Elk effects on sagebrush-grassland after fire on Yellowstones Northern Range

by Reyer Jan Rens

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

Abstract:
There continues to be concern for the shrub communities of the Northern Yellowstone Winter Range (NYWR). This concern for the decline of big sagebrush (Artemisia tridentata Nutt.) began during the first half of the twentieth century. It is not well understood how these communities will recover from the wildfires of 1988. Intense levels of herbivory allowed under the National Park Service (NPS) policy of natural regulation has generated additional concern. It was my objective to determine the effect of elk browsing on shrub community recovery from fire on the Black-tailed Deer Plateau of the NYWR. The null hypotheses I tested were: 1) that the shrubs of a mountain big sagebrush (A. t. vaseyana [Rydb.] Beetle) habitat type will recover from fire at the same rate with or without elk browsing, and 2) that elk herbivory would have no effect on the herbaceous component of this habitat type, regardless of bum treatment. I sampled 12 sites. Significant differences were found in the development of protected and browsed shrubs. Big sagebrush measurements were taken in and out of exclosures at 5 environmentally paired, protected and browsed sites dominated by sagebrush. Big sagebrush canopy cover at the 5 sites averaged 20.0% with protection and 9.7% where browsed ($P < 0.01$). Individual plants produced 76% more grams of forage for winter where protected ($P < 0.01$). Big sagebrush densities were not different ($P < 0.01$). Sprouting shrubs, rubber rabbitbrush (Chrysothamnus nauseosus (Pallas ex Pursh) Britt.), green rabbitbrush (C. viscidiflorus (Hook) Nutt.) and gray horsebrush (Tetradymia canescens DC.) made up a smaller part of the community and generally responded the same as big sagebrush. Coverages for all herbaceous species, perennial grasses, forbs, Idaho fescue (Festuca idahoensis Elmer), bluebunch wheatgrass (Agropyron spicatum (Pursh) Gould), and other grass species were compared by treatment. Some small differences were found in herbaceous components. Impacts on shrub communities from cumulative and interactive effects of wildfire and intense herbivory have implications for many NYWR values.

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NORTHERN RANGE

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APPROVAL

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Reyer Jan Rens

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

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Date April 20, 2001

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ABSTRACT

There continues to be concern for the shrub communities of the Northern Yellowstone Winter Range (NYWR). This concern for the decline of big sagebrush (*Artemisia tridentata* Nutt.) began during the first half of the twentieth century. It is not well understood how these communities will recover from the wildfires of 1988. Intense levels of herbivory allowed under the National Park Service (NPS) policy of natural regulation has generated additional concern. It was my objective to determine the effect of elk browsing on shrub community recovery from fire on the Black-tailed Deer Plateau of the NYWR. The null hypotheses I tested were: 1) that the shrubs of a mountain big sagebrush (*A. t. vaseyana* [Rydb.] Beetle) habitat type will recover from fire at the same rate with or without elk browsing, and 2) that elk herbivory would have no effect on the herbaceous component of this habitat type, regardless of burn treatment. I sampled 12 sites. Significant differences were found in the development of protected and browsed shrubs. Big sagebrush measurements were taken in and out of exclosures at 5 environmentally paired, protected and browsed sites dominated by sagebrush. Big sagebrush canopy cover at the 5 sites averaged 20.0% with protection and 9.7% where browsed ($P \leq 0.01$). Individual plants produced 76% more grams of forage for winter where protected ($P \leq 0.01$). Big sagebrush densities were not different ($P \leq 0.01$). Sprouting shrubs, rubber rabbitbrush (*Chrysothamnus nauseosus* (Pallas ex Pursh) Britt.), green rabbitbrush (*C. viscidiflorus* (Hook) Nutt.) and gray horsebrush (*Tetradymia canescens* DC.) made up a smaller part of the community and generally responded the same as big sagebrush. Coverages for all herbaceous species, perennial grasses, forbs, Idaho fescue (*Festuca idahoensis* Elmer), bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Gould), and other grass species were compared by treatment. Some small differences were found in herbaceous components. Impacts on shrub communities from cumulative and interactive effects of wildfire and intense herbivory have implications for many NYWR values.

CHAPTER 1

INTRODUCTION

Ungulates rely heavily on sagebrush (*Artemisia* L.) habitat types for winter foraging on the Northern Yellowstone Winter Range (NYWR) (Wambolt and McNeal 1987, Wambolt 1996, Wambolt 1998, Wambolt and Sherwood 1999). Dominant big sagebrush (*A. tridentata*) taxa on the NYWR are basin big sagebrush (*A. t.* Nutt. *tridentata*), Wyoming big sagebrush (*A. t. wyomingensis* Beetle and Young), and mountain big sagebrush (*A. t. vaseyana* [Rydb.] Beetle). All three are non-sprouting after disturbance such as fire. Wildfire at least temporarily eliminates these taxa (Wambolt et al. 1999). The 1988 wildfires renewed and escalated concern for sagebrush communities on the NYWR.

Effects of large ungulates on the NYWR have been debated since at least the 1920's. Biologists focused most on woody plants, primarily aspen (*Populus tremuloides* Michx.) and willows (*Salix* L.). There has been little concern for the decline of sagebrush on the NYWR over the last 35 years. During the early twentieth century, sagebrush communities within Yellowstone National Park (YNP) received much attention (Rush 1932, Wright and Thompson 1935, Cahalane 1943, Kittams 1950). In response, the National Park Service (NPS) constructed 10 exclosures in 1957 and 1962 partially to study the relationships between ungulate foraging and sagebrush. This was during a period of high elk (*Cervus elaphus nelsoni* Bailey) numbers on the NYWR. Eight of these exclosures still exist; 4 of which are totally in sagebrush habitat types, and all have significant portions within a sagebrush habitat type. Two burned completely during the large Yellowstone fires of 1988. These exclosures on the Black-tailed Deer Plateau contain primarily a mountain big sagebrush habitat type.

Recently, the relationship between ungulate foraging and sagebrush taxa on the NYWR has received increasing attention. Investigations have determined mechanisms that influence browsing patterns on sagebrush and intensity of use by ungulates (Personius et al. 1987, Striby et al. 1987, Wambolt and McNeal 1987, Bray et al. 1991, Wambolt et al. 1994, Singer and Renkin 1995, Wambolt 1996). These mechanisms are unique to sagebrush taxa and sagebrush-herbivore interactions on the NYWR (Wambolt 1998). Intense browsing has reduced big sagebrush populations on the NYWR (Wambolt 1996, Wambolt and Sherwood 1999, Wambolt et al. 1999). Loss of big sagebrush habitat can impact numerous wildlife populations (Welch 1997, 1999) and may cause long term reductions in some wildlife populations. Big sagebrush is particularly important for ungulates during winter as a nutritious forage (Welch and McArthur 1979) and for thermal and security cover. Given the importance of big sagebrush to wildlife, natural resource managers need to understand the dynamics of big sagebrush communities following fire, especially on ranges like the NYWR where browsing is intense.

Fire interacts with ungulate herbivory to influence vegetative community dynamics. This interaction is not well understood. This study was conducted to examine the interaction of fire with herbivory on community recovery. My objective was to investigate shrub and herbaceous community recovery on the Black-tailed Deer Plateau of the NYWR following the 1988 Yellowstone fires and under intense browsing. I did this by comparing shrub and herbaceous parameters between sites protected or unprotected from ungulate foraging on a portion of the NYWR burned in 1988.

CHAPTER 2

LITERATURE REVIEW

Importance of Big Sagebrush to Wildlife

Big sagebrush taxa dominate the largest vegetation type on the NYWR (Houston 1982). Sagebrush habitats that remain relatively free of snow during the winter are important winter foraging areas for ungulates on the NYWR (Wambolt and McNeal 1987, Wambolt 1996, Wambolt 1998, Wambolt and Sherwood 1999). Big sagebrush habitats on the NYWR may include basin big sagebrush, Wyoming big sagebrush, and/or mountain big sagebrush. Stands of big sagebrush types vary by site and microsite conditions from nearly pure stands of 1 taxon to mixed stands. Ungulates on the NYWR utilize all 3 taxa to differing extents but prefer mountain big sagebrush as a forage (Wambolt 1996).

Among ungulates, big sagebrush-grassland plant community types are particularly important to antelope (Barmore 1980, Norland et al. 1996), mule deer (*Odocoileus hemionus* ssp. *hemionus*) (Julander and Low 1976, Hobbs and Spowart 1984, Welch and Wagstaff 1992), and elk (McNeal 1984). These habitats provide important cover and forage during winter when other forages are less nutritious and unavailable (McNeal 1984, Welch and McArthur 1986, Welch and Wagstaff 1992). Ungulates meet protein requirements for maintenance of approximately 5.5-6.0% during winter (Nelson and Leege 1982) in part by consuming big sagebrush which maintains a crude protein level of approximately 12% (Welch and McArthur 1979). Winter protein content in Yellowstone elk rumens averaged 9.3% when percent crude protein of commonly used grass species and sedge species is < 4% and < 5% respectively (Houston 1982). Concurrently, bluebunch wheatgrass, the dominant grass of relatively snow-free portions of the NYWR, does not meet minimum protein requirements for gestation during fall and winter (Wambolt et al. 1997, Nelson and Leege 1982). Big sagebrush also has the highest digestibility among browse plants on the NYWR (Striby et al. 1987). Big sagebrush maintains 57% digestibility (Striby et al. 1987) during winter while bluebunch wheatgrass ranged from 21% to 23% in southwestern Montana (Wambolt et al. 1997).

Elk use big sagebrush dominated vegetative types during late fall and winter (McNeal 1984). However, elk depend more on grasses throughout the year (Morris and Schwartz 1957, Greer 1970). Winter severity and grass availability affect elk use of big sagebrush. Greer et al. (1970) found big sagebrush among the most frequent forage items in winter elk diets. Browse, including big sagebrush, averaged 17% of elk diets and increased in volume during severe winters across the NYWR (Houston 1982). Use of NYWR sagebrush habitats near Gardiner increased with number of elk in the area (Wambolt 1996). Big sagebrush comprised as much as 9% of elk diets on range areas depleted of sagebrush by past use (Rush 1932, Wright and Thompson 1935, Cahalane 1943, Kittams 1950). Harvest numbers from the special late elk hunt near Gardiner (mid-December through February) are a good indicator of winter severity when forage limitations force elk from the security of YNP into the Gardiner Basin. Wambolt (1996) found this elk harvest was positively related to utilization of sagebrush leaders. Deer also use big sagebrush at lower elevations of the NYWR. On part of the NYWR near

Gardiner, Wambolt (1996) found mule deer winter diets averaged 52% sagebrush over 10 years. The same study found percent dead crown on mountain big sagebrush was significantly correlated to plant browsing, indicating extremely high levels of use on sagebrush habitats in the Gardiner area of the NYWR. With adult elk and deer daily intakes of approximately 2% of body weight per day (Nelson and Leege 1982), a 200 kg elk and 54 kg mule deer will consume 4.0 kg and 1.1 kg of forage per day respectively. An elk consuming a minimal 9% sagebrush will consume approximately 0.36 kg of sagebrush per day and a mule deer consuming 52% sagebrush will consume approximately 0.57 kg of sagebrush per day. Given the current (1999) elk population of approximately 13,000, 4680 kg (5.2 tons) of sagebrush per day would be removed by elk, and the approximately 2000 mule deer would consume another 1140 kg (1.3 tons) of sagebrush per day on the NYWR.

Big Sagebrush Response to Ungulate Browsing on Yellowstone's Northern Range

Sagebrush responses to ungulate browsing are well studied. Several growth characteristics of big sagebrush make it less tolerant to browsing than other browse species (Bilbrough and Richards 1991). Because mountain big sagebrush is wind pollinated, seed heads are elevated above the canopy making them susceptible to browsing. Also, the productive buds on the distal ends of stems are vulnerable to browsing. Terminal leaders contribute most to biomass production, and production generally decreases toward the base of the plant. Shoots older than one year are unable to initiate new growth (Bilbrough and Richards 1993). Compensatory response by big sagebrush is significantly reduced if the current year's growth is removed (Cook and Stoddard 1960). Clipping shoots or removal of previous or current year's growth induced significant crown death, root death, and even plant mortality in mountain big sagebrush (Bilbrough and Richards 1993, Cook and Child 1971, Cook and Stoddard 1960, Wandera et al. 1992). Cook and Stoddard (1960) found that when half of plant crown was clipped, the intact portion of the crown grew back more vigorously while the clipped portion of the crown died. However, Painter and Belsky (1993) warn against the concept of compensatory growth in a natural setting. Patten (1993) applied this compensatory growth viewpoint to browsing by elk in YNP and concluded herbivory did not benefit grass or woody species including big sagebrush.

Mortality of sagebrush on the NYWR was attributed to heavy browsing by elk as early as the 1930's (Wright and Thompson 1935). More recently, nearly 80% of the ungulates in YNP forage on the NYWR during winter (Singer 1991), and Houston (1982) estimated elk represent 89% of the winter biomass of ungulates on the NYWR. High elk numbers have dictated high levels of browsing. Wambolt (1996) found 35% of mountain big sagebrush across the NYWR were killed by excessive browsing. Among surviving plants, crown die-back attributed to browsing averaged 44.7% among 3 big sagebrush subspecies. Sagebrush densities, canopy coverages and production of winter forage were all significantly greater on 19 protected sites compared with unprotected sites across the NYWR (Wambolt and Sherwood 1999). Ungulate use is depressing sagebrush community productivity on the NYWR. This is additive to the effects of wildfire on sagebrush loss discussed in the following section.

Big Sagebrush Response to Fire on Yellowstone's Northern Range

Fire has long been used to control or alter big sagebrush stands. Burning sagebrush has been a source of controversy between those who believe burning harms big sagebrush rangelands and those who believe fire benefits such rangelands. Peterson (1995) claims sagebrush removal does not automatically benefit wildlife while improving forage for livestock. He maintains that, in most cases, sagebrush removal is not necessary to properly maintain, manage, and improve rangelands.

Managers have attempted to mimic natural burning cycles of big sagebrush communities. However, the length of these cycles is debated, and also greatly altered by other man-induced actions such as other methods of sagebrush removal, livestock grazing, and proliferation of exotic species. Natural fire frequencies may range from 60 to 110 years (Whisenant 1990). On cheatgrass (*Bromus tectorum* L.) infested sagebrush areas along the Snake River in Idaho, stands may burn every 2 to 4 years, completely eliminating sagebrush and other native species (Whisenant 1990). Following a 30 year study in the Gravelly Mountains in southwestern Montana, Lomasson (1948) claimed sagebrush on sites favorable for growth will continue to reproduce indefinitely without disturbances such as fire. However, in more recent years with heavier browsing pressure, Petroni (1991) recommended burning stands in the same area every 20 years. In different areas, Wyoming big sagebrush recovered little 12 years after fire (Blaisdell 1953) or 18 years after fire (Wambolt and Payne 1986). Sagebrush stands require at least 30 years to recover significantly from burning (Harniss and Murray 1973, Watts and Wambolt 1996), while recovery from spraying, plowing, or rotocutting may take nearly 20 years (Watts and Wambolt 1996). Wambolt et al. (2001) compared burned and unburned portions of 13 sites in southwestern Montana 2 to 32 years post fire. Thirty-four of 38 comparisons showed significantly ($P \leq 0.05$) greater sagebrush canopy coverages, densities, and production of winter forage while native perennial bunchgrasses were not affected (Wambolt et al. 2001). Wambolt et al. (1999) found minimal recovery of mountain big sagebrush on the NYWR 19 years after fire. Canopy coverages were 12 times greater on unburned sites compared to burned sites, and established shrub densities on unburned sites were 15 times those of burned sites (Wambolt et al. 1999).

CHAPTER 3

METHODS

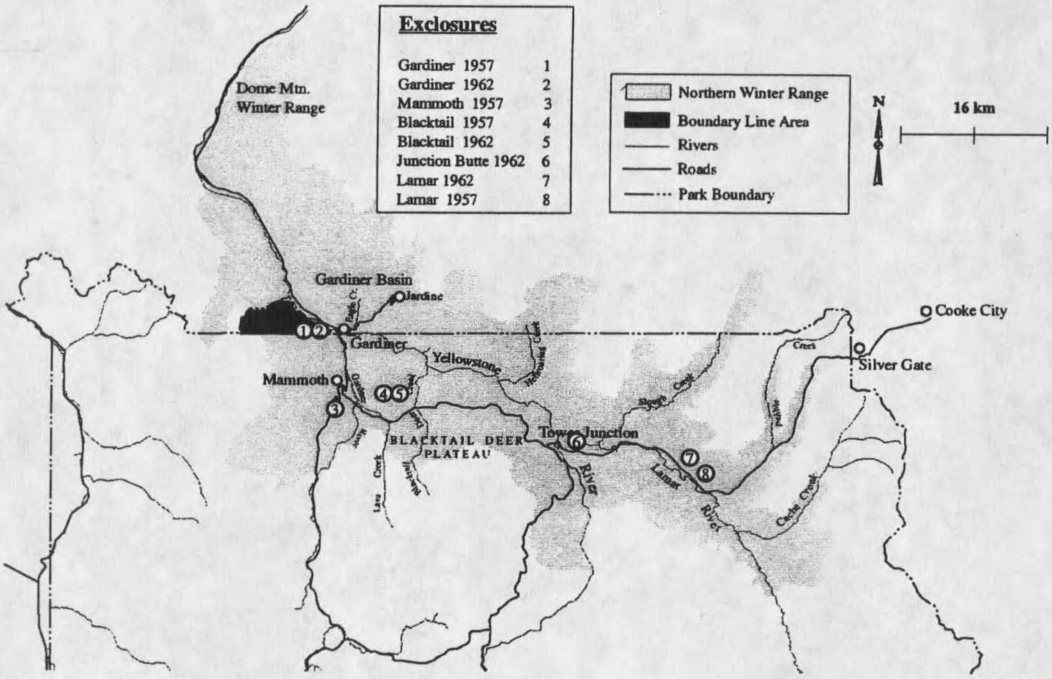
Study Area

Location

This study was conducted on the Black-tailed Deer Plateau of the Northern Yellowstone Winter Range (NYWR) in north central Yellowstone National Park (YNP). The NYWR occupies 100,000 ha over an 80 km stretch along the lower elevations in northern YNP and extends northward into Montana along the Yellowstone River drainage (Houston 1992) (Figure 1). The Lamar and Gardner Rivers also drain portions of the lowlands in YNP that are relatively free of snow. These conditions provide a reliable location for ungulate foraging (Houston 1982).

The 97.7 km^2 Black-tailed Deer Plateau of the NYWR (Coughenour 1991) covers a portion of the northern boundary of YNP approximately midway between Mammoth and Tower Junction. The 2 ungulate exclosures on the Black-tailed Deer Plateau used for this study are located on a ridge top and generally southeasterly facing slope in the approximate center of the NYWR. The NPS erected 1 exclosure near Black-tailed Deer Creek in 1958 and the other nearby in 1962 to evaluate the effects of ungulate grazing (Barmore 1980, Houston 1982, Singer and Harter 1996).

Figure 1. The Northern Yellowstone Winter Range. The Black-tailed Deer Plateau exclosures 4 and 5 were used because they were the only 2 completely burned in 1988.



Landscape

The NYWR contains portions of the Yellowstone, Lamar, and Gardner river drainages in the lowlands of YNP. The Yellowstone River drains the areas of the NYWR extending out of YNP, while the Gardner River drains lower and mid elevations in YNP, and the Lamar River drains mid and higher elevations of the NYWR. Foothills and mountains rise away from floodplains, and valleys are trough-like with foothills rising steeply from floodplains to rolling benchlands often at 50° to 60° slopes (McNeal 1984). These slopes are windswept and provide the majority of snow-free foraging areas for wild ungulates (McNeal 1984). North and east facing slopes provide timbered thermal cover for wintering ungulates (McNeal 1984).

The Black-tailed Deer Plateau is approximately one-third of the NYWR, and lies between the highest elevations drained by the Lamar River in YNP and the lower elevations in the Gardiner Basin outside YNP. The elevation on the Black-tailed Deer Plateau is approximately 2040 m above sea level, midway between the lower (1600 m elev.) and higher (2600 m elev.) elevations of the NYWR (Houston 1982, Coughenour 1991).

Climate

The climate across the NYWR is variable, although generally favorable for ungulates (Wambolt 1998). Gardiner, Montana (1616 m elev.) receives approximately 280 mm of precipitation, while Mammoth (1899 m elev.) receives approximately 400 mm, and Tower Falls (1912 m elev.) receives approximately 410 mm (Farnes 1991). Half of the precipitation is received as snow, and most rainfall occurs in spring and early summer (Farnes 1991). June usually has the most precipitation with about 50 mm (U.S. Weather Bureau Station, Mammoth, WY). Localized thunderstorms may be the only moisture in July and August. Elevation and precipitation on the Black-tailed Deer Plateau are similar to Mammoth and Tower Falls.

The growing season on the plateau is generally from mid-April to mid-September. The warmest month is July, which averages 17.3° C, although a killing frost may occur any month. Winter snows begin limiting ungulate movement and foraging sometime in November and snows recede in approximately mid-March. This concentrates animals for approximately four months on the NYWR. Elk numbers and amount of time spent on the NYWR depend in part on snow depths and densities (Farnes 1999).

Soils

Glacial scouring and deposition have had the largest influence on the soils of the Black-tailed Deer Plateau. The geologic parent material for soils in these exclosures is Pinedale glacial till including material from Absaroka volcanics, limestone, precambrian crystalline rocks, and tuff (Lane 1990).

Soils are generally characterized as Mollisols with a cryic temperature regime. The mean annual soil temperature falls between 0° C and 8° C (NOAA 1994). Alfisols and Inceptisols are common under forest canopies and on rock outcrops, respectively (McNeal 1984). Most of the plateau is depositional and soil profile depths may be several meters in certain areas. Soils texture is typically loam, gravelly loam, gravelly sandy loam, or very gravelly loam (Lane 1990) with coarse fragments ranging from gravel to boulders, respectively (McNeal 1984).

Vegetation

Sagebrush-grassland dominates much of the Black-tailed Deer Plateau and is often interspersed with heavily forested areas. Above 1770 m, the mountain big sagebrush and bluebunch wheatgrass habitat type dominates, especially on south facing slopes. Prairie junegrass (*Koelaria macrantha* Ledeb.), Columbia needlegrass (*Stipa columbiana* Macoun), arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh.] Nutt.), lupine (*Lupinus* spp. L.), and fringed sagewort (*Artemisia frigida* Wild.) were other herbaceous species associated with this vegetation type. Green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), rubber rabbitbrush (*C. nauseosus* (Pallas) Britt.), and gray horsebrush (*Tetradymia canescens* D.C.) were the sprouting shrubs associated with this vegetation type. Sprouting shrubs are those that sprout from roots remaining in the soil after disturbances such as fire.

The mountain big sagebrush and Idaho fescue (*Festuca idahoensis* Elmer) habitat type is also found at elevations above 1770 m, most often on north and east facing slopes. Mountain brome (*Bromus carinatus* H. & A.), common timothy (*Phleum pratense* L.), sticky geranium (*Geranium viscosissimum* F. & M.), common snowberry (*Symphoricarpos albus* [L.] Blake), and Wood's rose (*Rosa woodsii* Lindl.) are other species associated with this habitat type.

Sites with higher available moisture and deeper soils in areas such as depressions, may contain the basin big sagebrush and bluebunch wheatgrass habitat type. This type is extremely rare on the Black-tailed Deer Plateau. Common understory species include basin wildrye (*Elymus cinereus* Scribn. & Merr.), Columbia needlegrass (*Stipa columbiana* Macoun), and the exotic species smooth brome (*Bromus inermis* Leys) and crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.).

The Wyoming big sagebrush and bluebunch wheatgrass habitat type, usually found below 1980 m, is also found on the Black-tailed Deer Plateau, but is limited by the relatively high elevation. Common graminoids found with this community type are prairie junegrass, Indian ricegrass (*Oryzopsis hymenoides* [R. & S.] Ricker), needleandthread (*Stipa comata* Trin. & Rupr.), and green needlegrass (*Stipa viridula* Trin.). Common forbs include hairy goldenaster (*Chrysopsis villosa* [Pursh.] Nutt.), milkvetch (*Astragalus* spp. L.), and locoweed (*Oxytropis* spp. D.C.). Fringed sagewort, green rabbitbrush, rubber rabbitbrush, and gray horsebrush are common shrubs in this community.

Timbered areas commonly occur at higher elevations and northern slopes throughout the study area. The dominant species at these areas are Douglas fir (*Pseudotsuga menzeiesii* [Mirbel] Franco), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), whitebark pine (*Pinus albicaulus* Engelm.), lodgepole pine (*P. contorta* Dougl.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). Sedges (*Carex* spp.), rushes (*Juncus* spp.), willow (Salix spp. L.), quaking aspen (*Populus tremuloides* Michx.), and common snowberry often occur near creeks, springs, and other areas with higher moisture.

Native Ungulates

The Black-tailed Deer Plateau, as part of the NYWR, contributes to sustaining one of the largest wintering herds of Rocky Mountain elk known (Houston 1982). The NPS actively reduced herds by transplanting or intensive harvesting over a 35 year period until 1968, when the NPS adopted a philosophy of non-interference (natural regulation). Populations subsequently increased from less than 4,000 animals to more than 23,000 by 1988 (Coughenour and Singer 1996). The winter of 1988-1989 drastically reduced the herd by approximately 40%, but the population was estimated at 25,000 animals again in 1993 (Lemke 1999). Many elk also died in the winter of 1996-1997, but the population has slowly rebounded (Lemke 1999). In 1999, 11,742 elk were counted on the NYWR, compared with 11,692 in 1998. The northern Yellowstone elk population has decreased since the mid-1990's counts of 18,000-19,000 to the current level of 11,000-12,000 elk (Lemke 1999).

The Black-tailed Deer Plateau serves as a staging area for elk. Elk tend to congregate on the plateau prior to exiting YNP near Gardiner. This tendency is greatly influenced by winter severity. With increasing severity, elk spend less time on the plateau before exiting the Park. Some elk that congregate on the plateau may not leave during a less severe winter. In the last five years, 5,296-8,626 elk have migrated and wintered out of the Park (Lemke 1999). Many migrating elk spend some time on the Black-tailed Deer Plateau.

In addition to elk, mule deer, bison (*Bison bison*), antelope (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and moose (*Alces alces*) also winter on the NYWR. Mule deer populations fluctuate from year to year around 2,000 animals, and most are restricted to lower elevations around Gardiner. Most winters, bison also wander from YNP. In the winter of 1988-1989, 600 bison were harvested and nearly 1,100 were harvested in the winter of 1996-1997. Both winters were relatively severe causing more bison to migrate out of YNP. In the winter of 1993-1994, 3,529 bison were counted on the NYWR, almost twice the number in 1988-1989. The following winter, 1994-1995, numbers were up to nearly 4,000 (John Mack pers. com. Oct. 2000). In 1998, the Montana Department of Fish, Wildlife, & Parks and the Animal and Plant Health Inspection Service actively reduced numbers to 2,200 (John Mack pers. com. Oct. 2000).

Since 1993, the pronghorn antelope population on the NYWR has hovered just over 200 animals, approximately 50% of observed numbers in the late 1980's and early 1990's. In 1993 the population was estimated at 439 animals, and in 1999, 204 antelope were counted (Lemke 1999). During winter, antelope are restricted to the lowest elevations in the Gardiner Basin. Sagebrush is an important component of pronghorn diets, particularly during winter on the NYWR (Barmore 1980). Big sagebrush averaged 48.7% and total sagebrush averaged 67.2% in fecal samples of antelope over 3 winters (1985-1988) in the Gardiner area (Singer and Norland 1995). The decline in pronghorn numbers is attributed to declining sagebrush in their traditional wintering areas.

Bighorn sheep also inhabit distinct, isolated portions of the NYWR. The population is so small, 181 in 1999 (Lemke 1999), that impacts to winter forage for other ungulate species are negligible. Mountain goats, like bighorn sheep, occur in such small numbers, and inhabit such distinct, high elevation portions of the NYWR, that their impacts to winter foraging is also negligible. Moose, with a total NYWR population of 100 to 200 animals, are very sporadic occupants of portions of the NYWR (Tyers pers. com. Oct. 2000). They also have a minimal impact on the winter forage base for other ungulate species on the NYWR.

Burning History

There were 8 to 10 large fires on the portion of the northern winter range inside YNP in the last 300-400 years (Houston 1973). The extent of sagebrush-grass habitats burned by these fires is unknown. Humans have suppressed fires in YNP since 1886 with increasing sophistication. Nearly all fires were being suppressed on NYWR grasslands by the 1950's (McNeal 1984). In the 1970's, managers recognized fire as an integral part of natural systems and began to use it as a management tool. In 1972, 12,000 ha of winter range within YNP were designated as areas where wildfires would not be suppressed.

Minor fires occurred in YNP prior to 1988, but these were relatively insignificant. The fires of 1988 affected approximately 320,000 ha in YNP. Approximately 20,000 ha of this were non-forested and another 15,000 ha were undifferentiated (Despain et al. 1989). Non-forested burn was characterized as burned sagebrush shrublands, grasslands, meadows, wet meadows, and alpine meadows. Undifferentiated burn comprised burned areas that could not be reliably placed in canopy, mixed, non-forested, unburned, and undeliniated burn categories (Despain et al. 1989).

The predominant burn type on the Black-tailed Plateau of the NYWR was a non-forested burn type. Infrared and color aerial photographs taken in October of 1988 and July of 1991, respectively, indicate both exclosures used in this study were nearly completely burned in the 1988 wildfires. No fires have directly influenced the areas observed in this study since 1988. However, there have been minor burns in the area as in 1998 when a lightning started fire burned approximately 40 ha north of the exclosures.

Measurements and Analysis

Study Sites

Of the 8 exclosures presently remaining on the NYWR, I used the 2 burned during the 1988 Yellowstone wildfires for comparisons. These exclosures contained considerable environmental variation. The sagebrush habitat type within each exclosure was stratified to separate topographic, soil, and microclimatic variation to isolate differences in shrub parameters existing among various environmental conditions. Twelve sites were studied, (5 and 7 sites associated with the West and East exclosures, respectively). Each site contained browsed (outside exclosures) and protected (inside exclosures) areas that were environmentally paired. Pairing was accomplished by stratifying sagebrush habitats based on slope, and aspect (Coughenour 1991) (Table 1.). Sagebrush dominated 5 of the 12 sites. Sagebrush parameter comparisons were made for these 5 sites. Four of the 12 sites were dominated by sprouting shrubs and used for parameter comparisons of those taxa. All 12 sites were used in comparing canopies of herbaceous species. Only established shrubs were used in making density and forage production comparisons to avoid overestimation of these parameters. Inclusion of very young plants, which have high seedling mortality in the first few years after germination, would obscure differences between protected and browsed sites. (Mehus 1995). Established sagebrush plants were those with an average horizontal axis (canopy) $\geq$ 15 cm from 4 canopy measurements (Wambolt et al. 1994). Established sprouting shrubs were those having an average horizontal canopy axis $\geq$ 3 cm. Data were collected during the summers of 1998 and 1999.

Table 1. Characteristics of sites used in vegetation comparisons.

Site Number[1]	Exclosure	Slope Class	Aspect	Degrees from North
1	W	16-29	SE	132
2	W	30-44	S	160
3[3]	W	4-15	SSE	165
4[3]	E	0-3		
5	E	16-29	ESE	122
6[2]	E	4-15	E	82
7[3]	E	4-15	S	180
8[2]	E	16-29	SE	144
9[2]	W	16-29	SE	138
10[2]	W	16-29	SE	154
11[2]	E	30-44	ESE	116
12[3]	E	4-15	E	71

[1]All sites were used in herbaceous species comparisons.
[2]Sites used in sagebrush comparisons.
[3]Sites used in sprouting shrub comparisons.

Plant Measurements

On both sagebrush and sprouting shrub sites, means of canopy coverages and densities were compared by site and across sites. Means of sagebrush production of winter forage were also compared using forage prediction models based on subspecies and browse form class developed on the NYWR by Wambolt et al. (1994). At each of the 12 sites, ten-30 m transects were located inside the exclosure and another 10 transects outside the exclosure. Each site was stratified so that each transect would represent an equal sized portion of the entire site (Coughenour 1991, Wambolt et al. 1999). The line interception method developed by Canfield (1941) was used along each 30 m transect to obtain percent canopy coverage. This method determines canopy cover by adding segments of live vegetative species canopy ≥ 3 cm, falling directly below a transect line. Belt transects were used to determine shrub densities. Belt transects of 2 x 30 m were created along each 30 m line above by counting plants 1 m on both sides of the line transect. Only plants rooted within the belt transect were counted. To select 10 plants/line for production of winter forage measurements, the nearest plant to every third meter along the 30 m transect was measured. Means of protected transects were compared to means of unprotected transects.

Understory measurements were taken using methods described by Daubenmire (1959). A decimeter (20 x 50 cm) plot frame was used every third meter along the 30 m transect line to estimate canopy coverages by cover class. This resulted in 100 plots in the protected area of each site and 100 plots on the browsed area for each environmental pairing. Means of the 12 protected areas of sites were compared to means of the 12 paired browsed areas of sites. Cover classes were 0-5, 5-25, 25-50, 50-75, 75-95, and 95-100% (Daubenmire 1959). Herbaceous canopy cover was recorded for Idaho fescue, bluebunch wheatgrass, other grasses, and all forbs.

Analysis

Exploratory data analysis indicated unequal variances from site to site. Consequently, 2-sample Student's t-tests were used to compare means of shrub densities, estimated sagebrush production of winter forage, and canopy coverages of all species. Protected areas were compared to browsed areas for each site. Overall means from protected areas were compared to overall means of browsed areas on the 5 sagebrush sites, the 4 sprouting shrub sites, and on all 12 sites for herbaceous species. In order to make simultaneous inferences among sites at the P=0.05 level, the tests were adjusted using the Bonferroni (Neter et al. 1996, Wambolt and Sherwood 1999) procedure. This adjustment yielded overall comparative P-values of 0.01, 0.0125, and 0.0042 for the 5 sage sites, 4 sprouting shrub sites, and 12 understory sites, respectively.

CHAPTER 4

RESULTS AND DISCUSSION

Shrub Canopy Cover

Mountain Big Sagebrush

The overall comparison between browsed and unbrowsed treatments at the study sites dominated by mountain big sagebrush showed that sagebrush canopy cover was lower ($P \leq 0.0001$) on browsed areas than on unbrowsed areas. Comparisons across the 5 mountain big sagebrush study sites indicate sagebrush cover where unbrowsed was 2.1 times that of browsed areas (Table 2). The average canopy cover for all five sites was 20.0% inside and 9.7% outside the exclosures. These results clearly show effects of browsing on mountain big sagebrush recovery.

Table 2. Percent canopy cover of all mountain big sagebrush at 5 environmentally paired sites either browsed or protected.

Site	N transects/site	Protected (%)	Browsed (%)	Probability >t[1]
6	10	16.26	7.89	0.002
8	10	20.27	6.28	0.0001
9	10	24.81	10.95	0.0001
10	10	18.13	11.37	0.0453
11	10	20.53	11.88	0.0002

[1]The comparative P value for similar inferences is 0.01.

On unburned portions of the NYWR, Wambolt and Sherwood (1999) reported very similar results on areas with established communities that were protected from browsing for 32 to 37 years. They found average big sagebrush canopy cover on protected portions was 2.0 times greater ($P \leq 0.0027$) than on browsed portions over 19 sites. Canopy cover averaged 19.7% inside and 6.5% outside exclosures. Based on canopy coverages, these results indicate sagebrush in these communities has recovered to conditions of unburned areas of the NYWR studied by Wambolt and Sherwood (1999).

Blaisdell (1953) and Wambolt et al. (1999) describe effects of burning on sagebrush recovery. Blaisdell reported little re-establishment of mountain big sagebrush 12 years after burning in Idaho. On 7 NYWR sites burned 9 and 13 years previously, mountain big sagebrush cover averaged 1.2% while 33 unburned sites averaged 14.2% canopy cover Wambolt et al. 1999). The burned portions of the Wambolt et al. (1999) studies however, were located at low elevation portions of the NYWR near Gardiner, where there is little or no snow for protection from herbivory (Hoffman 1996, Wambolt et al. 1999). Higher elevations of the NYWR such as Black-tailed Deer Plateau and Lamar Valley, receive larger snowfalls (Appendix Table 13) and accumulations.

I found that the 5 sites had similar capabilities to support big sagebrush. The relationships between protected and unprotected portions of sites were consistent for vegetative parameters across the conditions represented by different sites. Effects of browsing coupled with fire have depressed canopy cover across browsed portions of all sites. Mountain big sagebrush cover in the protected portions of the study sites ranged from 16.3 to 24.8% and in the browsed portions from 6.3 to 11.9%. The higher cover at protected and browsed portions of some sites compared to protected and browsed portions of other sites may indicate a more favorable environment for sagebrush. These sites likely have better soil conditions from being in slight depressions and have probably endured less browsing due to increased snow depths compared to other sites (Appendix Table 13) (Wambolt and Sherwood 1999). Similarities of all sites are likely due to environmental conditions that are broadly the same across the Black-tailed Deer Plateau.

Sprouting Shrubs

Sprouting shrubs (rubber rabbitbrush, green rabbitbrush, and gray horsebrush) comprised much less canopy cover overall than did big sagebrush (Table 3). However, relationships were similar to big sagebrush. Sprouting shrubs had less cover ($P \leq 0.0001$) on browsed areas than on unbrowsed areas across the 4 sites dominated by sprouting shrubs. Comparisons across these 4 study sites found average canopy cover on protected sites was 2.9 times that of browsed sites (Table 3). Average canopy was 5.8% inside and 2.0% outside exclosures for the 4 sites. Site 4 was not significantly different ($P \leq 0.12$) when considering the Bonferroni adjustment for simultaneous inferences, although average canopy was 4.4% inside and 2.9% outside the exclosure.

Table 3. Percent canopy cover of all sprouting shrubs at 4 environmentally paired sites either browsed or protected.

Site	N transects/site	Protected (%)	Browsed (%)	Probability >t[1]
3	10	4.28	0.71	0.0007
4	10	4.41	2.87	0.1204
7	10	6.73	0.85	0.0003
12	10	7.62	3.65	0.0057

[1]The comparative P value for similar inferences is 0.0125.

These results do not logically follow what may be expected after wildfire. Rabbitbrush, because it is sprouting, should have benefited from disturbances such as the burn (Wambolt et al. 1999) and browsing (Wambolt and Sherwood 1999), and thus been plentiful until successionally replaced by the dominant big sagebrush taxa (Wambolt et al. 1999). Wambolt and Sherwood (1999) reported 2% canopy cover of sprouting shrubs in protected areas and 1.1% in the browsed locations ($P \leq 0.0027$) on unburned areas across the NYWR. These sprouting shrub canopy coverages were nearly half those found on areas burned 10 years previously (Wambolt and Sherwood 1999). Mehus (1995) found gray and green rabbitbrush canopies greater ($P \leq 0.001$) on areas of the NYWR burned (2.8%) than on unburned areas (0.3%) indicating burning at least temporarily benefits sprouting shrubs. These results concur with Blaisdell (1953), Young and Evans (1974), and Wambolt and Payne (1986) who found that green rabbitbrush dramatically increased following fire. Wambolt and Sherwood (1999) support my results suggesting that the intense levels of herbivory on the NYWR may have retarded sprouting shrubs, despite their resiliency to browsing.

Shrub Density

Mountain Big Sagebrush

The overall density comparison of established plants (crown cover ≥ 15 cm) of mountain big sagebrush between browsed and protected treatments showed that density might not be reduced ($P \leq 0.12$) by browsing. Established plant densities ranged from 45.9 to 147.8 per $60m^2$ where protected and 32.5 to 129.4 per $60m^2$ where browsed (Table 4). Individual comparisons of 4 of the 5 sites dominated by mountain big sagebrush showed no differences ($P \leq 0.05$) in number of plants. Site 11 showed more plants ($P \leq 0.018$) where protected (87.6 per $60m^2$) than where browsed (71.4 per $60m^2$).

Sites 9 and 10 were located in slight depressions, which likely accumulated more snow, protecting small plants and increasing moisture available during the growing season. These results indicate plant establishment is not affected by ungulate browsing a decade after fire.

Table 4. Number of big sagebrush plants (with a canopy ≥ 15cm) per $60m^2$ at 5 environmentally paired sites either browsed or protected.

Site	N transects/site	Protected (plants/$60m^2$)	Browsed (plants/$60m^2$)	Probability >t[1]
6	10	45.9	32.5	0.0707
8	10	74.4	42.7	0.0587
9	10	147.8	129.4	0.4575
10	10	99.1	103.9	0.7310
11	10	87.6	71.4	0.0180

[1]The comparative P value for similar inferences is 0.01.

Wambolt and Sherwood (1999), however, indicate browsing effects on unburned portions of the NYWR are intense enough to reduce plant densities. They found 30.5 plants per $60m^2$ inside and 15.3 plants per $60m^2$ outside exclosures ($P \leq 0.0027$). These differences were across sites continually browsed or protected for 32 to 37 years. Their study contained sites with mature productive stands, not plants trying to establish under intense levels of herbivory. Results from the Black-tailed Deer Plateau study sites do not concur with these findings perhaps due to the interactions of browsing and fire over the shorter time frame of 1 decade. Comparing burned and unburned portions of the Gardiner Basin of the NYWR, Wambolt et al. (1999) found an average of 52 plants per $60m^2$ across 33 unburned sites compared to 14 plants per $60m^2$ across 7 previously burned sites. These sites were studied 10 to 14 years after being burned. Recovery across these sites was under continuous intense levels of browsing. My results indicate browsing suppressed recovery, not induced decline because of intense levels of herbivory as in Wambolt and Sherwood (1999). Mehus (1995) and Wambolt and Sherwood (1999) both remark that there were situations with a large number of small (canopy ≤ 15 cm) sagebrush plants outside the exclosures. These were in open areas of sagebrush canopy where predecessor plants had been overbrowsed, allowing seedlings to establish. The interaction of browsing with fire has caused a similar effect on the Black-tailed Deer Plateau. This interaction along with the relatively short time since burning (10-11 years) has resulted in larger numbers of smaller plants outside the exclosures. An influx of these juvenile plants reaching established sizes outside the exclosure would skew densities and possibly production measurements, with more than would be expected in an area experiencing intense levels of herbivory. This would not be expected with a longer time for recovery and either a browsed vs. protected comparison or burned vs. unburned comparison.

Snow may protect these small plants at mid and higher elevations of the NYWR for several years before they are available for ungulate foraging (Wambolt 1998, Wambolt and Sherwood 1999). Hoffman (1996) found that out of the mountain big sagebrush plants in the Gardiner Basin of the NYWR that established in the 1978-1992 period, 47% established during 1988. Good seed production during that year was due to plentiful spring moisture followed by a winter with considerably more snow than prevailed through the 15 year period (Hoffman 1996). A large winter elk die-off (Lemke 1999) and a loss of forage from the 1988 fires were coupled with these conditions. Similar conditions for seedling establishment during the first season following the fires of

1988 occurred on my study sites and may account for higher densities of established plants than on unburned portions of the NYWR.

Sprouting Shrubs

Density of sprouting shrubs averaged 73.9 per 60m^2 where protected, compared to 82.2 per 60 m^2 on the browsed portions of the 4 sites (Table 5); however, the difference was not significant across all sites ($P \leq 0.47$). There were more plants on protected areas of sites 3 and 7, ($P \leq 0.003$), averaging 65.1 per 60m^2 where protected and 36.7 per 60m^2 where browsed. The S and SSE exposures of these sites likely subjected plants outside the exclosure to higher levels of browsing because of decreased snow amounts. Site 12 had more ($P \leq 0.0033$) plants where browsed (167.5 per 60m^2) than where protected (76.2 per 60m^2). Site 12 may show the effects of disturbance by a browsing caused increase in density. This site was also on an open slope facing E toward the Black-tailed Deer Creek valley, which receives less solar radiation during winter and likely accumulates more snow protecting plants outside the exclosure from browsing. Sprouting shrubs inside the exclosure on this site must compete with more grass cover (Table 8) along with litter accumulation.

Table 5. Number of sprouting shrubs (with a canopy ≥ 3cm) per 60m^2 at 4 environmentally paired sites either browsed or protected.

Site	N transects/site	Protected (plants/60m^2)	Browsed (plants/60m^2)	Probability >t[1]
3	10	67.0	43.3	0.0031
4	10	89.3	88.1	0.9328
7	10	63.3	30.1	0.0002
12	10	76.2	167.5	0.0033

[1]The comparative P value for similar inferences is 0.0125.

My results differ from Wambolt and Sherwood (1999) who studied unburned portions of the NYWR. Sprouting shrub densities on the Black-tailed Deer Plateau were not less where browsed; however, they found higher densities where protected, 16.6 per $60m^2$ compared to 13.1 per $60m^2$ ($P \leq 0.0027$), on the browsed portions of 19 sites (Wambolt and Sherwood 1999). My results indicate the response of sprouting shrubs was similar to big sagebrush on the upper portion of the NYWR at sites recovering from fire under intense levels of herbivory. However, higher densities of sprouting shrubs in this study are expected because of sprouting shrub response to burning (Mehus 1995, Wambolt et al. 1999). The area may not have recovered enough in 10 years to show impacts of herbivory on the sprouting shrubs similar to Wambolt and Sherwood (1999).

Mountain Big Sagebrush Production of Winter Forage

Mountain big sagebrush plants over the 5 sites dominated by the taxon produced 43% more ($P \leq 0.0004$) forage available in winter in the unbrowsed treatments than the browsed treatments (Table 6). Average grams of forage produced per plant was 55.3 where protected and 31.4 where browsed. Site 6 had the lowest density of the 5 sagebrush dominated sites. However, unprotected plants of site 6 were large which resulted in equal production of winter forage from sagebrush in and out of the exclosure. Site 9 had the highest densities and canopy coverages of the 5 sites. However, production of winter forage from the sagebrush was unusually small per plant due to the high densities. Forage produced for winter on site 9 where protected was 19.26 g/plant compared to 13.18 g/plant where browsed ($P \leq 0.1372$). This was likely due to a high number of newly established plants that had not yet developed large canopies. Variation in productivity where protected from browsing was likely dictated by differences in microclimates across the study area. Production of winter forage per mountain big sagebrush plant can be used with density to calculate production on a unit area basis (Wambolt and Sherwood 1999). Because densities were not different across sites ($P \leq 0.12$), the effects of browsing on plant size and shape are clearly shown by forage production comparisons.

Table 6. Average grams of winter forage produced per mountain big sagebrush plant at 5 environmentally paired sites either browsed or protected.

Site	N transects/site	Protected (g)	Browsed (g)	Probability >t[1]
6	10	63.76	67.41	0.8357
8	10	87.00	26.37	0.0022
9	10	19.26	13.18	0.1372
10	10	61.38	30.76	0.0033
11	10	45.02	19.40	0.0023

[1]The comparative P value for similar inferences is 0.01.

Production of forage for winter by mountain big sagebrush on the Black-tailed Plateau where protected was 176% that of browsed areas of sites. These results are similar to Wambolt and Sherwood (1999). They found mountain big sagebrush production of winter forage was 88% greater ($P \leq 0.0027$) on sites protected from browsing for 32-37 years compared to sites exposed to browsing (Wambolt and Sherwood 1999). These results contrast to Wambolt and Sherwood (1999) in amount of the difference in forage produced. This is expected because of the relatively short time since the burn for mountain big sagebrush recovery. Wambolt et al. (1999) found little recovery of big sagebrush 19 years after fire. Differences on the Black-tailed Deer

Plateau are not as drastic due to the long term effects of fire coupled with intense levels of browsing during recovery.

Mountain Big Sagebrush Establishment Conditions

My results support the assumption that sagebrush plants inside and outside the exclosures had equal opportunity to reestablish using viable seed in the soil as seed sources. Johnson and Payne (1968) indicate sagebrush reestablishment may be highly dependent on persistence of mature plants following disturbance. However, the Yellowstone wildfires of 1988 burned intensely enough to eliminate all mature mountain big sagebrush plants across the study area. After the fires had completed all their major runs, the NPS reported that fire perimeters included 321,270 ha within YNP as of September 19, 1988 (Despain et al. 1989). Approximately 6% (20,761 ha) of this was meadow, and sage/grassland burns. The Black-tailed Deer Plateau burned September 9, 1988 (Despain et al. 1989) as part of the North Fork Fire. Burns across the greater Yellowstone area varied in intensity. In grasslands and shrublands soil charring depths ranged from 1 to 5 cm (Despain et al. 1989). Less intense burning in the grass and shrub fires across the study area allowed for seed survival in the soil.

Sagebrush seed dispersion can be accomplished through wind, water, or animals (Tisdale and Hironaka 1981). Wind dispersal is the primary method of sagebrush seed dispersal (Wambolt et al. 1989), although Goodwin (1956) concluded water seems to be primary in seed dispersal of big sagebrush. A mature mountain big sagebrush plant can produce approximately 360,000 achenes (Harvey 1981). However, the majority of seed dispersal of sagebrush taxa occurs less than 4 m from the parent plant (Beetle 1960, Friedman and Orshan 1975, Harvey 1981, Tisdale and Hironaka 1981, and Wambolt et al. 1989). There were no potential parental plants left in or near the study area. This coupled with the limited ability of sagebrush taxa to disseminate seed farther than 4 m and the apparent even aged distribution of mountain big sagebrush plants across the study area, indicates reestablishment occurred from seed left in the soil after burning.

Readily available seed combined with favorable precipitation conditions of the winter of 1988-1989 allowed seedling germination and establishment (Wambolt et al. 1999). 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). Meyer (1994) suggests successful emergence of mountain big sagebrush seedlings may depend on the amount and timing of spring snowpack. Snow levels during the winter of 1988-1989 increased moisture to levels favorable for big sagebrush germination and establishment (Hoffman 1996). Average snowfall for 1947-1999 was approximately 185 cm. The winter of 1988-1989 received approximately 203 cm (Western Regional Climate Center). Early drought can be a large factor in causing seedling mortality (Meyer 1994), although seedlings may be able to withstand water shortages by early summer (Booth et al. 1990). June through August precipitation in 1989 was near average, receiving 97% of normal (Frank and McNaughton 1993). Average precipitation for June through August for 1948-2000 was 12.5 cm (Western Regional Climate Center). The same months for 1988 and 1989 had 4.1 cm and 11.9 cm respectively (Western Regional Climate Center). Evans and Black (1993) showed higher water availability during late summer increases reproduction in big sagebrush (subspecies not considered). However, there were no reproductive plants on the study area following the 1988 fire.

Many of the established mountain big sagebrush plants were approximately 10 years old in 1999 coinciding with favorable conditions for establishment during the late 1980's. Snow levels across the NYWR may protect smaller mountain big sagebrush plants from herbivory until they are approximately 5 years old, when they become large enough to contribute to forage and seed production of the community (Hoffman 1996). Increased snow levels along with habitat loss from the fires resulted in an approximately 40% reduction in elk numbers in the winter of 1988-1989 (Lemke 1999). Elk numbers took 5-6 years to recover to levels similar to 1988. This period of low herbivory levels, readily available seed, and favorable moisture conditions allowed sagebrush germinated in the late 1980's to become established.

Herbaceous Canopy Cover

Total Herbaceous Species

Total herbaceous canopy was not different ($P \leq 0.37$) when compared over all sites (Table 7). Mean herbaceous canopy across all sites was 51.3% and 52.4% inside and outside exclosures, respectively, with little variation between sites.

Table 7. Canopy coverage of all herbaceous vegetation at 12 environmentally paired sites either protected or unprotected.

Site	Protected (%)	Unprotected (%)	Protected SD	Unprotected SD	Probability > t[1]
1	56.78	58.92	7.84	9.58	0.5161
2	37.27	45.52	8.26	6.36	0.0223
3	49.32	51.20	5.11	3.65	0.3578
4	58.55	53.97	5.63	3.33	0.0401
5	64.47	55.34	8.68	3.41	0.0216
6	62.52	56.2	7.20	4.32	0.0285
7	52.35	42.45	3.19	3.40	0.0001
8	52.55	59.80	6.76	4.65	0.0167
9	39.20	42.92	6.43	6.70	0.2208
10	41.60	50.87	10.27	6.00	0.0240
11	48.60	56.90	6.28	6.10	0.0078
12	55.15	55.90	2.99	3.90	0.6356

[1]The comparative P value for similar inferences is 0.0042.

Understory canopy was not different on sites with higher shrub canopy. This is not surprising in light of other research (Blaisdell, 1953; Daubenmire, 1975; Peek et al., 1979; Anderson and Holte, 1981; Kuntz, 1982; Wambolt et al. 2001) which indicates the absence of increased herbaceous production from sagebrush control treatments. Wambolt et al. (2001), found herbaceous production was not different on portions of sites with reduced big sagebrush compared to unburned portions of sites across SW Montana burned 2 to 32 years previously. These results indicate mature shrub communities do not affect the herbaceous component of the community and that the herbaceous species do not increase in the absence of shrubs after control treatments.

Canopy coverages and biomass measurements are both useful to evaluate taxa in terms of their relative influence in an ecosystem (Daubenmire 1959). However, community comparisons using canopy cover measurements as in this study and biomass measurements used in other studies should not always be expected to be correlated 100%.

My results seem to fit with indications of Houston (1982), who suggests relative abundance and distribution of grasses have changed very little across Yellowstone's winter range since the 1800's. Fluctuations in perennial grasses and forbs were related more to growing conditions and occasionally to pocket gophers than to ungulate densities on higher elevations of the NYWR studied from 1954 to 1974 (Houston 1982). Increased winter snow depths often preclude heavy grazing of understory vegetation at mid to higher elevations of the NYWR. These conditions induce a decline in total range area available for foraging (Houston 1982, Farnes 1991) and also concentrate use on the herbaceous component of shrub communities at lower elevations. Because of these factors, large differences in understory species canopy would not be expected when comparing protected areas to areas available for grazing.

Houston (1982) also indicates climatic factors have a greater influence than elk grazing on perennial grasses and forbs. Coughenour (1991) concluded that elk winter grazing did not reduce productivity of herbaceous plants at sites on the NYWR. Frank and McNaughton (1993) found aboveground biomass on ungrazed areas to be significantly greater ($P \leq 0.0003$) across 4 protected sites compared to grazed sites. However, they used only 1 upland winter range site experiencing similar conditions to sites in this study.

The 1988 wildfire influenced all results in the study area. Singer and Harter (1996) document that elk herbivory had larger overall effects than burning when comparing grazing to fire effects on grassland production. Most herbaceous responses to burning are within the first few years following fire (Harniss and Murray 1973). Two years after burning in 1988, Singer and Harter (1996) report a 20% increase in grass production in sagebrush habitats on the Black-tailed Deer Plateau. However, Houston (1982) compared an unburned area and an area burned 9 years previously in the same area, and reported 138 g/m^2 air-dried weight of perennial grasses on the unburned area and 79 g/m^2 where burned. Longer term effects of fire on herbaceous understory vegetation in sagebrush habitats are highly variable and dependent on site conditions (Walhof 1997).

Perennial Grasses

Grasses apparently covered slightly more ($P \leq 0.0854$) of the area outside exclosures than where protected from grazing (Table 8). Mean cover was 36.7% and 38.6% inside and outside exclosures, respectively. The interaction of grazing with effects of fire can lead to varying results.

Table 8. Canopy coverage of all perennial grasses combined at 12 environmentally paired sites either protected or unprotected.

Site	Protected (%)	Unprotected (%)	Protected SD	Unprotected SD	Probability > t[1]
1	50.86	44.14	6.27	4.31	0.0277
2	23.10	31.27	7.19	5.85	0.0121
3	38.15	35.32	5.32	4.75	0.2263
4	41.97	39.4	6.72	2.92	0.2879
5	32.87	42.28	5.00	4.19	0.0011
6	49.40	41.85	6.13	4.93	0.0071
7	37.67	30.8	2.78	3.98	0.0002
8	38.15	46.67	5.50	5.96	0.0048
9	27.17	32.25	5.64	5.78	0.0623
10	28.92	36.35	8.60	3.45	0.0265
11	32.32	42.50	3.19	3.05	0.0001
12	39.75	40.92	2.84	2.43	0.3336

[1]The comparative P value for similar inferences is 0.0042.

Greater grass cover outside of the exclosures is nearly statistically significant, however, the difference is less than 2% cover and may not be directly indicative of ungulate effects. Grasses other than bluebunch wheatgrass and Idaho fescue contributed most to cover on sites 1 and 6.

These results may be at least partially from indirect effects of herbivory such as increased rates of nutrient cycling and alteration of plant nutrient allocation (Frank and McNaughton 1993, Singer and Harter 1996). Frank and McNaughton (1993) discuss possible mechanisms for the promotion of aboveground grassland production. They suggest stimulation of grassland production may be linked through direct and indirect effects of grazing by elk (Frank and McNaughton 1993). Plants may benefit from increased solar radiation from a more open canopy causing increased nutrient allocation to aerial parts. Regrowth may have higher photosynthetic rates leading to higher growth rates compared to ungrazed plants. In addition, soil moisture may be conserved, and soil irradiation and decomposition may increase (Frank and McNaughton 1993). Merrill et al. (1994) also suggest indirect effects of grazing, such as removal of standing dead material on microclimatic conditions, likely influence early growth of perennial grasses. Singer and Harter (1996) reported aboveground grass biomass was equal on grazed areas compared to ungrazed areas of the Black-tailed Deer Plateau prior to burning. However, 2 years after burning, grass production was 20% greater where burned (Singer and Harter 1996). Their results concur with Harniss and Murray (1973), who indicate that most herbaceous responses to burning are thought to occur the first few years following fire.

My results differ in that the whole study area was burned 10 years previously and differences between grazed and ungrazed herbaceous cover were small (< 1%).

Forbs

Forb cover was not different ($P \leq 0.27$) on portions of sites protected from herbivory compared to grazed portions (Table 9). Mean forb cover was 14.6% and 13.9% inside and outside the exclosures respectively.

Table 9. Canopy coverage of all forbs at 12 environmentally paired sites either protected or unprotected.

Site	Protected (%)	Unprotected (%)	Protected SD	Unprotected SD	Probability > t[1]
1	5.92	14.94	2.83	9.71	0.0266
2	14.17	14.25	4.75	1.95	0.9640
3	11.17	15.87	1.79	1.68	0.0001
4	16.57	14.57	3.94	.78	0.1479
5	31.59	13.06	6.67	3.91	0.0001
6	13.12	14.35	2.89	3.07	0.3703
7	14.82	11.65	2.64	1.79	0.0078
8	14.54	13.12	5.22	3.20	0.5187
9	12.02	10.67	2.93	5.35	0.3310
10	12.67	14.52	2.20	2.29	0.2217
11	16.27	14.40	6.70	3.46	0.4420
12	15.40	14.97	1.95	2.38	0.6670

[1]The comparative P value for similar inferences is 0.0042.

(Coughenour 1991) found slightly more forb biomass outside exclosures on unburned NYWR sites, 1 out of 2 years. Singer and Harter (1996) report significantly less ($P \leq 0.05$) forb biomass on grazed sites than on ungrazed sites before burning and no difference between grazed and ungrazed sites after burning in 1988. Singer and Harter (1996) found no change in forb production 2 years after burning, and Norland et al. (1996) reports slightly higher forb biomass 2 years following burning. Forb differences between grazed and ungrazed sites are likely influenced more by seasonal moisture differences than by grazing (Coughenour 1991).

Bluebunch Wheatgrass

Bluebunch wheatgrass cover was nearly greater ($P \leq 0.092$) where unprotected from grazing over all sites (Table 10). However, the overall difference of cover was less than 1% across all sites. Bluebunch wheatgrass covered 7.4% of protected areas and 8.3% of grazed areas. Sites ranged from 2 to 10% cover where protected and 2.5 to 12.8% where unprotected from herbivory.

Table 10. Canopy cover of bluebunch wheatgrass at 12 environmentally paired sites either protected or unprotected.

Site	Protected (%)	Unprotected (%)	Protected SD	Unprotected SD	Probability >t[1]
1	4.53	2.50	4.39	0	0.2032
2	8.70	9.00	3.27	2.34	0.8164
3	9.37	12.82	3.19	1.60	0.0068
4	10.07	10.42	2.17	2.43	0.7381
5	2.66	6.50	.44	2.43	0.0027
6	5.47	7.57	2.84	3.09	0.1313
7	10.10	6.37	3.18	1.81	0.0046
8	8.51	4.75	1.49	2.02	0.0002
9	4.37	7.70	1.59	2.42	0.0019
10	8.92	12.07	5.20	3.26	0.1220
11	7.80	7.10	2.55	2.17	0.5169
12	7.82	11.62	2.94	1.87	0.0028

[1]The comparative P value for similar inferences is 0.0042.

Prior to burning, Singer and Harter (1996) found less ($P \leq 0.05$) bluebunch wheatgrass biomass 1 out of 2 years where grazed compared to where ungrazed. However, they found no difference in bluebunch wheatgrass biomass on grazed areas of the Black-tailed Deer Plateau 2 years after burning (Singer and Harter 1996). Merrill et al. (1994) found green biomass of bluebunch wheatgrass higher in the spring where protected from grazing for 2 years. However, grazed and ungrazed green biomasses were similar by the end of the growing season on an unburned portion of the NYWR (Merrill et al. 1994).

Idaho Fescue

Idaho fescue cover was not different ($P \leq 0.78$) between protected and grazed areas over all sites (Table 11). Average cover inside exclosures was 14.5% and outside cover was 14.7%. These results differ from those of Singer and Harter (1996) who found greater ($P \leq 0.05$) biomass of Idaho fescue on grazed areas when compared to protected areas on unburned portions of the Black-tailed Deer Plateau. They also reported more biomass was also found on grazed portions of both burned and unburned areas two years after the fires of 1988. Merrill et al. (1994) describe identical responses of Idaho fescue to grazing as bluebunch wheatgrass. Longer term response of Idaho fescue to burning and herbivory effects are also more likely tied to climatic variations.

Table 11. Canopy cover of Idaho fescue at 12 environmentally paired sites either protected or unprotected.

Site	Protected (%)	Unprotected (%)	Protected SD	Unprotected SD	Probability > t[1]
1	6.89	18.51	3.60	5.67	0.0001
2	6.82	8.85	2.71	3.88	0.1923
3	21.65	11.62	3.15	2.82	0.0001
4	23.90	17.37	6.57	2.23	0.0126
5	14.91	11.50	2.32	2.43	0.0125
6	9.70	16.52	6.12	3.38	0.0063
7	12.65	5.75	1.97	2.22	0.0001
8	12.75	19.02	4.46	5.13	0.0081
9	16.12	12.37	2.69	3.63	0.0171
10	11.80	12.57	4.14	2.12	0.6045
11	13.55	22.82	3.10	3.58	0.0001
12	22.80	19.67	2.52	4.49	0.0709

[1]The comparative P value for similar inferences is 0.0042.

Other Grasses

The remaining grasses on the Black-tailed Deer Plateau collectively showed similar effects of grazing and burning as did bluebunch wheatgrass and Idaho fescue. There was no overall difference ($P \leq 0.49$) in cover inside exclosures compared to outside exclosures (Table 12). Grasses other than Idaho fescue and bluebunch wheatgrass covered 14.7% of protected areas and 15.5% of areas accessible for grazing. Both sites 1 and 6 were in slight depressions and on leeward slopes allowing these sites to accumulate more snow than other sites (Appendix Table 13). Site 1 was almost exclusively a grassland site although there was evidence of a few sagebrush plants prior to burning in 1988.

Table 12. Canopy cover of combined grasses at 12 environmentally paired sites either protected or unprotected (excluding bluebunch wheatgrass and Idaho fescue).

Site	Protected (%)	Unprotected (%)	Protected SD	Unprotected SD	Probability > t[1]
1	39.44	23.62	11.46	6.05	0.0021
2	7.57	13.42	3.71	2.26	0.0005
3	7.12	10.87	2.21	1.67	0.0004
4	8.00	11.60	2.44	2.12	0.0024
5	15.31	24.28	6.39	3.89	0.0044
6	34.22	17.75	6.98	3.67	0.0001
7	15.30	18.67	3.07	4.95	0.0810
8	17.27	22.90	8.44	6.20	0.1022
9	6.67	12.17	3.58	2.05	0.0005
10	8.20	11.70	2.32	3.59	0.0184
11	10.97	12.57	4.92	3.92	0.4321
12	9.12	9.62	1.96	3.73	0.7118

[1]The comparative P value for similar inferences is 0.0042.

Apparently, herbivory on herbaceous plants a decade after the wildfire has not greatly affected herbaceous composition at my study sites. The study area is not subject to as heavy a level of utilization as lower elevation areas of the NYWR because of snow conditions. When upper elevation sites are free of snow cover, animals are no longer confined to the NYWR. Differences, where detected, were very small. The effects of elk herbivory on grasses and forbs are difficult to separate from the effects of wildfire in my study area on this part of the NYWR.

CHAPTER 5

SUMMARY AND IMPLICATIONS

Management of the NYWR continues to draw controversy since it began nearly a century ago. The importance of large ungulate populations in the region, along with the fact that winter habitat is the primary determinant of their survival (Houston 1982), magnifies the attention of scientists and the public. The importance of sagebrush to the survival of many species through severe winters is one aspect of the contentious management of the NYWR. Loss of sagebrush habitats on the NYWR poses a serious threat to numerous wildlife populations dependant on the taxa, including elk, mule deer, antelope, and sage grouse.

The impact of ungulate browsing on established stands of mountain big sagebrush is documented. Shrub declines associated with browsing on the NYWR are described by Mehus (1995), Hoffman (1996), Wambolt (1998), Wambolt and Sherwood (1999), and Wambolt et al. (1999). Impacts of fire on mountain big sagebrush stands on the NYWR are also well studied. Wambolt and McNeal (1987), Wambolt (1998), Wambolt et al. (1999), and Wambolt et al. (2001) document minimal recovery of sagebrush stands following fire on the NYWR.

This study on the Black-tailed Deer Plateau found that mountain big sagebrush plants are establishing equally on areas protected or available to ungulate browsing 10 years following fire. Relatively rapid establishment was promoted by the best germination and establishment conditions of a 2 decade period. Sagebrush stands at these sites have not been exposed to as high a level of herbivory for prolonged periods as were some of the sites studied by Wambolt and Sherwood (1999), Wambolt et al. (1999), Wambolt et al. (1998), Mehus (1995), and Hoffman (1996). However, this study did find browsing affected the growth form of these young plants. Browsed plant canopies were smaller, thereby reducing the amount of forage they produce for wintering ungulates.

Rubber and green rabbitbrushes and horsebrush were impacted similarly. This is contrary to what may be expected (Wambolt and Sherwood 1999), because these shrubs are capable of sprouting from roots following disturbances such as fire and intense herbivory. It is notable that 10 years after fire, these sprouting shrubs show the same recovery pattern as mountain big sagebrush.

Results of herbaceous vegetation showed minimal effects from herbivory. On the Black-tailed Deer Plateau of the NYWR, grasses and forbs apparently do not experience levels of herbivory intense enough to alter communities. Grasses and forbs do not receive intense grazing pressure during mild months because ungulates are not confined to this part of the NYWR. During winter months, ungulates are precluded from intense grazing because herbaceous species are often under snow.

Given the importance of sagebrush communities to numerous wildlife species on Yellowstone's northern range, managers should consider strategies to reverse or halt the loss and reduction of this important forage and general habitat component. It can be concluded that the reduction in all shrubs across the NYWR and suppression of recovery on burned portions of the NYWR will detrimentally impact native ungulates. This will be especially important to their foraging requirements during severe winters. In addition, other species dependant on these sagebrush habitats will be impacted simultaneously to varying degrees.

LITERATURE CITED

Anderson, J.E. and K.E. Holte. 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. J. Range Manage. 34:25-29.

Barmore, W.J. 1980. Population characteristics, distribution and habitat relationships of six ungulates in northern Yellowstone National Park. Final Report. Yellowstone files.

Beetle, A.A. 1960. A study of sagebrush-the section *Tridentae* of Artemisia. Wyoming Agr. Exp. Sta. Bull. 368. 83 pp.

Bilbrough, C.J., and J.H. Richards. 1991. Branch architecture of sagebrush and bitterbrush: use of a branch complex to describe and compare patterns of growth. Can. J. Botany. 69:1288-1295.

Bilbrough, C.J., and J.H. Richards. 1993. Growth of sagebrush and bitterbrush following simulated winter browsing: mechanisms of tolerance. Ecology. 74:481-492.

Blaisdell, J.P. 1953. Ecological effects of planned burning of sagebrush-grass range on the upper Snake River Plains. U.S. Dept. of Agriculture Tech. Bull. No. 1075. Ogden, UT.

Booth, G.D., B.L. Welch, and T. Jacobson. 1990. Seedling growth rate of 3 subspecies of big sagebrush. J. Range Manage. 43;225-229.

Bray, R.O., C.L. Wambolt, and R.G. Kelsey. 1991. Influence of sagebrush terpenoids on mule deer preference. J. Chem. Ecol. 17:2053-2062.

Cahalane, V.H. 1943. Elk management and herd regulation - Yellowstone National Park. Trans. North Am. Wildl. Conf. 8:95-101.

Canfield, R. 1941. Application of the line interception method on sampling range vegetation. J. Forestry. 39:388-394.

Cook, C.W., and R.D. Child. 1971. Recovery of desert plants in various states of vigor. J. Range Manage. 24:339-343.

Cook, C.W., and L.A. Stoddart. 1960. Physiological responses of big sagebrush to different types of herbage removed. J. Range Manage. 13:14-16.

Coughenour, M.B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. J. Appl. Ecol. 28:71-82.

Coughenour, M.B., and F.J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecol. Appl. 6:543-593.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33:43-64.

Daubenmire, R. 1975. Plant succession on abandoned fields and fire influences in a steppe area in southeastern Washington. Northwest Science. 49:36-48.

Despain, D., A. Rodman, P. Schullery, and H. Shovic. 1989. Burned area survey of Yellowstone National Park: The fires of 1988. Div. of Research and Geographic Information Systems Laboratory, Yellowstone National Park, Wyoming. 14 pp.

Farnes, P.E. 1991. A scaled index of winter severity. Pages 135-138 in Proceedings of the Western Snow Conference. 12-15 April 1991, Juneau, Alaska, Colorado State University Press, Fort Collins, CO.

Farnes, P.E. 1999. Index of Winter Severity values for elk and bison for Yellowstone National Park for the 1999 winter up through March 1. Unpublished Report.

Frank, D.A., and S.J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia. 96:157-161.

Friedman, J., and G. Orshan. 1975. The distribution, emergence and survival of seedlings of *Artemisia herba-alba* Asso in the Negro Desert of Israel in relation to distance from the adult plants. J. Ecol. 63:627-632.

Goodwin, D.L. 1956. Autecological studies of Artemisia tridentata Nutt. Ph.D. Dissertation. Washington State University, Pullman, WA.

Greer, K.R., J.B. Kirsch, and H.W. Yeager. 1970. Seasonal food habits of the northern Yellowstone elk herds during 1957 and 1962-1967 as determined from 793 rumen samples . Mont. Wild. Invest. Lab. Progress Report No. W-83-R-12. 76p.

Harniss, R.O., and R.B. Murray. 1973. Thirty years of vegetal change following burning of sagebrush-grass range. J. Range Manage. 26:322-325.

Harvey, S.J. 1981. Life history and reproductive strategies in *Artemisia*. M.S. Thesis. Montana State University, Bozeman, MT.

Hobbs, N.T., and R.A. Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. J. Wild. Manage. 48:551-560.

Hoffman, T.L. 1996. An ecological investigation of mountain big sagebrush in the Gardiner basin. M.S. Thesis, Montana State University, Bozeman, MT.

Houston, D.B. 1973. Wildfires in northern Yellowstone National Park. Ecology. 54:1111-1117.

Houston, D.B. 1982. The northern Yellowstone elk, ecology and management. Macmillan Publishers, New York, New York.

Johnson, J.R., and G.F. Payne. 1968. Sagebrush reinvasion as affected by some environmental influences. J. Range Manage. 21:209-213.

Jorgensen, H. 1990. Big sagebrush and fire in the intermountain west. Unpublished literature review. 119 references. Montana Fish, Wildlife & Parks, Bozeman, MT.

Julander, O., and J.B. Low. 1976. A historical account and present status of the mule deer in the west. pp. 3-19. In: G.W. Workman and J.B. Low (eds). Mule deer decline in the west. Utah State University. Logan, UT.

Kittams, W.H. 1950. Sagebrush on the lower Yellowstone range as an indicator of wildlife stocking. Yellowstone files. 14pp. Mimeo.

Kuntz, D.E. 1982. Plant response following spring prescribed burning in an *Artemisia tridentata* ssp. *vaseyana-Festuca idahoensis* habitat type. Doctor of Philosophy Dissertation, University of Idaho, Moscow, ID.

Lane, J. 1990. Characterization and comparison of soils inside and outside of grazing exclosures on Yellowstone National Park's northern winter range. M.S. Thesis, Montana State University, Bozeman, MT.

Lemke, T. 1999. Northern Yellowstone Cooperative Wildlife Working Group 1999 annual report. Unpublished report. 1999. Montana Fish, Wildlife & Parks. 35 pp.

Lommasson, T. 1948. Succession in sagebrush. J. Range Manage. 1:19-21.

McNeal, A.F. 1984. Site characteristics and effects on elk and mule deer use on the Gardiner winter range, Montana. M.S. Thesis, Montana State University, Bozeman, MT.

Mehus, C.A. 1995. Influences of browsing and fire on sagebrush taxa on the Northern Yellowstone Winter Range. M.S. Thesis, Montana State University, Bozeman, MT.

Merrill, E.H., N.L. Stanton, and J.C. Hak. 1994. Responses of bluebunch wheatgrass, Idaho fescue, and nematodes to ungulate grazing in Yellowstone National Park. Oikos. 69:231-240.

Meyer, S.E. 1994. Germination and establishment ecology of big sagebrush: Implications for community restoration. Symposium on management, ecology and restoration of intermountain annual rangelands. U.S. Department of Agriculture, Forest Service General Technical Report. INT GTR-313:244-251. Boise, ID.

Morris, M.S., and J.E. Schwartz. 1957. Mule deer and elk food habits on the National Bison Range. J. of Wild. Manage. 21:189-193.

Nelson, J.R., and T.A. Leege. 1982. Nutritional requirements and food habits. 323-367. In: Elk of North America, ecology and management. J.W. Thomas and D.E. Toweill, (eds.). Stackpole Books, Harrisburg, Pennsylvania.

Neter, J., M.H. Kutner, C.J. Nachtsheim, and W. Wasserman. 1996. Applied Linear Statistical Models. Irwin Publishing. 4th Edition.

Norland, J.E., F.J. Singer, and L. Mack. 1996. Effects of the Yellowstone fires of 1988 on elk habitats. In: D. Despain and R. Hamre, (eds.) The ecological implications of fire in Greater Yellowstone: Second Biennial Conference on Science in the Great Yellowstone Ecosystem. Int. Assn. of Wildland Fire, 1996. 223-232.

Painter, E.L., and A.J. Belsky. 1993. Application of herbivore optimization theory to rangelands of the western United States. Ecol. Appl. 31:2-9

Patten, D.T. 1993. Herbivore optimization and overcompensation: Does native herbivory on western rangelands support these theories? Ecol. Appl. 3:35-36.

Peek, J.M., Riggs R.A., and J.L. Lauer. 1979. Evaluation of fall burning on bighorn sheep winter range. J. Range Manage. 32:430-432.

Personius, T.L., C.L. Wambolt, J.R. Stephens, and R.G. Kelsey. 1987. Crude terpenoid influence on mule deer preference for sagebrush. J. Range Manage. 40:84-88.

Peterson, J.G. 1995. Ecological implications of sagebrush manipulation: a literature review. Wildlife Management Division, Montana Fish, Wildlife & Parks, Project, W-101-R-2. 49 pp.

Petroni, M.A. 1991. Gravelly sagebrush. Final Environmental Impact Statement. U.S.D.A. Forest Service, Beaverhead National Forest, Ennis, MT.

Rush, W.M. 1932. Northern Yellowstone Elk Study. Montana Fish and Game Commission.

Singer, F.J. 1991. The ungulate prey base for wolves in Yellowstone National Park. In: R.B. Keiter and M.S. Moyce, (eds.). The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale Univ. Press. New Haven, Conn.

Singer, F.J., and M.K. Harter. 1996. Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. Ecol. Appl. 6:185-199.

Singer, F.F., and R. A. Renkin. 1995. Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. Great Basin Naturalist. 55:201-212.

Smith, and P.T. Tueller, compilers, Proc-Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. USDA Forest Serv. Gen. Tech. Rep. INT-276, Ogden, UT.

Striby, K.D., C.L. Wambolt, R.G. Kelsey, and K.M. Havstad. 1987. Crude terpenoid influence on in vitro digestibility of sagebrush. J. Range Manage. 47:231-234.

Tisdale, E.W., and M. Hironaka. 1981. The sagebrush-grass region: a review of the ecological literature. Univ. Idaho For. Wildl. And Range Exp. Stn. Bull. No. 33.

U.S. Weather Bureau Station. Mammoth WY.

Walhof, K.S. 1997. A comparison of burned and unburned big sagebrush communities in southwest Montana. M.S. Thesis. Montana State University, Bozeman.

Wambolt C.L. 1996. Mule deer and elk foraging preference for 4 sagebrush taxa. J. Range Manage. 49:499-503.

Wambolt, C.L. 1998. Sagebrush and ungulate relationships on Yellowstone's northern range. Wildlife Soc. Bull. 26:429-437.

Wambolt, C. L., W. H. Creamer, and R. J. Rossi. 1994. Predicting big sagebrush winter forage by subspecies and browse form class. J. Range Manage. 47:231-234.

Wambolt, C.L., M.J. Frisina, K.S. Douglas, and H.W. Sherwood. 1997. Grazing effects on nutritional quality of bluebunch wheatgrass for elk. J. Range Manage. 50:503-506.

Wambolt, C.L., T.L. Hoffman, and C.A. Mehus. 1999. Response of shrubs in big sagebrush habitats to fire on the Northern Yellowstone Winter Range. In: E.D. McArthur, W.K. Ostler, C.L. Wambolt, (compilers), Proceedings-Symposium on shrubland ecotones. USDA Forest Service Proceedings. RMRS-P-11:238-242. Fort Collins, CO.

Wambolt, C.L., and A.F. McNeal. 1987. Selection of winter foraging sites by elk and mule deer. J. Environ. Manage. 25:285-291.

Wambolt, C.L., and G.F. Payne. 1986. An 18-year comparison of control methods for Wyoming big sagebrush in Southwestern Montana. J. Range Manage. 39:314-319.

Wambolt, C.L. and H.W. Sherwood. 1999. Sagebrush response to ungulate browsing in Yellowstone. J. Range Manage. 52:363-369.

Wambolt, C.L., K.S. Walhof, and M.R. Frisina. 2001. Recovery of big sagebrush communities after burning in southwestern Montana. J. Environ. Manage. 61:323-348.

Wandera, J.L., J.H. Richards, and R.J. Mueller. 1992. The relationships between relative growth rate, meristematic potential and compensatory growth of semiarid-land shrubs. Oecologia. 90:391-398.

Watts, M.J., and C.L. Wambolt. 1996. Successional trends of Wyoming big sagebrush 30 years after 4 treatments. J. Environ. Manage. 46:95-102.

Welch, B.L. 1997. Seeded versus containerized big sagebrush gardens. J. Range Manage. 50:611-614.

Welch, B.L. 1999. Add three more to the list of big sagebrush eaters. In: E.D. McArthur, W.K. Ostler, C.L. Wambolt, (compilers), Proceedings-Symposium on shrubland ecotones. USDA Forest Service Proceedings RMRS-P-11. 171-174. Fort Collins, CO.

Welch, B.L., and E.D. McArthur. 1979. Feasability of improving big sagebrush for use on mule deer winter ranges. In: J.R. Goodin, and D.K. Northington (eds), Arid plant resources. Texas Tech University, Lubbock, Texas. 451-457.

Welch, B.L., and E.D. McArthur. 1986. Wintering mule deer preference for 21 accessions of big sagebrush. Great Basin Natur. 46:281-286.

Welch, B.L., and F.J. Wagstaff. 1992. 'Hobble Creek' big sagebrush vs. Antelope bitterbrush as a winter forage. J. Range Manage. 45:140-142.

Western Regional Climate Center. 2001. Monthly precipitation, monthly total snowfall. Yellowstone Park, Wyoming. (wrcc@dri.edu).

Whisenant, S.G. 1990. Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. In: E.D. McArthur; E.M Romney, S.D. Smith, P.T. Teuller, (compilers). Proceedings-Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-276:167-170. Ogden, UT.

Wright, G.M., and B.H. Thompson. 1935. Fauna of the National Parks of the United States: wildlife management in the national parks. Fauna Series No.2. U.S. Govt. Printing Office, Washington, D.C.

Young, J.A., and R.A. Evans. 1974. Population dynamics of green rabbitbrush in disturbed big sagebrush communities. J. Range Manage. 27:127-132.

Young, J.A., R.A. Evans, and D.E. Palmquist. 1990. Soil surface characteristics and emergence of big sagebrush seedlings. J. Range Manage. 43:358-366.

APPENDICES

APPENDIX A

SUMMARY TABLES

Table 13. Average snow depths (cm) for protected and unprotected portions of sites. Three stratified measurements were taken for each protected and each unprotected area for individual sites in February 1999. Average yearly snowfall 1948 to 2000 was 182 cm. Snowfall for winter 1998-1999 was 213 cm (Western Regional Climate Center, Yellowstone Park, Wyoming).

Site[1]	Protected (cm)	Unprotected (cm)
1	32.7	32.3
2	21.7	11.7
3[3]	23.7	8.7
4[3]	16.3	16.7
5	15.3	21.3
6[2]	39.0	34.3
7[3]	23.3	28.3
8[2]	34.0	27.7
9[2]	32.0	25.3
10[2]	34.7	29.0
11[2]	35.0	27.0
12[3]	18.3	12.3

[1]All sites were used in herbaceous species comparisons.
[2]Sites used in sagebrush comparisons.
[3]Sites used in sprouting shrub comparisons.

Table 14. Percent canopy cover of big sagebrush at 12 environmentally paired sites either browsed or protected.

Site[1]	N transects/site	Protected (%)	Browsed (%)	Protected SD	Browsed SD	Probability >t
1	9	0.95	0.32	1.43	0.47	0.2413
2	10	0.57	2.80	1.16	1.65	0.0027
3[3]	10	0.75	0.60	1.29	0.87	0.7575
4[3]	10	0.98	2.02	1.74	1.35	0.1540
5	8	0.49	0.55	0.72	1.06	0.9818
6[2]	10	16.26	7.89	5.16	5.22	0.0020
7[3]	10	4.51	6.44	4.52	2.26	0.2419
8[2]	10	20.27	6.28	5.55	4.38	0.0001
9[2]	10	24.81	10.95	6.43	3.87	0.0001
10[2]	10	18.13	11.37	8.22	5.58	0.0453
11[2]	10	20.53	11.877	5.03	3.11	0.0002
12[3]	10	0.35	0.52	0.89	0.58	0.6148

[1]All sites were used in herbaceous species comparisons.
[2]Sites used in sagebrush comparisons.
[3]Sites used in sprouting shrub comparisons.

Table 15. Number of big sagebrush plants (with a minimum canopy of 15cm) per $60m^2$ at 12 environmentally paired sites either browsed or protected.

Site[1]	N transects/site	Protected plants/$60m^2$	Browsed plants/$60m^2$	Protected SD	Browsed SD	Probability >t
1	9	4.66	1.22	3.90	1.48	0.0323
2	10	8.9	29.7	9.63	15.45	0.0020
3[3]	10	11.8	12.0	9.75	5.94	0.9564
4[3]	10	4.2	14.2	6.81	7.04	0.0047
5	8	6.0	4.6	3.78	3.85	0.4830
6[2]	10	45.9	32.5	19.09	11.05	0.0707
7[3]	10	37.3	56.1	23.43	12.87	0.0392
8[2]	10	74.4	42.7	16.34	44.81	0.0587
9[2]	10	147.8	129.4	49.6	58.42	0.4575
10[2]	10	99.1	103.9	27.47	33.69	0.7310
11[2]	10	87.6	71.4	15.44	12.20	0.0180
12[3]	10	6.0	7.3	7.15	7.09	0.6878

[1]All sites were used in herbaceous species comparisons.
[2]Sites used in sagebrush comparisons.
[3]Sites used in sprouting shrub comparisons.

Table 16. Average grams of winter forage produced per mountain big sagebrush plant at 12 environmentally paired sites either browsed or protected.

Site[1]	N transects/site	Protected (g)	Browsed (g)	Protected SD	Browsed SD	Probability >t
1	9	38.00	16.82	26.00	12.22	0.1154
2	10	9.72	25.91	1.36	22.08	0.0458
3[3]	10	8.98	9.63	1.65	1.07	0.3047
4[3]	10	28.75	26.58	18.03	28.16	0.8693
5	8	18.94	19.37	11.42	9.33	0.9345
6[2]	10	63.76	67.41	33.93	43.12	0.8357
7[3]	10	12.81	21.39	7.56	16.64	0.1620
8[2]	10	87.00	26.37	45.46	8.57	0.0022
9[2]	10	19.26	13.18	11.22	4.37	0.1372
10[2]	10	61.38	30.76	24.79	14.18	0.0033
11[2]	10	45.02	19.40	19.41	8.65	0.0023
12[3]	10	10.17	11.17	2.63	3.02	0.5231

[1]All sites were used in herbaceous species comparisons.
[2]Sites used in sagebrush comparisons.
[3]Sites used in sprouting shrub comparisons.

Table 17. Percent canopy cover of all sprouting shrubs at 12 environmentally paired sites either browsed or protected.

Site[1]	N transects/site	Protected (%)	Browsed (%)	Protected SD	Browsed SD	Probability >t
1	9	0.41	0.00	0.43	0.00	0.0224
2	10	2.91	0.03	3.30	0.09	0.0221
3[3]	10	4.28	0.71	2.26	0.48	0.0007
4[3]	10	4.41	2.87	2.55	1.55	0.1204
5	8	0	0	0.00	0.00	....
6[2]	10	0.36	0.58	0.57	0.90	0.5246
7[3]	10	6.73	0.85	3.41	0.85	0.0003
8[2]	10	0.64	0.05	0.86	0.10	0.0567
9[2]	10	0.79	0.29	0.67	0.28	0.0499
10[2]	10	4.34	0.31	6.12	0.32	0.0672
11[2]	10	1.45	0.09	2.24	0.16	0.0868
12[3]	10	7.62	3.65	3.42	1.66	0.0057

[1]All sites were used in herbaceous species comparisons.
[2]Sites used in sagebrush comparisons.
[3]Sites used in sprouting shrub comparisons.

Table 18. Number of sprouting shrubs (with a minimum canopy of 3cm) per $60m^2$ at 12 environmentally paired sites either browsed or protected.

Site[1]	N transects/site	Protected plants/$60m^2$	Browsed plants/$60m^2$	Protected SD	Browsed SD	Probability >t
1	9	3.11	0.22	3.06	0.67	0.0224
2	10	31.2	8.1	7.14	6.08	0.0001
3[3]	10	67.0	43.3	12.91	17.79	0.0031
4[3]	10	89.3	88.1	37.14	24.28	0.9328
5	8	3.0	0.8	2.50	0.89	0.0412
6[2]	10	6.8	18.7	4.85	22.71	0.1367
7[3]	10	63.3	30.1	17.78	14.22	0.0002
8[2]	10	4.3	2.9	4.27	2.77	0.3957
9[2]	10	11.4	18.4	8.04	10.98	0.1212
10[2]	10	22.8	7.3	20.36	3.74	0.0404
11[2]	10	13.9	11.4	20.20	5.32	0.7128
12[3]	10	76.2	167.5	21.37	73.18	0.0033

[1]All sites were used in herbaceous species comparisons.
[2]Sites used in sagebrush comparisons.
[3]Sites used in sprouting shrub comparisons.

APPENDIX B

SITE DIAGRAM

Figure 2. Site Diagram.