



Bitterbrush growth and reproductive characters in relation to browsing in southwest Montana
by William Wyatt Fraas

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in
Range Science

Montana State University

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Abstract:

Antelope bitterbrush (*Purshia tridentata* Pursh) stands in southwestern Montana appeared to be heavily browsed and to contain few seedlings. Growth and reproductive characters were measured on 10 ecologically diverse stands in relation to browsing levels. Stands averaged 0 to 60% browsing use of twigs on sampled branches. These rates were lower than in a previous study within the study area due to differences in sampling. Neither 1 season of rest from browsing nor 1 season of clipping previously unbrowsed plants affected bud densities.

Flower bud density was lower ($P < 0.001$) and long shoot (LS) bud density was higher ($P < 0.01$) on browsed than unbrowsed plants. Browsed and unbrowsed twigs within browsed plants did not differ in flower or LS density, indicating a plant-level effect of browsing. Browsing levels did not correlate significantly with either growth or flower production, but all 3 factors varied among stands ($P < 0.05$). Although observed seedlings were rare, few seedlings should be required to replace these long-lived plants.

Crude protein levels differed between stands ($P < 0.05$). Summer leaves contained twice the protein of stems ($P < 0.05$). Winter leaf protein levels declined 21% ($P < 0.01$).

Bitterbrush plants in a burned stand had a similar density to an adjacent unburned stand and produced per-branch growth rates similar to unburned plants, but were smaller ($P < 0.001$) 8 years after burning. Flower production was also less ($P < 0.001$), suggesting that these bitterbrush sprouts could take many years to reach full reproductive maturity. Plant communities differed between the burned and unburned plots. Burning bitterbrush stands on big game winter range could result in decreased shrub production for many years.

A bitterbrush stand exposed to livestock and big game use produced more LS growth per length of branch ($P < 0.01$) and had a higher leaf crude protein content in 1990 ($P < 0.05$) and higher stem crude protein content in 1991 ($P < 0.05$) than an adjacent bitterbrush stand receiving only big game use.

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Antelope bitterbrush (*Purshia tridentata* Pursh) stands in southwestern Montana appeared to be heavily browsed and to contain few seedlings. Growth and reproductive characters were measured on 10 ecologically diverse stands in relation to browsing levels. Stands averaged 0 to 60% browsing use of twigs on sampled branches. These rates were lower than in a previous study within the study area due to differences in sampling. Neither 1 season of rest from browsing nor 1 season of clipping previously unbrowsed plants affected bud densities.

Flower bud density was lower ($P < 0.001$) and long shoot (LS) bud density was higher ($P < 0.01$) on browsed than unbrowsed plants. Browsed and unbrowsed twigs within browsed plants did not differ in flower or LS density, indicating a plant-level effect of browsing. Browsing levels did not correlate significantly with either growth or flower production, but all 3 factors varied among stands ($P < 0.05$). Although observed seedlings were rare, few seedlings should be required to replace these long-lived plants.

Crude protein levels differed between stands ($P < 0.05$). Summer leaves contained twice the protein of stems ($P < 0.05$). Winter leaf protein levels declined 21% ($P < 0.01$).

Bitterbrush plants in a burned stand had a similar density to an adjacent unburned stand and produced per-branch growth rates similar to unburned plants, but were smaller ($P < 0.001$) 8 years after burning. Flower production was also less ($P < 0.001$), suggesting that these bitterbrush sprouts could take many years to reach full reproductive maturity. Plant communities differed between the burned and unburned plots. Burning bitterbrush stands on big game winter range could result in decreased shrub production for many years.

A bitterbrush stand exposed to livestock and big game use produced more LS growth per length of branch ($P < 0.01$) and had a higher leaf crude protein content in 1990 ($P < 0.05$) and higher stem crude protein content in 1991 ($P < 0.05$) than an adjacent bitterbrush stand receiving only big game use.

INTRODUCTION

Antelope bitterbrush (Purshia tridentata Pursh) is well-documented as a valuable food source for big-game animals (Kufeld 1973, Kufeld et al 1973). It is highly palatable, moderately nutritious, and common on many big-game winter ranges (Giunta et al 1978), although it seems to be declining in some areas (Winward and Finley 1983). Bitterbrush inhabits a wide range of habitats (Franklin and Dyrness 1973), mainly on open, well-drained sites (Nord 1965), and has been useful as a ground stabilizer on exposed soils (Nord 1959). Land managers have therefore been interested in propagation, growth, and management of bitterbrush to improve wildlife habitat and restore degraded lands.

Bitterbrush is known for its variability in habitat, morphology, and physiology. Habitats range from pine (Pinus spp.) understory (Sherman and Chilcote 1972) to open dune sands (Chadwick and Dalke 1965) and recent lava flows (Eggler 1941). Its growth form ranges from prostrate forms only 10 cm high to columnar forms over 3 m tall (Winward and Finley 1983). Color, shape, and size of leaves, stems, and seeds vary between and within populations (Alderfer 1977). Mowing and burning result in responses that range from death to vigorous sprouting (Clark et al 1982). While these variable attributes enable bitterbrush to inhabit and contribute to the widely divergent habitats in western North

America, they can also make management of the species more difficult unless the response of local populations is known.

A recent study (Guenther 1989) of the environmental relationships of several bitterbrush stands on the Montana Department of Fish, Wildlife, and Parks' Mount Haggin Wildlife Management Area (MHWMA) noted the wide range of habitats and growth of these stands. Guenther also found a high level of browsing on the bitterbrush plants and little successful reproduction during the previous decade. Those findings raised concerns for the future of bitterbrush stands on the important MHWMA mule deer winter range and increased interest in managing and enhancing the stands.

The specific objectives of this study were to examine growth and reproductive characters of separate bitterbrush stands and to relate these characters to browsing levels. I hypothesized that bitterbrush stands are not uniform in their reproductive and growth characteristics. Results from this study could increase our knowledge of how this plant responds to continued, heavy browsing pressure and could aid in formulating management strategies for bitterbrush stands and the winter ranges they often occupy.

LITERATURE REVIEW

Bitterbrush is highly variable in many of its attributes, including plant growth form and size; stem, leaf, and seed size and color; phenology; response to burning or mowing; occurrence on soil types, slopes, aspects, or as understory; growth and flowering rate; and insect resistance. These characters have generally persisted in common garden conditions. Several annotated literature reviews (Hall 1964¹, Basile 1967, Clark and Britton 1979) discuss many of these characteristics. This chapter provides a background of bitterbrush characters pertinent to this investigation.

Distribution

Bitterbrush is distributed throughout western North America, mainly from the 37th parallel northward into British Columbia, and mainly west of the continental divide (McArthur et al 1983). Southwest Montana represents part of the northeastern edge of its range. Bitterbrush intermingles spatially and genetically with cliffrose (Cowania stansburiana Torr.) and desert bitterbrush (Purshia glandulosa Curran.) on its southern boundary (Stutz and Thomas 1964), although hybrid characters are found nearly

¹. Hall, F.C. 1964. Literature review of bitterbrush (Purshia tridentata). USDA Forest Service, Pacific Northwest Region. Portland, Or. 48 p. Unpublished.

throughout its range. Bitterbrush is found generally on coarse, deep, well-drained soils, and on hot, dry, south-facing slopes (Nord 1965, Tew 1983).

Species Description

Bitterbrush is a semi-erect and diffusely branched shrub from 0.4 to 3 m tall, belonging to the rose family (Rosoideae, Rosaceae). Its roots are semi-taprooted and extend 10 to 20 feet deep (Cline 1960, McConnell 1961). Its leaves are mostly deciduous, 0.5 to 1.5 cm long, and wedge-shaped with revolute margins and 3 lobes at the tip. Leaves are variously glabrous to tomentose, usually dark green above and lighter to white below. Flowers are pale to bright yellow, 5-petalled, perfect, 1 to 1.5 cm in diameter, and often numerous. Seeds are teardrop-shaped, consisting of an achene within a papery husk about 0.5 to 1 cm long. Seeds are usually born singly. Viable seeds are light brown or grey, plump, and relatively large. There are usually about 40,000 of these seeds per kilogram (18,000 per lb). Mottled, shriveled, or small seeds are dead or produce weak seedlings.

Phenology

Bitterbrush phenology (Fig. 1) seems to vary more by season and climate than by ecotype (Shaw and Monsen 1983). Leaf growth begins in late spring, and is soon followed by

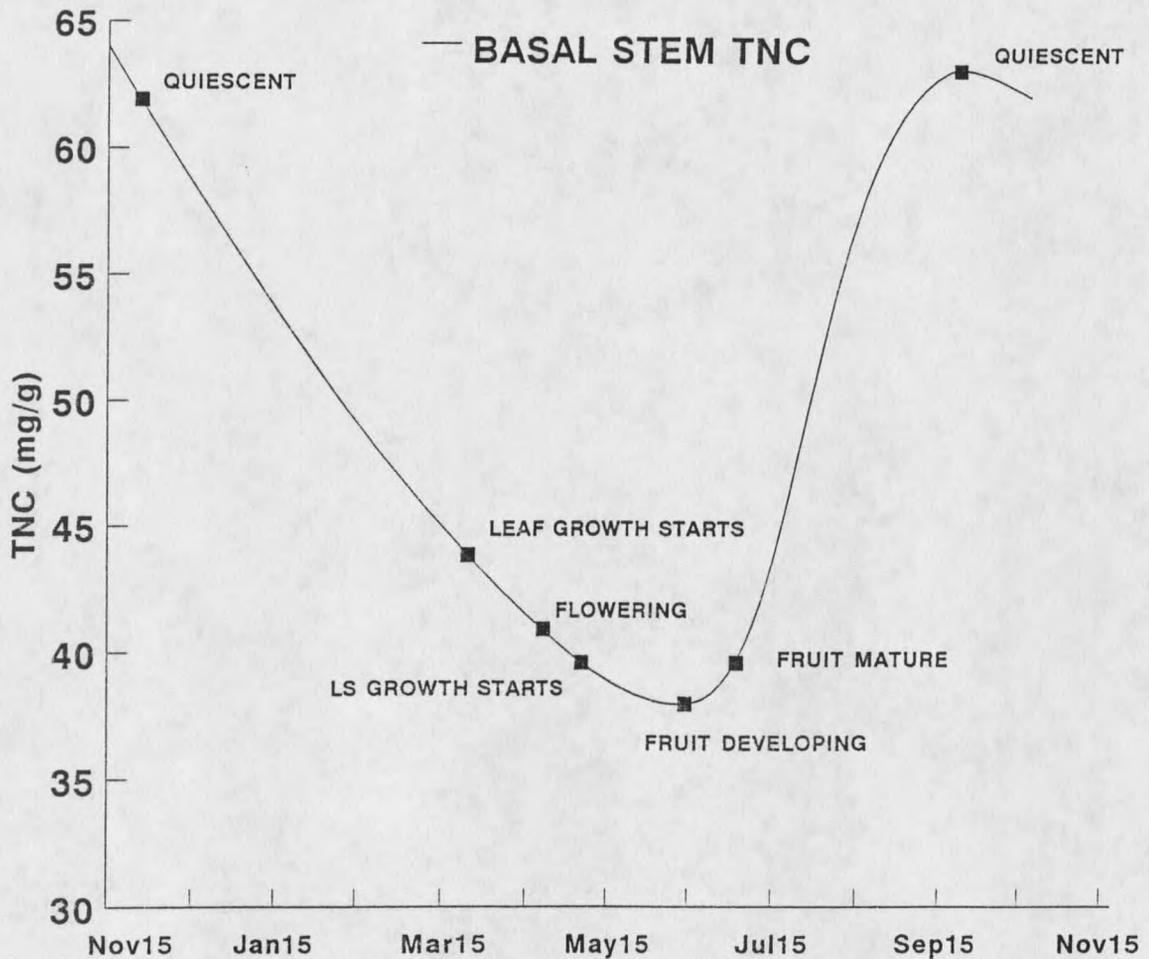


Fig. 1. Representative total nonstructural carbohydrate (TNC) concentration (mg/g) in basal stem region of bitterbrush (Menke and Trlica 1981) and average phenologic stage (Shaw and Monsen 1983). Leaf and long shoot (LS) samples were taken at or before seed maturity in early August for crude protein analysis.

flower bud formation. Flowers erupt from late May to late June and seeds are set within a month of flowering. New twigs (long shoots or LS) begin to elongate during flowering, extend most during seed set, and continue to grow until low soil moisture or cold halts growth in the fall.

Long shoot length seems to be strongly related to precipitation from the preceding fall through summer (Garrison 1953a, Shepherd 1971, Tueller and Tower 1979, Bilbrough 1990). Most leaves are deciduous, dropping in response to moisture stress in late summer or fall (Shaw and Monsen 1983), but some small leaves overwinter on some populations (Alderfer 1977).

Carbohydrate Cycle

The nonstructural carbohydrate cycle in bitterbrush (Fig. 1) is fairly typical of range plants (Cook 1966), with rapid depletion of soluble carbohydrates as leaf, flower, and seed growth ensues, followed by replenishment during late summer and gradual decline during winter until active plant growth resumes (Menke and Trlica 1981). Carbohydrate levels appear to be affected by season of biomass removal, being least disrupted by clipping during dormancy and most sensitive during seed-set, the stage of lowest reserves (Menke and Trlica 1983). Young twigs (less than 2 years old) contain less total nonstructural carbohydrate than older stems, but appear to be depleted more rapidly than older stems during active growth (McConnell and Garrison 1966).

Reproduction

Bitterbrush reproduction is a complex process (Evans et al 1983). Seeds are highly palatable to several species of rodents and entire seed crops may be harvested by granivores. Harvesting is not necessarily detrimental to reproductive success, however. Many of these rodents not only cache the seeds, but remove the papery husk, which contains a germination inhibitor, as does the pericarp (seed coat). Most caches are placed in open, exposed soil from 1 to 5 cm deep where 1 to hundreds of seeds overwinter and germinate in late spring. Some species of rodents apparently relish the emerging cotyledons and may devour the entire cache of sprouts.

If rodents fail to eat some of the seeds, however, seedlings from crowded caches are likely to die from competition for moisture and space. Overlooked or later-sprouting seedlings or seedlings from small caches are most likely to survive sprouting. Unburied seeds are less likely to germinate, as removal or weathering of the seed coat is necessary to diminish the effect of the germination inhibiting substance.

Rodents may not be the only agents of seed burial, as an incidence of apparent livestock trampling of seed into loose soil on a steep slope resulted in establishment of single seedlings rather than the usual clusters of rodent-cached seeds (Bunting et al 1985). Winter and spring soil

moisture adequate for soaking and leaching the inhibitor are necessary, as are favorable moisture conditions during the first 3 years. Hard frost in the late spring has been implicated in high seedling mortality and low seedling establishment. Seedlings are also susceptible to damage by damping-off fungus, cutworms, and grazing by rodents and large ungulates.

Some growth forms of bitterbrush can also reproduce vegetatively through layering. The prostrate growth forms growing on loose or moving soil are most likely to root from stems in contact with or covered by the soil (Nord 1965). Adequate moisture also seems to be a factor in frequency of layering success. Layered stems may eventually become separated from the parent plant and appear to be unique individuals.

Bitterbrush has been reported to be declining across its range (Nord 1965, Ferguson and Medin 1983, Winward and Finley 1983), often accompanied by a lack of successful reproduction (Guenther 1989). Anderson (1989) related such intermittent or rare seedling establishment of long-lived perennial plants to the infrequent occurrence of "safe sites" where and when ideal establishment conditions exist.

Nord (1965) termed bitterbrush establishment in California "spasmodic" as 5 to 7 years often elapsed between good seedling establishment years. Guenther (1989) found at least 1 plant established per year from 1930 through 1982,

with all 18 of his sites pooled, which suggested that adequate conditions for establishment occurred in that time span for at least 1 of his study sites every year.

Ferguson and Medin (1983) estimated that 1-2 plants per acre per year became established on their Idaho study site, inside and outside of a deer enclosure. Nord (1965) found seedling clusters of up to 3,900 per acre in California with yearly variations of up to 800%. He also found a strong moisture and altitudinal gradient associated with seedling establishment and noted that snowpack was much more effective than rainfall for providing good establishment conditions. These factors all suggest that bitterbrush seedling establishment often occurs intermittently in time and space, so that few seedlings would likely be found unless a large area were searched.

Browsing Response

The leaves and twigs of bitterbrush are eaten by many species of large ungulates, including cattle, sheep, goats, mule deer, elk, moose, and bighorn sheep (reviewed by Nord 1965), as well as by many insects (Furniss 1983). Wildlife use can occur year-round, depending on availability of bitterbrush, whereas domestic stock prefer other forages during spring and summer and turn to bitterbrush primarily when herbaceous foods senesce (Jensen et al 1972, Neal 1982, Reiner and Urness 1982, Urness 1982).

Season and degree of use affect bitterbrush growth. Martinsen (1960) found that moderate summer use of bitterbrush led to decreased LS growth, while Jones (1983) found that removal of most top growth during dormancy was not detrimental to LS growth. Regardless of season, bitterbrush appears to respond positively to any level of browsing pressure, at least for short periods. Unbrowsed plants have appeared to decrease their annual growth rate, and have produced less shoot growth than adjacent, moderately browsed plants (Gysel 1960, Peek et al 1979). This decrease can apparently occur in as little as 2 years after protection. One year of protection has been recommended for allowing maximum LS production (Tueller and Tower 1979).

Tueller and Tower also reported a "stagnation" effect. They found that plants clipped severely each year produced more than plants either rested for 5 years or only moderately browsed and then clipped severely. Although several researchers have recommended a maximum of 60% use of annual growth (Hormay 1943, Garrison 1953b, Steinhoff 1959, Martinsen 1960, Lay 1965, Shepherd 1971), higher levels for short periods have not been detrimental (Urness and Jensen 1983).

Browsing pressure appears to affect the ratio of LS and flowers produced. McNulty (1947) found fewer numbers of flowers produced at increasingly higher levels of browsing,

attributing the change to the number of lateral buds available to produce flowers. Garrison (1953b) and Urness and Jensen (1983) noted a similar trend of flower production. Ferguson and Medin (1983) stated that "old bitterbrush plants tend to reduce annual twig growth in favor of seed production unless continually stimulated by the browsing of animals." Bilbrough (1990) found that although clipping did not directly remove buds responsible for flowering, clipped bitterbrush was able to mobilize otherwise inactive buds for elongation and theorized that "heavy browsing would eventually reduce the number of buds available to produce flowers." She did not, however, determine whether varying browse levels affect the allocation of buds to flowers in successive growing seasons.

A close relationship exists between the use level of bitterbrush twigs and both the length and number of twigs removed. Several researchers have shown a relationship between the length and diameter of bitterbrush LS (Basile and Hutchings 1966, Jensen and Urness 1981). Guenther (1989) found a high correlation between the length of browsed leaders and the number of leaders browsed ($r=0.94$, $P=0.0001$) in southwest Montana, although counting browsed leaders resulted in a 10% higher estimate than did comparing leader length before and after browsing.

Watson and Casper (1984) contend that plants consist of nearly autonomous, repeated units. Bud allocation

"decisions" are thus made on a local (branch) level and are primarily influenced by photosynthetic assimilate (carbohydrate) supply and demand within each module. They hypothesized that defoliation could affect this relationship directly by removing the food supply, or indirectly by affecting the plant's roots, which could in turn affect water and nutrient supplies to the whole plant.

Stand Rejuvenation

Senescent bitterbrush stands have been subjected to a variety of treatments in attempts to increase leader production, including rotomowing (Jones 1983), topping (Ferguson and Basile 1966) and burning (Blaisdell and Mueggler 1956). Incidental treatments have included heavy grazing (Reiner and Urness 1982, Urness and Jensen 1983) and exposure to logging activity (Edgerton 1983). Many of these drastic treatments have resulted in increased LS lengths on remaining branches, whereas others have resulted in root sprouting with vigorous LS production from the new stems. These results depend on the ecotype involved; Leopold (1950) noted that fire eliminated bitterbrush in California, whereas Blaisdell (1953) described vigorous sprouting of burned plants in Idaho. Most researchers described increased average LS lengths, but did not report total production. Urness and Jensen (1983) found higher individual LS lengths but less total LS production on

heavily browsed compared to unbrowsed plants, resulting in a net production decrease in response to treatment.

Bitterbrush has appeared to respond differently to fire at nearly every site. Leopold (1950) noted that bitterbrush was exterminated by fire in California. Blaisdell (1953) and Blaisdell and Mueggler (1956) reported frequent sprouting after fire in Idaho. Bunting et al (1985) found that the decumbent growth form is most likely to sprout after fire, and that sprouting frequencies of bitterbrush in mountain big sagebrush (Artemisia tridentata Nutt. ssp. vaseyana [Rydb.] Beetle) habitat types tend to be lower than for other, more mesic habitat types. Rice (1983) attributed sprouting frequency to ecotype, soil moisture and type, season of burn, and fire intensity, to which Martin and Driver (1983) added amount of browsing pressure, site quality, and length of time since burning. Bitterbrush may also reestablish from seedlings, but seedlings or sprouts may require more than 5 to 10 years (Monsen and Shaw 1983, Bunting et al 1985) to reach sexual maturity. Murray (1983) found that bitterbrush production on burned sites was still below that of unburned sites 30 years after burning, which could have detrimental effects on big game winter range (Klebenow 1985).

Species associated with bitterbrush in southwest Montana respond variously to fire. Bluebunch wheatgrass (Agropyron spicatum Pursh) response has been mixed, ranging

from short-term (1-3 years) and long-term (4-30 years) decreases in canopy cover or production (Blaisdell 1953, Daubenmire 1975), to short-term increases (Uresk and others 1976), to no change (Peek et al 1979, Kuntz 1982, McNeal 1984, Mangan and Autenrieth 1985). Idaho fescue (Festuca idahoensis Elmer) is commonly damaged by fire (Pickford 1932, Blaisdell 1953, Nimir and Payne 1978, Hironaka et al 1983, Mangan and Autenrieth 1985). Sometimes 30 or more years are required for Idaho fescue to recover (Harniss and Murray 1973). Mountain big sagebrush rarely sprouts after fire (Blaisdell 1953, Pechanec et al 1954), although it can vigorously reestablish from seed (Hironaka et al 1983). Often plant species diversity increases after fire (Johnson and Strang 1983), but individual species tolerances vary widely (Blaisdell 1953, Ralphs et al 1975, Nimir and Payne 1978).

Root Nodulation

Bitterbrush has been found with root nodules containing species of the actinorhizal genus Frankia (Nelson 1983) and may be able to fix some of its needed nitrogen. However, nodulation decreases under dry conditions (Righetti and Munns 1981), which are common in bitterbrush stands. The extent of nodulation in each bitterbrush stand and throughout its range has not been established (Wagle 1958,

Nelson 1983).

Tiedemann (1983) found that soil nitrogen concentrations beneath bitterbrush plants were 3 times greater than in surrounding open areas, a development common to other desert shrubs (Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973). Although the surrounding soil areas seem to be depleted of nutrients, addition of detritus and nitrogen fixation from growing shrubs may result in a net gain in nutrients for a site. The role of such "fertile islands" in successional development of shrub sites is not known (Tiedemann 1983).

Protein Content

Protein is 1 of the most important nutrients for wintering ungulates (Dietz 1972). Welch et al (1983) estimated that crude protein levels of bitterbrush are not quite high enough to support their needs but postulated that protein content might vary with populations of bitterbrush. Differences in bitterbrush protein content between sites have been noted (Giunta et al 1978), although not between local habitat types (Morton 1976). Slausen and Ward (1986) found no difference in crude protein between 3 Colorado accessions in a common garden, but Welch et al (1983) found differences in a common garden test with plants from a wider geographical area. Nutrient concentrations have occasionally been altered by fertilizing bitterbrush plants

(Bayoumi and Smith 1976, Tiedemann 1983), but no differences have been found at varying browse levels (Dietz et al 1962, Shepherd 1971). Crude protein levels were higher when winter leaves were present (Dietz et al 1962), but winter leaf presence varies between populations of bitterbrush (Welch et al 1983).

Water Use Efficiency

Water use efficiency, or the ratio of water used (or lost in transpiration) to the amount of carbon fixed in photosynthesis varies with nitrogen and water availability for several desert shrubs (Toft et al 1989). Both of these variables vary from site to site in bitterbrush habitats (Cook and Harris 1950, Nord 1965). One measure of water use efficiency is the ratio of carbon-13, a naturally occurring stable isotope of carbon, to carbon-12, the most commonly occurring isotope of carbon. Carbon isotopes are differentially absorbed by plants, with ^{13}C being discriminated against. This discrimination decreases as the plant undergoes water stress, which allows more ^{13}C to be absorbed by plant tissues (Farquhar et al 1982). Since bitterbrush LS growth has been shown to be very sensitive to precipitation (Garrison 1953a, Shepherd 1971, Tueller and Tower 1979, Bilbrough 1990), there might be a relationship between carbon isotope ratios and bitterbrush growth rates.

No studies of water use efficiency or ^{13}C ratios have been conducted on bitterbrush.

METHODS

Study Sites

Selection

Study sites were chosen primarily to represent bitterbrush stands from a range of biotic and environmental conditions so that results might be useful to land managers operating in a variety of environments. In addition, sites were chosen to include plants protected from browsing pressure and to represent the effects of burning on bitterbrush in this portion of its range (Table 1).

Four of the original 18 sites on the Mount Haggin Wildlife Management Area (MHWMA) were selected for their representation of environmental extremes that Guenther (1989) correlated with bitterbrush growth and density (Table 2). Physical access to these sites ("Powerline", "Willow Creek", "Railroad Gulch", and "High Rye") and others is described in Appendix A.

Two sites were selected for their browse protection aspects. A big game exclosure was located on the Deerlodge district of the Deerlodge National Forest near Dry Cottonwood Creek ("deer exclosure"). A site near Maude "S" Canyon ("Butte"), on the outskirts of Butte, Montana was selected because of a lack of browsing impact by the local deer population.

Table 1. Browsing and burning effect classes for study sites.

Class	Sites
Continuous browsing	Powerline Willow Creek Railroad Gulch (browse) Railroad gulch (cage) 1990 High Rye Dry Cottonwood cattle exclosure (browse) Cattle exclosure (cage) 1990 Dry Cottonwood deer + cattle Steep Mountain burned Steep Mountain unburned
Continuous rest	Dry Cottonwood deer exclosure Butte (rest) Butte (clip) 1990
One season rest	Cattle exclosure (cage) 1991 Railroad Gulch (cage) 1991
One season clip	Butte (clip) 1991
Burn effect	Steep Mountain burned

The Dry Cottonwood site contained a 3-level exclosure system which allowed me to compare three levels of browsing activity. In addition to the deer exclosure, a livestock exclosure ("cattle exclosure", deer-only use) had also been constructed. Near the 2 exclosures, a bitterbrush stand that sustained cattle and big game browsing use ("deer + cattle") was also identified.

One site was selected to gauge the impacts of burning bitterbrush in southwest Montana. Two plots ("burned", "unburned") were situated on either side of the apparent burn line on Steep Mountain, 8 km northwest of Butte, Montana, on the Butte District of the Deerlodge National Forest.

Table 2. Relative levels for environmental and plant community characteristics of study sites¹ on the Mount Haggin Wildlife Management Area. These 4 of Guenther's (1989) 18 sites were chosen to represent extremes in factors he found to be correlated with bitterbrush density and growth characteristics.

Character	high	medium	low
elevation	2,4	3	1
bitterbrush cover	3	2	1,4
perennial grass cover	4	2	1,3
perennial forb cover	1,3	4	2
litter cover	3	2	1,4
bare ground	2	1,3,4	
soil organic matter	2	4	1,3

¹1=Powerline site (Guenther's site #2). 2=Willow Creek site (Guenther's site #5). 3=Railroad Gulch site (Guenther's site #10). 4=High Rye site (Guenther's site #14).

Description

The 10 study sites were located within a radius of 14.5 km of each other (Fig. 2). Long-term climatic records were available only from the Silver Bow County Airport (2 km south of Butte, MT), elevation 1,700 m. Precipitation there averages 250 to 350 mm per year with 49% received between April and July (NOAA 1991). Precipitation averages for the study period are presented in Appendix B, Table 14. Topographic characteristics of each site are presented in Table 3.

Habitat types of all sites except the Steep Mountain and High Rye sites were seral stages of Mueggler and

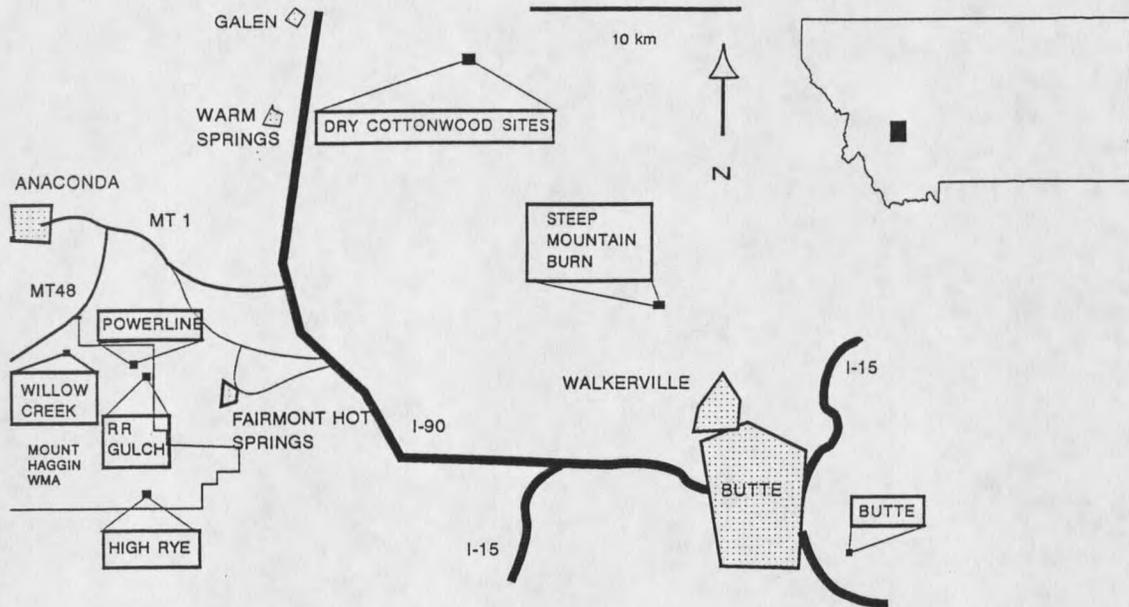


Fig. 2. Area map of study sites.

Table 3. Topographic characteristics of all study areas.

Site	Elevation (m)	Slope (%)	Aspect (degrees)
Butte	1730	26	234
Deer Exclosure	1830	12	225
Cattle Exclosure	1830	16	188
Deer + Cattle	1820	10	190
Burn	2010	21	220
Unburn	2010	24	180
Powerline ¹	1640	16	85
Willow Creek ¹	1780	31	110
Railroad Gulch ¹	1650	32	115
High Rye ¹	1940	38	120

¹From Guenther (1989).

Stewart's (1980) bitterbrush-bluebunch wheatgrass (Agropyron spicatum Pursh) habitat type. The dominant shrub on these sites was bitterbrush, but the understory vegetation appeared to have regressed from the described potential climax composition (Youtie et al 1988). The plant community on the Steep Mountain burn site was a bitterbrush-mountain big sagebrush (Artemisia tridentata Nutt. ssp. vaseyana [Rydb.] Beetle)-bluebunch wheatgrass association intermediate to the big sagebrush/bluebunch wheatgrass and bitterbrush/bluebunch wheatgrass habitat types of Mueggler and Stewart (1980). The plant community on the High Rye site corresponded to their bitterbrush-rough fescue (Festuca scabrella Torrey ex Hook.) habitat type. Site descriptions follow below.

Butte site. This site is located at the edge of Butte, Mt. on or near old mining claims and a city park. A housing subdivision is nearby, and a railroad grade is immediately upslope from the site. I found no evidence of browsing on these plants, although local residents complained of deer damage to their ornamental shrubs. The plant community consisted of bitterbrush, spotted knapweed (Centaurea maculosa Lam.), and scattered squaw currant (Ribes cereum Dougl.) and rose (Rosa woodsii Lindl.).

Dry Cottonwood Sites. This area is part of a big game winter range and cattle grazing allotment on the Deerlodge District of the Deerlodge National Forest. A three-level exclosure system is in place at this site for examining vegetation use by livestock and big game. A 0.4 ha big game exclosure ("deer exclosure") with a 2.4 m woven wire fence and a 0.4 ha livestock exclosure ("cattle exclosure") with a 3-strand barbed wire fence were constructed in approximately 1961. An additional site with big game and cattle use was chosen slightly downhill from the 2 exclosures.

There was scattered overstory of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) throughout all 3 plots. Understory vegetation consisted of a variety of species, with a high number of native perennial forbs. The area was in 1 pasture of a 4-pasture rotation cattle grazing system. Grazing was planned for sequential 1-month grazing periods for 3 out of 4 years with rest during the growing season every fourth year.

Steep Mountain Site. This site is located on the south flank of Steep Mountain. Precipitation on the site averages 400 to 450 mm per year (Ross and Hunter 1976). The area is part of a cattle-grazing allotment carrying 125 cattle for 1 to 2 months each summer in a 4-pasture rotation system (with growing season rest every fourth year) on the Butte Ranger District of the Deerlodge National Forest. The area is also winter range for mule deer and elk.

A prescribed burn was planned to "kill sagebrush and enhance grass and forb production for livestock and wildlife" (USDA 1981). Bitterbrush was to be left unburned due to its perceived high forage value for big game. The site was rested from livestock use in 1981 to increase fuel loads and was burned on November 3, 1981. Weather conditions at ignition were 37% relative humidity, air temperature of 11°C and 17-29 m/sec south wind. Soil moisture was not recorded. Several areas of bitterbrush were burned in the fire. The pasture was rested from livestock use until September 15 of the following year.

The burned and unburned plots were approximately 6 m on both sides of the apparent burn line on areas of nearly identical slope, aspect, and parent material.

Mount Haggin Wildlife Management Area Sites. The Powerline site is on a slope 50 m above a perennial stream on the northeast edge of the MHWMA big game winter range. The plant community consists of bitterbrush and spotted knapweed.

The Willow Creek site is near the top of a grassy ridge 150 m above Willow Creek. This site supports a relatively high amount of basin wild rye (Elymus cinereus Scribn. & Merr.), along with other perennial grasses and bitterbrush. This area is used as winter range by mule deer, elk, and moose.

The Railroad Gulch site is also in the deer and elk

winter range. This site occupies a mid-slope position 30 m above an intermittent stream. The plant community consists of bitterbrush and spotted knapweed.

The High Rye site is 1500 m higher in elevation than the other MHWMA sites and appears to receive the greatest snowpack. Guenther (1989) found the lowest amount of big game use at this site, although I found a herd of 250 elk bedded on the site in February 1991. It is near the top of a Douglas-fir-capped ridge 250 m above a perennial stream and near high meadows. The plant community on the site consists mostly of bitterbrush and rough fescue.

Livestock had access to the pastures containing the Powerline, Willow Creek and Railroad Gulch sites for a short time in the spring and fall of each year as cattle drifted through to other grazing areas (Michael R. Frisina, pers. comm.). The study sites received insignificant levels of livestock use. The High Rye pasture was part of a rotation grazing system (Hormay 1970) for about 200 cow-calf pairs and was intermittently grazed or rested in June or the fall.

Procedures

Study Plots

Study plots were selected to typify their communities for factors such as aspect, slope, soil type, bitterbrush density, and understory-overstory distribution. Five, 15-m

transect lines in each study site were placed perpendicular to the slope at 3-m intervals down the slope, comprising a study plot of 15 X 12 m (Guenther 1989). On the MHWMA sites I used Guenther's plots and transect lines.

Canopy Cover

Plant canopy cover was measured along these 5 transect lines in each study plot. Grass and forb canopy were estimated by species with a 2 X 5 dm quadrat and 6 canopy cover classes after Daubenmire (1959), with 10 quadrats per line. Litter, bare ground, and rock cover were also estimated for each quadrat. Shrub canopy cover was measured by the line intercept method (Canfield 1941). Live and dead shrub cover were recorded by species, with cover discontinuities greater than 8 cm recorded as changes in cover. Tree overstory cover was also estimated along these line intercept transects. This plant community information was collected in September of each year, after most annual growth had ended.

Density

Density of shrub species was measured in belt transects 2 m wide centered on the 5 transect lines (Guenther 1989). Live and dead plants rooted within the belts were recorded by species in August.

Plant Volume

Bitterbrush plant volumes were estimated each year from measurements of canopy thickness (maximum minus minimum height of canopy), length of major axis, length of minor axis perpendicular to the major axis, and calculation of ellipsoid volume. Live and dead canopy were recorded in August.

Bitterbrush Growth

For this paper, a bitterbrush "plant" is defined as a single stem or group of stems that appeared to have had a single point of origin. "Leaf cluster" refers to a bud which had produced a group of leaves and which had not elongated (less than 7 mm in length). "Long shoot" (LS) refers to a bud structure that had elongated (more than 7 mm in length) in the current growing season, and consisted of a stem and attached leaf clusters. "Flower" refers to a bud which had produced a flower. Leaf clusters or LS sometimes grew from buds adjacent to a flower bud and were tabulated separately. Flowers grew only on 1 year old or older stems, often on "short shoots" (SS), which had not elongated.

Ten bitterbrush plants rooted within 1 m of the transect lines were randomly selected on each plot for growth and reproduction measurements. Four branches were randomly chosen on each plant using a frame with 10-cm grids placed on top of the plant. Digits from a random number table identified grid intersections. The closest live

branch to a plumb line dropped through the grid intersection was marked with a numbered metal tag wired loosely to the branch. I deviated from totally random selection when I had the opportunity to use plants and branches previously marked by Guenther (1989). In those instances (at most 3 plants per site and 1 branch per plant), I incorporated Guenther's tagged branches into this study.

On each marked branch, age and length of each stem segment, number of flowers, leaf clusters, and LS, length of LS, and number of seeds produced were measured. Apical bud status of each terminal stem segment was recorded as browsed (within the past year), unbrowsed, or dead. Seeds were collected from each producing branch and were labelled as to apical bud status and number of seeds per flower: browsed, unbrowsed, or dead; single or double. Flowers were counted in early July, seeds were counted and collected in early August, and leaf clusters and LS were counted and measured in early September.

I compared measurements only from twig segments 3 years old or less, as little bud activity occurred on older twigs. Twig age was readily ascertained by examining annual growth scars after an initial trial of comparing growth scars with growth rings.

In 1991, twig segments on tagged branches had aged 1 year, so tags were moved to the terminal 3 year old segment on each original branch. Some branches, however, appeared

completely dead in July 1991. Tags from these branches were moved to nearby branches in a similar position on the plant. Where the whole plant was dead, the nearest plant along the transect line was tagged and measured as described previously.

Plant Age

Bitterbrush plant ages were determined by examining growth rings from basal stem segments (Nord 1965, Lonner 1972) cut from all plants in 1 X 12 m belt transects on either side of each study plot (Guenther 1989). Stand ages for the Dry Cottonwood deer and cattle exclosures were estimated from plants cut from a belt transect 1 X 24 m long located between the 2 exclosures. From 8 to 18 plants at each site were sampled in this manner. Stand ages for the MHWMA sites were taken from Guenther (1989), with 2 years added for time elapsed since his measurements.

Layering Frequency

I estimated bitterbrush layering frequency by counting the number of obviously layered branches. This proved to be difficult with sprawling plants, and imprecise with most plants due to the difficulty of determining when a plant had originated by layering or when the old stem had been covered with litter and soil.

Browsing Level

Terminal twig segments on each marked branch were observed for browsing use during the previous season. Due to Guenther's finding of high correlation between number of LS browsed and length of LS removed, I used the quicker measurement of counting browsed and unbrowsed twigs. Browsing level was estimated by dividing the number of browsed twigs by the number of terminal twigs on each branch. All branches were considered, regardless of availability to browsers, to determine plant response to removal of a percentage of all annual growth. This was the method employed by researchers who have expressed recommended use levels (Hormay 1943, Garrison 1953, Martinsen 1960, Lay 1965, Urness and Jensen 1983).

Abiotic Factors

Soil samples were obtained from a soil pit in each study plot except the burned plot. One sample was obtained for the burned and unburned pair of plots. The Montana State University Soil Test Laboratory performed organic matter determinations and total kjeldahl nitrogen analyses on all non-MHWMA soil samples. Mount Haggin Wildlife Management Area site information was derived from Guenther (1989). I determined texture (hydrometer method) and pH (with a 1:2 soil:water mixture on a Corning model 7 pH meter) for the samples.

Topographic information was recorded at each site.

Aspect was determined by taking a compass bearing from the major slope. Slope was measured with a clinometer. Elevation was determined from USGS topographic maps of each area.

Protein and Leaf:Stem Analysis

Long shoot material was collected from 10 plants in and around the study plots (except for the big-game exclosure, to avoid affecting the protected plants) for crude protein analysis and to determine leaf-to-stem ratios. Material was collected just before or at time of seed set in 1990 and 1991. This was estimated to be the period of maximum soluble carbohydrate drawdown for bitterbrush plants (Fig. 1, Menke and Trlica 1981). Material was also collected in February, when mule deer were concentrated on these sites. Plant material was oven-dried at 60°C for 48 hours. Leaves were separated from LS and weighed separately to determine leaf-to-leader ratios. Leaves and LS were then ground to approximately 1 mm diameter in a grinder (Janke & Kunkel kg, type A10). Pairs of samples were aggregated for dry matter and crude protein (kjeldahl nitrogen) analyses at the Oscar Thomas Nutrition Laboratory of the Montana State University's Department of Animal and Range Sciences.

All leaf and LS material was collected from the marked branches on each of 2 randomly selected plants at each site (except the Dry Cottonwood deer exclosure and High Rye sites) for comparison of total weights. Long shoot twigs

and leaves were separated as described above. Branch leaf clusters were separated from the branch. This current annual growth was then oven dried and weighed as described previously. Percent dry matter estimates were based on determinations made previously on similar material analyzed for protein. Weight ratios on a percent dry matter basis were calculated on the dried material. These ratios were averaged between the 2 plants from each site and were presented as site averages.

Carbon-13 Analysis

Six samples of summer 1990 leaf material were ground to 0.5 mm in a Wiley mill for carbon isotope concentration analysis (Toft et al 1989) at the Stable Isotope Ratio Facility for Environmental Research (Salt Lake City, Ut.). Three samples each were analyzed from the Dry Cottonwood deer enclosure and deer + cattle plot.

Seed Viability

Collected seeds were tested for percent germination and percent viability. Seeds from 1990 were stored in paper bags at room temperature (10-30°C) with the papery husks intact from August 1990 until May 1991. I removed the husks by rubbing the seeds between my fingers until the husks tore and fell away. The seeds were then placed in disposable petri dishes on a layer of Whatman #2 filter paper in preparation for a germination test (Young and Evans 1976).

The filter paper was moistened with tap water and the dishes were stacked on trays for storage in stratification and germination chambers in Montana State University's Plant Growth Center. The trays of seeds were cold-stratified at 2°C for 14 days, then moved into a germination chamber (Percival Mfg. Co., Boone, Iowa, model PGW-108) for dark incubation at 15°C for 4 weeks. Dishes were examined for germination weekly and were remoistened as needed. Seeds were considered germinated with radicle extension of 5 mm. After a four-week germination period, seeds were returned to the stratification room.

Seeds collected in 1991 were prepared similarly except that 3 layers of trimmed paper towel replaced the filter paper, which had dried out quickly. Since germination was poor for the 1990 seeds, a different process was attempted in August, 1991. AOSA (1985) prescribed a 24 hour soak and discard of water prior to a 4-week stratification period.

At the end of the stratification period, some of the 1990 seeds were still germinating, so all 1990 samples were rinsed with water and incubated alongside the 1991 seeds in September 1991. All seeds were placed in the same growth chamber as before for a 4-week dark incubation at 15°C. At 4 weeks, germination was still proceeding, so seeds were moved to a growth chamber (Hoffman Mfg. Co., Albany, OR, model SG30 germinator) at the Montana State Seed Test Laboratory for dark incubation at 15°C. Germination dates

(by week) were recorded for all dishes. Following the 8+ week germination period, remaining ungerminated seeds were dissected and recorded as live or dead (Nord 1956). These results were tabulated as number of seeds tested and percent live (Appendix B, Table 15).

I determined the effect of the apparent seed coat germination inhibitor in 2 ways. Embryos of some of the ungerminated seeds were excised and placed on moistened paper towel in plastic petri dishes at room temperature and ambient light (Nord 1956). Other ungerminated seeds were irrigated with fresh tap water every day (Meyer and Monsen 1989), under the same conditions as the excised embryos.

Additional seed samples from 1990 and 1991 were tested for viability at the State Seed Test Lab with a tetrazolium test in October 1991. I used the procedure of AOSA (1985) with a 24-hour to 1 week presoak in tap water, removal of the embryo to soak for 4 hours in a 1% unbuffered tetrazolium solution, and observation of stain absorption. There was good agreement between this technique and the excision technique of Nord (1956) in identifying live embryos.

Browsing Treatments

The MHWMA Railroad Gulch and Dry Cottonwood cattle exclosure (deer-only use) sites were selected to receive a plant protection treatment for the winter 1990-1991 browsing season. Twenty bitterbrush plants were randomly selected

within each study plot, instead of 10 plants as on the other plots. All 20 plants were measured in 1990, but 10 plants on each site were selected to be caged for the winter of 1990-1991. These 10 plants were covered with individual exclosures constructed of several types of wire mesh to discourage elk or deer use. These exclosures were erected in October 1990 and removed in June 1991. Plants were measured on the same schedule as in 1990.

Twenty plants at the Butte site were similarly selected and measured in 1990. In February 1991, 10 of these plants were randomly selected to receive a severe clipping treatment. All current year LS were removed by breaking and tearing by finger (leaving at most 1 cm of stem) to simulate a 100% browsing by deer on plants that had rarely, if ever, been browsed. Plants were measured on the same schedule as in 1990.

Data Treatment

Initial measurements of twig length, flowers, leaf clusters, seed, and LS numbers, LS length, and plant dimensions (Appendix B, Table 16) were used to determine averages, densities, volumes, and ratios. Data were summarized across all 4 branches per plant to create a branch average (hereafter termed a "plant average") for each datum category. Site averages resulted from averaging the 10 plant averages for each of the 10 study plots (100 plants).

Browsing level analyses were conducted by comparing the number of browsed and unbrowsed twigs on each plant. Only terminal twigs (those with no subsequent younger twigs) were used to determine browsing level. Unbrowsed twigs with obviously dead terminal buds were not used in browsing level comparisons. Browsed and unbrowsed twigs on a plant were each pooled across branches for comparison of browsing response on a plant level. These plant averages were then combined to create site averages (10 sites).

Winter "leader" crude protein levels were calculated with a weighted average of winter leaf and LS protein levels. The percentage of leaves and stems (from leaf:stem ratios, discussed earlier) was multiplied by the crude protein content of leaves and stems to give a "whole leader" protein estimate for comparison with other studies (Dietz et al 1962, Welch et al 1983).

Canopy cover data were summed for each of the 5 transect lines in each study plot to create site averages. Line intercept data were converted to percent canopy cover by dividing line length of each species by total line length (15 m). Canopy cover was summarized mostly by life form to enable comparison with Guenther (1989) and because individual species were too numerous to list (Appendix B, Table 17). Only live bitterbrush canopy cover is presented, although Guenther (1989) presented total (both live and dead) bitterbrush canopy cover.

Absolute plant species differences were of little interest between all sites, but were of concern on the Steep Mountain burn area. On this site, herbaceous species comprised only a few percent of total canopy cover, but they could be valuable indicators of change by their mere presence. Therefore, species data were presented as frequency of occurrence, rather than as percent canopy cover. Frequency was calculated by averaging the number of frames in which each species occurred for each transect line. Line averages were then averaged to create plot averages.

Shrub density was calculated per transect by dividing the number of plants found by the area observed in each belt transect (2 m wide by 15 m long). Results for the five transects per plot were averaged to create a site average and converted to plants per hectare.

Statistical Analyses

Occurrence of unequal variances for some comparisons (such as flower or seed numbers and species occurrence) required use of nonparametric statistical tests (Sokal and Rohlf 1981:429). Bilbrough (1990) also found unequal variances in her study of bitterbrush bud fates and relied on nonparametric analyses. Such tests were also used for comparisons with small sample sizes (such as plant densities or canopy cover, where $n=5$) (Snedecor and Cochran 1989:44). To maintain uniformity, most comparisons were therefore

conducted with nonparametric tests (Table 4). Several of these nonparametric tests utilized rankings and compared medians rather than means (Snedecor and Cochran 1989:135). Results are presented as means, however, for ease of comparison with published literature not using these statistical procedures. Differences were considered significant at $P \leq 0.05$.

Nonparametric tests included a Wilcoxon signed-rank

Table 4. Statistical tests, applications, and resulting test statistic used for comparisons in this study. Median test from Dixon and Massey (1969), others from Lund (1991). Results in tables and figures are presented as means. Differences were considered significant at $P \leq 0.05$).

Test ¹	Application	Parametric	Statistic
median	species frequency flower & seed numbers	No	χ^2
NPGR ²	species frequency canopy cover site-site bud densities growth measurements shrub densities protein carbon isotope ratio	No	U
NPPA ²	volume year-year seed success year-year flower number year-year canopy cover year-year	No	T
AVMF	site-year-treatment interactions LSD, mean separation	Yes	F t
MREG	correlation, regression	Yes	r

¹median=median test (Chi-square). NPGR=Mann-Whitney rank-sum test. NPPA=Wilcoxon signed-rank test. AVMF=multi-factorial analysis of variance. MREG=simple linear regression.

²These programs use a normal approximation for estimation of P-values.

test (Snedecor and Cochran 1989:140) for comparison of paired measures (such as the same plants between years), a Mann-Whitney rank-sum test (Snedecor and Cochran 1989:142) for comparison of group means, and a median (Chi-square) test (Dixon and Massey 1969:350) for comparisons with unequal numbers of observed values (such as species presence or seed production).

Interactions between years, sites, and treatments were analyzed with a multi-factor analysis of variance (Snedecor and Cochran 1989:297). This test assumed equal variances, so it was not relied on to determine main effects.

Relationships between pairs of data categories were compared with a simple linear regression or correlation test (Snedecor and Cochran 1989:173). Correlation was used when a dependence relationship could not be assumed.

Comparisons between sites were based on least significant difference (LSD) (Snedecor and Cochran 1989:235) at $P \leq 0.05$. Least significant differences were calculated as part of the analysis of variance for pairs of means, such as site-to-site or year-to-year comparisons.

Specific statistical tests were the NPGR (Mann-Whitney), NPPA (Wilcoxon signed-rank), AVMF (multi-factorial analysis of variance), and MREG (simple linear regression and correlation) programs of the MSUSTAT statistical program (Lund 1991), and the median test procedure described by Dixon and Massey (1969:350). The NPGR and NPPA programs

utilized a normal approximation for calculating P values (Dixon and Massey 1969:348, Snedecor and Cochran 1989:141).

The study plots represent only 1 observation point and are not replicated in this study. For some comparisons, each of the 5 transect lines in a plot served as pseudoreplicates. This lack of true replication reduces the power of inference possible from this study. Additional study plots would have been difficult to obtain due to my desire to continue study on previously established plots (Guenther 1989) and due to the few sites (such as exclosures) on the geographic edge of bitterbrush's range.

RESULTS AND DISCUSSION

Browsing Level

Average browsing levels for bitterbrush sites in this study ranged from 20 to 60% removal of all current annual long shoot (LS) growth (Table 5). These levels were seemingly well within the levels recommended by other researchers for long-term health and maintenance of the stands (Hormay 1943, Garrison 1953b, Steinhoff 1959,

Table 5. Browsing level (percent) for study sites for 1989, 1990, and 1991 based on number of twigs removed. Browsing level for 1989 was based on twigs available to browsers. Browsing level for 1990 and 1991 was based on all terminal twigs on sampled branches, regardless of availability. The Butte and Dry Cottonwood deer exclosure sites were unbrowsed.

Site	1989 ¹	1990	sd	1991	sd
BUTTE		0a ² B ³	-	0aD	-
DEER EXCLOSURE		0aB	-	0aD	-
CATTLE EXCLOSURE		45aA	15.2	39aABC	29.0
DEER + CATTLE		55aA	18.9	54aBC	24.1
BURN		48aA	18.6	50aBC	33.7
UNBURN		51aA	21.5	61aC	32.0
POWERLINE	97	51aA	15.4	40aABC	22.8
WILLOW CREEK	92	52aA	13.3	23bA	11.7
RR GULCH	100	53aA	20.5	37aABC	28.1
HIGH RYE	74	60aA	12.4	30bAB	31.3

¹From Guenther (1989).

²Row entries with similar lower case letters (ab) are not significantly different (Wilcoxon test, P>0.05).

³Column entries with similar upper case letters (ABCD) are not significantly different (LSD, P>0.05).

Martinsen 1960, Lay 1965, Shepherd 1971). However, these browsing levels were far below those reported by Guenther (1989), often for the same branches (Table 5).

One reason for this difference may lie in the techniques employed in choosing branches. Guenther chose twigs that were on the outermost portions of each plant and held a minimum of 4 LS, a technique employed in estimating relative use levels (Cole 1959, Patton and Hall 1966). In contrast, I randomly chose branches from throughout the plant; some were deep within the canopy and some had no LS in 2 years of observation. Although I observed browsed LS within all levels of canopy, and plants on all study plots were browsed (except those plots chosen for no browsing use), fewer of my branches may have been available to browsing deer or elk. This may have resulted in lower estimates of browsing pressure. However, this technique allows more accurate comparison with the findings of researchers who have made browsing level recommendations based on clipping portions of all current annual growth (Hormay 1943, Garrison 1953b, Steinhoff 1959, Martinsen 1960, Lay 1965, Shepherd 1971).

The Cole (1959) technique has been criticized for its shortcomings in correlating browsing levels to animal populations (Mackie and Lonner 1977). Based on results from my study, current browsing levels should not be detrimental to the plants on these study sites and do not require

manipulation through control of herbivore populations (Guenther 1979) to preserve these bitterbrush stands.

Browsing levels for the Mount Haggin Wildlife Management Area (MHWMA) sites (Table 5) were generally lower in 1991 than 1990 ($P < 0.001$). This was expected as big game animals moved onto the MHWMA winter range later in the season in 1991 (Michael R. Frisina, pers. comm.). This delay in use may have increased the disparity between Guenther's browse level measurements and mine because animals may not have been as concentrated or present for as long a time on the winter ranges during the years that I observed those sites.

Browsing Effects

Branch length represents the sum of each year's growth minus the cumulative reduction by browsing. In addition to the direct effect of removing twig material, browsing might also affect length by changing the potential for growth. Growth potential might be affected by the ability of the whole plant to grow, or by the number or type of buds available, either for the whole plant or for individual twigs.

Several researchers have attributed low growth rates to whole-plant effects on "vigor" (Hormay 1943, Garrison 1953b) or carbohydrate reserves (Menke and Trlica 1983) and have recommended moderate browse levels or specific seasons of

use. Tueller and Tower (1979) reported a lower growth rate in rested or lightly used plants than in those that were heavily browsed, terming this a "stagnation" effect.

Bilbrough (1990) found that clipped bitterbrush was able to mobilize inactive buds for elongation, and hypothesized that this would eventually alter flower and LS ratios. Although I could detect differences in bud density (buds per unit length of stem) between sites and treatments, and could construct bud frequencies from this information, I could not determine whether changes in frequency of flowers, leaf clusters, or LS were due to variable densities before browsing or to bud differentiation after browsing.

Therefore I will restrict my discussion to bud densities in the following sections.

Browsing Effects on Bud Density

Total bud density, expressed as the sum of the number of flowers, leaf clusters, and LS per unit length of stem, was similar for browsed and unbrowsed sites ($P > 0.10$) (Fig. 3). Total bud density differed, however, at the twig level ($P < 0.01$) when browsed and unbrowsed twigs were pooled for each site (Fig. 3), showing an effect of browsing on total bud production.

Browsed plants had a lower flower bud density ($P < 0.001$) and higher LS bud density ($P < 0.01$) than unbrowsed plants (Fig. 3). However, at the twig level (Fig. 3), flower or LS densities were similar ($P > 0.56$) between browsed and

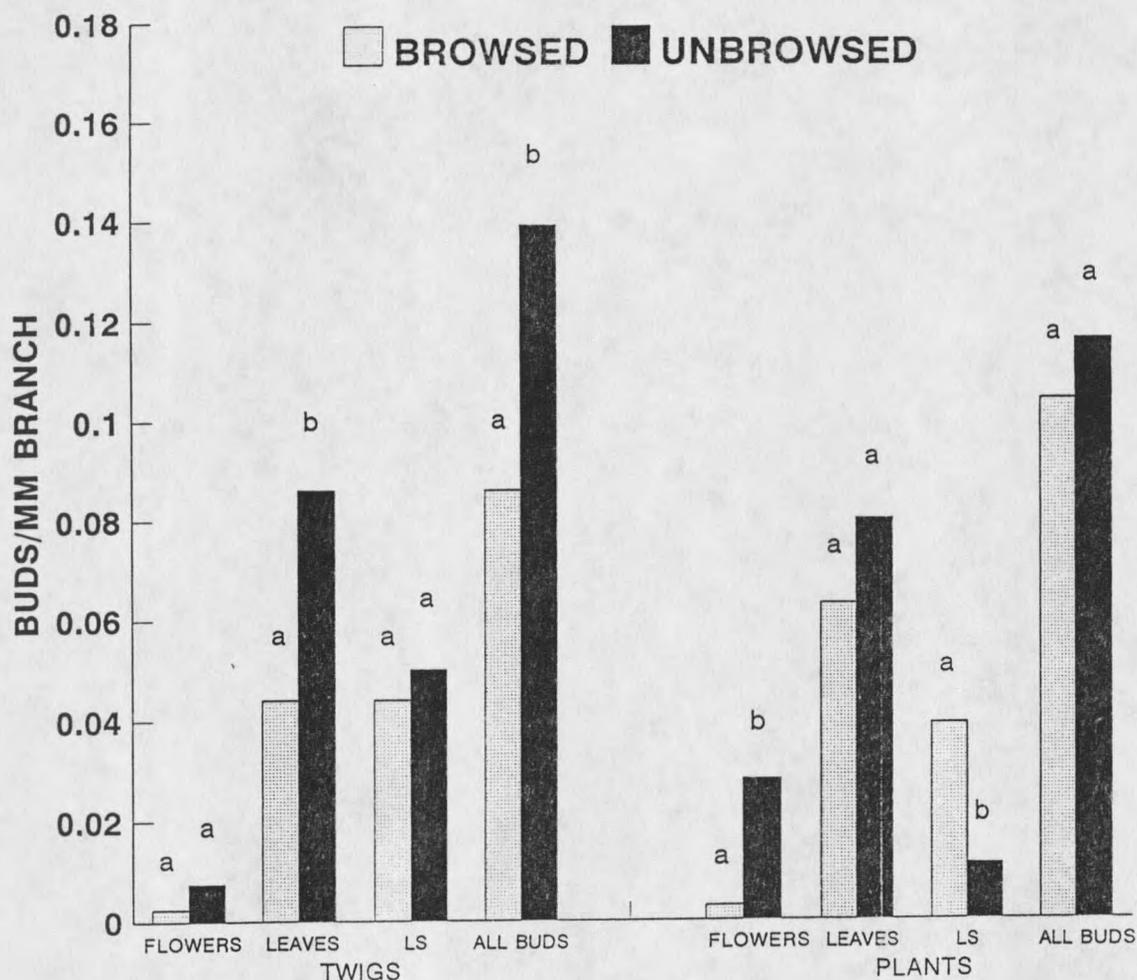


Fig. 3. Average number of buds per mm of branch (density) by type of bud structure (flowers, leaves, long shoots). Comparisons are between browsed and unbrowsed twigs on browsed plants (n=8), and between plant averages from browsed (n=7) and unbrowsed (n=2) sites. Pairs of bars with similar letters are not different (Mann-Whitney test, $P > 0.05$). Flower and long shoot bud densities on browsed plants differ from those on unbrowsed plants while they do not differ on twigs within browsed plants, indicating a whole-plant response to browsing.

unbrowsed twigs pooled for all browsed sites. Unbrowsed twigs from browsed plants had lower flower ($P < 0.01$) and higher LS ($P < 0.001$) bud densities than twigs from unbrowsed plants. This suggests that browsing affects both browsed and unbrowsed twigs on browsed plants, which is a plant-level response. Further, density of any of the 3 types of buds did not appear to depend on actual level of browsing per plant (0-100% of terminal twigs on sampled branches on plants exposed to grazing) ($r < 0.07$, $P > 0.22$). This suggests that any degree of browsing affects flower and LS production on the whole branch, and probably on the whole plant.

Root response may be related to a whole plant response to browsing. Cook and Stoddart (1960) found that sagebrush (*Artemisia tridentata*) branches clipped of most or all leaf buds died, perhaps because they could not supply enough of their own food to survive (Watson and Casper 1984). Root supplies of water and nutrients to clipped branches may have diminished as well, as Cook and Stoddart (1960) found a direct link between discrete portions of sagebrush canopy and discrete portions of the root mass. Carbohydrate stores could also be involved, as young stems (those most likely to be removed by browsing) experience the largest decline in carbohydrate levels during growth periods (McConnell and Garrison 1966). Since local carbohydrate sources contribute most to growing points (Watson and Casper 1984, Richards and Caldwell 1985), loss of young stems to browsing may

contribute to competition among remaining buds for scarce food supplies.

Loss of buds to clipping or browsing has been linked to changes in hormone levels (Maillette 1982) in silver birch, which might also affect root:shoot relationships. However, neither such hormonal effects nor discrete root-shoot interconnections have been studied for bitterbrush.

Leaf cluster bud density was 49% lower on browsed twigs ($P < 0.05$) compared with unbrowsed twigs (Fig. 3). This decrease did not appear between browsed and unbrowsed plants ($P > 0.61$) or between unbrowsed twigs from browsed plants and twigs from unbrowsed plants ($P > 0.80$), suggesting that this leaf bud response occurred only on browsed twigs. Possible mechanisms for this decline include increased mortality of leaf buds either by physiological effects or by higher leaf bud density at the distal (browsed) end of the twig. Physiological effects could include physical or chemical damage due to browsing or a change in resource allocation patterns within the plant to maintain flower and LS bud numbers at the expense of leaf bud numbers.

Treatment Effects on Bud Density

Total bud density did not differ between the protection treatments ($P > 0.30$), or between the clip treatments ($P > 0.70$) (Fig. 4). Similarly, bud densities for flowers, leaf clusters, or LS (Fig. 4) did not differ among protection treatments ($P > 0.11$) or the clipping treatment ($P > 0.38$).

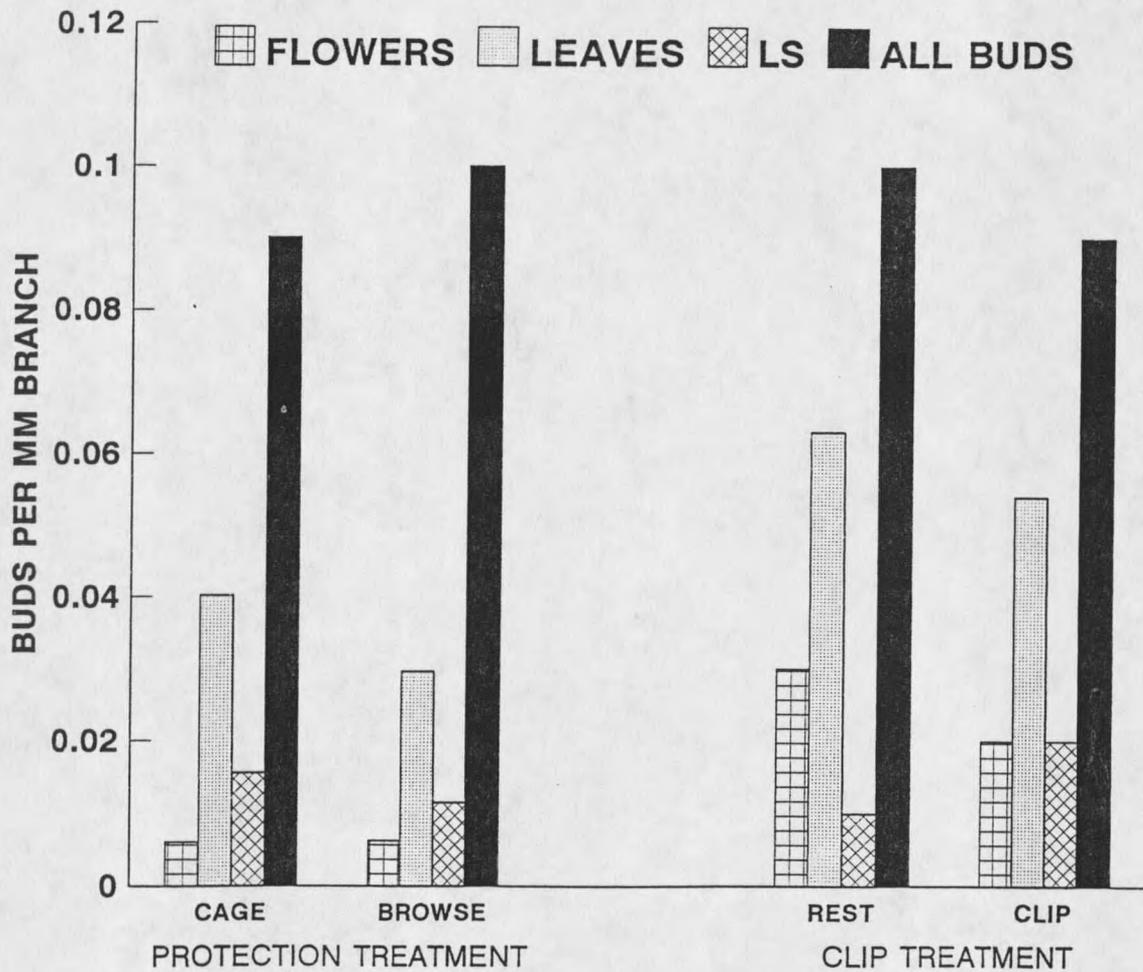


Fig. 4. Average number of buds per mm of branch (density) by type of structure (flowers, leaves, long shoots) for plants ($n=10$) at browse treatment sites in 1991. Caged plants were protected from browsing for 1 winter browsing season. Clipped plants had 90-100% of all current long shoots (LS) removed in February to simulate heavy browsing on otherwise unbrowsed plants. Bud densities did not differ between treatment pairs for any bud type (Mann-Whitney test, $P>0.05$).

These results are not consistent with previous reports. McNulty (1947), Ferguson and Medin (1983), and Bilbrough (1990) predicted more flowers on unbrowsed or protected plants; however, I found that neither 1 season of protection nor 1 season of clipping affected flower bud density.

Long shoot bud density was not affected by the treatments, either (Fig. 4). Tueller and Tower (1979) predicted that 1 year of rest from browsing would allow expression of maximum growth; I expected that a component of the predicted additional growth after protection would be more LS buds, but that apparently did not happen on these sites. However, Tueller and Tower's (1979) idea of stagnation may be applicable here, in that a residual effect of a plant's browsing or rest history may affect its degree or immediacy of response to browsing or rest.

Although browsing levels (Table 5) were the same for the 2 Steep Mountain plots ($P > 0.59$), flower bud density was lower on the burned plot (Table 6) than on the unburned plot ($P < 0.001$). Leaf cluster and LS densities were similar between the 2 plots ($P > 0.10$).

The Dry Cottonwood cattle exclosure plot had lower total bud densities than the unbrowsed deer exclosure plot ($P < 0.01$), whereas flower bud densities (Table 6) were lower ($P < 0.001$) and LS bud densities were higher ($P < 0.001$), just as with other browsed and unbrowsed comparisons.

Although browse levels (Table 5) were not significantly

different between the Dry Cottonwood deer-only (cattle exclosure) and deer + cattle plots ($P > 0.21$), there were differences in bud density (Table 6). Long shoot bud densities were lower on the deer-only plot than the deer + cattle plot ($P < 0.01$), but other bud densities did not differ ($P > 0.14$) between the two plots.

Browse Level Effects on Growth

Bitterbrush growth has many components. I measured old growth (3, 2, and 1 year old stem segments), long shoot (LS) growth (annual growth), leaf weights (leaf clusters), and plant volume. These are discussed separately.

Old growth. Total length of old growth twigs (total branch length) (Fig. 5) was considerably shorter on the browsed sites than on the unbrowsed sites ($P < 0.001$), reflecting the influence of browsing in modifying branch length. Accordingly, the Dry Cottonwood unbrowsed plot had longer branches than the deer-only plot ($P < 0.01$), whereas the deer + cattle plot had the shortest branches ($P < 0.05$) at this site.

Total branch length (Fig. 5) for the burned and unburned Steep Mountain plots did not differ ($P > 0.38$), which indicates that the combination of growth and browsing was similar between these plots for the previous 3 years.

Annual growth. The number of LS produced varied by site and year (Fig. 6), with fewer ($P < 0.05$) but longer ($P < 0.05$)

Table 6. Bud density (buds per 100 mm stem) for flowers, leaf clusters, and long shoots (LS) on all study sites in 1990 and 1991. The 2 unbrowsed study sites are at left.

Bud Type	Year	Butte	Deer Excl	Cattle Excl	Deer + Cattle	Burn	Unburn	Power Line	Willow Creek	RR Gulch	High Rye	Avg.
Flower	1990	7.5a ¹	6.9a	0.4a	0.7a	0.1a	2.9a	1.6a	3.5a	2.2a	5.0a	3.2X ³
	(sd)	0.4 F ²	0.7 EF	0.1 A	0.2 AB	0.3 A	0.2 BCD	0.2 ABC	0.2 CD	0.2 ABC	0.4 DE	2.5
Flower	1991	2.7b	2.5b	0.0a	0.7a	0.1a	1.1b	0.1a	0.3b	0.4b	0.1b	0.8W
	(sd)	0.2 C	0.3 C	0.0 A	0.1 AB	0.3 AB	0.1 B	0.0 AB	0.0 AB	0.1 AB	0.0 AB	1.0
Leaves	1990	10.7a	7.3a	8.1a	7.9a	10.3a	9.7a	8.9a	9.5a	10.0a	10.5a	9.4Z
	(sd)	0.3 C	0.2 A	0.2 ABC	0.2 AB	0.2 BC	0.2 ABC	0.4 ABC	0.6 ABC	0.3 BC	0.2 BC	1.1
Leaves	1991	6.3b	8.9a	6.7a	5.6b	4.1b	6.2b	8.2a	3.5b	8.6a	4.5b	6.3Y
	(sd)	0.4 ABC	0.4 C	0.2 ABC	0.2 AB	0.2 A	0.3 ABC	0.7 BC	0.2 A	0.3 BC	0.1 A	1.8
LS	1990	1.7a	1.1a	3.2a	6.1a	4.6a	3.2a	3.4a	3.1a	2.1a	3.0a	3.0X
	(sd)	0.1 AB	0.1 A	0.1 CD	0.2 E	0.3 D	0.2 CD	0.2 CD	0.2 BC	0.1 ABC	0.1 BC	1.4
LS	1991	1.0a	1.0a	2.4a	3.5b	2.3b	2.6a	4.7a	3.7a	3.3b	6.0b	3.1X
	(sd)	0.1 A	0.1 A	0.1 AB	0.1 BCD	0.2 AB	0.2 ABC	0.2 DE	0.1 CD	0.1 BC	0.2 E	1.5

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¹Site entries with similar letters (abcde) for year pairs are not significantly different (Wilcoxon test, P>0.05).

²Row entries with similar letters (ABCDE) are not significantly different (LSD, P>0.05).

³Column entries with similar letters (WXYZ) are not significantly different (LSD, P>0.05).

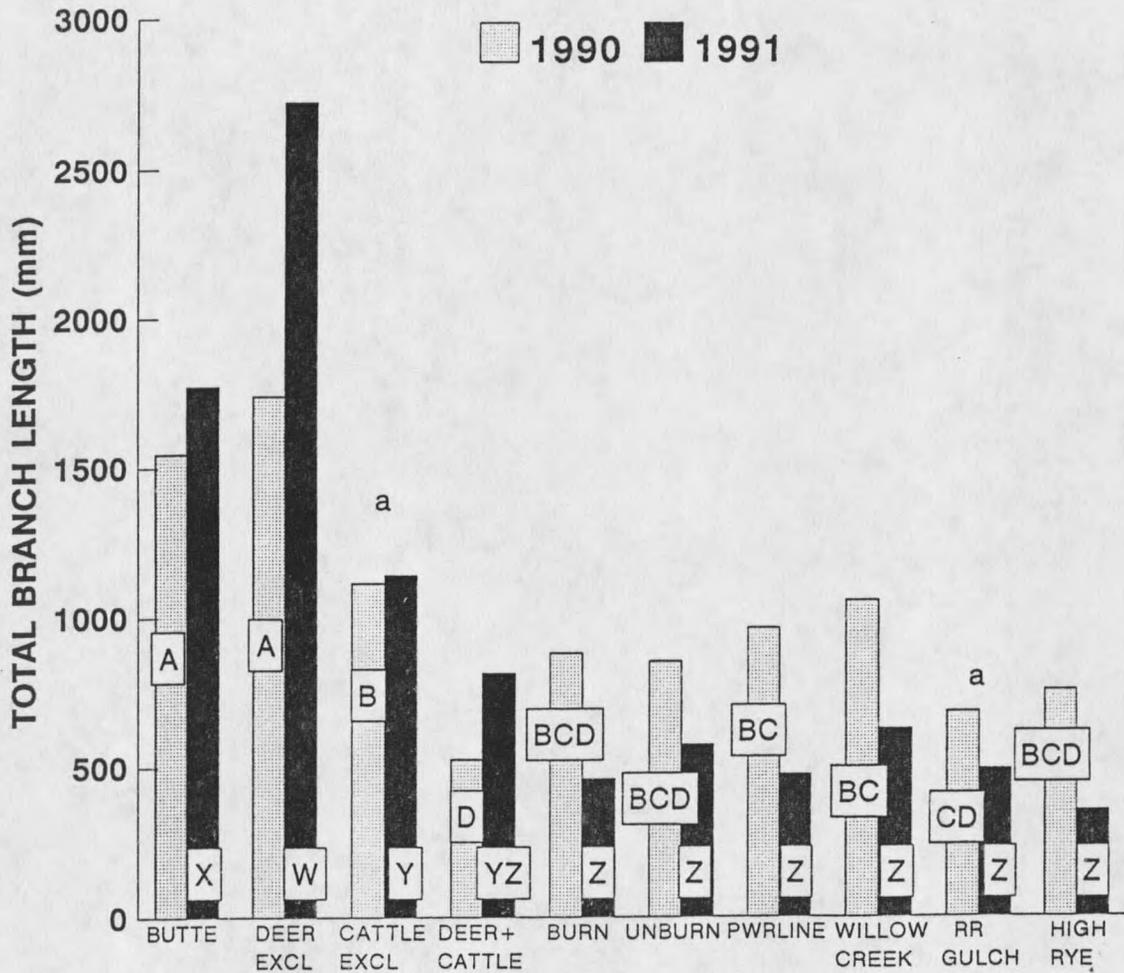


Fig. 5. Average total branch length (mm) of 1, 2, and 3 year old twig segments for plants ($n=10$) at all study sites. The 2 unbrowsed sites are at left. Site to site, within year differences (LSD, $P \leq 0.05$) are denoted by columns with unlike letters (ABCD=1990, WXYZ=1991). All sites showed year to year, within site differences (Wilcoxon test, $P < 0.05$) except those denoted by "a".

LS (Fig. 7) in 1991 than in 1990. However, the correlation between number and average LS length was not significant ($r = -.12$, $P > 0.60$). As discussed earlier (Fig. 3), LS bud density was highest on browsed plants ($P < 0.01$). However, LS bud numbers (Fig. 6) did not differ between browsed and

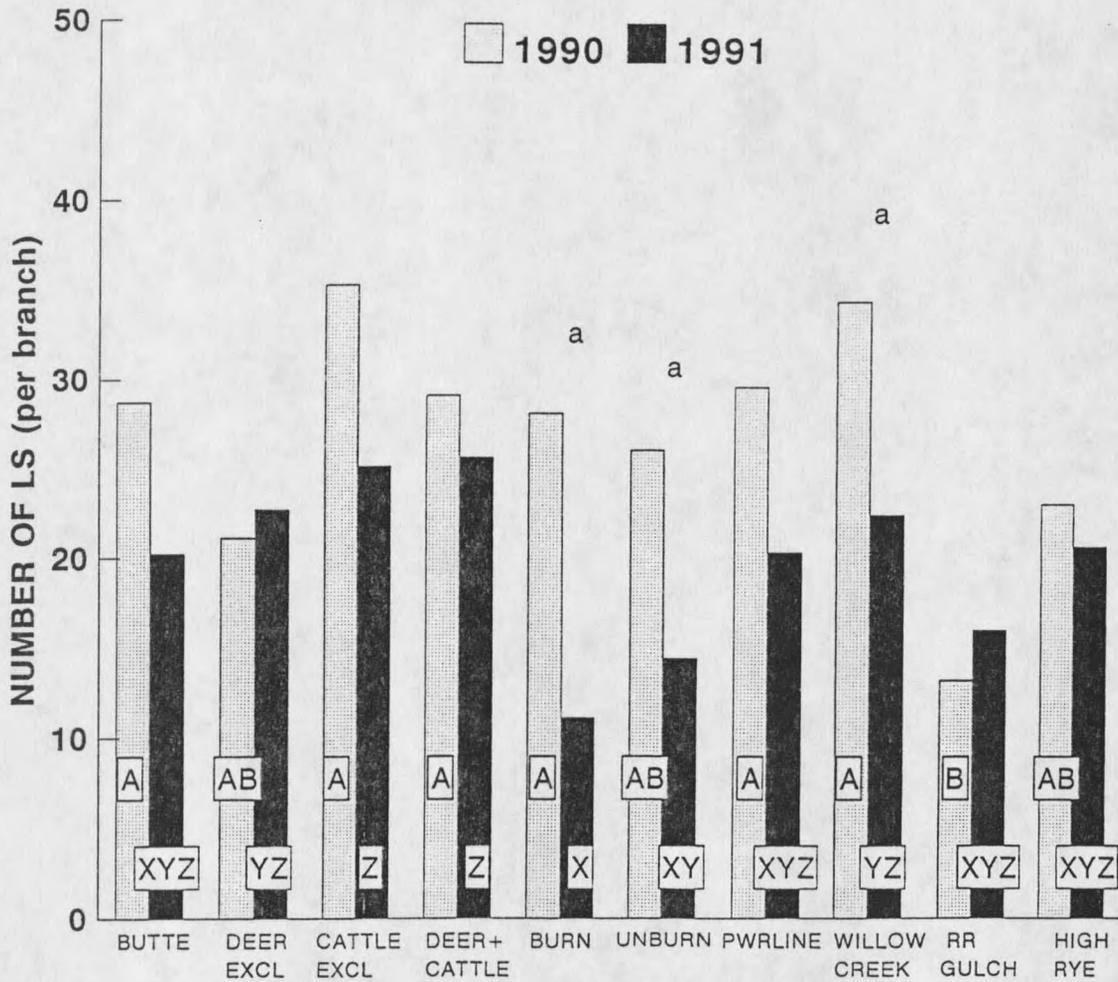


Fig. 6. Average number of long shoots (LS) per branch for plants ($n=10$) at all study sites. The 2 unbrowsed sites are at left. Site to site, within year differences (LSD, $P \leq 0.05$) are denoted by columns with unlike letters (AB=1990, XYZ=1991). Only those sites denoted by "a" showed a year to year, within site difference (Wilcoxon test, $P < 0.05$). Fewer LS were produced in 1991 than 1990 (Wilcoxon test, $P < 0.05$).

unbrowsed plants ($P > 0.89$) because of longer branches on unbrowsed plants than on browsed plants.

Annual LS growth (total LS length) (Fig. 8) was not significantly correlated to total branch length ($r < 0.45$, $P > 0.13$) across all sites. Although the sites with the

longest branches (unbrowsed) also had high LS growth, total LS growth was not significantly longer on unbrowsed than on browsed sites ($P>0.67$).

Long shoot length per unit length of branch varied

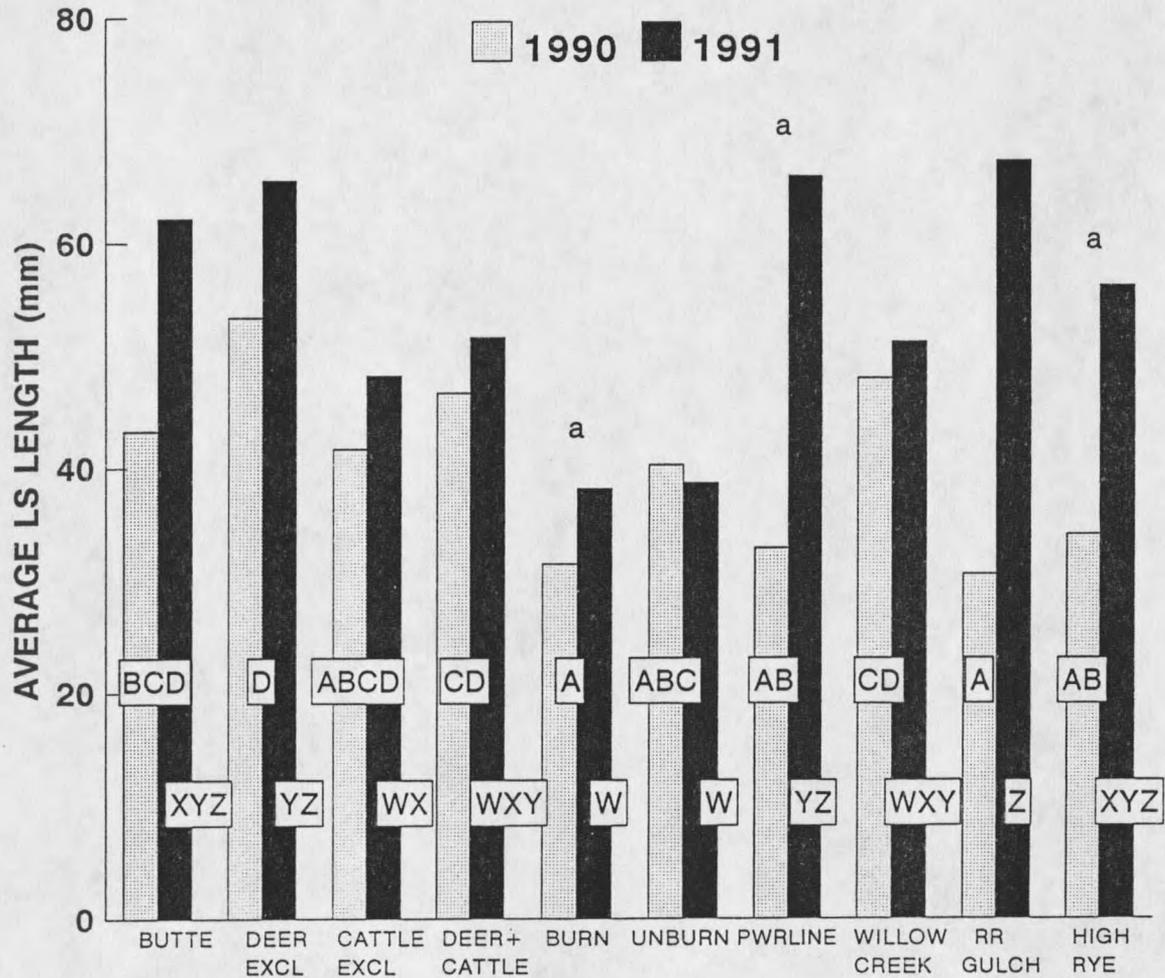


Fig. 7. Average ($n=10$) long shoot length (total long shoot length divided by number of long shoots) per branch for all study sites. The 2 unbrowsed sites are at left. Site to site, within year differences (LSD, $P\leq 0.05$) are denoted by columns with unlike letters (ABCD=1990, WXYZ=1991). Only those sites denoted by "a" showed a year to year, within site difference (Wilcoxon test, $P<0.05$). Average LS length was greater in 1990 than 1991 (Wilcoxon test, $P<0.05$).

between most sites and sometimes between years (Fig. 9). This growth rate appeared to increase on the MHWMA sites in 1991 although all other sites decreased. I found a significant year x group interaction ($P < 0.05$), but not a

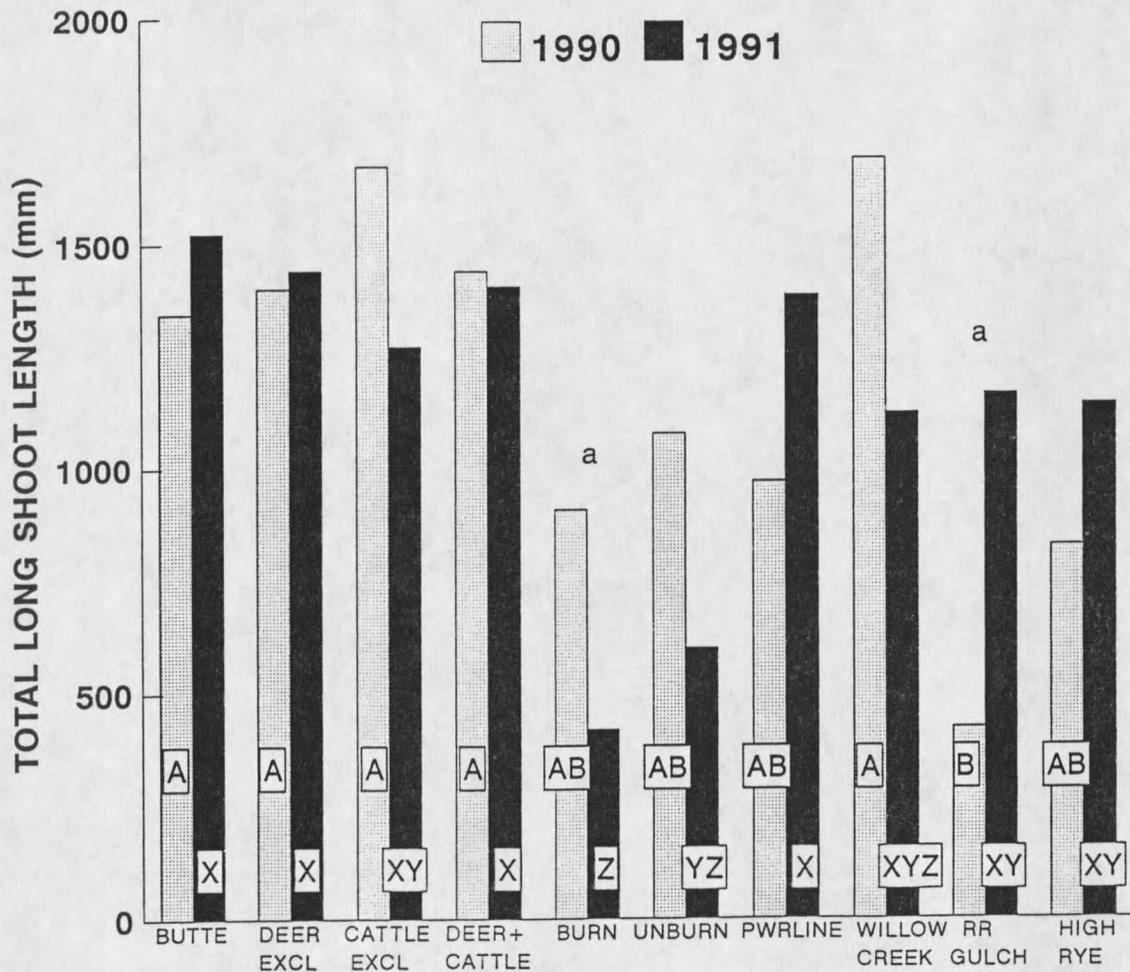


Fig. 8. Total long shoot (LS) length (mm) per branch ($n=10$) for 1990 and 1991 for all study sites. The 2 unbrowsed sites are at left. Site to site, within year differences (LSD, $P \leq 0.05$) are denoted by columns with unlike letters (AB=1990, XYZ=1991). Only those sites denoted by "a" showed a year to year, within site difference (Wilcoxon test, $P < 0.05$).

significant year or group difference ($P > 0.11$). The reason for this difference between sites and years is unknown.

At the Dry Cottonwood exclosure site, LS length per unit of stem (Fig. 9) was greater on the deer + cattle plot than the deer-only plot (cattle exclosure) ($P < 0.01$), and the deer-only plot tended to be greater than the unbrowsed plot ($P < 0.07$). This tendency supports Tueller and Tower's (1979) stagnation theory, which predicts relatively higher growth rates at relatively higher browsing levels. Reiner (1982) also reported that livestock grazing increased bitterbrush growth by reducing herbaceous competition during the growing season (see Plant Community, below).

Neither total LS length (Fig. 8) nor LS length per unit of branch (Fig. 9) differed between the burned and unburned plots ($P > 0.38$). Since both the growth rate and the browsing level (Table 5) were the same between plots, this suggests that browsers removed the same amount of LS material from each branch in each plot. There should have been more branches on the larger unburned plants, so browsers should have had more food in the unburned plot. However, I collected an inadequate number of samples to determine the degree of difference in total plant material removed from each plot.

The protection treatments on the Dry Cottonwood cattle exclosure and Railroad Gulch plots resulted in differing effects on total branch length and LS length per length of

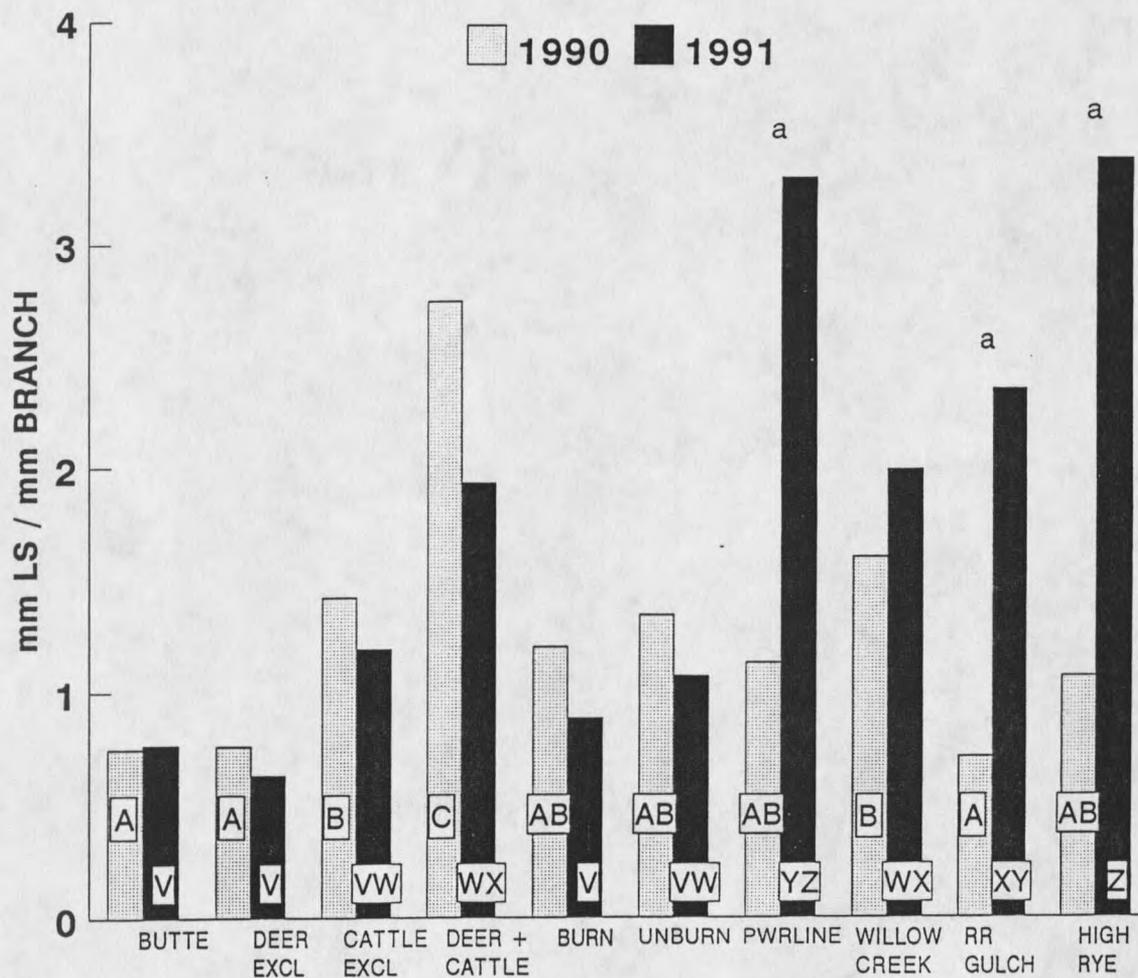


Fig. 9. Long shoot length per length of branch (mm/mm) ($n=10$) in 1990 and 1991 for all study sites. The 2 unbrowsed sites are at left. Site to site, within year differences (LSD, $P \leq 0.05$) are denoted by columns with unlike letters (ABC=1990, VWXYZ=1991). Only those sites denoted by "a" showed a year to year, within site difference (Wilcoxon test, $P < 0.05$).

branch (Fig. 10) between sites. Analysis of variance showed significant year x site ($P < 0.01$) and year x site x treatment ($P < 0.05$) interactions for LS length per length of branch.

Tueller and Tower (1979) had recommended 1 year of protection to allow maximum LS growth. That effect was not

apparent on these treatment plots. The clip treatment on the Butte plot resulted in no difference ($P>0.59$) in either total LS length or LS length per length of branch between clipped and unbrowsed plants (Fig. 10). Bitterbrush growth has been correlated with precipitation levels (Garrison 1953a, Tueller and Tower 1979), but that was probably not a factor between 1990 and 1991 growth levels. Precipitation for the 10 months preceding 1991 measurements was 1.0 cm below normal (Appendix B, Table 14).

Leaf weights. Long shoot leaf to stem weight ratios were similar between years ($P>0.28$) but showed some variation between sites (Table 7). These ratios reflect the amount of leaf and stem present and available on LS as a discrete unit to browsers and affect the nutrient content of each mouthful (see Protein, below). Figure 11 shows the weight relationships between twig leaf clusters, LS, and LS leaf clusters. From these results, about 72% of the branch leaf material was located on the LS. Adverse effects of summer and early fall browsing on bitterbrush vigor may be related to the ease with which much of a bitterbrush plant's photosynthetic material may be removed by browsing (Watson and Casper 1984). Martinson (1960) found that bitterbrush plants respond with less growth when clipped only lightly in summer or moderately in early fall. His findings correspond to the relative amounts of leaf material present at those

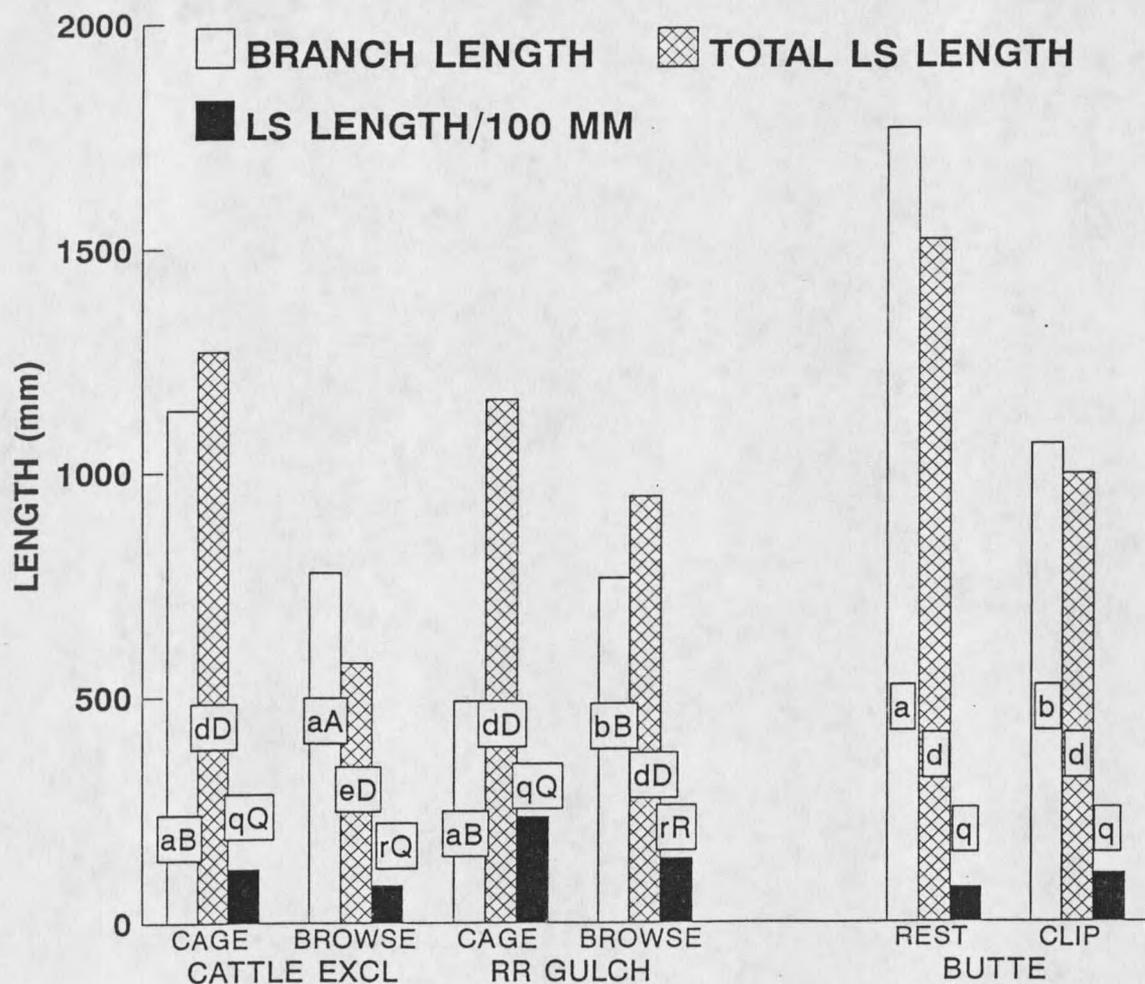


Fig. 10. Total branch lengths, total long shoot (LS) lengths, and LS length per mm of branch (mm) for browsing treatment sites in 1991 ($n=10$ for each) following treatment. Caged plants were protected from browsing for one winter browsing season. Clipped plants had 90-100% of all current LS removed in February to simulate heavy browsing on otherwise unbrowsed plants. Unlike lower case letters (ab=branch length, de=total LS length, qr=LS length/100 mm) denote differences (Mann-Whitney, $P<0.05$) between treatment pairs within categories and sites. Unlike upper case letters (AB, DE, QR) denote differences (Mann-Whitney, $P<0.05$) between cage treatment sites within categories and treatment. Analysis of variance showed a significant site \times treatment ($P<0.05$) interaction for branch length on cage treatment sites.

Table 7. Relative weights (percent) of bitterbrush leaf cluster, long shoot (LS) stem, and LS leaf. Dry Cottonwood deer enclosure and High Rye sites were not sampled. Figures are means of two plants per site.

Site	Leaf clusters (%)	LS stems (%)	LS leaves (%)
Butte	16	45	39
Cattle Enclosure	20	34	46
Deer + Cattle	14	38	48
Burn	29	32	39
Unburn	16	37	48
Powerline	8	39	53
Willow Creek	18	35	46
Railroad Gulch	10	47	42

times. When fewer leaves are present in early summer, less browsing would be required to remove much of the leaf material.

Live Plant Volume. Bitterbrush plants varied in size within and between sites (Fig. 12) and, as expected, rested plants were not the largest plants observed (Tueller and Tower 1979). At the Dry Cottonwood site, volumes of unbrowsed plants were similar to plant volumes in both the deer + cattle and the deer-only use area ($P > 0.06$).

Live bitterbrush volume in the burned area (Fig. 12) was 21% of the volume in the unburned area ($P < 0.001$). This represents a potentially large decrease in browse available to wintering ungulates, a condition which is likely to persist. Monsen and Shaw (1983) observed that LS production

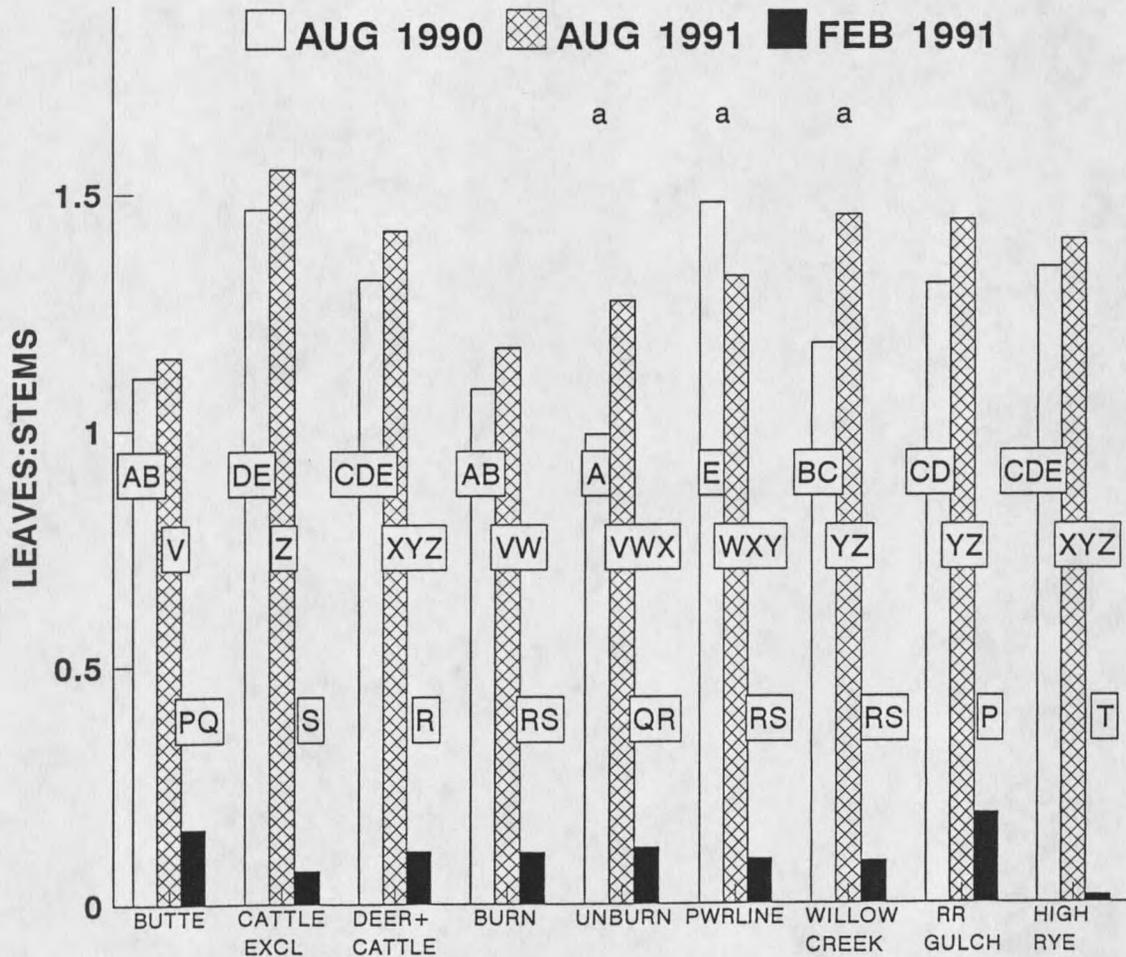


Fig. 11. Average ($n=10$) long shoot leaf to stem weight ratios for August 1990, August 1991, and February 1991. The Dry Cottonwood deer enclosure site was not sampled. Unlike upper case letters (ABCDE=August 1990, VWXYZ=August 1991, PQRST=February 1991) denote between site, within sample date differences (LSD, $P \leq 0.05$). Only those sites denoted by "a" showed a year to year, within site difference (Wilcoxon test, $P < 0.05$). Winter ratios were lower than summer (Mann-Whitney, $P < 0.01$) for all sites. August 1990 ratios across all sites were lower than August 1991 ratios (Mann-Whitney, $P < 0.01$).

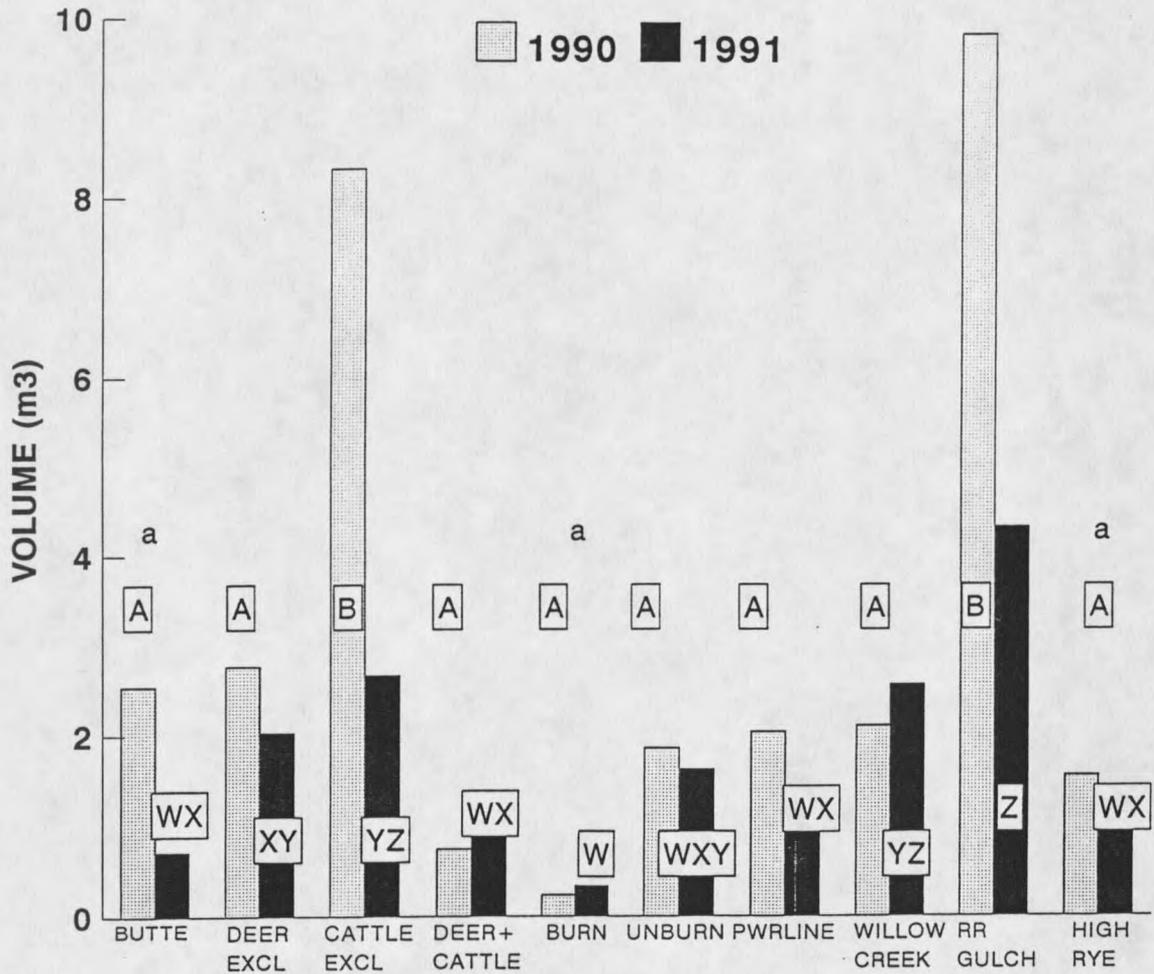


Fig. 12. Average ($n=10$) live plant volume (m^3) for all study sites in 1990 and 1991. The 2 unbrowsed sites are at left. Site to site, within year differences (LSD, $P \leq 0.05$) are denoted by bars with unlike letters (AB=1990, WXYZ=1991). Only those sites denoted by "a" showed a year to year, within site difference (Wilcoxon test, $P < 0.05$). Average live plant volume was greater in 1990 than 1991 (Wilcoxon test, $P < 0.05$).

on newly sprouted bitterbrush would require at least 5 years to recover if browsed, Pechanec et al (1954) reported a drop in production for 9 years, and Murray (1983) found that bitterbrush production was still below unburned sites 30 years after burning. Klebenow (1985) noted that mule deer

avoided large burned areas on Nevada winter range until bitterbrush and other shrubs had recovered, which often required 15 years.

Live plant volume (Fig. 12) decreased an average of 23% from 1990 to 1991 ($P < 0.05$) for all sites. This decline may represent an inability of bitterbrush to persist on these sites, however, this trend is not supported by canopy cover measurements (Table 8) for live bitterbrush cover, which did not change between years ($P > 0.40$). Tiedemann (1983) documented an approximate 20% decrease and subsequent recovery in live canopy cover over 3 years in apparent response to crop year precipitation. Major changes in average precipitation over this study period were not apparent (Appendix B, Table 14). Live plant volume changes (Fig. 12) of unbrowsed plants were similar to changes of plants in browsed plots ($P > 0.30$).

The protection treatment moderated the reduction of live plant volume (Fig. 13) between years ($P < 0.05$), when compared by analysis of variance. This implies an effect of browsing on branch death. However, the clipped plants on the unbrowsed Butte site showed apparently no reduction ($P > 0.19$) in average live plant volume over that of untreated plants (Fig. 13).

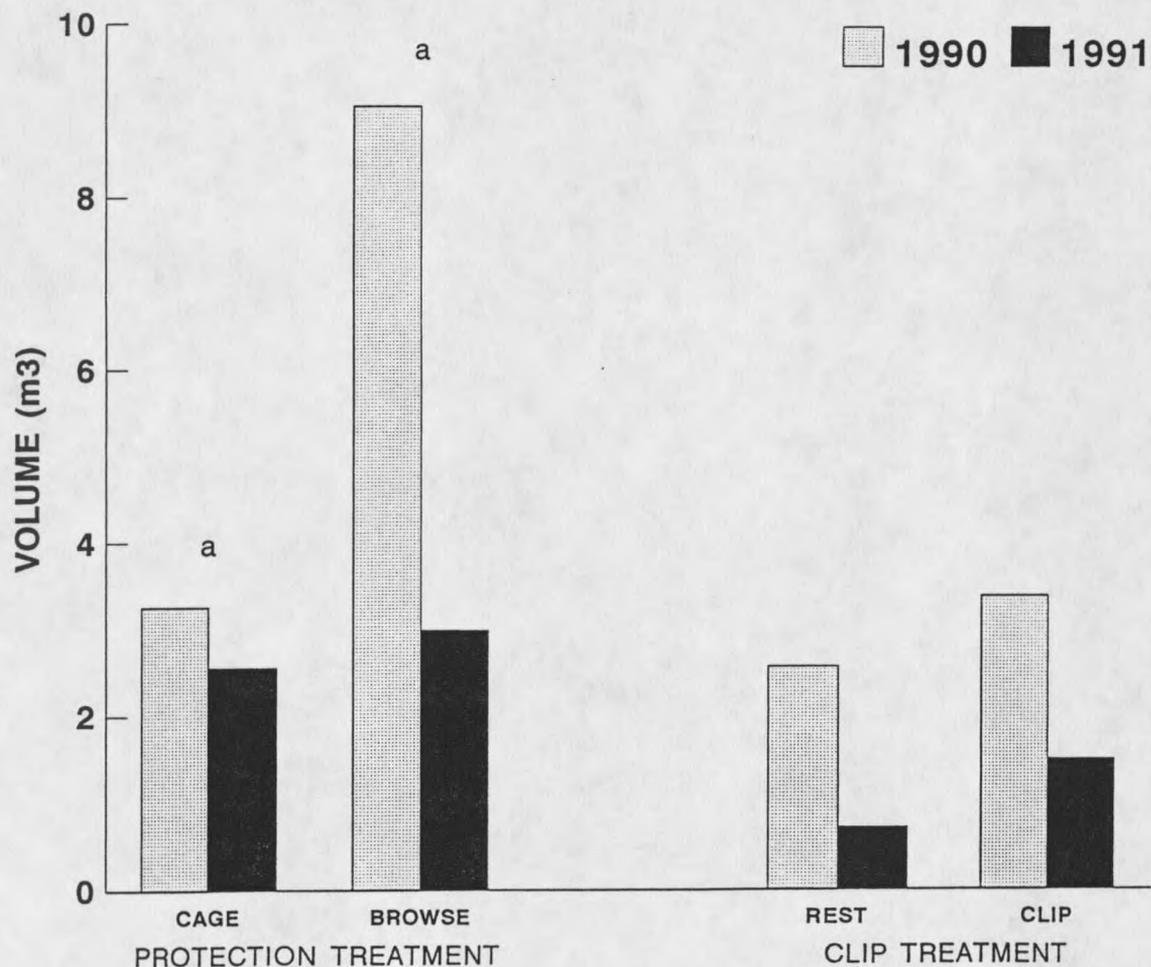


Fig. 13. Average ($n=10$) live plant volume (m^3) for browsing level treatment sites. Caged plants were protected from browsing for one winter browsing season. Clipped plants had 90-100% of all current LS removed in February to simulate heavy browsing on otherwise unbrowsed plants. Only those bars denoted by "a" differed between years (Wilcoxon test, $P<0.05$). Volumes did not differ (Mann-Whitney, $P>0.07$) between treatment pairs for either the protection or clip treatment. Year to year volume reduction was less (analysis of variance, $P<0.05$) for caged plants than adjacent browsed plants.

Table 8. Canopy cover (percent) of bitterbrush¹, non-bitterbrush shrubs, and perennial and annual grasses and forbs² on study sites for 1990 and 1991. Data were collected after most annual growth had occurred in September of each year.

Site		Bitter -brush	Shrub	Per. forb	Per. grass	Ann. forb	Ann. grass
Butte	1990	20.4	1.8	14.0	0.5	0.0	3.1
	1991	10.0	3.7	17.5	0.0	0.0	0.0
Deer Excl.	1990	22.2	3.2	3.0	7.4	0.0	6.5
	1991	15.6	5.2	9.0	13.3	0.6	10.4
Cattle Excl.	1990	13.3	7.6	12.8	14.7	0.0	0.4
	1991	10.2	8.3	6.3	11.8	0.0	0.6
Deer + Cattle	1990	13.3	7.9	2.8	9.2	0.0	0.4
	1991	10.2	16.5	3.2	14.7	0.0	0.3
Burned	1990	5.3	0.0	2.4	15.4	0.0	0.5
	1991	4.6	1.0	3.7	28.1	0.0	0.0
Unburn	1990	13.8	7.0	1.9	12.6	0.0	0.0
	1991	11.2	7.2	4.3	20.0	0.0	0.0
Pwrline	1990	21.0	0.4	11.4	0.3	0.0	1.2
	1991	17.3	0.0	14.2	0.7	0.0	1.4
Willow Creek	1990	33.7	0.4	1.2	15.6	0.0	0.1
	1991	40.7	0.8	1.2	14.5	0.0	2.7
RR Gulch	1990	22.4	0.0	12.3	0.3	0.0	1.5
	1991	32.3	0.0	13.0	0.5	0.0	1.0
High Rye	1990	21.4	0.8	3.4	20.9	0.1	0.1
	1991	17.8	3.5	7.4	30.0	0.0	0.0

¹Bitterbrush and other shrub canopy cover estimated from line intercept measurements (Canfield 1941). Figures are length of live canopy encountered along 5, 15 m transect lines, in percent.

²Grass and forb canopy cover estimated from canopy cover classes in 10 X 20 dm quadrats (Daubenmire 1959).

Carbon-13. Ratios of stable carbon isotopes showed no difference ($P > 0.10$) between plants from the 2 plots tested (Table 9), the heavily browsed Dry Cottonwood deer + cattle use plot and the nearly adjacent unbrowsed deer exclosure plot. These values are within the ranges reported for other cold desert plants (Toft et al 1989). Due to the cost and experimental nature of the analysis, few samples were tested. The high variability within plot samples in relation to the similarity of plot means requires a larger sample size to detect differences between sites such as these (Snedecor and Cochran 1989:441).

This carbon isotope ratio is often used to gauge water-use efficiency, because the proportion of ^{13}C in leaf material increases as leaves become water-stressed (Toft et al 1989). Since bitterbrush growth has been closely linked to precipitation (Tiedemann 1983, Bilbrough 1990), the carbon ratio might also indicate a relationship between water stress and relative growth rates. Long shoot length/mm branch was significantly different between the 2 sites ($P < 0.001$). Carbon isotope ratios did not reflect this difference (within the limits of the small sample sizes tested) and therefore do not appear to be related to bitterbrush LS lengths. One reason for this might be the time periods involved. The relationship between growth and precipitation has been correlated to mostly dormant-season precipitation, whereas ^{13}C ratios have been related to water

relations over the life of the leaf (Evans et al 1986), which begins after the dormant season.

Browsing Effects on Reproduction

Bitterbrush reproduction can occur by both sexual and vegetative means. The following sections discuss layering, flower production, seed production, and laboratory germination tests.

Layering. Nearly all plants observed had several obviously layering branches, although few appeared to have successfully rooted in the last several years. However, I was unable to adequately determine if nearby plants originated from buried or decomposed layering branches, from seed, or from root sprouting.

Flower Production. Flower production varied greatly from site to site (Fig. 14) and was lower in 1991 than in 1990 ($P < 0.05$). Flower numbers were highest on the 2 unbrowsed plots ($P < 0.001$). The longest branches and the lowest browsing level also occurred on the unbrowsed plots (Fig. 5 and Table 5). Despite this relationship, flower numbers did not appear to depend on either percent browsing level ($r < 0.19$, $P < 0.10$) or length of branch ($r < 0.16$, $P > 0.15$) on browsed plants. These results are contrary to the findings of McNulty (1947) and Garrison (1953b) and suggest that bitterbrush flower production on these sites did not change significantly on browsed plants despite actual level

Table 9. Carbon-13 ratios (parts per thousand) for bitterbrush long shoot leaves from deer + cattle (browsed) and deer exclosure (rested) plots. Results were not significantly different (Mann-Whitney, $P > 0.10$) for these two sites.

Sample Number	Isotope Ratio (0/00)
Deer + Cattle 1	-25.22
Deer + Cattle 2	-26.16
Deer + Cattle 3	-25.88
average	-25.75
Deer Exclosure 1	-25.55
Deer Exclosure 2	-26.46
Deer Exclosure 3	-25.16
average	-25.72

of browsing.

Plants unbrowsed for over 20 years had more flowers (Fig. 14) and higher flower densities (Table 6) than did browsed plants ($P < 0.05$). This is in agreement with Ferguson and Medin (1983), who observed more flowers on plants protected for 23 years. McNulty (1947) also found fewer flowers on plants browsed at successively higher levels. In this study, however, plants protected for 1 browsing season had similar flower numbers ($P > 0.90$) and flower bud densities ($P > 0.25$) as adjacent browsed plants (Fig. 4). Although plants clipped 1 season produced fewer flowers ($P < 0.05$) than adjacent unclipped, long-rested plants, the number of flower buds on the remaining length of stem (bud density) did not differ ($P > 0.38$) between clipped and rested plants. This lack of response in flower bud production rate might be

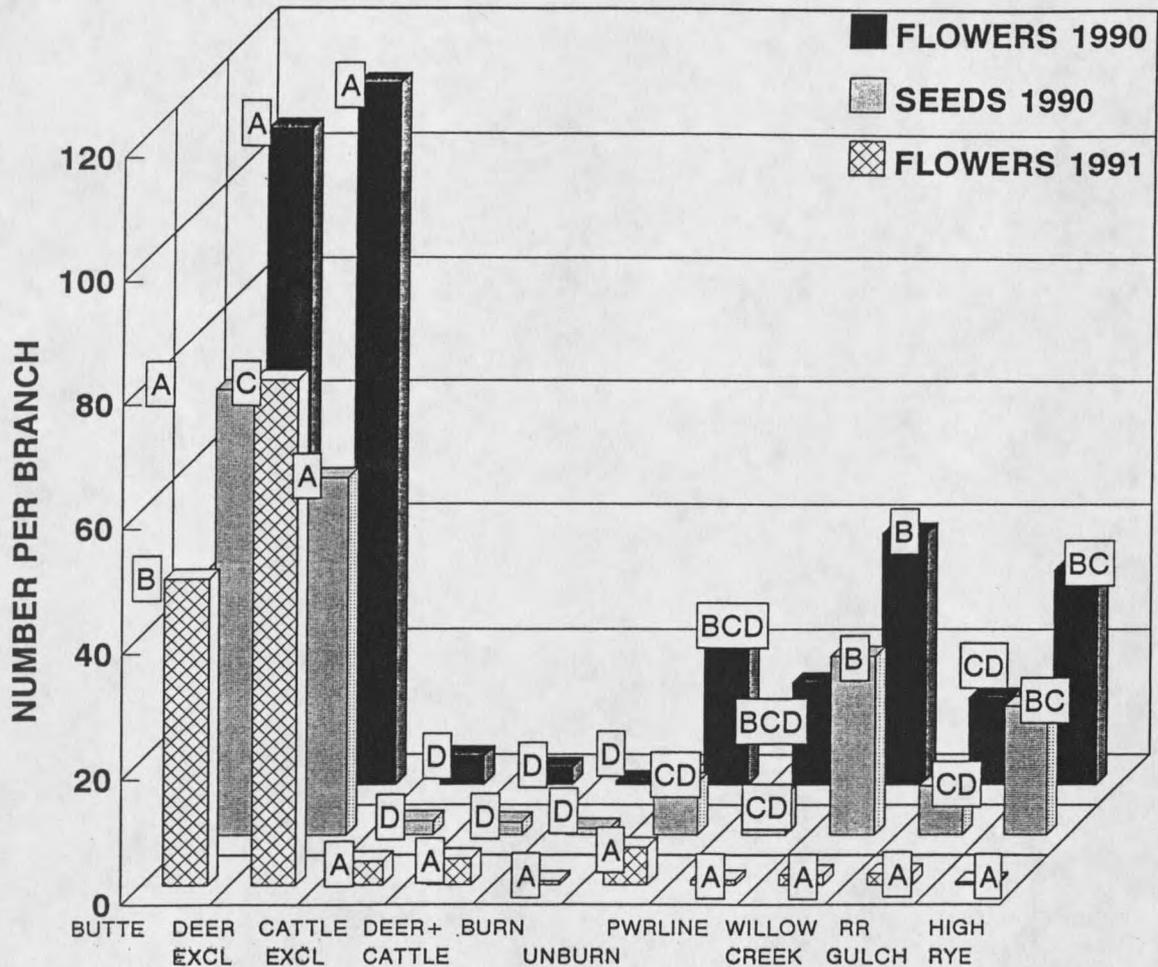


Fig. 14. Average ($n=10$) flower and seed numbers per branch for all study sites. Seeds are shown for only 1990 due to low seed numbers in 1991. Row values with similar letters do not differ (LSD, $P>0.05$). Flower and seed numbers were highly correlated to each other (simple linear regression, $r>0.97$, $P<0.001$). Fewer flowers were produced in 1991 than 1990 (Mann-Whitney, $P<0.05$).

explained by Tueller and Tower's (1979) idea of stagnation. Due to a residual effect of a plant's browse or rest history, flower production may not respond immediately to browsing or resting.

Flower production (Fig. 14) and flower bud density

(Table 6) were lower on the burned than the unburned plot ($P < 0.001$ for both). This agrees with observations (Monsen and Shaw 1983, Bunting et al 1985) that newly sprouted bitterbrush could require at least 10 years to reach reproductive maturity and contribute as a seed source. This delay in seed production could hinder the spread or recovery of bitterbrush on sites where little sprouting occurs or where few unburned plants remain to supply seeds.

Seed Production. Not all flowers produced seeds, nor were all seeds viable. Total seed production varied by site and by year (Fig. 14), mirroring the site and yearly relationships of flower production ($r > 0.97$, $P < 0.001$), which is in agreement with Nord's (1965) observation of cyclic seed production years. However, the percentage of seeds produced per flower (Fig. 15) was lower in 1991 than in 1990 ($P < 0.05$). This is also reflected in the lower percentage of live seeds produced as determined by tetrazolium testing (Table 10). Seed production was so low on many plots that further statistical analysis was precluded.

Germination. Seed viability (AOSA 1985) varied markedly between seeds produced in 1990 and those produced in 1991, except for the 2 Steep Mountain (burn area) plots (Table 10). This apparent decline in viability may have been related to the few seeds produced in 1991. I had difficulty finding seeds to collect in 1991 on many sites

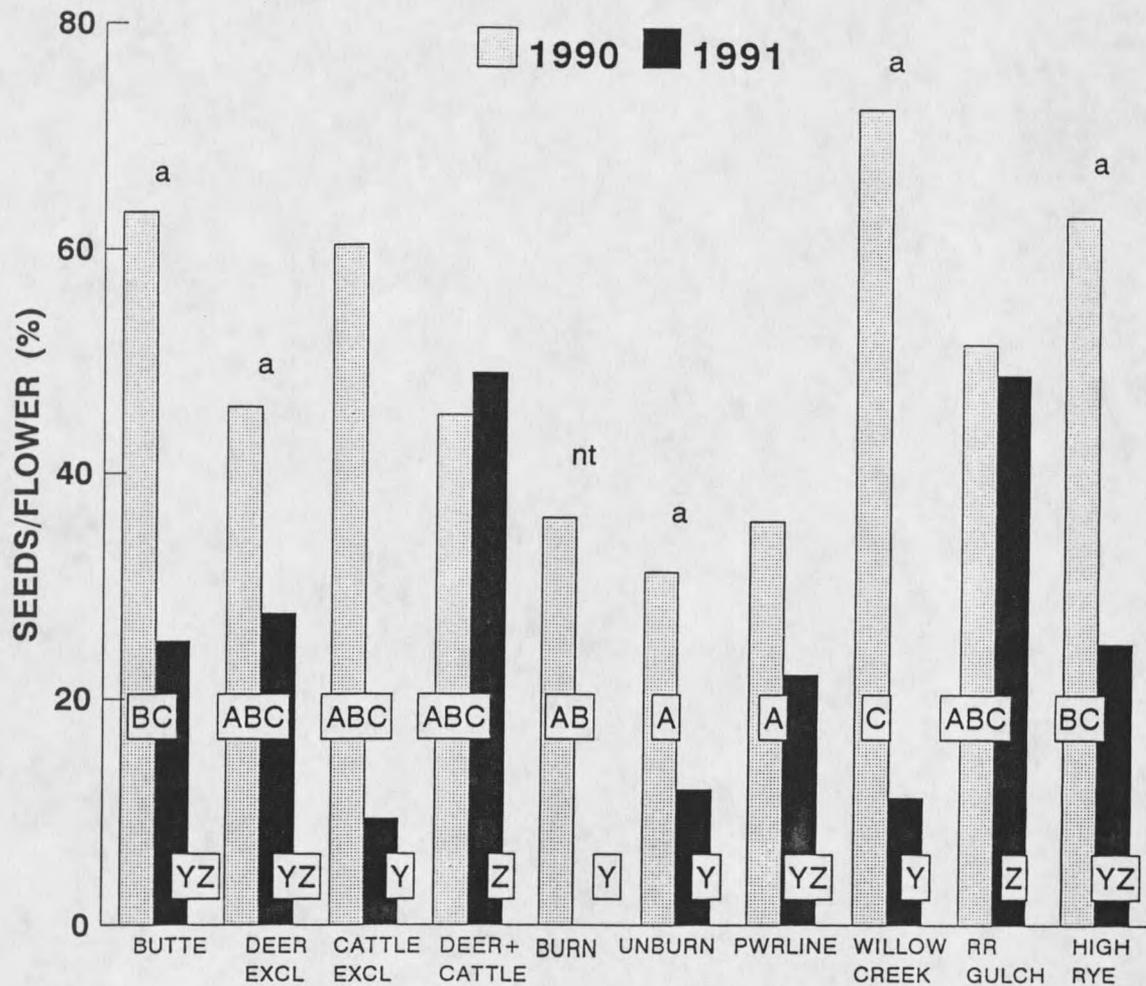


Fig. 15. Percentage of seeds produced per number of flowers produced (seed success) on all study sites in 1990 and 1991. Site to site, within year differences (LSD, $P \leq 0.05$) are denoted by bars with unlike upper case letters (ABC=1990, YZ=1991). Only those sites denoted by "a" showed a year to year, within site difference (Wilcoxon test, $P < 0.05$). "nt" denotes no test due to 0.0% seed success (Burned site, 1991). Seed success across all sites was lower in 1991 than 1990 (Wilcoxon test, $P < 0.05$).

Table 10. Seed viability (tetrazolium test) and number per kilogram for several sites in 1990 and 1991. Insufficient samples were collected for statistical analysis.

1990 Site	Viable (%)	Seeds per kg	1991 Site	Viable (%)	Seeds per kg
BUTTE	96	39,100	BUTTE	38	54,700
UNBURN	75	50,000	DEER EXCL.	27	63,000
POWERLINE	79	53,400	DOUBLE ¹	10	75,300
WILLOW CREEK	69	51,000	BURN	78	43,700
HIGH RYE	90	36,400	UNBURN	95	45,000
			POWERLINE	11	86,500
			HIGH RYE	28	61,000

¹Seeds from 2 flowers per hypanthium.

and probably collected fewer viable seeds from each site. I was unable to tetrazolium test enough seeds for statistical analysis, but the ultimate goal of such analysis would be to relate flower production to amounts of live seed produced for the various sites and treatments.

Germinable seed is expected to be full, plump, and relatively large (Nord 1965). Comparison of live seed and seed weight from these sites supports that expectation (Table 10), as heavier seed (fewer seeds per kg) was more viable ($r > 0.90$, $P < 0.001$). Seeds from many of these sites are small (50,000 to 86,000 seeds/kg) compared with Nord's (1965) figures of 35,000 to 43,000 seeds per kg in California. These small seeds may be related to the apparent inability of southwest Montana's bitterbrush plants to successfully reproduce by seed in recent years. However,

these results may not be an adequate reflection of the relationship between seed weight and viability because only the largest and fullest seeds were selected on each site. A random selection of seeds would be necessary to make such a determination.

Seed germination in growth chamber trials did not occur as described in previous reports. I employed 2 separate protocols (Young and Evans 1976, AOSA 1985), but seeds germinated neither as quickly nor as fully as expected with either procedure. Some seeds seemed to begin germination by breaking the seed coat, then apparently regained dormancy and did not progress further. Excising these embryos from the seed coat (Nord 1956) or repeatedly irrigating these seeds (Meyer and Monsen 1989) allowed most of them to continue germination (90% of excised seeds in 2 weeks, 50% of irrigated seeds in 4 weeks, and 90% of remaining seeds when excised). After the initial 4-week trial, many seeds became dry but still germinated, or seedlings dried out and later revived with addition of water. Such apparent stamina was not expected from Young and Evans' (1976) report of the necessity for precise control of temperature and moisture for complete germination. My observations suggest that these bitterbrush seeds are able to tolerate repeated wetting and drying episodes during germination and that seed coat removal or additional leaching of a germination inhibitor from the seed coat are necessary for many seeds to

successfully germinate.

I also found differences in rate and extent of molding of seed samples and its effect on seed germination. AOSA (1985) stated that mold indicates weak seed. I observed many mold-encrusted germinating seeds, although it appeared that fewer encrusted seeds than non-encrusted seeds from the initial germination test survived until dissection months later.

The expected germination time of 2-4 weeks after stratification was not adequate for these seed samples by at least 4 weeks. Data are presented in Appendix B, Table 15 with no further analysis.

Protein

Crude protein levels averaged 14 and 7% for summer LS leaves and stems, which agreed with previous reports for bitterbrush throughout its range (Dietz et al 1962, Bayoumi and Smith 1976, Morton 1976, Tiedemann 1983, Welch et al 1983). Protein levels also differed between sites ($P < 0.001$) and years ($P < 0.001$, Fig. 16). When all sites were pooled, summer leaf protein increased 11% between years ($P < 0.05$) and winter leaf protein decreased 21% from summer levels ($P < 0.001$). Long shoot crude protein did not vary significantly between years ($P > 0.59$) but was higher in summer 1991 than in the previous winter ($P < 0.05$).

The unbrowsed Butte site rated highest in crude protein

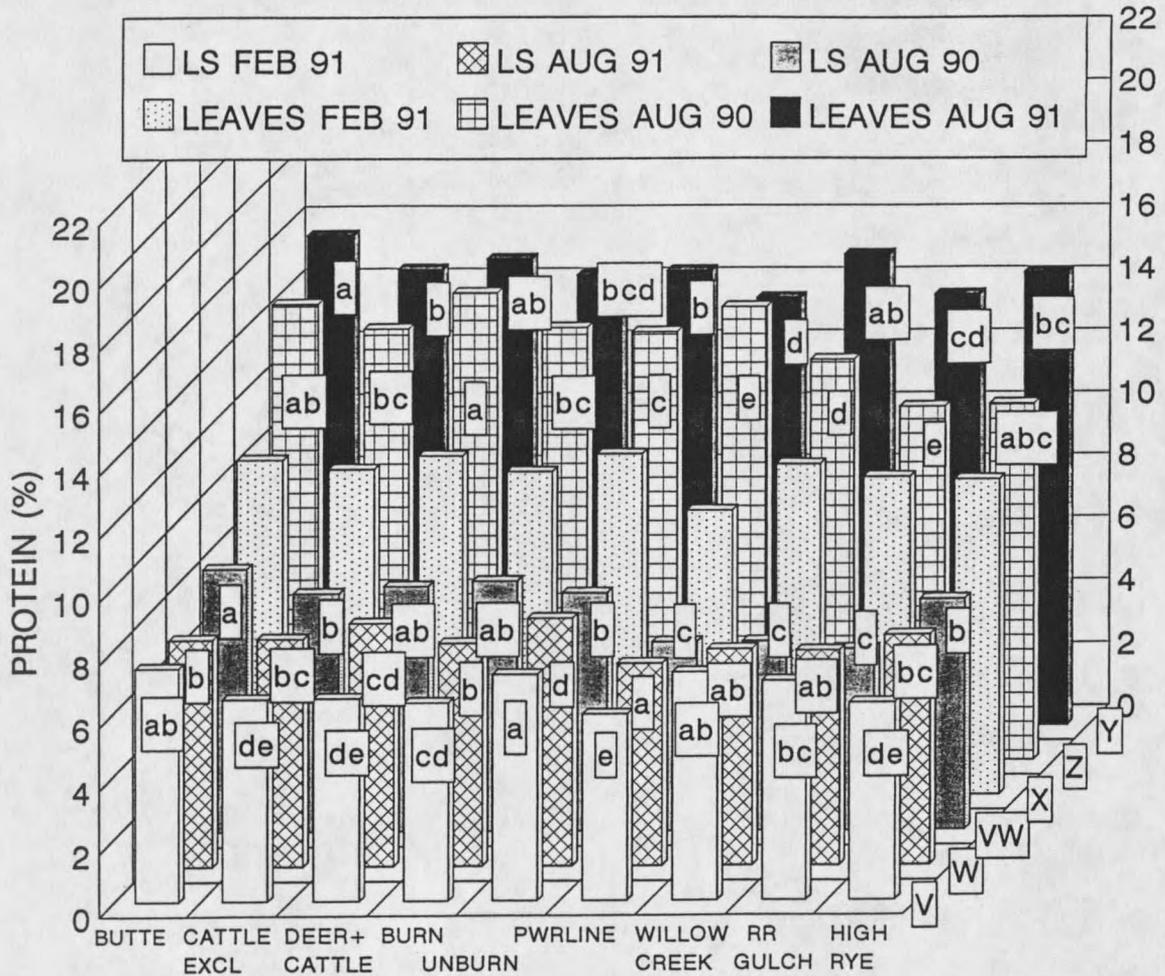


Fig. 16. Average ($n=5$) crude protein levels (%) of bitterbrush leaves and long shoots (LS) for summer 1990, summer 1991, and winter 1990-91. The Dry Cottonwood deer enclosure site was not sampled. Columns with similar lower case letters (abcde) are not significantly different (LSD, $P>0.05$) for each protein source and collection date. Insufficient winter leaf material ($n=1$) was gathered for statistical analysis within collection period. Similar upper case letters (VWXYZ) denote protein source and collection date averages that are not significantly different (LSD, $P>0.05$).

(Fig. 16) for 3 of the 6 measurements, although none were significantly higher than the next lower site ($P > 0.22$). Protein values for the MHWMA sites were lower for summer 1990 leaves ($P < 0.07$) and LS ($P < 0.01$) than for other sites and collectively rated lowest for 4 of the 6 measurements. These site differences were not expected from Morton's (1976) work, but were supported by that of Giunta et al (1978) and Welch et al (1983).

Bitterbrush crude protein levels (Fig. 16) on the deer + cattle site were higher than the adjacent cattle exclosure site for summer 1990 leaves ($P < 0.05$) and for summer 1991 leaders ($P < 0.05$). Other protein levels did not differ ($P > 0.29$) between these two sites. Although a difference in use might thus seem to affect protein levels on these sites, the unbrowsed Butte site had higher protein levels than browsed sites in 1990 ($P < 0.05$) and no difference in winter or 1991 ($P > 0.14$).

Related to these site and possible population (Alderfer 1977) differences are soil differences. Soil samples from shrub interspaces on the Dry Cottonwood, Steep Mountain, and Butte sites (Table 11) contained 49% more soil nitrogen at the Butte site than at the Steep Mountain site and 78% more than at the Dry Cottonwood site. Bayoumi and Smith (1976) found a positive response of bitterbrush protein levels to fertilization with nitrogen, although Tiedemann (1983) found slightly negative to no response to fertilization. However,

some desert shrubs accumulate nutrients under their canopy and deplete the surrounding interspaces (Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973), conditions for which I did not sample. Protein levels on my study sites are therefore not necessarily related to soil nitrogen levels.

Dietz et al (1962) alluded to the high protein level of leaves in winter, but did not quantify those levels. Welch et al (1983) reported that winter leafiness (presumably, weight of leaves compared with weight of stems) of plants

Table 11. Edaphic characteristics for study areas. Soil nitrogen was sampled at only 3 sites.

Site	pH	OM %	N ² %	Sand %	Silt %	Clay %	Textural class
Butte	5.6	2.6	0.11	63	24	13	sandy loam
Dry Cottonwood (all)	5.7	1.0	0.06	80	12	8	loamy sand
Steep Mountain (all)	6.3	1.1	0.07	67	23	10	sandy loam
Powerline ¹	5.8	1.4		65	15	20	sandy loam
Willow Creek ¹	5.2	3.6		65	18	17	sandy loam
Railroad Gulch ¹	5.7	1.0		72	18	10	sandy loam
High Rye ¹	6.7	2.8		69	15	16	sandy loam

¹From Guenther (1989).

²Total Kjeldahl nitrogen.

from Idaho, Colorado, Utah, and California ranged from 5.9 to 15.1% while combined leaf and LS crude protein ranged from 5.9 to 7.9%. These ranges are similar to values found for these Montana sites: leafiness of 1.5 to 15.8% and combined crude protein of 6.1 to 7.6% (Table 12).

Guenther (1989) reported that deer pellets from the MHWMA sites contained large amounts of Rocky Mountain juniper (Juniperus scopulorum Sarg.) and Oregon grape (Berberis repens Lindl.). Protein values for small winter samples of Oregon grape and juniper from the Willow Creek site were 8.4% and 6.9%, respectively. These values for bitterbrush and juniper are below those reported by Welch et al (1983) and below what they considered to be the necessary threshold of 8.9% crude protein for wintering deer. Hamlin and Mackie (1989) suggested that mule deer have more need for high quality forage in the fall, while building energy reserves, than in the winter. Bitterbrush in southwest Montana may supply this needed level of nutrients in the fall, as I observed delayed leaf-fall on wind-protected bitterbrush plants in late November 1990, but I did not sample plants at that time.

Plant Community

Canopy Cover

Canopy cover by life form varied from site to site and from year to year (Table 8). The unbrowsed Dry Cottonwood

Table 12. Winter crude protein content (percent) of bitterbrush long shoots (LS) (leaves and stems) and percent leafiness (weight of leaves per weight of stems) for study sites, February 1991. The Dry Cottonwood deer enclosure site was not sampled.

Site	CP (%)	sd	Leafiness (%)	sd
Butte	7.6 ^{a1}	0.46	13.6 ^{AB}	0.02
Cattle Exclosure	6.4 ^{cd}	0.32	6.5 ^D	0.02
Deer + Cattle	6.6 ^c	0.39	9.9 ^C	0.04
Burned	6.7 ^{bc}	0.33	9.6 ^{CD}	0.03
Unburned	7.6 ^a	0.44	10.5 ^{BC}	0.02
Powerline	6.1 ^d	0.22	8.5 ^{CD}	0.03
Willow Creek	7.1 ^{ab}	0.15	8.1 ^{CD}	0.03
Railroad Gulch	7.2 ^a	0.20	15.8 ^A	0.03
High Rye	6.1 ^d	0.47	1.5 ^E	0.01

¹Column entries with similar letters are not significantly different (Mann-Whitney, $P > 0.05$).

plot, for example, showed an 89% increase in cover of herbaceous life forms ($P < 0.05$) from 1990 to 1991. This supports Mueggler's (1983) observations of many-fold annual variation in graminoid and forb biomass production due to differences in growing season.

Grass canopy cover variation was particularly evident on the Steep Mountain burn site between years and plots. Perennial grass cover increased more than 50% in 1991 from 1990 on each of the burned and unburned plots ($P < 0.05$). This increase could reflect differing growing conditions each year (Appendix B, Table 14), or no cattle use of the site in 1991. Analysis of variance for perennial grass canopy cover showed more cover in the burned plot than in

the unburned plot over both years ($P < 0.01$), while forb cover did not differ between plots ($P > 0.90$).

The burned plot had more herbaceous plant species and a different community composition (Figs. 17 and 18, and Appendix B, Table 17) than the unburned plot. This trend was also reported by Johnson and Strang (1983) for other burns in the northern Rocky Mountain area. Several species were found in only the burned plot (Figs. 17 and 18), which agrees with published accounts of those species' response to fire (Blaisdell 1953, Harniss and Murray 1973, Nimir and Payne 1978, Pechanec et al 1954, Ralphs et al 1975).

I measured twice as much herbaceous canopy cover (Table 8) in 1990 in the cattle exclosure ($P < 0.05$) than in the deer + cattle plot, where cattle grazed from mid-July through late August. I found no difference in herbaceous plant canopy cover between the cattle exclosure and deer + cattle use plots in 1991 ($P > 0.90$), which was a year with late August through late September cattle use. This cover change could have affected competition between bitterbrush and herbaceous species for soil nutrients, resulting in an advantage for bitterbrush (Reiner 1982).

Canopy cover (Table 8) in the Dry Cottonwood unbrowsed plot was not significantly different for the deer-only plot for perennial grass (1990 $P > 0.06$, 1991 $P > 0.53$) or for non-bitterbrush shrubs ($P > 0.40$). Annual grass cover, however, was higher in the unbrowsed plot ($P < 0.01$). I found a

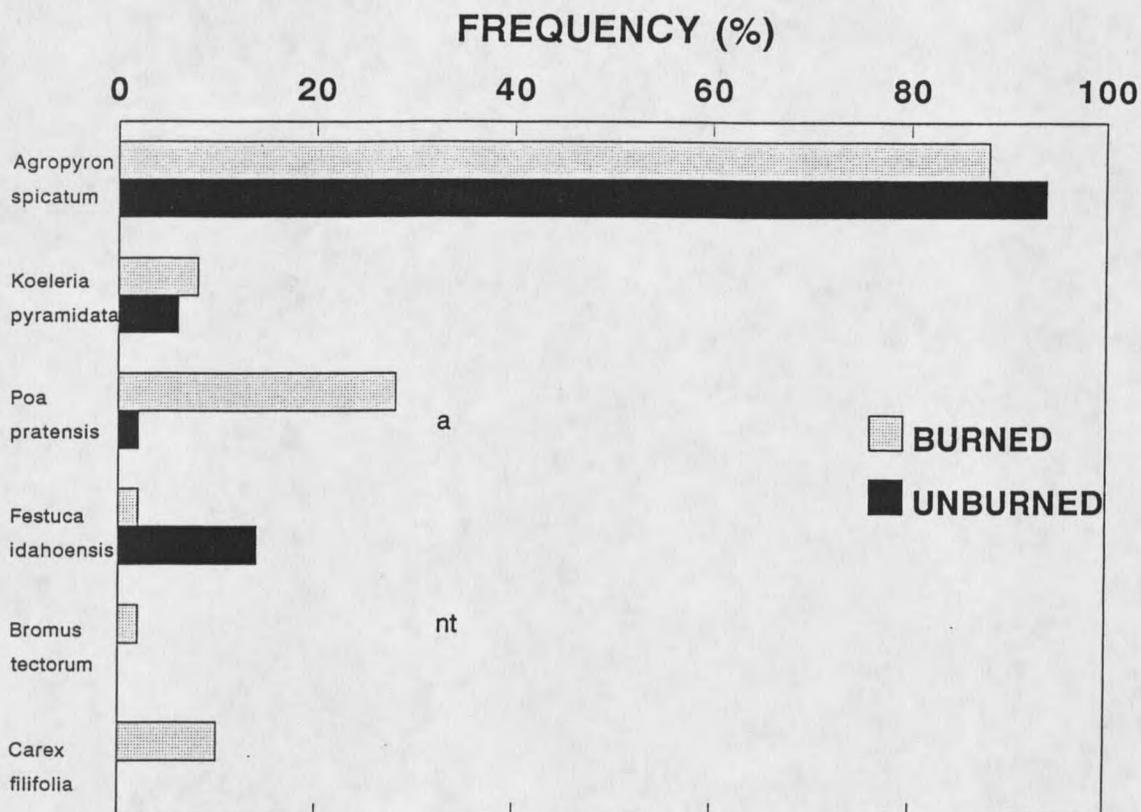


Fig. 17. Average (n=5) frequency of occurrence of graminoid species on the Steep Mountain burned and unburned plots in 1990. Several species occurred on only one of the two sites. Only those species marked with "a" showed a site to site difference (median test, $P < 0.05$). "nt" denotes no test due to low number of observations.

significant site x year interaction ($P < 0.01$) for total herbaceous vegetation, reflecting the differential response of the disparate plant communities (Appendix B, Table 17) on the 2 plots to yearly growing conditions (Appendix B, Table 14).

Guenther (1989) identified those sites with the fewest species as also having the greatest spotted knapweed (a

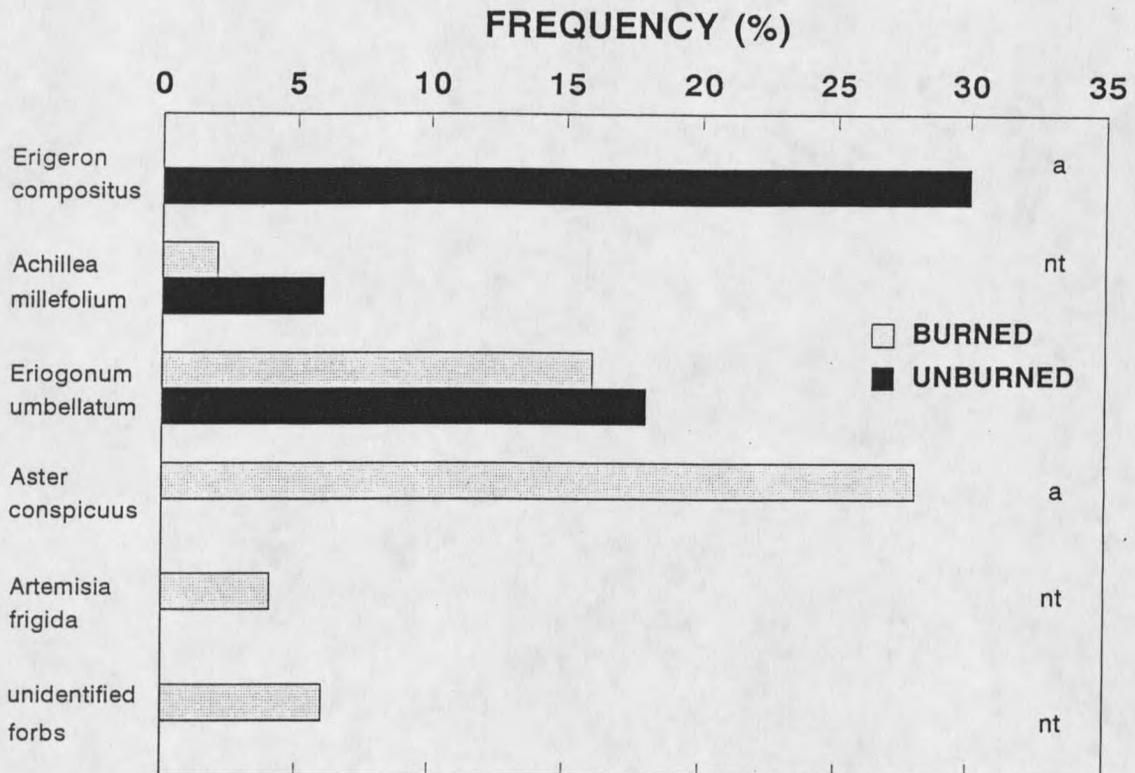


Fig. 18. Average (n=5) frequency of occurrence of forb species on the Steep Mountain burned and unburned plots in 1990. Several species occurred on only one of the two sites. Only those species marked with "a" showed a site to site difference (median test, $P < 0.05$). "nt" denotes no test due to low number of observations.

short-lived perennial forb) canopy cover ($r = -.57$, $P < 0.01$). The same trend, in terms of non-knapweed herbaceous canopy cover (Table 8), was apparent on my 10 study plots ($r = -.82$, $P < 0.001$). Bitterbrush canopy cover, however, was positively associated with knapweed cover ($r = .60$, $P < 0.05$). This correlation may be related to the low successional conditions, such as small amounts of litter and high amounts of bare ground (Appendix B, Table 18), under which

bitterbrush and knapweed show high establishment rates (Sherman and Chilcote 1972, Watson and Renney 1974).

Shrub Density

Bitterbrush density varied from site to site (Fig. 19). However, density at both unbrowsed sites (Dry Cottonwood deer enclosure and Butte) was similar ($P > 0.90$). At the Dry Cottonwood site, density was slightly lower in the deer-only use plot than in the deer enclosure plot ($P < 0.08$) while the deer + cattle plot was intermediate ($P > 0.40$).

Bitterbrush density (Fig. 19) at all 4 Mount Haggin WMA sites differed from each other ($P < 0.06$). While these sites represent a wide range of environmental and plant community diversity, Guenther (1989) was unable to find a significant correlation between bitterbrush density and any of the environmental factors that he measured. Nord (1965) reported California bitterbrush stands with up to 4,600 plants per hectare which occurred on sites with the least plant competition. In contrast, the High Rye plot was stocked at about 9,600 plants per hectare with as much competing species' cover (Table 8) as any other site in this study ($P > 0.20$).

At the Steep Mountain site, density of all shrubs (Fig. 20) was lower on the burned plot ($P < 0.05$), although bitterbrush density was the same for both plots ($P > 0.60$) and rubber rabbitbrush (Chrysothamnus nauseosus (Pallas) Britt. ssp. albicaulis (Nutt.) Hall & Clem.) increased on the burn

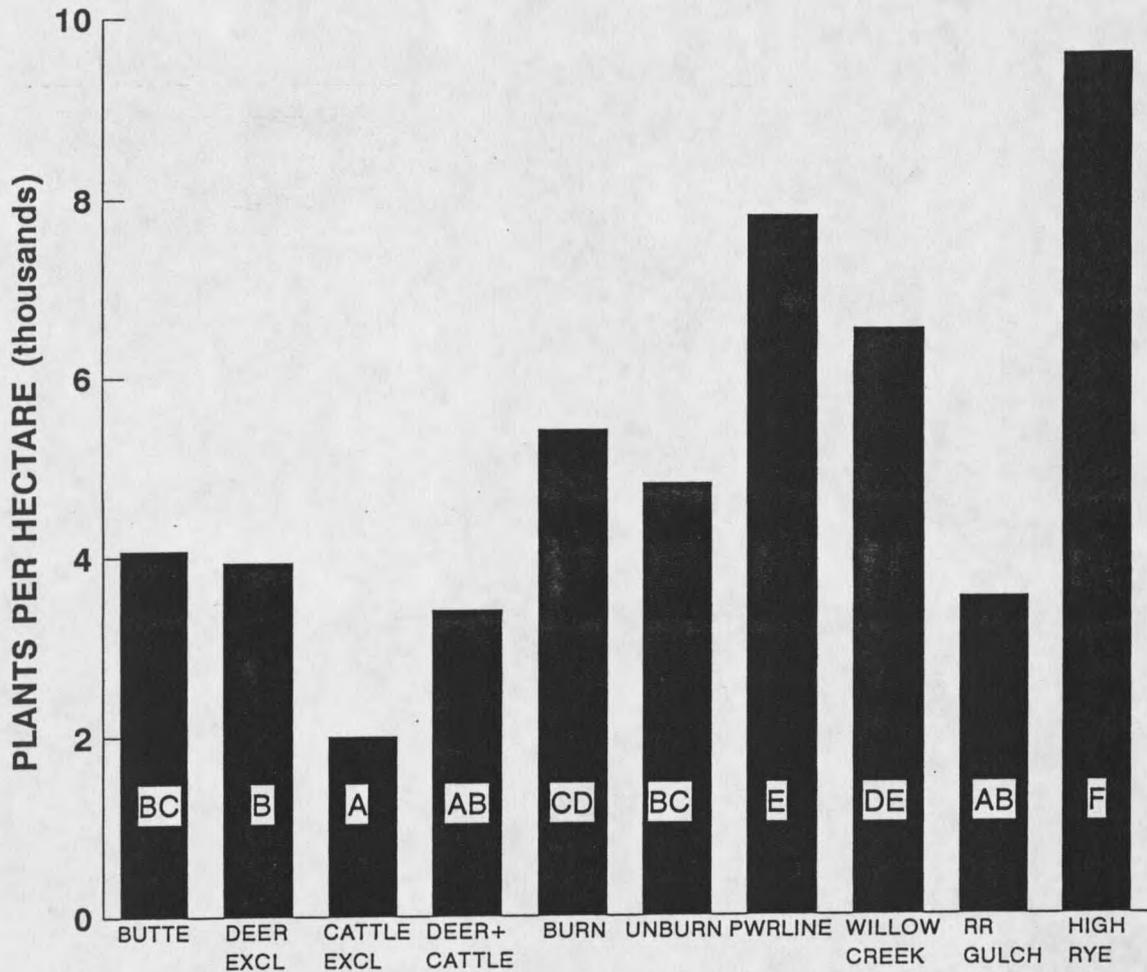


Fig. 19. Average ($n=5$) bitterbrush density (plants per hectare) on all study sites. The two unbrowsed sites are at left. Site to site differences (LSD, $P \leq 0.05$) are denoted by unlike letters (ABCDEF).

plot ($P < 0.01$). This decrease in total shrub density is probably a direct effect of burning on mountain big sagebrush, which rarely sprouts after fire (Blaisdell 1953, Pechanec et al 1954) and only occasionally grows from seed after fire (Hironaka et al 1983).

Bitterbrush exhibited either a strong sprouting or

seeding response, or both, to maintain a high density on the burn plot. Stem samples from the burn area showed that 50%

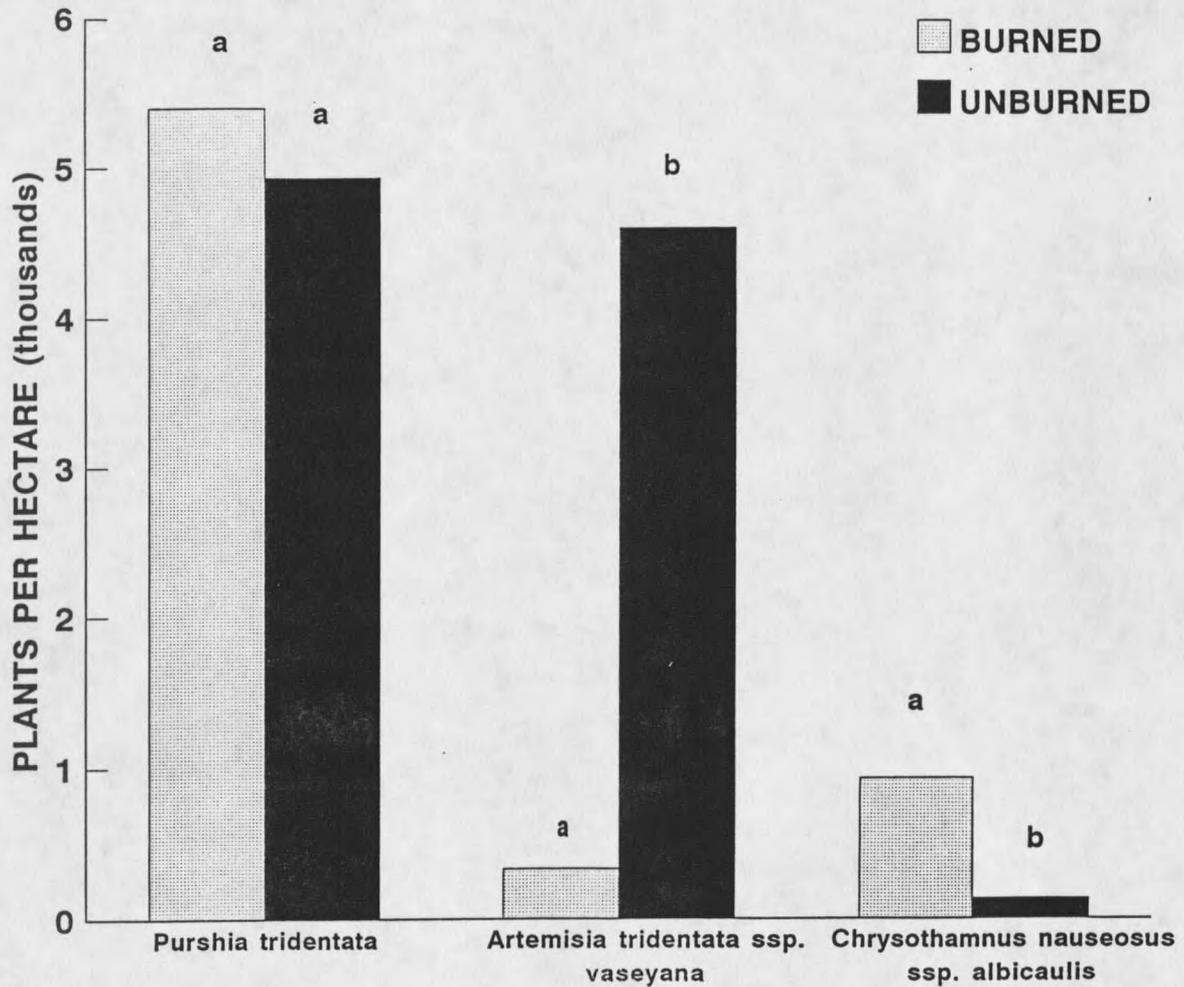


Fig. 20. Average (n=5) density (plants per hectare) of shrub species on the Steep Mountain burned and unburned plots. Pairs of bars with unlike letters are different (Mann-Whitney and median tests, $P < 0.05$).

of the sampled stems were older than the burn (more than 8 years old). This represents an unusually high sprouting response. Bunting et al (1985) reported that while the decumbent growth form (as found on these plots) is likely to sprout after fire, the sprouting frequencies of bitterbrush in mountain big sagebrush habitat types in Idaho and Montana averaged 29%, compared with at least 50% on this site. I could not determine whether the younger stems originated as new seedlings or as root sprouts, because old skeletons were not present on those plants (and may have been consumed in the fire).

Bitterbrush Stand Ages

Bitterbrush stands varied in average age from 25 to 40 years (Table 13). These ages are average for stand ages reported for Montana (Lonner 1972, Guenther 1989), California (Nord 1959), and eastern Washington (McConnell and Smith 1963). No young plants (less than 8 years old) were collected at any of the sites, as Guenther (1989) also reported.

Seedlings

We found a few seedlings, mostly by chance, although considerable time in 1990 was spent looking for seedlings in the study plots. Sprouts were located only at the Dry Cottonwood deer enclosure, Dry Cottonwood cattle enclosure, and Steep Mountain unburned sites, and none were found

Table 13. Bitterbrush stand ages for all study sites.

Site	average	n	min	max	sd
BUTTE	25	18	10	40	7.43
EXCLOSURES (both)	26	14	10	48	9.89
DCCG	25	15	10	46	10.50
BURN	13	8	7	30	7.70
UNBURN	26	15	13	33	5.54
POWERLINE ¹	40				
WILLOW CREEK ¹	25				
RAILROAD GULCH ¹	37				
HIGH RYE ¹	28				

¹Interpreted from Guenther (1989).

within the study plots. Sprouts usually occurred in groups of 2 to 7, with a few singles observed. All sprouts were less than 10 cm tall, and all appeared to be less than 5 years old. Nearly all of the sprouts located in 1990 survived into 1991, with no browsing damage observed.

This lack of seedlings was expected from previous reports of "spasmodic" (Nord 1965) or widely spaced seedling establishment. Probably only a very few bitterbrush plants per year normally establish (Ferguson and Medin 1983), depending on local weather conditions (Guenther 1989) or snowpack (Nord 1965), especially in mature stands (Anderson 1989).

SUMMARY AND CONCLUSIONS

Antelope bitterbrush is a palatable and nutritious food source for big game animals and often appears to be heavily browsed. Bitterbrush populations appear to be declining and seedling success is low in many areas, including southwest Montana. I examined bitterbrush growth and reproductive characters in relation to browsing levels on 10 sites in southwest Montana over two growing seasons. Conclusions which follow below should be considered specific for these sites, as local populations of bitterbrush differ in many respects, and because these study sites were not replicated and represent only one observation per site. Measurements and P values discussed below are presented in Appendix B, Table 19.

Browsing Level

Browsing levels of study sites averaged 20 - 60%, which are within the levels recommended by other researchers (Hormay 1943, Shepherd 1971) for health and maintenance of bitterbrush stands. Apparent browsing levels were lower in this study than in a previous one (Guenther 1989), probably due to a difference in sampling technique.

Growth

Bitterbrush plants on these southwest Montana sites exhibited both twig-level and plant-level responses to

browsing. Browsed twigs produced 1/2 the leaf cluster density as did unbrowsed twigs. Browsed and unbrowsed twigs on browsed plants produced 10% as many flower buds and 350% more long shoot (LS) buds per length of stem than did twigs on unbrowsed plants, which agrees with previous reports (McNulty 1947, Urness and Jensen 1983). These data indicate a fundamental difference in bud allocation patterns between browsed and unbrowsed bitterbrush plants and suggest that plants protected from browsing for many years should not be used as a standard for comparison with plants exposed to normal browsing pressures. It was not clear if the observed bud density changes occurred before (location on twig) or after (plant response) browsing, because location of buds was not mapped on each twig and fate of buds was measured only after browsing.

Actual level of browsing seemed to have little effect on bud densities. Regression analysis showed no significant relationship between browsing level on browsed plants and bud densities. Bud densities did not differ between control plants and plants treated with either one winter of browsing rest or with 100% clipping of all current growth following many years of no use.

Despite loss of stem length and buds in browsing, browsed plants produced the same amount of LS growth as did unbrowsed plants. Long shoot growth differed between rest treatment sites, however, and showed a significant site by

year interaction.

Live plant volume decreased 23% on both browsed and unbrowsed plants from 1990 to 1991. It is unknown whether this trend is due to temporary effects such as insect damage or weather fluctuations, or an inability of these bitterbrush plants to maintain themselves on these sites.

Both the number of LS produced and the average length of LS varied significantly each year, with 31% fewer and 23% longer LS in 1991. However, LS length and number of buds were not significantly related to each other and may have been responding to other variables, such as precipitation.

Based on these data, reducing browsing pressure for 1 season would appear to be of no immediate benefit to LS production on these bitterbrush stands. Such reductions might occur with some livestock grazing systems or with a mild winter that did not concentrate big game on winter ranges.

Protein

Bitterbrush crude protein levels varied between sites and years, with a 13.1% to 10.3% decline from summer to winter for bitterbrush leaves. Although most leaves had fallen by February, all sites contained plants with retained leaves at that time, which increased winter crude protein levels by 5% over twigs alone. Winter protein levels averaged 7.0%, which were below the estimated necessary

threshold of 8.9% for wintering deer. However, September through November protein levels might have been higher, as many plants retained leaves through that period. Protein levels from plants on 1 unbrowsed site were significantly higher for leaves and stems in 1990 but did not differ from browsed sites in winter or 1991.

Flowers and Seeds

Flower and seed production decreased 60% from 1990 to 1991, as did the number of seeds produced per flower. There appeared to be no correlation between browsing level and flower production among browsed plants, which was not expected from previous research (McNulty 1947, Garrison 1953b). However, browsed plants produced less than 16% as many flowers as did plants unbrowsed for many years, which agrees with previous reports (Ferguson and Medin 1983).

Seed viability declined from 1990 to 1991, based on tetrazolium tests. Seed weight also declined; lighter seed was less viable. Germination tests were inconclusive, except to show that seeds from these sites remained viable after several wetting and dessication events and many would germinate only after their seed coats were removed. Bitterbrush seeds can thus probably survive intermittent dry periods while germinating but seem to require seed coat removal or extensive leaching to remove germination inhibitors.

Stand Ages

Bitterbrush ages on these study sites were average (29 years), based on other reported stands (Nord 1965, Lonner 1972). Few seedlings were found, but others (Ferguson and Medin 1983, Anderson 1989) have indicated recruitment should be low for long-lived plants on sites such as these. Lack of normal-size or viable seed, or even of an entire seed crop would be inconsequential if bitterbrush recruitment needs are indeed low.

Burning Response

Bitterbrush plants on a burned plot had a strong sprouting response, maintaining the same density of plants as an adjacent unburned plot. Flower production was lower on burned plants, reaffirming that burned plants are reproductively immature for approximately 10 years after burning (Bunting et al 1965). This could delay spread of bitterbrush and recovery of sites with few unburned plants or where little sprouting occurs.

Growth rates, browsing levels, and total branch length were not significantly different between the burned and unburned plots, indicating that browsers "pruned" each branch to a constant length. Since burned plants were much smaller than unburned plants, even 8 years after burning, much less browse material was probably available from burned plants. Density and cover of all shrub species were lower

on the burned plot than on the unburned plot, reducing this plot's suitability as big game winter range.

Herbaceous plant canopy cover was higher in 1991 than in 1990 for both the burned and unburned plots. Perennial grass cover was higher on the burned plot over both years, while there was no difference in forb cover. More species were found on the burned plot, although some species were observed only in 1 of the 2 plots. This indicates a plant community shift as a result of burning, which could adversely affect animal species dependent on a mature shrub community.

Exclosure Plots

Some growth responses differed between bitterbrush study plots within a 3-level big game and livestock exclosure system. The deer + cattle plot had a higher LS bud density and greater LS growth per length of branch than the deer-only plot, although browsing levels were similar. Bitterbrush plants exposed to both deer and cattle browsing pressure had a higher crude protein content than plants exposed to only big game browsing use for summer 1990 leaves and summer 1991 stems, but did not differ from the deer-only plot for other protein measurements. Therefore, bitterbrush plants exposed to both big game and livestock use appeared to be at least as vigorous as plants exposed to only big game use.

In conclusion, I studied growth and reproductive characters of geographically and ecologically separate bitterbrush stands. Browsing levels were not excessive, but growth and reproductive characters did differ between browsed and unbrowsed twigs, plants, and sites. A prescribed burn reduced bitterbrush size and reproductive capacity while appearing to initiate a long term plant community shift. Combined cattle and big game use affected some bitterbrush growth characters differently than big game use only.

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APPENDICES

Appendix A
Study Site Access

Study Site Access

Sites are laid out in 15 X 12 m plots with beginning points of each of 5 internal transect lines (perpendicular to slope) marked with wooden stakes or 0.5 inch rebar with 6 inches of stake exposed. Stakes, bars, and landmarks (trees, bushes at corners) were marked with blue or orange survey flagging. Bars were painted orange. Many plants along the transect lines contained branches tagged with 1.25 in metal tags, which were often shiny and visible from a distance, aiding site location.

Dry Cottonwood exclosures:

Take the Galen exit from I-90 onto MT 273 for 0.8 miles. Turn left onto the dirt road for 0.4 miles, then turn right onto Dry Cottonwood Road (FS #85) for 0.6 miles. Turn left onto Sand Hollow Road (FS #9455). Take right fork (to Dry Cottonwood) at 2.5 miles. Park at large fir tree on south side 2 miles further. Exclosures are 50 meters south.

Study site in deer exclosure is 100' south of FS transect marker post in NW corner.

Study site in cattle exclosure is 100' south of FS transect marker post in NE corner.

Study site adjacent to exclosures is 30' south of mineral exploration pit located 200' southwest of SW corner of cattle exclosure.

Steep Mountain Sites

Take Main St. in Butte north into Walkerville. Turn left onto Main St. in Walkerville, go 0.3 miles to 2nd St. Take 2nd St. to right (north) and left around abandoned schoolhouse, 0.3 miles to intersection. Proceed straight, between corrals for 0.65 miles. turn left for 1.8 miles to burned-out farmhouse [4-WD from here]. Drive uphill past house foundation 0.15 miles (bear left) to USFS boundary fence. Drive 0.435 miles and park by large fir tree on south side. Proceed 75' on bearing 225° to burn line between two sites lying 20' to east and west.

Maude "S" Canyon

Take Continental St. exit in Butte from I-90 and turn north on Frontage Road 0.3 miles. Turn right onto M.S. Canyon access road and drive 0.4 miles to railroad tracks. Proceed 0.14 miles left (west) along tracks and park. From large rock (10' high, black face) on south side (below) of tracks, go 40' on bearing 50° to a large bitterbrush growing on a rock. Site lies south and west from here.

Powerline Site

From the Mule Ranch in the Mount Haggin Wildlife Management Area drive 12.5 miles north on MT 48. Turn right just past railroad tracks onto unpaved road for 2.5 miles. Turn right onto paved road for 1.9 miles and turn right onto dirt road. Follow this 0.9 miles through gate to right, continue 0.5 miles (bear left) to railroad crossing. Continue 0.4 miles past tracks and turn right (north) in draw bottom under powerline. Follow powerline road 0.9 miles over ridge, through stream crossing, and 0.2 miles uphill. Park on small flat area on right (east) side. Walk 150 yards on bearing 300° to a large rock (20' high). Walk 50 yards uphill on bearing 80° to site.

Willow Creek Site

From the Mule Ranch in the Mount Haggin Wildlife Management Area drive 10.1 miles north on MT 48. Turn right (east) onto the Cabbage Gulch Road. Drive 2.3 miles to ridgetop. Take left fork along ridge (north) for 0.9 miles. Park on flat spot near old log on ground to right (east). Site is on east slope of ridge 10 yards downhill.

Railroad Gulch Site

From the Mule Ranch in the Mount Haggin Wildlife Management Area drive 12.5 miles north on MT 48. Turn right just past railroad tracks onto unpaved road for 2.5 miles. Turn right onto paved road for 1.9 miles and turn right onto dirt road. Follow this 0.9 miles through gate to right, continue 0.5 miles (bear left) to railroad crossing. Continue 0.4 miles past tracks and turn right (north) in draw bottom under powerline. Drive uphill 0.3 miles and park near tree on right side of road (only tree nearby). Walk 80 yards on bearing 200° (toward small fir) to site.

High Rye Site

From Fairmont Hot Springs drive 0.1 miles east and take German Gulch Road to right (south). Drive 3.7 miles on main road (past intersection with mining road). Cross cattleguard and turn right (uphill). Drive 1.0 miles and park near culvert. Site is 50 yards uphill, to left and uphill of lone fir.

Appendix B

Tables

Table 14. Monthly normal and departure from normal precipitation (inches) and mean temperature (°F) recorded at the Silver Bow County airport (NOAA 1991).

Precip.	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
normal	.55	.38	.65	.98	1.73	2.37	1.11	1.27	1.12	.68	.45	.44
1987								.24	-1.25	-.68	-.29	.20
1988	-.08	-.20	-.10	.17	.28	-1.62	-.78	-1.12	-.01	-.26	.14	.17
1989	.75	.34	.56	-.9	.01	-1.56	.78	.37	.36	.40	-.04	.14
1990	-.09	-.27	.0	-.27	.45	-1.20	-.19	1.05	-1.05	-.42	.17	-.10
1991	-.10	-.23	.71	na ¹	.63	.01	na					
Temp.												
normal	15.5	21.5	26.3							41.0	27.5	19.6
1987										.8	2.9	-1.5
1988	-2.7	5.3	4.3							5.9	.8	-.8
1989	3.1	-14.5	1.7							-.9	5.4	-.7
1990	8.9	2.2	5.1							-1.6	5.0	-9.4
1991	1.8	11.4	3.6									

¹Records not available.

Table 15. Seed viability trial results. "Percent live" includes both germination and tetrazolium tests.

YEAR	SITE	TRIAL	SEED SOURCE ¹	%LIVE	n
1990	Butte	1	u	77.78	27
		2	u	86.21	29
		1	2	70.37	27
		2	2	68.97	29
		3	2	76.92	26
	Deer Excl	1	u	64.00	25
		2	u	41.67	24
		1	2	23.81	42
		2	2	55.56	27
		3	2	84.00	25
		4	2	46.15	26
		Cattle Excl	1	u	36.84
	2		u	35.00	20
	1		b	33.33	24
	2		b	37.04	27
	1		2	30.95	42
	2		2	44.44	27
	3		2	41.38	29
	Deer+Cattle		1	u	0.00
		2	u	13.04	23
		1	b	35.29	17
		2	b	19.05	21
		1	2	12.31	65
		2	2	41.94	31
		3	2	23.08	26
		Burned	1	u	58.33
	2		u	76.00	25
	1		b	93.75	16
	2		b	57.89	19
	1		2	73.91	23
2	2		47.83	23	
Unburned	1	u	47.62	21	
	2	u	26.67	15	
	1	b	37.04	27	
	2	b	44.00	25	
	1	2	24.00	50	
	2	2	52.00	25	
Powerline	3	2	56.00	25	
	1	u	53.85	26	

Table 15. Continued.

		2	u	44.00	25
		1	b	26.92	26
		2	b	25.81	31
		1	2	10.71	56
		2	2	40.74	27
		3	2	32.00	25
	Willow Creek	1	u	85.19	27
		2	u	64.00	25
		1	b	60.71	28
		2	b	92.59	27
		1	2	32.50	40
		2	2	39.39	33
		3	2	38.24	34
		4	2	39.47	38
	RR Gulch	2	u	62.50	24
		1	b	65.22	23
		2	b	62.96	27
		1	2	11.11	45
		2	2	55.56	27
		3	2	84.00	25
		4	2	62.96	27
	High Rye	1	u	22.73	22
		2	u	30.43	23
		1	b	38.46	26
		2	b	41.67	24
		1	2	9.62	52
		2	2	33.33	30
		3	2	28.57	28
<hr/>					
1990	Butte	1	x	90.48	21
in 1991 ²	Deer Excl	1	x	28.00	25
		2	x	51.43	35
	Unburned	1	b	30.00	20
	Powerline	1	x	51.61	31
		2	x	48.28	29
	Willow Creek	1	x	64.00	25
	High Rye	1	x	29.63	27
		2	x	28.57	28
<hr/>					
1991	Butte	1	u	39.47	38
		2	u	43.48	46
		1	2	3.13	32
		2	2	5.71	35
<hr/>					
	Deer Excl	1	x	32.00	25

Table 15. Continued.

	2	x	36.00	25
	1	u	28.00	25
	1	2	32.14	28
	2	2	23.33	30
Cattle Excl	1	x	50.00	38
	2	x	14.89	47
Deer+Cattle	1	x	25.00	16
	2	x	41.18	17
	1	u	28.57	21
	2	u	35.00	20
Burned	1	x	64.29	28
	2	x	81.48	27
Unburned	1	x	93.94	33
	2	x	95.12	41
	1	u	76.92	26
	2	u	84.62	26
	1	b	72.00	25
	2	b	90.32	31
	1	2	56.86	51
	2	2	69.23	52
Powerline	1	u	8.57	35
	2	u	7.89	38
	1	b	11.43	35
	2	b	8.82	34
	1	2	20.00	5
Willow Creek	1	x	3.64	11
	1	u	37.5	24
	2	u	61.11	18
	1	b	40.00	5
	1	2	8.77	57
RR Gulch	1	u	48.65	37
	2	u	28.57	42
	1	b	31.25	32
	2	b	17.14	35
	1	2	13.43	67
	2	2	20.59	68
High Rye	1	x	29.03	31
	2	x	41.38	29

¹u=from unbrowsed twigs. 2=from 2 seeds per hypanthium.
²b=from browsed twigs. x=mixed from browsed and unbrowsed twigs.
²Seeds collected in 1990 but tested with 1991 seeds.

Table 16. Bitterbrush measurements¹ for study sites and plants, 1990 and 1991.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTL SLN	TTL SEED	MAX LS	
1990	Butte	4	1188	47	142	29	1090	29	103	
		rest	5	1455	155	207	14	913	130	180
			8	1927	135	286	15	934	51	182
			9	1894	95	253	43	2674	58	175
			11	1089	55	104	6	183	11	105
			17	921	136	73	3	33	105	14
			23	1579	83	158	47	1786	68	90
			28	1216	158	109	19	573	145	137
			29	646	41	64	12	580	23	120
			31	3532	151	210	99	4682	93	230
			avg	1545	106	161	29	1345	71	134
			std	766	45	72	27	1333	43	58
1990	Butte	3	1525	42	112	25	3198	24	290	
		clip	6	1499	156	143	29	1193	125	122
			7	842	81	132	37	1461	73	96
			8	2111	314	194	30	1566	274	195
			12	1090	149	183	42	865	106	53
			13	1161	76	98	41	1936	51	150
			20	1755	218	159	35	1090	174	85
			26	1046	143	98	9	211	115	36
			27	580	74	44	0	0	40	0
			30	1060	141	92	31	1269	51	95
			avg	1267	139	126	28	1279	103	112
			std	431	76	44	13	850	72	79

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTL SLEN	TTL SEED	MAX LS
1990	Deer Excl	2	1783	217	109	3	92	111	48
		5	3620	79	271	62	5455	50	190
		6	1192	3	129	36	2217	0	197
		7	1694	164	152	7	468	74	208
		8	2111	157	82	7	315	95	98
		9	1191	108	92	3	93	58	37
		14	1131	112	57	25	1491	53	180
		18	1151	83	87	7	229	42	61
		19	1577	78	111	39	2422	37	124
		21	1936	127	158	22	1228	51	122
		avg	1739	113	125	21	1401	57	127
		std	711	56	57	19	1582	29	61
1990	Cattle Excl cage	4	755	23	75	26	1159	14	95
		5	503	21	49	20	882	13	130
		8	644	0	60	27	1180	0	98
		10	1452	0	67	44	2014	0	120
		12	797	0	82	16	423	0	110
		15	378	0	26	29	1074	0	76
		16	845	0	83	16	561	0	95
		22	750	0	71	12	376	0	90
		23	786	8	79	13	777	7	108
		25	652	1	84	9	352	1	150
		avg	756	5	68	21	880	4	107
		std	269	9	17	10	484	5	20

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TLLSLEN	TTL SEED	MAX LS
1990	Cattle Excl browse	1	1243	0	132	44	2060	0	153
		3	2828	2	280	85	4058	0	145
		6	1413	0	111	37	2469	0	180
		7	842	36	91	20	769	15	88
		11	1010	4	66	54	3403	4	182
		17	710	0	60	23	864	0	87
		18	732	0	46	36	1322	0	100
		19	790	0	64	15	362	0	52
		21	701	0	44	7	100	0	28
		24	873	3	50	32	1309	3	100
		avg	1114	5	94	35	1672	2	112
		std	614	11	68	21	1240	4	49
1990	Deer+Cattle	3	621	1	45	39	2022	0	140
		4	458	7	31	30	1751	5	140
		5	345	14	22	29	1095	14	112
		6	276	0	18	21	813	0	111
		8	335	3	37	27	750	0	70
		10	980	1	88	49	3544	0	155
		12	831	1	66	23	1722	1	190
		14	414	0	40	15	411	0	100
		17	684	0	33	38	1554	0	145
		21	308	0	28	20	729	0	110
		avg	525	3	41	29	1439	2	127
		std	230	4	20	10	866	4	32

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTL SLEN	TTL SEED	MAX LS
1990	Burn	1	828	0	73	37	1280	0	84
		6	1075	0	100	43	1496	0	105
		8	1172	12	107	21	479	1	38
		11	696	0	89	22	608	0	55
		12	686	0	64	38	1422	0	98
		13	567	1	72	23	933	0	105
		16	1030	1	104	24	517	1	40
		17	930	0	63	31	963	0	75
		18	981	0	74	35	920	0	55
		25	841	0	100	38	1048	0	65
		avg	881	1	85	31	967	0	72
		std	182	4	16	8	341	0	24
1990	Unburn	2	1049	23	92	35	1300	2	70
		7	558	10	55	30	1481	0	107
		9	611	3	54	29	934	2	82
		11	796	4	98	17	501	2	90
		14	623	20	65	28	1255	3	175
		15	789	17	107	29	1285	3	98
		16	1155	53	102	12	224	24	60
		21	1112	44	90	16	1395	19	150
		22	693	42	61	12	290	18	50
		24	1136	43	82	52	2101	10	125
		avg	852	26	81	26	1077	8	101
		std	225	17	19	12	560	8	38

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTLLEN	TTL SEED	MAX LS
1990	Powerline	4	888	19	100	23	650	12	83
		11	1325	1	139	52	1426	0	63
		13	760	1	90	26	631	0	55
		17	757	38	89	22	637	20	53
		18	524	6	33	41	1430	4	120
		24	1576	13	123	21	729	2	63
		29	1063	0	124	19	504	0	48
		32	677	3	57	24	1212	2	89
		35	949	51	96	37	1291	13	92
		38	1115	31	86	31	1178	10	81
		avg	963	16	94	30	969	6	75
		std	301	17	30	10	350	7	21
1990	Willow Creek	4	507	15	49	38	1589	11	116
		10	920	61	144	19	711	35	105
		13	901	49	76	29	978	43	89
		29	1101	74	244	32	1198	57	78
		32	1169	30	73	54	3344	26	205
		34	1612	68	133	47	2217	53	122
		42	556	9	35	14	775	9	128
		43	939	45	89	21	835	27	98
		45	1059	15	104	18	752	10	80
		47	1788	36	142	72	4496	14	146
		avg	1055	40	109	34	1690	29	117
		std	383	22	57	18	1227	17	36

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTL SLEN	TTL SEED	MAX LS
1990	RR Gulch cage	3	1057	10	70	48	2279	7	145
		5	474	10	80	10	289	8	58
		14	501	13	55	17	383	3	44
		16	693	13	72	5	192	2	75
		17	507	5	49	15	621	3	90
		19	1349	11	110	43	1726	3	90
		23	852	5	65	24	1273	0	110
		25	475	10	32	8	436	5	84
		28	373	1	39	12	277	0	43
		29	574	5	61	8	146	4	30
		avg	686	8	63	19	762	4	77
		std	295	4	21	14	702	3	33
1990	RR Gulch browse	2	263	3	31	14	581	0	258
		6	837	31	86	17	436	22	72
		7	1106	14	60	15	479	7	69
		8	1066	11	73	16	432	7	51
		9	516	8	74	9	283	7	63
		12	719	11	62	22	953	6	108
		15	638	8	70	14	341	6	48
		18	723	18	58	15	483	10	67
		24	445	25	59	4	124	12	48
		27	521	9	55	6	98	1	25
		avg	683	14	63	13	421	8	81
		std	253	8	14	5	231	6	62

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTLLEN	TTL SEED	MAX LS
1990	High Rye	4	953	4	71	40	1533	3	69
		6	1003	66	116	22	612	26	61
		7	689	18	68	27	678	12	68
		10	548	44	72	9	171	31	30
		14	720	84	87	23	699	51	65
		19	645	20	75	12	381	19	68
		21	416	24	56	14	441	11	78
		27	766	18	65	32	1250	11	100
		28	643	53	50	26	1189	35	89
		29	1172	12	116	25	1301	6	115
		avg	756	34	78	23	826	21	74
		std	215	25	21	9	435	14	22

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTLLEN	TTL SEED	MAX LS
1991	Butte rest	4	1262	66	192	7	321	15	52
		5	2001	69	21	13	801	20	160
		8	2446	82	172	41	3140	41	235
		9	1401	62	141	14	1355	15	300
		11	1188	4	78	9	789	0	215
		17	1073	34	43	10	370	15	80
		23	1969	14	0	0	0	6	0
		28	1608	31	95	11	593	4	90
		29	1153	15	59	25	2022	0	220
		31	3590	111	305	72	5831	28	475
		avg	1769	49	111	20	1522	14	183
		std	741	33	88	20	1687	12	132
1991	Butte clip	3	1416	0	13	18	2171	0	205
		6	883	27	14	13	415	4	70
		7	463	5	34	25	1312	5	142
		8	1799	65	39	10	188	14	55
		12	599	26	81	9	513	14	121
		13	1063	2	46	47	2428	0	126
		20	1562	9	117	12	450	0	122
		26	833	21	54	0	0	8	0
		27	643	12	41	14	661	0	130
		30	1363	0	74	26	1813	0	149
		avg	1062	17	51	17	995	5	112
		std	429	19	30	12	826	5	54

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTL SLN	TTL SEED	MAX LS
1991	Deer Excl	2	834	1	75	22	992	0	126
		5	5037	180	388	18	1024	34	200
		6	2399	88	183	44	2636	41	152
		7	2483	16	42	16	1427	0	210
		8	2225	34	117	12	1326	14	185
		9	1258	0	150	23	1398	0	115
		14	2502	187	326	11	511	75	73
		18	2183	57	240	12	630	6	110
		19	4333	191	574	44	2576	107	165
		21	3977	55	316	25	1887	19	155
		avg	2723	81	241	23	1441	30	149
		std	1264	73	155	12	695	34	41
1991	Cattle Excl cage	4	874	0	58	3	218	0	130
		5	878	19	85	7	395	3	110
		8	1438	0	127	18	634	0	114
		10	539	0	29	32	2586	0	205
		12	638	0	75	8	127	0	30
		15	0	0	0	0	0	0	0
		16	787	0	51	27	803	0	52
		22	953	3	84	7	233	0	60
		23	905	16	83	2	84	2	47
		25	765	0	85	21	652	0	84
		avg	778	4	68	13	573	1	83
		std	344	7	33	11	718	1	56

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTL SLEN	TTL SEED	MAX LS
1991	Cattle Excl browse	1	1445	0	122	33	1125	0	92
		3	1954	0	72	39	2491	0	235
		6	1935	0	67	26	1360	0	146
		7	1148	0	59	23	993	0	127
		11	590	0	50	17	310	0	28
		17	447	0	25	19	1155	0	160
		18	906	0	66	31	2064	0	116
		19	708	0	60	6	239	0	98
		21	1188	0	111	31	1886	0	144
		24	1080	0	73	26	1091	0	114
		avg	1140	0	71	25	1271	0	126
		std	492	0	27	9	681	0	51
1991	Deer+Cattle	3	616	0	34	17	1130	0	145
		4	584	2	37	4	75	0	40
		5	554	26	45	15	762	8	133
		6	431	0	21	22	767	0	96
		8	455	7	32	25	1528	1	155
		10	879	4	32	35	2450	4	155
		12	1235	3	71	35	1997	3	153
		14	630	0	23	34	1993	0	117
		17	2024	0	68	37	1563	0	150
		21	725	0	54	32	1781	0	110
		avg	813	4	42	26	1405	2	125
		std	461	8	17	10	681	3	35

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TLLSLEN	TTL SEED	MAX LS
1991	Burn	1	716	2	24	34	1271	2	87
		6	513	0	14	3	140	0	93
		8	384	0	13	8	332	0	85
		11	369	0	7	3	118	0	55
		12	557	0	26	12	559	0	86
		13	324	3	17	7	388	0	88
		16	380	0	24	4	57	0	18
		17	344	0	15	14	476	0	75
		18	598	0	12	7	246	0	65
		25	408	0	28	19	593	0	77
		avg	459	1	18	11	418	0	73
		std	123	1	7	9	334	1	21
1991	Unburn	2	624	7	32	31	1196	4	83
		7	871	6	20	25	968	0	78
		9	470	6	37	15	390	0	64
		11	589	8	62	20	1061	1	92
		14	453	1	46	5	141	0	52
		15	309	6	10	17	754	1	84
		16	539	7	37	10	266	1	69
		20	622	1	39	3	165	0	71
		22	586	10	24	2	26	2	14
		24	676	8	35	16	1005	0	165
		avg	574	6	34	14	597	1	77
		std	142	3	14	9	421	1	36

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTLLEN	TTL SEED	MAX LS
1991	Powerline	4	354	0	16	20	1264	0	133
		11	374	0	25	7	330	0	80
		13	305	0	10	27	2745	0	180
		17	521	1	57	22	1481	0	126
		18	517	6	41	18	1201	4	142
		24	920	1	41	24	1771	0	143
		29	429	0	23	21	1218	0	104
		32	707	0	31	29	1697	0	128
		35	270	0	16	16	1069	0	186
		38	342	0	97	19	1071	0	131
		avg	474	1	36	20	1385	0	135
		std	193	2	24	6	591	1	30
1991	Willow Creek	4	586	3	11	22	943	0	95
		10	501	6	35	21	808	1	105
		13	796	0	20	30	1244	0	154
		29	546	0	15	25	1087	0	118
		32	425	5	9	24	1995	2	370
		34	392	0	15	21	1271	0	140
		42	733	1	20	18	660	0	65
		43	308	0	21	6	289	0	121
		45	431	0	14	12	862	0	170
		47	1553	1	40	45	2052	0	190
		avg	627	2	20	22	1121	0	153
		std	340	2	10	10	526	1	80

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TTLLEN	TTL SEED	MAX LS
1991	RR Gulch cage	3	1988	13	154	30	1643	8	116
		5	460	2	6	4	139	2	68
		14	424	0	45	19	858	0	100
		16	805	0	45	22	1217	0	118
		17	651	0	56	17	1183	0	125
		19	909	0	72	20	1099	0	142
		23	751	0	31	5	261	0	101
		25	735	3	69	9	301	3	72
		28	518	0	97	22	2005	0	240
		29	390	0	47	12	756	0	160
		avg	763	2	62	16	946	1	124
		std	441	4	38	8	578	2	47
		1991	RR Gulch browse	2	558	0	23	27	1576
6	562			2	74	18	1113	2	124
7	729			0	48	18	1565	0	191
8	438			0	13	20	1748	0	190
9	639			0	44	24	1618	0	103
12	395			11	32	15	1354	5	216
15	336			0	32	6	313	0	80
18	409			2	49	16	1132	1	135
24	420			0	42	16	1065	0	134
27	419			3	52	5	158	0	44
avg	491			2	41	17	1164	1	133
std	119			3	16	7	516	2	51

Table 16. Continued.

YEAR	SITE	PLANT	TTL LEN	TTL FLR	TTL LVS	NO. LS	TLLSLEN	TTL SEED	MAX LS
1991	High Rye	4	221	0	7	15	1256	0	330
		6	224	0	10	22	1126	0	152
		7	500	0	13	25	1134	0	98
		10	453	0	18	32	1870	0	144
		14	295	4	16	6	384	1	99
		19	405	0	25	21	682	0	96
		21	322	0	15	17	799	0	111
		27	284	0	11	19	1063	0	120
		28	302	0	19	21	1144	0	125
		29	510	0	20	28	1958	0	145
		avg	352	0	15	21	1142	0	142
		std	102	1	5	7	460	0	66

¹TTL LEN = Sum of twig lengths (mm); TTL FLR = total flowers; TTL LVS = Total leaf clusters; NO. LS = Total number of long shoots; TLLSLEN = Total length of LS (mm); TTL SEED = Total seeds; MAX LS = Length of longest LS on branch (mm).

Table 17. Plant species encountered in quadrats (Daubenmire 1949) in study sites.

<u>SPECIES</u>	Butte	Deer Excl	Cattle Excl	Deer + Cattle	Burn	Unburn	Power Line ¹	Willow Creek ¹	RR Gulch	High Rye ¹
SHRUBS										
<i>Amelanchier alnifolia</i>	-	-	-	-	-	-	-	X	-	-
<i>Artemisia tridentata</i> <i>ssp. vaseyana</i>	-	-	-	-	X	X	-	-	-	-
<i>Chrysothamnus nauseosus</i>	-	X	X	X	X	X	X	-	-	X
<i>C. viscidiflorus</i>	-	X	X	X	-	-	-	-	-	X
<i>Purshia tridentata</i>	X	X	X	X	X	X	X	X	X	X
<i>Prunus virginiana</i>	-	X	X	X	-	-	-	-	-	-
<i>Pseudotsuga mensiesii</i>	-	X	X	X	-	-	-	-	-	-
<i>Ribes cereum</i>	X	-	-	X	-	-	-	-	-	-
<i>Rosa woodsii</i>	X	-	X	-	-	-	X ²	-	X ³	-
<i>Symphoricarpos albus</i>	-	-	-	-	-	-	-	X	-	-
GRAMINOIDS										
<i>Agropyron spicatum</i>	-	X	X	X	X	X	X	X ²	X	X
<i>A. trachycaulum</i>	-	-	-	-	-	-	-	X	-	-
<i>Agrostis stolonifera</i>	-	-	-	-	-	-	-	X ²	-	-
<i>Bromus inermis</i>	-	-	-	-	-	-	-	-	-	X ³
<i>B. tectorum</i>	X	X	X	X	X	-	X	X	X	X ²
<i>Carex filifolia</i>	-	-	-	-	X	-	X ²	-	-	X
<i>Distichlis stricta</i>	-	-	-	-	-	-	-	X ³	-	-
<i>Elymus cinereus</i>	-	-	-	-	-	-	-	X	-	-
<i>Festuca idahoensis</i>	-	X	X	X	X	X	-	-	-	-
<i>F. scabrella</i>	-	-	-	-	-	-	-	-	-	X
<i>Koeleria pyramidata</i>	-	-	X	X	X	X	-	-	-	X

Table 17. Continued.

<u>SPECIES</u>	Butte	Deer Excl	Cattle Excl	Deer + Cattle	Burn	Unburn	Power Line	Willow Creek	RR Gulch	High Rye
<i>Poa pratensis</i>	-	-	-	-	X	X	X ³	X	X	X
<i>P. secunda</i>	-	-	X	X	-	-	X ²	-	X ²	-
<i>Stipa comata</i>	-	-	-	-	-	-	X	-	X	-
<i>S. viridula</i>	-	-	-	-	-	-	-	-	-	X ²
unknown per. grass	-	-	-	-	-	-	-	X	-	X
FORBS										
<i>Achillea millefolium</i>	-	X	X	X	X	X	-	-	-	X
<i>Agoseris glauca</i>	X	-	X	-	-	-	-	-	-	-
<i>Allium cernuum</i>	-	-	X	X	-	-	X ²	-	-	-
<i>Antennaria microphylla</i>	-	X	X	X	-	X	-	-	-	X ²
<i>Apocynum androsaemifolium</i>	-	-	-	-	-	-	-	-	X ³	-
<i>Artemisia frigida</i>	X	X	X	X	X	X	-	-	-	-
<i>A. ludoviciana</i>	X	-	-	-	-	-	-	-	-	-
<i>Aster campestris</i>	-	-	-	-	-	-	-	-	-	X ³
<i>A. chilensis</i>	-	-	-	-	-	-	-	X ³	-	-
<i>A. conspicuus</i>	X	-	-	-	X	X	-	X ²	-	-
<i>Balsamorhiza sagittata</i>	-	-	-	X	-	-	-	-	-	-
<i>Gentaurea maculosa</i>	X	-	-	-	-	-	X	-	X	-
<i>Cirsium flodmanii</i>	-	-	-	-	-	-	X ³	X ²	-	X
<i>Comandra umbellata</i>	X	-	-	-	-	-	-	-	-	-
<i>Erigeron compositus</i>	-	-	-	-	-	X	-	-	-	-
<i>Erigeron sp.</i>	-	-	-	X	-	X	-	-	-	-

Table 17. Continued.

<u>SPECIES</u>	Butte	Deer Excl	Cattle Excl	Deer + Cattle	Burn	Unburn	Power Line	Willow Creek	RR Gulch	High Rye
<i>Eriogonum umbellatum</i>	-	X	X	-	X	X	-	-	-	X
<i>Erysimum asperum</i>	-	-	-	-	-	-	-	-	-	X ²
<i>Fragaria virginiana</i>	-	-	-	X	-	-	-	-	-	-
<i>Geranium viscosissimum</i>	-	-	-	-	-	-	-	-	-	X
<i>Heterotheca villosa</i>	-	-	X	X	-	-	X ³	-	-	-
<i>Linaria vulgaris</i>	-	-	-	-	-	-	-	-	-	X ³
<i>Lithospermum ruderales</i>	-	X	-	-	-	-	-	-	-	X ³
<i>Lupinus wyethii</i>	-	-	X	X	-	-	-	-	-	X
<i>Mentzelia laevicaulis</i>	-	-	-	-	-	-	-	X ³	-	-
<i>Opuntia polyacantha</i>	-	-	-	-	-	-	-	-	X ²	-
<i>Penstemon</i> sp.	-	X	-	-	-	-	-	-	-	-
<i>Phlox</i> sp.	-	-	-	X	-	-	-	-	-	-
<i>Potentilla gracilis</i>	-	-	-	-	-	X	-	-	-	X
<i>Sisymbrium altissimum</i>	-	-	-	-	-	-	X ³	-	-	X ³
<i>Solidago missouriensis</i>	-	X	-	-	-	-	X	X	-	X
<i>Taraxacum officinale</i>	-	-	-	-	-	-	-	-	-	X ³
<i>Tragopogon dubius</i>	-	X	-	-	-	-	-	-	-	-
Unknown annual forbs	-	X	-	-	X	-	-	-	-	X
moss	-	-	-	-	-	-	-	-	-	X ³

¹From Guenther (1989).²Additional species not reported by Guenther (1989).³Species reported by Guenther (1989) but not found in this study.

Table 18. Percent litter, bare ground, and rock at all study sites in September of 1990 and 1991, by canopy cover method (Daubenmire 1959).

Site		Litter	Bare ground	Rock
BUTTE	1990	34.5	8.1	4.0
	1991	54.7	31.8	5.4
DEER EXCL	1990	42.2	14.3	1.3
	1991	63.3	16.3	0.0
CATTLE EXCL	1990	40.5	27.4	1.6
	1991	54.6	26.0	1.6
DEER + CATTLE	1990	42.0	24.2	10.2
	1991	45.2	24.9	9.4
BURN	1990	13.0	34.6	20.3
	1991	21.0	50.3	25.7
UNBURN	1990	26.0	26.6	13.7
	1991	33.5	40.1	15.5
POWERLINE	1990	36.7	26.9	2.2
	1991	55.8	34.6	2.1
WILLOW CREEK	1990	31.5	29.3	1.2
	1991	43.9	36.2	6.5
RAILROAD GULCH	1990	42.5	26.3	0.1
	1991	49.6	38.6	0.2
HIGH RYE	1990	38.7	15.1	0.5
	1991	55.4	32.2	1.1

Table 19. Comparisons, measurements, and P levels discussed in CONCLUSIONS section.

contrast	type	mean	P<x	
browsing level (%)	1990	42	0.003	
	1991	52		
total bud density (bud/100 mm branch)	br.plant	10.4	0.11	
	unbr.plant	11.6		
	br.twig	8.6	0.01	
	unbr.twig	13.9		
flower bud density (bud/100 mm branch) (within browsed plants)	br.plant	0.3	0.001	
	unbr.plant	2.8		
	br.twig	0.25	0.56	
	unbr.twig	0.75		
leaf bud density (bud/100mm branch)	br. plant	6.3	0.61	
	unbr plant	8.0		
	br twig	4.4	0.05	
	unbr twig	8.5		
LS bud density (bud/100mm branch)	br. plant	3.9	0.01	
	unbr. plant	1.1		
	br. twig	4.4	0.75	
	unbr. twig	4.4		
treatment bud density (1991) RR Gulch	flowers cage	0.1	0.25	
	browse	0.4		
	leaves cage	8.7	0.88	
	browse	8.6		
	LS cage	2.4	0.11	
	browse	3.4		
	allbuds cage	11.1	0.45	
	browse	12.4		
	flowers cage	0.5	0.60	
	browse	0.0		
	deer excl.	leaves cage	7.8	0.15
		browse	6.5	
LS cage		1.6	0.12	
browse		2.3		

Table 19. Continued.

		allbuds cage	9.9	0.31
		browse	9.1	
		flowers rest	2.5	0.38
		clip	1.8	
Butte		leaves rest	6.3	0.55
		clip	5.4	
	LS	rest	1.2	0.38
		clip	1.9	
		allbuds rest	10	0.71
		clip	9	
browse level,	1990	burn	48.3	0.73
burn sites (%)		unburn	51.1	
	1991	burn	49.8	0.60
		unburn	61.2	
bud density,		flower 1990		
Dry Cottonwood		deer excl	4.7	0.001
sites		cattle excl	0.2	
(bud/100 mm		deer+cattle	0.7	0.14
stem)		leaves 1990		
		deer excl	8.0	0.24
		cattle excl	7.4	
		deer+cattle	7.7	0.21
	LS	1990		
		deer excl	1.1	0.001
		cattle excl	2.7	
		deer+cattle	4.8	0.002
		allbuds 1990		
		deer excl	13.9	0.007
		cattle excl	10.5	
		deer+cattle	12.3	0.20
browse level (%)	1990	cattle excl	45.5	0.21
		deer+cattle	55.2	
	1991	cattle excl	38.8	0.49
		deer+cattle	54.3	

Table 19. Continued.

LS number per branch	1990	27.2	0.05
	1991	19.9	
	browsed	23.9	0.90
	unbrowsed	23.2	
LS length (avg) per branch	1990	40.2	0.05
	1991	52.3	
total LS length (avg 90,91)	browsed	1156	0.67
	unbrowsed	1427	
LS len/mm stem	deer excl	1.4	0.06
	cattle excl	2.6	
	deer+cattle	4.6	0.001
	burned	1.0	0.67
	unburned	1.2	
live plant volume (m ³)	1990	3.2	0.04
	1991	1.7	
	deer excl	2.8	0.91
	cattle excl	8.3	
	deer+cattle	0.8	0.06
	burned	0.2	0.006
flower production	1990	35.8	0.01
	1991	14.5	
	browsed	80.0	.02
	unbrowsed	143	
	burned	0.8	0.001
	unburned	15.6	
seed success	1990	52.1	0.02
	1991	25.6	

Table 19. Continued.

protein (%)	leaves	1990	13.1	0.04
		1991	14.6	
		win91	10.3	0.000
	LS	1990	7.1	0.60
		1991	7.2	
		win91	6.5	0.01
canopy cover (%) perennial grass	90	burned	15.4	0.17
		unburned	12.6	
	91	burned	28.1	0.05
		unburned	20.0	
all herb. plants (avg. 90,91)	90	cattle ex	27.8	0.01
		deer+cattle	12.3	
	91	cattle ex	18.8	1.0
		deer+cattle	18.1	
		burned	25.1	0.01
		unburned	19.3	
non-bb shrubs	90	deer excl	3.2	0.46
		cattle excl	7.6	
	91	deer excl	5.2	0.40
		cattle excl	8.3	
bitterbrush density (plants/ha)	Butte		11.8	1.0
		deer excl	12.2	
		cattle excl	6.6	0.08
		deer+cattle	10.2	0.40
		burned	14.2	0.68
		unburned	14.4	
all shrub density (plants/ha)	burned	20	0.01	
	unburned	28.2		
chna dens	burned	2.8	0.008	
	unburned	0.4		
artr dens	burned	1.0	0.01	
	unburned	13.4		

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