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Bitterbrush (Purshia tridentata) regeneration processes in a ponderosa pine stand at the Lick Creek study area

Kristi D. Pflug
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BITTERBRUSH *(PURSHIA TRIDENTATA)* REGENERATION PROCESSES

IN A PONDEROSA PINE STAND

AT THE LICK CREEK STUDY AREA

by

Kristi D. Pflug

B. S. The University of Montana, 1997

presented in partial fulfillment of the requirements

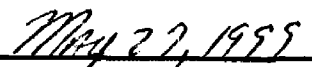for the degree of

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Bitterbrush *(Purshia Tridentata)* Regeneration Processes in a Ponderosa Pine Stand at the Lick Creek Study Area (77 pp.)

Director: Donald J. Bedunah $D.\,Bedunah$

   Lack of natural regeneration of bitterbrush (*Purshia tridentata*), an important browse species for elk and mule deer, is a problem throughout its range. To gain better understanding of the dynamics affecting bitterbrush seedling recruitment in a ponderosa pine (*Pinus ponderosa*) forest at the Lick Creek Study Area in the Bitterroot Mountains of Montana, the effects of four different forest management treatments (a control, and shelterwood cuts with no burn, a low fuel consumption burn, or a high fuel consumption burn) on flower production and seedling recruitment were monitored during 1997 and 1998. The impacts of animal predation on flower production, seed crop depletion and seedling survival were also observed using sets of caged, netted and uncaged plants. In addition, the viability of seeds from this area was compared with that of seeds from another local source.

   Flower production did not differ among forest management treatments in 1997 or 1998. Differences in flower numbers between caged and uncaged plants for both years ($p \leq 0.001$) indicated that browsing significantly impacted flower production. Differences in number of remaining seed among caged, netted and uncaged plants ($p < 0.050$) suggested that some reduction in seed crops may also be occurring due to seed depredation by rodents. No significant problems were found in seed viability or seedling survival on this site. The largest barrier to natural regeneration appears to be litter buildup on undisturbed sites, resulting in a lack of suitable locations for rodent caching and seed germination. No natural seedlings were observed in undisturbed areas. Therefore, disturbance of the organic horizon appears necessary if bitterbrush stands are desired as a future part of this landscape. It is my conclusion, based on data collected on natural seedling establishment and data on mature plants, that logging with or without low intensity fire could be beneficial to the stand by removing litter for seedling recruitment while still retaining a number of mature bitterbrush.

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INTRODUCTION

Antelope bitterbrush *(Purshia tridentata)*, one of the most wide ranging western shrubs, is found from New Mexico to British Columbia, and from Montana to California (U. S. Department of Agriculture 1937), in grasslands and open pine forests (Parish et al. 1996). In addition to its intrinsic value as an understory and grassland plant, bitterbrush is often an important food for mule deer *(Odocoileus hemionus)* and elk *(Cervus elaphus)*, and can be a major component of their winter diet. In a study by Austin and Urness (1983), bitterbrush was often the most heavily used browse species even when making up only 3% of the plant community. Moose *(Alces alces)*, bighorn sheep *(Ovis canadensis)*, yellow-pine chipmunk *(Eutamias amoenus)*, deermice *(Peromyscus maniculatus)*, chipping sparrow *(Spizella passerina)*, and blue grouse *(Dendragapus obscurus)* are among the other species that use bitterbrush for food and cover (Nord 1965, Gordon 1943; Mussehl 1960; Everett et al. 1978; Matlock-Cooley 1993).

During the last five decades, the lack of natural bitterbrush regeneration has become recognized as an increasing problem throughout much of its range (McNulty 1947, Sanderson 1962, Nord 1965, Peek et al 1978, Winward and Finley 1983, Fraas 1992, Clements and Young 1996, Young et al 1997). For example, in a study of bitterbrush in six forest types *(Pinus ponderosa-Juniperus scopulorum, Pinus ponderosa-Pseudotsuga menziesii, Pinus ponderosa-Abies concolor, Pinus flexilis, Pseudotsuga menziesii-Abies concolor, Abies concolor)* in Utah from 1957 to 1980, "*Purshia* population densities declined in all forest types over the study period... Average density

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loss ... was 35.9 percent in 20 years... Photographs taken in the initial and the 1978-80

sample demonstrate that many shrub individuals died and left no replacements" (Harper

and Buchanan 1983).

Bitterbrush stands in western Montana have shown a similar lack of regeneration

(Bunting et al 1985). Studies of the shrub-grass communities at and around the Mount

Haggin Wildlife Management Area in southwestern Montana have repeatedly stressed the

minimal amount of successful reproduction occurring in that region (Guenther 1989, Fraas

1992, Matlock-Cooley 1993). Such concerns have also arisen in the ponderosa pine

(*Pinus ponderosa*) forests of the Lick Creek Study Area in the Bitterroot National Forest

of western Montana. Mature bitterbrush is an important component of the understory

throughout much of this study area. However, until the 1997 growing season, very few

bitterbrush seedlings were observed on the study site. Ayers (1995) found only eight

bitterbrush seedlings in the area during the combined field seasons of 1993 and 1994.

Others have also reported little or no regeneration during the period of 1992 to 1996

(personal communication, Don Bedunah, Professor of Range Resource Management,

School of Forestry, University of Montana, Missoula, MT).

This investigation seeks to gain a better understanding of the causes of the lack of

bitterbrush seedlings at the Lick Creek study site. In order to test for and eliminate

possible causes of this lack of regeneration, I attempted to ascertain 1) if flowering was

occurring, and if there was a difference in flower numbers between several forest

management treatments; 2) if browsing had significant impacts on flower numbers; 3) if

there were significant differences in pre-seedfall seed depredation by ungulates, rodents or

birds, and insects; 4) if there were detectable differences in viability and germination between seeds collected from the site and seeds obtained from another local seed source that had been found to produce healthy seedlings under greenhouse conditions; 5) whether the Lick Creek study area sites and treatments offer suitable habitat for seed germination and seedling establishment; 6) whether browsing by either ungulates or rodents has noticeable impact on seedling survival rates during the first growing season; and 7) whether various physical site characteristics and forest management treatments have a significantly different effect on natural seedling establishment. Results from this study may help provide clarification of factors associated with lack of natural bitterbrush regeneration in the Lick Creek ponderosa pine forest and in similar bitterbrush stands throughout the western United States and Canada. This information could then suggest management action on restoration of regeneration in these stands, thus enhancing the future of this plant and benefitting the wildlife species which utilize it.

LITERATURE REVIEW

Species Description

Bitterbrush is a long-lived woody species, with ages of up to 162 years reported

from studies of annual ring counts from stands in California, Oregon, Colorado and Utah

(Giunta et al 1978). A member of the rose family, it has small (6 to 19 mm), three-lobed,

wedge-shaped leaves that vary in color from grayish to dark green and may be deciduous

or evergreen, depending on the ecotype (Giunta et al 1978). Small (8 mm) yellow or

cream flowers emerge in mid-spring to mid-summer, depending on latitude and elevation

(Giunta et al 1978). Flowers and buds tend to appear nearly simultaneously on plants in a

given stand, and last for one to 3 weeks. The flowers are perfect, regular, and five

petaled, and develop on second year or older plant growth (Shaw and Monsen 1983,

Giunta et al 1978). Cross-pollination by bees, wasps, or other insects is required for

successful seed production (Shaw and Monsen 1983, Giunta et al 1978). The fruit is a

pubescent, oblong achene, 6 to 12 mm long, with a persistent, pointed style, and contains

a single reddish or purple seed (Young and Evans 1983, Shaw and Monsen 1983, Giunta

et al 1978). The seed development and maturation process takes from 40 to 95 days.

Twig growth also begins during this period and persists until about one month after

seedfall. The duration and timing of flowering, seed production and leader growth vary

with latitude, elevation, and yearly fluctuations in climate (Shaw and Monsen 1983, Giunta

et al 1978).

Bitterbrush is considered a pioneering species (Klemmedson and Ferguson 1969),

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and is a symbiotic nitrogen fixer when inoculated with the actinomycete *Frankia* (Young et al 1997, Dalton and Zobel 1977, Righetti et al 1983). It grows best on coarse-textured, well-drained soils of neutral to moderately acid pH (Giunta et al 1978), with south slopes tending to support more bitterbrush stands than other aspects (Guenther et al 1993, Tew 1983). However, bitterbrush is not limited to these "ideal" sites. It grows in a wide variety of soils, elevations, latitudes, climates, and vegetation communities throughout western North America (Giunta et al 1978). Adaptation to this diversity of habitats, as well as to insects and fire, has led to a wide array of ecotypes with differing leaf color, shape and persistence; nutritive content and palatability; rate of growth; growth form; disease and insect resistance; and tolerance for cold, heat, shade, drought and fire (Hormay 1943, Nord 1965, Stanton 1959, Edgerton et al 1983, Giunta et al 1978, Alderfer 1977, Shaw and Monsen 1983, Davis 1983). Experiments in common gardens have shown that variations in these characteristics reflect parental seed source more than current habitat conditions (Edgerton et al 1983, Giunta et al 1978).

Growth form varies from tall and treelike to low and layering (Giunta et al 1978). The upright form has a crown arising from a small number of basal stems, and accumulates new growth primarily in the upper part of the plant. The decumbent form has many basal branches and acquires new growth throughout its crown (Shaw and Monsen 1983). Decumbent forms tend to bear less seed than erect forms (Shaw and Monsen 1983), often resorting instead to spreading via low branches that take root where they touch the ground (Giunta et al 1978). These two examples represent the extremes in bitterbrush growth form, with an entire gradient of forms occurring inbetween. In their survey of bitterbrush

stands of the northern Rocky Mountains of Montana and Idaho, Bunting et al (1985) found representatives of this entire spectrum, with the lowest, layering individuals being less than 1 m tall at maturity, and the tallest (non-layering) growing to more than 1.5 m high.

The growth form of a bitterbrush plant may affect the manner in which it sprouts. Columnar and subcolumnar forms may resprout after disturbance from a mass of ground level dormant buds around the stem, or from a callus of meristematic tissue formed above ground level beneath the bark (Blaisdell and Mueggler 1956, Bunting et al 1985, Driver 1983). Driver (1983) notes that this description is similar to that given by Daubenmire (1974) in describing a lignotuber, a budding structure often found in woody plants of areas with high fire frequency. Decumbent forms may resprout following disturbance from both the central bud mass and from bud masses formed at layering points (Bunting et al 1985, Giunta et al 1978). Whether or not a plant will resprout following disturbance may be affected by destruction of the sprouting organ (Edgerton 1983), phenological stage at the time of disturbance, carbohydrate reserves, and age (Martin and Driver 1983), as well as genetic factors (Driver 1983). Resprouting after fire may be influenced by other factors in addition to these, as covered in the "Fire and Bitterbrush" section of this paper. In addition to resprouting after disturbance, bitterbrush may also produce aerial stems arising from lateral roots. This type of resprouting is considered rare (Giunta et al 1978).

Browsing Dynamics

Bitterbrush often constitutes a major portion of elk and mule deer winter diet (Austin and Urness 1983, Gruell 1986), and is thought to be one of the few species able to maintain ungulate weight when used as the main food source (Giunta et al 1978). These animals find the leaves and terminal twigs, or leaders, extremely palatable, as well as nutritious. Reports have varied as to the response of bitterbrush to differing levels of browsing. Tueller and Tower (1979) and Peek et al (1978) found large decreases in productivity and increases in dead matter when plants were completely excluded from browsing. However, Buwai and Trlica (1977) found that vigor and biomass greatly decreased under steady browsing. The answer to these and other apparently conflicting reports is probably related to the amount and intensity of browsing. Giunta et al (1978) state that while mature bitterbrush must be browsed in order to maintain vigor, removal of more than 60% of leader growth per year may prove detrimental. They also state that timing of browsing is important, with winter consumption being less detrimental than use during the growing season.

Seed Production

Wild bitterbrush begin bearing seed when they are between eight and 20 years old, depending on local conditions (Giunta et al 1978). For flower and seed production to occur, the levels of physiological stress a plant has experienced during the current and preceding growing seasons must not have depleted plant resources. Studies of bitterbrush have shown that seed production is the time of lowest carbohydrate reserves, indicating

that this plant requires a large amount of carbohydrates to carry out this phase of the reproductive cycle (Fraas 1992, Menke and Trlica 1981, Shaw and Monsen 1983). Environmental factors noted to affect bitterbrush health (and, directly or indirectly, seed development) are summer precipitation, amount and frequency of browsing, and herbaceous competition (Sherman and Chilcote 1972, Giunta et al 1978, Martin and Driver 1983, Ferguson and Medin 1983). Levels of these factors ideal for successful seed production may come together rather infrequently, depending on location (Giunta et al 1978, Martin and Driver 1983). In Utah, seedcrops have varied by site from one to six year intervals (Deitschman 1974). Timing of seed maturation is also affected by locality and climatic conditions, with hot, dry sites ripening seed more rapidly (Meyer and Monsen 1989). Late spring or summer freezes can ruin entire seed crops (Evans et al 1983). Insects also take their toll, often significantly reducing both seed production and viability (Shaw and Monsen 1983).

Seed/Animal Dynamics

Almost all natural bitterbrush regeneration comes from the caches (buried seed stores) of rodents (Scholten 1983, Young and Young 1986), including chipmunks, squirrels, and deer mice (Vander Wall 1994, Clements and Young 1996). These caches suit the germination needs of bitterbrush seeds (discussed more fully in the next section) by offering a means of removing the germination inhibitor and of stratification over winter. Rodents remove the papery outer husks, which contain a germination inhibitor (Hormay 1943), and bury the seeds in the soil in groups of approximately 10 to 100 (Hormay 1943,

Evans et al 1983), depending on the type of caching involved. Some seeds are stored in larders within burrows ("larder hoarding") (Vander Wall 1990, Clements and Young 1996), which tend to be too deep in the ground for germination to occur (Matlock-Cooley 1993). Others are disseminated throughout the home range of the animal ("scatter hoarding") and buried one to two inches deep (Vander Wall 1990, Clements and Young 1996, Evans et al 1983). Scatter hoarding is important in spreading bitterbrush seed beyond the immediate vicinity of the parent plant (Martin and Driver 1983). The rodents may use these scatter caches for later consumption, but a number of caches are usually forgotten or left over, remaining in the ground throughout the winter. This provides natural stratification for the seeds (Evans et al 1983). The forgotten caches thus may become a source of bitterbrush seedlings (Clements and Young 1996, Sanderson 1962, Scholten 1983, Vander Wall 1994). Buildup of undecomposed organic matter tends to discourage this type of caching (Sherman and Chilcote 1972) and lead to larder caching only (Matlock-Cooley 1993).

Rodent population dynamics significantly affect whether or not these scatter hoards will produce seedlings. Low numbers of rodents may result in insufficient caching and dissemination of seed, but high numbers (especially when combined with a small seed crop) may result in consumption of most available seed and any resulting seedlings, and even in destruction of mature plants via stem girdling and consumption of the roots (Giunta et al 1978, Martin and Driver 1983, Hubbard 1965, Young et al 1997). In addition, many of the seeds that are cached but not consumed may be broken or otherwise nonviable. Studies by Evans et al (1983) showed that caches which averaged 12.5

seedlings also contained an average of eight ungerminated bitterbrush seeds per cache, with an average of one out of those eight that was not broken or empty. Incubation of these few entire seeds produced no germination.

Birds also eat bitterbrush seed, but usually to a much lesser extent than rodents (Giunta et al 1978). Some observers have also cited large numbers of seed harvested by ants (Young and Evans 1978, Brown et al 1979). However, compared to rodents, both birds and insects are much less frequently mentioned in relation to bitterbrush seed dynamics than rodents.

Seed Germination Physiology

A bitterbrush achene is composed of a dry paper-like covering made of residual flower parts, and the embryo, radicle, hypocotyl, and cotyledons, which are all covered by the seedcoat and pericarp (Young and Evans 1983). The paper-like covering must be removed in order for germination to occur, as trials in petri dishes have shown it usually inhibits the germination process (Hormay 1943, Evans et al 1983).

In addition, seed germination in bitterbrush requires certain species-specific environmental conditions to be met. The seeds must have a cool, moist overwintering in order to break dormancy (Meyer & Monsen 1989, Young and Evans 1976, 1981). Without this period of cool moisture (called stratification), only 5 to 20 percent of a seed crop will germinate (Young and Evans 1983). Many studies have concluded that under laboratory conditions, a moist prechill of four to six weeks at 2 to 5° C is sufficient for breaking dormancy in seeds from most sources (Meyer and Monsen 1989, Young and

Evans 1976, Meyer et al 1986, McHenry and Jensen 1967). Because the length of the actual cool-moist period experienced tends to vary from site to site under natural conditions, one might assume that seeds from different sources would have inherently different requirements for stratification length. However, in experiments with seeds from 28 different bitterbrush populations from differing habitats, Meyer and Monsen (1989) found no such relationships, leading to the conclusion that seasonal fluctuations in climate may have more effect on the degree of dormancy than do overall climatic norms for an area. Exposure to temperatures much above $6°$ C for periods of more than one day will either increase the level of dormancy (causing the seed not to germinate that growing season) or trigger premature germination (resulting in death if temperatures dip back below freezing) (Meyer & Monsen 1989). This indicates that under natural conditions it is very important to maintain a continual snowpack throughout the winter until time for germination in the spring.

Bitterbrush embryos will often germinate when dissected from the rest of the seed, implying that dormancy may be imposed by the seedcoat (Young and Evans 1983, Meyer and Monsen 1989, Hormay 1943). Most researchers agree that dormancy is probably maintained until enough oxygen is allowed to reach the embryo for germination to occur (Meyer and Monsen 1989, Come 1967, Young and Evans 1976, 1983). Bitterbrush seeds are able to imbibe water during dormancy (Young and Evans 1983). Depending on temperature, this water may carry the required oxygen to the embryo. Oxygen is more soluble in water at lower temperatures (Streeter 1935), and the embryo also needs less oxygen at lower temperatures (Come and Tissaoui 1972). In addition, Young and Evans

(1976, 1983) and Meyer and Monsen (1989) have inferred that there are germination inhibitors in the seedcoat which bind available oxygen to phenolic compounds. These germination inhibitors would be more effective at preventing germination when oxygen levels are low, since they would be more likely to capture most of the available oxygen. Thus, cold temperatures and moisture appear to work together to provide oxygen levels sufficient to meet embryo requirements and to overload oxygen trapping compounds in the seedcoat.

Some researchers have also concluded that periods of dry afterripening at warm temperatures (such as would be found on many bitterbrush sites after seedfall) may reduce dormancy levels, with greater periods of afterripening producing lower dormancy (Meyer and Monsen 1989). This even further implies that dormancy and germination processes are heavily influenced by seasonal site-specific climatic conditions. Laboratory results are therefore not necessarily good predictors of the field germination process. Investigations into natural field germination must take into account all of the fluctuating moisture and temperature conditions mentioned in this section, as together they constitute a complex and interlocking system for seed germination or lack thereof (Young et al 1997, 1993).

Rodent caches serve as an excellent system to meet seed stratification requirements under natural conditions. Burial of the seeds helps ensure greater moisture than if seeds were left on the soil surface (Young et al 1993). Snowpack alone may occasionally provide adequate stratification for surface-lying seeds, but consequent germinant survival is rare (Young et al 1993). In general, researchers agree that seeds must be buried for seedling establishment to occur (Meyer and Monsen 1989, Basile and Holmgren 1957,

Young et al 1993).

Hydrogen peroxide soaks have frequently been suggested as an alternative for stratification when undertaking artificial seeding (see, for example, Young and Young 1986). However, Meyer and Monsen (1989) found that hydrogen peroxide soaks did not break dormancy completely, and that the caustic properties which allowed this chemical to partially break down dormancy barriers apparently harmed the embryo itself. They also found that water soaks prior to stratification reduced the length of stratification required, but could not be used as a replacement for stratification.

Preliminary observations indicate that dormant bitterbrush seeds can survive to form a seedbank if germination conditions are not met. Giunta et al (1978) noted that seed stored for up to 10 years in a dry, unheated warehouse had 85 to 95 percent germination in subsequent tests. Young et al (1993) found that seeds which did not receive sufficient moisture for field stratification remained dormant in the seedbed, without rotting. Another experiment (Young et al 1997) found that some seeds planted in the field did not emerge until the second growing season after planting.

Natural Seedling Establishment

Several researchers have documented that large amounts of natural bitterbrush seedling establishment are a rare occurrence (Giunta et al 1978, Young et al 1993). Establishment tends to be variable in both time and space, with few seedlings per year or per hectare (Fraas 1992, Nord 1965, Ferguson and Medin 1983). Even with artificial seedings, percent seedling survival over the first growing season is quite small. Ferguson

and Basile (1967) found that although 68 percent of planted seed spots germinated, only 18 percent of these had successful seedling establishment at the end of the growing season. Monsen and Shaw (1983) found only one mature plant for every 120 seeds planted–a return rate of 0.8 percent.

Natural germination tends to occur soon after snowmelt, situating it at the juncture of adequate soil moisture and lowered risk of frost (Meyer and Monsen 1989, Ferguson 1972, Nord 1965). Seedling establishment rates thereafter are still highly correlated with soil moisture and temperature gradients (in terms both of late frost and exceedingly high heat) (Bunting et al 1985, Ferguson 1972). Surprisingly, intraspecies competition among seedlings within a cache does not appear to be detrimental to seedling survival. Rather, the success of a seedling group appears to be positively correlated with the number of seedlings it contains. This may be due to mutual shading, which helps to reduce soil temperature in the immediate vicinity of the seedling group. This pattern continues into subsequent growing seasons, at least through the third year (Ferguson and Basile 1967). Single seedlings have occasionally been observed in cow tracks, where presumably cattle have displaced seeds and then buried them in the soil as they step on them (Bunting et al 1985). However, this is relatively rare, and given the findings of Ferguson and Basile (1967), these plants would be expected to have a lower survival rate than those which germinate via the usual process of rodent caching.

Interspecific competition for soil moisture is considered a significant factor in seedling survival. This is especially true when the competition comes from herbaceous plants or invasive annuals such as cheatgrass (*Bromus tectorum*) or knapweed (*Centaurea*

maculosa) (Ferguson and Medin 1983, Guenther et al 1993, Hubbard 1956, Monsen and

Shaw 1983, Young et al 1993, 1997). Predation by rodents, rabbits and insects is also

frequently associated with seedling demise, particularly when the seedlings are still in the

cotyledon stage (Bunting et al 1985, Clements and Young 1996, Evans et al 1983). In

addition, seedlings may be trampled and crushed by wildlife, livestock or people (West

1968, Matlock-Cooley 1993).

Successful large-scale establishment of seedlings thus depends on the simultaneous

or sequential occurrence of a number of conditions which produce favorable seed

production, seed germination, and seedling survival. These factors (as discussed in detail

in this and the preceding three sections) come together fairly infrequently, resulting in

intervals between successful establishment of up to 20 years or more (Giunta et al 1978).

Fire and Bitterbrush

The role fire plays in the ecology of bitterbrush is intricate and highly

controversial. A review of existing literature regarding this subject requires careful

analysis of the various issues presented in order to sort through what initially appears to be

highly contradictory information. Some examples of the many apparently contradictory

reports follow. Nord (1965) recorded that 5 to 25 percent of bitterbrush resprouted after

5 wildfires in California, while another 8 wildfires resulted in no resprouting. Hormay

(1943) observed that 25 percent or more bitterbrush resprouted in only one post-wildfire

site in California. Leopold (1950) noticed that repeated fires at one site in California

stimulated bitterbrush growth, whereas fires at another site obliterated the species.

Blaisdell (1950) reported that bitterbrush density even 15 years after burning was negatively correlated with burn intensity, and that even light burns had only two thirds the number of plants of unburned sites. Driver (1983) noted 40 to 100 percent resprouting from prescribed spring burns in central Washington. This area had a pre-European settlement fire interval of 6.5 to 10 years. In an adjacent summer wildfire area, Driver (1983) found only 5 percent resprouting even three years after the burn. Martin (1983) found bitterbrush mortalities ranging from 77 to 100 percent for prescribed burns in central Oregon, but also noticed substantial reestablishment from seedlings.

Much of the apparent discrepancy in response appears to be related to whether the ecotype and individuals involved have specialized resprouting buds, whether those buds are destroyed in the fire, and whether the plant has enough energy reserves to resprout if it does have surviving buds. Britton and Clark (1985) noted that many (especially older) reports on burns and bitterbrush do not document these factors and the circumstances that would impact them.

Presence or absence of specialized buds for resprouting appears to be connected with past fire history of the community type and site involved. Bitterbrush is often found in communities with big sagebrush. Big sagebrush does not survive fire of any intensity or any form (Britton and Clark 1985, Blaisdell 1953). Murray (1983) noted that burning sagebrush-grass communities throughout the western United States tends to have a negative influence on the bitterbrush in those stands, which tend to be killed or to have low resprouting. In the two examples cited earlier from Leopold (1950), the area where bitterbrush was eliminated by fire was in a sagebrush stand, while the area of recurrent

fires which produced resprouts was in a ponderosa pine forest.

The presence of bitterbrush in pre-European high fire frequency pine forests has been a subject of some dispute. Many early hypotheses about pre-European settlement fire intervals in areas where bitterbrush is a climax species, and about the pre-European presence of bitterbrush in areas known to have had frequent fires, were based solely on initial (often poorly documented) reports of bitterbrush response to burns (see Wright 1979). These hypotheses have gone on to become assumptions in the minds of many. Driver et al (1980), Martin (1983), and other more recent works have questioned these assumptions, citing high fire frequencies as late as the 1920s in pine types where bitterbrush is recognized as a longstanding member of the community (Daubenmire and Daubenmire 1968). Driver et al (1980) observed that recent fires on their study site in the eastern Cascades significantly reduced bitterbrush populations, and that it took 15 to 20 years for the species to reestablish. However, core analyses of shrubs on the site showed that the oldest plants were 75 to 90 years old. Fire history studies of the area had indicated mean fire intervals of 7 to 10 years until 1927 (Driver et al 1980). This means that these oldest plants had in some way managed to maintain productivity in the presence of fire, perhaps through fire resistance or sprouting. In analyses of photo pairs (dated 1870 through 1982) of sites throughout the Intermountain western United States, Gruell (1986, 1982) observed that bitterbrush had increased in number, size, and distribution during the years of fire suppression. However, Gruell's captions on three of these early (1907 to 1909) photos indicate that bitterbrush was present on sites with known frequent fire intervals. This would corroborate statements by early observers (recorded in Weaver

1957) that various shrub species were present in the pine forests of the late 1800s, but were limited from attaining their present size and density by the frequent recurrence of fire (see also Johnson and Smothers 1976 and Rice 1983).

Martin and Driver (1983) have hypothesized that frequent fires on a given site might cause both long term and short term genetic selection for plants with sprouting capabilities. Davis (1983) noted that in many studies sprouting ability varied not only between ecotypes but also between individuals in an ecotype. Blaisdell and Mueggler (1956) found more postburn sprouting on a site that had previously been burned in 1939 than on a similar site with no recent fire history. Driver et al (1980) found that bitterbrush sprouts in their prescribed burn area on a ponderosa pine forest came from lignotubers located at or slightly below ground level. These lignotubers, or budding centers at the root crown, must not be destroyed if the plant is to resprout successfully (Giunta et al 1978). Soil texture and moisture, season of burning, and fire intensity all play a part in whether a fire destroys this vital budding organ (Rice 1983). Soils of higher bulk density and coarse fragment content have a greater potential to transfer heat to the root crown and are less likely to maintain moisture which could initially absorb heat and provide cooling action via vaporization. Soils with high organic matter or clay content transfer heat poorly, and also maintain more moisture (Driscoll 1963, Rice 1983, Martin and Driver 1983). Soil moisture is also affected by season of burn and local weather conditions, as is plant moisture. In general, spring burns appear to coincide with the greatest period of soil and plant moisture (Driver 1983), followed by fall and then summer (Bunting et al 1985, Blaisdell and Mueggler 1956, Clark et al 1982). Finally, high

intensity fires usually damage the sprouting organ and result in less sprouting than low intensity fires (Bunting et al 1985, Murray 1983, Rice 1983, Blaisdell 1950, 1953). Fire intensity is affected by season due to the soil and plant moisture factors noted above (Bunting et al 1985), but perhaps more importantly, after decades of fire suppression, it is also immensely affected by the amount of fuel buildup. Driver et al (1980) found that as the frequency of fire decreased, the intensity of the fires increased. Their research led them to believe that bitterbrush with the capability to sprout could survive frequent low intensity fires, but not infrequent high intensity fires.

Lastly, even if a plant does have budding capabilities which are not destroyed during burning, it still must have sufficient carbohydrate reserves if it is to resprout successfully. Carbohydrate levels are lowest in midsummer after seed production, taking the rest of the summer to recover (Menke and Trlica 1981, Bunting et al 1985). Thus, for both soil moisture and carbohydrate reasons, spring or fall burns appear to give the best chance for survival. Other pressures such as insect defoliation or excessive browsing may also deplete the energy stores needed for vigorous sprouts (Martin and Driver 1983, Hormay 1943).

Some authors have mentioned growth form as an important factor in achieving sprouting, claiming that decumbent forms sprout more readily than upright forms (Bunting et al 1985, Nord 1965). However, other studies have indicated that while form does influence the manner in which a plant sprouts, both forms may have ground level budding organs and thus have the potential to resprout following disturbance (Blaisdell and Mueggler 1956, Bunting et al 1985, Driver 1983).

Many more recent studies have indicated that fire can be very beneficial in obtaining seedlings. Fire reduces litter buildup and provides an initial reduction of competing vegetation, both of which are crucial for seedling establishment (Bunting et al 1985). Sherman and Chilcote (1972) and Matlock-Cooley (1993) found that rodent caching of bitterbrush seed was largely inhibited by buildup of litter and duff due to fire suppression. Sherman and Chilcote (1972) went on to predict that declines in bitterbrush populations could be expected if this trend were not reversed. An intense fire is more likely to effectively reduce herbaceous competition (Blaisdell 1950, Driver et al 1980), but some reduction is provided by low intensity fire as well. Perennial grasses may experience a period of accelerated growth due to nutrient release immediately after a fire, but this growth rate soon diminishes, allowing shrubs to reestablish dominance (Daubenmire 1952, Sherman and Chilcote 1972). Martin (1983) surveyed 21 prescribed burn units and found a general trend of increasing seedling establishment over time. The units assessed varied from three to eight years postburn at the time of the investigation.

In addition to its direct effects on sprouting, stand vigor and seedling establishment, fire or lack thereof in conifer stands may have a significant impact on mature bitterbrush vigor and the regeneration process via the density of tree canopy cover. Harper and Buchanan (1983) observed that in photos and records taken over a 21 year period in Bryce Canyon National Park (Utah), steady increases in forest canopy cover were accompanied by steady decreases in shrub understory, including bitterbrush. McNulty (1947) believed that the decline in bitterbrush was caused by overgrazing. However, Harper and Buchanan (1983) noted that domestic animals had been excluded

from the park since 1937, and that deer populations had declined throughout the period of their study (1957-1980). This implied to them that continuing increases in shade brought on by community succession under fire suppression were more responsible for loss of bitterbrush density in their area than was browsing pressure.

Some have suggested logging as an alternative form of disturbance for moving litter and reducing canopy cover and competition. Logging does remove some of the thick conifer canopy that has developed during fire suppression, allowing decreased shading and competition (Gruell 1982, Edgerton 1983). However, logging may result in less selection for more vigorous bitterbrush plants with less dead matter, which is an important potential benefit of low intensity fire. As in burning, logging operations that destroy the root collar will destroy any sprouting potential in bitterbrush (Edgerton 1983).

In conclusion, it seems likely that before European settlement, especially in pine forests, fire may have led to widely spaced, small bitterbrush (Rice 1983) with genetically selected sprouting capability (Driver et al 1980). Although fire suppression led to an initial increase in the size and density of bitterbrush (Driver et al 1980, Johnson and Smathers 1974, Weaver 1957), it has also resulted in more decadent stands, with little seedling establishment, senescent plants, and possibly even loss of selection for sprouting capability (Driver et al 1980, Sherman and Chilcote 1972, Martin and Driver 1983, Bunting et al 1985). When wildfires do occur in this post-fire suppression era, they tend to be of an intensity that consumes the stand and destroys any remaining vestiges of sprouting capability (Rice 1983). If vigorous stands of bitterbrush are to be maintained in the future, it appears that low intensity fire must be returned to their habitat in those areas

where fire was common before the era of fire suppression (Bunting et al 1985).

STUDY SITE

Selection

The Lick Creek Study Area offers a unique opportunity to investigate factors affecting bitterbrush regeneration. It has been the site of ongoing bitterbrush research since 1992, and detailed records from permanent study plots allow data comparison to extend outside the two year data collection period of my own study. In addition, management records exist for this ponderosa pine/Douglas-fir stand throughout most of its period under European administration (about 100 years), including records of tree basal area and stand entry dates, as well as many photos of the site taken approximately every 10 years since 1909 (Gruell et al 1982, Menakis 1994). A ponderosa pine forest restoration project was initiated in the area in 1992 (in conjunction with the original bitterbrush research), and offers additional resources for canopy and forest management data. These many sources of information can facilitate a depth of analysis not possible at many other sites.

History and Previous Project Synopsis

Before European management began, fires ignited by lightening or Native Americans (Gruell et al 1982, Barrett 1980, 1981) burned through this area at an average interval of 7 years and a range of 3 to 30 years (Gruell et al 1982, Arno 1976). These fairly light intensity surface fires maintained parklike stands of large ponderosa pine trees with open understories (Gruell et al 1982, Arno 1976). Studies from this and nearby sites

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reveal that these frequent surface fires date back to at least 1500 (Gruell et al 1982). The

last fire of this type on this site occurred around 1890 (Gruell et al 1982), and fire was

then excluded from the area for the next 100 years (with the exception of a light

underburn on a small portion of the area in 1981 [Menakis 1994]). Fire history resumed

when prescribed burns were carried out in May 1993 by personnel from the U. S. Forest

Service (Ayers 1995).

The US Forest Service undertook a timber sale in part of the current study area

from 1906 to 1911. Before the cutting began, the stand consisted primarily of mature and

old-growth ponderosa pine, ranging from 200 to 400 years old and averaging 124 trees

per hectare. The Forest Service removed about half of these trees and 63% of the basal

area in a selective cutting which targeted large trees (Gruell et al 1982). Another portion

of the current study area, which was private land at that time, was clearcut during the

same time frame (Menakis 1994; personal communication, Mick Harrington, Research

Forester, Fire Sciences Laboratory, Missoula, MT). Various parts of the study area were

reentered for thinning at different times over the next 60 years. These thinnings took

place in approximately 1952 to 1956 and 1962 to 1966, but not all areas were thinned in

the same manner or at the same time. After 1966, thinning treatments and dates became

even more differentiated, with records often being unclear as to the extent and area of the

treatments involved. The last such entry was apparently in 1980 (Menakis 1994).

According to historical documents researched by Gruell et al (1982), elk and mule

deer populations at this site have fluctuated greatly over the past 100 years. They were

apparently numerous in the late 1800s (Koch 1941), but declined drastically by 1913

(Janson 1967). The populations of these and other ungulates has since recovered, with

mule deer numbers peaking in the 1950s and elk numbers continuing to increase steadily

(personal communication, John Firebaugh, Biologist, Montana Dept. of Fish, Wildlife and

Parks, Missoula, MT). As for domestic animals, sheep were permitted to graze the area

until 1912, and use was apparently heavy toward the end of this grazing period (Gruell et

al 1992). Cattle grazing was permitted until 1992 (Ayers 1995).

In 1992, the U.S. Forest Service Intermountain Fire Sciences Laboratory, the

Bitterroot National Forest and the University of Montana initiated a cooperative study at

the Lick Creek Study Area to determine overstory and understory plant response to

ecosystem restoration research treatments. Roughly 49 ha of the area was divided into 12

units of approximately 4 ha each. These units were then randomly assigned one of four

treatments (a control, and shelterwood cuts with no burn, a low fuel consumption burn, or

a high fuel consumption burn) (see Appendix A). Each of these units was also assigned

twelve 0.04 ha plots, marked with a metal stake so that vegetation could easily be

surveyed and the location of various species of interest in each plot recorded by azimuth

and distance from the stake. The shelterwood cuts were completed in the fall of 1992,

reducing both basal area and trees per acre by about 50 percent to achieve an end average

of 13.1 m^2/ha in basal area and 277 trees per hectare on those treated units. Prescribed

burns were completed in May of 1993. Because of prevailing weather patterns, fuel

consumption, percent of area burned, and burn intensity did not actually differ

significantly between burns (Ayers 1995) (See Appendix B). This current study on

bitterbrush regeneration began in May of 1997.

Physical Description

The Lick Creek Study Area (Lat. 46°5' N., long. 114°15' W.) is located in the Bitterroot National Forest, 21 km southwest of Hamilton, Montana and 3 km north of Lake Como. Elevations range from 1311 to 1402 m, with slope varying from 5 to 70 percent. Aspects are generally southeast, south and southwest. The mean annual precipitation is around 56 cm, with approximately 50 percent in the form of snow. Soils are of granitic till parent material and are shallow to moderately deep, with some poorly drained areas and clay soils at the lowest elevations (Gruell et al 1982). The wettest months are normally May and June and the driest month is usually July. Average maximum temperature in July is 28.8° C, and average minimum temperature in January is -8.3° C (Menakis 1994).

Most of the habitat types (Pfister et al 1977) for the area studied are Douglas-fir (*Pseudotsuga menziesii*) types, with grand fir (*Abies grandis*) types also found on a very small percentage of the lower units (Gruell et al 1982, Menakis 1994). The dominant overstory before treatments was Douglas-fir and ponderosa pine *(Pinus ponderosa)*, with potential site indexes for these two species averaging 16 m tall at age 50 (Pfister et al 1977, Gruell et al 1982).

The Lick Creek area is considered an important local winter and spring range for mule deer and elk (U. S. Department of Agriculture, Forest Service informational brochure). White-tail deer and moose also frequent the area.

Observations during the two field seasons of this project indicated that bitterbrush

growing season tends to begin in early May and continue into late September. Flower

formation and anthesis tend to occur in late May through mid June, and seeds mature in

mid to late July, depending on weather conditions at the time.

METHODS

For successful bitterbrush regeneration, there must be flower and seed production, seed germination, and seedling survival. I examined each of these processes by:

•Counting flowers in designated plots on all forest management research treatments for two consecutive growing seasons.

•Tetrazolium viability tests and laboratory germination tests on seed collected from the study site, compared to seed obtained from another local seed source known to produce healthy seedlings under greenhouse conditions.

•Measuring germination and first growing season survival of planted seeds from a local seed source (known to be viable) on the different forest management treatments.

•Surveying for natural seedlings and recording ecological site data in designated study plots on all forest management research treatments.

In addition, I estimated the impact of browsing and predation on flower and seed production and on seedling establishment by:

•Counting flowers on paired sets of caged and uncaged plants in each forest management research treatment for two growing seasons.

•Comparing seed counts at the beginning of seed formation to remaining seed count three weeks later for caged, netted and uncaged plants.

•Comparing survival of caged to uncaged bitterbrush germinants established by seeding.

All statistical analyses were conducted using SPSS software version 8.0 (SPSS 1997).

Procedures

Flower Production in Different Forest Management Treatments

In May 1997, five 0.04 ha plots were chosen from each unit to undergo flower

counts for comparison across forest management research treatments. I selected five plots

because this was the minimum number of plots per unit which still contained live

bitterbrush plants as of the 1993 and 1994 field seasons. For those units having more than

5 plots with live bitterbrush, selection was made by first eliminating plots with less than 5

remaining live plants, and then randomly selecting from the remaining plots. I then

counted the number of flowers on every plant in all chosen plots during May and June of

1997 and 1998.

Location of previously caged plants (see next section) revealed that the different

forest management treatments no longer had the same number of previously caged

individuals. All analyses in this section on flower production per plot were therefore

conducted without flower count data from these previously caged plants to avoid any bias

that higher production by caged plants might bring into the analyses.

The resulting flower counts were analyzed both as average number of flowers per

plot and as average number of flowers per plant (to avoid any biases due to the number of

plants in a given plot before treatments were applied in 1992/93) for each unit.

Non-homogeneous variances and nonnormality for each year's set of both types of data

(despite many attempted transformations, such as log, square root, arcsin of square root)

necessitated the use of nonparametric multiple sample comparisons tests recommended for

these situations, including Kruskal-Wallis (Ott 1993) and the post-hoc comparisons of

Tamhane, Dunnett and Games-Howell (Day and Quinn 1989). Because none of these

tests would allow me to block by year, I also did Kruskal-Wallis on each year's data alone,

both with and without outliers. No interaction between treatment and year was found on

exploratory scatterplots.

Flower Production of Caged Versus Uncaged Pairs of Plants

Caging and other forms of exclosure have frequently been used to monitor the

impact of browsing on forage production in bitterbrush (Tueller and Tower 1979, Peek et

al 1978). In the fall of 1993, previous researchers on this study site randomly selected 20

plants from each forest management treatment and paired plants of close proximity and of

similar vigor and biomass, caging one plant from each pair in a 4.9 foot (1.5 m) high wire

cage (Ayers 1995). During May 1997, I located the original caged pairs to determine the

difference in flower numbers between caged (unbrowsed) and uncaged (browsed)

bitterbrush. Those pairs which had one or both members dead or missing were noted as

such, and flower count was obtained only for those pairs which were still viable during

May of 1997 and 1998.

The flower count data was compared between caged and uncaged plants as

number of flowers per plant. Non-homogeneous variances and nonnormality (despite

many attempted transformations) once again necessitated the use of nonparametric two

sample comparisons tests, including Kruskal-Wallis, Wilcoxon Signed Rank (used for

paired data), and Wilcoxon Rank Sum/Mann-Whitney (all recommended for

heterogeneous variances by Ott 1993 or Norusis 1997), as well as an approximate t-test

(recommended for heterogeneous variances and nonnormality, Day and Quinn 1989). The

various tests were conducted on data from both individual years and on combined years'

data.

Seed Depredation Ratios of Caged, Netted and Uncaged Plants

At the beginning of July 1997, I reviewed flower count data to find all of those

plants recorded which had produced at least 20 flowers. Of these, 15 plants per treatment

were randomly selected to be monitored for seed production, with 3 of these plants per

treatment randomly selected to be caged with large-square (4 x 7.5 cm opening) hardware

· cloth (to exclude ungulates), and another 3 to be covered with vexar netting (to exclude

all seed predators except insects). The number of plants selected for caging and netting

was related to the time and expense involved in enclosing plants and moving and replacing

these exclosures for seed monitoring. Seed count was recorded for every selected plant in

1997 and 1998, both at the beginning of seed production (late June or early July), and

again three weeks later (mid to late July), to determine the ratio of remaining seed count

to original seed count. This ratio was then used to compare the amount of seed lost

before seedfall among the three different sets of plants, in order to assess whether

ungulates, rodents and birds, or insects might be responsible for large amounts of seed

being harvested or browsed off before seedfall.

Because of non-homogeneous variances (despite many attempted transformations)

and unequal sample sizes, I used an approximate t-test, which makes adjustments for both

situations (Ott 1993, Day and Quinn 1989). Because this involved comparing three populations using a two sample test, I compared each one to the others by pairs (i.e., big cage v. net; big cage v. no cage; no cage v. net). Exploratory graphs indicated a significant difference between 1997 and 1998 data, so I did each set of t-tests for 1997/98 combined data, 1997 alone, and 1998 alone. Exploratory scatterplot analysis did not indicate an interaction between forest management treatment and caging treatment.

Laboratory Viability and Germination Rates of Lick Creek and Other Local Bitterbrush Seeds

Seed was collected from Lick Creek bitterbrush plants immediately outside the study plots during the last 2 weeks of July, 1997. Seed was collected by hand, with every effort made to select only those seeds which were large, unshriveled and blemish-free, in order to increase odds of viability (Meyer and Monsen 1989). I then cleaned the seed by hand, removing debris and rubbing it between my fingers to remove the remnant flower parts which contain germination inhibitors (Young and Young 1986). After hulling, black or spotted seeds were removed, as these are usually signs of insect infestation or nonviability (Giunta et al 1978). Although I originally collected over 800 seeds, only about 300 passed these culling standards and were thus considered healthy enough to undergo testing.

In order to facilitate judgement on the strength of the viability rates found in the Lick Creek seeds, I also obtained seed from Bitterroot Restoration, Inc., which had been collected that same season about 8 km south of Lick Creek (0.8 km up Rye Creek Rd,

south of Darby [personal communication, Matt Ogden, Seed Biologist, Bitterroot

Restoration, Inc., Corvallis, MT]). This seed source had produced healthy seedlings in

previous greenhouse trials done by Bitterroot Restoration. The BRI seeds had been

cleaned and culled in a manner similar to mine. Both sets of seeds were placed in dry,

cold storage (1° C) until use in the spring of 1998.

Sample sizes for tetrazolium and germination tests in other experiments have

ranged from four replications of 25 seeds each (Meyer and Monsen 1989) up to four

replications of 100 seeds each (Young et al 1983). Available seed from each source

dictated that I use four replications of 30 randomly selected seeds apiece from each seed

source for each of the two tests.

A. Tetrazolium Tests

I first prepared the seeds for dissection by placing each replication in a petri dish

between moist germination blotters and leaving them overnight at room temperature (18°

C) (Meyer and Monsen 1989, Grabe 1970) . I then excised each embryo by cutting the

seed coat at the cotyledon end and applying firm pressure to the radicle end with my

fingers (Meyer and Monsen 1989). Embryos were immediately placed by replication in

petri dishes and covered with a one percent solution of tetrazolium chloride prepared with

distilled water (Grabe 1970). They were then soaked for 12 hours at room temperature

(Meyer and Monsen 1989, Grabe 1970). After this period, I examined the embryos and

separated them in the staining dishes into germinable and non-germinable, using standards

detailed and diagramed in Grabe (1970). In general, viable embryos are stained

completely red or contain only minor unstained patches on the cotyledons (Meyer and

Monsen 1989).

Viability rates for each replication were computed as the ratio of viable seeds to the total number of seeds in that replication. Comparisons between seed sources were made using an approximate t-test and the nonparametric Wilcoxon Rank Sum/Mann-Whitney test (Day and Quinn 1989, Norusis 1997) because there were too few data points to evaluate normality.

B. Germination Tests

Seeds were stratified in the dark for six weeks at 2 to 5° C (Young and Evans 1983; Young and Young 1986; Meyer and Monsen 1989). I first soaked the seeds in a 5% bleach solution for 2 minutes to kill any bacteria or mold. Each replication of 30 seeds was then divided into three subsets of 10 seeds per petri dish, so that seeds could be spaced without touching each other, and layered between two sections of blotter paper (Young & Evans 1983, Meyer and Monsen 1989; personal communication, Matt Ogden, Seed Biologist, Bitterroot Restoration, Inc., Corvallis, MT). Seeds were kept moist with tap water throughout the stratification period (Young & Evans 1983, Meyer and Monsen 1989).

Petri dishes were moved to a dark growth chamber set at 15° C (Meyer and Monsen 1989) and monitored biweekly for moisture and germination. I recorded the number germinated at each examination and discarded germinated seeds. Seeds were considered germinated when the radicle had emerged 5 mm (Meyer and Monsen 1989, Young and Evans 1983). Ungerminated seeds were discarded at the end of four weeks (Meyer and Monsen 1989).

Germination rates for each petri dish were measured by computing the ratio of seeds that germinated to the total number of seeds in that dish. Comparison of germination rates between seed sources was conducted using an approximate t-test and the nonparametric Wilcoxon Rank Sum/Mann-Whitney test (Day and Quinn 1989, Norusis 1997) because there were too few data points to clearly ascertain normal distribution.

Germination and Establishment of On-site Seed Plantings in Different Forest Management Treatments

In November of 1997 I planted seeds from the BRI seed source (mentioned above) in the study area at Lick Creek to determine whether the site and the various forest management treatments were suitable for germination and seedling survival. Three plots of 10 seed groups each were planted in each of three forest management treatments (control, shelterwood cut, and low fuel consumption burn). The high intensity burn treatment was not used because of lack of sufficient seeds, and because the intensity and severity of the two burn treatments had in actuality been very similar (Ayers 1995). These plots were located around the perimeter of three flower count plots in each treatment, in a manner designed to capture most of the variation in aspect and slope of the given unit. The seeds were planted in groups of five each, at a depth of about 1 inch (2.54 cm) under mineral soil, to simulate natural germination conditions in rodent caches (Evans et al 1983, Matlock-Cooley 1993). Scarification of the sites occurred only to the extent that surrounding vegetation, litter and soil were disturbed by the planting process (an area of

approximately 6 inches [15 cm] diameter for each seed group). The artificial caches were unmarked in order to avoid attracting rodents (Young et al 1997). This fall planting gave natural scarification an opportunity to occur over winter. I inspected the sites biweekly in May and early June of 1998 to record the number of seedlings germinated. Germination rates for each of the plots were then computed by taking the percentage of seed groups that germinated out of the total number of seed groups in that plot.

I returned to the plots to count remaining seedlings in October of 1998, in order to assess seedling survival over the course of the first growing season (Ferguson & Basile 1967). Seedling survival rates for each of the plots were measured by taking the percentage of seedlings that were surviving in October out of the total number of seedlings in that plot in May and June.

Due to problems encountered in carrying out this test, I have deferred an account of statistical analyses to the appropriate "Results and Discussion" section.

Survival Rates of Caged and Uncaged Seedlings from On-site Seed Plantings

After the planted seeds (above) germinated in mid-May and June 1998, I randomly selected and caged one half of the emerged seedlings in each plot, using PVC seedling protectors (see Evans et al 1983 for similar caging studies). In order to assess the impact of browsing by rodents or ungulates on seedling survival during the first growing season, I returned to the plots to count live seedlings in October of 1998. Seedling survival rates for these two treatments (caged and uncaged) in each plot were measured by taking the percentage of seedlings in that caging treatment that were still alive in October out of the

total number of similarly treated seedlings in that plot in May and June. Due to

non-homogeneous variances, I used an approximate t-test for comparison (Day and

Quinn 1989).

I also conducted an experiment to monitor seedling depredation and survival over

winter and early spring, since browsing pressure from ungulates is greatest during this

time (Gruell 1986, Martin and Driver 1983). Forty one-season-old seedlings per plot

(donated by Bitterroot Restoration, Inc.) were planted on the three seeding plots (see

above) in each of the three seeding treatments (control, no burn, low burn) in late fall,

1997 (Leckenby and Toweill 1983). On one plot per treatment, half of the seedlings were

randomly selected to be caged upon planting. Survival and percent browsed were

recorded in May 1998. Non-homogenous variances made an approximate t-test

appropriate for this data as well.

Established Natural Seedlings in Fall 1998 in Relation to Site Characteristics and Forest Management Treatments

In order to determine whether various physical site characteristics (including forest

management treatments) have significantly different effects on natural seedling

establishment, I surveyed all flower count plots for one year old seedlings and germinants

in June of 1998. Germinants were easily distinguishable via their reddish-purple

cotyledons (Evans et al 1983), which were soon followed by small, three–lobed,

distinctively bitterbrush leaves. One year old seedlings at the beginning of the growing

season were usually 10 to 15 cm tall, and looked like new leaders on mature plants,

occasionally with two or three branches already forming (Carpenter 1983). Earlier work with artificially planted bitterbrush of both ages facilitated my recognition of the germinants and one year old seedlings under natural conditions. These surveys were conducted only on plots selected for flower count, due to the amount of time involved in collecting this data and the information detailed below for each plot. I returned to the plots to count live seedlings in October of 1998, in order to assess seedling survival over the course of the first growing season (Ferguson & Basile 1967).

At the time of the initial surveys in June, I also collected information on physical characteristics of each 0.04 hectare plot, including trees per hectare (of diameter at breast height [dbh] greater than or equal to 10 cm), trees per hectare of regeneration less than 10 cm dbh but greater than 61 cm high, tree basal area (m^2/ha), and average aspect and percent slope. The number of mature trees and tree regeneration per hectare was determined by counting all trees of that description within the 0.04 hectare plot, and multiplying that number by ten. Basal area was determined using a 10 BAF (basal area factor) prism, counting "in" trees as seen from the center of the plot, multiplying that number by ten to compute basal area per acre, and then converting that to basal area per hectare (Husch et al 1982). Aspect was taken using a compass, and percent slope using a clinometer.

In July 1998, I collected five samples from each plot of the top 8 cm of mineral soil for soil moisture evaluation. The samples for each plot were combined and brought back moist (in sealed plastic bags) to the laboratory. I then conducted analyses of current moisture content on each plot's combined sample by weighing the moist samples, drying

them in an oven at 105° C, and reweighing them. Soil water holding capacity was determined by saturating previously dried and sieved samples with water and equalizing water content on a pressure plate at -33 kPa. Results from these two procedures were used to calculate current soil moisture as a percent of water holding capacity at field capacity (Cassel and Nielsen 1986; personal communication, Tom DeLuca, Associate Professor of Soils, School of Forestry, University of Montana, Missoula, MT).

All of the plot data mentioned above, plus information collected during flower counts and from previous records for each plot (including forest management treatment, number of mature plants 1997 and 1998, flower count per plot 1997 and 1998, and original number of plants before treatment in 1992) were scrutinized for qualification as candidate variables in a logistic regression for presence or absence of survived seedlings in the fall of 1998. I did not combine data for the five subplots per unit, even though this entailed some pseudoreplication, because items such as slope and aspect cannot be averaged across such a large area without losing the variability they were intended to capture in the first place.

All work on this logistic regression was conducted using procedures established by Hosmer and Lemeshow (1989). I first examined scatterplots of possible explanatory variables versus the dependent variable to see if there was a need for second and third order terms. Then I ran each possible explanatory variable, plus the second and third order terms found above, through a univariate logistic regression. Variables with a resulting P-value of <0.25 were considered as candidate variables. After this I computed Pearson's r correlation among these candidate variables. I chose the variable with the

most biological significance from each group showing a correlation greater than or equal

to 0.60, and eliminated the other variables in that group (Hosmer and Lemeshow 1989;

personal communication, Jon Graham, Associate Professor of Mathematical Sciences,

University of Montana, Missoula, MT). Next, I ran multiple versions of a logistic

regression model containing all candidate variables still remaining after the screening

procedures listed above. Interaction terms which made biological sense were also

included in these model runs. Variables and terms were deleted from the model one at a

time, with the term of lowest significance deleted after each model run. The cutoff value

for inclusion in the model was a P-value less than or equal to 0.10.

Because bitterbrush is a relatively long-lived woody species and develops early and

late wood rings much like those of a tree (with life spans of up to 160 years), it can be

aged via annual ring counts (Giunta et al 1978, Peek et al 1978, Sherman and Chilcote

1972). In 1998 I obtained and aged a set of 24 bitterbrush cores from the study site. 12

cores were collected from the previously selective cut, and 12 from the previously clearcut

(1906-1911) areas, using a random walk to locate bitterbrush outside of study plots and a

handsaw to obtain cuts as close as possible to ground level (Peek et al 1978). Cores were

smoothed with a belt sander, stained with water, and aged under a binocscope (Sherman

and Chilcote 1972). Age estimates for missing core rings were made using the relative

ring width estimation methods for dendrochronology described in Arno et al (1997).

Similar methods have been used on bitterbrush by Sherman and Chilcote (1972). I then

looked for age classes of bitterbrush and the differences in age between them, in order to

see if a pattern existed indicating an approximate interval between seedling establishments

at our site (Giunta et al 1978) and to see if cycles revealed were consistent with

regeneration currently observed on the site. The number of cores assessed in this manner

was limited due to the amount of time and the destruction of bitterbrush involved, and was

intended for use only as a preliminary assessment, not as a statistically valid sample.

RESULTS AND DISCUSSION

Flower Production in Different Forest Management Treatments

Average flower count per plot was not statistically different between forest

management treatments (P>0.800) or years (approximate t-test P=0.255) (Fig.1).

Average flower count per plant also did not differ between treatments (P>0.550) but did

differ between years (P=0.074) (Fig. 2). I believe this difference between years was due to

variations in climate, including browsing pressure. Record-level snows in the winter of

1996-1997 were observed to keep elk at this wintering ground past the bud setting and

anthesis periods (mid to late June) of 1997. In 1998, most of the elk were gone by the end
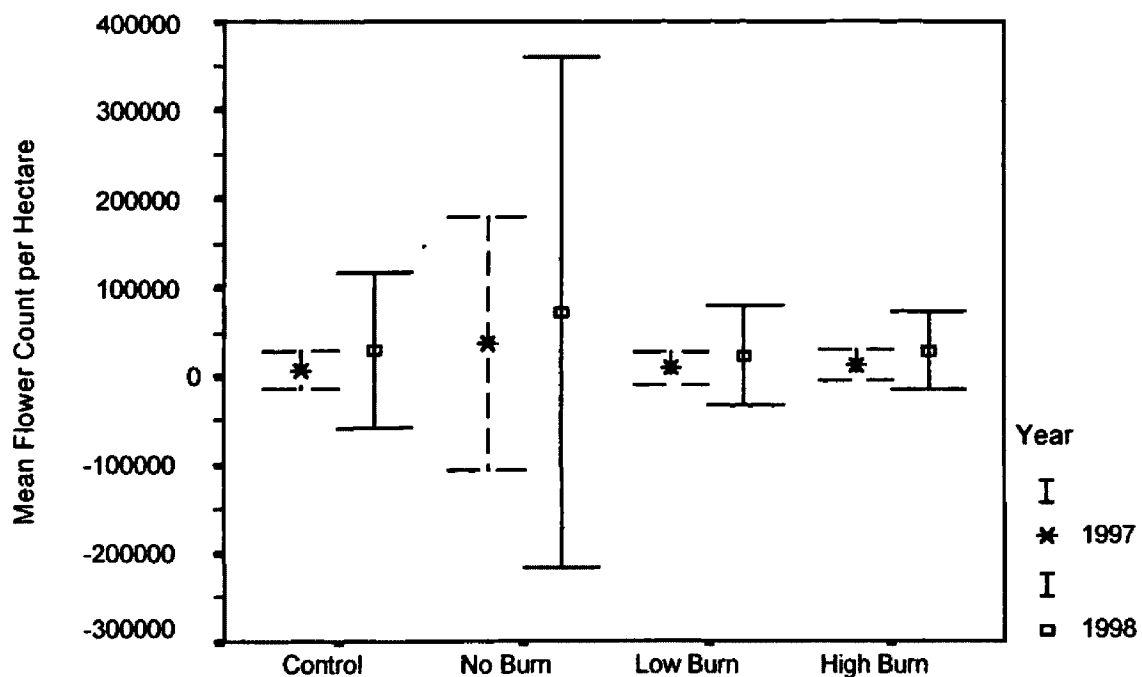
Fig. 1. Bitterbrush (*Purshia tridentata*) flower counts per hectare[1] for different forest management treatments in 1997 and 1998.

[1]Bars are 95% confidence intervals.

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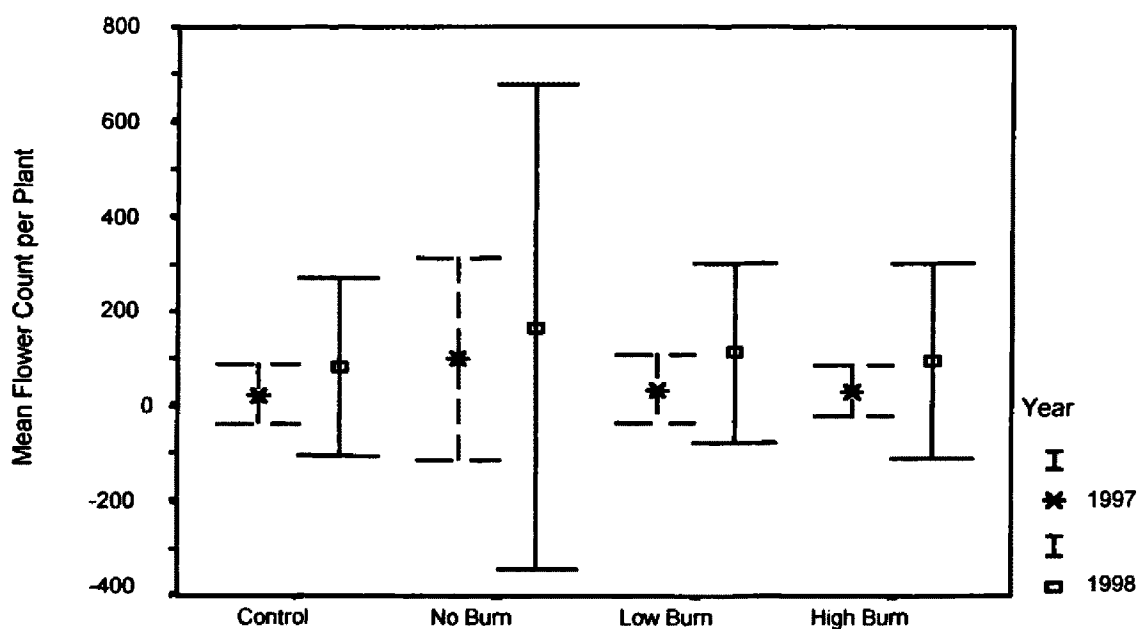
Fig. 2. Bitterbrush (*Purshia tridentata*) flower counts[1] ($\bar{x}$) per plant for different forest management treatments in 1997 and 1998.

[1]Bars are 95% confidence intervals.

of May. The combination of stress due to over-browsing and actual consumption of flower-producing plant material may have severely lowered flower production during the 1997 growing season. I observed many plants during the late spring and early summer of 1997 that had bark slippage on shoots which appeared to be one to two years old. Two year old leaders are heavily involved in flower production (Shaw and Monsen 1983). Even caged plants often had bark slippage and considerable twig breakage where apparently ravenous ungulates had pushed their heads as far as possible through the tops of the cages. I did not observe much bark slippage at all during the 1998 field season.

Flower Production of Caged Versus Uncaged Pairs of Plants
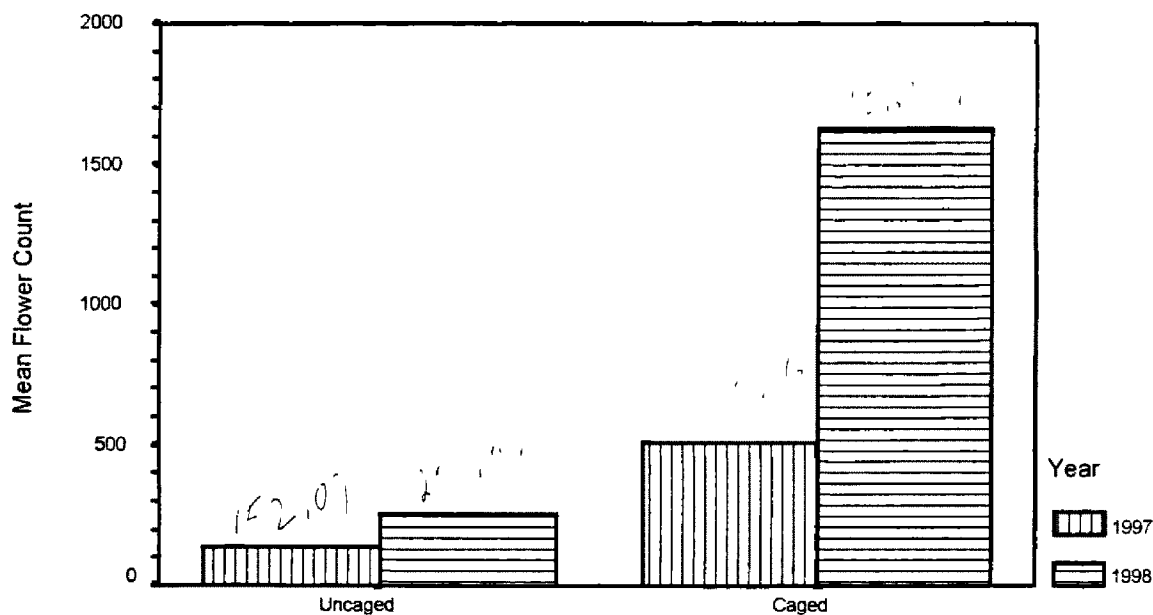
Fig. 3. Bitterbrush *(Purshia tridentata)* flower numbers per plant for caged and uncaged plants in 1997 and 1998.

Comparisons of flower numbers between caged and uncaged paired plants were significantly different for all tests ($P \leq 0.001$) for each individual year and for both years' data combined (Fig. 3). The greater flower numbers on caged plants show that browsing at the Lick Creek study area has a significant impact on flower production. Other researchers (Buwai and Trlica 1977, Guenther et al 1993) also found that browsing levels of ungulate populations in their study areas were detrimental to bitterbrush stands, causing decreases in vigor and biomass. However, Tueller and Tower (1979) found a 70% reduction in bitterbrush forage production after two years of caging. These sources make it appear that a balanced amount of browsing is needed to maintain vigor but not overly reduce biomass. Ferguson and Medin (1983) state that old bitterbrush will reduce leader growth and increase seed production if not browsed. Almost every one of the

caged bitterbrush at our site, however, exceeded its paired counterpart not only in flower numbers but also in vigor and size. Most caged plants were three to four times as tall as uncaged plants, and most of them completely filled their cage. Flowers during both seasons surveyed were so thick on these plants that it was almost impossible to count them. Visual comparison of these plants with their uncaged matches made it hard to believe that the two had ever had the same size and vigor. These plants had been caged for five to six years, but were showing none of the reduction in well-being predicted by Tueller and Tower (1979) or Peek et al (1978). A number of these caged plants displayed evidence of having been browsed where they extended through the cage at both top and sides. Perhaps this browsing stimulation was enough to keep the plants from becoming senescent. In light of the literature and the fact that these caged and relatively lightly browsed plants were much more vigorous than the uncaged plants, I must conclude that ungulate populations and browsing pressure at this study site are having a significant negative impact on vigor and flower production in this bitterbrush stand.

Seed Depredation Ratios of Caged, Netted and Uncaged Plants

Because exploratory graphs indicated a flattening out of remaining seed count to original seed count ratios across all treatments in the second year of data collection, I chose not to use analyses done on the two years' data combined. In 1997 there were significant differences (P<0.050) in seed count ratios among the caged, netted and uncaged treatments, but in 1998 there were no significant differences (P>0.150). Ratios
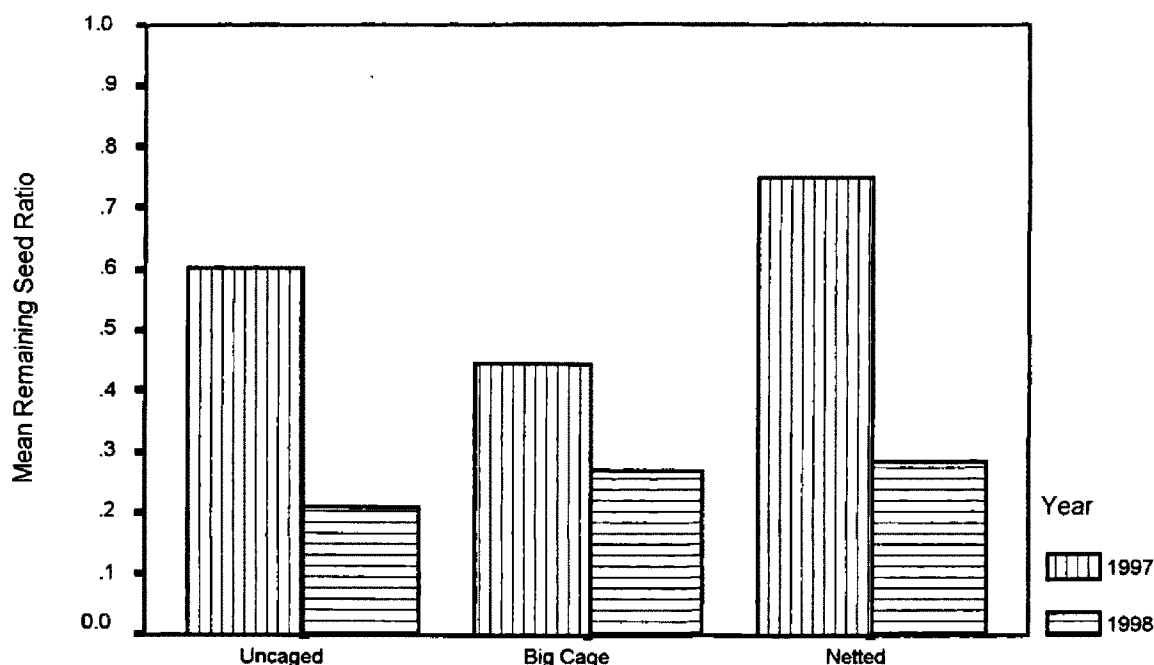
Fig. 4. Bitterbrush (*Purshia tridentata*) ratios of remaining seed count to initial seed count for caged, netted and uncaged plants in 1997 and 1998.

of remaining seeds to initial seeds for 1997 were 0.75, 0.60 and 0.45 for the netted,

uncaged and large-caged plants, respectively (Fig. 4). Apparently, nets kept rodents and

birds from consuming seeds, while cages with large openings provided these animals with

a safe, relatively predator-free place to feed. Indeed, on return in 1998, I observed a

number of caged plants with new chipmunk holes directly under the plant. The bias

created by possibly improving rodent habitat with these large cages makes it somewhat

difficult to view other trends. However, I do not think that ungulate disturbance or

browsing would have had much effect on these seed count ratios, because ungulate

populations on this site at this time of the season consisted of a few white-tail deer.

Some sources (Young and Evans 1978, Evans et al 1983) cite high seed depredation levels

by ants. I observed minimal ant activity on these plants during my ten months of field

work. The fact that plants with nets (designed to keep out all predators <u>except</u> insects) had the highest ratio of remaining seed in 1997 also indicates that this was probably not a significant factor at this site.

Ratios of remaining seed count to initial seed count for each treatment in 1998 not only failed to be significantly different from each other, but also were much lower than ratios in 1997 (Fig. 4). This may be an indication that most of the seeds had already ripened and fallen by the time of my second seed count that year. July and August of 1998 had record-level high temperatures and extremely low levels of precipitation. This may have caused most of the seeds to ripen and fall earlier than usual and so lowered the ratios in my counts. Meyer and Monsen (1989) confirm that during hotter, drier seasons plants develop and mature seed much more quickly--sometimes a week and a half more quickly. Because the seed production cycle is generally fairly consistent under characteristic climatic conditions for a given geographic location (Giunta 1978), I collected this 1998 data in exactly the same time frame as in 1997, to avoid bias that would come from collecting data at a different point in the seed cycle. Unfortunately, it appears that I still ended up at a different point in the cycle, due to climatic extremes. Constant observation of the seed maturation process (color etc.) might allow one to catch these "same cycle points" better than a using set number of weeks (Shaw and Monsen 1983).

Laboratory Viability and Germination Rates
of Lick Creek and Other Local Bitterbrush Seeds

Comparisons of tetrazolium and germination test results revealed no significant

difference in percent viability (P>0.45) or germination rates (P>0.55) between the Lick

Creek and Bitterroot Restoration seed sources (Fig. 5). In theory, tetrazolium and

germination tests should yield similar percentages (Meyer et al 1986, Meyer 1989, Grabe

1970). However, mold is frequently a problem in laboratory stratification and

germination, causing some authors to recommend tetrazolium testing only (Meyer et al

1986, Grabe 1970). I began stratification on 05-08-98, and had to rebleach moldy seeds

(with no radicle showing yet) on 05/15, 05/24 and 06/10. Once germination testing began,

I could not bleach or otherwise eliminate mold because the chemicals used would probably

also have killed the embryos. This contamination problem is probably the reason for the
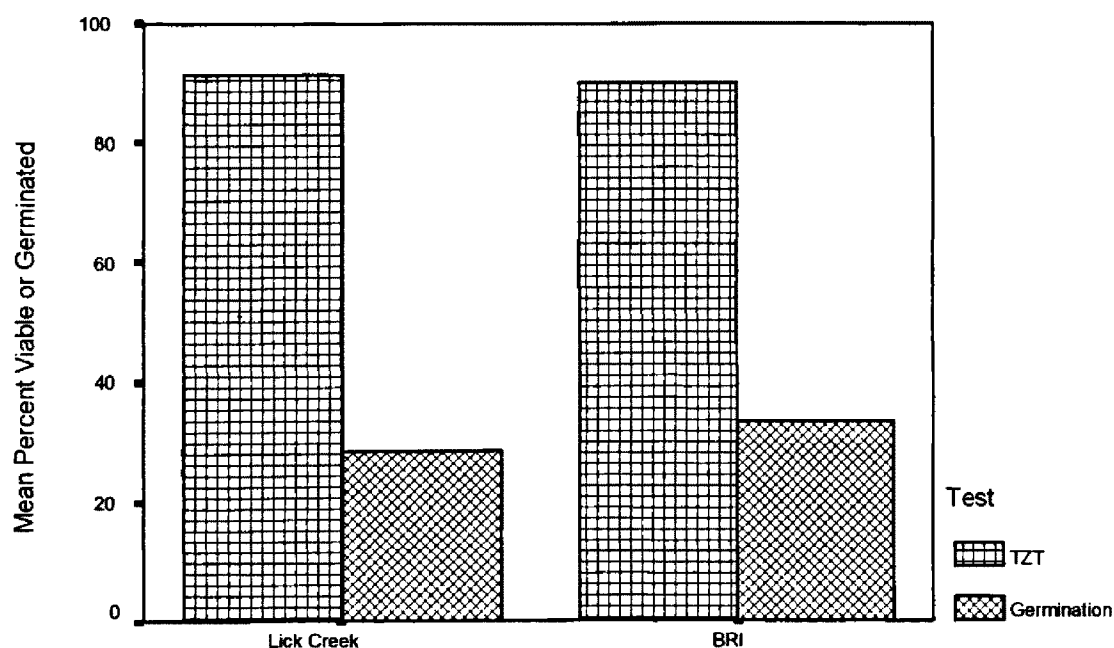
Fig. 5. Percent viable and germinated bitterbrush (*Purshia tridentata*) seeds from Lick
Creek and Bitterroot Restoration seed sources.

lower germination percentages (Meyer et al 1986). The high viability ratios found in

tetrazolium testing of both seed sources are consistent with those from other seed sources

which have been similarly culled to remove damaged and infested seeds, (Giunta et al

1978, Meyer and Monsen 1989), indicating that seed viability is not an explicit problem at

Lick Creek.

Germination and Establishment of On-site Seed Plantings in Different Forest Management Treatments

Because the ground was frozen at the time I planted seeds on the Lick Creek study

site, I used outside help to plant approximately 2/3 of the seeds. Although the planting

depths cited by my helper (2.5 to 5.0 cm under mineral soil) coincide with those cited by

Evans et al (1983) and Hormay (1943), only 7% of those seed spots germinated the

following spring (as compared to 75% of the seeds I planted), indicating that there were

probably problems in the planting procedures used. These seeds comprised all of the burn

and no burn seeding treatments, rendering comparison among forest management

treatments useless.

The 75% germination rate cited earlier was for seeds planted in the control area,

indicating that shading conditions at this particular control site are not too much for

germination to occur. Shading was also not a factor in seedling survival and

establishment, as 87% of these germinated seeds were still alive upon reinspection in

October 1998. This does not, however, imply that litter conditions also had no effect on

germination, because a 15.25 cm diameter circle around each planting was relatively litter-

free compared to the site around it. I did replace some of the litter following each planting in the fall, but not all of it because that would have prevented me from relocating the seeding spots the following spring.

Survival Rates of Caged and Uncaged Seedlings from On-site Plantings

An approximate t-test (P=0.290) indicated no significant difference in percent survival over the first growing season between caged ($\bar{x}$=0.70) and uncaged ($\bar{x}$=0.90) seedlings. These results should be viewed with caution because the seedlings monitored were located in the control area only (see section above), and predation patterns could differ between this area and those with other forest management treatments. The slightly lower mean for caged plants, though not significantly different from that of uncaged plants, could be due to greater shading by cages in this already well-shaded area.

Clements and Young (1996) found that rodents in their study area consumed the cotyledons on bitterbrush germinants and thus reduced early recruitment by 40%. Almost all of the planted germinants I found were still at the cotyledon stage, and only 13% did not make it past this stage. Germinants take about 10 days to reach the true-leaf stage (Clements and Young 1996), and as I checked the seed plots every three to four days, it seems likely that I would have noticed had consumption of cotyledons been much higher than I recorded. Thus, grazing of germinants was apparently not as significant a problem on this control treatment as it has been on some other study sites (Ferguson 1972, Evans et al 1983, Clements and Young 1996). All of the recorded 13% seedling mortality on this control site, however, was at the cotyledon/early true-leaf stage. I was able to

observe very little about this process in my survey of natural seedlings (see section below), because of the difficulty of finding germinants still at the tiny cotyledon stage when searching through larger areas where cache locations are unknown.

Of the one season old seedlings planted in the fall, 76% were still alive in spring, indicating a high overwinter survival rate. Of all seedlings planted on plots with no caging, 58% had been browsed. However, there was no significant difference (p=0.222) in survival between browsed and unbrowsed plants (Fig. 6a). Comparisons using Kruskal-Wallis (p=0.000) and Tamhane, Dunnett T3 and C, and Games-Howell (p≤0.050) indicated a significant difference among treatments in the number of seedlings browsed during winter. Browsed bitterbrush seedlings averaged 81, 64 and 29 percent for no burn, control, and burn treatments, respectively. However, I observed that ungulate use patterns of the various forest management treatments were different during the 1997 and
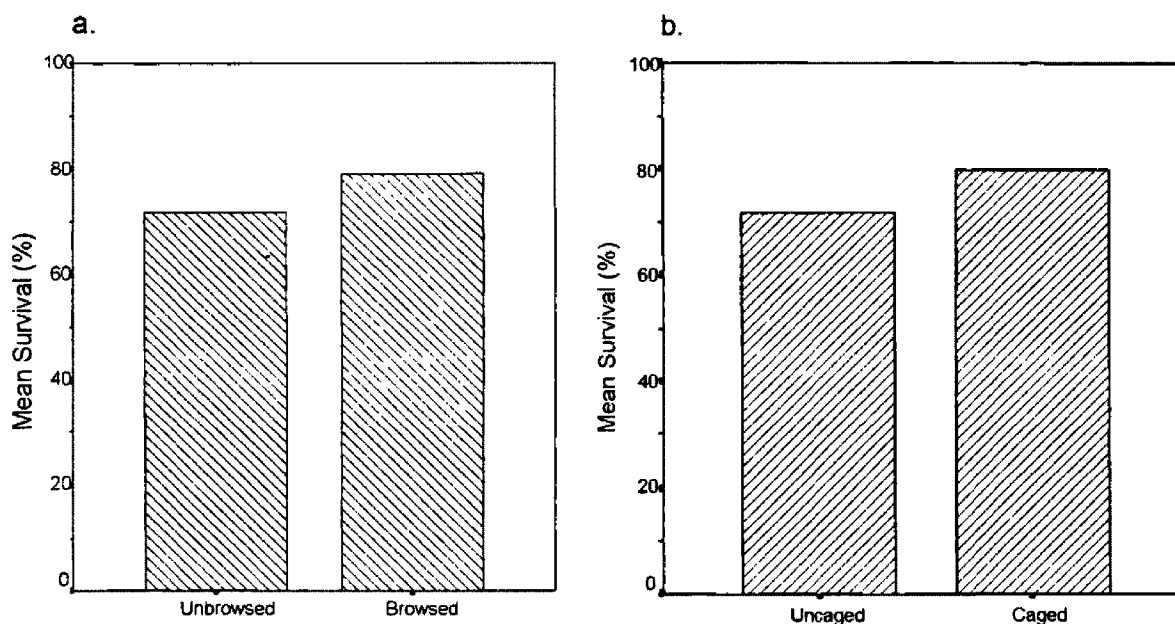
Fig. 6. Bitterbrush (*Purshia tridentata*) winter seedling survival (%) for browsed or unbrowsed plants (a) and caged and uncaged treatments (b).

1998 field seasons, so these numbers may not reflect constant preferences. Since there

was not a significant difference in percent survival between browsed and unbrowsed

seedlings, these use patterns were probably unimportant in determining seedling survival.

In plots where caging occurred, there was no significant difference (P=0.290) in

overwinter survival between caged and uncaged seedlings (Fig. 6b). This corroborates the

tests above that failed to show a difference in overwinter survival between browsed and

unbrowsed seedlings. Thus, I would conclude that at this site, overwinter browsing was

not a significant factor in seedling survival. Casual observations showed that most of the

seedlings were quickly covered with snow in late fall. Snowpack may thus serve as a

protective feature for bitterbrush seedlings.

Established Natural Seedlings in Fall 1998
in Relation to Site Characteristics and Forest Management Treatments

I found more bitterbrush seedlings on this study site during 1997 and 1998 than

had been recorded by other studies since 1992 (Ayers, 1995). However, the number of

seedlings was still not large enough to create a significant regression model which would

account for variation in seedling establishment patterns. Multiple attempts at linear

regression models failed to show any explanatory variables as significant, even though

many of the candidate variables are known to affect seedling establishment (refer to earlier

section in Literature Review on "Natural Seedling Establishment"; see also Appendix C).

Therefore, I attempted to use a logistic regression, binary response model (testing for

presence or absence of seedlings in each plot) to determine what site factors might be

most associated with regeneration or lack thereof. In repeated testing and comparison of logistic regression models, the only explanatory variable significant ($P \leq 0.100$) was the number of plants in 1997, as a first, second and third order term. However, this correlation was weak ($r=0.276$). A scatterplot of the number of plants in 1997 versus presence or absence of seedlings also failed to show any clear relationship between the two, as the ranges of "Number of plants" were the same for both presence and absence of seedlings (Fig. 7). Thus, , although field observation revealed visible differences in seedling survival associated with these various microsite characteristics, there were simply not enough positive (i.e., seedlings present) data points to be able to make significant statistical conclusions (personal communication, Jon Graham, Associate Professor of Mathematical Sciences, University of Montana, Missoula, MT).

However, apart from regression analyses, I believe these results provide some
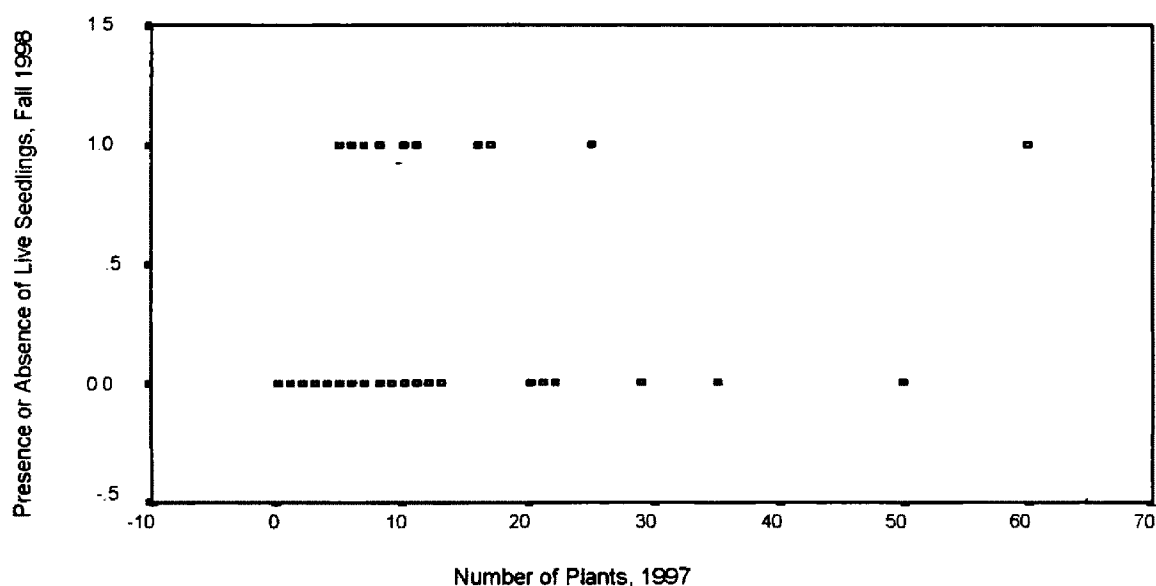
Fig. 7. Presence or absence[1] of bitterbrush (*Purshia tridentata*) seedlings, fall 1998, in relation to number of mature bitterbrush plants, 1997.

[1]0=absence; 1=presence

logical inferences that are compatible with previous research on the issue of bitterbrush

regeneration. Differences in numbers of seedlings between treatments were highly

significant when treatments were grouped as disturbed versus undisturbed (approximate t-

test p=.006). The combined disturbed sites averaged twenty seedlings per hectare,

whereas the undisturbed sites had no seedlings (Fig. 8). The one seedling I did observe in

a control ("undisturbed") area was where road work had clearly invaded a plot, allowing

some soil/litter disturbance in years past that contrasted sharply with the relatively

undisturbed area around it. Because this seedling was in an area which did not accurately

represent the associated treatment, it was treated as an outlier. This was the only seedling

I observed in any control area, either in or out of a designated study plot. In the disturbed
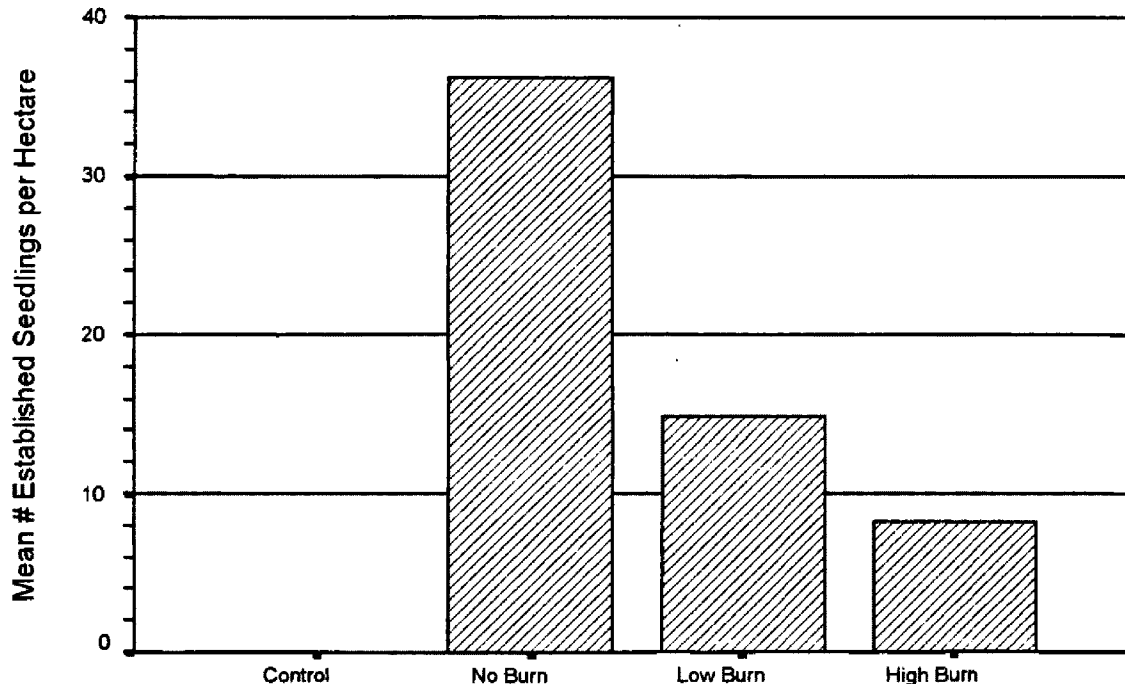
Fig. 8. Naturally established bitterbrush (*Purshia tridentata*) one year old seedlings and germinants per hectare in October 1998 for different forest management treatments.

areas, on the other hand, I observed many seedlings outside of the plots surveyed. One must keep in mind that bitterbrush is a very long-lived plant (Giunta et al 1978), and consequently may not need great numbers of seedlings to maintain the stand (Fraas 1992). Therefore, a difference between zero (or even one) and twenty seedlings per hectare could be quite significant in terms of long-term stand continuity on this site where pre-treatment (1992) bitterbrush numbers averaged 494 per hectare for plots included in this seedling survey. In view of these observations and of multiple literature references to the small number of seedlings usually involved in successful stand regeneration (Fraas 1992, Nord 1965), the number of seedlings found on these disturbed areas is probably of considerable importance for the future of this stand.

Results of mature bitterbrush annual ring counts (Appendix D) revealed a three to seven year interval between major age groups. The results also showed that when a period of regeneration did occur, it would last for two or three years. These results are based on a very small sample size. However, this would be consistent with the seedling information collected in 1998: the one year old seedlings germinated in 1997, which is five years after the youngest core age class, and this regeneration period is lasting at least two years because there were also germinants in 1998. These types of slightly varying and yet fairly consistent intervals are similar to those found in Utah (Deitschman 1974). Given the reduced snowpack and high temperatures of the 1998-1999 winter, I would not expect to see this regeneration cycle continue into the 1999 growing season (Meyer and Monsen 1989).

The dates for all of the regeneration periods found in my core studies fell within or

close to the amount of time observed by Martin (1983) for seedlings to reestablish on prescribed burn sites (3 to 8 years), as they coincided with or were within 10 years after dates of thinnings in the area (Menakis 1994, Ayers 1995). Classes farther from the dates of such disturbances had fewer representatives present in my analyses.

The number of cores obtained as part of this project was insufficient to conduct statistical analysis with meteorological data. Such work would be extremely time consuming and was outside the scope of this study. Further work could be done to obtain more cores and to try to link the dates obtained to weather summaries from the nearby Darby weather station in order to assess the climatic conditions related to regeneration cycles at our site. However, such work would need to be carried out with extreme caution, because a seedling class in a given year does not necessarily depend on that year's weather conditions alone, or even on those of the year before. For example, conditions might have been favorable one year for high seed production, but unfavorable for germination. Those seeds could then have remained in the seedbank for several years (Young et al 1993, 1997) until weather conditions were right for germination. This type of situation might even explain why there was such a large seedling crop in 1997 (showing up in 98 as one year old seedlings), in spite of having had no observed large seed crops in the area for at least five years (Personal communication, Don Bedunah, Professor of Range Resource Management, School of Forestry, University of Montana, Missoula, MT). Seeds from a previous seed crop may have remained in the ground until the high snowpack of the winter of 1996-1997 broke dormancy and provided enough spring moisture for good seedling establishment. This type of weather/seedling crop analysis is

very complicated and should not be oversimplified.

As noted by Giunta et al (1978), in order to have regeneration, there must be a good seed crop, a rodent population large enough to cache seeds but small enough to not consume all of them, and proper weather for stratification over winter, germination in the spring, and early seedling establishment. As stated above, it appears from core analyses that conditions for a good seedling crop occur approximately every three to seven years at this site (see Nord 1965, Giunta et al 1978, Martin and Driver 1983 for similar examples). However, if fire suppression is not providing the clearing of litter (undecomposed organic matter) needed for seedlings to establish, all the other conditions may be favorable, and yet the regeneration opportunity will be unsuccessful (Sherman and Chilcote 1972). This may be what is happening in many "declining", nonreproducing bitterbrush stands across the West. Matlock-Cooley (1993) conducted an intensive survey of rodent habits and noted that litter density on her study site caused these rodents to resort almost entirely to larder-caching, deep in their burrows where seeds were unable to germinate.

Fire/Bitterbrush Relationships at this Study Site

The need for litter removal in order to have successful regeneration inevitably leads back to the issue of the relationship between bitterbrush stands and fire. Fire was a regular source of disturbance in these forests before European management (Arno 1976), and served to reduce the litter buildup which is an obstacle to bitterbrush regeneration. The place of bitterbrush in these formerly low intensity, high frequency fire regimes in our

area needs to be more closely examined. Reconstruction of pre-European stand conditions for ponderosa pine forests has been done from tree age analysis as well as written descriptions of the period and photos (Arno et all 1995, Fiedler et al 1998). This type of analysis is much more difficult with bitterbrush because of three factors: 1) they do not show up as well in photos (especially if they were small or seedlings); 2) they were not as prominent and therefore not as consistently documented in historical records as huge ponderosa pine; and 3) historic bitterbrush stand inventory records are rare or nonexistent (unlike ponderosa pine inventories).

During the course of this project I reviewed many photos of our study site taken over the course of the past 90 years (some from Gruell et al 1982, others from the US Forest Service Region 1 Headquarters, Missoula, MT). Intensive study of these pictures with the aid of magnification revealed the presence of small, low-growing bitterbrush at low density (compared with today's largest stands) in a number of the areas photographed in 1909 (14 years after the last recorded fire, which is within the 3 to 30 year fire interval for the site recorded by Arno [1976]). As time since the last fire increases, bitterbrush in these photos become considerably larger and more dense, equaling today's largest stands on this site by the late 1920s in some photographs. However, vigor soon begins to decline as the canopy closes, and no regeneration is visible. When trees are removed in subsequent thinnings, the bitterbrush stands appear to regain vigor. The process viewed in these photograph series seems to indicate not only that these bitterbrush stands need some form of soil disturbance and tree canopy opening in order to maintain vigor and reproduce, but also that bitterbrush were probably present on this site during the era of

high frequency, low intensity fires (although in smaller form and numbers) (for example, see photo series accompanying USDA FS Photos 87357 and 86480).

Research by Ayers (1995) on this site in the two years following the 1993 prescribed burns found a 72% bitterbrush mortality due to fire exposure. This mortality was closely related to burn intensity. Although there was a substantial reduction in the number of plants on both burn and no burn treatments in relation to the controls, the remaining plants on the disturbed treatments had substantial increases in vigor and biomass in comparison to control area plants. These increases in vigor were greater in the burn areas than in the no burn areas (Ayers 1995).

In 1994, resprouts from treatment "mortalities" on the particular plots studied in this regeneration investigation were 4%, 23%, and 8% for no burn, low burn and high burn treatments, respectively (Ayers 1995). During the process of resurveying plants in these same plots in 1997 and 1998, I recorded an additional 11% resprouts in the no burn areas, 8% in the low burn areas, and 3% in the high burn areas. These were plants that were still recorded as dead in 1993 and 1994 data, but were alive (and often quite large and vigorous) by 1997 or 1998. This indicates that recovery time between disturbance and resprouting may be as much as six years. Minimal additional mortality occurred between 1994 and 1997. The percent of mature plants present in 1998 compared to 1992 was 79%, 69%, 40%, and 35% for control, no burn, low burn and high burn treatments, respectively. Thus, some mortality was experienced even on the control treatments. These numbers do not include seedlings, and so over time the percent population maintenance for the disturbed areas could be expected to become comparable to or even

surpass that of the control areas.

Less than 0.8 km from this study site, another low intensity prescription burn was conducted in 1996. Unlike the burns done at my site in 1993, this burn was truly low intensity (personal communication, Mick Harrington, Research Forester, Fire Sciences Laboratory, Missoula, MT). When I walked through this site approximately one growing season after the burn, I found only one dead bitterbrush. Every other bitterbrush I saw had apparently resprouted, even when burn marks on the stem and branches were quite evident. Although the initial bitterbrush numbers were substantially fewer than on my study site, the amount of resprouting seems to indicate that many individuals in this area still retain the capacity to sprout after fire, if the fire is of low enough intensity to avoid destroying sprouting organs. Less resprouting on our particular site was probably due to the intensity of our particular fires (Ayers 1995), but resprouts found as late as 1998 show that percent recovery is still increasing. Thus, while the recovery process after a higher intensity fire may take some time, it does occur.

SUMMARY AND CONCLUSIONS

The primary goal of this study was to gain a better understanding of the lack of bitterbrush regeneration at the Lick Creek Study Area. My investigations showed no significant problems in seed viability or seedling survival on this site. Some reduction in flower and seed production was experienced due to browsing by ungulates, and higher amounts of regeneration could be expected if browsing pressure at this site was reduced. A lesser reduction in seed production may be occurring due to seed depredation by rodents. However, the largest barrier to regeneration appears to be buildup of undecomposed organic matter on undisturbed sites, leading to a lack of suitable sites for rodent caching and seed germination. This same obstacle has been noted by a number of other researchers (Sherman and Chilcote 1972, Evans et al 1983, Ferguson and Medin 1983), including researchers nearby in southwestern Montana (Matlock-Cooley 1993, Fraas 1992).

Data collected on natural seedling establishment, in conjunction with other data on mature plants at this site, make it appear that a control (no disturbance) management plan would result in high numbers of older plants, but with little or no regeneration, leading to a senescent and non-self-sustaining stand. Lack of disturbances which simulate natural events also leads to senescence, poor vigor, and lack of regeneration in the larger ponderosa pine forest of which this bitterbrush stand is a part (Agee 1993). Burn treatments (after tree harvest), when conducted at the relatively high intensities that occurred on our site, may significantly reduce numbers of older bitterbrush plants but may

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also result in seedlings. These findings are consistent with those of Driver et al (1980) and Martin (1983). A lower intensity burn after tree thinning might result in less mature plant loss (as indicated by my observations on the nearby lower intensity burn), and yet still yield success in seedling establishment (Bunting et al 1985, Rice 1983). A shelterwood cut with no burn treatment may also result in minimal mature plant loss with successful regeneration. The type of treatment chosen may depend on the specific management objectives for a given area, both in terms of bitterbrush stand condition and in terms of timber and other interests.

Managers may even want to consider a mosaic of different treatments on the landscape as a simulation of mosaics created by fires in the past. Such mosaics provide more diversity of habitat and species (both flora and fauna) and less potential for landscape-scale forest stand replacement by insect, disease or fire (Camp et al 1996). Such a strategy could also allow different interests to be satisfied on different sectors in the area at different points in time (for example, a logged area leaving large bitterbrush for wildlife browse next to a logged and burned area aimed at temporarily reducing density by eliminating plants of poor vigor). However, if bitterbrush stands are desired as a future part of this landscape, it seems clear that disturbance of some sort will be necessary on at least some portion of it, for it is these very disturbances which have allowed this species (and others in this forest type) to remain as a viable component of this ecosystem for centuries. In this era of 90 years post-fire suppression, these stands cannot be left "untouched" and expected to survive. Failure to provide these disturbances may ultimately result in long term loss of this species, and of others which also depend on

disturbance for regeneration and maintenance.

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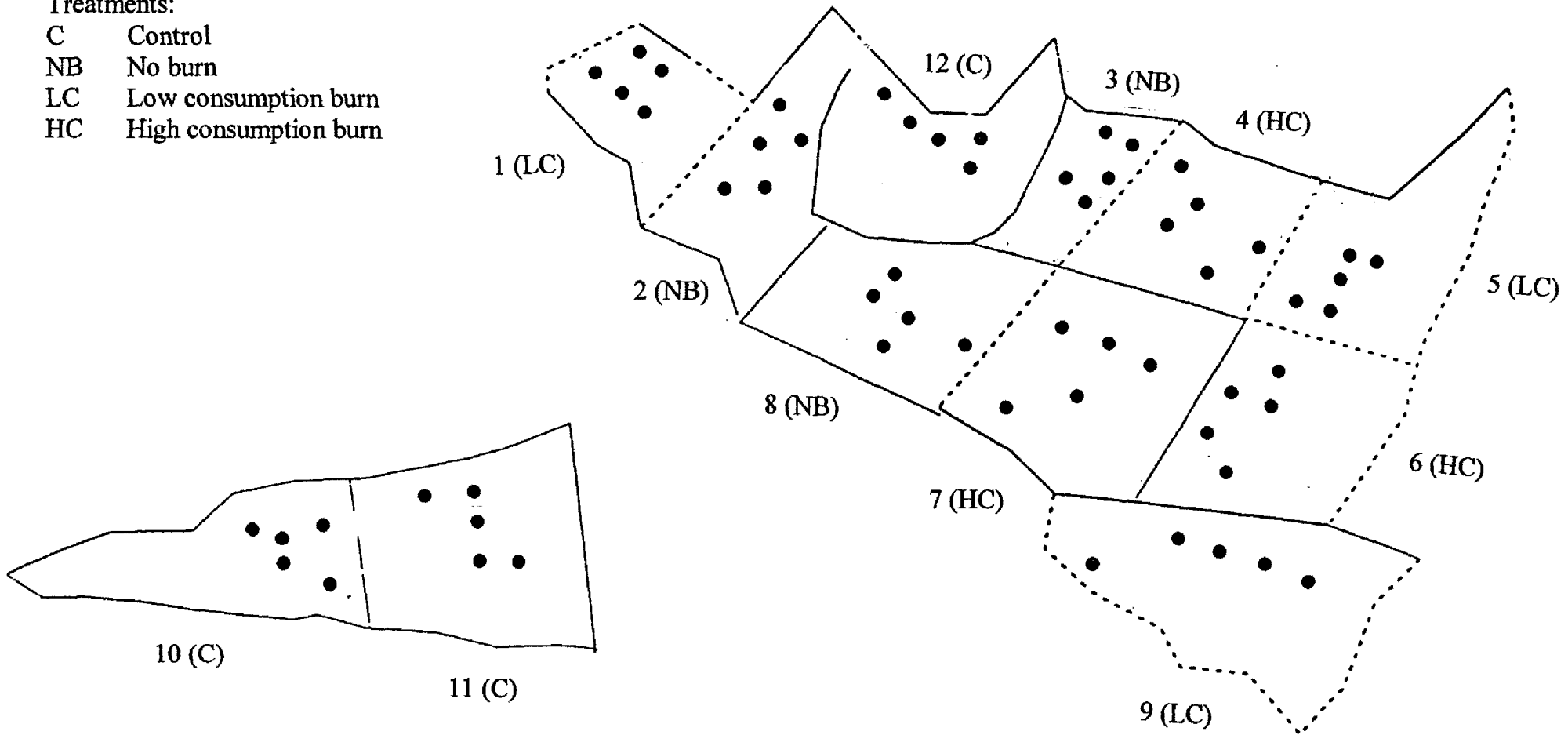
APPENDIX A: Relative Location of Units and Study Plots (map courtesy Intermountain Research Station, Missoula, Montana)

Units are labeled by number.
● indicates locations of plots used for this study.
Treatments:
C   Control
NB   No burn
LC   Low consumption burn
HC   High consumption burn

APPENDIX B:
Burn Intensities During 1993 Prescribed Burns
(information from Ayers 1995)

Numbers show percent of total area under the designated prescription that received the indicated intensity of actual burning.

Prescription	% actual heavy burn	% actual light burn	% unburned
High burn	43	13	44
Low burn	50	14	36

APPENDIX C:
Descriptive Statistics for Plots Containing
Established Seedlings in Fall 1998

	N	Minimum	Maximum	Mean	Std. Deviation
Aspect	11	138	223	183.64	24.98
Slope (%)	11	12	33	20.09	6.44
Soil moisture as a % of water holding capacity	11	18	82	40.36	17.78
# mature bitterbrush/ha, 1992	11	198	2422	813.22	775.98
# mature bitterbrush/ha, 1997	11	124	1483	393.13	388.28
# mature bitterbrush/ha, 1998	11	124	1557	397.62	405.06
Flower count per ha, 1997	11	346	180118	43864.27	59104.39
Flower count per ha, 1998	11	3064	369306	92596.61	131735.62
Tree basal area (m2/ha)	11	4.6	18.4	11.063	3.676
Trees per ha >10cm dbh	11	74	272	163.99	55.56
Trees per ha (regen <10cm dbh)	11	0	618	197.69	234.69

APPENDIX D:
Core Ages and Corresponding Establishment Dates

Age	Year	Source
32	1966	Lower units—skid row
32	1966	Upper units & above
28	1970	Lower units & area
28	1970	Lower units—skid row
28	1970	Lower units—skid row
26	1972	Upper units & above
21	1977	Upper units & above
21	1977	Upper units & above
20	1978	Lower units & area
20	1978	Upper units & above
19	1979	Lower units & area
19	1979	Lower units & area
19	1979	Lower units & area
19	1979	Upper units & above
19	1979	Upper units & above
18	1980	Lower units & area
18	1980	Upper units & above
15	1983	Lower units & area
15	1983	Upper units & above
15	1983	Upper units & above
14	1984	Upper units & above
10	1988	Upper units & above
9	1989	Lower units & area
6	1992	Lower units & area