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Proceedings— Research and Management of Bitterbrush and Cliffrose in Western North America

Salt Lake City, Utah, April 13-15, 1982



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U.S. DEPARTMENT OF AGRICULTURE

Proceedings— Research and Management of Bitterbrush and Cliffrose in Western North America

Salt Lake City, Utah, April 13-15, 1982

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FOREWORD

Purshia and closely related genera such as Cowania and Fallugia of the Roseaceae are important components of vegetative habitats on approximately 25 million acres (10 million ha) in Western North America. They occupy successional positions ranging from seral to climax, and show specific adaptations to soil type, climate, and vegetation associations. They form the mainstay of the diet of wintering mule deer throughout much of their range and provide vital watershed protection to otherwise unstable erosive land. Because of the N-fixing capability of Purshia and Cowania, shrubs of these genera play a role in the nitrogen economy of habitats where they are found.

Through the past several decades, a substantial amount of research has been conducted in habitats where these shrubs occur. Management programs have intensified to explore their utilization for wildlife, range livestock, and revegetation. However, to date there has been no effort to assemble the existing knowledge of these shrubs and to bring this information to individuals involved in research and management.

The purpose of this symposium proceedings is to develop the state-of-the-art and science of managing these shrubs and to provide land managers, scientists, and educators with a reference text.

The Bitterbrush and Cliffrose Symposium, held in Salt Lake City, Utah, April 13-15, 1982, drew some 120 participants from land management agencies, colleges and universities, and Federal research organizations. The symposium was sponsored by the USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, and Utah State University, Logan.

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WELCOMING REMARKS --

BITTERBRUSH AND CLIFFROSE SYMPOSIUM

Dr. Roger R. Bay

Director, Intermountain Forest and Range Experiment Station

I am pleased to see so many scientists and managers from throughout the Western United States here at this important symposium. Many of you have been involved in the study of, and the management of, bitterbrush and cliffrose for quite some time. We obviously believe these are important plant species and their proper management can contribute to better land and wildlife management. The Intermountain Forest and Range Experiment Station has had a variety of research effort on bitterbrush for well over 30 years, with some of the early work started in the Boise area in cooperation with other agencies. I think this symposium is timely.

I am pleased to see that many representatives of management agencies are involved with the program and are attending this meeting. Close working relationships between research groups and management agencies are a prime factor in moving technology from the study and discovery stage to application in the field. We at the Intermountain Station have had a particularly close working relationship with a variety of agencies involved in the management of bitterbrush. Here in Utah, the Utah Division of Wildlife Resources and the Station have worked together for more than 30 years, involving assignments of scientists and managers between the State division and our Shrub Sciences Laboratory in Provo. Not only do we cooperate in research studies, but the State's management agency ensures that results are put into practice immediately.

We've also enjoyed good cooperative work with other States such as the Idaho Department of Fish and Game, and the major Federal agencies, National Forest System, and the Bureau of Land Management in the Intermountain area. Such team work has contributed to our knowledge and management for the two important species we are addressing today.

The purpose of this symposium is to develop state-of-the-art information on the science and management of these shrubs, and to provide land managers, scientists, and educators with a reference text. This is certainly in keeping with one of our major goals at the Intermountain Station in recent years: to summarize, synthesize, and deliver to managers information about key subjects in the Intermountain and Rocky Mountain West area. We have been able to stress technology transfer efforts such as this only because we have been able to conduct the research studies over several decades. We have built up a reservoir of information from research as well as experience of managers. It is appropriate now to tap this reservoir and ensure that the knowledge is transferred to the right hands.

I hope this symposium will not be the only one of its kind. We have had some discussion on the possibility of continuing this kind of effort with other shrub species important to the Western United States. We would appreciate your thoughts and comments on this possibility.

We don't have any papers in the symposium addressing technology needs or the opportunities for future research. I would ask participants to consider this topic now and after this symposium. What are the new technology needs of resource managers? Where should the science agencies--such as Forest Service Research Stations, Agricultural Research Service, and universities--concentrate their future research efforts? The participants of this symposium represent the spectrum of agencies and institutions involved in both the research and management of shrub species. I hope you will have the opportunity to consider needs and agree on some recommended actions.

Section 1. Distribution, Taxonomy, and Habitat Classification



TAXONOMY, DISTRIBUTION, AND CYTOGENETICS OF PURSHIA, COWANIA, AND FALLUGIA (ROSOIDEAE, ROSACEAE)¹

E. Durant McArthur, Howard C. Stutz, and Stewart C. Sanderson²

ABSTRACT

The rosaceous genera Cowania, Purshia, and Fallugia are endemic to western North America. The five species of Cowania (C. ericifolia, C. mexicana, C. plicata, C. stansburiana, C. subintegra) and the single species of Fallugia (F. paradoxa) are more southern in distribution (Mexico and southwestern United States) than the two species of Purshia (P. glandulosa, P. tridentata) which extend from northern Baja California to British Columbia. Hybridization between C. stansburiana and P. tridentata is common where their ranges are sympatric, principally in Utah and Nevada. They both have $n = 9$ chromosomes, F_1 hybrids between them are fertile and reciprocal introgression is common. Purshia glandulosa is considered to have been derived from such hybrid products. Fallugia paradoxa has $n = 14$ chromosomes. Polyploidy was not found in individuals of 22 Cowania; 64 Purshia; seven Purshia X Cowania interspecific and intergeneric hybrids; and six Fallugia populations. Chromosome counts are presented here for the first time for Cowania ericifolia, C. mexicana, C. plicata, C. subintegra, and Purshia glandulosa; all $n = 9$. The $n = 14$ count for Fallugia paradoxa is a corrected count, it was formerly reported as $n = 9$. During the early Tertiary, Cowania and Fallugia may have had a common ancestor in the northern Mexican uplands, or more likely Fallugia may have had a separate origin. Purshia may have been derived directly from Cowania which has more southern distribution, more primitive traits, and a larger number of species; or from a common ancestor. Cercocarpus shares many of the primitive traits of Cowania and may be related to Cowania and Purshia; it is abundant in the fossil record.

¹Paper presented at the Bitterbrush and Cliffrose Symposium, Salt Lake City, Utah; April 13-15, 1982.

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INTRODUCTION

Cowania, Purshia, and Fallugia have been included as members of the tribe Dryadeae of the subfamily Rosoideae of Rosaceae (Rydborg 1908-1918). In common with many rosaceous genera, the three genera are economically important (table 1, Robertson 1974). They provide browse for livestock and wild herbivores, seed production for small animals, natural and manipulated soil binding, and esthetic beauty (Robertson 1974, Blauer and others 1975). These genera have a Western United States distribution, more northerly in the case of Purshia, but distinctly southwestern, extending well into Mexico, for Cowania and Fallugia. The genera have distributional and morphological analogues consisting of other rosaceous genera principally from the subfamilies Rosoideae and Spiraeoideae.

Table 1.--Subfamilies of Rosaceae with characteristic chromosome numbers and generic examples¹

Subfamily	Common <u>x</u> 's	Other <u>x</u> 's	Polyploidy present	Representative genera (x)
Rosoideae	7,9	8,14	Yes	Fragaria, Geum, Potentilla, Rosa, Rubus, Sanguisorba (7); Alchemilla, Coleogyne ² (8); Cercocarpus, Chamaebatia ² , Cowania, Dryas, Purshia (9); Fallugia (14)
Prunoideae	8	--	Yes	Exochorda, Osmaronia, Prunus (8)
Spiraeoideae	9	7	Yes	Physocarpus, Spirea (7,9); Aruneus, Chamaebatiaria ² , Holodiscus ² , Kelysea ² , Petrophytum ² , Lutkea (9)
Pomoideae	17	14,15	Yes	Quillaja (14); Vaquelinia (15); Amelanchier, Cotoneaster, Crataegus, Malus, Peraphyllum ² , Pyracantha, Pyrus, Sorbus (17)

¹References: Federov (1969), Ornduff (1967), Moore (1973, 1974, 1977), Goldblatt (1976, 1981), and tables 2 and 3.

²New chromosome counts (Sanderson and McArthur, unpublished).

In this paper we discuss the taxonomic and geographic settings of the group and present exhaustive chromosomal data. Based on those settings and data, we present hypotheses outlining possible evolutionary relationships.

FAMILY TAXONOMIC SETTING

The rose family consists of about 100 genera of herbs, shrubs, vines, and trees divided into 3,000 species not including apomictic microspecies of Rubus and Rosa and other genera (Robertson 1974; Bailey Hortorium Staff 1976). The family has usually been divided into six subfamilies, but with the recognition of Chrysobalanaceae and Neuradaceae as independent families, only four subfamilies remain: Rosoideae, Prunoideae, Spiraeoideae, Pomoideae (Robertson 1974; Goldblatt 1976; Jones and Luchsinger 1979). The subfamilies are distinguished, in general, from one another by ovary position, type of flower, type of fruit, and number of pistils (Johnson 1931; Lawrence 1951; Benson 1957; Jones and Luchsinger 1979). Members of the family occur worldwide but are much more common in the northern temperate region--especially western North America and eastern Asia (Raven and Axelrod 1974). All 13 tribes occur in North America, 12 of 13 in western North America. A total of 45 genera have species indigenous to North America; 42 genera are restricted to North America (Robertson 1974).

The family Rosaceae is one of 17 families in the order Rosales. According to the Takhtajan-Cronquist phylogenetic classification system of flowering plants, the Rosales were derived from the primitive Magnoliales fairly early in angiosperm history (Cronquist 1968). The Rosaceae was well represented by Paleogene time some 50 million years ago (Raven and Axelrod 1974).

BASE CHROMOSOME NUMBERS IN ROSACEAE

The basic (x) chromosome number for the family Rosaceae and for the Rosales as a whole is thought to be $x = 9$, although $x = 7$ also draws some support (Raven 1975; Goldblatt 1976; Lewis 1980). Within the family, base numbers of 7, 8, 9, and 17 are common (table 1), which has invited considerable speculation from cytogeneticists about phylogenetic relationships. Sax (1933) proposed that ancient, $x = 8$ and $x = 9$, taxa hybridized and with the subsequent doubling of chromosome numbers, produced the amphidiploid Pomoideae with $x = 17$. Stebbins (1950) suggested that the $x = 8$ and $x = 9$ plants were from the subfamilies Prunoideae and Spiraeoideae, respectively. Darlington and Moffett (1930) and Darlington (1963) suggested an alternative cytological scenario for the Pomoideae: $x = 17$ is derived from an $x = 7$ base with three chromosomes present three times and the other four present two times. Goldblatt (1976) challenged the Prunoideae and Spiraeoideae hybridization hypothesis on the basis of chemotaxonomical data. Robertson (1974) and Goldblatt (1976) suggested that Spiraeoideae are likely the primitive Rosaceae.

CHROMOSOME NUMBERS IN COWANIA, PURSHIA, AND FALLUGIA

Previously reported chromosome counts on 21 populations of Purshia tridentata (Sanderson 1969; Alderfer 1976), two populations of Cowania stansburiana (Baldwin 1951; Sanderson 1969), and a single collection of Fallugia (Baldwin 1951) were all $n = 9$ or $2n = 18$ diploids. Sanderson (1969) reported that hybrids between Purshia tridentata and Cowania stansburiana were normal diploids with nine pairs of chromosomes at meiosis. Our new counts (table 2) confirm the $x = n = 9$ status for Cowania (5 species) and Purshia (2 species) for 205 individuals from 93 populations and 1 interspecific and 5 intergeneric hybrid populations. Our counts cover most of the geographic range for Purshia and for Cowania stansburiana (fig. 1, 2; table 2). For the other Cowania species we obtained counts, from 1 to 3 plants, from 1 population each (table 2). Fallugia is not based on $x = 9$. Our counts for 6 widespread populations (table 2) were all $n = 14$. Baldwin's (1951) count of $2n = 18$ is apparently an error. Baker, Righetti, and Pinkava (personal communication) also recently obtained $n = 14$ counts for Fallugia. Although polyploidy is quite common in the Rosaceae as a whole (table 1), it did not occur in the populations we sampled for Purshia, Cowania, or Fallugia (table 2).

EVOLUTIONARY CONSIDERATIONS

Although the family Rosaceae in general is circumboreal in distribution and many of the taxa had Arcto-Tertiary distribution, several genera are richly represented in the Madro-Tertiary geoflora (Axelrod 1958). The Tertiary geoflora concept championed by Chaney and Axelrod (Chaney 1944; Axelrod 1950, 1958; Chaney and Axelrod 1959; Raven and Axelrod 1978) is based on fossil flora evidence and outlines three such floras for North America (fig. 3). In the southern half of the continent the Neotropical-Tertiary geoflora was dominated by broad-leaved evergreens. In the north, the Arcto-Tertiary geoflora was composed of a mixture of mixed temperate deciduous and evergreen species. In between these two and centered in the southern Rocky Mountains and adjacent present-day Mexico, the sclerophyllous and microphyllous Madro-Tertiary geoflora emerged (fig. 3). The Madro-Tertiary geoflora drew its constituent species from the stock of the other floras, but its plants of necessity became adapted to drier habitats.

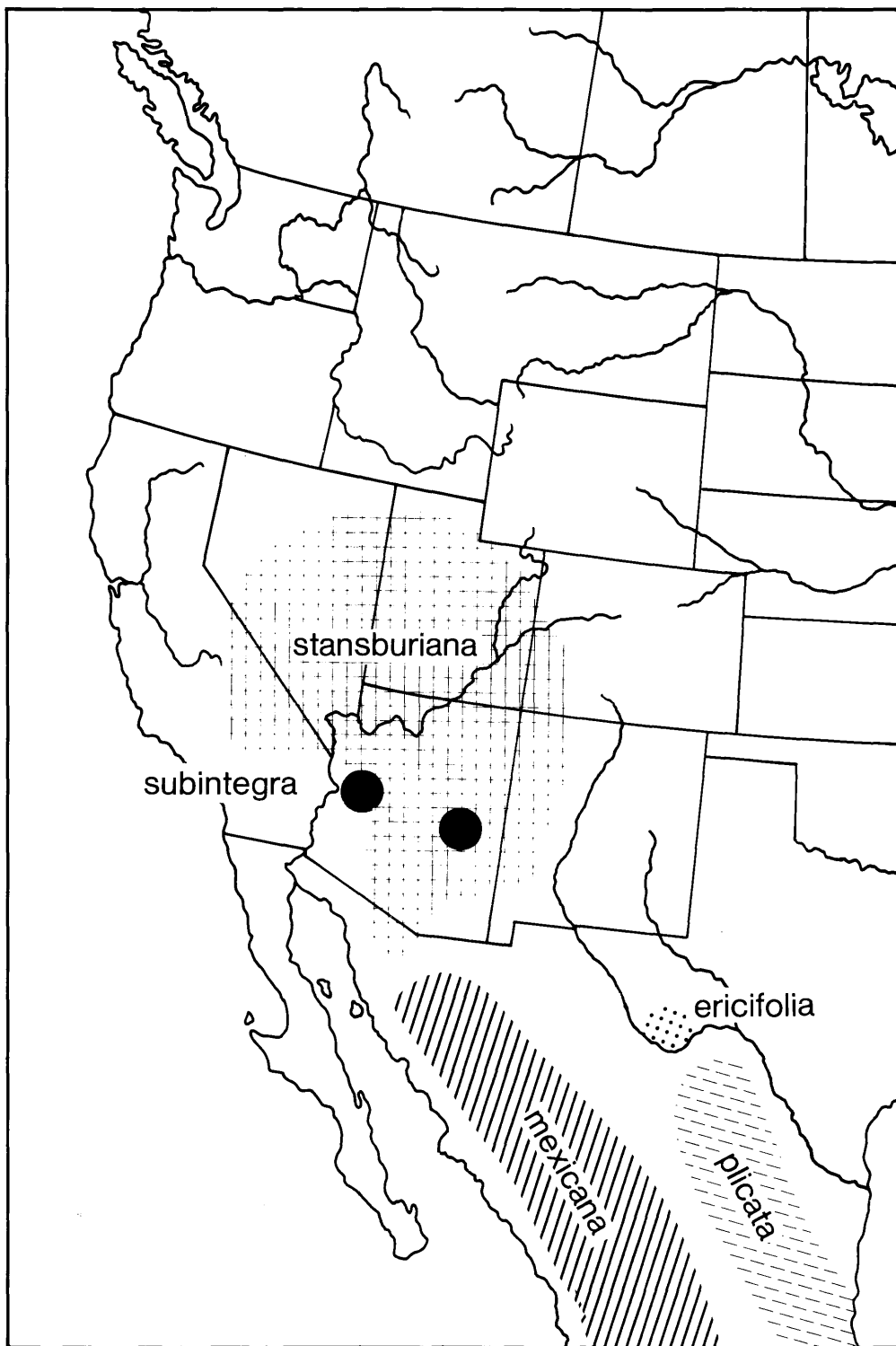


Figure 1.--Distribution of *Cowania* species (after Rydberg 1908-1918; Abrams 1944; Kearney and Peebles 1960; Vines 1960; Little 1976; Koehler and Smith 1981). Baker, Pinkava, and Righetti provided the location for the eastern population of *C. subintegra*.

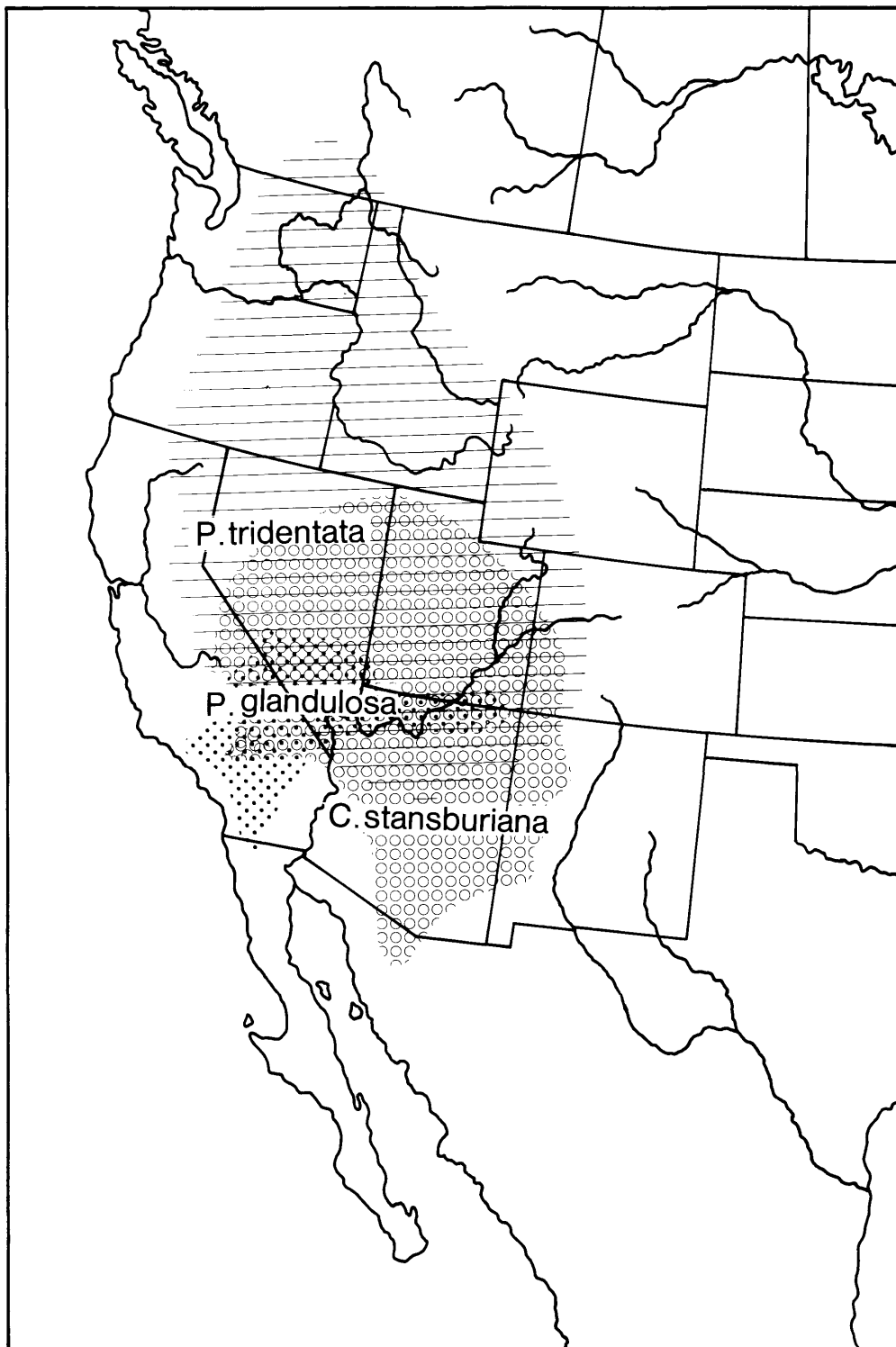


Figure 2.--Distribution of *Cowania stansburiana*, *Purshia tridentata*, and their derivative species *P. glandulosa* (after Stutz and Thomas 1964; Nord 1965; Koehler and Smith 1981).

Table 2.--Chromosome numbers of Cowania, Purshia, Fallugia, and hybrids

Taxa	Locale, collection number ¹	No. of plants sampled	<u>n</u> ²	<u>2n</u> ³
<u>Cowania ericifolia</u> Torr.	Dagger Flat, Big Bend National Park, Brewster Co., Texas, S&T, June 1978, 950 m.	1	9 ⁴	
<u>Cowania mexicana</u> D. Don.	Sombrerete, Zacatecas, Mexico, S, S&T, June 1978, 2 400 m.	2		18
<u>Cowania plicata</u> D. Don.	Iturbide, Nuevo Leon, Mexico, S, S&T, June 1978, 1 900 m.	3		18
<u>Cowania stansburiana</u> Torr.	Scipio, Millard Co., Utah	3		18
	Pine Valley, Washington Co., Utah, U8, 1 650 m.	2		18
	Kaibab Plateau, Coconino Co., Arizona, U15, 1 900 m.	3		18
	American Fork, Utah Co., Utah, U24, 1 550 m.	2		18
	Richfield, Sevier Co., Utah, U24, 1 700 m.	2		18
	Santaquin, Utah Co., Utah, U27, 1 550 m.	2		18
	Slaughter Creek, Washington Co., Utah, U35, 1 650 m.	2		18
	Fredonia, Coconino Co., Arizona, U37, 1 450 m.	2		18
	Prescott, Yavapai Co., Arizona, U38, 1 700 m.	2		18
	Canelo Hills, Santa Cruz Co., Arizona, U39, 1 700 m.	3		18
	Kaibab Plateau, Coconino Co., Arizona, U41, 1 900 m.	6		18
	Kyle Canyon, Clark Co., Nevada, U42, 2 150 m.	2		18
	Thoreau, McKinley Co., New Mexico, U43, 2 350 m.	7		18
	Connors Pass, White Pine Co., Nevada, U44, 700 m.	2		18

Table 2.--(Con.)

Taxa	Locale, collection number ¹	No. of plants sampled	<u>n</u> ²	2n ³
	Blanding, San Juan Co., Utah, U45, 1 900 m.	2		18
	Dave Valley, Lincoln Co., Nevada, U46, 1 950 m.	3		18
	Church Mtns., Millard Co., Utah, U49, 1 800 m.	2		18
	Willow Creek, Sevier Co., Utah, M&S 1348, 1 850 m.	1	9	
<u>Cowania subintegra</u> Kearney	Burro Creek, Mohave Co., Arizona, M 1344, 800 m.	3	9	
<u>Purshia glandulosa</u> Curran.	Jackson Springs, Washington Co., Utah, U2, 1 200 m.	2		18
	Caliente, Lincoln Co., Nevada, U7, 1 900 m.	2		18
	Pioche, Lincoln Co., Nevada, U8, 1 900 m.	1		18
	Ventura, Ventura Co., California, U13, 1 000 m.	4		18
	Oak Springs Summit, Lincoln., Nevada, U14, 1 900 m.	4		18
	Elbert Pass, Inyo Co., California, U15, 1 900 m.	2		18
<u>Purshia tridentata</u> (Pursh) DC.	Diamond Mtn., Uintah Co., Utah, U23, 2 300 m.	2		18
	Fairview, Sanpete Co., Utah, U26, 1 950 m.	1		18
	Mt. Pleasant, Sanpete Co., Utah, U31, 1 900 m.	4		18
	Janesville, Lassen Co., California, U29, 1 350 m.	4		18
	Fountain Green, Sanpete Co., Utah, U31, 1 850 m.	3		18
	Poontown Creek, Wasatch Co., Utah, U37, 2 500 m.	2		18

Table 2.--(Con.)

Taxa	Locale, collection number ¹	No. of plants sampled	<u>n</u> ²	2 <u>n</u> ³
	Maybell, Moffat Co., Colorado, U47, 1 850 m.	2		18
	Mountain Dell, Salt Lake Co., Utah, U54, 1 700 m.	2		18
	Blackfoot, Bingham Co., Idaho, U57, 1 400 m.	2		18
	Pioche, Lincoln Co., Nevada, U64, 1 950 m.	2		18
	Vernal, Uintah Co., Utah, U74, 1 750 m.	2		18
	Bryce Canyon, Garfield Co., Utah, U79, 2 400 m.	2		18
	Fillmore, Millard Co., Utah, U82, 1 700 m.	2		18
	Boise, Ada Co., Idaho, U83, 1 600 m.	2		18
	Bishop, Inyo Co., California, U87, 1 850 m.	3		18
	Mono Lake, Mono Co., California, U90, 2 600 m.	2		18
	Neola, Duchesne Co., Utah, U91, 1 850 m.	2		18
	Preston, Franklin Co., Idaho, U95, 1 700 m.	2		18
	Long Valley Jct., Kane Co., Utah, U103, 2 300 m.	4		18
	Montrose, Montrose Co., Colorado, U104, 1 800 m.	1		18
	Silver City, Juab Co., Utah, U106, 1 900 m.	2		18
	Santaquin, Utah Co., Utah, U107, 1 600 m.	2		18
	Elko, Elko Co., Nevada, U114, 1 600 m.	1		18
	Reno, Washoe Co., Nevada, U116, 1 550 m.	2		18

Table 2.--(Con.)

Taxa	Locale, collection number ¹	No. of plants sampled	<u>n</u> ²	2 <u>n</u> ³
	Silver City, Juab Co., Utah, U117, 1 900 m.	2		18
	Balm Creek, Baker Co., Oregon, U118, 1 100 m.	1		18
	Service Creek, Wheeler Co., Oregon, U119, 650 m.	2		18
	Izee, Grant Co., Oregon, U120, 1 350 m.	2		18
	Hat Rock State Park, Umatilla Co. Oregon, U121, 150 m.	2		18
	Oklahoma Gulch, Chelan Co., Washington, U123, 450 m.	2		18
	Hagerman Wildlife Management Area, Gooding Co., Idaho, U124, 900 m.	2		18
	Nahahum Canyon, Chelan Co., Washington, U125, 450 m.	2		18
	Wellsville Mtns., Box Elder Co., Utah, U126, 1 800 m.	2		18
	Cave Valley, Lincoln Co., Nevada, U127, 1 950 m.	3		18
	Blanding, San Juan Co., Utah, U128, 1 900 m.	3		18
	Diamond Range, Eureka Co., Nevada, U129, 2 200 m.	1		18
	Junction Valley, Cassia Co., Idaho, U130, 1 900 m.	2		18
	Deer Pasture, Millard Co., Utah, U134, 1 750 m.	2		18
	Canyon Mtns., Millard Co., Utah, U135, 1 800 m.	2		18
	Church Mtns., Millard Co., Utah, U136, 1 800 m.	2		18
	Church Mtns., Millard Co., Utah, U137, 1 800 m.	2		18
	Canyon Mtns., Millard Co., Utah, U138, 1 800 m.	2		18

Table 2.--(Con.)

Taxa	Locale, collection number ¹	No. of plants sampled	<u>n</u> ²	2 <u>n</u> ³
	Lava Beds National Monument, Siskiyou Co., California, U139, 1 300 m.	2		18
	Lava Beds National Monument, Siskiyou Co., California, U140, 1 300 m.	1		18
	The Dalles, Wasco Co., Oregon, U143, 200 m.	2		18
	Okanogan Valley, Okanogan Co., Washington, B20, 300 m.	1		18
	Bell Rapids, Twin Falls Co., Idaho, B38, 950 m.	2		18
	Ritter, Grant Co., Oregon, B76, 950 m.	2		18
	Six Mile Lake, Harney Co., Oregon, B97, 1 390 m.	1		18
	Verdi, Washoe Co., Nevada, B100, 1 550 m.	2		18
	Point of Rocks, Sweetwater Co., Wyoming, B101, 2 050 m.	1		18
	Weed, Siskiyou Co., California, B103, 1 100 m.	2		18
	Soda Springs, Caribou Co., Idaho, B104, 1 900 m.	2		18
	Aztec, San Juan Co., New Mexico, B128, 1 830 m.	1		18
	Plains, Sanders Co., Montana, B178, 800 m.	2		18
	South Pass, Fremont Co., Wyoming, B183, 2 300 m.	2		18
	Hoback Junction, Teton Co., Wyoming, B185, 1 870 m.	2		18
	Dulce, Rio Arriba Co., New Mexico, NM503, 2 150 m.	1		18
(HYBRIDS)				
<u>C. stansburiana</u>	Oakley, Cassia Co., Idaho,	2		18
X <u>P. tridentata</u>	U3, 1 500 m.			

Table 2.--(Con.)

Taxa	Locale, collection number ¹	No. of plants sampled	<u>n</u> ²	<u>2n</u> ³
	Junction Canyon, Cassia Co., Idaho, U3, 1 900 m.	2		18
	Wellsville Mtns., Box Elder Co., Utah, U4, 1 800 m.	1		18
	Payson Canyon, Utah Co., Utah, U41, 1 900 m.	5		18
	Nephi, Juab Co., Utah, U44, 1 700 m.	4		18
<u>C. stansburiana</u> X <u>P. glandulosa</u>	Snow Canyon, Washington Co., Utah, U5, 1 000 m.	2		18
<u>P. tridentata</u> X <u>P. glandulosa</u>	Benton Station, Mono Co., California, U5, 2 050 m.	1		18
<u>Fallugia paradoxa</u> (D. Don) Endl.	Hite, San Juan Co., Utah, S, May 1982, 1 050 m.	1	14	
	Willow Creek, Sevier Co., Utah, M&S 1347, 1 850 m.	1	14	
	Alpine, Brewster Co., Texas, Powell 3712, 1 400 m.	1	14	
	Pahcoon Springs Wash, Washington Co., Utah M 379, 1 050 m.	1	14	
	Pipe Springs, Mohave Co., Arizona, M 1345, 1 500 m.	2	14	
	Capitol Reef National Park, Wayne Co., Utah, M 1354, 1 650 m.	2	14	

¹Collection numbers: U = Seed accessions maintained by the Great Basin Experimental Station, Ephraim, Utah (USDA Forest Service, Intermountain Forest and Range Experiment Station and Utah Division of Wildlife Resources, cooperating); B = seed accessions maintained by Forestry Sciences Laboratory, USDA Forest Service, Intermountain Forest and Range Experiment Station, Boise, Idaho; M, M&S, S, S&T are authors' collections; NM = seed accessions maintained by Los Lunas Plant Materials Center, USDA Soil Conservation Service, Los Lunas, New Mexico; others are identified in Acknowledgements Section.

²n = gametic number from pollen mother cells.

³2n = somatic number from root tip meristems.

⁴An additional univalent also observed.

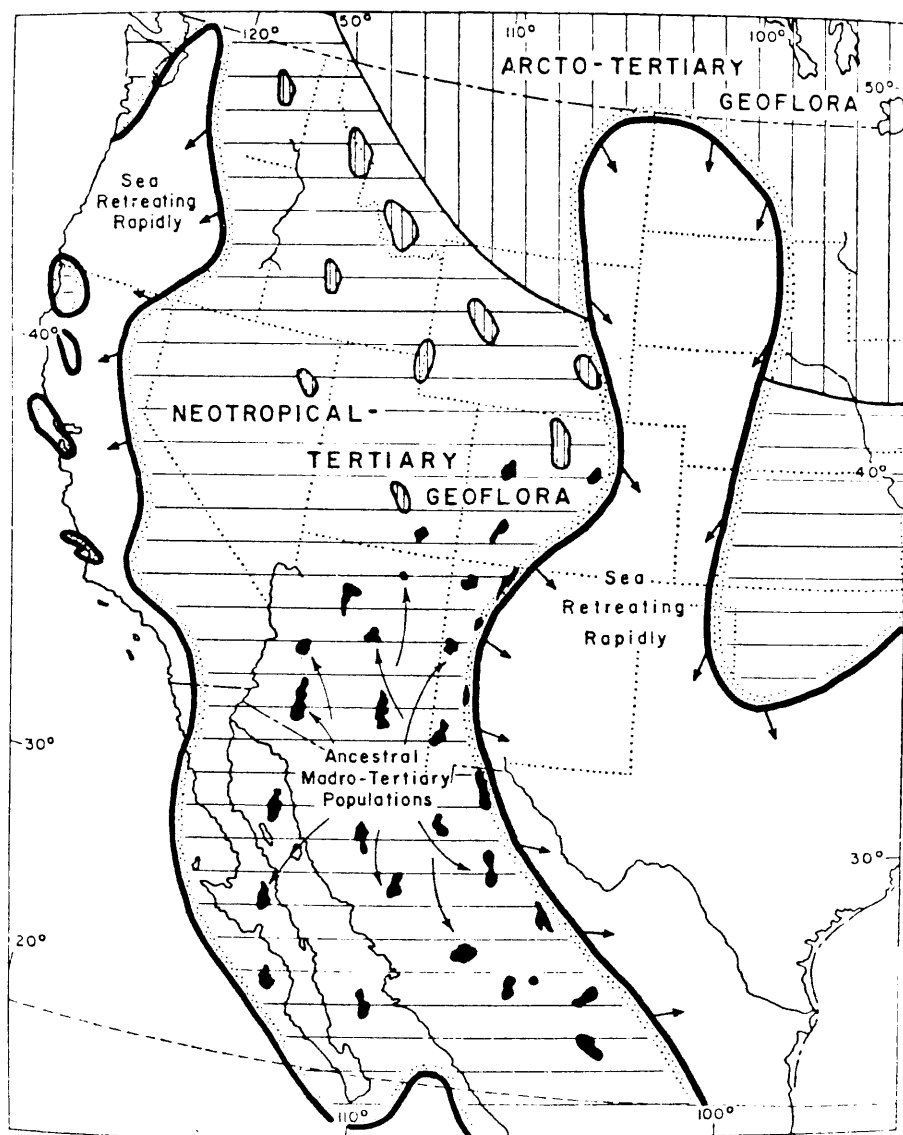


Figure 3.--Inferred distribution of ancestral Madro-Tertiary plants in pre-Eocene time (from Axelrod 1958).

Western Rosaceous Shrubs

We believe with Axelrod (1958) that rosaceous plant stocks available from the Arcto- and Neo-tropical geofloras became part of the more arid Madro-Tertiary geoflora. Apparently, these stocks evolved as new adaptations in the increasingly drier conditions of the Southwest. Axelrod (1950, 1958, 1977, personal communication) lists Amelanchier, Cercocarpus, Chamaebataria, Coleogyne, Cowania, Holodiscus, Lyonothamnus, Peraphyllum, Photinia, Prunus, Purshia, Rosa, and Vauquelinia as rosaceous genera occurring in the Madro-Tertiary geoflora. These genera represent all four rosaceous subfamilies (table 1).

The Madro-Tertiary geoflora is particularly rich in fossil records of Cercocarpus and Vauquelinia (Axelrod 1950, 1958). The records for Purshia and Cowania are more spotty. Purshia is recorded from the Pliocene some 10 million years ago (Axelrod 1958, personal communication). Cowania has not been recorded, although Axelrod (1977) suggested it was part of the mid-Eocene to Pliocene flora of 10 to 50 million years ago. An extinct fossil species of Fallugia is represented in the Creede, Colorado flora of 26.5 million years ago (Axelrod, personal communication).

Several rosaceous genera, all in the subfamilies Rosoideae and Spiraioideae, have $x = 9$ chromosomes, and Madro-Tertiary geoflora affinities (table 3). These species may be more closely related than placing them in separate subfamilies would indicate. Besides sharing the primitive $x = 9$ chromosome number, both sets share growth habit similarities and are mostly endemic to western North America, and sclerophyllous or microphyllous. The high rates of endemism (10 of 13 genera) and monotypicism argue for a Madro-Tertiary geoflora connection within scattered pockets of habitat. The main exceptions are the circumboreal Dryas, Physocarpus, and Spiraea. The $x = 9$ Rosoideae genera of table 3 may have more in common with Spiraioideae than with $x = 7$, mesic Rosoideae such as Fragaria, Potentilla, Rosa, Rubus, and Sanguisorba. For example, Chamaebatia of Rosoideae and its namesake Chamaebatiaria of Spiraioideae resemble one another very closely in leaf form although they differ in fruit type and growth habit. The Rosoideae species of table 3 have close distributional, morphological, and actinomycete nodulation ties (Benson 1957; Klemmedson 1979). Nevertheless, we question the subfamilial distinctness of the genera listed in table 3 in light of their apparent affinities.

Table 3.-- Rosaceous shrubs with Madro-Tertiary geoflora affinities, $x = 9$ ¹

Subfamily Rosoideae	No. of species	Distribution	Subfamily Spiraioideae	No. of species	Distribution
<u>Adenostoma</u>	2	California and western Mexico	<u>Chamaebatiaria</u> ²	2	Idaho, Utah, Nevada
<u>Cercocarpus</u>	7	Western North America including Mexico	<u>Holodiscus</u> ²	14	Western North America including Mexico, Columbia
<u>Chamaebatia</u> ²	2	California	<u>Kelseya</u> ²	1	Idaho, Montana, Wyoming
<u>Cowania</u>	5	Western North America including Mexico	<u>Lutkea</u>	1	Northwestern North America
			<u>Petrophytum</u> ²	5	Western North America
<u>Dryas</u>	4 ³	Circumboreal	<u>Physocarpus</u> ⁴	6 ³	North America and Asia
<u>Purshia</u>	2	Western North America	<u>Spiraea</u> ⁴	22 ³	Circumboreal

¹Shrubs of the subfamilies Rosoideae and Spiraioideae with species west of the Mississippi River. Chromosome number, number of species, and species distribution information compiled from Rydberg (1908-1918), Martin (1950), Raven and others (1965), Taylor and Mulligan (1968), Bailey Hortorium Staff (1976), and tables 1 and 2.

²Based on new chromosome counts (Sanderson and McArthur, unpublished).

³Only North American species included.

⁴Also includes $x = 7$ species (in the Asiatic portion of range).

Evolutionary History

The degree of relationship among taxa may be assessed, in part, by the fertility of hybrids between them. Reproductive isolation barriers are usually established by natural selection. They are, expectedly, most intense between species that have a long history of sympatric association (Stebbins 1974). Conversely weak isolation barriers are ordinarily indicative of recent evolutionary divergence or recent contacts between related, formerly allopatric species. We believe the weak isolation barriers between Cowania stansburiana and Purshia tridentata are indicative of their recent contact after a long separation. Although Cowania stansburiana differs in many attributes from Purshia tridentata, there is little restriction to their interbreeding.

An area including almost all of Utah and most of Nevada is an overlap zone for them (fig. 2), and hybrids are found at nearly every point of contact (Stutz and Thomas 1964). The only semblance of a reproductive isolation barrier is their partially disjunct flowering periods. Purshia tridentata usually flowers earlier than C. stansburiana, but in many places, C. stansburiana, growing on a south-facing or west-facing slope of a ravine, has its flowering period sufficiently advanced to overlap the retarded flowering period of P. tridentata growing on the adjacent north-facing or east-facing slopes. In such circumstances hybrids are abundant, mostly along the ridge tops separating the parental populations. The hybrids are highly fertile and often yield sizeable populations of hybrid segregants. More commonly, the hybrids backcross to the parents, providing genetic introgression from one species to the other. So common is introgressive hybridization that no population of bitterbrush yet examined in Utah is free from influence of earlier hybridization with cliffrose (Stutz and Thomas 1964; authors' unpublished observations). Introgression of bitterbrush into cliffrose is less common than introgression of cliffrose into bitterbrush, but that, too, occasionally happens. Such wholesale hybridization and subsequent introgression will undoubtedly provide numerous new adaptive products. Thus far only two have been detected: one to the south and one to the north of the overlap area (fig. 2). The southern adaptive derivative has been described as Purshia glandulosa. So recent is its origin that although it is uniform for those particular attributes that identify it as P. glandulosa, different populations are genetically distinct. This may reflect polyphyletic origins or chance fluctuations in occurrence of attributes not crucial for its establishment (Stutz and Thomas 1964). Koehler and Smith (1981) demonstrated that the flavonoid chemical complement of P. glandulosa is compatible with a hybrid ancestry.

North of Utah, beyond the geographic distribution of Cowania, some cliffrose characteristics are present in most bitterbrush populations (Stutz and Thomas 1964). A possible advantage to such introgressed populations may be a reduction in palatability to browsing animals. The magnitude of apparent introgression diminishes, as expected, with latitude, but even in a population in British Columbia a few plants bear stalked hypanthium glands, suggesting some influence of Cowania even at that northern latitude.

Because much of the overlap area of C. stansburiana and P. tridentata coincides with areas occupied by Pleistocene lakes and glaciers as recently as 12,000 years ago (Lindsay and Vickery 1967), the current distributions in the overlap areas are recent for both species. Their previous, probably disjunct, distribution allowed genetic divergence for many attributes, but provided little impetus for reproductive isolation.

Purshia and Cowania, while obviously related, differ in many attributes used in taxonomy (table 4): leaf size and shape, pubescence, glandulosity, time of flowering, number of stamens, number of carpels, deciduousity, and geographical distribution (Thomas 1957; Stutz and Thomas 1964). However, because some of the species hybridize in nature, yielding fertile progeny, some scientists (such as Cronquist, personal communication; Koehler and Smith 1981) thought it might be appropriate to combine them into one genus. The wisdom of such a rigid application

of a single criterion for genus definition in the face of their numerous differences is questionable. Therefore, we prefer to retain them as separate genera. Other rosaceous genera (such as Cydonia, Malus, Pyrus, and Sorbus) also have intergeneric fertility but are maintained as distinct genera (Watkins 1976).

Table 4.--Morphological characteristics of species of Cowania, Purshia, and Fallugia

Species	Leaves										Flowers								Bark
Species	Length (mm)	Width (mm)	Lobes (#)	Sinus depth (0-3)	Dorsal pubesc. (0-3)	Revolute margin (0-3)	Gland abundance (0-3)	Gland formality (0-3)	Glands stalked (0-3)	Pedicel length (mm)	Pedicel glands (0-3)	Sepal length (mm)	Sepal glands (0-3)	Hypanth. angle*	Hypanth. pubesc. (0-3)	Hypanth. glands (0-3)	Glands stalked (0-3)	Achenes/hypanth. (#)	Color
COME	7	4	3	3	0	3	3	3	0	4	1	4	2	c	2	0	1	8	bronze
COST	7	4	5	3	0	2	3	2	0	5	3	6	2	f	0	3	2	6	gray
COER	6	1	0	-	0	3	0	-	-	3	3	2	3	f	3	3	3	14	gray
COSU	9	4	1	1	1	2	0	-	-	7	0	3	0	f	1	0	-	5	gray
COPL	11	6	6	1	0	1	v	v	v	6	3	6	3	f	2	3	3	12	brown
PUGL	6	3	3	2	0	3	3	2	0	4	0	5	0	f	1	0	0	2	gray
PUTR	10	7	3	2	3	0	0	0	0	1	0	3	0	f	1	0	0	1	gray
FAPA	10	6	3	3	1	2	0	0	0	13	0	6	0	c	1	0	0	55	yellow

* companulate = 40°, funnellform = 70°

Seven species of Cowania have been described: C. alba Goodding, C. ericifolia Torr., C. mexicana D. Don, C. plicata D. Don, C. davidsonii Rydberg, C. stansburiana Torr., C. subintegra Kearney. The single collection of C. alba is almost certainly Purshia glandulosa or a hybrid (Rydberg [1913, p. 416] notes that the collection of C. alba may be a hybrid between C. stansburiana and P. glandulosa--and, we have observed such hybrids in the general area of the only collection made for C. alba). Cowania davidsonii is one of the common variants of C. stansburiana (Kearney and Peebles 1960). As shown in table 4 and figures 1 and 4, the other five species have distinctive differences and distributions.

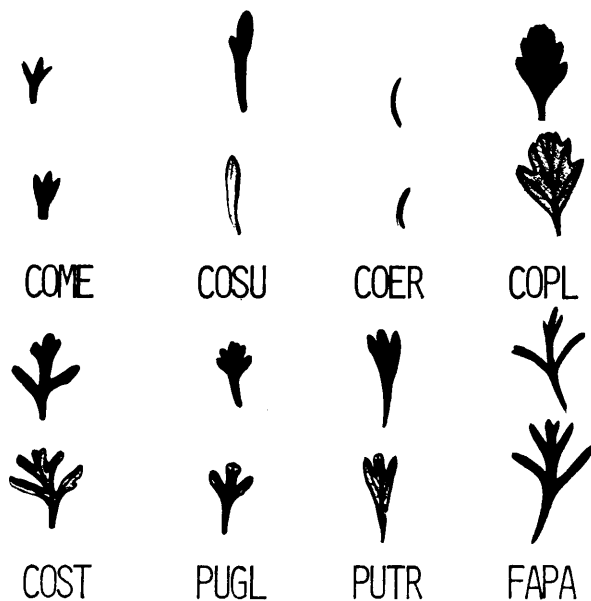


Figure 4.--Illustrated leaves of Cowania, Fallugia, and Purshia species (ca. X 1).

Cowania mexicana is found only on the slopes of the Sierra Madre Occidental in north-central Mexico. It is an erect, almost fastigate shrub 6.5 to 13 ft (2 to 4 m) high with short branches and conspicuously rusty-orange colored bark. The leaves are three-cleft with narrow entire lobes and deep sinuses (fig. 4) bearing nonstalked glands.

Cowania stansburiana grows northward from northern Mexico into California, Arizona, New Mexico, Colorado, Utah, and Nevada to about the 42° parallel. It usually grows in dry, well-drained shallow soils. It is usually 3 to 6.5 ft (1 to 2 m) tall, but some plants grow into small trees, 20 ft (6 m) or more in height. This species is frequently treated as a variety of C. mexicana (var. stansburiana [Torr.] Jeps.). We choose to accept it on the species level in a parallel treatment with the other Cowania taxa (table 4). It differs from C. mexicana in that C. stansburiana generally has more leaf lobes, a less revolute leaf margin, less glandular formality on leaves, a longer pedicel length, more pedicel glands, larger sepals, a more funnelform hypanthium angle, more stalked glands on flowers, and fewer achenes per hypanthium. The two taxa differ also in that C. stansburiana has glands on the hypanthium whereas C. mexicana has a pubescent hypanthium.

Cowania ericifolia has a restricted distribution in limestone rocks along the Rio Grande River in the Big Bend area of Texas. This short statured, straggling shrub has tiny needle-like leaves (fig. 4).

Cowania subintegra has been collected only near Burro Creek in west-central Arizona and near Bylas in southeastern Arizona. It grows in a calcareous shale with xerically adapted plants such as Larrea tridentata and Cereus giganteus. It is much like C. ericifolia in all respects except that many leaves have irregular and infrequent side lobes, and it is generally larger statured.

Cowania plicata is a very distinctive species, conspicuous because of its beautiful pink-crimson flowers. Its leaves are much broader than those of any other Cowania species (fig. 4) and are seasonally deciduous when grown in the Brigham Young University nursery in Utah. It grows in the Sierra Madre Oriental in northeastern Mexico in more mesic sites than do other Cowania species.

Fallugia paradoxa (D. Don) Endl. is monotypic and also shows minimal intraspecific variation. Although a common element in all of the deserts of southwestern North America (fig. 5), it is usually restricted to washes, seepage areas, and woodland margins, so it is somewhat more mesophytic than Purshia glandulosa and most species of Cowania. Superficially, because of its similarly lobed leaves and clusters of long, feather-tailed fruits, Fallugia appears to be closely related to Cowania (Benson 1957; Blauer and others 1975). However, its chromosome number (table 2, Baker, Pinkava, and Righetti unpublished) and floral characteristics (table 4) show that it is a distinctive genus. Furthermore, Fallugia also differs from Cowania, Purshia, Dryas, Cercocarpus and other $x = 9$ Rosidae shrubs (1) in not forming symbiotic actinomycete-induced nitrogen-fixing root nodules (Klemmedson 1979; Nelson in this proceedings; Righetti in this proceedings), and (2) in producing functionally dioecious plants (Blauer and others 1975; authors' personal observations). We are not certain if its primary alliances are with the $x = 9$ group of table 3 or with one of the $x = 7$ groups of table 1. Some of the $x = 7$ plants such as Potentilla have the dioecious habit of Fallugia. The curious case of the putative natural hybrids between Cowania and Fallugia (Blauer and others 1975) is apparently due to mutants of C. stansburiana. These plants have the $2n = 18$ chromosome number of C. stansburiana (authors' unpublished; Baker, Pinkava, and Righetti unpublished).

Purshia tridentata (Pursh) DC. is distributed from about the 37° N parallel northward into southern British Columbia, mostly on the western side of the Continental Divide (fig. 2). It differs from P. glandulosa and all of the Cowania species in being deciduous and having a much earlier flowering period (May-June). Other differences are listed in table 4.

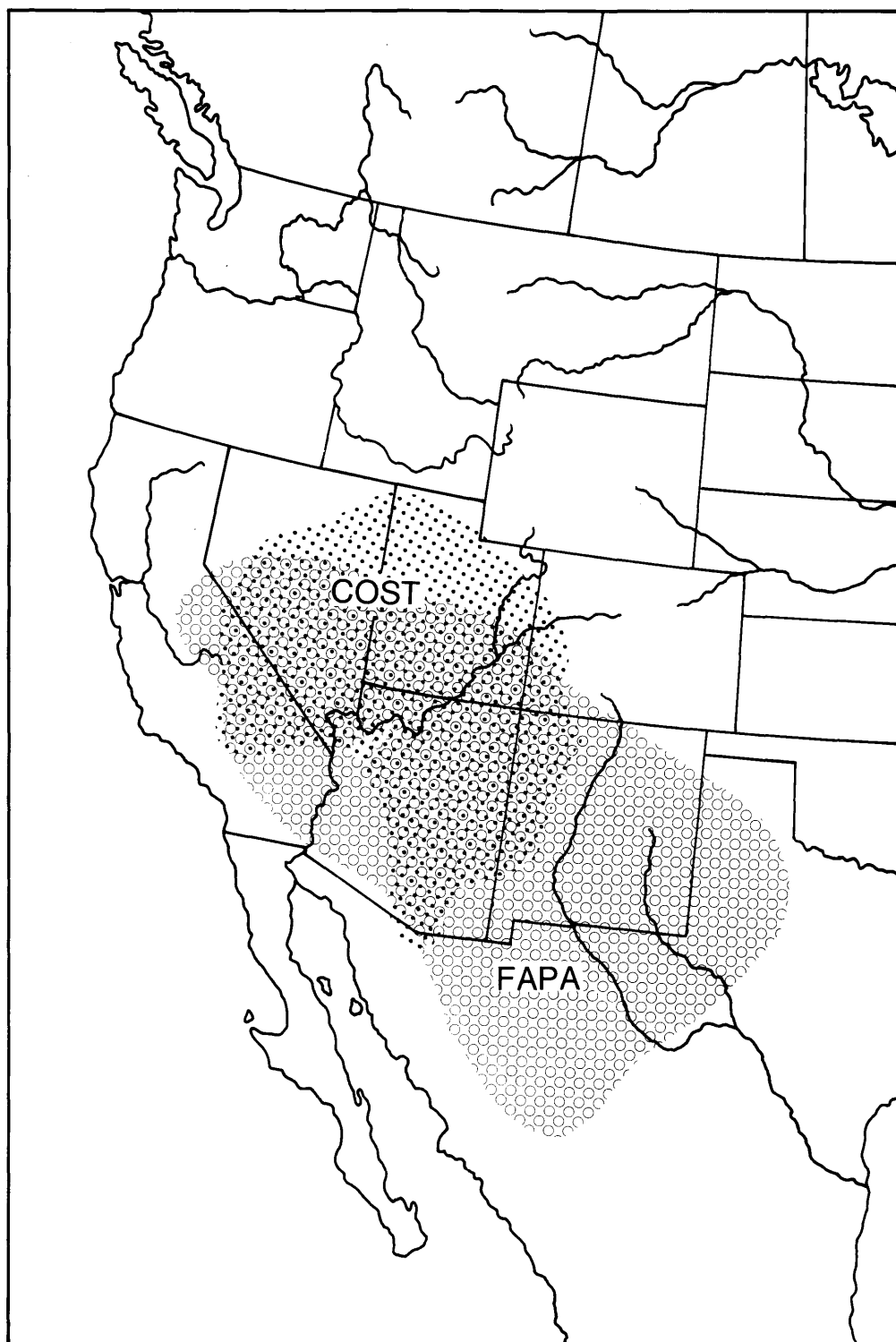


Figure 5.--Distribution of Cowania stansburiana (from fig. 2) and Fallugia paradoxa (after Kearney and Peebles 1960; Vines 1960).

Purshia glandulosa Curran is restricted to southern Utah, northern Arizona, southern Nevada, and southeastern California (fig. 2). Stutz and Thomas (1964) and Koehler and Smith (1981) report that it appears to be a hybrid derivative from Cowania stansburiana X Purshia tridentata parentage.

Cowania appears to be more ancient than Purshia. Furthermore, Cowania, has other attributes that make it attractive as ancestral stock. It has some apparent affinities with Cercocarpus, which has a demonstrated antiquity through an abundant fossil record (Axelrod 1950, 1958, 1977). We think it notable that Cowania and Cercocarpus both have long, plumose, persistent styles attached to their achenes. Furthermore, Cowania and Cercocarpus have a similar complement of isoenzymes, more similar, in fact, than do Cowania and Purshia (Leonard and others 1981). Their chromosomes are similar in size and staining behavior (authors' unpublished research). Both Cercocarpus and Cowania have higher numbers of species than the other Rosoideae of table 3; and they have better development in the south where the Madro-Tertiary geoflora underwent maximum development (figs. 1 and 3).

We make the proposal that Cowania is ancestral to Purshia. Its southern distribution, greater intraspecific differentiation, primitive traits (numerous flower parts and evergreen habit), and its apparent isoenzymatic and morphological kinship with the geologically widespread Cercocarpus make it a good candidate for primitive stock. Cowania appears to be among those desert shrubs that Axelrod (1958) proposed were derived from the Arcto- and Neo-tropical Tertiary flora following their emergence in the Sierra Madre region of Mexico during the Tertiary epoch. Its lobed, revolute-margined leaves appear to be adaptations that permitted it to accommodate the more xeric Madro-Tertiary environment and that have allowed it to continue as a desert shrub to the present. Cowania mexicana is probably most like the ancestral stock. From it, C. ericifolia was probably derived as a more extensive xerophyte bearing needle-like leaves that permitted it to occupy severely xeric sites. Cowania stansburiana apparently acquired multilobed leaves and numerous stalked glands that were necessary adaptations for spreading into the cooler drier climates to the north. Cowania subintegra with its subtle leaf-lobing may be an intermediate in the evolution of C. ericifolia or a separate spinoff in the line. Alternatively, it may be the product of hybridization between a previously more widespread C. ericifolia and C. stansburiana. Because C. plicata is so distinctive from the other Cowania species, it most likely diverged early in the evolution of the genus.

Purshia is also probably an early derivative from Cowania that subsequently evolved in isolation. Present contact between Purshia and Cowania is apparently very recent. An alternative hypothesis is that some ancestral stock gave rise to several related, but independent, entities from the evolving Madro-Tertiary flora, for example, Cowania and Purshia taxa. As mentioned above, Purshia glandulosa is clearly of recent origin (fig. 2).

Fallugia paradoxa was probably also a part of the Madro-Tertiary geoflora. It may have separated from Cowania-Purshia by chromosome number reduction or, more likely, it may be more closely related to $x = 7$ stock. In any case, it is now apparently genetically impoverished and narrowly niche-restricted.

Future evolution in this fascinating group of rosaceous plants will probably be most dramatic in the overlap areas of Cowania and Purshia. There, interhybridization is providing an unusually rich gene pool, probably much like that available during Tertiary when the merging of northern and southern species and the presence of moisture gradients provided similar extensive arrays of genetic combinations with resultant new adaptive themes.

CONCLUSIONS

Cowania, Purshia, and Fallugia are all derivatives of the rosaceous components of the Madro-Tertiary geoflora. Cowania with its more southern distribution, higher number of species, apparent antiquity, and affinity for Cercocarpus is probably most like the ancestral stock. Cowania mexicana may have been the springboard for the derivation of other species of Cowania and perhaps Purshia. Fallugia's relationship to Purshia and Cowania remains unclear. Although it shares several morphological traits with Cowania, it has many distinctive differences including base chromosome number.

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TAXONOMIC VARIATIONS OF BITTERBRUSH

(PURSHIA TRIDENTATA) IN OREGON¹

A. H. Winward and Jean Alderfer Findley²

ABSTRACT

Morphological and physiological characteristics of bitterbrush populations were examined in Oregon and northern California to determine which of the observed variations are genetic and which are environmental expressions. Four ecotypes were identified but extensive overlapping between populations was found. Specific characteristics studied indicated two separate trends for bitterbrush gene flow into Oregon.

INTRODUCTION

Bitterbrush (Purshia tridentata [Pursh] DC) is a palatable and nutritious shrub component of many western rangelands. Because of depletion over much of its range, considerable emphasis has been placed on its restoration during the past two decades. Many restoration attempts have met with either limited success or total failure. Although many factors have been explored to explain these failures, the possibility of genetic variation within this species often has been overlooked. Species such as bitterbrush that occupy broad environmental ranges have had ample opportunity for the development of such adaptive variations.

Many of us have observed a considerable amount of variation in bitterbrush. Height ranges from a low prostrate, layering form less than 1.6 ft (0.5 m) to large upright shrubs over 13 ft (4 m) tall. We have observed marked variation in leaf size, shape, color, and pubescence between areas as well as within a single population. Glandulation may occur on the hypanthia alone or on new leaders and leaves. Seed size, shape, and coloring varies markedly as does the hypanthium length. Growth form as influenced by leader and spur development likewise has shown distinct variation. In addition, we have observed major differences in the timing of such physiological functions as flowering and seed set over the shrub's geographic range.

Bitterbrush grows in association with a variety of vegetation types, including ponderosa pine, lodgepole pine, oak, juniper, or sagebrush. Sometimes it is a sole shrub dominant. Franklin and Dyrness (1973) recorded 18 recognized habitat types in Oregon of which bitterbrush was a major component.

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Soil characteristics supporting bitterbrush vary widely. Parent material may be basaltic, rhyolitic, pumiceous, or sedimentary (Nord 1965). Generally, soils are coarse-textured, deep, and well drained; however, Driscoll (1964) reported stands of bitterbrush on fine-textured, stoney soils.

Several authors indicate that many of the differences observed between populations of bitterbrush may be genetically influenced (Nord 1959; Wagle and Vlamis 1961; Plummer and others 1968; Klemmedson and Ferguson 1969). We initiated this study to ascertain if bitterbrush is composed of distinct genetic groups that can be recognized and used to better understand management requirements for this forest and rangeland shrub. A more detailed discussion of pertinent information on the ecology and taxonomy of antelope bitterbrush can be found in Alderfer (1977) from which this publication is a part.

STUDY APPROACH

We selected 18 areas in eastern Oregon and two areas in northern California for field studies of specific bitterbrush populations. Populations selected for intensive study were chosen to represent major differences in growth form and morphology of bitterbrush plants, elevations, geographical range, dominant associated species, and physical environment. Every effort was made to select sites that presented reasonably undisturbed conditions and a minimum of utilization on bitterbrush plants.

At each site, measurements were made and characteristics studied for 20 vigorous, mature, seed-bearing individuals of the local bitterbrush population. We placed a vegetative sample from each plant in a paper bag for later chromatographic studies. A voucher specimen was likewise pressed for the 10 even-numbered plants from each site. As the season progressed, we collected seeds and their accompanying hypanthia from each of the 20 plants at each area.

Based on visual inspection and measurement of material from the pressed samples, ratings were developed and assigned for leaf glandulation, pubescence, length, width, lobing, general shape, and bark coloration. In an effort to evaluate growth form, leader growth was recorded as strongly upright or multidirectional. Layering, dense or open branching, and spur production also were rated.

We selected 450 well-filled seeds from 17 populations. These seeds were germinated and grown in a common greenhouse environment to help determine which characteristics were genetically fixed versus those that might represent environmental expressions. Percent emergence, cotyledon height, and leaf pubescence, glandulation, and shape were recorded for comparisons between different populations and between parent plants and their progeny.

Vegetative material from 10 samples at each of 15 sites was used for chromatographic tests. Root tips from the germination trials were used in the chromosomal studies. We used a cluster analysis technique in grouping populations of bitterbrush that had similar characteristics.

RESULTS

Data from the 20 study areas showed some clustering of kinds or races of bitterbrush, but a lot of overlapping occurred between populations. We found evidence of a gene flow pattern among populations into Oregon. There has been a pattern of gene exchange northward through Utah, down the Snake River in Idaho, and into northeastern Oregon. Our data suggest that another line of gene exchange has

occurred westward from the Great Basin to the Cascade-Sierra Mountains and from there northward into Oregon and Washington. Major morphological differences between populations from these two areas of gene flow that showed in the cluster analysis are shown in table 1.

Table 1.--Major characteristics of two gene flow patterns found in Oregon.

	Idaho - Snake River	Cascade-Sierra
Leaves	Straight edge	Belled
Achenes	Long, indented	Filled
Hypanthia	Long	Short

In addition to these gene flow patterns, we found sufficient evidences to identify and describe four ecotypes of bitterbrush in Oregon. The pumice soils in the lodgepole pine region appear to have given rise to a local ecotype of bitterbrush characterized by small, dark green, heavily glandular plants that show a tendency toward prostrate growth form, layering, and lack of dense spur development (fig. 1).

In a similar and equally harsh but edaphically different environment at the top of Hart Mountain, another ecotype has developed. This ecotype is similar in growth form, color, layering, and glandulosity to the lodgepole pine ecotype, yet has certain distinctive features (fig. 1). Leaves at Hart Mountain are more belled and have shallower lobes, a striking white bark, and yellowish rather than redish glands. Seed set and shatter occurs in late summer versus early summer for the lodgepole ecotype.

We found two additional ecotypes representing tall plants with long, large leaves and heavy seeds, one in the Janesville area of northern California and the other along portions of the Snake River drainages in north eastern Oregon (fig. 2). Both locations have long growing seasons and deep soil, in contrast to the rather harsh environmental conditions that gave rise to the Hart Mountain and lodgepole pine ecotypes. These two tall ecotypes actually showed more dissimilarity than the low, layering ecotypes. Differences were particularly evident in the hypanthium length, achene shape and markings, glands on the hypanthia, leaf pubescence, and a distinct point on the outer leaf lobes (table 1).

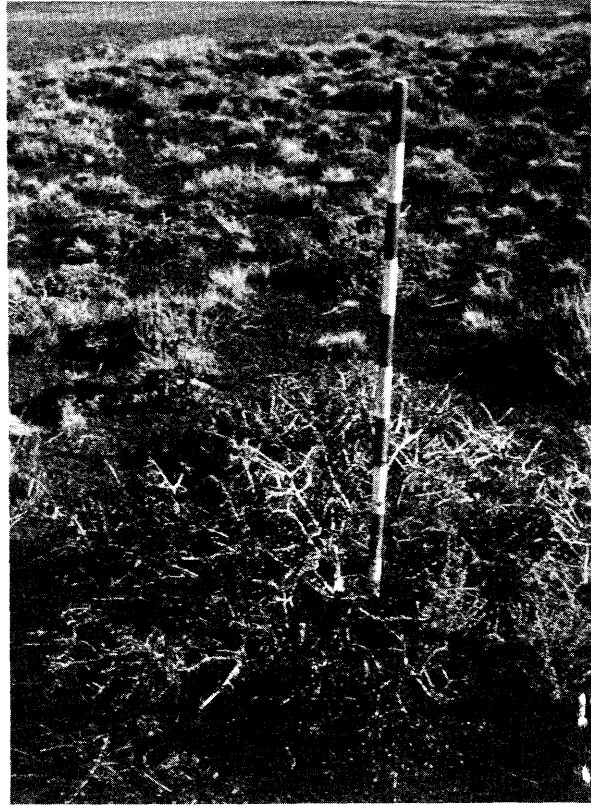


Figure 1.--Examples of low, layering ecotypes: Left - Lodgepole/Pumice, and right - Hart Mountain.



Figure 2.--Examples of tall, massive ecotypes: Left - Janesville, and right - Snake River.

However, in support of the ecotype concept for these four races, all retained many of their characteristics under common conditions in the greenhouse (fig. 3). Although morphology was variable within and between populations of these ecotypes, silhouettes in figure 4 demonstrate the general leaf shapes of each of the four Oregon ecotypes. These silhouettes also demonstrate that leaf morphology varies depending on its position on the plant. This characteristic can be useful in better understanding bitterbrush taxonomy, and it may be an important management feature. For example, size of overwintering leaves varies considerably among ecotypes, which, in turn, can influence the winter nutrient status of bitterbrush.



Figure 3.--Plants showing upright (left) and recumbent (right) growth form for plants grown in the greenhouse. Left - Snake River ecotype, and right - Lodgepole/Pumice ecotype.

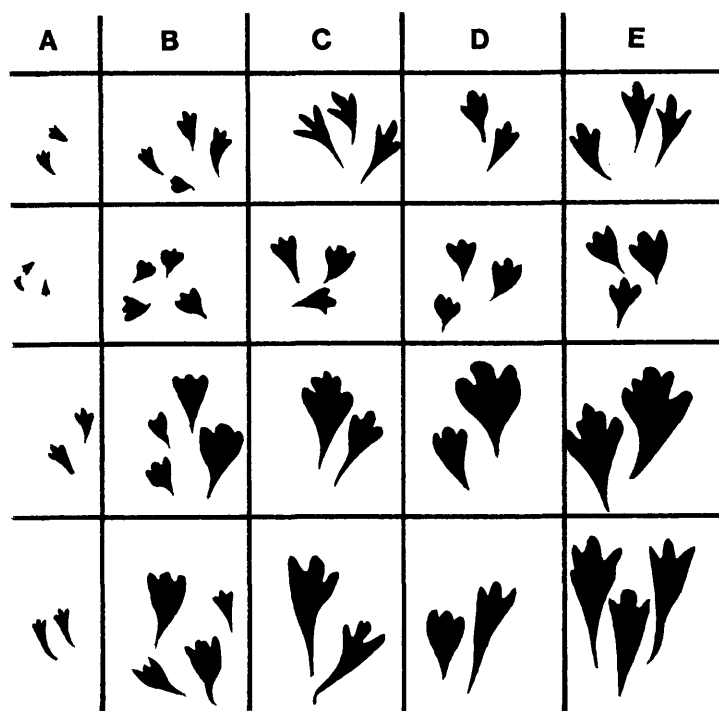


Figure 4.--Variation in leaf characteristics for the four Oregon ecotypes. Kind of leaf and/or position are as follows: A = overwintering; B = outside spur; C = inside spur; D = first leader; E = second and subsequent leader

The remainder of the bitterbrush populations studied appeared to represent merging of characteristics from two or more of the four described ecotypes.

Chromosome counts showed all bitterbrush populations studied were diploid ($2n = 18$). No evidence of polyploidy was found. In the chromatographic studies, we could not find adequate correlation between the flavanoid and phenolic spots and morphological characteristics, nor geographical distribution of bitterbrush. We did find four spots common to cliffrose (Cowania stansburiana Torr.) in sampling desert bitterbrush (P. glandulosa) obtained from southern California. This supports statements by other authors regarding introgression of cliffrose and desert bitterbrush (Nord 1965). These four spots were found only sporadically in antelope bitterbrush; yet, they likewise indicate that some populations of antelope bitterbrush may show introgression with cliffrose. However, no distributional pattern could be discerned for plants or populations containing these spots.

CONCLUSIONS

Because bitterbrush has the characteristic to outbreed (readily crosses with other bitterbrush plants in the vicinity) and because it is known to hybridize with cliffrose, it contains a diverse genetic reserve so that, in total, the species is well adapted to a number of diverse environments. This has been both an advantage and disadvantage to managers. The advantage is the wide diversity of material to choose from when selecting sources of bitterbrush for specific sites or uses. The disadvantage is that it is difficult to match the best genetic material to our particular needs. For managers contemplating bitterbrush seeding projects, seed source remains critically important. Indiscriminate choice of seeds may be responsible for our past and present seeding failures. We need to study tolerance ranges of all races of bitterbrush so we can better predict their limitations. For example, the two low layering ecotypes may be highly adapted for establishment on certain harsh sites. However, it would appear the Hart Mountain ecotype may be more successful on harsh, shallow soil sites in higher mountainous areas of the Western United States because it is adapted to the shorter frost-free growing season at these elevations.

A relationship was observed between taller plants and frost-free growing season. Seeds from the tall ecotypes may produce seedlings unable to survive where severe frosts occur frequently. Failure of some of our past seeding is likely related to selection of nonfrost tolerant ecotypes. If local or on-site seed is not available, we recommend that associated vegetation, soil type, and frost-free growing season of the seed source be matched as nearly as possible to the site selected for seeding.

Based on our study of the four ecotypes, we also recommend that the presoak treatment in thiourea to break bitterbrush seed dormancy be extended from the currently recommended 5 min. treatment to a 15-20 min. treatment. We found that a 5 min. soak was not adequate for all ecotypes studied, while the 15-20 min. soak broke dormancy in all ecotypes. A longer 20 min. soak is not recommended because it may damage the radicle of some types.

As we continue to understand more about the genetic nature of bitterbrush, we will most likely increase our ability to manage this complex and interesting shrub.

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BITTERBRUSH DISTRIBUTION AND
HABITAT CLASSIFICATION ON THE
BOISE NATIONAL FOREST¹

Ronald K. Tew²

ABSTRACT

On the Boise National Forest, bitterbrush occurs most abundantly between 3,200 and 4,500 ft (975 and 1371 m) elevation. Hot south-facing slopes have the greatest tendency to support bitterbrush at all elevations. On sites having deep soils, plants are tall and treelike, but they are prostrate on many of the harsher sites.

INTRODUCTION

Numerous classification and stratification schemes could be used to inventory natural resources. Most are used to identify units of land that have unique resource values or constraints. In mapping, some characteristics often used as a basis include soils, vegetation, landform, geology, and climate. These variables may be mapped independently or as an integrated system. The approach that has been followed here is an integrated inventory with emphasis on landform, geology, vegetation, and climate. Soil is given emphasis at lower levels in the inventory system.

Whatever approach is used, a base map is generally prepared that provides a common land resource frame of reference for various disciplines to relate to in land management planning. Advantages to such an approach from the standpoint of bitterbrush management include: (1) predictive capabilities are improved in a homogeneous setting; (2) there is a basis for extrapolation of information; (3) sampling variation is reduced when resource inventories are done in a relatively homogeneous environment; (4) there is a recognized unit of land for describing the location of available resources; and (5) there generally is better interdisciplinary communication when a common land base has been established as a reference point.

FOREST STRATIFICATION

The concepts of land systems inventory presented by Wertz and Arnold (1972), with modifications proposed by Bailey (1980), provided the framework for land

¹ Paper presented at the Bitterbrush and Cliffrose Symposium in Salt Lake City, Utah, April 13-15, 1982.

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stratification on the Boise National Forest. Bailey's ecoregion concept provided the first broad level of stratification using climate and potential vegetation as variables. Within ecoregions, "zones" were established by superimposing subsections as defined by Arnold (1975). These zones were distinguished on the basis of landform, climate, and geologic structure. Zones were divided into "landtype associations" as defined by Wertz and Arnold (1972).

All or portions of 21 zones were established to cover about 3 million acres (1.2 million ha) in the Boise National Forest. The general location and the approach used is shown in figure 1.

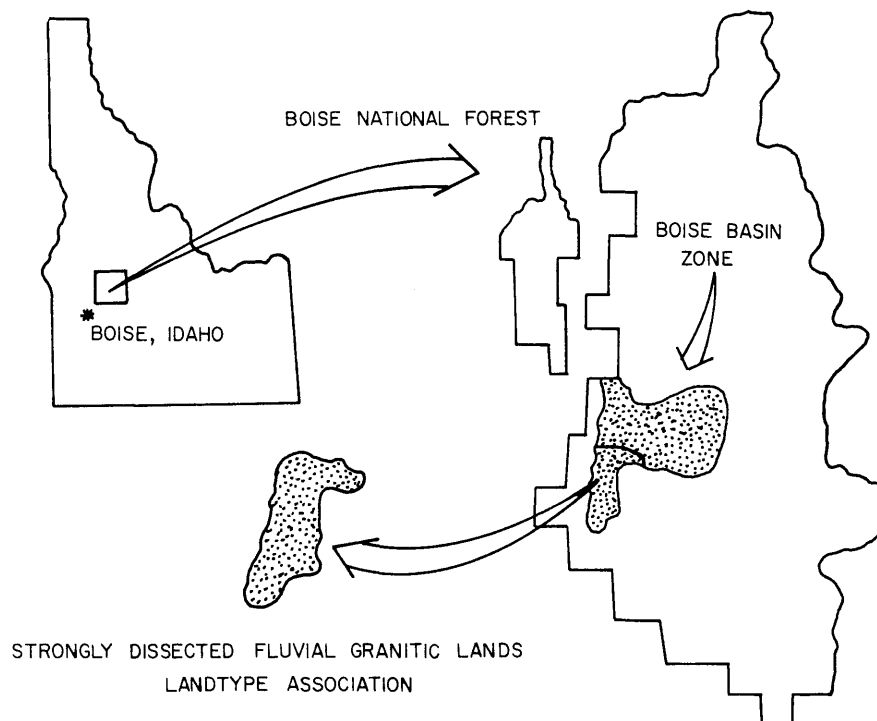


Figure 1.--General location of the Boise National Forest with an example of land stratification.

Generally three to five landtype associations were recognized in each zone. These divisions were based primarily on landform, geology, vegetation, and climatic factors. Slope forming factors, such as glacial and fluvial action, as well as water handling characteristics of the slopes, were also considered.

GEOLOGY AND SOILS

About 85 percent of the Boise National Forest lands are within the Idaho batholith where granitic parent materials dominate. The soils are sandy and often shallow to moderately deep, over fractured, and/or decomposed granite.

A few basalt flows and silicic volcanic lands occur on the southern end of the Forest where deeply cut canyons overshadow the streams. The west and central portion of the Forest has a limited acreage of structurally controlled basalt lands with long, steep, west-facing dip slopes. In these areas, soils are often shallow, cobbly, clay loams over hard bedrock. These differences in soil and geology have been taken into account in the Forest stratification process.

CLIMATE AND ELEVATION

The average annual precipitation ranges from 14 inches (36 cm) on the southern end of the Forest to a high of 70 inches (178 cm) on the northern end. The precipitation is closely tied to elevation ranging from 3,200 ft (975 m) to approximately 10,000 ft (3046 m). There is also a close link to latitude, with more moisture in the northern latitudes. Rain shadow effects are apparent throughout the area.

Summers are hot and dry with little moisture falling on the lower elevation slopes between June and September. Temperatures exceeding 90° F (32° C) are common during several weeks in July and August. The combination of high temperatures and relatively low rainfall makes conditions for plant growth quite severe. Even so, many species are able to adapt to the harsh climatic conditions by sending roots deep into the fractured granitic materials.

PLANT/HABITAT TYPE CHARACTERIZATION

Hironaka and Fosberg (1981) are cited as the authorities on habitat types. Scientific names follow Holmgren and Reveal (1966) except where tentative subspecies of big sagebrush (Artemisia tridentata ssp. spiciformis and Artemisia tridentata ssp. xericensis) are identified. In these cases, concepts presented by Hironaka and Fosberg (1981) are used.

BITTERBRUSH DISTRIBUTION

Purshia tridentata (Pursh) DC., (bitterbrush), occurs most abundantly between 3,200 and 4,500 ft (975 and 1371 m) elevation, although a few sites may have plants above 5,500 ft (1676 m). Hot south-facing slopes have the greatest tendency to support bitterbrush at all elevations, even though annual precipitation on sites supporting bitterbrush ranges from 14 to 35 inches (36 to 89 cm).

Bitterbrush habitat types occur on both volcanic and granitic parent materials. In each case, bitterbrush dominates only the relatively harsh sites, but dense stands of bitterbrush may occur on productive sagebrush habitat types as well.

On the southern end of the Forest, the Basalt Plains and Canyons landtype association contains several Artemisia arbuscula Nutt. var. arbuscula (low sagebrush) habitat types. Shallow, rocky, clay loam soils that are saturated in the spring for short periods are prevalent. Bitterbrush is not common on these habitat types. Only a few decadent plants are scattered along the edges of the communities. However, it is common to see several sagebrush habitat types mixed together, and the total landscape may have considerable bitterbrush present in a mosaic pattern.

Artemisia tridentata Nutt. ssp. vaseyana (Rydb.) Beetle/Agropyron spicatum (Pursh) Scribn. & Smith var. spicatum, (mountain big sagebrush/bluebunch wheatgrass) is by far the most common habitat type. Bitterbrush is a regular component on most of these sites. Because this habitat type covers the entire elevational range of bitterbrush on the Forest, there are many soil types involved. As a result, bitterbrush density, production, plant size, and shape varies considerably. Landform can vary from gently rolling hills to long, very steep slopes.

The Artemisia tridentata Nutt. ssp. vaseyana (Rydb.) Beetle/Festuca idahoensis Elmer (mountain big sagebrush/Idaho fescue) habitat type is most prevalent on steep north-facing slopes. Bitterbrush is generally sparse on these sites, although some plants are present.

The Artemisia tridentata Nutt. ssp. tridentata (basin big sagebrush) habitat types occur primarily at the lower elevations on depositional soils. These sites are productive because of the deep soils, and in some cases moisture is received from adjacent slopes. There are some areas where dense stands of bitterbrush occur and plants exceed 6 to 8 ft (1.8 to 2.4 m) in height. When this condition occurs, the sagebrush is generally sparse.

The Artemisia tridentata ssp. xericensis (x big sagebrush) habitat types are common between 3,500 and 5,000 ft (1066 and 1676 m) elevation. These sites are usually highly productive and have considerable species diversity. It is also common to find basin big sagebrush and mountain sagebrush on these sites. Bitterbrush does well and again produces large plants. Bitterbrush may be relatively abundant or somewhat sparse.

The Artemisia tridentata ssp. spiciformis/Bromus carinatus Hook. & Arn. (alpine big sagebrush/California brome) habitat type occurs on the high elevation glaciated landtype associations. Because of the high elevations and cool, moist climatic conditions, it is uncommon to find bitterbrush growing on these sites.

Zones and landtype associations occurring in the central portion of the Forest have vast amounts of bitterbrush growing on the granitic materials. Bitterbrush habitat types are common, especially on hot south-facing slopes. The slopes are generally very steep and considerable natural erosion is evident. Soils are shallow and have coarse textures. Plants are often prostrate with an abundance of dead wood present.

There are some unique slopes that are dominantly native grasslands. The slopes are long, very steep, and have a smooth graded appearance. Soils are shallow over granitic bedrock. On these slopes, bitterbrush may be observed in a few places. The plants usually follow the rock fracture lines across the slopes. Here the plants can anchor their roots deeply into the substratum.

The zone immediately north of Boise is unusual in that it is the only place on the Forest where vast stands of Aristida longiseta Steud. var. longiseta (red three-awn) are present. Some of the finer textured soils are in this zone. Here bitterbrush occurs most densely along a belt between 3,200 and 4,500 ft (975 and 1371 m) elevation. Several sagebrush species are commonly associated with the bitterbrush.

Along the west-central portion of the Forest, structurally controlled basalt lands with long, steep west-facing slopes are present. Here soils are shallow clay loams with a high coarse fragment content. Bitterbrush habitat types are common within this zone, and sagebrush habitat types are somewhat limited in extent. Red three-awn, which is so common a few miles to the east, becomes sparse on the volcanic materials.

On the high elevation glaciated landtype associations and on the high elevation meadows that occupy large acreages on the northern portion of the Forest, bitterbrush distribution becomes very limited. Precipitation is high, reaching 70 inches (178 cm) per year in some areas. Temperatures are cool and the growing season is short. Much of the land in this vicinity is covered with dense stands of timber, thus eliminating bitterbrush, except in a few scattered ponderosa pine stands at the lower elevations.

MANAGEMENT IMPLICATIONS

Because several big-game winter ranges occur on the Boise National Forest, it is essential that adequate food sources be maintained on key habitats. It is important to maintain a diversity of plants as well as an abundance of major food supplies. To

meet these demands, the Forest has been actively engaged in a bitterbrush planting and management program. Several factors have influenced program results: (1) gopher activity is intense on some landtypes where soils are deep; (2) seeds or seedlings adapted to specific habitat types have not always been as carefully selected as they should have been (that is, seed from large treelike bitterbrush plants on basin big sagebrush habitat types may not do as well on shallow soils where prostrate bitterbrush plants are commonly found); (3) summers are hot and dry, which creates a tremendous moisture stress on new plants during their first growing season; (4) it has not always been recognized that bitterbrush plants perform best on sites where roots can easily penetrate the soil or where fractures in the parent material provide channels that roots can anchor into, nor that bitterbrush competes well on the harsh dry sites because it is capable of sending roots into the fractured granitic materials; and (5) bitterbrush plants are often killed by fires that commonly occur during the hot summer months, which needs to be accounted for in any economic consideration.

CONCLUSIONS

Zones and landtype associations are units of land that have unique qualities from the standpoint of resource production potentials, management constraints, and opportunities for improvement. Only two broad levels of land stratification have been addressed here for the Boise National Forest as a reference framework. However, more detailed inventories have identified landtypes and range types. At both levels of stratification, bitterbrush distribution, plant height, shape, and production can be predicted.

By recognizing site potentials, constraints, and opportunities at various levels of land stratification, better land management prescriptions can be developed in future planning cycles. Communication between specialists can also be improved because specialists relate to common units of land that have been well described. The result should be more efficient bitterbrush management in the years ahead.

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Section 2. Growth Performance, Phenology, and Physiology



PERFORMANCE COMPARISON AMONG POPULATIONS OF BITTERBRUSH, CLIFFROSE,
AND BITTERBRUSH-CLIFFROSE CROSSES ON STUDY SITES THROUGHOUT UTAH¹

James N. Davis²

ABSTRACT

Since the late 1950s, 259 accessions of bitterbrush, cliffrose, and bitterbrush-cliffrose crosses have been grown on many diverse pinyon-juniper sites throughout Utah. Extensive plantings have helped to determine where each accession performs best. Some accessions perform well at many locations. Managers can use these accessions to meet a wide variety of site characteristics. Most areas of the West are represented by the 259 accessions.

INTRODUCTION

Bitterbrush (Purshia tridentata) [Pursh] DC) and Cliffrose (Cowania mexicana var. stansburiana [Torr.] Jeps.), because of their abundance and importance in the Western United States, have been the subject of many studies, most of them directed toward bitterbrush. Studies on bitterbrush commonly involve nutrition, palatability, germination, planting methods, genetics, general ecology, management, production, nitrogen fixation, and the effects of fire, cold, soil, and moisture relationships.

Most research has only hinted at the possible usefulness of the abundant genetic variation within or between populations of bitterbrush and cliffrose. To meet the needs of a wide variety of site and management problems, selection of divergent natural forms should be pursued.

Antelope bitterbrush in Idaho was found to resprout readily following fire and clipping trials (Blaisdell and Meuggler 1956). After such treatments were initiated on unburned and earlier (1939) burned-over areas there was less than 50 percent sprouting on the unburned areas as compared to 75 percent sprouting on the previously (1939) burned site for individuals that sprout after fire. Further selection had occurred on the previously burned site for individuals that sprout after fire. Hormay (1943) reported that hundreds of thousands of acres of bitterbrush in California had been destroyed by fire, and that only two occurrences of sprouting had been observed. Driscoll (1963) listed percent sprouting of bitterbrush on 13 burned areas throughout central Oregon. Percent sprouting ranged from 1 to 80 percent. He noted that there appeared to be little relationship between intensity of the burn and the degree of sprouting. Nord (1965) found resprouting of antelope bitterbrush after burning or cutting to occur infrequently in California, while desert bitterbrush (Purshia glandulosa Curran) resprouted frequently. Billings (1952) stated that bitterbrush in the western Great Basin is permanently lost by fire due to the fact that it rarely sprouts. Within some areas of critical big-game range, the reoccurring incidences of fire would be very detrimental. Therefore, the ability of bitterbrush to resprout after fire would be an excellent heritable characteristic to have.

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Many observers have noted other variable characteristics within populations of bitterbrush: seed dormancy (Nord 1965); leaf color (Hormay 1943; Stanton 1959), growth form and height (Hormay 1943; Stanton 1959; Plummer and others 1968), stem layering (Nord 1965; Plummer and others 1957), ability to fix nitrogen (Klemmedson and Feruson 1969), and nutritive content (Giunta and others 1978). Wagle (1958) reported wide variation in growth of bitterbrush ecotypes in response to latitude, elevation, and soils. Stanton (1959) found differences in cold tolerance between central Oregon and northern California populations. With this great amount of variation within and between species, managers must carefully consider which characteristics are best suited for their specific needs before seeding within a specific habitat type. Seed sources have been shown to influence survival of seeded stands of bitterbrush (Plummer and others 1957).

Giunta and others (1978) summarized the following attributes that bitterbrush ecotypes possess in varying degrees: growth form, fire tolerance, rate of growth, period of growth, seed production, drought resistance, nutritional qualities, heat tolerance, soil adaptation, cold hardiness, climatic adaptation, resistance to disease or insect damage, palatability to game or livestock, evergreen habit, vegetative reproduction, and shade tolerance.

STUDY AREAS AND METHODS

Since the late 1950's the project has evaluated 259 accessions of bitterbrush and cliffrose, with accessions originating from most areas throughout the Western United States. Of the 259 accessions, there were 141 accessions of antelope bitterbrush, 49 of cliffrose, 46 of antelope bitterbrush-cliffrose, and 1 of desert bitterbrush-antelope bitterbrush.

Species trials are currently located throughout Utah. However, special emphasis has been placed on the pinyon-juniper zone and adjacent associated community types. Table 1 lists the sites with their approximate elevation and the dominant vegetative type. These areas were selected to provide information on species vigor and their ease of establishment within the diverse pinyon-juniper sites and on the breadth of species and accession adaptation. Because most species trial sites were not protected from grazing animals, one cannot make fair or equitable comparisons between most characteristics of the different populations. The comparisons in this paper deal more specifically with longevity, vigor, and stand rating between populations of bitterbrush, cliffrose, and bitterbrush-cliffrose crosses.

When possible, performance ratings were made at least once each year the first 3 years after planting and thereafter at 3 to 5 year intervals. Performance ratings on plants grown on many sites began as early as 1956.

Plot size is variable, depending on how many species or accessions (populations) were to be planted on a site. Each selected accession was randomly planted at least twice on each site in shallow furrows 5 to 10 ft (1.52 to 3.05 m) long.

Species plot evaluations included some of the following characteristics: type of planting, location of site, date of planting, date of rating, species name, accession number (which included date and area from which the seed was collected), plot number, number of plants, plant density along the furrow, stand rating, average crown in inches, average weight in grams, rooted frequency along furrow, average percent utilization, state of development, growth habit, type of reproduction, seed production, and seedling vigor.

Table 1.--List of areas in a study of bitterbrush, cliffrose, and bitterbrush-cliffrose communities.

Area	Name	Location and county	Elevation in feet (meters)	Vegetation type
01	Dahl's Dugway	Ephraim Canyon, Sanpete	7,200 (2,195)	Mountainbrush
02	Rasmusson's	Ephraim Canyon, Sanpete	5,700 (1,737)	Pinyon-juniper: Sagebrush
03	Levan Dry Farm	Levan, Juab	5,200 (1,585)	Dry farm: sagebrush
04	Black Mountain	Salina Canyon, Sevier	6,000 (1,829)	Pinyon-juniper: sage- brush, cheatgrass brome
05	Pioneer Road	Fillmore, Millard	6,000 (1,829)	Pinyon-juniper: moun- tain brush
06	Fillmore Dump	Fillmore, Millard	5,400 (1,646)	Dry farm: sagebrush
07	Pinto	Pinto, Washington	6,000 (1,829)	Pinyon-juniper: moun- tainbrush
08	Ellickers	Summit, Iron	5,800 (1,768)	Homestead: sagebrush, pinyon-juniper
09	Brigham Burn	Brigham City, Box Elder	5,200 (1,585)	Sagebrush: cheatgrass brome
10	Major's Hillside	Ephraim Canyon, Sanpete	7,100 (2,164)	Pinyon-juniper: moun- tainbrush
11	Beaver Bench	Beaver, Beaver	6,300 (1,920)	Pinyon-juniper: sage- brush
12	Jackson Springs	Gunlock, Washington	4,000 (1,219)	Pinyon-juniper: black- brush, desert shrub
13	Indian Peaks Dry Farm	Indian Peak Wildlife Management Area, Beaver	7,000 (2,134)	Pinyon-juniper: sage- brush
14	Indian Peaks cleared area	Same as preceding	7,000 (2,134)	Pinyon-juniper: sage- brush
15	Indian Peaks Burn	Same as preceding	7,000 (2,134)	Pinyon-juniper: sage- brush
16	Ephraim Roadcut	Ephraim Canyon, Sanpete	6,800 (2,073)	Mountainbrush
17	Kamas	Kamas, Summit	7,000 (2,134)	Mountainbrush
19	Lake Hill	Ephraim Canyon, Sanpete	8,000 (2,438)	Aspen: fir
20	Orem Burn	Orem, Utah	5,000 (1,524)	Mountainbrush: sage- brush, grass
22	North Holden	Holden, Millard	5,600 (1,707)	Pinyon-juniper: sage- brush
24	Cyclone Flat	W. Blanding, San Juan	6,600 (2,012)	Pinyon-juniper
25	Alkali Point	E. Blanding, San Juan	6,100 (1,859)	Pinyon-juniper
26	Peter's Point	N. Monticello, San Juan	7,200 (2,195)	Pinyon-juniper: sage- brush
27	Huntington	Huntington, Emery	5,800 (1,768)	Pinyon-juniper: sage- brush
28	Fairview Canyon	Fairview, Sanpete	6,400 (1,951)	Mountainbrush
29	Hobble Creek	Springville, Utah	4,800 (1,463)	Mountainbrush: sage- brush
30	Manti Dump	S. Manti, Sanpete	5,900 (1,798)	Pinyon-juniper: sage- brush (blacksage)
31	Majors Nursery	Ephraim Canyon, Sanpete	7,100 (3,164)	Mountain brush
32	Triangle Mt.	Salina Canyon, Sevier	6,500 (1,981)	Pinyon-juniper
33	Indian Peaks	Indian Peaks Wildlife Management Area, Beaver	7,000 (2,134)	Pinyon-juniper
34	Wallsburg	Wallsburg, Wasatch	5,800 (1,768)	Sagebrush: cheatgrass brome

Table 1.-- (Continued)

35	East Manti	Manti, Sanpete	5,900 (1,798)	Sagebrush
36	Manti Sheep Trail	Manti, Sanpete	6,000 (1,829)	Pinyon-juniper: cheat-grass brome
37	Rabbit Gulch	E. Duchesne, Duchesne	6,300 (1,920)	Pinyon-juniper: sagebrush
39	John August Lake	John August Lake, Sanpete	10,300 (3,139)	Sub Alpine
41	Tobin Bench	Veyo, Washington	4,500 (1,372)	Blackbrush: pinyon-juniper, desert shrub
42	West Cedar City	Cedar City, Iron	5,700 (1,737)	Sagebrush: greasewood
43	Wingate Mesa	Fry Canyon, San Juan	6,900 (2,103)	Pinyon-juniper
44	Gunnison	Gunnison, Sanpete	5,200 (1,585)	Shadscale: salt desert
45	Marysvale	Marysvale, Piute	6,000 (1,829)	Pinyon-juniper
46	Rulon Mortenson's	W. Ephraim, Sanpete	5,700 (1,737)	Greasewood: saltbush
47	Taylor Flat	Browns Park, Daggett	5,800 (1,768)	Pinyon-juniper: sagebrush
48	Santa Clara	Santa Clara, Washington	3,000 (914)	Desert shrub
49	Bald Mountain	Ephraim, Sanpete	5,700 (1,737)	Pinyon-juniper
50	Nephi Canyon	Nephi, Juab	5,600 (1,707)	Pinyon-juniper: mountainbrush
51	Big Buck	Dutch John, Daggett	6,600 (2,012)	Pinyon-juniper: sagebrush, bitterbrush
52	Omans	Gordon Creek, Carbon	7,200 (2,195)	Sagebrush, pinyon-juniper
53	College Farm	Ephraim, Sanpete	5,600 (1,707)	Sagebrush: grass
54	Millville	Millville, Cache	5,000 (1,524)	Mountainbrush, sagebrush
55	Mona	Mona, Juab	5,800 (1,768)	Sagebrush: grass
58	Henry Mountains Deer and cattle out	Henry Mountains, Garfield	7,600 (2,316)	Pinyon-juniper
59	Henry Mountain Cattle out-deer in	Henry Mountains, Garfield	7,600 (2,316)	Pinyon-juniper
60	Chevron Chemical	Vernal, Uintah	6,600 (2,012)	Pinyon-juniper: black sagebrush grass
61	Springville	Springville, Utah	4,600 (1,402)	Sagebrush: grass
62	Pretty Valley	N. Manti, Sanpete	6,400 (1,951)	Pinyon-juniper: mountainbrush

*Site numbers not listed are "out".

A computer program helped organize, analyze, and summarize the large amounts of data. A synthetic index value was determined by selecting the best performing accession on each site. This was done by comparing the average stand value for each accession and giving 8 points for the best performing accession and as low as 1 point for the poorest "best of eight" accessions. Average rank value was then calculated (maximum rank value would be 8.0). To determine which accessions exhibited the best overall rating on the most sites within the state, the average rank value was summed with the total number of sites on which it was one of the best eight performing accessions. This summed value is the index value. The best overall performing accessions showed the highest index value.

The selection of the best performing accessions, as determined by computer analysis, is shown in table 2. Accessions with the largest index values are considered the best. Only the "five" best performing accessions were used in the table. Other terms used in table 2 include vigor, longevity, stand, and rank.

Table 2.--The best performing accessions of bitterbrush, cliffrose, and bitterbrush-cliffrose crosses

Species	Accession number	Accession origination	Average				
			Rank	Stand	Longevity	Vigor	Index
Cliffrose	U 9	Pioneer Rd. UT	7.5	6.8	15.2	6.8	24.5
	U 20	American Fork, UT	6.3	5.4	9.7	7.0	16.3
	U 16	Orem, UT	5.8	4.7	8.4	7.0	13.7
	U 22	Central, UT	7.0	6.2	8.1	5.5	13.0
	U 1	Oak Creek, UT	7.0	7.0	10.0	5.5	12.0
Desert bitterbrush	U 2	Moody Creek, UT	6.9	6.3	13.2	6.3	25.9
	U 5	George Creek, CA	7.1	5.9	12.2	NR*	21.1
	U 4	McMurray Meadows, CA	6.8	7.0	9.5	7.0	11.8
	U 8	Pioche, NV	6.7	6.8	10.2	3.0	9.6
	U 6	White Mountain Inyo Co, CA	8.0	4.5	20.0	6.0	9.0
Desert bitterbrush X antelope bitterbrush	U 1	Benton Station, CA.	7.8	6.2	7.0	6.9	11.8
Desert bitterbrush X cliffrose	U 5	Snow Canyon, UT	8.0	6.0	4.0	5.0	9.0
	U 3	Delmar Pass, NV	8.0	3.7	12.0	4.0	9.0
	U 4	Slaughter Creek Utah	8.0	2.0	3.0	6.0	9.0
Antelope bitterbrush	U 31	Fountain Green, UT	5.9	5.6	11.4	6.2	31.8
	U 3	Starvation Can., UT	5.6	5.1	8.4	NR	19.6
	U 28	Mt. Pleasant, UT	5.8	5.9	8.8	6.9	17.1
	U 14	Salt Lake Co., UT	7.1	6.2	7.4	6.0	12.5
	U 50	Spring City, UT	6.5	6.4	18.0	6.5	11.8
Antelope bitterbrush X cliffrose	U 10	S. Mt. Pleasant, UT	5.9	6.6	10.1	6.0	14.9
	U 16	Mt. Dell Res., UT	4.5	4.7	16.4	6.7	12.5
	U 11	Fountain Green, UT	7.2	7.3	25.2	4.5	12.2
	U 21	N. Mt. Pleasant, UT	6.5	3.6	10.9	4.0	10.5
	U 27	Enterprise, UT	6.3	4.6	6.5	6.2	10.3

*NR= No record, the project did not use vigor ratings until early 1970's.

Vigor is a subjective measurement or expression on a plant's appearance and how actively healthy and well balanced plant growth is. This is an average value for all sites it was grown on. The maximum value is 10. As subjective as this measurement is, it has been found to be very reflective of plant performance and found to be quite consistent among those who rate the species plots.

Longevity is the number of years the accession has grown on a specific site since the initial planting. This again is an average value for all sites on which it has been grown.

Stand is a combined value of percent cover (value of 1-5) and plant distribution along the furrow (value of 1-5). Because it is the only measurement that has consistently been used in rating species performance since the beginning of the project it is the best measurement that can be used to help determine which rank value each accession has. The maximum value for stand is 10.

Rank is an average value of how well each accession performed when compared with the other accessions for a given species on a site-for-site basis. Maximum value attainable is 8. Some species within table 2 do not list the five best accessions, because either there were not five accessions collected for a specific species, or the minimum parameters selected on the computer program were too stringent. Accessions having values less than 3 for vigor and 3 years longevity were dropped.

Most of the accessions were collected by private seed collectors for reasons that were not necessarily connected to the selection of characteristics that this project would have looked for, but were characteristics the seed collectors chose. In most instances seeds were collected from stands producing large amounts of seed that were easy to collect. Most such stands were usually composed of plants 3 ft (.91 m) or more in height, with an upright growth habit. Large amounts of seed would indirectly indicate good vigor, while an upright growth form would make it more useful in most situations for revegetation of deer winter range.

An additional study was initiated in 1980 at a nearby protected "common garden" with over 50 selected accessions of bitterbrush, cliffrose, and bitterbrush-cliffrose crosses to help in better determining differences in morphological, phenological, and genetic characteristics.

RESULTS AND DISCUSSION

Accession U9 had the best cliffrose index value (table 2). Accessions U20, U16, U22, and U1 were grouped closely together near the U9 index value. All these accessions are similar morphologically except that some appear to grow on more sites than others as indicated by their respective index values.

Desert bitterbrush accessions U2 and U5 were by far the best performing populations (table 2). Both are high elevation ecotypes that come from the most northerly populations of desert bitterbrush in Utah and California. The next three accessions (U4, U8, and U6) have somewhat lower index values as a group.

Only one accession (U1) of desert bitterbrush crossed with antelope bitterbrush has been collected and grown. However, U1 has good values for stand and vigor (table 2). It is from within the area where the most northerly populations of desert bitterbrush occur in northeastern California.

Only seven accessions of the desert bitterbrush crossed with cliffrose were grown on species trial plots. Of these seven, only three showed very much promise, and of these only accession U5 from Snow Canyon had an acceptable stand rating (table 2).

Antelope bitterbrush accession U31 (table 2) was by far the best performing population (index value 31.8). Technically, it was in a class by itself. It is a large, upright, robust plant. On the native site, it is on the average 6 to 8 ft (1.83 m-2.44 m) high and with a crown of 6 or more ft (1.83 m). Seed was collected from the original source and planted on a site near the mouth of Hobbie Creek Canyon to help develop a more dependable seed source for this accession. There, it has shown another good characteristic that is not evident on the native site. Whenever a stem or branch touches the ground it aggressively develops roots. The other accessions are grouped closely together with index values ranging from 19.6 to 11.8. All five of these accessions have very similar stand vigor ratings.

The antelope bitterbrush crossed with cliffrose accessions all have index values of almost the same magnitude (table 2). They were grouped so closely it is difficult to determine which is really "best" without first looking more closely at stand and vigor ratings. Overall, it would appear that U10 was the "best".

In summary, of all the 259 accessions grown on sites in Utah, only 24 exhibit good enough rank, stand, vigor, and index values to be of use when planted within the extensive pinyon-juniper type.

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SURVIVAL AND GROWTH OF APACHE-PLUME, STANSBURY CLIFFROSE, AND SELECTED
SOURCES OF ANTELOPE BITTERBRUSH IN NORTHEAST OREGON¹

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ABSTRACT

Performance of transplants from single geographic sources of Apache-plume and cliffrose and eight sources of antelope bitterbrush were evaluated for 6 years in a uniform garden on shrub-steppe rangeland. Growth and survival of most shrubs was good. A bitterbrush source from a forest ecotype was preferred by insects and suffered 76 percent mortality after three seasons of defoliation.

INTRODUCTION

Antelope bitterbrush (Purshia tridentata [Pursh] DC.)³ occurs in a wide array of environments throughout interior western North America. Adaptation to environmental features such as soils, climate, fire, and insects has resulted in ecotypes differing in morphology, growth form, palatability, fire tolerance, drought resistance, and other characteristics (Alderfer 1977; Guinta and others 1978; Monsen and Christensen 1975; Nord 1965). Knowledge of these attributes is needed for selecting plant materials for particular environments in range improvement projects as well as for genetic development of superior shrubs.

Plant materials for improving wildlife forage and cover are being evaluated in a uniform garden on the Keating mule deer winter range in Baker County, Oreg. The comparatively harsh environment of the garden is characteristic of many similar depleted shrub-steppe ranges that could benefit from range rehabilitation. Some promising species may be selected by land managers for operational projects. Most, however, will be evaluated further in outplantings representing a range of growing conditions.

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³Sources for scientific and common names of plants are Garrison and others (1976), Holmgren and Reveal (1966), and Plummer and others (1977).

This paper summarizes 6 years of Keating garden data on the survival and performance of transplants of eight geographic sources of antelope bitterbrush and single sources of Stansbury cliffrose (Cowania mexicana stansburiana [Torr.] Jeps.) and Apache-plume (Fallugia paradoxa [D. Don] Endl.).

STUDY AREA

The garden is on land administered by the Bureau of Land Management 30 miles (48 km) east of Baker, Oreg. It lies on gently rolling benchland above the Powder River canyon at an elevation of approximately 3,200 ft (980 m). Annual precipitation is 12 inches (300 mm), occurring mainly as winter snow. Intermittent spring and fall rains may also provide significant moisture, but the summers are droughty as is characteristic of the Pacific Northwest. Temperature extremes may reach -30° F (-35° C) in the winter and 100° F (38° C) during the summer; the frost-free growing season is estimated to be 145 days.

Soils are moderately deep and of granitic origin. They have been tentatively classified as fine, montmorillonitic, mesic, Calcic Argixerolls of the Brownscombe series.

Plant communities of the Keating range reflect past disturbance by fire, grazing, abandoned farming, and most recently, extensive grass seeding. The garden is in a portion of a standard crested wheatgrass (Agropyron desertorum Schult.) seeding that was fenced to exclude deer and livestock. Surrounding communities are characterized by basin big sagebrush (Artemisia tridentata tridentata Nutt.), rabbitbrush (Chrysothamnus spp. Nutt.), cheatgrass brome (Bromus tectorum L.), medusahead wildrye (Elymus caput-medusae L.), Sandberg's gluegrass (Poa sandbergii Vasey), numerous annual and biennial forbs, and scattered occurrences of bearded bluebunch wheatgrass (Agropyron spicatum [Pursh] Scribn. and Smith). Local ranchers and land managers suggest that antelope bitterbrush was once an important component of some communities. Scattered, heavily browsed bitterbrush shrubs now occur only in the steep, rocky canyon below the garden.

METHODS

Description of Shrub Sources

The sources of shrubs included in the garden are briefly described in table 1. Those of antelope bitterbrush represented an array of contrasting environments and ecotypes found in the Pacific Northwest.

The Janesville source is a vigorous, erect ecotype occurring on an area with sandy, granitic alluvial soils in northeastern California. It was included because plantings in Utah and Idaho have shown superior growth over other sources (Monsen and Christensen 1975).

Boise Basin, Garden Valley, and Fort Hall sources are from Idaho seed collections. The Boise Basin source is a decumbent, spreading ecotype on the granitic cobble of dredge piles north of Boise. The Garden Valley source is an erect ecotype on coarse, granitic soils also north of Boise. The Fort Hall source is a semierect form growing on alluvial materials in the Snake River drainage north of Pocatello, Idaho.

Table 1.--Descriptions of seed sources of antelope bitterbrush, Stansbury cliffrose, and Apache-plume evaluated in the Keating uniform garden, Oregon

Species source	Elevation	Precipitation	Frost-free period	Soils	Growth habit
	<u>m</u>	<u>mm</u>	<u>Days</u>		
<u>Antelope bitterbrush:</u>					
Janesville, CA	1,312	254	120	Granitic	Erect
Boise Basin, ID	1,220	762	75	Granitic	Decumbent
Fort Hall, ID	1,220	432	120	Alluvial	Semi-erect
Garden Valley, ID	1,098	508	90	Granitic	Erect
Hat Rock, OR	107	203	170	Lacustrine	Erect
Keating, OR	793	305	145	Granitic	Erect
Pringle Falls, OR	1,312	508	<20	Pumiceous	Decumbent
Warner Mtn., OR	1,830	508	<100	Basaltic	Decumbent
<u>Cliffrose:</u>					
American Fork, UT	1,281	381	120	Sedimentary	Erect
<u>Apache-plume:</u>					
Richfield, UT	1,616	330	100	Sedimentary	Erect

The Oregon sources have the greatest environmental contrasts in the group. The Hat Rock source is a vigorous, erect ecotype growing on sandy soils deposited over basalt adjacent to the Columbia River near Hermiston. This source is the lowest in elevation and has the hottest, driest, and longest growing season. The local Keating source was collected from shrubs in the rocky bluffs along the Powder River below the garden. It also represents an ecotype that developed in a harsh, dry environment with warm growing seasons. In contrast, the Pringle Falls source represents the other climatic extreme for antelope bitterbrush. This fine-leaved, decumbent ecotype occurs in dense stands exceeding 8,000 shrubs per acre (19,760/ha) (Edgerton, this symposium) that dominate the understory of extensive lodgepole pine (Pinus contorta Dougl. ex Loud.) communities in the pumice region of central Oregon. Light and temperature appear to limit growth more than moisture availability; frosts are common during the growing season. The Warner Mountains source of south-central Oregon and the Pringle Falls source are similar in morphology. However, the Warner Mountains shrubs developed on basalt-derived soils without a tree overstory and represent the highest elevation ecotype studied in the garden.

Neither Stansbury cliffrose nor Apache-plume are native to the Pacific Northwest. Both, however, have grown well in southern Idaho plantations. There is value in determining the amplitude of adaptability of these promising shrubs outside their native ranges. Their inclusion in plantings on depleted ranges could potentially increase the diversity of forage and cover available to wintering wildlife. Single Utah sources of each species were included in the uniform garden.

Planting

In April 1976 at three Keating garden locations, 10 shrubs of each source were transplanted in rows in a 6-ft (1.8-m) spacing (total of 30 shrubs of each source). Six of the bitterbrush sources and the cliffrose and Apache-plume shrubs were 6-month-old container seedlings grown in a greenhouse. Fort Hall and Garden Valley bitterbrush sources were 1/0 bareroot nursery stock. The estimated average seedling height at planting was 3 inches (8 cm).

Competing vegetation was removed by a disc plow prior to planting. Hand planting was accomplished using both planting bars and spades.

Garden Maintenance

Competing vegetation adjacent to the shrubs was removed twice each growing season by mechanical cultivation, primarily to provide uniform growing conditions for performance comparisons. The shrubs received neither fertilizer nor supplemental water.

The fence surrounding the garden protected the shrubs from deer and livestock browsing. Mice, rabbits, and gophers foraged on a few shrubs. Grasshoppers were present each growing season, with unusually high populations in 1977, 1978, and 1979. No insect control measures were used either within the garden or on the surrounding rangeland.

Measurements

Survival and performance of each transplanted shrub was assessed each year at the close of the growing season in September. We counted surviving plants and measured maximum height and crown spread. Total aboveground biomass was determined using a modification of the weight estimate technique of Pechanec and Pickford (1937); prior to data collection, technicians trained themselves to accurately estimate the individual shrub weights by clipping and weighing different sizes of branches.

Measurements were recorded in metric units and are so presented in this paper. We estimated relative vigor, flower and fruit production, and insect occurrence and damage.

RESULTS

Tables 2, 3, and 4 summarize growth of shrubs during the first six growing seasons as reflected by measurements of average maximum height, average maximum crownspread, and average aboveground biomass.

Table 2.--Height of antelope bitterbrush, Stansbury cliffrose, and Apache-plume shrubs in the Keating uniform garden, Oregon

	Mean maximum height $\pm$ 95 percent confidence interval					
Species and source	1976	1977	1978	1979	1980	1981
	----- <u>cm</u> -----					
<u>Antelope bitterbrush:</u>						
Janesville, CA	26 $\pm$ 2	44 $\pm$ 2	72 $\pm$ 3	76 $\pm$ 3	80 $\pm$ 3	88 $\pm$ 4
Boise Basin, ID	24 $\pm$ 2	41 $\pm$ 3	65 $\pm$ 3	69 $\pm$ 3	72 $\pm$ 3	76 $\pm$ 3
Fort Hall, ID	20 $\pm$ 7	31 $\pm$ 6	51 $\pm$ 6	50 $\pm$ 7	55 $\pm$ 5	61 $\pm$ 3
Garden Valley, ID	21 $\pm$ 3	38 $\pm$ 3	64 $\pm$ 4	67 $\pm$ 4	72 $\pm$ 4	78 $\pm$ 5
Hat Rock, OR	24 $\pm$ 3	40 $\pm$ 4	69 $\pm$ 5	71 $\pm$ 5	74 $\pm$ 5	83 $\pm$ 6
Keating, OR	25 $\pm$ 2	42 $\pm$ 4	67 $\pm$ 3	69 $\pm$ 3	72 $\pm$ 3	78 $\pm$ 3
Pringle Falls, OR	19 $\pm$ 3	34 $\pm$ 3	58 $\pm$ 4	52 $\pm$ 4	43 $\pm$ 14	47 $\pm$ 12
Warner Mtn., OR	22 $\pm$ 3	36 $\pm$ 4	64 $\pm$ 4	65 $\pm$ 4	62 $\pm$ 4	68 $\pm$ 5
All bitterbrush	23	38	64	65	66	72
<u>Cliffrose:</u>						
American Fork, UT	22 $\pm$ 2	34 $\pm$ 3	61 $\pm$ 3	64 $\pm$ 3	65 $\pm$ 4	80 $\pm$ 5
<u>Apache-plume:</u>						
Richfield, UT	47 $\pm$ 4	58 $\pm$ 4	80 $\pm$ 6	77 $\pm$ 4	88 $\pm$ 6	103 $\pm$ 6

Table 3.--Crown spread of antelope bitterbrush, Stansbury cliffrose, and Apache-plume shrubs in the Keating uniform garden, Oregon

	Mean maximum crown spread $\pm$ 95 percent confidence interval					
Species and source	1976	1977	1978	1979	1980	1981
	<u>cm</u>					
<u>Antelope bitterbrush:</u>						
Janesville, CA	17 $\pm$ 2	45 $\pm$ 4	88 $\pm$ 6	107 $\pm$ 6	114 $\pm$ 6	127 $\pm$ 7
Boise Basin, ID	21 $\pm$ 2	57 $\pm$ 3	108 $\pm$ 4	131 $\pm$ 4	130 $\pm$ 4	138 $\pm$ 5
Fort Hall, ID	24 $\pm$ 11	58 $\pm$ 11	100 $\pm$ 6	119 $\pm$ 9	118 $\pm$ 9	124 $\pm$ 10
Garden Valley, ID	17 $\pm$ 3	49 $\pm$ 6	95 $\pm$ 10	113 $\pm$ 9	124 $\pm$ 9	133 $\pm$ 10
Hat Rock, OR	22 $\pm$ 5	61 $\pm$ 6	108 $\pm$ 7	128 $\pm$ 7	129 $\pm$ 8	144 $\pm$ 9
Keating, OR	25 $\pm$ 4	61 $\pm$ 6	111 $\pm$ 9	130 $\pm$ 7	132 $\pm$ 6	137 $\pm$ 8
Pringle Falls, OR	40 $\pm$ 6	70 $\pm$ 6	104 $\pm$ 7	106 $\pm$ 7	93 $\pm$ 29	106 $\pm$ 22
Warner Mtn., OR	27 $\pm$ 5	59 $\pm$ 6	98 $\pm$ 6	113 $\pm$ 7	110 $\pm$ 7	121 $\pm$ 10
All bitterbrush	24	58	102	118	119	129
<u>Cliffrose:</u>						
American Fork, UT	16 $\pm$ 3	37 $\pm$ 4	66 $\pm$ 4	78 $\pm$ 6	80 $\pm$ 5	91 $\pm$ 7
<u>Apache-plume:</u>						
Richfield, UT	38 $\pm$ 4	56 $\pm$ 4	94 $\pm$ 8	98 $\pm$ 6	113 $\pm$ 11	141 $\pm$ 11

Table 4.--Aboveground biomass of antelope bitterbrush, Stansbury cliffrose, and Apache-plume shrubs in the Keating uniform garden, Oregon

	Mean dry weight $\pm$ 95 percent confidence interval					
Species and source	1976	1977	1978	1979	1980	1981
	<u>Grams</u>					
<u>Antelope bitterbrush:</u>						
Janesville, CA	5 $\pm$ 1	6 $\pm$ 10	683 $\pm$ 89	1	824 $\pm$ 65	2
Boise Basin, ID	5 $\pm$ 1	73 $\pm$ 23	658 $\pm$ 83		851 $\pm$ 49	
Fort Hall, ID	6 $\pm$ 5	39 $\pm$ 22	326 $\pm$ 97		490 $\pm$ 80	
Garden Valley, ID	7 $\pm$ 3	69 $\pm$ 17	563 $\pm$ 104		847 $\pm$ 113	
Hat Rock, OR	8 $\pm$ 3	78 $\pm$ 16	704 $\pm$ 143		799 $\pm$ 95	
Keating, OR	11 $\pm$ 6	83 $\pm$ 18	805 $\pm$ 138		867 $\pm$ 81	
Pringle Falls, OR	13 $\pm$ 6	81 $\pm$ 21	522 $\pm$ 115		164 $\pm$ 128	
Warner Mtn., OR	6 $\pm$ 3	69 $\pm$ 35	71 $\pm$ 130		653 $\pm$ 126	
All bitterbrush	8	70	604		687	
<u>Cliffrose:</u>						
American Fork, UT	3 $\pm$ 1	33 $\pm$ 7	394 $\pm$ 78		452 $\pm$ 43	
<u>Apache-plume:</u>						
Richfield, UT	12 $\pm$ 2	51 $\pm$ 7	262 $\pm$ 31		497 $\pm$ 121	

¹No data were taken because of grasshopper defoliation.

²No data were taken.

First Year

Moisture conditions during the spring and early summer of 1976 apparently favored the establishment and growth of shrubs. All of the container bitterbrush transplants survived the first season. Fort Hall and Garden Valley sources experienced 20 and 5 percent mortality, respectively, probably due to preplanting condition of the bareroot transplants.

Height and crown spread of shrubs tended to reflect characteristics of the parent stands. Janesville bitterbrush grew rapidly in height with a relatively narrow crown. However, crowns of the decumbent Pringle Falls bitterbrush source were twice as wide as high.

All of the Stansbury cliffrose and Apache-plume transplants survived. Growth of Apache-plume was exceptional, averaging over 40 cm in height (fig. 1).

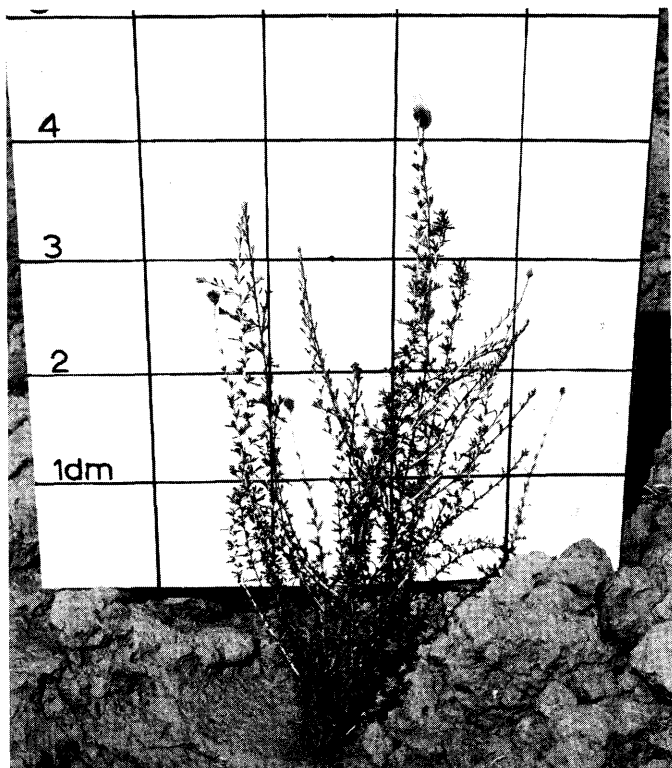


Figure 1.--Apache-plume transplant after one growing season (1976) in the Keating uniform garden, Oregon.

Second Year

Eastern Oregon experienced near-record drought during the 1976-77 winter and the 1977 growing season. Despite unfavorable growing conditions, mortality was negligible and all shrubs produced vigorous twig growth. Average height nearly doubled and increases in crown spread were even greater. Overall average above-ground biomass of the eight bitterbrush sources increased from 8 g to 67 g.

In early July 1977, an increasing abundance of grasshoppers was observed in the garden and on the surrounding rangeland. By mid-July evidence of extensive feeding was noted, first on oldman wormwood (*Artemisia abrotanum* L.), then on other shrubs including honeysuckle (*Lonicera* spp. L.), cherry (*Prunus* spp. L.), currant (*Ribes* spp. L.), antelope bitterbrush, cliffrose, and Apache-plume. On August 1 flushing counts on 25 circular plots (1-m diameter each) systematically located across the garden indicated an average density of seven grasshoppers per square meter. Genera and species identified from a partial collection included *Aulocara ellioti* (Thomas),

Arphia pseudonietana (Thomas), Melanoplus sanguinipes (F.), and Melanoplus foedus Scudder or M. f. fluviatilis Bruner.⁴ Estimates were not made of the number of each kind of grasshopper nor the extent of feeding by each.

Table 5 shows estimates of damage to leaves and bark. Apparently the Pringle Falls bitterbrush source was preferred over the other sources. Each of the shrubs of that source was nearly completely defoliated while feeding on other sources was largely confined to new growth near the tips of twigs (fig. 2). Occasional feeding was noted on the bark of small twigs of all shrubs.

Table 5.--Grasshopper damage to leaves and bark¹ and resulting mortality of antelope bitterbrush, Stansbury cliffrose, and Apache-plume shrubs in the Keating uniform garden, Oregon

Species and Source	Mean leaf area removed			Mean bark area removed			Mortality
	1977	1978	1979	1977	1978	1979	1977-81
	----- Percent -----						
<u>Antelope bitterbrush:</u>							
Janesville, CA	4	4	95	2	1	12	0
Boise Basin, ID	2	3	84	1	1	3	0
Fort Hall, ID	18	10	99	2	2	9	0
Garden Valley, ID	14	5	98	2	1	12	0
Hat Rock, OR	6	5	93	2	2	11	0
Keating, OR	7	6	100	1	2	14	0
Pringle Falls, OR	93	68	100	3	4	21	76
Warner Mtn., OR	20	20	100	2	2	14	7
<u>Cliffrose:</u>							
American Fork, UT	4	1	92	2	1	21	3
<u>Apache-plume:</u>							
Richfield, UT	23	22	66	8	5	24	7

¹Includes bark of twigs and large stems.



Figure 2.--Selective defoliation of antelope bitterbrush sources by grasshoppers; Pringle Falls, Oreg., source at left, Janesville, Calif., source at right.

⁴Identification by G. B. Hewitt, Research Entomologist, USDA, SEA, Rangeland Insect Laboratory, Bozeman, MT 59717.

Third Year

Survival remained high during 1978. All shrubs continued vigorous growth. Apache-plume and the Janesville bitterbrush source were tallest, as expected. Crown spread of several bitterbrush sources exceeded 1 m.

Grasshoppers during mid- and late summer reached a density of $5/m^2$ in early August. Again they fed most heavily on the Pringle Falls bitterbrush source, but defoliation was less severe than in 1977.

Fourth Year

During the 1979 growing season grasshoppers were responsible for considerable damage to range forage and agricultural crops throughout much of eastern Oregon. Grasshopper density in the Keating garden exceeded $15/m^2$. During early and mid-July they again fed on the Pringle Falls source, but as preferred forage became less available and insect maturity progressed, feeding shifted to all of the bitterbrush sources. Leaves, succulent new twig growth, and twigs and bark were devoured (table 5).

Fall survival remained high. Accurate growth measurements were difficult because of the material removed by grasshoppers. Accordingly, both height and crown spread of most shrubs showed little, if any, growth. The Pringle Falls bitterbrush source, which received 3 years of heavy defoliation, decreased 6 cm in average maximum height from 1978 to 1979.

Fifth and Sixth Years

Grasshopper populations were much lower during the 1980 and 1981 growing seasons, allowing recovery of most shrubs. Although most shrubs had many dead twigs, only the Pringle Falls bitterbrush source suffered extensive mortality as the result of previous defoliation; only 7 of 30 shrubs (23 percent) survived. Survival of other shrubs exceeded 90 percent (table 5).

Growth during 1980, the fifth season, showed the apparent effects of defoliation the previous year. All bitterbrush sources showed an average height increase of only 1 cm. Several sources decreased in height. Crown spread and biomass were similarly affected.

During 1981, growth of most shrubs overcame the lull of 1980. All bitterbrush sources, Stansbury cliffrose, and Apache-plume showed modest increases in height and crown spread during 1981. All of the bitterbrush sources and Apache-plume also produced both flowers and seeds.

DISCUSSION AND CONCLUSIONS

The Keating garden is a valuable field laboratory for evaluating plant materials for range rehabilitation. Surprisingly, introduced shrubs such as cliffrose and Apache-plume plus most native bitterbrush from an array of sources were established and performed well in the relatively harsh environment that included drought and repeated insect attacks (fig. 3). Total height growth of bitterbrush and cliffrose compares well with that reported for a cultivated Utah planting (Monsen and Christensen 1975).



Figure 3.--Antelope bitterbrush sources in the Keating uniform garden after six growing seasons (1981). The Janesville, Calif., source is at left, foreground. The seemingly vacant center row illustrates mortality of the Pringle Falls, Oreg., source due to consecutive seasons of selective defoliation by grasshoppers.

Apparently those bitterbrush sources deserving further testing in outplantings include Janesville, Boise Basin, Garden Valley, Keating, and Hat Rock. Apache-plume and cliffrose showed promise in this study and should also be further evaluated. The Keating source ranked high in all performance measurements. It was clearly superior in production of biomass in 1978, a positive indication of its capability for rapid establishment. This should be considered an advantage in harsh rangeland environments where conditions favoring establishment are often of short duration. Because of its adaptability to the local environment, the Keating source remains the most reliable choice for use in revegetation projects in similar habitats.

As expected, shrubs in the garden developed growth forms and other characteristics such as leaf shape and color that tended to reflect their parent seed sources. The tall, upright form of progeny from, for instance, the Janesville source may be of particular value for ranges where improvement of cover or shelter for wintering animals is an important concern. Decumbent, layering forms are likely to have value in soil stabilization.

To our knowledge, selective feeding by grasshoppers on particular shrub ecotypes is previously unreported in the rangeland and related literature. Most studies report that herbaceous plants are the major components of the diet. Preferences vary widely according to the grasshopper species, their nutritional needs at different stages of maturity, and the availability and maturity of forage species (Hewitt 1977). It is not unusual, however, for the diet to include shrubs. Allred (1941) reported extensive damage to big sagebrush stands in Wyoming and Montana. Holmgren and Basile (1959) noted that grasshoppers were a common problem in bitterbrush plantings, feeding on both seedlings and established shrubs. They found, as did our study, that defoliation in consecutive years can result in mortality.

In our study, grasshoppers repeatedly defoliated the Pringle Falls source. This ecotype developed in a cool forest environment where significant insect buildups are infrequent, and apparently it lacks the resistance present in rangeland ecotypes less vulnerable to insect attack. Such results suggest that more information on insect forage preferences could have far-reaching implications in selection of plant materials for range revegetation. They also underscore the importance of evaluating potential plant materials in uniform gardens and outplantings over a period long enough to afford a range of environmental conditions.

Plantings such as the Keating garden are of value in assessing the range of adaptability and relative productivity of promising species and ecotypes. They also increase our knowledge of more subtle characteristics, such as insect preferences, which might not be detected in native stands.

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PHENOLOGY AND GROWTH HABITS OF NINE ANTELOPE BITTERBRUSH, DESERT
BITTERBRUSH, STANSBURY CLIFFROSE, AND APACHE-PLUME ACCESSIONS¹

Nancy L. Shaw and Stephen B. Monsen²

ABSTRACT

Growth habits, growth rates, phenology, and seed production of antelope bitterbrush, desert bitterbrush, Stansbury cliffrose, and Apache-plume accessions grown on a common garden are described. The information aids in the selection of appropriate management practices and improved seed production efforts, and provides a basis for selecting accessions for breeding programs or revegetation projects.

INTRODUCTION

Extensive variation within many native Intermountain shrub species has evolved in response to the interaction of rich gene pools and diverse habitats (Stutz 1974; Giunta and others 1978). Accessions of important species have been selected from the array of available ecotypes for inclusion in range revegetation programs. Antelope bitterbrush (Purshia tridentata [Pursh] DC.) was used in early wildlife habitat restoration projects (Hormay 1943; Holmgren 1954; Plummer and others 1955). Specific accessions of this species have also improved esthetics and reduced erosion on disturbed sites (Tiedemann and others 1976; Monsen and Plummer 1978; Everett 1980).

The related species -- cliffrose (Cowania mexicana D. Don var. stansburiana [Torr.] Jeps.), Apache-plume (Fallugia paradoxa [D. Don] Endl.), and desert bitterbrush (Purshia glandulosa Curran.) -- have also proven of value in revegetation projects (Blauer and others 1975; Plummer and others 1968). These species are drought tolerant and are prime candidates for ornamental use on nonirrigated sites. Palatable forms provide important winter forage for deer, cattle, and sheep. Desert bitterbrush and Apache-plume are somewhat fire tolerant, frequently resprouting following burning. Apache-plume is an excellent erosion control plant for disturbed sites in dry areas as it spreads vegetatively. All three species have potential for breeding programs as all hybridize with antelope bitterbrush (Stutz and Thomas 1964; Stutz 1974; Blauer and others 1975).

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Trials in Utah, Nevada, and Idaho during the past 30 years have identified important accessions of these species and their range of adaptation, growth characteristics and value in plantings (Plummer and others 1968; Blauer and others 1975; Giunta and others 1978). But additional knowledge of each species' floral phenology is required if adequate supplies of commercial seed are to be produced on a regular basis (Van Epps 1974; McArthur and others 1978). Studies of the floral sequence and seed development of each accession would provide data required for breeding programs, management of wildland stands to maximize seed production or permit stand regeneration, prediction of seed collection dates, and development of technology required to augment seed production under agricultural conditions (West and Wein 1971; Hopp and Blair 1973; Blauer and others 1975; Giunta and others 1978; Everett and others 1980). Comparisons of even-aged accessions of individual species planted in a common garden would aid in the identification of genetic variation in growth habits, timing of phenological stages, seed production capabilities, and susceptibility of seeds to damage by biotic and abiotic factors.

In the present study, we examined the growth habits and floral phenology of five accessions of antelope bitterbrush, two accessions of desert bitterbrush, and one accession each of Stansbury cliffrose and Apache-plume that were planted in a common garden near Boise, Idaho (table 1). Native stands of several of these accessions have been the subject of ecological studies (Ferguson and others 1963; Nord 1965; Alderfer 1977; Menke and Trlica 1981). Each accession has been tested extensively in selection trials and seeding projects in the Intermountain region (Plummer 1968; Monsen 1975; Giunta and others 1978; Monsen and Plummer 1978; Davis, unpubl. data, Monsen, unpubl. data, Stevens, unpubl. data). Commercial seed dealers regularly collect large quantities of Stansbury cliffrose seed from the Utah County, Utah, site and antelope bitterbrush seed from the sites at Lassen County, Calif.; Moffat County, Colo.; and Ada County, Idaho.

SITE DESCRIPTION

The study was conducted at the Boise Shrub Garden approximately 17 miles (27 km) northeast of Boise, Idaho. The 40 acre (16-ha) deer-proof enclosure was constructed on an east-facing terrace of granitic colluvium. Slopes range from 8 to 15 percent. Soils are dark greyish-brown or yellowish-brown gravelly, sandy loams.

Undisturbed areas within the enclosure are dominated by stands of mountain big sagebrush (Artemisia tridentata Nutt. var. vaseyana [Rydb.] B. Boi.) and threetip sagebrush (Artemisia tripartita Rydb.). Scattered antelope bitterbrush shrubs occur throughout the site. Understory grasses include Idaho fescue (Festuca idahoensis Elmer), squirreltail (Sitanion hystrix Nutt.), and Sandberg's bluegrass (Poa sandbergii Vasey). Spurred lupine (Lupinus laxiflorus Dougl. var. calcaratus [Kell.] Smith), hermit milkvetch (Astragalus eremiticus Sheld.), and storksbill (Erodium cicutarium [L.] L'Her.) are common forbs.

Climate of the site is semiarid with an 11-year (1970-81) average annual precipitation of 17 inches (43 cm). Approximately 80 percent of the annual precipitation falls from October through April. Most summer precipitation occurs as infrequent, high intensity thundershowers. Total precipitation in 1979 (the first year of study) was 24 percent below average while 1980 precipitation was near normal. Seasonal distribution of the precipitation was erratic during both years. For 1970 through 1981, the frost-free season averaged 126 days, with average dates of last spring and first fall frosts May 26 and October 1.

Table 1.--Cliffrose, Apache-plume, desert bitterbrush, and antelope bitterbrush accessions grown at the Boise, Idaho, Shrub Garden.

<u>Species</u>	<u>Seed source</u>	<u>Elevation</u> <u>Ft</u>	<u>Annual</u> <u>precipitation</u> <u>Inches</u>
<u>Cowania mexicana</u> <u>stansburiana</u>	Utah Co., Utah (American Fork)	5,100	15.0
<u>Fallugia paradoxa</u>	Sevier Co., Utah (Richfield)	5,300	8.3
<u>Purshia glandulosa</u>	Mono Co., Calif. (Benton Hot Springs)	5,700	5.9
<u>Purshia glandulosa</u>	Washington Co., Utah (Snow Canyon)	3,800	7.1
<u>Purshia tridentata</u>	Lassen Co., Calif. (Janesville)	4,300	16.9
<u>Purshia tridentata</u>	Moffat Co., Colo. (Maybelle)	6,300	11.0
<u>Purshia tridentata</u>	Ada Co., Idaho (Lucky Peak Res.)	3,200	16.9
<u>Purshia tridentata</u>	Carbon Co., Utah (Starvation Canyon)	7,000	23.2
<u>Purshia tridentata</u>	Juab Co., Utah (Eureka)	6,400	15.4

METHODS AND MATERIALS

Planting

The seven bitterbrush accessions were planted in 1973, and the cliffrose and Apache-plume accessions were planted in 1974. Native shrubs were cleared from the area prior to planting. Containerized seedlings of the antelope and desert bitterbrush accessions and 1-0 bareroot stock of the cliffrose and Apache-plume accessions were planted at 8-ft (2.4-m) spacings in two replications of 25 plants each. To reduce competition, each seedling was hand planted in the center of a 9-ft² (0.8 m²) "scalp" from which approximately 2 inches (5 cm) of surface debris and soil, including weed seeds and roots, had been removed (Holmgren 1956). The site is mowed annually to control weeds and reduce the danger of wildfire. Rodent populations are controlled by baiting.

Data Collection

Five plants in each of the two replicated plots per species were selected at random for observations of leaf development, leader growth, and floral phenology. These observations were recorded for all nine accessions in 1979 and 1980. Survival, height, crown spread, vigor, and uniformity of the shrubs have been

recorded annually since 1975. Incomplete data are available for the desert bitterbrush plots.

Leader growth and leaf development observations were followed annually with tagging of 10 leaf fascicles and four terminal leaders on each marked shrub. Development of the first new leaf in each marked fascicle was recorded from the earliest date of observable growth until the leaf reached its mature size and was fully expanded. Length of each marked terminal leader was recorded periodically throughout the growing season.

Floral phenology was followed annually with tagging of 10 flower buds on each of the marked shrubs. Each bud was examined separately on each observation date and assigned a rating value based on its stage of development. The type and extent of any observed damage to each flower or fruit were also recorded.

Timing of observations was dependent upon the rate of phenological development. Leaf development and floral stages were recorded weekly. Flowering and seed development stages were observed biweekly for 2 to 3 weeks following anthesis. Leader growth was measured semimonthly in May, June, and early July during the period of rapid growth and monthly from July through September during decreased growth. Yearly plant measurements and ratings were recorded in August.

Meteorological data have been collected since 1971 at the USDA Forest Service, Lucky Peak Nursery approximately 0.5 miles (8 km) north of the Shrub Garden. Precipitation, maximum and minimum temperatures, wind speed, and wind direction are recorded.

RESULTS

Vegetative Development

Growth rates and growth habits of the nine accessions studied are reported in table 2. Of the Apache-plume shrubs, 60 percent survived through the 1981 growing season while survival of each of the remaining accessions exceeded 90 percent. Attrition of the Apache-plume accession appears to be related to a lack of cold hardiness. One or two plants have succumbed each winter and six shrubs were lost during the winter of 1976-77. Varying degrees of dieback and recovery of additional Apache-plume plants have been observed each year.

All accessions retained their native growth habits and morphological characteristics when grown in the common garden. Nord (1965), Plummer and others (1968), and Giunta and others (1978) also found these traits to be maintained for antelope bitterbrush accessions grown on a number of experimental plots. The growth habits of individual accessions became apparent during the first growing season following planting as a result of differential height and crown growth, variation in branch flexibility, and the development of additional basal stems. The Carbon County and Juab County, Utah, and Moffat County, Colo., antelope bitterbrush accessions are very similar in growth habits. Numerous basal branches grow in a diffuse pattern and new leaders are initiated over the entire crown of the shrub. The Lassen County, Calif., antelope bitterbrush exhibits an erect growth habit with the crown developing from a small number of basal stems and new leader development concentrated in the upper portion of the plant. The growth habit of the Ada County, Idaho, antelope bitterbrush is intermediate between the other two forms. The Apache-plume and Washington County, Utah, desert bitterbrush accessions exhibited the greatest variation in growth habit, ranging from erect to diffuse.

Table 2.--Performance of antelope and desert bitterbrush, Stansbury cliffrose, and Apache-plum accessions at the Boise Shrub Garden

Accession	Survival (%) ^{1/} (July 1981)	Growth habit	Layering (% in 1981)	Vigor ^{2/} (mean 1975-1981, PUGL mean 1979-1981)	Uniformity ^{3/} (mean 1975-1981, PUGL mean 1979-1981)
COMES ^{4/} Utah Co., Utah	94	Erect	0	8	8
FAPA Sevier Co., Utah	60	Erect-Diffuse	0	6	7
PUGL Mono Co., Calif.	96	Diffuse	0	8	6
PUGL Washington Co., Utah	92	Erect-Diffuse	0	8	7
PUTR Lassen Co., Calif.	96	Erect	0	8	8
PUTR Moffat Co., Colo.	100	Diffuse	8	7	8
PUTR Ada Co., Idaho	100	Erect-Diffuse	2	8	8
PUTR Carbon Co., Utah	100	Diffuse	36	8	8
PUTR Juab Co., Utah	98	Diffuse	0	8	8

^{1/} COMES and FAPA planted in 1973, PUGL and PUTR planted in 1974.

^{2/} 0 = dead ... 9 = high vigor

^{3/} 1 = growth form highly variable within the plot ... 9 = growth form uniform throughout the plot.

^{4/} COMES - Stansbury cliffrose; PUGL - desert bitterbrush; FAPA - Apache-plume; PUTR - antelope bitterbrush

Table 3.--Mean annual height and crown measurements in inches of antelope and desert bitterbrush, Stansbury cliffrose, and Apache-plume accessions at the Boise Shrub Garden

Accession		1975	1976	1977	1978	1979	1980	1981
		-----Inches-----						
COMES ¹	Height	15.7	26.0	39.4	41.7	39.8	45.3	63.0
Utah Co., Utah	Crown	18.5	23.6	28.0	35.8	51.6	60.2	63.8
FAPA	Height	15.7	21.7	33.1	30.7	73.6	32.3	38.2
Sevier Co., Utah	Crown	15.0	27.2	27.2	28.7	33.9	42.5	42.1
PUTR	Height	23.6	29.5	37.0	45.7	45.7	48.0	57.5
Lassen Co., Calif.	Crown	25.2	27.6	38.6	45.3	61.8	68.9	64.2
PUTR	Height	24.4	26.0	30.7	28.3	35.0	32.7	37.0
Moffat Co., Colo.	Crown	39.8	53.1	59.1	50.0	60.2	69.3	71.3
PUTR	Height	27.6	28.3	40.6	42.9	42.5	41.7	45.7
Ada Co., Idaho	Crown	33.5	43.7	53.1	54.3	64.2	75.2	74.8
PUTR	Height	24.4	25.6	26.8	31.1	31.9	35.0	40.9
Carbon Co., Utah	Crown	32.7	47.2	51.2	53.5	58.3	73.2	77.6
PUTR	Height	26.0	31.1	40.6	36.6	41.3	42.5	52.4
Juab Co., Utah	Crown	35.4	52.0	59.1	56.3	63.4	73.6	83.5

^{1/} COMES - Stansbury cliffrose; FAPA - Apache-plume; PUTR - Antelope bitterbrush

Antelope bitterbrush accessions that form stem layers are capable of spreading vegetatively and are not as dependent upon seed production for stand maintenance as are nonlayering forms. Layering forms are also generally more fire tolerant. The spreading crowns and extensive root systems add stability to sandy soils and steep slopes. New growth of these frequently low growing plants provides available forage for browsing animals, although they may be covered by snow during winter and early spring. Layering forms frequently produce less seed than upright forms, and seed collection is more difficult and time consuming.

Of the nine accessions studied, three of the antelope bitterbrush accessions exhibited stem layering (table 2). Of the Carbon County, Utah, plants, 36 percent formed stem layers. Native plants of this accession grow at a high elevation site with a short growing season. Under such conditions the plants may be dependent upon reproduction by vegetative spread. Nord (1965) observed that plants growing under similar conditions in northern California also produced numerous stem layers. Layering plants at Ada County, Idaho, are most numerous on steep cliffs or road cuts. Layering frequency is greater for Moffat County, Colo., plants growing on sand dunes (Wheeler, personal communication).

Mean annual height and crown measurements for seven of the accessions are reported in table 3. All accessions with the exception of the Ada County, Idaho, and Lassen County, Calif., antelope bitterbrush accessions exhibited slight to moderate amounts of dieback as a result of exposure to low temperatures during the winter of 1977-78, although only one Apache-plume plant was lost. The affected plants recovered during the succeeding growing season. Development of all plants from 1976 through 1979 was erratic and may have been the result of low temperatures during the winters of 1976-77 and 1978-79, low precipitation during the 1977 drought year, and low to moderate levels of grasshopper damage inflicted in 1978. More rapid growth was recorded during the 1980 and 1981 growing seasons.

Vegetative Phenology

An understanding of the timing of vegetative development in relation to flowering and seed production for each species is important in terms of management practices. Various management strategies and schedules may be designed to maximize seed or vegetative production and to control the growth form or size of the shrubs. Seed production and most vegetative growth of all four species studied occur in the spring and early summer during increasing temperatures and decreasing soil moisture levels. Timing of various phenological phases may vary from year to year depending upon climatic conditions. As a result, the use of observable phenological stages is preferable to the use of prescheduled dates in applying management techniques.

Initial leaf growth of each of the antelope bitterbrush accessions was observed between March 17 and 23 in 1979 and 1980 (table 4). Actual dates may have been slightly earlier as phenophases were recorded only weekly or biweekly. The first new leaf in most leaf fascicles expanded and attained mature size by mid-April at the time flower buds were beginning to develop. Although the Moffat County, Colo., accession initiated leaf growth slightly ahead of the others, differences in the timing and rate of leaf growth among accessions were minor.

Leader growth of all five antelope bitterbrush accessions was initiated during the first week of May in 1979 and 1980 at approximately the time when flower buds began to open (table 5). The initiation of leaf and leader growth occurred later in 1979 than in 1980. This pattern was observed in all nine accessions studied and may have resulted in response to the cooler early spring temperatures of 1979. The rate of leader growth remained low through May and increased in June and early July during fruit development and maturation. Growth rates diminished in July following

Table 4.--Phenological development of antelope and desert bitterbrush, Stansbury cliffrose, and Apache-plume accessions at the Boise Shrub Garden

Accession		Leaf growth initiated	First leaf expanded	Floral buds visible	Anthesis	Fruit development initiated	Leader growth initiated	Fruit mature
COMES ^{1/} Utah Co., Utah	1979	April 26	May 18	May 14	June 5	June 13	May 12	July 20
	1980	April 25	May 15	April 28	June 2	June 14	May 9	July 22
FAPA Sevier Co., Utah	1979	April 18	May 4	May 22	June 10	June 22	May 5	July 28
	1980	April 16	May 2	May 5	May 25	June 3	April 28	July 30
PUGL Mono Co., Calif.	1979	April 26	May 18	April 28	May 24	May 29	May 18	July 18
	1980	April 23	May 15	April 21	May 17	June 5	May 14	July 22
PUGL Washington Co., Utah	1979	April 26	May 18	April 28	May 25	May 28	May 20	July 18
	1980	April 23	May 15	April 21	May 21	June 4	May 14	July 21
PUTR Lassen Co., Calif.	1979	March 21	April 18	April 21	May 14	May 24	May 5	July 7
	1980	March 17	April 20	April 7	May 3	May 14	May 8	July 10
PUTR Moffat Co., Colo.	1979	March 21	April 22	April 21	May 15	May 24	May 5	July 7
	1980	March 17	April 23	April 14	May 4	May 12	May 8	July 10
PUTR Ada Co., Idaho	1979	March 21	April 18	April 24	May 13	May 24	May 5	July 7
	1980	March 17	April 15	April 22	May 6	May 16	May 8	July 10
PUTR Carbon Co., Utah	1979	March 21	April 18	April 21	May 14	May 25	May 5	July 7
	1980	March 20	April 20	April 14	May 4	May 11	May 8	July 10
PUTR Juab Co., Utah	1979	March 21	April 22	April 21	May 16	May 26	May 5	July 7
	1980	March 23	April 23	April 14	May 8	May 12	May 8	July 10

^{1/} COMES - Stansbury cliffrose; FAPA - Apache-plume; PUGL - desert bitterbrush; PUTR - antelope bitterbrush

Table 5.--Leader growth of antelope and desert bitterbrush, Stansbury cliffrose, and Apache-plume accessions at the Boise Shrub Garden.

Accession	1979 1980	May 15 May 13	May 30 June 3	June 13 June 12	June 28 June 26	July 27 July 21	August 29 August 12	September 20
-----Inches-----								
^{1/} COMES Utah Co., Utah	1979	—	0.7	2.5	3.1	4.1	4.2	4.6
	1980	—	1.5	3.4	6.2	6.4	6.4	
FAPA Sevier Co., Utah	1979	1.1	1.5	2.2	2.8	3.7	3.6	3.6
	1980	1.1	2.6	3.7	3.8	4.4	6.2	
PUGL Mono Co., Calif.	1979	—	1.7	2.3	2.7	3.5	3.5	3.6
	1980	—	1.0	1.6	2.0	4.6	4.6	
PUGL Washington Co, Utah	1979	—	1.0	1.9	2.7	3.0	3.0	3.0
	1980	—	0.9	1.5	1.9	3.0	3.0	
PUTR Lassen Co., Calif.	1979	0.9	1.6	2.2	3.1	3.0	2.9	3.0
	1980	0.9	1.5	1.5	4.6	5.1	5.2	
PUTR Moffat Co., Colo.	1979	0.6	2.1	3.4	4.1	4.3	4.2	4.2
	1980	0.4	1.4	2.5	2.8	3.7	3.7	
PUTR Ada Co., Idaho	1979	0.9	1.7	2.8	3.1	3.2	3.3	3.2
	1980	0.9	1.5	2.0	3.2	5.1	5.2	
PUTR Carbon Co., Utah	1979	0.7	1.7	2.5	3.0	3.1	3.0	2.8
	1980	1.0	1.5	1.5	2.1	2.4	2.4	
PUTR Juab Co., Utah	1979	0.8	1.9	3.2	3.8	4.0	4.1	4.1
	1980	0.7	1.5	1.9	3.5	4.8	5.2	

^{1/}COMES - Stansbury cliffrose; FAPA - Apache-plume; PUGL - desert bitterbrush; PUTR - antelope bitterbrush

seed shatter. Minimal leader growth occurred during late summer and fall. Leaf fall has been observed for all five antelope bitterbrush accessions in response to moisture stress during mid-summer.

Leaf development of the Stansbury cliffrose and desert bitterbrush accessions started between April 23 and 26 each year. Expansion of the first new leaf in each fascicle was completed by mid-May in an average of 22 to 24 days. Leader development of both species followed a pattern similar to that for bitterbrush. In contrast to antelope bitterbrush, leaf fall during the late summer months was minimal for these accessions.

Leaf growth of Apache-plume started in mid-April, approximately 1 week earlier than that of the Stansbury cliffrose and desert bitterbrush accessions each year. The first leaf in each fascicle expanded rapidly and reached mature size within approximately 16 days of the time flower buds began to appear. Leader growth was initiated slightly in advance of flower bud appearance and continued into August.

Floral Phenology

Antelope Bitterbrush. Flowers of antelope bitterbrush are regular, perfect, and perigynous. They are pollinated by bees, wasps, and other insect species and are self-incompatible (Blauer and others 1975). The flowers are approximately 0.3 inch (8 mm) in diameter with showy, cream-colored deciduous petals. Normally, there is one or occasionally two pistils and a single series of approximately 25 stamens. The fruit is a cartilaginous, pubescent achene with a persistent style. Seeds are purplish-black.

Initiation and progression of the flowering sequence was very similar for each of the five antelope bitterbrush accessions in 1979 and in 1980 (tables 4 and 6). Floral buds appeared on all five between April 14 and 21 in 1979 and between April 7 and 14 in 1980. Bud formation may have been delayed in 1979 relative to 1980 as a result of cooler temperatures and greater precipitation during the winter and early spring of 1979. However, rainfall during flower and fruit development totaled 0.7 inches (1.8 cm) in 1979 and 5.0 inches (12.6 cm) in 1980. Seed of each accession was collected on July 6 in 1979 and July 10 in 1980.

Flower buds appeared nearly simultaneously on most shrubs within each accession. The solitary flower buds develop at the tips of short lateral spurs on second year or older wood. Buds appeared slightly earlier, and flowers and fruits developed more rapidly, on branches near the ground. Production of flower buds was somewhat limited both years as the shrubs had not reached full maturity. Bud production was greatest and most uniform among plants of the Moffat County, Colo., accession and most erratic for the Juab County, Utah, accession. However, over 90 percent of the shrubs in each accession produced at least moderate numbers of flowers.

No consistent differences among accessions were observed in the timing of flowering or fruit development. On all accessions, flower buds developed and remained closed for 2 to 3 weeks before opening for several days. Two nights of below-freezing temperatures -- 28°F (-2°C) on May 28 and 31°F (-1°C) on May 29 -- were recorded during or following flowering in 1979 while none was recorded in 1980. No frost damage to the developing fruit was observed.

Table 6.--Seed production and duration of flowering and fruiting phases for antelope bitterbrush, desert bitterbrush, Stansbury cliffrose, and Apache-plume accessions at the Boise Shrub Garden

Accession	Flowering period	Fruit development	Total	Percentage of fruit with multiple pistils	Normal and spotted mature seed	
					Percent	seed
-----Days-----						
COMES ^{1/} Utah Co., Utah	1979	30	37	67	100	87
	1980	47	38	85	100	48
FAPA Sevier Co., Utah	1979	31	36	67	100	--
	1980	35	57	86	100	--
PUGL Mono Co., Calif.	1979	31	50	81	2	38
	1980	45	47	92	4	32
PUGL Washington Co,Utah	1979	30	51	81	15	33
	1980	44	47	91	28	59
PUTR Lassen Co., Calif.	1979	33	44	77	2	67
	1980	37	57	94	1	38
PUTR Moffat Co., Colo.	1979	33	44	77	12	65
	1980	28	59	87	15	55
PUTR Ada Co., Idaho	1979	30	44	74	11	56
	1980	24	55	79	7	47
PUTR Carbon Co., Utah	1979	34	43	77	17	21
	1980	27	60	87	20	39
PUTR Juab Co., Utah	1979	35	42	77	9	66
	1980	28	59	87	17	50

^{1/} COMES - Stansbury cliffrose; FAPA - Apache-plume; PUGL - desert bitterbrush; PUTR - antelope bitterbrush

The period of fruit development for the five accessions differed between years. Fruit developed to maturity in 42 to 48 days in 1979 and in 57 to 60 days in 1980. Duration of the entire flower and fruit development ranged from 74 to 84 days in 1979 and from 87 to 94 days in 1980. Blaisdell (1958) reported flowering and fruit development of 66 days for antelope bitterbrush growing near Dubois, Idaho, at an elevation of 5,500 ft (1 676 m) while populations growing at elevations between 6,122 and 8,963 ft (1 866 and 2 732 m)) in Cache la Poudre Canyon, Colo., were found to require from 102 to 125 days (Colorado Game, Fish, and Parks Dept. 1965).

A number of insects are known to damage or destroy the seed of antelope bitterbrush (Ferguson and others 1963; Basile and Ferguson 1964; Basile and others 1964; Furniss 1975; Ferguson 1967). Significant reduction in potential seed production often results from insect infestation (table 6). Spotted seeds, which normally exhibit reduced germinability, were counted with normal seeds during the fruit development period because they could not be identified without being removed from the achene. Frequently observed seed predators in the area of the Boise Shrub Garden include a gall midge (Mayetiola spp.), a gelechiid (Filatima sperryi Clarke), thrips (Frankliniella spp.) and one or more species of stink bugs (Chlorochroa spp.).

Mature seeds dehisce quickly. Although seeds on individual accessions develop very uniformly, at least small percentage of seeds generally ripen and are disseminated prior to collection. Of the marked flowers, 38 to 55 percent were producing normal or spotted achenes on June 30, 1980. Much of this seed was lost just prior to collection because of high winds and rainstorms. By July 10, 1980, fully developed, mature seeds were collected from only 14 to 24 percent of the originally marked flower buds.

Plantings of antelope bitterbrush in seed orchards or common gardens may create situations that increase the susceptibility of the shrubs to attack by damaging insects, because dense, pure stands are available for invasion. Populations of predators and parasites of seed-damaging insects are limited by site maintenance practices (Van Epps and Furniss 1981). Inadequate knowledge of the biology and ecology of most of these seed damaging species is available to determine whether control practices can be effectively applied. Seed loss because of wind storms and insect damage emphasizes the need for careful selection of seed production sites and the need for development of appropriate cultural techniques for each species.

Desert Bitterbrush. Flowers of desert bitterbrush are morphologically similar to those of antelope bitterbrush, but are approximately 0.7 to 1.0 inches (18-25 cm) in diameter. They are insect-pollinated and self-incompatible (Blauer and others 1975). Flowers normally produce three, or sometimes two, pistils. However, during the 1979 and 1980 seasons, an average of only 3 percent of the flowers of the Mono County, Calif., accession and 22 percent of the flowers of the Washington County, Utah, accession produced two pistils. No flowers with three pistils were observed. The achene is slightly smaller than that of antelope bitterbrush and has a more pronounced beak. Developing seeds are more yellow-green and mature seeds more reddish-purple than those of antelope bitterbrush.

Flower buds originate at the tips of spurs on second year and older growth. Only five shrubs of the California accession and 10 of the Utah accession produced significant numbers of floral buds in 1979. The number of shrubs to produce abundant flowers has increased annually since 1979, indicating that this species may be slower to reach maturity than antelope bitterbrush at the Boise location. The timing of flowering and fruit development stages was similar for both accessions (table 4) and lagged from 1 to 2 weeks behind the same stages for antelope bitterbrush. Flowering occurred after the last frost each year. Fruit development ranged from 47 to 51 days for the two sources over the 2 years. Flowering and fruit

development ranged from 81 to 92 days. Percentages of flowers to produce normal or spotted mature seed for the two accessions were quite low, ranging from 32 to 59 percent. The remaining seeds were all damaged or destroyed by insects.

Stansbury Cliffrose. Flowers of Stansbury cliffrose are regular, perigynous, and usually perfect. They are approximately 0.8 inches (2.0 cm) in diameter with 5 sepals, 5 petals, many stamens in 2 series and 4 to 12 pistils. The fragrant, pale yellow flowers are insect-pollinated and self-incompatible. The fruits are narrow, leathery achenes approximately 0.1 inches (0.3 cm) in length with long, white plumose styles. Approximately 90 percent of the flower buds are produced during the initial flowering period. Buds formed during this period are borne on short lateral spurs on second year or older wood. Stages of flowering and seed development lagged from 2 to 4 weeks behind those of antelope bitterbrush each year. Flowering occurred after the last frost each year. Fruit development required approximately 37 days each year. Flowering and fruit development was approximately 68 days in 1979 and 78 days in 1980.

Shrubs within this accession exhibited considerable variation in the number of flowers produced and seed maturation dates. Achenes mature fairly uniformly on individual shrubs from the initial group of floral buds. However, variation in seed maturation dates among shrubs necessitates almost daily seed collection as mature fruits dehisce quickly.

Additional flower buds form following initial flowering and throughout the summer, particularly following summer rains. These buds appear at the tips of leaders or spurs produced during the current growing season. Flowering at the Boise Shrub Garden has been observed well into October.

The only major type of damage observed on fruits of this accession involved the loss of all achenes from a single receptacle. This was probably insect caused because damage to the receptacle of some of these flowers was also observed. Also, the achenes of more than one flower on a branch were frequently removed while none of the flowers on nearby branches were affected. Initial damage was noted on June 15 in 1979 as flowering began. The percent of achenes lost by the time of fruit maturation was 13 percent in 1979 and 52 percent in 1980.

Apache-plume. The flowering habits of the Sevier County, Utah, Apache-plume accession have been described by Blauer and others (1975). Although some shrubs are dioecious, a majority are monoecious. Few flowers are fully bisexual. Pistillate flowers bear rudimentary, nonfunctional stamens, while staminate flowers bear rudimentary, nonfunctional pistils. Fruits are elongate achenes with plumose white and purplish styles.

Flower buds appeared later on Apache-plume than on the other species. Buds were first observed on May 22 in 1979 and on May 5 in 1980. Buds are formed on elongated peduncles originating from vegetative growth produced during the current season. They may be formed on lateral leaders, terminal leaders, or root sprouts. Buds may be solitary or several buds may develop in a small corymb. Flowering began about June 5 in 1979 and May 22 in 1980 following the last frosts of both growing seasons. The showy, white flowers are pollinated by a variety of Coleoptera and Hymenoptera. Unlike bitterbrush and Stansbury cliffrose, some Apache-plume flowers may be self-compatible (Blauer and others 1975).

Flower buds are produced continuously throughout the summer. Most buds develop over about 1 month following the appearance of the earliest buds. Consequently, the achenes do not ripen uniformly. The earliest buds produced mature fruit by July 28 in 1979 and by July 30 in 1980. The duration of the fruit development period for buds produced early in the season was 51 days in 1979 and 36 days in 1980. Flower

and fruit development required 67 days in 1979 and 86 days in 1980. Additional flowers were produced through early October both years.

The Apache-plume, desert bitterbrush, and Stansbury cliffrose accessions have become established, have developed to maturity, and have produced viable seed crops at the Boise Shrub Garden, which is north of their native ranges. Plantings of each species at similar locations within 15 miles (33 km) of the Boise Shrub Garden have survived as long as 26 years, although no natural reproduction has been observed. An opportunity exists to extend the range of use for these species.

CONCLUSIONS

The nine shrub accessions exhibited characteristic growth forms, cycles of phenological development and levels of tolerance to environmental conditions. The wide range of variability existing within the four Rosaceous species examined provides a strong genetic base for breeding and selection programs. Increased use of shrubs in wildland revegetation projects has created a demand for site-adapted varieties exhibiting desired characteristics and suited to current planting and management techniques. Although numerous accessions of these species have been included in research and site improvement plantings, commercial varieties are not yet available.

The five antelope bitterbrush accessions established readily and exhibited a wide variation in growth habits and seed production capabilities, although timing of their phenological phases was quite similar. Milder climatic conditions and a relatively long frost free season at the Boise Shrub Garden compared to the other seed source locations may have contributed to their success. The loss of seed as a result of wind storms and insect damage serves to emphasize the need for care in the selection of seed production sites and the requirement for the development of appropriate cultural techniques for each species.

The Apache-plume, desert bitterbrush, and Stansbury cliffrose accessions have become established and developed to maturity at the Boise Shrub Garden, which is located north of their native ranges. Plantings of each of these species at similar locations within 15 miles (9 km) of the Boise Shrub Garden have survived for as long as 26 years, although no natural reproduction has been observed. An opportunity exists to extend the range of use for these species.

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SEED PHYSIOLOGY OF ANTELOPE BITTERBRUSH AND RELATED SPECIES¹

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ABSTRACT

Dormancy of the seeds of antelope bitterbrush (Purshia tridentata [Pursh] DC), desert bitterbrush (P. glandulosa Curran), and cliffrose (Cowania mexicana var. stansburiana [Torr.] Jeps.) seeds is a major factor limiting successful artificial revegetation with these species. Dormancy is broken under natural conditions by cool-moist stratification. To enhance germination before artificially seeding these shrubs, land managers can stratify seeds or treat them with hydrogen peroxide. Even with optimum enhancement, the germination will rarely exceed 60 percent.

INTRODUCTION

The closely related members of the Rosaceae family, desert and antelope bitterbrush and cliffrose, are valuable browse species on western rangelands. In many areas, communities of these plants have deteriorated, and land managers have attempted to revegetate rangelands by planting seeds of these species.

One major hindrance to seeding all three species is dormancy of the seed. Many land managers and scientists have recognized the problem, and as a result, the seed ecology of antelope bitterbrush has been subject to research for 45 years. A bibliography of antelope bitterbrush literature, done over a decade ago, lists over 200 citations, many of which mention or are solely concerned with germination and seedbed ecology problems (Basile 1967). A more recent annotated bibliography (Clark and Britton 1979) also stresses the importance of seed and seedbed ecology for bitterbrush. The germination and establishment problems probably are as important to the regeneration of desert bitterbrush and cliffrose as they have been demonstrated for antelope bitterbrush, but much less research has been devoted to these species.

NATURE OF DORMANCY

Conflicting terminology has been used to describe the fruits of bitterbrush; for clarification, we will define the terms we use before proceeding with a review of the nature of dormancy. The perfect yellow flowers of antelope bitterbrush are borne singly at the end of short lateral leafy spurs. The fruit is an oblong achene about 0.13 to 0.5 inches (6 to 12 mm) long. The achene consists of the embryo or miniature plant, radicle, hypocotyl, and cotyledons covered by the seedcoat and pericarp. The pericarp, or ripened wall of the ovary, is soft and bright red when

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the seed is forming, but becomes very dark at maturity. The achene is dry and flinty when mature, and we will refer to it as a seed. When the seed of antelope bitterbrush is mature, it falls from the plant with a papery covering composed of remnant flower parts and tipped with a remnant of the style. Desert bitterbrush seeds have the same covering except the beaked style remnant tends to be more elongated. The seeds of cliffrose are completely enclosed in a thickened, funnellform remnant of flower parts and are tipped by long, feathery styles. Before entering commerce, the papery covering of bitterbrush seeds is normally rubbed free of the seed. The thickened covering of cliffrose seeds cannot be mechanically removed without damaging the seed. When we refer to a cliffrose "seed," the entire assemblage is included. Generally, when sold in commerce, the seeds of cliffrose have the feather style removed.

When the embryos of antelope bitterbrush seeds are dissected from the achenes, the embryos will germinate, indicating the dormancy is controlled by factors associated with the seedcoat and/or pericarp. Embryo dissection has been used as a quick viability check for antelope bitterbrush seeds (Nord 1956).

The seeds of antelope bitterbrush are largely dormant at harvest. Usually 5 to 20 percent of a seed lot will germinate without enhancement. Germination of antelope bitterbrush seeds is greatly enhanced by cool-moist stratification. This treatment simply consists of placing the seeds in a moist environment at a temperature too cold to allow germination. The term "stratification" originated from the forestry practice of placing seeds between layers of peat moss to form a stratified bed for winter chilling. The usual rationale given for germination enhancement from stratification is that the cool-moist period allows sufficient oxygen to reach the embryo to allow germination. We will expand on this concept in a later section on stratification.

Dormant antelope bitterbrush seeds do imbibe water. The seedcoat and pericarp do not interfere with moisture imbibition as is the case with hard-seeded legumes.

In addition to stratification, thiourea treatment can remove the inhibition to germination of antelope bitterbrush seeds (Pearson 1956). Thiourea belongs to a class of compounds called sulphydryls, a number of which have a markedly stimulatory effect on dormant seeds (Roberts 1973). In solution, thiourea is in equilibrium with the iso form: $\text{NH}_2\text{CSNH}_2 \rightleftharpoons \text{NH}_2\text{C}(\text{SH})\text{NH}_2$. One peculiarity of these compounds is that they can have an extremely narrow concentration range for optimum activity. Thiourea enhancement of antelope bitterbrush germination seems to be an ideal solution to dormancy as far as land managers are concerned. After soaking the seeds in the thiourea solution, they are dried. When the dried seeds are rewet after planting in the field, the thiourea is effective in enhancing germination. In contrast, once antelope bitterbrush seeds, or those of most other species, are stratified, the seeds must be planted immediately for the germination enhancement to be effective. If the stratified seeds are dried, not only is the advantage gained by stratification lost, but the seeds become nonviable. Three problems are associated with the use of thiourea-treated bitterbrush seeds: (1) the treatment has never been as effective in producing established stands in the field as laboratory results would indicate, (2) thiourea is labeled as a highly toxic substance to humans, and (3) thiourea-treated seeds must be seeded in the spring. Very little information is published about the response of cliffrose and desert bitterbrush seeds to thiourea, but in one trial, cliffrose seed germination was enhanced by thiourea treatment (Alexander and others 1974).

Antelope bitterbrush seeds have increased germination when treated with solutions of hydrogen peroxide (Everett and Meeuwig 1975). Hydrogen peroxide is a compound that has been shown to enhance germination of seeds of numerous species (Crocker and Barton 1953). Another major group of compounds that have been shown to

enhance germination is the gibberellic acids. Gibberellin has been used to substitute for the stratification requirements of antelope bitterbrush seeds (McConnell 1960).

Many land managers who have worked with seeding of antelope bitterbrush in the field believe seeds stored at cool and cold temperatures for a year germinate better than freshly harvested seeds. This response would be similar to an after-ripening requirement although such requirements usually do not respond to storage temperatures.

In summary, the seedcoat and/or pericarp of antelope bitterbrush seeds interfere with the germination of these seeds. This interference can be overcome by cool-moist stratification or by treatment with various chemicals, all of which have been shown to influence the pentose phosphate pathway of dormancy (Roberts 1973).

GERMINATION PROFILES

In a recent publication we developed germination profiles for antelope and desert bitterbrush and cliffrose seeds (Young and Evans 1981). We compared four basic germination treatments for each species: (1) control with no treatment before the seeds were incubated, (2) thiourea soaking before incubation, (3) hydrogen peroxide soaking before incubation, and (4) cool-moist stratification before incubation. The details of each treatment are given in subsections.

In all treatments, four replications of 100 seeds were used. Unless otherwise specified, we collected seeds in northern Nevada for antelope bitterbrush or purchased seeds from southwestern Utah for desert bitterbrush and cliffrose during the summer that they were produced and began testing in October of the same year. Seeds were stored in the laboratory in paper bags before testing. Usually, the seeds were hand threshed to avoid injury. The papery flower parts that persist around the achenes of antelope and desert bitterbrush were removed. The indurate portion of the funnellform flower of cliffrose that persists around the achene was not removed. Seeds were placed on a single thickness of germination paper in petri dishes and kept moist with tap water. Seeds were considered germinated when the radicle emerged 0.25 inches (0.5cm). The seeds were incubated in dark germinators.

Control Profiles

To develop profiles of the germination of seeds of each species in relation to temperature, we incubated the seeds at 55 constant and alternating temperature regimes. Constant regimes consisted of 0°, 2°, 5°, and then at 5° increments through 40°C. Alternating regimes consisted of 16 hours at each constant temperature alternating with 8 hours at each higher temperature in the profile daily. For example, 0°C alternated with 2°, 5°, 10°, 15°, 20°, 25°, 30°, 35°, and 40°C while 35°C alternated with 40°C only. Seeds were incubated for 4 weeks with counts made at 1, 2, and 4 weeks. Seeds were considered germinated when the radicle emerged 0.25 inches (0.5 cm).

The effects of constant and alternating temperatures on each species in terms of germination percentage were statistically analyzed using a quadratic response surface. This quadratic response surface was composed of a series of regression equations, one for each cold period (16 hours) temperature through the series of warm period temperatures (8 hours) with calculated values and their confidence limits (Evans and others 1982).

Thiourea

WARNING! Before considering any seed treatment with thiourea, remember it is a highly toxic chemical. The regulations of most public land management agencies prohibit the use of this material as a dormancy breaker.

We soaked the seeds of all three species in a 3 percent solution of thiourea for 30 minutes, allowed the seeds to dry, and then incubated them at the standard 55 constant and alternating temperatures used for germination profiles.

Hydrogen Peroxide

The seeds of all three species were pretreated by soaking for 6 hours in 1 percent hydrogen peroxide following the procedures of Everett and Meeuwig (1975).

RESULTS: GERMINATION PROFILES

Control

For the 55 temperature regimes of the standard germination profile, seeds of antelope bitterbrush averaged only 16 percent germination, but germinated significantly better ($P = 0.01$) than the other two species (table 1). Germination was very low for the seeds of cliffrose and desert bitterbrush.

Seeds of antelope bitterbrush germinated at a wide range of constant and alternating temperatures without pretreatment. Some germination occurred at 87 percent of the regimes tested (table 1). Optimum temperature regimes for germination were spread over a wide range of warm period temperatures from 15° to 30°C. Except for 10°/25°C (10°C for 16 hours/25°C for 8 hours in each 24-hour period), the optima occurred at 0° to 5°C cold period temperatures which, as will be seen in a later section, are the ideal temperatures for stratification of antelope bitterbrush seeds. Essentially, during the 4-week incubation period, antelope bitterbrush seeds were partially self-stratifying themselves at these incubation temperatures. Partitioning the profiles into percentiles indicated that 51 percent of the regimes had germination from 10 to 25 percent and 27 percent had germination below 10 percent (table 1).

The germination profile for desert bitterbrush seeds was considerably different with no evidence of self-stratification. There was no germination at 0°C or any temperature regime that alternated with 0°C. The optimum regimes were restricted to constant temperatures of 5° through 20°C except for 10°/15°C. Germination occurred at only 51 percent of the regimes tested, and an overwhelming 95 percent of the regimes had germination below 10 percent. Overall, germination of desert bitterbrush without pretreatment was very low.

Germination of cliffrose seeds was low at all temperatures, and some germination occurred at only 60 percent of the temperatures tested. The optimum temperature regimes for germination were scattered over a wide range and accounted for 27 percent of the possible regimes (table 1). Some of the optima occurred in the self-stratifying range of 0°/25°, 2°/30°, and 5°/20° through 5°/30°C, but others were the warm regimes of 20°/25° to 20°/30°C. On a percentile basis, 67 percent of the regimes had germination below 10 percent.

Thiourea

The soaking period we found to give optimum enhancement of germination for all three species and was used for the profiles was 30 minutes in a 3 percent solution of thiourea (Young and Evans 1981). This is a much longer soaking time than was originally proposed by Pearson (1956). He found that long-duration soaking inhibited germination. Antelope bitterbrush seeds have been shown to be sensitive to the temperature of the soaking solution with high soaking temperatures reducing subsequent germination (Neal and Sanderson 1975). It may be that high soaking temperatures led Pearson to discount the value of longer duration thiourea treatments in enhancing germination. The value of longer duration soaking in thiourea solutions was originally pointed out by the late Eamor Nord (personal communication).

Table 1.--Comparison of parameters synthesized from quadratic response surface for germination profiles for antelope bitterbrush, desert bitterbrush, and cliffrose seeds without treatment before incubation. See Young and Evans (1981) for complete profiles.

Parameters	Cliffrose	Desert bitterbrush	Antelope bitterbrush
	-----Percent-----		
Regimes with some germination	60	51	87
Mean germination	9	5	19
Regimes with optimum germination	27	11	22
Mean of optima	13	8	30
Germination percentiles:			
10	67	95	27
10-25	33	5	51
26-50	0	0	22
51-75	0	0	0
76-90	0	0	0
90	0	0	0

For the overall mean germination at the 55 constant and alternating temperature regimes tested, antelope bitterbrush seeds had significantly higher ($P = 0.01$) germination than the other species. Cliffrose seeds were intermediate in germination, and desert bitterbrush germination profiles had the lowest average germination.

Seeds of antelope bitterbrush germinated at all temperatures tested except $0^{\circ}/0^{\circ}$, $35^{\circ}/40^{\circ}$, and $40^{\circ}/40^{\circ}\text{C}$ after being treated with thiourea. The mean germination of regimes with some germination was 46 percent (table 2). Optimum temperature regimes occurred at 18 percent of the temperatures tested with an average germination of 65 percent. The optima occurred at temperatures from 10° to

25°C alternating with 2° to 10°C. Based on a percentile breakdown, 49 percent of the regimes produced germination between 51 and 75 percent, and only 11 percent had germination below 10 percent.

Seeds of desert bitterbrush germinated at 85 percent of the temperature regimes tested after treatment with thiourea (table 2). Besides 0°/0°C, desert bitterbrush seeds failed to germinate at 35°/35° or 40°/40°C and most of the temperature regimes that alternated with 40°C. Optimum regimes for germination were clustered around 15°/25°C and accounted for 15 percent of all regimes, with a mean germination of 43 percent. Based on percentile, 26 percent of the temperature regimes produced germination below 10 percent.

After treatment with thiourea, cliffrose seeds germinated at 93 percent of the temperature regimes tested (table 2). Only the very cold and extremely warm regimes failed to support some germination. Optima constituted 16 percent of the regimes in a tight cluster in the 20° and 25°C warm period temperatures, alternating with 2° and 15°C cold period temperatures. The mean germination at the optimum regimes was 66 percent. Based on percentiles, 29 percent of the regimes produced germination between 51 and 75 percent, and 15 percent had germination below 10 percent.

Table 2.--Comparison of parameters synthesized from quadratic response surfaces for germination profiles for antelope bitterbrush, desert bitterbrush, and cliffrose seeds soaked in a 3 percent solution of thiourea for 30 min. before incubation. See Young and Evans (1981) for complete profiles.

Parameters	Cliffrose	Desert bitterbrush	Antelope bitterbrush
	-----Percent-----		
Regimes with some germination	93	85	95
Mean germination	38	26	46
Regimes with optimum germination	16	15	18
Mean of optima	66	43	65
Germination percentiles:			
10	15	26	11
10-25	18	27	7
26-50	38	47	33
51-75	29	0	49
76-90	0	0	0
90	0	0	0

Stratification

Stratification of bitterbrush is intricately related to temperature and time. Hormay (1943) reported that the stratification requirements for bitterbrush seeds were 5 to 8 weeks at 0° to 5°C. This temperature range is supported by our investigation, but our results indicate that the duration can be shortened (Young

and Evans 1976). More importantly, excessively long stratification can reduce subsequent germination.

The usual recommended stratification period for antelope bitterbrush is 2 to 3 months (U.S. Department of Agriculture, Forest Service 1948). Petzold (as cited by Deischman and others 1974) found that short stratification periods of as little as 2 weeks gave adequate germination.

We have determined that osmotic and matric potentials of the soil, water, and fluctuations in seedbed temperatures can dramatically influence the degree of germination enhancement received from stratification.

No one knows for certain what is the mode of action for stratification enhancing seed germination; however, we (Young and Evans 1976) previously suggested a possibility based on the research of the French seed physiologist, Come (1967).

Embryos require very little O_2 in the environment to germinate. The lower temperature, the less O_2 is needed² (Come and Tissaoui 1972). The higher the temperature, the greater the O_2 requirement of the embryo, but the quantity of available O_2 decreases because at higher temperature it is less soluble and phenolic substances chemically react with the O_2 before it reaches the embryo. At 2°C, about 14 p/m O_2 are soluble in water, but only 10 p/m are soluble at 15°C (Streeter 1935). Because low temperatures increase solubility of O_2 in water and reduce both the requirements for it and the fixing capacity of the seedcoat, stratification enhances germination of antelope bitterbrush seeds.

Mean germination of desert bitterbrush (38 percent) at 55 constant and alternating temperatures after 2 weeks stratification at 5°C was significantly higher ($P = 0.01$) than that for the other species. The mean germination of cliffrose seeds (39 percent) was intermediate and that for antelope bitterbrush seeds (31 percent) was lowest.

The quadratic response surface for antelope bitterbrush germination reveals some germination at 91 percent of the temperature regimes tested. The optimum temperature regimes for germination were loosely clustered around 5°/15°C encompassing 23 percent of the temperature regimes with an average germination of 52 percent. Partitioning the profile into percentiles shows that 52 percent of the temperature regimes produced germination from 26 to 50 percent (table 3). Only 15 percent of the regimes produced germination greater than 50 percent. On the other end of the germination spectrum, 15 percent of the regimes produced germination of less than 10 percent.

Table 3.--Comparison of parameters synthesized from quadratic response surfaces of germination profiles for antelope bitterbrush, desert bitterbrush, and cliffrose seeds after cool, moist stratification. See Young and Evans (1981) for complete germination profiles.

Parameters	Cliffrose	Desert	Antelope
		bitterbrush	bitterbrush
		-----Percent-----	
Regimes with some germination	96	80	91
Mean germination	37	50	36
Regimes with optimum germination	15	11	23
Mean of optima	55	72	52
Germination percentiles:			
10	11	22	15
10-25	16	9	18
26-50	51	36	52
51-75	22	31	15
76-90	0	2	0
90	0	0	0

The quadratic response surface for germination of seeds of desert bitterbrush showed a lower number of temperature regimes that supported some germination than antelope bitterbrush, but a higher average germination (table 3). Desert bitterbrush seeds failed to germinate at 40°C or colder temperatures alternating with 40°C except for 15°/40°C. Optimum temperature regimes were tightly clustered at 10°/10°, 10°/15°, 10°/20°, 15°/15°, 15°/20°, and 20°/20°C. The mean of the optima was 72 percent. Partitioned into percentiles, 67 percent of the temperature regimes supported germination between 26 and 75 percent. The failure to germinate at most 40°C temperatures was reflected in the 22 percent of the regimes that produced germination below 10 percent.

Seeds of cliffrose had some germination at all temperature regimes except 0°/0° or 0°/2°C. The mean germination of the 52 regimes that produced some germination was 37 percent (table 3). The temperature regimes that produced optimum germination were clustered around 5°/25°C and extended to 2°/25°C. The mean of the optima was 55 percent. On a percentile basis, 51 percent of the temperature regimes produced germination in the 26- to 50-percent range and only 11 percent were below 10 percent.

Hydrogen Peroxide

The overall mean germination of antelope bitterbrush seeds (21 percent), pretreated with 1-percent H₂O₂ for 6 hours, was significantly higher ($P = 0.01$) than that for the other two species. Desert bitterbrush seeds had intermediate germination (19 percent), and the mean germination of cliffrose seeds (9 percent) was lower.

The quadratic response surface for percent germination of H_2O_2 treated seeds reveals some germination at 85 percent of the temperature regimes tested with a mean germination of 26 percent (table 4). The optimum temperatures for germination clustered around 10°/10°, 10°/15°, and 10°/20°C with a mean of 49 percent. Dividing the profile into percentiles resulted in 47 percent of the profiles having germination from 26 to 50 percent. A large proportion of regimes, 29 percent, supported germination only from 0 to less than 10 percent.

A quadratic response surface for percent germination of desert bitterbrush seeds treated with H_2O_2 was similar to that of antelope bitterbrush (table 4). Some germination occurred at 87 percent of the 55 temperature regimes tested.

Mean germination of the regimes with some germination was 13 percent. The number of regimes with optimum germination was 13 percent of the total, the same as for antelope bitterbrush. The mean of the optima was 37 percent. The optimum regimes were clustered around 10°/20°, 10°/25°, and 10°/30°C or slightly higher warm period temperatures than for antelope bitterbrush. The percentile distribution of germination and temperature regimes for desert bitterbrush germination was practically identical to those for antelope bitterbrush seeds.

The quadratic response surface for percent germination of cliffrose seeds treated with H_2O_2 reveals a limited germination response (table 4). Germination occurred at 62 percent of the temperatures tested with a mean of 14 percent. The optimum temperature regimes for germination spread over a relatively wide range of temperatures (20 percent of the total) from 10°/10° through 20°/25°C. The lack of germination enhancement of cliffrose seeds with H_2O_2 treatments is illustrated by the 62 percent of the temperature regimes with less than 10-percent germination.

Table 4.--Comparison of parameters synthesized from quadratic response of germination profiles for antelope bitterbrush, desert bitterbrush, and cliffrose seeds treated with hydrogen peroxide. See Young and Evans (1981) for complete profiles.

Parameters	Desert Cliffrose bitterbrush Antelope bitterbrush		
	-----Percent-----		
Regimes with some germination	62	87	85
Mean germination	14	23	26
Regimes with optimum germination	20	13	15
Mean of optima	25	37	49
Germination percentiles:			
10	62	27	29
11-25	31	31	24
26-50	7	42	47
51-75	0	0	0
76-90	0	0	0
90	0	0	0

DISCUSSION

Enough antelope bitterbrush seeds germinate without germination enhancement to suggest that through hybridization and selection, plant breeders might be able to greatly increase germination and reduce the strict stratification requirements. This is a long-term project, but certainly should be included in programs to shift seed collection of these species from native stands to seed orchards.

There are many constraints on the seeding of moist, stratified seeds, both from a mechanical handling standpoint and from the biological requirements. Essentially, one can only seed prestratified seeds in a seedbed that is conducive to continued germination. This means that drilling would be limited to short periods of time when temperature and moisture conditions are satisfactory in seedbeds. These seedbed conditions would have to be predicted because of the time required for stratification and the loss of viability with prolonged stratification. Despite all these drawbacks, stratification is the only germination enhancement technique available for many species. Development of drills to handle moist seeds should continue.

If effective rodent repellents could be developed, fall seeding of bitterbrush and cliffrose seeds probably would be the most desirable alternative. Pesticide restrictions have greatly limited the potential materials for use as repellents, and one should remember that any time a chemical is placed in close proximity to a seed, there is a distinct possibility of influencing germination. Equally important with the development of repellent is the continued study of rodent-seed ecology. The complex interaction of rodents and antelope bitterbrush seeds is well known. We assume that a similar relation exists for desert bitterbrush and cliffrose seeds under natural conditions. An unexplored possibility for enhancing regeneration of these species is to manipulate rodent populations or artificially feeding seeds into the rodent caching cycle with or without subsequent control of rodents.

Hydrogen peroxide offers an alternative method of enhancing germination of the bitterbrush species. Stratification gives a better enhancement of germination than hydrogen peroxide, especially for cliffrose seeds. The advantages for hydrogen peroxide are a shorter treatment time is required and the seeds can be dried. If we understood the nature of germination enhancement from hydrogen peroxide treatments, it might be possible to perfect the methodology to increase germination enhancement.

Practically, thiourea, the ideal germination enhancer for bitterbrush seeds, is a dead issue. Virtually all State and Federal land management agencies have outlawed the use of this material.

In the final analysis, we know a great deal about the germination of bitterbrush and cliffrose seeds. We also know that a great deal of work is required to develop this knowledge into a form that adequately answers the problems land managers face in trying to revegetate rangelands with these species.

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Section 3. Successional Relationships



ANTELOPE BITTERBRUSH SEEDLING ESTABLISHMENT
FOLLOWING PRESCRIBED BURNING IN THE PUMICE ZONE
OF THE SOUTHERN CASCADE MOUNTAINS¹

Robert E. Martin²

ABSTRACT

Antelope bitterbrush (Purshia tridentata) seedling establishment was surveyed on 21 units two to eight growing seasons after burning. Bitterbrush seedlings occupied from one-quarter to five times as many of the plots as did old plants, and regeneration was related to seasons since burn, site quality, and livestock grazing. Records were kept of bitterbrush seedlings, seedling groups, stems per group, and height and diameter growth.

INTRODUCTION

Antelope bitterbrush (Purshia tridentata) is one of the most important browse plants for big game in the Northwest. Because it is often detrimental to bitterbrush, fire has been restricted in big game winter range areas. However, in considering the amount of bitterbrush in many areas, we must question the presumed detrimental effect of fire. Fire was a frequent visitor to much of the pine bitterbrush type in the southern Cascade Mountains. Weaver (1959), Soeriaatmadja (1966), Martin and Johnson (1979), and studies by the Bend Silviculture Laboratory³ show that fire in this area was as frequent as once every 5 to 15 years, with the period between fires increasing as we go to higher, wetter, and cooler sites. Some of the areas in this study were clearcut and burned in the 1920's, yet bitterbrush is the dominant understory plant in the young pine stands.

Because of the predominance of bitterbrush in these stands, it must have effective mechanisms for regeneration after fire (Driver and others 1980). Regeneration might come from seedlings or sprouts, and many factors might affect both means of reproduction (Martin and Driver, in this proceedings).

This study was conducted to evaluate regeneration, particularly seedlings, on 21 prescribed burns. The purpose of the study was to evaluate reestablishment of bitterbrush on prescribed fires the first few years after burning by answering the following questions: Is there a relationship between percent stocking and time? How regular is the establishment over time? What is the stocking as percent of

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³Unpublished data, Silviculture Laboratory, Bend, Oregon.

old plants? What are height and diameter over age? What is height to diameter ratio? Can we see effects of land management, such as grazing? What percent of old plants sprouted?

PREVIOUS WORK

Bitterbrush is often considered intolerant of fire, taking many years to reestablish on a site following fire. (An extensive discussion on the factors affecting bitterbrush reestablishment after fire is given in the Martin and Driver paper in this proceedings.)

Hormay (1943) reported that a stand of bitterbrush 2 to 3 ft (61 to 91 cm) tall can become established on a favorable site 15 years after burning. He also reported that cheatgrass (Bromus tectorum) can impede seedling establishment; thus fire is quite damaging to bitterbrush stands. Blaisdell (1950) found the number of bitterbrush plants 15 years after burning varied inversely with the "intensity" of burn, and even light burns still had only about two-thirds the production per acre of the unburned site. He felt that sprouting ability was important in a shrub's rapid recovery after fire.

Multiple stemmed bitterbrush groups grow somewhat faster than single stem plants (Ferguson 1962). Ferguson and Basile (1967) have reported that the increasing seedling numbers in each group (or seed spot) increases the chance of survival.

Nord (1965) and Weaver (1967) state that bitterbrush recovers very slowly following fire. Wright and Bailey (1982) use this to hypothesize that fire occurs only about once every 50 years in the ponderosa pine-bitterbrush type. However, Driver and others (1980) indicate that bitterbrush has mechanisms to recover quickly from fire on the eastern slopes of the Cascade Mountains in Washington through seedlings established on heavily burned areas or by sprouting from a lignotuber just below the groundline.

There seems to be no concurrence on the susceptibility of bitterbrush to fire. Different areas and fire situations seem to yield different responses.

METHODS

I selected 21 prescribed burning units for survey of bitterbrush regeneration. These units were at five locations that ranged from the Deschutes National Forest in central Oregon to Lava Beds National Monument in northeastern California (fig. 1) and were in various ponderosa pine (Pinus ponderosa)-bitterbrush communities. Units had been burned from two to eight growing seasons before sampling in July and August 1980.

An arbitrary point on the boundary of each unit was taken as a starting point. The second-hand of a watch was used to obtain a compass direction for a transect, using the reciprocal direction, if necessary. After moving a suitable distance into the burn unit to avoid edge effect, sample plots were taken at uniform distances along the transect (fig. 2). If we encountered the edge of the unit, we made an offset and took plots along a transect on the reciprocal bearing (fig. 2). Distances between plots varied from unit to unit, depending on unit size.

Plots were 39.37 inches (1 m) radius. Two types of plots were taken--yes/no plots and count plots. On yes/no plots the following data were taken:

1. Bitterbrush seedlings present or not
2. Old bitterbrush plants present or not
3. Old bitterbrush plants sprouting or not

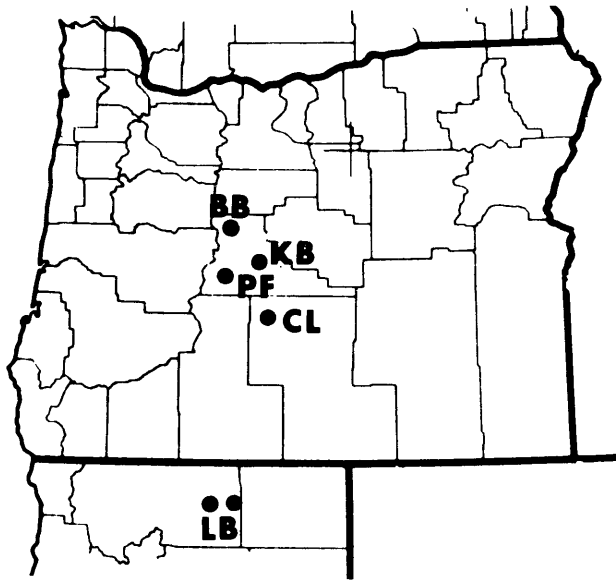


Figure 1.--Locations of burn blocks in central Oregon and northern California.

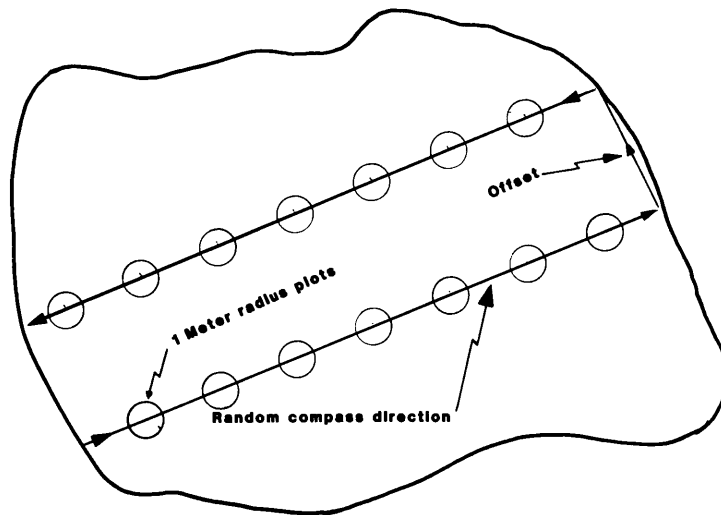


Figure 2.--Schematic of sampling system.

On count plots the following data were taken:

1. Number of bitterbrush seedling groups
2. Number of stems in each group
3. Distance from each seedling group to nearest tree and nearest old tree (>150 years)
4. Age of bitterbrush seedling
5. Height of bitterbrush seedling
6. Diameter of bitterbrush seedling
7. Number of old bitterbrush plants
8. Old bitterbrush plants sprouting or not.

Burning conditions and fuel consumption for each unit were available, but were used in only a general way in analysis. Other general information on units as well as site index and grazing pressure were recorded.

RESULTS AND DISCUSSION

Burn units varied from 0.2 to 50 acres (0.1 to 20 ha), and in site index at 100 years (table 1). The varying unit sizes could affect study results because of the differences in seed availability, rodent populations, grazing and browsing pressure, or microclimate.

Table 1.--Block characteristics of percent stocking, number of seedling groups, and number of stems per group for each location.

Burn location and block	Estimated site index	Date burned	Growing seasons since burn	Months since burn	Number of plots with old bitterbrush		Stocked plots Percent	New bitterbrush plants			Stems per seedling group			Plots new Plots old
					Percent	Percent		Number of groups	per plot	Range	X	S	Range	
Black Butte														
1	80	Oct. 1972	8	93	17	0	76	2.19	1.20	0-5	3.13	2.57	1-12	4.47
2	80	May 1973	8	86	87	1	75	5.13	2.77	0-11	2.72	2.39	1-12	.86
3	80	May 1974	7	74	12	0	69	1.78	0.94	0-5	2.90	2.70	1-11	5.42
4	80	Sept. 1975	6	58	88	12	72	4.32	2.51	0-11	2.17	1.72	1-9	.72
Pringle Falls														
Bob's corner														
1	78	May 1976	5	50	79	3	74	2.50	1.54	0-7	1.98	1.63	1-8	.94
2	78	Oct. 1977	4	33	84	2	90	3.63	2.08	0-9	3.74	3.78	1-15	1.05
3	78	Oct. 1977	4	32	39	0	34	3.50	1.97	0-8	4.39	5.90	1-33	.87
4	78	Oct. 1977	4	32	91	2	84	3.12	2.22	0-9	2.17	2.29	1-14	.90
5	78	Oct. 1977	4	32	91	1	74	1.74	1.44	0-6	3.20	3.96	1-21	.80
7	78	Oct. 1977	4	32	97	0	95	5.92	3.91	0-19	2.50	2.71	1-15	.98
Kelsey Butte														
A	75	March 1978	3	29	94	1	87	2.70	2.03	0-8	1.44	1.30	1-9	.92
E	75	May 1978	3	27	79	2	36	1.60	1.15	0-6	1.24	0.66	1-4	.44
Cabin Lake														
1	67	May 1976	5	52	93	0	32	1.50	0.91	0-5	2.10	2.59	1-12	.34
2	67	May 1976	5	52	98	0	36	1.10	0.31	0-2	5.41	4.33	1-14	.37
3	67	May 1976	5	52	89	0	9	1.33	0.71	0-3	2.00	1.76	1-6	.10
4	67	May 1976	5	52	93	0	10	1.30	0.48	0-2	3.08	3.50	1-13	.11
Lava Beds														
1 Upper Ice	78	June 1975	6	62	89	2	58	1.27	0.63	0-3	3.74	4.07	1-16	.64
2 Cave	78	August 1975	6	61	95	2	86	1.48	1.05	0-5	2.58	1.86	1-8	.91
3	78	Oct. 1975	5	59	78	23	40	1.67	0.96	0-4	4.09	3.63	1-15	.51
Caldwell	50	May 1977	4	39	90	10	26	1.07	0.41	0-4	1.07	0.27	1-2	.29
Black Lava Flow	78	June 1979	2	14	82	1	20	1.18	0.73	0-4	6.16	7.99	1-32	.24

Percentage of plots stocked with new bitterbrush plants ranged from 9 to 95 (table 1). Lowest stocking was recorded on the Cabin Lake burns, all of which have experienced heavy cattle grazing. The 5-acre (2.0 ha) burns are located in an area where no other fires have stimulated grass and forage production. Competition from grasses may also be a factor restricting bitterbrush reproduction (Hormay 1943). The Black Lava Flow burn, also low in stocking, had only 14 months between burning and sampling, which may account for its condition. It would probably restock at about the same rate as the three Upper Ice Cave burns, which are close by.

The Caldwell Butte burn at Lava Beds National Monument showed low seedling establishment but high sprouting. The site is quite dry, as indicated by the low site index, and only about 20 percent forested. Open areas with low fuel loading and lower interspecific competition probably account for the relatively high sprouting (Martin and Driver, this proceedings).

Perhaps more indicative of relative success in bitterbrush seedling establishment is the ratio of plots stocked with seedlings compared to those stocked with old plants--a percentage that ranges from 0.10 to 5.42 (table 1). The high percentages obviously come from units with low numbers of old plants and high numbers of seedlings. Any seedlings present before the burn would be missed in the counting, as there would be no postfire evidence of their presence. Generally, these would be relatively few, but would lower the table 1 ratio figures somewhat. Numbers of bitterbrush seedling groups per 33.8 ft² (3.14 m²) plot averaged from 1.07 to 5.92 in each unit, with an individual plot high of 19 (table 1).

Numbers of stems per seedling group also varied considerably, with units averaging from 1.07 to 6.16 and an individual plot high of 33 (table 1). The highest unit average was recorded on the Black Lava Flow burn, the most recent conducted.

Numbers of stems per seedling group tended to decline with the age of the seedling group, although the relationship was generally quite weak. Values of r^2 for regression of number of stems per group against age ranged from 0.1 to 0.73 in linear and polynomial regressions. In all except one of the 21 units, stems per seedling group was negatively correlated with age. This decline could result from both the death of individual stems in a group and the death of entire groups with large numbers of stems because of competition within the group.

Sprouting was generally low among the burn units (table 1). Upper Ice Cave 3 was burned late in the year with high fuel and soil moisture, which may account for the higher sprouting. Fuel consumption was low in the burn and did not cover the entire unit.

Analysis of variance indicates a highly significant difference ($P < 0.01$) among locations for plots containing bitterbrush seedlings (table 2). Calculations were made on all units and also after dropping two units at Lava Beds National Monument. The Black Lava Flow unit was dropped in the second analysis because it was burned only 14 months before counting and the Caldwell unit because it was of low site index and only about 20 percent forested. Further testing for individual differences among locations using the least significant difference technique (Steel and Torrie 1960) showed significant differences ($P < 0.05$).

<u>Location</u>	<u>Percentage of plots stocked</u>	
	<u>21 plots¹</u>	<u>19 plots^{1 2}</u>
Pringle Falls	75.17 ^a	75.17 ^a
Black Butte	73.00 ^{a b}	73.00 ^a
Kelsey Butte	61.50 ^{a b}	61.50 ^a
Lava Beds	46.00 ^{a b c}	61.33 ^a
Cabin Lake	21.75 ^c	21.75 ^b

¹Number followed by the same letter indicates no significant difference ($P < 0.05$).
²Black Lava Flow and Caldwell units were dropped.

Table 2.--Analysis of variance for plots stocked with bitterbrush seedlings in the five locations.

21 Blocks				
Among locations	4	8610.53	2152.63	4.49 ¹
Within locations	16	7184.14	449.01	
Total	20	15794.67		
19 Blocks (without Caldwell and Black Lava Flow)				
Among locations	4	7917.78	1979.44	5.13 ¹
Within locations	14	5402.75	385.91	
Total	18	13320.53		

¹Significant at 99 percent level of confidence.

Cabin Lake is different from all other locations when two units from Lava Beds are thrown out. This I attribute to cattle grazing and/or grass competition.

The regularity at which seedlings became established on different units also shows the reliability of regeneration following burning. In an attempt to assess this, I plotted cumulative regeneration percent against percent of seasons since burn (fig. 3a-d). Thus, a plot of 45° would indicate the regeneration had come in evenly over the years, as indicated by the diagonal line on each figure. Data from the Black Butte and Kelsey Butte units (fig. 3a) were mostly close to the 45° line, indicating regular annual regeneration over the years. The Pringle Falls units (3b) tended to have annual regeneration but lagged behind the line, perhaps indicating that many of each current year's seedlings are lost. On the other hand, both Cabin Lake and Lava Beds units (3c and d) had wide fluctuations from year to year in the cumulative regeneration. These units seem to have very good and very bad years for regeneration.

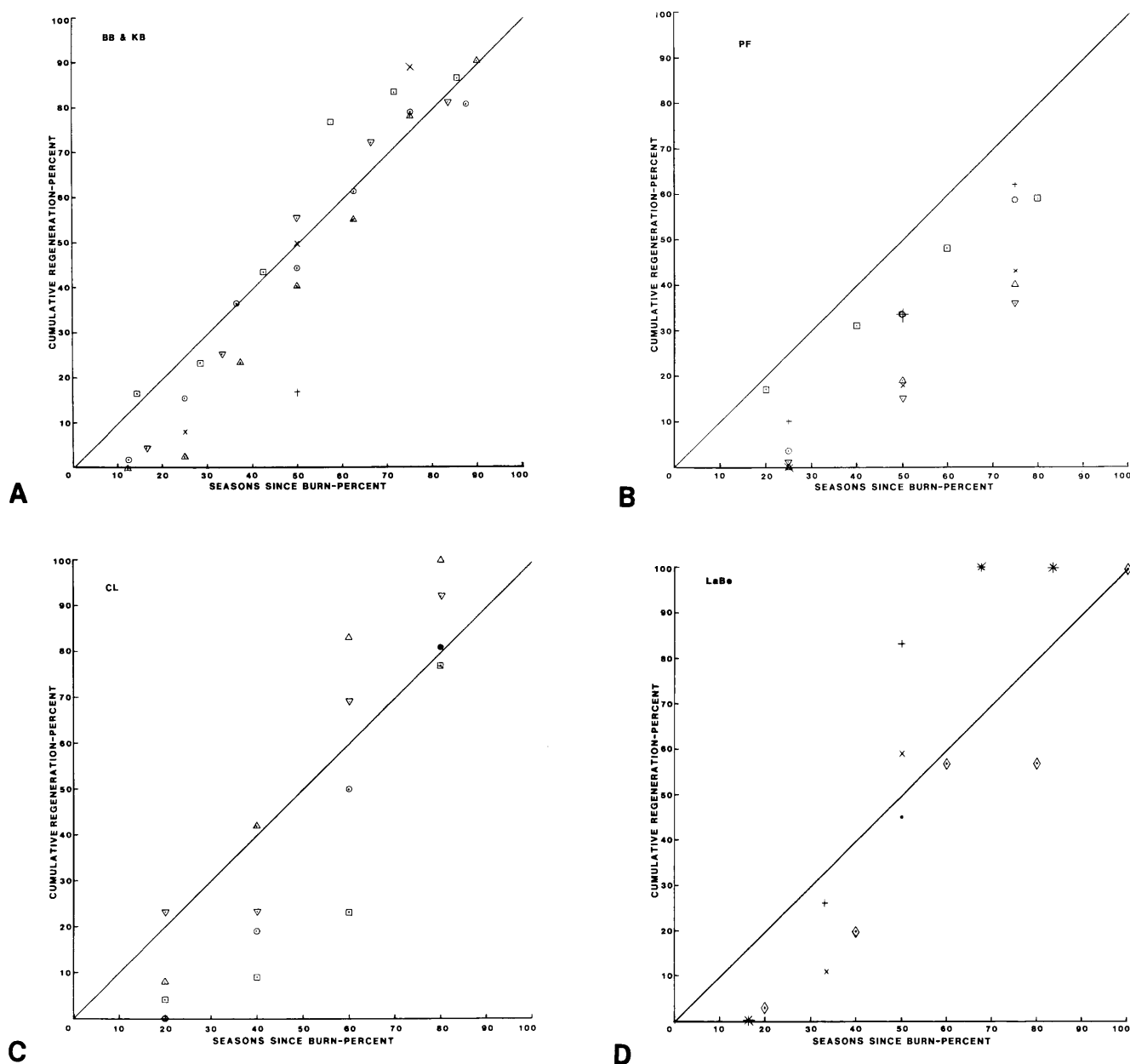


Figure 3.--Cumulative regeneration percent over percent of growing seasons since burn. Black and Kelsey Buttes (a), Pringle Falls (b), Cabin Lake (c), and Lava Beds (d).

To study the rate at which seedlings grow, I used several curve forms to regress height and diameter over age of seedlings (fig. 4 and 5). Curvilinear regression generally accounted for a little more of the variation than did linear regression, but so little was gained that the linear regressions are presented here. The regressions were not tested for significant differences, and there was great variability in the data. Values of r^2 for the regression of height over age varied from only 0.14 for Cabin Lake to 0.74 for Black Butte. In the regressions of diameter over age, r^2 ranged from 0.16 for Cabin Lake to 0.56 for Pringle Falls. All the regressions were highly significant ($P < .01$), and coefficients and F values are given in table 3. Using these figures I would expect bitterbrush plants (groups) to be 5 to 10 inches (12.5 to 25 cm) and 6 to 11 inches (15 to 28 cm) in diameter at 5 years of age, provided they are not extensively browsed. A plot of height/age versus the diameter/age lines indicates the plants (groups) on all units except the Pringle Falls unit to be about three-quarters as high as they are wide (fig. 6).

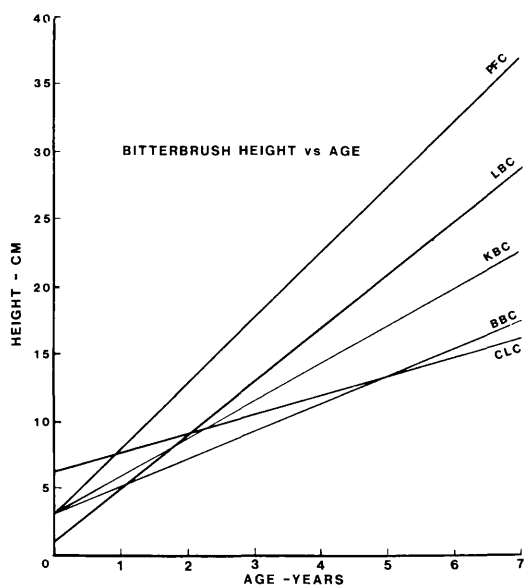


Figure 4.--Height of bitterbrush seedlings regressed over age. Low correlation has reduced the slope of all lines, but especially that of the Cabin Lake (CLC) regression.

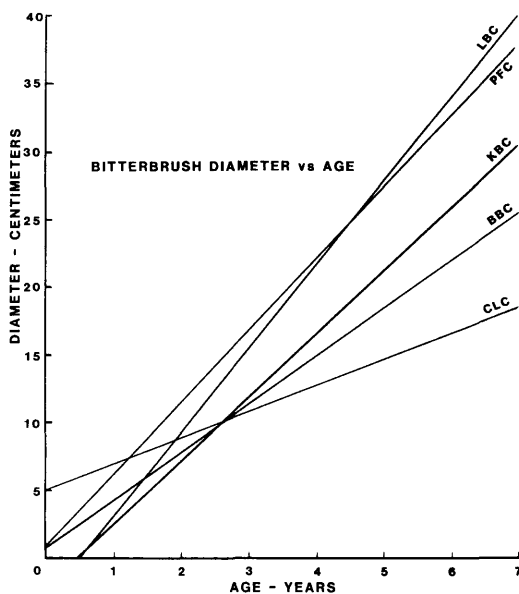


Figure 5.--Diameter of bitterbrush seedlings regressed over age. Cabin Lake had the lowest correlation, greatly reducing the slope of the regression.

Table 3.--Regression values for the highly significant linear regressions among diameter, height, and age of bitterbrush seedlings.

Location	Number observations	Intercept	Coefficient	R ²	F	S $\bar{x}$
<u>Diameter/age</u>						
Black Butte	290	.852	3.51	.55	349.0	5.63
Kelsey Butte	94	-2.28	4.67	.53	102.0	3.59
Pringle Butte	440	.885	5.26	.56	565.0	4.64
Cabin Lake	78	5.41	1.87	.16	14.6	4.82
Lava Beds	142	-3.14	6.16	.48	132.0	7.17
<u>Height/age</u>						
Black Butte	290	3.12	2.04	.55	357.0	3.24
Kelsey Butte	94	3.18	2.78	.36	52.5	2.99
Pringle Butte	440	3.19	4.86	.56	561.0	4.31
Cabin Lake	78	6.16	1.43	.14	11.9	4.08
Lava Beds	142	1.08	4.00	.46	117.0	4.93
<u>Height/diameter</u>						
Black Butte	290	3.64	0.499	.74	823.0	2.47
Kelsey Butte	94	5.38	0.449	.39	59.3	2.92
Pringle Butte	440	3.59	0.762	.68	59.3	3.69
Cabin Lake	78	6.21	0.319	.15	13.0	4.05
Lava Beds	142	4.29	0.557	.69	317.0	3.70

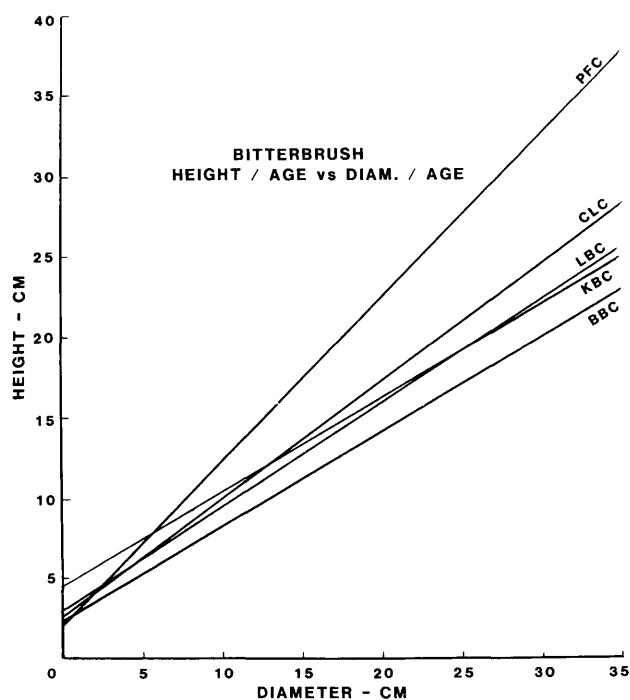


Figure 6.--A plot of height over age versus diameter over age from figures 4 and 5.

SUMMARY

Bitterbrush seedlings have become established rather quickly on prescribed burn units in ponderosa pine/bitterbrush communities in the southern Cascade Mountains of Oregon and California. These extensive communities are important as a game food source. Sprouting of old bitterbrush was generally low, and might be attributed to any of several factors such as plant age, stress from competition, fuel loads, low soil moisture, and burning conditions. The rapid establishment of seedlings would indicate that bitterbrush can regenerate by this means in ponderosa pine stands in pumice regions of the southern Cascade Mountains following fire. Use of fire in these stands could help develop a mosaic of vigorous young bitterbrush in mixture with older plants, perhaps enhancing wildlife habitat.

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THE ECOLOGY OF SHRUBS IN BRYCE CANYON NATIONAL PARK

WITH SPECIAL REFERENCE TO PURSHIA TRIDENTATA¹

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ABSTRACT

Shrubs contribute more cover than either forbs or graminoides in the forests of Bryce Canyon National Park. Purshia tridentata reaches maximum abundance in the ponderosa pine forests and declines steadily with increasing elevation. Purshia is the major understory species in the low elevation forests. The study covers mortality and establishment rates in six forest types over a 21 year period.

INTRODUCTION

Bryce Canyon National Park is in Garfield and Kane Counties, southcentral Utah. Elevation ranges from 7,915 ft (2,412 m) at park headquarters to 9,105 ft (2,777 m) at Rainbow Point, the highest spot in the park. Geology in the area is dominated by the rather soft Wasatch limestone that has eroded along the edges of the plateau to produce spectacular pink pinnacles and badlands that are the major scenic attractions of the park. Precipitation at headquarters averages about 15.9 inches (40 cm) annually (Eubank and Brough 1979). Precipitation is about equally distributed throughout the year with 25 percent in the January to March period, 22 percent in April to June, 33 percent in July to September, and 20 percent in the October to December interval. Mean annual temperature averaged 41.0°F (5°C) for the 1916-75 interval: January temperatures averaged 21.6°F (-5°C), while July had an average temperature of 62.9°F (17°C) (Eubank and Brough 1979). Deep snowpacks accumulate on the plateau in winter: April 1 water content of snowpacks at headquarters averaged 4.3 inches (11 cm), while water content of snowpacks at Rainbow Point averaged 8.7 inches (22 cm) (Whaley and Lytton 1979).

Although total annual precipitation is unknown for any location other than at headquarters, two general studies relate precipitation to elevation in Utah mountains. Lull and Ellison (1950) showed that annual precipitation in Ephraim Canyon on the Wasatch Plateau (central Utah) increased about 4.9 inches/1,000 ft (12.5 cm/305 m) rise in elevation. Harper and others (1981) reported a 3.0 inches (7.6 cm) increase in precipitation per 1,000 ft (305 m) rise in elevation in the Uinta Mountains of northeastern Utah. Assuming that the relationship between elevation and precipitation at Bryce Canyon National Park is similar to that observed elsewhere in the state, annual precipitation at Rainbow Point probably averages somewhere between 19.5 and 21.8 inches (49.5 and 55.4 cm).

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OBJECTIVES

The principle objective of this paper is to document the density of Purshia tridentata (bitterbrush) in various forest types within Bryce Canyon National Park for the intervals 1957-59 and 1978-80. The data base permits us to describe mortality and establishment rates for that species in six forest types over a 21 year period. We also provide information on associated shrubs, because such data should help managers to put the bitterbrush data into proper ecological perspective.

METHODS

Our report is based on 223 permanently marked study plots sampled in the summers of 1957-59 by Buchanan (1960) and sampled again in 1978-80. At each study plot, a 10.76 ft² (1.0 m²) quadrat was established to sample herbs and shrubs. Trees and tree reproductions at each plot were sampled using the quarter method of Cottam and Curtis (1956). A marking peg at each 10.76 ft² quadrat was used as the point from which quarter method distances were measured. All perennial plants in each quadrat were mapped onto gridded paper using a metal frame with 16 equal-sized subsections. About one-third of the study plots were photographed in the initial and again in the later sample.

The sampling points were spaced approximately 300 ft (91 m) apart on a transect that ran along the top of the plateau and nearly the entire length of the park. Direction of the transect was occasionally altered as it encountered park boundaries or edges of the plateau. Compass bearings along each leg of the transect were recorded; distance between plots was measured with a surveyor's chain. The transect began near Rainbow Point and terminated near the park boundary about 1 mile (1.61 km) north of Fairyland View point and some 3 miles (4.83 km) northeast of headquarters. In addition to vegetational characteristics, slope steepness and direction of slope exposure were also recorded at each sampling point. Elevations at sampling points were taken from topographical maps.

After data from the second sample were in hand, individual sampling points were assigned to one of six general forest types based on composition of the tree layer at each point. Finally, several sampling points within each forest type were randomly chosen for analysis for soil depth and other characteristics: those samples were taken in summer of 1981. Soil depth was estimated with a thin (0.39 inch, 1.0 cm) diameter steel rod fitted with a handle at right angles to its length. The sharpened, 3.28 ft (1 m) long rod was pushed into the soil until it struck material that the worker could not penetrate. Five depth samples were taken at each point, one at the center and one in each corner of the 10.76 ft² quadrat. Twelve subsamples of the surface 6 inches (1.52 dm) soil (litter layer removed) were taken at each sampling point with a tube sampler. Subsamples were uniformly distributed within the area delimited by the four trees sampled by the quarter method; subsamples were composited for analyses.

RESULTS

We recognized the following forest types at Bryce Canyon: Pinus ponderosa - Juniperus scopulorum (PIPO-JUSC), Pinus ponderosa - Pseudotsuga menziesii (PIPO-PSME), Pinus ponderosa - Abies concolor (PIPO-ABCO), Pinus flexilis (PIFL), Pseudotsuga menziesii - Abies concolor (PSME-ABCO), and Abies concolor (ABCO). Pinus ponderosa - Juniperus scopulorum forest dominated gently rolling, lower elevation sites, while Abies concolor was either the dominant or a successional aggressive species on higher elevation sites. Such sites also tended to be on steeper slopes than those that supported PIPO-JUSC forests (table 1).

Table 1.--General environmental conditions in six forest types at Bryce Canyon National Park. Forest types are identified by major tree dominants. Abbreviations used for trees in this and subsequent tables are as follows: Abies concolor (ABCO, white fir), Juniperus scopulorum (JUSC, Rocky Mt. Juniper), Pinus flexilis (PIFL, limber pine), Pinus ponderosa (PIPO, ponderosa pine), and Pseudotsuga menziesii (PSME, Douglas fir). All values reported are based on the sample sizes reported at the bottom of the table except for soil depth, which was based on sample sizes of 14, 7, 14, 28, 11, and 12 (left to right among forest types). The same letter in superscripts denotes means that do not differ significantly (P .05).

	Forest types					
	PIPO- JUSC	PIPO- PSME	PIFL	PSME- ABCO	ABCO	PIPO- ABCO
Ave. elevation (m)	2,437 ^a	2,519 ^b	2,600 ^c	2,626 ^{cd}	2,640 ^d	2,651 ^{de}
Ave. slope (%)	13.6 ^a	24.6 ^{bc}	26.3 ^b	18.4 ^d	18.0 ^d	17.7 ^{acd}
Ave. exposure	1.2 ^{ade}	0.8 ^{bc}	0.7 ^b	1.0 ^{ac}	1.5 ^d	0.9 ^{ce}
Ave. soil depth (cm)	36.5 ^a	25.1 ^{bc}	34.5 ^a	31.1 ^{ab}	39.5 ^a	21.6 ^c
Biotic characteristics in 1980 and (1959)						
Trees/ha	178 (84)	163 (101)	312 (221)	676 (300)	682 (436)	262 (138)
Saplings/ha	155 (102)	256 (114)	448 (191)	961 (516)	1,281 (680)	646 (202)
Living cover (understory)						
Forbs (%)	11.6 (11.9)	3.0 (5.0)	3.5 (3.0)	4.8 (5.8)	3.0 (3.0)	7.5 (8.0)
Grasses (%)	4.7 (5.3)	2.0 (4.0)	1.0 (1.0)	2.5 (4.1)	2.0 (3.5)	3.0 (7.0)
Shrubs (%)	11.7 (13.7)	12.0 (17.0)	13.5 (22.0)	8.0 (17.3)	3.0 (5.5)	12.5 (21.0)
Total understory cover (%)	28.0 (30.9)	17.0 (26.0)	18.0 (26.0)	15.3 (27.2)	8.0 (12.0)	23.0 (36.0)
No. plots/type	72	16	29	72	19	15

¹Exposures are coded according to a scheme suggested by Beers and others (1966): in that scheme, southwesterly slopes receive a value of 0.0, while northeasterly slopes are assigned a value of 2.0. Generally speaking, the larger the value, the cooler the site, all other things being equal.

Purshia tridentata achieved maximum abundance in the PIPO-JUSC forests at the lowest elevations (table 2). Purshia tended to become less important as elevation increased; the species was either absent or performed poorly in forests where Abies concolor was capable of doing well. Although bitterbrush occurred in 20 percent of the study plots of the PIPO-ABCO forest type that occupies shallow soils at the highest elevations (table 1), the population there suffered 33 percent mortality over the 1959-80 period and was unable to establish any new plants (table 2).

Purshia population densities declined in all forest types over the study period (table 2). Average density loss for the five forest types that had bitterbrush in 1957-59 was 35.9 percent in 20 years. Density losses were low in the PIPO-JUSC forests (21.4 percent) and maximal in the PSME-ABCO community (100.0 percent). Mortality was high in the limber pine forests too, but there, recruitments equalled mortality to give zero change in density (table 2). In general, mortality increased and recruitments declined with elevation.

Table 2.--Density (individuals/10 m²) of various shrub and subshrub species in the forests of Bryce Canyon National Park in 1980. Additional parameters for Purshia tridentata populations are given at the bottom of the table. An asterisk denotes a species that retains the bulk of its foliage during the winter (evergreen).

Species	PIPO- JUSC	PIPO- PSME	PIFL	PSME- ABCO	ABCO	PIPO- ABCO
<u>Artemisia nova</u> *	1.0	.0	.0	.0	.0	.0
<u>Arctostaphylos patula</u> *	3.6	8.1	5.5	2.5	.0	2.7
<u>Berberis repens</u> *	7.5	12.5	12.8	21.2	14.4	13.3
<u>Ceanothus martini</u> *	.8	2.5	1.7	.6	.0	.7
<u>Chrysothamnus depressus</u> *	16.7	3.8	5.9	4.2	.0	25.3
<u>Pachystima myrsinites</u> *	2.2	7.5	7.2	11.8	15.9	28.7
<u>Petradoria pumila</u>	.0	.0	.0	.7	.0	11.3
<u>Purshia tridentata</u>	6.1	1.9	1.4	.0	.0	1.3
<u>Rosa woodsii</u>	.4	.0	3.4	.6	.5	1.3
<u>Symphoricarpos oreophilus</u>	.7	4.4	6.9	7.6	1.1	3.4
<u>Tetradymia canescens</u> *	.8	.0	.0	.0	.0	.0
<u>Xanthocephalum sarothrae</u>	2.8	.0	.3	.0	.0	4.7
Other <u>Purshia</u> parameters						
Frequency (% in m ² quadrats 1959)	40.3	25.0	17.2	6.9	.0	20.0
Mortality (% from 1959-80)	39.3	50.0	100.0	100.0		33.3
Recruits (No./10 m ²)	1.4	.6	1.4	.0	.0	.0
Density change (% from 1959-80)	-21.4	-25.0	.0	-100.0		-33.3

The principle shrubs associated with Purshia in those forest types where it performed best were Arctostaphylos patula, Berberis repens, Chrysothamnus depressus, and Xanthocephalum sarothrae. Other species such as Pachystima myrsinites, Rosa woodsii and Symphoricarpos oreophilus occurred infrequently with Purshia but achieved best development at higher elevations than that species (table 2).

Although Purshia is a winter deciduous species, most of the shrub individuals in these forests are evergreen. Over 70 percent of the shrub or subshrub individuals were evergreen in all six of the forest types (table 2). Of the shrub individuals, 95 percent were evergreen in the most dense (and presumably darkest) forest type (white fir). The success of so many evergreen shrub species in the understory of the Bryce Canyon forests suggests that the characteristic has some adaptive value there. We will return to the question of possible adaptiveness of evergreen leaves.

Over the 21 years of observation, average understory cover declined in all six of the forest types (table 1). The average decline across all forest types was 31.3 percent. Cover of all lifeform groups in the understory declined, but grasses and shrubs declined much more than forbs (table 1). Overall, forbs declined about 9 percent in relative terms, but grasses (39 percent) and shrubs (37 percent) declined over four times faster. Undoubtedly, the declines were strongly influenced by the great increases in forest density and attendant shading: in 21 years, density of trees and saplings roughly doubled on the average in Bryce Canyon forests (table 1). Nevertheless, photographs taken in the initial and the 1978-80 sample demonstrate that many shrub individuals died and left no replacements even in quadrats not overshadowed by trees or saplings.

Although Cowania, the other Rosaceous shrub focused in this symposium, did not occur in our samples, we have compared soil physical and chemical parameters in the forest zone of best development of Purshia in this study with similar parameters in stands that support Cowania mexicana var. stansburiana in central Utah (table 3). Purshia is shown to occur on deeper, better developed and more fertile soils than Cowania (table 3). The smaller rooting volume (soil depth) at Cowania sites would be expected to magnify the differences noted for Cowania and Purshia sites in respect to amounts of essential nutrients per unit weight of soil. Our field experience suggests that these results are probably broadly representative for habitats occupied by these species throughout Utah. Cowania is often on rocky outcrops or coarse gravels, while Purshia seems to prefer better developed soils. These closely related species thus appear to have diverged along at least edaphic and climatic gradients. Modern distribution patterns suggest that Purshia is more tolerant of cold winters and dry summers than Cowania.

DISCUSSION

Major changes have occurred in the Bryce Canyon National Park forests during the 21 years of our study. Forests have become more dense and natural succession has altered their composition³. Those changes have been associated with less dramatic, but nevertheless large changes in the shrub layers of the forest understories. We have considered response of only Purshia tridentata here. The data provide many insights into ecological principles bearing on management of that species.

Our data show that bitterbrush in Bryce Canyon is most competitive at elevations below 8,200 ft (2,500 m). Although it did occur above those elevations at the park, it failed to perform well there: mortality was high -- an average of 71 percent above 8,200 ft as opposed to 39 percent below that elevation; and recruitments were low -- 1.30/100 ft² below and 0.46/100 ft² above 8,200 ft. Ream's (1963) data for species abundance in 25 northern Utah mountain communities support

³ Buchanan, H. and K. T. Harper. Successional dynamics of the forests of Bryce Canyon National Park, Utah. Unpublished manuscript.

Table 3.--Soil characteristics in the ponderosa pine-juniper forest type at Bryce Canyon National Park and in the Cowania mexicana var. stansburiana community in central Utah (data from Price and Brotherson, in press). Means of each value are followed by their standard deviation. The same letter in superscript denotes means for any given parameter that do not differ significantly (P .05)

	<u>Purshia</u> (PIPO-JUSC type)		<u>Cowania</u>	
Soil depth (dm) ¹	3.65 ^a ±	1.04	1.79 ^b ±	0.74
Soil texture				
Sand (%)	36.3 ^a ±	7.5	53.6 ^b ±	13.9
Silt (%)	33.1 ^a ±	7.3	27.9 ^a ±	8.5
Clay (%)	30.6 ^a ±	4.2	18.3 ^b ±	7.5
pH	8.2 ^a ±	0.1	7.7 ^b ±	0.4
"Available" phosphorus (ppm) ²	10.2 ^a ±	14.6	12.8 ^a ±	3.8
Exchangeable				
Calcium (%)	.91 ^a ±	0.23	0.58 ^b ±	0.09
Magnesium (%)	.08 ^a ±	0.02	0.02 ^b ±	0.01
Potassium (ppm)	242.0 ^a ±	161.0	176.0 ^a ±	102.0
Sodium (ppm)	50.0 ^a ±	16.0	97.0 ^a ±	121.0
Sample Size	8		10	

¹Actually soil penetrability with a thin probe. Sample size for this parameter at Bryce Canyon was 14.

²On Bryce Canyon soils, phosphorus was extracted with 0.2 N acetic acid, while in the Cowania study, the extractant was sodium bicarbonate. The former extractant usually frees more phosphorus than the latter on common soil samples.

our observations at Bryce Canyon. He found Purshia in greatest abundance below 6,250 ft (1,900 m) and lacking completely as a significant member of the vegetation above 7,400 ft. Since Ream's (1963) data were taken about 4° farther north, one would expect the species to perform best at lower elevations there than at Bryce Canyon.

Our data suggest that bitterbrush's ability to establish in marginal habitats must be heavily influenced by ephemeral, local conditions. Although the species had once established itself above 7,400 ft at Bryce Canyon, high mortality and poor reproduction suggest that it will not persist in those forest types. Since there is little evidence for significant climatic changes in the Bryce Canyon area during the past half century (McNulty 1947), we conclude that establishment of the species at the higher elevation sites must have been favored by past disruptions of the vegetative cover. Data summarized elsewhere suggest that ground fires and abusive grazing by domestic livestock in the early part of this century probably kept forests at Bryce open and less dark than at present³.

Others have earlier noted the decline of bitterbrush populations across Utah. As early as 1947, McNulty (1947) described a widespread failure of bitterbrush stands to reproduce in the state. McNulty (1947) blamed the poor reproductive success exclusively on overuse by grazing animals. Our data implicate another cause (community succession) for population declines in bitterbrush populations, even though ungulate grazers may also have been involved.

We tested McNulty's (1947) hypothesis of grazing pressure (domestic and wild ungulates) as the cause for population decline in bitterbrush. Because domestic grazers have been excluded from the park since about 1937 (see footnote 3), we confined our attention to mule deer, the only hooved grazing animal remaining there. The data show (table 4) that deer herd sizes in the area have apparently declined throughout the period 1957-80. Harvest rates from other herd units of Utah for the period 1966-72 were 2.05, 2.63, 3.70, 5.48, and 8.56 animals/km² of summer range (North Book Cliffs, Pine Valley Mountains, Elk Ridge, LaSal Mountains, and Blue Mountain herd units respectively)⁴. In comparison, harvest rates for mule deer were 2.79 (unit 50) and 1.85 (unit 60) animals/km² of summer range/year from 1961 to 1965, a period of heavy harvests for our study areas. Therefore, deer populations were not unusually large during the period when bitterbrush populations were declining in the park. Declining hunter success through the years also suggests declining deer populations (table 4). Admittedly, such data are difficult to interpret because grazing stress is the result of an interaction between number of grazers and number of available plants per unit area. Nevertheless, it seems likely that grazing pressure alone is not responsible for the observed decline in bitterbrush populations at Bryce Canyon National Park.

Table 4.--Number of mule deer harvested from herd units that surround or lie close to and have habitats similar to those at Bryce Canyon National Park. Unit 50 (Antimony) lies due north of the Park, and unit 60 (Paunsagunt Plateau) includes but has most of its area to the west of the Park. Data are averaged by 5-year intervals for 1951-80 for both units. For a time, unit 60 was subdivided to produce 60B. We combined results for those subunits for the years of their existence. Percent hunter success in the regular season (special hunts ignored) is also reported for the same intervals used for harvest data). Data are from Utah Division of Wildlife Resources (1960-81) reports.

Time interval	Herd unit				Type of hunt
	50		60		
	Harvest	% success	Harvest	% success	
1951-55	998	89.0	282	NA	Either sex
1956-60	1631	70.4	1429	83.4	Either sex
1961-65	1619	67.2	1988	59.7	Either sex
1966-70	613	68.2	743	55.0	Either sex
1971-75	569	46.6	525	39.4	Either sex 1971-73; buck only 1974 on
1976-80	219	31.6	209 ¹	24.8	Buck only

¹ area partially closed in 1980.
NA = data not available.

Mooney and Gulmon's (1982) considerations relative to leaf duration have relevance to this study in two ways. Their work suggests that the prevalence of evergreen-leaved shrubs at Bryce Canyon may be related to the uniform distribution of precipitation throughout the year and/or to low availability of phosphorus, a

⁴ Pederson, J. C. and K. T. Harper. Does summer range quality influence sex ratios among mule deer fawns in Utah? (In press).

critical element for plant growth (table 3). Also, full consideration of the comparative ecology of Purshia tridentata and Cowania mexicana var. stansburiana must include evaluation of the consequences of their difference in leaf duration. If Mooney and Gulmon's (1982) conclusions are broadly applicable, one would predict that bitterbrush (deciduous) should have higher photosynthetic rates and faster growth than its evergreen-leaved relative, Cowania. Their generalizations also suggest that the leaves of the former species should have higher protein levels and be more palatable to herbivores. Leaf duration may explain why bitterbrush has extended its range far into the summer-dry Great Basin and Pacific Northwest, while Cowania's range and abundance patterns are well correlated with the summer rain zone of the Southwest. Those observations conform to expectations suggested by the Mooney-Gulmon hypothesis relative to leaf duration: one would expect the evergreen species to perform best where the moisture supply was more uniform. The different edaphic preferences of these two shrubs also fit expectations for deciduous and evergreen taxa, with the evergreen species occurring where nutrients are more limiting.

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RESPONSE OF THE BITTERBRUSH UNDERSTORY OF A CENTRAL OREGON

LODGEPOLE PINE FOREST TO LOGGING DISTURBANCE¹

Paul J. Edgerton²

ABSTRACT

Logging and slash disposal caused extensive soil disturbance and physical damage to the bitterbrush understory. After 5 years, substantial recovery had occurred due to increased twig growth of surviving shrubs and establishment of shrub seedlings on disturbed soils. Apparent increases in herbaceous species added needed diversity to the forage resource.

INTRODUCTION

Lodgepole pine (*Pinus contorta* Dougl. ex Loud)³ forests of the pumice soil region of central Oregon are important summer range for mule deer (*Odocoileus hemionus hemionus*) and livestock. Antelope bitterbrush (*Purshia tridentata* [Pursh] DC.) dominates the understory over much of the area and is the major forage species (Stuth 1975). Advances in wood processing technology have resulted in the acceleration of timber harvest in these forests. Because the pumice soils are easily disturbed, land managers need a better understanding of the impact of logging on the understory in order to develop appropriate management strategies that will maintain or enhance the forage resource.

Bitterbrush response to logging disturbance has been studied on a timber sale on the Pringle Falls Experimental Forest in Oregon. Purpose of the study was (1) to determine the extent of soil disturbance and reduction of the shrub understory, and (2) to document subsequent understory recovery due to growth response of surviving shrubs and the establishment of new shrubs and herbaceous plants. An earlier paper (Edgerton and others 1975) reported initial disturbance and understory response. To further document understory recovery, this paper compares those data taken 2 years after disturbance with data collected at 5 years.

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³Sources for scientific nomenclature are Little (1953), Hitchcock and others (1955-1969), and Ingles (1965).

STUDY AREA

The study was conducted approximately 40 mi (64 km) southwest of Bend, Oregon. Elevation is 4,300 ft (1 310 m). Precipitation averages 20 inches (50.8 cm) annually, occurring mostly as winter snowfall. Frosts are common during the short growing season.

Soils and vegetation are characteristic of much of the level to gently rolling plateau. Soils are Typic Cryorthents, belonging to the Lapine series formed on pumice ejected from Mt. Mazama about 6,500 years ago. They are primarily composed of easily disturbed sand and pumice gravels, variable in depth, and underlain by buried soil (Cochran and others 1967). Lodgepole pine occurs in extensive, nearly pure stands on flats and in shallow depressions where it is the topographic climax species (Berntsen 1967). Youngberg and Dahms (1970) identified several forest types dominated by lodgepole pine with lodgepole pine/bitterbrush the most extensive. According to Volland's (1976) more detailed classification of plant communities of the pumice zone, the study area is best described as lodgepole pine/bitterbrush/forb. Other common understory plants include western needlegrass (*Stipa occidentalis* Thurb. ex Wats.), bottlebrush squirreltail (*Sitanion hystrix* [Nutt.] J. G. Sm.), Ross sedge (*Carex rossii* Boott), and least lupine (*Lupinus lepidus* Dougl.).

The study was conducted in three adjacent cutting units, 396 ft by 2,640 ft (121 m by 805 m) in size, separated by unlogged forest. The units are level and prior to logging supported a lodgepole pine forest relatively uniform in size and density. A diameter-limit harvest of trees 9 inches (23 cm) diameter at breast height (dbh) and larger reduced stems by 67 percent and basal area 78 percent. Logged stands averaged 114 trees per acre (282 per ha) with 20.5 ft² (4.7 m²) basal area. Adjoining unlogged stands averaged 339 trees per acre (837 per ha) with a basal area of 91.3 ft² (21.0 m²).

Logging and slash disposal occurred between 1969 and 1971. Most logs were yarded by rubber-tired skidders, but a D-4 crawler tractor was also used. Slash was piled by TD-6 and D-8 tractors with brush blades and burned on two units in 1970 and on the remaining one in 1971.

METHODS

Prior to logging, nine randomly located 100-ft (30.5-m) line transects were established in each unit and marked inconspicuously to minimize their influence on the operation of logging equipment. Ground disturbance caused by logging and slash disposal was estimated in November 1972 using the line interception method (Canfield 1941). Changes in bitterbrush crown area were measured by the line intercept method in November 1967, before logging, and in 1972 and 1975, 2 and 5 years after logging and slash disposal.

Comparative growth response of surviving shrubs was determined from linear measurements of current twig growth on randomly chosen secondary branches on 30 mature shrubs in each logged and adjoining unlogged stand. Measurements were taken at the end of the growing season and did not include lateral spur growth less than 0.4 inch (1 cm) in length.

Changes in bitterbrush density and age structure were determined from counts of shrubs on 27 circular plots, each 100 ft² (9.3 m²). The plots were systematically located in each logged unit and adjoining unlogged stand. Groups of young plants that likely had emerged from rodent caches were counted as single plants and care was taken to minimize errors due to layered and multiple stems commonly found in mature bitterbrush. Two years after logging, shrubs were classified as seedlings 1 to 3 years old, and ≥ 3 years. At 5 years, they were classified as current seedlings or established plants.

The data were studied using analyses of variance comparing (1) crown area before logging versus 2 and 5 years after logging, (2) twig growth in logged versus unlogged stands, and (3) shrub densities and age in logged versus unlogged stands at 2 and 5 years.

Lodgepole pine regeneration was surveyed on 27 circular plots, each 436 ft² (40.5 m²). These plots were systematically located in each logged unit. Additional data were taken to describe the development of associated understory vegetation. Percent canopy coverage of herbaceous species and other shrubs was estimated according to the technique described by Daubenmire (1959). Three transects of 30 plots, each 12 by 23 inches (30.5 by 58.4 cm), were randomly located perpendicular to the long axis of each logged unit and adjoining unlogged stand.

RESULTS AND DISCUSSION

The initial impact of logging and slash disposal on the soil and understory vegetation was severe and extensive: 90 percent of the ground surface was disturbed, of which 78 percent was classified as moderate (< 3 inches or 7.6 cm deep) or heavy (> 3 inches or 7.6 cm deep) disturbance (table 1). Average bitterbrush crown area (table 2) was reduced from 15.1 percent before logging to 4.3 percent 2 years after logging, a relative change of 72 percent.

Slash piling with a blade apparently caused more soil disturbance and shrub damage than did log skidding. Although skidding partially damaged shrubs, many survived. Slash piling, however, churned soils as deep as 12 inches (30 cm) in the piles and on fire lanes circling them, causing most shrubs to be broken, uprooted, or buried.

Fortunately postlogging recovery of the shrub understory has been equally dramatic. Logging created a favorable environment for more vigorous growth of surviving shrubs as well as the germination and establishment of new shrubs. Intercept measurements showed that crown area increased significantly ($P < 0.05$) from 2 to 5 years after disturbance to equal prelogging values.

Increased twig growth made an important contribution to recovery. Current annual twig growth of surviving shrubs in logged units significantly ($P < 0.05$) exceeded that of unlogged units both 2 and 5 years after logging (table 3). Surviving shrubs in the logged areas also appeared to be more vigorous and produced more twigs. In a similar plant community, Stuth and Winward (1976) reported that terminal and lateral leaders accounted for 71 percent of shrub production in logged areas, while short spurs produced more than one-half of the current production in adjoining unlogged stands. The fact that mule deer and livestock prefer leaders and seldom utilize spur growth (Stuth 1975) underscores the potential forage contribution of logged areas.

Table 1.--Ground disturbance due to logging and slash disposal

Disturbance class	Description	Percent of area in this condition
None	No disturbance	8
Light	Litter displacement only	12
Moderate	Soil disturbed < 7.6 cm	32
Heavy	Soil disturbed > 7.6 cm	46
Slash	Debris > 7.6 cm diameter	2
All classes		100

Table 2.--Changes in bitterbrush crown area following logging disturbance

Logging unit number	Prelogging	Crown area	
		2 years	5 years
		<u>Percent</u>	
1	14.9	3.7	21.7
2	14.8	3.8	20.4
3	15.5	5.4	18.2
Average	15.1	4.3	20.1

Table 3.--Current annual growth of bitterbrush twigs in logged versus unlogged lodgepole pine stands 2 and 5 years after logging

Logging unit number	Twig length			
	Logged		Unlogged	
	2 years	5 years	2 years	5 years
	<u>mm</u>			
1	69.2	80.0	35.6	46.1
2	68.4	70.9	38.8	43.0
3	81.1	73.4	30.8	41.7
Average	72.9	74.8	35.1	43.6

Rapid establishment of new shrubs, primarily on moderately and heavily disturbed soils, is reflected in shrub population densities shown in table 4. Just 2 years and subsequently 5 years after loss of 72 percent of the understory, shrub densities of logged and unlogged stands were not significantly different ($P > 0.05$), but there were significant differences ($P < 0.01$) in age structure. Logging converted an older mature stand to one dominated by younger plants. These understory changes are apparent in the photo comparison in figure 1. Shrubs established since logging accounted for nearly 70 percent of bitterbrush in logged stands but less than 10 percent in unlogged stands.

Table 4.--Bitterbrush density per hectare in logged and unlogged lodgepole pine stands

Age class	Unlogged	Logged	
		<u>Years after logging</u>	
		2 years	5 years
Current seedlings	1,274	1,593	2,868
Established since logging	2,048	13,827	19,577
Established before logging	20,421	5,641	5,641
All shrubs	23,743	21,061	28,086

Shrub densities exceeding 8,000 per acre (19,760 per ha) found in this study may seem unusually high. On most shrub-steppe ranges, 500 to 2,000 shrubs per acre (1,235 to 4,940 per ha) are considered adequate stocking (Hubbard 1962). Shrubs in these forest communities, however, are small in stature and many of those beneath the lodgepole canopy appear suppressed and low in vigor. Stanton (1959) reported comparable densities in similar lodgepole communities near La Pine, Oregon.

Successful recovery of the shrub understory in these forests depends on the number, size, and condition of surviving shrubs as well as the extent of soil disturbance and environmental conditions created by logging. Stuth and Winward (1976) noted that shrubs 8 to 16 inches (20 to 40 cm) in height had a higher survival rate and better growth response than did smaller plants. Shrubs taller than 16 inches (40 cm) were more easily damaged and didn't respond well to environmental changes. A good distribution of large plants, however, was suggested to maintain seed production for regeneration. Size of surviving shrubs was not measured in this study, but a wide range of size classes was observed. Ample regeneration is evidence of adequate seed production.

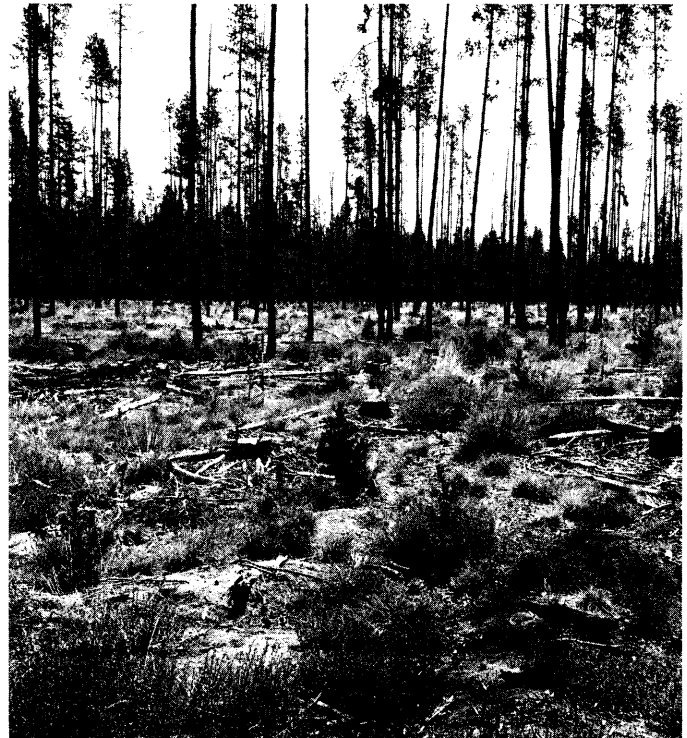
Environments of the logged units during the initial two seasons following disturbance apparently were conducive not only to seed production but also to subsequent germination of rodent caches and seedling establishment. The partial tree canopy remaining probably ameliorated harmful minimum growing season temperatures that commonly occur in clearcuts in the pumice region (Cochran and others 1967). Stuth and Winward (1976) found a significant correlation between density of successful caches and cover and/or density of the tree overstory. Cochran (1969) reported similar benefits of the tree canopy to lodgepole pine regeneration.



A



B



C

Figure 1.--Unlogged and logged lodgepole pine-bitterbrush forest: (A) Unlogged stands with mostly mature bitterbrush shrubs. (B) Logged stands 2 years after logging; 73 percent of bitterbrush were seedlings and small shrubs established since logging. (C) The stands 5 years after logging; 80 percent of bitterbrush were seedlings and young established shrubs. Lodgepole pine established since logging averaged 597 trees per acre (1,475 per ha).

Apparent increases in the quantity and diversity of native herbaceous vegetation also contributed to forage recovery. Five years after disturbance, average canopy cover of grasses and sedges was 1.9 percent and 5.7 percent in unlogged and logged stands, respectively. Ross sedge and bottlebrush squirreltail made the largest gains. Several forbs also were more abundant, with average cover increasing from 0.6 to 1.5 percent.

Reforestation is another important consideration in evaluating logging impacts in these forest communities. Rodents, insects, ungulate browsing, harsh microclimates, and soil factors often hinder seed production, germination, seedling establishment, and early growth. Fortunately, 5 years after disturbance, these logged units averaged 597 newly established trees per acre (1,475 per ha) as compared to 339 mature trees per acre (837 per ha) in adjoining unlogged stands. Successful regeneration is the primary goal of foresters, but wildlife managers realize that as logging progresses into adjacent stands, maintenance of deer habitat will depend on the development of suitable resting and escape cover in previously harvested stands.

CONCLUSIONS

Study results show that silvicultural treatments can enhance bitterbrush and other forage species in central Oregon lodgepole pine forests. Acceptable levels of soil and understory disturbance can be achieved by selection of appropriate harvest methods and equipment. Special attention should be given to developing silvicultural prescriptions that ameliorate harsh environmental extremes often limiting establishment of shrub and tree seedlings.

Where excessive tree regeneration is thinned, these and similarly harvested stands should serve as important forage areas for mule deer and livestock for, perhaps, 15 years or more. Consideration for other habitat requirements such as cover must be planned in adjacent stands to realize full benefit of this resource. To this end, foresters, biologists, and range managers must work together to assure a balance of habitats of appropriate size, arrangement, and stand condition.

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LONG-TERM CHANGES IN AN UNGRAZED BITTERBRUSH

PLANT COMMUNITY IN SOUTHWEST IDAHO¹

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ABSTRACT

Successional changes and the effects of winter browsing by deer were evaluated by periodically sampling the vegetation of an Idaho winter range site dominated by bitterbrush. Over 23 years of study, bitterbrush density decreased while canopy cover increased. Rabbitbrush density increased, but canopy cover remained relatively stable. Effects of slope exposure on vegetation changes were small. Variety of herbaceous perennials increased, whereas variety of annuals was static. Deer use was not a significant factor in vegetation change. Browse production probably decreased because of increasing age of bitterbrush shrubs. In light of slow vegetational change on bitterbrush-dominated winter range, land managers should consider rejuvenation of old stands by topping, or increasing stand density through revegetation.

INTRODUCTION

During the 1950's some land managers believed that bitterbrush (Purshia tridentata Pursh D.C.) stands in southern Idaho were deteriorating. As early as 1929, this same opinion was expressed regarding severely overgrazed ranges in Utah (Forsling and Storm 1929). In Idaho, bitterbrush was considered the most valuable forage shrub on many winter ranges used by mule deer (Odocoileus hemionus), and much speculation existed concerning the long-term trend of plant composition where bitterbrush was an important component. Winter ranges along the Middle Fork of the Salmon River and the South Fork of the Payette River sustained only a fraction of the number of bitterbrush plants that had flourished there during the 1930's and early 1940's (Holmgren and

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Basile 1956; Shaw and Nielson 1951). The decline of bitterbrush on the Payette River range was in part accelerated by fire that increased the density of cheatgrass (Bromus tectorum L.), which in turn provided severe competition for bitterbrush seedlings. Cicadas also damaged the bitterbrush on the Payette winter range in 1943. These factors, plus the large deer population at the time, resulted in a large decrease in bitterbrush stand density and productivity.

To gain further insight into plant succession, and to compare the changes in vegetation resulting from protection from deer browsing with those occurring on adjacent, unprotected areas, the study reported here was begun in 1955.

METHODS

In December 1953, the Idaho Fish and Game Department erected a 1-acre (0.4-ha) deer-and-cattle-proof enclosure on winter range north of the Boise River, in Boise County, Idaho. The enclosure is located about 0.5 mile (0.8 km) east of the mouth of Mores Creek at an elevation of 3,200 ft (976 m). The immediate area is within a major deer migration route and has historically sustained heavy concentrations of deer in most winters. Livestock grazing, although probably heavy in past years, has been limited to only occasional trailing of cattle since the early 1950's. About 60 percent of the area within the enclosure faces primarily southwest and the remainder faces east.

In the spring of 1955, twelve 50-ft (15.24-m) line transects were established within the enclosure: 6 on the southwest slope and 6 on the east slope. Twelve comparable line transects were established on the same slopes just outside the enclosure. Figure 1 shows a portion of the southwest slope, both inside and outside the enclosure, on which some of the transects were located. Each line transect also served as the downslope edge of a 4-ft by 50-ft (1.22-m by 15.24-m) belt transect and a 6-inch by 50-ft (15.24-cm by 15.24-m) belt transect.



Figure 1.--Portion of the southwest-facing slope of the study area, photographed in February 1954, a year before the study was started.

Data were recorded from the 24 transects in early June 1955, 1958, 1963, 1968, 1973, and 1978. The line transects were used to obtain data on canopy intercept of shrub species and basal intercept of all perennial plant species (Canfield 1942). Canopy intercept was measured to the nearest 0.1 ft (3 cm). The 4-ft by 50-ft belt transect was used to obtain density of all perennial plant species. Data on percent frequency and percent composition of perennials were obtained by dividing this transect into five 10-foot (3.05-m) segments, and recording data on perennials by transect segments. Data on percent frequency and density of annual species were similarly obtained by dividing the 6-inch by 50-foot belt transects into 50 segments of 1 ft each. Constancy of annual species was determined as the percent of 50-ft transects on which each species was encountered.

RESULTS

Shrub Cover and Density

Bitterbrush canopy cover increased slightly more rapidly on the areas exposed to deer browsing than on the areas protected by the enclosure. Over the 23-year study, the mean canopy cover increased from 24.2 to 32.2 percent (a 30 percent increase) inside the enclosure compared to an increase from 16.7 to 23.0 percent (a 38 percent increase) outside the enclosure (table 1).

Table 1.--Mean percent canopy cover of bitterbrush and rabbitbrush, on browsed and protected areas and by aspect of slope, for each year of sampling

	Year					
	1955	1958	1963	1968	1973	1978
<u>Bitterbrush</u>						
Browsed, SW	10.6	14.7	13.6	15.5	15.9	16.3
Browsed, E	22.8	21.6	20.5	21.5	26.2	29.6
Mean	16.7	18.2	17.0	18.5	21.0	23.0
Protected, SW	20.5	18.8	22.8	21.8	28.4	29.8
Protected, E	27.8	28.7	33.7	32.1	32.6	34.6
Mean	24.2	23.8	28.2	27.0	30.5	32.2
<u>Rubber rabbitbrush</u>						
Browsed, SW	3.4	3.3	4.8	3.1	3.6	4.7
Browsed, E	7.8	6.6	7.0	7.6	6.9	5.6
Mean	5.6	5.0	5.9	5.4	5.2	5.2
Protected, SW	3.4	2.7	4.3	3.9	5.7	5.8
Protected, E	1.1	2.5	1.9	2.1	2.9	3.6
Mean	2.2	2.6	3.1	3.0	4.3	4.2
<u>Total cover</u>						
Browsed	22.1	23.1	23.0	23.6	25.4	29.0
Protected	26.4	26.1	31.2	30.0	34.8	36.4
Southwest slope	19.0	19.8	22.6	22.2	26.8	27.8
East slope	29.6	29.6	31.6	31.6	34.3	37.6

Rubber rabbitbrush (Chrysothamnus nauseosus [Pallas] Britt.) was the only other shrub encountered on the transects, except for a couple of golden currant (Ribes aureum Pursh) shrubs on the east slope, outside the enclosure.

From 1955 to 1978, mean canopy cover of rabbitbrush inside the enclosure increased from 2.2 to 4.2 percent, while mean canopy cover outside the enclosure decreased from 5.6 to 5.2 percent. Thus, rabbitbrush remained a relatively stable component of the shrub stand throughout the 23 years of observations.

The effects of slope exposure on the bitterbrush-rabbitbrush stand were small. On the southwest-facing slope, both inside and outside the enclosure, both species increased in canopy cover while the percent composition remained essentially the same. On the east-facing slope, both species increased in canopy cover inside the enclosure, but rabbitbrush decreased while bitterbrush increased on transects outside the enclosure.

With respect to shrub density, the number of bitterbrush plants on protected transects decreased from 41 to 33 (a 20 percent decrease); 10 of the original plants died, but 2 new ones became established. On unprotected transects the number of bitterbrush plants decreased from 37 to 34 (an 8 percent decrease); 6 of the original plants died, but 3 new ones became established. Overall, bitterbrush density decreased from 726 to 626 per acre (294 to 253 per ha). The mean height of bitterbrush shrubs increased approximately the same amount on all transects--about 9 inches (23 cm) over the 23 years.

The number of rabbitbrush plants increased from 8 to 27 (a 237 percent increase) on transects inside the enclosure; 2 of the original 8 plants died, but 21 new plants became established. On transects outside the enclosure, the rabbitbrush plants increased from 16 to 58 (a 262 percent increase); 10 of the original 16 plants died, but 52 new plants became established.

Cover and Density of Herbaceous Perennials

Total basal intercept of perennial grasses and forbs decreased slightly, both inside and outside the enclosure, over the 23 years (fig. 2). However, the observed changes varied according to slope exposure. On the southwest slope basal intercept remained virtually constant (and very low) inside the enclosure, but increased slightly outside the enclosure over the last decade of the study period. Basal intercept of herbaceous perennials decreased by nearly an identical amount on east slopes inside and outside the enclosure.

While total basal intercept apparently declined, except on the unprotected southwest slope, total density of herbaceous perennials (including biennials, but excluding Sandberg bluegrass [Poa secunda Presl.], and needle-leaved phlox [Phlox aculeata Nels.]), steadily increased over the 23 years (table 2). Density of perennials appears to have increased more rapidly outside the enclosure than inside, but was unaffected by slope.

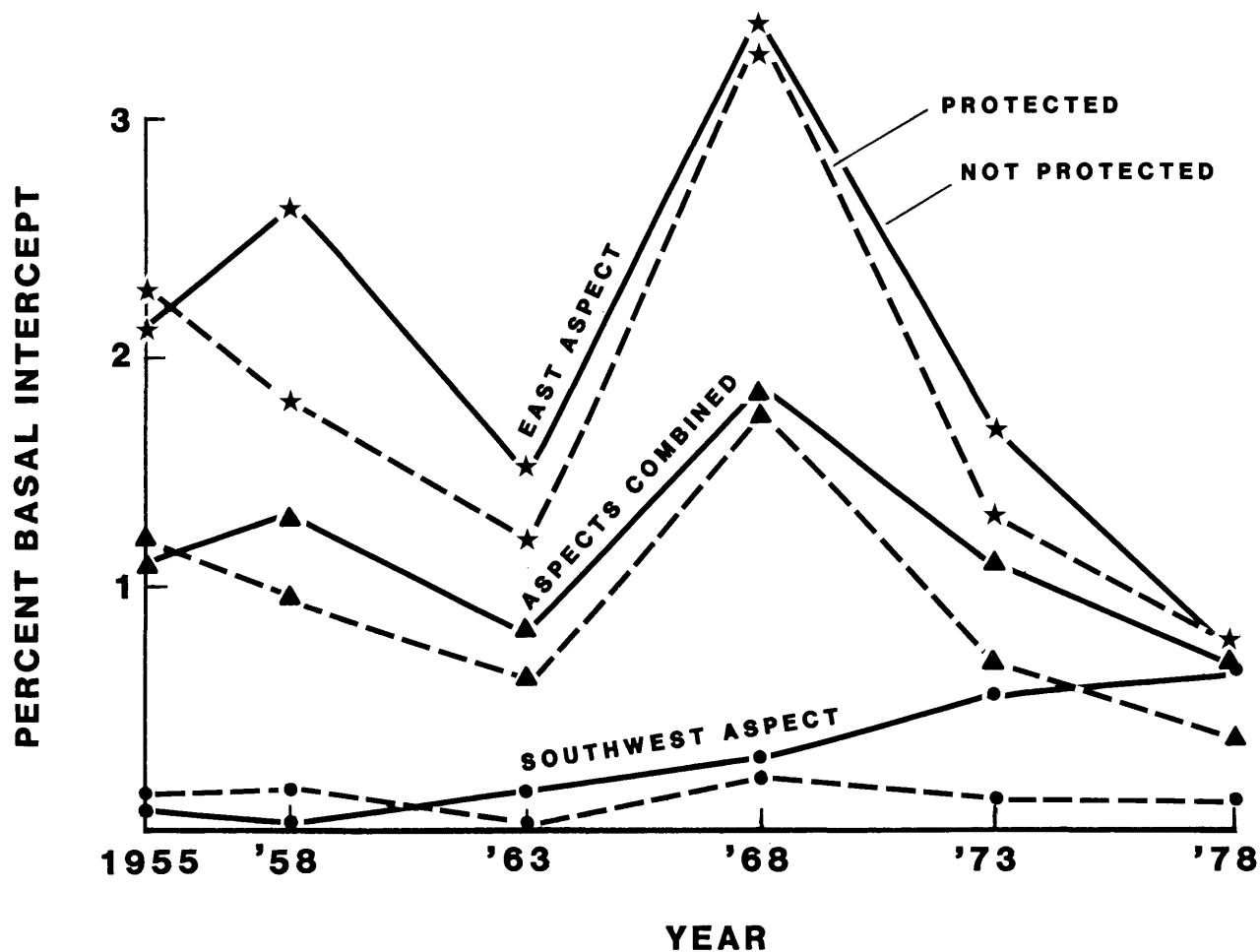


Figure 2.--Percent basal intercept of herbaceous perennials; 1955 to 1978, according to degree of protection and slope aspect.

Table 2.--Mean density (number per 100 ft²) of herbaceous perennials, excluding Sandberg bluegrass and needle-leaved phlox

	1955	1958	1963	1968	1973	1978
Protected, SW	1.7	1.8	1.4	1.5	7.6	7.8
Browsed, SW	.6	1.1	1.8	3.5	8.0	10.7
Protected, E	4.7	2.3	3.9	4.3	9.4	8.2
Browsed, E	4.9	3.8	7.1	5.8	17.2	17.8
Protected	3.2	2.0	2.6	2.9	8.5	8.0
Browsed	2.8	2.4	4.4	4.6	12.6	14.2
Southwest	1.2	1.4	1.6	2.5	7.8	9.2
East	4.8	3.0	5.5	5.0	13.3	13.0

The number of species of herbaceous perennials doubled between 1955 and 1978 on both slopes within the exclosure. Outside the exclosure, the increase in numbers of perennial species encountered was of roughly the same magnitude as inside the exclosure (table 3).

Table 3.--Number of species of herbaceous perennials recorded on each sampling date

	1955	1958	1963	1968	1973	1978
Protected, SW	8	7	9	8	13	16
Browsed, SW	3	4	6	6	8	7
Protected, E	9	7	12	12	17	18
Browsed, E	11	10	12	17	15	19

Annual Plant Species

The list of annual plant species encountered during the study remained essentially unchanged. However, populations of individual species fluctuated considerably, as indicated by frequency data. Cheatgrass (Bromus tectorum L.) frequency ranged between 90 and 100 percent on all transects in every year sampled except 1968, when it ranged from 90 to 100 percent on southwest slopes but dropped to a mean of 68 percent on east slopes.

In addition to the ubiquitous cheatgrass, common annual species on the study area have been bigflower groundsmoke (Gayophytum diffusum Torr. & Gray), large-flowered collomia (Collomia grandiflora Dougl. ex Lindl.), storksbill (Erodium cicutarium (L.) L'Her.), and bedstraw (Galium aparine L. var. echinospermum [Wallr.] Farwell). Some annuals were found almost exclusively on specific exposures: common clarkia (Clarkia rhomboidea Dougl.) and desert plectritis (Plectritis macrocera [T.&G.] Gray) characteristically occupied east slopes; dwarf monkey-flower (Mimulus nanus H.&A.) was found only on the southwest slope, while storksbill and wire-stemmed eriogonum (Eriogonum vimineum Dougl. ex Benth.) were common on southwest slopes but very rare on east slopes.

DISCUSSION

The purpose of this study was to learn more about the effects of protection from deer browsing on the dominant perennial plant species occurring on the Boise River winter range. After 23 years of periodic observations, it appears that changes are only slightly affected by the presence or absence of deer.

Anderson and Holte (1981) cited several recent studies suggesting that forest and shrub communities may be exceptionally stable in the absence of external disturbances. Their data from sagebrush-dominated rangeland in southeastern Idaho suggested that the population of dominant shrubs had been relatively stable over 25 years of protection from grazing. Voth (1979) found that changes in species numbers and in perennial cover were minimal between 1931 and 1977 on plots protected from livestock grazing. Some of her data were from winter range areas along the South Fork of the Boise River that were similar to our study area. On the other hand, shrub stands established as a result of drastic disturbances (such as wildfire) are often seral, and vegetative composition changes drastically within a decade or two.

In this study, the stands of bitterbrush inside and outside the enclosure have both decreased in density and increased in canopy spread. Thus, the bitterbrush population is thinning but the remaining shrubs are larger. Over the 23-year study, only five new bitterbrush plants have become established on the 0.1 acre (0.04 ha) sampled. If this is representative of the surrounding area, it suggests that approximately two new bitterbrush plants have become established per acre, per year. Bitterbrush reproduction can be expected to be poor where a well-stocked stand of old shrubs is complemented with a dense understory of cheatgrass and scattered herbaceous perennials, all of which provide severe competition and leave few openings for bitterbrush seedling establishment. Furthermore, the lack of livestock grazing (outside the enclosure as well as inside) decreased soil disturbance and encouraged the return of herbaceous perennials.

The slightly smaller increase in canopy cover of bitterbrush inside the enclosure than outside might be expected. This is because old bitterbrush tend to reduce annual twig growth in favor of seed production unless continually stimulated by the browsing of animals. The bitterbrush stands on the study area were mature at the study's start.

The population of rubber rabbitbrush exhibited a much more rapid turnover than the population of bitterbrush; 50 percent of the 24 plants tallied in 1955 had died by 1978, but 73 new plants had become established. More than 200 rabbitbrush seedlings were tallied on the southwest slope outside the enclosure in 1955, none of which survived to the 1958 sampling. In 1968, a total of 170 seedlings were recorded on all transects; 10 years later, 32 percent of these plants were still alive, but most were still very small, having exhibited a mean growth of 1 to 2 inches (2.5 to 5 cm) per year. Survival rates among the 1968 seedlings were 23 percent inside the enclosure, 37 percent outside, 13 percent on southwest slopes, and 39 percent on east slopes.

In southeastern Idaho, Anderson and Holte's (1981) data suggest a rapid turnover in the population of green rabbitbrush (Chrysothamnus viscidiflorus [Hook.] Nutt.), with no evidence of seral replacement of green rabbitbrush after 25 years of protection from livestock grazing.

The measured decrease in basal intercept of herbaceous perennials on east slopes, both inside and outside the enclosure, was due entirely to a decrease in the basal intercept of Sandberg bluegrass. Bluegrass basal intercept decreased 68 percent between 1955 and 1978 (fig. 2). However, the increase recorded in 1968 suggests that climatic variability affects the composition of a plant community and the vigor of individual species within the community. Bluegrass density also decreased on east slopes by 32 percent inside the enclosure and by 43 percent outside. Although the decrease in density of bluegrass agrees with the measured decrease in basal intercept, the relative accuracy of the density data is uncertain because of the difficulty in distinguishing individual plants of Sandberg bluegrass.

McLean and Tisdale (1972) observed a decrease in Sandberg bluegrass in several 29-year-old enclosures in British Columbia. Neal (1982) noted that heavy, early spring grazing by cattle on deer winter range in southern Oregon and northern California reduced the cover of all bunchgrasses except Sandberg bluegrass, which increased. Both Neal (1982) and McLean and Willms (1982) cite high the value of Sandberg bluegrass as early spring forage for mule deer.

Data from outside the enclosure show an overall decrease in basal intercept of herbaceous perennials over the 23-year study. However, this was due to the decrease in measured basal intercept of Sandberg bluegrass on the east slope, as mentioned above. On the unprotected southwest slope, total basal intercept increased from 0.24 percent in 1955 to 0.63 percent in 1978, due entirely to an increase in needle-and-thread grass

(*Stipa comata* Trin. & Rupr.). In 1955, only five needle-and-thread plants were tallied on the 12 southwest slope transects; this number increased to 26 by 1968, and to 66 in 1978.

The smaller increase in density of herbaceous perennials inside the exclosure may be a result of less soil disturbance, which in turn offers fewer favorable locations for the establishment of seedlings than may be available on the area used by deer.

Table 4 shows the overall change in density of the major perennial grasses and forbs between 1955 and 1978. One important change is the decrease in density of balsamroot on both protected and unprotected east slopes. Balsamroot numbers decreased from 23 to 3 and from 16 to 4 on east slopes inside and outside the exclosure, respectively. A general decrease in balsamroot would be important because it is a very long-lived species and is a valuable forage plant on deer winter ranges. Burrell (1982) found that balsamroot made up from 6 to 22 percent of the diet of mule deer in Washington, with the use of balsamroot increasing as the availability of bitterbrush decreased.

Table 4.--Overall change in density of major species of herbaceous perennials, 1955-1978

	Protected		Browsed	
	Slope aspect		Slope aspect	
	SW	E	SW	E
GRASSES				
<u>Agropyron inerme</u>	NC ¹	NC	NC	NC
<u>Poa bulbosa</u>	NC	NC	I ²	I
<u>Poa secunda</u>	NC	D ³	NC	D
<u>Sitanion hystrix</u>	NC	NC	NC	I
<u>Stipa comata</u>	I	-- ⁴	I	--
<u>Stipa thurberiana</u>	--	--	--	I
FORBS				
<u>Achillea millefolium</u>	I	--	--	--
<u>Arabis spp.</u>	I	I	I	I
<u>Balsamorhiza sagittata</u>	NC	D	--	D
<u>Delphinium spp.</u>	NC	I	--	I
<u>Phlox aculeata</u>	D	D	--	NC
BIENNIALS				
<u>Aster canescens</u>	I	NC	I	NC
<u>Erysimum capitatum</u>	--	I	--	I
<u>Phacelia heterophylla</u>	I	NC	I	NC

¹NC = no change.

²I = increase.

³D = decrease.

⁴-- = did not occur.

CONCLUSIONS

Data obtained from vegetative sampling over the 23-year study showed that deer use, which varied from extremely heavy to light, has not been a significant factor influencing vegetative composition or the trend in plant succession. Specifically, deer use did not prevent an increase in canopy cover or shrub height of bitterbrush, nor did deer use have any effect on the canopy cover or density of rubber rabbitbrush.

Although bitterbrush density decreased, individual bitterbrush shrubs became larger. Yet the shrubs probably are producing less available browse for wintering deer because of height and old age. This will be true especially when snow depth limits access to grass and forb species. The density of herbaceous perennials other than Sandberg bluegrass, balsamroot, and needle-leaved phlox has slowly increased, both inside and outside the enclosure.

Under those circumstances, managers should consider either rejuvenating old bitterbrush shrubs by topping (Ferguson and Basile 1966; Ferguson 1972) or increasing stand density and age class distribution by seeding or planting (Holmgren and Basile 1959; Medin and Ferguson 1980).

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Section 4. Management Strategies



ARTIFICIAL REVEGETATION USING ANTELOPE

BITTERBRUSH--A LAND MANAGER'S VIEW¹

Robert Carpenter²

ABSTRACT

Revegetation procedures using antelope bitterbrush (Purshia tridentata) are discussed from a land manager's point of view. Since 1976, approximately 600,000 seedlings have been transplanted on the Arrowrock Front deer winter range of the Boise National Forest.

Volunteers, YACC, seasonal employees, and contract labor have been employed to complete the field work. Items included in this discussion are: acquisition of seed and rearing, grading, storing, field planting, and transplant stock procedures. Survival varied greatly depending on quality of plants, time of planting, and planting method.

INTRODUCTION

In 1976, a major effort to rehabilitate the Arrowrock Front deer winter range using antelope bitterbrush (Purshia tridentata) was initiated. The area is located on the Boise National Forest and lies approximately 18 air miles (29 km) east of Boise, Idaho. Topography is typically steep and dissected. Slope gradients range from 15 to 80 percent. South facing exposures are dominant. Elevation ranges from 3,200 ft (980 m) to 5,200 ft (1592 m). Soils are granitic, coarse textured, and loose, with low waterholding capacity. Annual precipitation averages approximately 19.5 inches (49 cm).

IDENTIFY PLANTING AREAS

The first step in successful big game rehabilitation is to identify and select acceptable planting areas. These sites are frequently the more critical areas for wintering game animals. Data collected by observations during several years of average or more severe winters are necessary to determine the location of these ranges. Following this initial screening, the areas should be inventoried to determine soil and vegetative conditions.

1 Paper presented at Bitterbrush and Cliffrose Symposium, Salt Lake City, Utah April 13-15, 1982.

2 Range Conservationist, USDA Forest Service, Boise National Forest, Boise, Idaho.

ACQUIRING SEED

The acquisition of seed from plant populations that are adapted to the planting site is extremely important. It is best to acquire seed from plants growing on similar habitat types within the local area. When this is not possible, one should be very careful in selecting seed from unfamiliar seed sources.

The cost of seed is dependent upon such factors as demand, ease of collection, and available seed supplies. A discussion of seed collection may be obtained from various reports (Schopmeyer 1974; Shaw 1981; Plummer and Jorgensen 1978). During the past 7 years, bitterbrush seed costs have ranged from \$4.00 per pound (\$8.80/kg) to \$8.00 per pound (\$17.60/kg). All seed lots should be tested for viability and germination before planting. This can normally be completed through state seed laboratories or private seed companies. There are approximately 15,000 seeds per pound (6800/kg) of bitterbrush seed (USDA 1971).

SEEDING OR PLANTING

Once an area has been selected for treatment and seed has been acquired, two planting options are available. Both methods have economic and logistic advantages and disadvantages.

1. Seeds may be planted directly onto the site. For more information on direct seeding refer to Medin and Ferguson (1980).
2. Bareroot or containerized transplant stock can be propagated or acquired and field planted.

Transplant stock can be grown as bareroot or containerized plants.

CONTAINERIZED STOCK

Containerized stock is normally grown under greenhouse conditions. Plants are grown in special mediums composed of peat, vermiculite, and sand. Length of time from seed to plant varies from 5 to 10 months (Ferguson and Monsen 1975). Use of containerized stock on a large scale in Idaho Batholith soils has been thought to be unsuccessful for the following reasons:

1. The soil medium is not compatible with the native soils. The containerized plant medium is "spongy" because of the high peat and vermiculite content and in droughty climates seems to dry more rapidly than the native soils.
2. The roots tend to remain in the potting medium. They do not grow quickly into the native soils. If the potting soil dries out, the roots die.

BAREROOT STOCK

Bareroot stock can be grown in seed beds at a commercial or Forest Service nursery. At the Lucky Peak Nursery, Boise, Idaho, seed is planted either in the late fall (normally October) or in the early spring. The seed is allowed to germinate and grow for one season. Transplants of adequate size can be produced in one growing season.

Figure 1 illustrates possible planting and lifting schedules for year-old stock. Close coordination by field personnel with the nursery is required. Growing periods may vary depending on the location of the nursery.

Lifting Bareroot Stock																			
MONTHS	1981			1982												1983			
	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
	P ₁			Growing Season								L ₁							
	P ₂			Growing Season												L ₂			
				P ₃ Growing Season								L ₃							
				P ₄ Growing Season												L ₄			
P = Time seed is planted																			
L = Time seedlings are lifted																			

Figure 1 -- Possible planting and lifting schedules for year-old bareroot stock

At the Lucky Peak Nursery, plants are spring lifted between February 20 and March 10, but may be fall lifted between October 20 and November 10. Fall lifted shrubs can be stored over winter in nursery storage. Fall lifted seedlings may be planted in the late fall or early spring. We have planted shrubs during all months from October through April on the Arrowrock Front winter range. However, planting from November 20 until February 15, is dependent on the soils being thawed. Although it is possible to plant throughout the winter, the ideal time to plant is early in the spring to allow plants to establish an adequate root system. This must be done before the dry summer period. The seedlings should be planted so that they can break dormancy at the same time as the native plants. This allows the seedling the maximum amount of time for root establishment. The time frame for planting is very narrow.

Grading and Packaging

Following lifting, plants are taken into the packing shed where they are graded and packaged. Grading is the process of sorting out the usable from the "cull" plants. Variables involved in grading are:

1. Size of the plant stem
2. Size of the root system
3. Branching of the stem

Factor number 3, "branching of the stem," seems to be the best criterion to use for grading antelope bitterbrush. As a general rule, top branching indicates an adequate root system for field planting. Figure 2 illustrates the variability in size of plants lifted from the same seedbed.

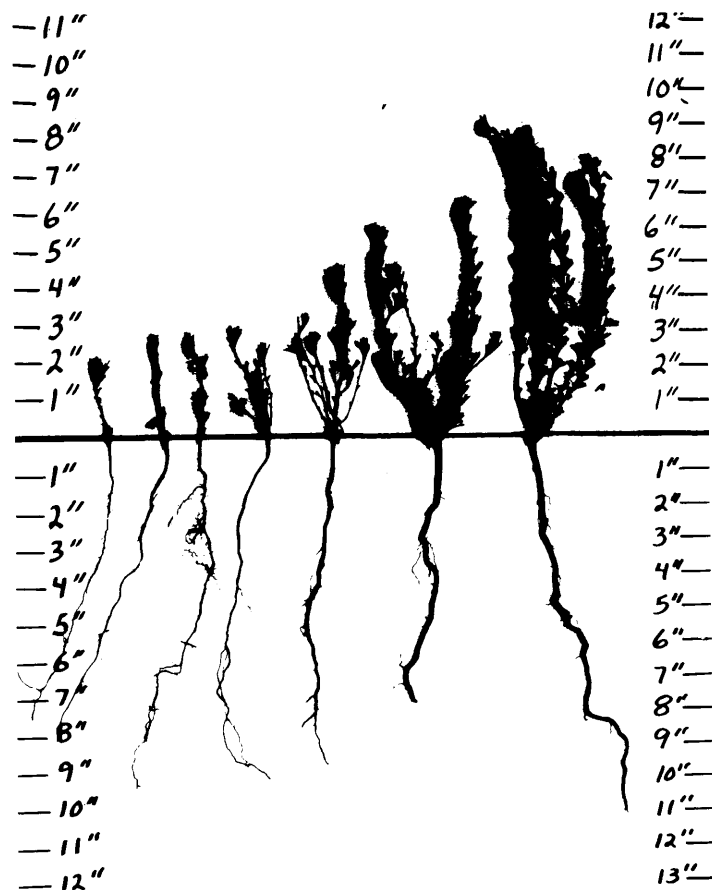


Figure 2. -- Illustrates variability in size of bitterbrush grown in the same seedbed

Packaging is completed at the nursery immediately following the sorting and grading process. Plants are packaged in either bags or crates with spagnum moss used as a packing medium.

Storage of Lifted Plants

Prior to shipment, plants are stored in coolers at the nursery. Plants are stored at temperatures between 28° and 34°F (-2 and 1°C) (Dahlgreen and others 1974).

Wrapping Plants

Seedlings should be removed from storage just prior to planting. Plants in a snow cache should be removed 1 day in advance of planting. This is particularly critical if the daytime temperature is above 50°F (10°C). Plants removed from storage should be dipped in a vermiculite solution and wrapped in wet burlap (Dahlgreen and others 1974). Plants should not be wrapped more than 2 to 3 days before planting. It is best to wrap the shrubs the night before planting. The warmer the weather, the more critical this factor becomes. Wrapping should be done where there is no wind, no direct sun, relative humidity is high and temperature is low.

PLANTING (SITE PREPARATION)

Site preparation is the first step in the actual planting process. Completion is reduced by scalping. "Scalping" is the process of removing the vegetation from the area to be planted. Tools used in scalping included McCleods, fire rakes, or hodads (Larson and Milodragoyich 1982). The scalp should be a minimum of 3 ft by 3 ft (.9m by .9m) (Holmgren 1956). It is essential to remove competition for a 1-2 year period. This permits the transplant to establish an adequate root system.

HAND PLANTING

The final and most critical step of the planting process is placing the plant in the ground. The importance of this step cannot be overemphasized. However, if the preceding steps are not completed correctly the plant may already be doomed when planted.

All planting on the Arrowrock Frong has been accomplished with planting bars. These come in a variety of shape and sizes. The most useful bar for this site has been the modified KCB bar. The blade has been modified to a 14 inch (35 cm) blade length. This provides adequate depth for the plants root system and usually prevents plants from being planted "too shallow." The steps in the planting process are shown below. These steps have been taken from the USDA, Forest Service Reforestation Handbook (1971). This method is often referred to as "slit" planting and is not permitted for tree planting in the Intermountain Region. Because of differences between tree and shrub root configuration, slit planting is a desirable planting method for shrubs on the Arrowrock Front. The following procedure is used with the modified KCB bar:

1. Use both hands to drive the bar full length in the ground at the proper angle near the center of the selected spot. Use foot on the step as needed. Repeated efforts may be required in some instances.
2. Withdraw the bar 1 inch (2.5 cm). Open the bottom of the hole by pulling the bar 4 to 6 inches (10-15 cm) toward the body while using the point where the bar enters the ground as a fulcrum.
3. Force the bar into the ground so the tip acts as a fulcrum and push the bar 6 to 8 inches (15-20 cm) away from the body. This should open the top of a rectangular hole approximately 14 x 3 x 2½ inches (35 x 7.5 x 6 cm).
4. Remove the bar from the hole without disturbing the soil faces. Bend over or drop to one knee.
5. Carefully remove one seedling from the carrier, shaking it gently to straighten the roots. Insert the shrub in the hole until the root collar is 2 inches (5 cm) below the soil surface.
6. Raise the shrub so the root collar is level with the soil surface. Make sure the roots are fully extended in a near natural position, not curled or twisted.
7. Thrust the bar into the soil 3 inches (8 cm) in front of the shrub while holding the seedling at the proper depth near the center back of the slit. Push the bar forward, forcing dirt into the top of the hole, securing the seedling in place. Release the seedling and stand up.

8. Drive the bar full length into the soil as before at the same point used above. Do not permit the bar to angle into the planting hole.
9. Withdraw the bar 1 inch and pull it 4 to 6 inches (10-15 cm) toward the body. This action closes the bottom of the hole.
10. Force the bar into the ground so the tip acts as a fulcrum and push the bar 6 to 8 inches (15-20 cm) away from the body. This action should close the top of the hole, leaving an open crimp hole.
11. Remove the bar and repeat steps 8, 9, and 10 once or twice so seedling is surrounded by firm soil.
12. Place heel across last crimp hole and step firmly to plug it. Check for firmness and stem position and proceed to next spot.

PLANTING INSPECTION

Major items to observe when completing planting inspections are proper firming of soil around seedling roots and depth of planting. These two factors when not followed as outlined account for 90 percent of all seedling mortality on the Arrowrock Front.

Firmness

Firming the soil around the roots is the most critical step in the planting process. Steps 7 through 12 in the planting process need to be strictly adhered to. If the soil is not compacted tightly against the roots, air spaces will remain, placing tremendous stress upon the plants. Failure to firm the soil around the roots accounted for 60 percent of the seedling mortality on the Arrowrock Front.

Depth

The second major reason for seedling mortality is improper planting depth. It is much more harmful to plant a seedling too shallow than too deep. The seedling should be planted with the root collar at the surface of the soil. The proper level is determined by the level of "solid soil", not loose soil (fig. 3). This becomes more difficult to gauge as the steepness of slope increases. As a general rule, the "solid soil" level will be the lower or downhill side of the planting hole. When the planting bar is used, an area approximately 6 inches (15 cm) in diameter is disturbed. On steeper slopes this may amount to 2-4 inches (5-10 cm) vertically. This loose soil should not be repacked around the stem as it is usually washed away during spring storms. Improper planting depth accounts for about 30 percent of all seedling mortality.

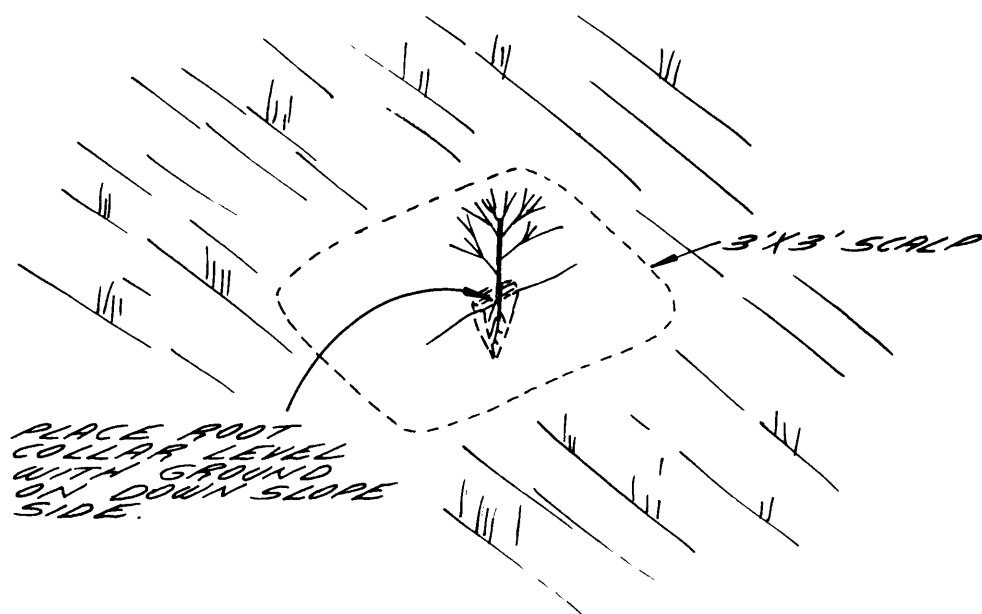


Figure 3 -- Diagram of scalp showing position of planting hole and root collar.

CONCLUSIONS

Large scale transplanting of bareroot shrub seedlings, primarily antelope bitterbrush, has been highly successful on the Arrowrock Front of the Boise National Forest. Between 1976 and 1982, nearly 600,000 seedlings were planted. Careful consideration of the following factors determines the success of planting projects:

1. Planting site selection.
2. Selection of seed adapted to site.
3. Timing of planting.
4. Grading of plants.
5. Storage and handling of lifted plants.
6. Planting practices.

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SEEDING ANTELOPE BITTERBRUSH WITH GRASSES
ON SOUTH-CENTRAL IDAHO RANGELANDS--A 39-YEAR RESPONSE

Stephen B. Monsen and Nancy L. Shaw²

ABSTRACT

The response of a 39-year old seeding of antelope bitterbrush and perennial grasses in south-central Idaho is discussed. The effects of livestock grazing upon shrub establishment and survival and the composition of the understory plants is presented. Natural establishment of shrub seedlings is also reported.

INTRODUCTION

Shrub seedings on western rangelands were initiated in the early 1940's and 1950's following revegetation studies in Idaho (Holmgren and Basile 1959), California (Hormay 1943), Washington (Brown and Martinsen 1959), and Utah (Plummer and others 1957). Antelope bitterbrush (Purshia tridentata) was soon recognized as a useful species to plant on game and livestock ranges. Nord and others (1967) found that seeds from this shrub could be easily collected, processed, and planted. Holmgren (1954) reported that the seeds germinated uniformly and the seedlings were quite vigorous.

Several factors caused erratic results from early shrub seedings. Problems often resulted from the lack of satisfactory planting equipment. Competition from annual weeds and established perennials reduced shrub seedling survival and establishment (Holmgren 1956; Hubbard 1956). Holmgren and Basile (1959) determined that rodent depredation of seeds and small seedlings was also a major deterrent to the establishment of antelope bitterbrush and other shrubs. In addition, livestock, rabbit, and game animal grazing was destructive to new plantings (Plummer and others 1966). Although such factors hampered early plantings, methods were developed to minimize these problems and facilitate seeding of shrubs on large acreages.

In the mid-1940's, agricultural drills and seeders were adapted to plant shrubs and grasses on game and livestock ranges. The equipment was modified to plant grass and shrub seed in separate drill rows to reduce competition between the two classes of plants. Numerous plantings of antelope bitterbrush and introduced grasses were established in south-central Idaho in the 1940's and 1950's. The seeded species have since reached maturity. Consequently, this study was instigated to evaluate the success of mixed plantings, particularly (1) the ultimate survival of seeded antelope bitterbrush, (2) recruitment of new antelope bitterbrush plants, and (3) the composition and herbage production of the seeded and native species.

METHODS

In summer 1942, a wildfire burned approximately 1,200 acres (486 ha) of rangeland in the Willow Creek and Case Creek drainages of the Mountain Home Ranger District, Boise National Forest, Idaho. Prior to burning, the sites supported a mixed stand of mountain big sagebrush (Artemisia tridentata ssp. vaseyana), antelope bitterbrush, and

¹Paper presented at Bitterbrush and Cliffrose Symposium, Salt Lake City, Utah; April 13-15, 1982.

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various bunchgrasses. In October 1942, about 45 acres (18 ha) within the Case Creek drainage were seeded with a tall upright form of antelope bitterbrush and a grass-forb mixture (table 1). The site was planted by coupling one 10-ft (3.1 m) and two 6-ft (1.8 m) John Deere double disc drills together. Seeds of the herbs were mixed together and planted with these drills (fig. 1). The antelope bitterbrush seed was planted separately from the herbs by blocking off the outside portion of one grain drill box and seeding antelope bitterbrush through one drop of the drill. Thus, the grasses and broadleaf herbs were seeded in a strip approximately 22 ft (6.7 m) wide. Antelope bitterbrush was planted in single rows spaced about 22 to 26 ft (7 m) apart. For the first 2 years after planting, the site was protected from livestock grazing. Thereafter, cattle grazed the area either in the spring or early summer.

Table 1.--Seeding mixture--Case Creek planting, October 1942

Species seeded	Seeding Rate
	lbs/acre
<u>Agropyron desertorum</u>	3.00
<u>Arrhenatherum elatius</u>	1.00
<u>Bromus inermis</u>	1.00
<u>Poa bulbosa</u>	1.00
<u>Melilotus officinalis</u>	.25
<u>Purshia tridentata</u>	1.60

In 1946, a 1-acre (0.41 ha) livestock-proof enclosure was erected to determine the effects of livestock use on the seedings. Ten drill rows of antelope bitterbrush, each approximately 133 ft (40.5 m) long, were included within the enclosure. Counts and measurements of all antelope bitterbrush plants in each row were recorded from 1949 through 1951. Similar data were not recorded for seeded shrubs outside of the enclosure. However, field observations were recorded during each of the first 7 years following planting. In 1981, the enclosure site was resampled 39 years after planting. Three outside areas similar to the enclosure in aspect, soil conditions, and orientation of the enclosure were selected for study at this time. Each outside area included five adjacent seeded rows of antelope bitterbrush, each 133 ft long.

All antelope bitterbrush plants within each drill row were individually measured to determine their maximum height and maximum crown. The number of seeded shrubs to occur in the protected and grazed areas are presented as plants per acre. A Student's t test was used to test for significant differences between average number of seeded shrubs per row in the enclosure and on the grazed sites (Sokal and Rohlf 1969).

Duncan's Multiple Range Test was used to determine differences among means for shrub heights and crowns (Steel and Torrie 1960).

In 1981, the cover and herbage production of all herbaceous and woody plants was estimated using 10.8 ft² (1 m²) square plots. Within each of the four study areas, four antelope bitterbrush plants were randomly selected from each of the five rows. A 10.8 ft² plot was located directly beneath each shrub. Four additional plots of the same size were established adjacent to each of these shrubs in a line perpendicular to the shrub row. The plot centered beneath the shrub was identified as quadrat 1. Successive quadrats away from the shrub were numbered in sequence from 2 through 5. This positioning allowed for comparison of the influence of the overstory shrub on the understory composition and production as a function of distance from the shrub.

The annual herbage production of each species within the frame was determined by ocular estimate. Plants in every fifth set of plots were clipped and weighed as a check against the ocular estimates. Clipped samples were then air dried and reweighed to provide dry weight conversion factors. Live ground cover for each species was determined by estimating the area occupied by the vertical projection of stems and foliage. The percent cover provided by litter and bare ground was also estimated and recorded. Production data were expressed in grams of herbage per meter square plot. Duncan's Multiple Range Test was used to determine differences among the means of species densities and yields for all quadrat positions both within and between the protected and grazed areas.

RESULTS AND DISCUSSION

In 1949, the first counts of antelope bitterbrush plants within the enclosure were made 7 years after planting (table 2). There was an average of one antelope bitterbrush plant per 7.6 linear ft (2.3 m) of seeded row. More than 99 percent of the seedlings recorded in 1949 survived, counting as mature plants in 1981. In the grazed area, a mean of one antelope bitterbrush shrub per 12 ft (3.7 m) of planted row survived in 1981. Compared to the enclosure about 36 percent fewer shrubs become established in the grazed areas.

Table 2.--Numbers of antelope bitterbrush plants to establish and survive--Case Creek, 1941 seeding.

	Exclosure site				Grazed areas			
	1949	1950	1951	1981	1949	1950	1951	1981
Mean number plants/ 133 ft row	17.5	17.5	17.2	17.2	--	--	--	11.0
Frequency (linear feet of row/plant)	7.6	7.6	7.7	7.7				12.0
No. plants/acre	197	197	194	194				124
Percent survival	100	100	99.5	99.5				--

Livestock grazing, although regarded as low or moderate in regards to the amount of grass removed, caused a decrease in the number of shrubs to establish and persist. Few game animals graze the study areas and have little influence on plant responses. Field records report that major losses of shrub seedlings to livestock grazing had occurred by 1946 when the plants were less than 4 years old. Field observation summarized by Holmgren in 1946 reported that: "The palatability of the shrubs soon became evident under light to moderate use as determined by the utilization of crested wheatgrass. The bitterbrush was grazed heavily and the removal of all current growth was not unusual."³

Apparently cattle grazing continued to be detrimental to shrub survival and plant vigor in grazed areas even after 1946. If the number of antelope bitterbrush plants was approximately uniform throughout the planted area in 1946, then differences in plant numbers recorded in 1981 in the grazed and protected areas could be due to the influence of continued livestock grazing. Seedling losses attributable to livestock grazing were observed from field inspections for 5 to 7 years after planting³. By 1949, cattle grazing had significantly reduced the size of the existing plants (table 3); plants growing within the enclosure were nearly double the size of the grazed plants. Undoubtedly annual grazing had a cumulative effect upon the small plants. Shrub seedlings that survived for the first 5 to 7 years apparently were

Table 3.--Measurements of 7-year old antelope bitterbrush plants in grazed and protected sites--Case Creek, 1949.

Treatment	Height	Crown diameter	Stem diameter	Yield
	-----inches-----			g/plant
Grazed areas	8.1 ^{a1}	7.0 ^a	0.3 ^a	5 ^a
Exclosure	15.8 ^b	13.2 ^b	0.3 ^a	35 ^b
Alone ²	19.3 ^c	19.2 ^c	0.5 ^b	60 ^c
With competition ³	14.6 ^b	11.3 ^b	0.3 ^a	25 ^b

¹ Figures in the same column not sharing the same letter superscript are significantly different at the .05 percent confidence level.

² Selected shrubs growing without other plants within a 30-inch (76.2-cm) radius.

³ Selected shrubs growing with other plants present within a 30-inch (76.2-cm) radius.

³ Holmgren, R. C. Boise, ID: Data on file at the Forestry Sciences Laboratory; 1946.

able to persist even though cattle grazing continued annually for nearly 40 years. A satisfactory stand developed even though the young plants were heavily browsed each year during the period of establishment.

Competition from other shrubs and herbs also affected the growth of the young antelope bitterbrush plants. Shrub seedlings encountered in locations where no other plants occurred within a 30-inch (76.2 cm) radius were significantly larger than seedlings that existed with competition (table 3). Hubbard and others (1962) reported that crested wheatgrass plants found growing within 2 ft (0.60 m) of young antelope bitterbrush reduced shrub vigor and size. At a separate planting established in the Willow Creek drainage in 1948, many antelope bitterbrush seedlings succumbed to intense competition from annual weeds during the first⁴ growing season. Heavy losses occurred even in areas protected from livestock grazing⁴.

In most areas throughout the Case Creek planting, antelope bitterbrush was able to establish and persist with the seeded herbs. Seeding the herbs in separate rows from the shrubs satisfactorily reduced competition between the seedlings. Seeded shrubs were uniformly distributed throughout the seeded rows. Plants were not clumped together, but appeared in a regular pattern. Spacing the seeded row of bitterbrush approximately 10 inches (25 cm) from the adjacent row of seeded grass provided a satisfactory 20-inch (50-cm) buffer for establishment of the shrub seedlings. Giunta and others (1975) found that a 24-inch (60 cm) width is required to establish shrubs in areas dominated by annual cheatgrass (*Bromus tectorum*). Rangelands can be successfully seeded in this manner unless a large number of residual plants remain after burning or other treatments. An influx of annual weeds can also reduce shrub seedling survival.

The combined effects of biological and climatic influences upon shrub seedling emergence and survival were significant. The ultimate attainment of mature plants was extremely low compared to the number of seeds planted. Assuming 24,000 antelope bitterbrush seeds per acre were dispersed in the Case Creek seeding, a return rate of only 0.008 percent was attained in the exclosure. This amounts to about one plant for every 120 seeds planted. Under these conditions approximately 12 seeds per linear ft (31 cm) must be planted to assure the attainment of one shrub per 10 ft (3.1 m) of seeded row. This amount must be increased if minimal grazing or other impacts are expected. However, increasing the seeding rate will not always compensate for expected losses. Competition, drought, or rodent damage may result in the death of all seedlings regardless of the amount of seed planted. Any disruption of new seedlings can seriously affect the success of the planting.

VEGETATIVE RESPONSE TO GRAZING, PROTECTION, AND SPACING OF THE SEEDED SHRUB ROWS

Seeded Antelope Bitterbrush

Antelope bitterbrush plants growing in the grazed areas have been moderately browsed by cattle. However, grazing of mature plants has not seriously interfered with plant growth (table 4). By 1981, shrubs within the exclosure were approximately 15 percent larger in both height and crown spread than those outside the exclosure. Grazing of the shrubs has reduced their size and confined the leader growth into a more compact area. A major portion of the shrubs have now grown out of the reach of the cattle. However, grazed plants remained vigorous and productive. Plants within the exclosure are widely branched and provide a more open canopy.

⁴ See footnote 1.

Table 4.--Average plant height and crown diameter of grazed and protected shrubs, Case Creek, 1981.

Sampling area	Plant height	Crown spread
	----- inches -----	-----
Exclosure	73.9 ^{a1}	100.6 ^a
Grazed area		
Sampling site 1	61.9 ^b	82.7 ^b
Sampling site 2	58.6 ^{bc}	82.4 ^{bc}
Sampling site 3	68.2 ^c	88.4 ^c

¹Figure in the same column sharing the same letter superscript are not significantly different at the 0.05 percent confidence level.

It is important that seeded antelope bitterbrush be able to persist through natural regeneration. To perpetuate themselves, new shrub seedlings must be able to establish amid the understory plants. Most seeded grasses, including desert wheatgrass (*Agropyron desertorum*), are highly competitive and may reduce the recruitment of bitterbrush seedlings. Since the Case Creek area was initially seeded in 1942, approximately 205 new shrubs per acre (506 shrubs per ha) have become established by natural reseeding within the exclosure. In the grazed areas 149 new shrubs per acre (368 plants per ha) have become established. The number of new shrubs found in the grazed areas is significantly lower than found in the exclosure site. The plants originated from seed produced by the mature shrubs that were established from the 1942 seeding. The new shrubs occur throughout the strip where grasses were planted. The entry of shrub seedlings has been slow, yet the seedlings have been able to establish amid the seeded and native bunchgrasses.

Native Shrubs

The number and production of mountain big sagebrush and rubber rabbitbrush (*Chrysothamnus nauseosus*) appear to be influenced by the presence of the seeded antelope bitterbrush. Both understory shrubs occupy less cover in quadrat number 1, beneath the canopy of the seeded bitterbrush, than in the other quadrats (table 5). The percent ground cover and production of sagebrush and rabbitbrush tend to increase with increasing distance from the bitterbrush rows. Both shrubs attain their maximum density in the open areas between the seeded rows of antelope bitterbrush. Ground cover for these two shrubs within and outside the exclosure was less than 10 percent for any quadrat position. In most instances, no significant difference in cover or herbage production is recorded for similar quadrat positions within or outside of the exclosure. The presence of seeded desert wheatgrass has also been important in controlling the invasion of these woody species. Seeding antelope bitterbrush rows at closer row spacings may be a means to control the reinvasion and density of mountain big sagebrush and rubber rabbitbrush.

Table 5.--Ground cover for grazed and protected sites recorded by meter quadrat portions--Case Creek, 1981

Species	Quadrat positions-1	Exclosure site					Grazed site				
		2	3	4	5	Percent	1	2	3	4	5

Seeded shrubs											
<u>Purshia tridentata</u>	38.0	2.8	0.6	1.6	3.5	51.2	3.9	0.2	--	--	--
Native shrubs											
<u>Artemisia tridentata</u> ssp. vaseyana	4.31	7.4	4.2	9.5	9.5	5.9	8.6	8.9	8.7	8.6	8.6
<u>Chrysothamnus nauseosus</u>	--	--	1.3	.3	--	--	.2	--	.1	--	--
Native forbs											
<u>Lupinus argenteus</u>	2.7	2.4	2.2	5.0	7.0	1.3	1.9	2.8	3.3	4.2	4.2
<u>Montia perfoliata</u>	2.2	--	--	--	--	--	--	--	--	--	--
Other perennials	--	--	--	1.6	.5	--	--	--	--	--	--
Annuals	3.7	--	--	--	--	.2	.1	.4	.2	.3	.3
Seeded grasses											
<u>Agropyron desertorum</u>	20.7	23.6	22.9	18.1	20.0	16.7	15.3	14.6	14.3	13.8	13.8
<u>Poa bulbosa</u>	3.3	6.2	9.0	11.1	7.9	2.7	5.1	7.0	7.9	8.8	8.8
Native grasses											
<u>Festuca idahoensis</u>	1.4	1.5	2.1	4.7	4.0	1.2	2.1	3.1	3.1	3.5	3.5
<u>Poa secunda</u>	--	.6	1.5	1.7	.3	.4	.3	.2	.4	.6	.6
<u>Sitanion hystrix</u>	3.0	1.0	1.7	1.1	2.5	.8	.1	.6	.1	.6	.6
Litter and moss	65.1	59.5	56.5	54.2	50.0	80.2	47.3	46.5	46.9	45.8	45.8
Bare ground	3.3	6.4	9.5	12.3	8.4	4.1	23.0	25.4	26.1	27.4	27.4

Broadleaf Herbs

Cover and production of perennial forbs was approximately 50 percent greater in the enclosure than in the grazed areas (table 6). Silvery lupine (Lupinus argenteus), arrowleaf balsamroot (Balsamorhiza sagittata) and aster (Aster spp.) are the dominant forbs in all areas. The presence and importance of these three perennials increased with increased distance from the seeded shrubs. These plants did better in the open without the shading influence of antelope bitterbrush. In contrast, the production and percent ground cover of shade tolerant Montia perfoliata decreased with distance from the overstory shrubs.

Seeded Grasses

The density and herbage production of desert wheatgrass was not reduced by the overstory influence of antelope bitterbrush (tables 5, 6). Significant differences in cover by this species did not occur among quadrats positions. Ground cover provided by desert wheatgrass was approximately 28 percent less outside the enclosure than within the enclosure. In addition, the outside areas produce 62 percent less herbage. Grazing reduced the live cover and significantly decreased grass vigor. Yet, desert wheatgrass has been able to persist as the dominant understory species in the grazed area. It appears practical to improve the production of desert wheatgrass by decreasing the spacing between the shrub rows. However, the optimum spacing for bitterbrush is not known.

Bulbous bluegrass (Poa bulbosa) responded quite differently from desert wheatgrass to the presence of overstory shrubs. This short-lived perennial maintained greater cover and herbage production in the openings than as an understory plant. A similar pattern was recorded for the grazed and nongrazed sites. Protection from grazing resulted in slightly higher cover and yield figures, although the differences were not significant.

Native Grasses

The ground cover and herbage yields for both Idaho fescue (Festuca idahoensis) and Sandberg bluegrass (Poa secunda) were significantly greater in the quadrats located away from the seeded shrubs. These two grasses require open conditions to fully develop. Squirreltail (Sitanion hystrix) responded oppositely. Plants located directly beneath the shrubs were more productive. The native grasses were slightly favored within the enclosure. However, plant composition did not differ significantly for any quadrat within or outside the enclosure.

Litter and Bare Ground

In both the grazed and nongrazed areas, the accumulation of litter was significantly greater at a .05 percent confidence level beneath the seeded shrubs than in any other quadrat both within and outside the enclosure (table 5). Litter in quadrat 1 was 65 percent for the enclosure site and 80 percent for the same position in the grazed area. Within the enclosure the percent litter in quadrats two through five was similar, although significantly lower than for quadrat one. In areas outside the enclosure a similar pattern was recorded. However, the percent litter outside the enclosure was less in quadrat positions 2 through 5 in comparison to each similar quadrat position within the enclosure.

The average percent of bare ground was quite low for all quadrats within the enclosure. Quadrat 1 averaged about 3 percent bare ground. This figure increased with distance from the shrub. Quadrats in the grazed areas had a significantly greater

Table 6.--Herbage yields for grazed and protected sites recorded by meter quadrat positions--Case Creek, 1981

Species	Exclosure site					Grazed site				
	1	2	3	4	5	1	2	3	4	5
Quadrat positions:	gr/m ² plot									
Seeded shrubs										
<u>Purshia tridentata</u>	440.0	14.3	2.7	9.3	51.3	702.0	39.5	1.3	4.2	--
Native shrubs										
<u>Artemisia tridentata</u>	39.5	58.8	27.6	67.8	81.3	44.0	80.4	68.6	64.1	55.1
<u>ssp. vaseyana</u>	--	--	.5	1.5	--	--	.2	--	1.4	--
<u>Chrysothamnus nauseosus</u>										
Native forbs										
<u>Lupinus argenteus</u>	12.0	9.4	10.1	20.4	32.7	7.7	7.8	12.6	16.6	18.6
<u>Montia perfoliata</u>	2.9	--	--	--	--	--	--	--	--	--
<u>Other perennials</u>	--	--	--	11.7	20.3	.7	.2	.6	.8	.1
<u>Annuals</u>	.7	--	--	--	--	--	--	--	--	--
Seeded grasses										
<u>Agropyron desertorum</u>	174.3	172.5	174.6	110.6	130.1	112.2	90.6	90.1	81.5	80.7
<u>Poa bulbosa</u>	3.2	4.3	6.3	8.1	7.5	2.3	3.1	5.2	5.8	6.9
Native grasses										
<u>Festuca idahoensis</u>	2.6	3.5	3.5	8.1	7.7	1.9	3.8	5.5	5.8	10.4
<u>Poa secunda</u>	--	1.3	2.1	1.5	.7	.7	--	.3	.7	.5
<u>Sitanion hystrix</u>	11.5	2.1	6.5	3.7	7.0	2.1	.2	.9	.2	1.1
Total understory vegetation	246.5	251.9	231.2	233.4	287.3	171.6	186.3	183.8	176.9	173.4
Total vegetation	686.5	266.2	233.9	242.7	338.6	873.6	225.8	185.1	181.1	173.4

percentage of bare ground than similar quadrats within the exclosure. Quadrat readings taken beneath the seeded shrubs were similar in the grazed and ungrazed area. However, the percent bare ground was significantly higher in all other quadrats in the grazed areas when compared to the protected site. The percent bare ground in quadrat positions 2 through 5 was similar in the grazed sites, but much higher than for quadrat 1.

CONCLUSIONS AND IMPLICATIONS

Seeding grass and shrub seeds in separate drill rows is a practical method of reducing competition between antelope bitterbrush and perennial grass seedlings. Grass rows should not be planted closer than 12 to 15 inches (30 to 38 cm) from the seeded shrub rows. A wider spacing of about 24 to 30 inches (60 to 76 cm) is more beneficial.

Few shrub seeds become established and develop into mature plants even when this method of seeding is used. However, only a small return is required to produce a satisfactory stand. Care should be given to assure that seeds are properly distributed and positioned in the soil. Livestock grazing should be curtailed for 1 to 4 years to allow shrub seedlings to establish. Thereafter, grazing should be carefully regulated to avoid destruction of the young plants. Established stands of desert wheatgrass limit the natural regeneration of antelope bitterbrush. In addition, moderate grazing by cattle in the spring and summer months also reduces shrub seedling establishment.

The presence and density of a bitterbrush overstory control the composition and yields of understory herbs and smaller woody plants. The shading provided by erect forms of antelope bitterbrush enhances the production of shade tolerant species. The production of desert wheatgrass is increased while the yields of Sandburg bluegrass and Idaho fescue are decreased. Shade tolerant broadleaf herbs also respond positively to the canopy coverage. However, certain important forbs require open conditions to attain maximum productivity. Tall antelope bitterbrush plants reduce the density of both mountain big sagebrush and rubber rabbitbrush. When seeded with competitive understory grasses, antelope bitterbrush can be used to control these two woody species.

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POTENTIALS FOR THE MANAGEMENT OF
BITTERBRUSH HABITATS BY THE
USE OF PRESCRIBED FIRE¹

Charles H. Driver²

ABSTRACT

Observations on the results of prescribed fire and wildfire in ponderosa pine-bitterbrush-pinegrass habitats indicate potentials for use in managing antelope bitterbrush. Prescribed burns in early spring and fall when soil moisture was high resulted in vigorous sprouting, whereas hot burns resulted in seedling establishment.

INTRODUCTION

Reports on the ecological characteristics of antelope bitterbrush (Purshia tridentata (Pursh) DC.) with respect to its reaction to fire appear to be diverse. Have we misinterpreted the true fire ecology of this species and thereby possibly overlooked a tool for managing this important shrub?

Fire is commonly reported (Hormay 1943; Billings 1952) to be very destructive to antelope bitterbrush, practically removing it from its dominant position within the plant community of a typical habitat. However, on some occasions (Nord 1965), it has been observed that a small percentage of the plants recover by sprouting after burning under the most "favorable conditions." On these rare occasions not more than 30 percent of the burned plants give rise to vegetative sprouts, most of which succumb before the end of the first growing season. Moreover, a few reports in the literature indicate that in some areas of its natural range, populations of antelope bitterbrush have exhibited abilities to sprout reasonably well following burning. In fact, Clark (1979) reports 30 to 50 percent of the plants of this species sprouted after being burned in eastern Oregon. In addition, Blaisdell (1953) reported individual plants tended to continue to give rise to sprouts after reburning.

My limited observations (Driver and others 1980) on the response of antelope bitterbrush to prescribed fire directed me to the question: How can a dominant plant species of a pristine climax vegetational community with a known history of frequent fire occurrence not express characteristics that ensure its survival and perpetuation?

To investigate the possibility of using fire as a management tool for the culture of antelope bitterbrush one should examine the status of our knowledge on the subject of prescribed fire as covered by Martin and Driver (this proceedings). In addition, to accomplish the use of fire as a management tool we should examine Barney's (1975)

¹ Paper presented at the Bitterbrush and Cliffrose Symposium, Salt Lake City, Utah, April 13-15, 1982.

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definition of fire management as the "integrating of fire related biological, ecological, physical and technological information into land management to meet a desired objective." I will follow this with Wright and others' (1979) statement on fire as a tool of management: "One of the most fruitful areas within which to practice these concepts is in that part of our wildlands used for range and wildlife purposes."

These statements establish my objectives in applying the ecological characteristics of this important shrub species in relation to fire, to the need for improving the condition of critical winter range for mule deer.

My initial observations (Driver and others 1980) on the abilities of antelope bitterbrush to sprout following an early spring prescribed fire triggered my interest in this subject.

Table 1 shows the surprising range of 40 to 100 percent of the burned bitterbrush plants sprouted vigorously following prescribed fires within the ponderosa pine-bitterbrush habitat in the early spring. The study area was the Entiat River drainage designated as South, located 20 miles (32.19 km) north of Wenatchee, Wash. The natural fire frequency of the study site was determined to be as low as 6.5 to 10 years during an 80-year period before white people frequented the area. When similar prescribed fires were tried, however, in the same area in the fall, bitterbrush sprouting was only observed to range from 0 to 5 percent. In addition, a survey of all bitterbrush plants within a 35 acre (14.16 ha) area within a large summer wildfire site indicated only 5 percent of the burned plants exhibited vigorous sprouting 3 years after the fire. This site was in the vicinity of the prescribed fire area (South); the wildfire had occurred 2 years previously.

The effects of fires on seedling establishment were evaluated. Observations were conducted in the same general area indicated as South in table 1, in which ponderosa pine fuels resulting from precommercial thinning operations had been piled and burned in early fall. Within the charred-remains areas, ranging from 1/100 to 1/50 acre (40.47 to 80.94 m²), all vegetation including pinegrass (*Calamagrostis rubescens* [Buckl.]) had been completely destroyed. Three years after the burns, individual seedlings were observed at the density equal to 300 seedlings per acre (table 2). The seedling establishment on the spring prescribed fire plots indicated a density of only 50 per acre (124 per ha).

Table 1. Relative effects of prescribed burns and wildfire on sprouting of antelope bitterbrush.

Season of burn	% Sprouting range plants	Precipitation pattern	Location
Spring	50-88	Spring snow	North site
Fall	0-74	Fall rain	
Spring	40-100	Spring snow	South site
Fall	0-5	Dry fall	
Summer	3	Dry summer	South site

Table 2. Relative effect of prescribed burns and wildfire on antelope bitterbrush seedling establishment.

Type of fire	Season of fire	Average density/acre
Pile and burn	Fall	300
Prescribed burns	Spring	50
	Fall	105
Wildfire	Summer	18 of 20 plants flowering at 3 years and seeding at 5 years

Because the fall burns appeared not to be conducive to bitterbrush sprouting on these South study sites, soil and live plant moisture were probably limiting factors. Typically, no measurable rainfall occurred in this area for the 60 day summer period. A similar habitat and area with a known early fall rain pattern, some 70 miles (112.65 km) north of the Entiat site, located west of Winthrop, Wash., was brought to my attention by the fuels manager officer of the USDA Forest Service. The Winthrop District fuels management group had conducted a series of spring and fall prescribed burns in the ponderosa pine/bitterbrush/pinegrass habitat type over a similar 3 year period.

We surveyed the results of these prescribed fires on bitterbrush sprouting and seedling establishment. On transects one chain wide (66 ft or 20.12 m) progressing entirely across the widest dimension of the burned area, all bitterbrush plants were observed. The presence and absence of sprouting was noted on all burned plants as well as the occurrence of seedlings. The burned stands ranged from 10 to 30 acres (4.05 to 12.14 ha). A summary of the results is noted as the North location in table 1 and as fall burns in table 2. Prescribed fire in the North sites apparently yielded similar results to that of the South sites with relatively high percentages of burned plant sprouting after the spring burns. However, the fall burns tended to result in higher percent sprouting than similar burns in the South site.

DISCUSSION AND CONCLUSIONS

The data in table 1 from the observed sites indicate that prescribed burns conducted in the early spring, when the soil and live plant moisture appear to be high, tended to result in more than half of the plants giving rise to vigorous vegetative sprouting.

Prescribed burning in the fall, especially at the South site, when the soil moisture was thought to be quite low, resulted in few of the burned plants sprouting. When prescribed burns were conducted at North site, which typically exhibited a late summer and early fall rain pattern, a somewhat higher percentage of plants sprouted.

Bitterbrush stand establishment following fire demonstrates interesting trends (table 2). At one end of the spectrum in the spring burn sites that typically exhibited a low rainfall pattern following the fire, only 50 seedlings per acre (124 per ha) were observed regardless of location. In contrast to this the fall burn sites exhibit twice the density of seedlings. The explanation for this latter observation, however, is complex because the South burned more completely than the North. The observations on the seedling establishment on the pile and burn treatment offer

somewhat of a lead in that hot burns greatly reduce the vegetative competition from pinegrass for at least 3 years following the fire. This effect is thought to be a significant factor to bitterbrush seedling establishment. Regardless of the true ecological processes responsible for these results, hot burns in small areas within similar habitats appear to provide for bitterbrush seedling establishment.

The response of the bitterbrush populations at the South sites exhibiting vigorous sprouting pose an interesting question: could there be a difference in this population due to the history of natural fire occurrence?

Interestingly, many of the plants that sprouted exhibited lignotubers. Daubenmire (1974) describes this as a structure that gives rise to many adventitious buds and is usually located at the soil interface on the main stem of a woody plant. Lignotubers have been commonly observed on many of the shrub species found in the California chaparral. The structure is commonly associated with woody plants in communities typically exposed to frequent fires.

This indicates that the population I have been observing could have resulted from a long period of selection for sprouting abilities by a history of high fire frequency. Such actions could have led to the development of a sprouting ecotype. This may have been a feasible function as demonstrated by Blaisdell's (1953) report of high sprouting rate following a reburn treatment.

In addition, Blaisdell and Mueggler (1956) reported that sprouts appeared to be derived in two ways: "from an existing mass of dormant buds wholly or partly encircling the stem at ground level, or from a callus of meristematic tissue formed beneath the bark after treatment and encircling the stem." The former description of meristematic tissue appears to fit that given by Daubenmire (1974) characterizing a lignotuber. Therefore, Blaisdell's (1953) and Blaisdell and Mueggler's reports (1956), along with my observations appear to establish the basis for further investigations into the occurrence or development of genetically controlled sprouting ability in this shrub species.

In conclusion, fire could be a functional tool in managing antelope bitterbrush in habitats similar to those in which these observations were made. More specifically, prescribed fire used in early spring at the time of high soil moisture should ensure the possibility of many of the plants of this species giving rise to vegetative sprouts resulting in vigorous growth. Hot fires, especially during periods of low soil moisture, can lead to seedling establishment if a seed source is available. Therefore, many aspects of fire can play a vital role in the management of this vital wildlife browse shrub. Much more specific information is needed, however, to accurately prescribe the conditions for burning and fully understand the functions of fire in accomplishing the goals of managing this vital shrub resource.

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RESPONSE OF ANTELOPE BITTERBRUSH TO BURNING AND SPRAYING IN SOUTHEASTERN IDAHO¹

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ABSTRACT

Long-term response (1936-1979) of Purshia tridentata is reported for an August 1936 prescribed burn and an accidental 2,4-D spray in 1961. On unburned plots bitterbrush yields in 1966 were more than twice those on burned plots. Spraying with 2,4-D in 1961 resulted in relatively large increases in bitterbrush yields in 1966 and declines in big sagebrush studies on spring and late summer burning are included.

INTRODUCTION

Antelope bitterbrush (Purshia tridentata Pursh. DC) is a highly preferred browse species for big game on winter ranges in the Western United States (Julander and Robinette 1950; Robinette and others 1952; Hoskins and Dalke 1955; and McConnell and Dalke 1960). However, on many winter ranges overgrazing, decadence, or encroachment by big sagebrush (Artemisia tridentata Nutt.) has severely reduced the availability of bitterbrush for big game. Prescribed burning and spraying with herbicides are two techniques commonly used by land managers to renovate sagebrush-bitterbrush stands to make them more productive. Such improvement practices as well as some wildfires have not always been beneficial for bitterbrush.

This paper reports the long-term results from burning and the effects of spraying with 2,4-D on the response of bitterbrush and associated shrubs (mountain big sagebrush A. tridentata ssp. vaseyana; green rabbitbrush, Chrysothamnus viscidiflorus [Hook] Nutt.; and gray horsebrush, Tetradymia canescens DC) in southeastern Idaho. Recent work on spring versus late summer burning on bitterbrush is also reported.

REVIEW OF LITERATURE

Work done in California (Hormay 1943) and in the Western Great Basin (Billings 1952) showed that the rarity of sprouting of bitterbrush following burning in these areas would permanently eradicate the species. Also in California, Countryman and Cornelius (1957) found bitterbrush was completely absent from a burned area 6 years after wildfire, while on an adjacent unburned area bitterbrush constituted 91 percent of the vegetal cover. Nord (1965) observed that bitterbrush sprouting was frequent to abundant on 5 of 13 burns he examined in California; only where appreciable sprouting occurred was recovery successful. He concluded that the recovery process was slow, often requiring 30 or more years to be complete.

In southeastern Idaho Blaisdell (1953) reported that bitterbrush production was less on burned areas compared to unburned areas 15 years following the Fremont County prescribed burn and similarly 12 years following the Clark County prescribed burn.

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The areas were burned in September 1932 and August 1936, respectively. In the year following the Fremont County fire 49, 43, and 19 percent of the bitterbrush plants had sprouted in areas of light, moderate, and heavy intensity burning, respectively. However, the fire reduced the number of the original live plants, which resulted in lower production.

In central Oregon Driscoll (1963) reported that bitterbrush sprouting varied from 1 to 80 percent of the plants following summer wildfires. He concluded that environmental factors were more important in regulating sprouting success than were burn intensities. Production was not reported, nor has productivity been followed over time for these burns.

If done at the right time, spraying with herbicides is less detrimental to bitterbrush than burning. Blaisdell and Mueggler (1956) examined a number of spray areas in southeastern Idaho and found bitterbrush was unharmed on four sites and only slightly damaged on a fifth. In a controlled study, Mueggler and Blaisdell (1958) found bitterbrush was severely injured by burning, but was favored by spraying with 2,4-D. Spraying with 2,4-D before bitterbrush flowers resulted in less crown mortality and effective reductions in big sagebrush (Hyder and Sneva 1962). Although spraying appears to be more beneficial to bitterbrush than burning, the accompanying reduction forbs may not be desirable.

STUDY AREA AND METHODS

Our study was conducted on the Upper Snake River Plains at the U.S. Sheep Experiment Station approximately 11 mi (18 km) northeast of Dubois, Idaho, in Clark County. Blaisdell (1953) described the general vegetal character prior to burning as a dense stand of big sagebrush 2 to 4 ft (0.6 to 1.2 m) high with a fairly continuous stand of perennial grasses. The perennial graminoids were thickspike wheatgrass (Agropyron dasystachyum [Hook] Scribn.), bluebunch wheatgrass (A. spicatum [Pursh] Scribn. & Smith), plains reedgrass (Calamagrostis montanensis Scribn.), bluegrasses (Poa L. spp.) and sedges (Carex L. spp.). He indicated the vegetation composition was roughly 35 percent perennial grasses, 5 percent perennial forbs, 5 percent annual forbs, 40 percent sagebrush, 15 percent perennial forbs, 5 percent annual forbs, 40 percent sagebrush, and 15 percent rabbitbrush, horsebrush, and other shrubs. Bitterbrush was a small component of the total.

Topography is typical of the Upper Snake River Plains with lava outcrops interspersed with deeper soil swales. Soils are derived from basalt and aeolian sources. Textures in the soil surface are sand to silt loams. Long-term precipitation records at the headquarters show that annual precipitation averages 11.6 inches (295 mm) per year, with extreme variability from year to year. May and June receive the most precipitation on the average.

In 1936, 400 plots 100 ft² (9.3 m²) were systematically established within 1 mi² (2.6 km²) (T11N, R37E, Sec. 15) area and were measured using the weight estimate technique (Pechanec and Pickford 1937). Current growth of shrubs was measured. In August 1936, the area was burned. After burning, each plot was rated for burn intensity using the following classification: (1) heavy burn - trunk or main stem consumed by fire; (2) moderate burn - larger branches of sagebrush remaining, but smaller branches and twigs consumed; (3) light burn - smaller branches and twigs unburned, on leaves consumed by fire; and (4) unburned - no evidence of fire either in the understory or sagebrush crowns.

The subsequent years (1937, 1939, 1948, 1966, and 1979) most plots were remeasured using the same weight estimate technique. Some plots were not measured

because of sampling reduction, lost plots, or reburned plots. The actual number measured in the above years were 400, 400, 373, 297, and 387, respectively.

A wildfire in 1947 burned over a portion of the original area. Therefore, 27 plots were not measured in 1948. An adjacent area was sprayed with 2,4-D in 1961 and some of the herbicide drifted over the burn area affecting 150 plots. These plots were identified prior to the 1966 sampling. In 1966 only three-fourths of the total plots were measured in an effort to reduce the sampling load. The difference in the numbers of plots sampled has a bearing on some of the discussions that follow.

Only 40 plots contained bitterbrush in 1936. These were associated with lava outcrops and swales, and after burning were related to burn intensity. Since there were so few plots in each classification a rigorous statistical analysis was not possible. Therefore, the approach taken in this paper has been to make inference based on trends.

Blaisdell (1953) reported the vegetation production response through 1948, but did not make a separate statistical analysis for bitterbrush because he believed the data were inadequate. Harniss and Murray (1973) evaluated the results of the same burn through 1966 and concentrated on the principal shrubs, but they did not consider the effects of the 1961 spraying. In this paper the effects of burning and spraying on bitterbrush are reexamined for the Clark County burn during the 43-year period from 1936 through 1979.

RESULTS AND DISCUSSION

The results in the following sections are based on all plots that contained bitterbrush in any one of the 6 measurement years. These plots are analyzed in terms of burn intensities (described in the methods section), subtypes (plots on lava outcrops or on swale areas), and treatments (those burned in 1936, those burned in 1936 and sprayed in 1961). For each consideration the data represent averages for the respective groups.

Effect of Burn Intensities

Yields of bitterbrush, big sagebrush, rabbitbrush, and horsebrush and the percentage of these yields to the unburned yields in 1936 are given in table 1.

Prior to burning in 1936, bitterbrush yields averaged 13.7 lbs/acre (15.4 kg/ha) and reached a peak in 1966 regardless of burn intensity. The effects of burn intensity continued to persist as evidenced by smaller percentage yield increases with more intense fires. In 1966, the average bitterbrush yield of 106.3 lbs/acre (119.1 kg/ha) on unburned plots was more than twice the average yield of burned plots at 52.4 lbs/acre (58.7 kg/ha). Bitterbrush yields in 1979 declined considerably from 1966 levels due to a severe outbreak of tent caterpillar (Malacosoma californicum) from 1977 to 1979.

Big sagebrush was severely damaged by burning; until 1966 yields on the burned plots were considerably lower than those on unburned plots. In 1966 the average yields of big sagebrush on these bitterbrush plots were higher than those in 1936 even though 48 percent of the plots had been sprayed with 2,4-D in 1961. Rabbitbrush and horsebrush yields were reduced the year following burning, but increased through 1948. A positive relationship existed in both species between yield and burn intensities. Rabbitbrush yield declined in 1966 and 1979, while horsebrush yields increased in 1966 than declined in 1979.

Table 1.--Mean yields in pounds per acre and percentage of 1936 yield for bitterbrush, big sagebrush, rabbitbrush, and horsebrush in relation to burn intensity and year. U.S. Sheep Experiment Station, Dubois, Idaho.

Species	Year	Mean yield	Percent of 1936	Mean yield	Percent of 1936	Mean yield	Percent of 1936	Mean yield	Percent of 1936
Bitterbrush	1936	9.5	0	17.0	0	13.2	0	15.3	0
	1937	20.3	114	0.3	-98	0.0	-100	0.9	-94
	1939	51.6	445	12.3	-27	8.0	-39	2.2	-86
	1948	31.9	237	20.2	19	12.8	-3	10.5	-31
	1966	106.3	1024	64.5	281	44.3	236	48.4	217
	1979	27.2	188	12.4	-27	17.9	36	12.9	-15
Big sagebrush	1936	166.9	0	128.6	0	140.0	0	148.1	0
	1937	382.3	129	15.2	-88	0.2	-100	0.1	-100
	1939	353.1	112	16.6	-87	1.2	-99	2.3	-98
	1948	399.5	139	46.9	-63	89.1	-36	10.5	-46
	1966	165.1	-1	197.3	53	187.8	34	156.3	6
	1979	171.3	3	163.3	27	164.6	18	176.3	19
Rabbitbrush	1936	32.5	0	49.7	0	22.5	0	16.4	0
	1937	18.4	-43	24.0	-52	22.2	-1	13.5	-18
	1939	22.7	-30	60.8	22	62.0	176	59.7	264
	1948	22.2	-32	69.8	40	53.9	140	67.6	312
	1966	11.9	-63	11.0	-78	15.4	-31	4.5	-73
	1979	11.0	-66	12.6	-75	20.3	-10	6.7	-59
Horsebrush	1936	8.6	0	19.7	0	17.3	0	28.0	0
	1937	7.5	-12	7.8	-61	8.8	-49	15.1	-46
	1939	12.3	44	18.4	-7	33.4	93	64.2	129
	1948	5.7	-33	36.0	83	50.9	194	82.6	195
	1966	10.3	20	64.4	227	24.0	39	28.6	2
	1979	6.1	-29	18.3	-7	14.5	-16	19.0	-32
Number of plots by burn intensity:		31		21		36		58	

In 1936 bitterbrush was present in 40 of the original 400 plots (10 percent) and in 103 of the 297 plots (35 percent) sampled in 1966 (table 2). Of the 146 plots containing bitterbrush in 1 of the 6 years sampled, 27 percent contained bitterbrush in 1936 and 71 percent in 1966. The occurrence of bitterbrush in plots in 1936 and 1977 increased from 7 to 26 on unburned plots (271 percent) and from 33 to 77 on burned plots (133 percent).

Bitterbrush was present in 2 of the 33 plots the year following burning. By 1939 bitterbrush had made substantial yield increases and was present in 4 additional nonburned plots. In contrast, yields were well below 1936 levels in the burned areas (table 1), and occurred in only 12 plots. Through 1966--30 years after burning--bitterbrush yields were lower in plots that were burned at higher intensities.

Blaisdell (1953) reported that bitterbrush sprouting was reduced with higher burn intensities. The results from the present study suggest that burn intensity was not the only important factor in regulating bitterbrush recovery. It is likely that bitterbrush became established from seed in the nonburned areas and from sprouting and seed in the burn areas (table 2). After 1939 any increases in bitterbrush were probably due to establishment from seed. Of the original 33 burned plots, only 10 contained bitterbrush in 1939, which suggests that these are plots in which bitterbrush sprouted. The others became established from seed.

Table 2.--Number of plots containing bitterbrush by burn intensity and year. U.S. Sheep Experiment Station, Dubois, Idaho.

Year	Unburned	Light	Moderate	Heavy	Total
1936	7	6	10	17	40
1937	5	1	0	1	7
1939	11	4	4	4	23
1948	17	4	7	14	42
1966	26	15	28	34	103
1979	18	15	21	36	90

Large increases in grass and forb yields in the burned areas may have influenced the establishment of bitterbrush more than the direct impact of the fire itself. Unfortunately, the unusually low numbers of plots containing bitterbrush at the time of the burn did not permit an assessment of the direct impact. However, burning appeared to have a very long-lasting effect on bitterbrush recovery. This possibly was due to the competitive effects of the other vegetation.

Between 1939 and 1948, during the period when grass and forb yields on the burned areas were greatest, only 13 new bitterbrush plots were established. Much of the increase in yield was due to the rhizomatous, thickspike wheatgrass, which is a vigorous competitor. The most establishment came between 1948 and 1966 as grass and forb yields declined and big sagebrush yields increased. During this period 52 plots became established in the burn areas (208 percent) compared to 9 in the nonburned areas (53 percent). These figures could lead the reader to believe burning enhanced establishment, but they are misleading. When the establishment percentages are calculated on the basis of the total nonburned and burned plots, then 50 percent of the nonburned plots contained bitterbrush compared to 31 percent in burned areas.

In 1979 there was a reduction in the number of plots containing bitterbrush due to a severe infestation of tent caterpillar. However, there is evidence to suggest establishment was continuing between 1966 and 1979. Of the 103 plots with bitterbrush in 1966, 46 did not contain bitterbrush in 1979; and 33 plots devoid of bitterbrush in 1966 contained bitterbrush in 1979. If one could assume no loss from tent caterpillar while incorporating the gain from newly colonized plots, nearly 45 percent of the plots would have contained bitterbrush in 1979.

Effect of Burning and Spraying

Yields of the four species and percentages of 1936 yields are shown in table 3 for plots that were burned in 1936, and for plots that were both burned in 1936 and sprayed with 2,4-D in 1961.

Bitterbrush yields in 1966 were 620 percent greater than 1936 yields on sprayed plots compared to 241 percent greater yield for nonsprayed plots. On sprayed plots

Table 3.--Mean yields in pounds per acre and percentage of 1936 yield for bitterbrush, big sagebrush, rabbitbrush, and horsebrush in relation to burning only and burning plus spraying with 2,4-D. U.S. Sheep Experiment Station, Dubois, Idaho.

Treatment	Year	Bitterbrush		Big sagebrush		Rabbitbrush		Horsebrush	
		Mean yield	Percent of 1936	Mean yield	Percent of 1936	Mean yield	Percent of 1936	Mean yield	Percent of 1936
Burned 1936	1936	13.2	0	141.3	0	37.4	0	20.0	0
	1937	6.9	-48	78.1	-45	26.9	-28	10.5	-47
	1939	16.3	24	77.0	-46	72.2	93	33.9	70
	1948	16.5	25	134.0	-5	77.5	107	48.5	143
	1966	45.0	241	243.7	72	16.5	-56	30.3	52
	1979	21.1	59	131.1	-7	15.2	-59	15.4	-23
Burned 1936+	1936	10.3	0	152.3	0	11.4	0	21.8	0
Sprayed 1961	1937	1.5	-85	97.4	-36	8.3	-27	12.2	-44
	1939	8.4	-18	87.3	-43	24.6	116	47.7	119
	1948	23.2	126	174.5	15	38.1	234	61.1	181
	1966	73.9	620	84.1	-45	1.7	-85	28.4	30
	1979	7.0	-32	219.1	44	4.6	-59	15.6	-28

Table 4.--Number of plots containing bitterbrush by treatment and year. U.S. Sheep Experiment Station, Dubois, Idaho*

Year	Burned only	Burned and sprayed
1936	21	15
1937	2	3
1939	10	11
1948	25	17
1966	43	53
1979	49	35

*Does not include plots reburned in 1947

big sagebrush yields declined from 174.5 to 84.1 lbs/acre (195.6 to 943. kg/ha) (107 percent) compared to an increase from 134.0 to 243.7 lbs/acre (150.2 to 273.1 kg/ha) (82 percent) on nonsprayed plots between 1948 and 1966. There were greater reductions in rabbitbrush and horsebrush yields between 1948 and 1966 on sprayed plots than on nonsprayed plots. In addition, the occurrence of bitterbrush in sprayed plots increased from 17 to 53 (212 percent) compared to an increase from 25 to 43 (72 percent) on nonsprayed plots over this same time period (table 4).

Spraying in 1961 resulted in increases in yield by bitterbrush and decreases by other shrub species. Most of the yield increases were due to reduced competition from the other shrubs. Spraying also permitted greater establishment compared to the nonsprayed areas. While the occurrence of bitterbrush on sprayed plots increased 212 percent and 72 percent in nonsprayed plots between 1948 and 1966, it is noteworthy that bitterbrush disappeared from 39 plots in sprayed areas between 1948 and 1966 compared to 19 in nonsprayed areas. Although it is not possible to determine exactly when the plots became established, the yields in many plots in 1966 were quite low, suggesting that establishment was recent and probably occurring after spraying.

One might expect that spraying and burning would have a similar effect on establishment due to increased grass production. An explanation for the greater

establishment of bitterbrush on the sprayed areas is elusive. One explanation is that establishment may have proceeded immediately following spraying and before competition from grasses became severe.

Effect of Site

Mean yields and percentages of the 1936 yields for the four shrub species are given in table 5.

Bitterbrush yields were greater in all years on plots associated with lava outcrops compared to plots in swales. The increase in numbers of plots containing bitterbrush from 1936 to 1966 was 137 percent in lava outcrop sites and 200 percent in swales (table 6). However, when viewed relative to the total number of plots, bitterbrush occurred in 56 percent of the plots in the rocky sites compared to 21 percent of the plots located in the swales. Undoubtedly, postburn responses of other vegetation influenced the establishment of bitterbrush through 1948. Thereafter, a greater increase occurred proportionately in the swale areas. Part of the increase was due to the effect of spraying.

Table 5.--Mean yields in pounds per acre and percentage of 1936 yield for bitterbrush, big sagebrush, rabbitbrush, and horsebrush in relation to lava outcrops and swale sites. U.S. Sheep Experiment Station, Dubois, Idaho.

Subtype	Year	Bitterbrush		Big sagebrush		Rabbitbrush		Horsebrush	
		Mean yield	Percent of 1936	Mean yield	Percent of 1936	Mean yield	Percent of 1936	Mean yield	Percent of 1936
Lava outcrops	1936	20.3	0	153.3	0	31.9	0	14.9	0
	1937	8.0	-60	80.4	-48	22.9	-28	8.2	-45
	1939	27.7	37	79.8	-48	64.0	100	29.2	96
	1948	28.9	43	155.5	1	50.1	57	36.5	145
	1966	98.3	385	200.8	31	11.3	-65	29.1	35
	1979	28.7	42	172.0	12	16.6	-48	10.3	-31
Swales	1936	7.0	0	141.0	0	20.0	0	25.4	0
	1937	1.2	-82	86.6	-39	13.2	-34	13.7	-46
	1939	2.0	-59	77.4	-45	40.5	103	49.4	94
	1948	8.0	15	135.1	-4	60.0	200	67.9	167
	1966	23.6	240	141.1	0	7.8	-61	37.8	49
	1979	4.9	-29	169.0	20	6.7	-67	20.1	-21

Table 6.--Number of plots and percentage of 1936 numbers in relation to lava outcrop and swale sites. U.S. Sheep Experiment Station, Dubois, Idaho.

Year	Lava outcrop		Swales	
	Number	Percent	Number	Percent
1936	27	100	13	100
1937	5	19	2	15
1939	17	63	6	46
1948	28	103	14	108
1966	64	237	39	300
1979	51	189	39	300

In the swales areas 51 percent of the plots contained bitterbrush for the first time in 1966 compared to 21 percent in the rocky areas. All plots were sprayed suggesting spraying may have had an important influence on the establishment of bitterbrush.

Prior to burning in 1936, bitterbrush occurred in more plots on rocky sites (27) than in plots in swales (13) (table 6). In every year thereafter bitterbrush continued to be more prevalent on the rocky sites. Today, observations across the entire U.S. Sheep Experiment Station indicate that bitterbrush is actually more prevalent and productive in the swale areas compared to the rocky sites. The difference between data from 1936 and the present observations may be due to the extended drought preceding the burn.

An examination of all plot records for 1936 revealed that grasses, forbs, and shrubs were greater in the swales than on rocky sites. The vegetation production averaged 546.0 lbs/acre (612 kg/ha) in the swales and 446.1 lbs/acre (500 kg/ha) on the lava outcrop plots. During the period of below normal precipitation, competition for soil moisture was probably more severe in the swale areas due to a greater demand from a more luxuriant vegetation. As demand exceeded availability certain species were stressed beyond their tolerance and were reduced. On the rocky sites, even under reduced soil moisture conditions, more water may have been available for the shrubby component resulting in less loss proportionately. Total biomass was still greater in the swale areas compared to the rocky areas in 1936 in spite of the possible larger reductions in yields in the swale areas.

Sites with a heavier understory fuel load preheat the overstory more rapidly and effectively. This and heavier overstory fuel load give rise to fire of greater severity. Consequently, in swale areas where fuels were heavier, it is expected that the increased burn intensity lowered sprouting of bitterbrush and resulted in lower yields.

Big sagebrush and rabbitbrush yields were more erratic after burning with respect to yearly response and site. Horsebrush, on the other hand, was more productive in the swale areas over the 43 years.

Spring Versus Late Summer Burning

The original plots were measured in 1979 to terminate the 1936 burn study and to provide initial data for a comparison of spring versus late summer burning. In late August and early September of 1979 two burns of 160 acres (65 ha) in size were conducted. In mid-April 1981 another quarter section was burned. The yields of the four shrubs are given in table 7 by treatment and year.

Bitterbrush yields increased from 23.6 to 91.0 lbs/acre (26.4 to 102.0 kg/ha) from 1979 to 1980 on the area burned in the spring. Plots that were not burned in both the spring and late summer burned areas, showed increases in bitterbrush yields from 33.1 to 158.2 lbs/acre (37.2 to 177.3 kg/ha) from 1979 to 1981. This indicates that bitterbrush was likely recovering from tent caterpillar damage and that environmental conditions were favorable.

As expected, burning in the spring or late summer caused reductions in yields of all shrubs. Although the postburn yields of bitterbrush were less in the spring burn area (12 percent) compared to the fall burned area (29 percent), studies conducted at

Table 7.--Mean yields in pounds per acre and percentage of yields for bitterbrush, big sagebrush, rabbitbrush, and horsebrush in relation to spring and fall burning. U.S. Sheep Experiment Station, Dubois, Idaho.

		Bitterbrush		Big sagebrush		Rabbitbrush		Horsebrush	
		Mean		Mean		Mean		Mean	
	Year	yield	Percent	yield	Percent	yield	Percent	yield	Percent
Nonburned	1979	33.2	100	149.1	100	18.8	100	15.0	100
	1980	90.8	274	149.8	100	20.9	111	21.0	140
	1981	158.2	477	122.6	82	13.5	72	35.2	235
Spring ¹	1979	13.6	100	271.0	100	16.0	100	18.2	100
	1980	91.0	100	205.0	100	2.7	100	18.5	100
	1981	11.2	12	28.0	14	0.7	27	10.4	57
Fall ²	1979	9.4	100	217.5	100	7.4	100	10.6	100
	1980	2.7	29	17.6	8	3.7	49	7.3	69
	1981	2.5	27	9.8	5	5.7	77	11.2	105

¹Percent based on 1980

²Percent based on 1979

the Sheep Station suggest that sprouting following spring burning will be greater than late summer burning (Murray³) and will ultimately give rise to greater yields.

Blaisdell (1953) reported that 43 percent of the bitterbrush plants sprouted when burned in September at a moderate intensity. However, when burned in the spring (mid-April) at the same intensity, bitterbrush sprouted at an 80 percent rate (Murray³). Even though conditions of the vegetation and weather conditions produce burns of similar intensity, factors such as soil moisture greatly influence sprouting. When soils are moist at the time of the burn there appears to be less damage at the root collar where sprouting occurs.

Even when sprouting occurs plants may die depending upon the severity of the winter. If young sprouts are protected by ample snow during the winter many will survive the subfreezing weather. However, if they are exposed, most will perish. In addition, if young sprouts are grazed during the first year, overwinter mortality will increase (Murray³).

MANAGEMENT RECOMMENDATIONS

Evidence from this and other studies conducted in the sagebrush-grass region of the Western United States suggests that burning in mixed sagebrush-grass stands does not enhance antelope bitterbrush yields. Recovery of bitterbrush from fire required many years even though individual sprouted plants may achieve greater yields in a relatively short time. The principal problems arise from the large numbers of plants that are killed immediately or have low sprouting success, or where competition from other species reduces establishment of new plants.

³Murray, Robert B. Sprouting of bitterbrush in response to spring burning. (Manuscript in preparation.)

If fire is being contemplated to maximize yields of bitterbrush, then burning should be conducted early in the spring or late in the fall. To minimize damage to grasses and forbs burns should be done while they are dormant in the spring or before regrowth occurs in the fall. High soil moisture at the time of the burn appears to enhance sprouting of bitterbrush. Therefore, it is important to establish periods when these conditions prevail in each locality in which prescription burning is to be used.

On the Upper Snake River Plains our experience indicates that burns can be conducted successfully during mid- to late April. The actual period may vary depending upon winter conditions, especially in the amount of snow. During this period snow has recently disappeared, soil moisture is high, daytime temperatures often rise to 60 to 70° F (15.6 to 21.1° C) drying the previous year's litter, moisture in sagebrush is less than 100 percent (dry weight basis), relative humidities often fall below 30 percent, and the height of new grass growth is less than 2 inches (5 cm). In some years inclement weather does not permit burning, and usually the time when burns can be conducted is limited to only a few days.

The long-term effects of burning on bitterbrush recovery are an important consideration for land managers whose primary goal is to rejuvenate bitterbrush stands. Burns should be conducted under environmental conditions that produce low-intensity burns to enhance sprouting. However, even with increased sprouting from spring or late fall burning, overwinter mortality and damage from either livestock or big game grazing on new sprouts lowers overall sprout survival. Therefore, to ensure maximum regeneration and yields in a relatively short time consideration should be given to the desirability for planting or seeding bitterbrush immediately following burning.

When burns are prescribed to improve forage conditions for sheep, enhancement of bitterbrush is usually not an objective even though it is highly palatable to sheep. Here the goal is to increase forage and reduce the amount of defoliated shrub branches. The shrub skeletons left following spraying or burns of low intensity are undesirable, because the skeletons pull wool. As a result, sheep tend to avoid such areas. Consequently, burning should be done when conditions promote more intense burns.

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BITTERBRUSH MANAGEMENT ON THE BOISE WILDLIFE MANAGEMENT AREA¹

Gerald C. Scholten²

ABSTRACT

By using cattle and sheep in a managed grazing system, 16,500 acres of mule deer winter range have been improved. Grazing is used to increase bitterbrush vigor, stimulate bitterbrush leader growth, and improve forage composition. Artificial revegetation by seed and seedlings is used to enhance bitterbrush population in selected areas.

INTRODUCTION

The Boise River Wildlife Management Area is managed under a cooperative management plan by the Idaho Department of Fish and Game, Idaho Department of Lands, USDA Forest Service, USDI Bureau of Land Management, U.S. Army Corps of Engineers, and Highland Livestock and Land Company. Technical assistance is supplied by the Soil Conservation Service and the Agriculture Research Service-Northwest Watershed Research Center. The Idaho Department of Fish and Game is responsible for implementing the management program with approval from the cooperating agencies and private landowner.

The current management objectives are: (1) improve mule deer winter range, (2) increase upland game production, (3) provide public hunting, and (4) provide for wildlife appreciation. Proper bitterbrush management is essential to achieve the first management objective.

DESCRIPTION OF AREA

The 16,500 acre (6600 ha) Boise Front management segment is located 3 miles (4.8 km) east of Boise, along the Lucky Peak Reservoir. The area is steep with slopes to 60 percent and elevations range from 2,800 ft (850 m) to 5,900 ft (1800 m). The area has numerous canyons that drain into the Boise River. It is intermingled with heavy clay, loams, and sandy granitic soils. Precipitation ranges from 12 inches (30.5 cm) at lower elevations to 26 inches (66.0 cm) above 5,000 ft (1520 m). Most of this is received during the late fall to early spring. Temperatures range from -23° to 108° F (-30° to 43° C). Bitterbrush (Purshia tridentata), big sagebrush (Artemisia tridentata), gray rabbitbrush (Chrysothamnus nauseosus), and willow (Salix spp.) are the most common browse species. Bluebunch wheatgrass (Agropyron spicatum), bottlebrush squirreltail (Sitanion hystrix), cheatgrass (Bromus tectorum), and Sandberg bluegrass (Poa secunda) are the most common grasses. Key forbs consist of arrowleaf balsamroot (Balsamorhiza sagittata), phlox (Phlox spp.), and hawksbeard (Crepis spp.).

¹Paper presented at the Bitterbrush and Cliffrose Symposium, Salt Lake City, Utah, April 13-15, 1982.

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Cattle and sheep graze the area in the spring and early summer. Some sheep use occurs again in the fall. During the winter, 800 to 4,600 mule deer, and occasionally elk, use the area. The wide difference in deer numbers using the area was found to be related to temperature and water content of snow above the 5,000 ft (1520 m) elevation. A multiple regression equation has been developed that shows this relationship:

$$Y = 2039 + 200X_1 - 524X_2 - 3X_3$$

where Y is deer animal unit months, X1 is the mean January temperature in C°, X2 is the mean February temperature in °C, and X3 is the snow water content in mm of the nearest snow course marker on January 1. The multiple correlation coefficient is $r = 0.91$ and the standard error of estimate is 303 (Johnson and others 1980).

MULE DEER FOOD HABITS

Information on plant preference by mule deer and season of use is needed in bitterbrush management and overall management of the winter range. To get this information, rumen samples were collected from deer hit by cars on State Highway 21, which runs through the middle of the management area.

Rumen samples from 45 road-killed deer during January to April from 1971 to 1975 were analyzed by the Idaho Department of Fish and Game laboratory in Boise. The results showed that peak use, 30 percent, occurred during January, when snows are usually the deepest. This is based on air dry weights. Sagebrush use is also high, 29 percent, during periods of deep snow. Use of grasses increases as spring green up occurs and shrub use declines. Sage and grasses are considerably more abundant than bitterbrush, which indicates the importance of bitterbrush in maintaining the wintering mule deer population.

CATTLE MANAGEMENT

In 1970 a rest season grazing system (Lacey and VanPoolen 1979) was implemented to improve mule deer winter range and watershed values. The program had two goals: (1) to improve perennial grasses, and (2) to improve bitterbrush. The objectives for perennial grasses were to restore vigor, increase their percentage composition, provide additional ground litter, increase soil moisture, and reduce soil temperature. The program objectives for bitterbrush were to provide for maximum hedging to increase vigor and provide more forage, provide the required 2 years of rest for maximum twig growth, and increase bitterbrush density through greater seed production and trampling of seed by livestock.

The system, started in 1970, consisted of eight pastures--four pastures ranged in elevation from 2,800 to 3,600 ft (850 to 1100 m), and four pastures from 3,600 to 5,900 ft (1100 to 1780 m). The treatments consisted of early grazing, grazing after seed ripe, and rest. Only four of the eight pastures were used in a given year. A total of 194 head of cattle were used from April 1, or when range readiness occurred, until November 30. Table 1 shows changes.

Three private landowners included their lands in the program to be managed for mule deer winter range. In return they were allowed to graze on the cooperative agencies' lands. During 1972 one rancher sold his land to the Department of Fish and Game and another dropped out of the program because of ill health. From 1970 to 1974 cattle numbers ranged from 91 to 194 head. Observations show that cattle preferred bitterbrush from mid-May through June and again in September and October.

In 1976 the program was modified to allow 108 head of cattle to graze for 7 months. The cattle had been using an adjacent Forest Service allotment. This change

allowed a winter range for mule deer and elk to be partially rested. The pastures and rotation system remained the same. Samples of bitterbrush, using a southwest regional twig diameter-length regression equation, developed by Ferguson and Marsden (1977), showed the overall use was reaching the desired 30 to 40 percent hedging. Observation indicated that we were not utilizing grasses sufficiently in some areas of the pastures, thus creating a "wolf" (tough, rank) plant community.

Table 1.--Changes in grazing seasons and cattle numbers

Years	Grazing season	Maximum cattle numbers
1970-74	April 1 to November 30	194
1975	No grazing	
1976-80	April 1 to October 31	208
1981-82	April 15 to July 31	375

In 1981 the program was again modified to 3.5 months, 375 head allotment beginning April 15 or when range readiness occurred. This was done: (1) to achieve 30 to 40 percent cattle use on bitterbrush in the use pastures, to stimulate leader growth, and to hedge the bitterbrush plant; (2) to utilize grasses and forbs to reduce competition for browse species; (3) to utilize grasses and forbs to prevent "wolf" plant communities from developing; and (4) to insure that the range was maintained in an early or mid-successional stage.

The rotation was changed from a low pasture, high pasture, high pasture, low pasture, to a low pasture, low pasture, high pasture, high pasture system because of a late growing season in the high pastures. The first use pasture would receive heavy use and the three remaining pastures would receive moderate use. A pasture would have heavy use once in 4 years followed by 2 years of rest. Results of 1981 measurements indicated a 22.9 percent use by cattle on bitterbrush, up from 1 to 10 percent under the previous systems. The cattle use, plus the 10 to 60 percent deer use, is expected to keep the bitterbrush plants in good form, class, and vigor (table 2).

Table 2.--Bitterbrush utilization by cattle and mule deer, 1978 to 1982

Year	Percent cattle use	Percent deer use
1978	10.3	38.6
1979	5.5	22.1
1980	1.0	10.4
1981	22.9	60.0

DOMESTIC SHEEP MANAGEMENT

Highland Livestock and Land Company has an exchange of use agreement with the Idaho Department of Fish and Game for 1,200 sheep for 30 days in the spring and 30 days in the fall. In return, the Department manages 875 acres of their private lands for mule deer winter range. The sheep cross the project in alternating strips so that the same areas are not used year after year. The spring sheep use was developed to utilize grasses and forbs, and the fall use is for seed trampling.

ARTIFICIAL REVEGETATION

Artificial revegetation has been accomplished using planting equipment that includes a transplanter for bare-root seedling, a modified corn-vegetable planter for seed, a Hanson browse seeder, rangeland drill, and aerial seeding. All types have worked with varying degrees of success, often dependent on moisture after planting. When scalping was used to reduce competition, the 8 ft (2.5 m) dozer blade provided the best survival rate with 7 percent for seed and 19 to 69 percent for seedlings. A 3 ft (1 m) wide scraper provided a 21.7 percent seedling survival rate while the offset disk provided less than 10 percent. Areas planted with no scalp ranged from 0 to 22 percent seedling survival. Aerial seeding, rangeland drill, and Hanson browse seeders have been used in fire revegetation projects with good success for grasses and shrubs. Estimated costs per acre for the various planting methods are listed in table 3.

Table 3. Cost of planting by various methods

Planting method	Seed/seedling	Pounds or number plants/acre	Cost/acre
Transplanter	Seedling	1,200/acre	\$96-\$150
Corn-vegetable planter	Seed	2-3 lb/acre	25-50
Hanson browse seeder ¹	Seed	3-4 lb/acre	25-75
Rangeland drill	Seed	12 lb	35-40
Aerial ²	Seed	12 lb	11

¹Used with other range treatment, cost of seed only.

²Based on 1975 prices.

Insects, rodents, disease, drought, and fire all contribute to losses of bitterbrush. Probably the most severe has been intense wildfires. A wildfire in 1980 left 70 percent of the bitterbrush plants killed with 26 percent resprouting and 4 percent of the burned plants still alive. In 1981 a wildfire killed 91 percent of the bitterbrush plants with only 2 percent resprouting and 7 percent of the burned plants still alive. The Boise Front has a history of wildfire, making fire control and prevention essential. This, coupled with good range management, is essential for enhancement of the mule deer population and watershed protection.

CONCLUSION

A well-managed grazing system can be used to enhance bitterbrush populations through hedging and periodic utilization of the grasses and forbs that reduce competition to the browse species. Artificial revegetation can be used to improve critical mule deer winter ranges. Soil type, moisture condition after planting, methods of planting, and rodent densities can play a key role in the success of the planting. Natural reproduction of bitterbrush has been occurring mainly from rodent caches. Wildfire prevention or control is essential in maintaining the bitterbrush populations. Prescribed burning may be a viable management tool to improve bitterbrush stands.

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ROTOMOWING ANTELOPE BITTERBRUSH--PRELIMINARY REPORT¹

Robert D. Jones²

ABSTRACT

In southeastern Idaho a hand pruning and rotomowing project was undertaken to try to improve the Juniper Mountain deer winter range. Results from the hand pruning trial indicated that the more heavily bitterbrush was pruned the better it responded with increased growth. Based on this, the rotomowing technique was developed. Preliminary results indicated this is a successful tool for this area.

INTRODUCTION

The deteriorating trend of an antelope bitterbrush (*Purshia tridentata* [Pursh] DC) deer winter range has been a problem facing land managers and big game managers for many years. Usually the areas in poorest condition are the most heavily used portions of the winter ranges. Managers may be reluctant to try new or unproven vegetation management techniques because they do not want to sacrifice what little deer winter range they have. The result is that the stand continues to deteriorate and the amount of critical forage available to the deer herd continues to decline.

Most managers today realize they need to try something to keep their bitterbrush stands in good condition or risk complete loss. Techniques they find in the literature include burning, chaining, rolling or crushing, riling, rotobeating, and rotomowing (Driscoll 1963; Ferguson and Basile 1966; Giles 1970; Guinta and others 1978; Schnoegas and Zufelt 1965). Different results using different techniques may occur with the same treatment due to various factors, including time of year the treatment was performed, phenological stage of the plant, soil conditions, climatic conditions, ecotypic variation of the plant stands, or a combination of these factors. After considering the variables the manager chooses the technique(s) and tests it on a site. This is what the Bureau of Land Management has done in selecting the rotomowing technique to maintain the Juniper Mountain bitterbrush deer winter range.

TREATMENT AREA

The Juniper Mountain area is 10 miles (16 km) northwest of St. Anthony, Idaho. Soils in the area were once active sand dunes that have been vegetated by antelope bitterbrush, rabbitbrush (*Chrysothamnus* spp.), basin big sagebrush (*Artemisia tridentata* spp. *tridentata*), chokecherry (*Prunus virginiana*), Utah juniper (*Juniperus osteosperma*), and numerous forb and grass species. Precipitation in the area ranges from 16 to 18 inches (40.6 to 45.7 cm) annually.

Bitterbrush stands in the area have matured and are beginning to show a downward trend in conditions. The sagebrush is overaged and overgrown and is providing very little forage to wintering deer, but it does provide hiding cover. Junipers found in the area are scattered. At this time they do not appear to be increasing.

¹Paper presented at the Bitterbrush and Cliffrose Symposium, Salt Lake City, Utah, April 13-15, 1982.

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METHODS

The first phase of the two-part rotomowing project was a study to determine if pruning bitterbrush would have a beneficial or detrimental effect on the plants. The second phase was to evaluate the response of bitterbrush to the rotomowing technique and big game response to the project.

In 1978 a hand pruning study was started to determine the effect and response of pruning on bitterbrush. Three transects, each consisting of 20 tagged plants, were established. Transect A served as a control transect and the plants remained unpruned. Transect B was moderately pruned with some of the lower and upper branches removed. Transect C was heavily pruned with most of the plant growth removed except one or two stems. By having the different levels of treatment we hoped to determine which pruning intensity stimulated the most regrowth.

Leader growth was measured to the nearest centimeter on each of the tagged plants following each of the next 2 growing seasons. The summarized data were then plotted to illustrate the relationship between pruning intensity and leader growth (fig. 1). Results showed favorable response from heavily pruned plants. Based on these results and the literature, the large-scaled rotomowing treatment was started in 1980. An 8-ft (2.44 m) rotary mower was powered by a rubber-tired farm tractor. The mower blades were held 12 to 14 inches (30.5 to 35.6 cm) above the ground to chop up the decadent brush, but to not damage the seedlings and younger growth in the stand. Each treatment area was irregular in shape and greater than 5 acres (2.02 ha) in size, but no larger than 40 acres (16.2 ha).

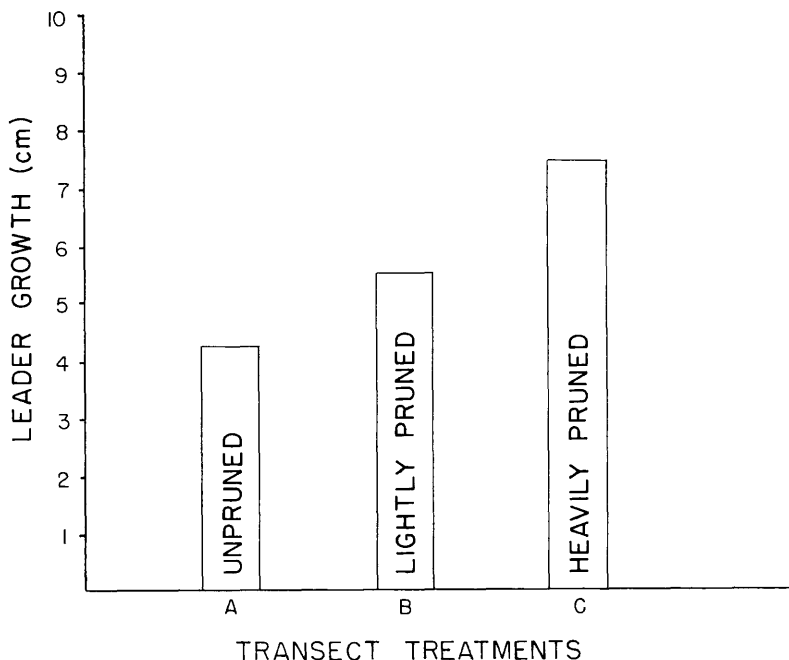


Figure 1.--Results from hand pruning study.

One treatment area was done in the fall and the others in the spring. Both the fall and spring treatments were done on dormant plants. A total of 400 acres (162 ha) were treated in the first project.

A 5-year monitoring study was established to document leader growth characteristics, big game vegetation use, and visual changes. Leader growth, to the nearest centimeter, is documented via four transects in the treated and untreated areas. The first years leader data were subjected to an analysis of variance. Six big game utilization transects were established in the treated and untreated areas.

RESULTS AND DISCUSSION

Results from the 2-year hand pruning study indicated that pruning increased the production of bitterbrush (fig. 1). Plants on transect A had an average leader growth of 4.16 cm. Plants on transect B, the moderately pruned transect, had an average leader growth of 5.46 cm. Plants on transect C, the heavily pruned transect, had an average growth of 7.30 cm. Although the original transect data could not be statistically analyzed, the general pattern through the treatment levels was that growth increased when plants were heavily pruned. These results, along with some smaller treated test areas, indicated probable success on a larger treatment project.

Data results between the mowed and the unmowed areas showed a significant difference in the average leader growth. No significant difference could be found due to the season of treatment (table 1). Leader growth in the treated areas was 15.8 cm and 13.7 cm for the fall and spring treatments, respectively (fig. 2). During the same growing season the untreated areas only produced average leader growth of 3.41 cm and 7.22 cm for fall and spring treatment areas, respectively.

Table 1.--Analysis of variance showing mowed versus unmowed and the effect of season and treatment results

BITTERBRUSH ROTOMOWING PROJECT			
	$F_{(1,48)} = 7.17, P$		
<u>Fall Treatment</u>	<u>DF</u>	<u>MS</u>	<u>F</u>
Mow versus unmow	1	1,228,998	246.34*
Error	48	4,989	
TOTAL	49	1,233,987	
<u>Spring treatment</u>			
Mow versus unmow	1	340,973	87.9*
Error	48	3,879	
TOTAL	49	344,852	
<u>Season</u>			
Spring versus fall	1	32,973	4.57 NS
Error	48	7,220	
TOTAL	49	40,193	

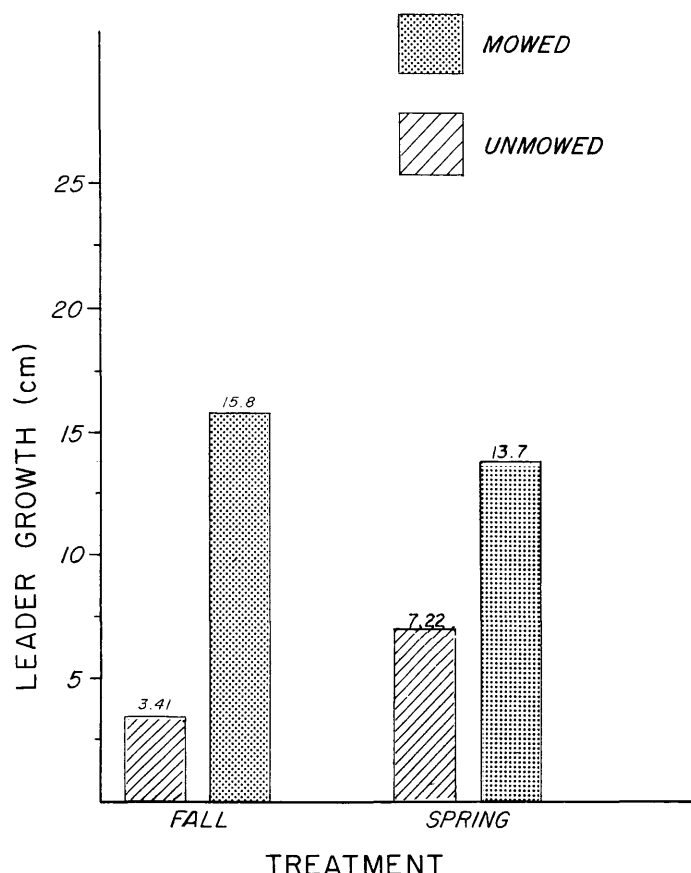


Figure 2.--Results from rotomowing showing leader growths from treatments in the fall and spring.

No mortality studies were done in the treatment areas prior to the project. Estimated mortality due to the treatment was less than 5 to 8 percent. This small loss is not expected to have a long-term detrimental effect on the productivity of the area.

Game and land managers want to know how long it will be before the treated areas produce usable forage and if temporary loss of production will be detrimental to wintering game. To answer these questions, the treatment areas were monitored throughout the winter months and vegetation utilization transects were read in the spring.

Results indicated that the treated areas had an average of 62 percent use (Idaho Fish and Game; and Hormay 1943) and adjoining untreated areas an average of 34 percent. Visual observations in the area supported the transect data. Deer were observed in the treatment areas every time they were visited; 77 animals were the most counted in a treatment area at one time. Because of such concentrations, the treatment areas had to be five acres (2.02 ha) or larger and numerous enough to accommodate the number of deer. The 25 to 40 acre (10.1 to 16.2 ha) treatment areas appear to be the most desired size, but there must be enough of them present to keep the use at an acceptable level.

Considerable flexibility is built into the use of this technique because season of treatment had no significant effect on the project success (fig. 2). Managers usually have to program for money in an annual work plan or have to accomplish a considerable amount of work during a limited time. The flexibility of the treatment allows two opportunities to accomplish the work during a field season when the money and/or time is available.

Two unexpected results developed from the treatment technique. The first was the increased production of grasses and forbs. Although deer winter diets consist mainly of browse, forbs and some grasses are used, particularly in the spring when greenup begins.

The second unexpected result was the possible segregation of use areas. Deer appeared to use the treatment areas while they were snow free and available, and then they moved into taller stands of bitterbrush when the snow had covered the treatment areas. This foraging response relieves browsing pressure on the taller stands of bitterbrush and sagebrush during periods of low snow accumulation. After snow has covered the shorter forage, the deer have a basically untouched forage supply to carry them through the deeper snow periods.

SUMMARY

Rotomowing antelope bitterbrush in the area west of St. Anthony, Idaho, initially appears to be a very useful technique in returning overaged and nonproductive big game winter ranges to highly desirable winter foraging areas. It can also be used on younger stands to avert deterioration.

A 5-year monitoring study was established to document the long term effects of the treatment. The first year's results showed there was an average leader growth, in the treated areas, of 15.8 cm and 13.7 cm for the fall and spring treatments, respectively. Big game use transects showed that deer, on an average, were able to use at least 62 percent of the vegetation during the first winter after a complete growing season. This high level of use indicates that treatment size and frequency must be considered during project layout in order to eliminate over-utilization and destruction by wintering big game.

Two unexpected results were gained from the project. There was increased grass and forb production in the treated areas. There also appeared to be a segregation of winter use areas by the deer.

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Section 5. Animal Relationships



ENTOMOLOGY OF ANTELOPE BITTERBRUSH¹

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ABSTRACT

Antelope bitterbrush is host to over 100 phytophagous insects, best known of which are species that defoliate, or infest fruits. Many other insect visitors range from perchers to pollinators to parasites and predators. In need of study are the susceptibility of ecotypes and hybrids; flower visitors; root infesters; plant disease vectors; and insect-plant community interrelationships.

INTRODUCTION

Antelope bitterbrush (Purshia tridentata [Pursh] D. C.) and its natural hybrids is a diverse shrub occurring in 11 western states and British Columbia on 340 million acres (138 million ha) over a wide range of climatic and soil conditions (Hormay 1943, Nord 1965). In its southern range, antelope bitterbrush intermingles with a close relative, desert bitterbrush (Purshia glandulosa Curran), insects of which are unstudied.

The use of antelope bitterbrush for browse by wild and domestic ungulates is addressed elsewhere in the symposium and in the literature (Basile 1967; Giunta and others 1978). What is not well publicized is its exceptional attractiveness to insects. Due largely to its wide occurrence and its abundant and fragrant yellow flowers, bitterbrush hosts an exceptional diversity of insects (Furniss 1972). Many are phytophagous in their habit, feeding on foliage, sucking juice, or infesting the bark or roots. Others are probably just perchers or somewhat chance visitors, perhaps attracted to the flowers; for example, parasitic wasps that are kept alive by nectar until their various insects hosts become available. Doubtless, many insects spread pollen from flower-to-flower in their travels, including flies and beetles besides the fabled bees. Others, such as spiders and predacious insects, lurk or hunt for their prey amongst the canopy.

Few of these insects have been identified and even fewer have been studied to determine their biology. Generally, only an immature stage is observed doing damage, whereas species descriptions are invariably based on the adult stage. In such instances, specific identification is impossible until the adult is reared from associated immature specimens, often a difficult or fruitless undertaking.

¹Paper presented at Bitterbrush and Cliffrose Symposium, Salt Lake City, Utah. April 13-15, 1982.

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METHODS

I used a standard aerial sweep net to collect insects in flight around bitterbrush. The net was also held beneath branches that were struck to dislodge insects on them (fig. 1). I gathered more detailed information by patient, close observation of shrubs for insects, webbing, defoliation, or galls. Branches were carefully clipped so as not to disturb insects on them, then scrutinized through a hand lens or microscope. That way, mites, eggs, and small insects could be seen. Branches were also enclosed in clear plastic bags and taken to the laboratory in a cooler where insects including larvae and parasitic wasps showed up on the inside surface. These same bags served as rearing containers for insects such as mature caterpillars that were about to pupate. Less mature insects had to be provided fresh foliage or were reared on potted plants in the greenhouse. This method avoided parasitism and enabled more intensive observations than were possible in nature.

Diapause was sometimes a problem in rearing immature insects to adults. I usually split specimens into lots for different treatment consisting of exposure outdoors over winter or refrigeration for 90 days in moist material in petri dishes; however, both methods resulted in high mortality.



Figure 1.--Insects were collected from bitterbrush by various means including an aerial net held beneath branches that were struck with a stick.

INSECTS OF BITTERBRUSH

What insects inhabit bitterbrush? Or a better question: What insects inhabit or benefit from bitterbrush and its hybrids, and how do they differ elevationally, geographically, seasonally, and by shrub age, phenology, and community makeup?

Unfortunately, bitterbrush insects are so poorly known that relatively few examples are available to answer these questions. A small and biased portion of the shrub's distribution has been sampled--and then only for a limited number of insects. The collecting tends to occur where cooperating range scientists conduct their work or where an outbreak is handy or happens to be reported. Perhaps 90 percent of my records came from the following areas: South Fork Salmon River, Payette River, and Boise River (Idaho); in the vicinity of Ephraim, Utah; and restricted localities in northern California, northeastern Oregon, and western Montana.

Ten years ago I listed 81 insects and mites that feed on antelope bitterbrush (Furniss 1972). The list has grown past 100 since then, and several times that figure will perhaps be collected eventually. Not included in the list is a much larger number of predacious insects and spiders (the latter are virtually unidentified, though common), parasites (although many are known, and all the phytophagous species

probably have them) and hordes of flower visitors. The roles of flower visitors are unstudied, but antelope bitterbrush is self-incompatible (Blauer and others 1975), and those insects likely play a profound role in pollination and hybridization.

TAXONOMIC DISTRIBUTION

The frequency of known phytophagous insects is shown in the following tabulation (Furniss 1972):

<u>Order</u>	<u>Family</u>	<u>Species</u>
Coleoptera	3	8
Diptera	1	3
Hemiptera	6	20
Homoptera	7	19
Lepidoptera	10	20
Orthoptera	1	5
Thysanoptera	1	1

Caterpillars (Lepidoptera), and sap-sucking insects (Hemiptera, Homoptera) constitute the most numerous species of insects collected from antelope bitterbrush, although their greater diversity does not preclude equal or greater importance of other orders. Because sap-sucking insects can transmit diseases of other plants, it is logical to investigate them as possible sources of disease on bitterbrush. So far, nobody has done so.

SOME COMMON AND IMPORTANT INSECTS

Most of the listed insects on bitterbrush are too poorly studied to permit their discussion. Some exceptions are presented here (see also Furniss and Barr 1975; and Furniss and Krebill 1972).

Species That Damage Flowers and Fruits

In April 1961, 600 flower buds were selected for weekly observation until seed drop, near Boise, Idaho (Ferguson and others 1963; Basile and others 1964). One hundred developing fruits on adjacent shrubs were collected weekly and examined for insect damage. Below are results of the study by percentage of plants damaged by insects (25 percent of seeds were normal):

Buds, flowers	
Thrips and unknown	6.5
Fruits, seeds	
Gelechiid caterpillars	5.0
Seed midge	6.8
Unknown insect	0.7
Shriveled or spotted	56.0 ³

The seed midge (believed to be a species of *Mayetiola*) had never before been reported on bitterbrush. We found that eggs were laid between the calyx tube and husk early in May. After hatching, up to a dozen orangish larvae mine through the husk and evidently feed on the developing seed, causing it to shrivel and blacken. The mature larvae form a puparium that, because of its appearance is called the flax-seed stage. Infested fruits are easily recognized by their more narrow appearance and because they persist on the plants (fig. 2) after normal fruits have dropped.

³About one-fifth of these seeds were black and shriveled, characteristic of the condition associated with feeding by *Chlorochroa sayi* Stal. The remainder were spotted, cause of which is unknown but thought to involve sucking insects.



Figure 2.--Fruits infested with midge larvae did not grow to normal width, and were retained long after normal seeds had dropped (January photo).

The gelechiid caterpillars were Filatima sperryi Clarke and Gelechia mandella Busck. After hatching, the first-instar caterpillars bore into the fruits and feed on the nutritious seeds, plugging the entry with their silk (fig. 3). Later they bore out through a clean hole and spin a silken web and tunnel to which they retreat when not feeding on leaves. The partially eaten leaves dry and cling to the silk. I have seen foliage of young shrubs in Valley County, Idaho, heavily damaged by these caterpillars. The webs gave the shrubs a silvery halo appearance when backlighted.

Feeding on fruits by Say's stink bug, Chlorochroa sayi (Stal) (fig. 4), was the cause of nonviable, blackened seeds (Ferguson and others 1963; Basile and Ferguson 1964; Ferguson 1967).



Figure 3.--Fruits destroyed by mining of first-instar gelechiid caterpillars. Entry holes are plugged by silk; caterpillars exit through open holes to feed thereafter on leaves.

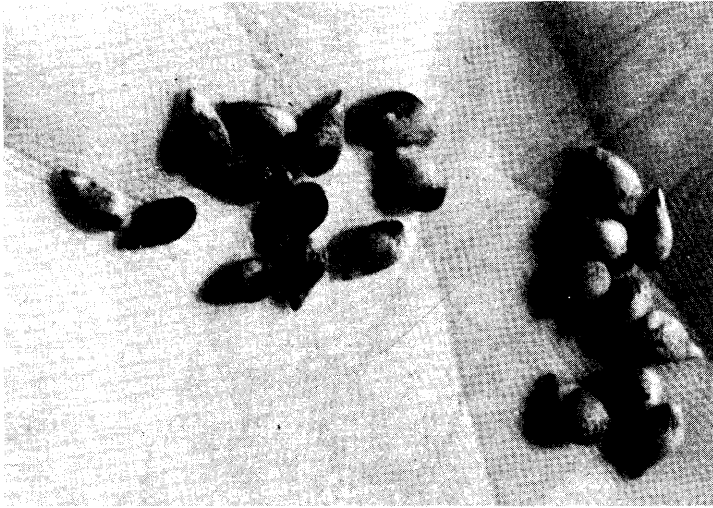


Figure 4.--Blackened appearance of seeds on left is due to feeding by stink bugs.

DEFOLIATORS

In a query to departments of fish and game in States and Provinces of Western North America and to other people involved with shrubs, I asked what insects were their greatest concern. Most replied that tent caterpillars (Malacosoma californicum Packard) on bitterbrush were most common. While I found this interesting, it is not representative of the true situation because the tents are conspicuous and most insects aren't. I have concluded after much experience that most insects are unseen by anyone. Their damage is often minor and nearly always subtle.

Although tent caterpillars have been recorded defoliating and killing bitterbrush over thousands of acres (Clark 1956), I have noted that tents (fig. 5) occur commonly on relatively few plants and seldom persist beyond a year. Nonetheless, this insect is potentially explosive, destined to give trouble at intervals. Duration of such outbreaks is apt to be short, however, due to a native virus that is rampant at high larval densities (Clark 1955; Clark and Thompson 1954).



Figure 5.--Tent caterpillars congregate on their tent when not feeding.

Recently, the walnut spanworm, Phigalia plumogeraria (Hulst) dramatically defoliated a seed orchard near Nephi, Utah (Furniss and Van Epps 1981; Van Epps and Furniss 1981). On May 17, 1979, the orchard appeared normal and plants were in full bloom on May 22. We now know that there had to be hundreds of thousands of larvae on the shrubs during those days--yet their presence went undetected until the next visit to the orchard on June 6 when the shrubs were found to be stripped of foliage and flowers. In the laboratory, I determined the walnut spanworm cycles through its larval (feeding) stage in an average of only 25 days at 70°F (21°C). The larvae had five instars, each exponentially greater in size than the previous one. The fourth and fifth instars (fig. 6) consume foliage at a rate many-fold that of earlier instars.

This event emphasizes a point: Vast populations of eggs or young caterpillars could be present, even in a small seed orchard, and nobody would know. Damage caused by loopers during their first two or three instars is subtle--consisting often of etching parts of leaf surfaces. But, with the increase in physical size to the fourth and especially the fifth instar, the larvae not only require much more food, but they are equipped with the strength and equipment to do so in large quantities. In these later instars, they reach out and guide edges of leaves into a notch in their labrum, whereby the leaf is fed into their cavernous mouths like hay entering a baler. Prior to the Nephi orchard defoliation, the walnut spanworm was unknown on bitterbrush, and unknown in Utah except for a few adults collected in flight.

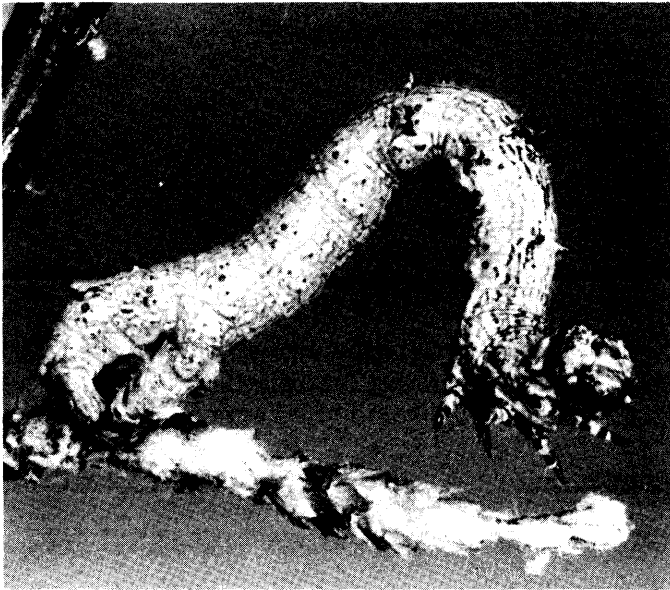


Figure 6.--A mature (fifth instar) walnut spanworm about to polish off the remnants of bitterbrush foliage. Such larvae stripped a Utah seed orchard of its leaves and developing fruits in 2 weeks.

The mountain mahogany looper, Anacamptodes animata profanata (Guen.), periodically attains epidemic numbers on bitterbrush. Prior to 1961, this species was known only from adult moths collected in flight without knowledge of its hosts or biology. Then it suddenly defoliated thousands of acres of curlleaf mountain mahogany in Owyhee County, Idaho (Furniss and Barr 1967). Intermingled bitterbrush and other shrubs were also defoliated. The infestation was reported by a rancher who was annoyed while riding his horse by webbing hanging from the tree-like mountain mahogany. I used that clue to relate the defoliation to presence of many pupae in the soil beneath defoliated shrubs. I subsequently learned that the pupae overwintered there and that adults emerged at night in the spring to lay eggs on the shrubs. The larvae vary amazingly in color and marking depending on factors such as crowding, host plant species, and environment, making their identification difficult.

Another defoliator, which I call the snailcase bagworm, *Apterona crenuella* Bruand (fig. 7), came here from Europe. Interestingly, the form (*helix*) that we have reproduces parthenogenetically--so we have only females, although both females and males occur in Europe. So far, not a great amount of damage has occurred to bitterbrush, which is but one of its many hosts.

Still another defoliator that appears to have been introduced, at least into Idaho, is the western tussock moth, *Orgyia vetusta gulosa* (Boisd.) (Furniss and Knopf 1971) (fig. 8). In the 1950's it defoliated bitterbrush and other shrubs near Idaho City. At that time, a smoke jumper contingent was in Idaho City, generating the possibility that some firefighter may have unknowingly brought back among his belongings the nucleus of this population. It seems to become epidemic only at fairly lengthy periods and is controlled by a native virus.



Figure 7.--Snailcase bagworm larvae on bitterbrush. The insect was introduced accidentally from Europe.

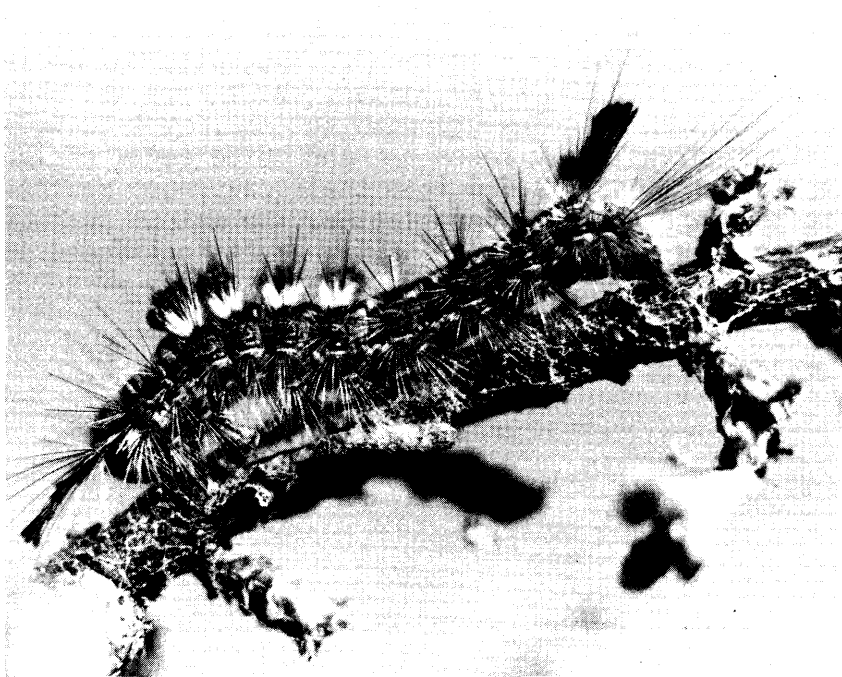


Figure 8.--This western tussock moth caterpillar is part of a disjunct population thought to have been accidentally introduced into southwestern Idaho from its more westward range.

CONCLUSIONS AND RECOMMENDATIONS

Although the diversity of insects on bitterbrush is actually a stabilizing factor in the plant community, the potential exists for outbreaks should natural controls fail or if new species are introduced.

Further research should include intensive study of predators (including spiders, which are virtually unstudied) and parasites of phytophagous insects; the kinds and relationships of flower visitors, including pollinators; root infesting insects; possible insect vectors of diseases of bitterbrush; differential susceptibility (or resistance) of hybrids and ecotypes to specific insects; surveying insect species and their abundance in the various bitterbrush provenances, and on hybrids and related species: Stansbury cliffrose and apache-plume; and insect-bitterbrush plant community interrelationships.

Whoever seeks to study bitterbrush insects will find that shrubs in general are looked on by many as undesirable, and likewise, shrub insects as being less important than those infesting trees. Researchers will also face difficulty in obtaining specific identification of bitterbrush insects because some are not described, others are described poorly, or the taxonomy of a group is confused. More often the insect stage concerned is immature and seldom included in the species description. Fortunately, however, I have usually succeeded in getting help from taxonomists to unravel the identity of important species (see Acknowledgments).

Caution should be taken to avoid directing research only on species causing the most obvious current damage or which are most abundant at the time. Some insects have remained at low levels for decades, only to explode and defoliate and kill extensive stands of shrubs. A concerned person should make every effort to study everything about those insects--then interpret their importance.

Finally, I recommend keeping an eye on other components of the bitterbrush community. Insects and other factors that adversely or beneficially affect the regeneration, vigor, and longevity of other vegetation can affect bitterbrush as profoundly as insects acting directly on bitterbrush. For those reasons, a good knowledge of community relationships is needed to develop management practices that benefit more than they harm.

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NUTRITIVE VALUE OF ANTELOPE AND DESERT BITTERBRUSH,

STANSBURY CLIFFROSE, AND APACHE-PLUME¹

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ABSTRACT

For range plants that are grown for animal consumption, nutritive value is of paramount importance, both qualitatively and quantitatively. A brief description is given concerning the digestive process and needs of consuming animals as a basis for judging the nutritive value of bitterbrush, cliffrose, and Apache-plume. Also discussed are the cyclic use of antelope bitterbrush and the feasibility of improving the winter level of its nutrients.

INTRODUCTION

For range plants that are grown for animal consumption, nutritive value is of paramount importance, both qualitatively and quantitatively. The nutritive value of any plant is judged by its ability to supply the nutrients to meet the physiological requirements of the consuming animal. Quantitatively the nutrient needs of animals vary according to species, age, size, and activity (National Academy of Sciences 1975; Maynard and others 1979). Qualitatively, nutrient needs of animals can be classified as energy-producing compounds, protein, minerals, and vitamins. (Water is also an important nutrient but is not considered in this paper.)

THE DIGESTIVE PROCESS

A basic understanding of the digestive processes and how different digestive tracts affect the digestive process is important in understanding the nutrient needs of range animals.

By definition, digestion is a process in which food is broken down into small particle size and finally solubilized for absorption and use in the body (Maynard and others 1979). Ingestion is the first step in the digestion process. In the mouth, food is broken up by mastication and mixed with saliva, which acts as a food softener and a lubricant. Large differences exist among animal species as to the extent food is masticated in the mouth. Ruminant animals such as cattle, sheep, and mule deer thoroughly grind grass by regurgitating and remasticating the food. Cattle are poor at grinding small seeds, whereas sheep and mule deer are able to break up small seed.

¹Paper presented at Bitterbrush and Cliffrose Symposium, Salt Lake City, Utah, April 13-15, 1982.

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From the mouth, the food moves down the esophagus into the stomach. The stomach can be a single compartment or four compartments. For the single compartment stomach (the abomasum), ingested food is exposed to hydrochloric acid and pepsin secreted by the gastric mucosa. Some microbial fermentation may occur in the single compartment stomach. From the stomach, the food passes into the small intestine where digestion continues and adsorption starts. Limited nutrient absorption and digestion occur in the last organ of the digestion tract, the large intestine.

The digestive tract of an animal includes the mouth, esophagus, stomach, small intestine, and large intestine. Digestive fluids are pumped into the tract from the liver and pancreas. Glands located along the digestive tract in the mucus lining also secrete digestive fluids into the tract. Based on the presence or absence of a compound stomach or large cecum, animals can be divided into two great groups; those depending on microbial fermentation to digest highly fibrous foods, and those lacking the ability to support microbial fermentation. Because the most economically important range animals have fermentation types of digestion (including cattle, sheep, goats, deer, elk, horses)³, a detailed discussion of their digestion process is needed.

Animals that depend on microbial fermentation can be divided into two groups; those with a compound stomach, called ruminants (cattle, sheep, goats, deer, elk), and those with a simple stomach and a large cecum (horses, rabbits). The ruminant stomach is divided into four compartments, rumen, reticulum, omasum, and abomasum. The rumen is the first and by far the largest of the compartments. Hastily eaten food is stored in the rumen under conditions that favor microbial fermentation--warmth (38° to 42°C), slight acidity (pH 6.8 to 6.0), and moisture. The food later is regurgitated, thoroughly chewed, and swallowed back into the rumen for additional microbial digestion. Muscular contractions by the rumen and reticulum keep the highly moistened food mass mixed. The coarse, less dense portion of the food mass is kept in the rumen by the muscular contractions of the rumen and reticulum for additional digestion. Macerated-digested food particles and the bodies of millions of microorganisms are forced into the reticulum and pass on to the omasum. In the omasum, large quantities of water are absorbed that concentrate the macerated-digested food mass and microbial mass. From the omasum the food and microbial mass is forced by peristaltic action into the abomasum where true digestion begins.

During the fermentation process, volatile fatty acids are formed, which in turn are absorbed directly by the rumen into the bloodstream. Volatile fatty acids are the major supplier of energy to the animal. Through microbial fermentation, the 10 essential amino acids needed by the animal are synthesized by the rumen microorganisms from plant protein, urea, and inorganic nitrogen. These amino acids may occur free in the rumen to be absorbed through the rumen wall and enter the bloodstream, or may be used to build microbial protein that becomes available to animals through regular enzymatic digestions. Rumen microorganisms also synthesize all the B vitamins needed by the animal. For animals capable of supporting microbial fermentation, protein quality and B vitamins are not a concern.

³For nonfermentation digestion tracts, the reader is referred to the following publications: Ensminger, M. E., and C. G. Olentine, Jr. 1978. Feeds and nutrition--abridged. The Ensminger Publ. Co., Clovis, California; Maynard, L. A., J. L. Lossli, H. F. Hintz, and R. C. Warner. 1979. Animal nutrition. 7th Ed. McGraw Hill Co., New York.

NUTRIENT NEEDS OF RANGE ANIMALS

From a quantitative point, the nutrient needs of animals vary according to species, age, size, and activity (National Academy of Sciences 1975; Maynard and others 1979). Qualitatively, nutrient needs of animals can be classified as follows: energy-producing compounds, protein, minerals, and vitamins.

Energy-Producing Compounds

Energy-producing compounds make up the single largest class of nutrients needed by animals (Dietz 1972; National Academy of Sciences 1975). Energy is needed to drive the various physiological processes of the body, and to provide movement and heat. Energy can be derived from a variety of compounds, including sugars, fats, pectins, starch, and protein, and in the case of ruminants and others with fermentation abilities, indirectly from cellulose and hemicellulose (Dietz 1972; National Academy of Sciences 1975; Maynard and others 1979). Some plant products including monoterpenoids and lignin do not furnish energy to the animal (Cook 1972; Short and others 1972; Maynard and others 1979).

The energy needs of animals are expressed in several forms such as total digestible nutrients, digestible energy, or metabolizable energy. Total digestible nutrients (TDN) is the sum of all the digestible organic compounds (proteins, sugars, cellulose, and so forth) with the digestible crude fat component being multiplied by the heat factor 2.25 (Maynard and others 1979). The TDN requirement of an animal is expressed as kilograms per animal per day or as a percent of the diet. Digestible energy (DE) is calculated by subtracting the gross calories in the feed from the calories in the feces (Maynard and others 1979). DE requirement of an animal is expressed as megacalories per animal per day or as megacalories per kilogram of dry matter. DE does not take into consideration losses of energy in the urine and in the form of combustible gases. When the energy losses in the urine and in the combustible gases have been subtracted, the remaining energy is called metabolizable energy (ME). Measuring the energy lost in the urine and combustible gases is expensive and subject to large experimental error (Dietz 1970). The ME requirement of an animal is expressed as megacalories per animal per day or as megacalories per kilogram of dry matter (Maynard and others 1979).

Energy needs of range animals vary according to weight and activity of the animal. Larger animals require more kilograms of TDN per day for a given activity than do smaller animals. A lactating female requires more kilograms of TDN per day than a nonlactating female of similar weight. On a constant weight basis, lactation requires a greater amount of energy than do other types of activities. Lactation is followed in descending order of energy needed by fattening, growing, gestation, and maintenance (National Academy of Sciences 1975).

Protein

Protein in animal bodies makes up a large, chemically related, but physiologically diverse group of compounds. Protein is the major organic compound of the organs and soft tissues of the body. All proteins are made from a common set of building blocks known as amino acids. Proteins are the chief component in a number of bodily structures: (1) skeleton muscle for external movement; (2) smooth muscle for internal movement (including breathing and the passage of food through the digestive tract); (3) cardiac muscle for the movement of blood; (4) tendons and ligaments for tying together body parts such as bones, muscles, and organs; (5) organs and glands such as the stomach, eye, pituitary, and skin (with its covering of hair); and (6) other structures including hemoglobin, cytochromes, and membrane.

Another functionally important group of protein compounds is enzymes, which provide the framework in which the chemical reactions of the body take place.

Because proteins are involved in so many bodily functions, the animal needs a liberal and continuous supply of them. Like energy, the protein requirement varies according to the weight and activity of the animal. For ruminants and other animals that have fermentation type digestive systems (horses, rabbits, burros), the quality of the protein is not important, only the quantity. The animal's protein requirement is expressed as grams per day of digestible protein or as a percent digestible protein in the diet. The requirement may also be expressed as grams per day of crude or total protein in the diet. As with energy, the greater the weight of the animal, the higher the protein needs. This assumes that activity is held constant. Protein needs for the various animal activities with body weight held constant is in the same order as for energy (National Academy of Sciences 1975).

Minerals

Mineral elements essential for the health of animals number about 15. Of these, seven are considered major elements: sodium, chlorine, calcium, phosphorus, magnesium, potassium, and sulfur. The remaining eight are classified as trace elements: iodine, iron, copper, molybdenum, cobalt, manganese, zinc, and selenium. These essential mineral elements constitute the major components of bones and teeth, maintain osmotic relations and acid-base equilibrium, play an important role in regulating enzymatic systems and muscular contraction, and are constituents of most organic compounds. They are also important in energy transfer (Ensminger and Olentine 1978; Maynard and others 1979).

Under most conditions, calcium and phosphorus are the mineral elements of major concern. Animal needs for calcium and phosphorus are expressed as grams per day per animal or as a percent of the diet. Larger animals under similar activity need greater amounts of calcium and phosphorus than do smaller animals. With size held constant, lactating animals require the most amount of calcium and phosphorus, followed by growth, fattening, gestation, and maintenance. The reader should note the requirement for energy and protein is greater for the fattening activity than for the growing activity (National Academy of Sciences 1975).

Vitamins

Vitamins are organic compounds needed by the body in relatively small amounts. They are unrelated chemically, but function as metabolic regulators (Maynard and others 1979). For animals capable of supporting microbial fermentation, only vitamin A is of major concern. Vitamin A combines with a specific protein of the eye to produce visual purple. Vitamin A is also important in normal development of bones, in normal power of disease resistance, and in maintaining healthy epithelium tissues. Because this vitamin is manufactured from the plant precursor carotene, the vitamin A requirement is expressed in terms of carotene, either as milligrams per animal per day or milligrams per kilogram of dry matter. With size held constant a lactating animal requires the most carotene, followed by growth, fattening, gestation, and maintenance (National Academy of Sciences 1975).

NUTRITIVE VALUE OF BITTERBRUSH, CLIFFROSE, AND APACHE-PLUME

Antelope bitterbrush, normally considered a winter forage for mule deer (Giunta and others 1978), is one of the major shrubs in their fall diet (Leach 1956; Tueller 1979; Medin⁴). After fall, the amount of antelope bitterbrush in the mule deer diet drops and the amount of big sagebrush or other shrubs increases to a peak in midwinter and starts declining in midspring (Leach 1956; Tueller 1979; Medin⁴). Leach (1956) observed on California winter ranges that the low use of bitterbrush during the winter months is not correlated with availability. A report on Colorado winter ranges by Medin⁴ agrees. Welch and Andrus (1977) reported heavy winter mule deer use on big sagebrush and rosehips but none on antelope bitterbrush on a Utah range. Even on ranges where the composition of antelope bitterbrush and big sagebrush was equal (27 and 29 percent, respectively) the mule deer consumed much more big sagebrush during winter (Leach 1956). This cyclic heavy use of antelope bitterbrush in the fall to big sagebrush use in the winter appears to be independent of the winter's severity (mild-open to cold with deep snow) (Leach 1956). Tueller (1979), however, attributed the low level of antelope bitterbrush in the diet of wintering mule deer in Nevada to short supplies of bitterbrush.

The Leach (1956), and Medin⁴ studies suggest that antelope bitterbrush may be primarily a fall forage for mule deer, that deer tend to switch from antelope bitterbrush to big sagebrush or other browse during the winter months, and that this switch is not necessarily due to short supplies of antelope bitterbrush. The importance of antelope bitterbrush as a winter forage for mule deer may not be as much as commonly held. But, its position as an important fall forage for mule deer needs to be emphasized.

Winter Digestibility

As explained earlier, total digestible nutrients is a measurement of energy in a forage. The total digestible nutrient requirement for wintering sheep (maintenance) is 55 percent (National Academy of Sciences 1975). Total digestible nutrient requirement for wintering mule deer is unknown but is probably close to that of sheep. Reported total digestible nutrient levels for antelope bitterbrush range from 39.7 to 54.8 percent; the mean is 47.5 percent (Bissell and others 1955; Dietz and others 1962; Smith 1952; 1957; Urness and others 1977). This compares to 64.8 percent for curlleaf mahogany, 63.4 for big sagebrush, 60.8 for juniper, 48.4 for mountain mahogany, 38.9 for chokecherry, and 36.2 for Gambel oak (table 1). Only curlleaf mahogany, big sagebrush, and juniper meet or exceed the total digestible nutrient requirement of wintering sheep and probably wintering mule deer. In general, dormant grasses are higher in total digestible nutrients than are most shrubs, and evergreen shrubs contain more digestible energy in the winter than do deciduous shrubs (Cook 1972; Welch 1981).

In vitro digestibility trials show that evergreen shrubs such as big sagebrush and curlleaf mahogany are more digestible than the deciduous shrubs (table 2). The in vitro digestibility of antelope bitterbrush is 25.1 percent. This compares to big sagebrush at 55.6 percent, black sagebrush at 53.1, chokecherry at 38.2, Gambel oak at 29.5, and mountain mahogany at 24.3 (see table 2 for other shrubs and references).

⁴Medin, D. E. Unpublished data on file at the Shrub Sciences Laboratory, Provo, Utah.

Table 1.--Total digestible nutrients of winter shrubs

Shrub	Total digestible nutrients (percent)	Reference*
Curleaf mahogany	64.8	2, 3, 6
Big sagebrush	63.4	1, 2, 3, 4, 5, 6
Juniper	60.8	2, 3
Mountain mahogany	48.4	3, 4, 6
Bitterbrush	47.5	2, 3, 4, 5, 6
Chokecherry	38.9	3
Gambel oak	36.2	3

*Reference

- 1 - Smith 1950.
- 2 - Smith 1952.
- 3 - Smith 1957.
- 4 - Dietz and others 1962.
- 5 - Bissell and others 1955.
- 6 - Urness and others 1977.

Table 2.--In vitro digestibility of winter shrubs

Shrub	Dry matter digestibility (percent)	Reference*
Big sagebrush	55.6	1, 2, 3, 4, 5, 6
Black sagebrush	53.1	8
Curleaf mahogany	51.6	1, 4
Rosehips (Sweetbrier rose)	49.1	4
Rubber rabbitbrush	45.9	6
Winterfat	44.7	8
Chokecherry	38.2	7
Saskatoon serviceberry	34.6	6
Gambel oak	29.5	5
Bitterbrush	25.1	1, 4, 6
True mahogany	24.3	1, 4

*Reference

- 1 - Urness and others 1977.
- 2 - Wallmo and others 1977.
- 3 - Sheehy 1975.
- 4 - Welch and Pederson 1981.
- 5 - Kufeld and others 1981.
- 6 - Ward 1971.
- 7 - Uresk and others 1975.
- 8 - Welch and others, in press.

Winter Crude Protein Levels

The protein requirement for wintering sheep and probably for mule deer is 8.9 percent (National Academy of Sciences 1975). Antelope bitterbrush has a reported winter crude protein content of 7.9 percent, desert bitterbrush 8.0 and cliffrose 8.4

(see table 3 for references). These values compare to big sagebrush at 10.7 percent, curllleaf mahogany at 10.1, fourwing saltbush at 9.6, chokecherry at 8.5, mountain mahogany at 7.8, Saskatoon serviceberry at 5.7, and Gambel oak at 5.4 (see table 3 for additional shrubs and for references). Only big sagebrush, curllleaf mahogany, and fourwing saltbush meet or exceed the crude protein requirement. In general, evergreen shrubs are higher in the winter level of crude protein than are deciduous shrubs, and deciduous shrubs are much higher in the winter level of crude protein than are dormant grasses (Cook 1972; Welch 1981).

Table 3.--Winter crude protein level of shrubs

Shrub	Crude protein (percent dry matter)	Reference*
Big sagebrush	10.7	1,2,3,4,6,8,9,10,12
Black sagebrush	10.2	10,12
Curllleaf mahogany	10.1	3,7
Fourwing saltbush	9.6	11
Chokecherry	8.5	3,5,10
Rocky Mountain juniper	8.5	1
Cliffrose	8.4	5
Utah juniper	8.0	3,5
Desert bitterbrush	8.0	3
Antelope bitterbrush	7.9	1,3,4,7,8,9
Mountain mahogany	7.8	1,5,8
Shadscale	7.7	10
Gardner saltbush	7.2	10
Rubber rabbitbrush	6.8	1,10
Saskatoon serviceberry	5.7	3,10
Gambel oak	5.4	5

*Reference

- | | |
|---|---|
| 1 - Dietz and others 1962. | 10 - National Academy of Sciences 1958. |
| 2 - Welch and McArthur 1979. | 11 - Welch and Monsen 1981. |
| 3 - Tueller 1979 | 12 - Sheehy 1975. |
| 4 - Bissell and others 1955. | |
| 5 - Smith 1950. | |
| 6 - Smith 1952. | |
| 7 - Trout and Thiessen 1973. | |
| 8 - Medin and Anderson 1979 (data converted to dry matter basis). | |
| 9 - National Academy of Sciences 1975. | |

Winter Phosphorus Levels

The phosphorus requirement for wintering sheep and probably mule deer is 0.24 percent (National Academy of Sciences 1975). Winter phosphorus content of antelope and desert bitterbrush is 0.13 and 0.10 percent, respectively (table 4). Both are well below the requirement. Even though aspen (0.23 percent), juniper (0.22), big sagebrush (0.22), Gardner saltbush (0.21), and other shrubs contain significantly higher levels of winter phosphorus than the two bitterbrushes, they do not meet the phosphorus winter requirement (see table 4 for additional shrubs and for references). In general, shrubs are significantly higher in winter levels of phosphorus than are dormant grasses (Cook 1972; Welch 1981).

Table 4.--Winter phosphorus level of shrubs

Shrub	Phosphorus (percent dry matter)	Reference*
Aspen	0.23	8
Big sagebrush	.22	1,2,3,4,5,6
Rocky Mountain juniper	.22	8
Gardner saltbush	.21	5
Chokecherry	.18	2,7
Saskatoon serviceberry	.17	2,7
Curlleaf mahogany	.17	2,3
Black sagebrush	.16	5
Fourwing saltbush	.15	4
Rubber rabbitbrush	.14	1,4,8
Mountain mahogany	.13	1,6
Antelope bitterbrush	.13	1,2,3,4,6
Shadscale	.12	4,5
Desert bitterbrush	.10	2

*Reference

- | | |
|---------------------------------------|--|
| 1 - Dietz and others 1962 | 6 - Medin and Anderson 1979 (data converted to dry matter basis) |
| 2 - Tueller 1979 | |
| 3 - Trout and Thiessen 1973 | 7 - Dietz 1972 |
| 4 - National Academy of Sciences 1958 | 8 - Short and others, unpublished data |
| 5 - National Academy of Sciences 1964 | |

Winter Carotene Levels

All shrubs furnish enough carotene to meet the winter vitamin A requirements for sheep and mule deer; dormant grasses furnish very little carotene. Range animals consuming large amounts of dormant grass could easily develop a vitamin A deficiency (Cook 1972; Welch 1981).

As a winter forage, antelope bitterbrush supplies more carotene, crude protein, and phosphorus, but less energy than does dormant grass. Desert bitterbrush and cliffrose may supply a little more crude protein and energy than does antelope bitterbrush. Several shrubs such as big sagebrush, fourwing saltbush, and curlleaf mahogany supply significantly more crude protein, phosphorus, and energy to the consuming animal than does antelope bitterbrush. The gradual dietary switch from an antelope bitterbrush base to a big sagebrush base observed by Leach (1956) and Medin⁵ could be the result of mule deer selecting for a higher nutritive plane in the diet in response to increasing environmental stress.

Improving the Winter Level of Nutrients

Dietz and others (1962) reported that the total digestible nutrient content of a winter sample of antelope bitterbrush containing a large amount of wintering green leaves was 52.5 percent. Presence of green leaves is an indicator of a high level of nutrients (Ensminger and Olentine 1978). The question becomes, was the antelope

⁵Medin, D. E. Unpublished data on file at the Shrub Sciences Laboratory, Provo, Utah.

genetically superior in producing wintering green leaves, or was the abundance of leaves due to unusual environmental conditions such as a warm-moist fall or winter? Alderfer (1976) and Monsen⁶ have observed that some populations of antelope bitterbrush retain more green leaves during the winter than others. Giunta and others (1978) report genetic differences among antelope bitterbrush in growth habit, adaptation, and so forth. If genetic factors are important in determining winter leafiness, then breeding and selection programs could be devised to maximize leafiness and winter nutrient content.

To broaden our understanding of the role that genetics might play in determining leafiness and crude protein, we undertook a study to determine the variation of winter leafiness, crude protein, and in vitro digestibility among five accessions of antelope bitterbrush, two accessions of desert bitterbrush, and one accession each of cliffrose and Apache-plume. All accessions were grown in a uniform garden. Desert bitterbrush, cliffrose, and Apache-plume were included because they can be hybridized with antelope bitterbrush (Blauer and others 1975; Koehler and Smith 1981). Significant variation among accessions would indicate that genetic factors are important in determining winter leafiness, crude protein levels, and in vitro digestibility. Locations of the accessions by county and state are given in tables 5 and 6.

Table 5.--Winter crude protein levels among accessions of Apache-plume, antelope bitterbrush, desert bitterbrush, and cliffrose grown in a uniform garden.
Data expressed on a dry matter basis

Accession	County and State	Crude protein (percent)
<u>Fallugia paradoxa</u> (Apache-plume)	Sevier, Utah	4.8*
<u>Purshia tridentata</u> (Antelope bitterbrush)	Moffatt, Colorado	5.9 ^a
<u>Purshia tridentata</u>	Juab, Utah	6.6 ^b
<u>Purshia tridentata</u>	Carbon, Utah	6.8 ^b
<u>Purshia tridentata</u>	Ada, Idaho	6.9 ^b
<u>Purshia tridentata</u>	Lassen, California	7.9 ^c
<u>Purshia glandulosa</u> (Desert bitterbrush)	Washington, Utah	8.6 ^{cd}
<u>Cowania mexicana</u> ssp. <u>stansburiana</u> (Cliffrose)	Utah, Utah	8.8 ^{cd}
<u>Purshia glandulosa</u>	Mono, California	9.3 ^d

* Means sharing the same letter superscript are not significantly different at the 95 percent level.

⁶Monsen, S. B. Unpublished data on file at the Forestry Sciences Laboratory, Boise, Idaho.

Table 6.--Winter leafiness among accessions of Apache-plume, antelope bitterbrush, desert bitterbrush, and cliffrose grown in a uniform garden. Data expressed on a dry matter basis

Accession	County and State	Winter leaves (percent)
<u>Purshia tridentata</u> (Antelope bitterbrush)	Ada, Idaho	5.9 ^{a*}
<u>Purshia tridentata</u>	Moffat, Colorado	7.4 ^{ab}
<u>Purshia tridentata</u>	Carbon, Utah	9.0 ^{abc}
<u>Purshia tridentata</u>	Juab, Utah	13.1 ^{bc}
<u>Purshia tridentata</u>	Lassen, California	15.1 ^c
<u>Fallugia paradoxa</u> (Apache-plume)	Sevier, Utah	27.3 ^d
<u>Cowania mexicana</u> ssp. <u>stansburiana</u> (Cliffrose)	Utah, Utah	47.5 ^e
<u>Purshia glandulosa</u> (Desert bitterbrush)	Washington, Utah	49.5 ^e
<u>Purshia glandulosa</u>	Mono, California	50.5 ^e

*Means sharing the same letter superscript are not significantly different at the 95 percent level.

From the uniform garden, we collected current year growth (stems with leaves, if present) from five plants for each accession. The five plants were chosen at random. Nitrogen content was determined by the Kjeldahl method and the crude protein level calculated (Association of Official Analytical Chemists 1980). Crude protein was expressed as a percent of dry matter. To determine *in vitro* digestibility, we used the Pearson (1970) *in vitro* digestibility method.

We used completely random analysis of variance to detect significance among the nine shrub accessions. Hartley's test ($\alpha=0.05$) was used to determine significant differences among accession means (Sendecor and Cochran 1967). Percentages were transformed to arcsin to avoid inequalities in the variance.

The winter crude protein content means for the accessions of antelope bitterbrush, desert bitterbrush, Stansbury cliffrose, and Apache-plume were 6.8, 9.0, 8.8, and 4.8 percent (dry matter basis), respectively. Significant differences in the crude protein levels were attributed to accessions (table 5). The Apache-plume was significantly ($\alpha=0.05$) lowest of all accessions tested. Desert bitterbrush from Mono County in California, contained the highest crude protein content of all accessions (9.3 percent), although not significantly higher than the Stansbury cliffrose (8.8), and the desert bitterbrush (8.6) from Washington County, Utah. Antelope bitterbrush from Moffat County, Colorado, contained significantly more (5.9) crude protein than the Apache-plume, but was significantly lower than the remaining. The antelope bitterbrush from Lassen County, California, contained significantly higher levels of crude protein (7.9) than the other antelope bitterbrush, but less than the two desert bitterbrush and Stansbury cliffrose accessions.

Winter leafiness also varied significantly among the accessions (table 6). The two desert bitterbrush and the cliffrose were significantly more leafy than the others. Apache-plume was significantly more leafy than any of the five antelope bitterbrush, but significantly less than the two desert bitterbrush and the

cliffrose. Leafiness ranged from 5.9 to 15.1 percent of current year growth among the five accessions of antelope bitterbrush.

In vitro digestibility also varied significantly among the accessions (table 7). The two desert bitterbrush and the cliffrose were significantly more digestible than the others. Antelope bitterbrush from Lassen County, California, was more digestible than antelope bitterbrush from Colorado, Utah, or Idaho.

Table 7.--In vitro digestibility of winter forage samples from accessions of Apache-plume, antelope bitterbrush, desert bitterbrush, and cliffrose grown in a uniform garden. Data expressed on a dry matter basis

Accession	County and state	Digested dry matter (percent)
<u>Purshia tridentata</u> (Antelope bitterbrush)	Moffat, Colorado	24.1 ^{a*}
<u>Purshia tridentata</u>	Juab, Utah	25.2 ^a
<u>Purshia tridentata</u>	Carbon, Utah	26.4 ^{ab}
<u>Purshia tridentata</u>	Ada, Idaho	28.3 ^{ab}
<u>Fallugia paradoxa</u> (Apache-plume)	Sevier, Utah	29.8 ^b
<u>Purshia tridentata</u>	Lassen, California	30.6 ^{bc}
<u>Purshia glandulosa</u> (Desert bitterbrush)	Washington, Utah	34.6 ^{cd}
<u>Purshia glandulosa</u>	Mono, California	37.0 ^d
<u>Cowania mexicana</u> ssp. <u>stansburiana</u> (Cliffrose)	Utah, Utah	37.6 ^d

*Means sharing the same letter superscript are not significantly different at the 95 percent level.

The relationships between leafiness and crude protein and between leafiness and digestibility were highly significant ($r=.80$ and $r=.92$, respectively). Because these data were generated on even-aged plants grown in a uniform garden, we concluded that genetic factors play an important role in determining winter levels of leafiness, crude protein, and in vitro digestibility in antelope bitterbrush, desert bitterbrush, cliffrose, and Apache-plume. Due to the limited number of accessions we used, we are expanding our gardens to include more accessions of antelope bitterbrush, desert bitterbrush, and cliffrose. We hope to locate superior strains for our breeding and selecting program aimed at increasing the nutritional quality of bitterbrush planted on fall and winter ranges of mule deer and livestock.

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GOAT USE IN FALL INCREASES BITTERBRUSH
BROWSE AND REDUCES SAGEBRUSH DENSITY¹

Philip J. Urness and Charles H. Jensen²

ABSTRACT

Bitterbrush responded to heavy fall grazing (100 percent of CAG) by Spanish goats with significant increases in twig production, while twig growth of big sagebrush generally decreased on plants used more than 70 percent (23 percent of those plants died). Thus, impact grazing favored bitterbrush and weakened big sagebrush, a desired result on ranges where quantity of sagebrush exceeds the forage needs of wintering big game.

INTRODUCTION

Attention has been focused recently on using domestic ungulates at various seasons and stocking intensities to manage for planned vegetational mixes on western North American rangelands. Spring grazing by cattle (Smith and Doell 1968) and sheep (Jensen and others 1972; Urness 1982) was compatible with winter use by deer and elk on Utah foothill ranges, provided domestic animals were removed before appreciable bitterbrush (Purshia tridentata Pursh [DC]) twig growth. Neal (1982) demonstrated similar responses of bitterbrush to early summer cattle use in northeastern California and south-central Oregon. Horses can be grazed on such ranges throughout summer without adverse impacts on bitterbrush or associated shrubs (Reiner and Urness 1982). Indeed, bitterbrush twig production can be increased by properly timed livestock grazing (Hubbard and Sanderson 1961). Anderson and Scherzinger (1975) reported a substantial increase in elk-carrying capacity on eastern Oregon rangeland where cattle were well managed. The unifying concept in these studies is that temporal separation allows livestock to utilize herbaceous forages that enhance the competitive capabilities of desirable shrubs, and/or improve the quality of herbaceous forage remaining for wintering big game.

Spanish goats have been used in the Southwest to decrease woody plants in pastures where interspecific competition and selective grazing have reduced more palatable forages (Huss 1972). Secondary benefits included lowered fuel loading (and risk of wildfire, Green and others 1979) and a marketable product--meat (Merril and Taylor 1976). Spanish goats were considered superior to other types for brush control; moreover, the authors indicated goats were productive on forage that sheep and cattle have difficulty utilizing.

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In Colorado, Gambel oak (Quercus gambelii Nutt.) sprouts were controlled by goats, and their use provided increased herbaceous forage for cattle (Davis and others 1975). High tannin levels in Gambel oak may limit the ability of goats to consume a monospecific diet (Nastis and Malechek 1981); however, when mixed with other nutritious forages, goats can perform well. This pattern likely occurs with other woody plants besides oaks. For example, goats were used to prune blackbrush (Coleogyne ramosissima Torr.) in winter to stimulate current season's growth and improve the quantity and quality of forage for cattle (Provenza and others³). Plants browsed heavily for four successive years produced significantly more current annual twig growth than unbrowsed plants. But high tannin content of current growth limited its palatability to goats and cattle (Provenza and Malechek⁴).

Thus, the literature indicates a highly specific response of different plant species to grazing, and the possibility that controlled grazing by different ungulates can accomplish certain range management goals. We have observed at several locations in Utah that some heavily used big game winter ranges supported well-developed stands of bitterbrush or cliffrose (Cowania mexicana D. Don). Other apparently similar sites that received light impacts by big game were dominated by big sagebrush (Artemisia tridentata Nutt.). Such vegetal patterns have variously been attributed to edaphic differences, but we hypothesized that the driving force in many cases was long-term differential use of more palatable associated shrubs favoring big sagebrush.

Conversely, if selective grazing by livestock or big game could be temporarily eliminated, a manager might develop a more desirable mix of palatable shrubs via impact use on big sagebrush. The latter species appears to have evolved chemical defenses against herbivory at the expense of grazing tolerance, in contrast to many shrubs in the family Rosaceae (bitterbrush and cliffrose included). This study, consequently, examined response of bitterbrush and big sagebrush to fall goat use at extremely heavy intensity to determine if such impacts could overcome the usual aversion of goats to big sagebrush (Narjisse 1981) to reduce its vigor and, perhaps, induce mortality.

STUDY AREA

In 1979 a 1.5-acre (0.6-ha) pasture was established in a big sagebrush-grass type about 4 mi (7 km) north of Hardware Ranch, Cache County, Utah. Vegetation was dominated by mountain big sagebrush (Artemisia tridentata ssp. vaseyana [Rydb.] Beetle), which accounted for nearly half of the total production (157 of 328 lb/acre; 176 of 368 kg per ha) and 80 percent of total shrub production. Green rabbitbrush (Chrysothamnus viscidiflorus [Hook.] Nutt.) was the second most abundant shrub. While bitterbrush was a common community component, it was not productive of current-annual-growth twigs (about 8 lb per acre; 9 kg/ha). All other shrubs combined yielded less than 2 percent of total production; of these, snowberry (Symphoricarpos oreophilus Gray) was most abundant.

³Provenza, F. D.; Bowns, J. E.; Urness, P. J.; Malechek, J. C.; Butcher, J. E. Biological manipulation of blackbrush by goat browsing; 1983. In press.

⁴Provenza, F. D.; Malechek, J. C. Diet selection by domestic goats in relation to blackbrush twig chemistry; 1983. In press.

Herbaceous plants comprised about 40 percent of fall forage, but that did not account for the amount consumed by cattle in spring and early summer. Common grasses were beardless bluebunch wheatgrass (Agropyron inerme [Scribn. & Smith] Rydb.), bluegrasses (Poa spp. L.), and Letterman needlegrass (Stipa lettermanii Vasey). Common forbs were Louisiana sage (Artemisia ludoviciana Nutt.), Pacific aster (Aster chilensis Nees), Fremont geranium (Geranium fremontii Torr. ex Gray), and mulesear wyethia (Wyethia amplexicaulis [Nutt.] Nutt.). Forbs were generally available as standing dead material by late fall due to heavy frosts.

Soils are the Goering and Yeats Hollow series of silt loams with moderate stoniness. Topography is moderately sloping toward the southwest. Precipitation at Hardware Ranch averages about 16 inches (400 mm); winters are usually cold and dry but snow depths at the study pasture often preclude midwinter use by elk or deer. Summers are warm and dry. The frost-free period is short (mid-June to mid-September), but frost can occur in every month.

METHODS

We established a grid with 40 equally spaced intersects in the square study pasture, and a buffer zone was maintained around the fenced boundary. A stake was driven at each intersect, and one major outer branch on the bitterbrush and big sagebrush plants nearest each stake was permanently marked with a numbered metal tag. Lengths of all current annual twigs on these branches were measured in fall 1979 and 1980 and residual lengths of those twigs were remeasured in spring 1980 (Smith and Urness 1962). The same procedure was followed for a control pasture, except 80 plants of each species were measured. Comparison of fall 1980 twig measurements on the goat-grazed pasture vs. the control reflected relative yield changes, while use was estimated by twig length differences between fall 1979 and spring 1980.

In summer 1980 heavy goat use had apparently stimulated numerous adventitious buds on older branches toward the axes of bitterbrush plants. A variation of the point-quadrat technique (Warren-Wilson 1960) was used to detect this response. We took 50 point-frame samples on as many plants in the goat-grazed and the control pastures. A frame consisted of a color-coded pole with a pin guide that could be adjusted to various heights. The pin was inclined at 32.5° from horizontal to sample within four vertical strata across a 20-inch (50-cm) column. The strata were 0-6.7, 6.7-20.1, 20.1-33.1, and 33.1-46.1 inches (0-17, 17-51, 51-84, and 84-117 cm) above ground level. These strata were used to determine where on the plant twig production occurred. All point contacts with bitterbrush were recorded as dead wood, old wood, bud clusters, or current growth twigs. Each twig contacted by the point was measured for length to provide a relative production estimate.

Stimulation of adventitious buds did not occur on big sagebrush. Therefore, twig length measurements on the tagged branches adequately estimated growth response on that species.

On October 8, 1979, we placed 83 Spanish goats (16 adult females, 23 yearlings, and 44 kids) in the pasture. Mean individual weights for the three age groups were 86.6 lb (39.4 kg), 57.9 lb (26.3 kg), and 33.5 lb (15.2 kg), respectively, at completion of the trial on October 30. Total weight of the lot was 4,183 lb (1 901 kg) and, based on 1,000 lb (454.5 kg) = 1 animal unit (AU), the intensity of use was 2.14 AUM/acre (5.29 AUM/ha). Goats were supplemented with 0.5 lb (0.23 kg) alfalfa hay per animal per day during the last 10 days of the trial to assure good animal condition for subsequent breeding experiments, thus weight responses were confounded and are not reported in this paper.

RESULTS

Utilization

Spanish goats exhibited a clear aversion to big sagebrush for the first 10 days, but readily consumed all grasses, forbs, and other shrubs. By the end of the 23-day trial little current-growth material remained on any plant species except big sagebrush (fig. 1). On the 10th day when most other forage was consumed, it appeared that goats would not eat any appreciable amount of sagebrush (similar phenomena have been observed with deer (Carpenter and others 1979). However, a storm deposited 13 inches (33 cm) of snow accompanied by unseasonably cold temperatures (min. averaged 21° F, 6° C, from October 21 to 30). After the storm, goats readily browsed some big sagebrush plants but ignored others, and by the end of the trial use averaged 44 percent (Welch and others 1981 reported mule deer responding in a like manner). Use of individual sagebrush plants ranged from 0 to 100 percent. About 40 percent of the marked plants were unused, another 20 percent were browsed between 1 and 70 percent, and 40 percent of the plants were used in excess of 70 percent.

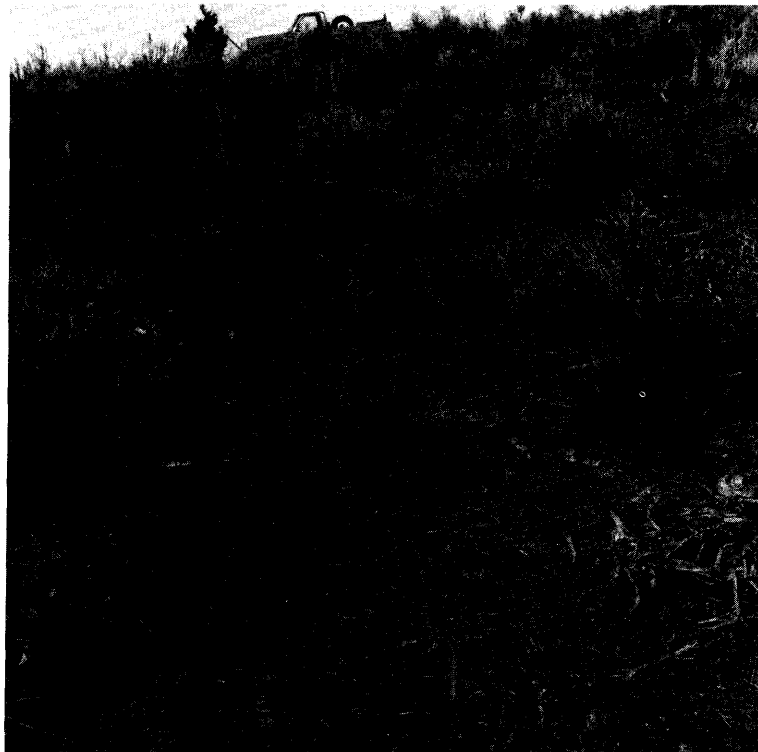


Figure 1.--Nearly complete use of available forage, including considerable litter, by goats in fall at Hardware Ranch. Only big sagebrush has current growth unused.

Bitterbrush use averaged 99.7 percent as determined by before-and-after-use measurements of current-growth twigs on peripheral branches. This was a conservative estimate, however, because a large quantity of older material was also consumed. Rarely have we observed such heavy use by other classes of ungulates; indeed, use was so extreme on some plants that even the bark was stripped from major branches (fig. 2).

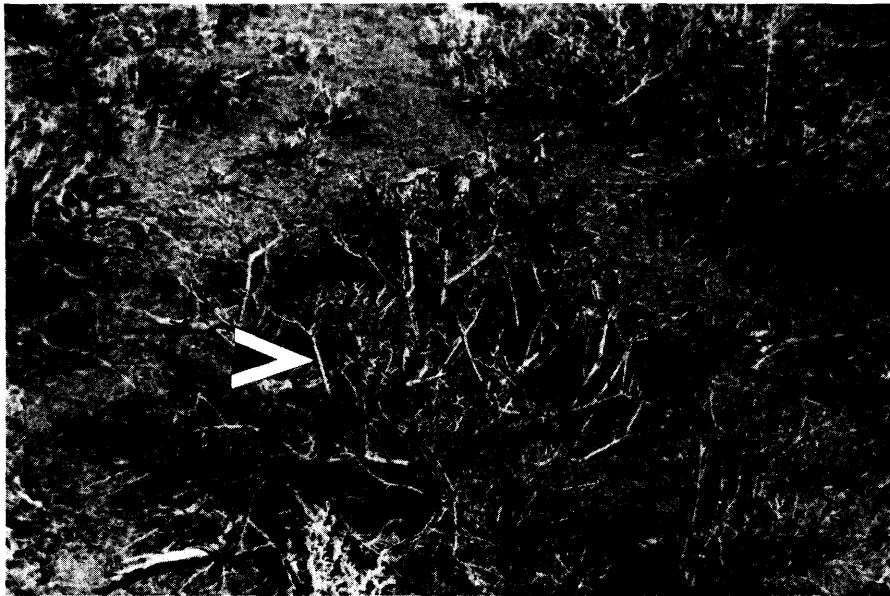


Figure 2.--Extreme use of bitterbrush including extensive bark stripping on older branches (arrows) by goats in fall at Hardware Ranch.

Subsequent Growth Responses

Big Sagebrush.--From 1979 to 1980, twig growth of big sagebrush decreased by 11 percent in the pasture grazed by goats and remained unchanged in the adjacent control pasture. Twig production on plants unused by goats increased 13 percent; it increased 35 percent on plants in the 1 to 70 percent use category. Twig growth decreased an average of 55 percent on plants used 70 percent or more (table 1).

Table 1.--Responses of big sagebrush plants to heavy fall grazing by Spanish goats at Hardware Ranch, Cache County, Utah

Use category	Mean utilization	1980 twig growth	Mortality
----- Percent	-----	Percent of 1979	Percent
0	0	113	0
1-70	40	135	0
71-100	91	45	23
Mean	44	89	10

These data indicate that utilization less than 70 percent was actually stimulatory to big sagebrush, but heavier use was harmful. Moreover, lightly used plants were more productive than unused ones. The decrease in production of plants used more than 70 percent was partly due to mortality. Also, about 25 percent of these plants increased in productivity despite heavy use.

Bitterbrush.--The two techniques used to estimate growth response of bitterbrush yielded substantially different results. Twig length measurements of tagged peripheral branches showed an overall decrease in production (table 2). Buds decreased by 98 percent when compared to the controls; the number of twigs declined 91 percent and total twig length decreased 32 percent. However, average twig length was far greater, indicating a strong first-year, compensatory growth response.

Table 2.--Responses of bitterbrush plants to heavy browsing in fall 1979 by spanish goats at Hardware Ranch, Cache County, Utah, as determined by twig length measurements on peripheral branches in 1980.

Measured characteristic	A	B	Percent B:A
	Control plants	Goat-browsed plants	
Percent Utilization, 1979	0	99.7	--
Number of buds, 1980	5,699	111	2
Number of twigs, 1980	1,228	111	9
Total twig length, 1980	3,558 inches (9 087 cm)	2,435 inches (6 172 cm)	68
Average twig length, 1980	2.91 inches (7.4 cm)	21.9 inches (55.6 cm)	751

Very heavy browsing obviously reduced production of peripheral branches, but that is an incomplete picture. Another difference was the absence of seed on the heavily used plants. For example, 1,228 of the 5,699 buds on the control plants initiated twigs in 1980; nearly 80 percent of all buds did not and can be assumed to be flower buds. In contrast, all 111 buds of heavily browsed plants produced twigs.

Twig length data did not accurately reflect bitterbrush response as illustrated by data from the inclined-point technique. Most adventitious buds arose on older branches near basal axes, not on younger peripheral branches (fig. 3). However, due to increased twig length, some twigs originating from adventitious buds extended well into the peripheral branches of heavily browsed plants. Twig production on these plants as determined by point-contact sampling increased 719 percent relative to control plants (table 3). Moreover, twig growth resulting from stimulation of adventitious buds was substantially greater in all strata following heavy goat use. Thus, twig production was significantly increased, a result consistent with that obtained by artificial pruning (Ferguson and Basile 1966).



A



B

Figure 3.--(A) Heavily used bitterbrush plant immediately after goats were removed from the pasture at Hardware Ranch. (B) The same plant two growing seasons after goat use showing excellent rejuvenation from basal adventitious buds.

Table 3.--Responses of bitterbrush to heavy fall (1979) browsing by Spanish goats at Hardware Ranch, Cache County, Utah, as determined from inclined-point-contact sampling in 1980

Measured characteristic	A	B	Percent B:A/100
	Control plants	Goat-browsed plants	
<u>Total point contacts per 50 frames</u>			
Old wood	32	18	56
Dead wood	17	34	200
Bud clusters	26	0	--
Number of twigs	38	70	184
	<u>Inches</u> (cm)	<u>Inches</u> (cm)	
Total lengths of contacted twigs per stratum			
0-17 cm	14 (36)	53 (135)	375
17-51 cm	116 (295)	774 (1 967)	667
51-84 cm	37 (94)	334 (875)	931
84-117 cm	0 (0)	31 (79)	--
Total	167 (425)	1,202 (3 056)	719

Point-contact sampling further revealed an increase in dead wood, a decrease in old wood, an absence of buds (except basal adventitious buds), and an overall increase in twig numbers for browsed shrubs. In our opinion, this comprehensive analysis of the entire plant is a more valid characterization of effective responses of bitterbrush to goat browsing.

Goats used all other plant species heavily, but their responses were confounded somewhat with spring grazing by cattle in 1979. Utilization in 1979 was estimated to be 73 percent on grasses, 45 percent on forbs, and 5 percent on shrubs. Big sagebrush received no use and bitterbrush use averaged 2 percent. Deer and elk use from late fall to early spring was also light because of research activity during fall and deep snow in winter. Cattle did not use the area in 1980. Therefore, the response of shrubs is attributed primarily to browsing pressure imposed by the goats.

DISCUSSION

An overwhelmingly conservative attitude has existed among range managers regarding allowable use levels on plants. Such concepts as "take half, leave half" or "60 percent use of key species is maximal" are perpetuated despite strong evidence that such practices, rigidly applied, are not always best. In fact, such concepts often allow selective grazing by herbivores of the more palatable species to a result opposite that of stated management goals; namely, an increase in less palatable competitive species such as big sagebrush. In grazing intensity-plant competition interactions, a number of factors are operative that ultimately have a strong bearing on the type of plant community that will develop.

In this study we were interested in the relative competitive advantage big sagebrush (low palatability) has over bitterbrush (high palatability) in traditional grazing systems. More specifically, whether a dramatic shift in grazing pattern both in terms of intensity (very heavy) and timing (fall, when physiological activity of both shrubs is minimal) could alter this competitive interaction to favor bitterbrush. Our data support a contention that temporary heavy use accomplished this purpose despite the fact that utilization of bitterbrush averaged twice that of big sagebrush. Further, earlier data indicated that bitterbrush can become more and sagebrush less prominent in the stand provided sufficient grazing pressure is imposed on other vegetational components in spring and early summer (Jensen and others 1972; Reiner and Urness 1982). Most likely a combination of growing-season and fall use will be necessary to significantly increase bitterbrush and decrease sagebrush dominance.

The selective use of big sagebrush at usually low overall grazing intensities presents still another problem. Since certain individual sagebrush plants are more palatable than others, they consistently sustain much higher use levels than less palatable ones, which likely leads to loss of the better plants over time. Certainly, mortality of 23 percent of the more palatable individuals in this study represents a potential trend. However, not all heavily used sagebrush plants decreased in production, indicating that some individuals possess greater resistance to browsing than others. To avoid or reduce selective grazing and the competitive advantage such a process conveys to less palatable plants, sufficiently heavy use must be imposed, at least periodically, to impact the entire population.

A short-term, high-intensity approach (Savory 1978; Heitschmidt and others 1982) might possibly achieve the desired result, yet our study confined large numbers of goats in a small area but failed to impose uniform use on big sagebrush, even with supplementation. It appears that any similar effort would require close confinement, supplemental feeding, and a longer time frame to be effective. Obviously the application of such an approach to a herd unit or grazing allotment is very limited.

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DYNAMICS OF ANTELOPE BITTERBRUSH SEED CACHES¹

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ABSTRACT

The natural regeneration of bitterbrush (Purshia tridentata [Pursh] DC.) is closely tied to the collection and seed caching activities of rodents. Predation by rodents and insects interfere with artificial vegetation of bitterbrush. Successful seeding of bitterbrush is dependent on understanding and adapting to the ecology of rodent populations.

INTRODUCTION

The perfect yellow flowers of antelope bitterbrush (Purshia tridentata [Pursh] DC.) are borne singly at the end of short, lateral, leafy spurs. The fruit is an achene about 0.13 to 0.5 inches (6 to 12 mm) long. The achene consists of the embryo comprised of radicle, hypocotyl, and cotyledons and is covered by the seedcoat and pericarp. The ovary wall or pericarp is fused to the actual seedcoat to form the achene. The achene is dry and flinty when mature, and we will refer to it as seed. When the seeds of antelope bitterbrush are mature, they fall from the plant with a papery covering composed of remnant flower parts tipped with a remnant of the style.

The papery covering of antelope bitterbrush seeds largely inhibits germination when the seeds are germinated in petri dishes (Hormay 1943). When the seeds are allowed to remain in the natural seedbed, presumably strict dormancy is imposed until this papery covering is rotted away (which probably occurs over winter). After overwintering the seeds can germinate. However, this is not usually the case in natural situations because almost the entire crop of antelope bitterbrush seeds is collected by rodents and Pogonomyrmex ants (Young and Evans 1978). When rodents collect bitterbrush seeds, they often remove the papery covering before caching 10 to 100 seeds in tight clusters buried about 2 inches (5 cm) deep in the soil (Hormay 1943). Apparently rodents discriminate among types of sites they use for caching. Accumulation of duff and litter discourages rodent caching activities (Sherman and Chilcote 1972). These caches remain in the soil over winter, and the seeds receive natural stratification (see Young and Evans this volume for details of stratification requirements). In the early spring, cotyledons of the germinating seeds form tight, rose-purple rosettes, identifying the cache locations. Rodents

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return to graze on the cotyledons which are rich in carotene which is often vital in the diet of the rodents in early spring (for examples of similar situations, see Beatley 1969 and La Tourrette and others 1971). If rodents failed to return and graze the seedlings, the seedlings would often die from intraspecific competition. Sloppy grazing by the rodents allows an occasional seedling to escape and possibly to become established. This highly complex regeneration system can be easily influenced by human activities but is hard to direct. Even if seedlings do escape rodent predation, other predators and diseases can cause mortality. Hubbard (1956) found variegated cutworm (Peridroma saucia [Hubmer]) damage on bitterbrush seedlings at the Doyle Experimental Area, Lassen County, California. Ninety percent of seedlings emerging in the spring of 1956 from seeds planted in the fall of 1955 were destroyed by worms. Nord (1965) described numerous insect species which are known to injure and destroy bitterbrush, including cutworms, tussock moth (Orygia vestusta [Boisduval]), green plant bug (Chlorochroa uhleri [Stal]), and the Great Basin tent caterpillar (Malacosoma californicum fragiles [Stretch]). Also, several damping-off fungi (Rhizoctonia solani [Kuehn]), Pythium ultimum [Taus]) were shown to be pathogenic on bitterbrush seedlings.

Our purpose was to investigate portions of the caching-regeneration system for antelope bitterbrush in order to more fully understand its functions. We believe that rodent grazing, insect feeding, fungal disease, and soil nutritional levels interact to greatly reduce seedling survival of antelope bitterbrush and that mortality caused by these factors is a function of density and depth of seed caching.

MATERIALS AND METHODS

Because of the impossibility of going to a given field location and automatically reproducing all portions of the antelope bitterbrush regeneration cycle, (seed production, rodent caching, and germination), experimental comparisons are more a function of opportunistic research. When we noticed the opportunity to experiment with the regeneration cycle we took advantage of the phenomenon. To bring balance to this necessarily disjunct approach we artificially reproduced portions of the cycle to establish meaningful experimental comparisons. All of these comparisons combine to create a rather complex experimental approach.

Studies of Natural Caches

In August 1980, about 16 ha of a mature stand of antelope bitterbrush burned in a wildfire located in Little Antelope Valley, Mono County, California. The stand constituted an important mule deer (Odocoileus hemionus [Rafinesque]) winter range and was situated on an alluvial fan just below the lower margin of the pinyon (Pinus monophylla Torr. and Frem.)/juniper (Juniperus osteosperma [Torr.] and J. occidentalis Hook. ssp. australis Vasek) woodlands of the eastern slope of the Sierra Nevadas. The soils were coarse-textured and derived from decomposing granite parent material. The wildfire was fast-moving and apparently very hot because stems of mountain big sagebrush (Artemisia tridentata Nutt. ssp. vaseyana [Rydberg] Beetle) burned to the soil level.

In the spring of 1981 many rodent caches of antelope bitterbrush seedlings were visible in the burned area. During early March we selected 100 seed caches in the burn and 20 in an adjacent unburned stand. The caches were randomly divided into groups of 20 and given the following treatments: (1) control caches in the burned area, (2) caches covered with rodent-proof caps made of 1 cm opening hardware cloth, (3) caches treated with 0.17 ounces (5 ml) of 0.03 percent solution of the insecticide diazinon, (4) caches treated with 0.17 ounces (5 ml) of 0.005 percent suspension of the fungicide benomyl, (5) caches treated with 0.17 ounces (5 ml) of

Studies of Artificial Caches

Field trials with artificial caches of antelope bitterbrush with variable numbers and depths of seeds were initiated in March 1982. Experiments were conducted at Doyle, Lassen County, California and Granite Peak, Washoe County, Nevada. Both sites are representative of the same type of plant community and soils found at Little Antelope Valley. Four replications in a randomized block design were used in all experiments. Seed caches were prepared in plastic boxes 4 x 4 x 3 inches (10 x 10 x 8 cm) with drainage holes. The boxes were filled with soil from the sites and compacted to comparable bulk densities. The seeds were placed on a fiberglass screen to facilitate recovery. Unless otherwise specified, antelope bitterbrush seeds collected at Lakeview, Oregon in 1981 were used. Depth treatments consisted of 100 seeds each planted: (1) on the surface, (2) at 0.4 inches (1 cm), (3) at 0.8 inches (2 cm), and (4) at 1.6 inches (4 cm) below the surface. Using deeper boxes in one trial at Doyle, the seeds were planted 10 cm deep.

In number of seeds-per-cache trials, seeds were planted at 0.4 inches (1 cm) depth with the number of seeds consisting of 1, 2, 5, 7, 10, 45, and 100 per box.

The boxes were carefully buried in the field according to the experimental design. Then the burial sites and surrounding area were raked and swept to blend in with the site. The boxes were recovered from the field after 1 week and the seeds were recovered by washing and screening the contents of the boxes.

Treatments testing olfactory sensitivity of rodents included caching at 1 cm in the soil 100 seeds of antelope bitterbrush with the papery flower parts attached. A second treatment consisted of caching at 0.4 inches (1 cm) 100 seeds that had been coated with two coats of plastic resin and baked dry. A third treatment consisted of finely grinding 100 antelope bitterbrush seeds and mixing the ground material with 100 seeds of crested wheatgrass (Agropyron desertorum, [Fisch.] Shult. cultivar 'Nordan'). This mixture and a treatment with 100 crested wheatgrass seeds, alone, were cached 1 cm deep.

To compare rodent preference for different sources of antelope bitterbrush we cached 100 seeds, 0.4 inches (1 cm) deep, from each of the sources collected in 1981: (1) Lakeview, Oregon, (2) Mono Lake, California (desert bitterbrush [Purshia glandulosa Curran]), (3) Chelan, Washington, (4) Tollgate, Idaho, and (5) Hotsprings, Montana. This experiment was repeated twice at Doyle; once in a randomized block with the boxes touching each other and once with the boxes randomly distributed in a 2.5 acre (1 ha) area.

Sherman live traps (baited with rolled oats) and rat-size snap traps (baited with rolled oats and peanut butter) were used on the study areas to determine rodent species present. Traps were set in lines of 10 stations, spaced 33 ft (10 m) apart, with one trap per station. Total trapping effort was 310 trap nights.

RESULTS

Natural Caching Studies

CHARACTERISTICS OF CACHES

In the area burned by wildfire in Little Antelope Valley, we found 3,600 rodent caches per acre (0.88 per m²) of antelope bitterbrush seedlings in the spring of 1981. In the unburned area only 650 caches per acre (0.16 per m²) were found. We

attributed the lower number of caches in the unburned area to rodent predation during the winter. There were numerous small rodent excavations indicating where caches had been raided. In the burned area, probably because of lack of cover, these excavations were not found.

In the burned area, the average number of antelope bitterbrush seedlings per cache was 12.5 with a range of 7 to 31. At the cotyledon stage of emergence, 30 percent of the antelope bitterbrush seedlings that we recovered from caches had evidence of damage apparently caused by insects. The underside of the cotyledons had been eaten leaving only the cuticle of the upperside of the seed leaves.

In the soil on the burned area from which caches were excavated for counting, we found an average of 8 ungerminated antelope bitterbrush seeds per cache. Careful examination of the seeds revealed an average of only 1 seed per cache that was not obviously broken or empty. Incubation of the entire seeds at 59°F (15°C) failed to produce any germination.

CACHES AND TREATMENTS

When we monitored through spring and summer the undisturbed seedlings of antelope bitterbrush growing from rodent caches at Little Antelope Valley, we found that all the seedlings in the burned control had died by June 19 (table 1). In the unburned control the seedlings started growing 2 weeks later, apparently because of shading caused by large shrubs, but they were all dead by June 12.

There were several apparent reasons for seedling mortality in the populations in relation to treatment and time. The first week after emergence the caches lost an average of 38 percent of their seedlings regardless of treatment. This we attribute to the lack of frost hardiness of antelope bitterbrush seedlings (unpublished data, R. L. Everett, Intermountain Forest and Range Experiment Station, U.S. Forest Service, Reno, Nevada). Antelope bitterbrush seedlings in the unburned control suffered a similar level of mortality in the first week even though they emerged 2 weeks later.

Rodent damage to seedling was never a factor in the burned area; therefore, the cage treatment was ineffective (table 1). In the unburned control, rodent damage was severe. Also, in the unburned control, late spring growth of cheatgrass (Bromus tectorum) formed a dense stand and offered severe competition for available moisture (Evans and others 1970). The burned area was virtually free of cheatgrass.

The addition of a complete nutrient solution to the caches hastened death of seedlings with all being dead by May 7 (table 1). Added nutrients may have increased moisture stress before the seedlings were deeply enough rooted to extract from the receding level of available water in the soil. The fungicide treatment did not markedly change the rate or date of total seedling death.

From March 17 to April 16, seedlings in the insecticide treatment had a mortality pattern similar to that observed in the burned control (table 1). After April 16, the rate of mortality in the insecticide-treated caches slowed and leveled off with 46 percent of the original seedling density surviving the summer. These seedlings reached the third true leaf stage by the end of the summer. By the spring of 1982 some antelope bitterbrush plants had become established in all of the insecticide-treated caches. We made an extensive collection of insects at the site, but entomologists did not consider any of the insects we collected as responsible for the type of seedling damage observed. In earlier studies, Hubbard (1956) found that wireworms destroyed bitterbrush seedlings.

Table 1.--Percent survival of antelope bitterbrush seedlings in rodent caches as related to date (March through July) and various treatments.
Experiment conducted in Little Antelope Valley, Mono County, California^a

Date	Percent survival					
	Unburned area	Burned area				
	Control	Control	Insecticide (diazinon) ^b	Fungicide (benomyl) ^c	Cages	Nutrient solutions ^d
March 17	--	100	100	100	100	100
24	--	60	69	68	59	56
31	100	40	56	60	27	43
April 14	70	38	51	59	12	12
16	50	34	50	27	7	6
21	37	14	44	17	5	1
May 7	21	13	46	12	4	0
21	10	9	46	9	2	0
June 3	2	7	46	4	1	0
12	0	2	46	0	0	0
19	0	0	46	0	0	0
July 6	0	0	46	0	0	0

^aNot all treatments were started on the same date. The unburned control was delayed 2 weeks because the seeds germinated slower and seedlings emerged later in the heavy shade of the large shrubs.

^b0.03 percent solution of diazinon.

^c0.005 percent solution of benomyl.

^d0.03 percent solution of 12-6-8 nutrient solution.

Artificial Caching Studies

A hard freeze in June 1981 destroyed much of the antelope bitterbrush seed crop on the eastern slope of the Sierra Nevadas, making it impossible to get a second year of data concerning natural caching. Using a different tact on the same general problem we artificially distributed caches of antelope bitterbrush seeds during the time when rodents were voraciously destroying the few natural caches that were germinating.

NUMBER OF SEEDS PER CACHE

When only one antelope bitterbrush seed was cached 0.4 inches (1 cm) deep, the rodents never bothered to dig it up at either location, even though the box containing the single seed was buried in an experimental design with other boxes that contained as many as 100 seeds (table 2). If two seeds were cached, rodents removed 75 percent of the seeds at both locations. At Doyle, if caches were composed of 10, 45, or 100 seeds, the rodents removed at least 98 percent of the seeds. Reichman and Oberstein (1977) showed that size (and depth) of seed caches affected their detection by rodents. Predation was not as high at Granite Peak, possibly because it is a higher and colder location than Doyle with less rodent activity at the same date.

Table 2.--Rodent predation of antelope bitterbrush seeds placed in artificial caches with different numbers of seeds per cache. Experiment conducted at Doyle, California and Granite Peak, Nevada. Seeds cached 0.4 inches (1 cm deep).

Number of seeds per cache	Percent predation by rodents	
	Doyle	Granite Peak
1	0	0
2	75	75
5	90	84
7	93	82
10	99	80
45	98	54
100	98	66

DEPTH OF BURIAL

At Doyle, rodents removed all of the antelope bitterbrush seeds cached on the soil surface (table 3). Only 8 percent of the seeds were recovered from burial at 1.6 inches (4 cm) after being exposed to rodent predation. At Granite Peak, predation was severe on the surface and at 0.4 inches (1 cm), but dropped to 50 and 47 percent at 0.8 and 1.6 inches (2 and 4 cm) burial, respectively. At Doyle, we also buried antelope bitterbrush seed 4 inches (10 cm) deep in special boxes. The rodents did not disturb these seeds. Because seeds are discovered by rodents primarily via olfactory cues (Howard and Cole 1967; Johnson and Jorgensen 1981), the low discovery rate of deeper caches is not surprising. Differences in rates of discovery between the two sites may be caused by a variety of factors including rodent species involved, soil moisture, etc. (Johnson and Jorgensen 1981).

Table 3.--Rodent predation in relation to depth of burial of antelope bitterbrush seeds. 100 seeds placed in all caches. Experiment conducted at Doyle, California and Granite Peak, Nevada

Depth of burial	Percent predation by rodents	
	Doyle	Granite Peak
Surface	100	91
0.4 inches (1 cm)	98	95
0.8 inches (2 cm)	99	50
1.6 inches (4 cm)	92	47

OTHER TREATMENTS

Leaving the papery bracts on the antelope bitterbrush seeds had no influence on subsequent predation of cached seeds. Likewise, coating the seeds with a plastic residue before caching them 0.4 inches (1 cm) deep did not markedly limit predation.

Rodents did not disturb caches of 100 seeds of crested wheatgrass. However, when the crested wheatgrass seeds were mixed with 100 finely ground antelope bitterbrush seeds before caching, the rodents completely excavated the boxes and chewed into small pieces the fiberglass screens that were placed below the seeds to aid in recovery.

SOURCES OF SEED

The five sources of bitterbrush seed that we tested, including one source of desert bitterbrush, appeared to be equally susceptible to predation by rodents (table 4). Where all the boxes of seeds were put together in an experimental design, this might be construed as baiting the rodents. Predation, however, appeared to be just as severe whether seeds were cached at random locations or in an area where the boxes were located adjacent to each other.

Table 4.--Rodent predation in relation to seed sources of antelope and desert bitterbrush. 100 seeds cached 0.4 inches (1 cm) deep. Seeds of different sources were placed in boxes that were both close together and widely spaced. Experiment was conducted at Doyle, California.

Seed source	Percent predation by rodents	
	Adjacent	Remote
Lakeview, Oregon	95	100
Mono Lake, California ^a	100	99
Chelau, Washington	100	100
Tollgate, Idaho	100	100
Hotsprings, Montana	99	97

^aDesert bitterbrush

Rodent Predators

The species of rodents we captured in these communities were: deer mice (*Peromyscus maniculatus*), Great Basin pocket mice (*Perognathus parvus*), least chipmunks (*Eutamias minimus*), and Panamint kangaroo rats (*Dipodomys panamintinus*). Gustafson (1974) trapped intensively (approximately 7200 trap-nights) in a plant community similar to those we trapped and located very near our Granite Peak site. He recorded the presence of other seed-eating rodents, including Ord's kangaroo rat (*D. ordii*), Great Basin kangaroo rats (*D. microps*), and dark kangaroo mice (*Microdipodops megacephalus*). According to Everett and others (1978), bitterbrush seeds are a highly preferred food source of deer mice, a rodent species credited with being the major consumer of artificially planted seed (Nelson and others 1970).

DISCUSSION

The collecting, caching, germination, and subsequent grazing of antelope bitterbrush seeds and seedlings form a very complex regeneration process. A similar process has been described for other plant species (Reynolds 1950; La Tourrette and others 1971; McAdoo and others 1983). This study points out the varied types of perturbations that are involved in the seedling establishment process. In designing a management program to enhance regeneration of antelope bitterbrush, managers and researchers must be cognizant of interacting effects of rodent activities and plant competition. In any plan they design for seeding antelope bitterbrush seeds in an artificial regeneration scheme, they must also recognize the great potential for seed predation by rodents. The depths at which seeds are typically planted in reseeding attempts 0.2 to 0.5 inches (0.5 to 1.3 cm) are ideal for discovery of seeds by rodents (Johnson and Jorgensen 1981). Also, the possible role of insect predation on antelope bitterbrush seedlings certainly deserves additional research.

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SUMMER USE OF BITTERBRUSH RANGELANDS BY MULE DEER¹

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ABSTRACT

Tractable mule deer were used to determine diet composition on summer rangeland characterized by bitterbrush, big sagebrush, and Utah juniper. Diets, composed mostly of forbs in spring, steadily shifted to bitterbrush dominance, reaching 91 percent in September. Based on available forage and percent dietary crude protein, the plant community was determined adequate for supporting mule deer. Management recommendations are discussed.

INTRODUCTION

The forage value of antelope bitterbrush (Purshia tridentata [Pursh] DC.)³ to Rocky Mountain mule deer (Odocoileus hemionus Rafinesque) has been well documented (Kufeld and others 1973). While most research dealt with use on winter ranges, the summer use of antelope bitterbrush appears to be important on ranges where high quality forages are limited.

In 1976 the Utah Division of Wildlife Resources identified 29 of 74 deer management units in which summer ranges were considered equal or more limiting in forage resources than the associated winter ranges (Hancock and others 1976). These units cover the western third and southeastern quarter of Utah, with similar ranges extending into portions of Nevada, Idaho, Colorado, and Arizona. Because they have lower precipitation and warmer temperatures than typical high elevation summer ranges, these units contain vegetal communities that are usually considered spring-fall or winter range types. They are characterized by plant communities containing curlleaf mahogany (Cercocarpus ledifolius Nutt.), Gambel oak (Quercus gambelii Nutt.), big sagebrush (Artemisia tridentata Nutt.), low sagebrush (Artemisia tridentata arbuscula [Nutt.] H.&C.), Utah serviceberry (Amelanchier utahensis Nutt.), and mountain snowberry (Symphoricarpos oreophilus Gray). Only limited acreages of high quality summer range, such as communities containing quaking aspen (Populus tremuloides Michx.), conifer, riparian, or upland meadows, are available, and consequently deer are forced to select less than optimal vegetal types. Nonetheless, these units have contributed a significant proportion (21 percent in 1981) to the total Utah deer harvest.

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³Scientific names are from Harrington, H. D. Manual of the plants of Colorado, Swallow Press, Inc., Chicago, Ill.; 1964, 666 pp. and Welsh, S. L., Moore, G. Utah plants, 3rd edition, Brigham Young Univ. Press, Provo, Utah.

Areas containing antelope bitterbrush are usually not considered summer range, especially where associated with pinyon-juniper (Olson and Logan 1973), yet many deer occupy these ranges throughout the summer. Consequently, the intent of this research was to investigate the adequacy of such ranges to support summering mule deer.

AREA AND METHODS

The study area was located in west-central Utah on the north slope of Sabie Mountain, which is part of the West Tintic Range. The elevation is 6,460 ft (1 970 m) and yearly precipitation averages about 9 inches (24 cm), received primarily during winter. Antelope bitterbrush occurs at varying densities within a singleleaf pine (Pinus monophylla Torr. & Frem.)-Utah juniper (Juniperus osteosperma Torr.) stand that dominates a zone extending from about 5,900 to 6,900 ft (1 800 to 2 100 m). Above and below the pinyon-juniper zone are treeless ranges dominated by big sagebrush. Although usually grazed in summer by cattle, no use occurred during the sampling period.

Mule deer diets were determined monthly from May through September 1981 using three tame, adult, female deer. Each sampling period consisted of observing a minimum of 1,000 bites per deer during a minimum of 2 feeding hours. Diets were determined as percent dry weight consumption by species using hand-plucked, simulated bites also collected monthly (Deschamp and others 1979). Deer grazed while roaming freely over a 740-acre (3-km²) area during diet sampling and were kept within a 1.0-acre (0.4-ha) on-site enclosure between trials to assure their being accustomed to the vegetation. Within the enclosure, they were fed alfalfa hay ad libitum to supplement natural forages. Although some dietary variations occurred between individual deer, generally the same forages were selected, and consequently diets were pooled.

Vegetal production was determined monthly from five permanent macroplots immediately following diet determinations. The macroplot locations were selected to accurately represent the range conditions within the diet sampling area. Each macroplot was 33 x 66 ft (10 x 20 m) and permanently marked with steel posts and wood stakes. Forage production was determined by encompassing each plot with a string and obtaining weight estimates for individual species. Weight estimates were obtained by one of the following three procedures: (1) Weight of species having uneven distributions, such as perennial forbs in which individual plants could be readily counted, was estimated by multiplying the number of plants counted by the mean weight of 3 to 10 clipped plants. (2) Weight of species having relatively uniform distributions, such as grasses and some annual forbs, was estimated by obtaining clipped weights on a unit area basis (often 10 ft² or 1 m²) and multiplying by the number of units within the macroplot. (3) Weight of individual shrubs was estimated using a reference branch, counting the number of equivalent branches on the shrubs, clipping the reference branch, and multiplying the clipped weight of the reference branch by the number of counted equivalent branches. These procedures were faster than conventional double sampling techniques and were adopted because of time constraints. However, to compare accuracy, a double sampling procedure using the macroplot-microplot approach was also completed during August (Poulton and Tisdale 1961; Deschamp and others 1979). Simply, within each macroplot, weight estimates were made on 40 randomly located microplots with every 10th plot clipped for regression calculation. Ground cover and plant canopy cover (table 3) were also estimated. Plant samples were collected monthly for converting to dry weight production, and those species comprising 1 percent or more of the diet during any month were analyzed for crude protein.

RESULTS

The diets of mule deer changed considerably throughout the summer (table 1). Consumption of antelope bitterbrush increased steadily reaching almost 92 percent by September. Consumption of three additional browse species declined in the late summer

diet because of low abundance and prior use by both wild and tame deer. In contrast, forbs comprised most of the diet in May, but declined rapidly throughout the summer. In May and June nine and seven forb species, respectively, comprised 1 percent or more of the diet, but by July only two remained important. Abundant grasses, big sagebrush, Utah juniper, and rabbitbrushes (Chrysothamnus spp. Nutt.) never exceeded 1 percent of the diet.

Table 1.--Mule deer diets (percent by weight) through the summer

Species	Month					Mean
	May	June	July	Aug.	Sept.	
BROWSE						
<u>Purshia tridentata</u>	8.2	23.1	59.9	79.8	91.7	52.5
<u>Symphoricarpos oreophilus</u>	2.9	5.8	6.5	4.9	1.2	4.3
<u>Amelanchier alnitolia</u>	4.4	6.5	2.5	1.8	.7	3.2
<u>Eriogonum microthecum</u>	T*	T	2.6	.7	.0	.7
4 others	.1	.1	1.0	.2	.8	.4
Total browse	15.6	35.5	72.5	87.4	94.4	61.1
FORBS						
<u>Commandra umbellata</u>	3.2	10.7	15.9	5.8	1.1	7.3
<u>Vicia americana</u>	24.4	10.9	.0	.0	.0	7.1
<u>Crepis accuminata</u>	10.3	19.1	.9	.6	.1	6.2
<u>Lithospermum ruderales</u>	7.7	5.5	9.1	4.7	3.7	6.1
<u>Astragalus</u> spp.	22.2	4.2	.0	.0	.0	5.3
<u>Agoseris glauca</u>	4.4	.7	.0	.0	.0	1.0
<u>Descuriana</u> spp.	1.8	3.0	.0	.3	.0	1.0
<u>Collinsia parviflora</u>	3.9	.0	.0	.1	.0	.8
<u>Delphinium nelsonii</u>	3.4	.0	.0	.0	.0	.7
<u>Allium accuminatum</u>	T	3.0	.0	T	.0	.6
26 others	2.9	7.3	1.5	1.1	.7	2.7
Total forbs	84.2	64.4	27.4	12.6	5.6	38.8
GRASSES						
Total grass	.2	T	T	.0	.1	.1

*T = < 0.1 percent.

Available forage, expressed as a percent of total production, showed generally less change over the summer (table 2). Available forage on antelope bitterbrush increased from May through July, but loss of leaves and flowers in August and September and continued use by deer resulted in a sharp decline. Browse species comprised the bulk of the production, and two most abundant species, big sagebrush and Utah juniper, showed little change in production. Forbs comprised only a small proportion of the forage production and declined sharply from the early summer months. Furthermore, many of the forbs were unpalatable to deer. Palatable forbs, such as American vetch (Vicia americana Muhl.), grew rapidly in early spring, but cured rapidly, decomposed, and were largely unavailable by July. A few species such as wayside gromwell (Lithospermum ruderales Dougl. ex Lehm.) had sufficiently coarse forage to remain intact through the summer. No important forb species grew in midsummer.

Table 2.--Available dry weight production percent by species through the summer

Species	Month					Mean
	May	June	July	Aug.	Sept.	
BROWSE						
<u>Purshia tridentata</u>	6.0	18.2	26.9	14.7	12.3	15.6
<u>Symphoricarpos</u>						
<u>oreophilus</u>	1.0	1.1	.3	.2	.1	.5
<u>Amelanchier alnifolia</u>	T*	T	T	T	T	T
<u>Eriogonum microthecum</u>	T	T	T	T	T	T
<u>Juniperus osteosperma</u>	34.6	26.7	27.2	33.2	31.0	30.5
<u>Artemisia tridentata</u>	29.6	34.7	29.8	30.3	36.9	32.3
<u>Chrysothamus</u>						
<u>viscidiflorus</u>	.3	1.5	2.6	1.6	1.8	1.6
3 others	T	.4	.7	1.9	2.2	1.0
Total browse	71.5	82.6	87.5	81.9	84.3	81.6
FORBS						
<u>Commandra umbellata</u>	.1	T	.1	T	T	.1
<u>Vicia americana</u>	.6	.1	T	T	T	.2
<u>Crepis acuminata</u>	.2	.2	.2	.2	T	.2
<u>Lithospermum ruderales</u>	.1	.1	.1	.1	.1	.1
<u>Astragalus spp.</u>	.6	.2	.0	.0	.0	.2
<u>Agoseris glauca</u>	.4	T	.0	.0	.0	.1
<u>Descuriana spp.</u>	.1	T	.0	.0	.0	T
<u>Collinsia parviflora</u>	1.5	.0	.0	.0	.0	T
<u>Delphinium nelsonii</u>	T	.0	.0	.0	.0	T
<u>Allium acuminatum</u>	T	T	T	.0	.0	T
<u>Opuntia spp.</u>	1.0	.1	.2	1.8	1.8	1.0
30 others	4.8	4.9	1.6	1.0	.9	2.7
Total forbs	9.4	5.8	2.2	3.1	2.8	4.7
GRASS						
Total grass	19.0	11.7	10.3	14.7	12.9	13.7

*T = < 0.1 percent.

Most species consumed by deer were highly preferred. The preference ration (percent dietary composition ÷ percent available production, Neff 1974) showed that all species comprising 1 percent or more of the monthly diets were preferred. Indeed, most had ratios greater than 4.0, suggesting they were highly preferred in relation to the total plant community (Austin and Urness 1982).

The relationship ($r^2=0.96$) between the macroplot procedures for estimating production and the double sampling technique using microplots showed good agreement (table 3). Ground and plant canopy cover were about average for this vegetal type (Olson and Logan 1973).

Table 3.--Vegetative production in lbs/acre as determined by macroplot estimation and microplot double sampling, ground cover (percent), and plant cover (percent) during August 1981

Species	Technique	
	Microplot	Macroplot
BROWSE		
<u>Purshia tridentata</u>	149.5	116.1
<u>Symphoricarpos oreophilus</u>	6.2	1.8
<u>Amelanchier alnifolia</u>	2.0	0.2
<u>Eriogonum microthecum</u>	0.6	0.8
<u>Juniperus osteosperma</u>	238.1	262.0
<u>Artemisia tridentata</u>	159.9	238.7
<u>Chrysothamnus vicidiflorus</u>	34.6	12.9
3 others	2.0	14.9
Total browse	593.1	647.4
FORBS		
<u>Commandra umbellata</u>	1.6	0.2
<u>Vicia americana</u>	0.7	0.2
<u>Crepis accuminata</u>	2.0	1.7
<u>Lithospermum ruderales</u>	6.9	1.1
<u>Opuntia spp.</u>	20.0	14.4
12 others	13.5	7.8
Total forbs	44.9	25.4
GRASS		
Total grass	125.9	116.1
TOTAL PRODUCTION	763.9	788.9
GROUND COVER		
Exposed soil	24.2	--
Litter	58.8	--
Rock	14.0	--
Basal vegetation	3.0	--
PLANT CANOPY COVER	37.2	--

The percent crude protein in the forage consumed changed considerably (table 4). Crude protein levels were high in May, but declined rapidly. The few forbs that remained available through the summer were lower in crude protein than the palatable browse species. For the composite diet, percent crude protein declined from about 18 percent in May to about 8 percent by late summer when no high quality forages were selected.

Table 4.--Percent crude protein for plant species comprising 1 percent or more of the monthly diet

Species	Month				
	May	June	July	Aug.	Sept.
BROWSE					
<u>Purshia tridentata</u>	13.8	10.7	8.9	7.9	8.2
<u>Symphoricarpos oreophyllus</u>	14.9	11.0	12.8	6.8	4.7
<u>Amelanchier alnifolia</u>	15.2	12.7	8.0	8.2	--
<u>Eriogonum microthecum</u>	--	--	10.2	--	--
FORBS					
<u>Commandra umbellata</u>	¹ 18.0	9.4	6.3	6.5	6.4
<u>Vicia americana</u>	17.2	8.6	--	--	--
<u>Crepis accuminata</u>	19.5	8.0	--	--	--
<u>Lithospermum ruderales</u>	20.9	13.1	7.9	6.4	6.4
<u>Astragalus spp.</u>	21.8	10.6	--	--	--
<u>Agoseris glauca</u>	20.2	--	--	--	--
<u>Descuriana spp.</u>	24.0	10.5	--	--	--
<u>Collinsia parviflora</u>	10.0	--	--	--	--
<u>Delphinium nelsonii</u>	11.6	--	--	--	--
<u>Allium Accuminatum</u>	--	9.5	--	--	--
Weighted percent in diet	18.1	10.0	8.7	7.7	8.1

¹Estimated.

DISCUSSION

Although Smith (1953) rated antelope bitterbrush relatively unpreferred as a summer deer forage--25th of 33 species assessed--it is important on low elevation summer ranges. Trout and Thiessen (1973) reported that antelope bitterbrush comprised 4, 1, 13, 22, and 5 percent of the monthly diets from May through September, respectively, from ranges where it made up less than 1 percent of the vegetal cover. They stated that where the shrub occurred, use by deer and cattle was heavy. Leach (1956), using rumen analyses from 29 and 16 deer, reported that antelope bitterbrush comprised 6.6 and 34.6 percent of the summer diets from two herds in California. Berg (1966) and Tueller and Monroe (1976), in comparing 13 low elevation summer deer habitats in Nevada, concluded that whenever antelope bitterbrush was found within a plant community, that community was invariably ranked among the highest in deer use. Berg (1966) further stated that the shrub was the most heavily used species in all areas where it occurred. Based on rumen analyses of sacrificed deer (five per sampling period), Doughty (1966), Deibert (1968), and Tueller (1979) reported it was an important forage in summer (table 5). The high dietary variation was caused by low sample size and changes in collection sites. Nonetheless, their data indicate the importance of antelope bitterbrush even though its maximum plant canopy cover was only 3.8 percent.

Table 5.--Proportion of antelope bitterbrush (percent dry weight and percent frequency of occurrence in mule deer diets from Fox Mountain, Nevada

Year	Month					
	May		July		September	
	Weight	Frequency	Weight	Frequency	Weight	Frequency
1964 ¹	1.7	40	50.7	100	38.8	100
1965 ¹	23.7	100	55.7	100	4.7	40
1966 ²	28.7	100	21.1	100	16.4	100
1967 ²	16.4	40	17.2	100	17.6	100

¹From Doughty 1966.

²From Deibert 1968.

Although our data showed that antelope bitterbrush had a considerably higher dietary contribution, especially in late summer, the study was conducted where other palatable browse species were sparse. If rumen analyses from wild deer had been used, the diet probably would have contained less bitterbrush and greater amounts of other species since mule deer generally have large home ranges which likely would have included other vegetal types (Rodgers and others 1978). Nonetheless, the important implication is that where it occurs on low elevation summer ranges antelope bitterbrush is readily consumed and preferred by deer.

Although nutritional parameters have not been strictly defined for mule deer maintenance or growth, forage quality (crude protein and digestibility) does effect carcass weights, productivity, and antler size (Julander and others 1961; Robinette and others 1973). Einarsen (1946) estimated 5 percent crude protein was the critical level for maintenance of black-tailed deer in Oregon, and Longhurst and others (1952) estimated this level was 7 to 8 percent for mule deer in California. Maintenance levels for adult white-tailed deer ranged from about 6 to 8 percent with optimal levels of 14 to 18 percent or higher (French and others 1955; Magruder and others 1957; Murphy and Coates 1966; Holter and others 1979). Summarizing these studies, about 7 percent crude protein appears to be an acceptable mean for body maintenance.

Consequently, for this study, the crude protein levels in the diet were excellent in May, adequate in June and July, and slightly above maintenance in August and September. Since bitterbrush followed the same nutritional decline but remained above 7 percent crude protein in this study, as well as in others (Doughty 1966; Trout and Thiessen 1973), we conclude that antelope bitterbrush is adequate for body maintenance of mule deer. Nonetheless, crude protein values of this shrub, as well as the combined diet, were considerably below those reported from high quality ranges where late summer values were generally above 12 percent (Collins 1979; Pallesen 1979).

CONCLUSIONS AND RECOMMENDATIONS

1. Antelope bitterbrush is an important summer forage, palatable to mule deer. The percent dietary contribution of the shrub increased through the summer as palatable forbs and other browse species became less available.

2. Although nutritionally far from optimal, pinyon-juniper and big sagebrush communities used by deer in summer and containing moderate quantities of bitterbrush should be considered as summer range. To estimate maximum potential summer deer-days/ha, the following procedure is suggested:

- A. Assume daily forage intake (dry weight) per deer is 3.3 lbs (1.5 kg) (Smith 1953; Bandy and others 1970).
- B. Assume bitterbrush comprises 50 percent of the summer diet (table 1).
- C. Assume 70 percent of bitterbrush's current annual growth is allocated for deer, with half (35 percent) utilized in summer.
- D. Divide half the allocated production, as determined in fall from ungrazed plots, by the daily bitterbrush consumption.
- E. Example using our figures:

$$\text{Maximum deer days per acre} = \frac{116.1 \text{ lbs/acre} \times .35}{1.65 \text{ lbs/deer-day}} = 24.6 \text{ (60.9 deer-days/ha)}$$

$$\text{Deer per mi}^2 \text{ over six months} = \frac{24.6 \text{ deer-days/acre}}{180 \text{ days}} \times \frac{640 \text{ acre}}{\text{mi}^2} = 87.5 \text{ (33.8 deer/km}^2\text{)}$$

Caution must be used in applying this procedure; lower figures result from higher intake rates, increased bitterbrush in the diet, or more conservative forage allocation, and vice versa. Consumption of the shrub, as well as other deer forages, by livestock must also be considered. Furthermore, other factors including water, animal behavior, and human disturbance may be more limiting than the forage resource. Robinette and others (1977) reported a density of 61.9 deer/mi² (23.9 deer/km²) on diverse low elevation summer range, but the extent of winter range was about half that of summer range.

3. Management of livestock should maximize forage availability, particularly bitterbrush, for deer while using the grass resource. Therefore, livestock should be grazed in mid- to late spring when grass is succulent, but before livestock use switches to bitterbrush and other browse (Jensen and others 1972). Berg (1966) reported that on seven areas where grazing was poorly controlled, livestock use of bitterbrush exceeded that of deer. On our study area, livestock grazing from about May 15 to no later than July 1 (Smith and Doell 1968) appears to be acceptable.

4. Since high quality forages are not available in late summer, the carcass condition and weight of deer would be expected, and apparently are, less than those of deer on high quality summer range (Austin 1982). This would likely result in increased mortality and decreased productivity (Julander and others 1961). Consequently, antlerless harvest of mature females should be conservative.

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Section 6. Soil-Plant Nutrient Relationships



OPPORTUNITIES AND APPROACHES FOR ENHANCING NITROGEN
FIXATION IN PURSHIA, COWANIA, AND FALLUGIA¹

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ABSTRACT

Although Purshia and Cowania are capable of nitrogen fixation, the ecological importance is not known. Limited observations suggest sparse nodulation may occur. There may be opportunities for enhancing nitrogen fixation utilizing an inoculum, species and ecotype selection, intergeneric hybridization, and plant breeding. Field trials are essential to demonstrate possible applications.

INTRODUCTION

Specific bacteria that infect plant roots allow the utilization of atmospheric nitrogen. The plants can then flourish and enrich the soil without expensive nitrogen fertilizer. Nitrogen fixation has long been exploited in agriculture. Rhizobium inoculants for specific legumes are commercially available and effective management of the legume symbiosis is a common agricultural practice.

Purshia (bitterbrush) and Cowania (cliffrose) are genera among certain woody angiosperms that have a symbiotic association with Frankia, an actinomycete somewhat similar to the better known legume-Rhizobium system. Both genera are important in

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ecological succession and are early colonizers on natural or human-induced disturbances. Symbiotic nitrogen fixation could contribute to their pioneer success. There is tremendous potential for adapting successful aspects of legume-Rhizobium agricultural practices to reclamation approaches using the actinorhizal association.

Lack of knowledge of the occurrence, effectiveness, and duration of nodules on Purshia and Cowania makes it difficult to estimate their ecological importance and level of nitrogen input. In some field observations, nodulation has not been encountered (Nelson, in this proceedings). It appears that many sites are sparsely nodulated (Dalton and Zobel 1977; Nelson, in this proceedings), and in some cases nodule biomass may be insufficient for appreciable nitrogen inputs (Dalton and Zobel 1977). Drought is a likely factor where soil samples collected from sparsely nodulated sites produce abundant nodules on well-watered, greenhouse-grown seedlings (Dalton and Zobel 1977; Righetti and Munns 1981). However, soils collected from native stands sometimes produce non-nodulated seedlings even in greenhouse trials (Wagle and Vlamis 1961; Klemmedson 1979; Righetti and Munns 1981). This is especially true in surface samples where moisture and temperature stresses may be severe (Righetti and Munns 1981).

Water may be the limiting factor, making nitrogen fixation of limited ecological importance. Fallugia paradoxa (Apache plume) may be non-nodulating (Righetti and Munns 1981; Nelson, in this proceedings) even though a hardy pioneer. This may have implications on the ecological significance of nitrogen fixation especially if Purshia, Cowania, and Fallugia all evolved from a common ancestor (McArthur and others, in this proceedings). However, it seems likely that nitrogen fixation would be an advantage for these pioneer species commonly found on drastically nitrogen-deficient sites. Although nitrogen fixation rates may be much less than those associated with agricultural legumes, the nitrogen requirement for these slower-growing shrubs is substantially less. Even if nitrogen fixation input into the ecosystem is small, it may enhance survival and establishment for the species involved.

Purshia has been grown in nitrogen-free media (Bond 1976a). Although the symbiosis can provide plants with a source of nitrogen, the challenge is to bring greenhouse successes to more difficult field applications. It is conceivable that nodulation could enhance initial plant establishment, but the enhanced success has to be compared to applied nitrogen. In nitrogen-deficient soils, 4-month-old, nitrogen-supplied, greenhouse-grown Purshia seedlings are generally three to four times larger than nodulated ones (Righetti and Munns 1982). It may not be wise to rely on symbiotic nitrogen if an initial nitrogen application is superior. Perhaps nodulated transplants with an established symbiosis could overcome the slow symbiosis establishment that has been reported (Bond 1976a; Dalton and Zobel 1977; Righetti and Munns 1981). However, a slow-release nitrogen fertilizer in the planting medium is relatively inexpensive considering the cost of labor and the transplants themselves. Some evidence has suggested that bare root transplants are superior to container-grown transplants (Carpenter, in this proceedings). This may create difficulties for a nodulated transplant scheme as maintenance of nodulation on bare root stock may be difficult. Even if fertilized for initial establishment, the effect of the nitrogen application will disappear. Continued growth on symbiotic nitrogen would be desirable.

We know very little about capabilities or opportunities for improvement of nitrogen fixation in these shrubs. With a vigorous research effort, nitrogen fixation may be enhanced. The economic establishment of a soil-enriching,

maintenance-free plant community may be obtainable. An evaluation of current research efforts and possible approaches to enhance nitrogen fixation in Purshia, Cowania, and Fallugia are presented in this paper. Studies are necessary on inoculation responses, soil fertility factors limiting nodulation, species and ecotype selection, genetic improvement, and intergeneric hybridization. Field trials will be required to evaluate any potential.

INOCULATION RESPONSES

Naturally occurring soil populations of the appropriate actinomycete seem to be adequate for actinorhizal systems inhabiting moist ecosystems, alder for example (Bond 1976b). In more xeric climates, insufficient soil populations may cause sparse nodulation. This is apparent from greenhouse trials in which soil collected from Purshia stands in eastern California was used as a growing medium with crushed nodules as an inoculum (Table 1). Nodules for the inoculum were collected at Truckee and Burcham Flat.

When inoculated with a P. tridentata crushed nodule inoculum, one of four non-nodulating soils (soil 4) and four sparsely nodulating soils (soils 3, 6, 8, 10) produced well-nodulated plants. Inoculation also increased nodule mass, total nitrogen, percent nitrogen, and shoot dry mass in some of the soils. Of the three soils failing to produce well-nodulated plants when inoculated, one produced plants that responded well to nitrogen additions but failed to nodulate under low nitrogen conditions (soil 9). A second produced severely stunted plants suggesting stresses other than nitrogen deficiency on the host (soil 2). The third (soil 7) produced plants that were not nitrogen deficient.

Subsequent studies have demonstrated that surface soil may bias the assessment of a site's nodulation capability for either Purshia or Cowania stands. Table 2 presents data from a greenhouse experiment in which Cowania seedlings were grown in surface and subsurface soil samples collected from 10 Cowania shrub communities in Arizona. Only three (soils 3, 9, and 10) of the 10 surface soils produced well-nodulated seedlings. Nodulation is usually better in subsoil samples, but even some subsoils produced few or no nodules.

Nodule masses display the same relationships as nodule number, but differences between sites and sampling depth are relatively smaller. Seedlings appear to compensate for fewer successful infections with an increase in mass per nodule.

Nitrogen inhibits nodulation, thus nitrogen-amended soils often produce fewer nodules. This is evident in the data and more apparent in shorter term experiments (Righetti and Munns 1982). Common soil nitrogen levels may inhibit nodulation, especially in surface samples. However, inoculation responses (table 1) and soil analyses indicate that nitrogen inhibition is not a major cause of sparse nodulation. It is possible that nitrogen levels not inhibitory in small container experiments with adequate water could be inhibitory in the field where drought might make nitrogen nonlimiting.

Table 1. -- Nodule number, nodule mass, shoot dry mass, and total nitrogen in the shoot for 4-month, *P. tridentata* seedlings grown in 10 different soils (from Righetti and Munns 1982).

Site identification	Nodule number	Nodule mass mg/plant (fresh)	Shoot dry mass mg/plant (dry)	Total N in shoot mg/plant
1. Burcham Flat				
uninoculated	40	90	190	4.23
inoculated	71	130	240	4.75
2. Cactus Flat				
uninoculated	0	0	173	2.02
inoculated	4	3	116	1.36
3. Chilcoot				
uninoculated	1	10	360	4.07
inoculated	56 *	203 *	396	7.48 *
4. Independence				
uninoculated	0	0	150	1.86
inoculated	29 *	143 *	230 *	4.14 *
5. Sherwin Hill				
uninoculated	34	166	380	7.11
inoculated	42	190	340	6.83
6. Shingle Mill Flat				
uninoculated	10	83	200	3.74
inoculated	82 *	180 *	316 *	7.58 *
7. Silver Lake				
uninoculated	0	0	1773	23.09
inoculated	0	0	2225	31.15
8. Truckee				
uninoculated	21	150	390	7.61
inoculated	66 *	206 *	470	9.54
9. Valyermo				
uninoculated	0	0	203	3.53
inoculated	1	10	236	3.04
10. Walker				
uninoculated	2	4	146	1.75
inoculated	41 *	130 *	280 *	5.29 *

*Indicates that values are significantly ($p = 0.05$) greater than the uninoculated treatment in the same soil.

Analysis of the data from several greenhouse trials reveals a correlation between a soil's ability to nodulate (as measured by nodule fresh mass per seedling) and the site's elevation (elev. squared, $r=0.340$, $p=0.032$) and precipitation (reciprocal precip., $r=(-)0.44$, $p=0.004$). Nodulation is often sparse or absent in samples collected from dry, low elevation locations. The most important physical or chemical soil parameter to correlate with nodulation is sodium bicarbonate-extractable phosphorus (log phosphorus, $r=0.392$, $p=0.012$). A forward multiple regression model utilizing the reciprocal of precipitation, the log of extractable phosphorus and sample depth ($r=0.344$, $p=0.05$) can account for 54 percent of the variability in nodule mass if one aberrant, high-nitrogen soil is omitted. Although

Table 2. -- Nodule number (nodules/plant) for 6-month, *C. mexicana* var. *stansburiana* seedlings grown in 10 different surface (0-20cm) and subsurface (20-40cm) soil samples with and without 56 ppm nitrogen.

	<u>Unamended</u>		<u>Nitrogen-supplied</u>	
	Surface	Subsurface	Surface	Subsurface
1. Big Springs	5	15	0	16
2. Desert View	0	1	0	0
3. Flagstaff	41	266 *	0 □	7 □
4. Fredonia	3	49 *	0	21
5. Grand Canyon	2	29	0	1
6. Jacob Lake	4	81 *	0	4 □
7. Payson	3	6	3	7
8. Prescott	6	18	3	4
9. San Francisco Peaks	29	46	8	85 *
10. Williams	46	23	35	10

* indicates that values are significantly ($p = 0.05$) different in the subsurface than in the surface soil.

□ indicates that values are significantly ($p = 0.05$) different in nitrogen amended treatment than in unamended treatment.

potassium (reciprocal potassium, $r=0.480$, $p=0.01$), magnesium (reciprocal magnesium, $r=0.387$, $p=0.05$), and sodium (reciprocal sodium, $r=0.411$, $p=0.01$) were also moderately correlated with nodulation, these variables add only 5.6% to the predictive capability of the model, and interpretation of these factors is difficult. Soil and environmental factors are important in determining the capability of a sample from a specific site to produce nodulated seedlings. Soil factors have also been correlated with the incidence of nodulation in the field.³ Although a suitable soil population of the microsymbiont may exist at some sites, other sites, especially from harsh locations, might benefit from an inoculation. In sites where these shrubs have not been previously established, a need for inoculation is more likely.

The successful isolation of *Frankia*, the actinomycete genus infecting susceptible angiosperms (Callaham and others 1978), will allow many applications. The endophytes infecting roots at a given site may not be the most effective. The importance of incompatibility between host and microsymbionts resulting in reduced efficiency may have been underestimated. Not all *Frankia* strains are equally capable of fixing nitrogen, and ineffective strains can be isolated from natural populations. Gains could probably be made through inoculation with compatible and superior

³Williams, S. E. Soil factors which influence nodulation of Rosaceous shrubs. Cand. J. of Microbiol. (in press).

strains, thus enhancing nitrogen fixation. This approach currently is being explored and an isolation of the first Frankia strain for a rosaceous species, Purshia, appears successful.⁴ The competitiveness of a superior strain with ineffective endogenous strains remains unanswered. However, if container-grown, nodulated transplants were utilized, one could be assured that at least in the short term a desirable and superior symbiosis exists. Although it appears that nodules may exist for quite some time, the longevity of nodules on these shrubs and the persistence of a superior symbiotic system cannot be predicted (Nelson, in this proceedings). If bare root transplants or seeding is the desired means of stand establishment, competition with endogenous strains may be more important. With the rapid gains occurring in endophyte culture, it may be possible to select for both competitiveness and effectiveness, circumventing problems with native ineffective strains.

SOIL FERTILITY FACTORS LIMITING NODULATION

Even with a suitable population and adequate moisture, optimal nodulation and nitrogen fixation could be limited by fertility constraints (Righetti and Munns 1981). In some cases, nitrogen-deficient seedlings are only sparsely nodulated even in the presence of an inoculum adequate for other soils (Righetti and Munns 1982). Salinity, soil reaction, and fertility factors may be important. Table 3 presents an example of fertilizer response.

Nodule mass, nodule number, total nitrogen in shoots, percent nitrogen in shoots and percent of root consisting of nodules generally increased with the fertilizer amendment. Nodule percentages were similar to previous studies in the same unamended subsoil (Righetti 1980) but approached solution culture values of 11 percent (Bond 1976a) when the soil was treated with phosphorus and sulfur. The increase is due to increased nodulation; root weight did not appreciably change with fertility treatments.

The response to the fertilizer amendment was more apparent for P. glandulosa than P. tridentata. Purshia tridentata appears to have a better symbiotic tolerance to low fertility. It may be possible to select appropriate adapted species or ecotypes capable of tolerating fertility constraints as well as modifying soils to alleviate fertility problems. The better symbiotic tolerance of P. tridentata to low fertility is further supported by data from Wagle and Vlamis (1961). In their 2-year study of plants grown in a nitrogen deficient soil that nodulated both species, shoot weights of P. tridentata were greater than P. glandulosa in unamended soils but similar in a soil amended with phosphorus, potassium and sulfur.

⁴Baker, D.; McCain, R.; Seling, E. Serologic and host compatibility relationships among the isolated Frankiae. Cand. J. of Microbiol. (in press).

Table 3.--Nitrogen fixation parameters (per plant) for P. tridentata and P. glandulosa seedlings grown in soils with different fertility treatments (from Righetti 1980)

Nitrogen fixation parameters	Unamended soil	Phosphorus and sulfur amended soil ¹
<u>P. tridentata</u> :		
nodule mass (mg)	183 □	365 *
nodule number	102 □	129 □
total N (mg)	13.8 □	18.33
% N	2.56 □	2.52 □
nodule % of root	4.9	10 *
<u>P. glandulosa</u> :		
nodule mass	65	278 *
nodule number	23	73 *
total N	6.73	14.43 *
% N	1.00	1.88 *
nodule % of root	2.3	9.0 *

¹ 50ppm phosphorus as $\text{Ca}(\text{H}_2\text{PO}_4)_2$ and 80ppm sulfur as $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$.

* indicates the parameter is significantly ($p = 0.05$) greater in the amended treatment.

□ indicates that the value reported for P. tridentata is significantly ($p = 0.05$) greater than the corresponding value for P. glandulosa.

SPECIES AND ECOTYPE SELECTION

Differences between the two Purshia species are not surprising considering their different ecological niches. Since ecotypes within both Purshia species, and Cowania mexicana var. stansburiana are known to vary tremendously across a wide range of properties, selection of superior nitrogen-fixing species or ecotypes for specific situations may prove valuable. There is some evidence that ecotypes vary in their nitrogen-fixing capability.

Differences in nodulation and growth for P. glandulosa seedlings grown from seeds collected from different locations have been observed (Righetti and Munns 1981). Dalton and Zobel (1977) reported that a P. tridentata ecotype from Utah produced ineffective nodules when grown in an Oregon soil that effectively nodulated other ecotypes. The potential and necessity for selecting appropriate species or ecotypes for a wide range of characteristics has been repeatedly emphasized throughout these proceedings, and nitrogen fixation is no exception. If the actinomycetes infecting these rosaceous plants is as variable as the hosts, a combined effort of selecting appropriate host-endophyte combinations could prove fruitful. In the short term, ecotype selection may be the best means of providing improved plant material.

GENETIC IMPROVEMENT AND INTERGENERIC HYBRIDIZATION

The remarkable variation within and hybridization between the two Purshia species provides a tremendous reserve for potential breeding programs. Hybridization between the two Purshia species and C. mexicana var. stansburiana with introgression in both directions enlarges possibilities that have been discussed in some detail (Stutz 1972; McArthur and others, in this proceedings). It is not surprising that putative hybrids between the two genera produce nodulated seedlings (Righetti and Munns 1981). Nitrogen-fixation capability could be included with whatever other characteristics are sought in breeding programs.

Fallugia paradoxa does not appear to be capable of symbiotic nitrogen fixation. Seedlings have been grown in native soils that produce nodules on related species without producing nodules on Fallugia (Righetti and Munns 1981; Nelson, in this proceedings), and field searches have failed to reveal nodulated plants (Nelson, in this proceedings). Expanding the host range of actinomycete-nodulated plants to include Fallugia could have important applications. Natural putative hybrids between F. paradoxa and C. mexicana var. stansburiana, a nitrogen fixing species, have been reported and attempts at artificial crosses appear successful (Blauer and others 1975). It is not known if the putative hybrid has a nitrogen fixation capability.

We have recently produced rooted cuttings of a natural putative hybrid growing at Ranger Pass, Kaibab National Forest in northern Arizona. Indole butyric acid (IBA) levels between 0 and 10,000 ppm have been tested. Rooting success increased from a negligible percentage at low levels to a maximum of 60 percent at 10,000 ppm IBA. At IBA concentrations of 3,000 ppm and above, rooting is complete within 45 days. Lower concentrations require up to 75 days to achieve their optimum rooting percentages. Although high levels of IBA produce a higher percentage of successfully rooted cuttings, less survive. None of the 10,000 ppm, IBA-treated cuttings survived. Since the putative hybrid is a unique living resource, a minimal amount of cutting material was used and a statistical evaluation was not possible. However, the following procedure is routinely used to produce cuttings of the C. mexicana var. stansburiana, F. paradoxa, the putative hybrid, and "F-2" hybrid seedlings.

Softwood cuttings (3 to 8 cm) are removed from field or greenhouse plants. If transportation is necessary, cuttings are stored in an ice chest during transportation to the laboratory. Upon arrival the distal ends of the cuttings are trimmed, brought in contact with a sponge saturated with a 2,000 ppm IBA, 50 percent ethanol, solution for 5 seconds, and placed in a sterile 30 percent peat, 70 percent vermiculite mix. Intermittent (15 seconds on, 7-minute interval) distilled water mist is applied for the rooting period (4 - 6 weeks). Plants are then transplanted into the desired media and returned to the mist bench. The interval between misting periods is gradually lengthened until mist is no longer required. A rooting of 33 percent with 80 percent survival is consistently achieved for field collected material. Greenhouse-grown material is more successful. Some of the rooted material has survived over a year and has been evaluated for nodulation and nitrogen fixation. Since the endophyte infecting Cowania roots has not been isolated, a soil mix known to produce nodulation in Cowania seedlings was used as a growing medium. Nodulation and acetylene reduction has been demonstrated for the putative hybrid cuttings and were similar to Cowania cuttings of the same size and age.

Approximately 40,000 seeds were collected from the putative hybrids in July 1981. Since Cowania is abundant and Fallugia is sparse at this Arizona location, these seeds are likely to be the product of a Cowania x putative hybrid backcross. Of these only 150 appeared filled, and we have successfully germinated nine, two of which died at an early stage. The remaining seven have remained vigorous and are

currently being vegetatively propagated. The poor fertility was not expected and is considerably less than what we have observed in some putative Purshia x Cowania hybrids. Although both Cowania and Fallugia have been reported as having a 9n chromosome number, Fallugia populations recently sampled are 14n (McArthur and others, in this proceedings), and the reports on Fallugia (Baldwin 1951) may be in error. If this is the case, a hybrid between two genera with different chromosome numbers would be unusual and could explain the poor fertility.

Although it appears that a thorough study on hybridization between Cowania and Fallugia could provide more information on the genetics of host susceptibility to nitrogen fixation, important questions need to be addressed. We doubt whether the putative hybrids are a genuine product of Cowania x Fallugia crosses. Anatomically, with the exception of pistil number, the putative hybrid closely resembles Cowania. Counts of chromosomes from root tips of putative hybrid cuttings and seedlings produced from putative hybrid seed were 18. A hybrid would likely have an intermediate number between 18 (Cowania) and 27 (Fallugia). It is likely that the small population reported consists of interesting Cowania mutants. It is important to verify reported artificial hybridization between these two genera (Blauer and others 1975) using chromosome counts and other characterization of the progeny. Another question arises on whether Fallugia is truly a non-nodulating genus. Field searches and greenhouse trials involving many different populations should continue.

If Fallugia still appears to be a non-nodulating genus after a substantial search, nodulated "F-1" hybrid seedlings would be an indication of the feasibility of host range expansion. If viable seedlings could be produced from a hybrid x Fallugia cross, a breeding program could conceivably produce a nodulated Fallugia-like species, and have long-term implications.

A short-term selection and vegetative propagation scheme could be initiated. Seedlings from a hybrid would be genetically unique and are likely to have varying degrees of Cowania or Fallugia character, depending on the pollen source and meiotic segregation of the hybrid gamete. These unique individuals could be reproduced vegetatively and tested for many characteristics including nitrogen fixation. Similar propagation schemes using seedlings derived from Cowania x Purshia hybrids could also be useful.

FIELD TRIALS

Although the opportunities and approaches for enhancing nitrogen fixation in the rosaceous shrubs have been discussed and optimism on the potential applications of actinomycete-nodulated plants has been expressed, some caution is also necessary. There are no convincing reports that nodulation and nitrogen fixation have a substantial impact on the ecosystems inhabited by these genera or if the plants receive considerable benefit from the symbiosis in establishment, growth, or longevity. Field trials are necessary to conclusively demonstrate potential application. Any studies comparing the establishment, growth and longevity of non-nodulated and nodulated plants will add valuable information. Utilizing plants of a desirable and tested ecotype, nodulated with an efficient Frankia strain, is essential. Comparing establishment of nodulated versus non-nodulated (and perhaps initially nitrogen-deficient) transplants could demonstrate an ecological importance of the process, but to thoroughly assess the potential application on marginal land, it is necessary to include a nitrogen control. If a soil is drastically nitrogen deficient, it may be unwise to avoid using an initial nitrogen application unless

assured that symbiotic plants will establish equal or better stands. Field studies augmenting water supply would be helpful in determining to what extent soil moisture is limiting nodulation and/or nodule function.

Nitrogen fixation is not a panacea and may only have an application on certain sites. It is difficult to demonstrate a nodulation response in short-run greenhouse experiments, so one might expect similar difficulties at some field sites. Long-term benefits may be more difficult to demonstrate than an establishment trial. It may be necessary to identify drastically nitrogen-deficient sites with low populations of native Frankia. Prior to expensive, long-term field trials it may be desirable to conduct greenhouse experiments with field-collected soil. This will assure that an inoculation response with the selected Frankia strain can occur at the field site.

Even with many questions unanswered, there is still cause for optimism. The importance of legumes in agricultural systems adds credence to goals of utilizing these actinorhizal nitrogen fixing systems on marginal land. Vigorous research should proceed.

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OCCURRENCE AND NATURE OF ACTINORHIZAE ON COWANIA
STANSBURIANA AND OTHER ROSACEAE¹

David L. Nelson²

ABSTRACT

Actinorhizal root-nodulation occurred on Cowania stansburiana, Purshia tridentata, P. glandulosa, Cercocarpus ledifolius, but not on the Fallugia paradoxa plants studied in natural stands. Over 6 years, annual percentage of Cowania plants sampled varied widely. Nodule necrosis and sloughing was common. Amount of nodulation on Cowania and Purshia in greenhouse tests was much higher than found in the field. Actinorhizal nodules on cliffrose are typical of those formed on other Rosaceae.

INTRODUCTION

Wildland shrub improvement and revegetation for restoration of wildlife habitats and disturbed landscapes in the Western United States are of increasing importance and interest (Plummer and others 1968; Monsen 1975; Thames 1977; Wright 1978). Enhancing the forage productivity of western livestock ranges is becoming more essential as competition increases for more direct use of agricultural plant products for human consumption. Biological nitrogen fixation could play a vital role in maintaining the nitrogen balance in plant ecosystems (Youngberg and Wollum 1970; Evans 1975; Wollum and Davey 1975; Silvester 1977). The nature of actinomycete symbiotic nitrogen-fixation in nonleguminous plants is of broad international interest (Uemura and Sato 1975; Nutman 1976; Becking 1977; Garber and Ruddat 1979). At present, 162 species in 19 genera in 7 families of woody Dicotyledons are known to form actinomycete-type root nodules (actinorhizae) (McArthur and others 1974; Bond 1976; Heisey and others 1980; Righetti and Munns 1980). Becking (1970) proposed the family Frankiaceae (Becking) for the species of Frankia Bunchorst (Actinomycetales) to which the actinorhizal microsymbionts belong.

Among western North American shrubs of the Rosaceae are species valuable for wildlife, livestock, and revegetation use (USDA Forest Service 1937; Blauer and others 1975). Certain species of this family function as symbiotic nitrogen fixers in plant community nitrogen balance (Wagle and Vlamis 1961; Vlamis and others 1964; Lawrence and others 1967; Lepper and Fleschner 1977; Klemmedson 1979). Of the Rosaceae, 12 species in 6 genera have been found to bear actinorhizal nodules (table 1). These genera belong to the subfamily Rosoideae, and all except Rubus belong to the tribe Dryadeae as described by Engler (1964). There is some question, however, on the significance of nitrogen fixation by shrubs in the more arid regions of the Western United States (Dalton and Zobel 1977; Kummerow and others 1978).

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Table 1.--Genera and species of the Rosaceae forming symbiotic, nitrogen-fixing actinorhizal nodules

Genera/species	Reference ¹	Nodulation evidence ²
CERCOCARPUS		
<u>C. betuloides</u> Nutt. ex T&G	Vlams and others 1964	GDN, NFD-(GT)
<u>C. ledifolius</u> Nutt.	Youngberg and Hu 1972	GDN, NFD-(GT)
	Lepper and Fleschner 1977	FND, NFD-(AR)
<u>C. montanus</u> Raf.	Hoppel and Wollum 1971	FND, NFD-(AR), MHDE
<u>C. paucidentatus</u> Britt.	Hoppel and Wollum 1971	FND, NFD-(AR)
CHAMAEBATIA		
<u>C. foliolosa</u> Benth.	Heisey and others 1980	FND, NFD-(AR, I ¹⁵ N)
COWANIA		
<u>C. stansburiana</u> Torr.	McArthur and others 1974	FND
	Righetti and Munns 1980	GDN, NFD-(AR, I ¹⁵ N)
DRYAS		
<u>D. drummondii</u> Richards	Lawrence and others 1967	FND, NFD-(I ¹⁵ N, GT), MHDE
<u>D. integrifolia</u> Vahl	Lawrence and others 1967	FND
<u>D. octopetala</u> L.	Lawrence and others 1967	FND
PURSHIA		
<u>P. tridentata</u> (Pursh) DC	Wagle 1958	FND
	Webster and others 1967	GDN, NFD-(I ¹⁵ N)
	Krebill and Muir 1974	MHDE
<u>P. glandulosa</u> Curran	Wagle 1958	FND
	Righetti and Munns 1981	GDN, NFD-(AR)
RUBUS		
<u>R. ellipticus</u> Sm.	Bond 1976b	FND
	Becking 1979	FND-(AR)

¹First information on the subject.

²FND = Field discovered nodulation; GDN = Greenhouse demonstrated nodulation; NFD- = Nitrogen fixation demonstrated; (AR) = Acetylene reduction; (I¹⁵N) = Isotopic ¹⁵N; (GT) = Greenhouse test, growth in nitrogen deficient soil; (MHDE) = Morphological-histological description of actinorhizae.

Although nitrogen fixation has been demonstrated for most rosaceous shrub species known to nodulate, there is little information on nodulation frequency in the field. In Cercocarpus, existence of actinorhizae on C. betuloides is based only on nodulation of plants reared from seeds in greenhouse pots in soil from a ponderosa pine site (Vlams and others 1964). C. ledifolius formed actinorhizae in greenhouse tests by Youngberg and Hu (1972) in soil known to nodulate species of Ceanothus, Alnus, and Purshia, but they found no actinorhizae on C. ledifolius in stands in central and eastern Oregon. The only record of field occurrence is on a single plant excavated in the San Bernardino Mountains of southern California (Lepper and Fleschner 1977). Hoeppel and Wollum (1971) found actinorhizae on C. montanus and C. paucidentatus on respective sites in the Sacramento and Pinos Altos Mountains of New Mexico but did not investigate nodulation frequency, although they mention that nodulation on C. montanus was more apparent than on the other species. In their

study of Chamaebatia foliolosa actinorrhizae, Heisey and others (1980) found no nodulation on plants in sites with 7.9 inches (20 cm) or more 0. soil horizon; their discovery of nodulation was in an area with little 0. horizon, but no information is given on frequency of plants nodulated. The first report of actinorrhizae on Cowania stansburiana by McArthur and others (1974) was based on our 1973 discovery in Salt Creek Canyon east of Nephi, Utah, but no details were given. Righetti and Munns (1980) have demonstrated both nodulation and nitrogen-fixation by Stansbury cliffrose in greenhouse tests using crushed nodules collected from seedlings of Purshia tridentata and P. glandulosa reared in the greenhouse in soil known to naturally nodulate Purshia. They did not find naturally occurring actinorrhizae on Stansbury cliffrose. The frequency of nodulated plants was not indicated by Lawrence and others (1967) on three species of Dryas studied in areas of recent glacier recession in Alaska, but accumulation of soil nitrogen under Dryas discs increased from 29 to 357 lb/acre (33 to 400 kg/ha) during the period of Dryas dominance. Wagle (1958) discovered actinorrhizae on P. tridentata and P. glandulosa in the field but did not study frequency of nodulation, nor did Righetti and Munns (1982) in their study.

Of the rosaceous shrubs, P. tridentata appears to be the most frequently nodulated, but little information exists on natural incidence. Examination of P. tridentata root systems in two sites in the pumice region of central Oregon by Dalton and Zobel (1977) revealed that 46 percent of 364 plants excavated bore nodules. This amount is lower than encountered with other actinomycete nodulated plants such as Alnus that are close to 100 percent nodulated (Bond 1974). Kummerow and others (1978) found only about one-tenth the nodule density per 1.3 yd³(m³) on southern California Ceanothus greggii A. Gray as reported on northern California Ceanothus spp. Both Kummerow and others (1978) and Dalton and Zobel (1977) concluded that the low nodulation frequency was probably related to the low moisture conditions in these semi-arid regions. Dalton and Zobel (1977) also showed that low temperatures could be a factor. They reasoned further that low amounts of nodulation probably did not result from low soil endophyte populations, because nodulation of plants grown in the same soil in greenhouses was complete. Nevertheless, nodulation in greenhouse tests does not occur in all soils taken from sites where known nodulating hosts such as Purshia spp. are growing (Wagle and Vlamis 1961; Righetti and Munns 1980). Addition of crushed nodule inoculum to known nodulating soil enhanced nodulation in greenhouse tests (Righetti and Munns 1981) suggests that endophyte population was well as other soil factors could be limiting nodulation. Soil N, P, and S levels apparently play a role in limiting or improving nodulation (Righetti and Munns 1981). Improved nutritional condition of the host resulting from a mycorrhizal presence, involving N, P, and Ca also apparently enhances nodulation by actinomycetes (Rose and Youngberg 1981).

The objective of this study was to provide information on occurrence and nature of actinorrhizae on C. stansburiana and other rosaceous shrubs in the field.

METHODS AND MATERIALS

We observed the nature and morphology of root nodules on Cowania stansburiana (Stansbury cliffrose) during the numerous root excavations made from 1973 through 1981.

The root systems of the following shrub species were examined for actinorrhizae: Cowania stansburiana (Stansbury cliffrose), Purshia tridentata (antelope bitterbrush), P. glandulosa (desert bitterbrush), Cercocarpus ledifolius (curlleaf mountain mahogany), and Fallugia paradoxa (D. Don) Endl. (Apache plume).

We studied the frequency of field nodulation of Stansbury cliffrose primarily on two sites, one in Salt Creek Canyon east of Nephi, Utah (elev. 5,900 ft or 1 800 m), and the other in lower Kyle Canyon (elev. 7,500 ft or 2 270 m) in the Spring Mountains of southern Nevada. Both areas were typical cliffrose sites with plants of wide age and size range. At the Salt Creek Canyon site, sparsely scattered Stansbury cliffrose, Cercocarpus betuloides and Juniperus osteosperma (Torr.) Little were the dominant shrubs on Jurassic, Arapien shale ridges. The area was highly eroded, and the soil was apparently of low fertility and extremely hard and difficult to dig. At the Kyle Canyon site, Stansbury cliffrose, Apache plume, Chrysothamnus spp., Ephedra spp., Atriplex spp., and Juniperus spp. were the dominant shrubs. The lower canyon cuts through a large bajada of predominantly limestone gravel.

We studied nodulation frequency on antelope bitterbrush on Round Mountain (elev. 7,600 ft or 2 320 m) and near Deadman Summit (elev. 8,000 ft or 2 440 m), Inyo County, California. At Round Mountain, Pinus jeffreyi Grev. & Balf. with an understory of Artemisia tridentata Nutt. and antelope bitterbrush formed the dominant vegetation. The soil was a soft volcanic ash strewn with basaltic rocks. At the Deadman Summit site, an almost pure understory of antelope bitterbrush occurred under a forest of P. jeffreyi. The soil was a coarse pumice. The two antelope bitterbrush sites were chosen partly because the soft soil allowed more complete exposure with less damage of the root systems.

At the Kyle Canyon, Round Mountain, and Deadman Summit sites, root excavations were made from 1974 through 1981. At yearly visits, all plants between 2 and 24 inches (5 and 61 cm) along 328 ft (100 m) transects were excavated with pick and shovel to a depth of 12 to 40 inches (30 to 100 cm). Roots extending beyond this depth were not examined. We recorded the range and average height of plants along with number of plants nodulated and number of nodules per plant. A single nodule or nodule cluster was judged as the product of a single infection. Both necrotic and actively growing nodules were included in the total. On the Stansbury cliffrose site at Kyle Canyon, we noted the number of actively growing and necrotic or sloughing nodules for each plant. At Kyle Canyon, excavations were made from 1974 through 1981 between July 9 and 16 (except October 9, 1974), excluding 1976. At other sites, plants were selected at random, except limited generally to plants 24 inches (61 cm) or less in height. The objective with species on these sites was to determine presence of nodulation only.

Rodents commonly make bitterbrush seed caches that result in multiple plant clumps. In 1979 at the Deadman Summit site, a disturbed area along a road recently invaded by antelope bitterbrush was selected for examination of nodulation frequency in multiple plant clumps. The objective was to examine the influence competition between plants in these clumps might have on nodulation frequency. We excavated all plants along a 984 ft (300 m) transect and noted clump height, number of plants, number of nodulated plants, number of nodules per plant, and condition of nodules.

A greenhouse test was made to research the possibility of actinorhizal formation in Apache plume and compare rates of nodulation among Stansbury cliffrose and the two species of bitterbrush. Soil was collected from the root zone of nodulated cliffrose plants at the Kyle Canyon site. After collection, we stored the soil in a coldroom at $34^{\circ} \pm 1^{\circ}\text{F}$ ($1^{\circ} \pm 0.5^{\circ}\text{C}$). Equal parts of the soil and a sterilized (autoclaved 2 hr at 250°F [121°C]) silica sand-vermiculite (Terra Lite) mixture were used as the test medium in Tinus-size (21.5 cu inches or 350 cc) containers (Spencer-Lemaire Inc., Edmonton, Canada). Seeds were leached for 72 hours in cold running tapwater to remove germination inhibitors, treated in 10 percent Clorox (5.25 percent Sodium Hypochlorite) to kill any surface seed-borne organisms, and then planted in washed, sterilized silica sand, in trays. In May, immediately after

emergence, seedlings were transplanted in the test soil and placed in the greenhouse. Plants received natural day lengths and lighting in a fiberglass-covered greenhouse. Temperatures were held at 75° and 61°F (24° and 16°C) in summer and 50° and 34°F (10° and 1°C) in winter day-night regimes.

We applied fertilizer (Plant Marvel, Plant Marvel Laboratories, Chicago, Illinois containing a 12-31-14 NPK ratio and trace elements S, B, Cu, Mn, and Zn) to all plants immediately after transplanting at a rate of .13 oz/gal (1 g/l) to soil saturation. Thereafter, no fertilizer was added. Plants were watered when dry to soil saturation. We used 25 plants per treatment. Greenhouse contamination from possible air-borne actinorhizal fungi was checked by growing the same number of plants of each species in soil that had been autoclaved. At 9 months after planting, the soil was washed from roots and number of nodules counted. Nodulation values were arrayed according to Newman-Keul's multiple range test (Steel and Torrie 1960).

RESULTS

The actinorhizal nodules found on Cowania stansburiana ranged from single unbranched lobes usually .25 to .38 inch (1 to 1.5 mm) in diameter by .25 to .76 inch (1 to 3 mm) long (extending laterally on secondary rootlets) to massive multibranched clusters up to 2 or 2.5 inches (5 or 6 cm) diameter. The majority of nodule clusters were 0.4 to 0.8 inches (1 to 2 cm) or less in diameter. The larger nodule clusters were usually attached to the larger laterals or main tap root within 3 to 6 inches (10 to 20 cm) of the soil surface. The average nodule clusters were nearly spherical, although when formed against a hard surface they were flat and fan-shaped. Tips of actively growing nodules were almost white, turning to a light tan proceeding proximally. Patches of rust-brown corky tissue formed an irregular mosaic pattern on the surface of the most enlarged portion of nodule lobes or branches. Continuing proximally three to four branching levels, branches became shrunk to about half their maximum diameter, with a dark-brown surface of sloughing cortical material. On young, actively growing nodules, initial branching was di-, tri-, and sometimes multichotomous. With larger or older nodule clusters, branching was more symmetrically dichotomous. Adjoining nodule lobes tended to branch dichotomously at a 90° angle to the opposing lobe, resulting in typical coralloid structures. Nodule clusters were found closely appressed on larger roots but were more commonly laterally or apparently terminally attached to smaller secondary roots. A closer examination revealed that nodules originated laterally as from the host pericycle. Frequently, as nodule clusters increased in size, an expression of apical-type dominance became evident (fig. 1). The root distal to a nodule point of attachment discontinued growth, shriveled, and died. Thereafter, the nodule appeared to be of terminal root origin. Increment growth of roots with attached nodules was often considerably greater than non-nodulated roots arising in the same vicinity. Expression of this apparent dominance was evident over all lateral roots arising proximally until the point where the nodulated root branched from a main root.

Table 2 summarizes data on the occurrence and frequency of nodulation on the various shrubs studied. Actinorhizal nodules were found on all species studied except Fallugia paradoxa. Of plants sampled, height ranged from 2 to 40 inches (5 to 102 cm) with an average of 12 inches (31 cm). The major portion of root systems of plants in this size range could be exposed when excavated to a depth of 12 to 40 inches (30 to 100 cm). Excavation of larger plants was too time-consuming to effectively include in the study. The data thus represents information on the smaller, likely younger, plants at the various sites. Within the 12 to 40 inch (30 to 100 cm) depths excavated, nearly all nodules were found in the upper 12 inches (30 cm) of the soil at all sites studied. From a total of all plants examined during the study, the percentage nodulated ranged as follows: 25.4 percent on Cowania stansburiana, 25.0 percent on Purshia tridentata, 12.5 percent on P. glandulosa, and 8.8 percent on Cercocarpus ledifolius.

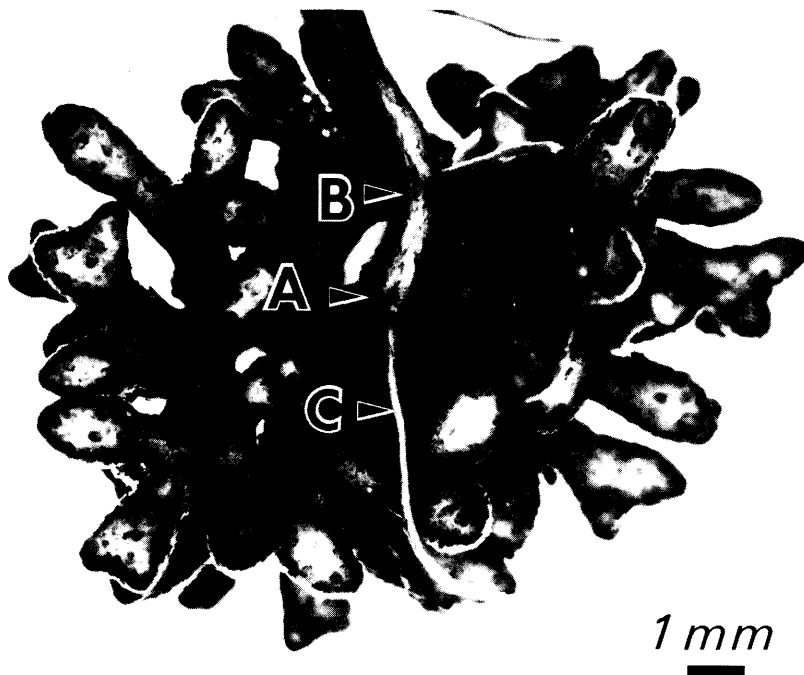


Figure 1.--1-year-old nodule cluster from Cowania stansburiana. Note nodule point of attachment (A), size of root proximal (B), and distal (C).

Table 2.--Frequency of actinorhizal nodules on shrubs in the field¹

Shrub species	Date ³	Location	Plant size ³ cm	Plants examined No.	Nodulated Percent
<u>Cowania stansburiana</u>	1973-74	Salt Creek Canyon Juab Co., Utah	15-31-102	48	8.3
	1979	Provo Canyon Utah Co., Utah	15-33-66	44	.0
	1974-81	Kyle Canyon Clark Co., Nevada	10-36-76	339 ⁴	32.2
<u>Purshia tridentata</u>	1974-77	Round Mountain Inyo Co., Calif.	5-25-91	294 ⁵	17.3
	1975-79	Deadman Summit Inyo Co., Calif.	5-25-61	884 ⁶	27.5
<u>Purshia glandulosa</u>	1973-79	Lida Summit Esmerelda Co., Nev.	15-36-61	50	12.5
<u>Cercocarpus ledifolius</u>	1973-79	Adams Head Mountain Garfield Co., Utah	8-31-46	57	8.8
<u>Fallugia paradoxa</u>	1973	Kyle Canyon Clark Co., Nev.	25-76	12	.0
	1975	Coal Creek Canyon Iron Co., Utah	25-36	15	.0

¹Plant root systems excavated by pick and shovel.

²Period of years excavations were made (not necessarily on all years included).

³Plant average height (center) and extremes.

⁴Total plants excavated on eight 328 ft (100 m) transects.

⁵Total plants excavated on five 328 ft (100 m) transects.

⁶Total plants excavated on seven 328 ft (100 m) transects.

On the more intensively studied Cowania transects at Kyle Canyon, percentage of plants nodulated varied from 53.1 percent in 1975 to 9.4 percent in 1979 (table 3). The average number of nodules per plant ranged from 2.6 to 7.7 for the 6 years. The highest number of nodules found on a single plant was 27, with the majority having from 1 to 3. An occasional plant would have many more nodules than usual so that in most years nearly half of the nodules found were on 1 or 2 plants. Many nodules were necrotic and appeared to be completely dead (fig. 2). Others had portions that were actively growing (fig. 3). The percentage of nodules with at least some actively growing portions varied from 67.8 to 6.4 over the 6 years. There was no apparent reason for the failure to find nodules on Stansbury cliffrose at the Provo Canyon site.

Table 3.--Occurrence of actinorhizal nodules on Cowania stansburiana in Kyle Canyon¹

Year sampled	Plant size ² cm	Nodulated plants	Total nodules	Nodule range ³	Plants nodulated	Active nodules
		Number			Percent	
1975	15-30-61	17	56	1-27 (65)	53.1	67.8
1977	8-33-51	13	49	1-20 (77)	40.6	47.5
1978	15-36-61	10	47	1-25 (70)	31.1	6.4
1979	10-28-61	3	23	2-12 (33)	9.4	17.4
1980	5-23-51	10	26	1-6 (90)	31.3	38.5
1981	8-36-61	5	32	1-19 (60)	16.0	18.6

¹Data from the first 32 plants 5 to 61 cm in height excavated on one transect each year.

²Left and right figure represents range extremes, center figure represents average height.

³First two figures represent range in nodule number per plant, figure in brackets is the percentage of nodulated plants with 1 to 3 nodules per plant.

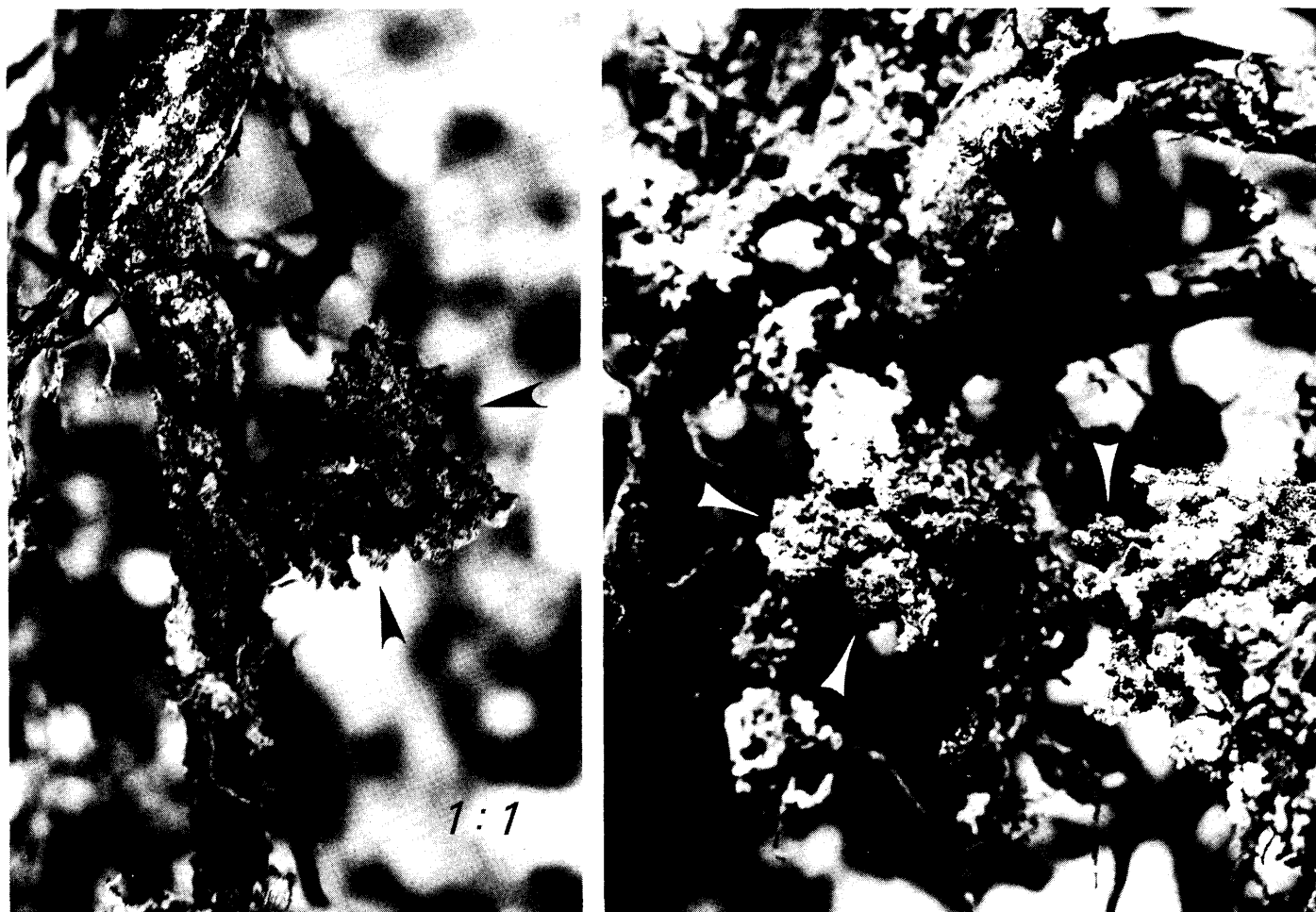


Figure 2.--Roots of a Cowania plant with numerous necrotic nodule clusters (arrows).

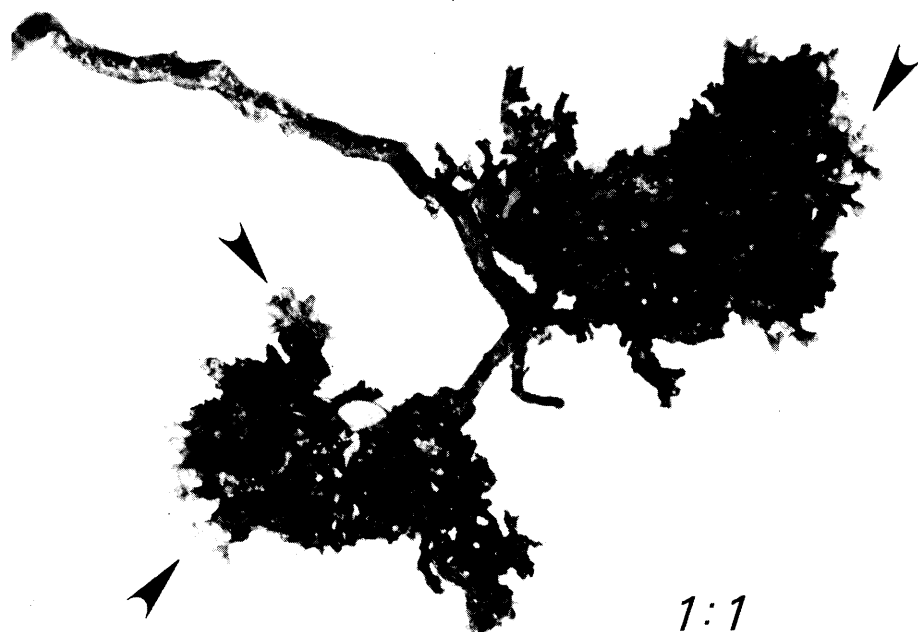


Figure 3.--Two partially necrotic nodule clusters. Note light colored active nodule lobes (arrows).

Data on nodulation of Purshia tridentata plants growing in multiple plant clumps as a result of rodent seed caches are given in table 4. We found up to 18 plants per clump, but those with more than 6 were not included because of the small numbers. With an increase in number of plants per clump from 1 to 6, the percentage of plants nodulated declined from 50.0 to 16.7, and the number of nodules on nodulated plants declined from 2.9 to 1.9. Only a low probability existed that any lack of correlation between increasing number of plants per clump and a decline in number of plants nodulated was not due to random chance, although the relationship is probably not linear. The percentage of actively growing nodules ranged from 83.3 to 18.2 with an increase in number of plants per clump, but there was no clear correlation.

In the greenhouse culture test, plants of all species formed actinorrhizae except Apache plume (table 5). No control plants formed actinorrhizae. The mean number of nodules per plant on Cowania was higher and clearly different from both Purshia species, but there was no clear difference between Purshia species. The variation in number of nodules per plant was high; for example, from 2 to 90 for Cowania. Nodule clusters appeared to be larger on plants with fewer numbers of nodules although no nodule mass data were taken. Nodules were distributed uniformly throughout root systems (fig. 4).

Table 4.--Correlation of Purshia tridentata actinorrhizal nodulation with number of plants per clump

Plants/ clump	Clumps	Clump height	Plants nodulated	Nodules/ nodulated plant	Active nodules	Active nodules/ nodulated plant
- - <u>Number</u> - -		<u>cm</u>	<u>Percent</u>	<u>Number</u>	<u>Percent</u>	<u>Number</u>
1	42	5-28-36	50.0	2.9	83.3	2.3
2	27	5-17-33	37.0	2.6	48.1	1.3
3	23	5-20-36	24.6	2.1	42.9	.9
4	26	5-19-33	28.8	1.5	60.0	.9
5	9	3-22-38	15.6	1.6	18.2	.3
6	11	5-21-30	16.7	1.9	28.6	.5
r			-.93	-.83	-.80	-.88
p			.01	.05	.05	.05

Table 5.--Comparison of Purshia, Cowania, and Fallugia nodulation rate in greenhouse culture test

Species	Seed Source	Percent nodulated ¹	Nodules/ plant, $\bar{x}$ ³	CV ³
<u>Purshia tridentata</u>	Okanogan, Washington	100	15.5a	48.4
<u>Purshia glandulosa</u>	Elbert Pass, California	100	11.8a	74.6
<u>Cowania stansburiana</u>	Kyle Canyon, Nevada	100	28.8b	72.6
<u>Fallugia paradoxa</u>	Richfield, Utah	0	0	0

¹Percent of 25 plants with nodules.

²Values followed by the same letter are not significantly different according to Newman-Keul's multiple range test at P = 0.05.

³Coefficient of variation.



Figure 4.--2-year-old Cowania plant from greenhouse test. Note distribution of nodule clusters throughout the root system.

DISCUSSION AND CONCLUSIONS

Root nodules on Cowania stansburiana, like other actinomycete-induced nodules, were modified roots. Nodules on Cowania, like Purshia, Cercocarpus, and Dryas, developed into distinctly indeterminate coralloid clusters. Nodule lobes on Cowania branch di- to multi-chorotomously by apparent division of the nodule tip meristem. No distinctly lateral or pericyclic branching, as in Ceanothus nodules (Strand and Laetsch 1977), was observed, and no nodule roots were observed as in Myrica nodules (Torrey and Callahan 1978). A closer comparison with the Alnus-type nodules may show that actinorhizal nodules of the Rosaceae are morphologically distinct. A definite apical-like dominance is expressed by actinorhizae of Cowania. Nodulated roots are distinctly larger than non-nodulated lateral roots of comparable age. This dominance is possibly a hormone-related phenomenon and likely ensures longevity of nodules, larger volume of vascular translocation, and more secure attachment of nodules. Presence of higher levels of growth hormone activity in actinomycete-induced nodules than in roots has been demonstrated in Alnus glutinosa (L.) Gaertn. nodules: indol-3yl-acetic acid (IAA) and others (Dullaart 1970), cytokinins (Bermudez DeCastro and others 1979), and IAA, cytokinins and gibberellin-like substances (Wheeler and others 1979). Interest has focused on their role in nodule development and microsymbiont function. The possibility of a hormonal role in a nodulated-root dominance needs to be considered.

Purshia glandulosa likely represents a stabilized hybrid between P. tridentata and Cowania stansburiana, and the three taxa form hybrid swarms where their ranges overlap (Stutz and Thomas 1964). Gene introgression occurs commonly, sometimes far beyond points of range overlap (Stutz and Thomas 1964; Nord 1965). Because of this close relationship, it is not unexpected that Cowania, as noted by Righetti and Munns (1980), would be found to form an actinorhizal symbiosis similar to Purshia. Fallugia paradoxa is classed in the tribe Dryadeae as are all nodulating Rosaceae, except Rubus, and is probably quite closely related to Cowania as indicated by experimental and possible natural hybrids (Blauer and others 1975). Fallugia did not nodulate in Cowania-nodulating soil in the greenhouse test in this study nor in those of Righetti and Munns (1981). Our limited sampling in the field was negative, and those excavated at Kyle Canyon were in a mixed stand with Cowania on which nodules were found. More extensive field sampling would provide a more reliable conclusion on existence of nodulation in this genus.

The frequency of nodulation in native rosaceous shrub species in this study was low, compared to other groups of actinorhizal plants that have been reported to be close to 100 percent nodulated. Frequency rates appeared generally lower than that found by Dalton and Zobel (1977) on P. tridentata in Oregon, and more comparable to that found on southern California chaparral Ceanothus spp. (Kummerow and others 1978). Information on frequency of nodulation in the field was limited by the method used in excavating root systems. Also, deeper roots were difficult to reach, and sampling was primarily limited to smaller plants. Although nodulation frequency on arid and semi-arid land species of Rosaceae appears low, there remains a potential for ecological significance because nitrogen is generally deficient in semiarid regions.

The frequency of nodulation of Cowania at the Kyle Canyon site appeared to vary considerably from year to year during the 6 years sampled. Possible explanations could be that (1) the sample size was too small to account for variation caused by low frequency, or (2) nodulation rate varied with fluctuating amounts of effective annual precipitation. Until this variation can be accounted for, it would seem that a true evaluation of frequency cannot be based on a single year's data. Wagle and Vlamis (1961) obtained no nodulation of Purshia plants grown in soil from the same Deadman Summit site where an average of 27.5 percent of Purshia plants nodulated were found (table 2) in this study. This disparity suggests that greenhouse bioassay of nodulation potential of field soil also needs further study.

The low percentage of actively growing nodules was unexpected, but there was no reason to think it was unusual. The yearly variation in amount of sloughing was roughly correlated with the percentage of plants nodulated. Nodules may slough during unusually dry years, or it could be a seasonal occurrence and the time of year that sloughing occurs varies with seasonal distribution of precipitation. Kummerow and others (1978) found few living and large amounts of decaying nodules on Ceanothus greggii in summer and fall when host water potentials were low. A single watered plant retained actively growing nodules into late summer. Time of year when sampling is done could, therefore, be an important factor in estimating frequency of field nodulation. The seasonal decomposition rate of sloughing or senescent nodules is unknown. Only portions of some nodules slough. One might speculate that evolution has been toward a system where nodules tend to slough during periods of low moisture, providing a flush of available nitrogen for rapid growth during short periods of high moisture. The reason for an occasional nodulated plant having many more nodules than usual was not evident. No apparent differences in soil moisture or other soil factors existed. Perhaps these plants were genetically more compatible symbionts, and differences are masked except when limiting soil factors are critical.

In the multiple-plant clumps of Purshia tridentata, the number of plants nodulated and possibly the number of actively growing nodules declined with an increase in number of plants per clump. It might be assumed that all plants within the clump are equally exposed to the soil-borne, nodule-endophyte propagules. A possible explanation for the decline would be a competition for water and soil nutrients such as N, P, and S that influence nodulation (Righetti and Munns 1980) and the nutrient deficient status of plants resulting from the competition. Proper balance of P and Ca in Ceanothus velutinus resulting from presence of vesicular-arbuscular mycorrhizae increased the frequency and function of actinomycete nodulation, according to information by Rose and Youngberg (1981). Nitrogen deficiency resulting from competition between plants in the clump should, however, tend to enhance nodulation.

The amount of nodulation of Cowania and Purshia plants in the greenhouse culture test was much higher than found on plants examined in the field. Moisture, temperature, and plant nutrient balance were possibly more favorable and could account for this difference although the study was not designed to test these factors. Initial addition of nitrate certainly did not greatly inhibit nodulation. Righetti and Munns (1981) tested soil factors and found that addition of P and S enhanced nodulation. Dalton and Zobel (1977) obtained similar increased rates of nodulation of Purshia in greenhouse tests. The number of nodules forming on Cowania was significantly higher than on the two Purshia species. And because the Cowania seed and test soil were from the same site and the Purshia seed source was different, there could be suggestion of endophyte-host specificity. The number-of-nodule basis for comparing nodulation among these species was a measure of infectivity rather than nitrogen-fixation. Size of nodule clusters appeared inversely correlated with higher numbers of nodules per plant, although no data were taken to establish this.

The difficulty encountered in culturing the Frankia endophyte in absence of its host, and failure thus far to find a natural saprophytic phase, suggest an obligate parasitism. In general, obligate parasites infect and grow better in a healthy, vigorously growing host. If nitrogen deficiency in the host enhances infection, it is inconsistent but perhaps unique with a Frankia obligate parasitism.

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RESPONSE OF BITTERBRUSH AND ASSOCIATED PLANT SPECIES TO
BROADCAST NITROGEN, PHOSPHORUS, AND SULFUR FERTILIZATION¹

Arthur R. Tiedemann²

ABSTRACT

The effect of three annual fall applications of a nitrogen (N), phosphorus (P), and sulfur (S) fertilizer on bitterbrush (Purshia tridentata [Pursh] DC) cover, leader growth, crude protein, and understory vegetation cover and biomass was studied in bitterbrush habitats in north-central Washington 1973 through 1976. Eight replications of treatments were established: unfertilized/not covered, unfertilized/covered, fertilized/not covered, and fertilized/covered. Nitrogen, P, and S were applied at annual rates of 67, 29, and 10 lbs/acre (75, 33, and 11 kg/ha) respectively. Bitterbrush cover varied widely among years from 16 to 32 percent (average of all treatments) and was a reflection of the August through February precipitation, but there were no significant differences among treatments for bitterbrush vegetative cover in any year. Current annual leader growth also varied among years in response to differences in August through February precipitation. In 1974, leader length of the fertilized/not covered treatment was significantly less than the fertilized/covered treatment indicating an attractant effect of fertilized plants for mule deer. Crude protein levels did not appear to respond to fertilization.

Biomass and cover of herbaceous understory responded significantly to fertilization and to fertilization and protection indicating that fertilization is an effective means of improving protective watershed cover. Calculated uptakes of N, P, and S by understory vegetation indicated that the major proportion of applied nutrients was available for bitterbrush growth.

The failure of bitterbrush to respond to fertilization is probably a consequence of the over-mature, decadent nature of these stands.

The relationships established between August through February precipitation and bitterbrush cover and leader growth should be a valuable predictive tool for bitterbrush production in this area.

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INTRODUCTION

Antelope bitterbrush (Purshia tridentata [Pursh] DC) is a prominent rosaceous shrub of low- to mid-elevation vegetative habitats (700 to 2,000 ft [200 to 600 m]) of the mid-Columbia region of eastern Washington (Daubenmire 1970; Franklin and Dyrness 1973). In addition to the documented importance of bitterbrush as a major component of the winter and early spring diet of mule deer (Odocoileus hemionus hemionus) (Burrell 1982), its continued productivity and vigor are essential to maintenance of watershed stability on these steep erosive slopes. Decadence and high plant mortality of bitterbrush are problems that have significance for continued wildlife productivity and land stability in many habitats where this plant is a major component of the vegetation. Driver and others³ surveyed bitterbrush communities in four mid-Columbia areas of north-central Washington using the rating system developed by Patton and Hall (1966)⁴. Two of the areas they surveyed were near areas of the present study. At all four locations, most plants were in mature or decadent age classes.

Absence of seedlings and young plants in these areas indicates a possible shift in community composition. Without recruitment of bitterbrush, vegetative composition may shift to dominance of annual and perennial grasses, forbs, and halfshrubs.

In some areas, no vegetation succeeds dying bitterbrush. The result is substantial erosion, road maintenance problems, and deterioration of water quality. Erosion establishes a subtle epicycle of reduced productivity and surface protection, reduced stability, increased erosion, and further reduction of productivity. The end result may be a soil material so low in nutrients and water-holding capacity that plant growth cannot be supported.

Commercial fertilizers hold promise for enhancing plant growth and restoring stability to unstable, eroding wildland sites. In other studies, soil nitrogen (N) and sulfur (S) have been determined to be moderately to severely deficient in amount and availability in several East Cascade soils (Tiedemann⁵ 1972; Tiedemann and Klock 1977; Klock and others 1971, 1975). Leman and Pittack⁵ conducted a field fertilization trial in eastern Washington, using 130 lb of N per acre (146

³Driver, Charles H., T. A. Hanley, I. Olmstead, and others. Decadence in antelope bitterbrush--a management problem and solution. Final report of a cooperative agreement with the Pacific Northwest Forest and Range Experiment Station. Copy on file at Forestry Sciences Laboratory, Wenatchee, Washington.

⁴S Seedling: Plant up to 3 years old that has become firmly established, usually less than 0.125 inch (.3 cm) diameter.

Y Young plant: Larger with more complex branching and more fibrous bark than seedling, does not show signs of maturity, usually between 0.125 and 0.2 inch (.3 cm and .5 cm) diameter.

M Mature plant: Complex branching, rounded growth form, larger size; seed produced on healthy plants; generally larger than 0.25 inch (.63 cm) diameter.

D Decadent: Plant, regardless of age, that is in a state of decline; usually evidenced by 25 percent or more dead branches.

⁵Leman, B., and C. C. Pittack. 1969. Pilot study. Pruning and fertilization of bitterbrush on the Swakane Game Range. Unpublished report on file with Chelan Co. PUD, Wenatchee, Washington.

kg/ha) applied to individual shrubs as Ortho unipel ANS 30-10-0-6 (N, phosphorus (P), potassium (K), and S) and Ortho unipel ANS 16-16-16-0 (NPKS). They found an increase in available forage on bitterbrush plants classed as mature, but did not obtain a response from plants classed as decadent. Bayoumi and Smith (1976) studied the response of native stands of antelope bitterbrush to applications of N and P fertilizer alone and in combination. Nitrogen applied at 30, 60, 96, and 149 lbs/acre (34, 67, 108, and 168 kg/ha) to individual bitterbrush plants resulted in statistically significant increases in twig growth, seed production, and crude protein percentages.

Neither of these fertilization studies addressed the integrated plant community response to fertilization. The prominence of cheatgrass (Bromus tectorum L.) in the bitterbrush habitats of the mid-Columbia necessitates an assessment of the total community response because cheatgrass responds readily to N and S fertilization (Klemmedson and Smith 1964) and may reduce the effectiveness of applied nutrients for bitterbrush. A more practical reason for evaluating the total community response is that aerial broadcast application is the only feasible means for fertilizing many sites--the results must reflect the response that would occur on an operational basis. A 3-year study to assess the response of bitterbrush habitats to N, P, and S fertilization had the following objectives:

1. Assess the fertility status of surface soils in three representative mid-Columbia bitterbrush habitats.
2. Evaluate effectiveness of three annual fall broadcast applications of a nitrogen-phosphorus-sulfur fertilizer for promoting growth and increasing crude protein content of bitterbrush.
3. Measure response of associated plant species to fertilization and estimate N, P, and S uptake by these species.
4. Measure mule deer use of bitterbrush and understory species in response to fertilization.

APPROACH

In the fall of 1973, eight sites were selected in the Entiat, Swakane, and Oklahoma gulch areas north of Wenatchee, Washington. These eight sites served as replications for the fertilizer study.

Areas of the study sites generally drain to the southeast into the Columbia River between Chelan and Wenatchee, Wash. All plots are situated on southerly facing slopes. Soils in all three areas are derived primarily from granitic parent material and are generally coarse and erosive (McColley 1976). Slopes are very steep, with relief of 30 to 40 percent. Bitterbrush is the predominant shrubby species. Big sagebrush (Artemisia tridentata ssp. tridentata) and serviceberry (Amelanchier alnifolia Nutt.) are the principal associated shrubby species. Prominent halfshrubs are snow eriogonum (Eriogonum niveum Dougl.), Wyeth buckwheat (E. heracleoides Nutt.), and Phlox (Phlox sp.). Arrowleaf balsamroot (Balsamorhiza sagittata [Pursh] Nutt.) and yarrow (Achillea millefolium L.) form the major portion of perennial forb cover. Cheatgrass (Bromus tectorum L.) dominates cover of gramineous plants, but bluebunch wheatgrass (Agropyron spicatum [Pursh] Scribn. and Smith) and western needlegrass (Stipa occidentalis Thurb.) are common.

Two different techniques were used to assess fertility of soils. The first involved determination of the concentrations of total N and total S in surface soils prior to fertilization. Total P was not measured in these soils because of a moratorium in effect at the time of the study preventing use of perchloric acid digestions at the Pacific Northwest Forest and Range Experiment Station.

Prior to fertilization in fall 1973, total N (Bremner and Tabatabai 1972), total organic carbon, pH (Black and others 1965), and total S (Tiedemann and Anderson 1971) were measured in soils from the surface 2 inches (5 cm) of areas beneath bitterbrush plants and an adjacent opening at each of the eight locations (replications). Areas under shrubs were sampled to serve as reference levels of nutrient constituents, organic carbon, and pH, that would be expected for this site in equilibrium with the climate, organisms, relief, and soil parent materials. The levels of nutrient constituents, organic carbon, and pH in open areas were indicative of soil fertility and soil chemistry throughout the study area and were used to indicate the potential for success of fertilization. A "t" test was used to evaluate differences in soil characteristics between areas under shrubs and open areas.

Availabilities of individual macronutrients; N, P, K, and S, the second parameter of fertility, were determined for surface soils of the study sites by the bioassay technique of Jenny and others (1950). Briefly, this greenhouse pot trial involves successive deletion of individual nutrients from a full nutrient treatment. Response to nutrient deletion is determined by measuring the biomass yield of a test species following a defined period of growth. Nutrient availability is expressed as the relative yield (RY) of each individual nutrient. Relative yield is the ratio of biomass yield with the treatment from which a nutrient was deleted to the yield with the full nutrient treatment. For example:

$$RYN = \frac{\text{yield of treatment with no added N}}{\text{yield with full nutrient treatment}} \times 100$$

Soils were collected from the surface 2 inches (5 cm) between bitterbrush plants near each of the sites for the fertilization study. These collection areas served as replications for the pot trial. Replication was carried through to the greenhouse. Soils were air dried to constant weight at about 20°C and sieved through a 4 mm mesh screen. After filling pots with 1200 g of soil, the following nutrient treatments were applied:

1. Check	No nutrients added
2. No nitrogen (N ₀)	N ₀ P ₁₀₀ K ₅₀ S ₅₀
3. No phosphorus (P ₀)	N ₁₀₀ P ₀ K ₅₀ S ₅₀
4. No potassium (K ₀)	N ₁₀₀ P ₁₀₀ K ₀ S ₅₀
5. No sulfur (S ₀)	N ₁₀₀ P ₁₀₀ K ₅₀ S ₀
6. Full nutrient treatment	N ₁₀₀ P ₁₀₀ K ₅₀ S ₅₀

Subscript refers to the approximate application rates in kg/ha.

Nitrogen was added as ammonium nitrate (NH₄NO₃), P as sodium mono-hydrogen phosphate (Na₂HPO₄), K as potassium chloride (KCl), and S as calcium sulfate (CaSO₄).

Ten seeds of bitterbrush were planted in each pot. Following establishment, plants were thinned to 3 plants/pot. Plants were grown under natural light in a greenhouse with day temperatures at about 27°C (80°F) and night temperatures at about 13°C (55°F). Distilled water was added as the soil surface dried. At the end of 22 weeks, plants were harvested and oven dried at 60°C to constant weight. A one-way analysis of variance was used to analyze statistical significance of differences among treatments for absolute yields (Steele and Torrie 1960). The Duncan multiple range test was used to separate differences among means of absolute yields. Relative yields were calculated but not tested statistically because they are determined from absolute yields.

For the field fertilizer trial, four 6.3 x 32.8 ft (2 x 10 m) plots were established at each of the eight sites. Half the plots at each of the eight

locations (replications) were fenced and covered with 3.3 inch (10 cm) mesh wire fence. Half the plots were fertilized with three consecutive, yearly, fall applications (1973, 1974, and 1975) of ammonium nitrate phosphate sulfate (27-12-0-4) at 67 lbs/acre (75 kg/ha) of N. Respective yearly application rates for P and S were 29 and 10 lbs/acre (33 and 11 kg/ha).

Design of the study was completely random, resulting in eight replications of the following sequence of treatments:

1. Unfertilized/not covered
2. Unfertilized/covered
3. Fertilized/not covered
4. Fertilized/covered

Protection of half of the plots was done to determine growth responses of bitterbrush and understory vegetation and response of bitterbrush crude protein to fertilization in the absence of mule deer use. Comparison of fertilized/covered and fertilized/not covered treatments provided an estimate of the attractant effect of fertilization for mule deer.

In the fall of each year (1973-1976), cover of bitterbrush and associated shrubby species was measured on a 2 x 32.8 ft (0.6 m x 10 m) permanent belt transect that bisects each plot. Cover was determined as a vertical projection of foliar vegetation on to the soil surface expressed as a percentage of the surface covered.

At the same time, 50 random leaders of the current annual growth were clipped from bitterbrush on each plot. After these were measured, leaves and stems were oven dried at 70°C, separated, and ground in a Wiley mill to pass a 60 mesh screen. Samples were analyzed for total N (Bremner and Tabatabai 1972). For the 1974 collection, all eight replications of each treatment were analyzed. In the following 2 years, small samples from each replication were composited by treatment. Total N values were converted to crude protein using a conversion factor of 6.25 (Cook and others 1962).

Except for 1973, cover and biomass of herbaceous understory vegetation were measured in the spring. In 1973, these measurements were made prior to fertilization in the fall. Biomass of herbaceous species was determined each year by clipping 2 ft by 2 ft (0.6 m by 0.6 m) quadrats at two random locations within each plot. Different locations were clipped in each year.

Differences among treatments for cover of bitterbrush, other shrubs, and associated herbaceous species, leader length, understory biomass, and crude protein (in 1974) were evaluated by analysis of variance with a completely randomized design (Steele and Torrie 1960). The Duncan multiple range test was used to determine significant differences among individual treatments. The principal hypothesis was that fertilization would have no effect on cover, leader length, crude protein of bitterbrush, and biomass productivity and cover of understory vegetation.

RESULTS AND DISCUSSION

Comparisons of Soil Characteristics

Soil reaction, as measured by pH of areas beneath shrubs, was more basic (6.96) than open areas (6.66). This difference was highly significant ($P = 0.01$). Romney and others (1977) also found a tendency for higher pH in areas under desert

shrubs than in bare areas, but Tiedemann and Klemmedson (1973) found no differences in pH of the surface 1.8 inches (4.5 cm) of soil between areas under mesquite (Prosopis juliflora [Swartz] DC) and adjacent open areas.

Higher levels of microbial activity and the resultant CO₂ generation would be expected to reduce pH in areas beneath shrubs compared to open areas. It appears, however, that cation input from litter through leaching and decomposition may be sufficient to displace H⁺ ions through mass action resulting in an increase (or no change) in pH. Leaching of plant tissue has been shown to remove up to 45 percent of cations such as calcium, magnesium, sodium, and potassium (Tukey and others 1958).

Total N was three times greater in soil from beneath bitterbrush shrubs than in open soils (0.12 percent compared to 0.04 percent). Total S and total C differences were similar. Total S under shrubs was 0.011 percent compared to 0.005 percent in open areas. Total C was more than twice as great under shrubs than openings (3.52 percent compared to 1.41 percent). These differences are highly significant ($P = 0.01$) and indicate that bitterbrush functions in a manner comparable to other desert shrubs in redistributing nutrients from open areas to areas beneath shrubs. Garcia-Moya and McKell (1970) and Tiedemann and Klemmedson (1973) observed that lateral roots of Larrea and Prosopis shrubs (respectively) deplete nutrients of surrounding open areas. Through deposition of leaves and other detritus to the zone beneath the canopy, islands of fertility are created. Symbiotic nitrogen fixation by bitterbrush (Wagle and Vlamis 1961) may also play a role in the N-enrichment patterns observed in the present study. However, the role of these fertile islands in successional development of shrub communities is at present not known.

In the case of bitterbrush in the present study, the N and S levels observed in openings are insufficient for adequate growth and development of many higher plant species. Even the levels of N and S under bitterbrush shrubs would be considered marginal for this climatic zone (Jenny 1930, 1941) and are at the lower end of concentrations observed in wildland soils in eastern Oregon and Washington (Geist and Strickler 1970; Tiedemann and Berndt 1972; Tiedemann and Klock 1977).

Soil Nutrient Availability

Yields (g/pot) of biomass in the nutrient availability trial for the check treatment (no added nutrients) were significantly less ($P = 0.05$) than yields of the full nutrient treatment (table 1). Yields of treatments from which N and S were deleted (N_0 , S_0), but with P and K added to each were the same as the check treatment indicating limited availability of N and S in these soils. With addition of N and S (P_0 and K_0 treatments), yields were increased to the same level as the full nutrient treatment. Availabilities of P and K were apparently sufficient since deletion of these caused no reductions compared to the full nutrient treatment.

Table 1.--Response of biomass yields to nutrient treatments in the greenhouse pot trial.

S ₀ (NPK added)	Check (No nutrients added)	N ₀ (PKS added)	P ₀ (NKS added)	Full (NPKS added)	K ₀ (NPS added)
----- g/pot -----					
2.26	2.48	2.48	<u>4.23</u>	4.59	<u>4.63</u>

Values (g/pot) with the same underline are not significantly different at P = 0.05.

Relative yields of S, N, P, and K were 49, 54, 92, and 101 percent, respectively. Jenny and others (1950) developed a relationship of relative yields of N and P from pot trials to the percent of field tests responding to added N and P for agriculture settings in California. For N, a relative yield of 30 percent denoted a soil low in N which would likely give a field response to added N. Relative yields of N above 50 percent indicated high N supplies and little chance of a field response to N fertilization. For P, the relative yield for a fertilizer response was 30 percent or less. There appears to be no comparable information for wildland settings. Comparison of RY values of N established by Jenny and others (1950) suggest little chance for a response of bitterbrush and associated species to fertilization (they did not develop RY values for S). However, considering the extremely low levels of N and S in surface soils and the RY levels of N and S in the 50 percent range, there is a strong potential for a response in the field setting to added N and S.

The very high relative yields of P and K indicate little possibility for a fertilizer response to addition of these elements.

Bitterbrush Responses to Fertilization

Since the response of bitterbrush to fertilization is the central focus of this paper, the data for associated shrub species is not presented. These generally made up less than 10 percent of the total shrub cover and were too variable for a valid statistical analysis of their response.

There were no significant differences among treatments for bitterbrush vegetative cover in any year. Cover varied widely from a low of about 16 percent in 1973 (average of treatments) to a high of 32 percent in 1974 and 1976 (fig. 1). Fluctuations in cover were a reflection of the August through February precipitation.

The current annual leader growth (average among treatments) also varied widely from 3.5 to 7.3 inches (9.0 cm to 18.6 cm) (table 2). As with cover, leader growth was responsive to August through February precipitation (fig. 1). This period's precipitation in 1973 was 4.8 inches (12.1 cm) and leader length (average of treatments) was 3.6 inches (9.2 cm). In 1974, leader length more than doubled to 7.3 inches (18.6 cm) in response to a precipitation increase to 10.4 inches (26.3 cm). The relationship to precipitation trends for bitterbrush cover and current leader growth may prove to be a useful tool in the future for predicting forage productivity in bitterbrush habitats where most of the precipitation occurs in the winter. Kindschy (1982) has shown a positive relationship between bitterbrush productivity and the current crop year precipitation (September 1 to June 30). Bitterbrush leader production (inches) = 0.593×-1.67 ($r=.622$).

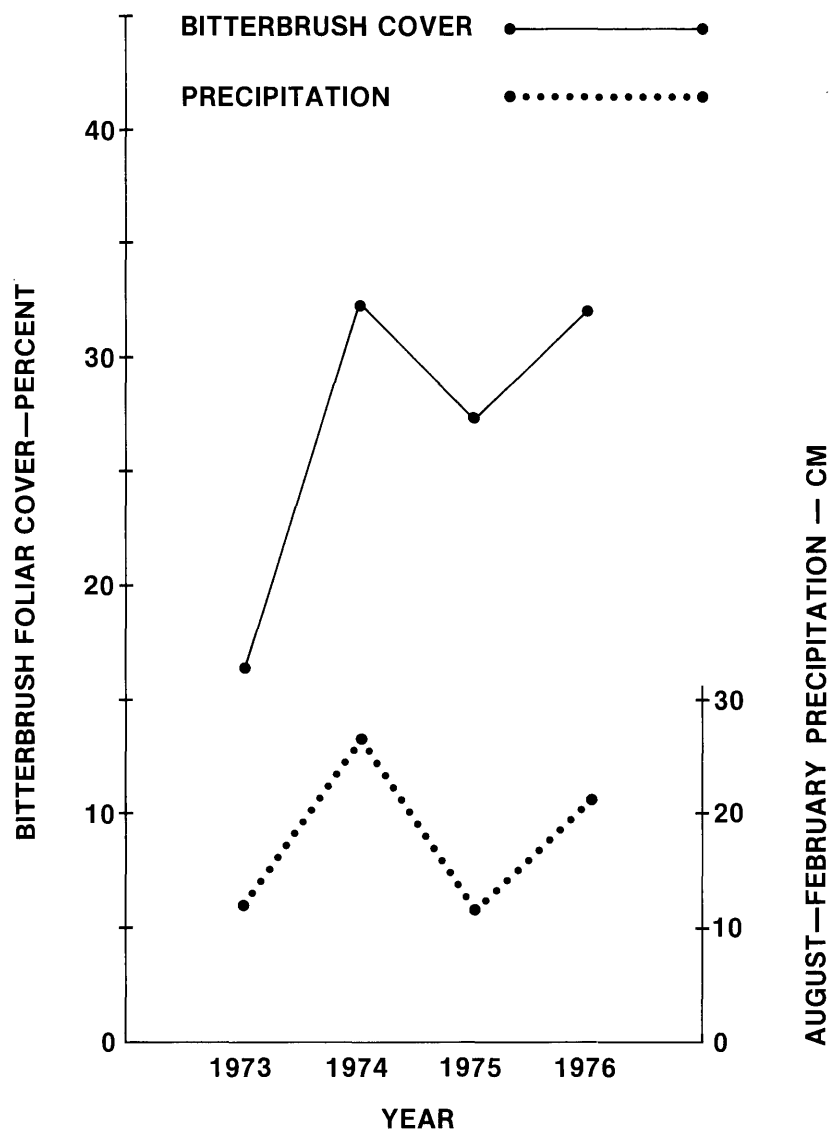


Figure 1.--Relationship of bitterbrush cover to August-February precipitation.

Table 2.--Length of 50 random bitterbrush leaders following fertilization and protection treatments.

	Unfertilized not covered	Unfertilized covered	Fertilized not covered	Fertilized covered	Mean	F-test
Prefertilization						
1973	9.0	8.9	9.3	9.5	9.2	NS
Postfertilization						
1974 ²	19.6 ^a	19.8 ^a	15.8 ^b	19.4 ^a	18.6	*
1975	10.1	8.7	8.5	8.8	9.0	NS
1976	9.1	8.9	9.1	9.8	9.2	NS

¹Inches = cm divided by 2.54

²Values with differing superscript letters are significantly different at P=0.05 according to the Duncan multiple range test.

*Significant at P=0.05.

NS = not significant

In 1974 there was a significant difference in length of leaders among treatments (table 2). The Duncan multiple range test revealed that average leader length of the fertilized/not covered treatment was significantly lower than the other treatments. In 1975 and 1976, there were no significant differences in leader length among treatments.

Current annual leader growth was measured in the fall to assess the growth response to fertilization; differences in leader length among treatments probably represent spring and summer use by mule deer. Shorter leader lengths on the fertilized/not covered plot are indicative of an attractant effect of fertilization similar to that observed by Bayoumi and Smith (1976) and reported in a summary paper by Duvall (1970). Greater use of the current annual leader growth on the fertilized/not covered plot in 1974 is probably also related to the "nutritional wisdom" of the animals, whereby they select forage that best provides for their physiological needs (Ivins 1952). It is not known why this apparent attractant effect of fertilization did not occur in 1975 and 1976. Perhaps in 1974, mule deer were confined to this part of their range for a protracted period into summer because of excessive snow depths at higher elevations. Snowfall in 1974 was more than twice as great as in 1975 and about 40 percent greater than 1976. The more open winters of 1975 and 1976 may have permitted earlier access to higher elevations so that spring and summer use of bitterbrush was less than in 1974.

Analysis of crude protein in leaves and stems of bitterbrush did not reveal any striking responses to treatments (table 3). For leaves, however, there was a strong variation among years ranging from 8.1 to 12.9 percent (average of treatments). Reasons for this difference are not known, particularly since the lowest values occurred after three applications of fertilizer. Crude protein values for stems in 1976 are also notable. Values for fertilized plots are lower than those for unfertilized plots in 1976. The reason for this is also not known.

Table 3.--Percent of crude protein in bitterbrush leaves and stems following three annual fall applications of 27-12-0-4 (NPKS) fertilizer at 247 lb/acre/year (278 kg/ha/year).

	Unfertilized not covered	Unfertilized covered	Fertilized not covered	Fertilized covered	Mean	F-test
	percent					
Leaves:						
1974	12.7	10.8	13.6	11.9	12.2	NS
1975	14.5	11.8	12.6	12.9	12.9	NT
1976	8.1	7.2	9.1	7.9	8.1	NT
Stems:						
1974	6.5	7.1	6.3	7.2	6.7	NS
1975	7.8	7.5	6.2	7.6	7.2	NT
1976	7.1	7.1	4.6	5.1	5.9	NT

NS = Not significant.

NT = No statistical test.

Herbaceous Understory Vegetation Responses

Response of herbaceous understory species was the most striking effect of fertilization observed in this study. Cover and biomass measurements of the herbaceous understory prior to fertilization in 1973 were not significantly different among treatments (tables 4 and 5), indicating that the replications selected for treatment were reasonably uniform. Vegetative cover was more uniform among plots than biomass prior to application of fertilizer (table 4).

Table 4.--Response of herbaceous understory vegetation cover to three annual fall applications of 27-12-0-4 (NPKS) fertilizer at 247 lb/acre/year (278 kg/ha/year).

	Unfertilized not covered	Unfertilized covered	Fertilized not covered	Fertilized covered	F-test
	percent cover				
1973, fall	6.9 ^{a1}	7.3 ^a	6.4 ^a	8.2 ^b	NS
1974, spring	17.8 ^{a1}	21.0 ^a	18.6 ^b	38.6 ^b	**
1975, spring	20.9 ^a	24.8 ^a	41.1 ^b	53.5 ^b	**
1976, spring	14.4 ^a	17.8 ^{ab}	30.8 ^{bc}	39.8 ^{cd}	**

** = Significant at P = 0.01.

NS = Not significant

¹ Values with different superscript letters are significantly different at P = 0.05.

On protected plots (fertilized/covered), fertilization increased cover and biomass of understory vegetation, 1974-1976, compared to both unfertilized treatments. In 1974 cover of the fertilized/not covered treatment was significantly less than that of the fertilized/covered treatment. The same response was observed for biomass in 1976 (table 5), but not for cover (table 4). Reduced cover in 1974 and reduced biomass in 1976 on the fertilized/not covered compared to the fertilized/covered treatment likely resulted from increased use of the fertilized forage similar to that observed for bitterbrush current annual leader growth.

The amounts of fertilizer N, P, and S potentially available for uptake by bitterbrush were determined by subtracting an estimated uptake by herbaceous understory vegetation from the amounts of each element applied. The differential herbage production between unfertilized/covered and fertilized/covered treatments (table 5) was used as the basis for this estimation. Concentration values of 1.6 percent total N and .26 percent total P in cheatgrass and bluebunch wheatgrass forage (Miller 1958) were used to convert herbage production values to uptake values for N and P. A value of .13 percent S in herbage was assigned based on the normal ratio of N:S in plant material of 12:1 (Allaway and Thompson 1966). The total production differential between the two treatments, 1974-1976, was 2,065 lb/acre (2,321 kg/ha). Resultant uptakes of N, P, and S during the 3 years were 33, 5, and 3 lb/acre (37, 6, and 3 kg/ha), respectively. These amounts are a relatively minor part of the total of 200, 88, and 29 lb/acre (225, 99, and 33 kg/ha) of N, P, and S applied. Therefore, most of the applied nutrients should have been available for uptake by bitterbrush.

Table 5.--Biomass of herbaceous understory vegetation in response to three annual fall applications of 27-12-0-4 (NPKS) fertilizer at 247 lb/acre/year (278 kg/ha/year) of N.

	Unfertilized not covered	Unfertilized covered	Fertilized not covered	Fertilized covered	F-Test
	kg/ha ¹				
1973	(477) ^{a2}	(715) ^a	(406) ^a	(206) ^a	NS
1974	(686) ^a	(827) ^{ab}	(1460) ^{bc}	(1636) ^c	**
1975	(709) ^a	(839) ^a	(1549) ^b	(1781) ^b	*
1976	(888) ^a	(1005) ^a	(968) ^a	(1642) ^b	+

NS = not significant

* = significant at P = 0.05.

** = significant at P = 0.01.

+ = significant at P = 0.10

¹ lb/acre = kg/ha X 0.89

² Values with different superscript letters are significantly different at P = 0.05.

CONCLUSIONS

Results indicate that fertilization of bitterbrush habitats in the areas tested would not be effective for promoting growth or crude protein of the bitterbrush. These results contrast with the work of Leman and Pittack (see footnote 5) and with results of the study by Bayoumi and Smith (1976). Both of those studies showed that N was effective in promoting growth and increasing crude protein contents of bitterbrush. However, the lack of fertilizer response of bitterbrush was the same as observed by Klemmedson and Ferguson (1969). In their study, bitterbrush grown in surface soil derived from granitic parent material either did not respond or displayed reduced productivity to added N when P, K, and S were also added. They concluded that bitterbrush may not have a high demand for N or that it may be a true pioneering species from this standpoint. A later study (Klemmedson and Ferguson 1973) demonstrated a positive response of bitterbrush in granitic soils to additions of sulfur. Wagle and Vlamis (1961) found that bitterbrush responses to the pot trial technique of Jenny and others (1950) varied depending on the type of soil. In a basalt-derived soil, P was deficient for bitterbrush, but N was adequate. In a pumice soil the response was reversed. They related the differential N response to the presence of nitrogen fixing nodules. Plants grown in the pumice soil in which N was limiting for bitterbrush growth produced no root nodules.

The stands chosen for this study are representative of much of the bitterbrush habitat in the mid-Columbia region. The majority of shrubs would be categorized as mature or decadent. Leman and Pittack studied fertilization of shrubs in this class, but added a pruning treatment that was probably responsible for most of the growth response they observed. Work by Ferguson and Basile (1966) tends to support this conclusion. They observed that topping of old bitterbrush shrubs increased twig production by 9 times. On mature form class 1 and 2 shrubs Leman and Pittack obtained a marked growth response to fertilization. Bayoumi and Smith (1976) were not specific about the age and form class of shrubs they studied, but it appears from a photograph that these were mature class shrubs. In the present study, lack of growth and crude protein response of bitterbrush appears to be related to the decadent nature of the plants. Plant senescence involves changes in meristematic activity and mobilization of nutrients and substrates (Leopold and Kriedemann 1975). In the case of decadent, over-mature bitterbrush, age probably affects the ability of shrubs to generate new roots, thereby limiting their capability to use fertilizer elements. Since herbaceous understory utilized only a small portion of the fertilizer, sufficient added N, P, and S probably were available for shrub uptake.

Another possibility is that low levels of S in these soils limits the development of bitterbrush roots throughout the life of the plants--a condition that may accelerate the senescence process and lead to decadence. Wagle and Vlamis (1961) found that S deficiencies limited root development of bitterbrush in pumice soils. Additions of S at a late stage in the life of the plants may not be effective in overcoming effects of long-term S deficiencies on root development.

Even though fertilization did not improve bitterbrush production in this study, there are two aspects of the results that deserve emphasis. The attractant effect of fertilization, as indicated by increased use of the fertilized/not covered plot, may be a potentially valuable aid to the land manager in controlling wildlife movement and utilization patterns. Additional research must be conducted to verify this response over several years involving more extensive areas.

Increases in cover and biomass of understory vegetation with fertilization have important implications for erosion reduction and restoration of land stability. Fertilization at the rates in this study approximately doubled the protective vegetative cover afforded the soil surface. In areas with active erosion, such as those in the present study, fertilization appears to be an effective means of improving surface protection.

The relationships established in this study among bitterbrush, cover, leader length, and precipitation need to be studied in terms of actual productivity values in pounds per acre (kg/ha) to be of maximum use to the land manager for predicting amounts of forage that are potentially available for wintering mule deer.

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Section 7. Fire Relationships



A LITERATURE REVIEW OF THE FIRE RELATIONSHIPS OF ANTELOPE BITTERBRUSH¹

Carol L. Rice²

ABSTRACT

The relationship of Purshia tridentata to fire is discussed through a review of the literature. The plant associations in which the species occurs and the fire frequencies of those associations are described. A presentation of the plant's adaptations to fire and factors affecting the response to fire follow. The management implications of these relationships are presented, including the possibility that prescribed fire may be used to enhance the management of this species.

PAST ROLE OF FIRE

Antelope bitterbrush occurs in a variety of plant associations. From the literature, these can be categorized into three zones: the ponderosa pine (Pinus ponderosa Dougl.), the steppe vegetation (sagebrush-grass [Artemisia L.]), and the juniper (Juniperus L.). Past fire frequencies can indicate how much fire the vegetative community can tolerate without being replaced, and what role fire might play in the ecology of bitterbrush.

Ponderosa Pine Zone

The past role of fire in the ponderosa pine zone has been well documented. According to Weaver (1957), early observers reported that while various shrub species were present in the pine forests in the 1880's and 1890's, they were never developed to the present size and density because of frequent and recurrent fires. He found the average interval between fires was 11 to 47 years. Arno (1976) reported the mean fire interval varying from 4 to 11 years in the climax ponderosa pine forests of the Bitterroot National Forest in Montana. Driver and others (1980) thought the mean fire interval of ponderosa pine stands was 7 to 10 years in Washington. In contrast, Wright (1978) stated that the ponderosa pine-bitterbrush communities in west-central North America burned every 50 years or so. This hypothesis is based on his observations and current knowledge of the susceptibility of bitterbrush to fire.

Johnson and Smothers (1976) studied the fire history and ecology at the Lava Beds National Monument and reported that "early travelers to southern Oregon and northern California remarked on the parklike appearance of ponderosa pine in this region."

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Today the forest is filled with an understory of mountain mahogany (Cercocarpus H.B.K. sp.) and bitterbrush. Although these were components of the original communities, frequent fires kept densities at a low level. They found the mean fire interval of the pine forest was quite frequent--a fire almost every 6 years.

Steppe Vegetation Zone

Franklin and Dyrness (1973) stated that fire and ungulate grazing in the steppe vegetation zone were apparently of limited importance in the Northwest before Europeans and their livestock arrived in the mid-1800's. Daubenmire (1970) (in Franklin and Dyrness 1973) says: "There is no evidence that the distribution of vegetation types or species in eastern Washington is related to the past use of fire." Wright and others (1979) noted that fire covered a large portion of the sagebrush-grass community in Yellowstone every 14 to 47 years; but, based on the vigorous response of horsebrush (Tetradymia canescens DC) to fire and the 30 years needed for it to decline, the probable frequency of fire would be about 50 years. They reasoned that if fires occurred every 20 to 25 years, many sagebrush-grass communities would have been dominated by horsebrush and rabbitbrush (Chrysothamnus Nutt. sp).

Juniper Zone

Wright and others (1979) reported that fire occurred every 10 to 30 years in the pinyon-(Pinus edulis Dougl.) juniper communities, and that fire kept junipers restricted to shallow, rocky soils and rough terrain. They remind us that the historic role of fire cannot be separated from the effects of drought and competition as the three play complementary roles in the distribution of vegetation.

Driscoll (1964) reported on a stand of bitterbrush in the juniper zone of central Oregon that had not been disturbed by man. Bitterbrush had a 9 percent shrub cover in the natural area, which constituted 40 percent cover of all perennial plants and 94 percent of the shrub cover. The plants were widely spaced (350/acre or 865/ha), restricted by soil types, averaged 5 ft (1.5 m) in height, and contained wide crowns. Driscoll also stated that wildfire appeared to have been a major factor in determining tree survival and distribution in the juniper-bitterbrush-Agropyron (Gaertn) association.

Young and Evans (1981) studied juniper-sagebrush stands in Lassen County, Calif., and reported that the most vigorous bitterbrush stands appeared to occur in old burns where juniper was reduced or eliminated.

In summary, the role of fire in habitats where bitterbrush is a component varies with vegetation zones. Fire occurring every 6 years or 50 years depending on the location, was important in the ponderosa pine zone. Fire does not appear to have been as frequent in the steppe vegetation zone, which has a mean fire interval as long as 50 years. Fire seems to have played a major role in the juniper zone, restricting distribution of tree species and other vegetation, and enhancing density of bitterbrush.

BITTERBRUSH AS A FUEL

The role of fire in a community is strongly influenced by its effects, which in turn is influenced by the fire behavior. Fuel is one manageable factor of those agents that determine fire behavior. Fuel characteristics may indicate season of fire, range of potential, fire intensity, and range of the rate of spread. Because any plant is a fuel, it is worthwhile to investigate bitterbrush as a fuel.

Some of the important characteristics concerning bitterbrush as a fuel are:

1. Available fuel loading (what is on the ground to burn).
2. The arrangement of fuel (horizontal and vertical continuity).
3. Distribution of diameter size classes of the available fuel loading.
4. Moisture content of the fuel.
5. Heat and ash content of the fuel (whether any volatile oils exist in high levels that might affect the fire behavior).

The fuel loading where bitterbrush occurs is generally light. Ponderosa pine forest communities where bitterbrush occurs probably have the heaviest loading because the pine produces much litter and contributes heavy fuels of larger diameters. However, Johnson and Smothers (1976) report that shrubs under ponderosa pine have the potential to greatly increase the available fuel loading. This, in turn, increases the likelihood of a conflagration that could destroy the entire community. In both the sagebrush-bitterbrush and juniper-bitterbrush communities, fuel loading is often so light that it will not carry a fire except under extreme fire weather conditions. Martin (1978) reported that fuels ranged from 1.4 to 4.3 tons/acre (3 137-9 633 kg/ha) (very light) in juniper associations and that the fuels were mostly the bunchgrasses, sagebrush, and bitterbrush. Meuggler and Stewart (1981) studied forage production (fuel production) of bitterbrush and found that average yearly production of the shrub component of the bitterbrush-Fescue scabrella (Torr.) habitat type (mainly bitterbrush) was 670 lb/acre (123 kg/ha). This was a yearly gross production of fuels; there is no estimate of the proportion decomposed and eaten yearly. Bitterbrush itself does not produce much fuel.

The arrangement of fuels varies in bitterbrush in a number of ways. The fuel arrangement of the decumbent ecotype of bitterbrush is different from the columnar ecotypes. The low, spreading form would be more accessible to the flames. In addition, the fuel arrangements differ in plant crowns. The crown may be dense and compact if heavily grazed or browsed, or may be wide and open otherwise. Martin and Dell (1978) mentioned an example of how the arrangement of fuels affects fire behavior in Planning for Prescribed Burning in the Northwest: "The needle drape in the bitterbrush will cause each plant to flare up; burners should be cautioned about this." Horizontally, the arrangement of fuel generated from bitterbrush is clumped, which is not conducive to fire spread, unless there are interspersed fuels such as grass, pine needles, or dense sagebrush.

The preponderance of dead fuel in bitterbrush itself is usually under 1/2 inch (1.2 cm) in diameter. The size, 1/4 inch (0.6 cm) or less, is considered "1-hour" fuel -- that is, the fuel reaches equilibrium with the atmosphere in 1 hour. In areas where a high dead-to-live ratio in bitterbrush plants exists, dead fuels can influence fire behavior to respond quickly to weather changes. However, because most are live fuels, the moisture in the plants would affect fire behavior to a greater extent. Live fuel moisture is typically highest during the spring and declines regularly until several inches of rainfall initiate an upward trend (Green 1981).

Nord and Countryman (1972) measured the moisture and ash content of nine shrub species in May 1971. They found the moisture content in bitterbrush foliage and stems to average 147 and 131 percent, respectively. Ash content is on the low side, but normal, at 3.8 percent of the foliage and stems. A high ash content tends to make the plant material less flammable.

Philpot (1969) found that the heat content of bitterbrush is average; thus, one would not expect explosive fires such as occur in chamise, which has a high ether extract content. As with other plants, the heat content of bitterbrush fluctuates with the season, but, unlike many other plants, it decreases in summer. The heat content in spring averages 5,040 calories/gram, lowers to 4,600 calories/gram in summer, then rises to 5,010 calories/gram in the fall. Heat content changes the flammability,

intensity, and rate of spread in fire. However, other factors are more important than heat content in determining fire behavior characteristics.

Adams (1980) reported that the fire behavior of prescribed burns on the Fort Rock Ranger District in Oregon in April and September was a function of the continuity of the fuel bed and the age and condition of shrubs--the younger stands (which tend to be discontinuous) did not support fire. Older stands (40 years plus) of the sagebrush-bitterbrush-bunchgrass plant community had consistent characteristics: flame length was 5 to 15 ft (1.5 to 4.6 m), intensity was 18-2,000 BTU/ft (kilocalories/meter-sec), and the rate of spread was 660 to 1320 ft/hr (201 to 402 m/hr). He reported that the fires were either nonburning or severe, with little intermediate fire behavior. Flammability appeared to be correlated to plant and stand age and presence of associated grasses, with the fuels being sensitive to weather changes.

RESPONSE OF BITTERBRUSH TO FIRE

Adams (1980) suggested that bitterbrush evolved in a fire climate. Mutch (1970) suggested that if a species were favored by burning, it would adapt to be flammable. Flammability can be enhanced by a concentration of fine fuels, low moisture content, high dead-to-live ratios, and high volatile oil content. Bitterbrush is mainly small diameter, its moisture content on the low side, its volatile oil content not extreme, and its dead-to-live ratio varies. Bitterbrush could respond to fire as do other plant species by reseeding into the site, surviving the fire and growing (freed from plant competition from other vegetation for some years), sprouting from adventitious roots just below the soil surface (sprout from the stem), or being completely eliminated from the site. Bitterbrush has, in fact, responded in all four of these ways.

Factors Affecting Sprouting Capability

The ability to sprout is only one adaptation for plant survival after fire. However, it is the most important adaptation in vegetation where bitterbrush occurs. Sprouting allows for better competition for moisture. It also seems to be the biggest determinant as to how long it takes for forage production to return to preburn state, and in some cases, whether bitterbrush would remain on the site at all. Why bitterbrush does or does not sprout has been variously attributed to fire intensity, genetic capabilities (different ecotypes), soil moisture and soil type, season of burn, and other factors.

FIRE INTENSITY

Blaisdell (1953) studied the ecological effects of planned burning on the sagebrush-grass range of the Upper Snake River in Idaho. He found that sprouting response of bitterbrush varied with fire intensity. Out of 800 bitterbrush plants, 49 percent sprouted after a light burn, 43 percent after a moderate burn, and 19 percent after a heavy burn. Bitterbrush was able to make a recovery (because of the sprouting that took place) after 34 growing seasons, but was still far below production of unburned sites. Blaisdell also reported that many bitterbrush plants sprouted soon after burning, made rapid growth, and gained dominance within 9 years.

Driver and others (1980) burned bitterbrush in a ponderosa pine-grass-bitterbrush habitat type with a light prescribed fire in the early spring in Washington and observed a 40 to 100 percent resprouting response. In a high intensity fire in an area where thinning debris had been piled and burned, they observed no sprouting. They concluded that bitterbrush can resprout following low intensity fires.

GENETIC CAPABILITIES

Sprouting in bitterbrush is affected by location within its range probably as a result of genetic variability. Wright and others (1979), in reviewing various ecotypes that exist in bitterbrush, stated that the decumbent ecotype generally resprouts after fire or top removal; this aggressive species is capable of revegetating severely disturbed areas after planting. The columnar forms on granitic soils in Idaho will generally resprout after fire or top removal, but resprouting seems to be dependent on fire intensity and soil moisture. Other ecotypes are more severely damaged by fire. Their review concluded that cool, spring burns in decumbent forms result in low mortality and high resprouting, but low seedling establishment. In fall burns, with good soil moisture, resprouting and layering occur in the decumbent ecotypes. They generalized that while fire harms the columnar ecotype more than the decumbent type, cool fall fires are least damaging to the columnar ecotypes. Fire harms bitterbrush more in fine-textured and calcareous soils than on coarse textured and well drained soils. Spring burning enhances sprouting.

Because one ecotype can be prevalent over large areas, previous studies that have explained variation in sprouting of bitterbrush by its location may have actually been observing a prevalent ecotype. Countryman and Cornelius (1957), finding that bitterbrush did not sprout on a northeastern California plateau after a moderate fire in August 1949, stated that a notable feature of burned plots was the complete loss of bitterbrush while, in contrast, bitterbrush was 91 percent of the forage on unburned plots. Nord (1965) noted that antelope bitterbrush is known to sprout in several locations in California. He reported that the only area outside California with frequent and abundant sprouting is eastern Idaho. Nord also reported that because soil moisture affected the degree to which bitterbrush stems were damaged, it was important in determining the degree of sprouting in a stand. When a rainstorm put out a fire or water was used to prevent fire from spreading, heavy sprouting occurred. Intensity is not a crucial factor, he states. Good sprouting is also most likely to develop along drainage channels, or in soils with good soil moisture retention. Where soil moisture was low, no sprouting occurred, regardless of the destruction suffered by the plant.

Sherman and Chilcote (1972) reported that resprouting of bitterbrush is infrequent in central Oregon. Five of 2,052 bitterbrush plants were sprouts, and 13 of those plants that had been cut below the soil surface had adventitious roots. Thus, it reproduced largely from seed. They noted, however, that although bitterbrush didn't sprout, because of a good adjacent seed source their plots were rapidly repopulated after fire, as indicated by a fire scar.

OTHER FACTORS

Environmental factors--Driscoll (1963) suggests that sprouting is not only controlled by genetics but also environmental factors, as well as intensity of the burn. In plots he studied in the ponderosa pine-bitterbrush-fescue and sagebrush-bitterbrush zones, he reported little difference between fire intensity and degree of sprouting. Where plants layered, the plant sprouted at the point of layering, not at the parent plant. Sprouting always occurred 2 to 3 inches (5 to 7.6 cm) below the soil surface. The frequency of sprouting was associated with soil texture and aspect. On north slopes, in loose coarse soils without pumice or cinders, bitterbrush had the highest sprouting with 80 percent. In fine textured stony soils, 1 percent sprouted. Where cinders and pumice were abundant, sprouting was minimal because, being porous, they transfer heat deeper, injuring the plant base more severely.

Season of burn--Adams (1980) stated in work done on the Fort Rock Ranger District in Oregon that bitterbrush sprouted 80 percent on a spring burn and 20 percent on a

fall burn. As previously noted, others have also observed a difference in sprouting in bitterbrush with spring, summer, and fall burns.

Carbohydrate reserve cycle--A large percentage of sprouts die 1 year after a fire. Klebenow and others (1976) reported that although sprouting was adequate on a site mortality after 1 year was widespread. One explanation rests in the carbohydrate reserve cycle in plants. Menke and Trlica (1981) reported that this cycle was a good screening tool for assessing relative effects of defoliation possibly by fire on different plant species. Plants that replenish reserves rapidly in the spring and minimize the time in low reserve status were least affected by defoliation.

Bitterbrush had a typical "V" shaped carbohydrate reserve cycle as shown in figure 1 (Menke and Trlica 1981). Burning when reserves in the taproot are lowest could most drastically affect the plant's ability to sprout. Lowest reserves occurred in the stem in May and June and in the taproot in late June to mid-July. Bitterbrush is unusual in that it doesn't completely replenish carbohydrate reserves until the fruit is fully

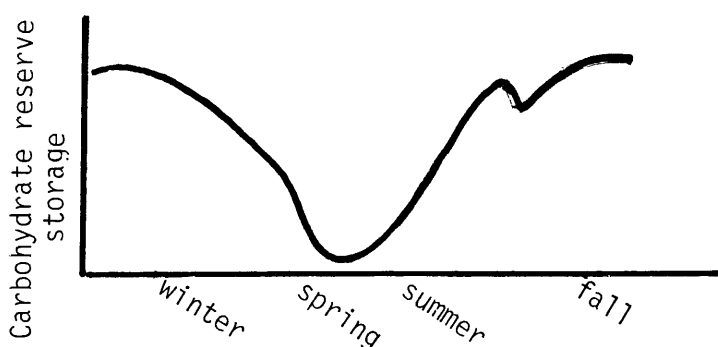


Figure 1. Graph showing carbohydrate reserve storage during winter, spring, summer, and fall.

developed, whereas most plants replenish those reserves somewhat earlier. No one has studied the possible variations in the carbohydrate reserve cycle in different ecotypes of bitterbrush, or documented the phenological stage of plant development when burned, but this approach could help anticipate when sprouting is likely to be most successful in order to optimize the time of the burn.

Factors Affecting Capability to Reestablish by Seed

Blaisdell (1953) stated that part of the recovery of bitterbrush, even where they sprout, comes from new plants established by seed, especially on high intensity fires where most of the old plants were killed.

Driver and others (1980), in developing their hypothesis of the role of fire in bitterbrush, reasoned that older plants (75 to 90 years) have maintained productive capacity for a long time through some mechanism, such as fire resistance, vegetative regrowth, or sprouting. They found that after an intense fire, where thinning debris had been piled and burned, bitterbrush and snowbrush ceanothus (Ceanothus velutinus Dougl.) seedlings were the only shrubs present. Grass was absent from the burn site, even though it was dominant before the fire. They concluded that bitterbrush can function as a pioneer plant in intense fires due to lack of competition from grass, and that the seedling mechanism works when there are infrequent intense fires in the vegetation type.

Sherman and Chilcote (1972) studied the distribution of bitterbrush in central Oregon in the open sagebrush and forest communities by measuring distances of rodent

caches from fire-scarred trees. They found the amount of litter on the ground was extremely important in determining the extent bitterbrush seedlings would appear on the site. The amount of litter was inversely proportional to the distance of caches from the fire-scarred tree used as a plot center. Rodents had a positive effect on seedling numbers because of their seed caches. Caches generally occurred where litter was light, and these locations resulted in higher seedling survival because of favorable pH, moisture, and other factors. Fire occurrence caused extensive seedling establishment. Seedling establishment declined gradually thereafter until another fire occurred.

Nord (1965) reported that seedling establishment varies considerably from year to year and from site to site even though precipitation, soils, and density are comparable. The soil must be moist to the depth of seeds in the fall, winter, and early spring for good seedling establishment. Nord also suggested that an alleopathy of associated plant's litter explains why the presence of litter and duff do not favor bitterbrush. He adds that sagebrush acts as a nurse plant for bitterbrush seedlings because of shade and other factors.

Wright and others (1979) reported that seedlings from the decumbent forms appear to be more competitive than from upright forms. Germination is generally higher in the low growing ecotype, and seedlings are favored by fall burning.

MANAGEMENT IMPLICATIONS

The perpetuation of healthy bitterbrush stands is a difficult management situation. Franklin and Dyrness (1973), building on Sherman's (1966) observations, stated that bitterbrush is the most readily eliminated of the common shrubs, although on some sites fire reduction, consequent competition, and increases in canopy density may have the same effect. This conclusion places the land manager in a dilemma on use of fire in bitterbrush on tree-covered sites. Light to moderate fires may enhance bitterbrush stands (Martin and Dell 1978; Sherman and Chilcote 1972; Driver and others 1980); however, they can generally be achieved only under prescribed conditions.

While bitterbrush has evolved under a fire regime, land management practices over the last 120 years have led to a general stagnation of bitterbrush stands in the West. Fires up to the mid-1800's were more frequent and resulted in grass ranges and pine forests both with widely spaced shrubs, including bitterbrush. Cattle grazing resulted in an increase in shrub cover because of a decrease in the fine fuels of grass litter and in the competition factor of grass in the understory. Bitterbrush cover increased, contributing to the increase in deer herds in the West.

More aggressive fire control measures that were introduced during the early 1900's have affected browse ranges in two ways. When fire control was effective, the shrub stands became decadent, with an increased average age of plants and with sagebrush becoming dominant. When more intense fires than occurred in grass stands of the precattle era occurred in these older browse stands, bitterbrush underwent severely reduced productive capacity.

Sherman and Chilcote (1972) concluded in their study of spatial and chronological patterns that bitterbrush is not a fire-resistant, but a fire-dependent species. Bitterbrush needs to have the litter cleared to enhance rodent caching. Under natural conditions, it is likely bitterbrush would occupy this niche indefinitely. They stated that fire control practices change the scenario. With intense fires because of fuel buildup, destruction of all plants is likely. If fire does not occur bitterbrush habitat will deteriorate and may be lost from portions of its present range.

In contrast, Weaver (1957) stated that bitterbrush's present distribution and extreme density over portions of the Klamath region of California are the result of human fire exclusion efforts over the last 40 to 50 years. Summerfield (1976) stated that bitterbrush is one the species most sensitive to fire in Nevada. If there is 15 to 25 percent composition by weight of bitterbrush on these sites, these areas should not be burned.

Leopold (1950) noted: "Along the lower fringe of ponderosa pine on the Truckee River, logging and recurrent fires have stimulated extensive growths of bitterbrush, on which a fine deer herd now winters. But, a few miles down the canyon toward more arid Reno, fire seems to wipe out both bitterbrush and sagebrush, giving rise to almost pure stands of cheatgrass. One cannot generalize, therefore, about where and when a given technique may be beneficial." This statement holds true today. Of the many factors affecting bitterbrush's response to fire, four are unalterable. Managers should know what is on the site and what influences these four factors bear on bitterbrush's response. The factors are the ecotypes present, what vegetative competition exists, soil texture, and soil moisture. Two factors helping determine fire's effect that can be manipulated by the potential burner are the season of burn and burn intensity.

Determining why bitterbrush reacts to fire as it does may depend on related ecological factors. For instance, intensity, soil texture, and soil moisture may all be related to how much damage is done to the stem; the question is what to use as an indicator to regulate damage. The genetic theory for explaining bitterbrush sprouting is uncompromising in that either the plants have or do not have adventitious buds. The percentage of buds in plant populations may vary, but if the population does not have specialized buds, bitterbrush will not sprout from the base even in the best conditions.

The literature displays many viewpoints of fire and bitterbrush. The author concludes that fire can and should be used in communities in which bitterbrush occurs under narrow conditions. Needing further research are the conditions necessary to meet range, wildlife, watershed, and silviculture objectives with prescribed fire.

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FACTORS AFFECTING ANTELOPE BITTERBRUSH

REESTABLISHMENT FOLLOWING FIRE¹

Robert E. Martin and Charles H. Driver²

ABSTRACT

Successful sprouting of bitterbrush after fire is controlled by such factors as plant genetics and morphology, plant age, competition, soil type, burning conditions, fuel load, past history, browsing pressure, and others. Seedling establishment depends on such factors as seed supply, rodent population, site, and others. Discussion centers on assessing the effects of fire on bitterbrush stands.

INTRODUCTION

Antelope bitterbrush (Purshia tridentata (Pursh) DC.) response to fire is of vital concern to land managers because the shrub is considered an important browse plant for big game throughout most of its range. Generally, investigators indicate fire is detrimental to bitterbrush in both the short- and long-term. However, bitterbrush is often abundant in systems where fire is known to have occurred frequently. Some investigators indicate burning with a cool, moist soil will give high sprouting percentage, while others state that no burning conditions give satisfactory bitterbrush regeneration after fire.

Such contradictions have led us to try to resolve the differences by considering the many factors affecting bitterbrush regeneration. Our grouping of the factors is for convenience of discussion. Many of the factors are interrelated, and we'll attempt to indicate this.

We'll cite only those papers that relate to factors being discussed. For a more complete review of literature on bitterbrush, the reader should consult Basile (1967) and Clark and Britton (1979).

SPROUTING

Many factors are important in determining whether or not bitterbrush sprouting will occur. While sprouting occurs readily on some areas, it may never in other

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areas because of genetic or other factors. In some cases, more frequent fire under more moderate conditions may be important in improving sprouting.

Genetics and Morphology

There appears to be a strong genetic influence in the ability of bitterbrush to sprout. Papers in this proceedings that cite the genetic variability in bitterbrush include: Davis, Driver, Edgerton and others, McArthur and others, Shaw, and Winward. Most of these studies, however, were not concerned with genetic variability in regard to response following fire.

Blaisdell (1950, 1953) pointed out that the ability of a plant to sprout is important in its rapid recovery after burning, and bitterbrush was intermediate in its ability to sprout. Wagle (1958) noted a great deal of variability in sprouting bitterbrush. In California, bitterbrush sprouting ranged from nonexistent to frequent on various burns, but was more common in the zone where hybridization occurred with desert bitterbrush, a good sprouter.

Bitterbrush sprouted anywhere from 3 weeks to 13 months after burning, or after top removal from dormant buds wholly or partly encircling the stem at ground level, or from a callus of meristematic tissue formed beneath the bark after treatment (Blaisdell and Mueggler 1956). The sprouts after burning were from buds protected by soil. The variability in bud location, callus formation, and time of sprouting might indicate genetic variability.

Driver and others (1980) observed that a large number of bitterbrush plants were sprouting from what appeared to be a lignotuber, according to the terminology of Daubenmire (1974). The lignotubers are swellings in the main stem at or just below the ground line. Because this characteristic has not been reported by other investigators, it may only be characteristic of bitterbrush in the area of central Washington where it was observed.

Morphology of bitterbrush appears linked to its sprouting ability. Decumbent forms are known to layer more readily than columnar forms, and location of adventitious buds around base may differ.³

Phenological Condition

The phenological condition of a plant at the time its top is removed, whether by fire or cutting, could greatly affect both its ability to sprout and the vigor of the sprouts. Food reserves of the plants generally are depleted rapidly during the fast early growing period when photosynthesis is unable to keep pace with utilization. Thus, removal of the top, or killing the top with fire, could leave the plant low in food reserves and with a less vigorous sprouting capability.

Several investigators have measured the levels of food reserves in plants throughout the year. Most measured total available carbohydrate (TAC) or total nonstructural carbohydrate (TNC). McConnell and Garrison (1966) found TAC dropped in all bitterbrush plant parts during leaf formation, flowering, rapid growth, and seed formation. As growth rate slackened, TAC began to increase throughout the

³Robert G. Clark and Carlton M. Britton, Texas Tech University, Lubbock. Personal communication.

plants. They felt bitterbrush carbohydrate metabolism would be harmed most by herbage removal during the depletion phase of the carbohydrate cycle between vernalization and early seed formation stages.

TAC was less affected than were herbage yield and morphological characteristics of antelope bitterbrush, and all were affected most by defoliation of bitterbrush during late spring and fruit development or seed shatter stages (Menke 1974). Multiple severe defoliations in one year were quite harmful. Buwai's (1975) results also showed bitterbrush herbage yield and vigor to be affected more than TNC. The plants were most affected by defoliations toward the end of the growing season. Plants that received three defoliations had greatly reduced herbage yield, but remained in good vigor. No plants with three or six defoliations had recovered after 14 or 26 months rest from grazing.

Trlica and others (1977) indicated plants defoliated during the fruit development phenological stage had shorter twigs than did those at other times. Herbage yields, vigor, and basal stem TNC levels were still lower in defoliated plants 14 and 26 months after defoliation than in nondefoliated plants.

Crude protein and apparent digestibility rose while crude fiber and crude fat dropped somewhat during the active growing period and fruit development of bitterbrush in central Oregon (Hickman 1975). He did not comment on the implication for survival after fire or crown removal.

On the applied side, Blaisdell and Mueggler (1956) noted that spring burning yielded more sprouting than burning in summer or fall, yet clipping date had little effect on sprouting. Phenological condition could be involved, but they felt other factors were more important. Jensen and others (1972) indicated that bitterbrush grazed by sheep even moderately during seed ripening will not produce more growth that year. Bitterbrush that were heavily grazed at that time appeared to lack vigor. Wagstaff (1980) reported that a 1975 summer wildfire eliminated almost all bitterbrush from a site. It is possible that the phenological condition contributed to that bitterbrush loss.

Plant Age

Very young and very old plants of a species may not sprout well. Our observations are that seedlings less than 5 years old and bitterbrush greater than 40 to 60 years of age do not sprout well. Perhaps the young seedlings have not yet developed the food reserves or layers to protect adventitious buds. Perhaps they've not yet developed the capability of forming the buds or meristematic callus, as it is called by Blaisdell and Mueggler (1956). Very old plants often seem to lack the vigor necessary to develop sprouts. This could be caused by any number of physiological factors, but it is likely a factor of the lack of food reserves in an already decadent plant.

Blaisdell and Mueggler (1956) point out that higher sprouting occurred after either burning or clipping of bitterbrush sprouts or new plants less than 15 years old than occurred on older plants; 7 to 10 clipped plants under 15 years old sprouted, whereas only 24 to 50 clipped plants older than 15 years sprouted.

The productivity of bitterbrush increased until an age of 60 to 70 years but then declined (McConnell and Smith 1977) in early heavy grazing and moderate late grazing. Whether or not this growth ability is also reflected in sprouting ability is not known.

Clark (1979) found no relationship between sprouting and age. One 92-year-old plant sprouted after being severed 5.9 inches (15 cm) above the ground lines.

Our own experience indicates that bitterbrush seedlings, say under 5 years, and older, decadent plants, perhaps older than 40 to 60 years, do not sprout.

Competition

Competition with other plants both before and after the fire will affect the ability of bitterbrush to reestablish itself. Before fire, competition will affect the general vigor of the plant, reducing its ability to sprout.

Hormay (1943) pointed out that bitterbrush is intolerant of shade and does best in forest openings and on slopes below the pine forest. Bitterbrush seedlings coming after fire often lost out in competition with cheatgrass (Bromus tectorum L.). He noted only two fires in California where sprouting had occurred and felt sprouting was not a main source of regeneration for bitterbrush.

Hubbard and others (1962) explored mortality in a mature bitterbrush stand where competition was a main source of mortality. The bitterbrush was in competition with itself and with crested wheatgrass (Agropyron desertorum Fisch.) They recommended not over 2,200 bitterbrush plants per acre (5,434 plants/ha), or about a 4.5 ft (1.4 m) spacing, for a good site. They cited a personal communication from E. C. Nord where he recorded an average stocking of 778 plants per acre (1,922 plants/ha) with a maximum of 1,420 plants (3,507 plants/ha). Sanderson and others (1963) felt this maximum might be too few in artificially seeded areas.

Sanderson and others (1963) checked the perennial grass competition by weeding out all plants except bitterbrush. Very significant responses in leader length were recorded for bitterbrush plants in both good and poor condition. The grass competition affected vigor as expressed by leader length, which could in turn affect mortality.

Western juniper (Juniperus occidentalis Hook.) and bunchgrasses are important competitors of bitterbrush in the Devil's Garden area of northern California (Hubbard 1965). Reduction of either competitor would leave more moisture and nutrients for bitterbrush, thus improving its vigor. McConnell and Smith (1965, 1970a) recorded an increase in grasses, forbs, and shrubs following thinning of ponderosa pine (Pinus ponderosa Dougl.) stands in eastern Washington. Antelope bitterbrush yield increased about 2 lbs/acre (2.2 kg/ha) for each 1 ft (0.3 m) increase in spacing and 1 lb/acre (1.1 kg/ha) for each 1 percent decrease in canopy. Total shrub (mostly bitterbrush) increment was 45 lb/acre (50.5 kg/ha), or a 1,100 percent increase, at 18.7 and 26.4 ft (5.7 to 8.1 m) spacings compared to 15 lbs/acre (16.8 kg/ha), or 166 percent increase, at 13.2 ft (4.0 m) spacing. The original stand was 2,800 trees/acre (6,916/ha) or an average spacing of 3.9 ft (1.2 m).

Partial cutting of a lodgepole pine (Pinus contorta Dougl.) stand from 91.3 to 20.5 ft²/acre (21.0 to 4.7 m²/ha) basal area in a central Oregon pumice site resulted in an average of 108 percent increase in twig length on mature bitterbrush plants (Edgerton and others 1975). They felt numbers of twigs were also increased, but had no supporting data.

Stuth and Winward (1976) recorded the effects on bitterbrush of clearcut logging in lodgepole pine in central Oregon. Although 43 percent of the plants were lost in logging, the leader length and general vigor of the remaining plants increased considerably.

Burning of bitterbrush in southeastern Idaho did not increase its yield because of large numbers of plants killed, low sprouting success, and competition from other plants (Murray, this proceedings).

Soil Type

Soil type can affect bitterbrush sprouting after fire especially through coarseness of the surface soil. Because sprouting occurs from adventitious buds or meristematic callus at or just below the soil surface, a soil that reduces heat transfer to these areas should enhance sprouting. Loose, pebbly soils may allow the fibrous bark and other organic matter in the surface soil to burn, thus causing more heating of the plant below ground. Finer soils may retain more surface soil moisture through capillarity, thus reducing combustion and temperature rise of the plant tissues just below ground line.

Nord (1959, 1965) reported antelope bitterbrush growing on soils developed from a wide range of parent materials including granitic, rhyolitic basaltic, pumiceous or sedimentary sandstone, and shale rock. He reports that it grows best on coarse textured soils that are well drained, very permeable, and slightly acid. It gives way to other plants on heavier textured, poorly drained, or basic soils. He indicates sprouting is related to the degree of damage at or just below ground line.

Driscoll (1963) reported the best sprouting of bitterbrush following two wildfires in central Oregon was on coarse-textured, nonstony soils without cinders or pumice. Fine-textured, stony soils have low sprouting. The least sprouting was where cinders or pumice were present.

Giunta and others (1978) maintain that sprouting is better on finer textured soils. Our casual observation indicates we are getting less sprouting following fire where soils are very coarse and pebbly. This is especially noticeable on the coarse "popcorn" pumice sites where we have burned.

Soil Moisture

High surface soil moisture has been reported by many investigators as necessary for or improving bitterbrush sprouting (Blaisdell 1953; Blaisdell and Mueggler 1956; Nord 1965; Pechanec and others 1965; Wright and Britton 1976; Martin and Dell 1978; Martin and Johnson 1979; Adams 1980; Olson and others 1981; Volland and Dell 1981; and Murray, this proceedings). Early spring and late fall are recommended for burning, when the soil is cool (Martin and Dell 1978; Martin and Johnson 1979; Adams 1980; Murray, this proceedings). The lower soil temperature requires more heat to be added to bring the protected plant tissue to the lethal temperature. Wildfires, which generally occur during the summer when soils are warm and dry, may account for the low sprouting afterwards.

Burning Conditions

Conditions under which burns are conducted may also affect bitterbrush sprouting. Fuel moisture, particularly that in the duff (H layer) if present, is closely related to soil moisture, and may contribute to sprouting response. The condition of the

site after burning was used by Blaisdell (1950, 1953) to classify the "intensity"⁴ as light, moderate, or heavy. Sprouting was inversely related to intensity, but even on the light burns less than 50 percent of the bitterbrush sprouted; 43 percent sprouted on the moderate burns, and 19 percent on the heavy burns.

Blaisdell and Mueggler (1956) reported that burned bitterbrush sprouted less readily than bitterbrush with complete tops removed. Since date of top removal did not vary with season, they believe the "intensity" of burn is what caused better sprouting in the spring. An August fire had a high rate of sprouting, but the sprouting occurred where water was sprayed to control spread of the fire.

Mueggler and Blaisdell (1958) reported a late August fire to be very damaging to bitterbrush. Countryman and Cornelius (1957) reported complete loss of bitterbrush for 6 years following an August wildfire in northern California.

Nord (1959) reported only one fire in California, an early January burn, where sprouting occurred on more than 25 percent of the bitterbrush, and in 1965 he stated that conditions during burning are important. Pechanec and others (1965) reported that in eastern Idaho and parts of Utah, high percentages of bitterbrush have sprouted after light burning. Wagstaff (1980) reported no bitterbrush sprouting following a summer wildfire in Utah.

Prescription conditions and variable fire effects on bitterbrush based on timing and conditions during burning were mentioned by Martin and Dell (1978), Martin and Johnson (1979), and Olson and others (1981) for areas in central Oregon and northern California. Highest sprouting at Lava Beds National Monument followed a late fall burn where duff had a high fuel moisture so that little of it was consumed (Martin, this proceedings).

Driver and others (1980) gave data on bitterbrush sprouting following a spring burn in central Washington. Similarly, Adams (1980) observed 80 percent sprouting of bitterbrush following a spring burn versus 20 percent sprouting after a fall burn. He cited burning conditions as one of the factors contributing to the difference.

More recently, Laven and Omi (this proceedings) and Murray (this proceedings) cited spring burning conditions as being most favorable for bitterbrush resprouting.

History

What has happened on a site in the past might influence the sprouting of bitterbrush. Over a long time, frequent fire might cause genetic selection of plants for those with better capability to sprout. In the short term, frequent fire might enhance sprouting by keeping fuel loads down or maintaining plant vigor.

Blaisdell and Mueggler (1956) noted that bitterbrush sprouting following a 1953 burn was better on a site previously burned in 1939 than on an unburned site regardless of the date of burning. They speculated the reasons might be burn "intensity," greater ability of younger plants to sprout, or even genetic differences.

⁴"Intensity" as used by Blaisdell is what many today refer to as "severity." We would prefer to use terms such as "fuel consumption" or "heat load," both of which could be measured or calculated, as indicators of the amount of heat supplied to the base of the plant. Intensity is technically the rate of heat release per unit of fire front (Byram 1959), and may or may not be related to the heat delivered to the base of the plant.

In a hypothesis, Driver and others (1980) pointed out that antelope bitterbrush, to be a dominant member of the plant community, should exhibit characteristics that insure its survival and perpetuation in such habitat environments. They used the ponderosa pine-pinegrass (Calamagrostis rubescens Buckl.)-bluebunch wheatgrass (Agropyron spicatum [Pursh] Scribn. & Smith)-bitterbrush habitats of central Washington as an example. Since these habitat types have a high fire frequency and bitterbrush is common, they concluded that bitterbrush must have mechanisms to cope with fire.

Fuel Load

The amount of fuel on a site can be a factor in bitterbrush sprouting after fire, although this is generally not mentioned in the literature. The fuel load is probably also related to competition, especially pine, and perhaps the length of time since fire and plant age. We have observed that sprouting of bitterbrush is low in the pine stands of central Oregon and northern California (Martin, this proceedings), even when these are burned with cool, moist soil and duff.

Browsing Pressure

Browsing pressure before and after fire can affect the ability of antelope bitterbrush to sprout and of the sprouts to survive. Some browsing appears to maintain plant vigor, but excessive or repeated browsing can be detrimental. Considered along with browsing will be grazing by domestic livestock, defoliation by insects, and cutting.

Hormay (1943) observed that plants weakened by previous grazing or caterpillar infestation may be seriously damaged or killed by a single heavy defoliation. Plants not previously weakened may recover quickly after a heavy attack by caterpillars, and 50 percent defoliation prevents flowering the next year.

Moderate clipping or topping of bitterbrush tends to enhance twig growth or crown characteristics (Garrison 1953; Ferguson and Basile 1966; Lesperance and others 1970; Ferguson 1972a; Trlica and others 1977). Heavy defoliation, browsing or clipping, or repeated clipping can harm plants and reduce forage (Hubbard 1965; Nord 1965; Menke 1974; Buwai 1975; McConnell and Smith 1977).

Ferguson (1968) noted that browsed young bitterbrush remained smaller than protected plants and had a slightly lower survival rate. Browsing one-third to one-half of the annual growth increased mortality. However, mechanically removing one-third to one-half of the bitterbrush canopy did not cause mortality (Ferguson 1972a). Twig production was stimulated by topping.

Jensen and others (1972) have shown sheep grazing does not decrease winter browse for wildlife provided the grazing is done before rapid twig elongation in the spring. Grazing later in the year used browse that would have been available for the coming winter.

McConnell and Smith (1977) indicated that heavy early-season grazing produces greater current twig yield per plant than does moderate late-season grazing. The heavy early-season grazing produces more mortality, however.

SEEDLING ESTABLISHMENT

Establishment of plants from seedlings is often the main way bitterbrush regenerates. In some areas, sprouting will be poor or absent following fire, regardless of conditions, and establishment from seed is necessary. Artificial seeding and planting is used in many areas where bitterbrush has been lost or was not present.

Seed Supply

An ample source of seed is a critical factor for seedling establishment of any species. Natural seed production has been discussed by only a few investigators; more have dealt with losses and distribution of seed.

Hormay (1943) stated that bitterbrush reproduces mainly from seed. Heavy seed crops on bitterbrush are a relatively infrequent occurrence in Utah, according to Giunta and others (1978).

Rodent Population

Rodents are important in the dissemination and destruction of seeds and may also destroy seedlings once established. Most bitterbrush seedlings develop from rodent seed caches (Hormay 1943; Nord 1959 and 1965; Hubbard 1965; West 1968; Sherman and Chilcote 1972; Giunta and others 1978; Evans and others, this proceedings). Many authors point out that successful seedling years depend on having a good seed year combined with a relatively low number of small mammals so that some cached seed are left for germination.

Rodents may transport the seed up to 1,000 ft (304.8 m) (Nord 1965). West (1968) reports that up to 90 percent of bitterbrush seedlings develop in clusters and estimates that 50 percent of the shrubs that develop may result from small mammal plantings. Other mammals and birds may also transport seed, and migratory Indians may at one time have accounted for long-distance movement of bitterbrush seed because it was used for medicinal purposes (Nord 1965).

Rodents cache the seed for later use. If rodent populations are high enough so seed production does not exceed their needs, essentially no cached seeds are left for seedling establishment (Hubbard 1965).

Rodents may also damage bitterbrush seedlings. Mice, and perhaps other rodents, rob seed spots⁵ planted in the fall (Holmgren and Basile 1956). Meadow mice (*Microtus montanus*) severely damaged bitterbrush by girdling in northeastern California and Oregon in the late 1950's (Hubbard and McKeever 1961).

Site

Quality of a site in relation to the strains of bitterbrush is important to good bitterbrush seedling establishment. Although many abiotic and biotic factors enter

⁵ A seed spot is the location where one or more (usually more) seeds have been planted. Usually two or more seed spots may be located close together in a single scalped area.

into site quality, we'll primarily consider moisture, nutrients, and macro- and micro-climatic conditions.

Many investigators mention site, most often in connection with artificial regeneration. Hormay (1943) and Nord (1965) mentioned site in terms of natural and artificial regeneration. Giunta and others (1978) pointed out site factors, particularly moisture and winter conditioning temperatures, as being important factors. Soil moisture and soil surface temperature are also important in bitterbrush seedling establishment (Ferguson 1972b).

Burning Conditions

The conditions under which wildfires or prescribed burns occur can have an effect on bitterbrush seedling establishment. Blaisdell (1950) reported that the number of bitterbrush seedlings varied inversely with the "intensity" of a prescribed burn. Sherman and Chilcot (1972) indicated that rodents prefer to cache seeds in mineral soil, so burning must remove the duff. Driver and others (1980) observed good bitterbrush seeding where debris piles had burned out, which left ash and mineral soil and removed competition. They pointed out that infrequent, more severe fires may lead to more bitterbrush seedling establishment.

Plant Competition

Competition with other plants for moisture, nutrients, and light is important to bitterbrush seedling establishment. Serious competitors may be grasses, forbs, shrubs, or trees.

Depletion of soil moisture by competing vegetation was strongly related to bitterbrush seedling growth and mortality (Hubbard 1956). Heavy competition from native vegetation and crested wheatgrass was compared with plots weeded the first year and third year. After 3 years, plants with no competition were five times as tall as those under heavy competition and suffered only one-third the mortality.

Sanderson (1962) recorded 88 percent bitterbrush seedling survival in a rototilled area versus 4 percent in an undisturbed area during a year of low precipitation. Bitterbrush responded to thinning of ponderosa pine stands in Washington (McConnell and Smith 1965, 1970a).

Percent survival of seedlings in a seedling spot was directly and strongly related to the number of seedlings (Ferguson 1962; Ferguson and Basile 1967). Thus, intraspecific competition was less important than the many factors that may help one or more of the seedlings in a group to survive.

Dealy (1970) showed that release from competition improved crown cover of 4-year-old bitterbrush more than its height growth. Protection from browsing was more effective than release from competition, but the combination of the two treatments was much more effective than either treatment alone.

Dietz and others (1980) showed that seeded bitterbrush survive two and a half times better after 10 years on an old burn site than in an open ponderosa pine stand. Growth was also better on the old burn site.

Bitterbrush seedlings have become established where slash accumulations have burned out, eliminating herbaceous vegetation for several years (Driver and others 1980).

Browsing Pressure

Browsing of bitterbrush seedlings by domestic livestock or wildlife reduces growth and survival. Animals may browse or graze in different ways, but excessive pressure can be very harmful. Proper browsing on adequately established plants can be stimulatory.

Lightly grazed pasture had a significantly higher density of bitterbrush plants than did a heavily grazed pasture (McConnell and Smith 1970b). Dealy (1970) indicated that protection from browsing significantly increased height and crown cover of 4-year-old bitterbrush seedlings. Monsen (this proceedings) has shown bitterbrush seedlings to establish in sites protected from grazing, and Martin (this proceedings) has shown four burn sites with heavy grazing to have significantly fewer bitterbrush seedlings than other burn units.

We have observed, but not measured, many young bitterbrush seedling groups that were completely or partly clipped off by either deer or cattle in partial or clearcut ponderosa pine areas after slash disposal.

INSECTS AND DISEASES

Insects and diseases may affect any phase of the bitterbrush life cycle. Some species may kill plants or reduce the vigor of young or old plants, making them susceptible to other agents. Others may reduce flowering or viable seed production or destroy seed or young seedlings. A better understanding of the insects and diseases affecting bitterbrush stands is needed, especially in connection with various patterns of manipulation and use.

Grasshoppers damage bitterbrush seedlings (Holmgren 1956). Edgerton and others (this proceedings) described the differential preference of grasshoppers for various provenances of bitterbrush. Hubbard (1956) described the destruction of bitterbrush seedlings by cutworms and wireworms, which destroy the cotyledons and roots, respectively.

Krebill (1972) compiled an annotated list of diseases for bitterbrush and other western shrubs, and Furniss and Krebill (1972) discussed the effects of insects and diseases on western shrubs. Furniss (this proceedings) discusses insect associates of bitterbrush, and Scholten (this proceedings) mentions insect problems in establishing bitterbrush in a wildlife management area.

ARTIFICIAL SEEDING AND PLANTING

Bitterbrush establishment following fire is presently dependent upon artificial seeding or planting in some areas. Few or no bitterbrush have been present or are left following fire, thus making artificial regeneration necessary.

Seed orchards and provenance studies have been established in many areas to provide seed. These are not without problems, as described by Edgerton and others, Shaw, VanEpps and Christensen, and Alder (all in this proceedings). But production of seeds or seedlings is generally successful. Guidelines for artificially regenerating bitterbrush stands or factors affecting success have been given by Hormay (1943), Nord (1956), Sanderson and Hubbard (1961), Plummer and others (1968), Dealy (1970), Steven and others (1974), Dietz and others (1980), and by Carpenter, Monsen, and Scholten (all in this proceedings).

SUMMARY

Successful regeneration of bitterbrush following fire is dependent on many factors. There is much overlap between the needs for sprouting of old plants versus natural seedling establishment, but each has unique requirements.

Sprouting is dependent on many factors. Some plants apparently are genetically not inclined to sprout whereas others have developed lignotubers from which sprouts emerge. Season of the year during which fires occur doesn't appear to be as important in obtaining sprouts as is a cool, moist soil condition. Whether lack of sprouting following fire during seed set and shatter is a phenological condition or due to lack of soil moisture has not been resolved.

Plant age and competition appear to affect sprouting ability, as both can affect general plant health and vigor. The degree to which these are responsible for sprouting capability again has not been determined. Plants in timbered areas have displayed less sprouting than nearby stands in the open. Animal browsing and pests as well as diseases can affect plant health and also alter sprouting capability.

The amount of fuel and burning conditions appear to change sprouting capability, but these factors have not been separated from other factors. Generally, fuel buildup will be greater in timber stands, thus confounding fuel load with tree competition.

A cool moist soil is a primary factor aiding bitterbrush sprouting. This factor alone will not cause good sprouting; some other critical factors may not be present.

Human protection of some stands to the point where they are old and decadent, where excessive fuel has accumulated, plant competition has developed, or the plants have not developed sprouting capability, has actually led to bitterbrush stands that are more susceptible to fire.

Natural seedling establishment following fire depends on seed supply, rodent population, site conditions in critical seedling years, plant competition, burning conditions, and browsing pressure. Generally, a good year to get seedlings started requires an excellent seed crop, a proper balance of rodents to cache the seed but not use it all, and a growing season in which soil moisture is not depleted too quickly. Plant competition and site conditions are factors in soil moisture depletion. Freezing and excessive heat may also be critical site factors. Burning conditions that destroy plant competition and create a good ash and mineral seedbed can aid establishment. Finally, excessive browsing and grazing by domestic livestock or wildlife can contribute to mortality or retard growth of bitterbrush seedlings.

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Bitterbrush and cliffrose are perhaps the most widely managed shrubs in Western North America. This proceedings of 27 papers is a collection of our current knowledge on research and management of bitterbrush, cliffrose, and other rosaceous shrubs in Western North America. Subjects include: (1) distribution, taxonomy, and habitat classification; (2) growth performance, phenology, and physiology; (3) successional relationships; (4) management strategies; (5) animal relationships; (6) soil-plant nutrient relationships; and (7) fire relationships.

KEYWORDS: rosaceous shrubs, Purshia, Cowania, Fallugia, Rosaceae, distribution, taxonomy, habitat classification, growth, phenology, physiology, succession (plants), management, animals, soil nutrients, nitrogen fixation, fire

The Intermountain Station, headquartered in Ogden, Utah, is one of eight regional experiment stations charged with providing scientific knowledge to help resource managers meet human needs and protect forest and range ecosystems.

The Intermountain Station includes the States of Montana, Idaho, Utah, Nevada, and western Wyoming. About 231 million acres, or 85 percent, of the land area in the Station territory are classified as forest and rangeland. These lands include grasslands, deserts, shrublands, alpine areas, and well-stocked forests. They supply fiber for forest industries; minerals for energy and industrial development; and water for domestic and industrial consumption. They also provide recreation opportunities for millions of visitors each year.

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