloid beetle, Gnathium eremicola Macswain, has beelike mouthparts and feeds primarily upon nectar. The other species are pollen feeders.

Another flower inhabitant, the western flower thrips (Frankliniella occidentalis (Pergande)) feeds on developing seeds. Furniss (1983) reported this insect destroyed approximately 6 percent of the buds on antelope bitterbrush (Purshia tridentata (Pursh) DC.). The impact of this thrips on rabbitbrush seed has not been quantified.

CONCLUSIONS

Green rabbitbrush is fed upon by a variety of insects, each attacking a specific part of the host plant. Little biological information is known about most of these insects and the impact of their feeding activities is not well documented. Despite the pressure these phytophagous insects exert on their host, we have observed little plant mortality. Therefore, it seems green rabbitbrush, under most conditions, can withstand a substantial amount of insect damage. More research is needed if we are to gain a better understanding of the insect-plant relationships that exist and the role insects have in the regulation of Chrysothamnus populations.

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SNOW DEPTH AND INCIDENCE OF A SNOWMOLD DISEASE ON MOUNTAIN BIG SAGEBRUSH

David L. Sturges and David L. Nelson

ABSTRACT: A snowmold disease of mountain big sagebrush (Artemisia tridentata ssp. vaseyana), induced by an unidentified fungus, was discovered in Wyoming in 1973. Snowmold was present on 2 percent of sagebrush plants where maximum snow accumulation was less than 16 inches (40 cm), and 93 percent of plants where maximum accumulation exceeded 47 inches (119 cm). The disease reduces the canopy area or kills mountain big sagebrush plants in areas of deeper snow accumulation.

INTRODUCTION

Big sagebrush (Artemisia tridentata) is a hardy shrub, well adapted to the semiarid environment that typifies much of the West. It has few natural enemies, but mortality attributable to biological agents has been reported. Gates (1964) described an infestation of aroga moth (Aroga websteri) on sagebrush-grass rangeland in eastern Oregon that affected thousands of acres. Two species of leaf-feeding beetles belonging to the genus Trirhabda also damage sagebrush. Pringle (1960) found big sagebrush in British Columbia was defoliated by T. pilosa and felt that the insect could destroy about 50 percent of a stand. An estimated 2,000 acres (810 ha) of threetip sagebrush (A. tripartita) in Wyoming were host to T. attenuata (Fisser and Lavigne 1961). Voles (Microtus spp.), by girdling the trunk of sagebrush, have caused extensive stand damage on a localized basis (Mueggler 1967; Tabler 1968; Frischknecht and Baker 1972).

In 1973 we discovered a snowmold fungus on mountain big sagebrush (A. t. ssp. vaseyana) in southcentral Wyoming. We have since collected the same fungus on mountain big sagebrush in Utah, Colorado, and other areas of Wyoming. The disease was not found on Wyoming big sagebrush (A. t. ssp. wyomingensis) or black sagebrush (A. nova), which grow on sites with little snow accumulation. Our observations suggested that incidence of snowmold on mountain big sagebrush increased as snow depth increased. This study, conducted at the Stratton Sagebrush Hydrology Study Area, was designed to test the hypothesis that occurrence of snowmold is related to snow depth.

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David L. Sturges is a Research Forester, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. David L. Nelson is a Research Pathologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT. Research was conducted in cooperation with the Bureau of Land Management, U.S. Department of Interior.

DESCRIPTION OF THE SNOWMOLD FUNGUS

The snowmold fungus is most prominent immediately after snowmelt when a dense, cottony mycelial growth covers infected sagebrush shoots (fig. 1). Mycelial development occurs while sagebrush plants are covered by snow. The snowmold fungus initially kills a small patch of tissue which then expands in subsequent years as additional healthy tissue is infected. Dead portions within the sagebrush crown are fringed by mycelial mats of recent origin. An entire branch or plant can eventually be killed. The fungus was inactive during the 1977-78 and 1980-81 winters when precipitation was extremely low; however, the organism remained viable and resumed growth when snow conditions were again favorable. Because of the slow advance of the fungus and its perennial character, the incidence of snowmold in any year reflects growing conditions over a number of previous winters.

We have isolated the fungus in other studies and demonstrated its pathogenicity to sagebrush (Nelson and Sturges 1982). It has not sporulated in the laboratory when grown in vitro, nor have we found a sporulating stage in nature. Hyphal septation is typical of the Ascomycetes (Nelson and others 1983), but until a sexual spore stage is found the organism must be placed in the Fungi Imperfecti, meaning sexual reproduction is unknown. Unique knobby projections on the walls of hyphae permit positive recognition of the fungus when hyphae are viewed under the microscope.

STUDY SITE AND EXPERIMENTAL METHODS

The Stratton Sagebrush Hydrology Study Area is located in southcentral Wyoming 18.6 miles (30 km) west of Saratoga. Elevation ranges from 7,600 feet (2 316 m) to 8,100 feet (2 469 m). Meteorological and hydrological information have been collected at the site since 1967. Average annual precipitation was 20.69 inches (52.6 cm), and average annual temperature was 36.8 °F (2.7 °C), during the 14-year period from 1969 to 1982. Approximately 75 percent of precipitation was snow. Strong winter winds relocate snow;

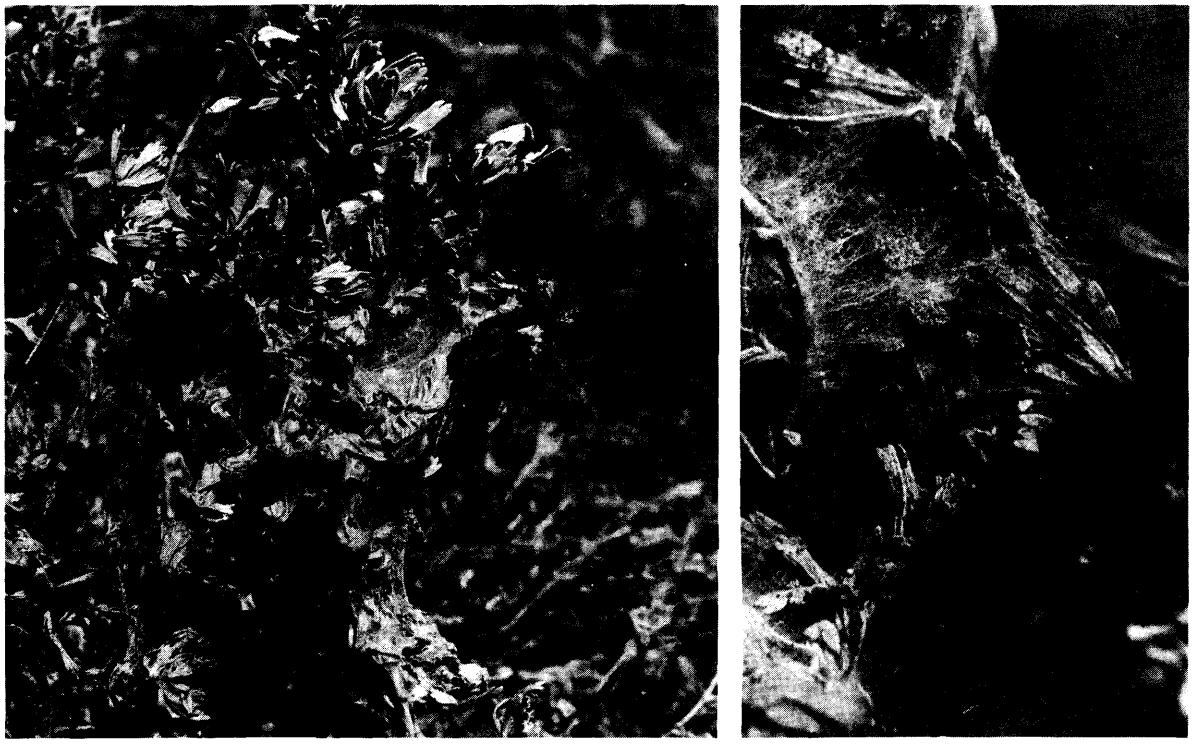


Figure 1.--A dense, web-like mycelium covers the infected portion of a sagebrush plant at the close of snowmelt (left). Closeup view of fungus mycelium on a sagebrush twig (right).

maximum accumulation varies from a few inches on windward slope and ridge areas, to more than 20 feet (6.1 m) in topographically induced depositional zones. Mountain big sagebrush inhabits areas of deeper snow, while Wyoming big sagebrush and black sagebrush are found on sites that retain little snow. Mountain big sagebrush is typically found on soils belonging to the Haggerty series where A and B horizons have a combined depth of 46 inches (117 cm). Mixed stands of Wyoming big sagebrush and black sagebrush grow on soils of the Kimmons series where A and B horizons have a combined depth of 20 inches (50 cm), or on the Roxyal series where the A horizon is 6 inches (15 cm) deep and a B horizon is lacking. Soils belong to the Cryoborall Great Soil subgroup.

The relationship between snow depth and incidence of snowmold was estimated from data collected on five transects in Loco Creek watershed (fig. 2). Transects were established in October 1979 and ranged from 527 feet (161 m) to 1,433 feet (437 m) in length. Loco Creek flows east, and the watershed has predominantly north-facing and south-facing slopes. Transects 1-4 began near the stream channel and extended toward the southern watershed boundary. Transect 5 was in the upper reaches of the watershed and extended in a northeast-southwest direction across a side drainage. All transects crossed a zone of deep snow accumulation and terminated in stands of low-growing Wyoming big sagebrush and black sagebrush. Snow depths were measured from the 1979-80 winter through the 1982-83 winter, by probing with an aluminum rod

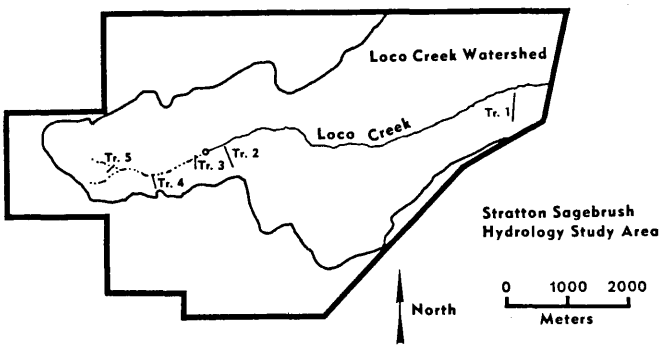


Figure 2.--The relationship of snow depth to incidence of snowmold was determined from data collected on five transects within Loco Creek watershed.

(Jairell 1975) at intervals of 25 feet (7.6 m). Information was collected about April 1, prior to the start of snowmelt. Accumulation of snow on seven index transects that cross major depositional zones in Loco Creek watershed was also measured annually beginning with the 1967-68 winter (table 1). Information from these transects indicated relative size of the snowpack during this study.

The incidence of snowmold was measured in June 1980. Sample sites were located in six strata based on snow depths measured earlier in the spring. Strata were: <24 inches, 24-35 inches,

Table 1.--Annual water content of snow on index transects that cross major depositional zones within Loco Creek watershed

Winter	Index transect 1	2	3	4	5	6	7	Yearly average		Winter ranking
	Inches							In.	Cm	
1967-68	42.9	46.6	55.1	28.2	31.1	77.2	29.0	44.3	113	[1]7
1968-69	28.4	31.7	36.9	19.5	20.6	56.2	21.7	30.7	78	12
1969-70	25.9	31.6	42.8	28.4	25.2	66.2	23.0	34.7	88	11
1970-71	44.4	44.6	55.5	28.1	31.0	71.5	30.0	43.6	111	8
1971-72	49.7	44.2	58.5	34.0	32.5	74.4	24.4	45.4	115	6
1972-73	31.8	39.0	40.4	24.4	28.2	60.8	25.9	35.8	91	10
1973-74	54.1	55.7	70.9	25.4	31.8	82.3	30.0	50.0	127	2
1974-75	41.3	52.2	56.8	27.3	32.3	82.0	28.4	45.8	116	5
1975-76	50.1	51.8	58.1	30.6	31.3	79.2	27.7	47.0	119	4
1976-77	1.5	5.4	8.1	9.8	5.7	15.1	5.4	7.3	19	15
1977-78	26.7	30.6	33.6	19.3	19.7	61.7	18.2	30.0	76	13
1978-79	67.0	67.5	82.4	42.1	45.4	91.1	42.9	62.6	159	1
1979-80	48.8	52.0	53.7	34.1	33.1	81.3	29.6	47.5	121	3
1980-81	.0	.5	.3	.1	.2	1.5	.1	.4	1	16
1981-82	45.2	42.2	52.1	31.4	28.7	74.5	26.7	43.0	109	9
1982-83	21.9	28.1	32.3	18.8	22.1	51.9	20.3	27.9	71	14

[1]The winter with the greatest snow accumulation in the 16-year period is ranked #1, the winter with least snow accumulation is ranked #16.

36-47 inches, 48-59 inches, 60-71 inches and >71 inches (<60 cm, 61-90 cm, 91-120 cm, 121-150 cm, 151-180 cm, and >180 cm). The location of snowmold sample sites in each stratum was randomly selected from snow measurement points in the stratum. An attempt was made to place four snowmold sampling sites within each snow-depth stratum. Placement of snowmold sampling sites on each transect is shown in figure 3.

Snowmold incidence was measured on belt transects 4.4-feet (1.3-m) wide which extended perpendicularly from snow transects so that sagebrush on individual belt transects would have a uniform snow cover. Orientation of belt transects was randomly determined. The first 25 sagebrush plants on a belt transect were categorized as either infected or not infected, based on the presence of mycelium from the previous winter. The height of the first 10 plants on a belt transect was recorded. The distance to the 25th plant was also recorded to enable sagebrush density to be calculated.

STATISTICAL ANALYSIS OF DATA

Data relating snowmold incidence to snow depth were analyzed by analysis of variance within a factorial experimental design. The variance

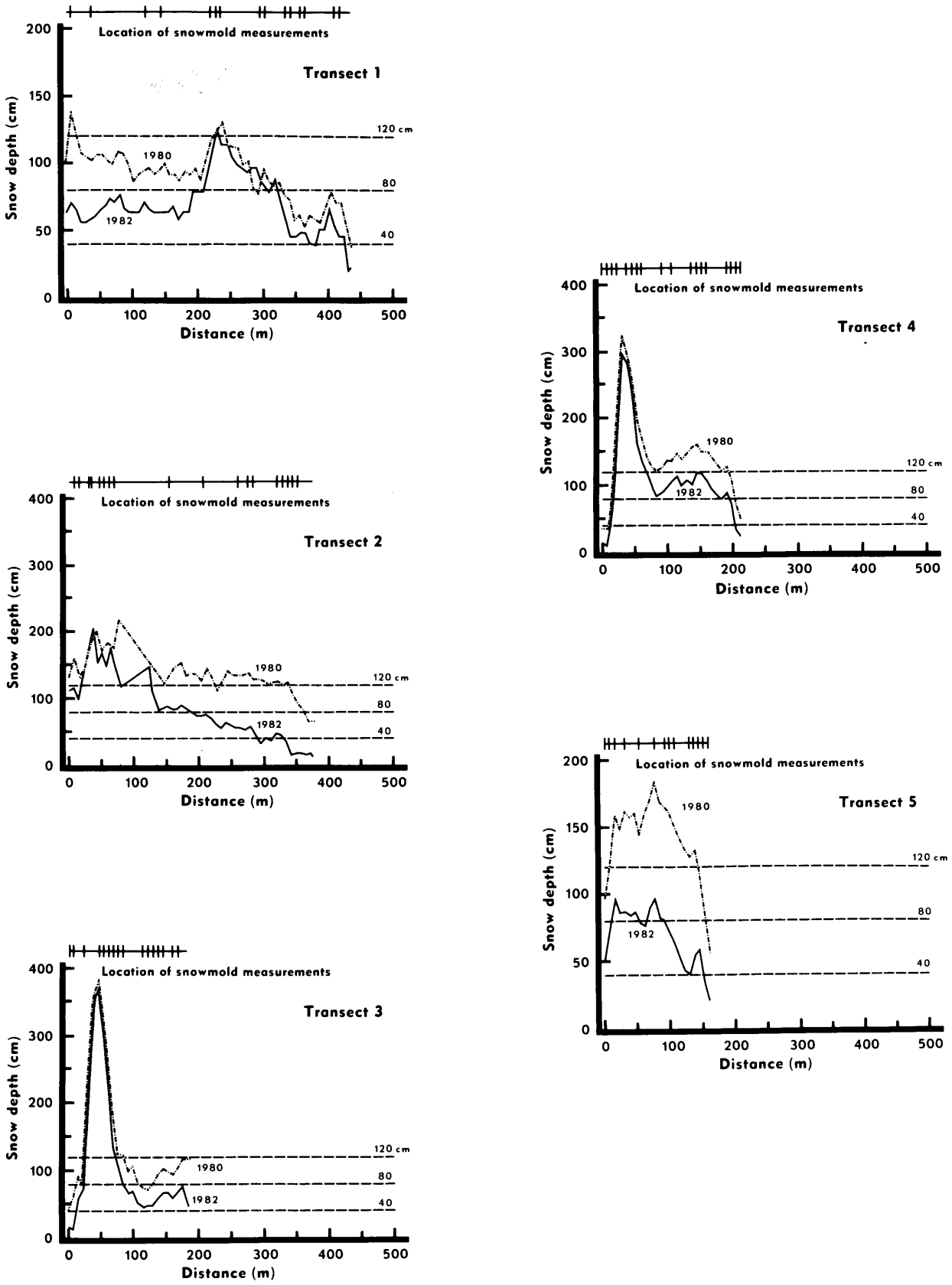


Figure 3.--Snow depths in the 1979-80 and 1981-82 winters on the five transects where incidence of snowmold was measured. The location of snowmold sampling points is also shown.

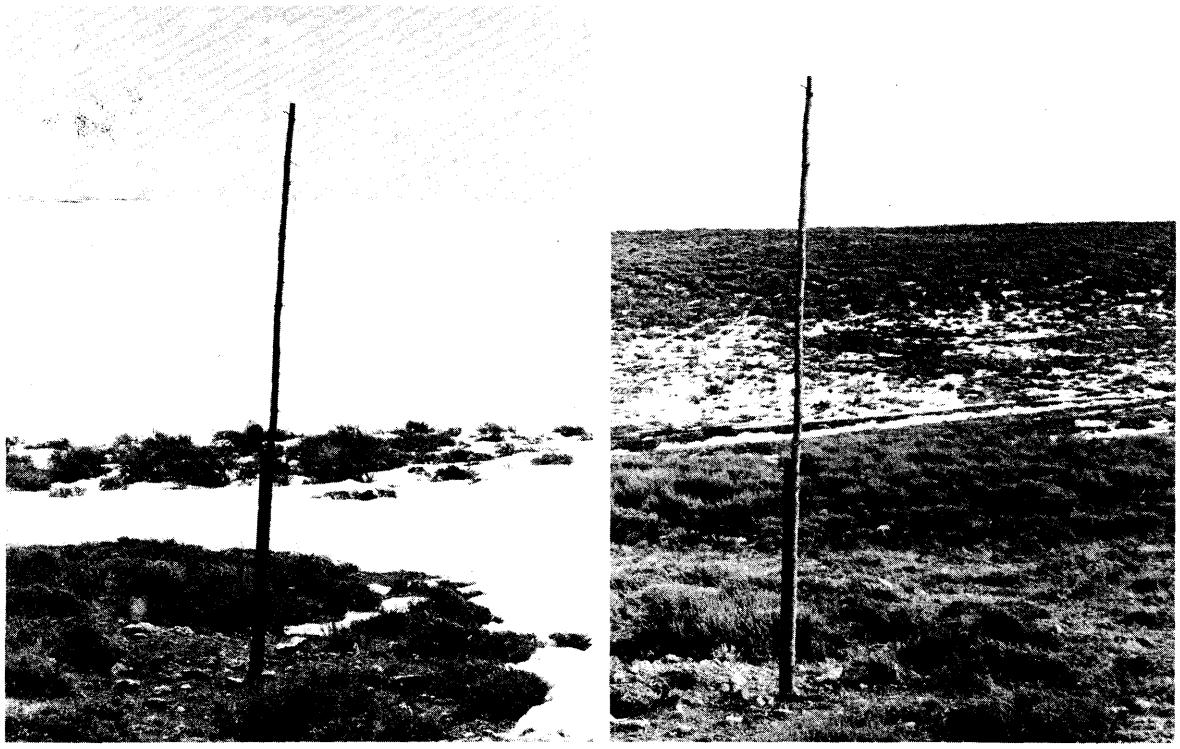


Figure 4.--More than 11.5 feet (350 cm) of snow accumulated on transect 3 in the incised channel of Loco Creek at maximum accumulation in the 1979-80 and 1981-82 winters (left). The fungus was inactive in winters when snow failed to cover sagebrush, indicated by conditions on transect 3, April 4, 1981 (right).

model permitted identification of significant differences in snowmold incidence between transects, between snow depth strata, and an interaction between depth strata and transects. Differences in snowmold incidence between snow depth strata were tested for significance using procedures described by Gabriel (1963) for dichotomous data. Sagebrush density data and sagebrush height data were also subjected to analysis of variance. Treatment means were tested for significance using Kramer's modification of the Tukey multiple range test (Dunnett 1980). A 0.05 probability level indicates statistical significance in this paper.

RESULTS

Snow Accumulation

Strong southwesterly winds relocate snow following precipitation events. The depth of snow accumulation at any location reflects the interaction between winter precipitation, vegetation height, and topographic position. Annual variations in snow accumulation between 1968 and 1983 are shown in table 1 for index transects in Loco Creek watershed. The pattern of deposition on the five transects utilized for snow measurements in this study was consistent from year to year, though annual snow depths were quite different. Yearly variations are indicated by data for the 1979-80 and 1981-82 winters (fig. 3). The deepest snow, more than 10 feet (305 cm), was present on transects 3 and 4 which cross the incised channel of Loco Creek.

Based on 16 years of information from permanent watershed transects, snow accumulation in the 1979-80 winter was the third highest, accumulation in the 1981-82 winter was average, and accumulation in the 1982-83 winter was the third lowest (table 1). Precipitation in the 1980-81 winter was the lowest ever recorded and snow failed to cover sagebrush plants (fig. 4).

Relationship of Snow Depth to Snowmold Incidence

The snowmold disease acts in a chronic rather than acute fashion. Presence of the fungus in a sagebrush stand reflects snow conditions over a number of preceding winters. Data on snowmold incidence were collected after snowmelt in 1980, but snow accumulation in the 1979-80 winter was very large. We felt that the relationship between snow depth and snowmold incidence should be based on snow conditions in an average winter, rather than conditions in a winter with either an extremely large or an extremely small snowpack. Thus, data collected in the 1981-82 winter, which represented an average snowpack, were used to relate incidence of snowmold to snow depth. A number of snow-depth strata on different transects lacked a single observation when snow depths measured in the 1981-82 winter were related to

snowmold incidence. Consequently, snow depths were restratified into four strata: 0-15 inches, 16-31 inches, 32-47 inches, and >47 inches (0-39 cm, 40-79 cm, 80-119 cm, and >119 cm).

Average incidence of snowmold for the four snow-depth strata is shown in figure 5. Differences attributable to transects and to snow-depth strata were significant. The interaction between snow-depth strata and transect location was not significant, indicating that the increase in snowmold incidence with increasing snow depth was similar on all transects. Incidence was very low where snow was less than 16 inches (41 cm) deep, but increased sharply as snow depth increased to 47 inches (119 cm). Differences in snowmold incidence between the two deepest snow-depth strata were not significant.

Relationship of Snow Depth to Sagebrush Density and to Sagebrush Height

The height and density of sagebrush were also related to snow depth. Average stand density decreased 34 percent going from a 0 to 15-inch (0 to 39-cm) snow depth, to a 16 to 31-inch (40- to 79-cm) depth, while average stand height nearly tripled (fig. 5). These figures reflect replacement of Wyoming big sagebrush and black sagebrush, which grew in locations where snow was less than 16 inches (40 cm) deep, by mountain big sagebrush, which grew in locations where snow was more than 15 inches (39 cm) deep.

Differences between sagebrush density in the three deepest snow-depth strata were not significant. The interaction between snow depth and transect location was significant for sagebrush density, unlike the analyses for incidence of snowmold or sagebrush height. The change to mountain big sagebrush from black sagebrush-Wyoming big sagebrush is not always sharply defined, particularly if there is a gradual change in snow depth with increasing slope elevation. Thus, sample sites on some transects where snow was defined as less than 16 inches (40 cm) deep were inhabited by mountain big sagebrush, while other sample sites defined as having snow deeper than 15 inches (39 cm) were inhabited by black and Wyoming big sagebrush.

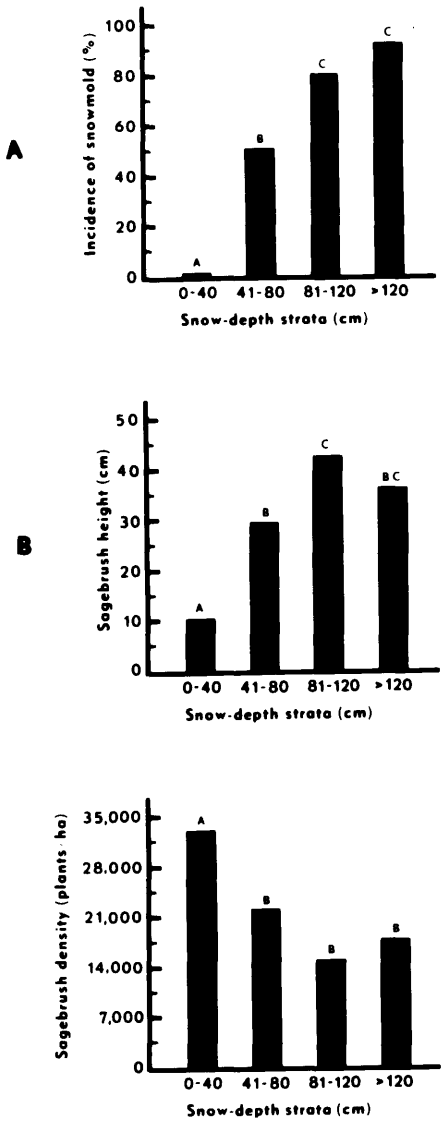


Figure 5.--The relationship between snow depth and (A) incidence of snowmold, (B) sagebrush height, and (C) sagebrush density. Any two means having different letters are significantly different.

DISCUSSION

Study data indicated that about 16 inches (40 cm) of snow were required for growth of the snowmold fungus. It is unlikely that snow depth per se was the primary factor influencing development of the disease. Rather, areas of deeper snow probably provide a suitable environment for growth. Laboratory studies show that snowmold fungus is adapted to a low-temperature regime (Nelson and Sturges 1982). Optimum in vitro growth of fungus mycelium occurred near 53.6 °F (12 °C), but some growth did occur at a temperature of 24.8 °F (-4 °C). The threshold snow depth that enables the fungus to grow probably varies somewhat with climatic regime. The crucial factor is having a snowpack temperature at or slightly below the freezing point of water sufficiently long for the fungus to grow.

Excessively cold temperatures in the snowpack probably prevent appreciable fungus growth in early winter months at the Stratton site. Maximum daily air temperatures are below freezing by mid-November and remain below freezing until late March. In the spring, the snowpack must warm to 32 °F (0 °C) before melt begins. Once snow melts, sagebrush is exposed to the desiccating effects of the atmosphere. Thus, there is a relatively short period of time in the spring when snowpack temperatures are warm enough for appreciable growth of the snowmold fungus.

Development of the fungus probably takes place while the snow surface is well above the

sagebrush canopy. Snowmelt is extremely rapid once the snow surface reaches the sagebrush canopy. Vegetation reradiates incoming short-wave solar radiation as long-wave radiation, which greatly accelerates snowmelt. Melt rates of 2.4 inches (6 cm) of water per day have been measured at the Stratton site (Sturges 1977). Assuming snow has a 35 percent water content, about 6.7 inches (17 cm) of snow are required to provide 2.4 inches (6 cm) of water. Thus, it is possible for snow to completely melt from a stand of Wyoming big sagebrush and black sagebrush in a single day.

Snow depths under 16 inches (40 cm) coincided with a low incidence of snowmold, and also with sites inhabited by stands of Wyoming big sagebrush and black sagebrush. The low incidence of snowmold in these stands might be attributed to a resistance of black sagebrush and Wyoming big sagebrush to snowmold. Tests we conducted in the laboratory demonstrate that the fungus can grow on both the Wyoming and basin (A. t. spp. tridentata) subspecies of big sagebrush as well as black sagebrush. Thus, we believe that the low incidence of snowmold on these sites reflects the fact that about 16 inches (40 cm) of snow are required to provide sufficient time for the fungus to fulfill growth requirements, rather than reflecting differences in susceptibility of sagebrush subspecies to snowmold.

Snowmold caused a substantial reduction in mountain big sagebrush cover at the Stratton study location. Transect 2 traversed an area where the effects of spraying sagebrush on soil water use and on vegetation production have been studied since 1969 (Sturges 1983). Snowmold was first observed at the site in 1973. The canopy cover of mountain big sagebrush was measured in 1969 before the fungus was active and again in 1980 after it had been active for a number of years. Canopy cover decreased 34 percent in those 12 years, a significant reduction attributable primarily to the snowmold.

Vegetative production measurements, which included the current annual growth of sagebrush, also indicated a decline in importance of sagebrush. Annual vegetative productivity decreased from an average of 1,271 lb/acre (1 424 kg/ha) in the 3-year period, 1971-73, to an average of 916 lb/acre (1 026 kg/ha) in the 2-year period, 1980-81. Annual forb and grass production differed by only 6 lb/acre (7 kg/ha) in the two periods. Thus, the decrease in total production is attributable to loss of sagebrush.

Additional studies are needed to determine the ecological role of the snowmold fungus in the mountain big sagebrush zone. Lack of suitable agents has prevented the use of biological control methods in management of sagebrush rangeland. There may be a potential for using the snowmold organism to thin mountain big sagebrush stands where environmental conditions are suitable for its growth.

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Section 6. Ecology

SAGEBRUSH OVER TIME:

A PHOTOGRAPHIC STUDY OF RANGELAND CHANGE

Kendall L. Johnson

ABSTRACT: The nature of the big sagebrush zone in presettlement times is an enduring question that cannot be answered definitively. Comparison of presettlement photographs with modern retakes of the same sites, however, provides useful information. This study compares 20 current photographs of Rocky Mountain sagebrush rangeland with those taken by William H. Jackson during the 1870's as a member of the U.S. Geological and Geographical Survey of the Territories (Hayden Expedition). The photographs were selected to illustrate different site responses: (1) sagebrush decrease or destruction, (2) sagebrush stability, (3) sagebrush increase or establishment, and (4) combination effects. Comparative analysis indicates that: (1) the reaction of big sagebrush stands to use and management is highly site-specific and a function of the kind of use and site characteristics; (2) shifts in composition and density of species have occurred but their magnitude cannot be assessed, although they probably range from slight to major change; (3) there has been no major shift in sagebrush distribution as a result of use; and (4) the appearance of the landscape today is a fair indication of its appearance in presettlement times.

INTRODUCTION

Perhaps the most enduring question among students of western plant ecology is the nature of the big sagebrush zone prior to European settlement. Was it mainly a grassland with sagebrush present only as a savanna? Many people think so, which leads to the belief that much of the present sagebrush-dominated land is the result of early and continued abusive use. The thought has become a kind of conventional wisdom, and the source of many "sagebrush-infested" statements (Cottam and Stewart 1940).

Or was the big sagebrush zone largely a shrubland, with sagebrush as a clear dominant? Many students of sagebrush think this was the case, pointing to the climax adaptation of the shrub. This leads to belief that sagebrush stands may have increased in density as a result of land use, but do not represent a major shift in vegetation type. In this view, the sagebrush zone appeared then much as it does now, at least in broad-scale or regional terms (Hironaka 1979).

Paper based on an address presented at the Symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

Kendall L. Johnson is Extension Range Specialist, Range Science Department, Utah State University, Logan, UT.

It is a controversy that will never be satisfactorily resolved for a very simple reason: lack of information. There are no definitive records of presettlement vegetation, hence proponents of any position in the argument must rely on indirect and circumstantial evidence which, by its nature, is open to different interpretations. The result is often that additional heat, but little light, is directed to the question.

It is true, however, that some kinds of circumstantial evidence are more compelling than others. Among these are landscape photographs taken before the effects of settlement, especially those of cultivation and livestock grazing, became significant. Comparison of such photographs with modern retakes of the same scenes offers a degree of insight into pristine vegetation not otherwise available. This study is an examination of ecological change in central Rocky Mountain sagebrush rangeland, based on comparison of photographs separated by well over 100 years. In this effort I try to show how sagebrush rangeland looked in the 1870's and how it looks today, speculate on the probable causes of the changes observed, and from that infer the relative ecological stability of the sites involved.

This pursuit was made possible by the efforts of William Henry Jackson, an early and exceptionally able practitioner of the then-new art of landscape photography in the 1870's. His photographs make it possible for us to gain some insight into the role of big sagebrush on presettlement rangeland and how that role may extend into the present time.

THE EARLY WEST IN DESCRIPTION

Aside from the remaining relict areas, large and small, the only evidence of early western vegetative conditions lies in the descriptions found in the journals, reports, and diaries of the first explorers and travelers. Their observations, however, were normally fragmentary, frequently conflicting, and sometimes puzzling. This is because nearly all of the early observers were in the West for practical reasons having nothing to do with vegetation, aside from its value as forage for trail stock. Most were simply traveling through the intermountain country to Oregon and California. A few were trappers, prospectors, hunters, and later, homesteaders. Almost none were observers of the country for itself. Therefore, their descriptions of vegetative conditions were usually both incidental and very general. For instance, Wislizenus (1912) observed that west

of Fort Laramie "the country continued hilly, sandy, poor as to grass, but so much the richer in sage brush," a description that leaves the reader wondering about the relative values of "poor" and "richer."

A major consequence is that the historical records are open to various and sometimes sharply different interpretations. For instance, Stewart's (1941) survey of historical records of Utah range ecology emphasized an abundance of grass in presettlement times. On the other hand, Vale (1975) maintained that the historical records established sagebrush as an ecological dominant in the intermountain West. Indeed, Young and others (1979) argued that the historical records could be used to justify any preconceived opinion of pristine vegetation. While that position may be extreme, there is no doubt that written history does not provide a definitive description of presettlement vegetation.

There are two partial exceptions to this general pattern: the scientific and military surveys, both designed to obtain specific information about the western territories. The scientific surveys were prompted by construction of the transcontinental railroad, which generated professional and public curiosity about the West. After the Civil War, Congress authorized several formal efforts to describe the land and its resources (Schmeckebier 1904). Surveys headed by Clarence King (1867-72), F. V. Hayden (1867-79), John Wesley Powell (1871-79), and George M. Wheeler (1871-79) explored, mapped, and documented in great detail major portions of the West, before being discontinued in favor of the U.S. Geological Survey in 1879.

The other main source of early formal information about the West was the U.S. Army. Charged with defense during the Indian Wars, the Army mounted numerous survey expeditions to the West to meet its strategic and tactical responsibilities. Prominent examples are the two Fremont expeditions across the Rocky Mountains in the 1840's (Fremont 1845), the 1849-50 Stansbury expedition to the Great Salt Lake (Stansbury 1852), the 1874 Custer expedition to the Black Hills (Ludlow 1875), and the 1859 Simpson exploration of the Great Basin (Simpson 1876).

All of the scientific and military surveys gained a wealth of detailed and reliable information on the natural resources of the West. But it must be remembered that the primary objective of survey personnel concerned with vegetation was the occurrence of species rather than the relations between them. Indeed, ecology had yet to be defined as a formal discipline, and so survey descriptions of vegetative conditions, while improved, were still not definitive.

Probably the most significant Survey was the long-running (1867-79) U.S. Geological and Geographical Survey of the Territories, informally known as the Hayden Expedition for its leader and director Dr. Ferdinand Vandiveer Hayden, a medical doctor become geologist. Dr. Hayden was instrumental in persuading Congress to authorize a series of annual expeditions to the central Rocky Mountains, including the famous 1871 Yellowstone survey that proved instrumental in establishment of the first national park. It is notable that the 1871 survey achieved its significance through the then-new medium of landscape photography. Through it verbal descriptions of the natural wonders of the Yellowstone, previously rejected as only tall tales, acquired visual support and thus credibility. So photography was a development that became a standard part of survey organization.

THE EARLY WEST IN PICTURES

A survey staff typically included several professional scientists in disciplines such as geology, minerology, botany, soils, zoology and meteorology. Due to the need for pictorial representation of striking features of the landscape, several of the surveys also employed or allowed volunteer service of artists. The noted landscape painter Thomas Moran, for instance, accompanied the 1871 Hayden expedition to the Yellowstone. Several of his landscape oils of later years were of subjects first sketched on the trip, including the now-famous painting of Yellowstone Falls. Once photography became a usable field technique, all of the surveys used it to provide visual evidence of notable features. The early survey photographers, John K. Hillers (Fowler 1972), Timothy H. O'Sullivan (Horan 1966), and William H. Jackson (Jackson 1940), were of great service in attaining survey objectives, and together created a scientific and artistic record of enormous value.

Jackson and the Hayden Expeditions

William Henry Jackson was for 9 years (1870-78) the staff photographer for the several Hayden expeditions. His survey service was the foundation of a distinguished photographic career and the basis of his critical standing as a photographer (Szarkowski 1963). Through the expeditions he became not only one of the first, but one of the best, landscape photographers.

Jackson's association with the Survey began almost accidentally, as the result of a chance encounter with F. V. Hayden on the newly constructed transcontinental railroad in 1869. Jackson was taking pictures of the railroad and of natural features near the grade for a commercial purpose. The next summer, Hayden stopped at Jackson's studio in Omaha on his way to conduct the 1870 Survey in Wyoming Territory, and invited him to accompany the expedition as official photographer. Although he was not offered a salary, Jackson accepted readily for only keep and expenses, control of the negatives, and the satisfaction of contributing art to science!

This was the first time the Survey had carried a photographer, and Hayden reported that Jackson produced about 400 negatives on the trip (Hayden 1871). By the end of the expedition, Jackson had become a permanent and salaried member of the Survey staff. Thus began the photographic library

that caused Current (1978) to observe: "They [the photographs] remain the earliest benchmark against which change--geological, ecological, botanical--can be measured." It is against this background that the photographs of natural landscapes taken by W. H. Jackson become significant. They open a window on the past through which comparisons with modern conditions can be made. The photographs help evaluation of the early writings and improve deductions on how, why, and to what extent changes have occurred. Jackson's work is an original contribution to photography, and an example of art in the service of science.

METHODS

This study is an appraisal of ecological changes in the sagebrush-grass rangeland of southern Wyoming, southern Idaho, and northern Utah. It is based on a comparison of Jackson photographs with modern retakes over 100 years later, employing mainly the photographs taken during the 1870 Hayden expedition, with some additional views from the 1871 and 1872 expeditions, and from an 1869 trip along the railroad. These were collated by Jackson as part of a descriptive catalog (Jackson 1875). All views now available in the USDI Geological Survey photographic library in Denver were inspected, and a decision made on their suitability for comparative study. Over 100 photographs were chosen that best illustrated rangeland conditions of the 1870's, and that offered a reasonable prospect of relocation. Twenty photosites that illustrated different responses to the use and management of sagebrush-grass rangeland over the past century were selected for this study (fig. 1).

Procedures

Over a 12-year period, 1974-1985, each Jackson photosite was relocated through time-consuming search in the field, aided by knowledge of the countryside and comparison of expedition maps and reports with modern references. Once the general location was found, the exact photopoint was relocated by detailed inspection of photo features. In a few cases, change had either obliterated the photopoint or made it impossible to see the subject from the original point. In such instances, suitable offset views were taken. All photographs were relocated with enough precision for comparison.

Once a photopoint was located, comparison photographs on both black and white and color films were taken, and appropriate notes made of date, time of day, line-of-sight direction, and photographic exposure. Directions to the site were recorded, and the point was marked on the ground for subsequent visits.

Information gathered on the site included a list of major plant species growing in the photopoint area (species nomenclature generally followed Hitchcock and Cronquist [1973] except that the Triticeae grasses were named according to Dewey [1984]). A ground-cover index (GCI) was generated by a 50- or 100-pace transect located on the photo line of sight, adjusted for physical conditions (NAS/NRC 1962). At every step of the right foot (1 pace), records were made of cover conditions (bare ground, rock, litter, vegetation) defined by a point at the toe of the boot sole. The GCI was regarded as the percentage of covered ground (total of all classes except bare ground).

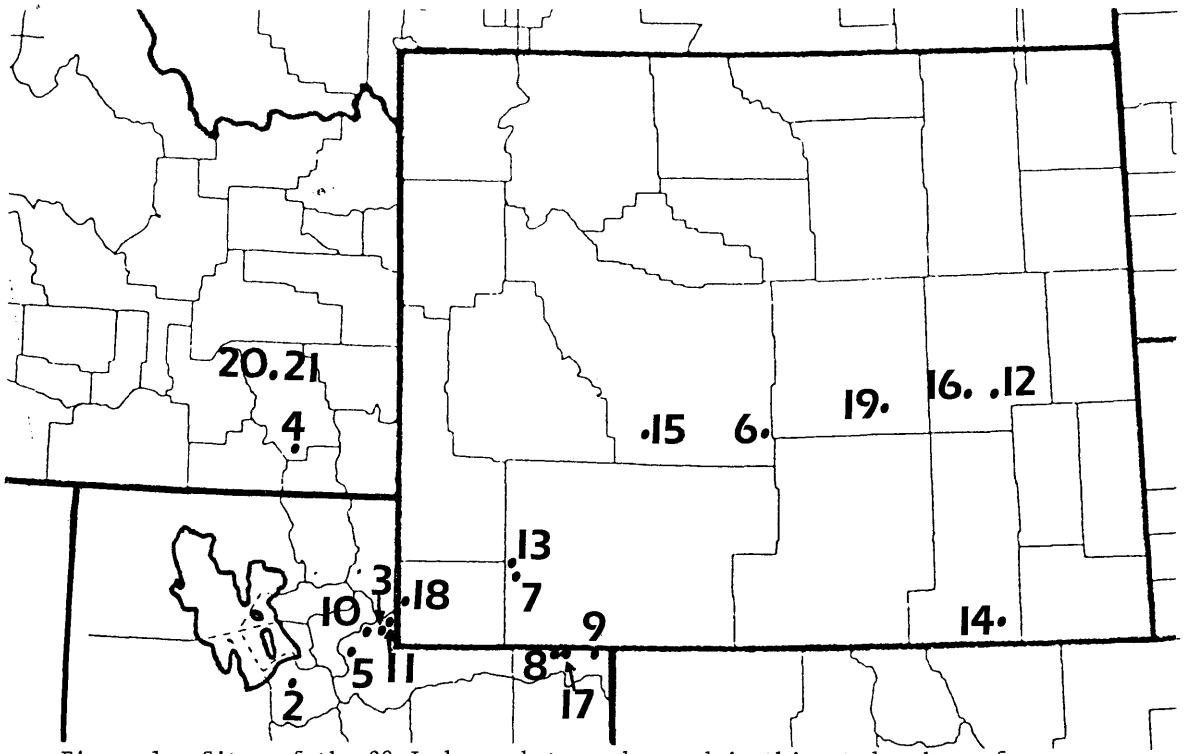


Figure 1.--Sites of the 20 Jackson photographs used in this study, drawn from his 1869 railroad trip and the 1870, 1871, and 1872 Hayden Expeditions. Numbers correspond to figures at the end of this paper.

Descriptive notes were made of site conditions, erosion patterns, soil characteristics, grazing use, and cultural changes. Field estimates of apparent range condition (ARC) and of apparent range trend (AT) were completed.

Subsequently, one or more visits were made to each photosite to obtain comparison photographs having the same light conditions as the original Jackson view. These photographs were made as close to the original date (determined from expedition records) and time of day (determined from photo shadow patterns) as possible. At this time all previously gathered site information was reviewed and additional observations were made.

Analysis

The several Hayden expeditions produced thousands of photographs of the presettlement West. Those surviving to the present provide much valuable information about the land. Identification of range sites, vegetation types, dominant plant species (especially shrubs), and a general appraisal of apparent range condition are all possible in the photographs. The collection is particularly valuable in its illustration of conditions before the advent of cultivation and domestic livestock. We see in the Jackson pictures pristine western rangeland.

But as estimators of early ecological conditions, the photographs have several inherent limitations. First and most important, interpretation is restrained both by the nature of the expedition and by the photographer's choice of subject. The basic perspective of the Survey was geological, and so many photographs are of bluffs, pediments, and unusual rock formations--more than their relative importance in the landscape might merit. In addition, Jackson was interested in the most photo-worthy subjects from an artistic, as well as a naturalistic, point of view. This caused a definite bias in subject selection toward the striking features of the landscape, especially on the often featureless rangeland traversed by the 1870 survey. In a technical sense important to the present purpose, Jackson did not take pictures of rangeland as such. Therefore, evidence of the ecological conditions of the day is usually incidental to the primary focus of the photographs.

Second, and also very important, the shallow oblique angle and distant orientation in the normal perspective of landscape photographs rule out detailed evaluation of many ecologically important characters. Although dominant plant species usually can be recognized, no definitive information can be gained on species composition, relative plant density, or ground cover. Analysis is confined to the perspective of the camera lens.

Another limitation occurred because the bulky cameras, slow films, and laborious wet-plate photographic process of the 1870's were often unequal to the atmospheric conditions of time and place. Few pictures were taken on windy days, for instance, because rapid movement of vegetation exceeded photographic capability. In addition, blowing dust made wet-plate negatives even more difficult to handle properly; under such circumstances photographs were usually not taken, even though potentially valuable studies were missed.

Lastly, the physical conditions of 1870 travel sometimes imposed restrictions. The number of glass plates an expedition could carry was limited, chemicals and water were sometimes in short supply, accidents and mishaps occurred, and backtracking was infrequent. Consequently, glass-plate negatives destroyed in accidents often could not be replaced, and views flawed by errors in exposure or development were frequently retained.

These characteristics limit, but do not destroy, the utility of the photographs as baseline evidence in a study of ecological change. We cannot identify or conclude as much as we might wish, but what is possible is also valuable.

Presentation

The comparison of each Jackson photograph with its retake was based on site description, appraisal (physical/cultural and ecological), and historical or pictorial qualities. Based on the overall analysis, each site was assigned to one of four change classes:

1. Sagebrush decrease or destruction
2. Sagebrush stability
3. Sagebrush increase or establishment
4. Combination effects.

The photo pairs are presented sequentially within the four change classes, without regard to geographic location. The photosites are identified by the place names assigned by Jackson, and all of the original photographs carry the USGS collection numbers. Figure numbers are identical to the photosite numbers in figure 1.

RESULTS

Sagebrush Decrease or Destruction

Most discussion of the ecological history of big sagebrush (Artemisia tridentata) does not include an argument for its decrease. It is well to remember, however, that European occupation of the sagebrush ecosystem has induced numerous instances of precisely that consequence.

View of the Wasatch Mountains (fig. 2).--One of the most graphic examples of sagebrush decrease has taken place in the Salt Lake Valley. The photosite is now in urban Salt Lake City, and cannot be relocated precisely. But it does not matter, for it is obvious that a large area of big sagebrush has been permanently removed. Estimates of GCI, ARC, and AT are inapplicable at this site due to the advanced stage of urban development.

It is reasonable to suppose that the 1872 photo also represents the presettlement conditions of 25

years earlier, and can be used to help evaluate conflicting verbal descriptions of the Salt Lake Valley such as those of Clayton (cited in Stewart 1941), who reported much grass, and Hayden (1870) who called it "a vast sage plain". It appears that Hayden had the more correct general description while Clayton may have described the somewhat better-watered areas of the initial settlement.

Castle Rocks (fig. 3).--While not as extreme as figure 2, other photographs show evidence of use and management resulting in the decrease of sagebrush. The 1869 photograph of Castle Rocks at the head of Echo Canyon in Utah shows a vigorous, dominant stand of big sagebrush. Based on modern information, we can speculate that the size and density of the shrubs must surely have suppressed herbaceous production. Ecological change evident in the retake photo is certainly due to repeated fires, likely started by locomotive embers on the railroad grade which destroyed the original photopoint. Marks of at least two fires are evident. High on the slope, secondary succession since an early fire has produced a sparse stand of bluebunch wheatgrass (Pseudoroegneria spicata) and Indian ricegrass (Oryzopsis hymenoides), with scattered rubber rabbitbrush (Chrysothamnus nauseosus), serviceberry (Amelanchier alnifolia), Utah juniper (Juniperus osteosperma), and big sagebrush.

A more recent fire lower on the slope, generally below the road cut as indicated by the juniper skeletons, has removed the bluebunch wheatgrass. A fairly even stand of needle-and-thread (Stipa comata), Great Basin wildrye (Leymus cinereus), cheatgrass (Bromus tectorum), and Indian ricegrass dominated by thistles (Cirsium spp.) is now in place. The slope is formed of alluvial deposits, with a great deal of water-worn cobble on the surface. Generally the hillside is unstable (GCI = 61, about half cobble), and in low fair condition with a slight upward trend. If there is a continued absence of fire, big sagebrush may again establish dominance, but more likely it has been permanently reduced on this site.

Camp on Gooseberry Creek (fig. 4).--The influence of agricultural development in southern Idaho can be seen in the photo comparison of a stream bottom surrounded in 1871 by sagebrush-grass uplands. A small relict area, pinched off between a road and the cultivated valley bottom, on the far channel slope indicates that big sagebrush then formed an open savanna (Hull and Hull 1974). The shrub now provides about 20 percent crown cover within a dominant stand of bluebunch wheatgrass and a rich variety of forbs, mostly arrowleaf balsamroot (Balsamorhiza sagittata), yellow salsify (Tragopogon dubius), western yarrow (Achillea millefolium), scarlet gilia (Gilia aggregata), and many others. Accumulation of litter has produced a dense ground cover (GCI = 94), indicating that the site has not been grazed or burned for many years. Range condition is high good to excellent with a slight downward (stagnant) trend.

Outside the relict area native vegetation has been replaced by intensive agriculture. The rolling uplands are in dryland wheat production and the valley bottom grows barley and alfalfa. Like hundreds of thousands of acres elsewhere, former sagebrush lands are now farmland.

Death Rock (fig. 5).--A uniform stand of big sagebrush occurred on the flood terraces at the mouth of Echo Canyon, already in 1869 the site of Echo City, Utah. In the years following, the area became part of a major transportation corridor. The original grade of the old Lincoln Highway was built right through the photopoint. Several railroad and highway grades plus interchanges for both are now in the near vicinity. The construction activity plus one or more fires have destroyed the sagebrush stand. In its place now is a weedy herbaceous community dominated by prickly lettuce (Lactuca serriola), tumblemustard (Sisymbrium altissimum), pepperweed (Lepidium perfoliatum), yellow salsify, and cheatgrass. Fair amounts of Louisiana sagewort (Artemisia ludoviciana) and needle-and-thread can be found. Scattered clones of Gambel oak (Quercus gambelii) and skunkbush (Rhus trilobata) inhabit the rocky outcrops with an occasional big sagebrush. The old highway grade is almost entirely rubber rabbitbrush.

The numerous weeds have produced abundant litter (GCI = 90), but range condition is very low. Long-term trend is slightly upward, but it is by no means certain that secondary succession will reestablish the former sagebrush stand to any significant degree, even though vigorous sagebrush communities persist nearby.

These examples could be multiplied across the entire sagebrush ecosystem. Nearly every acre of upland now devoted to intensive agriculture has been broken out of natural vegetation dominated by sagebrush. Most of the buildings, roads, canals, railroads, and other forms of construction have occupied former sagebrush land. Together with repeated fire, these kinds of changes have reduced the presettlement distribution of sagebrush, often permanently.

Sagebrush Stability

A surprising number of big sagebrush sites photographed by Jackson evince no discernible change more than 11 decades later. Keeping in mind that the photographs do not allow detailed evaluation of changes in plant composition or density, site stability is still evident.

Granite Ridges on the Sweetwater (fig. 6).--A protected cove off the Sweetwater River in central Wyoming supported a vigorous, dominant stand of big sagebrush in 1870. Today big sagebrush remains dominant, joined by rubber rabbitbrush and low rabbitbrush (Chrysothamnus viscidiflorus). The herbaceous population is dominated by needle-and-thread, Indian ricegrass, prairie sandreed (Calamovilfa longifolia), purple prairie clover (Petalostemon purpureum), and prickly pear (Opuntia polyacantha). Low use is indicated by litter buildup in the crowns of plants and in the between-plant spaces (GCI = 67).

Aside from the increase in size and density of the juniper trees in the rocks, this sandy, protected site retains in every way its appearance of 1870. Both the sagebrush dominance and the productive potential of Jackson's time remain, indicating a high degree of site adaptation and ecological stability [ARC: high good; AT: stable].

Badlands on Blacks Fork (fig. 7).--Stability of another kind can be seen in the sharply etched vegetative types surrounding Church Buttes in southwestern Wyoming. The 1870 view shows a stark sandstone outcrop surrounded by a highly saline outwash area from the butte, and areas of deep sand accumulation. Vegetal cover remains very low (GCI = 13) on the saline outwash, composed almost entirely of saltsage (Atriplex gardneri) and shadscale (Atriplex confertifolia). Big sagebrush and low rabbitbrush remain dominant on the sandy "islands" with an understory (GCI = 70) of Indian ricegrass, needle-and-thread, western wheatgrass (Pascopyrum smithii), and annual forbs.

The productive potential of this site was and remains very low. More than a century after the original photograph there is no visible change; the photographs could be interchanged without loss of information at either time [ARC: good; AT: stable].

A Natural Cave (fig. 8).--In 1870 Jackson photographed a sandstone cave near the confluence of Henrys Fork and the Green River which is now just off Linwood Bay on Flaming Gorge Reservoir. The surrounding slopes form a very sandy range site dominated in 1870 by shrubs. The retake view shows a marked increase in size and density of the distant trees but otherwise very little change. The shrubs are primarily big sagebrush with some low rabbitbrush and a few fourwing saltbush (Atriplex canescens). Herbaceous species are mainly needle-and-thread, Indian ricegrass, sand dropseed (Sporobolus cryptandrus), hoary aster (Machaeranthera canescens), fringed sagewort (Artemisia frigida), and prickly pear. On this site, shrub density and ground cover (GCI = 62) appear the same as they were in 1870. Were it not for the change in the junipers, the two views would be virtually identical [ARC: high fair to low good; AT: stable].

The photosite is now within Flaming Gorge National Recreation Area, and the reservoir has created greater physical isolation. Both factors will work toward future stability in use and management of the area.

Scene Near the Head of Red Creek (fig. 9).--Sometimes a major physical change does not induce a corresponding change in vegetation. An example is the headwaters of Red Creek east of Flaming Gorge, where the intermittent stream channel appears to be much more deeply incised today than it was in 1870, and a deep roadcut has been put through the near slope. Yet the vegetation on the sagebrush flat across the valley (GCI = 62) and on the slope (GCI = 44) remains much the same, probably because the soil profiles were already drained. Big sagebrush and both low and rubber rabbitbrush are the dominant shrubs, with abundant needle-and-thread, western wheatgrass, Indian ricegrass and cheatgrass. Livestock use is evident. During the period, juniper trees underwent a decrease and then an increase in the channel area, and a small increase on the foreground and on the far slope [ARC: low fair; AT: stable].

Thus the area displays vegetative stability in spite of major physical change, probably because the essential growing conditions for the vegetation have not been altered. It is likely that these circumstances will continue indefinitely into the future.

Tower on Castle Rock (fig. 10).--In the absence of natural or artificial disturbance, it appears that big sagebrush has the capacity to maintain itself within a community of poor ecological condition. The 1869 photograph of sagebrush just west of Castle Rock in Echo Canyon (fig. 3) shows a vigorous, dominant stand. It is reasonable to suppose that the dense shrubs suppressed herbaceous production in 1869, because they continue to do so today. Big sagebrush is by far the dominant shrub on the site, with scattered low rabbitbrush, bitterbrush (Purshia tridentata), and wild rose (Rosa woodsii). Indian ricegrass is the principal grass, with infrequent bluebunch wheatgrass and Great Basin wildrye, and a general distribution of cheatgrass.

Site conditions have been such that several gullies have developed on the area, including one very deep drainage immediately in front of the photopoint. There is abundant sign of past and current heavy livestock use. Apparent range condition is low fair and apparent trend is downward due to erosion (GCI = 59), but sagebrush remains very vigorous and stable and probably will continue to be so until disturbed to a significant degree.

From these examples of sagebrush stability it is possible to conclude first that big sagebrush was an important plant dominant of late 19th century Rocky Mountain rangeland, second that the shrub represents a genuine climax for these sites, and third that the use and management of the past 115 years have not significantly altered that status.

Sagebrush Increase or Establishment

That big sagebrush has increased markedly as a result of abusive land use is a near-axiom in the ecological history of the sagebrush zone. There is no doubt that such land use has taken place or that sagebrush has increased in distribution or density in some areas. The Jackson photo comparisons contain examples of apparent sagebrush increase or establishment as a response to site conditions of the past decades.

Wahsatch, Utah (fig. 11).--In 1869 a grassy meadow with scattered shrubs (probably gray horsebrush [Tetradymia canescens]) surrounded old Wahsatch Station on the Utah-Wyoming border. In the time since, the meadow shows signs of intense early

use, probably as a result of livestock shipments from the station. In addition, the area was affected greatly by major construction associated with the station, railroad, and highway. These impacts are indicated by the advance of now-mature sagebrush into the meadow. With abandonment of the station these uses abated; subsequent use allowed establishment of a dense sward (GCI = 85) which excluded further sagebrush invasion. The meadow is now dominated by western wheatgrass and alkali bluegrass (Poa juncifolia), with some prairie junegrass, bluebunch wheatgrass, needle-and-thread, Great Basin wildrye, and numerous forbs. There is little sign of grazing use.

Under current management trends, Wahsatch Station will likely continue as a stable meadow excluding further sagebrush increase and even reducing the existing population as the shrubs expire [ARC: high good; AT: upward].

Fort Fetterman (fig. 12).--Ecological changes leading to an increase in sagebrush can be traced to probable grazing mismanagement on some sites. In 1870 Fort Fetterman on the North Platte River was sited on shortgrass prairie with a slight shrub presence, probably Wyoming big sagebrush (A.t. ssp. wyomingensis). In the decades since, a significant increase in sagebrush has occurred, probably initiated by animal concentrations associated with the military post and continued by heavy livestock grazing after the fort was abandoned. The herbaceous understory is now very patchy and hummocky blue grama (Bouteloua gracilis) and threadleaf sedge (Carex filifolia) in low production (GCI = 59). A general distribution of cheatgrass and absence of forbs indicate sheep range. Unless there is some disturbance of the site, it is likely to remain a degraded big sagebrush stand for some time to come [ARC: poor to low fair; AT: downward].

Camp on Blacks Fork (fig. 13).--Blacks Fork in southwestern Wyoming is a desert stream which at this point in 1870 was supporting a grassy meadow lined by trees and shrubs. In the years since, a shrub type developed (GCI = 53), dominated by big sagebrush with some rubber rabbitbrush and occasional black greasewood (Sarcobatus vermiculatus). Grasses still evident in scattered clumps include western wheatgrass, alkali sacaton (Sporobolus airoides), inland saltgrass (Distichlis stricta), and bottlebrush squirreltail (Sitanion hystrix), with some Kentucky bluegrass (Poa pratensis) and Great Basin wildrye in the protection of shrubs. Forbs are mostly weedy annuals. The riparian shrubs are now reduced to a few decadent stems of narrowleaf cottonwood (Populus angustifolia) and silver buffaloberry (Shepherdia argentea) with no reproduction.

These changes are likely due to impoundments and diversions of water upstream, which have lowered the water table and drained the meadow. In addition, because desert streams are oases, the meadow has likely undergone heavy livestock and wildlife utilization. These trends will probably continue to make the meadow warmer and drier than it was in Jackson's time [ARC: poor; AT: downward].

Summit of Black Hills (fig. 14).--Sometimes an increase in big sagebrush occurs as an unintended result of other management programs. Shortgrass plains vegetation similar to that in the 1869 view normally is found on the Laramie Mountains (referred to as the Black Hills in Jackson's time) in southeastern Wyoming. The major visual change in the scene is the establishment of limber pine (Pinus flexilis) and big sagebrush on slopes and in swales having increased snow accumulation. The change is due at least in part to the early use of fences to protect grade cuts from blowing snow. The fences lasted a long time (materials can still be found on the ground), and it is likely they improved site water relations sufficiently to allow shrub and tree development. Now the trees are acting as their own snowfence, continuing the change. An excellent herbaceous understory (GCI = 76) now includes western wheatgrass, needle-and-thread, bluebunch wheatgrass, prairie junegrass (Koelaria cristata), fringed sagewort, and western yarrow (Achillea millefolium). The new community appears very stable, and most likely will continue to slowly expand [ARC: good; AT: stable].

Atlantic City, South Pass (fig. 15).--The increase in big sagebrush on some sites has no ready explanation. One example is the valley above Atlantic City near South Pass, dominated in 1870 by a willow flat (Salix spp.). Patches of quaking aspen (Populus tremuloides), indicated by the numerous snags and down wood, appear to have occupied most of the foreground at one time.

A great deal of change has taken place since 1870, primarily through dredging of the river and road construction. These operations drained the willow flat sufficiently to allow the establishment of conifers. Secondary succession since 1870 has produced a mature stand of aspen. Concurrently, big sagebrush has increased in density substantially, on both the immediate foreground and the distant slope at right center, in response to an unclear ecological impetus. Whatever the reason, big sagebrush has clearly expanded its presence, and now forms a stable community (GCI = 68), with bitterbrush and Idaho fescue (Festuca idahoensis) as dominants [ARC: low good; AT: stable].

Sagebrush Combination Effects

As might be expected, the ecological changes affecting sagebrush density and distribution are not monodirectional on many sites. Various combinations of decrease, increase, and stability can be found, illustrating the hazards of making too-wide assertions about cause and effect in the big sagebrush ecosystem. The dynamic integration of site conditions and land management must be included in the appraisal.

Camp on the Box Elder (fig. 16).--Opposite trends in ecological change have taken place on the Box Elder drainage in central Wyoming. The 1870 view shows a uniform sagebrush-grass community of moderate shrub density. Today the entire bottomland has been put into cultivation, accompanied by an increase in trees. Only the foreground slope

resembles its former condition (GCI = 61), with Wyoming big sagebrush, winterfat (Ceratoides lanata), and yucca (Yucca glauca) the dominant shrubs. Major grasses are blue grama, threadleaf sedge, needle-and-thread, and prairie junegrass; fringed sagewort, prickly pear, and sunflower (Helianthus pumilus) are the most important of numerous forbs. Lower on the slope, black greasewood, rubber rabbitbrush, and fourwing saltbush occur in a blue grama-sedge sod. There is little sign of livestock use on the slope, and it has every evidence of long-term stability. Thus total change in the bottoms contrasts with stable uplands in the Box Elder drainage [ARC: high fair; AT: stable].

A Perpendicular Bluff (fig. 17).--The 1870 photograph of a sandstone bluff (across the canyon from the natural cave in fig. 8 shows a sagebrush-grass community on a sandy range site at the right and a salt shrub stand on the shale outwash slope at left. Today the sagebrush-grass stand remains stable, with big sagebrush, rubber rabbitbrush, sand dropseed, needle-and-thread, and Indian ricegrass as dominants. Shadscale and saltsage with scattered big sagebrush remain on the outwash slope but are much reduced, probably due to disease or insect predation on the short-lived salt shrubs. Bottlebrush squirreltail is now present on the slope in abundance. The swale bottom is still occupied by black greasewood. Stability and change are thus concurrent effects of site ecology, but big sagebrush has remained largely the same [ARC: fair (shale), good (sand); AT: stable].

Evanston Coal Mines (fig. 18).--Frequently the conditions for either sagebrush increase or decrease are attributable to an intensive local disturbance such as mining. For instance, the 1871 view of an Evanston coal mine shows a salt desert shrub community, likely saltsage and winterfat, already heavily influenced by land-disruptive activities associated with the mine and probably by unmanaged grazing as well. The near-certain consequence was that big sagebrush and rubber rabbitbrush assumed almost total control of the site. Only remnant saltsage and winterfat plants survived, with perennial herbaceous plants largely confined to protection of the shrubs. Short of major disruption of the shrubs, it was likely that this site would remain a big sagebrush stand in degraded condition [ARC: poor; AT: slightly downward].

Rapid industrial development of the surrounding area is now under way, resulting in destruction of the sagebrush stand and exposure of bare soil. The remaining sagebrush is as before, but will likely soon give way to development as well. At the same time the steep, rocky slope above the site (GCI = 61) continues to support a shrub-grass community, primarily big sagebrush and bluebunch wheatgrass, in high fair to good condition and stable trend. Thus conditions promoting increase, decrease, and stability of sagebrush have all occurred on this site.

Jackson Canyon (fig. 19).--The 1870 view of a rough cleft in Casper Mountain shows a stable, well-vegetated, intermittent stream channel. The canyon slopes apparently were burned some years previously, replaced in secondary succession by shrubs. Flood flows in the years following have greatly increased deposition of coarse material downstream. The coarse sediments are now dominated by dense silver sagebrush (Artemisia cana). Shrub cover on the uplands is mainly true mountain mahogany (Cercocarpus montanus), with skunkbush, big sagebrush, bitterbrush, and black sagebrush (Artemisia nova). Herbaceous vegetation is primarily bluebunch wheatgrass, prairie junegrass, and threadleaf sedge, with a variety of forbs (GCI = 73). Cheatgrass generally infests the bottomland, probably due to heavy human and livestock use plus the effects of floods. A general compound of both ecological change and stability in sagebrush is evident here [ARC: fair; AT: downward (outwash)].

Portneuf Canyon (fig. 20 and 21).--All of the responses of sagebrush to the use and management of the past 100 plus years can be seen in the modern comparison with Jackson's 1872 views of Portneuf Canyon in Idaho. Big sagebrush has been removed in agricultural development of the stream bottom, together with construction of highway and railway lines. It has also given way to dryland wheat farming on the distant ridges, to construction of an interstate highway, to a limestone quarry, and to urban development (Inkom). The sum of all these influences equals a clear reduction of sagebrush distribution in the canyon.

On the bench in the left foreground of figure 20, however, it appears that sagebrush has increased in size and density, possibly as a result of grazing management. Range condition appears to be in low fair condition, although litter contributed by annual species is high (GCI = 76). Major grasses are Sandberg bluegrass (Poa secunda) and bluebunch wheatgrass with general cheatgrass.

At the same time, it is probable that little change has occurred on the basaltic plateau in the center distance because it is far too rough and broken for the plow and unsuitable to extensive livestock grazing. Except for the increase of juniper, it gives every evidence of site stability. Big sagebrush is by far the dominant shrub, with bitterbrush, skunkbush, and rubber rabbitbrush. Sandberg bluegrass and bluebunch wheatgrass dominate the drier ridges, while Kentucky bluegrass and western wheatgrass are found in the run-in areas. Ground cover is high (GCI = 81 with bare lava rock accounting for 38 points) [ARC: good; AT: stable (plateau)].

Thus at one location, decrease, increase, and stability of big sagebrush can be observed, with each response dictated by the particular combination of environmental factors in operation at that point.

DISCUSSION AND CONCLUSIONS

The Jackson photo comparisons contribute clear evidence toward understanding the ecological history of Rocky Mountain sagebrush rangeland since settlement. As a whole, they lend credence to the following observations:

1. Big sagebrush has a highly site-specific reaction to the use and management imposed on it during European settlement. Whether sagebrush increases, decreases, or remains stable is a function of both the kind of use and site characteristics.

2. There is little doubt that shifts in composition and relative density of both herbaceous and woody species have taken place on most sites. There is no means of assessing the relative magnitude of such changes, however. Based on general and circumstantial evidence alone, it is highly likely that a spectrum of change has occurred, again as a function of kind of use and site characteristics. That spectrum will range from virtually no change to total change, that is, entire replacement of native vegetation.

3. While it is clear that changes in sagebrush density have occurred, it is equally clear that there has been no major shift in sagebrush distribution as a result of use. The Jackson photographs provide evidence for the basic stability of rangeland types: grassland remains grassland, shrub stands retain their outlines, and low potential sites remain so. Only where extensive disturbance has taken place, and not always even then, can sagebrush be found today where it was absent in Jackson's time.

4. In macroterms, the appearance of the landscape today is a fair indication of its presettlement appearance. There is no basis for assuming that much of the big sagebrush distribution is a disclimax or a seral stage toward grassland. The photos support those who assert overall stability in sagebrush rangeland.

Thus it seems that a fair summary of the effects of use and management over the last 115+ years on Rocky Mountain sagebrush rangeland would be that although major change has occurred locally through the direct intervention of man, in any regional or broad-scale definition the sagebrush type remains essentially the same. In following the trail of Jackson, one must conclude that sagebrush <u>is</u> where sagebrush <u>was</u>.

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1985

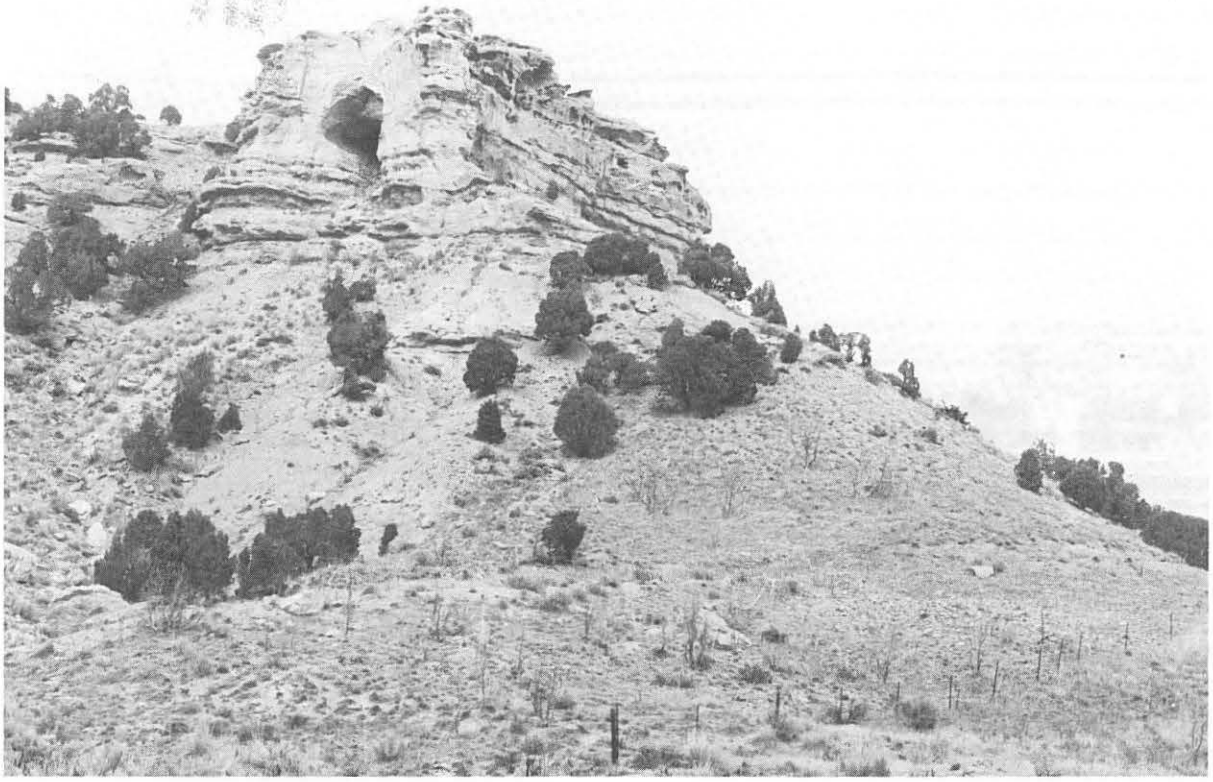


SE

1872

USGS 148

Figure 2.--View of the Wasatch Mountains now in urban Salt Lake City.



1984



N

1869

USGS 26

Figure 3.--Castle Rocks at the head of Echo Canyon, UT.



1985

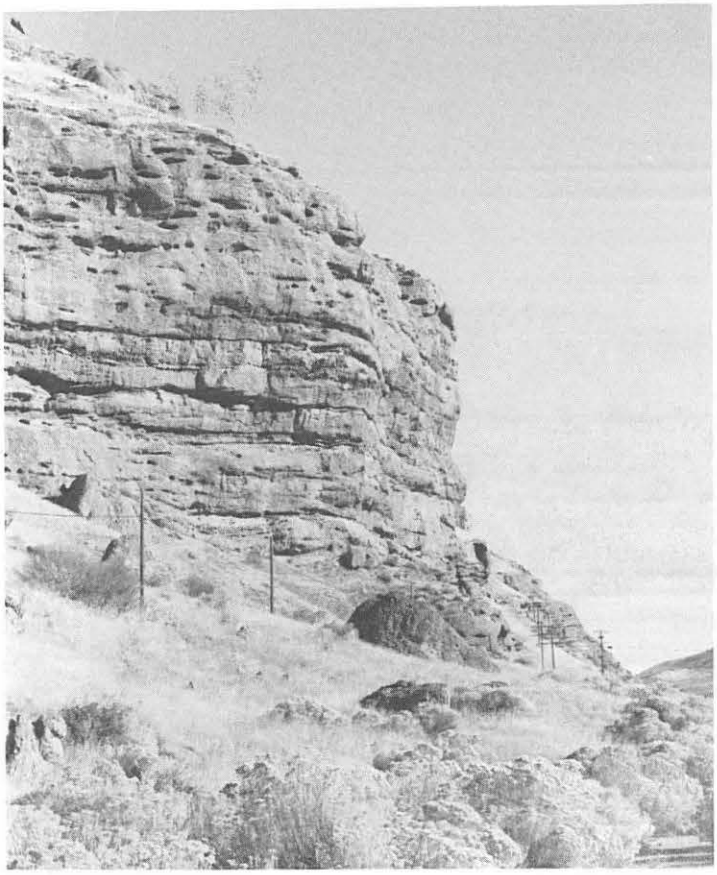


SW

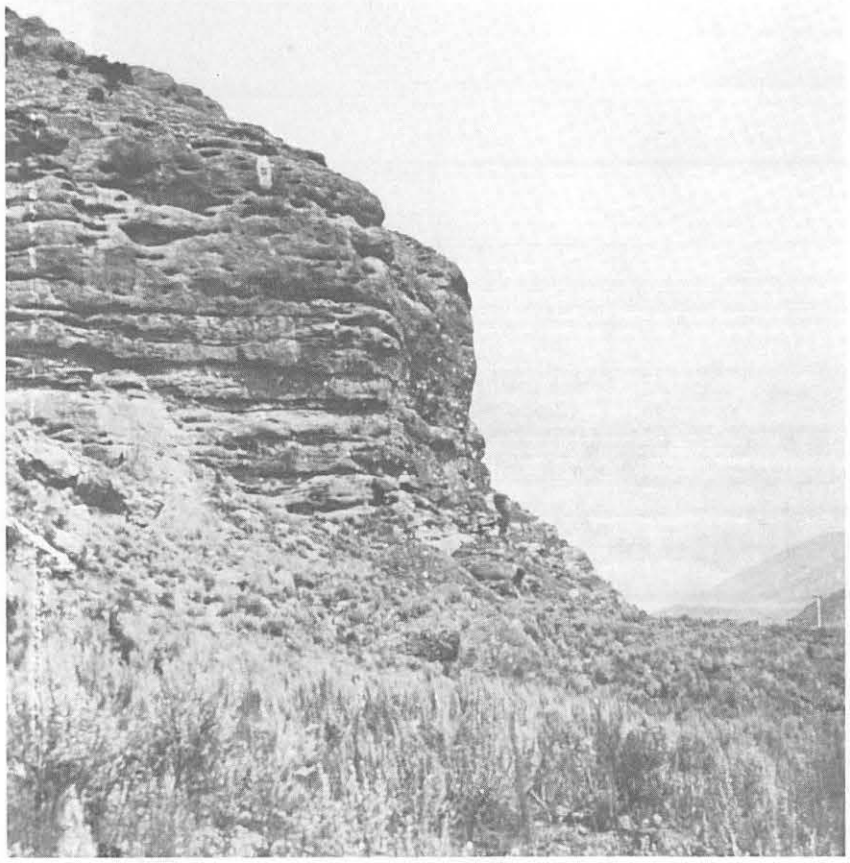
1871

USGS 54

Figure 4.--Camp on Gooseberry Creek in southern Idaho.



1985



NE

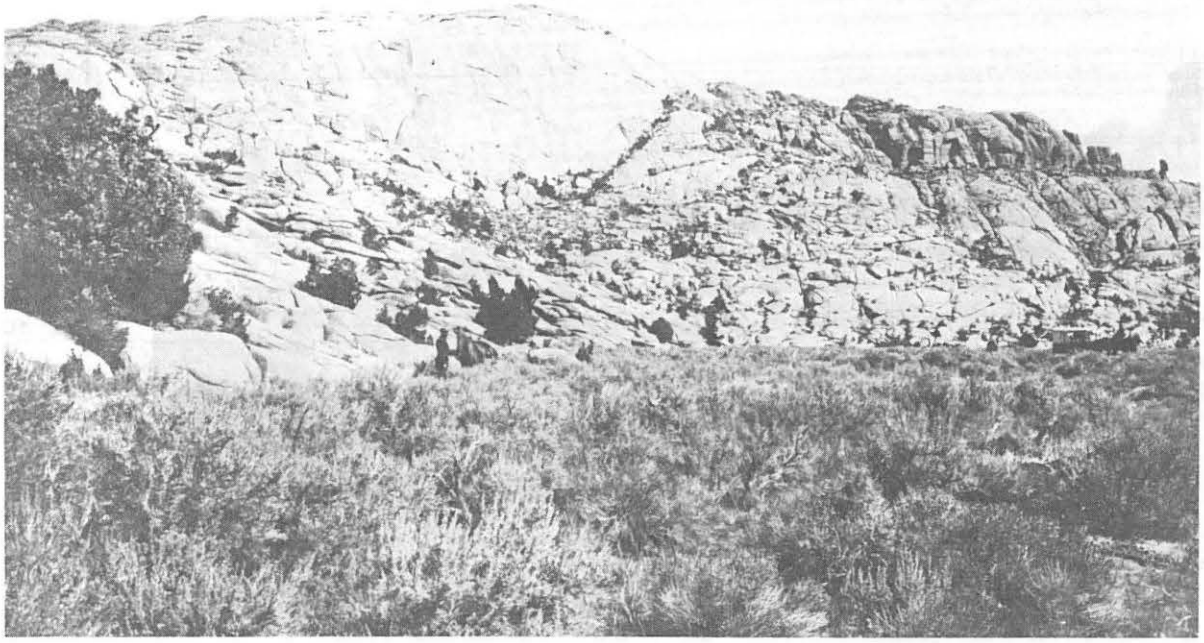
1869

USGS 765

Figure 5.--Death Rock at the mouth of Echo Canyon, site of Echo City, UT.



1978



NE

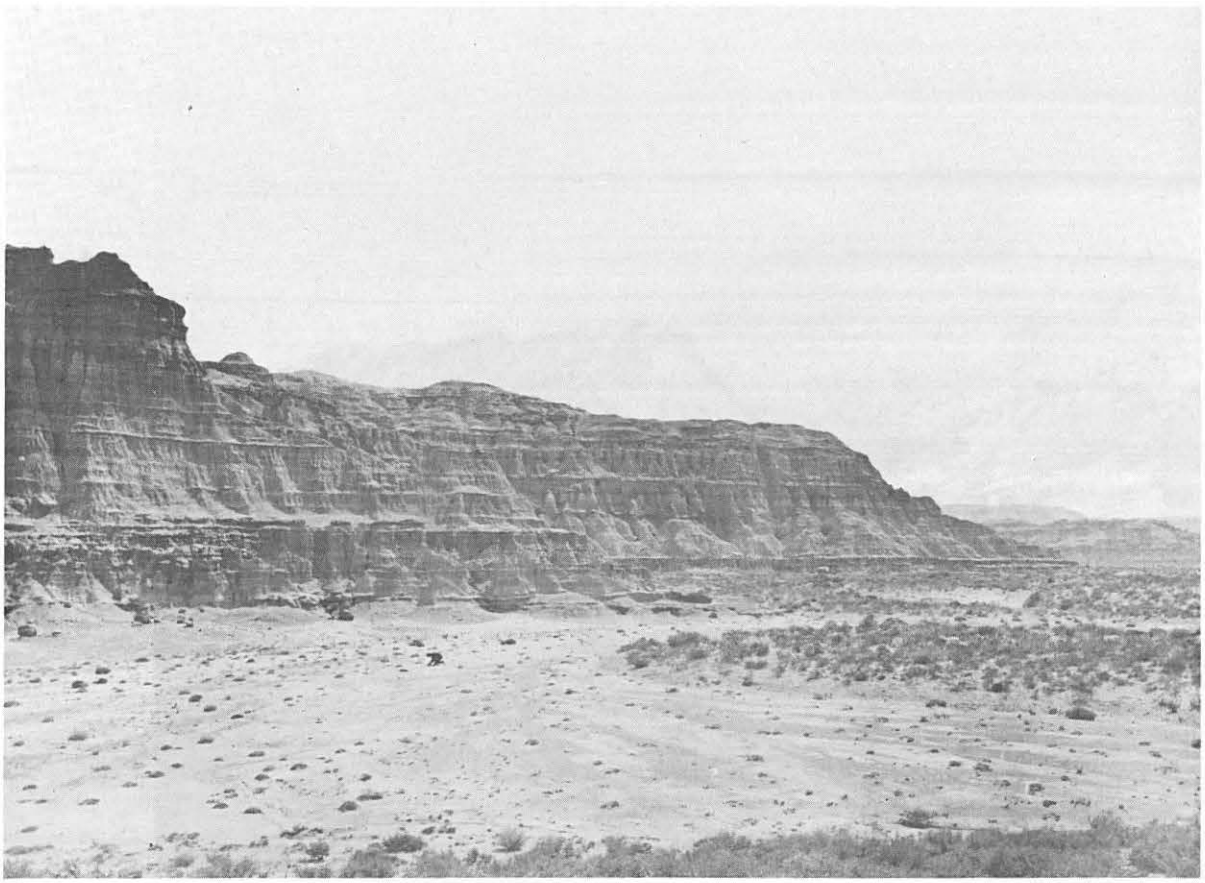
1870

USGS 291

Figure 6.--Granite ridges off the Sweetwater River in central Wyoming.



1978



SE

1870

USGS 308

Figure7.--Badlands on Blacks Fork, now called Church Buttes, in southwestern Wyoming.



1984



W

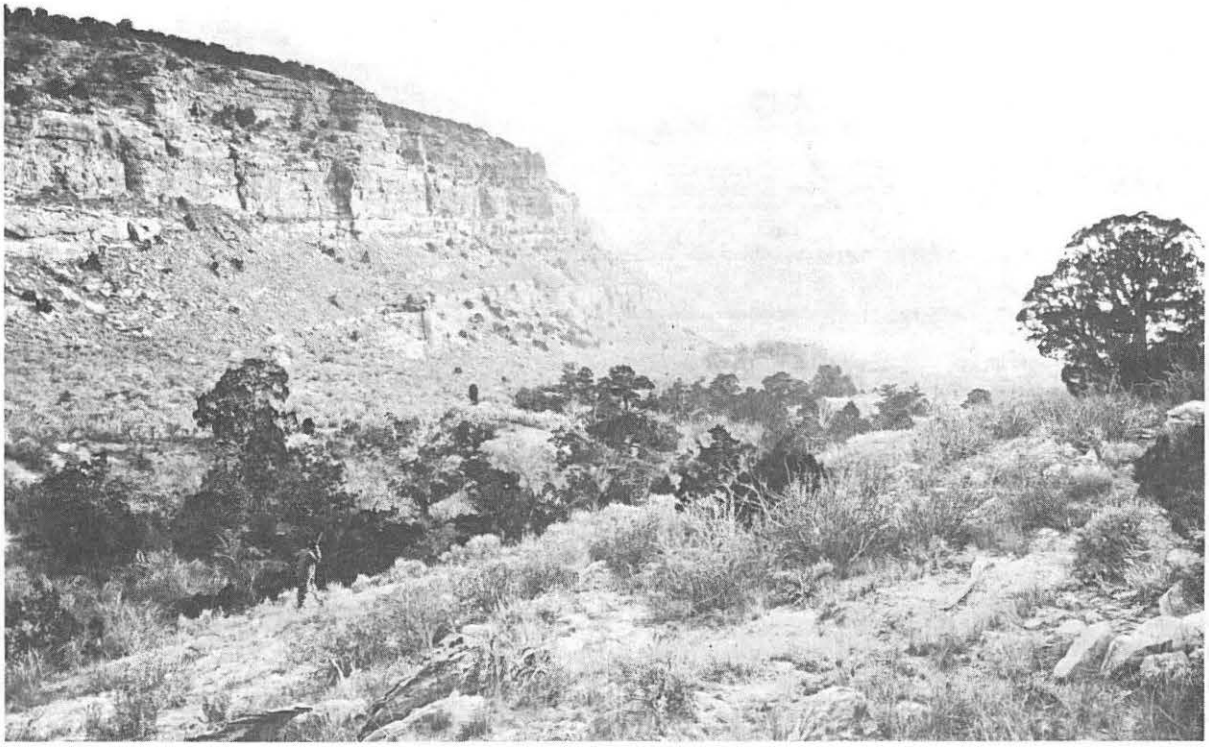
1870

USGS 330

Figure 8.--Sandstone cave near confluence of Henrys Fork and Green River, now Flaming Gorge Reservoir, UT.



1978

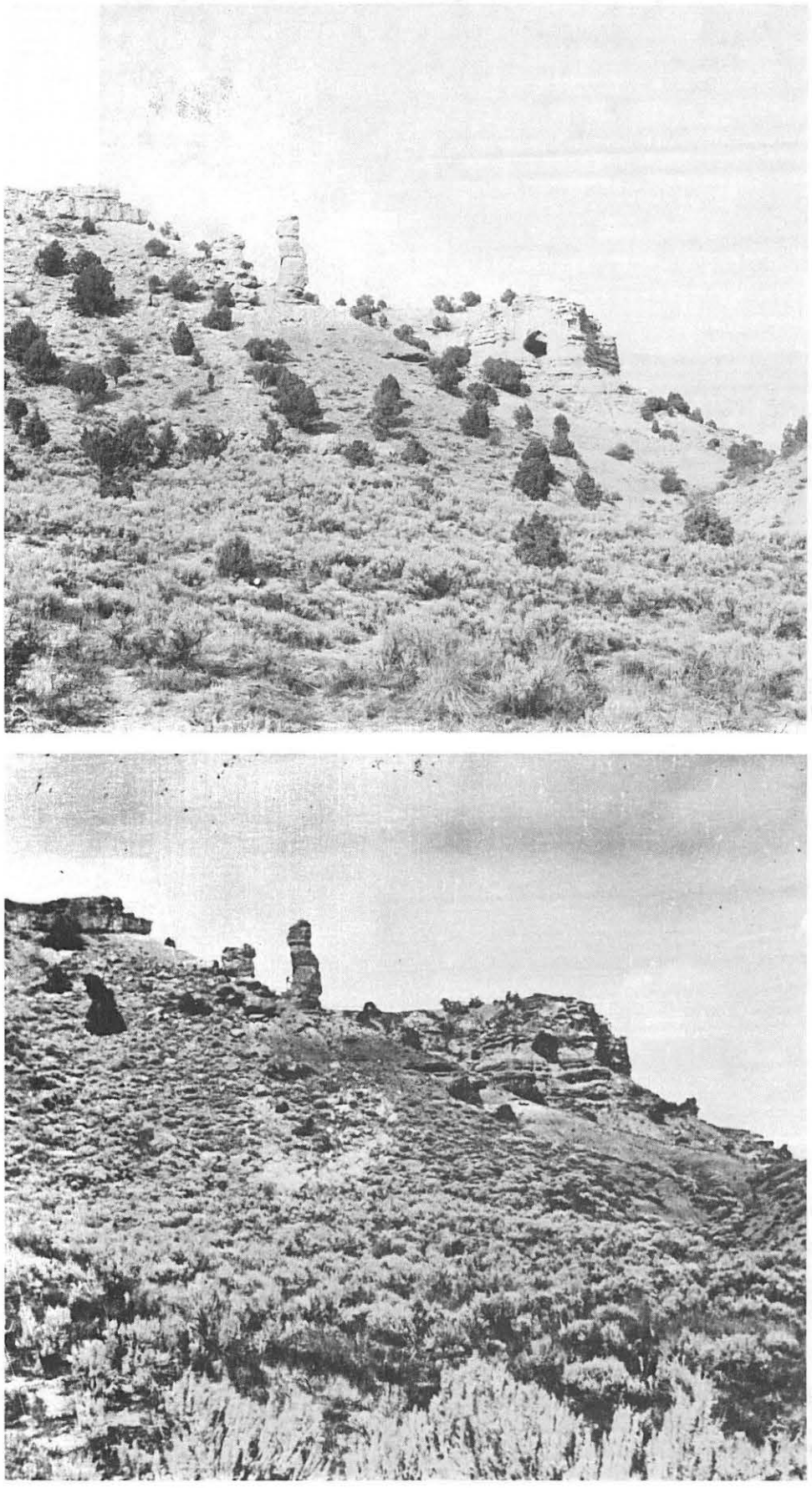


NE

1870

USGS 335

Figure 9.--Headwaters of Red Creek east of Flaming Gorge Reservoir, UT.



1985

NE

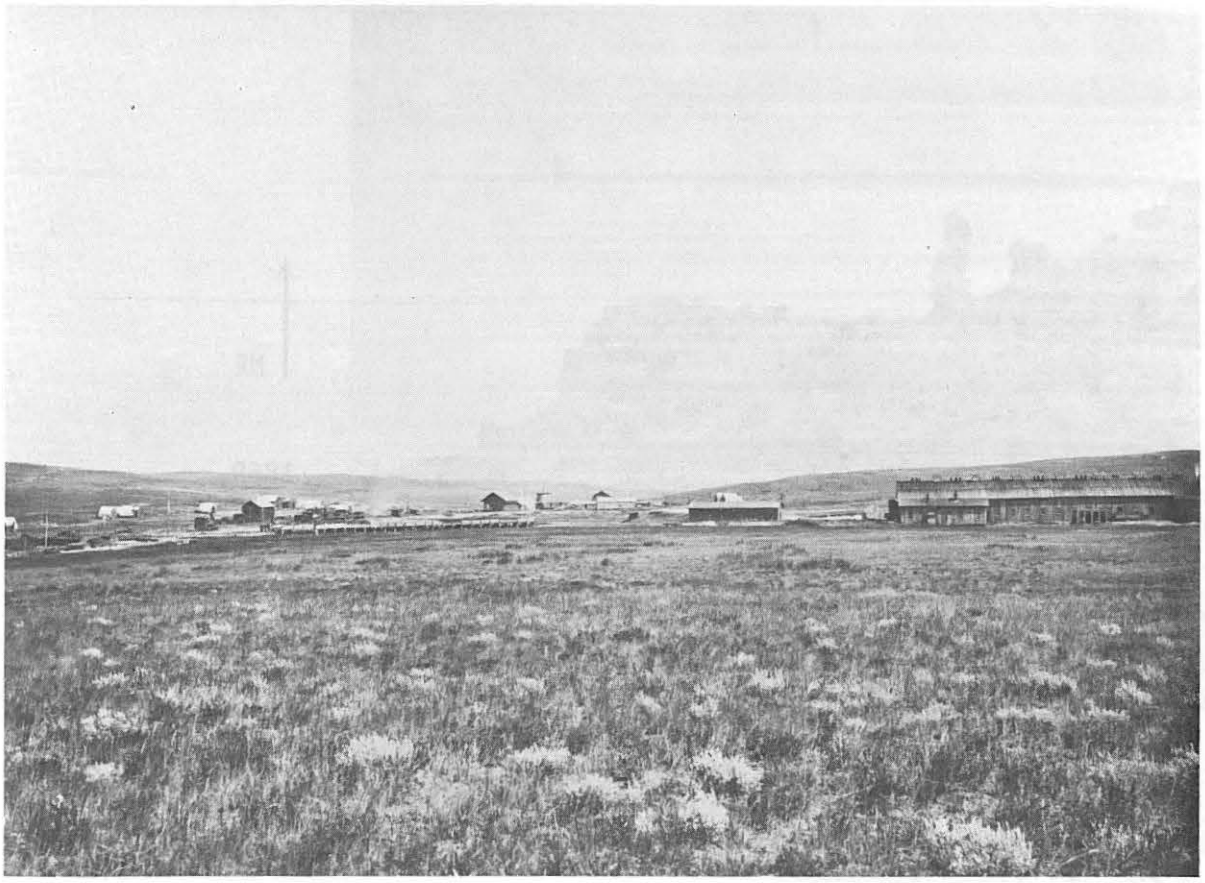
1869

USGS 812

Figure 10.--Tower on Castle Rocks in Echo Canyon, UT.



1985



N

1869

USGS 22

Figure 11.--Site of old Wahsatch Station near the Utah-Wyoming border.



1977



NW

1870

USGS 256

Figure 12.--Site of Fort Fetterman on the North Platte River, central Wyoming.



1978



SW

1870

USGS 305

Figure 13.--Camp on Blacks Fork near Church Buttes in southwestern Wyoming.



1978



NE

1869

USGS 837

Figure 14.--Summit of Black Hills near Laramie, WY.



1979



E

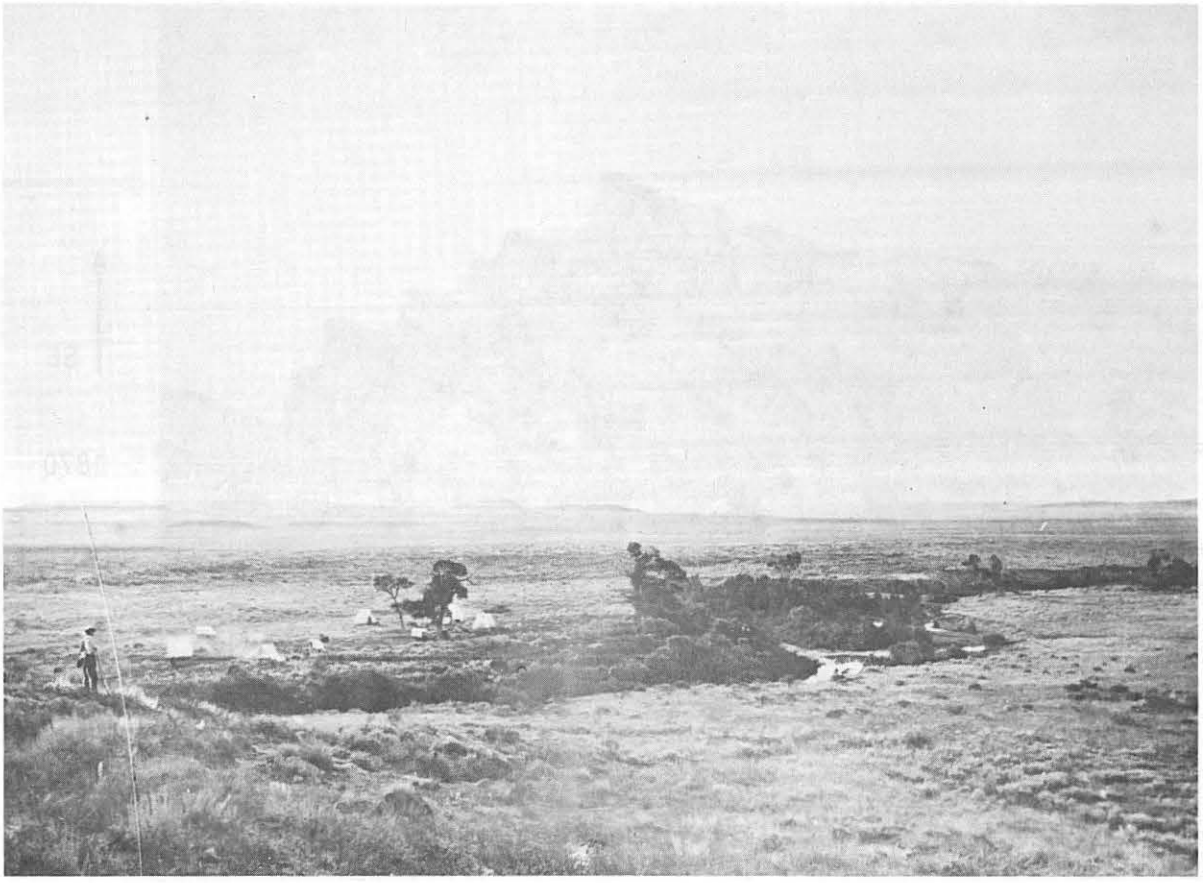
1870

USGS 302

Figure 15.--Atlantic City, near South Pass, WY.



1977



W

1870

USGS 270

Figure 16.--Camp on the Box Elder in central Wyoming.

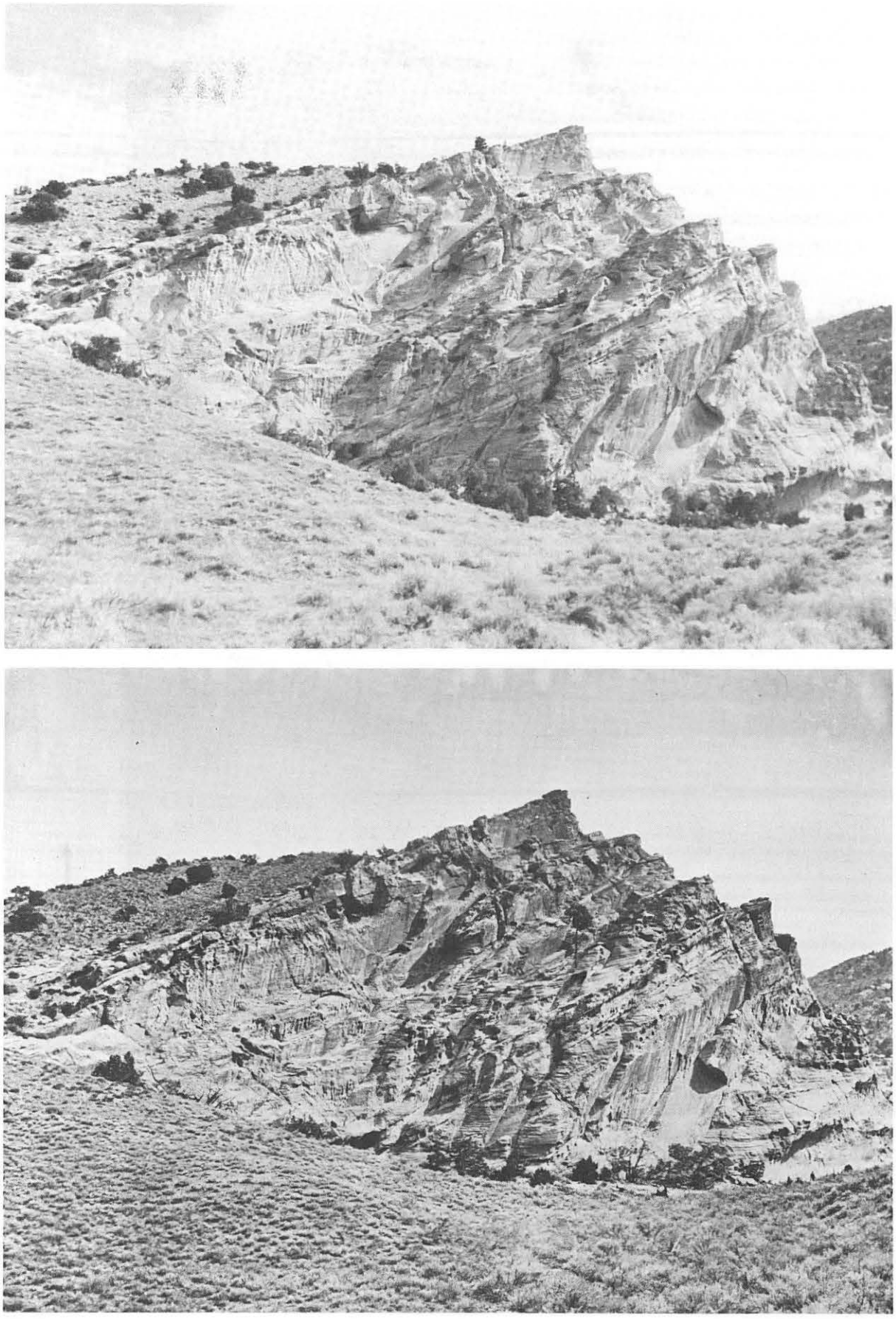


Figure 17.--Perpendicular bluff near Flaming Gorge, UT (see fig. 8).

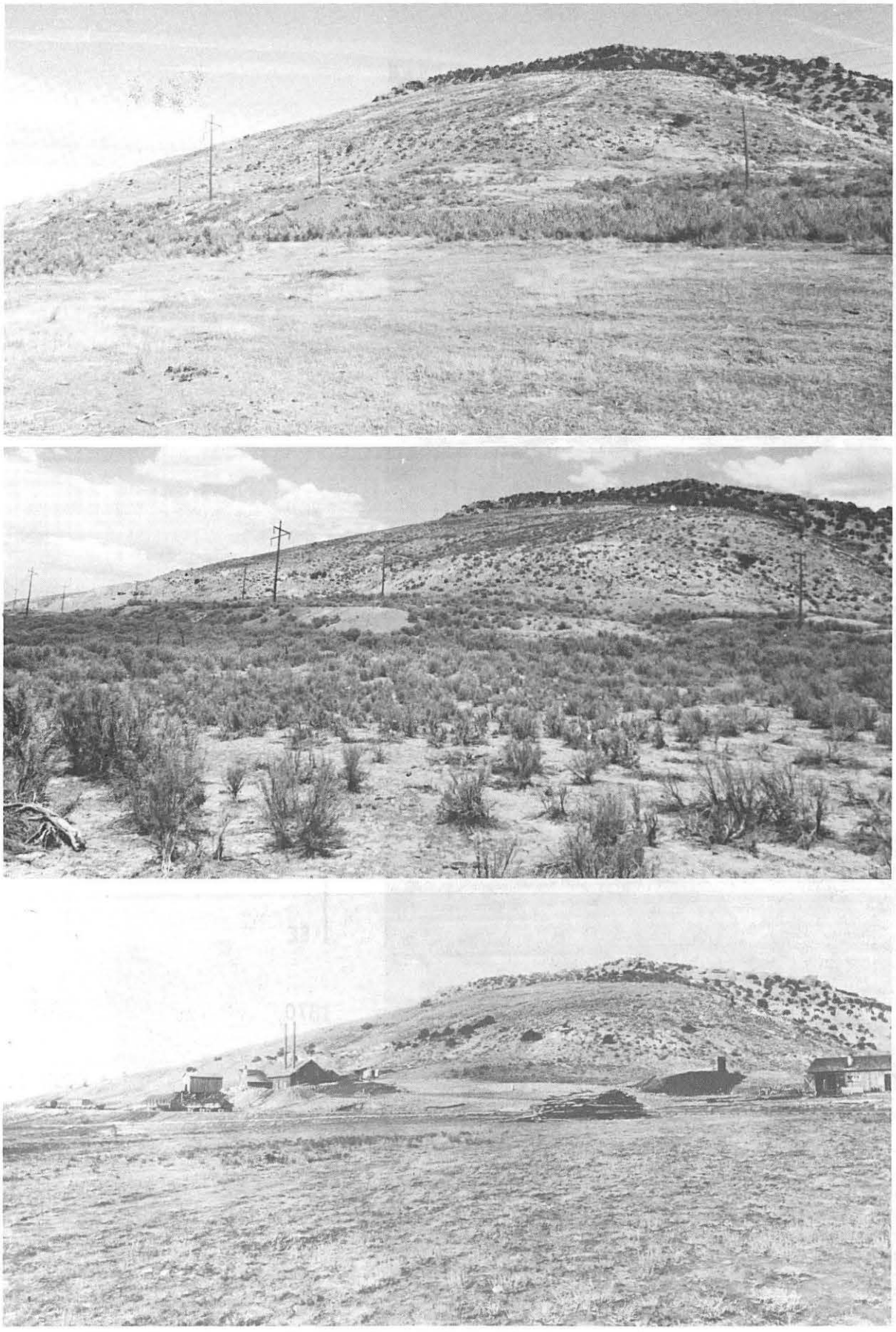
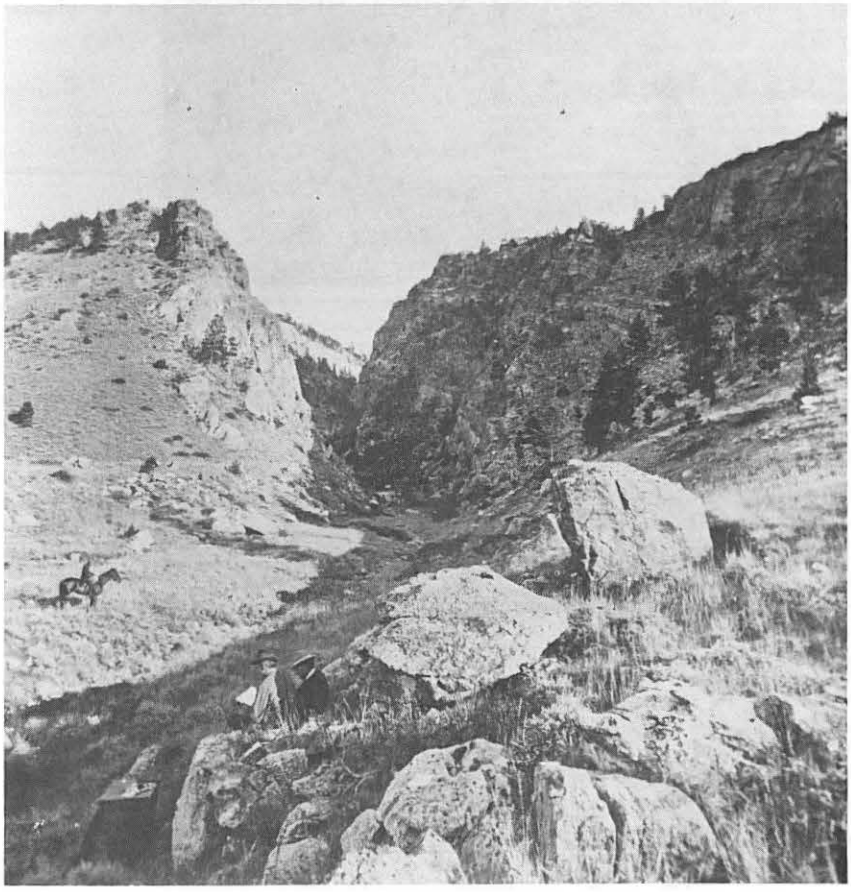


Figure 18.--Evanston coal mines, Evanston, WY.



1977



SE

1870

USGS 869

Figure 19.--Jackson Canyon in the Casper Mountains, WY.



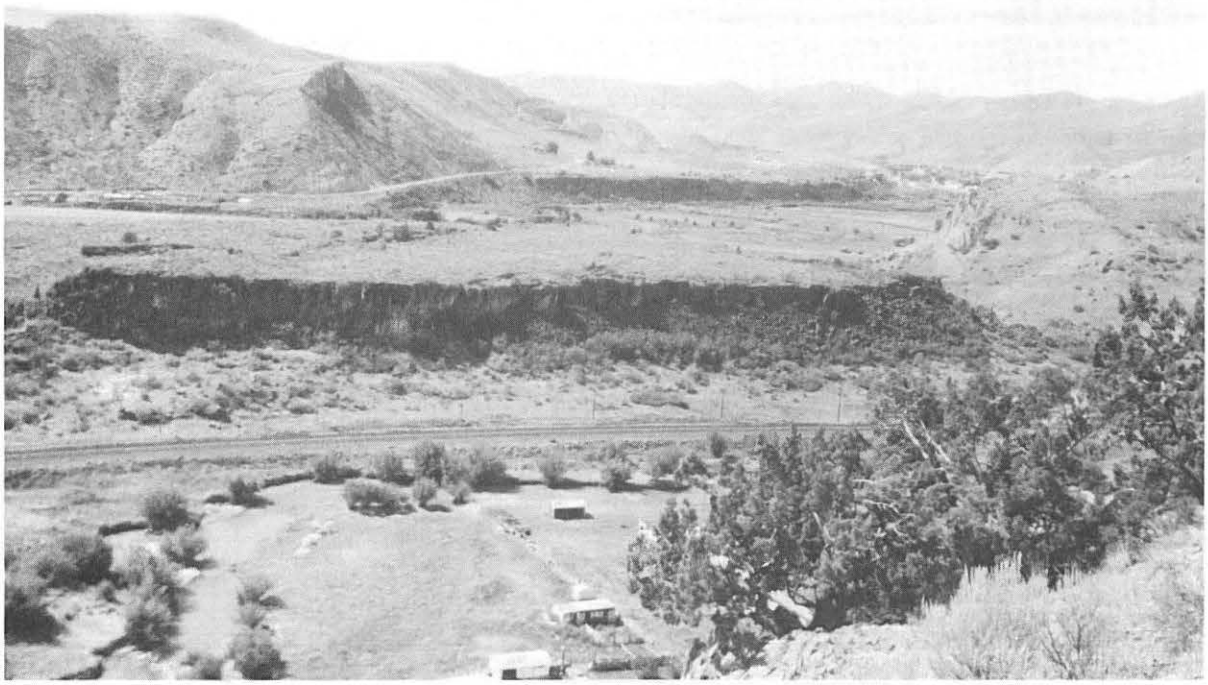
1985

S

1872

USGS 155A

Figure 20.--Portneuf Canyon near the town of Inkom, ID.



1985



NW

1872

USGS 157

Figure 21.--Portneuf Canyon near the town of Inkom, ID.

COMPARATIVE LEAF ANATOMY OF SAGEBRUSH: ECOLOGICAL CONSIDERATIONS

Leila M. Shultz

ABSTRACT: Measures of leaf anatomy are compared with environmental parameters in examining the degree to which sagebrush leaf structure is adaptive. Specimens examined [all members of Artemisia L. subgenus Tridentatae (Beetle) McArthur] are ranked numerically according to habitat aridity gradient and analyzed for trends in anatomical structure according to that gradient. Field-collected specimens are compared to collections from a uniform experimental garden in order to segregate environmentally plastic variation from that which is inherited. Genetically controlled anatomical variation occurs among species in palisade length:width ratios, epidermal thickness, relative volumes of air space, palisade, parenchyma, and relative volumes of xylem. The Xeromorphy Index is a measure of the relative amount of water-conducting tissue in the leaf and reflects the degree of adaption of a species to water stress. Multiple regression analysis shows how various aspects of anatomical structure and leaf morphology may be used in a predictive model relating leaf structure to habitat.

INTRODUCTION

Few studies have addressed ecological or functional aspects of leaf anatomy, largely because of the difficulty of dealing with this morphologically and anatomically most variable of plant organs. Since Haberlandt's (1924) early and largely speculative work on physiological plant anatomy, few studies have directly addressed functional aspects of leaf anatomy. Shields (1950) reviewed earlier works which dealt with leaf xeromorphy and structural influences. Since 1950, ecological studies of leaf anatomy have been limited to descriptions of general trends in xeromorphy and even these have been few. They exist primarily in the work of Philpott (1961), Pykko (1966), Mortenson (1973), and Bocher (1979). The lack of supporting physiological data hinders the consideration of anatomical structure in a functional context.

Paper presented at the Symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

Leila M. Shultz is Research Associate Professor and Curator of the Herbarium, Department of Biology, Utah State University, Logan, UT.

Because the information in this paper would be enhanced by companion physiological studies, much of the discussion is meant to stimulate that interaction and further study. To date, little effort has been made to correlate anatomical structure with habitat gradient or with physiology. This is due in part to the difficulty in quantifying anatomical structure. While quantitative microscopic methods have long been available, they have been largely ignored in the study of leaf anatomy. This study diverges from other descriptive ecological studies in the adoption of methods of quantitative anatomical measurement.

In spite of the predominance and ecological importance of sagebrush in western North America (fig. 1), structural studies of this shrub are practically nonexistent.

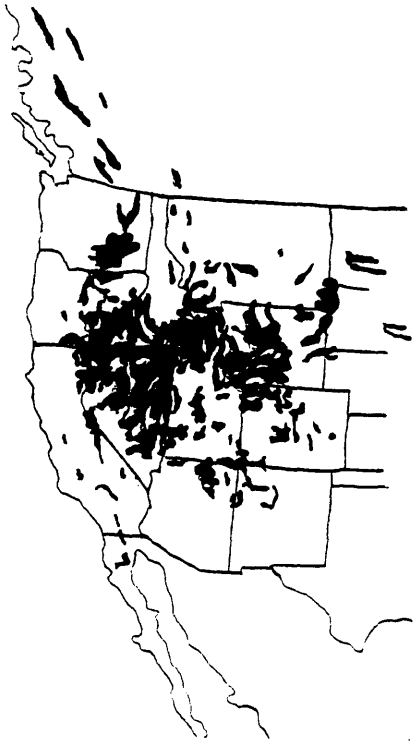


Figure 1.--Map of western North America showing the collective range for all members of Artemisia subgenus Tridentatae.

Previous work in leaf anatomy of Artemisia is limited to the developmental and morphological study of one species, A. tridentata Nutt. by Diettert (1937). The dissertation of Shultz (1983b) provides the first report of leaf anatomy for the 15 other taxa in the sagebrush complex. Two studies in wood anatomy address the ecological significance of structure. Moss (1940) reports the presence and discusses the significance of interxylary cork in stems of sagebrush, and Carlquist (1966) reports data that indicate that there is little variation among species in wood structure. However, the species possess a general pattern which is adaptive to desert habitats.

The principal questions addressed in this study are: (1) What is the range of variation in sagebrush leaf structure; (2) what aspects of leaf anatomy are genetically controlled rather than environmentally modified; and (3) how does anatomical structure correlate with ecological parameters? A related question, but one not explored in this paper, concerns those anatomical structures which show a phylogenetic rather than an ecological distribution. This topic is covered in Shultz (1983b). Patterns of leaf structure discussed here do show taxonomic patterns and may be used to define populations at the level of subspecies.

METHODS

Sampling

Collections for anatomical preparation were made of all sagebrush taxa, in the field, during late summer and fall of 1980, 1981, and 1982. Experimental garden collections were made from the University of Wyoming experimental sagebrush garden established by Alan Beetle. Sixteen of the eighteen taxa of sagebrush have been grown there under uniform environmental conditions. This experimental garden material provided a base of comparison in determining whether certain anatomical structures are environmentally induced or genetically controlled. Detailed measurements are based on those attributes which differ insignificantly between field and garden collections, and are presumably under genetic control.

Mature, late-season leaves were taken from vegetative shoots and fixed in the field. A total of 84 populations were sampled, with leaf sections prepared for microscopic study. Twenty-two collections were selected for intensive anatomical measurement. All anatomical material is vouchered with herbarium specimens and anatomical slides deposited at the herbaria of Utah State University (UTC) and Rancho Santa Ana Botanic Garden (RSA).

Microtechnique

Leaf sections are from mature, late-season leaves fixed in FPA (5 parts formalin: 5 parts glacial acetic acid: 90 parts 70 percent ethyl alcohol). Entire shoots were pickled in order to determine relative age and position of leaves examined. Leaves were dehydrated through a tertiary butyl alcohol series and embedded in a high melting-point paraffin. Leaf sections were cut from a rotary microtome at 10-12 micron thickness. Longitudinal (paradermal) sections and transections were stained with safranin and fast-green, and prepared according to standard microtechnique (Johansen 1940). All measurements are from a high-resolution Leitz compound microscope, at 100 to 400X.

Fiber macerations are from leaves soaked in nitric acid for 24 hours at 58 °C and stained with safranin. Figures for fiber length represent average lengths; all fibers in a leaf were counted.

Scanning electron micrographs are from leaves fixed in glutaraldehyde, dehydrated through an alcohol-freon series, critical-point freeze-dried, and sputter-coated with gold paladium.

Morphometric Analysis

Several measurements are presented here for their utility in defining anatomical adaptions to xeric habitats. The Xeromorphy Index (Shultz 1983a, 1983b) is a measure of relative amounts of water-conducting tissue (xylem) within a leaf. Measurements are from leaf sections cut at 10-12 um. The area occupied by the xylem is calculated geometrically and measured in proportion to all other leaf tissue. The Xeromorphy Index (X) is calculated by dividing the area of the leaf transection (T), by the total vessel area (V), figured in mm^2. V is calculated by sampling 60 vessels in each transection and calculating an average diameter, figuring area as $2\pi r^2$ then multiplying that figure by the total number of vessels in the leaf. This was calculated by projecting the transection onto graph paper and calculating area by squares occupied.

The ratio expressed as "X" remains constant regardless of the position of the section within the leaf and therefore may be calculated from any point in the leaf. The formula calculated relative amount of xylem in the leaf. The higher the Xeromorphy Index (X), the less the amount of conductive tissue in the leaf.

Tissue volumes are figured from a point-intercept sampling method that was devised for this study. The calculation of volumes of palisade, air space, veins (includes xylem, phloem, and accompanying tissues), and water-storing parenchyma (bundle sheaths and their continuations) is modeled from a random sampling technique reported by Parkhurst (1982). Rather than measure from photographs, I took measures directly through the ocular microscope and increased the sample number. Ninety randomized dots were plotted on a grid micrometer. The dots were counted directly from the leaf section, with intercept counts recorded at five different positions in each leaf, providing a random sample of leaf tissues.

Table 1.--Morphological and anatomical data for *Artemisia* collections

Artemisia species	Collection[1] number	Habitat[2] type	Average[3] vessel diameter (μm)	Average leaf area (cm^2)	Xeromorphy[4] Index	Epidermal thickness (μm)	Palisade length/ width	%Palisade volume	%Air volume	%Bundle sheath
arbuscula ssp. *arbuscula*	4510	x	5.5	.28	217	4.0	3.2	47	9	33
arbuscula ssp. *longiloba*	4460	sx	4.5	.08	102	6.0	3.0	53	7	30
cana ssp. *bolanderi*	5680[5]	sx	5.7	.37	128	3.5	3.0	51	25	30
cana ssp. *cana*	5451[5]	m	11.3	.20	111	10.3	4.0	54	14	30
cana ssp. *viscidula*	5421[5]	sx	6.9	.65	141	5.7	3.4	64	8	22
cana ssp. *viscidula*	4500	sx	8.7	.80	85	4.8	3.6	62	16	18
nova	4595	x	4.4	.09	186	5.7	2.3	39	11	35
nova	4557	x	5.4	.10	205	5.5	2.0	48	5	35
pygmaea	4560	xx	4.2	.01	514	8.5	2.1	71	5	14
pygmaea	4576	xx	3.6	.03	496	11.5	2.2	71	5	23
rigida	St. John s.n.	x	5.4	.09	190	4.8	2.8	60	6	34
rothrockii	4707	x	7.6	.29	249	8.5	2.2	41	21	28
rothrockii	5669	x	7.0	.34	250	6.0	2.1	64	11	15
spiciformis	5715	sx	6.8	.65	144	3.2	2.8	49	19	28
tridentata ssp. *parishii*	4600	sx	7.2	.15	110	3.0	2.5	44	3	36
tridentata ssp. *tridentata*	5272	sx	7.0	.45	165	2.8	2.8	37	15	25
tridentata ssp. *vaseyana*	5474	sx	7.1	.60	73	2.8	2.8	46	17	33
tridentata ssp. *vaseyana*	5456[5]	sx	6.8	1.23	80	4.5	3.1	39	24	22
tridentata ssp. *wyomingensis*	5463[5]	x	6.7	.26	200	4.0	2.0	42	6	40
tridentata ssp. *wyomingensis*	McArthur U-80	x	6.3	.75	290	6.8	2.3	55	5	30
tripartita ssp. *rupicola*	5439[5]	x	6.5	.48	201	4.5	2.8	53	9	27
tripartita ssp. *tripartita*	5461[5]	sx	8.4	.13	82	5.9	3.3	45	13	33

[1]Collection number: Shultz, unless otherwise noted. All collections at UTC.
[2]Habitat classifications: m = mesic, sx = semi-mesic, x = xeric, xx = extreme xeric.
[3]Average vessel diameter: average of 30 vessels, from primary veins.
[4]Xeromorphy Index: area of leaf-area of vessels (in transection).
[5]Samples from University of Wyoming - Uniform Experimental Garden.

Percent volumes are calculated from a sample of 450 point intercepts with the number of intercepts with different types of tissue calculated as a percentage of the whole leaf. Graphs are shown with lines for simple linear regressions and r^2 correlations. All graphs are from data summarized in table 1.

RESULTS

The habitat classification (table 2) is a qualitative ranking that is roughly based on patterns of precipitation, soil texture, and my field experience. Taxa are ranked within categories by increasing aridity. More information may be found in habitat descriptions presented in another paper in this symposium (Shultz 1985).

Table 2.--Sagebrush habitat classification

Species ranked in order of increasing aridity: m=mesic; sx=semi-xeric; x=xeric; xx=extreme xeric

Species	m	sx	x	xx
1. A. cana ssp. cana	x			
2. A. cana ssp. viscidula		x		
3. A. cana ssp. bolanderi		x		
4. A. tridentata ssp. vaseyana		x		
5. A. tripartita ssp. tripartita		x		
6. A. tridentata ssp. tridentata		x		
7. A. tripartita ssp. rupicola		x		
8. A. spiciformis		x		
9. A. arbuscula ssp. longiloba		x		
10. A. arbuscula ssp. thermopola		x		
11. A. tridentata ssp. parishii		x		
12. A. rothrockii			x	
13. A. arbuscula ssp. arbuscula			x	
14. A. rigida			x	
15. A. tridentata ssp. wyomingensis			x	
16. A. nova			x	
17. A. pygmaea				x

Qualitative and quantitative data for leaf morphology and anatomy of all species and subspecies of sagebrush (Artemisia subgenus Tridentatae [Beetle] McArthur) are presented for specimens collected from the field as well as from the uniform garden. Conclusions are drawn from aspects of anatomy that do not vary between the controlled and field conditions, or those structures that are apparently genetically controlled. Data for these measures are summarized in table 2.

Leaf Structure and Shape

Leaf architecture of the Artemisia tridentata complex fits a classic xeromorphic pattern in overall reduction in size, closely spaced veins, absence of spongy mesophyll, and a generally thick leaf lamina.

The basic anatomical pattern is illustrated in figures 2-5. Tissues are labeled in the schematic diagram of a leaf section shown in figure 6. The mesophyll of sagebrush leaves is composed entirely of palisade cells and lacks a spongy mesophyll. The xylem is composed entirely of vessels, with no tracheids. Fibers that accompany the veins are either gelatinous (in Artemisia rothrockii) or lignified (all other species). The prominent internal layer of non-photosynthetic parenchyma is the bundle sheath, with continuations and extensions. Resin ducts are present in all of the species and are associated with the veins and adjacent to the xylem. Leaf shape as well as the trend to size reduction in arid habitats are schematically shown in figure 7. All leaves have one central primary vein, two prominent lateral veins, and an intricate network of tertiary minor veins (figure 8).

Data for average leaf area are graphed with the habitat classification in figure 9. Leaves are entire (A. cana), pinnatifid (A. pygmaea), or three-lobed (all other species).

Leaves develop on lateral shoots with internodes shortened to the extent that the leaves are clustered into tight "buds". This arrangement is often referred to as a dolichoblast shoot. The leaves outermost in the cluster develop first. These leaves elongate rapidly in spring after overwintering and are termed "ephemeral" because they drop early in the spring and are easily identified by their unusually large size.

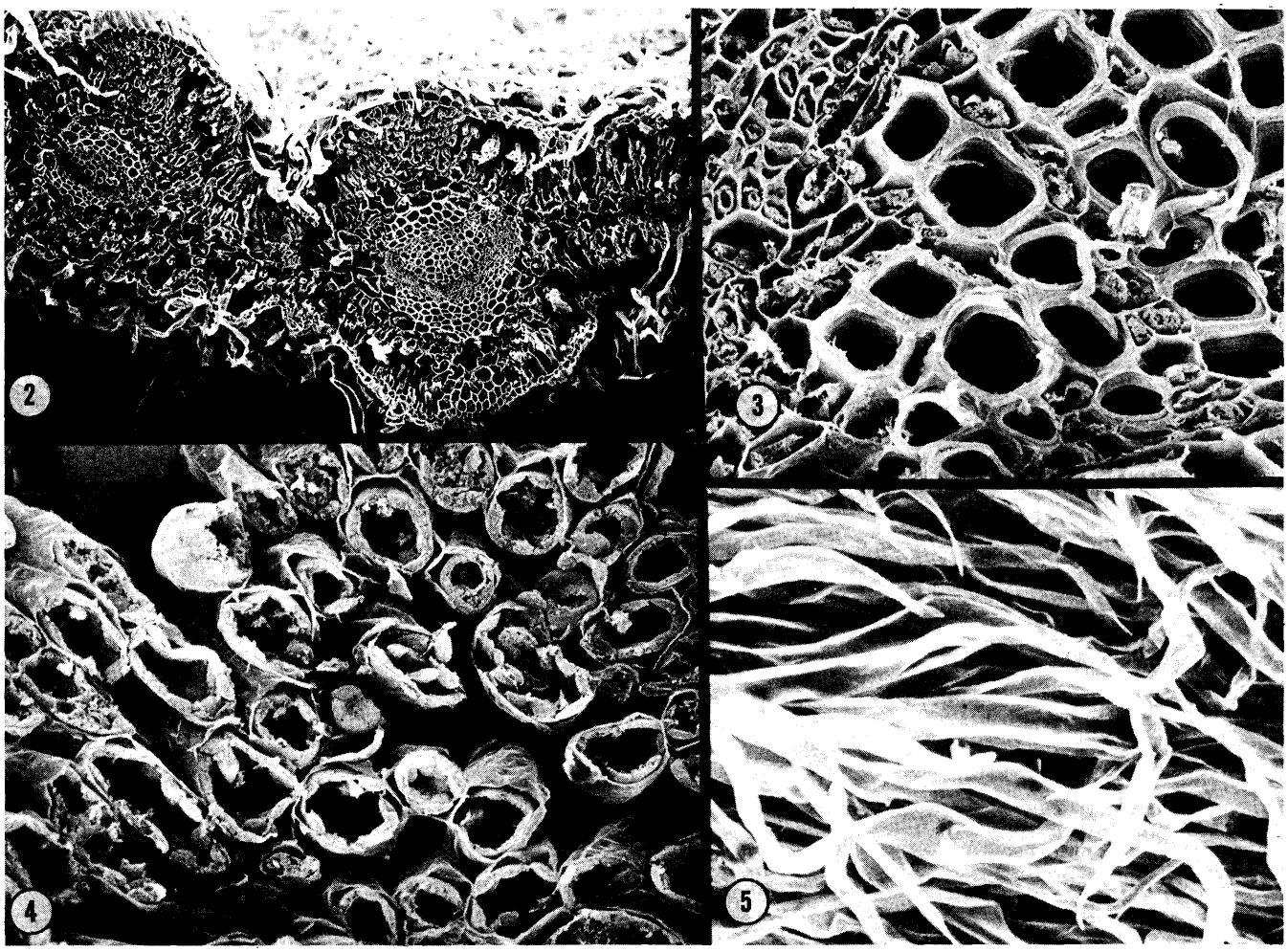
Species of sagebrush are either evergreen with leaves that remain photosynthetically active throughout the winter months, or deciduous after the plants have set seed. The drought-enduring evergreen species are Artemisia tridentata Nutt., A. arbuscula Nutt., A. nova A. Nels., A. pygmaea A. Gray, and A. rothrockii A. Gray. The deciduous, or drought-evading species are A. cana Pursh, A. tripartita Rydberg, and A. rigida (Nutt.) A. Gray.

Leaf hairs (trichomes) are either glandular or air-filled, T-shaped hairs (fig. 3).

The glandular hairs are biseriate, eight-celled, and contain the liquids that give sagebrush its characteristic odor. The T-shaped hairs are uniseriate, two-celled, and filled with air. The air-filled hairs form a dense cover on the leaf surface and are the cause of the silvery appearance of sagebrush.

Anatomical Measures

Xeromorphy Index.--Plants in the wettest habitats have more xylem per unit area than plants in the driest habitats. A high Xeromorphy Index indicates low relative volumes of xylem in the leaf. I devised this measure as a quantitative measure of xeromorphy. The Index shows a high correlation with habitat classification based on aridity (fig. 10).



Figures 2-5. Scanning electron photographs of Artemisia tridentata ssp. vaseyana (Shultz 4425). Figure 2.--Leaf cross-section with two of the three major veins, 140X. Figure 3.--Detail showing helically-thickened vessel walls, 1700X. Figure 4.--Detail of palisade cells. Note interconnecting plasmodesmatal strands, 1700X. Figure 5.--Detail of T-shaped hairs on leaf surface, 500X.

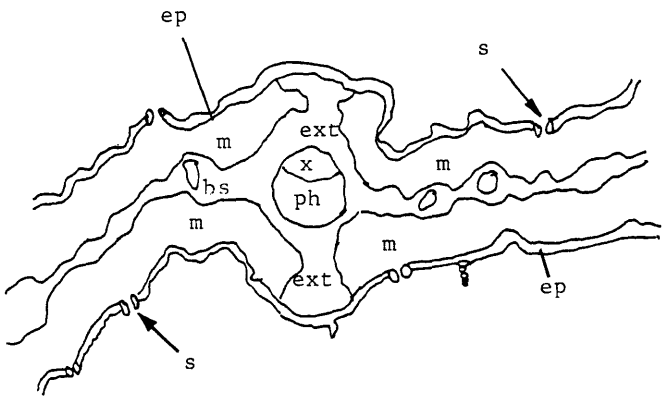


Figure 6.--Schematic diagram of typical sagebrush leaf section showing position of tissues: bs, bundle sheath; ep, epidermis; ext, bundle sheath extension; m, mesophyll (all palisade in sagebrush species); ph, phloem; s, stomatal pore; x, xylem.

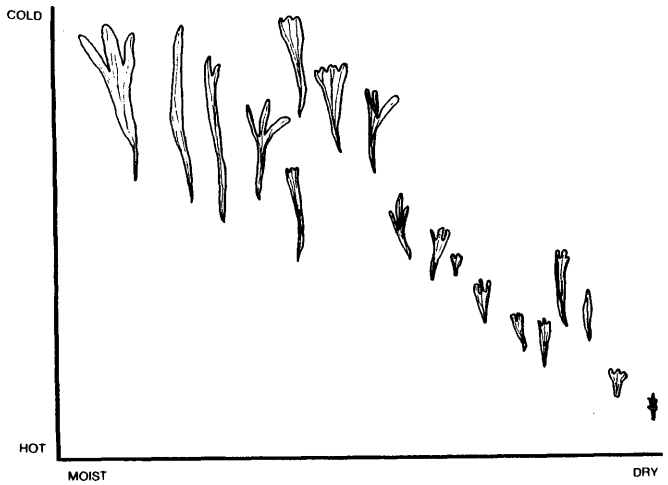


Figure 7.--Leaf morphology of Artemisia showing the trend for leaf reduction in progressing from cold, moist habitats, to hot, dry habitats. Each leaf represents one taxon within the sagebrush complex.

Stomates.--Stomates occur on both upper and lower surfaces and appear to be evenly distributed in most taxa. With the exception A. pygmaea, which has sunken stomates, guard cells are even with the plane of the epidermal wall. Where glandular trichomes are sunken in pits in the epidermal surface, stomates occur at the upper edge of the pit. Guard cells range from 8 to 14 microns wide and 15 to 25 microns long.

Schlerenchyma.--Schlerenchyma is present as fibers and as sclerified walls of the bundle sheath parenchyma. Counts of total fiber number and fiber lengths were made for a few leaves and lengths are presented in table 3.

Epidermal thickness.--Epidermal walls and their cuticles are generally thinnest in the species of mesic habitats. This relationship is shown by plotting average epidermal thickness against the xeromorphy index (fig. 11). Measures are from the area directly over the midvein, where there is no protective covering of hairs and the epidermis and cuticle are thickest. Measures range from 2.5 to 11.5 microns thick (table 2).

Air space volume.--Air space volumes range from 5 to 25 percent. Increasing amounts generally correlate with a decrease in palisade density.

Bundle sheath volume.--Bundle sheath parenchyma completely encircles each vein and forms continuations between all veins with extensions from major veins to the upper and lower epidermal surfaces. This results in a continuous sheet of water-storing tissues embedded within each leaf. Volumes range from 14 to 40 percent of total internal surface.

Volumes roughly increase in species along a continuum from dry to wet habitats, but show the closest correlation with changes in volume of palisade tissue (fig. 12).

Palisade cell length.--The longest palisade cells occur in the most mesomorphic species and the shortest in the most xeromorphic species. The relationship of palisade length to habitat is shown in fig. 13.

Vein densities.--Vein densities range from an average 4.4 per millimeter to 14.3 per millimeter across the width of the leaf. This represents a greater density than reported for sun leaves of deciduous dicots (Wylie 1951) and is adaptation to aridity in that dense vascularization aids in maintaining even internal moisture balances.

Vessel area.--The difference in average vessel diameters among species corresponds to the habitat gradient, with the the widest vessels found in the wettest habitat and the narrowest in the driest habitats. Relative volumes of vessels also decrease with aridity, as discussed in the explanation of the Xeromorphy Index (fig. 14). The percentage of space occupied by veins in the leaf (table 2) does not correspond to the area occupied by the individual vessels. Apparently, as xylem vessels decrease in diameter and number, there is a concurrent increase in other tissue within the veins such as interxylary parenchyma and fibers.

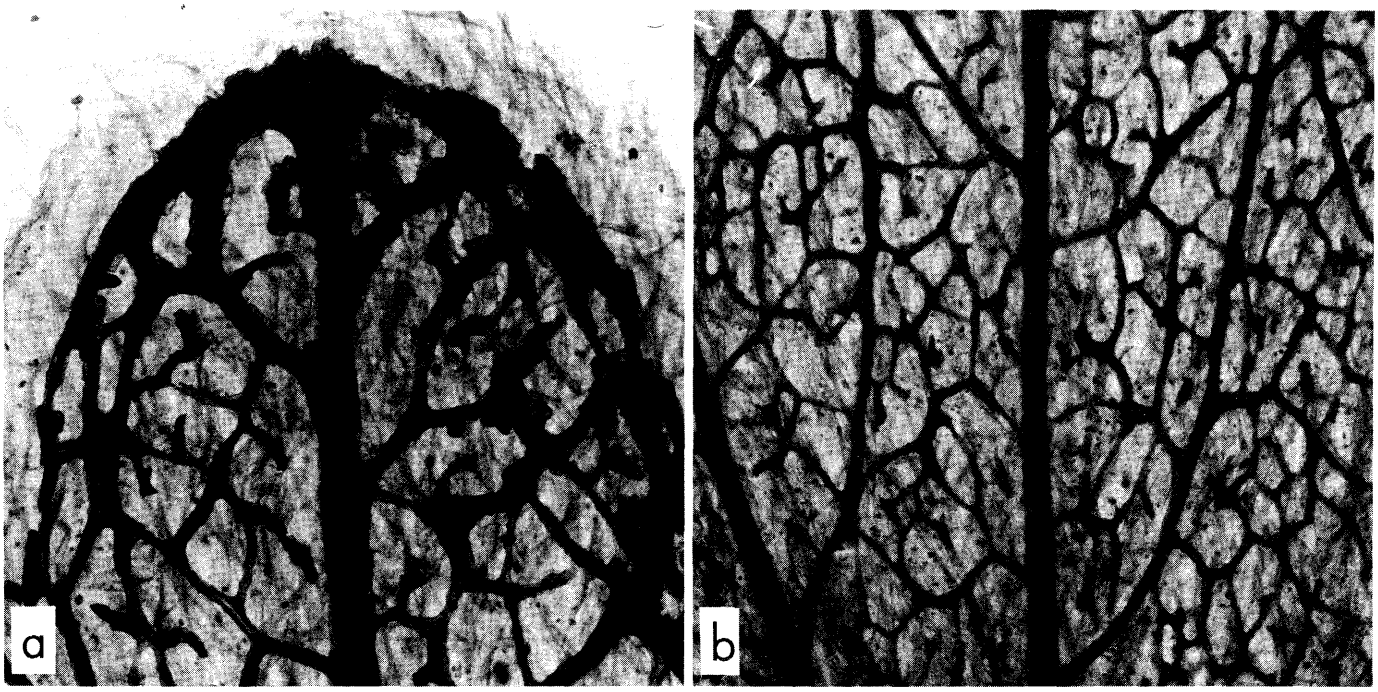
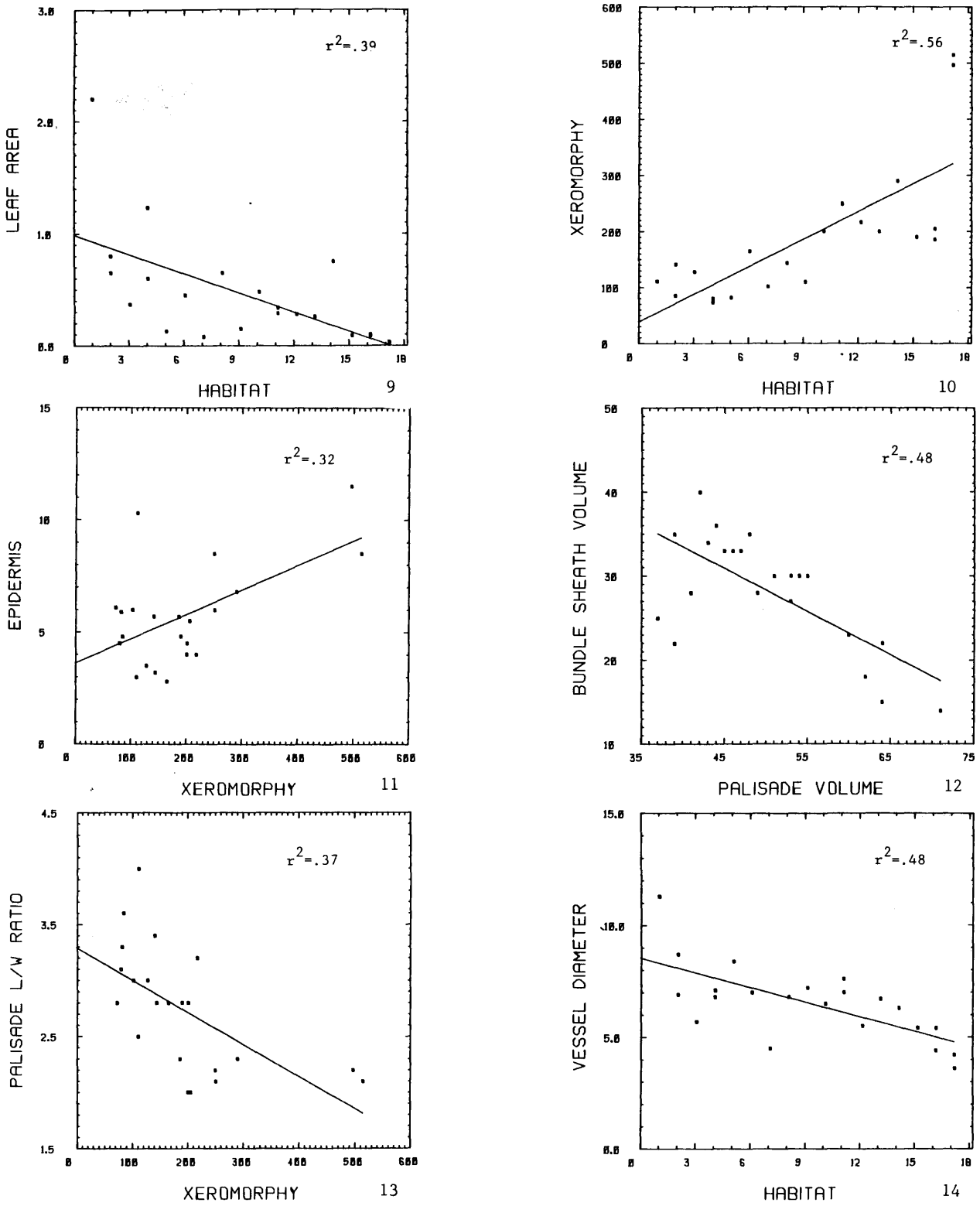


Figure 8.--Vein patterns of Artemisia tridentata ssp. vaseyana, from a leaf clearing. Figure 8a.--Terminal vein ending in one of the leaf lobes. Note hydathodal region at tip of vein and conspicuous sclerified bundle sheath cells. Figure 8b.--Shows central primary vein with secondary and tertiary veinlets.



Figures 9-14.--Correlations of anatomical data to various parameters, as indicated in the separate figures. All data are from table 2.

Figure 9.--Comparison of leaf area to habitat.
Figure 10.--Comparison of habitat to xeromorphy index (from tables 1 and 2).
Figure 11.--Comparison of Xeromorphy Index to epidermal thickness (from table 2).
Figure 12.--Comparison of palisade volume to bundle sheath volume (from table 2).
Figure 13.--Comparison of the Xeromorphy Index to the palisade l:w ratio (from table 2).
Figure 14.--Comparison of the habitat index (table 1) to average maximum vessel diameters (table 2).

DISCUSSION

Leaf structure is obviously correlated to plant habitats and thus plays a significant role in plant function. Figure 15 diagrammatically shows the relationship of leaf structure to physiological measures of water loss and provides a useful reference for the following discussion of leaf structure and function.

Because comparative physiological and ecological data are lacking for the species of sagebrush, I am limited to a discussion of ecological aspects of leaf anatomy in relation to general and rather crude patterns of habitat aridity. Ideally, the data presented in this study would be correlated with physiological data. While extensive studies have been made of Artemisia tridentata (Caldwell 1979), data are not available for other species of sagebrush. We know from the work of Caldwell and his associates that both stomatal resistances and water potentials are high in Artemisia, as expected for xeromorphic shrubs. Until physiological data are available for other species, this work will rest as a report of anatomical structure as it relates to general trends in environmental gradients.

The leaf arrangement as short clusters on leafy shoots may be adaptive in cold as well as dry environments in that the tight leaf clusters are self-insulating and provide protection from rapid temperature changes, from cold as well as from heat. The shading effect of overlapping leaves may be especially important in the summer time and provides protection to developing leaf primordia. Leaf hairs are among the first structures differentiated from the leaf primordia and both glandular and air-filled hairs cushion and surround the layers of leaves in the fascicle. Protective features of leaf hairs are thus available during rapid meristematic growth.

The ecological significance of hairs on leaf surfaces varies according to type of hair as well

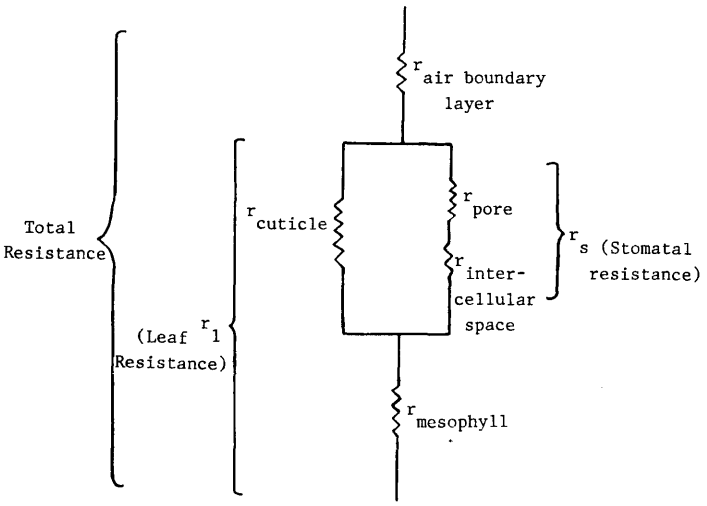


Figure 15.--Model of total leaf resistance to water loss showing roles played by various structures within the leaf (redrawn from Kramer 1983).

as varying between species. Studies of Encelia indicate that the importance of pubescence is in modifying the heat load of the plant. Hairs increase light reflectance which in turn regulates leaf temperature at a thermal optimum for photosynthesis (Ehleringer and others 1976; Ehleringer and Mooney 1978).

In Encelia, hairs are simple and there is no stalk as in the T-shaped hairs of Artemisia. The elevated hair layer in Artemisia T-shape creates a dead air space next to the epidermal surface and the dense cover of hairs extends the leafy boundary layer as well as reducing heat load by increasing light reflectance. Thus, the T-shaped hairs of Artemisia probably function in reducing transpiration by trapping air and raising relative humidity of the leaf surface as well as

Table 3.--Fiber length and abundance

Taxon (Artemisia)	Collection	Leaf Length	Fiber Length	Fiber No.
A. arbuscula ssp. arbuscula	Shultz 4510	12 mm	575 um	108
A. arbuscula ssp. longiloba	Shultz 4460	5 mm	289 um	67
A. cana ssp. viscidula	Shultz 4508	12 mm	727 um	53
A. nova	Shultz 4550	10 mm	531 um	88
A. pygmaea	Shultz 4560	4 mm	370 um	1400
A. rigida	St. John s.n.	n.a.	738 um	630
A. rothrockii	Shultz 4706	7 mm	677 um	198
A. tridentata ssp. parishii	Shultz 4600	n.a.	857 um	40
A. tridentata ssp. vaseyana	Shultz 4442	7 mm	376 um	13
A. tripartita ssp. tripartita	Ballard 6	12 mm	396 um	31

functioning in reducing leaf temperature. Glandular hairs form the site of synthesis of anti-herbivore compounds that significantly contribute to the success of sagebrush. Gland cells exude monocyclic and acyclic monoterpenes (Stangl and Greger 1980) as well as sesquiterpene lactones (Kelsey and Shafizadeh 1980).

Microscopic differences in anatomical structure are closely correlated to the habitats in which different species and subspecies of sagebrush occur. Several measures are presented here for the utility in defining anatomical adaptations to xeric habitats. These difference are measured as: (1) variance in relative volumes of leaf tissue; (2) differences in leaf surface to volume ratios; (3) variance in leaf size; and (4) variance in amounts of water-conducting area in the leaf. These data are summarized in table 2. The discussion of anatomical variation deals with ecologically significant aspects of the variation.

The relationship of the Xeromorphy Index to habitat (fig. 10) suggests the physiologic importance of relative amounts of xylem in leaf tissue. The diminution of water-conducting tissue in increasingly arid habitats apparently provides a means of conserving water.

The individual water conduits, or vessels, vary in width and abundance according to habitat. The widest vessels in the sagebrush complex occur in the species of mesic habitats (Artemisia cana) and the narrowest in the most xeric habitats (A. pygmaea). For structural reasons, it is reasonable to assume that narrow vessels have a greater resistance to negative tensions in the water column and that wide vessels would be more likely to collapse from the pull of high negative water tensions. Negative water potentials of -70 bars have been reported for A. tridentata (Dina and Klikoff 1973) and presumably higher negative tensions would be found in species of drier habitats.

Although limited quantitative data are available, stomatal densities do not appear to be a sensitive indicator of environmental gradients among species of sagebrush. Stomatal densities do not vary greatly among the taxa, except for Artemisia pygmaea, which has approximately twice the stomatal density of other species. As expected from habitat and growth form, A. pygmaea also has the most xeromorphic leaf structure. The largest guard cells and pore openings are found in the polyploid species A. rothrockii, A. tridentata ssp. wyomingensis, and A. spiciformis (McArthur and Pope 1975; McArthur and others 1981). Larger pore openings would obviously compensate for lower stomatal densities, but these measures remain to be calculated when corresponding water relations data are made available.

Fiber length apparently correlates more with leaf length than with habitat parameters. Correlations here become circular, however, in that leaf length is somewhat relative to leaf size, which in turn correlates to habitat (figures 8 and 9). Fiber abundance dramatically increases with habitat aridity (table 3). The most mesomorphic species have the fewest fibers (Artemisia cana and A. tridentata ssp. vaseyana); the greatest number occur in the most xeromorphic taxon, A. pygmaea.

Transport and storage of water appears to be the major function of the bundle sheath. An internally embedded layer of water-storing and transporting tissue should be a considerable advantage in leaves where water is limited, and appears to be a very effective specialization in desert plants. Because the sheath separates veins from photosynthetic parenchyma (fig. 6), water must move through the sheath before reaching the mesophyll. The sheath continuations provide a route for movement of water--internally in the intervein connection, and outwardly in connection to the epidermis, a layer which also provides lateral water transport. Since the sheath parenchyma cells are all contiguous they inhibit air movement between upper and lower portions of the leaf. The simple pits between the cells allow the free exchange of water. Stomates occur on both upper and lower leaf surfaces and provide the means of gas exchange to the mesophyll above and below the water-storing parenchyma.

Storage of metabolites and waste products appears to be another function of the sheath parenchyma. The visible amount of material within the sheath increases during the growing season. Late season leaves show an especially high amount of stainable materials. Changing concentrations of sugars in the sheath cells is an effective means of making osmotic adjustment within the leaf.

The significance of differing relative volumes of airspace is not clear since there is no simple correlation with environmental gradients. Generally, the smallest air volumes and therefore the most densely packed palisade are found in plants growing in the driest habitats. However, species growing in extremely arid habitats occasionally have very high volumes of air space, such as Artemisia rothrockii. Other factors such as internal layers of cuticle and shapes of palisade cells should be considered in the evaluation of the internal water balances. An optically refractive layer surrounds the palisade cells of A. rothrockii. This is similar to the internal cuticular layers reported by Frey-Wyssling and Hauserman (1941), and would reduce water loss from palisade cells. This protection from water loss in well-aerated leaves would explain the unexpectedly high volumes of air space in A. rothrockii.

Species of Artemisia that are winter-deciduous generally have greater volumes of air space than the evergreens; the drought-enduring evergreens generally have a more densely packed palisade and lower volumes of air space. The significance of an internal aerating system has been explored by a number of workers. Turrell (1944) found that internal to external surface ratios and transpiration rates are positively correlated with the volume of intercellular air space. Schroder (1937) demonstrated that unwatered plants show a 30 to 52 percent decrease in intercellular air

space. Likewise, the lesser amounts of intercellular air space in evergreens (Nius 1931) may be a corollary of reduced air space in water-stressed plants. Low amounts of internal air may have a limiting effect on rates of CO_2 exchange. Mooney and Dunn (1970) observed that limitation of water loss by evergreens during periods of drought may result in reduction of the rate of CO_2 exchange between the ambient air and chloroplasts.

Physiological studies suggest that, for structural reasons, leaves with a mesophyll composed entirely of palisade have greater photosynthetic efficiency than leaves with spongy mesophyll. This is due to the maximal exposure of chloroplasts to light and carbon dioxide in the elongate palisade cells. Because of the large surface area of palisade, up to 1.6 to 3.5 times are great as that of spongy mesophyll (Turrell 1936), there is also a greater potential for water loss. Experimental studies show that water deficits as well as high light intensities contribute to increased development of palisade. Perhaps even though internal surfaces are increased, the overall reduction of external surface is of critical importance to plant water relations.

Table 4 shows the results of a multiple regression analysis in which habitat classification is compared to four variables: the Xeromorphy Index, volume of air space, epidermal thickness, and palisade length:width ratio. For reasons already discussed, one variable alone does not demonstrate leaf xeromorphy. However, these four aspects of leaf anatomy used in a model show greater than 85 percent correlation to habitat and may be used in predicting fitness of a leaf structure to arid habitats.

Table 4.--Regression analysis using habitat as the dependent variable

Range: 1-22

	Coefficient	Standard error
Constant	3.413	0.490
Xeromorphy index	9.999	.999
Leaf area index	-.308	.179
Percent air volume	-.013	.010
Epidermal thickness	-.030	.039
Palisade L/W ratio	-.358	.158
R-SQ.: 0.893	Corr. R-SQ.	0.860

SUMMARY

Leaves of Artemisia fit a xeromorphic pattern in a number of measures. Ecologically significant anatomical variation exists in the amount of palisade tissue, amount of water-storing parenchyma, degree of palisade packing, vessel diameters, and relative amounts of xylem within the leaf. With increasing aridity, compensation in leaf structure occurs in: (1) relative amounts of water-conducting tissue, expressed as a high Xeromorphy Index; (2) amount of air space or internal cuticular layers; (3) vessel diameter; (4) palisade length/width ratios, and (5) epidermal wall thickness. While there is not a precise linear correlation of habitat and trends within any one of these measures, that they act together as a leaf system is demonstrated by the high correlation of these five measures with habitat in a multiple regression analysis.

Inasmuch as quantitative measures of leaf structure fit within a model with a high predictive value for habitat aridity, we can assume that leaf structure and function are intimately related. The demonstration of how leaf tissues work together as a system is basic to an understanding of the relationship of leaf anatomy to physiology.

Sagebrush leaf structure exhibits considerable interspecific variation and is obviously well-adapted to arid habitats. The flexibility of the genetic program that governs this structure may explain to a large degree the rapid evolution and extensive colonization of sagebrush in the west.

Quantification of the habitat parameters and their correlation with anatomical structure provide information on the patterns of diversification of sagebrush and how these species have adapted to the cold deserts of the Great Basin. It is within this evolutionary context that we should continue to explore the relationship of plant structure and function.

ACKNOWLEDGMENTS

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SOME EDAPHIC AND COMPOSITIONAL CHARACTERISTICS OF ARTEMISIA TRIDENTATA AND ASSOCIATED PLANT COMMUNITIES IN SOUTHEASTERN UTAH

Kimball T. Harper and Richard A. Jaynes

ABSTRACT: The major plant communities of the Kaiparowits Plateau below the pinyon-juniper zone include mat saltbush, green molly-shadscale, shadscale-grass, grassland-mixed shrub, blackbrush, and sagebrush. The first three communities occur on the lower benches at about 4,265 ft (1 300 m) elevation and are separated by strong edaphic differences. The latter three communities occupy upper benchlands at 4,922 ft to 5,577 ft (1 500 to 1 700 m). Soil texture and chemistry are similar among these vegetational types, but soils are consistently deeper and less stony under grassland mixed-shrub vegetation. The distribution of blackbrush and sagebrush shows little correlation with either edaphic or microclimatic variables. Their distribution may be attributable to unequal ability of those species to reinvade after fires. Increasing site xericness was correlated with less vegetative cover and fewer species per unit area sampled. Shrubs and grasses showed marked differences in site preferences. Shrubs performed best on ridge crests and shallow soils, while grasses preferred bases of slopes and deeper, sandy textured soils.

INTRODUCTION

Abundant coal of low sulfur content occurs on the Colorado Plateau portions of Utah, Arizona, Colorado, and New Mexico. Power companies, required to meet more stringent standards for sulfur dioxide emissions from coal-powered electrical generating plants, have used progressively more coal from Colorado Plateau mines. Since much of the coal is extracted from open-pit mines, a major problem facing energy developers is stabilization of disturbed areas. Revegetation using adapted species is the most economical means of stabilizing mine wastes, but even after more than a decade of intensive revegetation research in the more arid sections of the Plateau, revegetation programs still do not always yield fully acceptable results. On sites where topsoil characteristics and topography have been significantly altered, land managers may not be able to use adjacent natural vegetation as a model of appropriate species combinations for reclamation. Better procedures are still needed for deciding which species to plant, how to plant them, and what the sustainable limits for plant cover are at any given site. Such knowledge would also help managers know whether a reestablished plant cover is approaching the potential for the site. Before such management problems can be resolved adequately, the natural ecology of each site must be understood.

Prior workers in the arid environments of the Colorado Plateau have identified edaphic and topographic factors that are influential in controlling the distribution of certain plant communities. Community types and soil-vegetation relationships in the shadscale zone of Grand County, UT, were investigated by West and Ibrahim (1967). They reported that edaphic discontinuities correlated well with vegetational changes. Gates and others (1956) found that soil factors, such as salinity and one-third atmosphere soil moisture, were significantly correlated with changes in some plant communities in the Great Basin.

In a study of grassland communities in northern Utah, Harner and Harper (1973) theorized that site mesicness increased from slope top to slope base positions as a result of differences in water infiltration. They suggested that ridgetops retain less moisture due to overland flow of precipitation. Midslope positions often receive roughly as much "run on" as runoff. Slope bases were considered to be more mesic than other positions due to more "run on" than runoff. They concluded that the relative contribution of perennial forbs and grasses increased as sites became more mesic. Loucks (1962) also found slope position to be a good index of available soil moisture in local situations.

Early revegetational research produced few techniques that would guarantee success in truly arid regions (Bleak and others 1965; Plummer and others 1968). Plummer (1966) noted that early rehabilitation plantings in the arid zone had been done on a "let's see what happens" basis.

Later workers recognized the need to more precisely identify environmental factors

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Kimball T. Harper is Professor of Botany, Brigham Young University, Provo, UT; Captain Richard A. Jaynes is Legal Officer, USA-SPT Command Hawaii (3RBAA), Fort Shafter, HI.

exerting the greatest influence on revegetation (National Academy of Sciences 1974). In the past decade, better procedures and plant materials have become available (Aldon 1978; Frischknecht and Ferguson 1979; McKell and others 1979), but much still remains to be done. A better understanding of the relationships between soils, topography, precipitation, and natural vegetations would substantially improve planning for reclamation projects (Hutchings 1966; Cook and others 1974; Alvarez and others 1974; Harper and others 1975).

Our purpose here is to describe the major plant communities below the pinyon-juniper zone on the Kaiparowits Plateau and to quantify their relationship to climatic, edaphic, and topographic variables. The results should clarify environmental-vegetational relationships in the area and help workers select more appropriate species for specific situations. We will illustrate how our results can be applied to increase success of revegetation projects in the area.

DESCRIPTION OF THE STUDY AREA

Vegetation and associated soils of the Kaiparowits Basin were sampled on upper and lower benchlands northeast of Glen Canyon City, Kane County, UT. Abrupt changes in elevation give a step-like aspect to topography in the study area. Soil parent material for the sandy loam upper benchland sites (ca. 5,085 ft [1 550 m]) is the Straight Cliffs sandstone formation with some localized influence from Mancos shale. Soils on the lower benchlands (ca. 4,363 ft [1 330 m]) range from clay soils derived from Tropic shale to sandy clay loams derived from Straight Cliffs or Dakota sandstones.

The study area is characterized by elements of both cold and warm desert vegetation adapted to approximately 8.7 inches (22 cm) of mean annual precipitation (fig. 1). Two precipitation peaks occur in most years: one in winter (January and February) and the other in July and August. Precipitation and temperature data were collected near Glen Canyon at 3,900 ft (1 189 m) elevation. Synoptic climatological patterns for the region of concern suggest that precipitation should average about 1.9 inches (4.8 cm) more per year on the upper as opposed to the lower benches. Long-term regional patterns also predict that annual temperatures will average about 1.3 °F (0.7 °C) lower on the upper benchland (Betancourt 1984).

METHODS

Twenty-four sites were studied in various plant communities on apparently undisturbed upper and lower benchland area. Where possible, sites were paired for contrasting exposures supporting broadly comparable vegetation and soil. At each site, three 0.05-acre (0.02-ha) stands were established along a topographic gradient with one stand at each of the top, middle, and basal slope positions. At each stand, exposure was measured

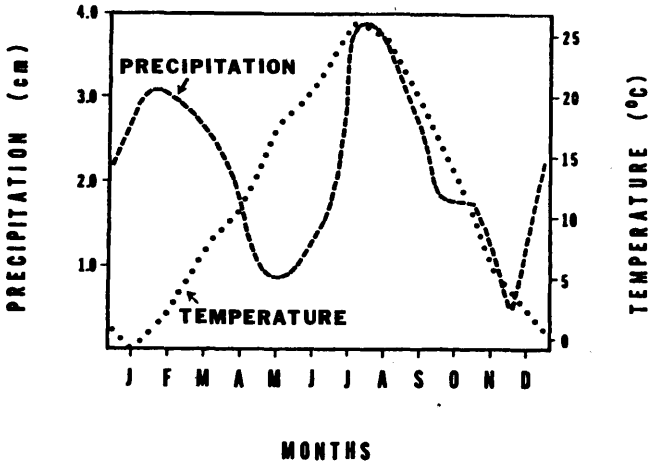


Figure 1.--Average precipitation and temperature at Glen Canyon City, Kane County, UT, for the period January-December 1972-75. Data supplied by Dr. B. W. Wood. Data collection was supported in part by Arizona Public Service Commission and California Edison Company.

in degrees from north and converted to an index of plant growth potential using a procedure described by Beers and others (1966). Their index utilizes potential solar radiation on a slope to approximate water and temperature stresses to organisms. The method assigns a value of zero to southwestern exposures and 2.0 to northeastern exposures: intermediate exposures receive values between zero and 2.0.

Vegetational data were collected at all stands during the period May 13-30, 1975. Twenty-five quadrats (each 2.7 ft^2 [0.25 m^2] in size) were spaced regularly over the surface of each stand. Data recorded for each quadrat included: (1) cover classes for living tissue, litter, and surface rocks larger than 0.16 $inches^2$ (1 cm^2) (Daubenmire 1968), (2) relative contribution of shrubs, perennial forbs, perennial grasses, and annuals to total living cover, and (3) presence for all vascular species.

Data recorded for each stand included a list of all species rooted therein, steepness of slope, and average soil depth from 20 random penetrometer readings. In addition, a composite soil sample was collected within each stand. The sample consisted of 12 cores (0.75 inch [1.9 cm] diameter and 6.0 inches [15 cm] deep) taken at regular intervals across the surface of the stand. Water infiltration rates (cm/min) were recorded at each site with ring infiltrometers. The infiltration rate for a stand was taken to be the average time required for disappearance of each of three successive 0.4-inch (1.0 cm) aliquots of water into initially dry soil. Percent rock is calculated as the average of percent rock cover (rocks >1 cm^2 [0.16 $inches^2$]) and rock content (diameter >2 mm [0.88 inch]) expressed as percent dry weight of the soil.

Independent	Dependent
Slope position (top=1, middle=2, bottom=3)	Percent total living cover
Exposure (Beers and others 1966 index)	Percent composition shrubs
Soil depth (cm)	Percent composition perennial forbs
Clay (percent)	Percent composition perennial grasses
Sand (percent)	Percent composition annuals
Percent rock	Average number species/quadrat
Slope steepness (percent)	
Infiltration rate (cm/min)	
Elevation (m)	
pH	
Salinity (ppm)	

A stepwise multiple regression procedure was used to provide predictive equations for various parameters of vegetation (Wikum and Wall 1974). The independent and dependent variables are above. Multiple regression provides an estimate of how various environmental factors interact to influence plant frequency and/or cover. The analyses were performed using data from our field samples and an arbitrary minimum F-value of 2.0 for admission of an independent variable to the analysis. The program terminated automatically when no remaining independent variable produced an F-value of 2.0 or more.

RESULTS

Community Characteristics

The communities differ in respect to soil texture, elevation, and soil salinity (table 1). The vegetative types can be conveniently grouped according to position in the landscape. Mat saltbush (Atriplex corrugata), green Molly (Kochia americana)-shadscale (Atriplex confertifolia), and shadscale-grass (primarily galleta [Hilaria jamesii], but also with considerable Indian ricegrass [Oryzopsis hymenoides]) occur on the lower benchlands. The upper benchlands support a mosaic pattern of the following three vegetative types: grassland-shrub (Indian ricegrass, galleta, sand dropseed [Sporobolus cryptandrus], blue gramagrass [Bouteloua gracilis], shadscale, matchweed [Gutierrezia sarothrae], and Brigham tea [Ephedra torreyana]); blackbrush (Coleogyne

Table 1.--General characteristics of environment and vegetation associated with the six vegetative types recognized. The standard deviation follows the mean for each value

	Mat saltbush	Green Molly/ shadscale	Shadscale/ grass	Grassland/ shrub	Blackbrush	Sagebrush
No.of study sites	6	6	21	21	12	6
Abiotic characteristics						
Elevation (m)	1,308±5	1,279±3	1,335±26	1,522±47	1,583±65	1,659±5
Slope (percent)	6.8±5.0	3.5±2.3	8.5±5.6	4.0±2.2	5.7±2.7	4.7±4.0
Texture (percent)						
Sand	13.8±4.2	47.3±7.0	64.4±11.4	74.4±8.8	72.7±6.1	70.5±3.0
Silt	22.0±3.0	17.2±3.1	13.0±5.9	8.1±4.9	6.7±3.3	11.0±3.5
Clay	64.2±4.2	34.3±4.9	24.4±8.4	17.3±5.1	20.7±3.4	18.3±2.7
Ave. percent rock (>1 cm)	2.0±0.9	36.2±4.1	16.9±8.6	5.6±9.2	6.4±6.5	11.8±4.8
Ave. soil depth (cm)	49.5±16.4	17.7±4.4	31.7±14.7	46.7±21.6	22.2±14.9	19.2±4.9
Infiltration rate (cm/min)	1.8±0.6	0.7±0.3	2.6±1.2	3.1±1.5	3.3±3.3	1.1±0.5
Soil pH	8.1±0.1	7.6±0.4	7.9±0.4	8.0±0.3	8.1±0.2	8.1±0.1
Salinity (ppm)	11,200±10,500	353±120	490±450	281±470	147±47	133±10
Biotic characteristics						
Living cover (percent)	12.0±6.8	14.6±4.0	19.4±6.4	27.0±6.5	26.2±6.8	21.8±4.2
Composition of cover (percent)						
shrubs	46±16	36±7	34±15	34±11	43±18	40±11
perennial forbs	2±3	14±5	6±4	16±8	11±4	20±11
perennial grasses	7±18	18±15	33±18	40±17	26±23	25±17
annuals	14±12	32±15	27±14	10±7	20±12	15±13
Species richness						
No. spp./0.25m^2	2.0±0.9	2.8±0.7	3.2±0.9	3.6±0.8	3.3±0.9	4.1±0.4
No. spp./0.05 ha	6.8±4.1	23.5±4.6	25.0±4.7	26.8±4.2	23.5±4.1	25.8±2.0

Table 2.--Average percent absolute frequency of the most abundant species in each of the six vegetative types recognized in this study. The frequency values of the 10 commonest species in each type are underlined. Each species is listed for all communities of occurrence. Frequency is the percentage of quadrats in a stand that contains the species in question

Species (life-form[1])	Mat saltbush	Green molly/ shadscale	Shadscale/ grass	Grassland/ shrubs	Blackbrush	Sagebrush
Androstephium breviflorum(F)	4	1	4	6		
Artemisia tridentata(S)						40
Aster arenosus(F)			2	9	5	15
Astragalus lentiginosus(F)		17		3	1	1
Atriplex confertifolia(S)		16	26	6	3	
Atriplex corrugata(S)	47			1		
Bouteloua gracilis(G)				6	9	15
Camissonia eastwoodiae(A)	23		1			
Chaenactis macrantha(A)		27				
Chaenactis stevioides(A)		1	14	4	15	16
Cleomella palmerana(A)	43					
Coleogyne ramosissima(S)				2	32	
Cymopterus purpurascens(F)		19	1	3		
Ephedra torreyana(S)			2	17	19	5
Eriogonum deflexum(A)			7	11	1	1
Eriogonum inflatum(A)	3	1	21			
Festuca octoflora(A)		9	16	14	18	27
Gilia leptomeria(A)	1		23	28	20	25
Gilia scopulorum(A)				8	40	57
Grayia spinosa(S)				4	12	3
Gutierrezia sarothrae(S)		1	12	34	11	51
Hilaria jamesii(G)	1	14	40	55	36	34
Kochia americana(S)		32		1		
Langloisia setosissima(A)		21	10	1		
Lappula occidentalis(A)		14	2	1		1
Lepidium montanum(F)			2	14	17	39
Mentzelia albicaulis(A)		1	6	24	25	14
Oryzopsis hymenoides(G)	11	21	17	25	9	25
Phacelia demissa(A)	40	15	20			
Salsola iberica(A)	22	6	23	9		
Sporobolus cryptandrus(G)			3	10		

[1]Letter following plant name indicates life form; S=shrub, G=perennial grass; F=perennial forb; A=annual.

ramosissima); and big sagebrush (Artemisia tridentata) (tables 1 and 2).

The distribution of vegetative types on the lower benchlands mirrors local parent materials (table 1). Exposures of Tropic shale support mat saltbush and widely spaced plants of Indian ricegrass (table 2). In years of above-average precipitation, adapted annual plants may flourish. In 1974, Cleomella palmerana, Phacelia demissa, and Camissonia eastwoodiae were abundant on sites derived from Tropic shale. Soils derived from Wahweap sandstone are dominated by shadscale and galleta grass on the lower benchlands and contain far less soluble salt and more sand than associated soils derived from Tropic shale. Although precipitation is probably comparable among the lower benchland study areas, the less saline, lighter-textured soils derived from the Wahweap sandstone supported about 60 percent more (in relative terms) plant cover than associated soils formed from Tropic shale. Floristic richness and vegetational composition also differ significantly on those two substrates with the former supporting a richer flora, relatively less shrub and annual plant cover, and relatively more perennial herb cover (table 1).

In areas where erosion has washed Tropic shale materials over rubble from Wahweap sandsone, green molly and shadscale grow intermixed with galleta, Indian ricegrass, and a variety of native annuals (tables 1 and 2). Surface soil characteristics at such sites are intermediate between those for exposures of Tropic shale and Wahweap sandstone in respect to texture, but such sites often have more stones in the profile than either of the other soils (table 1). Species richness (number of kinds of vascular species/quadrat or per stand) and vegetational composition on the alluvial soils that are derived from both Tropic shale and Wahweap sandstone are intermediate to values for those parameters on either of the parent materials alone (table 1).

On the upper benchlands, the three vegetational types sampled occurred on soils that were similar in respect to both textural and chemical characteristics (table 1). Nevertheless, soils underlying the grassland-shrub type were

significantly deeper than those under either blackbrush or sagebrush stands. The latter two community types characteristically appear on steeper ridges where natural erosion is slowly, but steadily, removing surface material to adjacent, less steep terrain. The grassland/shrub community often occurs on such sites where natural soil development is supplemented by light alluvial depositions from nearby, low ridges. The grassland/shrub, blackbrush, and sagebrush communities are similar in respect to total plant cover and dominant species, but the grassland/shrub type consistently supports relatively more grass and less shrub and annual plant cover than the two brush communities (tables 1 and 2).

The blackbrush and sagebrush sites in our data set are essentially identical for soil texture and soil depth, salinity, and pH (table 1). Sagebrush stands occur at slightly higher elevations in the area, but the difference is never large. The elevation difference should produce slightly more precipitation and somewhat cooler temperatures at the sagebrush sites, but the difference does not seem large enough to eliminate the possibility of blackbrush invading such sites. It is known that sagebrush reinvades rapidly after wildfire (Blaisdell and others 1982), but blackbrush reinvades so slowly that even after 35 years it may not be an important component of the vegetation (Callison and others 1983). Fire scars in the woody vegetative types of the upper benchlands of our study area demonstrate that wildfires do sweep the area at least occasionally. We suggest that although there is a widespread tendency for blackbrush to dominate the shallowest, residual soils overlying coarse-textured rock in our study area, the current patterning of sagebrush and blackbrush on soils of intermediate or greater depth may be related to the history of local fires. Sagebrush may now occur on some sites that once supported blackbrush. The ability of sagebrush to reinvade after fire should give it an advantage over blackbrush on transitional sites where both species can survive.

Predictive Equations

When mine spoils are to be revegetated, it would obviously be helpful to know how much plant cover one might reasonably expect a particular combination of soil and topography to support in a given climatic zone. It, likewise, could be useful to know if species of a particular life-form class might be at an advantage on a particular site.

Our data demonstrate that soil texture is a strong variable that exerts a profound influence on both plant cover and species (fig. 2). Other single variables that significantly affected many biological parameters were elevation, slope position, and soil depth. Elevation probably exerts its effects through precipitation and ambient temperature; both would have a tendency to

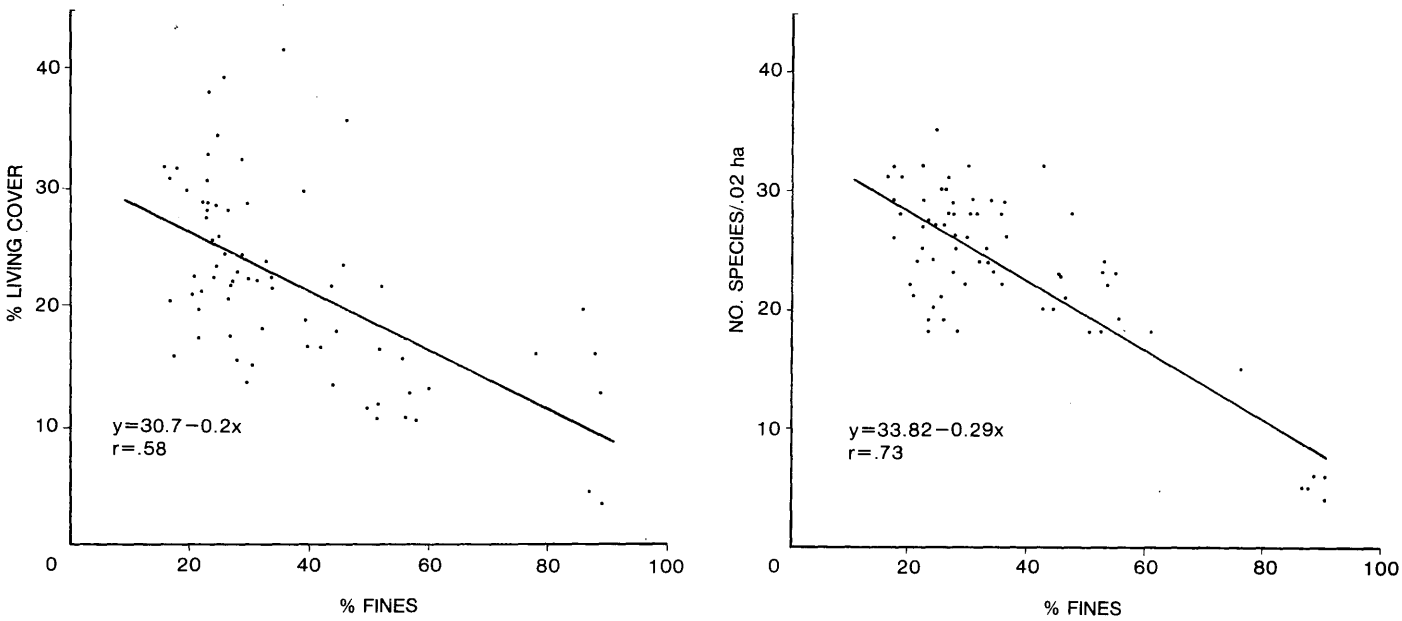


Figure 2.--Influence of soil fines (percent silt and clay summed) on living plant cover (left) and number of vascular species per 0.05-ac (0.02 ha) stand (right) at 72 stands on the Kaiparowits Plateau, Kane Co., UT. Data collected in May 1975. Since precipitation for the period October 1, 1974 through May 21, 1975 was almost 46 percent (2.49 inch [6.1 cm]) above the long-term average and mean monthly temperature for those months was 3.5 percent (ca. 1.48°F [0.7°C]) below long-term average, cover and species richness values probably overestimate long-term averages for those parameters (U.S. Dept. Commerce 1974, 1975).

Table 3.--Multiple regression equations for various vegetational parameters. For these analyses, data from 72 stands in six vegetation types have been pooled. All equations are significant at the 0.01 level

Dependent variables	Regression equation	R^2
Total living cover	Y= 53.3 -0.22 Sa -0.33 Ro -0.54 Cl -0.0003 Sal	0.59
Shrub cover (percent total cover)	Y= -9.2 -4.44 SP -0.24 SD +0.29 Cl +0.92 %S +0.035 El	.33
Perennial forb cover (percent total cover)	Y= -20.3 +0.19 Ro -0.10 Cl -0.40 %S +0.024 El	.30
Perennial grass cover (percent total cover)	Y= 62.1 +8.64 SP +0.37 SD -0.71 Cl -0.78 S -0.027 El	.47
Annual cover (percent total cover)	Y= 50.6 -3.16 SP +0.51 Cl -0.024 El	.40
No. species per 0.25 m^2 quadrat	Y= 1.0 +0.16 SP +0.007 SD -0.03 Cl +0.002 El	.32

Key to symbols: Cl=percent clay, Sa=percent sand, El=elevation (m), Sal=salinity (ppm), Ro=percent rock, Percent S=percent slope, SP=slope position, SD=soil depth (cm) (See Methods for coding).

make more water available for plant growth as elevation increased. Others have elsewhere noted the effects of slope position on both living plant cover and composition (relative contribution of shrubs, grasses, forbs, and annuals) in local situations (Harner and Harper 1973; England 1979; Moretti and Brotherson 1982). Soil depth has an impact on both water and mineral resources available to roots at any particular point.

Multiple regression equations relating six dependent parameters (living cover, species per quadrat, and relative importance of shrub cover, perennial grasses or forbs, or annuals) to environmental variables at the 72 study sites are given in table 3. In all cases, the equations account for a highly significant amount of the variation in the dependent variables using five or fewer variables. Multiple correlation coefficients for the analyses ranged from a high of almost 0.77 for total cover to a low of 0.55 for forb cover.

The relative success of each of the four life-form groups (shrubs, perennial grasses, perennial forbs, and annuals) was dependent on a unique set of variables. Although percent clay in the soil was a component of each equation for life-form groups, it was positively correlated with annuals and shrubs, but was negatively correlated with relative success of perennial grasses and forbs. Elevation also appears in all four equations; but is positively correlated with shrub and forb success, but negatively associated with grasses and annuals. Slope position is a component of three of the equations (not significantly correlated with forbs). Slope position is negatively correlated with success of shrubs and annuals, but positively associated with an increasing grass component in the vegetation (table 3). Slope steepness was a component of three of the life-form group equations. The variable was positively correlated with shrubs and negatively related to success of both perennial grasses and forbs.

As we have shown elsewhere (Jaynes and Harper 1978), the major species of table 2 also respond strongly to the same variables shown to be significant for success of the various life-form groups here. Persons interested in predictive equations for performance of individual species should consult that paper.

The number of species encountered per quadrat was positively correlated with slope position (greatest at slope base), soil depth, and elevation; and negatively associated with increasing amounts of clay in the soil.

DISCUSSION

Vegetational patterns in the Kaiparowits Plateau region are primarily controlled by variation in soil parameters, especially within a given range of elevation. Where topography is relatively simple and elevational variation is moderate, as it was in this study, climatic and microclimatic parameters do not exert overwhelming impacts. Soil texture, slope position, and slope steepness were particularly potent variables. Their impact was probably expressed through soil moisture available for plant growth. Although increasing elevation is a nonclimatic variable, it appears to be a surrogate variable that has effects similar to decreasing temperature and increasing precipitation. In general, our multiple regression equations (table 3) suggest that available soil moisture is the most critical variable controlling both amount of plant growth and kinds of plants that can tolerate specific sites. Any of the many edaphic and topographic variables that affect soil moisture available to plant roots appear to be important to plants in the Kaiparowits region.

In this paper, we have not emphasized statistical analysis of individual plant species, since we chose to focus on regional patterns, and no plant species occurred in all six of the ecosystems considered. Our analyses suggest that species of similar life-form and/or longevity tended to respond somewhat similarly to the environmental complexes encountered in this study. Such a broad generalization will inevitably have many exceptions, but a variety of studies demonstrate that plants of similar life-form have much in common in respect to rooting depth (Stewart and others 1940), tissue

water content (Sharif and West 1968), phenology (Rabinowitz and others 1979; Kemp 1983), tissue chemical content (Harner and Harper 1973; Pederson and Harper 1979; Woodward and others 1984), and reproductive biology (Ostler and Harper 1978; Harper 1979). Those similarities were apparently sufficiently distinct among life-form groups that each group responded differently from all other groups (table 3) with many of the intergroup differences being statistically significant.

Assuming that our results for life-form group responses to environment are real and applicable in other deserts, managers concerned with revegetating disturbed lands can profitably use such relationships to determine a mix of life-forms most likely to succeed on a particular site. Once that decision is made, attention can be directed toward selection of well-adapted species in each life-form class. Such an approach seems more likely to result in successful, self-sustaining revegetation attempts than one in which species are selected without regard to life-form and predicted success of various life-forms on the site.

The soil and topographic variables considered in our study can be easily quantified at specific reclamation sites. When overburden materials are severely disturbed, growing conditions of resultant sites may be so different from those on nearby, undisturbed soils that little relevant information about suitable species for reclamation can be inferred from the natural plant cover. In such cases. equations such as those in table 3 (but derived from local samples) may provide useful guidelines for the kinds of species needed and the amount and composition of vegetation that can be expected when the reseeded cover finally comes to equilibrium with the local environment.

As Aldon (1984) has noted, "Mining reclamation specialists and government regulators need sound criteria for judging when reclamation is complete and expensive bonds can be released." The methods outlined here provide a realistic, manageable method for estimating how much plant cover a site can be expected to support. They also permit managers to predict the life-form spectrum that is "natural" for a specific site and a level of species richness (number of species per unit area) that approximates that of undisturbed sites having similar physical and chemical properties.

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COMPOSITIONAL PATTERNS WITHIN A RABBITBRUSH (CHRYSOTHAMNUS) COMMUNITY OF THE IDAHO SNAKE RIVER PLAIN

Roger Rosentreter

ABSTRACT: Species compositional patterns of an area dominated by Chrysothamnus nauseous ssp. consimilis and Poa sandbergii were investigated south of Boise, ID. Two species associations, (1) rabbitbrush-Poa-moss and (2) lichen soil crusts, were identified. These associations correlated with sites of contrasting soil depth, light intensities, and salt concentrations. Lichen soil crusts produce few fire-supporting fuels and may function as refugia. They appear to influence the post-fire composition of the entire study area.

INTRODUCTION

The ecology of plant communities can be viewed at various spatial scales, ranging from fine-grained patterns of competition or microclimate to global distribution patterns. Depending on the size of our observational window, different factors are important in controlling the distribution and abundance of plant species. This paper gives a descriptive account of the interspecific relationships within a single plant community. The high diversity and abundance of soil cryptogams in this plant community as well as the larger more obvious vascular plants, are described.

Often, the results of plant studies conducted over the course of only 1 or 2 years merely reflect the weather conditions of those years rather than elucidating the long-term controlling biotic and abiotic factors. Cryptogams such as lichens are long-lived, persistent plants with slow growth rates. Unlike any other plants, lichens are not greatly influenced by short-term weather conditions. This makes them ideal indicators of long-term climatic and environmental factors.

Generally lichens growing as thin crusts over soil are difficult to physically preserve intact and as a result are poorly known taxonomically. Ecological studies of plants are normally preceded by taxonomic studies, but this was not the case for this study in southwestern Idaho. In fact, only a few of the taxa in the study area were previously reported in Idaho (Schroeder and others 1975).

Cryptogamic soil crusts are common in seral rabbitbrush communities and continue to exist in the later successional Artemisia communities. Most of the cryptogamic lichen taxa in the study area have worldwide distribution and are reported from many other arid biomes (Rogers 1977). Arid-zone lichen floras from various continents are very similar, perhaps because of the wide ranging dispersal of their small fungal spores (Rogers 1977).

For example, Caloplaca tominii Savicz, characteristic of the Fulgensio-Calopacetum tominii synusia found within the Artemisia/Agropyron community of the Canadian Yukon, was reported new to North American by Nimis (1981). Besides Caloplaca tominii, the Canadian Yukon plant community contains several lichen species that commonly occur in the southwestern Idaho study site. Caloplaca tominii also occurs in the Artemisia/grasslands of Russia (Savicz 1930) and northern Afghanistan (Poelt and Wirth 1968).

Studies of lichen communities that do not include associated vascular plant communities cannot produce correlating relationships or indicator values. Vascular plants and lichens read environmental factors differently and on separate time scales (McCune and Antos 1982). Each group of plants can provide information which may complement or explain something about the other. Descriptive studies such as this one are important for providing baseline data, identifying environmental indicators, and generating hypotheses. This study also attempts to evaluate the enhancement of vascular plants by cryptogams. In North America, there have been several phytosociological and floristic studies in arid habitats including those of Looman (1964a and 1964b), Anderson and others (1982), and Nash and Moser (1982).

STUDY AREA

The study area was located in Ada County south of Boise, ID. Elevation was 2,780 ft (848 m). The area is presently in a seral stage dominated by Chrysothamnus nauseosus ssp. consimilis and Poa sandbergii. Chrysothamnus nauseosus commonly resprouts after fires. Potential

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Roger Rosentreter is the State Botanist, U.S. Department of the Interior, Bureau of Land Management, Boise, ID.

vegetation for the site is Artemisia tridentata ssp. wyomingensis/Agropyron spicatum habitat type (Hironaka and others 1983). This study area has an uncommonly high frequency of rabbitbrush, yet other nearby disturbed areas are dominated by cheatgrass and lack any shrub cover.

The soils in the study area were derived from basaltic parent material and loess over alluvial and lacustrine sediments. These soils fit the Chilcott and Sebree complex series which occur on nearly level or gently sloping positions (USDA 1980; Barker and others 1983). The Chilcott soil is a fine, montmorillonitic, mesic Abruptic Xerollic Durargid (USDA 1980). The Sebree soil is a fine-silty, mixed mesic Xerollic Nadurargid (USDA 1980). Mean annual precipitation is approximately 10 inches (25 cm). The site contained numerous randomly occurring natric, (slick) spots which contain shallow Sebree soils of poor drainage and a very low percentage of vascular plant cover. Natric spots are areas of high salt concentrations in the soil (Barker and others 1983).

The area has a history of environmental disruptions. Historically, it was impacted by travelers using the Oregon Trail (Yensen 1980), and presently it is grazed by sheep and cattle in both the spring and winter. Since the area is near Boise, ID, which is a large city, human disturbance includes assorted off road vehicle use, target shooting, rodent hunting, and bird watching. The Snake River Birds of Prey Natural Area is also nearby.

METHODS

Sampling Methods

Sampling took place in the spring. One hundred forty plots, 20 per transect line, were placed on seven different randomly distributed transect lines within the apparently homogenous Chrysothamnus nauseosus ssp. consimilis-Poa sandbergii community. Each transect line end point was marked with a permanent wooden stake and referenced by compass bearings. Plots were 7.9 X 19.7 inches square (2 X 5 dm) and were placed one meter apart along the transect lines. All species present were recorded by Daubenmire cover classes (Daubenmire and Daubenmire 1968). Soil depth to the duripan horizon and presence of vesicular porosity were recorded for each plot sampled. (Vesicular porosity is associated with low organic matter in the soil, USDA 1980).

Nomenclature of vascular plants, mosses, and lichens follows Hitchcock and Cronquist 1973, Conard 1956, and Hale and Culberson 1970, respectively. Taxonomic concepts for the lichen Aspicilia desertorum (Kremp.), Meresh. follow Weber (1962 and 1967) and the genus Psora follow that of Schneider (1979).

DATA ANALYSIS

Species Ordination

A polar ordination was used for the species ordination; it was prepared using the computer program SWAN (McCune unpublished). Several species were grouped for analysis due to difficulty in distinguishing them at the species level when sampling. Those species groups included: (1) Large mustards-Erysimum occidentale and Lepidium perfoliatum; (2) mosses other than Tortula which included Polychidium piliferium, Ceratodon purpureus, Bryum argenteum, Bryum spp., and Funaria hygromitrica; (3) Caloplaca spp. which included Caloplaca tominii, C. citrina, C. vitellina, and Candelariella terrigena; (4) Collema spp.--Collema tenax and Polychidium albociliatum. Other incidental species present but not treated in the ordination analysis follow:

VASCULAR PLANTS
Allium nevadense
Elymus cinerus
Microsteris gracilis
Ranunculus glaberrimus
Salsola kali
Sitanion hystrix

LICHENS
Acarospora schleicheri
Dermatocarpon cinereum
Diploshistes scruposus
Lecanora pergibbosa
Lecidea glaucophaea
Lecidea uliginosa
Massalongia carnosa
Parmelia elegantula
Peltigera rufescens
Physconia detersa
Psora cernata
Psora decipiens
Psora lurida
Psora luridella
Psorotichia nigra
Tonnia caeruleonigricans

LIVERWORTS
Clevea hyalina
Riccia beyrhichiana

FUNGI
Galerina spp.
Geastrum spp.
Ompholina ericetorum
Tulostroma spp.

Subjective end-stand selection ordinated the species in species space. This ordination was done on two axes. The first axis was between a natric indicator species, Lecanora muralis, and bare non-natric soil lacking vesicular porosity. The second axis was between a small shallow-rooted ephemeral species, Draba verna, and a larger diffuse deeper-rooted winter annual, Bromus tectorum. Species of this ordination were:

1. Chrysothamnus nauseosus ssp. consimilis
2. Chrysothamnus nauseosus (dead shrubs)
3. Poa sandbergii
4. Vulpia octoflora
5. Ranunculus testiculatus
6. Myosurus aristatus
7. Draba verna
8. Lithophragma bulbiferia
9. Large mustards
10. Bromus tectorum
11. Gayophytum ramosissimum
12. Tortula ruralis
13. Other mosses
14. Lecanora muralis
15. Caloplaca spp.
16. Lecidea sp. nov.
17. Dermatocarpon lachneum
18. Thrombium epigaeum
19. Arthonia glebosa
20. Collema spp.
21. Cladonia pyxidata
22. Aspicilia desertorum
23. Texosporium santi-jacobi
24. Bare non-natric soil

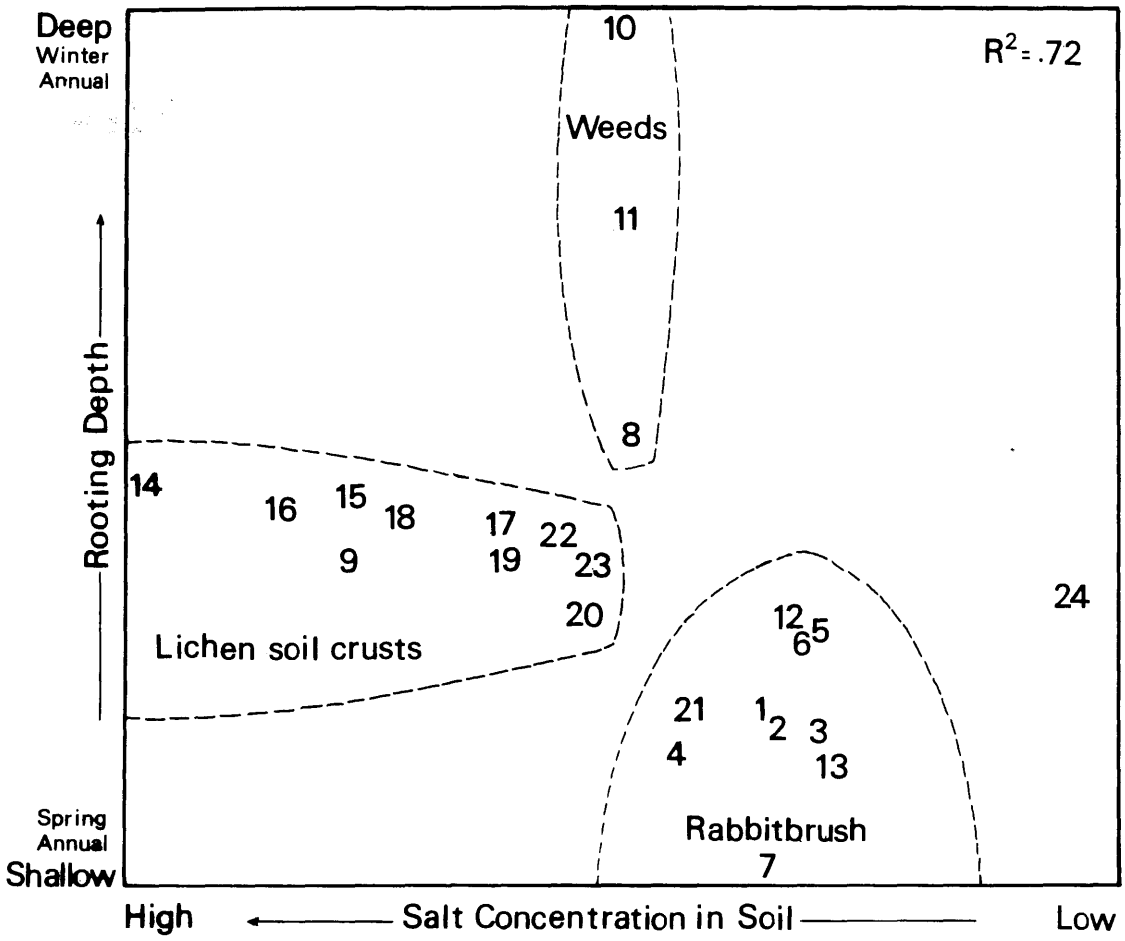


Figure 1.—Polar ordination of a rabbitbrush community.

RESULTS AND DISCUSSION

Discussions below are related to the ordination of species in Figure 1. The ordination of species suggests that the rabbitbrush community had two distinct species groups (1) the rabbitbrush-Poa-moss group and (2) the lichen soil crusts group. This ordination provides a helpful graphic representation of species similarity. This graphic presentation of the community structure allows for interpretation by both continuum and discrete ecological points of view. The other species cluster was composed of the weedy species. The weeds occurred centrally in the ordination showing that they have little site preference. In the field these weedy species obscured the pattern of the more site specific species.

Relationships Between Species Groups

The two species groups were predominantly separated by the first axis of the polar ordination (fig. 1). This axis was related to contrasting salt concentrations and resulting soil characteristics and represented a complex of factors associated with shallow natric soils. Shallow, natric or high sodium, soil sites accumulate silts and salts from local internal drainage. Sodium molecules bind the silt particles together, sealing the soil surface, preventing water penetration and creating standing water. These sites are called slick spots (USDA 1980). Water is lost by evaporation that concentrates the salts. Vascular plants' higher metabolic oxygen requirements preclude them from occupying such flooded anaeorobic sites. The shallow soil depth 1 to 4 inches (2 to 10 cm) and the duripan horizon restrict root penetration. Lichen soil crust species have low metabolic requirements making them tolerant of periodic flooding. Lichens lack roots and thus are not hindered by the shallow soil depth. Soil properties that characterize conditions of poor aeration appear to control the distribution of these species groups. This is similar to the reasons for the distribution pattern of big and low sagebrush, Artemisia tridentata and A. arbuscula (Hironaka and others 1983). These soil relationships point out that botany does not stop at the surface of the ground. The shallow natric soil sites lack shrubs and have little to no vascular plant cover. This results in little competition for light, moisture, nutrients, or space.

The second axis of the polar ordination was also related to soil depth. This axis appeared to separate vascular plant species which have roots and not the lichen species.

Relationships Within Species Groups

Rabbitbrush-Poa-moss.--The rabbitbrush-Poa-moss group occurred on the deeper non-natric soil, which was by far the more productive site. This rabbitbrush group contained only one lichen species, Cladonia pyxidata which occurs in many other more moist vegetation types. Cladonia pyxidata appears to be closely allied to this species group. All the moss species were closely associated with rabbitbrush, as was Poa sandbergii. One moss species, Polychidium piliferium, occurred on the dead portions of the short-lived perennial, Poa sandbergii clumps. In addition, seedlings of Poa sandbergii were most commonly found growing in beds of the moss Tortula ruralis. Several small shallow-rooted ephemeral annuals also occurred in these moss beds.

Lichen soil crusts.--The lichen soil crusts group was on the shallower, less productive, natric soil site. This group contained few vascular plants, only the large mustards Erysimum and Lepidium. These mustards are salt tolerant and mature in late spring and summer after the natric sites lose their standing water. This site lacked vascular plant cover sufficient to carry a fire.

One lichen, Texosporium santi-jacobi, a monotypic genus, is noteworthy for its uncommon ornamentation and large spore size (30 to 45u). It is one of the few narrow North American endemic lichens, it is a disjunct from the Mohave Desert of California. There is no apparent reason for this disjunct pattern. This is the only known population in Idaho despite intensive searching in southwestern Idaho.

The lichen species most narrowly defined spatially occurred close to Lecanora muralis. The narrowly defined (salt-tolerant) species were those lacking asexual fragmentation. In contrast, lichen species capable of asexual reproductive fragmentation were more broadly defined, such as, Arthonia glebosa, Caloplaca tominii, and Collema spp. These latter lichen species were more similar to the rabbitbrush species group and some could be considered weedy species. Rogers (1977) reported a similar species of Collema to be a pioneer species in arid Australia. Lichens which reproduce by fragmentation are often better indicators of environmental conditions because they lack sensitive "seedling" stages of growth. Seedlings often require very different conditions than do mature plants.

These natric sites produce few fire-supporting fuels and may function as fire refugia for those species occupying the site. Weedy lichen species surviving within the natric sites then may reinvade the burned rabbitbrush-Poa-moss sites. The study area's species richness and abundant lichen cover may characterize this mottled pattern of natric sites as refugia from fire. The refugia provide the plants necessary for rapid reinvasion. Refuge sites also may provide firebreaks and cool spots in fires which promotes the resprouting of rabbitbrush. Supporting this concept is the fact that large Lecanora muralis individuals on the natric sites were estimated to be over 60 years old (annual increment 2 to 3 mm) (Hale 1974), yet the area burned only 17 years ago (BLM fire records).

This fire refugia concept suggests that the compositional pattern of species is fire dependent. Therefore, the presence of refugia sites appears to influence the postfire species composition of the entire study area.

Grazing by sheep and cattle may also affect the relationships among species groups. The lack of vascular plants on the open natric sites may be the result of livestock use of the easier accessed open areas. Also, compaction and trampling by livestock may encourage the crustose growth form of lichens. The study site does have a heavy cover of cryptogams. In contrast, Rogers and Lange (1971, 1972), Rogers (1974), and Anderson and others (1982) report less lichen cover on heavily grazed areas. The heavy lichen cover on this site may reflect the importance of natric spots in promoting lichen growth. It appears that dispersal sites are more important than the grazing pressure on the influence of lichen cover in this sagebrush/grassland habitat type. The natric sites also had heavier textured silty soils which have been reported to be favorable for lichen cover (Anderson and others 1982).

CONCLUSIONS

The lichen soil crusts group is apparently a climax edaphic group. If plant succession were allowed to occur without major disturbances, the rabbitbrush-Poa-moss species composition would change while the lichen soil crusts group would not.

Rabbitbrush stands appear to be favorable for lichen growth because they lack leaves in the winter and early spring; this allows penetration of sunlight to the soil surface. Rabbitbrush stands also collect blowing snow, and increase soil surface temperatures and humidity on sunny winter days.

This community was composed of a rabbitbrush-Poa-moss species group and a lichen soil crust group. The species composition pattern of this rabbitbrush community appears to be determined by fire and edaphic conditions. The edaphic pattern contained slick spots which act as fire refugia for lichen species. These slick spots also influence fire behavior, resulting in cooler fires which promote rabbitbrush resprouting. Thus, slick spots influence species composition on both slick and nonslick spots. In contrast, areas nearby which lack slick spots burn hotter and are dominated by cheatgrass.

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POPULATION DYNAMICS OF TWO SAGEBRUSH SPECIES AND RUBBER RABBITBRUSH OVER 22 YEARS OF GRAZING USE BY THREE ANIMAL CLASSES

Richard Stevens

ABSTRACT: Density and growth performance of basin big sagebrush, white rubber rabbitbrush, and black sagebrush plants associated with grazing (blacktail jackrabbits, mule deer, and cattle) located in a fourway exclosure were identified and measured 2 (1964), 11 (1973), and 22 (1984) years following chaining and seeding of a juniper-pinyon site in central Utah. Considerable reproduction came from seed produced by native shrubs. Many shrubs were not killed by chaining. With no grazing, rabbit use only, deer use only, and rabbit and deer use combined, total numbers of big sagebrush and rabbitbrush plants decreased substantially between 1973 and 1984. With rabbit, deer, and cattle use combined these two shrubs and black sagebrush increased steadily.

INTRODUCTION

A majority of the winter and spring livestock and big game ranges in the Great Basin are located in the juniper-pinyon and sagebrush types (Ruess and Blanch 1951; Plummer and others 1970; Dwyer 1975). During the past three to four decades many of these rangelands have been treated mechanically or chemically and seeded (Plummer and others 1968; Vallentine 1971; Jordan 1982). Seed mixtures have included various grasses, forbs, and shrubs (Stevens 1983). Depending on site characteristics, species seeded and site preparation and seeding techniques, establishment of seeded species has been quite variable (Plummer and others 1970a, 1970b; Stevens and others 1977; Keller 1978; Jordan 1983), with shrub establishment being the most erratic. Reproduction of on-site species has been influenced by the density, condition, and age of the plants left on the site following treatment.

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Richard Stevens is Project Leader, Game Range Restoration Studies, Utah Division of Wildlife Resources, Great Basin Experimental Range, Ephraim, UT.

Establishment success from direct seeding of basin big sagebrush (Artemisia tridentata ssp. tridentata), black sagebrush (A. nova), and white rubber rabbitbrush (Chrysothamnus nauseosus ssp. albicaulis) has ranged from poor to excellent (Van Epps and McKell 1980; Crofts and Carlson 1982; Colbert and Colbert 1983; Luke and Monsen 1984; Monsen and Richardson 1984). These three shrubs establish not only from artificial seeding, but by natural spread from remnant plants (Daubenmire 1975; Young and Evans 1978; Monsen and Richardson 1983; Young and others 1984).

The inclusion of sagebrush and rabbitbrush seed in a herbaceous seeding can increase total production, enhance grass yields (Plummer 1959; Frischknecht 1963), improve the nutritive value of the seeding (Welch 1983), increase available winter forage, enhance snow entrapment, improve the esthetics of the seeding, and reduce the chances of destructive insect infestations (Haws 1978).

This study was designed to gain a better understanding of how basin big sagebrush, black sagebrush, and white rubber rabbitbrush respond to removal of competitive vegetation, direct seeding, natural invasion, and grazing by deer, rabbits, and cattle.

AREA

The Fountain Green Wildlife Management Area is located 5 miles (8 km) northeast of Fountain Green, Sanpete County, UT. A portion of the area was chained and seeded with a mixture of grasses, forbs, and shrubs in the fall of 1962. White rubber rabbitbrush seed collected from Wales Canyon, 18 miles (29 km) southeast of the site and seed of basin big sagebrush collected on the site were included in the seed mixture. Black sagebrush was not seeded. Prior to treatment, the site supported juniper-pinyon (Juniperus osteosperma-Pinus edulis) with a fairly good understory of basin big sagebrush and lesser amounts of Indian ricegrass (Oryzopsis hymenoides), western wheatgrass (Agropyron smithii), black sagebrush, and white rubber rabbitbrush.

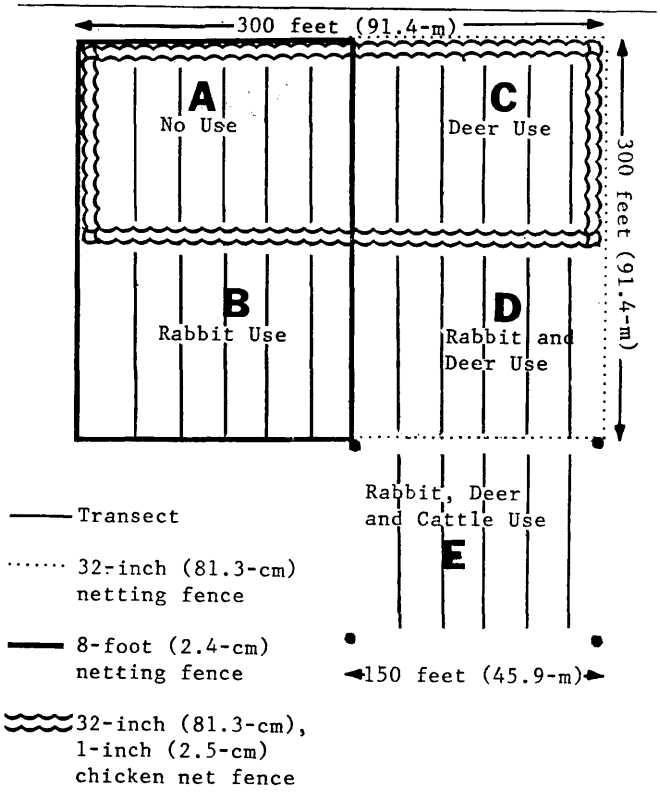


Figure 1.--Fountain Green fourway exclosure and comparable outside area. Five grazing treatments.

Following seeding a 300- by 300-foot (91.4- by 91.4-m) fourway exclosure (fig. 1) was built. The exclosure is located on a southeast exposure with an 8 percent slope. Soil is described as Deer Creek stoney silt loam (USDA 1981). Average annual precipitation during the 22-year study period was 14.73 inches (37.4 cm), with a high of 24.57 inches (62.4 cm) in 1983 and a low of 6.67 inches (16.9 cm) in 1976. The exclosure consisted of four 150- by 150-foot (45.7- by 45.7-m) sections. One section was open only to mule deer (Odocoileus hemionus) (treatment C), one to blacktail jackrabbits (Lepus californicus) (treatment B), one to both deer and rabbits (treatment D), and another closed to these animals and cattle (treatment A). An outside area of comparable size was open to deer, rabbits, and cattle (treatment E). Rabbit populations were high, being near or at peak the first 4 years following seeding. Mule deer numbers were moderate and remained fairly constant. Spring (May-June) use by cattle started 4 years after seeding and continued annually through 1981.

METHODS

Within each of the five sections, five permanent 100- by 1-foot (30.5- by 0.3-m) belt transects were randomly established to measure herbaceous growth and ground cover (fig. 1).

Percent cover of all herbaceous and woody species and production of herbs were recorded in 1964, 1965, 1967, 1972, 1977, and 1982. Ground cover was determined using a point sampling technique. A point was dropped at 6-inch (15.4-cm) intervals along each 100-foot (30.5-m) line (1,000 points per grazing treatment) with the first item encountered being recorded.

Cover data for 1964, 1972, and 1982 will be used as these 3 years corresponded the closest to the years that all shrubs were mapped and measured.

All shrubs and trees were mapped and their locations, widths, heights, and age classes recorded in all five grazing treatments in 1964, 1973, and 1984 (fig. 2). The following classes were applied. Basin big sagebrush and white rubber rabbitbrush height and age classes were: 0-5 inches (0-12.7-cm) (seedlings and young plants), 5-20 inches (12.7-50.8-cm) (immature plants), and over 20 inches (50.8-cm) (mature plants, producing seed). Black sagebrush classes were: 0-3 inches (0-7.6-cm) (seedlings and young plants), 3-10 inches (7.6-25.4-cm) (immature plants), and over 10 inches (25.4-cm) (mature plants).

Cover data are presented as trends. Shrub numbers are the total population of each species.



Figure 2.--Fountain Green exclosure, 1976. Total protection (treatment A, no grazing) section (I) and comparable outside (O) area (rabbit, deer, and cattle use). Note difference in shrub densities between sections and absence of forbs (alfalfa and Utah sweetvetch) in outside area.

RESULTS

Direct Seeding

The number of basin big sagebrush and white rubber rabbitbrush plants that resulted from direct seeding is unknown. The majority of the reproduction may or may not have originated from residual plants. The area was seeded in 1962; 2 years (1964) later shrubs were counted and measured. There were 52 basin big sagebrush; 1 seedling, 48 immature, and 3 mature plants. Nine white rubber rabbitbrush plants were immature; 1 was mature. Only one black sagebrush plant (mature) was located. Increase in shrub numbers after 1964 resulted from seed production off residual plants.

Cover, Production, and Numbers

Data indicate that total grass and forb production is more a factor of annual precipitation than it is of grazing treatments.

Percent cover appears to be a reliable indicator of community changes influenced by grazing treatments. Daubenmire (1968) reports similar results. Increases in shrub cover in all grazing treatments (fig. 2) corresponded with increased number of shrubs (fig. 3) and increased shrub size (figs. 4, 5, 6, 7, 8, and 9). The greatest increase in shrub cover (17 percent) was associated with the greatest increase in shrub numbers, and the largest number of mature shrubs. The greatest increases occurred where cattle, deer, and rabbits grazed jointly (treatment E).

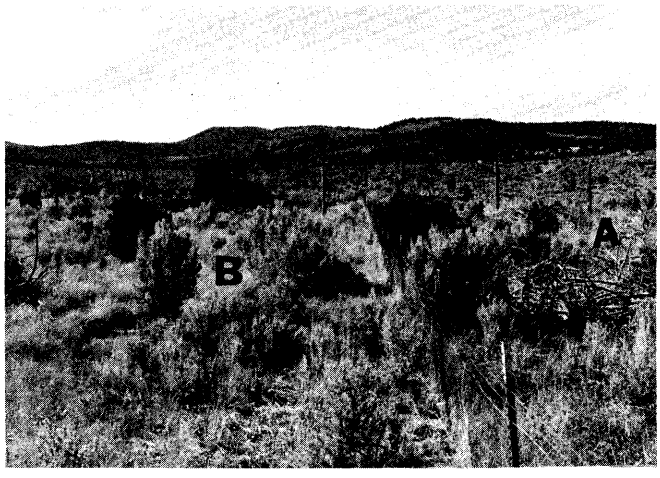


Figure 3.--Fountain Green Exclosure, 1976. Total protection from grazing (treatment A) (right) and rabbit use (treatment B) sections (left).

Forbs and grasses.--In 1964, 2 years following chaining, forbs attained their greatest amount of cover (13-29 percent) (fig. 4). The majority of the forbs were weedy annuals. On most juniper-pinyon improvement projects, annual forbs normally increase dramatically immediately following chaining. Once the seeded perennials became established, annual forbs decreased in number and cover until in 1972, when annuals made up less than 0.5 percent of the total cover. The seeded perennials, alfalfa (Medicago sativa var. Ladak), small burnet (Sanguisorba minor), and Utah sweetvetch (Hedysarum boreale) by 1972 had become firmly established and accounted for the majority of the forb cover. Under total protection from grazing (fig. 4, treatment A), perennial forb cover increased between 1964 and 1982. By 1982, forb cover under total protection was much higher (16.8 percent) than where rabbit (2.5 percent), or deer (6.2 percent), or rabbit and deer (3.8 percent) use occurred (treatments B, C, and D). Forb cover under cattle, deer, and rabbit use together (treatment E) steadily decreased from 18.2 to 1.9 percent.

Bare ground (fig. 4) steadily decreased (24.5 to 6.9 percent) where no grazing occurred (treatment A); however, there was an increase (16 to 25 percent) in bare ground where cattle, deer, and rabbits grazed together (treatment E). The increase in bare ground corresponds with: (1) increases in shrub numbers, and (2) decreases in forb cover. Litter (25 percent) and rock (5 percent) cover changed little over the study period.

Cover (25 to 35 percent) by grasses remained fairly stable over the years of the study and between grazing treatments. The first 2 to 3 years following chaining and seeding, the native grasses (Indian ricegrass and western wheatgrass) made up over 50 percent of the grass cover. As the seeded species established, they slowly became dominant. In 1982, native grasses under cattle, deer, and rabbit use did, however, maintain themselves as an important community component (over 30 percent). There were fewer trees alive in 1982 than in 1964; however, those alive had increased in size.

Basin big sagebrush.--Total number of shrubs appear to have been affected by grazing treatments (fig. 6). Within each of four grazing treatments; A. total protection; B, rabbit use; C, deer use; and D, rabbit and deer use combined, the total number of shrubs and the number of immature shrubs increased dramatically between 1964 and 1973 (A, 8 to 426; B, 15 to 558; C, 7 to 358; D, 3 to 453) and then decreased substantially between 1973 and 1984 (A- 426-333; B- 558 to 401; C- 358 to 173; D- 453 to 274). Only with combined rabbit, deer, and cattle use did number of shrubs increase from 1964 to 1973 (19 to 233) and again between 1973 and 1984 (233 to 465). Number of mature plants, however, increased during each time period in all grazing treatments.

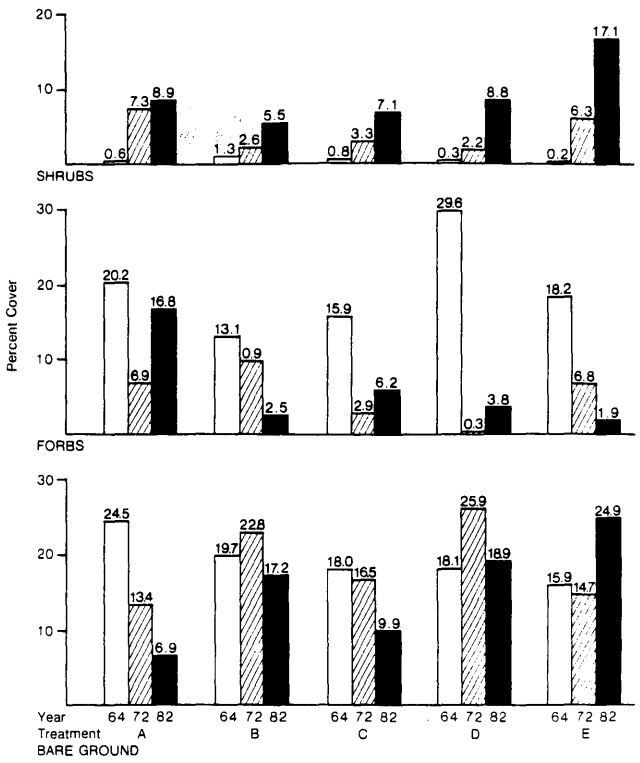


Figure 4.--Percent bare ground and percent ground cover of forbs and shrubs in 1964, 1972, and 1982, Fountain Green exclosures, five grazing treatments.

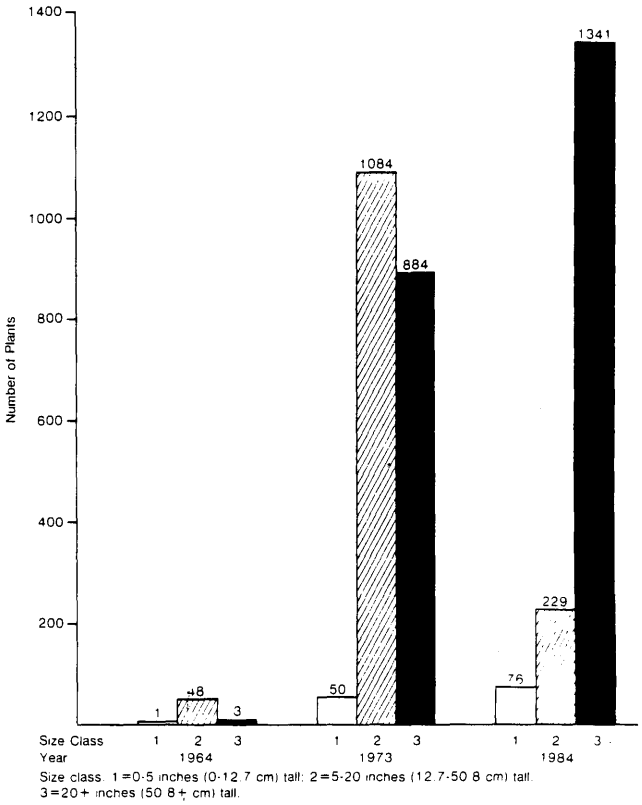


Figure 5.--Total number of basin big sagebrush plants (three size classes) in 1964, 1973, and 1984, Fountain Green exclosure.

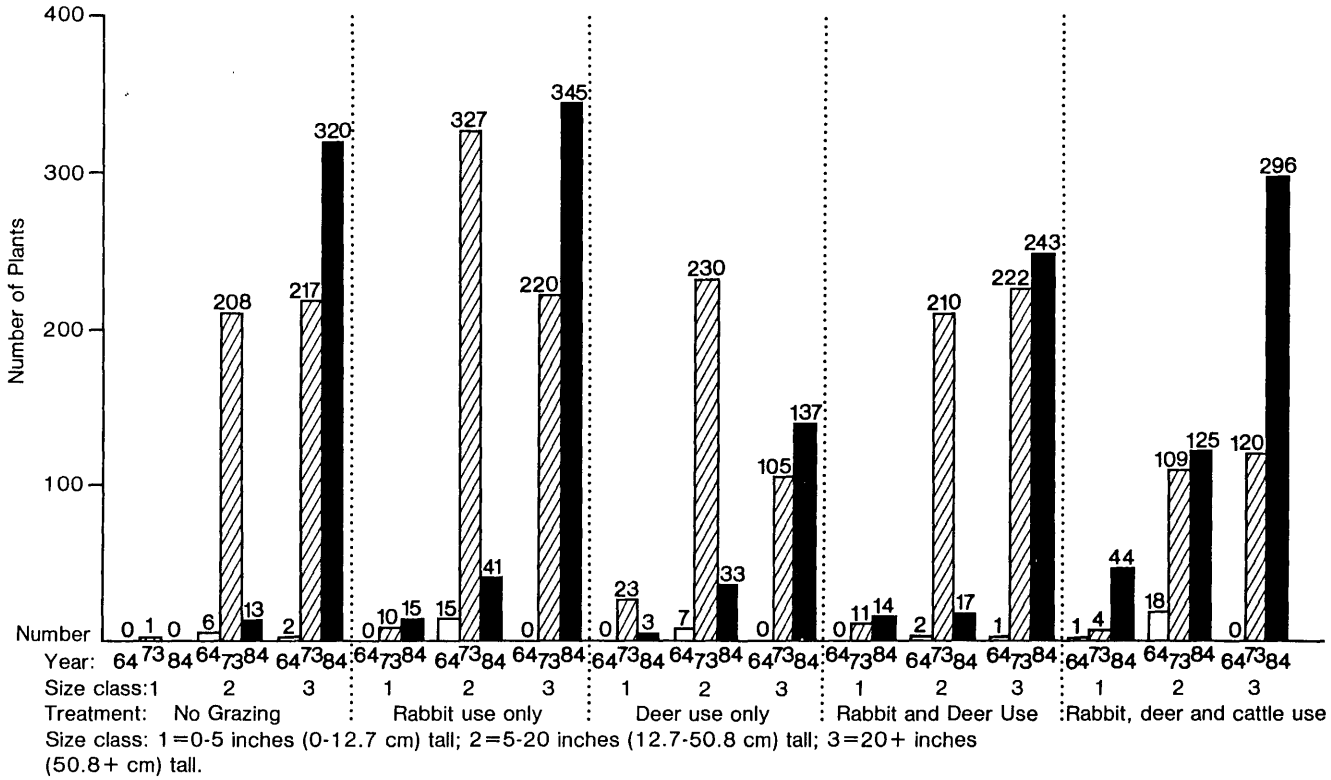


Figure 6.--Total number of basin big sagebrush plants (3 size classes) in 5 grazing treatments, Fountain Green exclosure, 1964, 1973, and 1984.

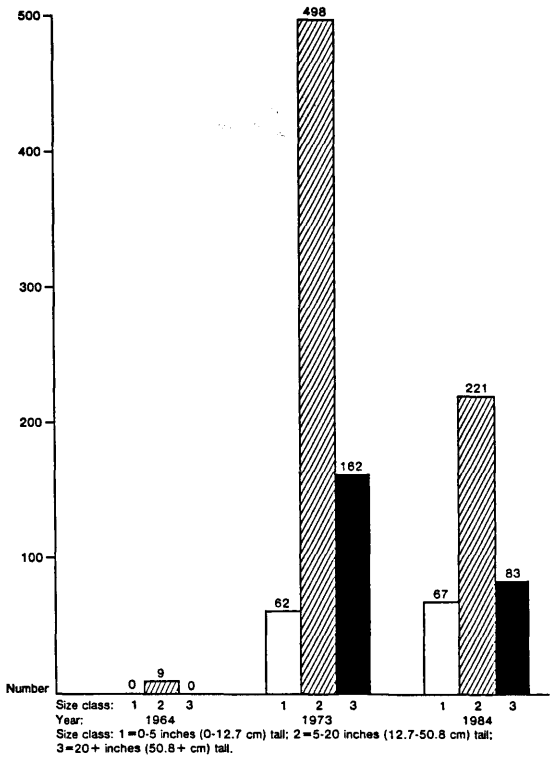


Figure 7.--Total number of white rubber rabbitbrush plants (three size classes) in 1964, 1973, and 1984, Fountain Green exclosure.

Fifty-two big sagebrush plants were present within the five grazing treatments in 1964. By 1973 there were 2,018 and in 1984 there were 1,646. Of the 52 original plants, 42 were alive in 1973 and 29 in 1984. About one-half (1,084) (fig. 5) of the 2,018 plants recorded in 1973 were immature; only 884 were mature. In 1984 there were 229 immature and 1,341 mature plants. Total number of plants increased dramatically between 1964 and 1973 followed by a substantial decrease between 1973 and 1984. Seedling numbers, however, showed a steady increase: 1 in 1964, 50 in 1973, and 76 in 1984.

White rubber rabbitbrush.--There were only 10 (9 immature, 1 mature) rabbitbrush plants in all grazing treatments in 1964. A dramatic increase to 622 plants occurred by natural spread between 1964 and 1973, followed by a nearly 40 percent decrease in numbers between 1973 and 1984 to 371 shrubs (fig. 7). Death of immature and mature plants between 1973 and 1984 accounted for the decrease. Number of seedlings was constant: 62 in 1973 and 67 in 1984.

There was at least a 65 percent reduction in the total number of rabbitbrush plants in four of the grazing treatments (total protection, rabbit, deer, and combined rabbit and deer use) (fig. 8) between 1973 and 1984. However, with combined rabbit, deer, and cattle use, rabbitbrush numbers increased from 47 to 239 during the same period.

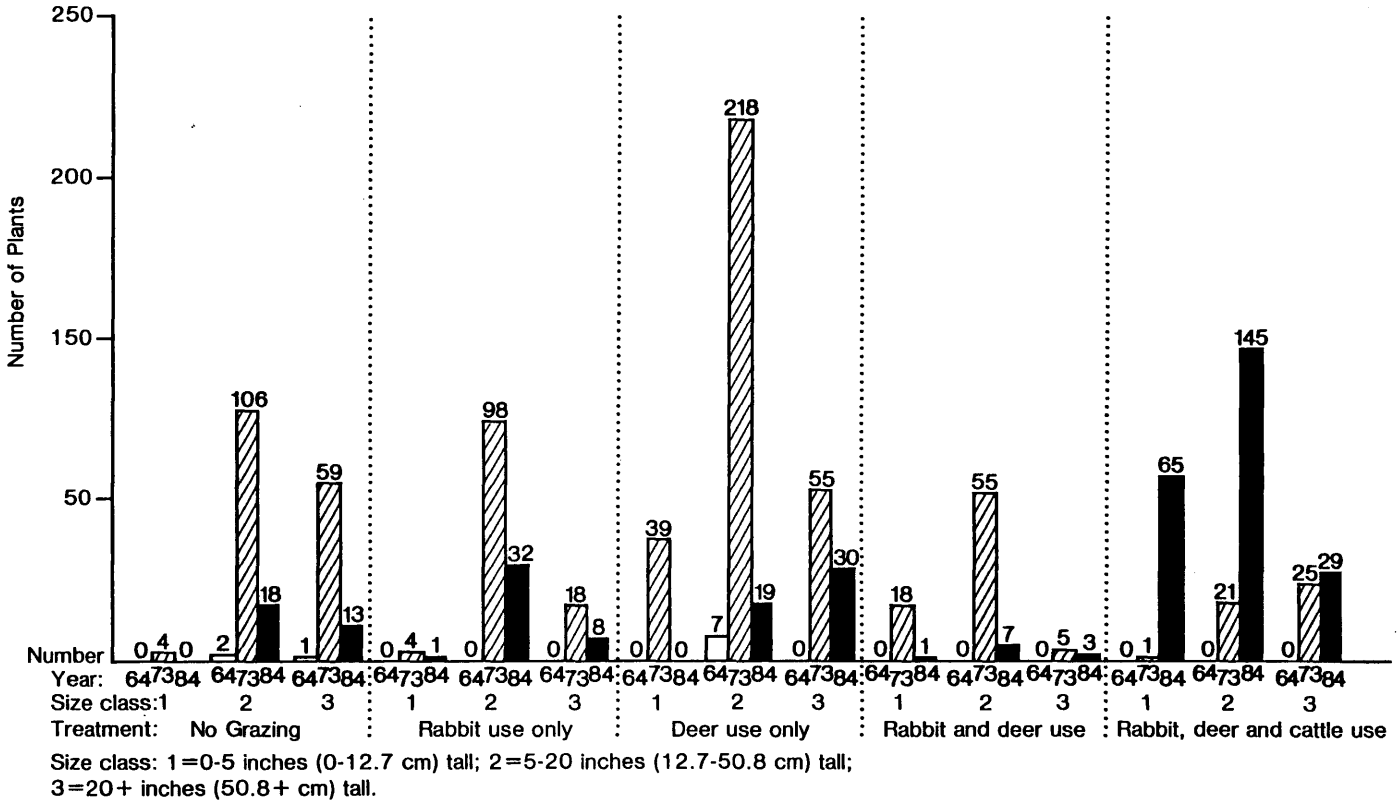


Figure 8.--Total number of white rubber rabbitbrush plants (3 size classes) in 5 grazing treatments, Fountain Green exclosure, 1964, 1973, and 1984.

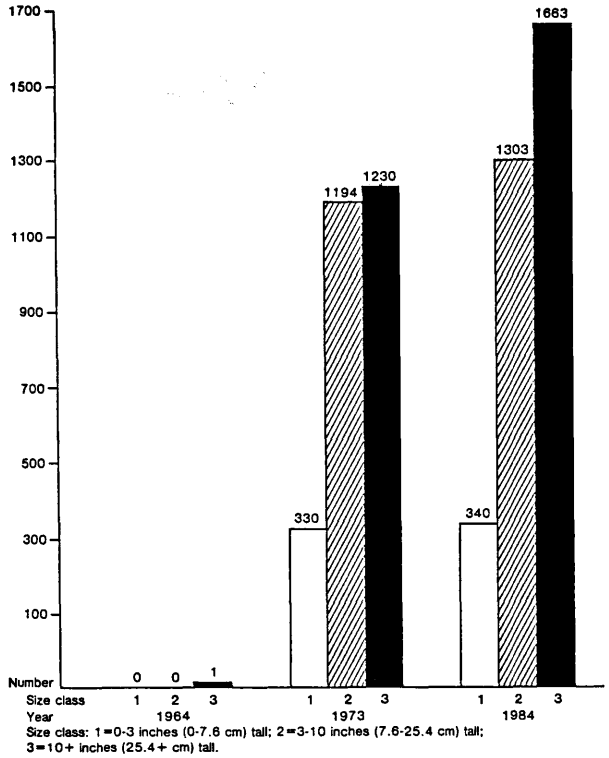


Figure 9.--Total number of black sagebrush plants (three size classes) in 1964, 1973, and 1984, Fountain Green exclosure.

Black sagebrush.--Within all five grazing treatments, shrub numbers were similar. Grazing treatment effects on shrub numbers were not evident. There was however, a dramatic change in total number of plants in all treatments over 22 years. One black sagebrush plant (mature) was located in 1964, 2,754 in 1973, and 3,306 in 1984.

Numbers of seedlings (fig. 9) in 1973 and 1984 were constant. Increases occurred in numbers of immature (1,194 to 1,303) and mature (1,230 to 1,663) plants.

SUMMARY

Fountain Green Wildlife Management Area was chained and seeded to a mixture of grasses, forbs, and shrubs in 1962. Basin big sagebrush and white rubber rabbitbrush were included in the seed mixture. Black sagebrush was not seeded. Chaining did not kill all the shrubs within the study area. All shrubs associated with a 300- by 300-foot (91.4- by 91.4-m) exclosure on the area were located and mapped in 1964, 1973, and 1984. Because of the short viability period of big sagebrush and rubber rabbitbrush seed (Stevens and others 1981; Jorgensen n.d.), only those shrubs on the sites in 1964 could have originated from seed planted in 1962. Goodwin (1956) reports that big sagebrush seed can move in the direction of prevailing winds up to 108 feet (33 m). Frischknecht (1962) followed big sagebrush reproduction in a crested wheatgrass (A. cristatum) seeding and reported that the maximum distance progeny spread from parent plants was 42 feet (12.6 m). Our observations are in line with these literature reports.

Numerically, black sagebrush increased the most of any shrub and did not appear to be affected by the presence or absence of grazing. Where rabbits, deer, and cattle grazed jointly for 22 years, big sagebrush and rubber rabbitbrush numbers showed the greatest sustained increase. This was the only grazing treatment that: (1) had a substantial increase in bare ground; (2) had the least amount of introduced perennial grasses; (3) had the lowest density of seeded perennial forbs (fig. 2); and (4) had the greatest amount of soil disturbance from grazing animals.

Big sagebrush, rubber rabbitbrush, and black sagebrush have been recognized as invader species (Frischknecht 1963; Christensen 1963), especially where the perennial grass community has been weakened. Vallentine (1979) also reported that continual early spring grazing encouraged invasion of big sagebrush. Continued early spring grazing by cattle occurred in the study area for 13 years; this may account for the continual increase in big sagebrush, black sagebrush, and white rubber rabbitbrush, along with an associated increase in bare ground and decrease in forbs and introduced grass cover (fig. 2).

Increased shrub numbers did not appear to adversely affect grass and forb forage production where no grazing occurred, or where rabbit use, deer use, and rabbit and deer use combined took place.

Basin big sagebrush, black sagebrush, and white rubber rabbitbrush were easily established, from direct seeding or residual plants in established stands of introduced and native perennial grasses and forbs.

ACKNOWLEDGMENT

Funds were provided by the U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station and Federal Aid in Wildlife Restoration Project W-82-R, Job 7.

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INFILTRATION ON OREGON LANDS OCCUPIED BY THREE SUBSPECIES OF BIG SAGEBRUSH

Sherman R. Swanson and John C. Buckhouse

ABSTRACT: High-intensity, short-duration rainfall events were simulated in the shrub interspaces on sites populated by three subspecies of big sagebrush, Artemisia tridentata ssp. tridentata, wyomingensis, and vaseyana, at four locations in eastern Oregon. Statistical analysis of infiltration during the final 15 minutes of each run showed large variability. Infiltration decreased as soil particle size decreased, organic ground cover decreased, bulk density increased, and extractable sodium increased. Infiltration was significantly lower on soils with vesicular porosity in the surface.

INTRODUCTION

Infiltration is necessary for precipitation to become part of the soil moisture available for plant growth. Infiltration of precipitation during the growing season can be especially important to herbaceous plant growth. Vegetation can in turn be influential in promoting infiltration, especially when percolation dominates the process.

The concept of using habitat types as a classification tool on western watersheds was promoted by Buckhouse and Mattison (1980) and Pfister (1981). The success of this concept depends on how well plant communities reflect watershed characteristics such as ground cover, above and below ground plant structure and phytomass, and soil structure, depth, texture, and organic matter.

Tisdale and Hironaka (1981) stressed the value of Artemisia tridentata (big sagebrush) subspecies in synecology. Winward (1980) briefly described management implications for A. tridentata subspecies.

Wyoming big sagebrush, A. tridentata ssp. wyomingensis, dominates the most xeric habitats of big sagebrush subspecies. It generally occurs below 6,000 feet (1 800 m) on moderately deep, well-drained soils. Grasses form the majority of the understory vegetation and most forbs are annual. There is a considerable amount of bare ground which cryptogams may occupy, 5 to 25 percent even under pristine conditions.

Basin big sagebrush, A. tridentata ssp. tridentata, occupies deep, well-drained soils and much of its range has been converted to cropland. More perennial forbs grow in these stands. Herbaceous production is from 1-1/3 to 2 times greater than in A. tridentata ssp. wyomingensis stands.

Mountain big sagebrush, A. tridentata ssp. vaseyana (var. pauciflorus) (Goodrich and others 1985), resides in the upper foothill and mountain areas from 3,500 ft (1 100 m) to 9,000 ft (2 700 m) elevation. It occupies moderately deep, well-drained soils with moisture available most of the summer. The herbaceous layer is more diverse, with commonly three to four times more species, and more productive by 1-1/2 to 2 times than on A. tridentata ssp. wyomingensis sites.

Our objectives were twofold: (1) Look for characteristic differences in infiltration rates among sites occupied by the three subspecies; and (2) identify aspects of the soil and vegetation that control and/or indicate differences in infiltration rates.

STUDY AREA AND METHODS

At each of four widely spaced eastern Oregon locations, (fig. 1) Millican, Squaw Butte, Frenchglen, and Baker, three sites for each of the three subspecies were selected; a total of 36 sites. Each site was relatively homogeneous and representative of a common habitat type in relatively high ecological status. The vegetation on most sites was classified as mid-seral or high seral. However, all but one of the A. tridentata ssp. tridentata sites were classified as low seral, often because of Bromus tectorum (cheatgrass) abundance. In general, A. tridentata ssp. vaseyana sites were in the best condition. To facilitate use of the Rocky Mountain infiltrometer (Dortignac 1951), each site was selected for nearness to a road, slight slope, and scarcity of large rocks that would interfere with placement of subplot frames.

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Sherman R. Swanson is Assistant Professor, Department of Range, Wildlife, and Forestry, University of Nevada-Reno, Reno, NV. John C. Buckhouse is Associate Professor, Department of Rangeland Resources, Oregon State University, Corvallis, OR.

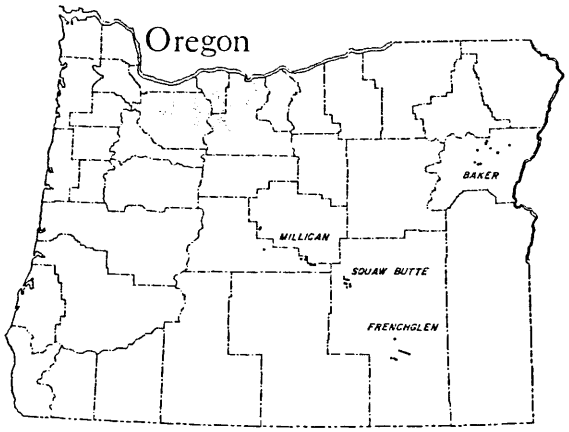


Figure 1.--Location of study sites.

Vegetation and soils were described in 1980. Vegetation was surveyed with three frequency transects of ten 1- by 2-foot (30- by 61-cm) plots each (Pieper 1978). Soils were described, sampled, and classified at the family level according to standard Soil Conservation Service (USDA Soil Conservation Service 1975) definitions.

All A. tridentata ssp. wyomingensis sites except one were Aridisols, whereas all A. tridentata ssp. vaseyana sites were Mollisols. The A. tridentata ssp. tridentata sites were about evenly divided between these soil orders. Five of the Millican sites have been heavily influenced by surficial deposits of Newberry Crater or Mazama pumice (tephra).

All twelve A. tridentata ssp. vaseyana sites and half the A. tridentata ssp. wyomingensis had Festuca idahoensis (Idaho fescue) as the understory dominant (Doescher 1982). Three of the remaining A. tridentata ssp. wyomingensis sites were A. tridentata ssp. wyomingensis/Stipa thurberiana (Thurber's needlegrass) habitat type; two were A. tridentata ssp. wyomingensis/Poa sandbergii (Sandberg's bluegrass) habitat type; and one was A. tridentata ssp. wyomingensis/Stipa comata (needle-and-thread grass) habitat type (Hironaka and Fosberg 1979). Half of the A. tridentata ssp. tridentata sites were A. tridentata ssp. tridentata/Elymus cinereus (basin wild rye) habitat type (Hironaka 1979); three were A. tridentata ssp. tridentata/Agropyron spicatum (bluebunch wheatgrass) habitat type; and one was A. tridentata ssp. tridentata/Stipa comata habitat type (Hironaka and Fosberg 1979).

The following summer (1981) a Rocky Mountain infiltrometer (Dortignac 1951) was used on each site to simulate high-intensity rainfall and measure infiltration and soil erosion in shrub interspaces. The 5 inches/h (12.6 cm/h) simulated storms represented events with a return period of well in excess of 100 years (Miller and others 1973). At least 30 minutes before each run, subplots were prewet with a fine-spray watering can until ponding began. (Ponding was possible on one tephra-dominated site which produced no runoff.) Each run lasted 28 minutes with samples collected after 3 minutes and at subsequent 5-minute intervals.

Eighteen subplots grouped into six plots were placed in representative shrub interspaces on each site. At each subplot, slope was measured with an Abney level and percentage coverage of each soil surface morphology type was visually estimated along with surface pavement, litter, cryptogams, bunchgrass base, and canopy cover. Litter and bunchgrass were combined to form the term organic ground cover. Training for ocular estimation of cover was done in the field with a 100-point frame.

Samples of the top 2.4 to 3.9 inches (6 to 10 cm) of each major soil surface morphology type were collected from two locations on the site to determine stone-free bulk density (Blake 1965), organic matter (Walkley and Black 1934), percentage medium and coarse sand, fine sand, silt, and clay in the fine-earth fraction (Day 1965), and extractable sodium (Peech and others 1947).

The three sites of each subspecies at each location served as replications for a randomized complete block experimental design with locations as the blocking factor and subspecies as the treatment. Simple and stepwise multiple correlation and one-way analysis of variance used sites or, where appropriate, plots or subplots as replications. Tukey's procedure was used for multiple comparisons of equal sample size and Scheffe's test was used with unequal sample size. Significance tests were made at the 0.1 probability level (Steel and Torrie 1980).

RESULTS

Average infiltration curves for the 36 sites were highly variable. Some sites showed almost no reduction in infiltration rate during the 28-minute run, while others showed rapid reduction in water intake before infiltration stabilized. Analysis focused on the last 15 minutes of the run (average final infiltration rate). Average final infiltration rates varied from just over 1 to just under 5 inches per hour (<3 - >12 cm/h). Habitat type and climax understory species showed no significant correlation with final infiltration rates. Although mean infiltration rates appeared generally lower for sites occupied by A. tridentata ssp. wyomingensis and for sites at Squaw Butte, statistical differences were not confirmed due to a significantly inconsistent variation between subspecies at the four locations (fig. 2). Differences in infiltration rates between sites supporting different subspecies were significant only at Frenchglen where sites occupied by A. tridentata ssp. wyomingensis had lower infiltration rates than A. tridentata ssp. vaseyana sites (fig. 3).

Differences in infiltration rates could, however, be partially explained by other site parameters. Surface soil and vesicular porosity

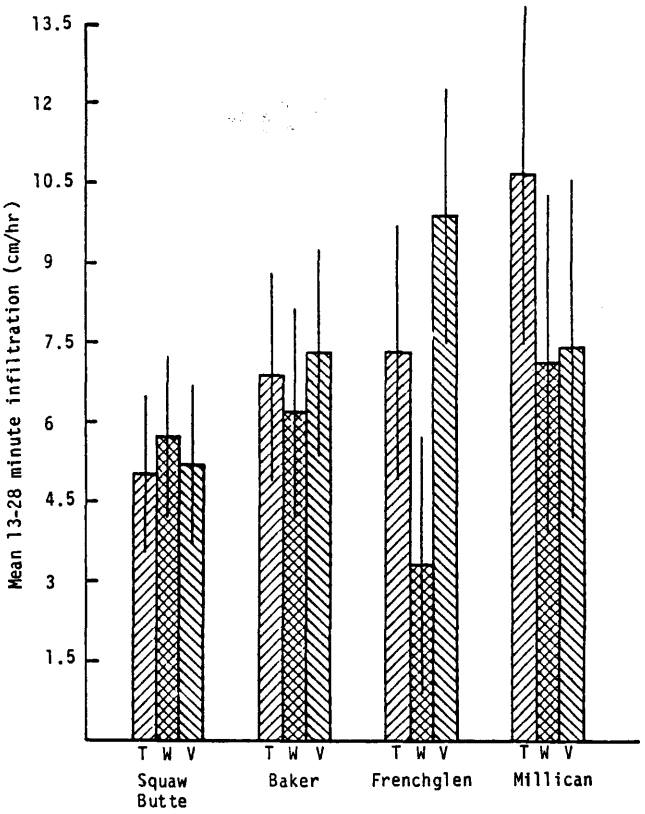


Figure 2.--Infiltration by location and subspecies. T = A. t. ssp. tridentata, W = A. t. ssp. wyomingensis, V = A. t. ssp. vaseyana. At a location, subspecies with nonoverlapping confidence intervals are significantly different at the 0.1 level of probability.

had lower rates of infiltration (fig. 4). Soils with loamy sand texture had significantly higher infiltration rates than soils with loam, sandy loam, or silt loam textures (inches/h 10.28, 6.62, 6.36, and 5.76 cm/h respectively). Although Borolls appeared to have higher mean rates of infiltration than other suborders, differences were nonsignificant between soil orders or suborders. Using stepwise multiple linear correlation, medium and coarse sand (0.25 to 2 mm) in the surface soil within each subplot accounted for 23 percent of the variability in average final infiltration rate (table 1). Combining organic ground cover with medium and coarse sand accounted for an additional 17 percent. Variables that were significantly correlated with final infiltration but did not improve multiple correlation included bare ground, clay, silt, bulk density, and organic matter. The amount of sodium in surface soils accounted for 11 percent of infiltration variability. Sediment concentration in runoff was also significantly related to infiltration (Swanson and Buckhouse 1984).

Five sites at the Millican location with surficial deposits of tephra had higher average final infiltration rates than the other 31 sites (3.58 and 2.56 inches/h, 9.1 and 6.5 cm/h respectively).

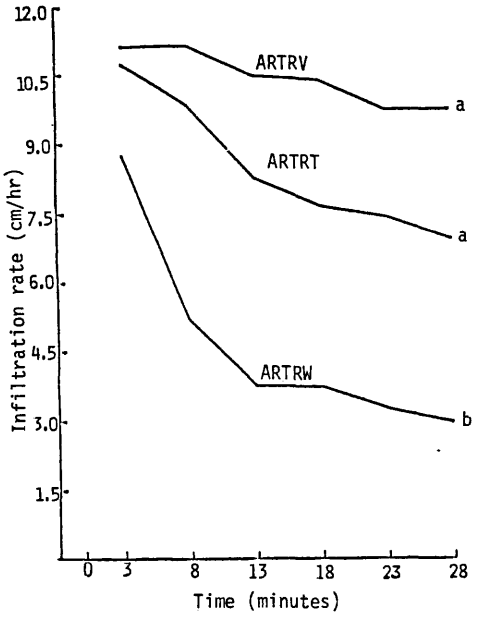


Figure 3.--Average infiltration curves for each subspecies at Frenchglen. Each line represents a total of 18 plots on three sites. The same letter at the end of two curves indicates a nonsignificant difference in infiltration rate during the last 15 mintes.

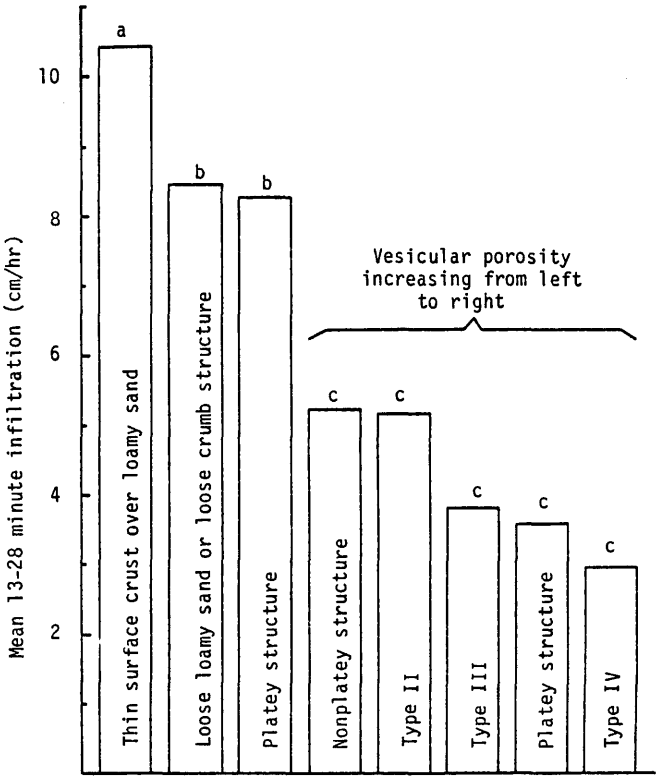


Figure 4.--Surface soil morphology and infiltration. Types II, III, and IV were described by Eckert and others (1977). Type II has many well-developed cracks; Type III has fewer well-developed cracks; and Type IV has few narrow cracks. Surface soil morphological types with differenct letters are significantly different at the 0.1 level of probability as determined by Scheffe's test.

Table 1.--Correlation analysis of soil surface and surface soil factors in 633 subplots with average final infiltration rate

Site factor	Stepwise R^2	Simple r
Medium and coarse sand (0.25 - 2mm)	Step 1 = .23**	.48**
Organic ground cover	Step 2 = .40**	.40**
Fine sand (0.05 - 0.25mm)		-.05NS
Bare ground		-.35**
Clay (<0.002 mm)		-.34**
Silt (0.002 - 0.05 mm)		-.27**
Bulk density		-.26**
Organic matter		.11**
Coarse fragments (>2 mm)		.01NS

**Indicates significance at the 0.01 level of probability.

Because of this difference, data analysis was repeated with these sites omitted. In that analysis, both soil order and suborder were significant descriptors for explaining infiltration rate. Mollisols had higher infiltration rates than Aridisols (2.8 and 2.08 inches/h, 7.25 and 5.29 cm/h respectively). Borolls had higher infiltration rates than Orthids (3.91 and 2.06 inches/h 9.94 and 5.23 cm/h respectively). In stepwise multiple linear regression, organic ground cover accounted for 29 percent of the variation, and percentage coarse fragments in the surface soil added just about half a percent to the multiple R^2. Surface soil morphology and habitat type analyses were essentially unchanged.

DISCUSSION

Shrub canopy zones generally have higher rates of infiltration than shrub interspaces because of differences in soil morphology, organic matter, and surface litter cover (Blackburn 1975; Brock and others 1982). This study, which examined infiltration in the shrub interspaces, can be taken as an indication of the response of the least absorbent parts of the site, but not of the site as a whole.

It was interesting to note that only at Frenchglen, which had the largest elevational difference among subspecies sites, was there a significant difference in infiltration rate among subspecies. Perhaps a wider and more representative elevational range elsewhere would have had study-wide significant differences in infiltration rates.

Regression analyses that included tephra sites supported the work of Rauzi and Kuhlman (1961), who found more rapidly declining infiltration rates on fine-textured soils. All correlation analyses, but especially the one omitting the tephra sites, support the conclusion that organic ground cover promotes infiltration (Branson and Owen 1970; Lang 1979; Meeuwig 1970). This relation between infiltration and organic ground cover may partially explain the higher infiltration rates found on Mollisols and especially Cryoborolls which have more organic matter in their surface layers. Increased organic matter can contribute to aggregate stability and a soil structure that is generally more favorable to infiltration. Soils with vesicular porosity are generally low in organic matter and are more frequently Aridisols.

The correlation of sodium with decreased infiltration may be an indication of the clogging effect of easily detached soil particles released by the dispersing action of sodium (Singer and others 1982).

Vesicular porosity occurs when air bubbles deform soil pores; hence it is an indication of soil instability under nearly saturated conditions. Infiltration rate can be reduced in these soils, as this and other studies have found (Blackburn 1975; Eckert and others 1977), because low aggregate stability leads to few surface pores and these are easily clogged by readily detached soil particles (McIntyre 1958). In addition, vesicular pores dampen the potential gradient by: (1) decreasing the soil particle surface area per unit volume; (2) increasing the depth to which a given quantity of water must penetrate before being absorbed; and (3) increasing the distance between the soil surface and the wetting front over which soil potential forces must pull.

Winward (1970) found that the occurrence of particular subspecies of big sagebrush did not correlate with soil texture. With this in mind, average infiltration rates in the last 15 minutes were adjusted using percent medium and coarse sand as a covariable. Even with this adjustment, tests for differences by subspecies, location, and condition class were nonsignificant.

CONCLUSIONS

The distribution of vegetation and process and infiltration are interdependent and controlled by many of the same factors. This correlation may aid managers in their attempt to understand rangeland hydrology; however, this investigation

indicates that vegetation identification must remain only one of many tools. Subspecies of big sagebrush, taken alone, were not shown to be reliable indicators of infiltration rates. They reflected significant differences in only one of four locations and that location had large differences in elevation among sites occupied by A. tridentata ssp. vaseyana and A. tridentata ssp. wyomingensis. Observable site parameters that did relate to increased infiltration rates were the absence of vesicular porosity, loamy sand texture, and greater amounts of organic ground cover.

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BIOLOGY AND ECOLOGY OF SAGEBRUSH IN WYOMING:

I. SOIL CHARACTERIZATION AND RESEARCH METHODS

Herbert G. Fisser

ABSTRACT: Monitoring of vegetation, grazing, and environmental factors in semiarid regions of western Wyoming, USA, was initiated in 1960. Plant community dynamics data have been recorded annually at 41 locations for 21 years. This paper gives a general portrayal of the Wyoming research sites. The methods of sampling are described. The climate is continental, average annual precipitation is 9 inches (22 cm) and mean annual temperature is 44 °F (7 °C). Yield and cover data of herbaceous species were obtained primarily with transects of 20 1- by 1-foot (30- by 30-cm) quadrats. Shrub yield was obtained with a weight-unit-estimation procedure. Intensive phenodynamics monitoring was conducted for ten years at 12 geographically diverse sites. Productivity data were derived by a weight-unit index procedure. Soil profile description, precipitation, and temperature were recorded. Annual photographic records have been maintained. The ERHYM model and precipitation-yield index procedures have been tested.

INTRODUCTION

Most rangelands of Wyoming are dominated by shrubs (Beetle 1960; Porter 1962; Küchler 1964). In Wyoming the most common and widely-dispersed shrub is Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis). Mountain big sagebrush (A.t. ssp. vaseyana) and basin big sagebrush (A.t. ssp. tridentata) are common, but restricted to smaller areas (Beetle and Johnson 1982).

Wyoming shrub ranges have supported a viable cattle and sheep industry for over 100 years (Nelson 1898; Vale 1975; Kearl 1980). Livestock management and that of pronghorn antelope (Antilocapra americana), mule deer (Odocoileus hemionus), and elk (Cervus elaphus) populations must meet ever increasing land use competition and economic stress (Kearl and Freeburn 1980; Olson and Gerhart 1982; Heady 1984). Ecological research for sagebrush was addressed 40 years ago (Robertson 1947). Efforts by W. M. Johnson (1969) and K. L. Johnson (1978) exhibited increasing awareness of the importance of sagebrush rangelands to agricultural, wildlife, and energy development industries.

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Herbert G. Fisser is Professor of Range Management at the University of Wyoming, Laramie.

These ecological studies were initiated in 1962 (Fisser 1962, 1963a). Various aspects of this research have continued to the present through cooperative support from the University of Wyoming Range Management Department and the Bureau of Land Management (BLM) (Fisser 1984a). A great variety of interests have been considered during the many years of monitoring on more than 100 locations encompassing the semiarid shrublands of western Wyoming.

The objectives of this and the following companion papers in this proceedings are: (1) to characterize sagebrush-related research in Wyoming, (2) to identify sagebrush response to grazing and chemical shrub control, (3) to show vegetation/precipitation trends with regression, and (4) to apply a hydrology-based forage production model.

DESCRIPTION OF RESEARCH SITES

Herbage production and cover were obtained primarily in the Big Horn and Wind River Basins of Wyoming. One location was a relic site near Thermopolis, WY, reported by Passey and Hugie (1962). All others were fenced exclosures of 2 to 6 acres (1 to 3 ha) that had been installed by the mid-1960's. Also included was an exclosure near Farson, WY, in the Little Colorado Desert and four exclosures south and west of Kemmerer, WY, on the Bear River Divide. Later, others were established to extend the geographic locations eastward toward Casper, WY, and southward toward Baggs, WY, and Manila, UT (Fisser and Kleinman 1974). Long-term herbage production data from five locations have been selected for presentation in this report (fig. 1).

Location and Geology

The name, county location, legal description, and year of establishment of each of the five research sites are given in table 1. Bud Kimball and Smilo occur in the Big Horn Basin; and the remainder occur in the Wind River Basin to the south. These basins formed during the Laramide Revolution beginning in late Cretaceous and extending through Eocene time. Regional uplifting of mountains, faulting and warping, and regional degradation and sediment deposition occurred during the Pliocene and Pleistocene, giving Wyoming its present unique ecology and high elevation (Love 1960).

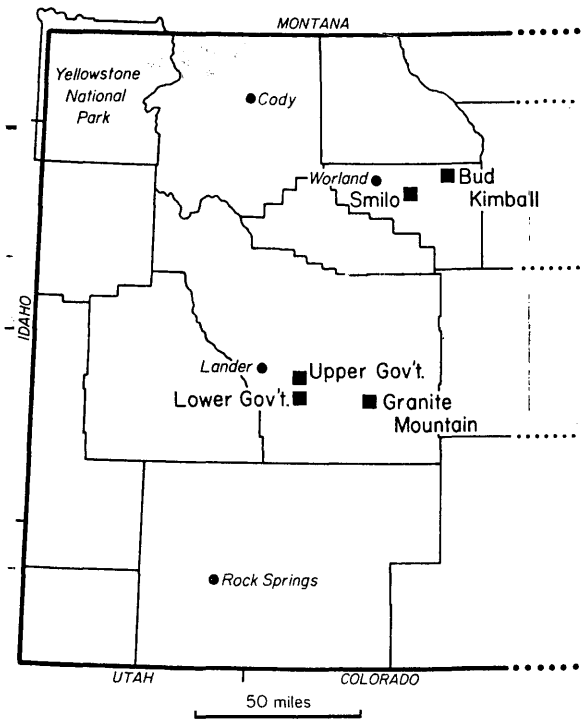


Figure 1.--Research locations in western Wyoming.

Soils and Topography

Soils are typical Aridisols derived under arid climates and exhibit poorly differentiated horizons. Most clay has been leached to lower horizons in the development process. Soluble salt concentrations are low and pH is well within tolerance ranges for growth of most species common to the sagebrush/grass region (Soil Survey Staff 1967; Ries 1973). Soil classification information is also given in table 1. Important differences in horizon thicknesses and textural values occur among sites; these affect soil moisture relationships (table 2).

Topography is generally level to slightly rolling with a general landscape of hills and plains. Slope values range from 0.5 to 5.5 percent. Exposures of the five sites are generally easterly from 30 to 110 degrees. Elevations range from 4,600 to 7,100 feet (1 400 to 2 160 m) (table 1).

Climate

The climatic region is continental, characterized by great diurnal and seasonal temperature variation, abundant sunshine, and mean annual precipitation of 8 to 11 inches (20 to 28 cm). Mean annual temperatures for the study sites were derived by extrapolation from nearby U.S. Weather Service Stations. Data extremes range from 110 °F (43 °C) in the Big Horn Basin to a low of -50 °F (-45 °C) at the Granite Mountain site in the Wind River Basin.

Table 1.--Location, general soil classification, and topographic information of the five research locations in western Wyoming

	Smilo	Bud Kimball	Lower Government	Upper Government	Granite Mountain
County	Washakie	Washakie	Fremont	Fremont	Fremont
Legal description TWSP	45N	46N	32N	33N	31N
RANGE	91W	89W	98W	97W	99W
SECTION	SWSE 14	NENW 29	NWSE 22	NWSW 32	NESW 7
Soil great group	Natrargid	Haplargid	Camborthid	Haplargid	Haplargid
Soil subgroup	Haplic	Ustollic	Borollic	Borollic	Borollic
Soil family (time)	Montmoril-lonitic mesic	Montmoril-lonitic mesic	loamy, mixed	loamy, mixed	loamy, mixed
Soil series	Absted	Ulm	Yamack	Almy	Forelle
Slope (percent)	5.5	2.0	0.5	0.5	0.5
Exposure (degrees)	076	110	085	080	030
Elevation (feet)	4,600	4,700	5,500	5,925	7,100
Elevation (meters)	1 400	1 430	1 675	1 805	2 165

Daily weighted mean seasonal temperatures of U.S. Weather Service Stations nearest each exclosure location are presented in table 3. On-site recorded seasonal precipitation was greatest during winter and spring (table 4). Although amounts vary from year to year, summer and fall precipitation occur consistently. This represents a major climatic variation from the Intermountain and Pacific Northwest region west of the Continental Divide where precipitation is almost completely absent during summer/fall, is greater in winter than spring, and where winter temperatures are adequate for early growth.

Vegetation

According to Küchler (1964) the sites in the more northerly Big Horn Basin occurred in the wheatgrass-needlegrass shrub steppe zone (Agropyron-Stipa-Artemisia). Those in the Wind River Basin occurred in the sagebrush steppe zone (Artemisia-Agropyron). The two categories were combined by West (1983) because of the small area of the former and because adequate literature was unavailable.

Wyoming big sagebrush and basin big sagebrush are the dominant shrubs (appendix I). Another frequently encountered shrub is Douglas or low rabbitbrush (Chrysothamnus viscidiflorus). The primary perennial grass is western wheatgrass; others include Sandberg bluegrass (Poa sandbergii), mutton bluegrass (P. fendleriana), prairie junegrass (Koeleria cristata), and needle-

Table 2.--Detailed physical and chemical soil characersistics including textural class, bulk density, and porosity of the A and B horizons

	Smilo	Bud Kimball	Lower Government	Upper Government	Granite Mountain
Soil A horizon depth (inches)	0-4	0-5	0-3	0-3	0-2
Soil A horizon depth (cm)	0-10	1-13	0-8	0-8	0-5
Soil B horizon depth (inches)	4-11	5-8	3-11	3-16	2-17
Soil B horizon depth (cm)	4-28	13-20	8-28	8-41	5-43
Soil coarse sand (percent)	16.2	3.4	34.2	7.1	13.4
Soil fine sand (percent)	22.2	14.7	21.0	12.8	19.6
Soil silt (percent)	31.9	49.0	12.8	43.1	34.5
Soil clay (percent)	29.7	32.9	32.0	37.0	32.5
Textural class	clay loam	silty c.l.	sandy c.l.	silty c.l.	c.l.
Bulk density A horizon	1.3	1.6	1.3	1.2	1.1
Bulk density B horizon	1.7	1.5	1.7	1.6	1.5
Porosity (percent) A horizon	49	52	52	54	59
Porosity (percent) B horizon	37	42	35	38	44
pH A horizon	7.9	7.8	8.1	7.1	7.6
pH B horizon	8.3	7.9	8.5	7.4	7.5
Sol. salts A horizon (mmho/cm^2)	0.6	0.7	0.7	0.8	0.7
Sol. Salts B horizon (mmho/cm^2)	0.5	1.4	0.6	0.6	0.5
$CaCO_3$ A horizon (percent)	0.5	0.6	0.6	0.7	0.6
$CaCO_3$ B horizon (percent)	0.6	0.5	0.5	0.5	10.5

and-thread (Stipa comata). Additional perennial grass and grasslike species which occurred irregularly are bottlebrush squirreltail (Sitanion hystrix), blue grama (Bouteloua gracilis), Indian ricegrass (Oryzopsis hymenoides), and threadleaf and needleleaf sedge (Carex filifolia and C. eleocharis). The introduced annual cheatgrass brome (Bromus tectorum) on occasion responds with dramatic increase following sagebrush control but is usually limited by competition from associated perennial species, as is the native annual sixweeks grass (Vulpia octoflora). Common mat-form and succulents include Hood's phlox (Phlox hoodii), Hooker sandwort (Arenaria hookeri), plains pricklypear (Opuntia polyacantha), and rose pussytoes (Antennaria rosea).

History and Use

Trappers and explorers were familiar with what is now Wyoming early in the 1800's. The majority continued westward toward California and Oregon, but by the 1820's a number of trappers were living in the State. By the 1860's, immense numbers of cattle and sheep were being trailed into Wyoming from Texas and Oregon (Frink 1954). The Big Horn Basin, one of the last areas of the State to be settled, was bypassed by most emigrants and stockmen. In 1871, however, J. D. Woodruff began a cattle enterprise on the Owl Creek area and built the first cabin in the Big Horn Basin (Duhig 1948).

Table 3.--Mean daily temperature (°F) by season, taken from U.S. Weather Service Stations nearest each of the five research sites

Season	Number of days	Smilo Worland	Bud Kimball Tensleep	Lower Government Lander	Upper Government Sand Draw	Granite Mountain Jeffrey City	Mean
Winter	183	28	32	28	30	25	29
Spring	76	57	54	54	53	50	54
Summer	61	70	68	69	69	65	68
Fall	45	54	51	55	55	49	53
Mean*		44	45	43	44	40	44

* Adjusted and weighted for days per season

Table 4.--Long-term seasonal precipitation data for the five research locations in western Wyoming

Season	Smilo	Bud Kimball	Lower Government	Upper Government	Granite Mountain
	- - - - - - - - - - - - - - - - - Inches - - - - - - - - - - - - - - - - -				
Winter October 16 - April 15	2.8	2.9	3.6	3.0	2.6
Spring April 16 - June 30	3.5	3.9	4.9	4.4	3.8
Summer July 1 - August 31	1.1	1.2	1.1	0.9	1.3
Fall September 1 - October 15	1.1	1.6	1.4	1.4	1.1
Annual	8.5	9.6	11.0	9.7	8.8

Little is known concerning the amounts and kinds of vegetation that were present during the early settlement years. In a diary written while traveling the Oregon Trail through the Wind River Basin, J. Dinwiddie wrote, "There is nothing but sand and sage" from the Sweetwater Crossing to South Pass, on the Wind River Range (Booth 1928). Generalized aspect, viewed in a similar context today, would not be much different. The disastrous loss of stock during the winter of 1866-67 is believed to have been the result of overgrazing as well as late spring storms (Frink 1954).

METHODS

Vegetation Monitoring

Introduction.--Earliest field research efforts, beginning in 1962, investigated vegetation cover and production of herbaceous species, primarily in the context of forage production. Area cover of all species was recorded. Only annual and perennial grass and grasslike species and single-stem annual and perennial forbs were clipped for determination of production. In 1971, study of biomass development of shrubs, mat-form, and succulent species was initiated with weight-unit-estimation procedures. In 1973, intensive studies were developed to record phenodynamics at 12 locations distributed from near Casper, Wamsutter, Manilla, Sage, Big Piney, Farson, and several locations in the Wind River and Big Horn Basins. Procedures to estimate community productivity were initiated in 1979.

Area cover and production.--Basal cover of herbaceous species and crown cover of shrub, half-shrub, and mat-form species, including the succulent plains pricklypear, was recorded (Fisser 1961; Fisser and Ries 1971). Area cover and herbage production studies on sagebrush-grass sites were conducted using transects of 20 quadrats, 1- by 1-foot (30- by 30-cm) spaced systematically along a randomly located 100-foot (30-m) steel tape. Cover percentages of all herbaceous, semiwoody, and woody species were estimated within each square foot unit. Data of shrub crown cover and basal cover of plains pricklypear, Hood's phlox, and Hooker sandwort were not combined when comparing area cover to herbaceous production since this group of plants was not clipped. Forage production was determined by clipping herbaceous species at ground or crown level at near peak standing crop. Exclosures were clipped on or near the same date each year. Clippings were oven dried at 158 °F (70 °C) for 24 hours prior to weighing.

Shrub production.--Beginning in 1971, shrub production was obtained by modified double-sampling during September and October. The technique involved a rapid weight-unit-estimation procedure. Estimates were made of transects consisting of 20 quadrats, 4- by 5-foot (1.2- by 1.5-m) spaced from 6 to 12 steps apart. The number of weight-units in each plot was estimated individually by two persons and then checked for accuracy. Weight-units were determined prior to the estimation procedure (Fisser and Ries 1972).

Phenodynamics.--To study the relationship of plant phenodynamics with vegetation production and environmental factors, an intensive monitoring program was initiated in 1973 at 12 research locations widely distributed in western Wyoming (Fisser and Kleinman 1974). Phenophase descriptions and stages were established for four primary species: western wheatgrass (Agropyron smithii), bluebunch wheatgrass (A. spicatum), big sagebrush (Artemisia tridentata), and black sagebrush (A. nova). A general phenology inventory scale was established for use on all other species.

Twenty individual plants of each of the four principal species were permanently located along 100-foot (30-m) lines in the 12 exclosures. Every 5 feet (1.5 m) on the line, directions along and from the line to the closest plant were recorded. Measurements of big sagebrush and black sagebrush included plant size, age, twig length, and seed stalk length. Measurements of western wheatgrass and bluebunch wheatgrass included plant size, age, leaf width and height, spike height, number of spikelets per seed head, and seed head development.

Separate scores were assigned for vegetative and reproductive development because plant individuals of semiarid regions seldom flower consistently. Time-lapse precipitation accumulation, maximum-minimum air temperatures, soil moisture and temperature, and site-characteristic photographs were recorded at each observation date (Fisser and Kleinman 1975).

Multiple step-wise regression was utilized to determine cause and effect relationships and correlations among environmental variables and plant development (Fisser and others 1977). In addition, a curvilinear regression model with a logrithmic growth curve and asymptotic limit was utilized to identify time-related phenologic development differences of species and life-form groups (Kinucan and Fisser 1984). These were then investigated to identify best plant predictors of climate variation.

Productivity.--Beginning in 1979, plant and community productivity relationships, with temporal and environmental changes, were studied using early- and late-season total population clipping and weight-estimation procedures. These were supplemented with multiple-period biomass sampling of individual culms and buds of the four prime species (Fisser and others 1980).

Beginning at least by the time of early standing crop estimation, individual plants of each prime species were clipped. Those selected represented the average phenology of a given prime species as indicated by the values of average phenology on the transect lines. The specimens to be clipped were selected at locations near the corresponding phenology transect line. At the first date each year, 40 specimens of each species were selected. Twenty were clipped and individually bagged with exclosure, species, and date identification. The remaining were identified with soft plastic-covered wire, placed on the ground in the case of

grasses and at the major twig base in the case of the sagebrushes. These were clipped at the next sampling date, at which time an additional set of 20 plants were identified with the soft, colored wire for subsequent sampling date clipping.

Selection of productivity units at the observation time prior to the clipping date was incorporated into the field procedures because of the intended extrapolation of prime species productivity data to that of the plant community. Productivity measures of entire plant populations typically involve clipping all species at frequent intervals throughout the growth season (Dickenson and Dodd 1976). Such data provide estimates of total standing crop at each date. They also require extensive work force and time allocation requirements that are totally beyond the limits of the present study (12 locations geographically distributed over an area representing the western two-thirds of Wyoming).

With data for both early and midseason community standing crop, and with productivity data of four prime species at frequent intervals throughout the growing season, essentially April through October, extrapolation and interpolation can be utilized to express coefficients of weight-phenology related development of the prime species to those of the community populations (Fisser 1984b). Thus, there appeared to be an apparent conceptual need, when developing the present field procedures, for time-extended relations of phenology-productivity unit selection and actual harvesting of the individual plants.

The procedures described in this report may not as closely depict true productivity values of community populations as clipping of all species would determine. The expression of standing crop at frequent intervals, derived from the productivity weight units integrated with early and late community standing crop, does provide, however, a valid characterization of community productivity dynamics (Fisser 1984c). In addition, the interrelation of prime species productivity units with phenologic progress will provide detailed description of phenodynamics and related standing crop values of these species (Fisser and others 1983)--data not available elsewhere that could be applied to the semiarid sagebrush-grass region typical of western Wyoming.

Time-variable environmental factors will influence both productivity and phenology. By interpretation of cause-effect responses, the biotic and environmental data will provide information useful for predicting growth and phenodynamics. Thus, future vegetation inventory processes can estimate probable crop production at any time during the growth season, subject to moisture and temperature benefits or restraints.

Productivity units of the wheatgrasses were individual culms. Selection was based primarily on the phenology average of the permanent transect lines. Height of culms, although uniform for most plants at a given stage of development, was specifically removed from the observer selection process.

Productivity units of the sagebrushes were individual twig tip initiation buds and initially included one node from the previous season's development. The inclusion of the added node was a minimal part of the productivity unit weight and was included to simplify the field procedure that required identification of a new bud twig as well as a uniform specified point at which it was to be removed from the shrub. The soft, colored wire was located at the base of the twig and did not affect bud growth development. Phenologic development, representative of the adjacent permanent phenology transect, defined the observer selection criteria. Length of current year twig development was used only if it related to identification of phenology that became definitive in some late-season reproductive stages (Fisser and others 1982).

Environmental Measures

Precipitation gauges with standard 8-inch (20-cm) orifice diameter were established at a few locations during the late 1950's (Fisser and others 1961). In 1960, and during subsequent years, smaller gauges were located at many research sites. A network of 70 gauges, spaced at 6 to 12 mile (10 to 20 km) intervals, was established initially throughout the Big Horn and Wind River Basins. A map with locations is given in Fisser (1963b). These gauges were metal cylinders with an orifice diameter from which 1 inch (2.54 cm) of precipitation would equal 100 ml (Fisser and others 1966). More than 200 gauges have been installed, primarily by the BLM, and are distributed over much of western Wyoming. Precipitation is recorded seasonally (Fisser and others 1966).

During the 1960's, a neutron probe was utilized to determine soil moisture (Fisser and others 1963). Gravimetric sampling with king tubes was conducted at several locations during the 1970's and early 1980's (Fisser and others 1977).

Ambient and time-lapse air temperature changes were recored with maximum- minimum thermometers. Soil temperatures at 1-, 8-, 15-, and 22-inch (2.54-, 20.35-, 38.1-, and 55.88-cm) depths were obtained from permanently placed thermographs (Fisser and others 1963). At sites of phenological studies, soil temperatures were obtained with thermometers inserted into the hole created by the king tube for soil moisture sampling (Kleinman and Fisser 1976; Fisser and others 1977).

Soil criteria were determined with the assistance of the BLM and the United States Department of Agriculture Soil Conservation Service personnel. Profile pits were excavated and characterized at all research locations. Samples were taken from each profile for detailed laboratory analysis (Ries 1973).

Photographic Record

Color and black-and-white photographs were taken to maintain a permanent visual record of research activities and temporal variation of vegetation and site conditions (Fisser and Ries 1973). A closeup photograph of each vegetation production transect and of those transects with permanent 1- by 1-foot (30- by 30-cm) quadrats was taken to show the first two quadrats. A general photograph was also taken showing distant vegetation and skyline. A single 2- by 20-foot (0.6- by 6.1-m) and 4- by 4-foot (1.3- by 1.3-m) quadrat for each exclosure characterizing grazing, chemical, and vegetation types was selected as a permanent photographic record site. Photographs were taken from one or more corners of each exclosure to provide visual expression of vegetation inside and outside the fenced units.

For 3 years during the phenodynamics study, closeup photographs of specific sagebrush branches, plains pricklypear clumps, and grass plants were taken at approximately 2-week intervals during the growing season. Observation of these segmental records exhibited a surprising characteristic in the production of reproductive stems. A specific branch usually alternated biennially, producing only vegetative growth one year, and producing seed the next (Kleinman 1976). Especially during years of moisture and temperature stress, it seems apparent that these shrubs are able to conserve their energy output related to development of reproductive structures and increase root components by restricting aerial growth to solely vegetative features.

Models and Forecasting

The generalized overview of modeling which has been approached in our research relates primarily to the water-balance climate model developed by Wight and Hanks (1981). In this model, which is identified by the acronym ERHYM, the herbage yields are determined as a function of the ratio of actual to potential transpiration values. Availability of input data, relative simplicity, and low computer costs make this model a viable tool for both research and resource management.

The major components of the ERHYM model require maximum and minimum temperature, daily precipitation and daily solar radiation climatic values. Soil information that is utilized includes albedo values of the soils, the water holding capacity, and infiltration rates. Daily update of soil water content is estimated by the model as related to the precipitation budget, evapotranspiration, and plant growth characteristics of the site. The vegetation components are identified by a crop coefficient and transpiration coefficient, as well as relative root distribution and a relative growth-curve factor. Growth is estimated on the basis of the ratio of potential evapotranspiration to actual evapotranspiration. The model integrates several aspects of range environment including amount of precipitation and daily distribution of precipitation. Evaporative demands of the vegetation are also taken into account. Soil moisture by horizon is a major factor and contributes to accurate prediction of rangeland yield.

The effectiveness of ERHYM depends upon its ability to simulate an accurate soil-water balance. Because there is little summer runoff at the sites in Wyoming, the soil-water components of the model were tested using single growing season runs in which actual, field-measured soil water values were used to initialize the model. Continuous runs were utilized to test the model's ability to predict over-winter recharge. For yield predictions, the model is run in a continuous mode from 1965 through 1980 to match the available yield data. Overall, the ERHYM performed reasonably well on two sagebrush rangeland sites of western Wyoming. Additional validation trials are being conducted to determine the best crop coefficient and transpiration coefficient to improve the accuracy and long-term forecasting ability of the model. The results of this study indicate that the ERHYM model has a wide range of potential applications in research and management of semiarid rangelands.

Studies to determine the simple relationship of herbage production to precipitation were conducted. Many studies which attempt to show quantitative relationships of herbage yield with precipitation have generally been unsuccessful. This is due primarily to the variable temporal distribution of precipitation and the fact that range plants respond to soil moisture only during certain phenological stages and little, if any, during fall and winter in the northern United States. Use of seasonal or combinations of monthly precipitation have helped account for the distribution effects.

Since precipitation herbage-yield relationships often exhibit a very site specific dependency, the development by several researchers has involved the use of ratios of long-term values. A yield and precipitation index model for herbage yield, then, may be adjusted and forecasts can be made with some reasonable expectation of success. The analyses of Wyoming research site data show that the winter-spring precipitation gives the best overall prediction results. These analyses also suggested that combining the herbage yield from several locations gave most consistent results.

Whether a model can be utilized to predict and forecast vegetation interactions with differing climatic variables through time is dependent upon the quantitative characteristics of the model and of course, on the interpretative evaluation of those conducting the research. With long-term climate records and reasonably long-term data of herbage production, an accurate estimate of expected forage yield may be developed by those concerned with the ecology of semiarid rangelands.

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Appendix I.--Plant names, growth characteristics, and occurrence at the five research sites in western Wyoming by plant class.

Plant name	Plant class	Smilo	Bud Kimball	Lower Govt.	Upper Govt.	Granite Mtn.
I. Shrubs, half-shrubs, mat-form, succulent						
Machaeranthera glabriuscula	Half-shrub	X	X			
Artemisia tridentata ssp. tridentata	Shrub	X	X	X		
Opuntia polyacantha	Succulent	X	X	X	X	
Machaeranthera grindelioides	Half-shrub		X			
Gutierrezia sarothrae	Half-shrub		X			
Phlox hoodii	Mat-form		X	X	X	X
Haplopappus acaulis	Mat-form		X			X
Ceratoides lanata	Half-shrub			X		
Chrysothamnus viscidiflorus	Shrub			X	X	X
Antennaria dimorpha	Mat-form				X	
Phlox multiflora	Mat-form				X	
Antennaria rosea	Mat-form				X	X
Artemisia tridentata ssp. wyomingensis	Shrub				X	X
Leptodactylon pungens	Shrub				X	
Eriogonum ovalifolium	Mat-form					X
II. Perennial Grasses and Grasslike						
Bouteloua gracilis	Grass	X				
Sitanion hystrix	Grass	X		X		X
Agropyron smithii	Grass	X	X	X	X	X
Poa secunda	Grass	X	X	X	X	X
Stipa comata	Grass	X	X	X	X	X
Stipa viridula	Grass		X			
Koeleria cristata	Grass		X	X	X	X
Oryzopsis hymenoides	Grass		X	X		X
Carex eleocharis	Sedge			X		
Poa fendleriana	Grass					X
III. Perennial Forbs						
Crepis occidentalis		X				
Cryptantha bradburiana		X				
Castilleja angustifolia		X	X		X	
Cymopterus montanus		X	X		X	
Astragalus missouriensis		X	X		X	X
Machaeranthera canescens		X	X		X	X
Sphaeralcea coccinea		X	X	X	X	
Allium textile		X	X	X	X	X
Erigeron pumilus		X	X	X	X	X
Lomatium orientale		X		X		
Penstemon cleburnei		X			X	
Calochortus nuttallii			X			
Chaenactis douglasii			X			
Delphinium geyeri			X			
Lomatium simplex			X			
Sedum stenopetalum			X			
Zigadenus venenosus			X			
Viola americana			X	X	X	
Viola nuttallii			X	X	X	
Lewisia rediviva			X		X	
Musineon divaricatum			X		X	
Crepis modocensis			X			X

(con.)

Appendix I. (Con.)

Plant name	Plant class	Smilo	Bud Kimball	Lower Govt.	Upper Govt.	Granite Mtn.
Astragalus diversifolius				X		
Astragalus drummondii				X		
Oenothera caespitosa				X		
Oxytropis sericea				X		
Astragalus purshii				X	X	
Crepis acuminata				X	X	
Tragopogon dubius				X	X	
Agoseris glauca				X	X	X
Astragalus missouriensis				X		X
Gilia congesta					X	
Arabis holboellii					X	X
Lesquerella ludoviciana					X	X
Comandra pallida						X
Erysimum asperum						X
Erigeron compositus						X
Lithophragma parviflora						X
Lithospermum ruderale						X
Penstemon laricifolius						X
Penstemon eriantherus						X
Senecio canus						X
Trifolium gymnocarpon						X
IV. Annuals						
Androsace septentrionalis	Forb	X				
Salsola kali	Forb	X				
Machaeranthera tanacetifolia	Forb	X	X			
Vulpia octoflora	Grass	X	X			
Chenopodium leptophyllum	Forb	X		X	X	
Gilia pumila	Forb	X		X	X	
Plantago patagonica	Forb	X		X	X	
Plantago spinescens	Forb	X		X	X	
Bromus tectorum	Grass	X	X	X	X	
Descurainia pinnata	Forb	X	X	X	X	
Lepidium densiflorum	Forb	X	X	X	X	
Lappula redowskii	Forb	X	X	X	X	X
Sisymbrium altissimum	Forb	X		X		X
Chenopodium album	Forb		X			
Monolepis nuttalliana	Forb		X	X		
Collomia linearis	Forb			X		
Gilia leptomeria	Forb			X		
Mentzelia albicaulis	Forb			X		
Thlaspi arvense	Forb			X		
Microsteris gracilis	Forb			X	X	
Gayophytum ramosissimum	Forb			X	X	
Camelina microcarpa	Forb			X		X
Cordylanthus ramosus	Forb			X		X
Arabis lignifera	Forb				X	
Bromus japonicus	Grass				X	
Eriogonum cernuum	Forb				X	
Oenothera contorta	Forb				X	
Gymnosteris parvula	Forb					X

BIOLOGY AND ECOLOGY OF SAGEBRUSH IN WYOMING

II. GRAZING, SAGEBRUSH CONTROL AND FORAGE YIELD

Herbert G. Fisser

ABSTRACT: In conjunction with a 21-year aridland research effort in western Wyoming, effects of use of the herbicide 2,4-D and livestock grazing restrictions were evaluated at five research sites. Shrub reinvasion dynamics have been diverse. Early, rapid establishment was consistently related to beneficial growing season weather, intensive summer grazing, poor initial control, and increasingly mesic site character. Annual herbage production of sagebrush often increased with removal of livestock grazing. Grass and forb production always increased following sagebrush control and maintained increased levels throughout the life of the study.

INTRODUCTION

Big sagebrush (Artemisia tridentata) occurs over vast areas of western rangelands and is a dominant shrub on over 130 million acres (53 million ha) in the 11 western states. In Wyoming alone, big sagebrush covers more than 30 million acres (12 million ha) of rangeland (Beetle 1960). Historically, this shrub has been a prominent feature of the West. Reports of early travelers through the West, when much of the vegetation was presumed to be in pristine condition, indicate that sagebrush was very common and even a nuisance. Since those times, many believe that big sagebrush has prospered and expanded its range due to overgrazing by livestock (Ellison 1960; McArthur and others 1985).

This paper reports herbage production changes on basin big sagebrush (Artemisia tridentata ssp. tridentata) and Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis) rangelands aerially treated with 2,4-D (2,4-dichlorophenoxy acetic acid) in the butyl ester formulation. Herbage production was monitored on both treated and untreated native rangelands under grazed and deferred conditions. Data reported here encompass 20 years following the control of big sagebrush with this herbicide (Fisser 1984).

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Herbert G. Fisser is Professor of Range Management at the University of Wyoming, Laramie.

The objectives of this study were to:
1. Evaluate sagebrush control practices.
2. Evaluate and compare long-term annual herbage production changes of (a) grazed and nongrazed treatments and (b) chemical control and natural treatments. 3. Interpret vegetation changes related to long-term effects of grazing exclusion and chemical treatment.

REVIEW OF THE LITERATURE

Sagebrush Distribution

Big sagebrush is the most widely distributed and abundant member of the group of woody shrubs collectively called sagebrush. It normally occurs as a dominant overshrub with understory of perennial grasses and forbs. It also grows in association with a variety of other shrubs such as bitterbrush (Purshia tridentata), serviceberry (Amelanchier alnifolia), and the rabbitbrushes (Chrysothamnus spp.) (Winward 1980). Although its volatile oils tend to make it unpalatable and may interfere with digestion, big sagebrush does, in many instances, provide high-quality forage for both livestock and wildlife. These volatile oils vary among subspecies, areas, seasons, and sometimes individual plants (Johnson 1976; Wallmo and others 1977).

Since the first identification of the species big sagebrush by Thomas Nuttall in 1841, three subspecies of this species have been recognized (Beetle 1960; Beetle and Young 1965). These three distinct subspecies are adapted to different growing conditions, but under some field conditions all may be found growing together (Beetle 1977).

Basin big sagebrush has probably the widest distribution and is the most common big sagebrush at elevations of 5,000 feet (1 500 m) and below (Winward 1980). It is an open, spreading shrub from 2 to 6 feet (0.6 to 1.8 m) tall and under favorable conditions can become treelike. This subspecies inhabits both wet and dry sites as well as strongly alkaline and nonalkaline deep-soil sites, but seldom occurs on shallow-soil sites (Beetle 1960; Beetle and Young 1965; Johnson 1976).

Wyoming big sagebrush is the most common big sagebrush in Wyoming and the most palatable of the subspecies. It is a dwarf shrub from 4 to 12

inches (10 to 30 cm) tall, found on dry, shallow-soil sites at medium elevations of 5,000 to 7,000 feet (1 500 to 2 130 m) in Wyoming. This subspecies is found with basin big sagebrush, but always occupies the poorer soil sites of hilltops and flats (Beetle and Young 1965; Johnson 1976).

The third subspecies, mountain big sagebrush (A. t. ssp. vaseyana), is the common big sagebrush at elevations of 7,000 feet (2 130 m) and higher. Characteristic growth form is a compact, flat-topped shape 1 to 3 feet (0.3 to 1.0 m) tall. Characteristic habitat sites are deep-soil, snow accumulation zones on mountain slopes (Beetle 1960; Beetle and Young 1965; Johnson 1976).

All three subspecies share characteristics of being long-lived perennial shrubs reproducing entirely by seeds (Brunner 1972). Growth starts later in the season than for most plants. Flowering does not take place until August or September and is a function of seasonal weather conditions, especially precipitation (Robertson 1971; Tueller 1973).

Much of the original range of sagebrush has been altered since the settlement of the West (Young and others 1979). Many thousands of acres of land have been plowed under and used for the production of agricultural crops. Other sagebrush ranges have been replaced by urban development, reservoirs, and transportation systems. The majority of sagebrush-dominated lands still exist, however, both under Federal (U.S. Department of the Interior, Bureau of Land Management and U. S. Department of Agriculture, Forest Service) and private ownership. The primary functions of these lands are for watershed protection, livestock production and wildlife habitat (Hedrick and others 1966).

Use of 2,4-D Herbicide

The discovery and development of the herbicide 2,4-D was documented by Peterson (1967). Many preliminary field studies were conducted. Findings supported allegations that 2,4-D uniformly killed broad-leaved weeds. After this, there was a dramatic increase in the marketing and use of 2,4-D as a herbicide. In 1962, it was used in Vietnam for chemical warfare, 20 years after initial studies and following widespread use to benefit agriculture. Several formulations of 2,4-D can be produced for use as herbicides or growth regulators. It can be obtained as an emulsifiable acid, amine salts, mineral salts, or esters (Klingman and Ashton 1975). The 2,4-D ester is the herbicidal form most commonly used for spraying big sagebrush.

Ester formulations of 2,4-D are generally considered to be the most toxic because:(1) volatility permits absorption of the gases through stomata, and (2) wetting action of the oil-like ester and oil carrier translocation of the chemical is also greatest during rapid growth when large amounts of food are being translocated and stored in the roots (Klingman and Ashton 1975).

Susceptibility of big sagebrush to 2,4-D was first demonstrated in 1946 and 1947, just after the chemical had been introduced to the market (Cornelius and Graham 1951). The first test in Wyoming stemmed from a cooperative effort between the U. S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station and the Bureau of Land Management (BLM) in 1949 (Hull and Vaughn 1951; Johnson 1958). These tests proceeded on rangeland sites southeast of Lander, WY. From 1965 through 1976, as shown in table 1, almost 2 million acres (800 000 ha) of big sagebrush rangeland were sprayed in Wyoming (Freeburn 1978).

Table 1.--Total acres of sagebrush sprayed in Wyoming by federal agencies and individuals, 1953-1976 (Freeburn 1978)

Year	Ranchers in coop. with ASCS [1]	Bureau of Land Management	National Forests	Great Plains cooperative program	Private [2]	Total
1965	81,838	34,942	6,800	9,124	9,063	141,767
1966	76,760	54,929	3,276	1,714	7,505	144,184
1967	123,861	37,510	2,740	5,584	11,728	181,423
1968	96,601	27,808	1,331	8,607	18,345	152,692
1969	96,573	22,558	8,659	8,875	10,339	147,004
1970	92,036	11,290	11,390	27,805	17,643	160,164
1971	95,000	1,000	1,571	18,143	16,716	132,430
1972	99,057	0	0	25,339	11,032	135,488
1973	45,299	0	1,130	17,909	16,605	80,943
1974	22,873	0	0	22,263	15,680	60,816
1975	69,199	3,850	0	15,111	10,678	98,838
1976	0	0	0	20,082	0	20,082
Total	1,131,304	292,799	94,892	180,616	207,749	1,907,360

1 ASCS - Agricultural Stabilization and Conservation Service
2 Using minimum expanded estimate.

Although techniques for maximizing the percent kill of big sagebrush have been standardized, the ensuing herbage production, longevity of forage increases, and reestablishment of sagebrush have been highly variable among sites. On the areas sprayed in Wyoming during 1949 with a 97 percent sagebrush kill, the production of native perennial grasses exhibited a threefold increase in 2 years (Hull and others 1952).

This same study area, located 25 miles (40 km) southeast of Lander on the Beaver Rim, was the focus of analysis by another researcher. W. M. Johnson (1969) followed up the earlier studies to investigate long-term effects of chemical control on this site. These long-term effects were examined to determine longevity of the big sagebrush control project. Johnson indicated that the increased herbage production on the sprayed area was nullified 6 years after spraying and concluded that in this area the life expectancy of a big sagebrush chemical control project was 14 to 17 years.

Cornelius and Graham (1951) tested the susceptibility of big sagebrush to 2,4-D in 1948 on the Lassen National Forest in northeastern California. At an application rate of 1 pound (454 g) acid equivalent of the butyl ester in 20 gallons (75.7 L) of water per acre (0.4 ha) of land, 85 percent of the big sagebrush plants were destroyed. One year following spraying, production of the three major perennial forage grasses, Idaho fescue (Festuca idahoensis), western needlegrass (Stipa occidentalis), and bottlebrush squirreltail (Sitanion hystrix) increased 2.5 times over that on the unsprayed area. Also, reproduction of grasses on the sprayed area was over three times greater than on the unsprayed plots. The researchers were unsure if native grasses would recover as well in competition with a thick stand of the annual grass, cheatgrass brome (Bromus tectorum).

Another study with 2,4-D was initiated at the Squaw Butte Experiment Station, Burns, OR, by Hyder and Sneva (1956). In 1952, they applied 2,4-D butyl ester to a 40-acre (16 ha) pasture at 2 pounds (0.9 kg) of acid per acre (0.4 ha) on a site where the annual precipitation was nearly 11 inches (280 mm). However, in 1953, 15.68 inches (398 mm) of precipitation were received, stimulating an increased herbage production on the sprayed area of 3.25 times over that on the native range. In 1954, precipitation was recorded at only 6.77 inches (172 mm) while herbage yield was still three times that of the native range. It was suggested that increased grass production was not only due to a release from competition for moisture, but also from increased nitrogen availability. Many perennial grasses are much better competitors for moisture than big sagebrush, but the shrub has the advantage in competition for available nitrogen (Robertson 1947). Hyder and Sneva (1956) also found that individual grass species responded differently to sagebrush control measures.

A later study at the Squaw Butte Experiment Station compared the spraying of big sagebrush on both fair- and poor-condition livestock ranges (Hedrick and others 1966). Annual precipitation for a 20-year period was 11.8 inches (300 mm). For the 8 years of study, herbage yields on fair-condition range averaged 200 pounds per acre (224 kg per ha) for untreated ranges and 387 pounds per acre (434 kg per ha) for sprayed ranges. On the poor-condition range sites, herbage production averaged 122 pounds per acre (137 kg per ha) on untreated and 489 pounds per acre (548 kg per ha) on sprayed plots. On both sites, over 85 percent of the sagebrush plants were killed. Cheatgrass was the main source of the high yield on the poor-condition range plots. Herbage production for all plants fluctuated most on both the untreated and treated plots in poor range condition.

Alley and Bohmont (1958) discussed the results of big sagebrush spraying in 1952 with 2,4-D butyl ester. Their study sites were located in the Big Horn Mountains of Wyoming at an elevation of 8,200 feet (2 500 m), with an annual precipitation of 22 inches (559 mm). During their 5-year study period, air-dry native grass production increased fourfold from 526 pounds per acre (589 kg per ha) on the unsprayed to 2,075 pounds per acre (2 325 kg per ha) on the sprayed range (Alley 1965). These increases occurred where 75 percent or more of the big sagebrush had been killed. They also determined that livestock consumed 60 percent of available forage on sprayed sites and only 25 percent of the forage on unsprayed areas.

Fisser (1968) conducted a study to evaluate soil moisture, soil temperature, and herbage production changes following chemical control of big sagebrush on two sites. One was a xeric site in the Big Horn Basin and the other a more mesic upland site in the Wind River Basin of Wyoming. During the 5-year study, herbage production following chemical control increased on both sites and was greatest on the mesic site. Soil moisture withdrawal rates were similar at both sites, but less moisture was taken from the grazed treatment locations than from the nongrazed protected areas. High soil water withdrawal rates and cool soil temperatures following chemical control, combined with protection from grazing, were also related to an increased root abundance associated with the treatments (Orpet and Fisser 1979; Sturges 1980).

Response of vegetation and soil water to sagebrush control was reported by Sturges (1983) for a study site near Saratoga, WY, at an elevation of more than 7,000 feet (2 130 m). Productivity of mountain big sagebrush on 2,4-D sprayed sites was nearly twice that of the untreated areas 10 years after treatment. Sagebrush mortality was 96 percent. Sagebrush control clearly modified the soil water regime. Sagebrush reestablishment, however, appeared to have a minimal influence on the soil water regime for 11 years following treatment.

A survey of big sagebrush control projects in Wyoming was completed for the years 1952-64 by Kearl (1965). He ascertained that the length of life of a spray project was regulated by the percentage of sagebrush controlled and the management practices after control. Life expectancies for areas sprayed between 1952 and 1957 were estimated at 15 years while sites sprayed between 1958 and 1960 revealed life expectancies of only 10 years. Later control programs, with improved methodology, resulted in potential effective life spans of 30 to 40 years. His survey reported forage increases ranging from 0 to 400 percent, with most common increases between 100 and 200 percent (Kearl 1973).

DESCRIPTION OF STUDY AREAS

During the late 1950's and early 1960's, trials to test the ability and requirements for control of sagebrush with the chemical 2,4-D were initiated at a number of locations in the Big Horn Basin, Wind River Basin, and areas near Kemmerer, WY (Fisser and Whysong 1969). Five separate areas, all located in Wyoming and on BLM lands, were selected for discussion in this report. Exclosures were erected on these sites to monitor the effects of livestock grazing and exclusion on the chemically controlled and native vegetation. These exclosures, Smilo, Bud Kimball, Lower Government Draw, Upper Government Draw, and Granite Mountain, were constructed by the BLM. They are located in north-central and west-central Wyoming (fig. I-1, Fisser, this proceedings). The soils of the study sites are all typical of those derived under arid climates (aridisols), and exhibit poorly differentiated horizons. Salt concentrations are low and pH is within the tolerance range for the growth of most sagebrush-grassland species (Ries 1973).

The immediate topography of these sites is generally level to moderate to gently sloping while the overall landscapes are rolling hills and plains. Slope values range from 0.5 percent to 5.5 percent on exposures of 30 to 110 degrees. Elevations vary from 4,600 feet (1 400 m) at the Smilo site to 7,100 feet (2 160 m) at the Granite Mountain site. Bud Kimball, Lower Government Draw, and Upper Government Draw exist at elevations of 4,700 feet (1 430 m), 5,500 feet (1 676 m), and 5,925 feet (1 805 m), respectively. Greater detail of site characteristics is given in the first paper of this series (Fisser, this proceedings).

METHODS

The exclosures were constructed by the BLM during the summers following early June application of herbicide. In the Wind River Basin, two exclosures, Lower Government and Upper Government, were treated and established in 1958. The two Big Horn Basin exclosures, Smilo and Bud Kimball, were completed in 1961. The Granite Mountain exclosure in the Wind River Basin was treated and installed in 1962.

The herbicide 2,4-D butyl ester was strip-sprayed by air under the supervision of the BLM. The chemical was applied in a mixture with diesel oil at the rate of 2 gallons per acre (18.7 L per ha). Precipitation was recorded seasonally on April 15, July 1, September 1, and October 15 with gauges at each location.

Research on grass and forb production by the University of Wyoming was initiated in 1962, while shrub production studies began in 1968. Living herbaceous plant material was clipped at or near peak growth for the purpose of estimating annual production. All the study plots of grasses and forbs were clipped (Fisser 1963).

Grasses and forbs were sampled in 20 1- by 1-foot (30- by 30-cm) quadrats located at 5-foot (1.52-m) intervals along a 100-foot (30-m) tape (Fisser 1963). These tapes were located on all treated and untreated sites by a restricted random process so as not to coincide with lines of previous years.

Shrub biomass was sampled at a later date than grasses and forbs since most shrubs, including big sagebrush, exhibit maximum yearly growth at a later time. For estimation of shrub production, a modified double sampling method was employed (Fisser and Whysong 1969). A 4- by 5-foot (1.2- by 1.5-m) quadrat was used. Twenty quadrats were located at 6-pace intervals along a randomly located line within each of the treatment areas (Fisser 1968).

Photographs of all lines were taken prior to collection of data. Percent cover for all individual species of grasses and shrubs was estimated within each quadrat prior to clipping separately by species. Vegetation samples were ovendried at 158 °F (70 °C) for 24 hours.

ANALYSES

Data from the five research locations were combined for presentation in this report. Simple linear regression was used to determine the seasonal precipitation groups which most closely related to vegetation dynamics. Vegetation classes subjected to analysis were annual yield of perennial grasses, all grasses and forbs, all species, and big sagebrush. These records were compiled for each of the treatment combinations: 1. native-nongrazed, 2. native-grazed, 3. shrub control-nongrazed, and 4. shrub control-grazed. The t test of paired means for years was used to compare all combinations of long-term yields among grazing and chemical shrub control treatments from the five research locations.

RESULTS

Two kinds of information will be presented in this report. The 21-year precipitation record and long-term yield data, with appropriate quantitative analysis, will be analyzed for the five research sites combined. Secondly, the general nature of the five exclosures identified

in the previous report will be descriptively characterized. The narrative will present a discussion of vegetation responses to the grazing treatment, the chemical shrub control treatment, and interactive environmental variables. It has been readily apparent over the years that annual monitoring is necessary because of dynamic vegetation response to treatment impacts and environmental changes. Without annual data accurate interpretation of interactive responses would not be possible.

Grouped Site Analysis

Precipitation.--The 21-year record of precipitation presented in figure 1 identifies three seasonal periods most closely related to vegetation yield, combined over the five sites. Mean total winter plus spring precipitation was 7.1 inches (180 mm)(table I-4, Fisser, this proceedings) with standard error of 1.52 inches (38.6 mm). Yield of perennial grasses and forbs was most closely related ($p < 0.001$) to the sum of winter plus spring precipitation. Mean annual values ranged from a low of 6.42 inches (166 mm) at Smilo, to a high of 7.14 inches (181 mm) at Upper Government. The similarity of these data among the five sites is an expression of overall climate control induced by the mountains of the Continental Divide to the west. The Big Horn Basin sites were, in general, more xeric than those to the south in the Wind River Basin. Variation among years, however, can result in any one of the sites receiving greatest precipitation (Ries 1973). No temporal trend in any of the seasonal precipitation groupings was discernible.

The precipitation for the winter season, October 16 to April 15, was next most closely related to herbage yield, more so than the spring precipitation by itself. Although 32 percent of mean annual precipitation occurred during the winter (table I-4, Fisser, this proceedings), standard error of the mean was only 0.82 inches (21 mm). Spring moisture provided 43 percent the total, 4.1 inches (104 mm), but exhibited much greater annual variation; standard error of the

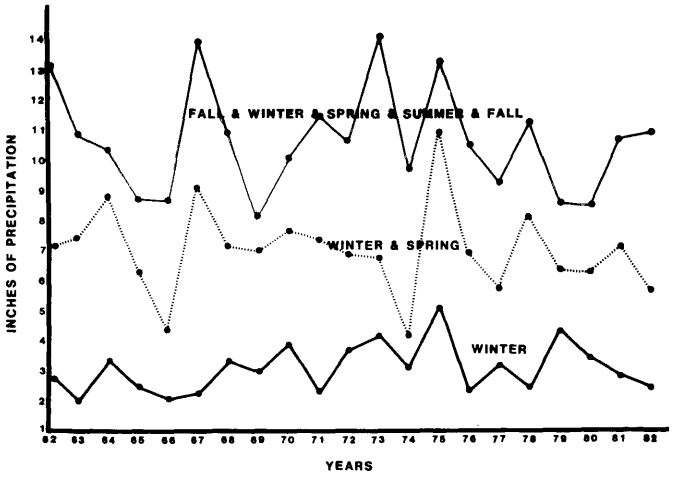


Figure 1.--Mean precipitation (inches) of five western Wyoming research locations, for 21 years, compiled for three seasonal categories.

mean was 1.46 inches (37 mm). Winter precipitation for the 21 years on the five sites averaged 3.0 inches (76 mm). Lowest mean annual value was 2.85 inches (72 mm) at Smilo, and the highest at Lower Government was 3.43 inches (87 mm). Somewhat surprisingly, winter precipitation at Granite Mountain was similar to that at Smilo, while Bud Kimball and Upper Government were intermediate and considerably less than at Lower Government (Fisser 1984).

The mean annual plus current fall precipitation was 10.63 inches (270 mm) with standard error of 1.76 inches (45 mm). Lowest mean annual value was not at Smilo as for the previous categories, but at Upper Government, with 9.11 inches (231 mm). This obviously was an expression of lesser amounts of fall and summer precipitation at this location than at the others. Greatest precipitation was recorded at Lower Government with 11.65 inches (296 mm). The precipitation value of this five-season period--previous fall, winter, spring, summer, current fall--was useful because of the strong relationship with total biomass of all species, and especially with that of shrub species. The latter, because of deep root systems and late summer-early fall maturation, were able to use deep water from previous fall and winter occurrences and from the current year's fall moisture because their yield was obtained during the fall period.

Vegetation.--In this report the mean annual yield of perennial grasses is used to show response, over time, to the grazing and chemical shrub control (spray) treatments. The nongrazed sites yielded 155 percent of the grazed (fig. 2). The shrub-controlled sites yielded 171 percent of the unsprayed.

The mean annual production of perennial grasses at the five sites, for 21 years, is shown for each of the four treatment combinations in table 2. The t-test of paired mean differences was highly significant ($p < 0.001$) for all comparisons except for the differences between grazed-shrub control and nongrazed-untreated, which was, however, significant at $p \leq 0.1$.

Table 2.--Mean annual yield (pounds per acre) of perennial grasses by grazing and chemical treatments at the five western Wyoming research locations

Treatment	Mean yield	Group means	Stand. error of the mean
Grazed - unsprayed	168		8.56
Nongrazed - unsprayed	216	192	13.48
Grazed - sprayed	239		12.84
Nongrazed - sprayed	416	328	20.44

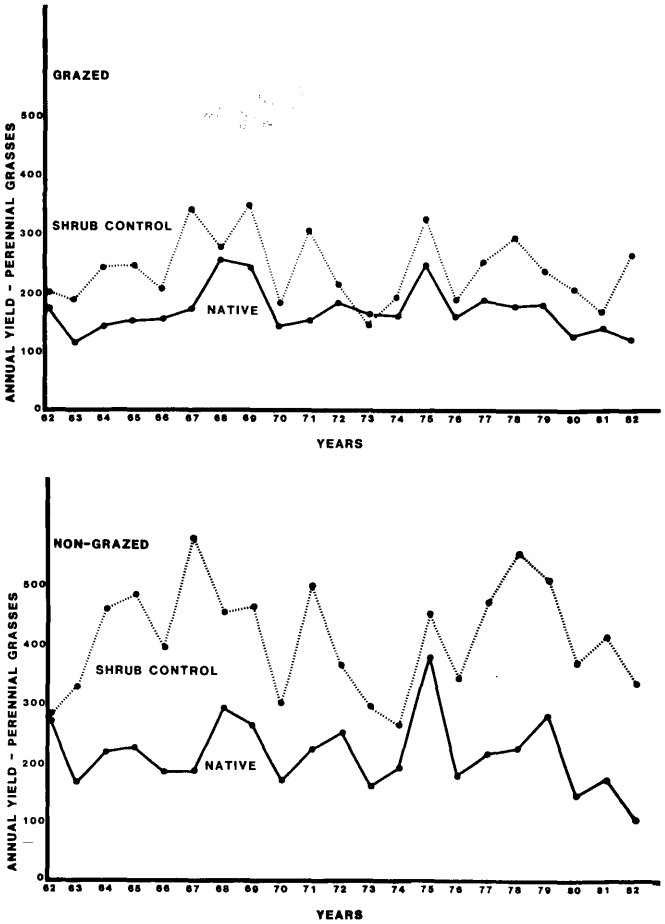


Figure 2.--Mean annual perennial grass yield (pounds per acre), for grazed (above) and nongrazed (below) treatments of five research locations in western Wyoming.

Changes with years were relatively similar among the five sites. Greater variation of yield over years occurred under the nongrazed treatment, however, showing that the moderate use noted on these sites did tend to inhibit herbaceous response (fig. 2). The yield dynamics of the nongrazed-sprayed sites were much greater than any of the other three treatment combinations. This would be expected in light of freedom from the influence of shrub dominance and release from grazing stress (Hedrick and others 1966).

Although some reinvasion by sagebrush, primarily on the intensively grazed sites, was evident, the high perennial grass response to the chemical shrub control treatment has been maintained. The trends exhibited in records extending well over 20 years beyond the chemical application indicate that beneficial effect, as suggested by Kearl (1973), may well persist for as much as 40 years. Continued monitoring of interactive environmental, grazing, and chemical treatment relations will be necessary to determine how long the shrub control impacts and benefits continue (Winward 1980). It is apparent that changes caused by chemical shrub control are long-term, at least on the semiarid sagebrush rangelands investigated in Wyoming.

Individual Site Characterization

Smilo exclosure.--The Smilo site is the most xeric and warmest during summer of the five selected locations. Although lower growing than normal in its more common occurrences along drainage sites, the dominant shrub is basin big sagebrush (fig. 3). Poor ecological condition was apparent in 1961. Very little perennial understory existed then. The most important perennial grasses are western wheatgrass (Agropyron smithii), blue grama (Bouteloua gracilis), bottlebrush squirreltail (Sitanion hystrix), Sandberg bluegrass (Poa secunda) and needleandthread (Stipa comata).

The response of perennial grasses to protection from grazing has been extremely limited. Initial response to chemical shrub control was positive but was severely restricted by a climatically induced population explosion, coincident with long, warm, moist, spring and moist, summer weather, of the annual cheatgrass in the mid-1960's. Striking differences between the unsprayed and chemically controlled sites have persisted. The nongrazed sagebrushes, especially in the chemically treated site, were vigorous. Some exhibited enhanced growth and reproduction, but they did not reestablish in abundance. Total grass and forb production on both untreated sites remained relatively stable. Precipitation was a dominant factor, as was the eroded soil of the site. The cheatgrass explosion indicated that shrub control practices should be restricted to better condition rangelands, at least if ecological condition increase is a primary goal. Very long-term beneficial values may be obtained on these sites, however, with stabilization of soils.

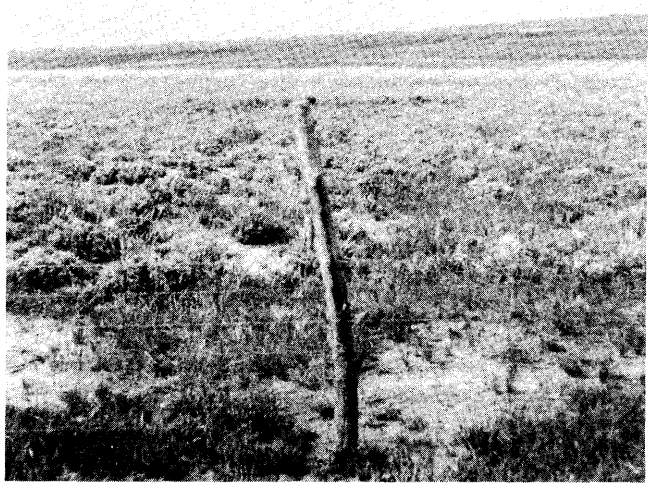


Figure 3.--The Smilo exclosure southeast of Worland was in low ecological condition, with abundant annual weeds, in 1961.

Bud Kimball exclosure.--Basin big sagebrush, as at Smilo, is dominant at the Bud Kimball exclosure (fig. 4). Ecological condition was fair at the time of establishment. The most prominent grasses were western wheatgrass and sandberg bluegrass. Others of lesser importance were Indian ricegrass (Oryzopsis hymenoides), junegrass (Koeleria cristata and needleand-thread. Good chemical control, better ecological condition, and greater site potential than at Smilo resulted in positive response to protection from grazing and the chemical treatment (fig. 4). Cheatgrass did not become a dominant. Sandberg bluegrass and western wheatgrass increased significantly after shrub control, and moderately with protection from grazing. Bluebunch wheatgrass (Agropyron spicatum) did become established in a corner of the exclosure but was never encountered during sampling for vegetation yield. Increased sagebrush was evident on the shrub control site by 1980, but perennial grass yield was little affected. Yield was much more responsive to precipitation dynamics than at the xeric Smilo site.

Lower Government exclosure.--The basin big sagebrush dominant at the Lower Government (LG) site is almost 3 feet (1 m) tall and exhibits typical characteristics of growth on sandy soil with a relatively shallow permanent aquifer (fig. 5). Western wheatgrass is the most prominent grass on native range. Needleandthread exhibited striking response to the combination of protection from grazing and chemical shrub control. Sagebrush inside the exclosure, especially a few bushes remaining in the shrub control area, exhibited good growth while those outside the exclosure had a hedged appearance. Protection from grazing induced only moderate response of understory perennial grasses because of the dominant influence of big sagebrush.

As at Smilo, wheatgrass was most abundant on the sprayed area protected from grazing. It contrasted, however, in that the initially better ecological condition, greater site potential, and cooler summer temperatures favored dominance by perennial grasses. Outside the exclosure, because of damage to sagebrush from animal trailing and minimal perennial grass presence, cheatgrass was more abundant than on the nearby grazed sprayed site. Even under intensive grazing, perennial grass yield on the treated site, in contrast to the xeric, low condition Smilo site, was adequate to restrict cheatgrass and other annuals.

The perennial grasses continued exhibiting strong interspecific competitive response after sagebrush became rather abundant. Even when the physiognomic aspect of the herbicide-treated site was essentially identical with that of the nonsprayed range, understory perennial grass and forb yield, cover, and density maintained beneficial effects of the chemical treatment throughout the study period.

Upper Government exclosure.--Wyoming big sagebrush is dominant at the Upper Government exclosure (fig. 6). Protection from grazing produced little vegetation change except when compared to sites of extreme overuse. Vegetation composition is significantly different from other rangelands in that junegrass is the most common understory species. Other species of lesser importance are western wheatgrass, Sandberg bluegrass and needleandthread. The continued abundance of junegrass on untreated range occurs as a result of site potential for multiple climax expression and the stability of vegetation on these sites dominated and controlled by sagebrush (Heady 1973).



Figure 4.--The Bud Kimball sagebrush control site protected from grazing showed abundant perennial grass yield and little sagebrush invasion even in 1981.

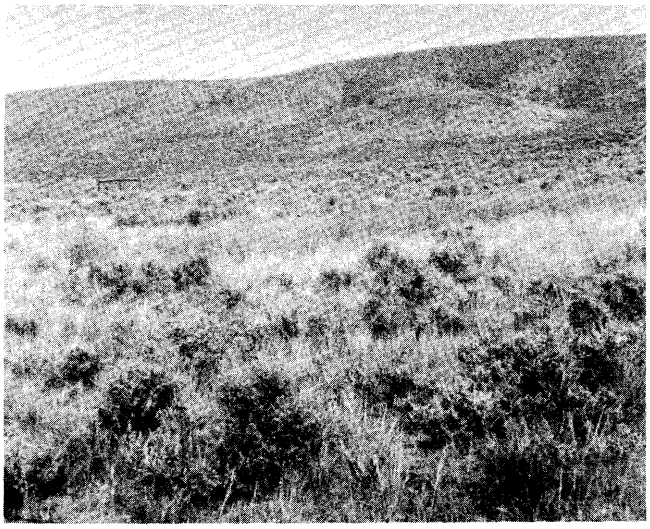


Figure 5.--Lower Government exclosure of basin big sagebrush showing limited reinvasion.

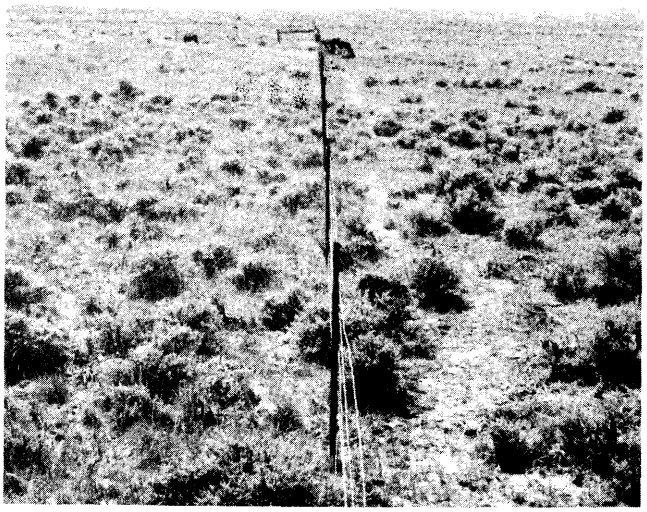


Figure 6.--Intensive use of grasses at the Upper Government exclosure, primarily junegrass, in the foreground, and generally reduced size of Wyoming big sagebrush bushes, is apparent. Greater sagebrush invasion is evident on the grazed-sprayed strip.

Yield of perennial grasses and forbs was much greater on the 2,4-D treated site than on the untreated range. With removal of sagebrush, grass composition has begun shifting from an overriding dominance by junegrass to needleandthread. Annuals were never abundant.

Shrub yield was similar for the unsprayed sites, both ungrazed and grazed. Protection from use allowed cover and growth of sagebrush plants to increase in contrast to the minimal changes on the grazed site. Livestock and wildlife effectively inhibited sagebrush because of browsing and mechanical damage. Under the herbicide treatment sagebrush yield was similar, whether grazed or not, but density increased during later years as a result of grazing stress and reduced competitive ability of herbaceous species.

Herbage yield fluctuations, as a result of changing growing conditions, were greatest on the sprayed site and on the area protected from livestock use. Sagebrush presence effectively limited herbage response to beneficial moisture and temperatures. Where sagebrush reinvasion was noted, perennial grass and forb yield was still greater than on the unsprayed areas.

Granite Mountain exclosure.--While the Wyoming big sagebrush was very effectively controlled at the Upper Government exclosure, a rather poor kill was obtained at the Granite Mountain exclosure (fig. 7). As a result, reinvasion of the shrub was more evident and rapid than at other locations. Partially killed shrubs began rapid growth within a few years inside the exclosure, but density increase was only moderate. Outside the exclosure sagebrush response following spraying was expressed primarily by density increase, as growth and size were inhibited by livestock and wildlife impact. Sagebrush size and density changed little on the grazed-nonspray sites. Those inside the exclosure, however, exhibited more seedheads and longer stems than those of the grazed area, an evident result of protection from livestock and pronghorn antelope.

Mutton grass (Poa fendleriana) was a dominant at this site, evidently in response to somewhat greater summer precipitation and cooler summer temperatures than at any of the other locations. Deeper B horizon, good porosity, low bulk density, and pH of soil all contributed to a vegetation complex similar to that of foothill sites with much greater precipitation than at the Granite Mountain location.

Perennial grass and forb yields changed little over the years on the untreated shrub-dominated sites, whether protected from grazing or not. With chemical shrub control, however, herbaceous species exhibited much increase, especially mutton grass, western wheatgrass, Sandberg bluegrass, and to some extent needleandthread. Greatest production increases occurred inside the exclosure of course. Summer cattle grazing occasionally severely inhibited growth outside the exclosure and apparently also was responsible for some sagebrush reinvasion.

This site has the highest yield potential of the five locations. Despite the weak sagebrush control, and partially because the site was in at least fair ecological condition when treated, annuals were never abundant. In addition, the positive response of perennial grasses to shrub control continued and appeared little influenced by the presence of sagebrush within the spray area of the exclosure. A similar, but less striking response of herbaceous species was also noted in the sprayed-grazed area outside the exclosure.



Figure 7.--At the Granite Mountain exclosure large and scattered Wyoming sagebrush bushes indicate poor chemical control, little intraspecific competition, but strong interspecific competition from perennial grasses.

DISCUSSION

Response to protection from grazing, with no shrub control, was minimal in terms of understory perennial grass and forb species. Sites of low ecological potential, and those in poorest ecological condition, exhibited weakest response. Conversely, sites of highest potential and better ecological condition responded well. Protection from grazing on untreated range allowed growth of big sagebrush plants that was not exhibited on the grazed sites. Grazing use on sagebrush outside the exclosures was always evident.

Continued moderate grazing on untreated sites did not appear detrimental to herbaceous species. In contrast, the grazing allowed little vegetation response by herbaceous understory species or by the overstory shrubs, to potential benefits of years with good growing conditions. Whether or not big sagebrush is considered a climax dominant on these sites, its present abundance effectively controls herbage yield dynamics, and the removal of grazing can hardly be expected to have immediate effects on these long-lived plants.

Beneficial vegetation response to chemical shrub control was most evident: (1) with protection from grazing, (2) on sites of highest ecological condition at time of treatment, (3) on sites with greatest yield potential, and (4) when annuals remained minimal components of vegetation populations.

Unless grazing use was destructive, the impacts were moderate, and in most situations provided benefit to the perennial herbaceous species by reducing interspecific competition with annuals and reinvading shrubs. Sites in poor ecological condition required greater recovery time than those in higher condition. Dynamic herbage production response is positively related to yield potential. Sites of low yield potential often may not provide adequate returns from increased forage to be cost-effective for a shrub control treatment. However, the treatment can have a very important long-term value in soil movement reduction, that may well be much more important than the minimal value associated with the limited temporal vegetation yield changes.

Presence of annuals is more expected in the warm, xeric areas of the Big Horn Basin than in the Wind River Basin to the south. When poor condition, low potential, and invasion by annual weeds combine, the expected perennial grass increase after shrub removal can be minimal. In some instances the great herbage yield of annuals may be used as forage, but the continued danger of excessive erosion persists.

It is apparent that multiple pathways of vegetation succession exist. Even with almost complete removal of sagebrush and its controlling influence over the community, each of the study areas exhibited site-specific species composition. Vegetation components and consequent community dynamics, it seems, should be expected to show different paths toward climax. To assume that all must eventually achieve essentially uniform composition would, first of all, ignore the concepts of natural stability on these semiarid ranges. As noted by West (1985), the process of succession is real and can be described, but predicting the paths and dynamics of change is difficult. Secondly, each site exhibits some physical or chemical environmental characteristics not present at others. These often minor factors may differentially influence different plant species. Interactive response may be so minimal that most common field sampling procedures are unable to detect significance. Long-term abundance and lack of expected change according to typical or expected successional progression can be interpreted ecologically by general knowledge of unique growth characteristics of the vegetation and individual species.

SUMMARY AND CONCLUSIONS

Precipitation and herbage yield were monitored for 21 years at five locations in western Wyoming. Interactive responses to environmental influences, to grazing-nongrazing, and to chemical shrub control-no shrub control treatments, were investigated. Each of the five research locations exhibited unique physical, chemical, or biotic characteristics. Precipitation was surprisingly similar among the sites. Response to precipitation amounts and shrub control treatments by perennial grasses was highly significant.

Grazing generally caused only minimal stress and reduction to forage yield except for sites subjected to atypically extreme use. Protection from grazing did not, by itself, benefit herbaceous species adequately to be identified as a potential management plan.

Herbicide spraying caused very significant positive forage responses. These responses were, on occasion, limited by poor ecological range condition, low ecological potential, poor control of the shrubs, and continued intensive grazing. Beneficial effects of the spraying, at least in terms of increased perennial grass forage yield, are expected to persist for many years into the future. With moderate grazing these grasses can maintain abundance and yield in spite of competition from the perennial shrubs.

ACKNOWLEDGMENTS

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BIOLOGY AND ECOLOGY OF SAGEBRUSH IN WYOMING:

III. PHENOLOGY

Herbert G. Fisser

ABSTRACT: Phenology of sagebrush was recorded at 12 locations in Wyoming representing the Big Horn Basin, Wind River Basin, Shirley Basin, Little Colorado Desert, Red Desert, and the Bear River Divide from 1973 through 1982. The quantitative scoring system distinguished vegetative from reproductive development. Herbage production and phenology of all species were also obtained. Phenological "phase," "stage," and "substage" characterization terms and phrases were established for distinctive appearance changes and integrated with a numerical scale. Regionally related phenodynamic differences were irregular and basically controlled by climatic factors. The increased precision of phenological characterization, with potential for detailed phyllochron distinction, provides a sensitivity level more nearly equivalent to commonly measured values of environmental factors such as soil moisture and temperature, soil texture, ambient temperature, precipitation, and others.

INTRODUCTION

Most reports of phenodynamics commonly portray annual life cycles with flowering, seed set, and maturation. Many perennial species of semiarid communities, however, seldom consistently flower each year. Vegetative structures do usually complete the entire phenophase cycle, from growth initiation through senescence, even if reproductive structures fail to develop. Development of individuals or populations has been investigated, but little effort has been extended toward the phenodynamics of entire communities. Furthermore, few reports are available that quantitatively evaluate phenodynamic interactions within or among communities and with environmental variation.

This investigation of plant phenology was conducted in central and western Wyoming for 10 years, from 1973 to 1982, at 12 diverse locations, all dominated by big sagebrush (*Artemisia tridentata*)(Fisser and Kleinman 1974). Black sagebrush (*A. nova*) was present at several of the sites (Hargis 1980). The program was a cooperative effort between the U.S. Department of the Interior, Bureau of Land Management (BLM), and the University of Wyoming, Department of Range Management.

Paper presented at the Symposium: Biology of *Artemisia* and *Chrysothamnus*, Provo, UT, July 9-13, 1984.

Herbert G. Fisser is Professor of Range Management at the University of Wyoming, Laramie.

The objectives of this study were to: (1) investigate both vegetal and reproductive phenologic patterns, (2) investigate whether these patterns were environmentally influenced, and (3) interpret these phenomona in an ecological context.

REVIEW OF LITERATURE

The term "phenology" is said to have been coined by the early botanist, Charles Morren (Lieth 1970). Henry David Thoreau has been credited as the father of phenology in the United States by Leopold and Jones (1947). Their work was exceptionally important because it identified regional phenologic variation as resulting not only from weather influences but also from integral genetic and site variation differences. Phenology has a variety of definitions. Newman and Beard (1962) described phenology as the art of observing life cycles in plants and animals. The U.S. International Biological Program Committee (Lieth 1974) expressed it as "the study of the timing of recurrent biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species."

The contemporary approach to phenology has become strongly oriented toward obtaining records with detailed descriptions of time sequences of plant development (Turner and Klipple 1952; Caprio 1966; Dierschke 1972; DePuit and Caldwell 1973; Dickenson and Dodd 1976; Kleinman 1976; Sauer and Uresk 1976). West and Wein (1971) proposed a digitized procedure to reduce the qualitative nature of phenology reporting and to approach interpretation with data more amenable to statistical analysis.

Big sagebrush was observed in Nevada by Robertson (1943). He noted that this shrub exhibited an early increase in photosynthetic activity from its winter dormant state that gave it a strong competitive ability for reinvasion of rangeland reseeded areas. Its root system gave the plant an opportunity to avoid short-term temporary growing season drought which caused severe stress to reseeded grasses with shallow and less comprehensive root systems (Brunner 1972).

The description of Wyoming big sagebrush as a distinct subspecies (*Artemisia tridentata* ssp. *wyomingensis*) by Beetle and Young (1965); the identification of significant root system differences of Wyoming big sagebrush and basin big

sagebrush (A. t. ssp. tridentata) by Nichols (1964); and the differential water acquisition ability of sagebrush from that of herbaceous species (Fisser 1968) provided the information that Wyoming rangeland yield was closely related to sagebrush dynamics as well as environmental criteria.

Hyder and Sneva (1962), at the Squaw Buttes research station in Oregon, were among early researchers to study chemical control of big sagebrush. They recognized that abundance and yield of this shrub was highly variable. Climate and site characteristics were noted as being extremely influential to growth of this shrub as well as to its rate of development.

DESCRIPTION OF STUDY AREAS

Location, Climate, and Soils

Intensive studies of plant phenology were initiated in 1973 on 12 locations in western Wyoming (fig. 1). These locations represent the Big Horn Basin, the Wind River Basin, the Little Colorado Desert, and Bear River drainages. The sites were all on sagebrush-dominated rangelands identified in general as semiarid. The areas of study express a broad ecological amplitude. The 12 research locations encompass the majority of western Wyoming, some 200 miles (325 km) from north to south and 225 miles (365 km) from east to west, an area of some 45,000 mi^2 (120 000 km^2). Elevation range is 2,300 feet (700 m), from 4,920 to 7,220 feet (1 500 to 2 200 m)(Kleinman 1976).

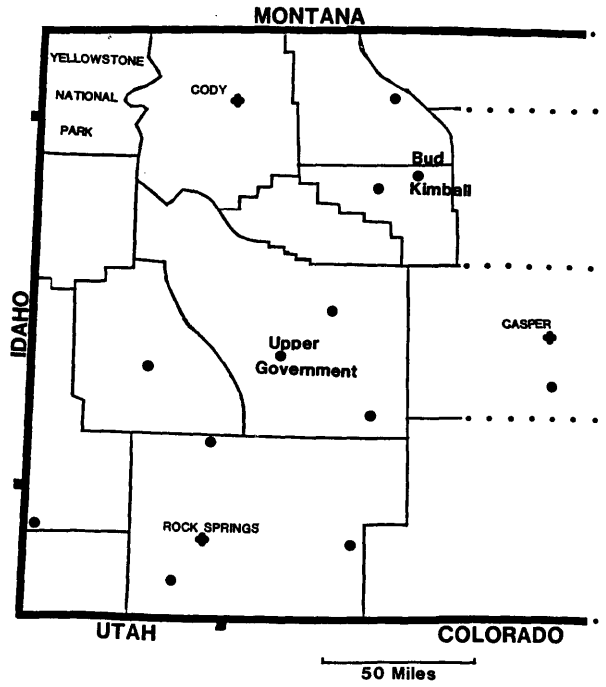


Figure 1.--Map of central and western Wyoming showing geographic distribution of 12 intensive phenology research locations(represented by the black dots.

Average annual precipitation is 8.7 inches (220 mm). Values are as low as 6.7 inches (170 mm) and as great as 11.0 inches (280 mm), a range of 4.3 inches (110 mm). Approximately three quarters of all precipitation occurs during winter and spring. The remainder is almost equally distributed during summer and fall.

Range of mean annual temperatures among sites is 12 °F (7.0 °C), from 35 to 47 °F (1.4 to 8.5 °C). Approximately 100 days are frost free. Mean seasonal temperatures range from 48 to 57 °F (9 to 14 °C) in the spring, and from 57 to 73 °F (9 to 14 °C) in the summer. Summer and winter temperatures often exceed 100 °F (38 °C) and -20 °F (-29 °C), respectively, and extremes of 110 °F (38 °C) and -50 °F (-45 °C) have been recorded (Kinucan 1983).

Soils are of two orders--Aridisol and Entisol. Diagnostic horizons are characterized by calcic and argilic components, and pH is moderately alkaline (Young and Fisser 1979).

Vegetation and Animals

In addition to big sagebrush, the dominant at all locations, associated woody species include black sagebrush (Artemisia nova), Douglas and rubber rabbitbrush (Chrysothamnus viscidiflorus and C. nauseosus), winterfat (Ceratoides lanata), broom snakeweed (Gutierrezia sarothrae), and occasionally gray horsebrush (Tetradymia canescens), spiny hopsage (Grayia spinosa), Utah juniper (Juniperus osteosperma), true mountain mahogany (Cercocarpus montanus), and western serviceberry (Amelanchier alnifolia). Kuchler (1964) identified the areas as sagebrush steppe and wheatgrass-needlegrass-shrub steppe zones.

The prevalent grass is western wheatgrass (Agropyron smithii). Other common genera are Poa, Koeleria, Oryzopsis, Stipa, and Sitanion. The annual cheatgrass brome (Bromus tectorum) was seldom present, reflecting the nonMediterranean climate of the region.

Forage utilization occurs primarily from cattle and sheep. Abundant pronghorn antelope (Antelocapra americana), mule deer (Odocoileus hemionus), feral horses (Equus caballus), and a variety of small mammal, reptile, and avian species are present.

METHODS

Plant phenology for all species was identified by developmental phases (table 1). Numerical scores were assigned from 1.0 to 8.0 for description of vegetative development and from 9.0 to 18.0 for reproductive development (Hargis 1980). Each phase was further subdivided at the decimal level (Fisser and Hargis 1982). These described visually apparent vegetal changes and reproductive development, when present. All flowering species at each study area were included in the inventory.

Table 1.--Numerical scoring values for vegetative and reproductive phenophases of big sagebrush developed during the 10-year intensive phenological research program in Wyoming

Score	Phenophase description
1.0	Winter dormancy
2.0	Vegetation bud development
3.0	New leaf development
4.0	Twig elongation
5.0	Twig elongation completed
6.0	Vegetative parts browning
7.0	Fall leaf - shed and/or regreening
8.0	Winter dormancy (revert to 1.0)
9.0	Floral bud development recognizable
10.0	Bloom initiation to 10 percent bloom
11.0	Midbloom - 10 to 25 percent bloom
12.0	Late bloom to seed formation
13.0	Seeds in milk stage
14.0	Seeds in dough stage
15.0	Seeds maturing
16.0	Seed cast - floral parts browning
17.0	Fall reproductive regreening
18.0	Winter dormancy (revert to 8.0)

Phenological observations were made at approximately 14-day intervals through the April to September growing season. At each location 20 individual sagebrush plants were identified along a permanent 100- foot (30-m) tape by coordinate distances at 5-foot (1.5-m) intervals. Cumulative precipitation, maximum and minimum air temperature, soil moisture, and soil temperature were obtained concurrently at each location (Fisser and Kleinman 1974; Kleinman 1976).

ANALYSES

Temporal phenological scores were combined by species, sites, and years. These arrays exhibited broad variability, as would be expected. Phenological sample adequacy was approached with a slight modification to the common test

$$n = \frac{t^2 s^2}{e^2}$$

with e set at $\pm$ 0.2 phenophase (Kinucan and Fisser 1984). A nonlinear growth form model was used to quantify phenologic patterns among species and among species groups of differing life-forms, both within and among sites (Ralston 1981; Kinucan 1983).

For this report, the phenological data of big sagebrush at two sites, the Bud Kimball in the Big Horn Basin and the Upper Government over 100 miles (160 km) distant in the Wind River Basin, are presented (fig. 1). A test of paired means by site over years was used to derive indication of similarities and differences. Detailed analyses combined for all 12 sites have been presented (Fisser and others 1983; Kinucan 1983; Kinucan and Fisser 1984).

RESULTS

The phenological records of big sagebrush at the Bud Kimball (BK) and Upper Government (UG) sites are graphically displayed in figure 2. At BK early spring warmup in 1982 caused early expression of new vegetative development, but later cool temperatures and moderate growing season precipitation caused normal progression through the leaf and stem phenophases. Adequate moisture and moderate later summer temperatures maintained an almost linear vegetative phenologic development rate. The early growth initiation was also reflected by earlier than normal floral bud manifestation. Optimum weather conditions during summer and fall caused slow reproductive development.

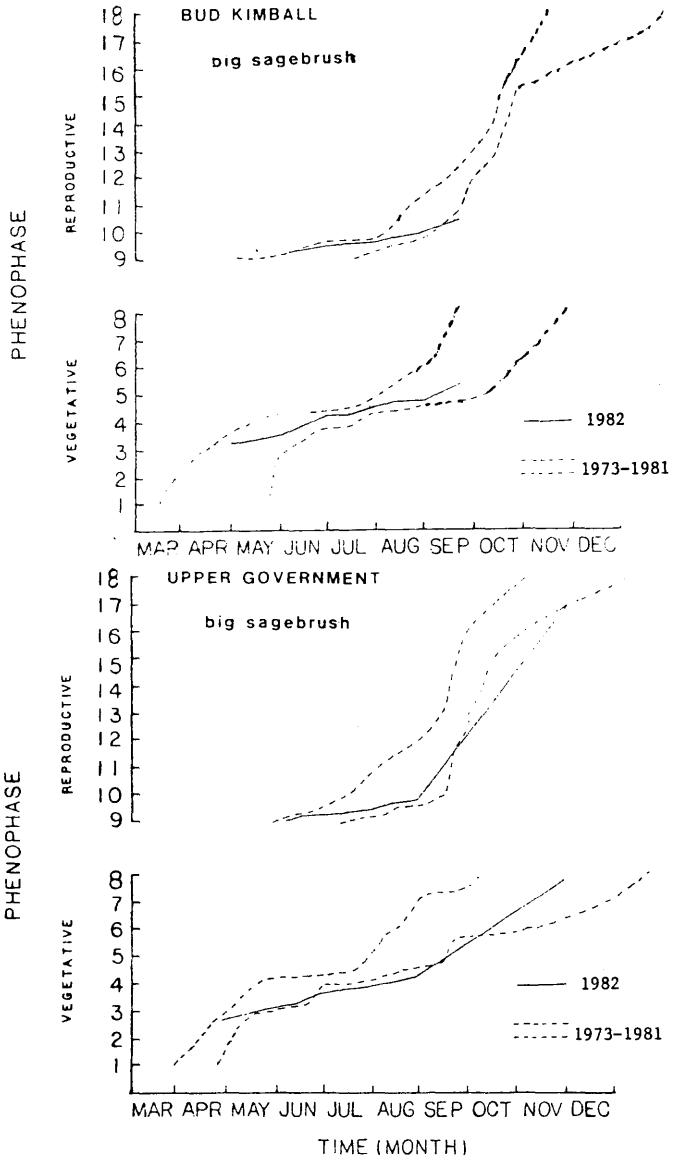


Figure 2.--Ranges of vegetative and reproductive phenological development of big sagebrush at the Bud Kimball (upper) and Upper Government (lower) research locations. Climatic variability during the 10th year of study (1982) caused such slow development that phenological values exceeded the limits of the previous 9 years.

At UG, vegetative growth development in 1982 also initiated early. Atypically cool spring temperatures and good moisture, however, maintained a slower rate of development than normal for the summer months. As a result, vegetative phenology exceeded the bounds set during the first 9 years during the midsummer growing period. Reduced fall moisture availability increased the vegetative phenologic progression rate so that maturation occurred near normal time. Big sagebrush reproductive expression at UG was early also, and the development rate was slower than during 1973 to 1981, until increased progression occurred during the fall.

The lower elevation (1 430 m), warmer temperatures, and commonly less winter snow cover at BK compared to UG (1 805 m) contributes to its earlier growth expression. The more moderate late spring-summer temperatures at UG, however, contribute to a slower vegetative phenologic progression rate than at BK (table 2). The slower development rate generally contributes to enhanced sagebrush herbage yield. The 29-day longer period noted for mean vegetative phenological development at UG was obviously in response to greater late fall soil moisture availability than at BK. Reproductive phenophase was initiated earliest at BK, but UG was generally more advanced during the later growing season. The higher elevation of the latter site reduced the reproductive phenophase time to 164 days compared to 186 at BK.

Table 2.--Julian dates of phenophase attainment at the Bud Kimball (BK) and Upper Government (UG) sites and mean days of difference of UG from BK for the 10-year mean records from 1973 through 1982

Phenophases	Julian dates		Days of difference
Vegetative	BK	UG	
1.0	108	104	4
2.0	116	113	3
3.0	128	135	-7
4.0	163	175	-12
5.0	248	235	13
6.0	267	266	1
7.0	290	293	-3
8.0	305	330	-25
(1-8)	(197)	(226)	(-29)
Reproductive			
9.0	162	171	-9
10.0	233	228	5
11.0	247	238	9
12.0	265	255	10
13.0	277	267	10
14.0	289	277	11
15.0	294	289	5
16.0	305	298	7
17.0	327	308	19
18.0	348	335	13
(9-18)	(186)	(164)	(22)

Environmental constraints resulted in a short growing season during which plant development was quite active unless limited by extreme temperature or drought. Cold spring temperatures generally suppressed rate of early development. Midsummer drought and warm temperatures caused an increased maturation rate and initiated senescence. The shrubs were influenced by early season, cool temperatures; however, late season development was curtailed little by surface moisture unavailability. Deep-rooted woody plants were able to utilize water from 1 to 5 feet (0.3 to 1.3 m) below the surface at depths not available to the roots of most herbaceous species.

These two sites were not at the complete extremes when compared to the other 10 locations. They do, however, represent diverse environmental characteristics rather easily explainable in terms of precipitation and temperature differences.

Those that received the least annual precipitation received the greatest proportion during winter and spring. Differences in effective moisture among sites thus were minimal because the dominant cool season species were able to efficiently utilize spring precipitation (Kinucan and Fisser 1984).

Mean annual temperature differences among sites had little effect on phenological development rates. The only significant thermally related differences in mean phenological development among species or growth forms, among sites, occurred when mean annual temperatures differed by at least 9 °F (5 °C). Soil temperature was one of the major primary driving factors that affected rate of phenological development. Significant changes in plant growth occurred with as little as 1 °F (0.5 °C) change in soil temperature. Relationships between soil moisture and phenological development rate were less obvious (Kinucan 1983).

Other environmental phenomena that were quite important in driving and regulating plant growth were: precipitation from fall through spring, soil moisture at various depths, and maximum and minimum air temperatures. Field data interpretation was based on multiple regression and step-wise selection analysis procedures. These were used to substantiate or reject hypotheses relating to comparative similarity, phenological information, and 15 environmental variables (Kinucan and Fisser).

Within sites, vegetative phenodynamics of species within growth forms such as big and black sagebrush exhibited significant similarity throughout the growing sequence ($p \leq 0.01$). Seven perennial grasses expressed group similarity patterns ($p \leq 0.01$): Sandberg bluegrass (*Poa secunda*), bottlebrush squirreltail (*Sitanion hystrix*), bluebunch wheatgrass (*Agropyron spicatum*), western wheatgrass (*A. smithii*), needleandthread (*Stipa comata*), Indian ricegrass (*Oryzopsis hymenoides*), and junegrass (*Koeleria cristata*). Although not statistically different, they of course, did not develop identically (Young and Fisser 1979). The sequence of development, from most rapid to slowest, generally occurred in the order as listed.

Significant similarity among growth forms was noted only for the perennial forbs, such as scarlet globemallow (Sphaeralcea coccinea) and low fleabane (Erigeron pumilus), that developed synchronously with the grass species. Phenological patterns of annuals were highly variable and quite sensitive to environmental factors that prevented long-term patterns from forming.

The patterns of phenological development that were consistent and repeated among sites were (1) early and rapid perennial grass development, (2) closely following development of perennial forbs, and (3) later development of shrubs with the most protracted sequence of phenological phases.

Developmental differences noted among growth forms can, in part, be attributed to differential partitioning of limited water resources once cold spring temperatures were no longer a limiting factor (Hughes 1977). Soil moisture at shallow depths and to 24 inches (60 cm) was depleted by late June or early July (Fisser 1968). At that time the grass species reached vegetative maturity. The forbs, which developed more slowly early in the season, generally began senescing by late June. Although there were noticeable variations in phenologic progression for portions of the season, there were no statistically significant differences in season-long development. At some sites, development started late in the season due to cold temperatures. Even with a late start, however, most herbaceous plant species at all sites reached maturity and senesced at the same time as at the other sites where spring growth initiation may have been as much as 40 days earlier.

This "catching up" of development demonstrates a vegetative phenophase condensation phenomenon. This, in essence, is a compression of the entire sequence of development into a shorter than normal time period. Reproductive phenology is not nearly as flexible and, as noted earlier, at these latitudes and elevations, may not even be initiated because of environmental stresses.

Within semiarid rangeland communities of Wyoming, various groups of species exist that express similar patterns of phenological development. These phenologically similar groups tend to be found among species with similar growth forms and rooting habits. Phenological similarities within group forms can be attributed to likenesses in moisture acquisition and cold temperature avoidance, in part controlled by similar morphological features. Conversely, differences among growth forms may be explained by these same attributes.

Within growth-form groups, variation was also minimized as a result of a vegetative phenophase condensation phenomenon. Although this phenomenon also occurred between growth forms, significant differences ($p \leq 0.01$) were evident, demonstrating a true difference in growth form strategies and niche specialization. Observations of the unique cumulative patterns of vegetal development expressed by growth forms led to speculation that adaptations to water and temperature stress are functions of growth form, which, in turn, dictates phenologic expression.

SUMMARY

A numerical scoring system was used to monitor vegetative phenodynamics independently of reproductive development. Many plant species of semiarid regions produce flowers and seeds inconsistently from year to year. The complete sequence of annual herbage growth response to climatic and environmental conditions usually progresses from spring bud initiation through leaf maturation during summer and fall. Sometimes extreme climatic stress can actually force early spring or summer dormancy and senescence of even the vegetative growth. A numerical quantification of plant growth phases can be used to better identify the plant response relationship to environmental driving variables

This study was conducted at 12 diverse semiarid sagebrush locations in Wyoming from 1973 through 1982. Intensive study of big and black sagebrush and western and bluebunch wheatgrass involved 20 plants of each species, at each location, which were monitored at 2- to 3-week intervals during the growing season. Permanent transect lines were installed to simplify relocation of each plant. Phenology of the four prime species was monitored to identify subphase appearance changes that were definitive for each. All other plant species were monitored using rather general and classical development phases and with lesser definition of subphase changes.

Big sagebrush phenology from a drier and lower elevation site (BK), and from a more mesic, higher elevation site (UG), were presented to show dissimilarities and likenesses of annual vegetative development. Intrinsic site differences that modified the rate of phenologic progression were apparent. Occasional weather extremes, at any location, caused development rate changes that superceded the inherent progression dynamics expected at a site.

Precipitation, seasonal air temperature extremes, and soil moisture most directly influenced phenologic progression, as would be expected. Plant species with similar growth forms, and especially similar root structure characteristics, exhibited similar phenodynamics. Vegetative phenology was more flexible than reproductive. Ability to extract soil moisture for a longer time in the fall by the deep-rooted shrubs such as sagebrush was exhibited by later seed maturation as well as a longer leaf development period than grasses and forbs. A perennial grass understory enhanced infiltration which provided long-term moisture availability and a greater competitive ability by the shrubs.

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BIOLOGY AND ECOLOGY OF SAGEBRUSH IN WYOMING: IV.

VALIDATION OF A RANGELAND PRODUCTION MODEL (ERHYM) FOR SAGEBRUSH SITES

J. Ross Wight, Herbert G. Fisser and Clayton L. Hanson

ABSTRACT: A rangeland model (ERHYM) was tested with long-term herbage yield records (1965-82) from two sagebrush-grass range sites in central Wyoming. Soil water and soil temperature data for 1963 to 1968 from one of the sites were used to validate the model's soil water balance and soil temperature components. The model accounted for about 50 percent of the variation in the field-measured total yields for the two sites. There was good agreement between the model-predicted and field-measured soil water and soil temperature.

INTRODUCTION

ERHYM (Ekalaka Rangeland Hydrology and Yield Model) is a climate, water-balance model initially developed to predict herbage yields as a function of climate (Wight and Neff 1983). Since its initial development, ERHYM has undergone a series of modifications and improvements. A runoff routine from the CREAMS model (Knisel 1980) that is based on the SCS curve number procedure, a soil temperature simulation routine from the EPIC model (Williams and others 1983), and a climate generating routine from the SPUR model (Wight 1983) have been added to enhance its accuracy and utility. ERHYM is a physically based, process-oriented model and should function effectively when the state variables and model parameters are properly quantified. It has a wide range of potential applications as a tool for researching and managing the rangeland ecosystem.

ERHYM was initially developed and validated for a mixed grass prairie ecosystem (Wight and Hanks 1981). It was successfully applied to a sagebrush-grass range site in southeastern Montana (Wight and Neff 1983). Some preliminary testing of ERHYM's water-balance and soil temperature routines was accomplished using data from sagebrush-grass range sites in southwestern Idaho (Wight and others 1983; Wight 1984). The availability of long-term precipitation and herbage production records for the Wind River Basin region of central Wyoming provided the opportunity to test and validate ERHYM on sagebrush-grass range sites in another geographical region (Fisser, these proceedings).

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J. Ross Wight is Range Scientist, Northwest Watershed Research Center, Agricultural Research Service, U.S. Department of Agriculture, Boise, ID; Herbert G. Fisser is Professor of Range Science, University of Wyoming, Laramie, WY; Clayton L. Hanson is Agricultural Engineer, Northwest Watershed Research Center, Agricultural Research Service, U.S. Department of Agriculture, Boise, ID.

PROCEDURE

Site Description

Yield and climatic data from two sagebrush-grass range sites in the Wind River Basin of central Wyoming were used in this study. Soils at both sites are classified as fine, loamy, mixed soils of the Aridisol order. Big sagebrush (Artemisia tridentata) is the dominant cover and western wheatgrass (Agropyron smithii), mutton bluegrass (Poa fenderiana), and sandberg bluegrass (P. sandbergii) account for most of the forage production on both sites. Site elevation and average annual precipitation are 7,106 feet (2 166 m) and 9.88 inches (25.1 cm), respectively, for the Granite Mountain site and 6,230 feet (1 899 m) and 9.33 inches (23.7 cm), respectively, for the McGraw Flats site. Herbage dynamics for the study period are shown in table 1.

Climatic Data

Precipitation was collected in simple aluminum raingauges installed at the exclosure of each study site. The raingauges had a diameter of 2.79 inches (7.09 cm) so that each 100 mL of water collected in the gauges was equivalent to 1.0 inch (2.54 cm) of precipitation. Oil was added to the gauges to prevent evaporation, and antifreeze was added during the winter months to prevent freezing. Precipitation was recorded four times each year: April 15, July 1, September 1, and October 15.

A daily precipitation record was developed for each study site by prorating the site precipitation records with nearby U.S. Weather Bureau stations using a reciprocal distance squared method such as the one by Wei and McGuinness (1973). Daily precipitation records obtained in this manner are generally satisfactory for predicting herbage production, but may induce a few day-to-day discrepancies between simulated and field-measured soil water content values. Daily solar radiation obtained from the climate-generating routine of the model and air temperatures from the U.S. Weather Bureau station

Table 1.--Dynamics of field-measured and model-predicted herbage yields for Granite Mountain and McGraw Flats

	Sample size	Mean yield	Range	Standard deviation
	Years	Lb/acre[1]		
Field-measured				
Granite Mountain				
Grasses and forbs	16	263	186-404	61
Shrubs	10	196	91-363	93
Total	10	460	299-633	118
McGraw Flats				
Grasses and forbs	18	238	82-370	84
Shrubs	12	223	0-382	110
Total	12	462	82-680	174
Model-predicted				
Granite Mountain				
Grasses and forbs	16	263	184-300	29
Total	10	460	322-593	85
McGraw Flats				
Grasses and forbs	18	237	166-293	56
Total	12	459	235-564	122

[1] Lb/acre x 1.12 = kg/ha.

at Lander, WY, were used for most of the simulations. The model was also run using "generated" maximum and minimum air temperatures.

Soil water content and soil temperature were measured at the Granite Mountain site periodically during the summer months of 1963, 1965, 1967, and 1968. Soil water was measured by the neutron scatter method at soil depths of 6, 12, 18, 24, 36, 48, and 60 inches (15, 30, 46, 61, 91, 122, and 152 cm). Soil temperatures were measured at depths of 1, 8, 15, and 22 inches (2.5, 20.3, 38.1, and 55.9 cm).

Herbage Yield Data

Herbage yields were determined both inside and outside an exclosure at each study site by clipping the herbaceous vegetation by species at ground or crown level from 20 1- by 1-ft (2.5- by 2.5-cm) quadrats spaced systematically along a randomly located 100-ft (30-m) steel tape. Twenty quadrats inside and 20 more outside the exclosure were clipped at each site each year. Annual site yield was determined as the average of all 40 quadrats. The vegetation was clipped within 1 month following peak standing crop. Beginning in 1971, the yield of shrubs and mat-forming species was obtained during late September and October by using a modified double-sampling technique. Weight units were estimated on 20 4- by 5-ft (1.2- by 1.5-m) quadrats inside and 20 quadrats outside the exclosure. Three of the weight units for each species were clipped and weighed to calibrate and check estimations. On areas outside the exclosures, where grazing had occurred prior to clipping, utilization estimates by species were used to adjust the yield estimates. Although herbage yields inside the exclosures were slightly higher than outside, the year by grazing treatments (inside and outside the exclosures) were generally not significant, and so the data from both inside and outside the exclosures were combined to provide a larger sample size.

Model Validation

The effectiveness of ERHYM as a forage yield model depends on its ability to simulate an accurate soil water balance. Because there is little summer runoff from these sites, the soil water-balance component of the model was tested using single growing season runs in which actual field-measured soil water values were used to initialize the model at the beginning of each growing season. Soil water measurements that coincided with the beginning of the growing season were available only in 1963 and 1965. Continuous runs, 1963 to 1967, were utilized to test the model's ability to simulate overwinter recharge. For yield predictions, continuous runs

for 1965 through 1980 for the Granite Mountain study site and 1965 through 1982 for the McGraw Flats study site were used to match the available yield data. In continuous runs, the soil water content variables were not reinitialized at the beginning of each growing season with field-measured soil water data. They were model simulated values carried over from year to year.

The model's ability to simulate soil temperatures was evaluated by comparing model-predicted soil temperatures at the Granite Mountain site with field-measured values for 1963-1968.

RESULTS AND DISCUSSION

Five years of soil temperature measurements on the Granite Mountain site provided data for validating the model's soil temperature routine. Accuracy of model-predicted temperatures (fig. 1; table 2) appears adequate for the needs of the water-balance component for the model. In the model, soil water uptake from the subsurface soil layers is reduced to zero as soil temperature decreases from 63 to 32 °F (17 to 0 °C). Above 63 °F (17 °C) soil temperature has no effect on soil water uptake. While such a temperature constraint is necessary to represent the effects of soil temperature on water uptake, the model is not sensitive to small deviations from actual soil temperature values because most of the evapotranspiration takes place when the soil is relatively warm.

A major test for the model is its ability to simulate soil water content. If the model can accurately simulate the seasonal soil water regime, then the model-calculated yield indices (actual transpiration/potential transpiration) are also assumed to be reasonably accurate. The best test of the water balance component is single growing season simulations where the model can be initialized with actual beginning soil water content values. A comparison of field-measured and model-predicted soil water contents for the Granite Mountain site in 1965 (fig. 2) indicates the model's ability to simulate soil water regimes for a single growing season. Similar results were obtained for 1963.

Simulating continuous soil water regimes over the winter is more difficult. To account for the processes of snow accumulation, snowmelt, and infiltration into frozen or partially frozen soils requires model complexity beyond the scope of ERHYM. In ERHYM, precipitation is accumulated as snow when temperatures are below freezing, and snow is melted by a simple temperature-driven algorithm from CREAMS (Knisel 1980) when air temperatures are above freezing. There are no adjustments of SCS curve numbers to reflect the effects of frozen soil on runoff. Nevertheless, the model-predicted soil water for a 5-year period at Granite Mountain compared reasonably well with field-measured soil water, indicating the model's ability to simulate continuous year-round soil water regimes (fig. 3). Only in 1965 were there major discrepancies at the beginning of the growing season between field-measured and model-predicted values.

Correlation coefficients for field-measured versus model-predicted herbage yields for 1965-80 for Granite Mountain and 1965-82 for McGraw Flats are presented in table 3. The model was better able to predict total yields than the grass-plus-forbs or shrub yields. Yields were based on a calculated actual transpiration/potential transpiration (T/T_p) ratio. The calculated transpiration value represents the total vegetation complex, and it is not partitioned by species; however, where the production of one component, such as sagebrush, is relatively

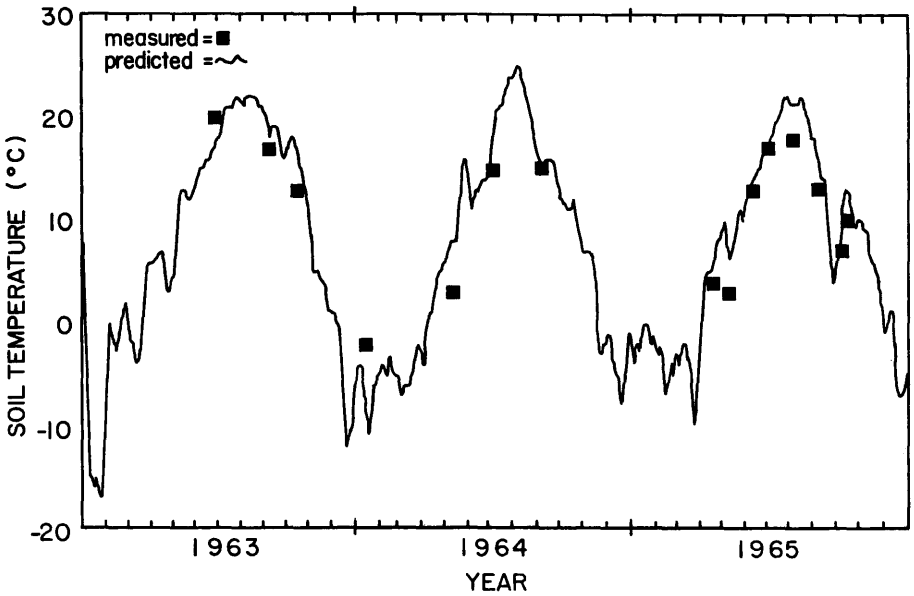


Figure 1.--Comparison of field-measured and model-predicted soil temperatures at the 18-inch soil depth, Granite Mountain, WY.

Table 2.--Correlation between field-measured and model-predicted soil temperatures at the Granite Mountain site

Comparisons	Sample size (n)	Soil depth[2] (inches) 6	12	18	24
		r-value[3]			
Single year simulations[1]					
1965	8	0.90	0.89	0.94	0.94
1967	9	.81	.87	.87	.87
Continuous simulation					
1963-65	27	.76	.83	.89	.88

[1]The model was initialized each year using field-measured soil water content values.

[2]Soil depths of 6, 12, 18, and 24 inches are equivalent to 15, 30, 45, 60 cm.

[3]All correlation coefficients (r) are different from 0.0 at the 0.10 probability level.

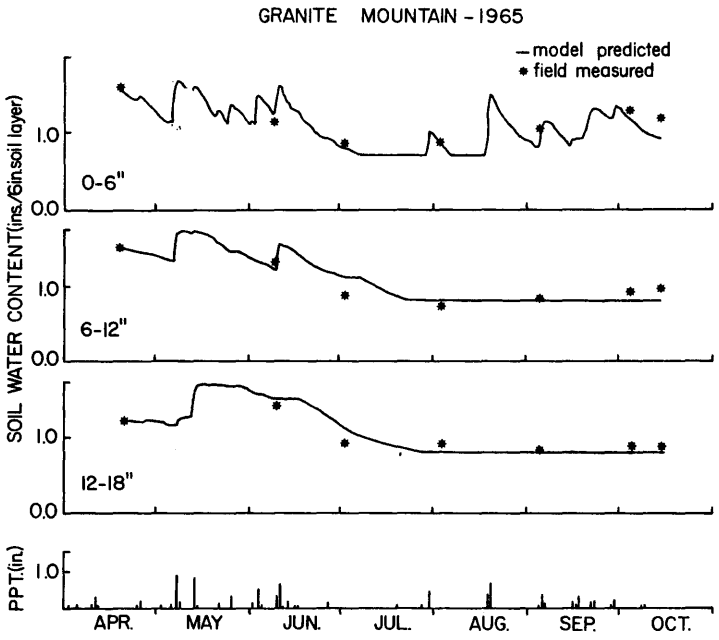


Figure 2.--Comparison of field-measured and model-predicted soil water for a single growing season at the 0-6-, 6-12-, and 12-18-inch (0-15-, 15-30-, 30-45-cm) soil depths.

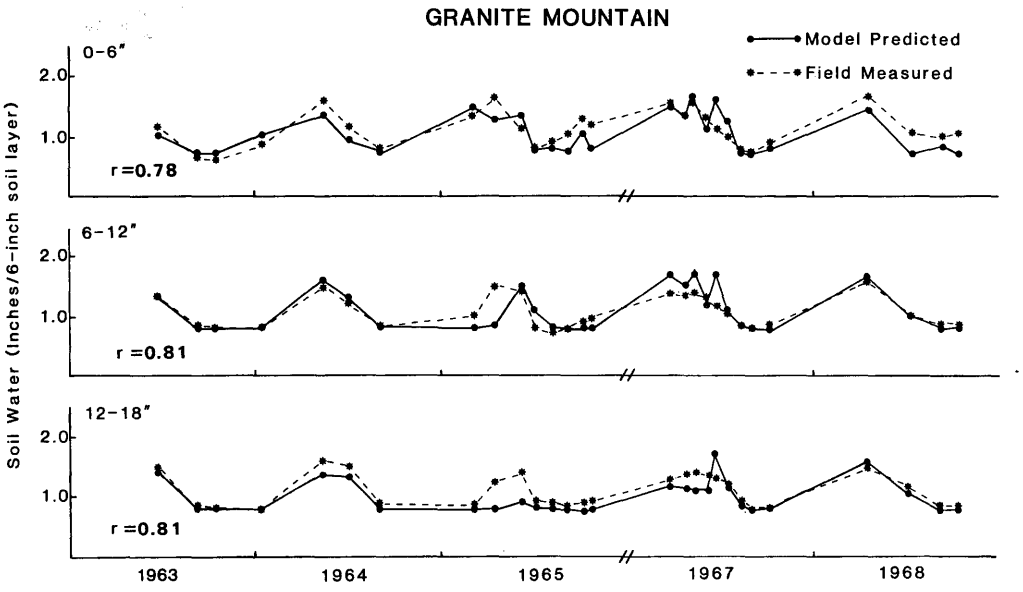


Figure 3.--Comparison of field-measured and model-predicted soil water for the 0-6-, 6-12-, and 12-18-inch (0-15-, 15-30-, and 30-45-cm) soil depths.

Table 3.--Correlation between field-measured and model-predicted herbage yields for 1963-82

Vegetation	Study site			
	Granite Mountain		McGraw Flats	
	Mode 1[1]	Mode 2[2]	Mode 1	Mode 2
	r-value			
Grasses and forbs	[3]0.40a	0.47a	0.68a	0.68a
Shrubs	0.34	0.39	0.49	0.58
Total	0.69a	0.68a	0.72a	0.77a

[1]Mode 1 simulations used actual air temperature values from the U.S. Weather Bureau Station in Lander, WY.

[2]Mode 2 simulations used model-generated air temperature values.

[3]Correlation coefficients followed by "a" are different from 0.0 at the 0.10 probability level.

stable, the model may have utility for predicting annual production of the other components, such as grasses and forbs.

Departures from a 1-to-1 relationship between model-predicted and field-measured values ($r = 1.0$) reflect large yield sampling errors; the model's inability to simulate T and T_p without error; and the lack of a 1-to-1 T/T_p - yield relationship. High sampling errors in the yield data are reflected by average coefficients of variation of 52, 49, and 36 percent for the grasses plus forbs, shrubs, and total yield, respectively, for the two study sites. While sampling variability of this magnitude is common on sagebrush-grass rangelands, the high variability of the actual herbage yield estimates adds to the difficulties of model development and validation.

Variation in annual production as determined from field samples was relatively small, especially in the grasses-plus-forbs component (table 1). On the Granite Mountain site, 75 percent of the annual yield was within a 90 percent sampling confidence interval of the 16-year mean. The correlation coefficient between model-predicted and field-measured grasses plus forbs yield was only 0.47. Yet, 75 percent of the model-predicted yield was within a 90 percent confidence interval of the associated field-measured yield values. For the Granite Mountain grasses-plus-forbs yield, the single long-term mean was as effective for predicting annual yields as the model. For total yield, the yearly variation was much greater. Only about 20 percent of the Granite Mountain and McGraw Flats total annual yields was within a 90 percent sampling confidence interval of the long-term mean yield. Comparison of ranges and standard deviations for the field-measured and model-predicted yields in table 1 indicates that the model represented the total yield dynamics better than that of the forbs plus shrubs.

The use of stochastic-generated air temperatures had very little effect on predicted yields, compared to the use of actual weather station air temperatures (table 3). For long-term simulations, it appears that generated solar radiation and air temperature values are adequate.

SUMMARY

Overall, the ERHYM model performed reasonably well on the two sagebrush range sites in central Wyoming. With better quantification of the state variables and model parameters such as crop coefficient and transpiration coefficient, model accuracy would likely be improved. The results of this study indicate that the ERHYM model has a wide range of potential applications in researching and managing sagebrush-grass rangelands.

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BIOLOGY AND ECOLOGY OF SAGEBRUSH IN WYOMING: V.

HERBAGE YIELD DYNAMICS AND SEASONAL PRECIPITATION RELATIONSHIPS

Clayton L. Hanson, Herbert G. Fisser, and J. Ross Wight

ABSTRACT: We investigated the linear relationship between seasonal precipitation and total herbage production at seven rangeland sites in central Wyoming. Total winter-plus-spring precipitation was the best herbage yield indicator where, on the average, 1 inch of precipitation produced 58 pounds of ovendry material. We also found that the coefficients in the herbage yield-crop year precipitation model proposed by Sneva and Hyder (1962b) and Sneva and Britton (1983) were different from the coefficients that gave the best linear relationship based on site data from central Wyoming.

INTRODUCTION

In many studies, simple or multiple linear regression analyses, using herbage yield as the dependent variable and seasonal precipitation as the independent variable, have been used to develop predictive equations. However, attempts to correlate annual herbage yields of semiarid rangelands with annual precipitation have generally been unsuccessful. This is due primarily to the variable distribution of precipitation and to the fact that range plants generally have the greatest rate of growth during the spring and early summer and little, if any, growth during fall and early winter. Use of seasonal or combinations of monthly precipitation have helped account for the distribution effects and, in many situations, have provided reasonably accurate herbage yield estimates. In Canada, Smoliak (1956) found that May and June precipitation provided good estimates of yield ($r = 0.86$). In North Dakota, Rogler and Haas (1947) correlated April-July precipitation with annual herbage yields ($r = 0.76$). Also in the Northern Great Plains, Power and Alessi (1970) and Wight (1978) found that May was the best single month to index annual herbage production. Sneva and Hyder (1962a) reviewed studies in the intermountain region which indicated that winter and spring precipitation were closely correlated with annual herbage production.

Precipitation-herbage yield relationships developed through regression techniques tend to be site specific. To overcome this dependency, Sneva and Hyder (1962b) and Sneva and Britton (1983) expressed herbage yield and "crop-year" precipitation as ratios of long-term medians.

In this study, we investigated the linear relationships between seasonal precipitation and total herbage yield at seven sites in central Wyoming where precipitation and yield records were available from 1971 through 1982 (Fisser, these proceedings). We also used the same data set to develop a yield-precipitation index model as proposed by Sneva and Hyder (1962b) and Sneva and Britton (1983) for herbage yield adjusting and forecasting. They found that one set of parameters could be used to represent the intermountain region and we wanted to know if their parameter values could be used outside the intermountain region.

METHODS

Site Description

The seven central Wyoming study sites were located in the Wind River Basin, which is both a structural and drainage basin. Its northern boundaries contact the southern portions of the Owl Creek and Big Horn Mountains. The Wind River Range forms the west and southwesterly boundaries, while the southeast and eastern limits are the Sweetwater Escarpment and the Rattlesnake Mountains. The basin is asymetrical in shape with lowest elevations near the Owl Creek Mountains. Elevations range from 4,000 to 7,200 feet (1 219-2 195 m).

The Wind River Basin has a semiarid climate. At Riverton, mean annual precipitation is 8.54 inches (21.7 cm) and mean annual temperature is 43.2 °F (6 °C). The seven central Wyoming sites used in this study are listed in table 1. Site elevation ranged from 5,220 feet (1 591 m) at the Shoshoni #7 location to 7,100 feet (2 164 m) at the Granite Mountain area. Annual precipitation varied from 8.09 inches (20.5 cm) at Shoshoni #7 to almost 10.00 inches (25.4 cm) at Lower Government.

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Clayton L. Hanson is Agricultural Engineer, Northwest Watershed Research Center, Agricultural Research Service, U.S. Department of Agriculture, Boise, ID; Herbert G. Fisser is Professor of Range Science, University of Wyoming, Laramie, WY; J. Ross Wight is Range Scientist, Northwest Watershed Research Center, Agricultural Research Service, U.S. Department of Agriculture, Boise, ID.

Table 1.--Annual and seasonal precipitation and herbage yield for seven study sites in central Wyoming

Site	Elevation	Slope	Aspect of slope	Average precipitation		Average herbage yield[1]		
				Annual[2]	Winter-spring[3] season	Inside	Outside	Means of inside and outside
	Feet	Percent	Degrees	-------Inches-------		-------Lb, ovendry weight-------		
Sweetwater	6150	3.0	145	8.88	6.33	460	436	448
McGraw Flat	6650	1.0	63	9.19	6.31	539	484	512
Granite Mountain	7100	0.5	30	9.03	6.32	524	490	507
Lower Government	5500	0.5	75	9.97	7.52	728	648	688
Upper Government	6080	0.5	90	9.03	7.22	535	422	479
Lander Ant	5350	1.5	143	8.33	6.66	302	325	314
Shoshoni #7	5220	0.5	15	8.09	6.12	326	338	332

[1]Average total herbage yield based on the years used in this study.

[2]Average based on 1960 through 1982 record.

[3]Average based on 1971 through 1982 record.

Soils were Aridisols, including mixed, typic, and frigid Haplargids. They exhibited moderate percolation, were well drained, of moderate alkalinity, and contained a zone of increased effervescence ($CaCO_3$) in the lower "B" horizon. Sand and clay content was variable and the textural class was loamy. The "A" horizon was usually about 3 inches (7.6 cm) thick and the "B" horizon about 15 inches (38.1 cm) thick.

PROCEDURES

Herbage production was obtained in an exclosure and adjacent grazed area at each site. Production was determined by clipping herbaceous species at ground or crown level. Clipping was conducted on or near the same date each year at each study site. Production sampling was initiated each year shortly after July 4 beginning on sites dominated by Gardner saltbush (Atriplex gardneri), which was treated as an herbaceous species. All new annual growth was clipped at that time for determination of total production. Clipping was completed by August 22 each year. Clippings were ovendried at 158 °F (70 °C) for 24 hours prior to weighing.

On areas where animal use had occurred prior to clipping, estimates of utilization were made by species. These estimates were made at the time each plot was clipped. Utilization values were averaged by species for 20 plots and used to adjust production for herbage lost by herbivory. Calculated production estimates given in table 1 were corrected for utilization and represent total production.

An estimate of total production was derived for each site by adding the shrubby and mat-forming species production to the clipped production.

Shrub, mat-forming, and pricklypear herbage production was obtained using a modified double-sampling technique during September and October. Weight units were estimated on 20 randomly located macroquadrats, 4 ft by 5 ft (1.2 m by 1.5 m), subdivided into 6-inch (15.2-cm) squares. Macroquadrats were 6-12 steps apart across the study area.

Shrubby species larger than 36 square inches, primarily big sagebrush (Artemisia tridentata Nutt.), were estimated using the 6-inch square as one weight unit. Mat-forming plants and shrubs smaller than 6 square inches were estimated by weight units of characteristic plant shape and size. Three of the weight units for each species were clipped for weight determination. Each sample was dried in an oven at 158 °F (70 °C) for 96 hours. The average weight in grams for the three weight units, multiplied by the total number of estimated units in 20 quadrats, was converted to pounds per acre as an estimate of annual production. At the same time clipped production data were collected during July and August, pictures of the transects were taken to give a pictorial history from year to year at each study location.

Precipitation data were recorded using metal raingauges installed at each exclosure. The raingauges were constructed with a diameter of 2.79 inches (7.09 cm) so that each 100 mL of water recorded in the gauge was equal to 1.0 inch (2.54 cm) of precipitation. Oil was added to each gauge after reading to prevent evaporation. During the winter months antifreeze was added in known amounts to prevent the gauges from freezing and breaking. Precipitation data were collected four times a year: April 15, July 1, September 1, and October 15.

Regression procedures were used to determine the relationships between annual and seasonal precipitation and total herbage yield by site where the precipitation periods were: (1) fall, September 1 through October 15; (2) winter, October 16 through April 15; (3) spring, April 16 through June 30; and (4) summer, July 1 through August 31. The relationships between seasonal precipitation and the herbage yield from inside and outside the exclosures, and the average of the yield from inside and outside the exclosures were investigated. For the final analyses, the annual yields from inside and outside the exclosures were used as separate samples.

Total winter and spring precipitation by site was used to develop the precipitation indices in the Sneva and Hyder model. Herbage yield indices were developed at each site by using the yields inside and outside the exclosures as separate samples.

DISCUSSION

Regression analyses were used to determine which precipitation season or combination of seasons was the best herbage yield predictor. Initial analyses showed that the winter-spring season gave the best overall prediction results. These analyses also suggested that using the herbage yields from inside and outside the exclosures as separate samples gave the most consistent results. Table 2 is a summary of the regression equations computed from the seasonal precipitation and herbage production at each of the seven study sites.

The slopes of the regression lines varied from 52 to 64/1b/acre (58 to 72 kg/ha) of herbage per inch of precipitation with a mean value of 58, which indicated that 1 inch of winter-spring precipitation produced about 58 lb (26 kg) of herbage (table 2). This was among the lower values Sneva and Hyder (1962a) found for the intermountain area; their values ranged from 33 to 132 lb of herbage/inch (6 to 23 kg/cm) of precipitation. Rogler and Haas (1947) reported about 74 lb/inch (13 kg/cm) of seasonal precipitation for central North Dakota. Smoliak (1956) found that 1 inch of spring and summer precipitation would produce 78 lb (35 kg) at the Manyberries Range Experimental Farm in southeastern Alberta.

Correlation coefficients (r) were significantly different from zero at the 0.01 level, which indicated that there was a linear relationship between seasonal precipitation and total herbage yield. However, the r^2 values for Lower Government and Shoshoni #7 were 0.44 and 0.34, respectively, which reduced the usefulness of the equations developed for these two sites. The 1974 herbage yields were not used in the final analyses of the Lower Government, Upper Government, and Shoshoni #7 sites because herbage yields were so much greater than the measured precipitation would indicate that using the 1974 data would have prevented developing useful prediction equations. The apparent reason for this discrepancy was that the previous fall precipitation was between 4 and 5 inches (10.2 and 12.7 cm). There was only 1 year in the data series when this was the case, so no conclusions could be made about the effect of large fall precipitation amounts on herbage yields at these sites or the other four sites in this study.

The 1976 data were not used for the Granite Mountain, Lower Government, and Upper Government sites because yields were very low relative to the available precipitation, and, again, would have prevented us from developing useful prediction equations. It is not known if the low

Table 2.--Summary of regression analyses of seasonal precipitation (X) vs. total herbage production (Y) from both the exclosure and grazed area at each study site

Site	Regression equation Y = a + bX			Correlation coefficient[1]
	a	b	n^2	r
Sweetwater	88	57	24	0.73
McGraw Flat	108	64	24	.81
Granite Mountain	111	63	22	.82
Lower Government	249	58	20	.66
Upper Government	66	57	20	.74
Lander Ant	-35	52	24	.82
Shoshoni #7	0	54	22	.58

[1]All correlation coefficients are significantly different from zero at the 0.01 level.

[2]Annual herbage yields from inside and outside the exclosures were separate samples (n = number of years x 2).

yields were due to sampling or other conditions such as seasonal climatological variations.

Sneva-Hyder Index Procedure

The same winter-spring precipitation and herbage yield data sets used for the final regression analyses were used to develop herbage forecasting equations based on the Sneva-Hyder procedure (Sneva and Hyder 1962b; Sneva and Britton 1983). Results are summarized in table 3. As shown in table 3, the slope varied from 0.63 at Lower Government to 1.10 at Shoshoni #7, with a mean value of 0.87 when all site data were grouped. The correlation coefficients (r) were all significantly different from zero, which indicated that there was a linear relationship between the precipitation index and herbage yield index, as with the other regression analyses. The r^2 values were below 50 percent for the Lower Government and Shoshoni #7 sites.

The single regression equation obtained for the seven sites was:

$$Y = 0.87X + 16 \quad (r = 0.71) \qquad (1)$$

where Y is the yield index (percent of median value x 100) and X is precipitation index (percent of median value x 100). Both the slope and intercept of equation (1) were significantly different from the equation proposed by Sneva and Britton (1983). Their equation was:

$$Y = 1.23X - 23 \quad (r = 0.83) \qquad (2)$$

This suggested that the herbage yield-precipitation relationship in the Wind River Basin of Wyoming was different from that of the sample areas used by Sneva and Britton. The crop-year precipitation (September 1-June 30) used by Sneva and Britton was about the same as the season used in this study, so other factors, such as soils and climatic regime contributed to the discrepancy between the two equations. Hanson and others (1983) found that the Sneva-Hyder (1962b) equation represented conditions at the low-elevation areas on the Reynolds Creek Experimental Watershed in southwest Idaho; this also suggested that the precipitation-herbage yield relationships were different between the intermountain region and the Wind River Basin.

The results of this study indicated that the precipitation-herbage yield index procedures proposed by Sneva and Hyder were good procedures for forecasting herbage yield. However, study results suggested that the coefficients in the equation were different for different areas of the country and, therefore, coefficient values must be computed for other areas than the intermountain region.

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Table 3.--Summary of regression analyses of seasonal precipitation (X) vs. total herbage yield (Y) where Y and X are expressed in percent of the median value[1]

Site	Regression equation Y = a + bX			Correlation coefficient[2]
	a	b	n[3]	r
Sweetwater	20	0.80	24	0.73
McGraw Flat	24	.92	24	.83
Granite Mountain	22	.78	22	.83
Lower Government	37	.63	20	.70
Upper Government	12	.89	20	.83
Lander Ant	-11	1.05	24	.83
Shoshoni #7	0	1.10	22	.58
All sites	16	.87	156	.71

[1]See Sneva and Britton (1983).

[2]All correlation coefficients are significantly different from zero at the 0.01 level.

[3]Annual herbage yields from inside and outside the exclosures were separate samples (n = number of years x 2).

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Section 7. Physiology and Growth

PHOTOSYNTHESIS, GROWTH, TRANSPIRATION, AND ^{13}C RELATIONSHIPS AMONG THREE SUBSPECIES OF BIG SAGEBRUSH (ARTEMISIA TRIDENTATA NUTT.)

Carolyn T. Frank, Bruce N. Smith, and Bruce L. Welch

ABSTRACT: Twenty-one accessions of three subspecies of big sagebrush (Artemisia tridentata ssp. tridentata, ssp. wyomingensis, and ssp. vaseyana) were grown in a uniform garden to test the relationship between $\delta^{13}C$ values and photosynthetic efficiency. Individual plants were measured for rates of photosynthesis, transpiration, growth, and $\delta^{13}C$ values. As growth rates increased, so did $\delta^{13}C$ values. Increase in growth indicated an increase in photosynthetic efficiency (CO_2 uptake/H_2O loss). Differences in $\delta^{13}C$ values among subspecies correlated with photosynthetic adaptations to different environmental conditions.

INTRODUCTION

Most plants fix carbon initially into 3-phosphoglyeric acid and are termed C_3 plants (Winter and others 1982). Among other characteristics, these plants exhibit a characteristic range of isotopic discrimination values for the naturally occurring, stable isotopes of carbon. Isotopic values reflect either environmental influences (Smith and others 1976; Vogel 1980) or genetically determined differences in diffusional or enzymatic fractionation (Park and Epstein 1960).

Artemisia tridentata (big sagebrush) is widespread throughout the Intermountain West and varies in size, growth rate, palatability, digestibility, and chemical composition (Welch and McArthur 1979; Welch and Pederson 1981; McArthur and Welch 1982). This paper examines $\delta^{13}C$ values for 21 accessions of A. tridentata grown at a common site as an indication of genetic differences in photosynthetic efficiency within this species.

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Carolyn T. Frank is a graduate research assistant, Department of Botany and Range Science, Brigham Young University, Provo, UT; Bruce N. Smith is Dean, College of Biology and Agriculture, Brigham Young University. Bruce L. Welch is principal research plant physiologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT.

MATERIALS AND METHODS

Plant material was grown in a garden established by the Forest Service, U.S. Department of Agriculture, in Springville, UT. Three subspecies of Artemisia tridentata (Nutt.), ssp. vaseyana, ssp. wyomingensis, and ssp. tridentata, were collected from 21 accessions throughout the Intermountain West, the majority from Utah. Of the 21 accessions, 10 were A. t. ssp. vaseyana, seven were A. t. ssp. tridentata, and four were A. t. ssp. wyomingensis. Each accession was represented by 10 plants. The resulting 210 plants were planted at random on a 3- by 3-m grid. Table 1 lists the locations of seed collection sites. Growth rates were determined by measuring the annual length of 15 leaders per plant. Leader lengths were measured from the terminal leaf bud scars to the tip of the current terminal leaves. Leaders were selected at random over the entire crown of the plant. The 15 measurements were pooled together to calculate a plant mean.

The rate of photosynthesis for each plant was determined using the CO_2 depletion method described by Ehleringer and Cook (1980). We, however, added a probe to determine temperature and relative humidity. Carbon dioxide was measured in an infrared gas analyzer operated in the absolute mode.

Transpiration rates were determined using temperature and relative humidity data collected with the gas samples. Leaf samples from each plant were air dried and then combusted using the sealed tube combustion technique of Sofer (1980). After combustion, plant samples were analyzed on an isotope ratio mass spectrometer. Results were expressed as:

$$\delta^{13}C_{PDB} = \left[\frac{R_{sample}}{R_{standard}} - 1 \right] X\ 1000$$

where R = mass 45/mass 44 of sample or standard.

The current year's growth on 10 different branches of each plant was measured during the last week of October 1981 and 1982.

Regression analyses were used to determine the relationship among $\delta^{13}C$ values, growth rates, transpiration rates, and photosynthetic rates. Standard deviations were calculated from the data obtained in each of these areas. Also, an analysis

Table 1.--Collection sites for big sagebrush subspecies used to determine rates of photosynthesis and growth

Subspecies	Accession	County and State	Elevation (m)
vaseyana	Colton	Utah, UT	2260
	Sardine Canyon	Cache, UT	1800
	Benmore	Tooele, UT	1900
	Petty Bishop's Log	Sanpete, UT	2380
	Durkee Springs	Sevier, UT	2350
	Clear Creek Canyon	Sevier, UT	2130
	Pinto Canyon	Washington, UT	1850
	Indian Peaks	Beaver, UT	2140
	Hobble Creek	Utah, UT	1500
tridentata	Clear Creek Canyon	Sevier, UT	1720
	Big Brush Creek	Uintah, UT	1830
	Loa	Wayne, UT	2140
	Dove Creek	Dolores, CO	2070
	Evanston	Uinta, WY	2020
	Wingate Mesa	San Juan, UT	2060
	Dog Valley	Juab, UT	1700
wyomingensis	Evanston	Uinta, WY	2130
	Kaibab	Coconino, AZ	2340
	Trough Spring	Humboldt, NV	1400
	Milford	Beaver, UT	1540

of variance was conducted to test for significant differences among the 20 accessions and subspecies.

RESULTS

Growth rates were related to $\delta^{13}C$ values among subpsecies (fig. 1). Tridentata with the highest average growth rate also produced the highest average $\delta^{13}C$ value (table 2). Wyomingensis had the second highest growth rate, and its $\delta^{13}C$ value was second highest. Subspecies vaseyana showed the lowest average growth rate and had the lowest $\delta^{13}C$ value. In 1981, however, vaseyana had the second highest growth rate and isotopic value; wyomingensis was lowest in both values. The rate of photosynthesis was highest in accessions with high rates of growth, transpiration, and $\delta^{13}C$ values. While photosynthetic rates for all accessions followed transpiration rates, this correlation was not as strong as for $\delta^{13}C$ values and transpiration rates.

The average photosynthetic rate was higher in June than in August. Transpiration was also greater in June than in August. This trend in transpiration could be seen at the level of subspecies and accessions as well. As can be seen in figure 2, $\delta^{13}C$ values decreased from June to August.

Comparison of $\delta^{13}C$ values and transpiration rates among the subspecies showed a tendency for $\delta^{13}C$ values to become more negative as transpiration increased (fig. 2). The growth rate of each subspecies is given in figure 3; tridentata had the highest growth rate followed by wyomingensis and vaseyana.

Table 2.--Growth rates and $\delta^{13}C$ values for three subspecies of big sagebrush for 1981 and 1982. All values ± one standard deviation

	1981		1982	
Subspecies	$\delta^{13}C$ o/oo[1]	Growth rate[2] (cm/yr)	$\delta^{13}C$ o/oo[3]	Growth rate[4] (cm/yr)
tridentata	-27.6 ± 1.14	28.8 ± 8.70	-28.2 ± 1.08	32.7 ± 7.91
vaseyana	-28.0 ± 0.95	23.3 ± 6.14	-29.3 ± 0.78	21.6 ± 2.27
wyomingensis	-28.2 ± 0.87	20.1 ± 3.27	-28.7 ± 0.62	26.4 ± 6.23

[1]Means are significantly different at $P < 0.25$.
[2]Means are significantly different at $P < 0.005$.
[3]Means are significantly different at $P < 0.10$.
[4]Means are significantly different at $P < 0.025$.

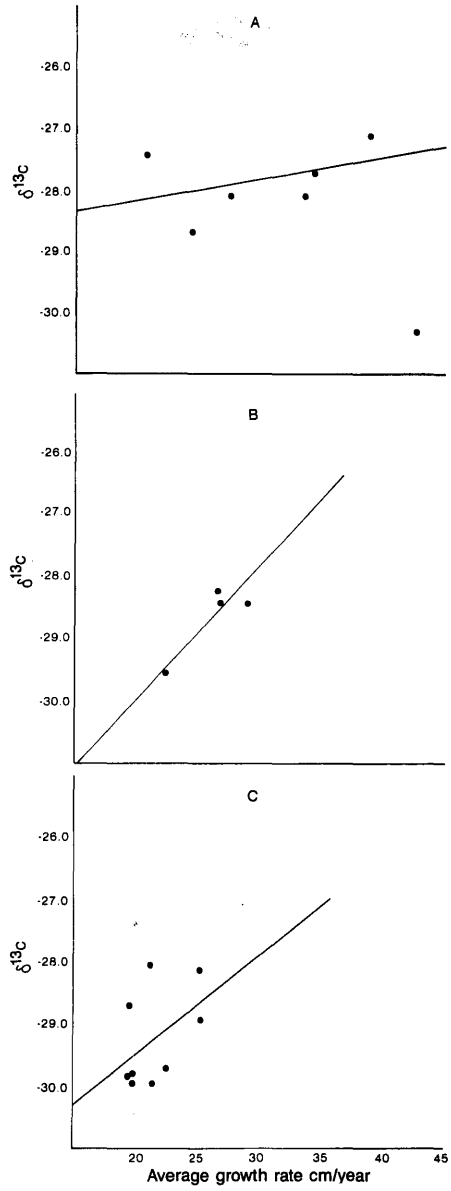


Figure 1.--Average growth rate (1982 vs. $\delta^{13}C$ in the three subspecies of Artemisia tridentata: (a) tridentata, (b) wyomingensis, (c) vaseyana. All three subspecies show a positive correlation: as $\delta^{13}C$ increases, growth rates also increase.

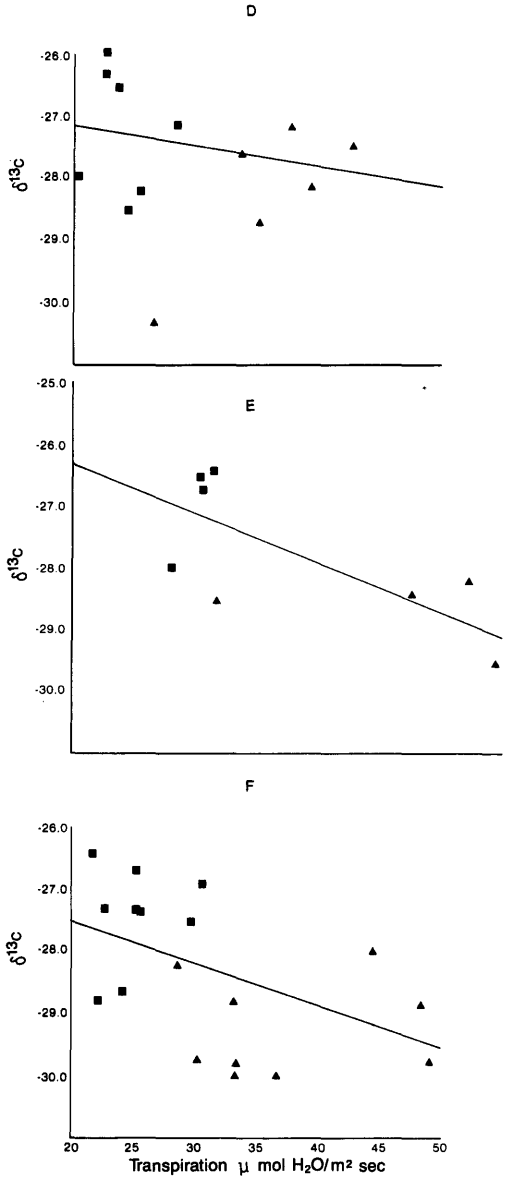


Figure 2.--Average $\delta^{13}C$ value vs. average transpiration rate in three subspecies of Artemisia tridentata: (d) tridentata, (e) wyomingensis, (f) vaseyana. All three subspecies show a negative correlation: as $\delta^{13}C$ increases transpiration decreases. Triangles represent June measurements and squares represent August measurements.

DISCUSSION

Theoretically there should be a close relationship between photosynthetic rate and dry matter production (Gaskel and Pearce 1981). Our results showed a direct relationship between growth rate and $\delta^{13}C$ values. As photosynthesis becomes more efficient, its $\delta^{13}C$ values became less negative.

Distribution of Artemisia tridentata subspecies occurs along a moisture gradient (McArthur 1983) (fig. 4). Presumably this distribution occurs because of genetic differences in environmental requirements since differences were maintained among subspecies when grown in a common garden (McArthur and Welch 1982). Genetic adaptation to different environments can be reflected in $\delta^{13}C$ values (Smith and others 1976). Vaseyana generally grows in cooler, more mesic sites than the other two subspecies. Its need to reduce water loss would, therefore, be less than that of wyomingensis which is adapted to harsh, dry soils, or tridentata which is found in the heat of the lower elevations (fig. 4). Vaseyana would not have to be as conservative with moisture. Tridentata, on the

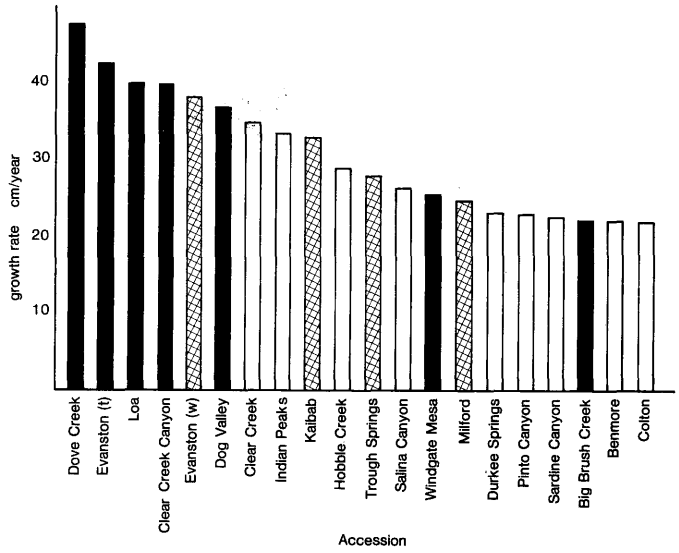


Figure 3.--Maximum growth rates attained by each accession. Solid bars, tridentata; hatched bars, wyomingensis; and open bars, vaseyana.

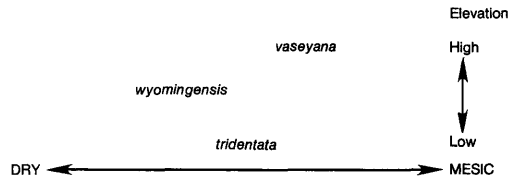


Figure 4.--Distribution of Artemisia tridentata subspecies along a moisture gradient in combination with elevation (McArthur 1983).

other hand, would require a greater water use efficiency. This, too, is reflected in higher $\delta^{13}C$ values and higher growth rates for tridentata. Wyomingensis generally grows on drier sites than tridentata, but at higher elevations with different precipitation patterns and soil conditions.

Subspecies of big sagebrush that exhibit rapid growth also show high rates of photosynthesis (reflected in less isotopic fractionation) and high rates of transpiration. Late summer rates of photosynthesis and transpiration were less than those measured in the spring perhaps due to decreased water availability. A general correlation was noted between photosynthesis, transpiration, and conditions at sites where the three subspecies naturally occur.

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COMPARISON OF PRODUCTION IN TWENTY-SEVEN ACCESSIONS OF FOUR SAGEBRUSH TAXA

James N. Davis and Richard Stevens

ABSTRACT: Vegetative production was compared on an equal annual stem length basis for 27 accessions of four sagebrush taxa, black sagebrush (Artemisia nova), and three subspecies of big sagebrush (A. tridentata), grown in a common garden at Ephraim, UT. Production was a measure of oven dried weight, stem weight, and total weight (stem and leaf material together) per cm of annual leader growth. There were few singularly outstanding accessions evident but there were some consistent trends. A trend index value was used to help indicate each accession's overall level of performance. The amount of variation between species and among accessions of sagebrush on an equal length basis was significant. In general, when comparing the production of the four sagebrush taxa on the basis of equal annual leader lengths A. tridentata ssp. vaseyana > A. tridentata ssp. tridentata > A. tridentata ssp. wyomingensis > A. nova.

INTRODUCTION

Considerable effort has been put into sagebrush research. Early work emphasized sagebrush control to help improve livestock ranges. More recent research has recognized many positive values for planting sagebrush (McArthur and Plummer 1978). Sagebrush has been shown to be one of the most important browse plants for wintering mule deer in many Intermountain areas (Leach 1956; Plummer and others 1968; Robinette 1977; Tueller 1979). Sagebrush is highly variable in many morphological and physiological characteristics (McArthur and others 1979; Johnson 1983). For example, sagebrush has been shown to have considerable variation in digestibility (Welch and Pederson 1981), growth rate and size (McArthur and Welch 1982), crude protein (Welch and McArthur 1979), and preference (Welch and others 1983). Many improvements can be selected for through this high amount of variation that occurs within and between sagebrush taxa.

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James N. Davis is research biologist and Richard Stevens is Project Leader for game range restoration studies with the Utah Division of Wildlife Resources stationed at the Intermountain Research Station's Shrub Sciences Laboratory, Provo, UT, and the Great Basin Experimental Range, Ephraim, UT.

Preference is an important characteristic to take into consideration when choosing species and/or accessions for seeding or outplanting, but the literature relating to preferential use is inconclusive with regard to the factors correlated to preferred use (Narjisse 1981; Radwan and Crouch 1978; Scholl and others 1977; White and others 1982). Preference has often been equated to the amount or percent use of the annual leader growth. These measurements have been used by researchers to make comparisons among taxa and accessions, and among years on critical wintering areas. These measurements have helped managers to set guidelines on how much use of the shrub annual leader growth can be consumed and still maintain plant vigor. But, percent use does not provide information on the amount of forage produced and consumed per plant. The problem of differing plant size is usually apparent and can be corrected for. Percent use when used for comparisons between different sagebrush accessions or taxa assumes that annual leader growth between and among taxa is the same, this could lead to some problems if not corrected for or recognized. Equal lengths of plant material have also been assumed equal in weight; they are not. Plant size differences have a strong genetic component and are important in annual forage production (McArthur and Welch 1982; Barker and others 1983). This could be an important concept to consider when choosing accessions for outplanting because forage production could be increased without increasing plant size or numbers. This study was designed to show if there are differences in production among or between sagebrush taxa when they are compared on the basis of adjusted equal annual leader lengths.

METHODS

Four taxa were chosen because of their natural abundance, use by wildlife, and availability within the same common garden at Ephraim, UT. They included: nine accessions of basin big sagebrush (Artemisia tridentata ssp. tridentata), four accessions of Wyoming big sagebrush (A. tridentata ssp. wyomingensis), seven accessions of mountain big sagebrush (A. tridentata ssp. vaseyana), and seven accessions of black sagebrush (A. nova) (table 1).

Five plants from each accession were randomly chosen from a common garden at Ephraim, UT, in late October of 1982. Four complete branches were randomly clipped off and separated into

Table 1.--Locations for sources of accessions of sagebrush taxa

Species	Subspecies	Accession	Location	County, State
tridentata	tridentata	U- 6	Snow Creek	Humbolt Co., NV
		U- 50	Fremont Road	Sevier Co., UT
		U- 55	Leonard Creek	Humbolt Co., NV
		U- 70	Moab	Grand Co., UT
		U- 74	Dove Creek	Dolores Co., CO
		U- 76	Clear Creek	Sevier Co., UT
		U- 79	Dog Valley	Juab Co., UT
		U- 82	Big Brush Creek	Uintah Co., UT
		U-107	Highway 28	Sweetwater Co., WY
tridentata	wyomingensis	U- 1	Trough Springs	Humbolt Co., NV
		U- 8	80/189 interchange	Uinta Co., WY
		U- 9	Milford	Beaver Co., UT
		U- 10	Decker Mine	Big Horn Co., MT
tridentata	vaseyana	U- 1	Hobble Creek	Utah Co., UT
		U- 9	Ephraim Canyon	Sanpete Co., UT
		U- 15	Sardine Canyon	Cache Co., UT
		U- 19	Salina Canyon	Sevier Co., UT
		U- 23	Pinto Canyon	Washington Co., UT
		U- 63	Carey	Blaine Co., ID
nova		U- 5	Manti	Sanpete Co., UT
		U- 7	Gunnison	Sanpete Co., UT
		U- 14	Alton (south)	Kane Co., UT
		U- 15	Alton (west)	Kane Co., UT
		U- 17	Desert Range	Millard Co., UT
		U- 18	Pine Valley	Millard Co., UT
		U- 22	Steinakers Res.	Uintah Co., UT

stems and leaves. Total stem length was measured to the nearest centimeter. The stems and leaves were oven dried and weighed separately. The data were summarized in tabular form in the following categories: weight of leaves per cm of stem, weight of stems per cm, total weight (stems and leaves) per cm of stem, and leaf weight as a percent of total weight. Categories for leaf weight, stem weight, and total weight will total correctly except for some small rounding errors. Percent leaf weight, however, sometimes will be slightly off the arithmetic totals from the table data because percent leaf weight was done on an equally weighted basis. All weights are in grams. A nested analysis of variance model was used (SAS User's Guide: Statistics 1982). A Newman-Kuel multiple means comparison test was used when there were significant differences among the means (Steel and Torrie 1960).

A trend index was used to better describe which accessions performed the best. This was done by giving each accession or species a score of 1 through n. The score received depended on its placement with regard to the others in the group, one point for first (the highest weight value), two points for second (the second highest weight value), etc. Each species' or accession's scores were summed for all categories. The species or accession with the smallest score was considered the best or most productive.

RESULTS

There were significant differences among the selected taxa of sagebrush (table 2). There was no one decidedly superior taxa in each category, but a definite trend was evident. Mountain big sagebrush was the most productive in all categories except for percent leaf weight. It had a trend index value of 5 out of a possible best score of 4 points. Mountain big sagebrush was 14 percent more productive than basin big sagebrush, 17 percent more productive than Wyoming big sagebrush, and 43 percent more productive than black sagebrush when compared on an equal length basis.

Basin Big Sagebrush

There were significant differences among accessions within the taxa. There was no decidedly superior basin big sagebrush (table 3), but for three of the four categories, the Clear Creek (U-76), Snow Creek (U-6), and Wyoming (U-107) accessions were consistently among the best. The one category in which two of these three accessions were not the best was weight of stems per cm. It is interesting to note that if you take the mean of the three best accessions, it was 21 percent more productive than the closest accession to it in total production and 37 percent more productive than the Fremont Road accession which is the lowest in total production. The trend index

Table 2.--Vegetative production (oven dry weights in grams) comparisons for equal stem lengths among four sagebrush taxa[1]

	$ARTR^{v}$	$ARTR^{t}$	$ARTR^{w}$	ARNO
Weight of leaves per cm	.193	.186	.147	.094
	$ARTR^{v}$	$ARTR^{w}$	$ARTR^{t}$	ARNO
Weight of stems per cm	.152	.145	.117	.106
	$ARTR^{v}$	$ARTR^{t}$	$ARTR^{w}$	ARNO
Total weight per cm	.346	.303	.293	.200
	$ARTR^{t}$	$ARTR^{v}$	$ARTR^{w}$	ARNO
Percent leaf weight	60.5	54.0	49.5	45.1
	$ARTR^{v}$	$ARTR^{t}$	$ARTR^{w}$	ARNO
Trend Index values[2]	5	8	11	16

[1]The means connected by a line are not significantly different at the .05 percent level. $ARTR^{t}$=basin big sagebrush, $ARTR^{w}$=Wyoming big sagebrush, $ARTR^{v}$=mountain big sagebrush, ARNO=black sagebrush

[2]Lower values indicate higher overall productivity (minimum value=4, maximum value=16).

scores ranged from 8 to 30. The three best accessions had trend index scores of 8 (Clear Creek), 11 (Snow Creek), and 12 (Wyoming).

Mountain Big Sagebrush

Low-elevation ecotypes of mountain big sagebrush have some of the best potential because of their apparent preferential use by wintering mule deer (Welch and others 1981). In general, either Pete Bishop (U-9) or Hobble Creek (U-1) were the best performing accessions of mountain big sagebrush (table 4). Accessions Pete Bishop (U-9) and Hobble Creek (U-1) had trend index values of 11 and 14, respectively, among values ranging from 11 to 30. To help illustrate the variability in total production between accessions, Pete Bishop (the most productive) was 42 percent more productive than Pinto Canyon (the least productive) when equal lengths were compared.

Wyoming Big Sagebrush

There was no decidedly superior Wyoming big sagebrush accession, but there was a noticeable trend. The Trough Springs (U-1) and Highway Interchange (U-8) accessions were the top two in three of the four categories with trend indexes of 6 and 9 respectively (table 5). Trend index values ranged from 6 to 15. With these two accessions producing a mean total weight of 0.362 grams per cm, they were 31 percent more productive than the Milford accession (U-9) and 48 percent more productive than the Decker Mine accession (U-10).

Table 3.--Vegetative production (oven dry weight in grams) comparisons of equal stem lengths for accessions of basin big sagebrush[1]

	ACCESSIONS								
	U-76	U107	U- 6	U-79	U-70	U-55	U-74	U-50	U-82
Weight of leaves per cm	.272	.261	.225	.173	.171	.168	.161	.127	.118
	U- 6	U-55	U-74	U-82	U-76	U107	U-79	U-50	U-70
Weight of stems per cm	.139	.130	.124	.118	.114	.112	.110	.108	.099
	U-76	U107	U- 6	U-55	U-74	U-79	U-70	U-82	U-50
Total weight per cm	.386	.374	.364	.298	.286	.283	.270	.236	.235
	U-76	U107	U-70	U- 6	U-70	U-74	U-55	U-50	U-82
Percent leaf weight	70.0	67.1	63.2	61.3	59.1	56.4	56.3	53.0	50.4
	U-76	U- 6	U107	U-55	U-74	U-79	U-70	U-82	U-50
Trend index values[2]	8	11	12	19	21	22	24	30	33

[1]The means connected by a line are not significantly different at the .05 percent level.

[2]Lower values indicate higher overall productivity (minimum value=4, maximum value=36).

Table 4.--Vegetative production (oven dry weight in grams) comparisons for equal stem lengths among accessions of Mountain big sagebrush[1]

	ACCESSIONS						
	U- 9	U- 1	U-13	U-15	U-23	U-63	U-19
Weight of leaves per cm	.324	.212	.180	.169	.161	.150	.148
	U-15	U- 1	U-19	U-63	U- 9	U-13	U-23
Weight of stems per cm	.190	.170	.168	.155	.152	.130	.115
	U- 9	U- 1	U-15	U-19	U-13	U-63	U-23
Total weight per cm	.447	.382	.359	.316	.310	.306	.276
	U- 9	U-23	U-13	U- 1	U-63	U-15	U-19
Percent leaf weight	67.3	55.5	55.1	54.1	51.0	46.3	45.7
	U- 9	U- 1	U-15	U-13	U-63	U-19	U-23
Trend index value[2]	11	14	18	23	24	28	29

[1]The means connected by a line are not significantly different at the .05 percent level.
[2]Lower values indicate higher overall productivity (minimum value=4, maximum value=28).

Black Sagebrush

No one accession of black sagebrush was significantly more productive, but the trend was for Walt James (U-17), West Alton (U-15), and Steinakers Reservoir (U-22) to be the most productive (table 6). They had trend index values of 9, 10, and 12 respectively. Trend index values ranged from 9 to 24. The Walt James (U-17) accession was 46 percent more productive than the Manti accession (U-5), when they were compared on an equal basis.

DISCUSSION

Literature on sagebrush has generally shown that there are usually clear choices as to which species or accession is the most preferred. However, no one has been able to determine which components of sagebrush affect its preferential use by wildlife. Maybe these results can give some explanation why this is so. When preference is determined by measuring percent removal of the current year's growth and also by assuming that equal stem lengths weigh the same, these assumptions could confound the results. For example, if two accessions (Pinto Canyon and Ephraim Canyon) of the same taxon and about the same size with average annual leader growths of 9.3 and 8.2 cm respectively (McArthur and Welch 1982) were both utilized at 5 cm, the Ephraim Canyon accession would have still provided 42 percent more forage. A correction factor is necessary to take into account total use per plant. Such a factor could be determined by sampling each accession or species and obtaining a value for oven dried weight per unit of stem length. This could be used to determine the differences in use (actual weight); the amount used could then be adjusted by this weight correction factor, allowing for a more accurate determination of how much of each species or accession has been consumed. This study showed that each accession and taxa does differ in productivity on a per unit length basis.

Table 5.--Vegetative production (oven dry weight in grams) comparisons for equal stem lengths among accessions of Wyoming big sagebrush[1]

	ACCESSIONS			
	U- 1	U- 8	U- 9	U-10
Weight of leaves per cm	.207	.145	.143	.093
	U- 8	U- 1	U- 9	U-10
Weight of stems per cm	.199	.172	.106	.105
	U- 1	U- 8	U- 9	U-10
Total weight per cm	.379	.344	.250	.198
	U- 9	U- 1	U-10	U- 8
Percent leaf weight	55.7	53.5	46.4	42.2
	U- 1	U- 8	U- 9	U-10
Trend index value[2]	6	9	10	15

[1]The means connected by a line are not significantly different at the .05 percent level.
[2]Lower values indicate higher overall productivity (minimum value=4, maximum value=16).

Table 6.--Vegetative production (oven dry wright in grams) comparisons for equal stem lengths among accessions of black sagebrush[1]

	ACCESSIONS						
	U-17	U-22	U-15	U-18	U- 7	U-14	U- 5
Weight of leaves per cm	.121	.115	.110	.101	.074	.070	.067
	U-15	U-22	U-17	U-14	U-18	U- 5	U- 7
Weight of stems per cm	.154	.129	.121	.111	.080	.076	.073
	U-15	U-22	U-17	U-18	U-14	U- 7	U- 5
Total weight per cm	.264	.244	.242	.181	.181	.147	.143
	U-18	U-17	U- 7	U- 5	U-15	U-22	U-14
Percent leaf weight	55.4	49.2	48.2	45.5	40.5	40.1	36.7
	U-17	U-15	U-22	U-18	U- 7	U-14	U- 5
Trend index value[2]	9	10	12	14	21	22	24

[1]The means connected by a line are not significantly different at the .05 percent level.
[2]Lower values indicate higher overall productivity (minimum value=4, maximum value=28).

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GROWTH RATE OF BIG SAGEBRUSH AS INFLUENCED BY ACCESSIONS, SITES, SUBSPECIES, AND YEARS

Bruce L. Welch and E. Durant McArthur

ABSTRACT: To aid in the development of improved cultivars of big sagebrush (Artemisia tridentata) for use on mule deer winter ranges, growth rate tests were conducted on accessions grown in a uniform garden. Genetically superior accessions were identified. To determine if genetic superiority is maintained in native stands, 21 accessions then were established on three different range sites. All three subspecies of A. tridentata were represented. Current-year leader growth was measured on each site for 5 years. Statistical tests detected significant ($P < 0.05$) effects due to accessions, sites, subspecies, and years. Genetic superiority, as determined under uniform garden conditions, was maintained across accessions, sites, subspecies, and years.

INTRODUCTION

Big sagebrush (Artemisia tridentata Nutt.) is the single most used winter mule deer (Odocoileus hemionus hemionus) forage in the Great Basin area of the Western United States (Leach 1956; Plummer and others 1973; Tueller 1978; Tisdale and Hironaka 1981; Blaisdell and others 1982). Because it is used so intensively, several characteristics of accessions of big sagebrush grown in uniform gardens are being studied by Forest Service and Utah Division of Wildlife Resources scientists (Welch and McArthur 1979; Welch and others 1981; McArthur and Welch 1982). The principal aim is to develop superior cultivars of big sagebrush for use on mule deer winter ranges. Characteristics being studied under winter conditions are: in vitro digestibility, crude protein content, monoterpenoid content, browsing preference, drought resistance, site adaptation, disease and insect resistance, seedling vigor, establishment methods, and annual growth rates or production. The last characteristic, growth rate, is the subject of this report.

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Bruce L. Welch is principal research plant physiologist, and E. Durant McArthur is supervisory research geneticist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT.

Other studies have demonstrated significant genetic growth rate differences among accessions and subspecies of big sagebrush growing in a uniform garden (Welch and McArthur 1979; McArthur and Welch 1982). The most productive accessions were of the subspecies tridentata (McArthur and Welch 1982). The apparent genetic growth rate superiority of the Dove Creek accessions (subspecies tridentata) was maintained on two other sites (McArthur and Welch 1982). Our purpose was to: (a) expand the knowledge base concerning the growth rates of 21 accessions of big sagebrush as influenced by site with age held constant, and (b) choose superior accessions for a breeding and selection program.

MATERIALS AND METHODS

Three outplanting sites were selected within the elevational range of most Utah mule deer winter ranges (1 370-2 140 m): near Springville, UT; 3 km east of Nephi, UT (Salt Creek Canyon); and 15 km west-southwest of Helper, UT (Gordon Creek Wildlife Management Area).

The Springville site at 1 402 m, is a basin big sagebrush habitat type. Soil is Pleasant Grove gravelly loam, 6 to 10 percent slope, with deep, well-drained, gravelly or cobbly soils on alluvial fans. Weathered limestone is the parent material. Soil permeability is moderately rapid. Roots can penetrate to a depth of 1.5 m or more. About 9 cm of available water is held by this soil to a depth of 1.5 cm. Soil pH ranges from 7.4 to 7.9. Average annual precipitation is 35 to 45 cm. The mean annual temperature is 8.9 to 11.1°C, and the frost-free period is 150 to 170 days (Swenson and others 1972).

The Salt Creek Canyon site (1 676 m) is a basin big sagebrush habitat type. Soil is a Rofiss gravelly clay loam, 4 to 15 percent slope. It is a deep, well-drained alluvial soil. Parent material is Arpien shale. Soil permeability is moderately slow. Effective rooting depth is 1.5 m or more. Soil pH ranges from 8.2 to 8.6. Average annual precipitation is 30 to 35 cm. The mean annual temperature is 7.2 to 8.3°C, and the frost-free period is 100 to 120 days (Soil Conservation Service 1981).

The Gordon Creek Wildlife Management Area, at 2 130 m, is a Wyoming big sagebrush habitat type. Soil is of the Atrac series (Atrac very fine sandy loam, 1 to 6 percent slopes). This series consists of deep, well-drained soils. Parent material is sandstone. Effective rooting depth is 1.5 m or

more. Soil pH ranges from 6.6 to 8.0. Average annual precipitation is 30.5 to 35.6 cm. The mean annual temperature is 7.2 to 8.3°C, and the frost-free period is 100 to 120 days (Soil Conservation Service 1981).

At each site, the vegetation was killed by disking. Subsequent weeds were removed by hand and mechanical means. Deer-proof fences were built around each site. Each site was planted (spring 1978) with containerized stock of 21 accessions of big sagebrush. Table 1 lists the accession collection sites. Each accession was represented by 10 plants and each plant was an experimental unit within the accession. The resulting 210 plants were placed at random on a 3- by 3-m grid for each site.

Table 1.--Collection sites for 21 accessions of big sagebrush used to determine the influence of site on growth rates

Subspecies	Accessions	County and State	Elevation
			(m)
vaseyana	Colton	Utah, UT	2260
	Sardine Canyon	Cache, UT	1800
	Benmore	Tooele, UT	1900
	Petty Bishop's Log	Sanpete, UT	2380
	Durkee Springs	Sevier, UT	2270
	Salina Canyon	Sevier, UT	2130
	Clear Creek Canyon	Sevier, UT	2130
	Pinto Canyon	Washington, UT	1850
	Indian Peaks	Beaver, UT	2140
	Hobble Creek	Utah, UT	1500
tridentata	Clear Creek Canyon	Sevier, UT	1720
	Big Brush Creek	Uintah, UT	1830
	Loa	Wayne, UT	2140
	Evanston	Uinta, WY	2020
	Wingate Mesa	San Juan, UT	2060
	Dog Valley	Juab, UT	1700
wyomingensis	Evanston	Uinta, WY	2130
	Kaibab	Coconino, AZ	2340
	Trough Springs	Humboldt, NV	1400
	Milford	Beaver, UT	1540

Growth rates were determined by measuring the annual length of 15 leaders per plant. Leader lengths were measured from the terminal leaf bud scars to the tip of the current terminal leaves. Leaders were selected at random over the entire crown of the plant. The 15 measurements were pooled together to calculate a plant mean. Measurements were taken during mid-November in 1979, 1980, 1981, and 1982. For the first year (1978) plant height was considered to be the height of the transplanted seedling.

The three subspecies of big sagebrush, Artemisia tridentata ssp. tridentata, ssp. vaseyana, and ssp. wyomingensis, were represented in this study. Of the 21 accessions, 10 were vaseyana, seven were tridentata, and four were wyomingensis. This gave the capability of testing for subspecies effects on growth rates.

Two three-way analyses of variance ($P < 0.05$) were performed on the data collected. Main effects for the first were sites, year, and accessions. For the second, the main effects were sites, year, and subspecies. Newman-Keuls multiple range test ($P < 0.05$) was used to compare treatment means.

RESULTS AND DISCUSSION

The overall mean big sagebrush annual leader length for all years, sites, and accessions was 22.9 cm. The two three-way analyses of variance detected effects due to all variables--year, site, subspecies, and accession.

The mean annual leader length for 1978 (24.1 cm) was significantly greater than for 1980 and 1981 (table 2). Annual leader lengths for 1979 and 1982 were not significantly less than 1978.

The Gordon Creek site produced smaller annual leader length (22.0 cm) than the Springville and Salt Creek sites (table 3).

Subspecies wyomingensis (17.3 cm) produced less leader length than subspecies vaseyana and tridentata (table 4). Subspecies vaseyana (20.4 cm) produced less leader length than subspecies tridentata.

Table 2.--Mean annual leader length of 210 big sagebrush plants grown for 5 years at three sites. Data are expressed as centimeters of current year's growth

	Years				
	1978	1979	1980	1981	1982
Length (cm)	24.1^{c*}	22.9^{abc}	21.5^{a}	22.5^{ab}	23.7^{bc}

*Means sharing the same superscript are not significantly different ($P < 0.05$).

Table 3.--Mean annual leader lengths of 210 big sagebrush plants grown for 5 years at three sites. Data are expressed as centimeters of current year's growth

	Site		
	Gordon Creek	Springville	Salt Creek
Length (cm)	22.0^{a*}	23.0^{b}	23.8^{b}

*Means sharing the same superscript are not significantly different ($P < 0.05$).

Table 4.--Subspecies mean annual leader lengths of big sagebrush plants grown for 5 years at three sites. Data are expressed as centimeters of current year's growth

	Subspecies		
	wyomingensis	vaseyana	tridentata
Length (cm)	17.3^{a*}	20.4^{b}	29.6^{c}
Number of plants per subspecies	120	300	210

*Means sharing the same superscript are not significantly different ($P < 0.05$).

The Dove Creek accession (41.4 cm) produced more annual leader length than the other accessions. Dove Creek represents subspecies tridentata (table 5). Other subspecies tridentata accessions with significantly longer leader lengths than vaseyana and wyomingensis accessions were Loa, Dog Valley, Evanston, and Clear Creek Canyon. Pinto Canyon (23.2 cm), Hobble Creek (23.1 cm), Salina Canyon (23.0 cm), and Indian Peaks (22.4 cm) were the fastest growing accessions of subspecies vaseyana.

Also, the three-way analyses of variance detected significant two-way interactions between site:accession and year:accession. Data shown in tables 6 and 7 explain the reason for the interactions. Across sites (table 6), some shifting in the ranking of accessions occurred.

Table 5.--Mean leader lengths of 21 accessions of big sagebrush grown on three sites for 5 years (10 plants per accession per site). Data are expressed as centimeters of current year's growth

Accession	Length (cm)
Petty Bishop's Log (v)*	15.3^{a**}
Trough Creek (w)	15.5^{a}
Evanston (w)	15.8^{a}
Big Brush Spring (t)	16.7^{ab}
Colton (v)	17.2^{ab}
Milford (w)	17.2^{ab}
Benmore (v)	18.8^{bc}
Clear Creek Canyon (v)	20.1^{cd}
Sardine Canyon (v)	20.2^{cd}
Durkee Springs (v)	20.6^{cde}
Kaibab (w)	20.7^{cde}
Wingate Mesa (t)	20.9^{cde}
Indian Peaks (v)	22.4^{def}
Salina Canyon (v)	23.0^{ef}
Hobble Creek (v)	23.1^{ef}
Pinto Canyon (v)	23.2^{f}
Clear Creek Canyon (t)	30.8^{g}
Evanston (t)	30.9^{g}
Dog Valley (t)	33.0^{h}
Loa (t)	33.1^{h}
Dove Creek (t)	41.4^{i}

* v = Artemisia tridentata ssp. vaseyana, w = ssp. wyomingensis, t = ssp. tridentata.

** Means sharing the same superscript are not significantly different ($P < 0.05$).

This shifting also occurred across years (table 7). The shifting caused the interactions to be statistically significant. However, the Dove Creek accession maintained its genetically superior growth rate on all three sites and across all 5 years (tables 6 and 7). This strengthens our justification for including the Dove Creek accession in our selection and breeding program (Welch and McArthur 1979; McArthur and Welch 1983).

The Hobble Creek accession maintained its ranking among the fastest growing vaseyana on all sites and for the first 3 years (tables 6 and 7. Our interest in the Hobble Creek accession stems from its high browse preference ranking (Welch and others 1981).

This study, along with others demonstrates that growth rate differences among subspecies and accessions of big sagebrush reflect genetic influences (Welch and McArthur 1979; Barker 1981; McArthur and Welch 1982). The plants maintain growth pattern differences in native stands as well as in uniform gardens.

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Table 6.--Ranking (out of 21) and mean annual leader growth of six accessions of big sagebrush grown on three sites. Data represent a 5-year average. Data are expressed as centimeters of current year's growth

Site	Accessions											
	Dove Creek		Hobble Creek		Pinto Canyon		Salina Canyon		Petty Bishop's Log		Trough Creek	
	R*	L**	R	L	R	L	R	L	R	L	R	L
Gordon Creek	1	40.4	6	23.0	7	22.8	9	20.4	16	16.4	21	14.5
Springville	1	44.6	7	23.6	8	22.9	6	24.9	21	13.0	18	16.5
Salt Creek	1	39.3	9	22.6	6	23.9	7	23.9	20	16.3	21	15.3

*Ranking of 21 accessions.
**Mean accessional annual leader length for 5 years.

Table 7.--Ranking and mean annual leader growth of six accessions of big sagebrush grown on three sites. Data represent a three-site average. Data are expressed as centimeters of current year's growth

Year	Accessions											
	Dove Creek		Hobble Creek		Pinto Canyon		Salina Canyon		Petty Bishop's Log		Trough Creek	
	R*	L**	R	L	R	L	R	L	R	L	R	L
1978	1	41.3	7	27.5	8	25.8	6	27.6	15	19.7	19	14.1
1979	1	43.7	6	24.3	7	23.3	8	23.2	19	15.2	20	14.0
1980	1	40.2	6	22.2	8	20.7	9	20.4	21	14.1	20	14.6
1981	1	38.4	10	21.5	6	22.1	8	22.0	21	14.2	20	16.9
1982	1	43.7	12	19.6	6	24.3	9	21.8	21	12.9	17	18.2

*Ranking out of 21 accessions.
**Mean accessional annual leader length for three sites.

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GROWTH AND INTERNAL WATER STATUS OF THREE SUBSPECIES OF ARTEMISIA TRIDENTATA

Richard F. Miller, Paul S. Doescher, Tony Svejcar and Marshall R. Haferkamp

ABSTRACT: Plant growth, leaf senescence, plant water potential, and soil water were measured for three subspecies of Artemisia tridentata. Plant water potentials for the two subspecies growing on the more mesic sites proved to be more responsive to changes in climate. Persistent leaves remained on the plants for one winter and two growing seasons.

INTRODUCTION

Artemisia tridentata dominates 90 million acres (36.5 million ha) in the Western United States, constituting the most abundant and widespread of the woody species characteristic of the extensive sagebrush/grass region. Three taxa of A. tridentata have been reported by Beetle (1960), Beetle and Young (1965), Winward (1970), and Winward and Tisdale (1977). They vary morphologically and phenologically, and have distinct ecologic and hydrologic requirements.

Taxa studied were Artemisia tridentata subspecies tridentata (ARTRT), wyomingensis (ARTRW) and vaseyana (ARTRV). A fourth subspecies spiciformis is described in this proceedings (see McArthur and Goodrich) but was not a part of our study. The objectives of this study were to record plant growth, leaf abscission, and seasonal and diurnal fluctuations in water potential of these subspecies and to relate these factors to air temperature and soil water.

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Richard F. Miller is Range Scientist, Eastern Oregon Agricultural Research Center, Oregon State University, Burns, OR; Paul S. Doescher is Assistant Professor, Department of Rangeland Resources, Oregon State University, Corvallis, OR; Tony Svejcar is Research Agronomist, U.S. Department of Agriculture, Agricultural Research Service, El Reno, OK; Marshall R. Haferkamp is Range Scientist, U.S. Department of Agriculture, Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR.

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STUDY AREA

Work was conducted on the Squaw Butte Experimental Range, situated in southeastern Oregon on the northern fringe of the Great Basin. The study was conducted from mid-May 1981 through November 1982.

The 40-year mean precipitation on the area is 11.8 inches (30 cm). The 1980-81 and 1981-82 crop year (September 1-August 30) precipitation levels were 83 and 117 percent of the mean, respectively.

The three sites selected for study were representative of the following three habitat types (Doescher 1983): Artemisia tridentata ssp. wyomingensis-Stipa thurberiana, A. tridentata ssp. tridentata/Elymus cinereus, and A. tridentata ssp. vaseyana/Festuca idahoensis. Sites were all within 2 miles (3.2 km) of each other (table 1). Macroclimate and soils, except for soil depth and rock content, were similar among all three sites.

METHODS

Phenology for each subspecies was recorded once every 2 weeks from mid-May through November 1981 and March through November 1982. In 1982, stem elongation and leaf fall were also measured. Twenty stems were permanently marked on each site prior to plant growth, and length was measured weekly from March through November. To measure persistence and timing of winter-persistent leaf fall, approximately 300 overwintering leaves on each site were marked with ink in March 1982 prior to new leaf development. To evaluate the proportion of leaf biomass abscissing in August, cheesecloth leaf traps were placed over 10 individual branches just prior to initial leaf fall (August 1) on each site. Leaves collected in the traps were removed on August 16, dried for 48 hours at 140 °F (60 °C) and weighed. Leaves remaining on the stem were also removed at this time, dried, and weighed.

Table 1.--Vegetation and soil characteristics of the study area

Plant communities	Elevation	Shrub cover	Herbaceous biomass	Soil classification	Soil texture of surface horizon	Soil depth
	Feet	Percent	Lbs/acre			Inches
ARTRV/FEID	5,082	15	613	Typic Haploxeroll	Loam	60
ARTRT/ELCI	4,498	20	555	Xerollic Durorthid	Sandy Loam	47
ARTRW/STTH	4,498	15	545	Xerollic Durorthid	Sandy Loam	18.5

Internal stem xylem water potential (ψw) of the three subspecies was measured during the 1981 and 1982 growing seasons by means of a pressure bomb (Scholander and others 1965; Waring and Clary 1967). Units for ψw are expressed in Megapascals (MPa). Diurnal measurements were taken at 5 a.m., 8 a.m., 11 a.m., 2 p.m., and 5 p.m. at 2-week intervals from June through July and monthly from August through October in 1981. In 1982, measurements were taken at 2-week intervals from May through July and then monthly to November. Diurnal patterns reported in the text were selected to characterize different temperature and soil water conditions. All other diurnals recorded followed a similar pattern to those selected. Seasonal ψw measurements, expressed over time are for both predawn (5:00 a.m.) and midday (2:00 p.m.) measurements. Plant water potentials are generally highest (plant least stressed) during the predawn hours and lowest during midday when evaporative potentials are generally the highest. Foliar samples for ψw readings were enclosed in a moist plastic bag, placed on ice for all three sites and then measured in a pressure bomb within 0.5 hour of collection. Two readings on three shrubs for each subspecies were recorded for each determination. Each pair of readings was treated as a subsample in the analysis of variance. Mean squares for subsamples and sample units (shrubs) were pooled so sample size for ψw measurements was 6 rather than 3 for each subspecies (Steel and Torrie 1960). Mean ψw for similar dates between years, and predawn and midday ψw were compared with the Student t test ($P<0.05$)

Soil moisture was measured gravimetrically at two depths (1-12 inches [2.5-30 cm] and 12-18.5 inches [30-47 cm]) in the ARTRW habitat type, and three depths (1-12 inches [2.5-30 cm], 12-24 inches [30-60 cm], and 24-48+ inches [60-120+ cm]) in the ARTRT and ARTRV habitat types. Soil moisture was sampled in conjunction with ψw measurements. Soil moisture release curves were used to convert percent soil moisture to soil water potential for each site.

Temperature and precipitation data were collected by means of standard Weather Bureau instruments located within 2 miles (3.2 km) of all three study sites. Air temperatures were recorded on the individual sites, but did not vary more than 3.6 °F (2 °C) from the Squaw Butte weather station, or site to site.

RESULTS

Climate 1981 and 1982

The 1981 growing season was drier and warmer than the 1982 growing season (fig. 1). During the 1982 crop year, 4 inches (10.2 cm) more precipitation was received than in 1981, allowing greater recharge of soil water at the lower depths. Although June and July temperatures were similar in both years, August and September temperatures in 1981 were warmer. In 1981 and 1982, respectively, degree days (based on 65 °F [18.3 °C]) totaled 190 and 117 in August and 68 and 27 in September (National Oceanic and Atmospheric Administration 1981, 1982).

The relatively high soil moisture during early June 1981 (fig. 2 a, b, and c) can be accounted for by above-normal spring precipitation which resulted in a moist upper 12 inches (30 cm) of soil. However, the persistence of relatively high soil water later in the 1982 growing season, also shown in the figures, was due to more soil water being available at depths below 12 inches (30 cm) than in 1981.

Phenology and Growth

Sequence of phenological development was similar for all three subspecies (fig. 2). Timing of leaf and stem development was similar for ARTRW and ARTRT, while ARTRV lagged behind by 2 weeks. ARTRV caught up with the other two subspecies by late June. ARTRW slowed stem elongation earlier than the other two subspecies (fig. 3). The most rapid rate of vegetative stem elongation measured was 0.04 inches/day (1.0 mm) for both ARTRW and ARTRT, and 0.07 inches/day (1.8 mm) for ARTRV. Reproductive stems were differentiated by mid-June for all

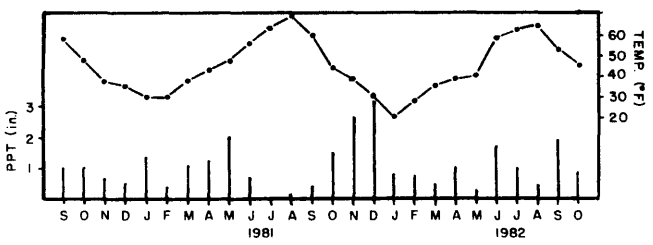


Figure 1.--Seasonal precipitation and maximum and minimum air temperatures for the Squaw Butte Experimental Range in 1981 and 1982.

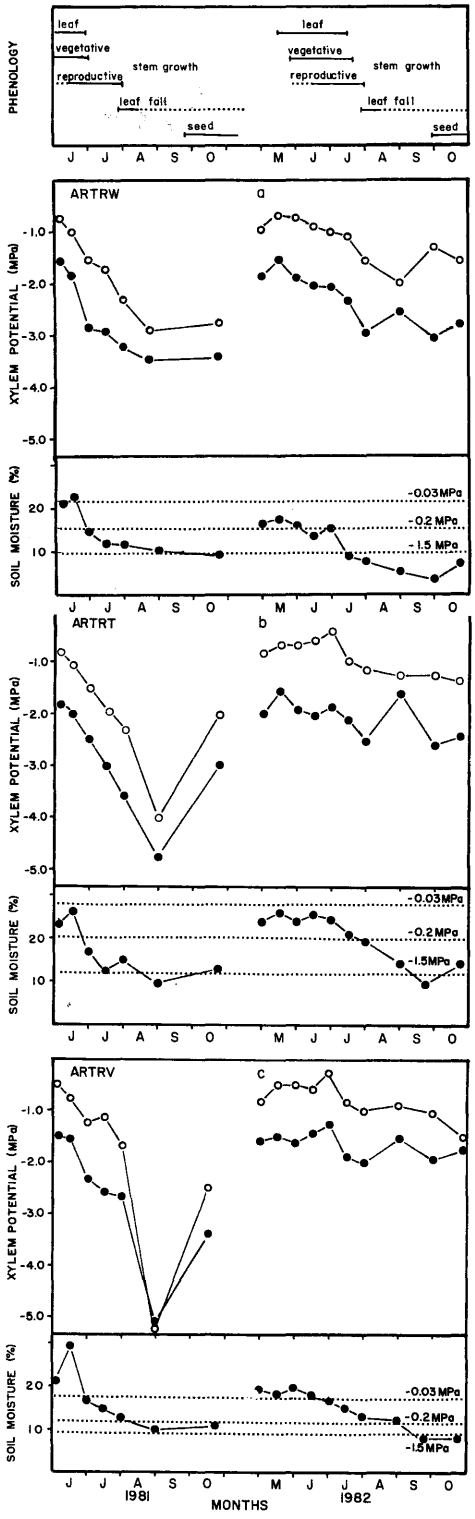


Figure 2.--Phenology and stem xylem water potential (MPa) and soil moisture in the wettest horizon on the site for two growing seasons for a) Wyoming big sagebrush (ARTRW), b) basin big sagebrush (ARTRT) and c) mountain big sagebrush (ARTRV). Plant phenology (----) for reproductive stems during the period they could not be separated from vegetative stems and leaf fall was minimal, restricted to ephemeral leaves.

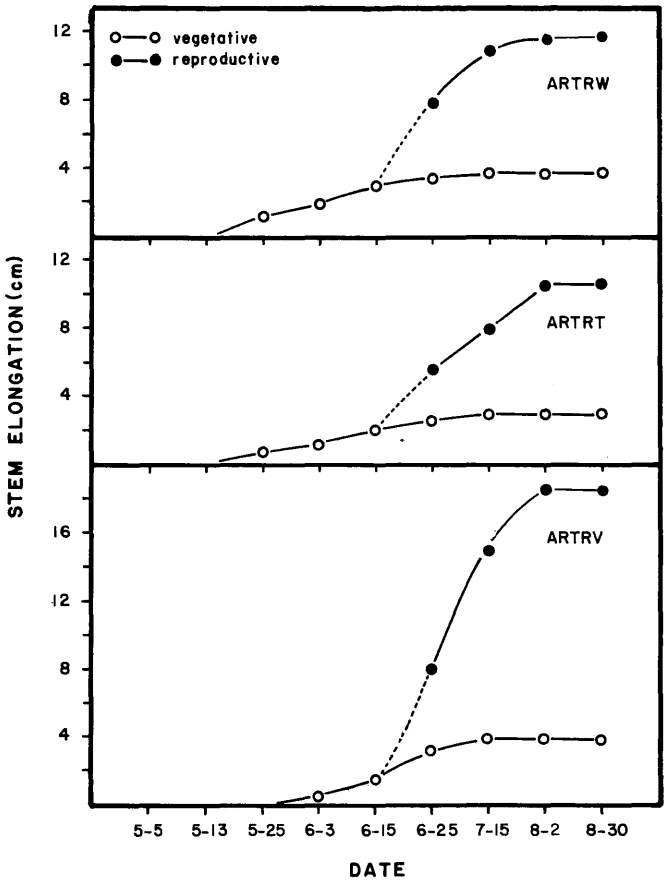


Figure 3.--Reproductive and vegetative stem elongation for the three subspecies during 1982.

three subspecies. At this time, vegetative stem elongation slowed down and terminated while reproductive stems rapidly grew for approximately 4 more weeks at maximum rates of 0.17, 0.15, and 0.25 inches/day (4.3, 3.8, and 6.4 mm) for ARTRW, ARTRT, and ARTRV, respectively. Although ARTRW reproductive stems grew at a faster rate than ARTRT, duration of rapid elongation was shorter. Termination of vegetative stem and leaf growth coincided with soil moisture tensions below -0.20 MPa.

Less than 2 percent of the marked winter persistent leaves fell from the plants between March and July on all three subspecies. During August, hot temperatures, low soil water, and low internal plant water potentials resulted in loss of 53 percent of the total leaf biomass on all three subspecies. Leaf senescence began in late July for ARTRW and ARTRT, with leaf abscission beginning by the first of August. The pattern was similar for ARTRV, however, the events occurred 10 days later. The entire crop of 1981-82 winter-persistent leaves fell in August 1982. The majority of ephemeral leaves also fell during this time. Ephemeral leaves continued to fall until early November, but at a slower rate. By late October, reproductive stems were leafless and drying on ARTRW and ARTRT, and seeds were in the hard dough stage. In contrast leaves on ARTRV reproductive stalks were falling, and seeds were in the dough stage.

Seasonal Water Potential

Predawn ψw during the two growing seasons ranged from -0.70 to -2.80, -0.45 to -3.90, and -0.34 to -5.80 MPa for ARTRW, ARTRT, and ARTRV, respectively (fig. 2a, b, and c). Midday ψw ranged from -1.45 to -3.44, -1.59 to -4.74, and -1.33 to -5.55 MPa for ARTRW, ARTRT, and ARTRV, respectively. Sharp declines in ψw occurred in both years for all three subspecies when soil water dropped below -0.20 MPa. Predawn ψw from July through October for ARTRW and mid-June through October for ARTRT and ARTRV were significantly less negative ($P<0.05$) in 1982 than 1981. The largest differences (significant at $P<0.05$) in ψw between years existed in ARTRT and ARTRV during late August and early September.

Diurnal Water Potential

Diurnal ψw patterns for the three subspecies of ARTR are represented in figures 4 and 5. The greatest differences (significant at $P<0.05$) between predawn and midday ψw occurred when soil moisture was readily available and midday temperatures were warm. When soil water was limited, as on August 31, 1981, little diurnal change occurred in ψw. The relationship of ψw between subspecies in late August was reversed between years. In 1981, ARTRW ψw were higher (least stressed) than ARTRT and ARTRV growing on the more mesic sites. In 1982, these results were reversed with ARTRV having the highest ψw in August. The data are interpreted to show: (1) a subspecies growing on a more mesic site may or may not have a lower water stress value, based on ψw, than subspecies growing on drier sites, and (2) the relative difference in ψw between subspecies can greatly change from year to year.

DISCUSSION

Phenology

The entire leaf crop which persisted through the winter was shed in late July and early August. Although leaves were not marked in 1983 and 1984, biweekly observations throughout the spring and summer, and monthly throughout the fall and winter on the Squaw Butte Experimental Range showed this pattern to be consistent. Spot checks throughout eastern Oregon also showed the leaf fall pattern to be similar. These data are interpreted to show winter-persistent leaves remain on the plant for two growing seasons and one winter. Abscission of winter-persistent leaves did not occur during the rapid growth phase of the plant. When soil water levels dropped below -0.20 MPa in the wettest horizon, vegetative stem elongation and leaf development terminated, and winter-persistent leaves began to senesce. These results are in contrast to Diettert (1938) and Branson and others (1976) who report that leaves persisting through the winter were shed in the spring as new leaves developed. Differences in leaf fall among these studies may be due to differences in location of plants studied. In eastern Oregon, springs

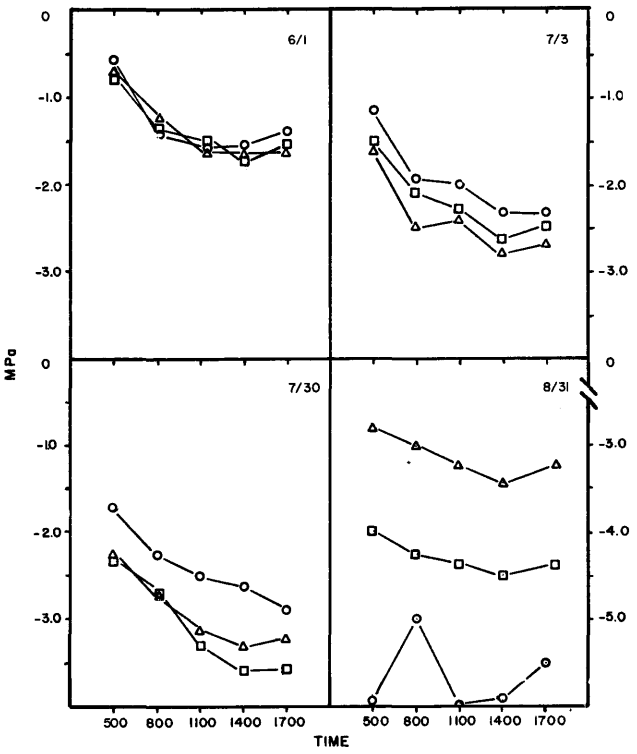


Figure 4.--Diurnal cycles of stem xylem water potentials in 1981 for Artemisia tridentata ssp. wyomingensis (△——△), tridentata (□——□) and vaseyana (○——○). Each point is a mean of six observations per time period.

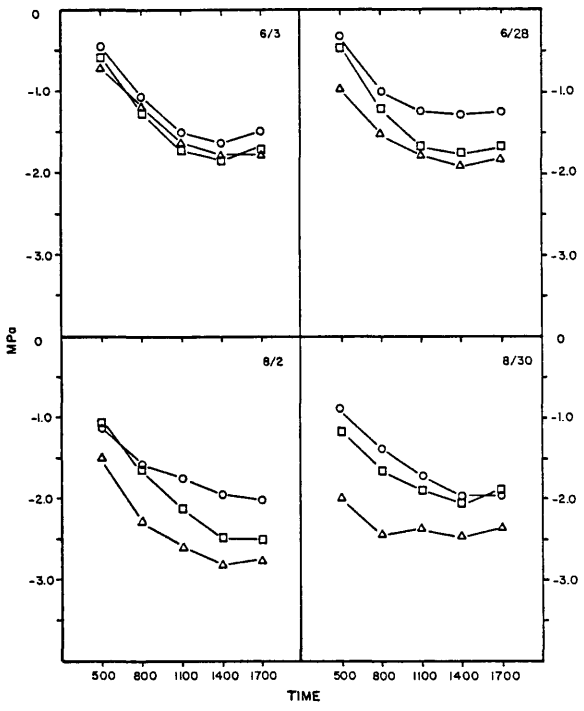


Figure 5.--Diurnal cycles of stem xylem water potentials in 1982 for Artemisia tridentata ssp. wyomingensis (△——△), tridentata (□——□), and vaseyana (○——○). Each point is a mean of six observations per time period.

are typically wet and summers dry. In Colorado where the other two studies were conducted, springs are relatively drier than summers. In addition we found 53 percent of the leaf biomass falling in early August (last year's perennials plus current year's ephemerals) from the plant, whereas Branson and others (1976) estimated leaf fall as 85 percent of the total number of marked leaves. Because ephemeral leaves are initiated earlier than perennial leaves, and if the previous year's winter-persistent leaves are still present, the period when leaf marking is done will influence the proportion of leaf types in the sample. The number of previous and current year's perennial leaves and the ephemeral leaves marked will determine the percent of marked leaves remaining on the plant.

Plant Water Potentials

Maximum and minimum ψw were consistent with other work on A. tridentata (Barker and McKell 1983; Branson and Shown 1975; Campbell and Harris 1977; DePuit and Caldwell 1973; Dina and others 1973; Everett and others 1977). DePuit and Caldwell (1973) suggested differences between minimum ψw (-2.1 MPa) in their study and Dina's (1970) results (-6.4 MPa) may have been due to climatic conditions and location. In our study, similar differences occurred between ARTRT and ARTRV in 1981 and 1982, but on plants at the same location. Minimum predawn ψw occurring in 1981 was -3.8 MPa for ARTRT and -5.8 MPa for ARTRV. In contrast, -1.3 MPa for ARTRT and -1.6 MPa for ARTRV occurred in 1982. Differences in minimum ψw between years in this study may be attributed to more precipitation in 1982, causing greater soil moisture recharge at the deeper depths, and cooler temperatures in August and September for 1982. This study would support the hypothesis that climatic conditions have a major influence on minimum ψw occurring during the growing season.

Although ARTRT is thought to exist on a more mesic site than ARTRW, ψw in 1981 did not reflect this. In June, July, and August, ARTRT ψw were either similar or more negative than ARTRW values. This may have been caused by the existence of a larger plant evaporative surface in the ARTRT community, which contained a taller canopy and greater shrub canopy cover than ARTRW. In a year of poor soil water recharge at deeper soil depths and high evaporative demands (1981), ARTRT was more water stressed based on the ψw than ARTRW. When adequate water was available (1982), then ARTRT was the least water stressed of the two. Although ARTRV ψw, in comparison to the other two subspecies, was consistent with growing on a more mesic site early in the growing season, it had the lowest ψw in late August 1981. Again, this may be attributed to lack of soil water and a high plant evaporative surface (due to higher herbaceous productivity measured by Doescher, 1983) as compared to ARTRW. Miller and Poole (1979) found a similar pattern on the more mesic communities in southern California shrublands, where both leaf area and internal plant water stress were greater than on the drier sites.

Differences in ψw for ARTRW were not nearly as great between years as they were for ARTRT and ARTRV (fig. 2 a, b, and c). ARTRW ψw did not seem to be as responsive to differences in climate between years as ψw of the other two subspecies. This may be due to several reasons:

1. Sites with shallower soils have more limited storage for above-average precipitation, as compared to sites with deeper soils.
2. More xeric communities have less evaporative surface (lower leaf area) and/or
3. subspecies may differ morphologically and/or physiologically.

CONCLUSIONS

Although big sagebrush is well adapted to arid environments, active vegetative growth occurred only at soil water tensions at or above -0.2 MPa. Soil water tensions between -0.03 and -0.2 MPa represent approximately 30 percent of the total water found in the soil profile. Once soil water decreased below -0.2 MPa, plant water potentials sharply decreased, active vegetative growth was terminated, and leaf abscission initiated. In August, plants reduced leaf biomass by over 1/2. Caldwell (1979), in a review of sagebrush physiology, reported photosynthesis is inhibited by moderate plant water stress. He speculated that success of the plant must depend on the display of numerous leaves during the cool season of the year when moisture stress had not yet developed. This would point out the importance of maintaining winter-persistent leaves throughout the spring.

Just because plants grow on a relatively more mesic site does not mean soil moisture will be higher or internal plant water stress less. These communities have developed strategies to exploit the larger available water resource by developing more extensive root systems and larger evaporative surfaces than more xeric communities. In years when precipitation doesn't fully recharge the soil, the more mesic communities may be subject to greater plant water stress.

Timing of abcission of the perennial leaves needs to be more thoroughly studied throughout the range of A. tridentata. In eastern Oregon, persistent leaves overwintered and fell from plants during the midsummer drought period of the following growing season.

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SEED PAPPUS AND PLACEMENT INFLUENCES ON WHITE RUBBER RABBITBRUSH ESTABLISHMENT

R. Stevens, K. R. Jorgensen, J. N. Davis, and S. B. Monsen

ABSTRACT: Using present seed cleaning and seeding techniques, seedling establishment of white rubber rabbitbrush from direct seeding has generally been poor. To facilitate handling and seeding, seed pappus is removed. Seeds are generally broadcast seeded and deposited in or on the soil in no particular position. Results indicate removal of seed pappus reduces seedling establishment. Greatest number of seedlings established when seeds were placed upright in the soil. Seeding techniques and equipment need to be developed that will assure proper seed placement and maximum seedling establishment.

INTRODUCTION

White rubber rabbitbrush (Chrysothamnus nauseosus (Pallas) Britt. ssp. albicaulis [Nutt.] Rydb.) is looked upon as a useful range shrub for livestock and wildlife (Hanks and others 1975; McArthur and others 1978, 1979; Wasser 1982) and a useful species for stabilization (USDA 1974; McArthur and others 1974, 1978; Thornburg 1982).

White rubber rabbitbrush normally produces seed annually. Seedlings naturally establish on rangelands and reclamation sites, especially disturbed areas where competition is lacking or is slight (McArthur and others 1979). Thousands of seedlings can be found in bare and disturbed soils, under and next to mature plants. Most do not, however, develop beyond the seedling stage. Seedlings are not very competitive and may be suppressed by herbaceous species. In some cases, grass production can be enhanced in the presence of this overstory shrub (Plummer 1959; Frischknecht 1963; Plummer and others 1968).

With present seed cleaning and seeding techniques, establishment from direct seeding has been variable, but generally very poor.

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Richard Stevens, Kent R. Jorgensen, and James N. Davis are Wildlife Biologists, Utah Division of Wildlife Resources, stationed at Ephraim and Provo, UT. Stephen B. Monsen is Botanist/Biologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT.

For example, Van Epps and Stevens (1984) planted 400,000 (estimated, number of seeds per gram) cleaned white rabbitbrush seeds (83 percent germination), each in three seeding treatments: (1) on top of undisturbed soil, (2) on top of undisturbed soil followed by disturbance, and (3) on top of disturbed soil followed by disturbance. Of the approximately 1.2 million seeds planted, less than 0.1 percent produced seedlings. Generally, with rabbitbrush, there is a great difference between the seedling potential and the actual number of seedlings established. King (1966) reported similar results with Taraxacum. Only 50-125 seedlings established for 10,000-20,000 seeds planted.

The fruit of rabbitbrush is technically a spindle-shaped achene (USDA 1974). For the purpose of discussion, we will consider an achene a seed. The terminal, or crown end of each seed bears a ring or crown of hairs, known as the pappus. The basal end includes the basal attachment scar.

Seed is generally hand-collected. To reduce volume and to facilitate handling and seeding, seed is run through a hammermill or debearder and screened and fanned to remove the pappus (USDA 1974; Plummer and Jorgensen 1978). Seed cleaned in this manner is 15 to 20 percent pure. With additional cleaning, seed can be cleaned up to 95 percent pure. Seed with less than 70 percent purity can only be seeded aerially, by hand, or through a thimble seeder. Seed over 70 percent pure can be drilled.

Two major differences between naturally seeded and artificially planted seed are the absence or presence of the seed pappus and subsequent placement of the seed in the soil. The pappus aids in wind dispersal of the seed (McArthur and others 1979). The presence of the pappus also aids in positioning a seed with the basal end down in contact with the soil. Seed can be deposited in soil cracks, cavities, or left lying on top of the soil. To maximize germination, the area of the seed that is the most efficient in absorbing water should be in contact with the growth medium. Sheldon (1977) reported that Taraxacum officinale is very sensitive to seed position. The highest germination occurred in seed having the basal attachment scar in direct contact with the soil. He further reported that the pappus also played an important role in seed placement and germination of Leontodon autumnalis, Senecio

viscosus, S. jacobaea, and Sonchus oleraceus. The awn, which is a seed appendage, like the pappus, of Avena fatua (Thurston 1960) orients and helps bury the seed. The removal of the awn of these seeds substantially reduced germination.

The pappus can act as an anchor to prevent seed movement before and during germination and establishment of surface-seeded species. Anchoring the seed to the growth medium has been reported to be very important in seedling establishment of winterfat (Booth and Schuman 1983). Once the radicle emerges it has to penetrate the soil. If the seed is not anchored, it can and will move along the soil surface with little or no radical penetration. This can result in rapid dehydration of the radicle and/or seedling (Sheldon 1977). There is also a possibility that the pappus may absorb and hold moisture, which may assist germination. It is not known how the pappus of white rubber rabbitbrush responds to moisture. Sheldon (1977) reported three types of pappus response to moisture: remaining open, closing and opening, and collapsing.

When broadcast or drilled, white rubber rabbitbrush seed with pappus removed can end up in or on the soil in any number of positions (upright, upside down, horizontal, buried at any depth, or on the surface). Lack of seeding success could be influenced by seed cleaning (removing pappus) and seed placement. A greenhouse study was carried out to determine what effect these two factors have upon seedling establishment.

METHODS

Seed was collected in Salt Lake County, UT, in November 1983. Plump, full seeds were selected and divided into two lots. Using hand tweezers the pappus was removed from all seed (cleaned seed) in one lot (A). Care was taken to ensure that seeds were not damaged. The pappus was left on seeds (uncleaned) in the second lot (B).

Germination Study

Germination tests were conducted on four samples of 100 seed for lots A and B. Seeds were placed between moist paper and put in a refrigerator at 34-38 ^{o}F (1.1-3.3 ^{o}C). Germination counts were made every other day for 60 days. Germination was recorded when the radicle length reached 5 mm.

Emergence Study

Seed (8 per block) were planted in 12 treatments in a completely randomized block design. There were six treatments for each of lots A and B, with four replications per treatment, for a total of 32 seeds per treatment.

Planting treatments were: [1]Lot A cleaned seed (pappus removed): (1) seed vertical, crown up, half of seed out of soil (⊣); (2) seed vertical, crown up, seed crown 1-2 mm below soil surface (⊤); (3) seed vertical, basal end up, half of seed out of soil (⊣); (4) seed vertical basal end up, basal end 1-2 mm below soil surface (⊤); (5) seed horizontal and buried 1-2 mm below soil surface (⊤); (6) seed horizontal on soil surface, no covering (⊢). Lot B uncleaned seed (pappus on): (7) seed vertical, crown up, half of seed out of soil (⊣); (8) seed vertical, crown up, seed crown 1-2 mm below soil surface (⊤); (9) seed vertical, basal end up, half of seed out of soil (⊣); (10) seed vertical basal end up, basal end 1-2 mm below soil surface (⊤); (11) seed horizontal and buried 1-2 mm below soil surface (⊤); and (12) seed horizontal on soil surface, no covering (⊢). Seed were planted individually with tweezers in a 3:1 sand-perlite mix. Daily watering from below eliminated soil or seed movement. Emergence (appearance of colyedon above ground), growth, development, and establishment (production of first post-colyedon leaves) were recorded for 30 days following seeding.

Newman-Kuels' multiple means comparison test was used to determine differences between means.

RESULTS

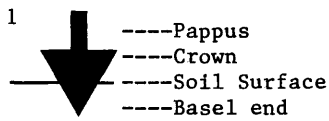
Germination

Removal of the seed pappus (cleaned seed) had no effect on germination of white rubber rabbitbrush seed. Mean percentage germination of cleaned seed was 91.1 and uncleaned seed 91.0.

Seed Cleaning Response

Significantly more seedlings from uncleaned seed than from cleaned seed were alive (with leaves) 30 days after seeding (table 1). Between cleaned and uncleaned seed there was no significant difference in the number of seeds that emerged over 30 days (table 2). However, a larger number of seedlings from cleaned seeds died or failed to develop post-cotyledon leaves (tables 1 and 3). Survival between emergence and 30 days was greater for uncleaned seed than cleaned seed (tables 1 and 2). Furthermore the greatest mortality occurred with cleaned seeds

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[1] 

that were seeded uncovered or partially covered as shown below as percent survival:

	Seed not covered or only partially covered	Seed covered
Seed with pappus	60	64
Seed without pappus	29	69

Clean seed planted on the surface or partially covered produced the greatest number of seedlings with exposed radicles. Most seedlings with bent or extended and exposed radicles died or failed to produce leaves.

Table 1.--Percentage of white rubber rabbitbrush seeds that produced live plants with at least two true leaves 30 days following seeding with various amounts of seed coverage for cleaned and uncleaned seed

Seed	Seed not covered or partially covered	Seed covered	Mean of noncovered, partially covered, and covered seed
pappus attached (uncleaned)	[1]45a	31a	38
pappus removed (cleaned)	20b	18b	19

[1]Numbers followed by the same letter are not significantly different at the 5 percent level.

Table 2.--Percentage emergence of cleaned and uncleaned white rubber rabbitbrush seed that were seeded with various amounts of covering

Seed	Seed not covered or partially covered	Seed covered	Mean of noncovered, partially covered, and covered seed
Uncleaned (pappus attached)	[1]75a	48b	61
Cleaned	70a	26b	42

[1]Numbers followed by same letter are not significantly at the 5 percent level.

Seed Placement

Seed placement had a significant effect on the number of live seedlings 30 days after seeding (tables 3A and 3B). Uncleaned seed planted upright with the crown up and basal attachment scar in contact with the soil produced the greatest number of seedlings (69 percent) (table 3A). There was no significant difference between the number of seedlings resulting from seed being covered or uncovered; however, the trend was for more seedlings from seed not covered or partially covered than from covered seed. Seedling success was significantly higher (table 3B) (41 percent success) from seeds planted upright (treatments 7, 8, 1, 2) with basal attachment scar in contact with the soil than from seeds planted horizontally (28 percent) (treatments 11, 12, 5, 6) where the basal attachment scar may have contacted the planting medium, or seeds planted upside down (17 percent) (treatments 9, 10, 4, 3) where the basal attachment scar had no soil contact (table 3B).

SUMMARY

Results from germination tests indicate the difference in seeding success was not influenced by germination, but rather by seed placement and positioning.

Uncleaned seed (pappus on) planted upright, and half buried produced the most seedlings (69 percent) of any treatment. Forty-one percent of the seeds planted upright produced seedlings with leaves, whereas only 28 percent of the seed planted horizontally and 17 percent of the seed planted upside down produced seedlings. Significantly more seedlings were produced (38 percent) from uncleaned seed than from cleaned seed (19 percent). Survival between emergence and 30 days was least (45 percent) for cleaned seed, especially those planted on the surface or partially buried (29 percent). Survival for uncleaned seed was 62 percent.

CONCLUSIONS

The pappus attached to white rubber rabbitbrush seed is generally removed to facilitate seed handling and planting. Cleaned seeds are often broadcast aerially and are thus deposited in or on the soil, in no particular position. Seedling establishment is generally very low.

Results from this study indicate that the presence or absence of the pappus does not affect laboratory germination, but does play an important role in seedling emergence and establishment. Greatest number of seedlings occurred when seeds were placed upright in or on the soil with the basal attachment scar in contact with the soil. Rabbitbrush seed are wind-dispersed and deposited; the seed pappus acts as a parachute and helps position the seed properly in the soil. The pappus can also act as an anchor, preventing movement of the seed during germination and radical penetration into the soil. Without the pappus, the seed can move along the soil surface or out of the soil exposing the radicle. Seedlings with bent and

Table 3.--Percentage of white rubber rabbitbrush seeds that produced live plants with at least two true leaves 30 days following seeding in 12 seeding treatments

A-Influenced by seed coverage

Seed not covered or partially covered		Seed covered	
Treatment	Percent	Treatment	Percent
[1]7-	[2]69a	11-	44ab
1-	44ab	8-	31bc
12-	38bc	5-	22bc
9-	9bc	2-	19bc
3-	9bc	10-	19bc
6-	6bc	4-	13bc

[1]See text footnote 1.
[2]Numbers followed by the same letter are not significantly different at the 5 percent level.

B-Influenced by seed positioning

Seed position	Percent
Seeded upright, treatments	
7- , 8- , 1- , 2-	[1]41a
Seeded horizontal, treatments	
11- , 12- , 5- , 6-	28b
Seeded upside down, treatments	
9- , 10- , 3- , 4-	17b

[1]Numbers followed by the same letter are not significantly different at 5 percent level.

exposed radicles generally do not produce healthy leaf-producing seedlings.

Uncleaned (pappus on) rabbitbrush seed is difficult to seed with most aerial or ground seeding equipment. If seeding success is to be improved, planting equipment and techniques need to be developed that will assure proper rabbitbrush seed placement.

ACKNOWLEDGMENT

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EMERGENCE, SEEDLING GROWTH, AND CRUDE TERPENOID CONCENTRATIONS IN A SAGEBRUSH GARDEN

Rick G. Kelsey

ABSTRACT: A sagebrush garden was established with seed collected from 16 populations of seven taxa in Montana. Emergence ranged from 0 to 80.5 percent. Relative seedling survival was near 74 percent or greater the first year and 90 percent or greater the second. Fertilizing the second season did not influence survival, but it doubled length, and doubled or tripled leaf biomass. Seedling crude terpenoid concentrations were lower than in parental plants and fertilizing did not affect accumulation of these compounds.

INTRODUCTION

Botanical and chemical characteristics of sagebrush indicate these shrubs have potential as a renewable source of high energy compounds and organic chemicals (Kelsey and others 1982; Kelsey, this proceedings). The epidermal surface of sagebrush leaves is covered with cuticular waxes and glandular trichomes containing monoterpenes and sesquiterpene lactones (Kelsey and Shafizadeh 1980). These hydrocarbons are readily extracted with solvents and can be removed without drying or grinding the tissue. The extract, referred to as crude terpenoids, can be converted to a high quality synthetic crude oil (biocrude) by hydrogenating (Kelsey, this proceedings).

For big sagebrush the greatest quantities of crude terpenoids have been observed in Artemisia tridentata ssp. tridentata, usually reaching 20 percent or greater of leaf dry weight, at peak concentrations in fall and winter (Kelsey and others 1982; Striby and others 1982; Personius and others unpublished data). This is also the fastest growing of the three common big sagebrush subspecies (McArthur and Welch 1982). Unlike traditional agricultural plants, species with the greatest potential for producing biocrude in arid and semiarid regions of the United States may have only low to moderate annual biomass yields (McLaughlin and others 1983).

In our studies, production of epidermal chemicals by sagebrush leaves has been shown to be independent of defoliation. In addition, partial defoliation did not adversely affect growth the following season, implying that plants could be harvested on an annual basis if clipping was not too severe (Kelsey, this proceedings). Cutting the entire crown is an alternative harvesting method that would kill the plants, except for Artemisia cana Pursh and A. tripartita Rydb. which root-sprout (Beetle 1960; McArthur and others 1979). Complete crown harvesting could be used on areas where shrub eradication was the desired objective, or where shrubs could be rapidly reestablished.

Sagebrush can be readily established by transplanting seedlings from nursery stock and native stands (Plummer and others 1968; 1970; Long, this proceedings). These shrubs are prolific seed producers (Harvey 1981), and under laboratory conditions, germination can exceed 80 percent (Sabo and others 1979; Stidham and others 1980; Harvey 1981). Field germination and emergence are frequently far less (Harvey 1981). Aside from germination data, very little information is available on the early growth stages of sagebrush seedlings, particularly in the field. The objective of this study was to plant a sagebrush garden from seed and measure emergence, growth, biomass productivity, and crude terpenoid concentrations of seedlings, and evaluate the results in terms of biocrude production.

MATERIALS AND METHODS

In October 1981, a garden site was selected in the Missoula valley near Fort Missoula on a Typic Cryoborol soil formed in alluvial material. Elevation was 960 m. Mean annual temperature is 6.2 °C (April-October 1982, 12.9 °C; 1983, 12.4 °C) and precipitation 32.6 cm (April-October 1982, 23.0 cm; 1983, 28.1 cm) (Cordell 1971; NOAA 1982, 1983). Native vegetation was scraped from an 18- by 18-m area and the soil rototilled. Sixteen 3- by 3-m plots were marked, each separated by a 1 m buffer zone on all sides. A single plot was prepared for each seed source. Flower stalks were collected in November from 16 populations of seven taxa in Montana: Artemisia tridentata Nutt. ssp. tridentata (Upper Red Rock Lake, Bannack, Perma); A.t. ssp. vaseyana (Rydb.) Beetle (Reynolds Pass, Sagecreek, Lavalle Creek); A.t. ssp. vaseyana var. spiciformis (Osterh.) Beetle (Upper Red Rock Lake); A.t. ssp. wyomingensis Beetle & Young (Bannack Flats, Ramsay, Miles City Livestock and Range Research Station); A. cana Pursh ssp. cana (Sappington, Miles City Livestock and Range Research Station); A.c. ssp. viscidula (Osterh.) Beetle (Sawpit

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Rick G. Kelsey is Research Associate Professor, Department of Chemistry, University of Montana, Missoula, MT.

Creek); A. tripartita Rydb. ssp. tripartita (Monida, Badger Pass, Ovando).

Also, in one population of each taxa, three parental seed source plants were tagged and leaves sampled. Samples were sealed in Ziploc plastic bags, transported on ice to the laboratory, and stored in a freezer. They were analyzed for crude terpenoid concentrations as described by Kelsey (this proceedings). Approximately one year later, at the end of the first growing season for garden seedlings, tagged big sagebrush plants (A.t. ssp. tridentata, Perma; A.t. ssp. wyomingensis, Ramsay; A.t. ssp. vaseyana, Lavalle Creek) were sampled again and analyzed for crude terpenoid concentrations.

Dry seeds were cleaned by screening and then blowing in a commercial seed cleaner. Seed numbers were estimated by weight after accurately counting the number of seeds in 5 to 10 small weighed subsamples from each population. To help visualize dispersal, seeds were mixed with sawdust in a hand-held seeder and sown onto bare ground in late February 1982. Garden plots were randomly assigned. Number of seeds sown per plot varied considerably, from as few as 97/m^2 to 6,995/m^2 (table 1).

Seedling density was estimated in June and October 1982. Twenty-four quadrats (8 per line) were randomly positioned on 3 parallel transect lines located 0.5, 1.5, and 2.5 m from the north edge of each plot. Quadrat size (table 1) was varied between plots to accommodate the different seedling densities. In October, seedlings were collected to measure length, biomass, and crude terpenoid concentrations. Individuals were gathered from a separate set of parallel transect lines each located 0.5, 1.5, and 2.5 m from the west edge of each plot. Nine quadrats, equal to the size used for seedling counts, were positioned at 30-cm intervals along each line. Seedlings closest to the line were clipped at ground level until a desired 10 g of fresh leaf tissue was collected from the whole plot. They were sealed in Ziploc plastic bags, transported on ice to the laboratory, and stored in the freezer.

Thirty of these seedlings were randomly selected for length measurements, from the clipped stem to the tip of the longest live green leaf, when the crown was tightly pressed against a rule. For the majority of seedlings, length measurement was a close approximate of height, but on a few plots some seedlings did not stand upright. A portion of their stem laid on the soil surface before bending up to support the crown. Each successive group of 10 measured seedlings were briefly rinsed in a beaker of water to remove soil particles adhering to the leaf surface. After patting dry, the 10 seedlings were placed into an aluminum pan to air-dry. Dried seedlings were separated into leaves and stems, ovendried at 100 °C overnight, desiccated 30 minutes and weighed. Seedlings not used for length and biomass measurements remained frozen and were analyzed for crude terpenoid concentrations.

Table 1.--Emergence and relative seedling survival, for single plots, during the first growing season, 1982

Taxa[1]	Collection site	Quadrat size[2]	Seeds sown	Seedling density[3] June	Seedling density[3] October	Emergence	Relative survival
			Number per square meter			Percent	
Att	Red Rock Lakes	1	2,367	[4]298 ± 144	313 ± 131	12.6	105.0
Att	Perma	3	6,995	347 ± 204	[5]402 ± 218	5.0	115.9
Att	Bannack	1	2,438	316 ± 120	240 ± 136	13.0	76.0
Atw	Miles City	4	2,811	1,888 ± 1,210	1,470 ± 994	67.2	77.9
Atw	Ramsay	2	2,750	621 ± 240	583 ± 229	22.6	93.9
Atw	Bannack Flats	1	97	38 ± 33	40 ± 31	39.2	105.3
Atv	Sage Creek	1	3,348	167 ± 58	158 ± 98	5.0	94.6
Atv	Lavalle Creek	1	723	109 ± 69	140 ± 60	15.1	128.4
Atv	Reynolds Pass	1	353	0	0	0	0
Atvs	Red Rock Lakes	1	143	0	0	0	0
Acc	Sappington	3	2,936	1,884 ± 959	1,712 ± 753	64.2	90.9
Acc	Miles City	3	4,439	3,573 ± 1,279	3,094 ± 1,107	80.5	86.6
Acv	Sawpit Creek	1	1,193	111 ± 82	82 ± 71	9.3	73.9
Atptp	Ovando	1	1,422	7 ± 13	7 ± 9	0.5	100.0
Atptp	Badger Pass	1	977	4 ± 11	7 ± 13	0.4	175.0
Atptp	Monida	--	[6]0	---	---	---	---

[1]Att, Artemisia tridentata ssp. tridentata; Atw, A.t. ssp. wyomingensis; Atv, A.t. ssp. vaseyana; Atvs, A.t.v. var. spiciformis; Acc, A. cana ssp. cana; Acv, A. cana ssp. viscidula; Atptp, A. tripartita ssp. tripartita.
[2]Dimensions in centimeters, 1 = 30 by 15; 2 = 17.5 by 15; 3 = 12 by 7.3; 4 = 9.5 by 7.3.
[3]Seedling densities were not significantly different between June and October on any plot.
[4]± Standard deviation.
[5]Plot damaged and soil disturbed in spots by mole activity.
[6]Floral stalks were collected at this site but the heads contained no seed.

In March 1983, before spring growth had begun, each plot was subdivided by digging a 4-6 cm wide trench through the center. The west one-half then received 260.7 g of commercial lawn fertilizer (29-3-3, N-P-K). This was equivalent to 168 kg of nitrogen per hectare used by Bayoumi and Smith (1976). The east one-half of each plot was untreated. Seedling density was estimated in June 1983, by the same procedure used in 1982, except that along each line four quadrats were randomly positioned in the fertilized side and four in the unfertilized side. Also, two seedlings closest to the transect line in each quadrat were measured for height. Final seedling counts were made in late October (eight plots) and early November (three plots) 1983, referred to as October for the purpose of discussion. Quadrat sampling was the same as in June, but all seedlings in the quadrats were clipped at ground level and handled as described above. Length, leaf biomass, and crude terpenoid concentrations were determined as in 1982, except rinsing soil from leaves was unnecessary. After quadrat sampling was completed, additional seedlings were collected in November and combined with the quadrat seedlings for analysis of crude terpenoid concentrations.

Grasses and forbs germinated and grew on all plots, but not in great densities the first year. Spotted knapweed (Centaurea maculosa Lam.) was one of the most abundant and serious competitors. To estimate competition from knapweed during 1983, all plants (including those in a rosette stage) were counted in each quadrat and clipped at ground level in October-November 1983. Clippings were put into paper bags, ovendried 24 hours at 60 °C, adjusted to room temperature for a minimum of 30 minutes, and then weighed.

Seedling length and leaf biomass were compared for fertilized and unfertilized subplots of each seed source using the Student t-test. Seedling densities (June vs. October in 1982 and 1983) were analyzed by the Student t-test for paired comparisons, at the 0.05 level of probability. Product-moment correlation coefficients were calculated to determine relationships between seedling densities and total seedling biomass 1982, leaf biomass 1983, and plant length 1982, 1983 (Sokal and Rohlf 1981).

RESULTS

Large quantities of seed were sown, when available, to compensate for the poor emergence and survival reported by Harvey (1981). Emergence was variable, ranging from 0 to 80.5 percent (table 1). Artemisia tridentata ssp. vaseyana and A. tripartita ssp. tripartita were poorest and A. cana ssp. cana the best, followed by A. tridentata ssp. wyomingensis (table 2). Habitat characteristics of the latter two taxa were the most different from those at the garden site (an A.t. ssp. vaseyana habitat). Miles City seeds, the best performers, were collected the greatest distance from the garden. Emergence was not complete on some plots the first week in June, as indicated by an increased seedling density in October. June is normally the wettest month in the Missoula valley (Cordell 1971), and conditions are ideal for sagebrush germination. Late germination and emergence replaced seedlings that died, making it difficult to measure survival accurately. This may explain why summer survival was extremely high, 74 percent or greater on every plot (tables 1 and 2). Consequently, these values should be considered as relative survival. There was no significant difference in seedling densities between June and October (table 1) on any plot.

Table 2.--Emergence, relative survival, length, and biomass, by taxa, the first growing season, 1982

Taxa[1]	Emergence	Relative survival	Length	Total seedling biomass	Leaf biomass
	-- Percent --		Millimeters	Milligrams dry weight per 10 seedlings	
Att(3)	10.2	99.0	29	244	159
Atw(3)	43.0	92.4	25	175	109
Atv(2)	6.7	111.5	32	325	209
Atvs(1)	0.0	---	--	---	---
Acc(2)	72.4	88.8	35	226	136
Acv(1)	9.3	73.9	[2]26	[2]242	154
Atptp(1)	0.5	137.5	[2]--	[2]---	---

[1]Abbreviations same as table 1. Number of plots averaged in parentheses.
[2]These were not sampled because of the small seedling number.

At the end of the first growing season, seedling length ranged from 23 mm for A. tridentata ssp. wyomingensis from Bannack Flats to 39 mm for A.t. ssp. vaseyana from Lavalle Creek (table 3). Although seedlings of the latter taxa were tallest based on plots, A. cana ssp. cana seedlings were tallest based on taxa (table 2). High seedling densities did not influence plant size. There was no correlation between October densities (table 1) and seedling length (r^2 = 0.21) or biomass (r^2 = 0.02).

Seedling biomass of A.t. ssp. vaseyana was greatest, largely a result of the Lavalle Creek plot from seeds collected locally near Missoula (tables 2 and 3). Biomass of A.c. ssp. cana was less than A.t. ssp. vaseyana because of greater leaf senescence and loss. As expected, short A.t. ssp. wyomingensis produced the least dry matter.

Seedling crude terpenoid concentrations were low relative to parental plants collected the previous year (table 4) and compared to three parental populations resampled after clipping the garden seedlings in early November 1982. Mature shrubs in their natural habitats produced approximately twice the concentrations of crude terpenoids (table 4).

Table 3.--Seedling length and biomass, for single plots, at the end of the first growing season, October 1982

Taxa[1]	Collection site	Length	Total seedling biomass	Leaf biomass
		Millimeters	Milligrams dry weight per 10 seedlings	
Att	Red Rock Lakes	[2]27 ± 9	198 ± 26	129 ± 15
Att	Perma	31 ± 12	247 ± 156	160 ± 94
Att	Bannack	30 ± 10	287 ± 125	188 ± 84
Atw	Miles City	26 ± 9	195 ± 38	122 ± 29
Atw	Ramsay	25 ± 6	157 ± 31	96 ± 18
Atw	Bannack Flats	23 ± 6	173 ± 42	108 ± 22
Atv	Sage Creek	24 ± 9	228 ± 49	164 ± 35
Atv	Lavalle Creek	39 ± 1	422 ± 33	254 ± 11
Atv	Reynolds Pass	---	---	---
Atvs	Red Rock Lakes	---	---	---
Acc	Sappington	32 ± 10	193 ± 31	113 ± 18
Acc	Miles City	37 ± 12	258 ± 79	158 ± 54
Acv	Sawpit Creek	26 ± 10	242 ± 32	154 ± 25
Atptp	Ovando	[3]---	[3]---	[3]---
Atptp	Badger Pass	[3]---	[3]---	[3]---
Atptp	Monida	---	---	---

[1]Abbreviations same as table 1.
[2]± Standard deviation.
[3]These were not sampled because of the small seedling number.

Table 4.--Crude terpenoid concentrations in parental populations (1981, 1982) and garden seedlings (1982, 1983)

Taxa[1]	Collection site	Parental plants[2]		Garden seedlings[3]		
		1981	1982	1982	1983 unfertilized	1983 fertilized
		Percent leaf dry weight				
Att	Red Rock Lakes	---	---	8.4	11.6	12.9
Att	Perma	[4]22.9 ± 3.3	24.6 ± 3.0	12.4	15.3	18.6
Att	Bannack	---	---	10.7	13.5	13.6
Atw	Miles City	---	---	15.0	15.1	14.1
Atw	Ramsay	18.1 ± 2.1	19.7 ± 3.3	9.5	11.4	11.0
Atv	Sage Creek	---	---	8.0	9.5	9.0
Atv	Lavalle Creek	11.3 ± 0.6	15.1 ± 1.1	7.0	10.1	9.6
Atvs	Red Rock Lakes	13.9 ± 0.9	---	---	---	---
Acc	Sappington	16.2 ± 7.5	---	9.3	10.2	10.7
Acc	Miles City	---	---	10.2	11.5	9.2
Acv	Sawpit Creek	8.2 ± 0.9	---	2.2	---	---
Atptp	Ovando	18.2 ± 3.5	---	---	---	---

[1]Abbreviations same as table 1.
[2]An average of three plants per collection site, 1982 plants were the same as 1981.
[3]Duplicate analysis per collection except six sites in 1982 with limited leaf material.
[4]± Standard deviation.

Relative seedling survival through the second summer was excellent (tables 5 and 6), averaging 90 percent or greater (table 6) for all taxa except fertilized A. cana ssp. viscidula. Seedling densities were not significantly different between June and October, although densities on several plots were greater in October. Some of this increase could have been due to variation and/or sampling error, and some probably resulted from residual seed in the soil that emerged after June sampling, since increases were observed mainly on plots sown with 2,000 or more seeds/m^2 (tables 1 and 5). Conditions during June and July 1983 were excellent for germination, with lower than average temperatures and above normal precipitation (NOAA 1983). The largest increases in seedling numbers were observed on A. cana plots (table 5) where lateral

Table 5.--Relative seedling survival, for single plots, during the second growing season, 1983

Taxa[1]	Collection site	Treatment[1]	Seedling density[2] June	Seedling density[2] October	Relative survival	Establishment[3]
			Number per square meter		Percent	
Att	Red Rock Lakes	F	[4]262 ± 136	280 ± 164[a]	106.9	11.8
		C	231 ± 169	227 ± 127[a]	98.3	9.6
Att	Perma	F	[5]287 ± 198	[5]191 ± 191[a]	66.6	2.7
		C	171 ± 129	171 ± 151[a]	100.0	2.4
Att	Bannack	F	[5]164 ± 111	[5]162 ± 93[a]	98.8	6.6
		C	198 ± 167	[6]200 ± 167[a]	101.0	8.2
Atw	Miles City	F	1,311 ± 591	1,527 ± 908[a]	116.5	54.3
		C	1,225 ± 562	1,282 ± 980[a]	104.7	45.6
Atw	Ramsay	F	495 ± 103	488 ± 114[a]	98.6	17.8
		C	510 ± 190	423 ± 164[a]	82.9	15.4
Atw	Bannack Flats	F	29 ± 27	[7]16 ± 22[a]	55.2	16.4
		C	29 ± 29	27 ± 20[a]	93.1	27.7
Atv	Sage Creek	F	151 ± 69	133 ± 60[a]	88.1	4.0
		C	140 ± 56	167 ± 96[a]	119.3	5.0
Atv	Lavalle Creek	F	122 ± 40	[7]129 ± 56[a]	105.7	17.8
		C	84 ± 49	71 ± 51[b]	84.5	9.8
Acc	Sappington	F	1,667 ± 947	1,747 ± 776[a]	104.8	59.5
		C	1,598 ± 811	1,884 ± 1,244[a]	117.9	64.2
Acc	Miles City	F	2,785 ± 1,244	[7]3,436 ± 1,153[a]	123.4	77.4
		C	2,534 ± 1,221	3,059 ± 1,233[a]	120.7	68.9
Acv	Sawpit Creek	F	89 ± 47	[7]51 ± 44[a]	57.3	4.3
		C	64 ± 53	78 ± 56[a]	121.9	6.5
Atptp[8]	Badger Pass	F	18 ± 27	[9]---	---	---
		C	13 ± 16	---	---	---

[1]Abbreviations same as table 1. Treatment, F = fertilized; C = control.
[2]Seedling densities were not significantly different between June and October on any plot. When fertilized and control of the same plot are followed by different letters, they are significantly different ($p < 0.05$).
[3]Number of seedlings in October 1983 as a percentage of the number of seeds sown in February 1982.
[4]± Standard deviation.
[5]Soils on the fertilized half of this plot were heavily disturbed by mole activity, burying and killing seedlings in some spots.
[6]Moderate mole damage.
[7]Some plot damage from mouse trails.
[8]The Ovando Atptp plot was vandalized during the winter and could not be used.
[9]Not sampled.

Table 6.--Relative seedling survival, establishment, length, and leaf biomass, by taxa, at the end of the second growing season, 1983

Taxa[1]	Treatment[1]	Relative survival	Establishment	Length	Leaf biomass
		Percent		Millimeters	Milligrams dry weight per 10 seedlings
Att(3)	F	90.8	7.0	73	445
	C	99.8	6.7	40	250
Atw(3)	F	90.1	29.5	66	301
	C	93.6	29.6	28	100
Atv(2)	F	96.9	10.9	93	485
	C	101.9	7.4	36	267
Acc(2)	F	114.1	68.5	66	234
	C	119.3	66.6	39	79
Acv(1)	F	57.3	4.3	78	217
	C	121.9	6.5	34	166

[1]Abbreviations same as table 1. Number of plots averaged in parentheses. Treatment, F = fertilized; C = control.

branching below soil level, or vegetative sprouts from existing seedlings, may have contributed to the higher counts (Walton, personal communication).

Seedling density was similar on fertilized and unfertilized plots in June and October (except for A.t. ssp. vaseyana from Lavalle Creek in October, table 5). However, fertilization resulted in increased productivity of grasses and forbs, particularly knapweed (table 7). Visual observations suggested competition was more severe on the fertilized portion of each plot. High shrub densities did not increase seedling mortality (table 5). Moderate to heavy soil disturbances from mole activity occurred in two A.t. ssp. tridentata plots and may have reduced seedling numbers of the Perma collection (table 5). Mouse trails were observed on several fertilized subplots, but mice had minimal impact on the young seedlings.

Table 7.--Knapweed density and biomass on the sagebrush seed plots, October 1983

Taxa[1]	Collection site	Treatment[1]	Knapweed Plants	Knapweed Biomass
			Number per square meter	Grams dry weight per square meter
Att	Red Rock Lakes	F	140 ± 56	271 ± 174
		C	140 ± 78	168 ± 97
Att	Perma	F	80 ± 58	175 ± 179
		C	76 ± 29	202 ± 111
Att	Bannack	F	82 ± 56	177 ± 155
		C	84 ± 44	116 ± 101
Atw	Miles City	F	130 ± 144	332 ± 388
		C	130 ± 115	126 ± 102
Atw	Ramsay	F	130 ± 69	384 ± 246
		C	160 ± 91	200 ± 133
Atw	Bannack Flats	F	96 ± 58	260 ± 198
		C	116 ± 42	168 ± 87
Atv	Sage Creek	F	109 ± 49	265 ± 150
		C	84 ± 44	168 ± 80
Atv	Lavalle Creek	F	193 ± 89	382 ± 203
		C	158 ± 58	236 ± 58
Acc	Sappington	F	194 ± 160	473 ± 394
		C	126 ± 137	347 ± 189
Acc	Miles City	F	69 ± 80	230 ± 112
		C	171 ± 137	245 ± 164
Acv	Sawpit Creek	F	196 ± 124	336 ± 169
		C	111 ± 51	150 ± 103

[1]Abbreviations same as table 1. Treatment, F = fertilized; C = control.

Fertilized seedling were significantly taller (1.5-2.7 times) than controls on all plots in October (table 8) as indicated by their length measurements. Length, however, was not correlated (r^2 = 0.04) with seedling density. Fertilized (table 6) A. tridentata ssp. vaseyana seedlings were tallest, followed by A. cana ssp. viscidula and A. tridentata ssp. tridentata (this taxon did have one plot with plants taller than the A.c. ssp. viscidula, table 8.) Without fertilization, A.t. ssp. tridentata seedlings were tallest, A.c. ssp. cana second, and A.t. ssp. vaseyana a close third. Seedlings of A.t. ssp. wyomingensis were shortest (except the Miles City fertilized plot) regardless of treatment. Artemisia cana ssp. cana seedlings were also short when fertilized (table 6), because of their deciduous nature. Seedling length on unfertilized subplots, in October 1983, had increased very little from the previous year (tables 3 and 8) indicating nutrient unavailability was limiting growth.

Leaf biomass of fertilized plants was 1.3 to 3.2 times greater than that of unfertilized controls (tables 6 and 8). Leaves were noticeably larger on fertilized seedlings. Fertilized A.t. ssp. tridentata from Bannack produced the most biomass per plot, but A.t. ssp. vaseyana produced the most biomass per taxa. This same relationship was observed for unfertilized seedlings. The

Table 8.--Seedling height (June), length (October) and leaf biomass (October), for single plots, at the end of the second growing season, 1983

Taxa[1]	Collection site	Treatment[1]	June height	October[2] length	Leaf biomass[2]
			Millimeters		Milligrams dry weight per 10 seedlings
Att	Red Rock Lakes	F	[3]80 ± 39	68 ± 26[a]	336 ± 100[a]
		C	38 ± 22	32 ± 10[b]	159 ± 39[b]
Att	Perma	F	62 ± 30	66 ± 29[a]	372 ± 67[a]
		C	28 ± 13	43 ± 16[b]	178 ± 26[b]
Att	Bannack	F	91 ± 36	84 ± 31[a]	628 ± 80[a]
		C	40 ± 22	45 ± 15[b]	414 ± 37[b]
Atw	Miles City	F	64 ± 24	73 ± 33[a]	300 ± 135[a]
		C	32 ± 9	32 ± 10[b]	104 ± 14[a]
Atw	Ramsay	F	61 ± 19	62 ± 28[a]	302 ± 38[a]
		C	24 ± 7	26 ± 6[b]	95 ± 16[b]
Atw	Bannack Flats	F	66 ± 25	62 ± 15[a]	---
		C	30 ± 12	27 ± 9[b]	---
Atv	Sage Creek	F	86 ± 38	85 ± 31[a]	541 ± 84[a]
		C	29 ± 13	32 ± 9[b]	328 ± 104[a]
Atv	Lavalle Creek	F	107 ± 42	100 ± 34[a]	429 ± 16[a]
		C	41 ± 11	40 ± 10[b]	205 ± 58[b]
Acc	Sappington	F	67 ± 28	66 ± 20[a]	218 ± 88[a]
		C	42 ± 14	38 ± 11[b]	82 ± 16[a]
Acc	Miles City	F	71 ± 20	66 ± 16[a]	249 ± 34[a]
		C	41 ± 13	40 ± 10[b]	76 ± 14[b]
Acv	Sawpit Creek	F	80 ± 38	78 ± 36[a]	217 ± 124[a]
		C	38 ± 11	34 ± 12[b]	166 ± 35[a]
Atptp[4]	Badger Pass	F	71 ± 32	[5]---	[5]---
		C	27 ± 8	---	---

[1]Abbreviations same as table 1. Treatment, F = fertilized; C = control.
[2]When fertilized and control of the same plot are followed by different letters, they are significantly different ($p < 0.05$).
[3]± Standard deviation.
[4]The Ovando Atptp plot was vandalized during the winter and could not be used.
[5]Not sampled because of small seedling numbers.

smallest leaf biomass in October was collected from subspecies of A. cana (except untreated A.c. ssp. viscidula). This is somewhat misleading because A. cana has more foliage earlier in the growing season, but is nearly deciduous, losing a greater portion of its leaves than big sagebrush subspecies. Fertilizing doubled or tripled leaf dry matter productivity for over two-thirds of the taxa (tables 6 and 8). Foliage biomass was not correlated ($r^2 = 0.32$) with seedling density in October. Some unfertilized seedlings had less leaf dry weight in 1983 than they did in 1982 (tables 2,3,6, and 8).

Crude terpenoid concentrations were not affected by fertilization (table 4). Concentrations in October 1983 were greater than one year earlier, but they were still lower than those recorded for mature parental plants in their natural populations, from the previous two years.

DISCUSSION

As expected from other studies (Harvey 1981; McArthur and Welch 1982) the emergence and growth of sagebrush, under uniform environmental conditions, varied considerably between taxa, within taxa from different geographic sources, and between individuals originating from the same population.

These results have important implications in terms of utilizing sagebrush species as biocrude producing plants. Undoubtedly, it would not be possible to grow an annually harvested crop of sagebrush plants from seed, even if plants were provided with ideal conditions. Sagebrush simply does not grow fast enough. However, since the shrubs can be partially defoliated without damaging growth (Kelsey, this proceedings), there would be no need to start from seed each year. Establishment from seed could still be important for sites that required complete shrub harvesting at periodic intervals, or where existing sagebrush plants were removed for replacement with a more productive form. Since sagebrush can be readily transplanted (Plummer and others 1968, 1970), nursery stock could be grown in gardens or in greenhouses (Long, this proceedings). Sagebrush seed is one of the least expensive to collect relative to other western shrubs (Plummer and others 1968).

The good germination and growth of A. cana ssp. cana, particularly those from Miles City, show that a variety of taxa can be grown on a given site. Successful establishment of various taxa was partially the result of favorable weather conditions during the study period and other beneficial environmental characteristics of this particular habitat. The same taxa may have responded differently in other environments or weather conditions.

Artemisia cana ssp. cana and A. tripartita ssp. tripartita might be more desirable than A. tridentata for biocrude production because they root-sprout (Beetle 1960; White and Currie 1983). The crude terpenoid concentrations in these two taxa were higher than in A. tridentata ssp. vaseyana (table 4). Further studies of A. cana would be necessary to determine optimal harvest time because of its deciduous nature.

Seedling growth responded quite positively to the application of fertilizer (tables 6 and 8), but there was no change in crude terpenoid concentrations. A similar growth response was observed when mature sagebrush was fertilized (Bayoumi and Smith 1976). For many plants, an inverse relationship exists between growth and chemical concentrations (McLaughlin and Hoffmann 1982; McLaughlin and others 1983). Various types of compounds, i.e., terpenes, lipids, and hydrocarbons, accumulate in plants subjected to stresses such as lack of water, insufficient nutrients, or herbivory (Bryant 1981). In sagebrush, the accumulation of epidermal compounds appears independent of stress associated with moderate to heavy defoliation (Kelsey, this proceedings), or growth stimulated by fertilization (this study). Consequently, increasing biomass production of these shrubs, by optimizing growing conditions, would directly increase the yield of epidermal chemicals from the plant, but without changing concentrations. Faster growing strains, or taxa, could be used to replace less productive populations.

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GERMINATION PROFILES FOR FIVE POPULATIONS OF BIG SAGEBRUSH

Raymond A. Evans and James A. Young

ABSTRACT: Seeds from two sources of mountain big sagebrush (Artemisia tridentata Nutt. ssp. vaseyana [Rydberg] Beetle), and three sources of basin big sagebrush (A. tridentata Nutt. ssp. tridentata) were tested from collections made in the same stands in 2 consecutive years. Germination tests were conducted at 55 constant and alternating temperatures. Basin big sagebrush seeds had higher germination at several categories of temperatures than seeds of mountain big sagebrush.

INTRODUCTION

The potential of seeds to germinate at various constant and alternating temperatures is one of the basic parameters governing the periodicity of germination and establishment of plants in wildland seedbeds. Obviously, temperature interacts with other microenvironmental parameters, such as moisture availability and seedbed soil conditions. However, determining germination-temperature response provides an important start toward understanding the complex interactions that affect germination. This study was undertaken to determine germination of big sagebrush seeds in relation to 55 different constant and alternating temperatures.

METHODS

Seeds of big sagebrush were collected in November 1982 and 1983 at five sites in western Nevada where reciprocal gardens of big sagebrush plants were located. The sites ranged from low-elevation (1 500 m) sagebrush communities, adjacent to the salt desert, to the lower fringes of the pinyon/juniper (Pinus/Juniperus) woodlands at 1 800 m elevation. Precipitation on the sites varied from 150 mm to 300 mm. Granite Peak and Churchill Canyon site #5 supported mountain big sagebrush and the other three sites, basin big sagebrush. Seeds were collected from natural stands, allowed to dry to moisture equilibrium, hand threshed, and cleaned with an air screen.

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Raymond A. Evans and James A. Young are Range Scientists with the U.S. Department of Agriculture, Agricultural Research Service, Reno, NV.

Seeds were stored in paper bags in the laboratory until tested. Tests were conducted 30 days, 6 months, and 12 months after harvest.

In all germination tests, four replications of 25 seeds each were used. Tests were conducted in petri dishes with the seeds placed on top of one thickness of germination paper and moistened with tap water.

Tests were conducted in dark germinators for 4 weeks with germination counts made weekly. Unless otherwise specified, seeds were considered germinated when the radicle emerged (0.25 cm).

Constant temperatures used were 0, 2, 5, 10, 15, 20, 25, 30, 35, and 40 °C. Alternating temperature regimes consisted of 16 hours at each lower constant temperature (cold period) and 8 hours at all possible higher temperatures (warm period) in each 24-hour period. For example, 0 was alternated with 2, 5, 20, 15, 20, 25, 30, 35, and 40 °C, whereas 35 was alternated with 40 °C only.

The effects of constant alternating temperatures on percentage germination were statistically analyzed using a quadratic response surface (Ott 1977). A quadratic response surface was developed for each cultivar or accession using multiple regression techniques. Estimated germination values and their confidence limits were derived from the quadratic response surface of each species for each cold-period (16 hours) temperature through the series of warm-period (8 hours) temperatures (Evans and others 1982). The generalized quadratic equation used in calculating expected values was:

$$Y = A_0 + A_1X_1 + A_2X_2 + A_3X_1 + A_4X_2 + A_5X_1X_2$$

where Y = percent predicted germination, A_0 = intercept, A_1 through A_5 = coefficients, X_1 = cold temperature, and X_2 = warm temperature. The intercept and coefficients were determined by multiple regression for individual species. The resulting values for A_1 through A_5 represent partial regression coefficients where the effect of one variable on germination is altered by the inclusion of the remaining variables. Calculated regression lines with confidence limits were compared with actual seed germination data.

We compared the germination percentage of the seeds tested at constant and alternating

temperatures with categories of seedbed temperatures that were developed on the basis of microenvironmental monitoring in the field (Evans and others 1970; Evans and Young 1970, 1972). These temperature categories were:

Very cold: 0, 0/2, 2, and 0/5 °C.

Cold: 0/10, 0/15, 2/5, 2/10, 2/15, 5/15, and 5/10 °C.

Cold fluctuating: 0/20 through 0/40 °C, 2/20 through 2/40 °C.

Moderate: 5/15 through 5/25 °C; 10 through 10/30 °C; 15 through 15/35 °C; 20 through 20/35 °C; 25 and 25/30 °C.

Fluctuating: 5/30, 5/35, 5/40, 10/35, 10/40, and 15/40 °C.

Warmer: 20/40, 25/35, 25/40, 30, 30/35, 30/40, 35, 35/40, and 40 °C.

A series of germination profile characteristics was generated from the response surfaces: (a) mean germination, (b) mean germination in the regimes producing some germination, (c) percentage of regimes with some germination, (d) percentage of regimes with optimum germination, (e) mean of germination optima, and (f) maximum germination (Young and Evans 1982). We define optimum germination as that equal to or greater than the maximum mean germination minus one-half its confidence interval (P=0.01).

RESULTS AND DISCUSSION

Variation Between Years

There was no significant (P=0.05) difference between the average germination for the seeds of big sagebrush produced at each location between 1982 and 1983 (table 1). Based on previous experience, we find it unusual that seeds from the same parents in different production years do not have marked differences. Generally, year-to-year variations in environmental conditions will have a big influence on seed germination.

Differences Among Locations

For this presentation, we averaged profiles for the 2 years and present mean germination parameters (table 2). Seeds produced at Churchill Canyon #1 and #3 had higher average germination at the 55 constant and alternating temperatures (table 2). Both of these locations support basin big sagebrush communities. Seeds from the other basin big sagebrush location, Medell Flat, and the mountain big sagebrush community at Churchill Canyon #5 were intermediate in germination. Seeds from the remaining mountain big sagebrush community at Granite Peak were significantly (P=0.01) lower in germination.

For certain species, germination may occur at only a few temperature regimes, but be very high at those restricted temperatures. This was not the case for the seeds used in this study. The germination mean of temperature regimes with some germination was very similar to the overall mean germination (table 2). Germination occurred at more than 90 percent of the temperatures tested; only the highest temperature regimes failed to produce germination. Optimum germination occurred in 12 to 19 percent of the temperature regimes tested (table 2). Maximum germination and germination at optimum temperatures were quite high except for the seeds of mountain big sagebrush produced at Granite Peak.

Distribution of Optimum Temperatures

Only two temperature regimes, 10/20 °C and 15/20 °C, were always optimum for seed germination (table 3). The range of temperature regimes that supported optimum germination at least once was quite wide, encompassing 19 regimes or 35 percent of those tested. Seeds of mountain big sagebrush produced at Granite Peak had the widest range of optima and those of the same subspecies produced at the Churchill Canyon #5 location had the narrowest, 29 and 9 percent of all regimes tested, respectively.

Cool-Moist Stratification Requirements

McDonough and Harniss (1974) reported that seeds of mountain big sagebrush collected in Idaho had

Table 1.--Mean germination of optima, and maximum germination for big sagebrush seeds produced at five locations in 1982 and 1983

	Year of seed production					
	Mean germination		Mean of optima		Maximum germination	
Location	1982	1983	1982	1983	1982	1983
	percent					
Granite Peak	34	35	59	55	63	57
Medell Flat	51	59	78	89	81	92
Churchill Canyon #1	59	69	84	93	87	95
Churchill Canyon #3	71	69	93	91	95	93
Churchill Canyon #5	48	46	82	75	86	79

Table 2.--Germination parameters synthesized from quadratic response surfaces for germination at 55 constant and alternating temperatures for five sources of seeds of big sagebrush. Figures are means for seeds produced at the same site in 1982 and 1983[1]

Germination parameter	Locations				
	Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5
	percent				
Mean germination	34c	55b	69a	70a	47b
Mean germination of regimes with some germination	36	57	66	72	51
Regimes with some germination	96	97	97	98	93
Regimes with optimum germination	19	12	17	15	15
Mean of optima	57	84	89	92	79
Maximum germination	60	87	91	94	82

[1]Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test.

Table 3.--Frequency of temperature regimes that supported optimum germination in quadratic response surfaces based on 55 constant and alternating temperatures. Seeds of big sagebrush from five locations produced in 1982 and 1983 used for a total of 10 response surfaces

Cold period temperature-	Warm period temperature - 8 hours °C									
16 hours, °C	0	2	5	10	15	20	25	30	35	40
0				10	10					
2				10	10	20				
5				20	30	10				
10			10	40	100	80	40			
15				40	100	90	60			
20					60	60				
25										
35										
40										

enhanced germination following cool-moist stratification at 0 to 2 °C for 30 days. The temperature regimes and the duration of incubation used in this study essentially produced self-stratifying incubation conditions. We have subjected seeds from all five sources to cool-moist stratification enrichment with potassium nitrate or gibberellin as substitutes for stratification requirements without enhancing germination above that obtained with a nonpretreated profile (Evans and Young, unpublished data).

Relating Temperature Profiles to Seedbed Temperatures

At moderate seedbed temperatures, the same pattern in regard to mean germination in relation to location was apparent that existed for overall mean germination (table 4). Seeds from Churchill Canyon #5 and Medell Flat were intermediate, and seeds from Granite Peak were markedly lower.

The germination of seeds from all sources was significantly (P=0.05) lower at very cold compared to moderate temperatures (table 4). However, the relative percentage decrease was less for mountain big sagebrush than for basin big sagebrush seeds (table 4). At cold seedbed temperatures, germination of Granite Peak mountain big sagebrush was 98 percent of what it was at moderate seedbed temperatures. The average germination of basin big sagebrush sources was 26 percent lower than that observed at moderate seedbed temperatures.

Germination of cold-fluctuating seedbed temperatures is an important category because the small seeds of big sagebrush are normally dispersed to the soil surface where they are exposed to widely fluctuating temperatures during germination. High incubation temperatures tend to depress germination of both mountain and basin big sagebrush seeds for the sources tested (table 4). This depression is roughly equal for the two subspecies, 67 percent for mountain and 65 percent for basin big sagebrush. However, under cold-fluctuating incubation regimes (combination of warmer and very cold temperatures), there is a disproportionate depression in germination of the mountain big sagebrush seeds. Compared to moderate temperatures, the cold-fluctuating regimes depressed the germination of the mountain big sagebrush sources 40 percent and of the basin big sagebrush seeds only 27 percent (table 4).

Table 4.--Germination of seeds from five sources of big sagebrush at categories of seedbed temperatures based on monitoring of seedbed environments in the field. Data represent the mean for seeds produced in 1982 and 1983[1]

Categories of seedbed temperatures	Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5
			percent		
Moderate	48 fg	75 a-c	83 a	86a	69 b-d
Very cold	33 ik	25 kl	32 j-l	41 hi	28 j-l
Cold	47 gh	57 ef	57 ef	65 c-3	53 fg
Cold fluctuating	31 j-l	53 fg	66 c-e	80 ab	39 bi
Fluctuating	24 k-m	44 g-i	76 a-c	76 a-c	59 d-f
Warmer	13 m	21 lm	30 i-l	36 h-j	27 j-l

[1]Means followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's multiple range test.

Relation to Establishment from Direct Seeding in Field

For all locations and seasons of seeding, where direct seeding resulted in seedling establishment, seeds of mountain big sagebrush outperformed seeds of basin big sagebrush (Young and Evans, this proceedings). The results of seeding reciprocal gardens in the field appear to be opposite of what the results of the temperature profiles suggest. Several factors have to be considered in interpreting the results.

First, the field data are based on emergence and/or persistence of seedlings compared to radicle emergence in the laboratory data. These different data bases allow the introduction of unaccountable variables. One of the most important of these may be the susceptibility of big sagebrush seedlings to injury by frost. Seeds of most cultivars of alfalfa (Medicago sativa L.) have excellent germination even at slightly subfreezing temperatures, but the seedlings are very susceptible to frost injury (Young and Evans, unpublished data).

The percentage of mountain big sagebrush seed emergence in the field often neared the optimum germination percentages for these seeds in laboratory tests. Either the potential of spring seedbeds to support germination is greater than we have evaluated, or some factor enhances mountain big sagebrush seed germination in the field compared to in the laboratory.

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SEEDLING ESTABLISHMENT OF FIVE SOURCES OF BIG SAGEBRUSH IN RECIPROCAL GARDENS

James A. Young and Raymond A. Evans

ABSTRACT: Establishment rates of five populations of big sagebrush (Artemisia tridentata Nutt.) by direct seeding and transplantings were investigated in five reciprocal gardens. Seeds (achenes) of mountain big sagebrush (A. tridentata ssp. vaseyana [Rydberg] Beetle) had the highest germination and establishment even on basin big sagebrush (A. tridentata Nutt.) sites. There were large differences in establishment of big sagebrush by direct seeding between years and among collections and sites. Initial results indicated that mountain big sagebrush plants were more vigorous than basin big sagebrush.

INTRODUCTION

Reciprocal gardens constitute a valuable research concept for the partitioning of phenotypic from inherent variability in populations of native plants. The potential of this concept was illustrated by the classic study by Clausen and others (1948).

The division of big sagebrush (Artemisia tridentata Nutt.) into subspecies that occupy relatively distinct ecological sites provided a suitable species for application of the concept of reciprocal gardens (Beetle 1960; Beetle and Young 1965; Winward and Tisdale 1977).

Our purpose was to study the establishment from seed and transplants of five populations of big sagebrush grown in reciprocal gardens in Nevada.

METHODS

Seeds (achenes) were collected from big sagebrush populations growing on five different sites in western Nevada in 1982 (table 1). The collection and garden sites ranged from the 1 460-m elevation sagebrush communities adjacent to chenopod desert communities, to the lower fringes of the pinyon-juniper (Pinus/Juniperus) woodlands at 1 830 m. The sites were located in the first mountain ranges east of the Sierra Nevada Mountains, within 160 km of Reno, NV. The soils at Granite Peak and Medell Flat locations are derived from decomposing granite or quartz diorite. The soils of Churchill Canyon are developed on alluvium from volcanic and metavolcanic sources.

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James A. Young and Raymond A. Evans are Range Scientists, U.S. Department of Agriculture, Agricultural Research Service, Reno, NV.

Direct Seeding Experiments

During December 1982, corresponding to the time of natural seed dispersal, we seeded in pots 100 seeds of sagebrush from each of the five populations. The 15-cm diameter pots were filled with soil from each location and buried to the soil surface. The burial sites at each of the five locations were in areas cleared of all vegetation. A randomized block design was used with six replications. Seeds were sprinkled on the soil surface, then left uncovered.

As soon as seedlings were noted, we counted the number of living seedlings per pot on a weekly basis. At the same time, the number of naturally occurring big sagebrush seedlings in the surrounding plant community was estimated by counting seedlings in 100 randomly located quadrats 0.01 m^2 in area. Direct seeding was repeated in March and December 1983, and March 1984.

In an additional six-replicated experiment established during December 1983, we filled two sets of pots for burying at each location with a sandy loam-textured soil that had been dried and screened for use in greenhouse planting. The pots were filled and watered repeatedly until the soil was compacted and nearly level. At each location, one set of these pots was seeded by sprinkling seeds from each of the five populations on the soil surface as in the original experiments. The second set of pots had 20 colored glass marbles 1.25 cm in diameter placed on the soil surface before seeding. The marbles covering the soil surface prevented rapid evaporation from the soil surface and provided a more favorable microenvironment for seed germination and seedling growth.

Transplant Experiments

Seeds collected from each location in December 1982 were used to grow seedlings in 15-cm plots in the greenhouse. The seedlings were transplanted to the gardens in May 1983. The

Table 1.--Characteristics of the five plant communities where Artemisia tridentata seeds were collected and reciprocal gardens located

Location	Elevation (m)	Artemisia tridentata subspecies	Soils	Estimated annual precipitation (cm)
Granite Peak	1830	vaseyana	Typic Haplargids	30
Churchill Canyon #5	1830	vaseyana	Typic Argixerolls	30
Churchill Canyon #3	1690	tridentata	Typic Torripsammonts	25
Churchill Canyon #1	1460	tridentata	Typic Torripsammonts	15
Medell Flat	1520	tridentata	Typic Durargids	20

experiment was repeated with seeds collected in December 1983 and seedlings transplanted in May 1984. In each garden, 100 seedlings from each source were planted in a randomized block design. Seedling survival was recorded in October 1983 and April 1984. In April 1984, the height and maximum and minimum crown diameters of each plant were recorded. A biomass index was calculated from these data.

Precipitation was recorded at the garden. Because the gardens have been used for experiments for about 20 years, we had considerable precipitation data. Typical of weather in the Great Basin, the winter of 1982-83 was one of the wettest on record, and the winter of 1983-84 after January 1 was virtually without precipitation.

RESULTS AND DISCUSSION

Direct Seeding Experiment - December 1982

In March 1983, the first emergence was apparent from the fall seeding (fig. 1). Greatest initial emergence, 36 percent, occurred at the lowest and most arid site (Churchill Canyon #1). The two higher elevation mountain big sagebrush sites had no emergence (fig. 1). The relation between elevation and emergence continued through the early spring, except the number of seedlings at the lower elevation declined as emergence at higher elevations increased. Churchill Canyon #5 had very limited emergence throughout the spring.

The interplay in emergence among sites illustrates the basic role temperature and available moisture play in controlling germination in the Great Basin during spring germination periods. Because precipitation is largely out of phase with temperatures that permit growth, seeds in a sagebrush seedbed seem to be almost always too cold or too dry to germinate. The higher elevation sites have the greatest precipitation, but often are markedly colder than the more arid sites at lower elevation. Remember that the winter of 1982-83 ranks as one of the wettest in western Nevada's recorded history (table 2). Despite abundant precipitation at the Churchill Canyon #5 site during the spring of 1983, favorable temperatures and available moisture for germination in the seedbed never coincided (fig. 1).

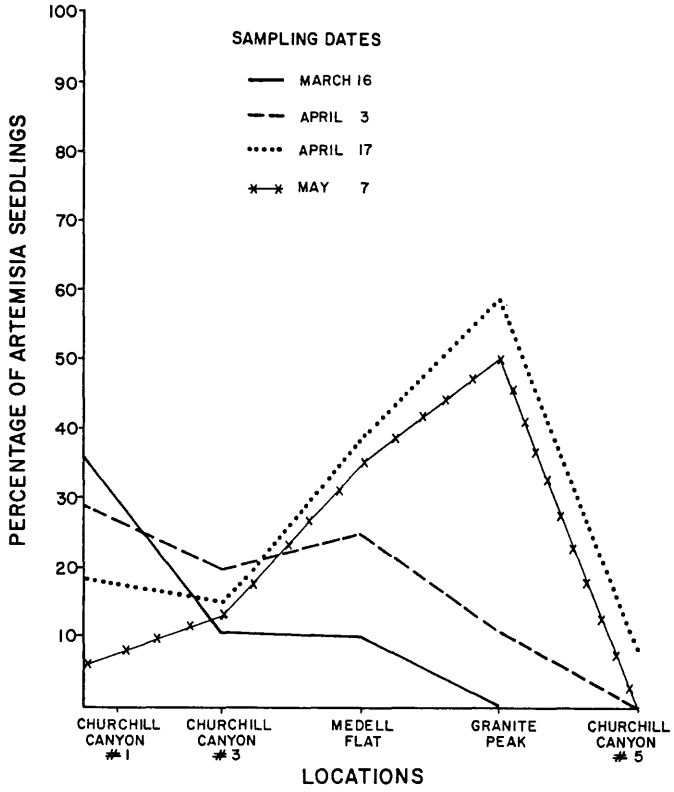


Figure 1.--Percent emergence of Artemisia tridentata seedlings in five reciprocal gardens at four sampling dates during the spring of 1983.

There was sufficient soil moisture at some sites during the spring and early summer of 1983 that the sagebrush seedlings persisted, even in relatively dense stands, in the artificial environments of the buried pots (table 3). The greatest seedling survival was at Granite Peak and Medell Flat. Seeds from Churchill Canyon #5 failed to germinate and establish at their site of collection, but had 82 percent seedling survival at the other mountain big sagebrush site. At the most arid site, Churchill Canyon #1, there were no differences among the sources in establishment by August 1, 1983.

Table 2.--Precipitation (cm) at the five seed collection and reciprocal garden locations in 1982-83 and 1983-84

Location	September-December		December-March		March-June		Total	
	1982-83	1983-84	1982-83	1983-84	1982-83	1983-84	1982-83	1983-84
	cm							
Granite Peak	13.2	11.7	21.3	8.4	10.2	2.3	44.7	22.4
Medell Flat	10.4	8.6	17.5	7.4	7.9	1.8	35.8	17.8
Churchill Canyon #1	7.6	4.8	10.7	5.1	5.3	1.0	23.6	10.9
Churchill Canyon #3	10.2	7.4	16.8	4.8	7.4	1.3	34.4	13.5
Churchill Canyon #5	13.0	12.7	20.6	5.8	9.9	1.5	43.5	20.0

Table 3.--Percentage establishment of big sagebrush seedlings in five reciprocal plantings. Seeds planted December 1982, data collected August 21, 1983[1]

Source	Garden location					Means of sources
	Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5	
	percent					
Granite Peak	28bc	63a	0c	0c	0c	18y
Medell Flat	10bc	35b	5bc	3bc	0c	11z
Churchill Canyon #1	13bc	33bc	3bc	0c	2c	10z
Churchill Canyon #3	8bc	25bc	5bc	5bc	0c	10z
Churchill Canyon #5	82a	25bc	3bc	0c	0c	22y
Means of locations	28y	37y	3z	2z	0z	

[1]Means of sources at individual locations followed by the same letter (a through c) are not different at the 0.05 level of probability as determined by Duncan's multiple range test. Overall means (locations and sources compared separately) followed by the same letter (y or z) are not different at the 0.01 level of probability as determined by Duncan's multiple range test.

Direct Seeding Experiment - March 1983

Despite abundant precipitation in the spring of 1983, sagebrush seedling establishment was much lower from spring seeding than fall seeding (tables 3 and 4). There were no statistical differences (P=0.05) among the sources in establishment, but the two sources of mountain big sagebrush had the numerically highest establishment.

Direct Seeding Experiment - December 1983

There were three treatments in the direct seeding experiments established in the fall of 1983: (1) using the soils found on each site (duplication of the 1982 experiment), (2) using a constant soil at all sites, and (3) using a constant soil with marbles to provide favorable microtopography.

Using the soils native to the site for the direct seeding experiments produced big sagebrush seedlings only at the relatively low-elevation Medell Flat and Churchill Canyon #1 sites (table 5). Substituting a uniform soil at all locations produced similar results. The addition of marbles to the soil surface to provide more favorable microtopography increased seedling establishment at all locations except Churchill Canyon #5 (table 5). The two sources of mountain big sagebrush had higher establishment rates than the basin big sagebrush sources.

Table 4.--Percentage establishment of big sagebrush seedlings in five reciprocal plantings. Seeds planted March 1983, data collected August 1, 1983

Source	Garden location					Means of sources
	Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5	
	percent					
Granite Peak	8	12	0	0	0	4
Medell Flat	2	2	2	0	0	1
Churchill Canyon #1	4	0	0	0	0	1
Churchill Canyon #3	2	2	0	0	0	1
Churchill Canyon #5	24	8	0	0	0	6
Means of locations	8	5	0	0	0	

Table 5.--Percentage establishment of big sagebrush seedlings in five reciprocal plantings. Seeds planted March 1982, data collected April 30, 1984

Location	Treatment	Source of seeds: Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5	Means of location
		percent					
Granite Peak	Location soil	0	0	0	0	0	0
	Constant soil	0	0	0	0	0	0
	Constant soil/marbles	18	2	4	6	10	8
Medell Flat	Location soil	4	0	0	0	16	4
	Constant soil	6	2	0	0	14	4
	Constant soil/marbles	36	8	6	10	32	18
Churchill Canyon #1	Location soil	6	0	0	0	4	2
	Constant soil	0	0	0	0	6	1
	Constant soil/marbles	18	4	6	0	24	10
Churchill Canyon #3	Location soil	0	0	0	0	0	0
	Constant soil	0	0	0	0	0	0
	Constant soil/marbles	6	0	0	0	3	2
Churchill Canyon #5	Location soil	0	0	0	0	0	0
	Constant soil	0	0	0	0	0	0
	Constant soil/marbles	0	0	0	0	0	0
Means of sources	Location soil	2	0	0	0	4	
	Constant soil	1	0	0	0	4	
	Constant soil/marbles	16	3	3	3	14	

The presence of microtopography, provided by the marbles, greatly enhanced the potential of the seedbed to support germination of the quite small big sagebrush seeds. This microtopography modified soil moisture, relative humidity, and temperature in the proximity of the big sagebrush seeds (Evans and Young 1972).

Direct Seeding Experiment - March 1984

Direct seeding in the spring of 1984 gave similar results to the 1983 fall seeding on the soils of the site (data not shown). Seedlings emerged only at Medell Flat and Churchill Canyon #1.

Transplant Experiments

The gardens have not been established long enough for survival to be a meaningful statistic.

Initial establishment in the first growing season was over 95 percent in all gardens for all sources.

In April 1984, we sought to evaluate differences in the sizes of the plants from the various sources in the reciprocal gardens. To take into account differences in growth form (some plants are upright and others nearly decumbent) we calculated an index of above ground biomass as follows:

$$\text{biomass} = \text{height} \times \frac{\text{maximum} + \text{minimum diameter}}{2}$$

The largest plants for all gardens were the mountain big sagebrush plants from the Granite Peak and Churchill Canyon #5 sites (table 6). The basin big sagebrush plants were, after 1 year in the gardens, significantly (P=0.05) smaller.

Table 6.--Biomass (cubic meters) of Artemisia tridentata transplants in five reciprocal gardens. Biomass calculated by Biomass = $\frac{\text{height} \times \text{maximum} + \text{minimum diameter}}{2}$. Data taken April, 1984 on plants transplanted to garden during May, 1983[1]

Source	Garden location: Granite Peak	Medell Flat	Churchill Canyon #1	Churchill Canyon #3	Churchill Canyon #5	Means of sources
Granite Peak	21b-d	26b	14e-g	13f-h	8hi	16a
Medell Flat	18c-f	15d-g	6i	6i	4i	10b
Churchill Canyon #1	24b	13f-h	4i	5i	6i	10b
Churchill Canyon #3	20b-e	22bc	5i	5i	5i	11b
Churchill Canyon #5	18c-f	39a	9g-i	13f-h	5i	17a
Means of locations	20b	23a	8cd	9c	5d	

[1]Means followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's multiple range test. Overall means for sources and locations compared separately.

The gardens supporting the largest plants were at Granite Peak and Medell Flat. Both of these sites have soils derived from decomposing granite compared to mixed alluvium from volcanic or mesovolcanic sources for the soils of the other sites. Plant size of the big sagebrush transplants was smallest at Churchill Canyon #5.

INTERPRETATION OF INITIAL RESULTS

This type of study obviously becomes more meaningful as the time base of observations increases. However, the initial results suggest some interactions of site potential and inherent potential of various collections of big sagebrush.

Seedling establishment of big sagebrush is obviously a rather high-risk venture, even in years of above average precipitation. In perspective, we should remember that, considering the longevity of big sagebrush plants, recruitment to the population is probably not required annually.

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FOLIAGE BIOMASS AND CRUDE TERPENOID PRODUCTIVITY OF BIG SAGEBRUSH (ARTEMISIA TRIDENTATA)

Rick G. Kelsey

ABSTRACT: In spring, overwintering sagebrush leaves expanded in size diluting the concentration of chloroform extractable epidermal chemicals (crude terpenoids). Between June and December leaf biomass decreased one third, and crude terpenoid concentrations doubled. Fifty percent defoliation in late winter did not adversely affect growth, or crude terpenoid concentrations. Plants survived complete defoliation in late winter when leaf primordia and twigs were undamaged. A synthetic crude oil was made from the crude terpenoid extract. Sagebrush has the botanical and chemical characteristics of a desirable biocrude producing plant.

INTRODUCTION

Leaves of big sagebrush (Artemisia tridentata Nutt.) have been described as a two-component chemical system (Kelsey and others 1982). The epidermal surface represents the external component and is characterized by hydrocarbons and oxygenated hydrocarbons in the form of terpenoids stored in glandular trichomes (Kelsey and Shafizadeh 1980) and waxes that are part of the cuticle (Silva Fernandes and others 1964; Thomas 1976). These compounds are readily accessible and easily removed by washing fresh whole leaves in organic solvents. Drying and weighing the extract provides a quantitative measure of the epidermal chemicals, also called crude terpenoids (Kelsey and others 1982). Because of their high concentrations, and ease of removal, crude terpenoids might provide a renewable source of oxygenated hydrocarbons for energy, chemical feedstocks, or specialty chemicals. Compounds in glandular trichomes are also of interest because of their potential as chemical defenses against herbivores (Kelsey and others 1983), pathogens, and associated vegetation (Klarich and Weaver 1973; Weaver and Klarich 1977; Kelsey and others 1978).

Constituents within leaves represent the internal chemical component characterized by cell wall polymers, protein, nonstructural carbohydrates, and some lipids. Extraction of crude terpenoids with chloroform removed all of the monoterpenes, greatly reduced ether extractives (crude fat), had minimal effect on protein content, and concentrated nonstructural carbohydrates in the residue (Kelsey and others 1982). This suggests an improved nutritional quality and potential for use as a livestock feed. Removing crude terpenoids increased digestibility by an average of 15 percent in vitro, using rumen fluid from sheep (Striby and others 1982).

Yield of crude terpenoids from a plant depends on the quantity of foliage and concentration of epidermal chemicals. Peak foliage biomass occurs after spring growth, before overwintering leaves begin to drop, when crude terpenoids are at their lowest concentration. Conversely, in fall and winter, leaf biomass is minimal and crude terpenoid content is at its highest (Kelsey and others 1982). In which season would the greatest yield of epidermal chemicals from a plant occur?

In spring, sagebrush growth began when all overwintering leaves (not just those near the leaf primordia) expanded and became physiologically active, as indicated by increasing quantities of crude protein and total nonstructural carbohydrates (Kelsey and others 1982). Simultaneously, there was a decline in crude terpenoid concentration. Data suggested the epidermal chemicals were diluted by increased leaf size. If so, crude terpenoid concentration should remain relatively constant when measured in quantity per leaf rather than quantity per unit of dry matter. If chemicals remain on the epidermal surface during spring growth, the yield per plant should remain high, but extraction would require processing more tissue.

Portions of a sagebrush crown can be harvested without adversely affecting its growth. The response depends upon the amount of tissue removed and phenological stage, or season harvested (Cook and Stoddart 1960; Wright 1970; Cook 1971). Partial defoliation by herbivores (rabbits, sage grouse, antelope, and mule deer) can occur throughout the year, but is usually most frequent during late fall, winter, and early spring months when other sources of forage are unavailable (Sundstrom and others 1973; Wallestad 1975; Green and Flinders 1980; Welch and others 1981). Bryant (1981) reports that adventitious shoots sprouting from boreal trees after heavy browsing by snowshoe hares contain significantly higher concentrations (at least double) of ether-soluble resins compared to mature-growth-form twigs. Higher resin contents in the adventitious

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Rick G. Kelsey is Research Associate Professor, Department of Chemistry, University of Montana, Missoula, MT.

shoots make them unpalatable to hares, thus providing the trees with some protection against herbivory. Could chemical changes associated with herbivore defoliation of sagebrush influence palatability of the regrowth? If defoliation does cause changes in crude terpenoid concentrations, what are the implications for producing high energy compounds?

The objectives of this research were to provide answers for the following questions:

1. During what time of year would the yield of epidermal chemicals from whole sagebrush plants be greatest?
2. When overwintering sagebrush leaves expand during spring growth, is there a change in the quantity of epidermal chemicals on the leaf surface?
3. What effect does defoliation have on the growth and vigor of sagebrush plants, and what is the crude terpenoid concentration in the regrowth?
4. Could sagebrush be used as a renewable source of biocrude chemicals, or other commercial materials?
5. Do data from the above experiments provide new insight into the hypothesis that epidermal chemicals of sagebrush constitute a chemical defense mechanism against herbivores.

MATERIALS AND METHODS

Crude Terpenoid Analysis

In the field, plant samples collected for crude terpenoid analysis were placed in Ziploc plastic bags, transported on ice to the lab, sealed in a second Ziploc bag, and stored in the freezer. Fresh frozen tissue was considered fresh since freezing caused no external signs of tissue damage. Before analysis each sample was frozen with liquid nitrogen; leaves were dislodged and separated from the woody tissue and then resealed in a plastic bag until adjusted to room temperature. If leaves could not be analyzed immediately, they were returned to the freezer in double plastic bags. After reaching room temperature, duplicate samples were weighed for extraction (2-8 g) and moisture content determination (1-2 g, 100 °C overnight 15 hours, cooled in a desiccator 30 minutes, then weighed). Leaves were washed for five minutes with chloroform (24 ml per g of fresh tissue) then filtered through coarse paper (Schleicher and Schuell sharkskin, cut to 14-cm diameter) into a preweighed flask. Chloroform was removed on a roto-evaporator with reduced pressure and a water bath (30-40 °C). Final traces of chloroform were removed by increasing the water bath temperature to 60-65 °C for one hour. The flask was wiped dry, desiccated for 30 minutes, and weighed.

In previous experiments, all crude terpenoid measurements have been restricted to leaf tissue in order to make accurate comparisons quantitatively on a seasonal basis and between taxa. Inclusion of woody tissue has been avoided because the proportion in current year's growth varies considerably between taxa. This experiment was conducted to see how crude terpenoid concentrations in other tissues compare with those in the leaves. A large composite sample of basin big sagebrush (Artemisia tridentata Nutt. ssp. tridentata) was collected at Perma, MT, on August 31, 1981, sealed in a plastic bag, transported on ice, and stored at subfreezing temperatures. Four tissues (leaves, twigs, twigs with attached leaves, and flower heads) were analyzed in triplicate for crude terpenoids.

Study Site

The study site for all field experiments discussed below was located in a stand of mountain big sagebrush (A. tridentata ssp. vaseyana (Rydb.) Beetle) at Lavalle Creek near Missoula, MT. The area was grazed each summer by cattle, but this had minimal effect on the experimental plants.

Overwintering Leaf Measurements

Previous studies demonstrated that all overwintering leaves expanded in length and width during spring (Kelsey and others 1982). Accompanying increases in dry weight could dilute the crude terpenoids, causing a decreased concentration when expressed as a percentage of dry weight. Effects of dry matter changes were eliminated by measuring the quantity of crude terpenoids from 200 overwintering leaves before and after spring growth. On March 9, 1982, prior to any growth, eight mature shrubs were tagged and sampled. Two hundred leaves were analyzed for crude terpenoids (using the same ratio of solvent to tissue given above), 100 were ovendried (as above), and 10 were measured fresh for length and width. All leaves were randomly selected. The same plants were resampled June 8, 1982, after leaf expansion. Before freezing with liquid nitrogen, all new tissue was removed, and the remaining overwintering leaves were analyzed again as described.

Spring Changes in Twig Biomass

To measure changes in foliage biomass during spring growth, five mature plants were selected for study on April 2, 1982. Three pairs of twigs were marked on each plant. Each pair was carefully chosen to be approximately equal in length, amount of woody tissue, and number of leaves. One twig of each pair was clipped, returned to the laboratory, and air-dried. Leaves and woody tissue were separated, then ovendried and weighed. The second twig of each pair was clipped June 8, 1982, and processed in the same manner.

Spring and Fall Foliage Biomass

Seasonal change in leaf biomass was determined on 10 pairs of mature plants. On June 17, 1982,

shrub pairs growing in close proximity were chosen for similarity in crown dimensions (length, width, height) and leaf biomass (ocular estimate). One plant of each pair was clipped at ground level, returned to the laboratory, and air-dried. Leaves were separated from woody stems, ovendried, and weighed. The remaining plants were clipped December 2, 1982, and the procedure repeated.

Effects of 50 Percent Defoliation

The following experiment was designed to determine what effect removing 50 percent of the sagebrush foliage in late winter would have on plant growth, biomass, and crude terpenoid concentrations. On March 10, 1982, prior to the start of spring growth, five pairs of shrubs were marked and measured (maximum live crown length, maximum live crown width perpendicular to length, and height of tallest vegetative branch). Pairs were growing close to one another and had similar crown sizes and leaf biomass. Between March 23 and 26, 1982, the treatment plant of each pair was clipped to remove 50 percent (ocular estimate) of the leaf tissue on every twig throughout the crown. Clippings were carefully gathered, sealed in a plastic bag, transported to the lab on ice, and weighed fresh. Duplicate subsamples were ovendried to calculate dry weights and percentage of leaf tissue. The remaining fresh tissue was frozen and analyzed for crude terpenoids. A small sample of leaves was gathered from the control plant at the same time the treatment shrub was clipped; it was frozen and analyzed for crude terpenoids. One year later between March 8 and 21, 1983, plants were clipped a second time and analyzed as before. At the end of the second growing season, on November 22 and 29, 1983, live crown dimensions were remeasured for all plants. Foliage samples were clipped from both treatment and control plants. After determining fresh leaf weight, subsamples were removed for duplicate moisture determinations and the remaining fresh leaves were analyzed for crude terpenoids. To measure total leaf biomass on the plants, each was clipped at ground level after the foliage sample had been taken. Air-dried leaves were separated from woody tissue, ovendried, and weighed. Dry weights of leaf samples collected for crude terpenoid analysis were added to the leaf biomass for a total.

Effects of Complete Defoliation

In previous sagebrush clipping experiments, plants were defoliated by cutting twigs to remove some portion of the current year's growth (Cook and Stoddart 1960; Wright 1970; Cook 1971) in a manner similar to ungulate grazing. Carbohydrates are stored in twigs at high concentrations during the early portion of spring growth, but then decline as new vegetative stems mature and flower stalks develop (Coyne and Cook 1970). To determine how plants would respond if completely defoliated, without damaging leaf primordia or twigs, three pair of plants were selected as described in the previous experiment. Live crown dimensions were measured and all overwintering leaves carefully picked from the treatment plant (one pair set up on March 8, 26, and 30, 1982). The leaves were ovendried and weighed. One year later the defoliation was repeated (March 1, 2, 3, and 8, 1983); leaves were weighed fresh, analyzed in duplicate for moisture content, and the remaining fresh tissue frozen for crude terpenoid analysis. A small leaf sample was also collected from each control plant for crude terpenoid analysis. At the end of the 1983 growing season (November 22, 1983), live crown dimensions were remeasured, leaf samples were gathered for crude terpenoid analysis, and plants were clipped at ground level. Whole plants were air-dried; the leaves were removed, ovendried, and weighed. Leaf dry weights from samples used for crude terpenoid measurements were determined as in the previous experiment and then added back for total leaf dry weight per plant.

Biocrude Production

Crude terpenoid extract is a mixture of monoterpenes, sesquiterpene lactones and cuticular waxes (Kelsey and others 1982) with a 21 percent oxygen content. Conversion of this material into a synthetic crude oil by hydrogenation was tested by Dr. Alan Peterson, Marathon Oil Company, Littleton, CO, using 200 g of extract, prepared as described above, but on a larger scale.

Screening for Biologically Active Compounds

Many terpenoids that occur in glandular trichomes on the epidermis of plants are biologically active, possessing antiherbivory, antifungal, antimicrobial, and herbicidal properties (Kelsey and others 1984). To test for active compounds with potential agricultural uses, crude terpenoid extracts were fractionated and sent to Dow Chemical Company, Walnut Creek, CA, for screening in a series of bioassays. Activities of interest included insecticidal, herbicidal, bactericidal, and fungicidal. In phase I of testing, crude terpenoid extracts were prepared from frozen foliage (stems and leaves combined) of eight sagebrush taxa: A. tridentata ssp. vaseyana--high-elevation chemotype (Kelsey and others 1973; Bhadane and others 1975); A. tridentata ssp. vaseyana var. spiciformis (Osterh.) Beetle; A. tridentata ssp. tridentata; A. tridentata ssp. wyomingensis Beetle & Young; A. tripartita Rydb. ssp. tripartita; A. nova Nels.; A. cana Pursh ssp. viscidula (Osterh.) Beetle; and A. longiloba (Osterh.) Beetle collected between August 31 and September 4, 1981. A sample of A. tridentata ssp. vaseyana--low-elevation chemotype (Kelsey and others 1973) collected March 27, 1981, was also extracted.

Each extract was further fractionated into three components. Before removing all chloroform from the extract, it was transferred to a 3-neck round-bottom flask and dried on a roto-evaporator for one hour with vacuum and a 60-65 °C water bath. The residue was distilled with steam delivered to the extract by a glass tube inserted

through a rubber stopper in one of the three openings. Monoterpenes passed into a condenser and were collected over a column of water. The oil was drained into a vial, water drops removed with a pipette, and traces of water eliminated by leaving the open vial in a desiccator overnight. This was fraction 1. Water had condensed in the 3-neck flask during steam distillation and was evaporated on the roto-evaporator. The non-volatile residue left in the flask was dissolved in hot ethanol, transferred to a separatory funnel, and diluted with an equal volume of water. This solution was washed with several portions of hexane that were combined, evaporated, and dried (as for chloroform above) to give fraction 2. The ethanol-water was then extracted with chloroform which was evaporated and dried to give fraction 3. Leaves washed with chloroform for the crude terpenoid extract were air-dried and ground to pass a 20 mesh screen. This tissue was further extracted in methanol (10 ml per g) for 30 minutes with occasional stirring. The solution was filtered through sharkskin paper, evaporated, and dried (as above) to give fraction 4.

Since fraction 3 of all taxa, except A. tridentata ssp. vaseyana var. spiciformis, possessed some degree of fungicidal activity in phase I, this fraction was selected for futher study. Forty grams of fraction 3 were prepared for each of the following taxa: A. tridentata ssp. vaseyana; A. nova; A. tridentata ssp. tridentata; A. tripartita ssp. tripartita; and A. cana ssp. viscidula, collected between July 23 and September 17, 1982. Using column chromatography (7 x 68 cm column, packed wet with silica gel 60-200 mesh, and eluted with dichloromethane or chloroform with increasing amounts of ethyl acetate) these taxa samples were each divided into five parts and sent to Dow for further testing. Nine sesquiterpene lactones and two unknown flavonoids present in the extracts, but isolated previously, were also sent for testing.

Statistical Analysis

All data were analyzed statistically using the t-test for paired comparisons (Sokal and Rohlf 1981) at the 0.05 level of probability, unless otherwise stated.

RESULTS

Crude Terpenoid Content of Woody Twigs and Flower Heads

Leaves had the greatest concentration of crude terpenoids (table 1) and woody twigs the least; flower heads were intermediate. Samples containing leaves attached to twigs had the second highest concentration, just below leaves alone.

Spring Changes in Overwintering Leaves

Overwintering leaves increased in length and width on all eight plants examined (table 2).

Table 1.--Crude terpenoid concentrations in various tissues of basin big sagebrush (Artemisia tridentata ssp. tridentata)

Tissue	Crude terpenoids
	Percent dry weight
Leaves	[1]26.6 ± 1.0
Twigs with leaves	21.2 ± 1.0
Twigs	7.7 ± .6
Flower heads	14.4 ± .4

[1]± Standard deviation.

Table 2.--Changes in length, width, dry weight, and crude terpenoid concentrations for overwintering mountain big sagebrush leaves, during spring growth

	Amount of change[1]			
Plant	Length	Width	Dry weight	Crude terpenoids
	Millimeters per 10 leaves		Milligrams per 100 leaves	Milligrams per 200 leaves
1	10.5	2.4	740.6	12.8
2	3.9	1.7	102.6	-16.1
3	11.8	2.2	725.7	31.4
4	4.0	1.3	-18.4	12.7
5	2.5	.0	103.8	-.9
6	2.6	.4	144.0	17.7
7	4.0	.7	206.1	-1.6
8	.7	.5	-49.4	-3.3
$\bar{X}$	[2]5.0	[2]1.2	[3]244.3	6.6

[1]Numbers represent amount of increase for the growth period between March 17 and June 8, 1982. - indicates decreases.
[2]Lengths and widths were significantly greater ($\alpha = 0.05$) in June.
[3]Dry weights were significantly greater ($\alpha = 0.10$) in June.

Table 3.--Paired twig biomass before (April) and after (June) spring growth of mountain big sagebrush, 1982

Plant	Biomass: Woody twig April	Woody twig June	Leaves April	Leaves June	Total April	Total June	Percent leaves in total: April	Percent leaves in total: June
	Milligrams dry weight							
1	[1]118	314	251	615	369	929	68.6	66.9
2	169	370	254	725	423	1,095	59.3	66.6
3	137	404	340	843	477	1,247	72.1	69.6
4	105	169	295	523	400	692	75.0	76.7
5	124	297	229	638	354	935	66.0	68.8
[2]$\bar{X}$	133	[3]321	272	[3]679	405	[3]1,000	67.7	[4]69.2

[1]An average of three twigs per plant, except plant 4 with two twigs.
[2]Averages calculated from 14 twig measurements on each date, instead of the five plant averages in the table.
[3]Significantly greater than the April value ($\alpha = 0.001$).
[4]Not significantly different from the April value ($\alpha = 0.05$).

This was accompanied by an increase in leaf weight for six of the eight plants. Overall, average dry weight of 100 leaves increased by 244.3 mg. These changes in leaf sizes were statistically significant. Crude terpenoid concentrations increased in four plants and decreased in four others. Three decreases, however, were quite small. The average concentration increased 6.6 mg per 200 leaves between March and June, but the difference was not significant. This supports the hypothesis that a spring decrease in crude terpenoid concentrations in old overwintering leaves, prior to new leaf growth, is primarily a dilution effect from increased dry matter. Consequently, the quantity of epidermal chemicals per leaf remains about the same, or maybe increases slightly.

Spring and Fall Foliage Biomass

Total twig biomass increased 2.5 times between April 2 and June 8 (table 3), with leaf (2.6 times) and woody twig (2.5 times) biomass changing in the same proportions. The ratio of leaf to woody tissue remained constant at about 2:1. Between June and December, leaf biomass decreased an average of 30.8 percent per plant (table 4). At the same time, average crude terpenoid concentration increased from 6.3 percent to 11.2 percent. Plants harvested in December would have provided 10 percent more crude terpenoid extract from about two-thirds the quantity of dry matter present in the spring.

Table 4.--Harvestable leaf biomass and crude terpenoid extract from mountain big sagebrush in spring and fall, 1982

Plant pair	Leaf biomass: June	Leaf biomass: December	Leaf biomass: December as percent of June	Estimated[1] crude terpenoid yields: June	Estimated[1] crude terpenoid yields: December
	Grams dry weight			Grams	
1	39.2	35.2	89.9	2.5	3.9
2	96.2	58.6	60.9	6.1	6.6
3	43.1	22.6	52.4	2.7	2.5
4	119.3	72.9	61.1	7.5	8.2
5	178.5	79.8	44.7	11.2	8.9
6	61.9	36.0	58.2	3.9	4.0
7	34.8	41.9	120.3	2.2	4.7
8	56.7	47.6	84.1	3.6	5.3
9	125.1	69.4	55.5	7.9	7.8
10	62.1	40.4	65.0	3.9	4.5
TOTAL	[2]816.9	504.4	$\bar{X}$ = 69.2	51.5	56.4

[1]June yields were estimated using the June 8, 1982 average crude terpenoid concentration measured for 200 overwintering leaves, from each of eight plants ($\bar{X}$=6.3 percent). This compared with the 6.6 percent crude terpenoid concentration measured for all leaves in the crown on June 5, 1980 (see fig. 1, Kelsey and others 1982). November yields were calculated using the November 22 and 29, 1982, average crude terpenoid concentration ($\bar{X}$=11.2 percent) from seven control plants in the 50 percent and complete defoliation experiments.
[2]June values were significantly larger ($\alpha = 0.05$).

Effects of 50 Percent Defoliation

Prior to clipping, treatment and control plants had similar crown sizes (table 5) and crude terpenoid concentrations (table 6) in the 50 percent defoliation experiment. After two growing seasons, control plants had significantly increased their crown sizes. Crowns of four defoliated plants were also larger, but still significantly smaller than controls. Nevertheless, treated plants continued to produce substantial foliage (table 7). At the end of the experiment, four out of five control plants had more foliage biomass than their corresponding treatment plants, but the difference was not significant. Each year after spring growth was complete, it was difficult to visually distinguish which shrubs had been clipped just a few months earlier. Defoliation had no effect on crude terpenoid concentrations (table 6).

Table 5.--Effect of 50 percent late winter defoliation, for two consecutive years, on crown size of mountain big sagebrush

Plant pair	Crown size[1] Before clipping, March 1982[2]	Eight months after second clipping, November 1983[3]	Percent change
	- - - Centimeters - - -		
[4]1T	135	170	+26
1C	172	234	+36
2T	256	261	+2
2C	251	272	+8
3T	340	376	+11
3C	388	410	+6
4T	301	297	-1
4C	304	333	+10
5T	142	153	+8
5C	165	206	+25

[1]Crown length, width, and height measurements added together.
[2]When the experiment began, crown sizes of treatment and control plants were not significantly different.
[3]When the experiment ended, treatment crowns had not changed significantly from the start, but they were significantly smaller than control crowns. Control crowns did increase significantly in size during the experiment.
[4]T = treatment, 50 percent defoliated; C = control.

Table 6.--Effect of 50 percent late winter defoliation, for two consecutive years, on the crude terpenoid concentrations of mountain big sagebrush leaves

Plant pair	Crude terpenoid concentration: Before clipping, March 1982	One year after first clipping, March 1983	Eight months after second clipping, November 1983
	- - - Percent dry weight - - -		
[1]1T	7.5	10.5	10.1
1C	5.6	10.9	10.1
2T	9.8	16.2	13.0
2C	8.6	13.1	-
3T	7.8	10.9	11.4
3C	11.3	11.6	12.6
4T	9.6	14.1	13.0
4C	8.4	12.5	11.6
5T	7.1	11.3	11.2
5C	8.5	12.4	9.7
$\bar{X}$T	[2]8.4	[2]12.6	[2]11.4
$\bar{X}$C	8.5	12.1	11.0

[1]T = treatment, 50 percent defoliated; C = control.
[2]No significant difference between treatment and control.

Table 7.--Biomass from 50 percent late winter defoliated mountain big sagebrush, after two consecutive years of treatment

Plant pair	Twig and leaf biomass from 50 percent clip: First clipping, March 1982	Second clipping, March 1983	Total leaf biomass: Eight months after second clipping, November 1983	Percent leaf in 50 percent clippings: March 1982	March 1983
	- - -Grams dry weight- - -				
[1]1T	14.6	30.5	[2]62.7	79.2	80.5
1C	-	-	91.1	-	-
2T	29.6	59.2	68.7	78.5	79.0
2C	-	-	97.7	-	-
3T	78.4	192.3	195.6	69.1	78.4
3C	-	-	367.2	-	-
4T	45.1	88.3	161.4	67.7	73.0
4C	-	-	151.8	-	-
5T	18.9	43.4	44.7	71.2	75.0
5C	-	-	57.5	-	-
$\bar{X}$				73.1	77.2

[1]T = treatment, 50 percent defoliated; C = control.
[2]No significant difference between treatment and control group.

Effects of Complete Defoliation

The response of completely defoliated plants appeared to be dependent on the amount of competition from associated shrubs. Plants in pair 1 were both growing with little competition from other sagebrush. The treated plant increased crown size and maintained leaf dry matter at 70 percent of the control (tables 8 and 9). Plant pair 2 grew closer to other shrubs and experienced more competition than pair 1. Live crown of the treated plant decreased 26 percent from its original size; leaf biomass was 53 percent of control. The third plant pair grew side by side, with completely overlapping root systems, but no competition from other shrubs. Weakening the competitive ability of the treated plant would directly benefit the control. Results indicate this type of relationship existed. Live crown size for the defoliated plant decreased 19 percent; leaf dry weight was only 7 percent of the control. Release from competition resulted in a 59 percent increase in the control crown size, the largest increase of any plant in either defoliation experiment. Live crown size of controls and treatments did not differ significantly at either the beginning or end of this experiment. Although foliage biomass was consistently greater on all control plants at the end of two years, this difference was not significant due in part to the small sample number. Leaf sizes were smaller on treated plants in both defoliation experiments, but the difference was most obvious when foliage had been completely removed. Crude terpenoid concentration was consistently higher in defoliated plants after the first year, but it was not significant (table 10). After a second treatment, crude terpenoid concentrations were equal in the two groups.

Table 8.--Effect of complete late winter defoliation, for two consecutive years, on crown size of mountain big sagebrush

Plant pair	Crown size[1]		
	Before defoliation, March 1982	Eight months after second defoliation, November 1983	Percent change 1982-83
	- - - -Centimeters- - - -		
[2]1T	[3]188	[4]204	8.5
1C	164	218	32.9
2T	149	110	-26.2
2C	149	156	4.7
3T	95	77	-18.9
3C	129	205	58.9

[1]Crown length, width, and height measurements combined.
[2]T = treatment, completely defoliated; C = control.
[3]No significant difference between treatment and control group.
[4]No significant difference between treatment and control group; controls March 1982 vs. controls November 1983; or treatments March 1982 vs. treatments November 1983.

Table 9.--Effect of complete late winter defoliation, for two consecutive years, on leaf biomass of mountain big sagebrush

Plant pair	Leaf biomass		
	First defoliation, March 1982	Second defoliation, March 1983	Eight months after second defoliation, November 1983
	- - - - - - Grams dry weight - - - - - -		
[1]1T	45.6	62.3	[2]63.4
1C	-	-	91.1
2T	12.8	14.5	12.9
2C	-	-	24.2
3T	10.0	13.2	8.1
3C	-	-	124.7

[1]T = treatment, completely defoliated; C = control.
[2]No significant difference between treatment and control group.

Table 10.--Effect of complete late winter defoliation, for two consecutive years, on crude terpenoid concentrations of mountain big sagebrush

Plant pair	Crude terpenoid concentration	
	One year after first defoliation, March 1983	Eight months after second defoliation, November 1983
	- - - - - Percent dry weight - - - - -	
[1]1T	[2]17.6	[2]13.7
1C	12.5	12.0
2T	16.5	9.9
2C	10.1	13.1
3T	14.4	14.7
3C	13.5	12.4
$\bar{X}$T	16.2	12.8
$\bar{X}$C	12.0	12.5

[1]T = treatment, completely defoliated; C = control.
[2]No significant difference between treatment and control group.

Biocrude Production

Plant products have the potential to be utilized as renewable sources of fuels and chemicals (Weisz and others 1979; Buchanan and others 1980; Calvin 1980; Johnson and Hinman 1980; Buchanan and Duke 1981; Wang and Huffman 1981). Monoterpenes and sesquiterpenes can be burned directly as liquid fuel (Calvin 1980; Wang and Huffman 1981) or catalytically cracked into gasoline (Weisz and others 1979; Calvin 1980). Experiments at Marathon Oil indicated that direct catalytic cracking of the crude terpenoid extract in a conventional fluid catalytic cracking unit was not an attractive method for producing liquid fuels, because of the relatively high oxygen (21 percent) content. A desired alternative was to produce a synthetic crude oil (biocrude) by hydrogenating the extract to remove oxygen. The resulting oily liquid contained 87.97 percent carbon, 11.94 percent hydrogen, 0.11 percent nitrogen, 0.07 percent sulfur, and no oxygen, and could be refined by conventional methods. There is reason to believe that crude terpenoids could be upgraded by hydrotreating more easily than processing either shale oil or residual oils.

Screening for Biologically Active Compounds

In phase I of the screening program for biological activity by Dow Chemical Company, 36 plant extracts (four from each of nine chemotypes) were tested. Extracts had no agriculturally significant herbicidal or insecticidal activity. Twenty-five extracts were antimicrobial at 500, 250, or 100 ug/ml, and most were inhibitory toward more than one bacterial species. Anaerobic microbes were more sensitive to the extracts than aerobic bacteria. Of all four fractions from a taxa, the hexane soluble compounds in fraction 2 were most antimicrobial, followed by 3, 4, and 1. Artemisia nova fractions inhibited the greatest number of bacterial species.

Extracts demonstrated a rather broad spectrum of fungicidal activity for six fungi species, but mainly against Piricularia oryzae (systemic rice blast) and Plasmopara viticola (grape downy mildew). Four fractions inhibited systemic rice blast and 15 were active toward grape downy mildew. Within a sagebrush taxa fraction 3 was most frequently active, followed by 2, 4, and 1.

In phase II, the five most active third fractions were prepared fresh, divided into five parts by column chromatography and each part bioassayed. In addition, pure crystalline sesquiterpene lactones, known to be present in the extracts, were tested. With the exception of A. tridentata ssp. tridentata, all five column parts from each sagebrush taxa were inhibitory to rice blast growth. Grape downy mildew was no longer available for testing, but based on results of phase I this fungi would also have been inhibited by these fractions. Surprisingly, none of the sesquiterpene lactones inhibited systemic rice blast fungi, suggesting the active constituent(s) was not a major terpenoid compound. Unfortunately, Dow was phasing out their fungicidal research and was unable to further evaluate this activity.

DISCUSSION

In recent years, the possibility of utilizing plant constituents as a renewable source of high energy compounds (biocrude), and organic chemicals has been given serious attention (Buchanan and others 1980; Johnson and Hinman 1980; Wang and Huffman 1981). Plants capable of growing in semiarid and arid regions of the Southwestern United States and Mexico (Campos-Lopez and Roman-Alemany 1980; Johnson and Hinman 1980; McLaughlin and Hoffmann 1982) have been considered good candidates for development because they grow in hot, dry, sunny areas where inadequate water supplies have traditionally limited agriculture. Botanical as well as chemical characteristics of these plants are important (Buchanan and others 1978). Furthermore, methods used in conventional agriculture may have to be modified in order to function within the constraints associated with arid environments. A common goal for many plant growers and breeders has been to maximize dry matter production, but according to McLaughlin and others (1983) this may be inappropriate for biocrude crops on arid lands.

Sagebrush is already prolifically abundant in semiarid regions of the western United States ranging from Mexico to Canada (McArthur and Plummer 1978; McArthur and others 1979). Its presence has been estimated on 1.1 million square kilometers at varying densities (Beetle 1960). Although the plants play an important role as winter forage for wildlife and in soil stabilization (McArthur and others 1979), there are many areas where populations are more than adequate, or not needed at all. These shrubs, having evolved in western North America (McArthur and Plummer 1978; McArthur and others 1981), are adapted and well suited to their semiarid environments. It's unlikely they could be easily eradicated and replaced by other biocrude-producing plants. There are many examples illustrating that sagebrush can reinvade sites where it has been destroyed (Bleak and Miller 1955; Johnson 1969; Harniss and Murray 1973). When big sagebrush is heavily clipped, growth will decrease substantially, and it can kill the plants (Cook and Stoddart 1960; Cook 1971); but, as indicated in this study and in others (Wright 1970; Cook 1971), the crown can be partially defoliated every year in fall or winter without detrimental effects on growth or concentration of epidermal chemicals. If shrub eradication was the primary objective for a site, whole plants could be harvested and extracted. Continuous biocrude production might be achievable by partial crown harvesting on a yearly basis. To minimize physiological damage to the plants, cutting could take place any time of the year

except spring and early summer (Cook 1971). Fall or winter harvesting would have the least impact on plant growth (Wright 1970; Cook 1971), and crude terpenoid concentrations would be at their maximum. Silver sagebrush (A. cana) and threetip sagebrush (A. tripartita) might be ideal for yearly harvesting since they regrow from root sprouts (Beetle 1960; White and Currie 1983). Optimal harvest time for silver sagebrush would differ from big sagebrush because of its deciduous nature (Beetle 1960).

At first thought, the potential for using sagebrush as a biocrude-producing plant might seem limited; however, on close examination the possibility appears feasible. This is especially true if one accepts the premise that traditional agricultural concepts may have to be modified in order to effectively utilize arid and semiarid lands in this country (McLaughlin and others 1983).

Our studies have demonstrated that sagebrush produces chemicals (a complex mixture of hydrocarbons and oxygenated hydrocarbons) on its epidermal surface that are easily removed by solvent extraction (Kelsey and others 1982). Crude terpenoids are obtainable without drying or grinding the plant tissue and once isolated they can be converted to a crude oil. Chemical yields could be increased by further extracting the leaves with a more polar solvent, ethanol or methanol (McLaughlin and Hoffmann 1982; Adams and McChesney 1983) and including the woody tissues that contain about 8 percent extractables (Shafizadeh and Buckwa 1970). Accumulation of crude terpenoids on the leaves is not affected by enhanced growth from fertilization (Kelsey, this proceedings), or stress caused by heavy defoliation (this study). Increasing biomass productivity would directly increase the plant yield of biocrude chemicals.

Chemical analysis suggests that extracted foliage also could be used as a livestock feed provided that large quantities of woody tissue were not included (Kelsey and others 1982). Ethanol-extracted sagebrush leaves combined with alfalfa were readily consumed by sheep, and the mixture provided adequate nutrient quality for a maintenance diet (Striby and others 1983). In vitro digestibility of sagebrush was significantly improved after extraction with chloroform (Striby and others 1982). If shrub damage was not an important consideration, cutting near the end of spring would provide maximum foliage quantity and nutrient quality for livestock feed after extraction. Crude terpenoid yields would still be high, although greater volumes of plant material would have to be processed.

Other botanical characteristics of sagebrush contribute to its desirability as a biocrude plant. Seed production is prolific (Harvey 1981). Being wind-pollinated, the flower stalks rise above the canopy so that seed collection is fast, easy, and inexpensive (Plummer and others 1968). Germination in the lab and field varies from poor to excellent depending on a variety of factors (McDonough and Harniss 1974; Harniss and McDonough 1976; Sabo and others 1979; Stidham and others 1980; Kelsey, this proceedings). A newly germinated sagebrush seedling is not very hardy and is susceptible to damage or death by frost, drought, competition, pathogens, and herbivores. Seedling survival in the field can be very low (Harvey 1981). Even though few seedlings are observed in natural sagebrush stands (Johnson 1969; Harniss and Murray 1973; Hazlett and Hoffman 1975), reproductive success is adequate to populate 1.1 million square kilometers (Beetle 1960) and reinvade areas treated for shrub eradication (Bleak and Miller 1955; Johnson 1969; Harniss and Murray 1973). Problems with new seedling mortality can be reduced by transplanting older seedlings from nursery stock and native stands (Plummer and others 1970; Long, this proceedings), or possibly rooted stem cuttings (Everett and others 1978). Growth is dependent on taxa, geographic origin of the taxa, chromosome numbers, and environmental influences (Harniss and McDonough 1975; McArthur and Welch 1982; Kelsey, this proceedings). Big sagebrush, the most widespread and abundant species, will grow on a variety of soils (Passey and Hugie 1962; McArthur and others 1979). It is interesting to note that basin big sagebrush (ssp. tridentata) is the fastest growing big sagebrush subspecies (McArthur and Welch 1982) and also produces the greatest quantities of crude terpenoids (Kelsey and others 1982). Out of 77 shrub species evaluated, big sagebrush had the best suitability index for use in restoring big game ranges in Utah (Plummer and others 1968). Many of the highest rated botanical characteristics--establishment, persistence, natural spread, growth rate, herbage yield, and availability of current growth--are also indicators of a good biocrude species.

The function of sagebrush chemicals as a defense against herbivores has just begun to be studied. The problem is very complex because the shrubs produce a variety of compounds that might be involved (monoterpenes, sesquiterpene lactones, highly volatile nonterpenoids, and phenolics) and their activities may be influenced by synergistic effects (Kelsey and others 1983). There is also a range of potentially affected herbivores (insects, livestock, and wildlife). Their responses to the various groups of compounds may be different. For example, Narjisse (1981) found that sheep discriminate against sagebrush monoterpene odor, whereas goats discriminate against the taste. Welch and others (1983) reported no correlation between the monoterpene content of five sagebrush taxa and their differential preference by mule deer. Much more needs to be learned before chemical interactions between sagebrush and herbivores can be fully understood.

Nevertheless, various observations and current knowledge imply that sagebrush plants are protected by a chemical defense mechanism. Native herbivores (pygmy rabbits, sage grouse, mule deer, and antelope) that have coevolved with the shrubs are heavy users compared to introduced domestic species (horses, goats, sheep, and cattle) (Sundstrom and others 1973; Hansen and

Reid 1975; Wallestad 1975; Olsen and Hansen 1977; Johnson 1979; Green and Flinders 1980; Narjisse 1981; Hanley and Hanley 1982). Given free access to the three subspecies of big sagebrush, mule deer prefer to utilize ssp. vaseyana over ssp. tridentata (Welch and others 1981; Sheehy and Winward 1981) even though the latter is more digestible (Welch and Pederson 1981; Striby and others 1982) and maintains a higher crude protein content during winter (Welch and McArthur 1979). Monoterpenes do not appear to be associated with this selection preference (Welch and others 1983). We have found other chemical differences that might be influencing mule deer. Subspecies tridentata consistently produces larger quantities of crude terpenoids, and it has greater concentrations of highly volatile nonterpenoid compounds such as methacrolein (Scholl and others 1977; Kelsey and others 1982; Striby and others 1982; Personius and others, unpublished results). In selection tests, grasshoppers preferred sagebrush extracted with chloroform over fresh tissue from the same plant (Geiselman and Kelsey, unpublished observations).

Furthermore, terpenoid constituents in glandular trichomes are concentrated on the tissue surface where they can most effectively exert a variety of biological activities (Kelsey and others 1984). Sagebrush monoterpenes and sesquiterpene lactones are located in glandular trichomes (Kelsey and Shafizadeh 1980) and these compounds are known to be antimicrobial (Nagy and others 1964; Nagy and Tengerdy 1967, 1968; Oh and others 1968; Weaver and Klarich 1976; Picman and Towers 1983), phytotoxic (McCahon and others 1973; Klarich and Weaver 1973; Weaver and Klarich 1977), and allergenic (Mitchell and others 1970; Mitchell and Dupuis 1971; Mitchell and Epstein 1974). It is not known if the highly volatile methacrolein is a glandular constituent, but it is recognized as a volatile animal toxin and mucus tissue irritant (Lewis and Tatken 1980). These shrubs are certainly armed with an arsenal of defense compounds.

Effectiveness of a chemical defense is dependent on the type of active compounds present and their quantities. Concentrations and compositions of sagebrush epidermal chemicals are genetically controlled with distinct differences between taxa (Kelsey and others 1982, 1983; Kelsey, this proceedings; Personius and others, unpublished results). Crude terpenoid concentrations are also influenced by environmental factors affecting growth; quantities vary from year to year within the same plant, depending on growing conditions (Kelsey and others 1982, and this study). Degree of protection is then regulated by genetic and environmental control of biosynthesis. As demonstrated in this study, sagebrush lacks the ability to increase crude terpenoid concentrations in response to defoliation, as a means of providing additional protection for the plants. Consequently, palatability of browsed sagebrush should remain relatively constant from year to year. Indeed, sagebrush taxa grazed by mule deer do maintain their level of palatability between years, as documented by animal preference for the same plants (Welch and others 1981).

During spring growth, overwintering leaves expand and increase their size diluting epidermal chemicals per unit of dry matter. Because active chemicals are concentrated on the surface rather than distributed throughout the tissue, increased size may have minimal impact on the protective quality of these compounds. This would seem particularly true for volatile deterrents (methacrolein) detectable by the olfactory sense of herbivores. If this is the case, overwintering leaves could expand without jeopardizing their defense. Conversely, if spring growth does weaken the chemical defense, it happens when plants may require less protection. Decreased apparency (Feeny 1976) results from the production of new foliage on associated vegetation that can be utilized by the herbivores (Willms and McLean 1978). Also, it may be unnecessary to have older leaves fully protected because shortly after leaf expansion stops they begin to senesce and drop from the plant. Although overwintering leaves are important for early spring metabolic activity, the plants can survive without them, particularly if the primordia remain undamaged.

Short internodes between sagebrush leaves cause rosette-like clusters near the stem tip (Diettert 1938). Older leaves surrounding the primordia could provide chemical protection until glandular trichomes have formed on newly developing leaves. Early appearance of glands (Diettert 1938) on the leaves is also suggestive of their protective role.

SUMMARY

1. Sagebrush crude terpenoid concentrations were highest in leaves (26.6 percent dry weight) followed by twigs with leaves (21.2 percent), flower heads (14.4 percent), and twigs (7.7 percent).
2. During spring, overwintering sagebrush leaves increased in length, width, and dry weight causing a dilution in the concentration of crude terpenoids. The quantity of epidermal chemicals remained about the same on each overwintering leaf as it expanded.
3. Twig biomass increased 2.5 times during spring growth, maintaining a 2:1 ratio of leaf to woody tissue.
4. Total plant leaf biomass in December was 30.8 percent lower than in June. Average leaf crude terpenoid concentrations were 11.2 percent and 6.3 percent, respectively. Whole plants harvested in December would provide quantities of crude terpenoid extract equal to, or greater than, whole plants harvested in June at peak foliage biomass.

5. Fifty percent defoliation of sagebrush plants in late winter for two consecutive years did not adversely affect growth and vigor. Crude terpenoid concentrations of defoliated plants did not differ from paired untreated controls.
6. Plants completely defoliated for two consecutive years, without damaging twigs or leaf primordia, continued to produce foliage. Growth and vigor seemed to depend on competition from other shrubs. Crude terpenoid concentrations of the regrowth remained similar to those of the untreated controls.
7. Hydrogenating the crude terpenoid extract to remove oxygen produced a high-quality crude oil (biocrude) that could be refined by conventional methods to liquid fuels and other organic chemicals.
8. Crude terpenoid extracts contained compounds that were antimicrobial, particularly toward anaerobic bacteria. Growth of several fungi was inhibited by extracts; two of the most sensitive fungi were causal organisms of systemic rice blast and grape downy mildew.
9. Based on botanical and chemical characteristics, sagebrush has potential to be used as a biocrude-producing plant in semiarid environments where it is adapted and occurs naturally.
10. Epidermal chemicals of sagebrush appear to function as a defense against herbivores.

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CHRYSOTHAMNUS NAUSEOSUS: A POTENTIAL SOURCE OF NATURAL RUBBER

W. K. Ostler, C. M. McKell, and S. White

ABSTRACT: Five taxa of rabbitbrush (Chrysothamnus nauseosus [Passas] Britt.) were evaluated for their potential for rubber production in a nine State area in the Western United States. Slope, aspect, elevation, geologic substrate, soil texture, pH, EC, soil phosphorus and potassium, plant height and diameter, plant weight, and plant water stress were all measured. Results indicate that rubber concentration is higher under stress conditions. Differences in rubber and resin contents were also identified among the five taxa. Chrysothamnus nauseosus ssp. consimilis var. viridulus had significantly greater percentages of rubber and resin content than the other four taxa. Age was shown to be positively correlated with rubber percentage.

INTRODUCTION

The genus Chrysothamnus (rabbitbrush) of Western North America belongs to the largest and most advanced of the flowering plant families, Compositae (Asteraceae, the sunflower family). The occurrence of rubber in C. nauseosus (rubber rabbitbrush) has long been known. The Western American Indians used rabbitbrush latex for chewing gum. In 1904, the presence of rubber in C. nauseosus was brought to the attention of the botanical world by A. J. Davidson, who sent a specimen to the University of California for identification and noted the Indians' use of it as gum (Hall and Goodspeed 1919). Fifteen years later, it was brought to national attention with the publication of Hall and Goodspeed's paper (1919) on Chrysothamnus rubber. They concluded that over 150,000 tons of rubber were available in native stands of Chrysothamnus in the Western United States, but very little research toward commercialization was done.

Initial work on rabbitbrush rubber quality was reported in a study by Dr. David Spence, Chairman of the Subcommittee on Rubber and Allied Substances of the National Research Council (Hall and Goodspeed 1919). He reported that the rubber was of good quality, vulcanized readily, and merited further investigation.

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W. K. Ostler is senior scientist, C. M. McKell is Vice President of Research, and S. White is a scientist for NPI, Salt Lake City, UT.

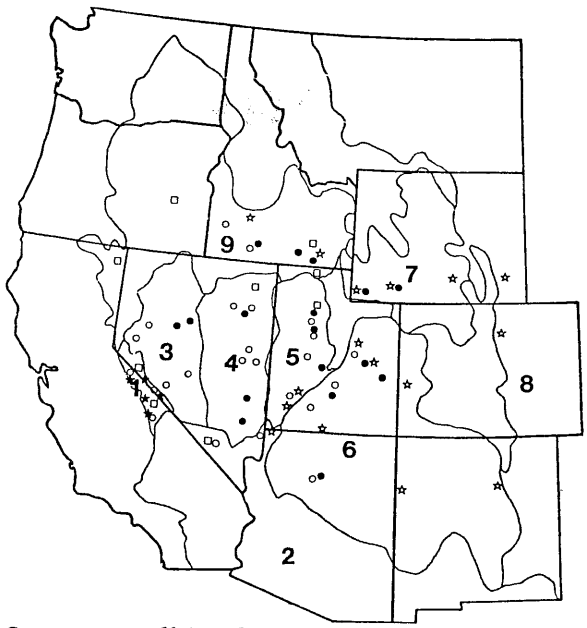
During World War II, the U.S. Department of Agriculture became interested in a domestic source of natural rubber due to potential blockages of foreign imports (Trumbull 1942; Doten 1942). Guayule (Parthenium argentatum) was eventually selected over rabbitbrush and other species for planting during the Emergency Rubber Project of the 1940's, principally because a guayule rubber production plant was operating in California and rubber had been commercially produced in Mexico and California.

The USDA recently evaluated over 100 plants having potential as hydrocarbon crops and rated rabbitbrush as having a very high potential for development (Buchanan and others 1978a, 1978b).

With this as a basis, NPI was able to obtain funding from National Science Foundation Small Business Innovation Research to evaluate rabbitbrush as a commercially viable rubber-producing species. The objectives of this study were to: (1) identify those subspecies of Chrysothamnus nauseosus that have a high rubber content, (2) identify environmental factors that may influence rubber accumulation, (3) determine growth rates and potential yields on agricultural and natural systems, and (4) initiate preliminary tests on rubber quality.

STUDY AREA AND TAXA OF INTEREST

The study area encompassed a major portion of the range of C. nauseosus in nine western states. A map of the area and study sites by subspecies is shown in figure 1. The area was divided into nine regions, based on floristic and physiographic features (Cronquist and others 1972) and included those recognized by Hall and Goodspeed (1919) in their work on rabbitbrush. Five high-yielding subspecies of C. nauseosus, previously identified by Hall and Goodspeed (1919) were the taxa of interest for this study. These include: C. n. ssp. consimilis; ssp. consimilis, var. viridulus; C. n. ssp. hololeucus, C. n. ssp. albicaulis, and C. n. ssp. graveolens. Chrysothamnus n. ssp. c. var. viridulus was recognized as a subspecies by Hall and Goodspeed in 1919, but is currently placed as a variety of C. n. ssp. consimilis (Anderson 1966). Due to its uniqueness from C. n. ssp. consimilis, in this analysis, it was kept as a unique taxa.



□C. n. ssp. albicaulis, ○ssp. hololeucus; ☆ssp. graveolens, ●C. n. c. var. consimilis; ★var. viridulus.

Figure 1.--The nine regions within the 10 states where field studies and rabbitbrush sampling sites occurred.

METHODS

Field Analysis

Within each region, three sample sites were selected for each of the subspecies found within that region. At each site, data were taken to identify the physical and biotic characteristics of the rubber rabbitbrush stand. Parameters measured included: slope, aspect, location, elevation, and geological substrate. In addition, a soil sample was taken at each site for analysis. Soils were analyzed for texture, pH, EC, phosphorus, and potassium (USDA 1969).

Six plants at each site were selected randomly for sampling using a criterion of size distribution. Height and two diameter measurements were recorded for each of these plants. Water stress readings (atm) were also taken using a Campbell J-14 plant pressure gauge.

To obtain a biomass volume value of the stand and determine growth rates, all six plants were cut at the soil line and weighed with a portable scale. The section at the base of each cut shrub was returned to the laboratory to determine age. A branch representative of the entire plant was removed from the plant and returned to the laboratory for chemical analysis to determine rubber content. A flowering sample was also collected and pressed at each site for taxonomic verification.

Chemical Analysis

Upon arrival at the laboratory, plants were oven dried at 140° F (60° C) for 48 to 72 hours and then defoliated. Each dried defoliated plant was then processed through a Wiley mill using a 20-mesh screen and placed in a glass jar prior to extraction.

The extraction procedure was as follows: the contents of each jar, containing the milled residue of six plants, was shaken to thoroughly mix the material. A 30 to 40 g sample was removed and the oil extracted with acetone in a 500 ml Soxhlet apparatus for a minimum of 24 hr at 0.5 cycles/minute. This yielded a mixture of low molecular weight oil and high molecular weight resin. Each high molecular weight sample was further extracted for 24 hr with hexane to remove the natural rubber compounds.

The resultant hydrocarbon fraction from several different extractions was subsequently analyzed by nuclear magnetic resonance (NMR). This was used to determine the microstructure of chrysil rubber in order to compare it with published data for hevea rubber.

Data Analysis

The data were analyzed on a Univac 1176 using the statistical package, SPSS, developed at the University of Chicago and available nationwide (Nie and others 1975).

RESULTS AND DISCUSSION

Environmental Analysis

A total of 66 sites were sampled. Overall averages for the parameters sampled are given in table 1. The average rubber yield for all five subspecies combined was 1.3 percent. Total hydrocarbon content averaged 21 percent (rubber, oil, resin). Average height of all shrubs sampled was 29.1 inches (0.7 m), the average weight was 3.8 lb (1.7 kg), and the average age was 5 years. Plants grew in a wide variety of soils, however, the soils were generally sandy with fairly high pH's (7.9) and high EC's (4.1). Rubber yields were low, as would be expected when averaging many populations. There was a wide divergence among individual plants and subspecies; individual yields ran as high as 6.57 percent.

A stepwise multiple regression was performed to determine if environmental factors, including plant size and age, influenced rubber content. The top five factors entering the stepwise regression were slope, elevation, stress, silt, and electrical conductivity (table 2). The results were significant at the 0.01 level, but only 28 percent of the variation was accounted for even with all five variables included in the regression equation. Again this is not unexpected since several taxa were involved in

Table 1.--Mean and standard deviations for environmental factors taken on the 66 rubber rabbitbrush sites over the entire study area

Environmental factor	Mean	Standard deviation
Crown diameter (in)	40.2	5.7
Crown diameter (in)	34.4	4.8
Height (in)	29.1	5.4
Weight (lbs)	3.8	2.6
Age (yr)	5.1	1.6
Water stress (atm)	17.4	4.6
pH	7.9	.6
Sand (%)	59.3	20.7
Silt (%)	29.1	15.3
Clay (%)	11.9	6.1
Phosphorus (ppm)	11.4	12.9
EC (mmhos/cm)	4.1	3.1
Potassium (ppm)	207.1	116.1
Elevation (ft)	5305.3	1462.6
Slope (degrees)	4.1	4.4
Rubber (%)	1.3	.7
Oil (%)	5.7	2.6
Resin (%)	14.0	4.0

Table 2.--The top five factors that entered the multiple regression to determine what factors were associated with rubber concentrations (n=66)

Independent variables	Cumulative R	Sign	Significance
Slope	0.315	-	0.05
Elevation	0.412	-	0.01
Stress	0.459	+	0.01
Silt	0.502	-	0.01
Soil EC	0.531	+	0.01

the analysis. The parameters selected by the multiple regression indicate that rubber concentration is higher under stress conditions. Another rubber-producing species, guayule, has been noted to produce similar response (Campos-Lopez and McGinnis 1978; Ostler and others 1983).

It has been shown that rubber content is greater in older tissues, particularly near the soil line (Hall and Goodspeed 1919). A regression was run to determine average increase in rubber content in successively older tissues (fig. 2). The regression shows a significant linear relationship between age of the tissue and rubber content. This relationship is important when considering the economics of growing rabbitbrush commercially because not only will weight of the plants increase over time, but the rubber content of the plants will also increase, giving a multiplication effect.

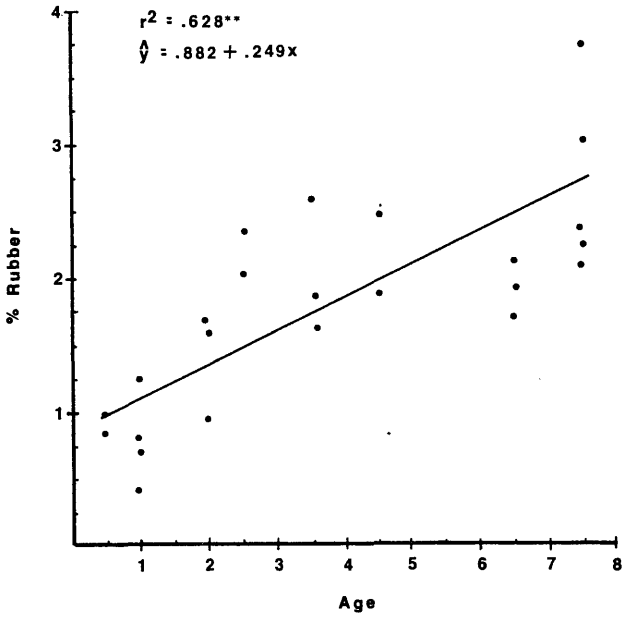


Figure 2.--Regression of rubber content and age (data extracted from Hall and Goodspeed 1919).

Analysis of Subspecies

To assess the influence that the genetic makeup of the plant may exert on rubber production, an analysis of variance was performed using subspecies as an independent variable to test its effect on the other parameters sampled. Only three parameters were significantly different among the subspecies. The one that is particularly interesting is rubber content (fig. 3). Chrysothamnus nauseosus ssp. consimilis var. viridulus is significantly higher than any of the other subspecies including C. n. ssp. c. var. consimilis. Indeed, var. viridulus average values for rubber content more than doubled C. n. ssp. hololeucus, the closest subspecies. This suggests that rubber content has strong genetic controls. Efforts to increase rubber production should be directed at selecting high rubber-producing strains.

A multiple regression performed on C. n. ssp. c. var. viridulus showed that plant size, measured as crown diameter, also is associated positively with rubber content. The "r" value was 0.893, which is significant at the 0.05 level. (Note: there were only three degrees of freedom).

Separate multiple regressions were run for each of the remaining subspecies using rubber content as the independent variable. The rankings of the dependent variable differed for each subspecies, but the same factors identified in the multiple regression using all sites were the major factors common to most subspecies, i.e., stress +, elevation -, EC +.

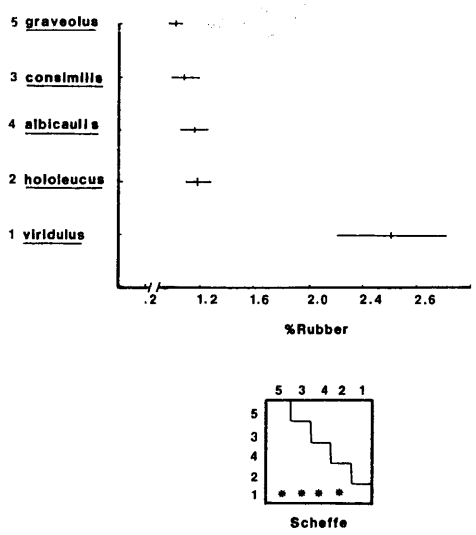


Figure 3.--The results of the analysis of variance for the percentage rubber content in rabbitbrush. The means and standard errors are located in the upper graph. Below are pairwise comparisons using the Scheffe procedure.

Growth Rates

To determine growth rates and yield in the field, the average weight (table 1) was divided by the average age. This yielded a value of .75 lb/yr (340 g/yr). This assumes that the growth is linear, which is certainly not true for the entire life of the plant, but may be appropriate for the first several years.

Growth rates from plants that had been clipped or hedged and allowed to grow for 2 years yielded average values of 1.1 lb/yr (510 g/yr) (McKell and Van Epps 1980; McKell and others 1981). These values are probably very comparable to what would be expected from an agricultural setting of Chrysothamnus in which harvest would take only the above-ground growth and leave the root system intact for regrowth.

Using the conservative growth rate of 1.1 lb/yr (500 g/yr), one can then calculate potential yields from agricultural systems. If one assumes 3 ft (91 cm) centers for the planting, this would require 4,842 plants/acre (11 964 plants/ha). At this spacing, in 5 years the canopy would be completely closed given average crown dimension obtained from this report. In 5 years, these plants would yield 533 lb of rubber per acre (598.2 kg/ha).

These figures are very conservative. Only two percent rubber content is assumed and growth rates are predicted to be the same as in native stands, which have generally high competition rates. If the plants contained a rubber content equivalent to the best native stock found, the yield would increase to 1,600 lb of rubber per acre (1 794 kg/ha) over 5 years. At 1983 prices of $0.46/lb (Wall Street Journal, Feb. 8, 1983) this would yield $736.00/acre or $1,812/ha worth of rubber. With competition control, these figures may increase conservatively at least another 50 percent, enabling reduction in the growing time to 3 years.

Rubber Quality

NMR analysis was performed on fresh extracted samples of C. n. ssp. albicaulis to determine the type of bonding of the carbon chain. Chrysothamnus n. ssp. albicaulis was selected because it grows very near NPI's research facility. Extracting and processing could be done quickly to avoid any decomposition of the rubber molecules. The results of the NMR as well as a comparison with hevea are shown in figure 4. The peaks are nearly identical and confirm that the rubber is composed of cis-isoprene molecules.

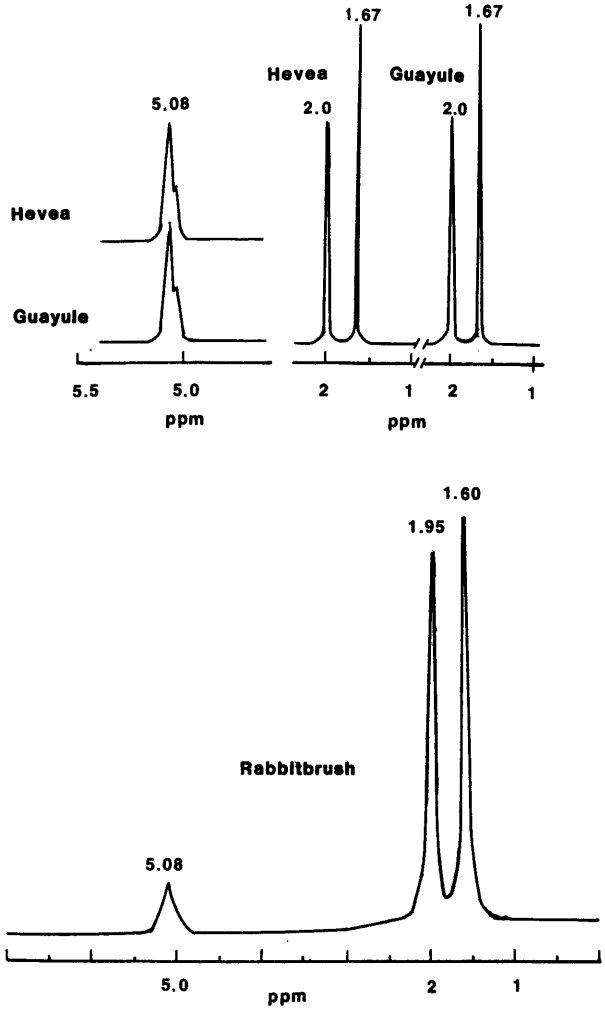


Figure 4.--Results of Nuclear Magnetic Resonance (NMR) of hevea, guayule, and rubber rabbitbrush. Rabbitbrush is on a larger scale.

Preliminary tests on rubber quality have all been encouraging, confirming the hypothesis that chrysil rubber is a good quality rubber. Second level studies on quality need to be undertaken to determine its acceptance and usefulness in the market place.

Analysis of Resins and Oil

Another aspect that would enhance the economic feasibility of growing Chrysothamnus nauseosus commercially is the discovery of a high percentage of resins and oils in rabbitbrush tissue (table 1). Preliminary results showed that resins averaged 14 percent and oil six percent. The resin may prove to be a more valuable resource than the rubber. The samples for resin and oil were from 1- to 2-year-old growth. Their values are higher than those determined by whole plant analysis, but these would be the portions most easily harvested in a plantation-type operation.

To test if subspecies varied in their resin content, an analysis of variance was performed. The results were very similar to those reported for rubber content. Only C. n. ssp. c. var. viridulus was significantly different from the other subspecies (fig. 5). This further strengthens the value of C. n. ssp. c. var viridulus as the subspecies with which to start selective breeding and improvement for commercial production.

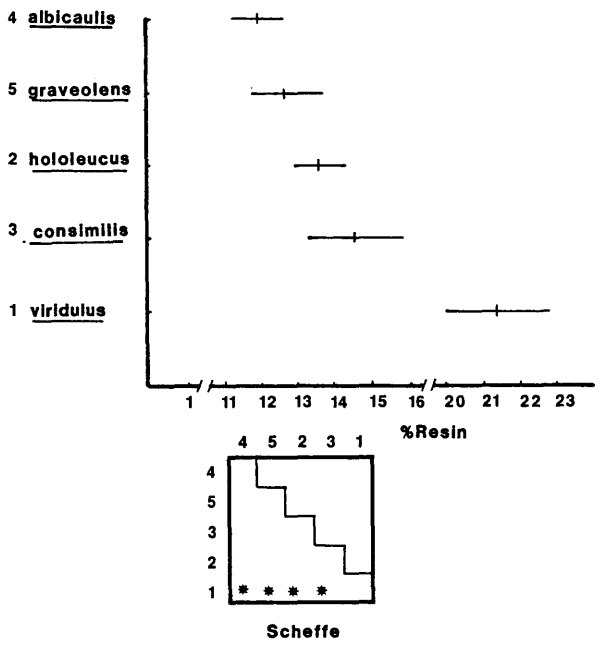


Figure 5.--The results of the analysis of variance for the resin content. The means and standard errors are located in the upper graph. Below are pairwise comparisons using the Scheffe procedure.

CONCLUSIONS

This study was beneficial in several areas which needed to be confirmed and verified before further work could be undertaken on the development of this potential source of domestic rubber. Perhaps the most important is the domination of genetic influence on Chrysothamnus nauseosus rubber production as illustrated by the analysis of variance. Having a strong degree of genetic constancy is important to breeding programs and subsequent trial plots.

Subspecies of C. nauseosus are also capable of interbreeding (McArthur and others 1978, 1979; McArthur 1984). This would facilitate the transfer and selection of genes for higher rubber content to other subspecies. Genetic amplitude is extremely great in these subspecies of rabbitbrush. They occur throughout western North America from hot desert valleys of California and Arizona to cold valleys and foothill slopes of southern Canada. The species characteristically occupies marginal land and invades into abused or overgrazed areas. It is very salt tolerant and actually shows slightly higher rubber content when in a stressful environment.

Average rubber values are low, but one must recognize that no genetic selections have been made on rabbitbrush. Indeed, less than 500 plants have ever been tested for rubber content. If individual specimen contents discovered thus far run as high as 6.57 percent (Hall and Goodspeed 1919), it appears feasible that this figure could be doubled by genetic selection, as has been done with guayule (McGinnes and Haase 1975; Campos-Lopez and McGinnes 1978). The growth rates of rabbitbrush are very high in comparison to guayule.

Rabbitbrush is widely distributed throughout western North America where winter temperatures are often below -20° F (-30° C). Thus, its potential range for cultivation and growth far exceeds that of any other rubber-producing plant in the area. In addition, it grows on marginal land and alkaline soils currently unused or unusable for agricultural crops. Rabbitbrush is also very resistant to mowing or harvesting. It rapidly resprouts from a cut stump, making it ideal for a continuous cropping system with several harvests through the life of the plant. The potential for rubber production from rabbitbrush appears very promising. Research should be directed toward genetic selection and improvement.

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CONTAINER NURSERY PRODUCTION OF ARTEMISIA AND CHRYSOTHAMNUS SPECIES

Lynn E. Long

ABSTRACT: Several thousand sagebrush and rabbitbrush seedlings are grown each year at Plants of the Wild Nursery in eastern Washington. Seed is stratified and sown directly into Ray Leach Supercells. Temperatures, soil moisture, and nutrients are carefully monitored throughout the growing season. By mid-August plants are of sufficient size to undergo a hardening process. Plants can be shipped in early fall or spring.

INTRODUCTION

Plants of the Wild is a native plant nursery located approximately 50 miles south of Coeur d'Alene, ID and Spokane, WA in Tekoa, Whitman County, WA. Since 1980 we have grown native plants for reclamation and revegetation projects throughout the West. Our current production is over 250,000 plants per year. We maintain a growing inventory of 1, 2, and 5 gallon plants. We are in an ideal location for growing a wide range of native plants. Located in the Intermountain region of the Northwest, we are adjacent to the dry desert regions of eastern Washington, eastern Oregon, and southern Idaho and yet within a very short distance of the forests of western Washington, western Oregon, and northern Idaho. It is largely for this reason that our plant list is so diverse. We grow 75 species of plants ranging from red alder and mountain huckleberry to fourwing saltbush and antelope bitterbrush. Included in this list are Artemisia cana, A. frigida, A. tridentata ssp. tridentata, A. tridentata ssp. wyomingensis, A. tridentata ssp. vaseyana, and two species of rabbitbrush, Chrysothamnus nauseosus and C. viscidiflorus.

THE CONTAINERS

Our standard tube is the 10 inch^3 Ray Leach Supercell. This tube has several advantages over other types of containers, including the ease with which plants can be consolidated both after germination and before hardening and shipping. Since each tube is a separate unit, tubes in which germination did not take place can be removed. Moreover, before moving to the shadehouse for hardening and eventual shipping, undersized plants can be removed and allowed to grow for a longer period in the greenhouse. This allows more effective utilization of our greenhouse space and shipment of only the strongest plants.

Paper presented at the Symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

Lynn E. Long is nursery manager and plant pathologist at Plants of the Wild Nursery (Palouse Seed Co.), Tekoa, WA.

GROWING MEDIUM

Growing medium is composed of 50 percent sphagnum peat and 50 percent number 2 horticulture grade vermiculite. Dolomite lime is added to the medium at the rate of 5 pounds (11 kg) per cubic yard, along with 5 pounds (11 kg) of calcium carbonate lime. This raises the pH to neutral or slightly alkaline when growing sagebrush, rabbitbrush, or other species that prefer an alkaline soil. The coarse vermiculite allows for better root aeration and drying, which is important in growing many desert species.

SEED SOURCES

Seed is obtained from commercial sources throughout the Western United States. Since many of our plants are grown on a speculation basis, it is impossible to exactly match seed sources with planting sites for these plants. However, whenever possible we grow plants on a contract basis and occasionally customers will collect site-specific seed. This, of course, requires planning and enough lead time to collect the seed and grow the plants.

SEED GERMINATION

Due to erratic germination of sagebrush and rabbitbrush seed, we normally try to obtain several seedlots of each species. This will ensure that one or more seedlots will contain viable, nondormant seed. A germination test is performed on each seedlot before it is sown. A few seeds are placed on a moistened blotter in a tray and subsequently placed in a germinator set at 68° F (20° C). Germination should be complete within 10 to 14 days. The results determine whether to sow a particular lot, and, if so, how much seed to place in each tube. In the past, germination of sagebrush and rabbitbrush seed has been erratic and unpredictable. Seed that is over 1 year old is more likely to be dormant, or dead, than fresh seed. Frequently, however, seed that is less than 1 year old will show high viability as indicated by a tetrazolium test, but will fail

to germinate. These lots are obviously dormant. Attempts were made to break this dormancy by stratifying the seed at 41° F (5° C) for up to 6 months and by subjecting stratified seed to freezing and thawing. Neither technique appreciably increased germination levels. It is for this reason that several different seedlots of fresh seed are tested before sowing.

When seed is received from the supplier it is held in a viable, nondormant state until planting by placing the seed in polyethylene bags three layers thick. Bags are then sealed and stored at 37° F (3° C). It is possible to keep seed in this state for several months. At the same time that germination testing is done, the remaining seed is soaked overnight in water and then placed in a porous cloth bag. This bag is then placed in a tray and covered with vermiculite. The seed is stratified at 41° F (5° C) for up to 15 days. This stratification provides a more rapid and uniform germination.

The seed is sown directly into the Supercell tube, normally in April or May. The quantity of seed sown depends on the outcome of the germination test. Enough seed is placed into each tube to assure that at least one germinant will be present. Approximately 1 month after seeding the plants are thinned, leaving only the strongest plant in each tube. Stratified seed is sown by hand due to the moistened condition. Once the seed is sown, a thin (ca. 1 mm) layer of Perlite is sprinkled over the seed. This covering acts as a mulch and holds moisture at the seed level. The seed is lightly sprinkled with water at least three times per day to replenish moisture. Germination should begin within 2 or 3 days. Sprinkling continues until germination is nearly complete, usually within 10 to 14 days.

WATERING AND FERTILIZING

Once germination is complete, fertilization begins. We use commercial fertilizers that contain all the major and minor elements needed. To begin, we use a 9-45-15 formulation at the rate of 100 ppm nitrogen followed in 3 weeks with 20-10-20 at the rate of 200 ppm nitrogen. The seedlings are fertilized each time they are watered, normally with 20-10-20; but if growth is too rapid 9-45-15 is used for one or two waterings. Our main concern is to develop a good caliper and root system with a proportional shoot. Therefore, watering and fertilization are most critical. To avoid root rot and to prevent the plants from becoming spindly, they are not watered until the soil is nearly dry. At that time we water to saturation.

GROWING TEMPERATURES

The growing temperature for sagebrush is approximately 80° F (27° C), but average greenhouse temperature at the time of germination in the early spring is normally 65° F (18° C). Desert plants are placed on benches near the exhaust fans to take advantage of the warmer temperatures in those areas of the greenhouse. Temperatures near the exhaust fans are usually 10 to 15 degrees warmer than temperatures near the intake.

DISEASE PROBLEMS

Diseases are rarely a problem on sagebrush or rabbitbrush when grown as summer crop. However, Botrytis infections occasionally occur, especially in the early spring when plants are dense and do not dry out before nightfall. Under these conditions, we regularly spray every 2 weeks with one of the following three fungicides on a rotating basis: Benlate, Ornalin, and Rovral. Later in the year we do not spray unless we see evidence of infection. One of the primary predisposing factors of Botrytis in sagebrush is the indeterminate germination that is so common in this species. Normally plants are thinned approximately 1 month after seeding, but they also need to be thinned a second time several weeks later. If this is not done, late germinants will produce a layer of lush, spindly growth under the main canopy where the humidity is quite high. Botrytis can easily become established on this later growth and will rapidly move to the larger plants. Sagebrush is the only species that seems to require this second thinning, but improved plant growth and health are well worth the extra time which the operation requires.

COLD HARDENING AND SHIPPING

Plants 4 months old are 8 to 10 inches (20 to 25 cm) tall and ready for hardening. The goal is to reach this stage by mid-August. To harden, the plants are watered heavily to remove nitrogen. They are then transferred to a shadehouse providing 47 percent shade. Once the plants are set outside under shade they are not watered again until they exhibit signs of wilting. At this point, the soil is saturated with water and fertilized using a low nitrogen, high phosphorus formulation of 9-45-15. This process subjects the seedlings to moisture and nutrient shock. The plants are further stressed by the shadehouse environment. Wind, nonoptimum temperatures, and shade all combine to slow the rate of top growth and further the development of roots and stem caliper.

By late September the plants are ready to be shipped. Sagebrush and rabbitbrush are shipped throughout the Western United States. Customers include private nurseries, mining companies, State game and highway departments, as well as several federal agencies. Those plants that are not shipped by late fall are overwintered outside and are shipped in the spring.

We constantly monitor our plants and adjust growing schedules and conditions as we learn more about growing these two species. We have found, however, that the procedures outlined here produce strong, healthy plants that are in prime condition for outplanting.

PRELIMINARY REPORT ON TISSUE CULTURE PROPAGATION OF BIG SAGEBRUSH (ARTEMISIA TRIDENTATA)

Walter M. Neville and E. Durant McArthur

ABSTRACT: From a single explant of big sagebrush (Artemisia tridentata ssp. vaseyana), 65 shoots were produced in 140 days using Murashige and Skoog's medium modified by Linsmaire and Skoog, supplemented with 7.1 x 10^{-6} oz/qt (0.2 mg/L), 6-benzyladenine, and 2 percent sucrose.

INTRODUCTION

Big sagebrush (Artemisia tridentata) can be propagated from seed and from cuttings (Alvarez-Cordero and McKell 1979). A method of propagation, more rapid than stem cuttings of a single plant, that has genetic characteristics of interest is in vitro or tissue culture propagation (Murashige 1974). A species related to big sagebrush, tarragon (Artemisia dracunculus L. var. sativa), has been propagated by tissue culture (Garland and Stoltz 1980). To develop a rapid method of propagation of big sagebrush, we used the tissue culture method developed by Garland and Stoltz (1980) for tarragon. We are interested in big sagebrush propagation because of its increasing use in revegetation plantings and potential for genetic improvement (McArthur and Plummer 1978; Welch and McArthur 1979).

METHODS AND RESULTS

Seeds of A. tridentata ssp. vaseyana collected at Diamond Fork, Utah County, UT, were placed between moist paper towels, placed in a closed container, and alternately located in a cold 37 °F (3 °C) dark place for about 12 hours and in a warmer 73 °F (23 °C) lighted place for about 12 hours. In about a week the seeds started to sprout.

One-week-old seedlings were sterilized with a 0.525 percent solution of sodium hypochlorite (a one-tenth dilution of Purex bleach) for 10 to 15 minutes and then washed with sterile deionized water. The seedlings were excised using sterile technique into four segments: solitary cotyledons, cotyledons with a 0.04-inch (1-mm) hypocotyl stem, hypocotyl stems, and roots.

The various explants were placed on culture medium consisting of Murashige and Skoog (1962) salts, Linsmaire and Skoog (1965) organics, 6 x 10^{-3} oz/1.057 qt (170 mg/L) $NaH_2PO_4 \cdot H_2O$, 2 percent (w/v) sucrose, 0.7 percent agar (w/v), and 7.1 x 10^{-6} oz/1.057 qt (0.2 mg/L) 6-benzyladenine. The sucrose and tissue culture medium were obtained from KC Biological, Lenexa, KS; the agar (Phytagar) and 6-benzyladenine, GIBCO Labs, Santa Clara, CA; the monosodium phosphate, reagent grade, J. T. Baker Chemical Co., Phillipsburg, NJ. The pH of the medium was adjusted to 5.7 - 5.8. Sucrose and agar were dissolved with heating, 0.17 oz (5 ml) of culture medium was pipetted into 0.68 oz (20 ml) borosilicate glass scintillation vials, and sterilized for 22 minutes in a steam sterilizer.

The cultures were incubated at 64 to 71 °F (18-24 °C) in light from a 27-watt cool-white fluorescent lamp at a distance of 17 inches (43 cm) with a photoperiod of 16 hours light, 8 hours dark.

In 6 weeks of culture only the explant consisting of cotyledon with hypocotyl stem produced shoots. After 140 days of culture and 3 transfers at 4 to 6 week intervals, 65 shoots were produced. By the third transfer the cultures lost vitality, and on the fourth transfer only 30 viable shoots remained.

The decline of the culture could have been caused by not having an optimum hormone concentration or by not dividing and transferring the shoots at durations shorter than 4 to 6 weeks. Other possibilities exist.

In future work, we will explore the effects on the vitality and logarithmic-like growth rate of the cultures of different hormone concentrations and intervals of 3 to 4 weeks (at the beginning of shoot elongation) for the division and transfer of the shoots.

Paper presented at the Symposium: Biology of Artemisia and Chrysothamnus, Provo, UT, July 9-13, 1984.

Walter M. Neville is President, Deseret BioResearch, Midvale, UT. E. Durant McArthur is Supervisory Research Geneticist, Shrub Sciences Laboratory, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT.

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Third in a series of proceedings of symposia on wildland shrubs, this publication brings together current knowledge of plants belonging to two important genera. Topics addressed by the 54 papers include distribution, systematics, genetics, revegetation and control, animal relationships, ecological relationships, entomology, pathology, and physiology.

KEYWORDS: Compositae, wildland shrubs, sagebrush, rabbitbrush, wormwood, southernwood, tarragon, mugwort, wormseed

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