An ecological investigation of moutain big sagebrush in the Gardiner basin
by Trista Lynn Hoffman

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

Abstract:
Mountain big sagebrush (Artemisia tridentata ssp. vaseyana [Rydb.] Beetle) is the dominant taxon on the Northern Yellowstone Winter Range (NYWR). The purpose of this study was to aid management by increasing ecological knowledge of mountain big sagebrush in the Gardiner basin within the NYWR. Specific objectives included: determining age structure of mountain big sagebrush communities, modeling site and mountain big sagebrush characteristics that influence the taxon’s production and age structure, and studying the taxon’s response to burning.

During 1993, mountain big sagebrush plants on 33 sites were classified as "large," "small" or "dead," and aged by counting growth rings. "Large" and “small” plants averaged 32 and 6 years old, respectively. Nearly half of the “small” plants were 5 years old, the result of optimal conditions for establishment in 1988. "Dead" plants averaged 41 years of age. A bimodal peak in establishment of mountain big sagebrush corresponded with large reductions in the northern Yellowstone elk population.

Mountain big sagebrush stands that were heavily and lightly browsed by ungulates were compared. Heavily browsed sites were found at significantly ($P<0.05$) lower elevations (2047 m on heavily browsed sites compared to 2179 m average for lightly browsed sites) and on steeper slopes (20.6% on heavily browsed sites and 12.7% on lightly browsed sites). Mountain big sagebrush were significantly older and more productive on heavily browsed sites. Average stand ages were 35 years, and production averaged 143.9 g/plant for heavily browsed sites compared to 28 years and 99.1 g/plants for lightly browsed sites.

Models with age, production, deadcrown and "small" plant density of mountain big sagebrush as dependent variables were developed. Variability in stand age of mountain big sagebrush was best explained by browsing levels, the density of "small" mountain big sagebrush shrubs present, the percentage of deadcrown, and the amount of live cover ($R2=0.68$, $p<0.0001$). Production of mountain big sagebrush was determined by stand age, the depth of the soil A horizon, and the slope of a site ($R2=0.26$, $P<0.05$). The amount of deadcrown in mountain big sagebrush plants was related to the amount of live cover, the stand age, and the soil sand fraction ($R2=0.59$, $P<0.03$). The density of "small" sagebrush plants was related to elevation, the stand age, the slope of the site, and the amount of ungulate browsing ($R2=0.42$, $P<0.004$).

Characteristics of 7 prescribed burned mountain big sagebrush sites were compared with the 33 unburned sites to determine the amount of recovery of mountain big sagebrush 10 to 14 years following burning. Mountain big sagebrush canopy coverage on unburned sites averaged 12 times that of burned sites and shrub densities on unburned sites exceeded burned sites by 12 times for “small" plants and 15 times for "large" plants.

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APPROVAL

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Trista Lynn Hoffman

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

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ABSTRACT

Mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* [Rydb.] Beetle) is the dominant taxon on the Northern Yellowstone Winter Range (NYWR). The purpose of this study was to aid management by increasing ecological knowledge of mountain big sagebrush in the Gardiner basin within the NYWR. Specific objectives included: determining age structure of mountain big sagebrush communities, modeling site and mountain big sagebrush characteristics that influence the taxon's production and age structure, and studying the taxon's response to burning.

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CHAPTER 1

INTRODUCTION

Big sagebrush (*Artemisia tridentata* Nutt.)/grassland comprises the largest vegetation type in the western United States (Colbert and Colbert 1983) dominating 60 million ha (Beetle 1960). Since the 1930's, control of sagebrush has been a primary objective of many land managers, with the intent of improving grass and forb production for livestock (Best 1972). Today, big sagebrush is widely recognized as valuable forage and cover for many big game species, (Kufeld et al. 1973, Welch and Peterson 1981, Wambolt and McNeal 1987, Ngugi et al. 1992), game and nongame birds, (Best 1972, Reynolds 1981, McAdoo et al. 1989) and other wildlife (Mullican and Keller 1986). Ironically, land managers are increasingly engaged in reducing big sagebrush for the purpose of benefiting wildlife or livestock.

There is much conjecture about the age at which big sagebrush reaches peak production. While some believe that big sagebrush declines in production or vigor after a certain age (Petroni 1991, West et al. 1984), details and the interrelationships with environmental factors related to these theorized declines are unclear. Decadence, degradation, and senescence are terms commonly used in the literature (Roughton 1972, Evans and Young 1978, Sinclair 1984) and in management plans relating to big sagebrush (Anonymous 1979, Anonymous 1982, Petroni 1991), but their meaning is vague. This study was initiated in an attempt to clarify relationships of mountain big sagebrush (*Artemisia* *tridentata* ssp. *vaseyana* [Rydb.] Beetle) communities regarding the taxon's viability as a climax dominant. A second goal was to obtain a better understanding of the relationship between age and production in mountain big sagebrush. This information should aid the management of the taxon.

The objectives of this study were 1) to determine the age structure of mountain big sagebrush stands, 2) to model habitat variables which influence the presence and age class distribution of young sagebrush, 3) to model the relationships among site and plant characteristics to stand production and age structure, and 4) to evaluate the response of mountain big sagebrush in selected burns.

CHAPTER 2

LITERATURE REVIEW

Age Structure and Senescence of Big Sagebrush

Because plant age is helpful in determining the nature of the vegetative community structure and in predicting successional or other ecological changes, age determination of big sagebrush individuals and populations has been of interest to scientists since the 1940's (Cottam and Stewart 1940, Lommason 1948, Stewart et al. 1956). Scientists recognized early on that sagebrush size was not necessarily proportional to age (Cottam and Stewart 1940, Pase 1956), and Ferguson (1964) established annual ring analysis as the only acceptable means of aging big sagebrush. It was also established early on that while big sagebrush may be a long lived species with shrubs documented as old as 100 (Cottam and Stewart 1940) to 200 years (Ferguson 1964), stands generally reach a maximum age of 40 to 50 years (Lommasson 1948, Blaisdell 1953, Roughton 1972).

While determination of big sagebrush age structures is a relatively straightforward process, the ecological status of sagebrush is often an issue of controversy. The use of the terms senescence, decadence or degradation to describe a variety of shrub characteristics demonstrates that several viewpoints exist regarding shrub dynamics.

Senescence in shrubs has been described as a state of physiological decline (Reid 1985) or a post-reproductive state (Gastuk et al. 1980, Zammit and Zelder 1993). Senescence has also been defined as a class of shrubs with at least 50% dead canopy (Young and Palmquist 1992). Peet and Christenson (1980) considered senescence to be a shift in the balance between competitive plant relationships as the vegetative community ages, resulting in successional replacement. Clearly the use of this term is inconsistent in the literature.

Decadence is a term used even more loosely and often without a clear definition. Roughton (1972) described big sagebrush stands with the largest number of individuals older than 55 years as decadent. However, he did not consider subspecies differences, and individuals less than 9 years were not included in his assessment. West et al. (1984), described plants with an apparent loss of vigor and reduced growth rate as decadent. Other uses of this term have referred simply to woody species in a generally undesirable state in need of human manipulation to achieve a more desirable condition (Anonymous 1979, Anonymous 1982, Petroni 1991).

Degradation is a third term used with little qualification to describe big sagebrush stands (Evans and Young 1978, Sinclair 1984). Again, this term seems to connote an undesirable condition.

The age or physiological stage in which big sagebrush is most desirable or of most benefit to wildlife has not been determined in the literature. In antelope bitterbrush (*Purshia tridentata* [Pursh] DC), age and productivity were positively related until 60 or 70 years of age, and then productivity declined (McConnell and Smith 1977). No relationships between age and yield have been determined for big sagebrush.

According to the "self-thinning rule" (Westoby 1984), plant mortality in even-aged stands (those that may be produced by a disturbance such as fire, for example) is driven by an accumulation of biomass, causing crowding and competition. The result is that the longevity of plants is not dictated by time, but rather by growth rate. Plant longevity is actually increased on sites with poor growing conditions. This counter-intuitive principle was confirmed in mountain big sagebrush by Bilbrough and Richards (1991) where, under favorable growing conditions, this shrub grows rapidly and has a short lifespan.

Germination and Seedling Establishment of Big Sagebrush

Germination patterns for big sagebrush have been described by Weldon et al. (1959) and Payne (1957). Although different germination ecotypes may occur in mountain big sagebrush (Meyer and Monsen 1992), germination generally occurs in late winter or spring with few or no seeds remaining in the seed bank (Meyer and Monsen 1991). Greenhouse studies found that optimal germination temperatures for mountain big sagebrush are 15-20° C (Young et al. 1991), and seedling growth may be reduced by a below-average temperature regime (Harniss and McDonough 1976). Seedling growth rate is rapid, reaching a maximum at approximately 11 weeks (Booth et al. 1990). It then diminishes considerably, probably as a strategy to survive when available water declines.

In a natural setting, seed production is not a limiting factor for mountain big sagebrush recruitment (Young et al. 1989). However, germination and recruitment of basin big sagebrush (*Artemisia tridentata.* ssp. *tridentata* Nutt.) was found to be sporadic with numerous seedlings emerging certain years and few or none in others (Daubenmire 1975, Humphrey 1984). In undisturbed stands of mountain big sagebrush, seedling recruitment is reduced due to competition by mature plants (Meyer 1994). Seedlings are generally excluded until older plants reach at least 40 years of age and begin to break down or die, allowing recruitment to occur in canopy openings (Lommasson 1948). Interspecific competition may also negatively influence seedling survival (Owens and Norton 1992).

On disturbed sites where competition by mature big sagebrush shrubs does not inhibit seedling growth, recruitment is still episodic and depends on a number of factors including precipitation events, seedbed characteristics, interspecific competition, and possibly the amount and timing of spring snowpack (Daubenmire 1975, Booth et al. 1990, Owens and Norton 1990, Young et al. 1990, Meyer 1994). In addition, crowded seedlings undergo a process of self-thinning based on seedling size and proximity to other seedlings (Ross and Harper 1972). These patterns of seedling recruitment complicate efforts to predict turnover in big sagebrush stands or to predict the recovery of this shrub from disturbance.

Production Estimation in Big Sagebrush

Managers often need to know the carrying capacity or the forage base of a given range. Consequently, numerous procedures have been used to estimate forage production of big sagebrush. Davis et al. (1972) found a strong relationship between widths of big sagebrush growth rings and production (subspecies was not considered). This method, along with others such as the weight estimate technique (Pechanec and Pickford 1937) involve destruction of plants as well as considerable time and cost to perform (Uresk et al. 1977). Scientists have since established non-destructive methods for determining big sagebrush production.

Many production estimates are based on an assumption of an appropriate shape of a shrub crown, and the dimensions associated with that shape. Using different plant shapes to calculate relationships varies between species (Murray and Jacobson 1982). Rittenhouse and Sneva (1977) used an elliptical crown shape to predict production in Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle and Young). Tausch (1989) measured the two longest perpendicular axes across in the crown along with crown height in low sagebrush (*A. arbuscula* Nutt.). These measurements were also used by Guenther et al. (1993) in bitterbrush. Wambolt et al. (1994) found that depending on the subspecies of big sagebrush, combinations of crown measurements and height related accurately to the amount of winter forage produced by big sagebrush. This methodology has been repeated by Mehus (1995) Wambolt and Fortney (1995), and Hoffman and Wambolt (in press).

Relationships between shrub dimensions and biomass are calculated using linear or nonlinear regressions. Both regressions were used by Guenther et al. (1993) for bitterbrush production estimates. Although Tausch (1989) felt that nonlinear regression was more appropriate to reduce systematic bias resulting in under or overestimation of biomass, linear regression is the most common analysis used (Rittenhouse and Sneva 1977, Dean et al. 1981, Wambolt et al. 1994). Wambolt et al. (1994) determined that linear regression was reasonable because nonlinear relationships were not observed in plots of dependent versus independent variables. Most of the studies above reported strong relationships between measured shrub parameters and biomass production.

Mountain Big Sagebrush Response to Ungulate Browsing

The response of mountain big sagebrush to ungulate browsing is well studied and fairly well understood. Several growth characteristics of this shrub make it less tolerant to browsing than other species (Bilbrough and Richards 1991). Because mountain big sagebrush is wind pollinated, flowering stems are elevated above the canopy making them susceptible to browsing. Branches and stems of this shrub grow linearly, and most of the productive buds are on the distal ends of stems where they are vulnerable to browsers. The terminal leaders contribute the most to biomass production, and production generally declines toward the base of the plant. In addition, mountain big sagebrush is unable to initiate new growth from shoots older than 1 year (Bilbrough and Richards 1993). Therefore, if the current year's growth is removed, compensatory response by mountain big sagebrush is significantly reduced.

Mountain big sagebrush has been shown to lose vigor, undercompensate, or even die following browsing. Bilbrough and Richards (1993) found that simulated browsing by clipping shoots resulted in decreased shoot biomass. This effect was increased with increased clipping to the point of branch mortality by the removal of all the current year's long shoots. Wandera et al. (1992) was also able to induce mortality in mountain big sagebrush by removing 90% of the previous year's growth. Cook and Child (1971) observed 100% mortality of big sagebrush (subspecies not considered) that were clipped twice in one year (winter and spring). Cook and Stoddard (1960) found that removal of current year's growth on half of a big sagebrush crown (again, subspecies not considered) resulted in mortality of that portion of the crown, plus mortality of a distinct portion of the root system. By contrast, the removal of half of the current year's growth on each twig (thereby distributing the effect of the treatment more evenly) produced an overall loss of vigor and biomass production with mortality of only small twigs and branches. Apparently, plant parts that are not productive are not supported by the remaining productive parts (Watson and Casper 1984).

Decline or mortality of mountain big sagebrush by browsing has been observed in a natural setting by a number of researchers. As early as the 1930's, heavy browsing by elk was credited for big sagebrush losses within Yellowstone National Park (YNP) (Wright and Thompson 1935). McArthur et al. (1988) observed 11 times as many dead mountain big sagebrush plants on an area heavily browsed by mule deer than a nearby area that was partially excluded from deer by an interstate highway and fence. Partial crown mortality was 64% higher on the browsed site compared to 17% in the excluded area. While studying utilization levels of 4 sagebrush taxa in southern Montana, Wambolt (in press) found that 35% of mountain big sagebrush were killed by excessive browsing. Browsing also caused increased crown dieback which was estimated at 58.7% during the study. Hoffman and Wambolt (in press) noted decreased production and vigor in Wyoming big sagebrush subject to heavy browsing compared to protected plants. In particular, reproductive structures were virtually eliminated by browsing.

Some studies have claimed that browsed plants may respond by growing more or growing faster than unbrowsed plants. Cook and Stoddard (1960) found that while the clipped half of a big sagebrush crown died, the intact portion grew more vigorously than in untreated plants. Paige and Whitham (1987) found that the removal of reproductive structures in scarlet gilia (*Ipomopsis aggregata* [Pursh] Grant), a short-lived forb, resulted in a 210% increase in biomass and a 240% increase in seed production. Dyer et al. (1991) found that repeated mowing of a plot of smooth brome (*Bromus inermis* Leyss.) resulted in

29% more aboveground biomass compared to untreated plots. Painter and Belsky (1993) warn however, that overcompensation by browsed or grazed plants may occur only rarely in a natural setting with no evolutionary or applied significance. They suggest further, that the nature of compensatory growth may depend on both the species and the environmental circumstances that influence the plant. Patten (1993) applied this viewpoint to browsing by elk in YNP and concluded that neither grass nor woody species (including big sagebrush) were benefited by browsing.

Use of Fire to "Improve" Big Sagebrush Stands

Fire is perhaps the most commonly used tool to control or alter big sagebrush stands. The practice of burning big sagebrush has been a source of controversy between those who believe that fire benefits big sagebrush rangelands, and those who believe that such rangelands are harmed by burning. Jorgenson (1990) and Peterson (1995) compiled comprehensive literature reviews pertaining to the implications of burning big sagebrush.

Managers have sometimes attempted to replicate natural burning cycles of big sagebrush, but there is debate as to the length of those cycles. In the Gravelly Mountains of southwestern Montana, burning of mountain big sagebrush every 20 years was recommended to maintain stand vigor (Petroni 1991). However, Lommasson (1948), following a thirty year study in the same area, maintained that these stands may maintain themselves indefinitely without disturbances such as fire. Other studies in southwestern Montana found little recovery of Wyoming big sagebrush after 12 years (Blaisdell 1953) or 18 years (Wambolt and Payne 1986), and a similar result was found in mountain big sagebrush after 19 years

(Mehus 1995). At least 30 years are required for stands to show significant recovery from burning (Harniss and Murray 1973, Watts and Wambolt 1996). Whisenant (1990) determined that the natural fire frequency along the Snake River Idaho was 60-110 years. However, he also found that in areas occupied by cheatgrass (*Bromus tectorum* L.), an exotic annual, burns may occur as often as 2-4 years, effectively eliminating big sagebrush as well as many other native species. .

The terms decadent, degraded and senescent are sometimes used as explanations for the necessity to burn big sagebrush to improve wildlife habitat (Anonymous 1982, Petroni 1991). However, Jorgenson (1990) found no references relating the use of fire to "rejuvenate decadent sagebrush stands." The reduction of fuel loads was the only suggested value for this practice (Charley and West 1975). Evanko (1949) found that burning may significantly increase the height of sagebrush seedlings (subspecies not considered), but the importance of this finding is not clear. Peterson (1995) found that there was no relationship between plant age and crude protein content in mountain big sagebrush. Therefore, burning does not necessarily improve the nutritional content of big sagebrush. These studies, or lack thereof, indicate that the role of fire in big sagebrush stand "improvement" is unclear. In fact, Rasmussen (1994) noted that fire has "very limited applicability" to maintain big sagebrush, and Harniss and Murray (1973) warn that degradation of vegetation and soil result from haphazard burning practices.

CHAPTER 3

STUDY AREA

Location

The study was conducted on a portion of the Northern Yellowstone Winter Range in southwestern Montana. The study area extends from Buffalo Mountain, 6 km northeast of Gardiner, to Dome Mountain, roughly 23 km to the northwest (Fig. 1). It is bounded by the Absoraka-Beartooth Wilderness on the east and the Gallatin Mountains on the west. The majority of sampling sites (28) was located in the Gallatin National Forest on the east side of the Yellowstone River. Five sites were located on National Park Service (2) or Forest Service (3) land on the west side of the river.

Landscape

The Yellowstone River is a prominent feature dividing the study area in half and serving as an elevational base away from which the foothills and mountains rise. The river floodplain is narrow, and the valley is trough-like with foothills rising steeply from the floodplain to rolling benchlands often at 50-60° slopes (McNeal 1984).

Volcanic activity has left a prominent mark on the northern Yellowstone valley. Northwest of Gardiner, basalt benches extend as far as Little Trail Creek and throughout the study area, basaltic outcrops and talus slopes may be found. Dacitic and andesetic breccias are common extrusive volcanic rocks dating to the Eocene Epoch (Fraser et al. 1969). In

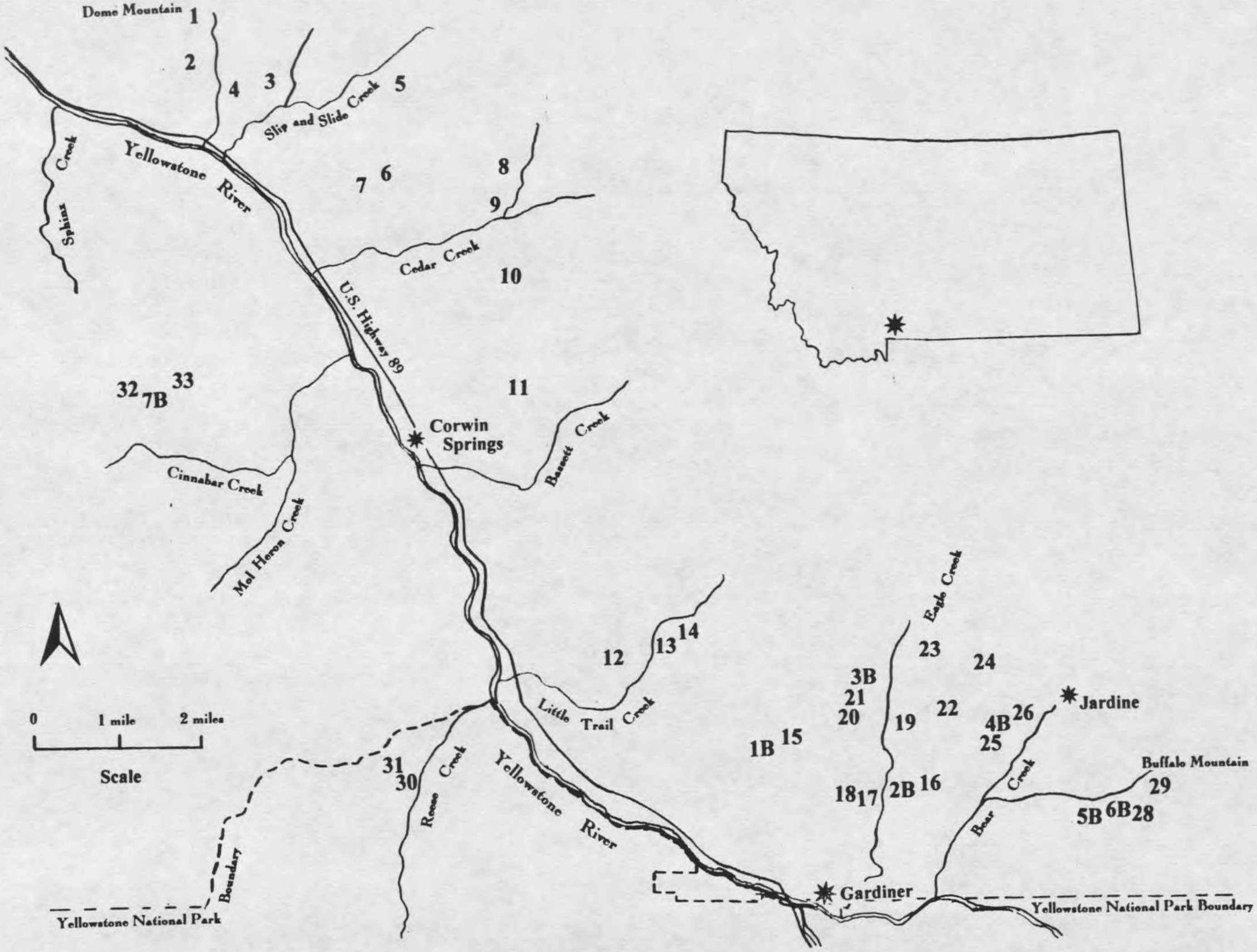

Figure 1. Map of the Gardiner Basin showing study sites (1-33 unburned and 1B-7B burned).

some areas, these rocks are the materials for extensive landslides and earthflows.

Glacial activity has also played a prominent role in the topographic expression of the study area. During the Pleistocene, 3 glacial advances occurred over the study area (Blackwelder 1915). During the third advance, the Pinedale, which peaked around 15,000 years ago, the study area was covered by the northern Yellowstone outlet glacier, a portion of the northern Yellowstone glacier (Pierce 1979). The northern Yellowstone glacier covered 3400 km^2 and averaged 700 m in thickness. In addition to moraines and glacial erratics deposited high on the walls of the valley, the withdrawal of the glaciers left the valley walls in steep and unstable condition (Good 1982). The result was a number of landslides and slumps that extend from Yankee Jim Canyon to Cinnabar Mountain. Two large earthflows are still active on either side of the Yellowstone River at the mouth of Slip and Slide Creek (Fraser et al. 1969).

Climate

The mountains surrounding the study area produce orographic effects on both a large and a local scale. The Gallatin Range creates a distinct rain shadow along the Yellowstone River, where annual precipitation averages 305 mm. The nearby benchlands receive 406 mm of precipitation, while the mountains may receive 760 mm annually (Farnes 1975).

Because half of the annual precipitation is in the form of snow, a water deficit by late summer is common. June is the wettest month with about 50 mm of precipitation (U.S. Weather Bureau Station, Mammoth, WY). In July and August, localized thundershowers may be the only source of moisture.

The growing season in the Gardiner valley is strongly influenced by elevation, but it is generally from mid-April to mid-September. The warmest month is July which averages 17.3 °C. A killing frost may occur in any month.

Soils

Glacial scouring and deposition are strong influences on the soils of the study area. Parent materials include granites and limestones deposited by glaciers as well as basalts and breccias. The soil regolith in the study area may range from a few cm in areas scoured by glaciers, to over 1.5 m in depositional areas.

Mollisols are the dominant soil order in the area, and soil groups may range from Aridic Haploborolls to Pachic Argiborolls. Alfisols may be found in forested areas and Inceptisols occur near outcrops of basalt and bedrock.

Soil textures are most commonly loams and sandy loams, although a wide variety of textures are present. Because much of the area is dominated by glacial till, most soils have a skeletal structure. Coarse fragments range from gravels to large boulders 3-4 m in diameter. Glacial erratics are common, especially in the southern portion of the study area.

Because the majority of precipitation in the study area comes in the winter, the soil moisture regimes are typically ustic. Soil temperatures are characteristically cryic.

Vegetation

Sagebrush-grassland habitat types dominate the study area. From cover types mapped in this study (Unpublished map, Trista Hoffman, U.S.D.A. Forest Service, Gardiner

District), sagebrush-grassland covers approximately 11617 ha. Three sagebrush species are represented. Tall three-tip sagebrush (*Artemisia tripartita* ssp. *tripartita* Rydb.) is found only in small isolated patches of a few ha on west-facing slopes of the OTO ranch. Black sagebrush (*A. nova* Nels.) occupies approximately 115 ha in pure stands and 325 ha in stands mixed with big sagebrush taxa. It occurs from the OTO ranch to Eagle Creek, with localized patches on the west side of the Yellowstone River. This sagebrush occupies elevations below 2100 m and is associated with shallow calcareous soils.

Big sagebrush occurs throughout the valley and 3 subspecies are present. Basin big sagebrush has a patchy distribution and dominates approximately 20 ha, while 315 ha are mixed with other sagebrush taxa. Small stands of basin big sagebrush may be found below 2100 m along irrigation ditches and agricultural fields, below talus slopes or in other areas with deep soils or conditions of high soil moisture. Wyoming big sagebrush grows in extensive stands in the dry glacial outwash along the Yellowstone River and associated benchlands below 2100 m. Approximately 4600 ha of this taxa are found in pure stands while 1100 ha are mixed with other sagebrush taxa. Mountain big sagebrush is the dominant shrub in the study area occupying 5520 ha in pure stands and 1150 ha in mixed stands. It may be found from 1800 m to 2500 m in elevation in a wide range of soil types. The above distribution areas do not include areas that were originally sagebrush habitat types, but have since been converted to agricultural fields, roads or buildings, or have not been restored to sagebrush cover following burning (see page 19).

At lower elevations mountain big sagebrush is associated with bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Scribn.), but across most of the study area, it is found with

Idaho fescue (*Festuca idahoensis* Elmer). Other prominent grasses associated with this shrub are prairie junegrass (*Koeleria macrantha* Ledeb.) and needleandthread (*Stipa comata* Trin. & Rupr.) in drier areas and columbia needlegrass (*S. columbiana* Macoun) and basin wildrye (*Elymus cinerus* Scribn. & Merr.) in sites with more moisture. A list of most of the plant species found in the study area may be found in McNeal (1984).

Several forest habitat types occur in the study area and are classified according to Pfister et al. (1977). Limber pine (*Pinus flexilis* James) is present at low elevations, and Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) stands are found at high elevations or near streams. Both of these species are associated with either bluebunch wheatgrass or Idaho fescue.

Ungulate Wildlife

As part of the Northern Yellowstone Winter Range, the study area sustains one of the largest wintering herds of Rocky Mountain elk (*Cervus elaphus nelsoni*) in the world (Houston 1982). In the early 1960's, the National Park Service (NPS) managed elk populations intensively, reducing herds by transplanting or intensive harvesting. In 1967, the NPS adopted a philosophy of non-interference with elk populations, and elk numbers increased from less than 4000 animals to more than 23,000 by 1988 (Coughenour and Singer 1996). The winter of 1988-89 drastically reduced the herd, but by 1993, it had recovered to an estimated 25,000 animals.

Some believe that elk are artificially concentrated on the northern winter range due to the disruption of traditional migration routes by human activity (Tyers 1981). Most of the elk spend the summer at high elevations in YNP or the adjacent Absoraka-Beartooth Wilderness. In winter, the concentration of elk on the study area varies, depending on the severity of the weather. Large herds may move out of the YNP only every 2 or 3 years (Houston 1982), but they may travel as far as 115 km to reach the Gardiner valley (Craighead et al. 1972). In the most severe winters, the area around Mammoth and Gardiner may be the only portion of the northern winter range that remains open and available for animals (Turner et al. 1994).

While elk are the most conspicuous winter ungulates on the northern winter range, the area is also critical habitat for mule deer (*Odecoileus hemionus hemionus*). Deer arrive on the winter range from the adjacent mountains in October, and remain until June. In the winter of 1992, mule deer reached a population high of approximately 2550 animals in the study area. Each year, 50-75% of the deer are found on the east side of the Yellowstone River (Unpublished report, Tom Lemke, Montana Fish, Wildlife & Parks).

Less common occupants of the study area include bighorn sheep (*Ovis canadensis*), especially near MacMinn Bench, Bear Creek and Bassett Creek. A population of pronghorn antelope (*Antilocapra americana*) occupies low elevations from Beattle Gulch to the Gardiner River. Bison (*Bison bison*) occasionally wander out of Yellowstone Park and into the study area, especially during severe winters. Moose (*Alces alces*) are other sporadic visitors.

Livestock Grazing History

In 1926, most of the public land within the study area was withdrawn from homesteading and added to the Gallatin National Forest system. Many grazing allotments were eliminated to provide more forage and cover for wildlife. Five allotments remain and occupy approximately 700 ha. Four allotments are grazed from June 16--October 16 each year while the fifth is grazed from June 16--September 30 annually (Unpublished, U.S. Forest Service, Gardiner District, Montana).

Burning History

By studying fire-scarred conifers, Houston (1973) determined that in the last 300-400 years, there were 8 to 10 large fires on the portion of the northern winter range inside YNP, although it is not clear how much burning occurred in sagebrush-grass habitats. Human fire suppression began in 1886 and has increased in sophistication ever since. By the 1950's, almost complete fire suppression in the grasslands of the Northern Yellowstone Winter Range was accomplished (McNeal 1984).

By the 1970's, fire was recognized as an integral part of the ecosystem as well as a useful management tool. In 1972, 12,000 ha of winter range within the Park were designated as range where wildfires would not be suppressed. The Forest Service, under pressure to minimize livestock/wildlife conflicts, began controlled burns in the late 1970's. Between 1979 and 1995, approximately 1170 ha were burned largely by prescribed burning (Unpublished map, Trista Hoffman, U.S.D.A. Forest Service, Gardiner District) to "improve range condition" by conjectured reduction in sagebrush and increases of herbaceous plants (Tyers 1981). Nearly 280 ha of the total was burned incompletely, due to adverse burning conditions or low fuel loads. Between 1965 and 1993, approximately 100 ha of the total burned as a result of wildlfires. In 1994 a wildfire on Deckard Flats consumed 525 ha of sagebrush habitat types. However, little sagebrush remained in this area due to previous prescribed burning and heavy browsing by ungulates migrating out of YNP. The study area was out of the range of the massive fires that burned YNP in 1988.

Human Settlement

Human settlement within the study area is one of the most important factors influencing wildlife habitat and movement. Residences, roads, fences, and recreationalists are among the obstacles that animals meet when they move from one part of the winter range to another. The human population of the study area, including Gardiner, Corwin Springs, Jardine, and outlying communities, is nearly 1600 in 650 houses (U.S. Bureau of the Census 1992). Most of the valley bottom between Gardiner and Yankee Jim Canyon is privately owned. Gardiner has a population of approximately 375 people, and is a major entrance to YNP. It lies directly in the path of migrating wildlife. Because large numbers of animals pass through this area, it is a popular stop for thousands of tourists on their way to and from YNP.

Jardine, a small mining town of about 30 persons, is 6 km northeast of Gardiner. Despite the small size of the town, the presence of the mine creates additional obstacles for wildlife. Wild ungulates encounter roads, heavy machinery, and leach ponds. The town of Corwin Springs lies along the Yellowstone River in the center of the study area. It has perhaps 400 people, but its population has changed dramatically in the last 15 years due to the activities of the Church Universal and Triumphant (CUT) which owns much of the private land in the area. In addition to increasing housing in the Corwin Springs vicinity, the CUT has stepped up agricultural production in both crops and livestock. These activities, like similar activities throughout the Gardiner valley, influence the quality of wildlife habitat and wildlife movements on the winter range.

CHAPTER 4

METHODS

Site Selection

During 1992, the extent of mountain big sagebrush within the study area was mapped using aerial photographs and ground confirmation. Between June and August, 1993, 33 unburned and 7 prescribed burned mountain big sagebrush sites were selected throughout the study area (Fig. 1, Appendix A: Tables 11-14). Adequacy of sample testing indicated that 33 sites provided a sufficient sample to account for the variation expected during the study.

A study site was defined as a stand of mountain big sagebrush that appeared relatively homogenous in terms of outwardly apparent characteristics such as slope, aspect and elevation. Confirmation of the mountain big sagebrush subspecies was made in the lab using an ultraviolet light (Stevens and McArthur 1974). Each study site was at least 0.25 ha in size (40x60 m) and ranged up to 3 ha. Sites were selected not by how well they appeared to represent the study area, but by whether they were thought to help characterize the full range of 1 or more of the parameters to be measured. The full range of values could then be used to develop models to illustrate the influence of these parameters on the age, production or establishment of mountain big sagebrush.

Measurements

Plant Measurements

Measurements of plant parameters began near the end of June, 1993. The majority of sagebrush growth for the year occurred before this time. Long shoots and leaves were fully elongated, and an annual growth ring was well established in the stem xylem. Therefore, measurable production increases by sagebrush plants were not expected over the remainder of the summer. The plant parameters measured included browse form class, percent cover of live and dead sagebrush, density of large, small and dead plants, percent dead crown, production and age.

The overall appearance of a sagebrush plant determined the browse form class assigned to the plant. Browse form classes were described by Creamer (1991). Plants that receive repeated heavy browsing develop a dense canopy and a hedged appearance. Lightly browsed plants have a more open canopy with linear growth due to the annual extension of terminal leaders. Usually, all of the plants on a site exhibited nearly the same browse form class.

At each site, 2 line transects, 30 m long, were established with the slope of the site. The transects were parallel to one another and 10 m apart. Measurements from the transects were pooled. Belt transects of 60 m^2 were established by measuring 1 m on each side of the line transect.

A plumb bob was used to determine live and dead cover to the nearest 1 cm along the transects. Live cover included any leaves, current year leaders or seedheads that intercepted the line transect. Dead cover referred to the intercept of dead sagebrush branches that were still elevated above the ground.

Plant density was determined by counting all sagebrush plants rooted within the belt transect. Plants were divided into “large,” ”small” and “dead” categories. A “large” plant measured at least 22 cm across the widest portion of its crown. These minimum measurements were derived from the minimum size requirements for use in the sagebrush production models developed by Wambolt et al. (1994). Plants smaller than these minimums were not considered to be significant contributors to the production of a site but were important as representatives of the younger age classes. Dead plants were separated from woody litter by the requirement of at least 1 main stem still rooted in place, and some portion of the stem remaining above the ground.

An ocular estimate of the percentage of dead crown area was made for each “large” sagebrush. This measurement estimated the loss of potential production on a site by mountain big sagebrush. Estimates were made to the nearest 10%.

Production was defined after Wambolt et al. (1994) as the amount of winter forage available to wildlife from mountain big sagebrush plants. Production measurements were made on 10 "large" plants per line transect. Each line transect used for cover was marked at 10 increments, 3 m apart, and the plants most closely rooted to each mark were measured for production.

Four measurements were recorded for each plant to model production. The major axis referred to the longest horizontal line between living plant tissue across the plant crown. The minor axis was a similar line perpendicular to the major axis. Two additional axes were measured perpendicular to one another and set at 45^0 angles to the intersection of the major and minor axes. The modeled forage production per plant was multiplied by the density of "large" plants to determine the mass of sagebrush forage available on a per ha basis.

Each of the 20 plants measured for production was cut at the base and transported to the lab for aging. Twenty "small" plants were collected in the same manner for aging. Twenty dead plants were also collected, but because dead plants were uncommon and often not found near the 3 m marks, these plants were collected by walking through the site and cutting the first 20 plants encountered. Often, dead stems were rotted or colonized by ants and had to be discarded, and on some sites, it was not possible to collect 20 specimens.

Annual growth rings were counted in cross-section (Ferguson 1964, Taha 1972). Sagebrush cross-sections were sanded smooth and a fresh razor was used to take a thin veneer off the surface. This removed the surface pores that were filled with sawdust or impurities and clarified the annual growth rings. A light coating of vegetable oil was sometimes used to highlight rings before counting with a 10x hand lens under a full spectrum light.

Site Measurements

Site parameters included elevation, aspect, slope, soil characteristics and associated vegetation. The elevation of a given site was estimated from its position on USGS topographical maps. Aspect was the general direction that the site faced, and it was measured with a compass as the degree difference from magnetic north. Slope was measured using a compass and plumb bob. Two measurements for slope were taken perpendicular to the aspect and 180° from each other. These estimates were averaged.

Areal canopy cover of grasses and forbs was estimated using 20 x 50 cm plots spaced 3 m apart along the transect lines (Daubenmire 1959). Ocular estimates of percent coverage were made for the grasses and forbs separately. Twenty plots were averaged for each site.

Soils were collected from a pit dug between the 2 transects. The depth of the A horizon was measured to the nearest cm, and a sample of this soil was collected at a 15 cm depth. Particle size analysis was determined using the Bouyocous method (1936), and organic matter was analyzed according to Page et al. (1982).

Analysis

Student's *t*-tests were used to compare parameters on heavily browsed sites versus lightly browsed sites, and burned sites versus unburned sites. Stepwise linear regression (Sokal and Rohlf 1981) was used to model habitat and mountain big sagebrush variables. Initially, both forward and backward stepwise regressions were used. Each variable required a significance level of 0.15 to enter the model. Forward regressions provided slightly higher R^2 values, thus were used in the final analysis.

To avoid collinearity among related variables, all variables were entered into a correlation matrix to determine their associations. Next, all variables were compared using simple linear regressions to determine which ones explain the most variation independent of the others. Variables that were likely to measure the same parameter, such as percent dead sagebrush cover and density of dead sagebrush, were highly correlated, and were obvious candidates for collinearity problems. Therefore, those collinear factors that explained the least variation were not entered into the models (Lund, personal communication 1995). Reducing the number of variables in each model also prevented regressions from becoming artificially inflated (Wambolt and McNeal 1987). The models were based on the remaining independent variables: elevation, percent slope, percent sand, depth of the A soil horizon, ungulate use, live sagebrush cover, density of "small" shrubs, percent deadcrown, production per shrub, and average stand age.

CHAPTER 5

RESULTS AND DISCUSSION

Age Distribution of Mountain Big Sagebrush

The age distribution of individual "large" mountain big sagebrush is shown in Figure 2. Large (≥22 cm) plants are the major contributors of sagebrush forage in the study area. Ages of individual “large” mountain big sagebrush plants ranged from 5 to 88 years with an average age of 32 years. Because no "large" plants were less than 5 years old, it appears that 5 years are required for a mountain big sagebrush plant to reach an age where it is large enough to contribute notably to the forage base. Crisp and Lange (1976) found in Australia that in *Acacia burkettii*, plants younger that 8 years had high mortality rates, and were not considered established members of the vegetative community. Roughton (1972) excluded all plants less than 9 years old in his discussion of sagebrush age classes. When mountain big sagebrush is burned, recovery to pre-burn levels of forage production is not a rapid process and requires almost a decade for shrubs to attain any notable level of production. Therefore, frequent burning of sagebrush will result in reduced forage production by sagebrush.

Even though 5 or more years are required to establish a mountain big sagebrush shrub as a productive individual, the population of sagebrush in the study area is relatively young. The age classes with the largest number of individual plants were between 25 and 35 years old. When plants were grouped as stands (20 plants measured per stand), the average stand

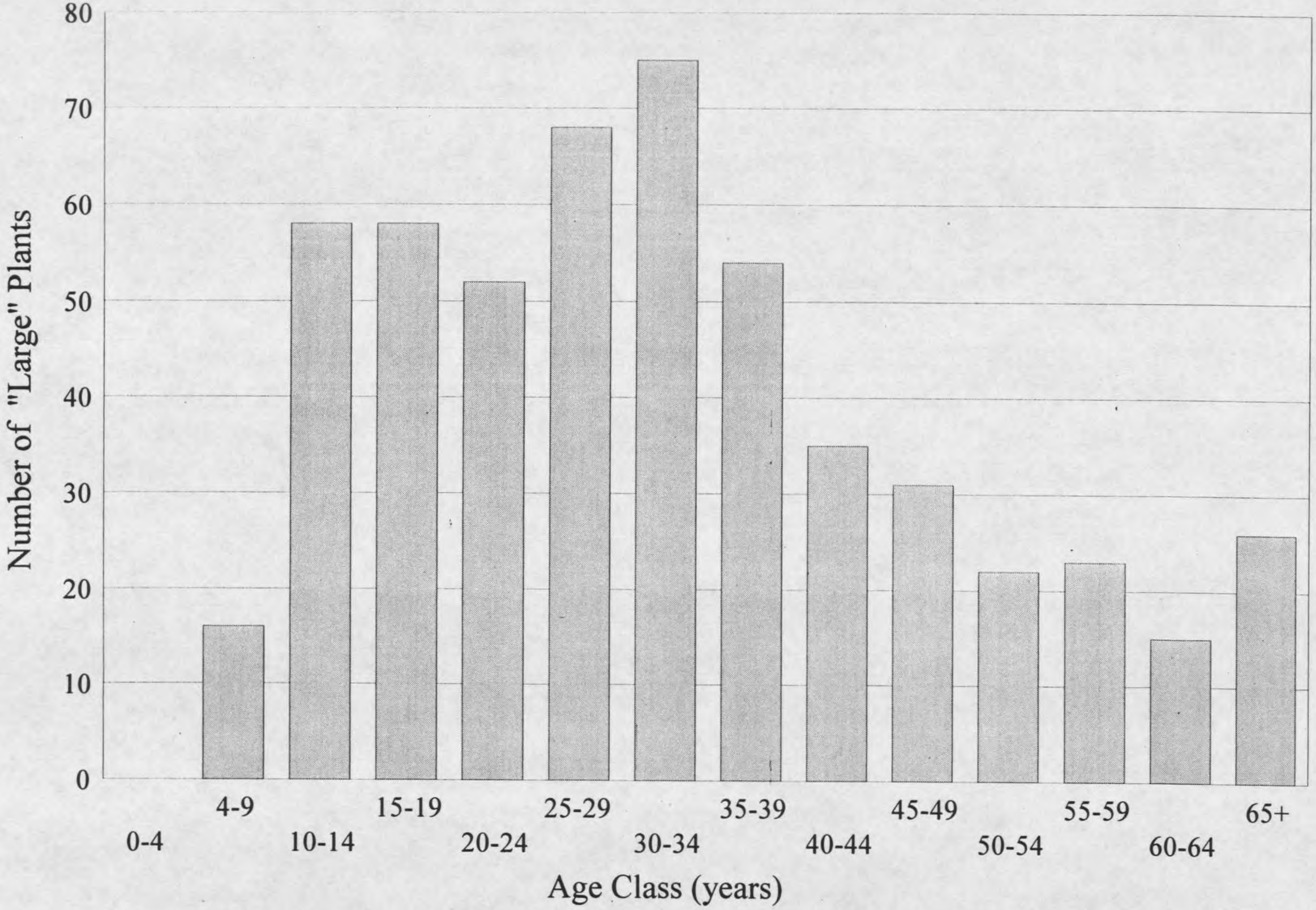

Figure 2. Age distribution of 660 “large” (>22 cm) mountain big sagebrush plants from 33 sites in 1993.

age (n=33) ranged from 18 to 45 years with an average overall stand age of 32 years in 1993 (Table 1, Appendix A: Table 11). Therefore, the average stand age was identical to the average individual age. Only 12% of the individuals exceeded 50 years of age, and 5% were older than 60 years.

Table 1. Averages and ranges of plant characteristics for mountain big sagebrush sites.

	$\bar{x}$	Std. Dev.	Maximum	Minimum
Percent Live line cover	14.2	0.1	38.8	3.0
Percent Dead line cover	5.5	0.0	15.0	0.1
Density “large” plants/m^2	0.9	0.3	1.5	0.4
Density “small” plants/m^2	1.0	1.0	4.0	0.1
Density “dead” plants/m^2	0.2	0.1	0.7	0.1
Production (g/plant)	127.6	73.6	330.1	34.8
Percent Deadcrown	22.5	7.2	43.2	11.1
Age “large” stand	32.2	6.4	45	18
Age “small” stand	6.1	0.5	25	1
Age dead stand	40.7	7.5	56	20

While big sagebrush have been reported to live as long as 200 years (Ferguson 1964), no mountain big sagebrush in the study area had such a long lifespan. The oldest plant recorded was a dead individual of 109 years. The oldest living plant was 88 years of age. In southwest Montana and southern Idaho, the majority of mountain big sagebrush were aged 11-20 years (Brown 1982), and the next most common age class was 21-30 years. Although the length of time since the last disturbance (such as fire) was not discussed, only 3% of plants were older than 50 years. In Nevada, the average longevity of big sagebrush (subspecies not considered) was estimated at 30 to 40 years (Wallace and Romney 1972, from West et al. 1979). The oldest big sagebrush plant (subspecies not considered) observed by Roughton (1972) in Colorado was 72 years old. On 2 sites, he found that 60-75% of shrubs were between 5 and 35 years of age (the 0-4 year age class was excluded). By excluding age classes below 9 years, he found that the majority of sagebrush on a third site was between 50 and 59 years old. He described this age structure as "decadent" even though thousands more plants were observed between 1 and 9 years old than all the other age classes put together. This description is misleading since thousands of plants were selectively eliminated from discussion. Although the shrub communities may have begun a cycle of self-rejuvenation as described by Lommasson (1948), stands were described by Roughton (1972) as if the young members were of no consequence.

In the Gardiner valley, mountain big sagebrush are not decadent. Every site has young age classes well represented and the majority of plants is less than 50 years of age. Because none of the 33 sites have been drastically disturbed (as with fire, spraying, etc.), this relatively young condition has maintained itself, with sagebrush plants establishing, maturing, dying and being replaced in a relatively short period of time (around 50 years) in the absence of human intervention as expected from a climax dominant. This indicates that burning or other means of sagebrush manipulation is not necessary to maintain sagebrush stands in a productive state or to prevent them from becoming "decadent."

The data from dead mountain big sagebrush plants are also evidence that mountain big sagebrush stands turn over relatively rapidly without outside intervention, although sampling was necessarily limited to plants that were generally small and free of heartrot, the average age of the sample of dead plants was 40.7 years (Table 1). While this does not establish the age at which mountain big sagebrush are likely to die, the estimate comes from 440 observations, which indicates that turnover by age 41 is not uncommon. Lommasson (1948) reported 40 years as the stand age at which old mountain big sagebrush plants begin to senesce, breaking down and creating natural openings in which young plants may establish. Recruitment by seedlings in closed stands of mountain big sagebrush occurs only infrequently due to intraspecies competition (Meyer 1994). However, patterns for seedling establishment are not always clearly related to natural openings associated with aging stands. They may also be influenced by environmental factors such as soil moisture or seed production (Tyrrell and Crow 1994).

The year of establishment for "small" mountain big sagebrush individuals is shown in Figure 3. These plants have a crown diameter below 22 cm. Such small plants do not contribute notably to the production by mountain big sagebrush in the study area. Plants that were over 20 years old and still “small” were found in areas with adverse growing conditions such as very dry, shallow soils on exposed ridgetops.

Individual "small" mountain big sagebrush plants range from 1 to 25 years old. Out of 660 “small” plants sampled, nearly one half were 5 years old (germinated in 1988) when sampled in 1993. This age dominated on all 33 sites. When plants were grouped as stands (20 "small" plants per stand), the average age (n=33) ranged from 4 to 11 years with an overall average age of 6 years (Table 1, Appendix A: Table 11).

Crisp and Lange (1976) proposed a model for age structure of shrubs that under hypothetical natural conditions, mortality is highest in young and old individuals, with

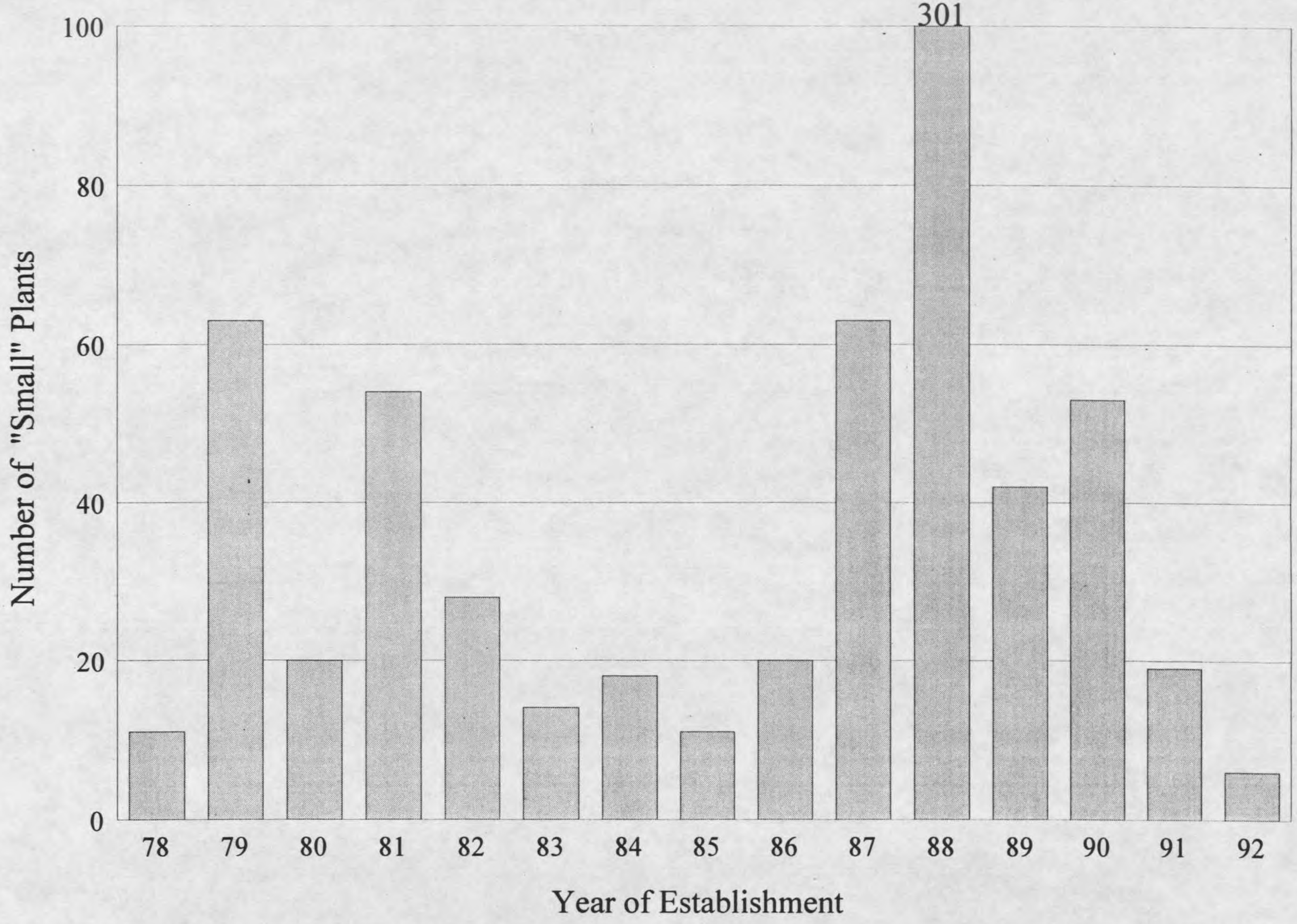

Figure 3. Year of establishment from 1978 to 1992 of 640 “small” (<22 cm) mountain big sagebrush plants from 33 sites.

reduced mortality in mature, but relatively young plants. Figure 4 is a simplified graph of this distribution. A sharp decline in surviving individuals would occur early after germination, followed by a period of reduced mortality. Eventually, mortality rates would again increase after plants reached a critical age.

The average stand establishment dates of "large" and "small" mountain big sagebrush plants are shown in Figure 5. Data were collected from different populations (see "Methods") and should not be combined to form a continuous age structure.

The survivorship curve (Fig. 5) from this study area is quite different from the hypothetical curve (Fig. 4). Within the age distribution for "large" plants, several stands have average ages that date to the late 1940's and early 1950's. Stand ages do not pre-date the 1940's because, as a whole, mountain big sagebrush in this area were found to average 41 years in a sample of 440 dead plants (Table 1). The stands at the older end of the curve probably represent the lifespan of mountain big sagebrush. This lifespan is influenced in part by the large ungulate population that has been present since these plants germinated.

In the late 1950's and early 1960's, mountain big sagebrush establishment generally increased, reaching a peak in 1961 (Fig. 5). This event was followed by a general decrease in recruitment by the late 1960's. This is inconsistent with the hypothesis that decreased mortality is observed in mature but relatively young plants (Crisp and Lange 1976). If one assumed that plants germinate and establish equally each year and that survival followed the hypothetical curve in Figure 4, then many more site ages should have been observed in the late 1960's and early 1970's. However, by the 1970's, establishment of mountain big sagebrush is extremely low.

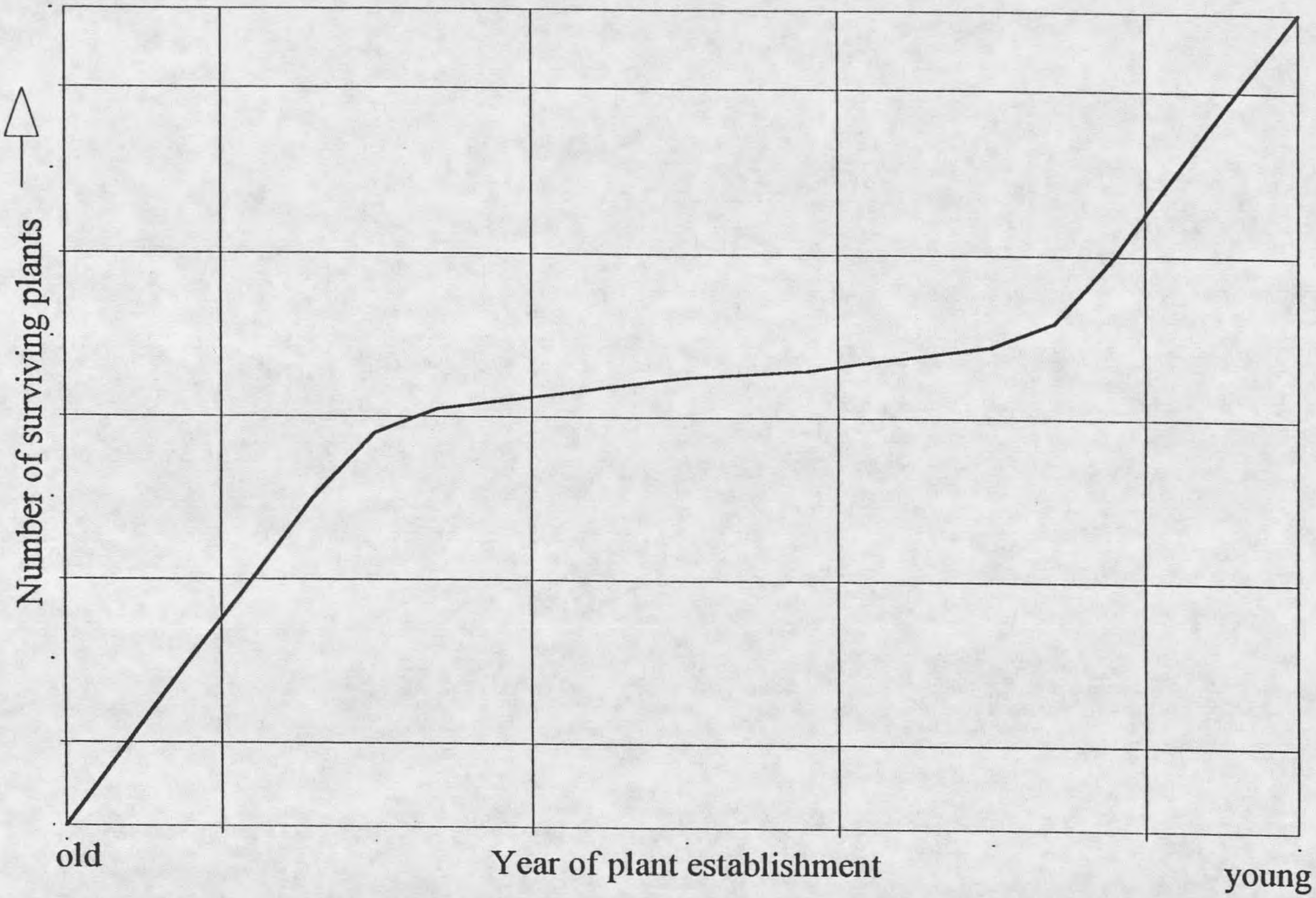

Figure 4. Hypothetical survivorship curve described by Crisp and Lange (1976). Shrub mortality is highest during the early years after establishment and again long after establishment with reduced mortality in middle age classes.

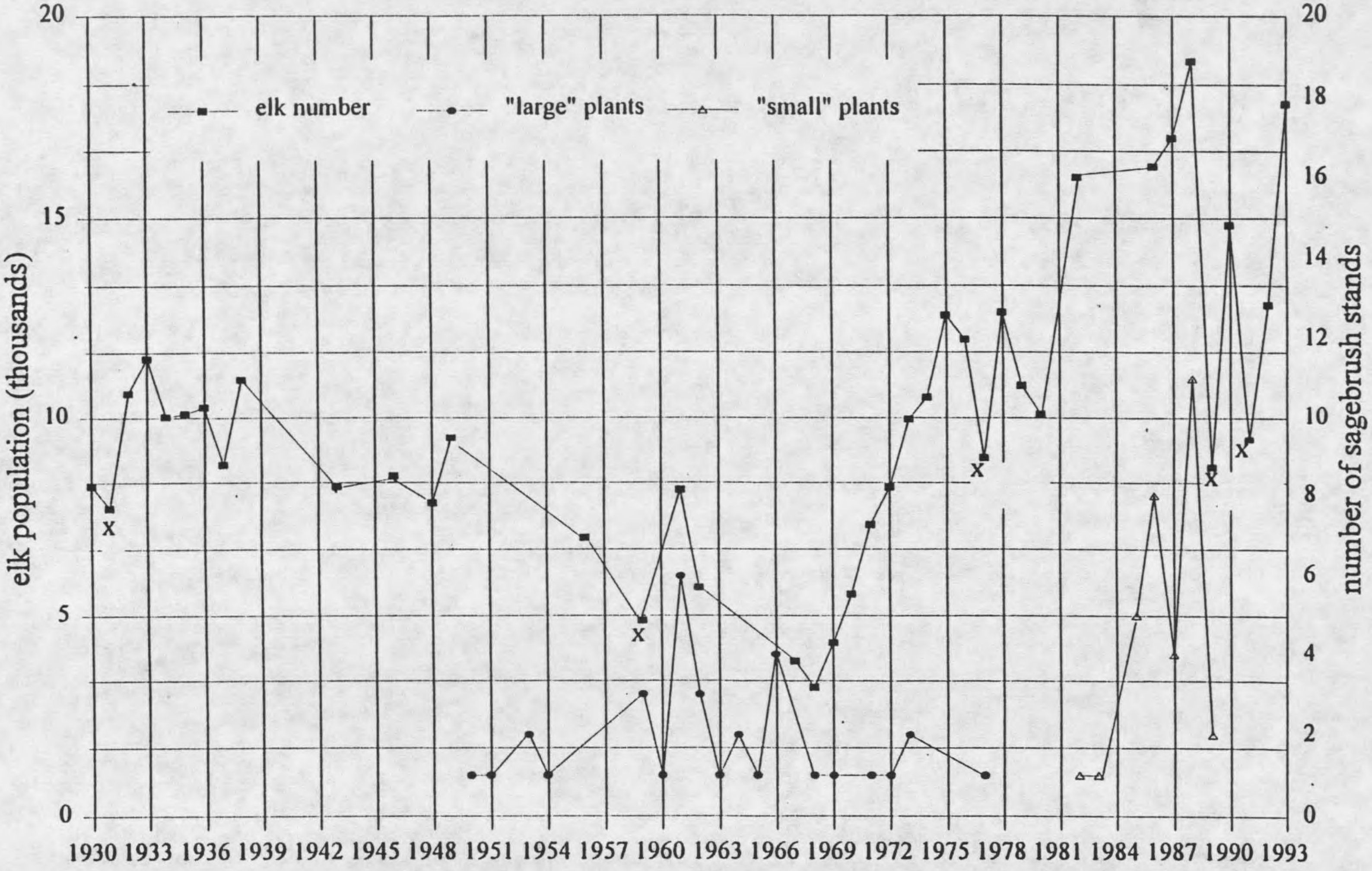

Figure 5. "Large" and "small" mountain big sagebrush stand establishment dates and elk winter counts (Unpublished report, Tom Lemke, Montana Fish, Wildlife & Parks, Houston 1982, Coughenour and Singer 1996), on the NYWR (X = poor count).

According to the hypothetical age distribution model (Fig. 4), "small" mountain big sagebrush should have high mortality rates that perhaps slow as the plants get older and begin to mature. Because nearly half of the "small" plants measured were 5 years old, their distribution also contrasts with the hypothetical model. Establishment peaks dramatically in 1988. This type of establishment is not apparent during other years.

The bimodal curve of the 2 age distributions of mountain big sagebrush corresponds to 2 distinct reduction events for the Yellowstone elk population (Unpublished report, Tom Lemke, Montana Fish, Wildlife & Parks, Houston 1982). Removals of 6365 animals in 1955-56 (mostly from outside YNP) and of 5135 (mostly from within YNP) in 1961-62, primarily by shooting, cut the elk population approximately in half each year (Houston 1982). During the winter of 1988-89, snow conditions, coupled with habitat loss from the Yellowstone fires, resulted in approximately a 40% loss of the herd (Unpublished report, Tom Lemke, Montana Fish, Wildlife & Parks).

Declines in the elk herd during these 2 periods may partly explain the difference between the curves in this study and the hypothetical curve. A reduction in herbivory and trampling may have resulted in increased establishment and survival of mountain big sagebrush, while declines in establishment occurred while elk populations were high.

Episodic germination due to other environmental conditions may also play a role in determining the age distribution observed in this study. Daubenmire (1975) found that in basin big sagebrush, recruitment of seedlings may be delayed for years until favorable moisture conditions occur for germination and establishment. Humphrey (1984) also found similar results, although big sagebrush subspecies was not considered. Microtopographic characteristics of the seedbed and timing of precipitation are critical for germination of mountain big sagebrush (Booth et al. 1990, Young et al. 1990). Successful emergence of mountain big sagebrush seedlings may depend on the amount and timing of spring snowpack (Meyer 1994). In addition, weather conditions, especially early drought are the primary factors in causing seedling mortality (Meyer 1994), although seedlings may be able to withstand water shortages by early summer (Booth et al. 1990).

Temperature and precipitation records from the years 1977 to 1992 show unusual climatic conditions that may have contributed to the large number of plants that germinated in 1988 (Table 2). The late summer of 1987 was one of the wettest in the 15 year interval. This moisture corresponded with a period of mountain big sagebrush flowering and seed production. An increase in water availability during late summer has been shown to increase the growth of reproductive tissues of big sagebrush (subspecies not considered) (Evans and Black 1993). The spring of 1988 was also one of the wettest of the 15 years sampled, but was followed by a drought in the summer and fall. A moist spring would promote seed germination of many plant species, but a summer drought would likely hamper growth of competing plants. Mountain big sagebrush, which is drought tolerant relatively soon after emergence (Booth et al. 1990), would have higher survival rates.

Table 2. Precipitation extremes during the 15 year period between 1977 and 1992.

	Month	Precipitation (mm)	Ranking for 15
1987:	July	910	Wettest
	August	410	4th Wettest
1988:	April	490	2nd Wettest
	May	920	Wettest
	June	120	Driest
	July	240	3rd Driest
	August	36	Driest

The age structure of "large" and "small" mountain big sagebrush illustrates 2 major episodes of establishment. The event in the late 1950's and early 1960's may be accounted for in part by the dramatic declines in the elk population. Detailed climatic conditions for this period were not found. In 1988, unusual climatic conditions, coupled with approximately a 40% reduction in the Yellowstone elk herd may have created an ideal situation for mountain big sagebrush establishment.

Ungulate Use of Mountain Big Sagebrush

Several significant correlations were found between the ungulate use of a mountain big sagebrush site as determined by browse form class and other characteristics of that site. The slope of a site, the age of the plants and the mass of forage produced per plant were positively correlated with the use of sagebrush ($P \leq 0.05$, Table 3). Results from Student *t*-

tests indicated that winter forage produced per plant was higher ($P \leq 0.09$, Table 4) on sites that were heavily used by ungulates. Several studies have shown that plants that are defoliated may initiate compensatory growth that exceeds the growth prior to defoliation (Paige and Whitham 1987, Dyer et al. 1991). However, mountain big sagebrush is not considered to be browsing tolerant (McArthur et al. 1988, Wandera et al. 1992, Bilbrough and Richards 1993), and the amount of difference in plant growth between high and low use sites cannot be entirely attributed to compensatory growth. In fact, mountain big sagebrush compensates poorly for lost tissue (Bilbrough and Richards 1993). Sites that are heavily used by ungulates are probably particularly productive. Even when browsed, they produce more forage than lightly used sites. Ungulates often use sites with steep slopes and southern exposures which are free of snow in the winter (McNeal 1984, Wambolt et al. 1987). The model shown on page 51 indicates that sites with steeper slopes have mountain big sagebrush stands that are more productive. These sites may be attractive to ungulates for their forage potential or for other characteristics such as hiding and thermal cover.

The age of mountain big sagebrush is also an important factor that determines ungulate use of a site. High use sites had an average age of 35 years, while low use sites had an average age of 28 years. Student's *t*- tests found that sites that receive the most use by ungulates are generally older ($P \leq 0.002$, Table 4). This observation demonstrates the serious implications for management plans that advocate frequent burning of big sagebrush to produce young stands for the benefit of wildlife.

Table 4. Student's *t*-test comparisons of heavy and light browse use on mountain big sagebrush as determined by shrub form class (Wambolt et al. 1994).

	H/L[1]	n	$\bar{x}$	std err	*t*-stat	Prob ≥ |*t*|
Elevation	H	21	2047	26.4	2.9	0.006
(m)	L	12	2179	36.6		
Percent slope	H	21	20.6	2.6	-2.0	0.05
	L	12	12.7	2.4		
Age (years)	H	21	35	1.2	-3.5	0.002
	L	12	28	1.7		
Forage	H	21	143.9	15.1	-1.7	0.09
per plant (g)	L	12	99.1	21.9		
Percent forb	H	21	26.6	3.4	2.8	0.009
cover	L	11[2]	43.1	5.1		
Soil organic	H	21	3.0	0.3	2.0	0.05
matter	L	11[2]	3.9	0.4		

[1] H=heavy use site, L=light use site

[2] Data for this variable were not collected from one site.

A significant negative relationship (r = -0.47, $P \leq 0.01$) was observed between browse form class of mountain big sagebrush and elevation. Student's *t*-tests comparing form classes showed that more heavily used sites were found at low elevations ($P \leq 0.006$, Table 4). These results are similar to those of Guenther and Wambolt (1993) who found elevation to be the most important factor in deer utilization of bitterbrush winter range. Snow depths over 460 mm prevent use of an area by deer (Regelin et al. 1977). In the Gardiner basin during the winter of 1980-81, deer were not observed at elevations above 2300 m (McNeal 1984). Although elk were capable of feeding above 2500 m in 1.5 m of snow, they generally concentrated below 2100 m in the winter of 1981-82.

Mountain Big Sagebrush Models

Introduction

The following 4 models describe the relationships between site and/or mountain big sagebrush characteristics and the following dependent variables: the average age of mountain big sagebrush stands, the percentage of deadcrown observed in a stand of mountain big sagebrush, the density of "small" mountain big sagebrush, and the forage produced by "large" mountain big sagebrush. These dependent variables were selected because they describe "decadence" or "senescence" in terms of any of the definitions used by the literature: age structure, productivity, or a post-reproductive state. Understanding the underlying influences that affect these variables give insights to what causes "decadence" or "senescence" in a mountain big sagebrush stand.

Average Age of Mountain Big Sagebrush Stands

Six parameters were entered into a model to characterize the maturity of mountain big sagebrush stands (Table 5). These parameters are included in the correlation matrix in Table 3. The following model had higher predictive power than any other model in this study.

Browse form class is the primary variable in the model. This does not imply that browsing increases the age of a sagebrush stand, but demonstrates that older stands may have characteristics that are attractive to ungulates. These stands subsequently receive more use which is reflected in their form class.

Table 5. Forward stepwise linear regression analysis using the average age of a stand of mountain big sagebrush as the dependent variable (Y)[1].

Step	Independent variable (X)	Cumulative R^2	Individual signif. of F	Model signif. of F
1	Browse form class	.25	.004	.004
2	Density "small" shrubs (number/m^2)	.36	.04	.002
3	Percent deadcrown	.46	.03	.0006
4	Live line cover (m)	.55	.03	.0002
5	Elevation (m)	.62	.04	.0001
6	Percent sand	.68	.05	.0001

[1] $Y = 36.0 + 4.6X_1 - 1.1X_2 - .04X_3 + .6X_4 + .2X_5 - .004X_6$

The negative relationship between "small" plant density and stand age typifies the recruitment pattern observed by Lommasson (1948) where sagebrush seedlings did not occur in stands that averaged <40 years of age. Only 4 sites in this study averaged >40 years. The lack of "small" plants on the sites is a function of the relatively young age of "large" plants. If older stands had been found, the negative trend may not have been observed.

This model agrees with Martin et al. (1981) that a stand of sagebrush that exhibits little deadcrown is likely to be young. However, deadcrown in this study contributes only 0.10 to the cumulative R^2. Managers should exercise caution when describing the maturity of a sagebrush stand by the amount of deadcrown observed. Mountain big sagebrush plants that grow rapidly under favorable conditions often die at a relatively young age (Bilbrough and Richards (1993). Therefore, one cannot assume that plants with large amounts of deadcrown are old plants.

The amount of live cover had nearly the same predictive power for age as the amount of deadcrown. This is another indication that as stands mature, they may be characterized by a greater amount of both live and dead material produced. Because line cover is a commonly measured parameter in range studies, it should also be used with caution to describe the maturity of sagebrush. Although older plants are likely to be larger, they may also be more widely spaced or have dead portions that would reduce the amount of cover observed. Therefore, measuring cover alone is not enough to determine the maturity of a stand of mountain big sagebrush. Intermediate aged stands may have the most canopy coverage.

The age model exemplifies some of the readily conspicuous qualities of mountain big sagebrush stands in the Gardiner Valley. Stands on this winter range that appear mature are often heavily hedged by ungulate browsing and have numerous plants with visible deadcrown that may be present due to both natural mortality and browsing. The high amount of living plant cover is also apparent although most sites have few seedling shrubs. According to the model, older stands are not only used more by ungulates, but they have characteristics, such as increased cover, that are attractive to ungulates. As demonstrated in the age distribution section (pages 28-38), mature stands are dominated by relatively young plants which turn over rapidly. This model suggests that ungulates may benefit most from the oldest stands available.

Percentage of Deadcrown in Mountain Big Sagebrush

The amount of deadcrown observed in a stand of mountain big sagebrush plants was negatively related to the amount of live sagebrush cover and the percentage of sand (Table 6). Age was positively related to the amount of deadcrown.

Table 6. Forward stepwise linear regression analysis using the percentage of deadcrown of mountain big sagebrush as the dependent variable (Y).[1]

Step	Independent variable (X)	Cumulative R^2	Individual signif. of F	Model signif. of F
1	Live line cover (m)	.36	.003	.0003
2	Ave. stand age (years)	.47	.02	.0001
3	Percent sand	.59	.01	.0001

[1] $Y = 23.1 - 1.6X_1 + .5X_2 - .3X_3$

The amount of live or dead cover measured on a line is dependent on 3 variables: shrub size, shrub density, and the percent of live shrub crown. Ocular observations of deadcrown agree with Tauch (1989) that small plants have less dead material in their crown than large plants. However, shrubs that have high amounts of deadcrown and appear "decadent" are not necessarily senescent or dying. Site 32 had among the lowest dead cover and density values observed (2.7% and 0.13/m^2 respectively), but had the highest percent deadcrown on living plants (43.2%). This suggests that dead cover is more a function of the density of dead shrubs than the amount of dead material in the crown of a plant.

As the average age of a stand of sagebrush increased, the percent of deadcrown also increased ($R^2 = 0.47$, $P \leq 0.02$). Martin et al. (1981) suggested that young sagebrush have little deadcrown compared to older shrubs. A relatively old sagebrush stand that is dense and has a high percentage of deadcrown, fits the loosely defined term of "decadent." However, as the model for winter forage production per plant indicates (Table 8), older plants are more productive than younger plants. Although young stands may have little dead material, they have not attained the size, density or productivity necessary to produce the amount of forage that older stands produce. Therefore, despite the amount of deadcrown or the "decadent" or "overmature" condition of older mountain big sagebrush stands, these stands are the most important producers of forage. Such stands perhaps should not be viewed as decadent or in need of manipulation simply because they contain considerable amounts of dead plant material.

Density of "Small" Mountain Big Sagebrush

A good indicator of the recruitment of seedlings and young established mountain big sagebrush plants is the density of plants below (22 cm crown diameter). The density of these "small" plants was negatively related to elevation, age and percent slope, while the amount of browsing had a positive relationship (Table 3). The model is shown in Table 7. Elevation and age contributed fairly equally to the final R^2.

Forb cover is positively correlated with elevation ($r = 0.40$; $P \leq 0.05$). The increase in precipitation and organic matter associated with increasing elevation results in sites that are potentially very productive. The inverse relation between "small" shrubs and elevation may be attributed to competition of these shrubs with a productive forb community. At several high elevation sites, small sagebrush were completely covered by a dense canopy of forbs such as arrowleaf balsamroot (*Balsamorrhiza saggitata* [Pursh] Nutt.) and sticky geranium (*Geranium viscossissimum* Fisch). McConnel and Smith (1977) believed that similar competition in bitterbrush communities reduced the survival rate of seedling shrubs.

Table 7. Forward stepwise linear regression analysis using the density of "small" mountain big sagebrush on a site as the dependent variable (Y).[1]

Step	Independent variable (X)	Cumulative R^2	Individual signif. of F	Model signif. of F
1	Elevation (m)	.15	.03	.03
2	Ave. stand age (years)	.28	.03	.01
3	Percent slope	.36	.06	.005
4	Browse form class	.42	.13	.004

[1] $Y=611.7 - 37.7X_1 - 4.4X_2 - .06X_3 + 2.0X_4$

The average age of "large" shrubs had a negative relationship with the density of "small" plants (Table 7). As plants become older, they become larger (see model for "age"), increasing the canopy coverage of a site and leaving few available recruitment sites for establishing shrubs. As seen in the model for average age of sagebrush stands (page 44), few stands were old enough to break down and allow seedlings to establish in shrub interspaces. Intraspecies competition by mature mountain big sagebrush severely restricts seedling recruitment (Meyer 1994). Lommasson (1948) determined that sagebrush seedlings did not establish under thick stands, and even when stands had aged sufficiently for the canopy to break down and open up, seedlings only established during periods of favorable moisture conditions. Sagebrush recruitment was most successful in stands over 50 years of age. Similar results were found in chaparral where seedlings were seldom observed in mature stands that were under 50 years of age (Keeley 1992). Although individual plants in this study were older than 50 years (as old as 88 years), the highest average age of a stand was 45 years. Perhaps "small" plants are negatively associated with increasing age because mature stands in the study area are not particularly old.

The negative relationship in the model between "small" plant numbers and percent slope (Table 7) is probably related to microclimatic characteristics of a site. Steep slopes have a higher incidence of solar radiation and are less likely to retain surface runoff. Moisture availability during early establishment of seedling mountain big sagebrush is critical (Meyer 1994). Steep, dry sites probably have a higher mortality rate of young mountain big sagebrush. Slope is not correlated with the density of "large" plants, so microclimatic effects are more pronounced in seedling plants and have less influence on those plants that survive and are able to establish. Apparently, survivorship is high enough that overall densities of mature stands are not affected by slope.

The positive relationship between browsing by ungulates and "small" plant density (Table 7) is probably attributed to a reduction in competition by associated plant species. Although grass cover shows no correlation with ungulate use of sagebrush, forb cover has a significant negative association ($r = -0.45$, $P \leq .0.01$, Table 3). Either forb competition is naturally low on heavily browsed sites, or it is reduced by ungulate browsing. Forb cover is positively correlated with elevation (r=0.40; $P \leq 0.05$) while ungulate use is negatively correlated with elevation (r = -0.47; $P \leq 0.01$). McArthur et al. (1988) suggested that sagebrush seedlings did not survive because of competition with annual forbs. Pechanec et al. (1954) found that sagebrush abundance was increased with livestock grazing.

Mountain big sagebrush stands that have numerous "small" plants may be characterized as being located at low elevations on sites with shallow slopes. They are usually older stands that are heavily used by ungulates. These factors make sense biologically because lower elevation sites are known to receive more use, older stands are more likely to have characteristics favorable for seedling recruitment, and moister soils may be found on shallower slopes.

Mountain Big Sagebrush Winter Forage Production

Three variables, age, soil depth, and percent slope were entered into the model with winter forage production per plant the dependent variable (Table 8). Age was significant ($P \leq 0.05$) as was soil depth ($P \leq 0.10$). Percent slope was not significant individually, but became significant upon entry into the model. The low predictive value of this model ($R^2 = 0.26$) indicates that other factors or interactions besides those measured, or parameters on a different temporal or spatial scale are responsible for the growth potential of mountain big sagebrush (Pearson et al. 1995).

Although its contribution to the model is small, average stand age is the most important parameter to predict the forage produced by mountain big sagebrush. The relationship between stand age and production is positive which suggests that older plants are likely to be more productive. McConnel and Smith (1977) found that bitterbrush productivity increased with age until shrubs were 60-70 years old. Further studies may determine whether such a relationship exists with sagebrush.

Table 8. Forward stepwise linear regression analysis using winter forage production in g per plant of mountain big sagebrush as the dependent variable (Y)[1].

Step	Variable	Cumulative R^2	Individual signif. of F	Model signif. of F
1	Average stand age (years)	.12	.05	.05
2	Soil 'A' horizon depth (cm)	.20	.10	.04
3	Percent slope	.26	.14	.03

[1] $Y = -101.6 + 4.6X_1 + 1.3X_2 + 1.66X_3$

The depth of the soil A horizon was also important in the model although it did not appear significant in the correlation matrix (Table 3). This variable contributes only 0.08 to the cumulative model. Likewise, the correlation between percent slope and forage production was not significant, although the model indicated that slope had a slight influence on forage production (0.06 contribution to the cumulative model). Clearly, the growth and forage production of mountain big sagebrush is a complex process not easily quantified by simple field measurements. Management of this species should therefore reflect the difficulty in predicting production.

Although no significant correlation was found between plant size and density in this study, the 8 sites that ranked the highest in production per plant, which is a function of plant size, also had less than the average density of plants ($0.87/m^2$) in the "large" category (Appendix A: Table 11). Sites with low production per plant were observed to have variable plant densities. This may indicate that for some sites, environmental factors such as nutrient or water availability may affect shrub density as much or more than plant size. As sagebrush plants grow larger, they often become more widely spaced (Westoby 1984). McNeal (1984) found a significant negative relationship between the size and density of sagebrush plants on sites within the study area.

This model suggests that as mountain big sagebrush plants age, their level of forage production increases. If this is the case, then the most important contributors to the forage base of mountain big sagebrush are the oldest plants in a stand. Eliminating the older plants will result in a decline in available winter forage. This will probably result in more browsing pressure on younger plants, perhaps arresting stand development in areas where herbivore numbers are high.

Other Correlations and Relationships

Correlations among several soil parameters were consistent with other studies conducted in Montana (Table 3). For example, elevation was well correlated with soil organic matter ($r = 0.39$, $P \leq 0.05$). Sims and Nielsen (1986) found similar results and concluded that as elevation increases, precipitation increases and decomposition rate declines resulting in higher organic matter content. The lack of correlation between organic matter and clay content was also consistent of both studies. Munn et al. (1978) found a strong relationship between overall site production and both soil organic matter and A horizon thickness. In this study, a relationship was observed between organic matter and production of grass (r = 0.55, $P \leq 0.01$), and forbs (r = 0.56, $P \leq 0.01$). Sagebrush production was not correlated with any soil parameters.

Several correlations in this study differ from those found by McNeal (1984). He found that grass production had a significant negative association with increasing sagebrush density (r = -0.47, $P \leq 0.01$). This association was not observed in the current study. Because McNeal (1984) included 3 big sagebrush subspecies found in the Gardiner basin together in his correlation matrix, one would expect a different grass/shrub dynamic than in a matrix with only mountain big sagebrush.

McNeal (1984) also found that slope was positively correlated with elevation (r = 0.42, $P \leq 0.01$), relating to the rise of the Absoraka Mountains. This was not observed in the current study probably because of the way sites were selected. This study purposely selected sites that appeared to have 1 or more extremes for the parameters of interest. For example, a high elevation site with low slope would be unusual, and would be selected to represent an extreme for 1 or more of the parameters studied. McNeal (1984) had no such requirement for selection of sites.

Mountain Big Sagebrush Recovery from Burning

All 7 burned areas that were sampled indicated that within the study area recovery of mountain big sagebrush following fire is slow. Maximum, minimum and average values for site and shrub parameters may be found in Table 9, while individual observations are shown in Appendix A:Tables 13-14. The sites had burned between 9 and 13 years previous to sampling, but none showed significant recovery. Mountain big sagebrush canopy cover averaged 1.7%, but this number was highly dependent on a single site (5B) which had 6.7% sagebrush cover. This was the only burned site to exceed 1% canopy cover of sagebrush. Three sites (1B, 3B, and 4B) had 0% canopy cover. This compares with an average cover of 14.2% for unburned sites. These results also agree with Mehus (1995) who observed in a burn near Gardiner, Montana, that 3 big sagebrush taxa produced a total of 2.5% cover on a site burned 19 years previous to sampling. Mountain big sagebrush contributed 0.07% of this percentage.

Table 9. Characteristics of mountain big sagebrush on 7 burned sites.

Site	Year Burned	Percent live cover	Density "large" plants/m^2	Density "small" plants/m^2	Total density shrubs/m^2
1B	1982	0.0	0.0	0.0	0.0
2B	1979	0.4	0.1	0.0	0.1
3B	1978	0.0	0.0	0.0	0.0
4B	1979	0.0	0.0	0.1	0.1
5B	1984	6.7	0.2	0.3	0.5
6B	1984	0.8	0.1	0.1	0.1
7B	1982	0.3	0.0	0.1	0.1
Average		1.2	0.1	0.1	0.1

Student's *t*-test comparisons between burned and unburned sites are shown in Table 10. The results show that canopy coverage of unburned sagebrush is over 12 times that on burned sites. Mehus (1995) found that the combined coverage of 3 sagebrush taxa was 11 times higher in unburned sites.

Mountain big sagebrush density was also reduced by burning. Two sites (1B and 3B) had no plants at all rooted within the belt transect. Two additional sites (4B and 7B) had only 1 "large" plant rooted within the belt transect. The highest density of "large" plants observed on a burned site was 14 per transect (0.23 plants/m^2) at site 5B. These values compare with an average density of 52 plants per transect (0.86/m^2) on unburned sites. Student's *t*-tests (Table 10) indicate that this difference is highly significant ($P \leq 0.0000$).

Table 10. Student's *t*-test comparisons of burned and unburned mountain big sagebrush sites.

	B/U[1]	n	$\bar{x}$	std err	*t*-stat	Prob > |t|
Percent cover of	B	7	1.2	0.3	4.6	0.0001
sagebrush	U	33	14.2	0.4		
Density of	B	7	0.06	1.9	7.5	0.0000
"large" plants/m^2	U	33	0.86	2.9		
Density of	B	7	0.08	2.1	2.2	0.04
"small" plants/m^2	U	33	0.91	10.5		
Percent grass	B	7	52.6	10.8	-2.2	0.04
cover	U	32[2]	35.9	2.9		
Percent forb	B	7	29.0	7.8	0.4	0.67
cover	U	32[2]	32.3	3.1		

[1] B=Burned site, U=Unburned site

[2] Data for this variable were not collected from 1 site.

The density of "small" mountain big sagebrush plants followed a similar trend as that of "large" plants. Two sites (1B and 3B) had no "small" plants within the belt transect, and the maximum density was observed on site 6B with 16 plants (0.05/m^2). While some unburned areas also had low numbers of "small" plants (as low as 0.03/m^2) the average density of "small" plants on unburned sites exceeded the average on burned sites by 11 times.

These results are similar to Mehus (1995) who found that mountain big sagebrush was significantly reduced by burning in the Gardiner basin. He found minimal recovery of this taxon 19 years after wildfire with only 0.07 plants/m^2 compared with 0.54 plants/m^2 on unburned sites. The results also follow Blaisdell (1953) who found little re-establishment of mountain big sagebrush 12 years after burning. Harniss and Murray (1973) examined the same area as Blaisdell (1953) after 30 years and found that sagebrush had almost recovered to pre-burn levels. Wambolt and Payne (1986) and Watts and Wambolt (1996) found that Wyoming big sagebrush exhibited a similar pattern. Eighteen years after burning, this subspecies had only recovered 12%, but after 30 years, it had returned to just below its original level of canopy coverage. The oldest burned site in this study was burned 14 years before sampling.

One of the most important factors that influences the recovery of mountain big sagebrush from burning is the degree of elimination of parent plants by fire (Johnson and Payne 1968). Big sagebrush does not resprout after fire nor does it rely on seed stored in the soil for recovery following disturbance such as fire (Noble and Slatyer 1980). Instead, big sagebrush is dependent on seed dispersal. Big sagebrush seed generally does not persist in the soil seedbank for more than 1 year (Young and Evans 1989). While plants as young as 2 years are capable of producing seed (Young et al. 1989), no plants growing in burned areas less than 10 years old had reproductive stalks. Some of the plants aged were older than the burns, indicating that they had not established after the fire, but had merely survived it. These residual plants represent the most important seed source for stand regeneration (Frischknect and Bleak 1957). However, either because there was low density of parent plants for seed production or because conditions for seedling recruitment were not favorable, no sagebrush seedling recruitment appeared to accompany surviving shrubs.

Although seed dispersal by big sagebrush has been documented as far as 30 m (Young and Evans 1989), 75-90% of the seed fall within 1 to 3 m of the parent plant (Young and Evans 1989, Wagstaff and Welch 1990). Wind is the primary carrier of seed (Wagstaff and Welch 1990), but is ineffective as a long-distance means of dispersal for re-colonization of disturbed areas (Frischnect and Bleak 1957, Johnson and Payne 1968). In a large, thorough burn that leaves few or no remnant seedbearing sagebrush, recovery may be hindered by the difficulty in dispersing to the center of the burned area.

Site conditions including precipitation, soil moisture, and plant competition are additional factors that play a role in the recovery of mountain big sagebrush after burning. As discussed in the age distribution section (pages 28-38), mountain big sagebrush establishment is sporadic and is often related to favorable precipitation patterns. Because of the delay in reestablishment of big sagebrush after disturbance, this shrub is described as “late successional” requiring either a mature community or specific conditions for establishment to occur (Humphrey 1984, Noste and Bushey 1987).

Survival of mountain big sagebrush seedlings is also influenced by interspecific competition. While Noble and Slayter (1980) described big sagebrush as tolerant to competition by other species, others found that competition reduced the recovery of big sagebrush (Humphrey 1984, McArthur et al. 1988, Owens and Norton 1990). Competition by grasses inhibits the establishment of sagebrush seedlings (Pechanec et al. 1954, Frischknect and Harris 1968, Owens and Norton 1990). High grass vigor in this study area may have reduced the establishment of seedlings after burning (Mehus 1995). In the present study, Student's *t*-tests comparing grass and forb cover of burned and unburned site found no difference in forb cover, but found significantly ($P \leq 0.03$) higher grass cover on burned sites (Table 10). These results disagree with McNeal (1984) who found significantly higher forb cover on 1 of 2 burned sites in the same study area while grasses were decreased by burning. The differences can probably be attributed to the length of time between burning and sampling. McNeal (1984) sampled only months after burning, while in this study, sampling took place between 10 and 14 years post-burn giving grasses time to recover.

Other studies have found variable responses of grasses and forbs to burning. Some reported no change in forb composition (Duvall and Linnartz 1967) while others reported increases (Mueggler and Blaisdell 1958). Decreases in forb production have commonly been observed (Blaisdell 1953, Wambolt and Payne 1986, Watts and Wambolt 1996). Responses by grasses are also variable and often depend on the species or season of burning. McNeal (1984) found no difference in grass production on burned and unburned sites in the Gardiner basin. Fraas et al. (1992) reported an increase in canopy coverage of Kentucky bluegrass (*Poa pratensis* L.), a decline in Idaho fescue, and no change in bluebunch wheatgrass 8 years after burning. Jorgensen (1990) and Peterson (1995) explore in detail the effects of burning on the forbs and grasses associated with big sagebrush.

In addition to seed dispersal, sporadic germination and plant competition, the degree of ungulate browsing in the study area is another factor that has resulted in slow recovery of mountain big sagebrush after burning. All of the sites sampled within burns were in areas where ungulate browsing was classified as "high" according to the browse form class of neighboring unburned shrub stands. Mountain big sagebrush is the sagebrush taxon most preferred by browsing ungulates on the study area (Wambolt in press) and is a particularly important shrub for mule deer on the winter range (McNeal 1984, Wambolt and McNeal 1987, Mehus (1995), Wambolt in press). In severe winters in the Gardiner basin, utilization by ungulates is magnified, especially at lower elevations or on steep south facing slopes, and is credited with mortality of many shrubs (Wambolt in press). Because mountain big sagebrush is intolerant to browsing (Bilbrough and Richards 1993), the high numbers of ungulates on the winter range have created a long term impact for this shrub (Fortney and Wambolt 1995, Wambolt in press). Burning mountain big sagebrush simply concentrates browsing on surviving or reestablishing shrubs. Overall, this browse species is declining on the winter range and burning will probably accelerate this decline.

Browsing has the capacity to substantially reduce seed production in sagebrush. Heavy browsing on Wyoming big sagebrush at lower elevations of the study area nearly precluded the growth of reproductive structures (Hoffman and Wambolt in press). These results concur with Decker and Pyke (1989) where reproductive stems and flowers increased in big sagebrush after browsing was excluded. In YNP, Kay and Chaddie (1991) found a similar effect on heavily browsed willows, which produced no aments on stems within reach of ungulates. Combined effects such as browsing with the difficulty of seed dispersal by a limited number of parent plants that may survive burning will greatly restrict the ability of mountain big sagebrush to re-establish after fire.

CHAPTER 6

SUMMARY AND MANAGEMENT IMPLICATIONS

Although management and manipulation of big sagebrush have been studied extensively, they remain controversial. On the Northern Yellowstone Winter Range, controversy is magnified by the large size of the ungulate populations, their economic importance to the region, and the fact that winter habitat is the primary determinate of their survival (Houston 1982, Pearson et al. 1995). Management decisions for the climax dominant sagebrush taxa in the Gardiner basin have serious biological and social implications.

If "decadence" is a term defined in plants as a post-reproductive state (Gastuk et al. 1980) or a state of physiological deterioration (Reid 1985), then the stands of mountain big sagebrush in the Gardiner basin are not decadent. Undisturbed stands were much younger on average than the "decadent" stands described by Roughton (1972) with only 12% of individuals as old or older than Roughton's averages. In addition, plants often died and were replaced by 41 years of age, indicating that stands turn over at a relatively young age. Burning mountain big sagebrush on the Northern Yellowstone Winter Range for the purpose of creating young non-decadent stands of sagebrush is counter-productive because , with the exception of heavy browsing effects, the taxon shows little decadence.

Mountain big sagebrush establishment and survival is largely dependent on environmental conditions that include both climatic factors and the presence of browsing ungulates. In this study, "large" shrub establishment coincided with declines in the northern

Yellowstone elk herd. "Small" plant establishment was related to both a decline in the elk herd and unusual precipitation patterns. An increase in shrub survival with reduced pressure from browsing indicates that ungulates is important in the age dynamics of the mountain big sagebrush population. Decreased browsing or trampling on seedling shrubs may allow establishment in years when elk numbers are low. This establishment may also be dependent on favorable climatic conditions. These forces complicate the predictability of establishment, and therefore the results of management decisions. For example, it would be difficult to determine establishment or production levels of mountain big sagebrush following prescribed burning if ungulate numbers and climate play key roles in determining shrub establishment.

The impact of ungulate browsing on established stands of mountain big sagebrush on the Northern Yellowstone Winter Range is documented. The utilization levels found on this winter range (Mehus 1995, Wambolt in press) exceed the amount believed to reduce vigor in this taxon (Cook and Stoddard 1960, Bilbrough and Richards 1993). Shrub declines associated with browsing in the Gardiner valley are described by Fortney and Wambolt (1995), Mehus (1995), Hoffman and Wambolt (in press), and Wambolt (in press). This study found that sites heavily used by ungulates were characterized by older plants that produced more forage than plants on lightly used sites. These sites have more productive potential. Therefore, while mountain big sagebrush on these sites are vigorous in terms of forage production, this production is attributed to site potential and may be reduced, especially over the long term, by excessive browsing. Regardless of the site potential, once a plant community has been altered, as with fire, wildlife respond to the existing vegetation, not the potential (Scott et al. 1993). For example, if a site has the potential to produce a shrub community, but a grassland community exists because of frequent burning, wildlife that depend on shrub communities will be detrimentally affected.

Models illustrated several points regarding the community structure of mountain big sagebrush stands. Several models shared 1 or more of 4 independent variables: stand age, elevation, percent slope and browing intensity. For example, the dependent variables of percentage of deadcrown, forage production and density of "small" shrubs were all influenced by the age of a mountain big sagebrush stand. Likewise, elevation was an important factor in characterizing the age of a stand as well as the density of "small" plants. The commonality of these independent variables among models suggests that the models themselves are related, and that each model reflects a part of the complex community structure of mountain big sagebrush.

The models indicate that stands of mountain big sagebrush that are older are more beneficial to wildlife. They exhibit more browsing by ungulates, and they produce more forage than younger stands, even though they also have larger amounts of deadcrown. The age distribution data indicate that stands are able to maintain a relatively young age structure in the absence of disturbance. Therefore, the models emphasize that artificial manipulation of mountain big sagebrush to benefit wildlife is not necessary in the Gardiner basin.

These results agree with Mehus (1995), that mountain big sagebrush recovery following fire on the Northern Yellowstone Winter Range is insignificant. Sagebrush productivity has been significantly reduced in burned areas. Burning often does not increase plant diversity, but concentrates the abundance of certain species, especially annuals such as cheatgrass (Hassen and West 1986). Burned areas in the Gardiner basin are not attractive to elk and are avoided by mule deer (Wambolt and McNeal 1987). Burning mountain big sagebrush stands that provide cover and forage to ungulates will only concentrate herds onto remaining undisturbed areas and accelerate the decline of mountain big sagebrush that is already heavily browsed.

Wildlife winter range in the United States is declining due to encroachment of human development (Regelin et al. 1977), and the Northern Yellowstone Winter Range is no exception. Because undisturbed stands of mountain big sagebrush provide numerous benefits to wildlife and are capable of remaining in a productive state without human intervention, managers must carefully consider the consequences of manipulating them. Burning may reduce or remove big sagebrush as a contributor to the forage base (Mehus 1995). In some unburned areas in southern Montana, big sagebrush has increased (Arno and Gruell 1983). However, browsing precludes increases on the Northern Yellowstone Winter Range (Fortney and Wambolt 1995, Mehus 1995, Hoffman and Wambolt (in press), and Wambolt (in press). High ungulate populations may also preclude establishment of this shrub, regardless of burning. The magnitude of the ungulate population is an important force causing declines in mountain big sagebrush, but burning will cause a cumulative impact by removing established plants and concentrating browsers on the plants that remain.

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APPENDIX A

CHARACTERISTICS OF INDIVIDUAL MOUNTAIN BIG SAGEBRUSH SITES

Table 11. Characteristics of mountain big sagebrush on 33 unburned sites

Site	Browse form class[a]	Percent live line cover	Percent dead line cover	Density "large" plants/m²	Density "small" plants/m²	Density dead plants/m²	Forage production (g/plant)	Percent deadcrown	Avg. age "large" plants (yrs)	Avg. age "small" plants (yrs)	Avg. age dead plants (yrs)[b]
1	L	20.83	7.72	1.08	0.23	0.22	62.03	18.22	23	_	39
2	L	14.33	6.71	0.70	0.42	0.22	73.40	18.82	33	5	44
3	H	5.89	3.20	0.83	0.92	0.25	140.59	20.75	29	6	31
4	H	12.70	4.17	0.80	0.63	0.17	201.48	19.47	34	8	46
5	L	38.81	8.18	1.53	2.53	0.27	117.07	14.65	29	5	39
6	H	4.98	1.37	0.63	0.35	0.13	45.57	30.57	34	11	20
7	H	13.21	3.19	1.05	1.57	0.12	136.67	21.18	29	6	43
8	H	22.45	5.84	0.93	2.10	0.23	150.37	11.61	31	6	43
9	H	9.55	8.69	0.82	4.02	0.35	166.15	30.08	31	7	29
10	L	11.11	9.30	1.13	1.08	0.32	70.84	28.27	29	8	28
11	H	8.79	4.06	0.97	0.70	0.33	93.18	25.17	34	8	--
12	H	6.55	1.78	1.03	0.93	0.10	94.32	24.70	26	7	56
13	H	12.85	5.74	0.73	0.28	0.27	174.97	30.71	44	5	43
14	H	14.17	0.54	0.77	0.07	0.17	91.04	31.30	42	7	45
15	H	11.48	3.76	0.57	0.27	0.22	259.49	20.87	45	7	40
16	H	10.11	8.94	0.72	0.32	0.13	324.59	22.80	33	7	34
17	H	11.33	2.59	0.70	0.68	0.12	143.84	20.30	36	8	48
18	H	9.55	3.61	0.62	0.05	0.12	219.67	15.47	35	5	31

Table 11 (continued).

Site	Browse form class[a]	Percent live line cover	Percent dead line cover	Density "large" plants/m^2	Density "small" plants/m^2	Density dead plants/m^2	Forage production (g/plant)	Percent deadcrown	Avg. age "large" plants (yrs)	Avg. age "small" plants yrs)	Avg. age dead plants (yrs)[b]
21	L	11.43	8.13	0.55	0.35	0.45	85.78	33.95	34	4	41
22	L	17.53	12.95	0.52	0.23	0.28	84.67	15.81	22	5	26
23	L	11.02	2.59	0.75	0.17	0.32	68.83	24.46	36	5	45
24	L	13.26	15.09	0.58	0.48	0.72	330.07	31.64	32	5	37
25	H	19.36	2.79	0.98	0.33	0.12	110.79	17.78	34	6	--
26	H	8.38	4.83	0.83	0.67	0.10	34.76	28.02	30	8	41
27	H	10.62	7.77	0.57	1.82	0.58	116.31	25.07	41	5	50
28	H	13.47	7.55	0.68	0.07	0.23	190.09	27.71	36	7	50
29	L	15.29	3.45	0.90	0.07	0.37	57.87	15.87	24	5	39
30	L	31.45	4.32	1.47	1.20	0.15	130.58	12.86	33	5	38
31	L	18.90	1.02	1.25	2.88	0.07	51.25	11.11	18	7	--
32	H	2.95	2.69	0.42	3.28	0.13	74.88	43.24	34	7	--
33	H	26.87	8.69	1.37	0.45	0.11	137.54	21.57	42	10	--

[a] H=heavy browse form class, L=light browse form class (Wambolt and McNeal 1987).
[b] Sample size varied according to available plants.

Table 12. Physical characteristics of 33 unburned mountain big sagebrush sites.

Site	Legal Description	Elevation (m)	Percent Slope	Aspect (degrees)	Soil A horizon depth (cm)	Percent sand	Percent clay	Percent grass cover	Percent forb cover
1	T7S R7E Sec.26 SW/NW	2195	4	279	--	--	--	--	--
2	T7S R7E Sec 35 NW/SW	2073	16	293	32	49	14	68	58
3	T7S R7E Sec 35 SE/NW	1963	16	311	32	51	20	39	40
4	T7S R8E Sec 35 SW/SE	1871	35	215	24	52	18	18	5
5	T7S R8E Sec 31 SW/SE	2103	23	291	27	46	21	58	46
6	T7S R8E Sec 6 SW/SW	2088	4	175	20	32	25	19	14
7	T8S R7E Sec 12 NE/NE	2073	19	235	23	50	15	24	25
8	T8S R8E Sec 5 SE/SW	2085	25	123	47	45	20	23	10
9	T7S R8E Sec 8 NE/NW	1951	14	135	31	42	22	45	41
10	T8S R8E Sec 17 NE/NW	2109	21	293	39	35	25	65	35
11	T8S R8E Sec 20 SE/NW	1951	7	259	25	43	19	43	30
12	T9S R8E Sec 4 NE/NE	2316	16	220	24	41	21	23	18
13	T9S R8E Sec 10 NW/NE	2188	43	275	65	60	11	36	19
14	T9S R8E Sec 10 NW/NE	2027	8	245	39	65	9	35	36
15	T9S R8E Sec 11 SE/SE	1975	25	166	41	61	13	24	19
16	T9S R9E Sec 18 NW/SE	1975	36	345	54	23	35	57	30
17	T9S R8E Sec 13 NE/SW	1975	23	90	33	50	19	35	8
18	T9S R8E Sec 13 NE/SW	1975	37	150	28	60	15	10	5
19	T9S R9E Sec 7 SW/NE	2134	14	214	53	33	25	35	52
20	T9S R9E Sec 12 NE/SW	2243	28	82	48	55	14	49	43

Table 12 (continued).

Site #	Legal Description	Elevation (m)	Percent Slope	Aspect (degrees)	Soil A horizon depth (cm)	Percent sand	Percent clay	Percent grass cover	Percent forb cover
21	T9S R9E Sec 12 NE/SW	2256	11	178	30	48	18	2	59
22	T9S R9E Sec 7 NW/SE	2207	20	240	49	45	22	30	53
23	T9S R8E Sec 6 SW/SE	2271	14	282	30	46	14	12	46
24	T9S R9E Sec 5 SW/SW	2323	2	260	59	38	24	42	57
25	T9S R9E Sec 8 SW./SW	2109	26	70	48	42	12	44	61
26	T9S R9E Sec 8 SW/NE	2073	37	219	33	37	35	22	9
27	T9S R9E Sec 17 SW/NE	2024	7	281	22	52	21	48	30
28	T9S R9E Sec 16 SW/SE	2353	8	245	48	36	20	59	29
29	T9S R9E Sec 21 SE/SE	2377	9	340	39	52	11	35	46
30	T9S R9E Sec 13 NE/NE	1966	13	85	60	44	20	23	11
31	T9S R9E Sec 13 NE/NE	1996	0	65	95	40	27	9	14
32	T8S R7E Sec 22 SW/SW	1935	6	209	23	11	40	41	49
33	T9S R7E Sec 22 SW/SE	1975	18	73	28	46	25	53	34

Table 13. Characteristics of mountain big sagebrush on 7 burned sites.

Site	Year Burned	Percent live line cover	Density "large" shrubs/m²	Density "small" shrubs/m²	Total density shrubs/m²
1B	1982	0.00	0.00	0.00	0.00
2B	1979	0.36	0.08	0.03	0.11
3B	1978	0.00	0.00	0.00	0.00
4B	1979	0.00	0.02	0.05	0.07
5B	1984	6.70	0.23	0.27	0.50
6B	1984	0.80	0.05	0.08	0.13
7B	1982	0.30	0.02	0.10	0.12
Average		1.17	0.06	0.08	0.13

Table 14. Physical characteristics of burned sites.

Site	Legal Description	Year burned	Elevation (m)	% slope	Aspect (degrees)	Soil A horizon depth (cm)	% sand	% clay	% grass cover	% forb cover
1B	T9S R8E Sec 11 SE/SE	1982	2097	11	193	24	66	8	32	19
2B	T9S R9E Sec 18 NW/SE	1979	1987	31	337	22	46	21	72	61
3B	T9S R8E Sec 12 NE/SW	1978	2164	9	91	95	56	14	88	46
4B	T9S R9E Sec 8 SW/SW	1979	2109	34	49	52	51	14	70	57
5B	T9S R9E Sec 16 SW/SW	1984	2085	5	245	37	53	20	54	30
6B	T9S R9E Sec 16 SW./SW	1984	2353	8	245	76	52	14	68	34
7B	T8S R7E Sec 22 SW/SW	1982	1942	0	241	20	43	28	52	13

APPENDIX B

MOUNTAIN BIG SAGEBRUSH PRODUCTION EQUATIONS

Table 15. Mountain big sagebrush forage production equations[1] from Creamer (1991).

Low use mountain big sagebrush:

$$\ln(F) = .647 + .034(MJ) + .031(AC) - .002(C1)$$

High use mountain big sagebrush:

$$\ln(F) = .489 + .037(MJ) + .050(AC) - .0003(C1)$$

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[1] Equation parameter abbreviations: F = forage (g), MJ = major axis (cm), AC = average cover (cm), C1 = circular area (cm^2), HT = height (cm).

Mud damaged.
Cleaned as well as
we could.

5/2010