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The Yellowstone Sage Belts 1958 to 2008: 50 Years of Change in the Big Sagebrush (*Artemisia tridentata*) Communities of Yellowstone National Park

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ABSTRACT

*In 1958, 13 belt transects were established within the ungulate winter range in the northern portion of Yellowstone National Park to study how shrub communities were affected by grazing from ungulate populations. Between 1958 and 2008, the belts have been measured and photographed by different researchers at least once per decade, which has resulted in a comprehensive 50 year time series of how these communities have responded to climatic change, herbivory, and natural disturbance. In this study, we compare the percent cover, seedling establishment, and plant survival in these communities at two points in time (1958 and 2008); and explore which factors – climatic, herbivory, or disturbance – were most influential to changes in canopy cover and number of seedlings after 50 years. The recovery of the big sagebrush community after the North Fork fire is also discussed. Herbivory has controlled tree growth on the shrub belts. Climate and lack of disturbance have resulted in an increase in big sagebrush (*Artemisia tridentata*) cover on many shrub belts inside and outside of exclosures. Invasive annual species have become important drivers of vegetation change at the lowest elevation site.*

In Monaco, T.A. et al. comps. 2011. Proceedings – Threats to Shrubland Ecosystem Integrity; 2010 May 18-20; Logan, UT. Natural Resources and Environmental Issues, Volume XVII. S.J. and Jessie E. Quinney Natural Resources Research Library, Logan Utah, USA.

INTRODUCTION

In 1957, Yellowstone National Park (YNP) managers embarked on an experiment to examine how ungulate populations affected vegetation in the northern portion of the park where many migratory species like elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and bison (*Bison bison*) spend their winter months (Edwards, unpublished letter). At the time, controversies over whether ungulate populations were too high and whether the browse vegetation was being overgrazed had existed for decades. As early as the 1930s, researchers raised concerns about declines in big sagebrush species possibly being related to overgrazing by overabundant populations of pronghorn (*Antilocapra americana*) and elk (Rush 1932). In 1950, Kittams concluded that big sagebrush was declining in many areas of the park for a combination of reasons, including physical breakage by browsing ungulates in winter, absence of seed production, and excessive browsing by pronghorn and elk at lower elevations in the park (Kittams, unpublished paper). In 1957, there were approximately 5000 elk in the park, 550 bison, 200 mule deer, and 150 pronghorn (Yellowstone National Park 1997). YNP managers were severely criticized

for allowing the populations of several of the ungulate species, especially elk and bison, to increase to levels that were thought to be detrimental to their winter range habitat and forage even though a policy of permitted hunts and culling kept the elk and bison herds at unnaturally low populations throughout the 1950s and 1960s (National Research Council 2002). Ranchers, park administrators, range managers, and park visitors believed that the range was being overgrazed, but little scientific data existed to support this belief (Yellowstone National Park 2005). By 1957, the National Park Service was concerned enough about the vegetation, the management issues, and particularly the declines in sagebrush, to initiate research that would provide scientific data to inform the debate and the regulation of ungulate populations in the park.

STUDY SITES

The ungulate winter range at the heart of the ungulate-management controversy consists of approximately 550 mi² (140,000 ha) of grassland, shrubland, and forest that extends across the northern boundary of the park (figure 1). The species that seasonally occupy this area include bison, elk,

pronghorn antelope, Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*), moose (*Alces alces*), and mule deer (Barmore Jr. 2003). Since the 1980s, mountain goats (*Oreamnos americanus*) have also occupied and utilized this area as winter range (Yellowstone National Park 1997).

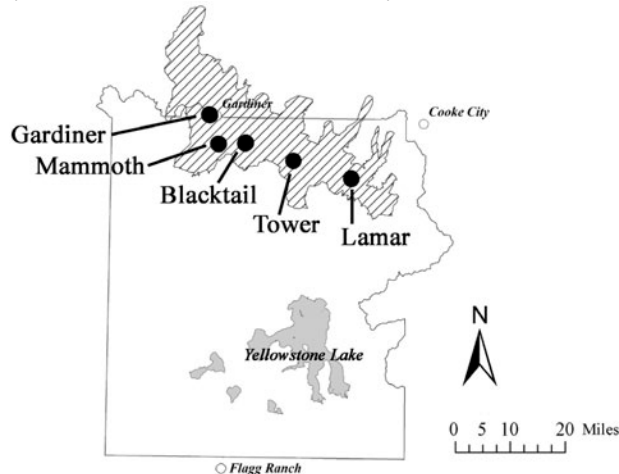


Figure 1. Boundary of the big-game winter range (striped area) and locations of the exclosures constructed in 1958 (dots). Winter range boundary provided by the Yellowstone Spatial Analysis Center.

In 1957, big-game exclosures were constructed at five locations across the northern winter-range area (figure 1). Park managers wanted to ensure that the study sites were designed and located so that they would provide for “detailed studies [for research] and demonstration areas to explain the wildlife range problem with the public” (Edwards, unpublished letter). The Tower exclosure was dismantled by 1962 because of a controversy over its visibility to the public, but the four remaining original exclosures still exist. In 1961, four additional exclosures were constructed to enhance the experimental design. They were constructed near the existing exclosures at Gardiner, Blacktail and Lamar and at a new location at Junction Butte. Because this study is focused on changes after a full 50 years, I do not address the changes that have occurred in the 1961 exclosures, although many of the same trends have occurred in them as in the 1957 exclosures.

Each ungulate exclosure constructed for the experiment is bounded by a fence over eight feet (2.4 m) tall that encloses approximately 5 acres (2 ha). The entire study design included two types of transects in both the original and 1961 exclosures – belt transects for mapping changes in sagebrush/browse, willow, and aspen; and line

transects (i.e., the Parker transects) for tracking changes in grasses, forbs, and shrubs; plus a square quadrat (9 ft²) for measuring percent cover changes in forbs and grasses. Two sagebrush belt transects were established at each location – one inside and one outside of the exclosure – for a total of eight belts to study changes in shrub cover in the 1957 exclosures (figure 2). Each belt transect was 5 ft (1.5 m) wide by 50 to 100-ft (15.2 to 30.5 m) long with the corners permanently marked with rebar. Originally the belt transects were called “sage belts” or “browse belts” depending on location. The dominant shrubs in the communities were, and still are, big sagebrush (*Artemisia tridentata*), green rabbitbrush (*Chrysothamnus viscidiflorus*), gray rabbitbrush (*Chrysothamnus nauseosus*), and horsebrush (*Tetradymia canescens*).

The line transects were established inside and outside of each exclosure in a paired configuration where slope, aspect, and elevation were matched as closely as possible between the inside and outside lines (figure 2). Each line transect was 100 ft (30.5 m) long and the total numbers of paired line transects vary with location. Because this study is focused solely on the shrub (particularly big sagebrush) changes over 50 years, the change in vegetation on the line transects will not be addressed in this paper except to put the design of YNP’s experiment and the fire effects after the 1988 fire in context. Photos could not be located for sage belts that were affected by the 1988 fires, so the nearest line transects are used to describe the fire-effects at the affected exclosure.

Together the eight sagebrush or browse belts presented in this analysis encompass a range of elevations, moisture conditions, soil depths, vegetation types, and disturbance effects and the unique characteristics of each study area enhance the overall study design. Similar sample sites were grouped by Singer and Renkin (1995) based on elevation, snowpack, precipitation, and big sagebrush species. Their characteristics include:

Low-elevation site: The Gardiner sage belts are the most northern sage-belt sites and are located near the town of Gardiner, Montana (figure 3). This area is the lowest in elevation (5400 ft; 1650 m) and driest of all the 1958 sage-belt sites (Barmore Jr. 2003). Precipitation averages 30 cm/yr (Singer and Renkin 1995). It is also within a spring and fall migration path for antelope (White 2009), and used by elk and mule

deer throughout the year (Houston 1982). Within the past five years, the area has been heavily invaded by non-native annual grass and forb species that currently affect total soil moisture and native-plant germination and growth in this part of the park (Hektner 2009). Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) is the dominant sagebrush subspecies at the Gardiner site (Singer and Renkin 1995).

Mid-elevation site: The Mammoth sage belts are located in an area of active geothermal activity at Mammoth Hot Springs. They are less than 0.25 mi (0.4 km) from the hot springs, at an elevation of 6400 ft (1950 m), and situated within open areas of coniferous forests. Non-native species occupy the area, but most are perennials or grasses located along horseback riding and hiking trails.

High-elevation sites: The Blacktail sage belts are at approximately 6700 ft in elevation in rolling terrain between wetlands (below) and coniferous forest (above). They receive an average of 55 cm/yr precipitation. They are adjacent to a popular hiking trail used by tourists for backcountry access and fishing, but tourists cannot access the sage belts inside the exclosures without permission. The Lamar sage belts are located along US Highway 212 near the Lamar River. They are in an area heavily used by bison during the summer months and by visitors who watch the bison and elk herds. The Lamar sage belts are at 6700 to 6800 ft (2050 to 2070 m) in elevation, and they exist on steeper hillsides than any of the sage belts. They receive an average of 55 cm/yr of precipitation. The dominant big sagebrush subspecies at these sites are mountain big sagebrush (*Artemisia tridentata vaseyana*) and basin big sagebrush (*Artemisia tridentata tridentata*) (Singer and Renkin 1995).

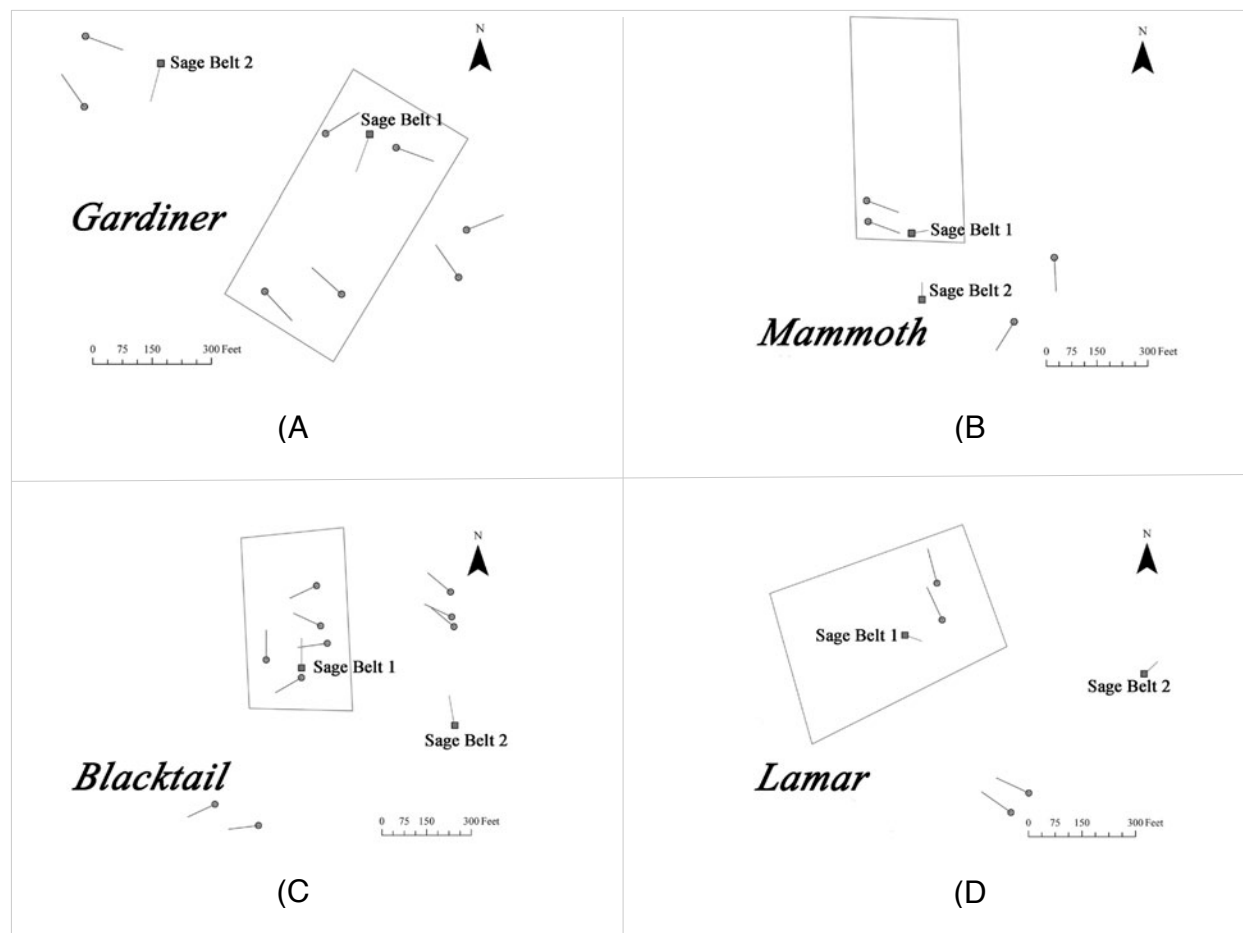


Figure 2. Locations of sagebrush belts (squares) and line transects (dots) within the (A) Gardiner, (B) Mammoth, (C) Blacktail, and (D) Lamar 1958 exclosures (outlined) that comprise part of Yellowstone National Park's natural experiment design. Sage-belt transects are labeled with their names. Bearing of each belt transect and line transect is indicated by directional lines.

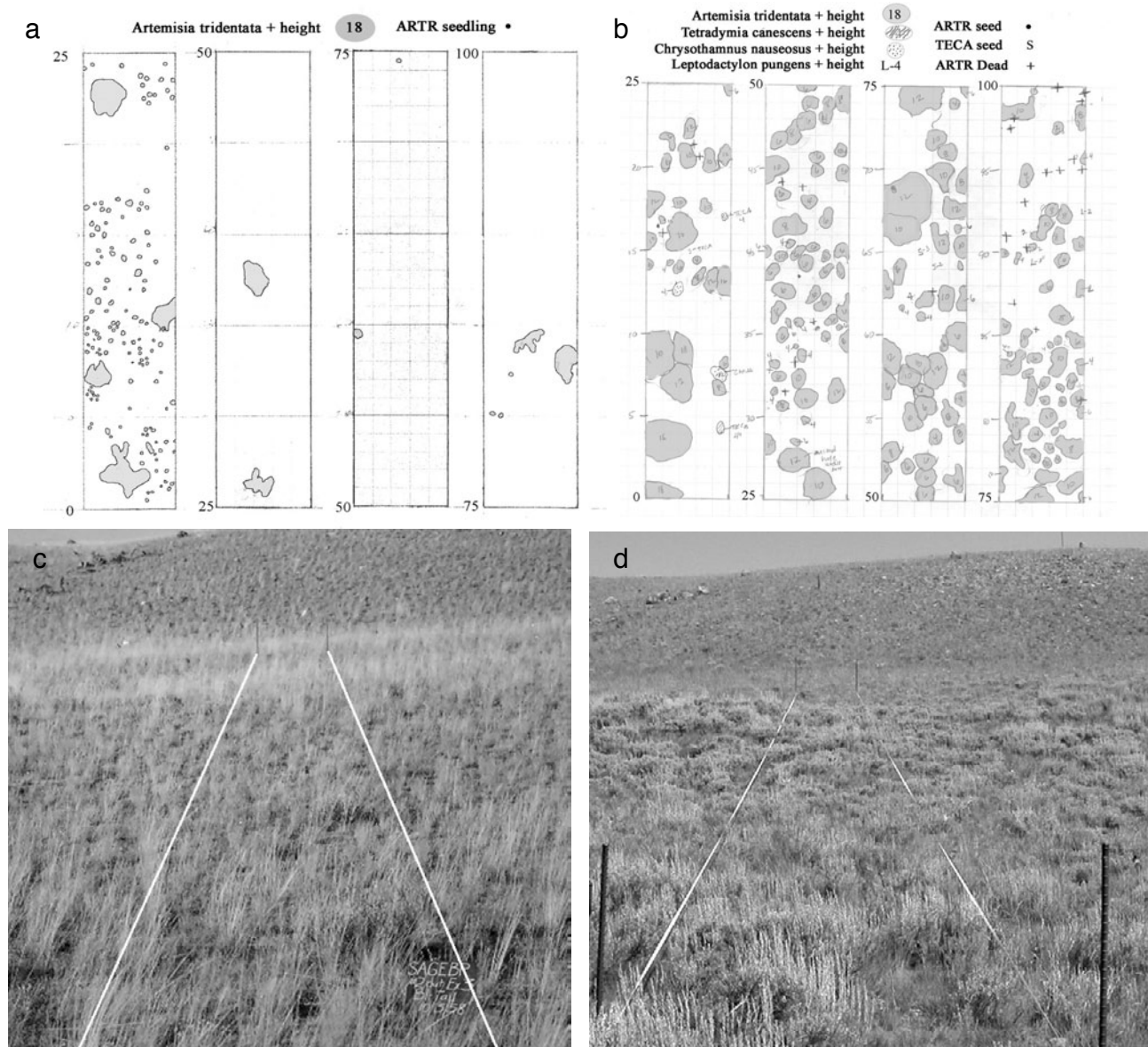


Figure 3. Data collection method from the Blacktail Sage Belt #2 (outside enclosure). (A) 1958 data form showing mapping of the aerial extent of sagebrush, species present, height of plants, seedlings, and dead shrubs (line in feet; tape location digitally enhanced); (b) 2008 data form showing mapping of the aerial extent of sagebrush and other shrubs, species present, height of plants, seedlings, and dead shrubs; (c) 1958 photo of belt transect corresponding to 1958 sample form; and (d) 2008 photo corresponding to 2008 sample form. Historic photo and data by Denton and Kittams (1958); 2008 photo by Art Sikkink.

METHODS

Sampling

The belt transects, which include the sagebrush or browse belts, were first sampled in 1958 by Gail Denton (Botany and Bacteriology Dept., Montana State College) and W.J. Kittams (YNP biologist) (Denton, unpublished data; Denton and Kittams, unpublished data; Kittams and Denton, unpublished data). Sampling consisted of mapping the location of each plant and the extent of the crown canopy by

species. The heights and dead vs. alive plants, by species, were recorded (figure 3a). The location and height of all seedlings and all dead shrubs were also identified. A photo point was established at the beginning of each sage belt during the original sampling and a photo was taken as part of the sampling procedure. Between 1958 and 2008, the belt transects have been sampled six times in much the same way, although height and/or seedling data were not measured in some years. Photos have been taken at similar locations on the belt transect each time the sage belts have been resampled.

In 2008, the eight 1958 sage belts were revisited for the 50th anniversary of YNP's experiment. The sage belt transects were sampled in the same way that they were sampled in 1958; namely by mapping the aerial extent of each plant to scale on graph paper, recording the species and height of each live shrub, mapping all seedlings by species at their germination location, and recording the location of all dead plants (figure 3). Photos were taken as per the sampling procedure and they were used in this study to augment descriptions of vegetation change at each sample location.

Evaluating Effects Of Burning Sagebrush In The Sage Belt Transects

Only the YNP North Fork Fire in 1988 burned any of the exclosure sites in this study. Its effects on the big-game exclosures were outlined in an unpublished report filed with YNP in September 1989 (Harter 1989). The report stated that the Blacktail exclosures were the only exclosures affected by the 1988 fires and that all three of the sage belts at Blacktail burned (Harter 1989). After the fire, minimal data was collected from the sage belts because there was little vegetation to map; burn severity estimates were made for the general area. Seedling heights and total seedlings were recorded, but individual seedling locations were not mapped according to the historic sampling protocols (Harter 1989). Because neither the sage nor transect belt photos from the 1989 fire have yet been located in the YNP archives, the best evidence of how the North Fork fire affected the sage belts are the changes that occurred on one transect line (Blacktail 58 C2T2), which is located within 10 ft (3 m) of the beginning of the inside belt transect (figure 2c). This paper uses data and photographs from the line transect to show fire effects and sagebrush recovery from the burn pictorially.

Data Analysis

This study was a qualitative and pictorial assessment of change within Yellowstone's experiment. Both historical and 2008 to-scale drawings were analyzed by (1) counting the number of grid squares covered by each shrub (by species) to determine a total canopy coverage of each species and (2) counting the number of seedlings, by species, on each belt transect for the two sample years. Change was assessed using tabular data, non-parametric statistical comparisons, and photographic records. Changes in canopy coverage and seedling counts between 1958 and 2008 were assessed graphically,

and Wilcoxon paired-samples tests were used to test for significantly different values in canopy cover and seedling counts between the two years. Locations inside and outside the exclosures were calculated separately (n=8). Significant differences were assessed if p-values were <0.05.

Climatic trends in maximum and minimum temperature (°F) and precipitation (inches) at the exclosures were assessed using data from the Mammoth Hot Springs weather station, which has been collected since 1955. Missing observations were not adjusted in any way.

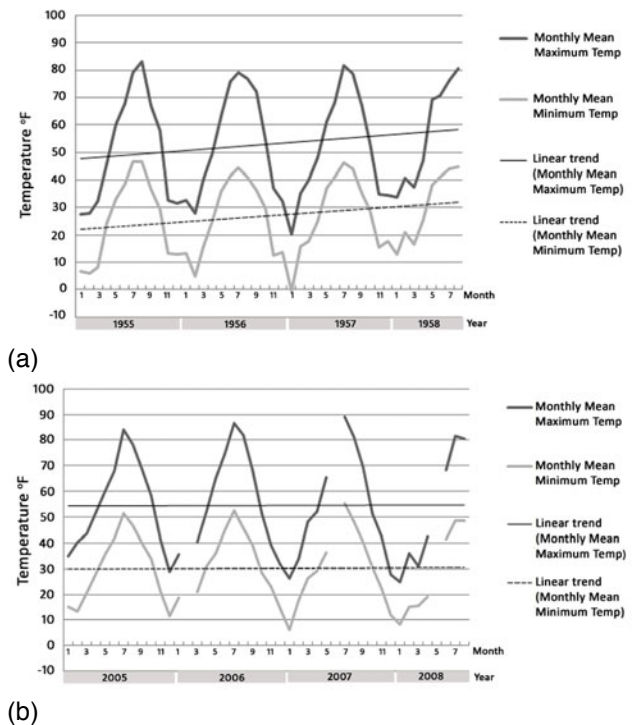


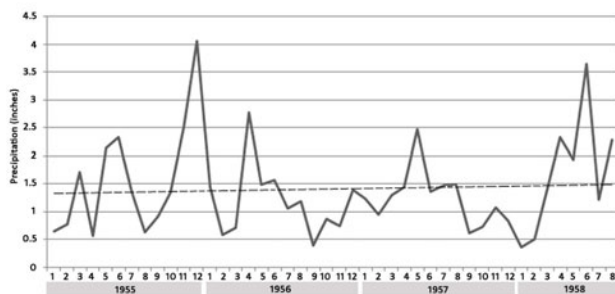
Figure 4. Monthly mean maximum and minimum temperatures in °F at Mammoth Hot Springs weather station in the four years prior to sampling the exclosure areas from (a) 01 Jan 1955 to 31 Aug 1958 and (b) 01 Jan 2005 to 31 Aug 2008. Linear trend lines are shown as solid and dashed lines.

RESULTS

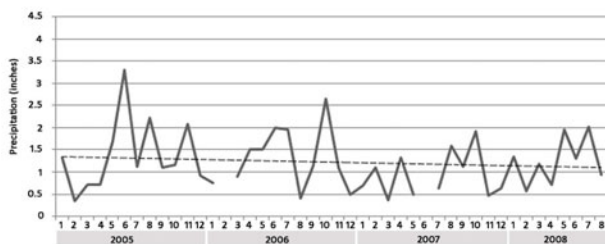
Climatic Trends (Mid-Elevation)

In the four years preceding 1958 and 2008, the park was experiencing different trends in temperature (figure 4a and 4b) and moisture conditions (figure 5a and 5b). The average annual temperature for the four-year period preceding sampling in 1958 was 39.8°F (4.3°C) and the average yearly precipitation was 16.44 in (41.8 cm) (National Climate Data Center

2010). The trend in mean monthly maximum and minimum temperature over that period was of gradually increasing temperatures and precipitation (figure 4a). The average annual temperature for the same period prior to sampling in 2008 was 41.33°F (5.2°C) and the average yearly precipitation was 14.25 in (36.2 cm). The trend in minimum and maximum monthly mean temperatures was flat while monthly precipitation declined each year (figure 5 b). The minimum and maximum temperatures in 2008 were at approximately 30 and 55°F (figure 4b), which were slightly higher than the mean minimum and maximum temperature in 1958 (figure 4a). In contrast to the spring and summer of 1958, which had an average of 2 inches (5 cm) rain each month before the initial sampling at the exclosures took place (figure 5a), the monthly precipitation in the spring and summer months before sampling in 2008 averaged approximately 1 in (2.54 cm). In general, the same trends that existed in 1958 continued at the mid-elevation weather station through 1974.



(a)



(b)

Figure 5. Monthly precipitation in inches at Mammoth Hot Springs weather station in the four years prior to sampling the exclosure areas from (a) 01 Jan 1955 to 31 Aug 1958 and (b) 01 Jan 2005 to 31 Aug 2008. Month number and year are shown on x-axis. Linear trend is shown as dashed line.

Compositional Changes Within The Belt Transects

Shifts in vegetation from dominantly grass to sagebrush have occurred on both grazed and ungrazed and low- and high-elevation sagebrush belts during the past 50 years (figure 6). Six of the

eight belt transects showed increases in canopy cover of big sagebrush that ranged from 5 to 45 percent. The largest increase in canopy cover occurred on the outside sagebrush belt at Mammoth (figure 6). The smallest increases occurred in the Lamar area. The average increase on the six belt transects was 24 percent. The remaining two belts had decreases of <5 percent each. Statistically, the differences between the eight location-year pairs were significant (p -value = 0.04).

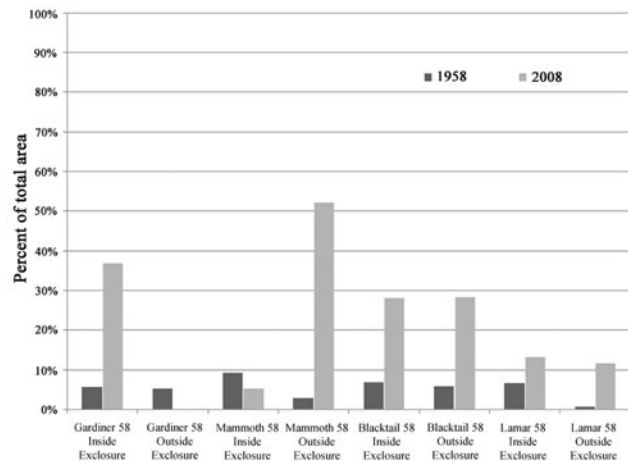


Figure 6. Differences in *Artemisia* cover between 1958 and 2008 for the eight sage belts established in 1957 and sampled in 1958.

The low-elevation, grazed site at Gardiner, the mid-elevation, ungrazed site at Mammoth (inside), and the high-elevation, ungrazed site at Lamar exhibited the most dramatic changes in composition over the 50 years. At Gardiner's outside sage belt, all shrubs that were part of the community for 30 years or more had died by 2008 (figure 7b). The native grass-*Artemisia* community that existed in 1958 (figure 7a) was replaced almost completely by short, non-native annuals, including annual wheatgrass (*Agropyron triticeum*), desert alysium (*Alyssum desertorum*), Japanese brome (*Bromus japonicas*), and cheatgrass (*Bromus tectorum*) (figure 7b). The same changes did not occur inside the Gardiner exclosure, where big sagebrush cover increased by 31 percent between 1958 and 2008. Inside the Mammoth exclosure, vegetation composition and structure changed from an *Artemisia tridentata*-dominated, open canopy community (figure 8a) to a community dominated by *Juniperus* and *Pseudotsuga menziesii* with an understory of *Symphoricarpos* (figure 8b). Conifers covered 30 percent of the belt in the Mammoth

exclosure after 50 years. On its paired belt outside of the exclosure, which contained less than 3 percent percent *Artemisia tridentata* in 1958 (figure 9a), sagebrush increased to 52 percent total cover by 2008 (figure 9b) and conifers occupied 0.01 percent of the belt.



(a)



(b)

Figure 7. Sagebrush reduction in Gardiner Sage Belt #2 (outside the exclosure). (A) In 1958, the belt contained mostly native grasses and sagebrush (YNP archive photo); (B) by 2008, the native grasses were gone, the sagebrush was dead, and the native community had been replaced by several non-native, annual forbs and grasses (Art Sikkink photo). Belt 100 ft (33.3 m) ends are marked with arrows in both photos.

The Lamar sage belts follow similar trends as those at Mammoth. Early photos of the inside belt transect show mostly grass and minor big sagebrush (figure 10a). All of the species that were identified on the inside belt transect in 1958 (Denton and Kittams, unpublished data) were still present in 2008, but aspen (*Populus tremenoides*), chokecherry (*Prunus*

virginiana), and service berry (*Amelanchier alnifolia*) had expanded to cover approximately 25 percent of the inside belt. Rose (*Rosa* sp.), snowberry (*Symphoricarpos* sp.), horsebrush (*Tetradymia canescens*), and green rabbitbrush (*Chrysothamnus viscidiflorus*) were also common shrubs inside the exclosure (figure 10b). In contrast, the belt transect that was open to grazing at Lamar had the same types of shrub species that were mapped in 1958, but all were too small to show on the photograph (figure 11a). All (except big sagebrush) were less than 4 in (10 cm) tall and presumably kept short by grazing. By 2008, canopy cover of big sagebrush had expanded to cover over 10 percent of the outside belt area (figure 11b).



(a)



(b)

Figure 8. Tree invasion in Mammoth Sage Belt #1 (inside exclosure) after 50 years of protection from grazing. (A) Originally, the belt was a sparse sagebrush and grass community (YNP archive photo); (B) by 2008 it was dominated by conifers and snowberry and consisted of less than 10% sagebrush (Art Sikkink photo).

In the areas where tree invasion was not a factor, big sagebrush coverage expanded approximately the same amount both inside and outside of the exclosures (figure 6), indicating that herbivory was not negatively affecting big sagebrush canopy cover. On the inside sage belts at Mammoth and Lamar, tree encroachment effectively decreased the area available for shrub growth so big sagebrush coverage shows a decline in total coverage between 1958 and 2008 (figure 6). It had not yet been eliminated from either site by 2008.



(a)



(b)

Figure 9. Sagebrush expansion in Mammoth Sage Belt #2 (outside the exclosure). (A) In 1958, the belt was dominated by grass with small sage plants and many seedlings (YNP archive photo); (B) by 2008, the belt was filled with sagebrush and trees were encroaching on its northern edge (Art Sikkink photo).

Whether total shrub diversity changed between 1958 and 2008 was hard to evaluate because, for most of the sites, big sagebrush was the only shrub mapped in 1958. Other shrubs were mapped on the same belts nine years later in 1967, but in 1958 the focus

was on big sagebrush and how it was affected by grazing. The only exception was the data collected on the belts at Lamar. At Lamar, several species of shrubs and trees were mapped in 1958 and 2008 so comparisons of diversity between the two years were easily made. The data showed that diversity increased at this high elevation site on belts both inside and outside of the exclosure. In 1958, there were six species of shrubs mapped on the inside sage belt and seven mapped on the outside belt. By 2008, there were eight species of shrubs plus aspen seedlings on the inside belt; and eight species on the outside belt (Sikkink, unpublished data 2008b). The two additional species included Oregon grape and green rabbitbrush.



(a)



(b)

Figure 10. Tree invasion in Lamar Sage Belt #1 (inside exclosure) after 50 years of protection from grazing. (A) Originally, the belt consisted of small plants of sagebrush, serviceberry, rose, snowberry, horsebrush, and green rabbitbrush, which were mapped on the sample form but are not obvious in the photo (YNP archive photo); (B) by 2008 all of the original species have grown and expanded, aspen and chokecherry have invaded the plot, and sagebrush is restricted to the last 20 ft (6 m) of the belt (Art Sikkink photo).



(a)



(b)

Figure 11. Sagebrush expansion in Lamar Sage Belt #2 (outside of the enclosure). (A) In 1958, the belt contained small sagebrush, serviceberry, green rabbitbrush, rose, horsebrush, and chokecherry (YNP archive photo); (B) by 2008, the original species were still present, Oregon grape had established, and the sagebrush had expanded to over 10% of the area (Art Sikkink photo).

Trends In Seedling Survival on Sage Belt Transects

Seedling counts differ by sample year and elevation (figure 12). In 1958, seedlings were much more common in the low to mid elevations (Gardiner and Mammoth) than they were in 2008. The average loss in number of seedlings at these locations was 18. At the higher elevations (Blacktail and Lamar), the opposite trend occurred in that there were more seedlings in 2008 than in 1958 both inside and outside of the enclosures. The average increase in number of seedlings for these two areas was 8. The difference in seedling counts between years was not significant (p -value = 0.55).

Fire Effects on the Shrub Communities

The shrub and grass communities of the enclosure areas have been remarkably unaffected by fires during the past 50 years. None of the transect lines or sage belts had burned prior to the NorthFork Fire in 1988. In 1988, records show that only the Blacktail enclosures were affected by fire and the entire set of sage belt transects had burned. The most recent sampling prior to the fires was in 1981 (Rominger and Cassirer, unpublished data). At that time, the southwest corner of the enclosure and the hillside outside the southwest was filled with mature sage plants (figure 13a). By 1994, the same area inside the enclosure was occupied by tall grass and young sage plants with extensive new growth on the branches; outside the enclosure, sage was scarce on the hillside (figure 13b). By 2008, mature sage was again abundant inside the enclosure (figure 13c), but sage still had not recolonized much of the hillside. In comparison to transect C2T2, the inside sage belt shows the same structure and composition (figure 13d). From 1981 to 2008, sagebrush increased from 14 to 28 percent in coverage inside of the enclosure and from 10 percent to 28 percent cover on the outside sage belt; and by 2008, there was very little evidence that the Blacktail sage-belt communities had burned at all except for a few fire-scarred stems and/or elevated root crowns on the shrubs, which indicated that the duff around the base of the plant had burned (Sikkink, unpublished data 2008b).

When compared to the other high-elevation sites at Lamar, sagebrush cover increased at both sites in both the grazed and protected areas (figure 6). By 2008, the Blacktail site showed the greatest increase in canopy cover (average 21 percent vs. Lamar average 8 percent) even though both of its big sagebrush belt transects had burned.

DISCUSSION

During the 50 years of YNP's experiment, the sage belts inside and outside of the enclosures have provided data on the relationships between herbivory and big sagebrush growth in the park. Today, new factors, such as climate change, tree invasion, and invasive non-native annual species, are also becoming important factors for change in the vegetation communities of YNP's northern winter range. When YNP's experiment began, the belt transects consisted mainly of native grasses. Big

sagebrush comprised less than 10 percent of the total area on any transect, regardless of whether it was grazed or protected from grazing by the exclosures (figure 6). Today, big sagebrush occupies a substantial area in most of the belt transects in both grazed and protected areas. Fluctuations in big sagebrush canopy cover, numbers of big sagebrush plants, seed leaders, and seedling survival on these belt transects have all provided different perspectives on vegetation change in the northern winter range throughout the duration of the experiment. Each new study fuels ongoing controversies over whether ungulate herbivory is the source of change in the big sagebrush communities and whether the ungulate population exceeds the carrying capacity of the northern range.

In this study, the effect of grazing on the vegetation of northern winter range is less clear-cut than some previous studies. Where Wambolt and Sherwood (1999) concluded unequivocally that herbivory was responsible for declines in canopy cover at all exclosure areas, this study found that there was an increase in sagebrush canopy cover at all belt transects except for Gardiner's outside belt (a low-elevation site) and Mammoth's inside belt (a mid-elevation site). Only Gardiner had an obvious decrease in big sagebrush that could be attributed, at least in part, to herbivory because big sagebrush was flourishing inside the exclosure and not outside. The results of this study agree more with Singer and Renkin (1995) who also found that big sagebrush cover increased in low-elevation areas where big sagebrush was protected from grazing but canopy cover increased in both grazed and ungrazed belts at high elevations. At the mid-elevation site, canopy cover of big sagebrush decreased between 1958 and 2008 because a majority of the shrub belt became covered by conifer trees. This result conflicts with Baker (2006) who stated that "the invasion [of conifer species], like juniper and Douglas fir, into sagebrush areas are not due to fire exclusion but other factors (i.e., grazing)." The area of tree invasion at the mid-elevation site is within the exclosure and well protected by grazing.

Differences in canopy cover between grazed and protected areas that were found in this study and those that were reported by Wambolt and Sherwood

(1999) can be explained in a number of ways. First, data on canopy cover were collected using different sampling methods. Data for this study were collected within the original, permanently-marked sage belt transect using historic mapping techniques. Wambolt and Sherwood (1999) sampled lines not associated with the original belt transects and used a line intercept method to determine canopy cover. Whereas this study focused solely on big sagebrush, Wambolt and Sherwood (1999) included both big sagebrush and other shrub species in some analyses. They also sampled both 1957 and 1962 exclosure areas, except for the burned areas at Blacktail, and included data from all of the areas in their statistical analyses. Singer and Renkin (1995) used methods comparable to the methods used in this study for their canopy cover results, but used circular plots inside and outside of six exclosures for utilization rates, biomass production, recruitment, and consumption. Differences in results and interpretations for all of the studies can also be attributed to the time frames that were sampled. Wambolt and Sherwood (1999) focused on herbivory and differences in vegetation cover within a single time frame. Singer and Renkin (1995) and this study compared differences between two points in time. This study concentrated only on the differences between the original data and new data collected in 2008, whereas Singer and Renkin (1995) included data from the 1960s and 1980s. If data from other sample years were included in the analysis for this study, interpretations would likely be different because some features, such as number of seedlings, have varied more over time.

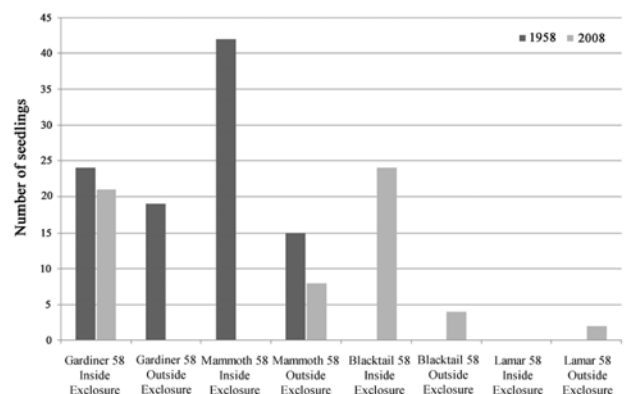


Figure 12. *Artemisia tridentata* seedlings present in the sage belts in 1958 and 2008. Differences in seedling counts between years are not statistically significant using a paired-sample Wilcoxon test (p -value=0.55).

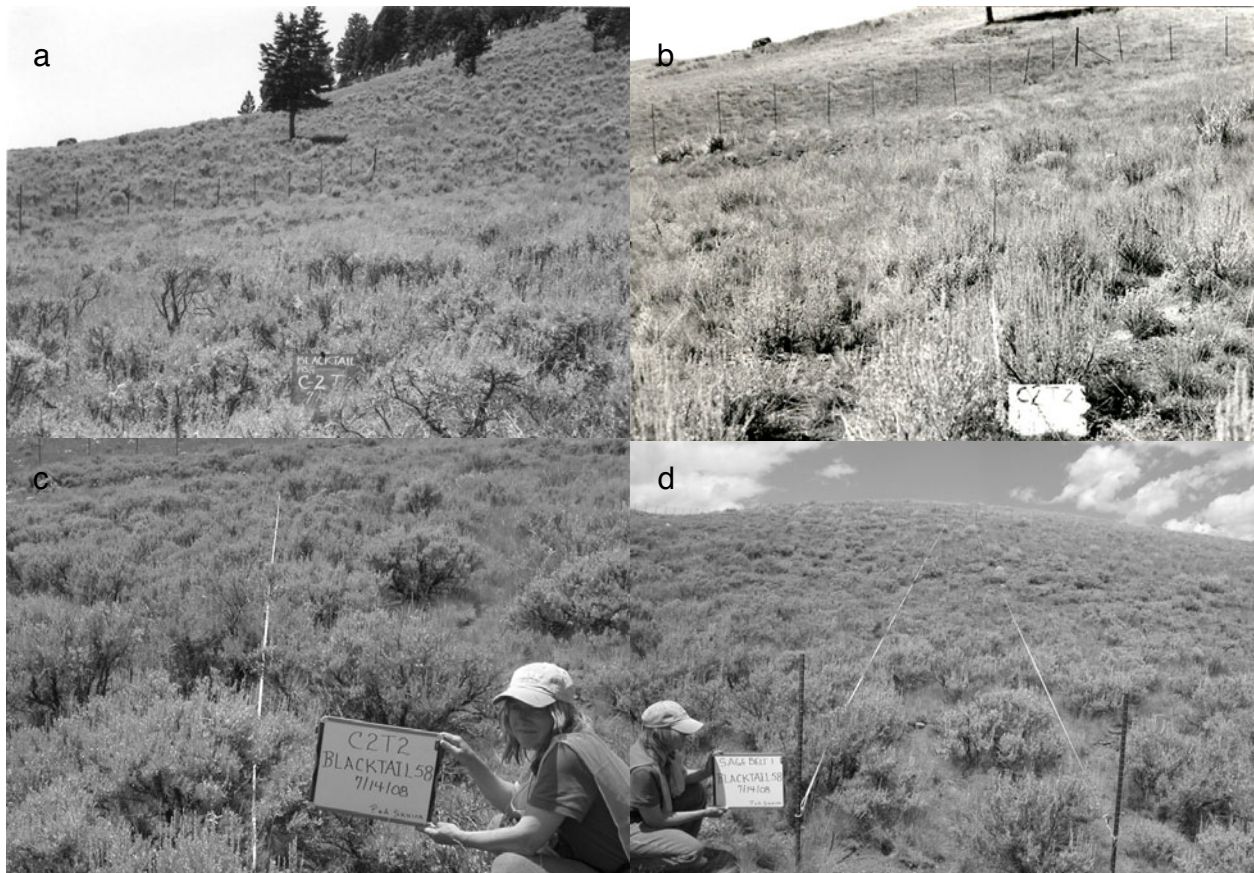


Figure 13. Effects of the 1988 North Fork Fire on *Artemisia* inside and outside of the Blacktail 58 enclosure. (A) Transect line C2T2 in 1981, prior to the North Fork Fire; (B) young sage regrowth on C2T2 six years after the burn in 1994; (C) mature sage on C2T2 in 2008; (D) sage growth on the sage belt adjacent to transect C2T2 in 2008. 1981 and 1994 photos from the YNP archive collection; 2008 photos by Art Sikkink.

In 2008, herbivory was still a dominant factor driving vegetation change at the low-elevation site in Gardiner, which agrees with several other studies (Houston 1982; Kittams, unpublished paper; Singer and Renkin 1995; Wambolt and Sherwood 1999). Inside the Gardiner enclosure, big sagebrush was flourishing in 2008 (figure 6), native shrub seedlings were relatively abundant (figure 12), and native grasses and forbs were present in amounts similar to those in 1958. Outside of the Gardiner enclosure, however, all shrubs had died, seedlings were non-existent, and non-native annuals had replaced most native grasses and forbs. The dramatic differences in shrub canopy cover and seedling establishment between the grazed and ungrazed areas leave little doubt that herbivory is very important in the area but it is not the only factor. Herbivory may be interacting with other factors to accelerate community change. Winter moisture for germination and warm, dry conditions during summer for growth create a favorable environment for growth of the annual non-native species, such as annual wheatgrass, brome,

and alyssum. These species have blanketed the landscape outside of the Gardiner enclosures in the past five to six years and affected soil moisture for growth and germination of the native species (Hektner 2009). How the declines in native species can be mitigated in the future is the subject of several new studies on restoration by the park that are occurring in the Gardiner area (Hektner 2009).

From the beginning of YNP's experiment to the mapping of the sagebrush belts in 2008, precipitation, temperatures, and grazing factors have changed dramatically. In 1958, the enclosure areas were sampled during a period of higher precipitation and cooler maximum and minimum mean temperatures than in 2008. Grass dominated all of the belts, and shrubs were kept small by grazing at the high elevations (indicated in the initial maps at Blacktail and Lamar). Ungulate populations were much smaller in 1958 than in 2008 because they were repressed by big-game hunting and culling within the park during the 1950s and 1960s (Singer and Renkin 1995;

Yellowstone National Park 1997). After four years of declining precipitation and higher temperatures preceding 2008, the high elevation sites showed the same percentages of sagebrush cover inside and outside of the exclosures, even though ungulate populations have increased significantly during the same time period. If herbivory alone were controlling the canopy cover of big sagebrush, cover in the outside belts should be much less than the inside belts, which is not the case for any of the mid- to high-elevation sites. Therefore, other factors besides herbivory must be contributing to the increase in big sagebrush cover. Climate and/or lack of disturbance are possible interrelated factors to explain these increases.

At mid to high elevations, herbivory and climatic effects are also important to controlling the growth and proliferation of trees. Conifers, service berry, and chokecherry, all regenerated and expanded in canopy cover when protected from herbivory by the exclosures. Similarly, data from willow and aspen belts inside and outside of the exclosures show that willows and aspens were able to grow to maturity inside of the exclosures, but they only existed as seedlings outside of the protected areas (Sikkink, unpublished data 2008a, c). Therefore, herbivory has been important to tree growth outside the exclosures at mid and high elevations as suggested by Wambolt and Sherwood (1999) and Kay (1995). However, mortality of willow and aspen trees has also increased inside the exclosures with the drier and warmer conditions of recent years (Bilyeu et al. 2008; Rogers 2008; Sikkink, unpublished data 2008a, c), suggesting that interactions between climate factors and herbivory affect growth and expansion at these elevations just like at Gardiner.

The shrub and grass communities of the exclosure areas have been remarkably unaffected by disturbance agents like fire during the past 50 years, but the belt transects at the Blacktail exclosures show how these high-elevation sites recovered from the North Fork fire in 1988. Six years after the sage belts burned, new plants and seed leaders were evident (figure 14b). By 20 years post fire, big sagebrush had surpassed its pre-fire canopy coverage percentages on both the inside and outside belt transects. The results from the Blacktail belts suggest that climate has controlled the recovery process of big sagebrush in the Blacktail area more than herbivory because the canopy coverage percentages are similar inside and

outside of the exclosure. The speed of recovery at Blacktail is remarkable in light of other studies that have followed the recovery of big sagebrush areas after burning (Cooper et al. 2007; Wambolt et al. 1998; Wambolt et al. 2001). Wambolt (1998) found that areas of Wyoming big sagebrush in the Gardiner Basin, which burned in 1974, recovered very little in 19 years. Welch and Criddle (2003) found that mountain big sagebrush recovered to 70 percent of pre-burn cover within 35 years. Colket (2003) showed that Wyoming big sagebrush in southeastern Idaho took 53 to 92 years to fully recover. Baker (2006) estimated even longer recovery rates of 50 to 450 years depending on big sagebrush type. Other studies have shown that big sagebrush recovery from burning is accelerated by dispersal of seed from nearby plants (Longland and Bateman 2002; Wroblewski 1999) or with soil seed pool immediately following a fire (Sugihara et al. 2006). Unlike the burn at Gardiner basin, the North Fork fire at Blacktail occurred in mountain and basin big sagebrush at high elevation where environmental and soil conditions were vastly different and seed sources were available from nearby areas.

Although most of the sites currently have abundant shrub cover and many mature shrub plants, the future of the shrub communities in YNP rests in production of seed to produce new plants, seedling survival, and maintaining community diversity. In 1958, when temperatures were cooler and precipitation more abundant, seedlings were more common at low to mid elevations. In 2008, under different climatic conditions, seedlings were much more common at the mid- and high elevation sites than they were at low elevation (figure 10), although the differences between the two years were not statistically significant at any location. The effect of grazing on big sagebrush seedling numbers is also not clear cut. In 2008, the low-elevation site at Gardiner showed seedling survival only inside the exclosure. The mid- to high-elevation sites at Mammoth and Lamar had seedlings only on the outside belts; but Blacktail had seedlings on both the inside and outside belts. It remains to be seen whether seed and seedlings will become more abundant with changes in climatic conditions. Evaluating changes in shrub diversity over time cannot be done using only the 1958 data because only big sagebrush was mapped in 1958. One thing is certain, this study does not show a decline in sagebrush canopy cover and the number of seedlings on most of the belt transects in YNP's

winter range as suggested by Wambolt (2005). All but two sage belt transects showed significant increases in big sagebrush canopy cover since 1958.

The controversies surrounding management of the northern range and whether it is being overgrazed or degraded over time will not be answered solely by the YNP sage belts because shrubs are not the preferred food for many ungulate species in the park (Singer and Renkin 1995). They do, however, constitute a portion of the diet of all ungulate species on the winter range (Singer and Renkin 1995; Wambolt 1998). Big sagebrush is a preferred food for pronghorn and mule deer, but not for elk or bison (Barmore Jr. 2003; Houston 1982; Singer and Renkin 1995). Even though big sagebrush comprises a small portion of an individual elk's diet, the numbers of elk on the northern winter range can have significant impacts on big sagebrush cover (Yellowstone National Park 1997). Individual transects, which provide data on grass, forb, and shrub composition inside and outside of the exclosures, will be more useful to evaluate changes in the grass and forb diversity and frequency that are most important for ungulate forage. In fact, Houston (1982), Coughenour et al. (1991) and Reardon (1996) have all addressed rangeland change using these transects and reported that the effects of herbivory were not significant on the exclosure sites between 1958 and the 1990s. This study focused on the trends in big sagebrush because that was the focus when the experiment was initiated in 1958. To determine the effect of herbivory on other shrub species in the northern range, the study must be expanded to include data for the years between 1958 and 2008 when mapping of the belts included other shrub species.

After 50 years, the sage belts indicate that climate (moisture and temperature), lack of fire, and tree invasion are major factors influencing change in these sagebrush communities. The results also suggest several interesting questions on the effects of invasive species in the park: such as, are the non-native species at Gardiner significantly changing the growing conditions for the long-lived species or are they simply taking advantage of climatic, management (past and present), and disturbance factors that facilitate their growth? Alternately, are the invasive species now a competitive or physical force for change at low elevations because of their dominance at Gardiner? Finally, the results suggest that changes in seedling survival are occurring in the winter range

that could affect future regeneration of sage in some areas. Yellowstone's experiment has provided valuable insights into the drivers of vegetation change over the past 50 years. It will continue to be important to park researchers and managers as they attempt to sort out the effects of herbivory, climate change, invasive species, and changing fire regimes on Yellowstone's vegetation over the next 50 years.

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