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

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 ($P<0.0l$) 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.

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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 1964[1], 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

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[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

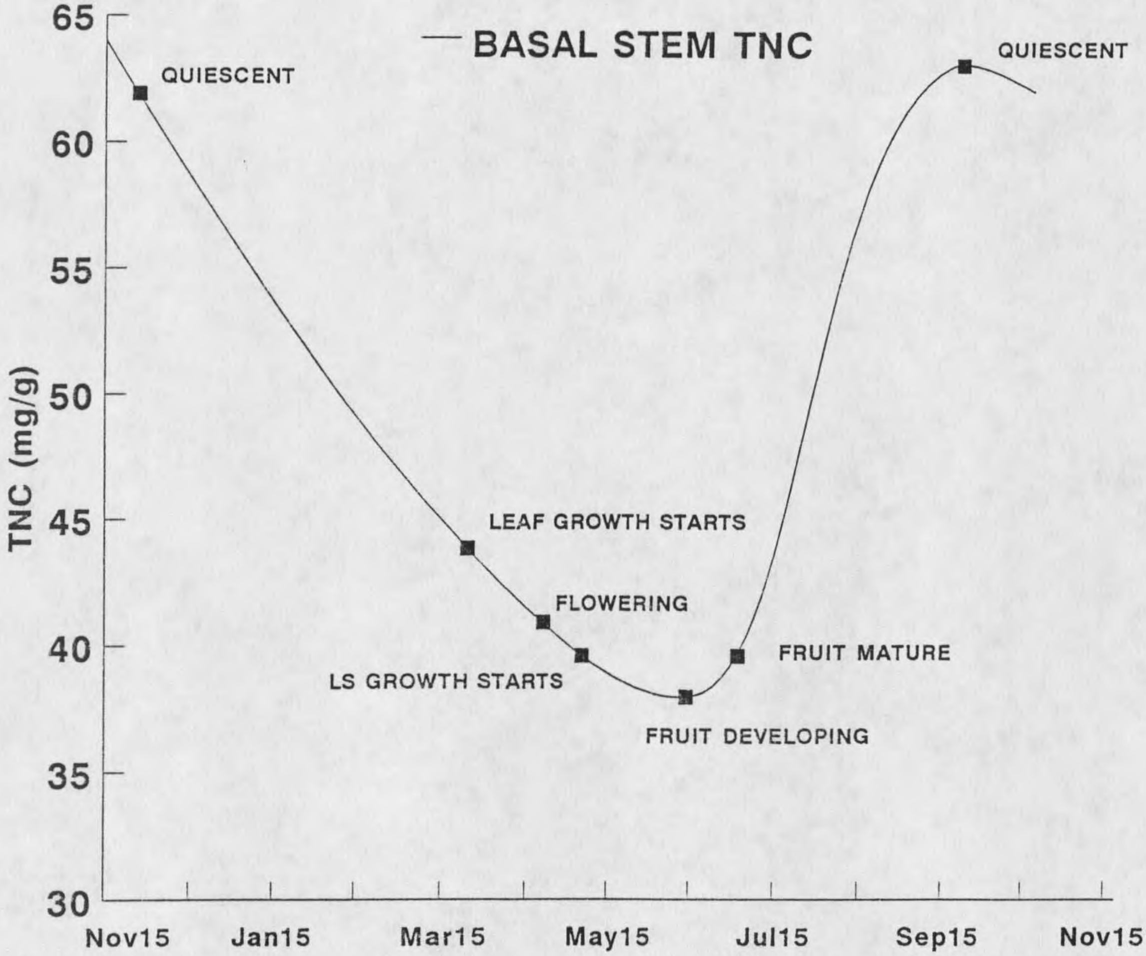

Fig. 1. Representative total nonstructural carbohydrate (TNC) concentration (mg/g) in basal stem region of bitterbrush (Menke and Trlica 1981) and average phenologic stage (Shaw and Monsen 1983). Leaf and long shoot (LS) samples were taken at or before seed maturity in early August for crude protein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

[1]1=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

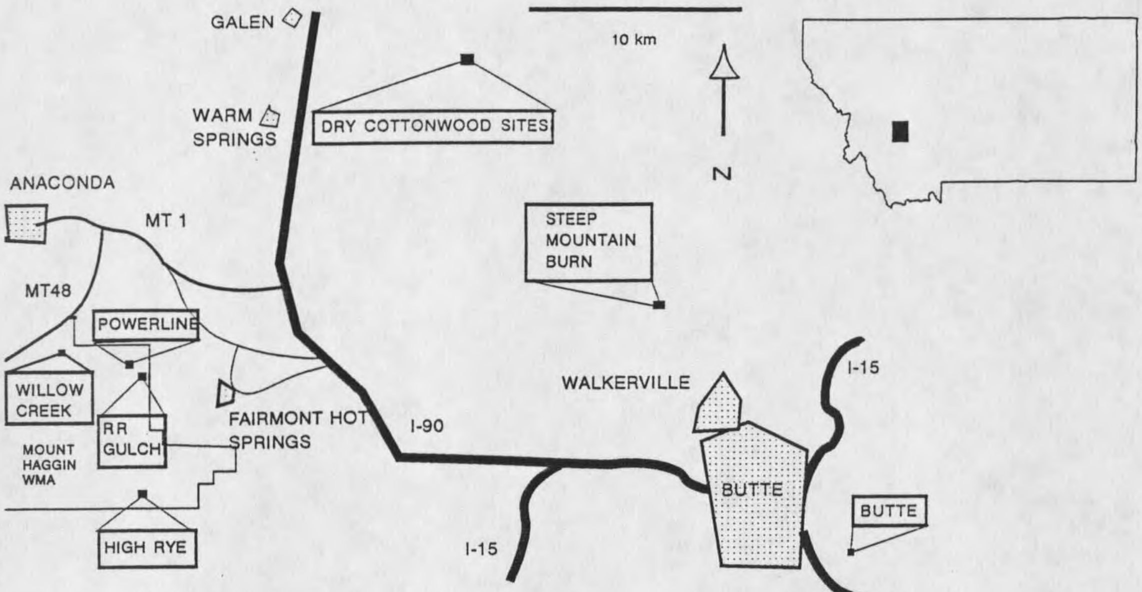

Fig. 2. Area map of study sites.

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

[1]From 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 rest-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