RESEARCH ARTICLE

Aspen Stand Conditions on Elk Winter Ranges in the Northern Yellowstone Ecosystem, USA

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ABSTRACT: Aspen *(Populus tremuloides)* stands inside and outside Yellowstone National Park (YNP), Wyoming, USA, were compared to test whether the lack of overstory aspen recruitment observed in YNP extended to winter ranges of elk *(Cervus elaphus)* in adjacent national forests. Remote sensing and field-collected data were obtained from aspen stands in YNP (n = 93), the Gallatin National Forest (n = 63), and the Sunlight/Crandall elk wintering area (n = 54) of the Shoshone National Forest. Remote sensing results indicated aspen canopy coverage decline in all three sites from the 1950s to the 1990s, but the proportional rate of decline was greater in YNP than in the national forest sites. Field data indicated that the density of live aspen overstory stems were significantly lower in YNP compared to the two national forest sites. Live aspen stems < 10 cm diameter at breast height were observed in YNP only in stands located in scree habitats, but were commonly observed in the national forest sites. Among the three study areas, no significant differences were observed in density of aspen ramets, the percentage of browsed ramets, or the density of conifers within aspen stands. However, the two national forest sites had a higher percentage of aspen stands containing ramets > 100 cm tall and a lower incidence of bark scarring on overstory aspen stems compared to YNP. Within YNP, aspen stands on scree habitat had a lower percentage of browsed ramets and more stems in small size classes compared to aspen stands in other habitat types. Collectively, these results indicate that while aspen cover has declined across all sites, the national forest sites have had successful recruitment of replacement overstory aspen stems. In contrast, overstory aspen in YNP are recruiting only in areas protected from browsing, such as on scree habitat. We suggest that differences in ungulate densities and foraging behaviors may explain the differences in aspen regeneration observed among the three sites.

Index terms: browsing, elk, *Populus tremuloides*, ungulates, Yellowstone National Park

INTRODUCTION

Quaking aspen *(Populus tremuloides)* is an adaptable species that is the most widely distributed tree in North America. Within Yellowstone National Park (YNP), aspen occurs principally on the northern range, the lowest elevation area within the park and important winter range for Rocky Mountain elk *(Cervus elaphus)* and other ungulates. Aspen also occurs on lands adjacent to YNP's northern range in the Gallatin and Shoshone National Forests. Aspen occupies only about 1% of the land area of YNP, but is considered ecologically significant since it is one of the few deciduous species in the area, provides habitat for numerous bird species, supports a variety of plant associations, and is used as browse by several ungulate species (St. John 1995, Dieni and Anderson 1997).

Aspen reproduces both sexually and asexually (DeByle and Winokur 1985). Asexual, or vegetative reproduction, dominates in the western United States, where aspen ramets are produced from meristems developed in the root system of existing clones (Schier et al. 1985). Individual aspen stems may live up to 200 years, but the parent clones are thought to be thousands of years old (Barnes 1966). In YNP, > 95% of the current aspen overstory consists of trees > 80 years old (Ripple and Larsen 2000). As these older stems die, they are not being replaced, resulting in a loss of biomass and canopy coverage in aspen stands. During the 20th century, the loss of aspen canopy coverage on YNP's northern range has been estimated at between 50% (Houston 1982) and 95% (Kay and Wagner 1994). In some YNP aspen stands, the overstory has been eliminated and the clones currently persist in a shrub form with ramets < 1 m tall (Despain 1990).

Kay (1994) has proposed that in the pre-European era, heavy predation by Native American hunters kept the elk population low enough to allow for aspen recruitment in the Yellowstone area. Ripple and Larsen (2000) proposed that a trophic cascade relationship involving wolves, elk, and aspen may have been a major factor influencing aspen recruitment in pre-European times, with wolf predation affecting elk browsing patterns in spatially specific ways. Unfavorable climatic conditions during the 20th century have also been proposed as a cause of aspen decline in YNP (Houston 1982, Meagher and Houston 1998). Suppression of wildfire may also play a role in aspen decline in western North America (Houston 1973, Bartos and Campbell 1998). Romme et al. (1995) suggested that an interaction of fire, climatic variation, and elk abundance controlled the dynamics of aspen overstory recruitment on Yellowstone's northern range.

Ungulate browsing has been identified as a major factor in preventing aspen from recruiting new overstory stems in YNP and elsewhere in western North America (Grimm 1939, Krebill 1972, Kay 1990, Bartos 1994, Romme et al. 1995, Huff and Varley 1999, National Research Council 2002). In the northern Yellowstone area, elk browsing of aspen occurs primarily in winter and takes two principal forms. Elk will repeatedly browse the leaders and twigs of aspen ramets and prevent their escapement to sapling or tree form. Elk also eat the bark of mature trees, leaving the black, scarred bark characteristic of aspen on YNP's northern range today.

The National Research Council report (2002) recommended that landscape scale aspen studies be conducted in the northern range area, comparing conditions inside and outside YNP borders. We developed a comprehensive aspen age structure analysis for elk winter ranges in the northern Yellowstone area, comparing YNP with adjacent elk winter range in the Gallatin and Shoshone National Forests, concluding that the National Forest areas contained significantly greater percentages of younger aspen stems (Larsen 2001, Larsen and Ripple 2003). Kay (1990) compared aspen recruitment in the Eagle Creek drainage of the Gallatin National Forest with recruitment in YNP, concluding that Eagle Creek stands had lower ramet densities but a greater diversity of overstory aspen size classes. St. John (1995) studied aspen on the northern range in the Gallatin National Forest, but did not compare his results with YNP conditions. He did conclude that ungulate browsing (both elk and domestic livestock) were negatively affecting aspen overstory recruitment in the Gallatin National Forest and predicted that current management practices would lead to further deterioration of aspen clones and changes in their understory plant communities. Suzuki et al. (1999) studied aspen stands in Rocky Mountain National Park and the adjacent Roosevelt National Forest in Colorado and concluded that aspen were not declining on a landscape level, but were failing to regenerate in local elk wintering areas due to excessive browsing of ramets.

We designed a remote sensing and field-based study to compare aspen stand conditions on YNP's northern range with National Forest areas adjoining the park to the north and east. The remote sensing data was used to quantify the change in aspen canopy coverage from the 1950s-1990s. The field transect data were used to analyze the variation in current aspen stand structure in our study areas. By analyzing both data sets, our objective was to compare aspen stand conditions inside and outside of Yellowstone park boundaries. Variables used to assess and compare the condition of aspen stands included the density of aspen ramets, the percentage of browsed ramets, the density and diameter class distribution of the overstory, the change in canopy coverage over a 38 year span (37 years in the National Forest areas), the extent of bark damage to large stems, and the extent of conifer encroachment in aspen stands. Elevation, aspect, and aspen habitat type data were also collected to test for differences among sites.

METHODS

Study Site

The study area included the northern range of YNP and the Gallatin National Forest, along with the Sunlight and Crandall Creek basins in the Shoshone National Forest (Figure 1). The Gallatin and Sunlight/Crandall study areas were selected because they are elk wintering areas in close geographic proximity to YNP's portion of the northern range. Since the management, livestock grazing history, and hunting regulations significantly differ between YNP and the Gallatin National Forest, these two areas of the northern range were considered separately.

The northern range lies in the valleys of the Yellowstone, Lamar, and Gardiner Rivers. It occupies 99,401 ha within YNP and 53,262 ha within the southern portion of the Gallatin National Forest. The northern range is the wintering area for the largest elk herd in the YNP area (Lemke et al. 1998). Houston (1982) describes the vegetation and climate of the area. The northern range and Sunlight/Crandall basins both consist of big sagebrush *(Artemisia tridentata)* dominated steppe, with islands of Douglas fir *(Pseudotsuga menziesii*) and aspen, with more continuous conifer forests above 2000 m.

The elk winter range in the Sunlight and Crandall Creek basins of the Shoshone National Forest were also included for comparative purposes. The Shoshone study area consisted of 43,798 ha within the Sunlight and Crandall Creek areas, an area corresponding to the elk winter range established by the Wyoming Department of Game and Fish (Figure 1). The Sunlight and Crandall Creek basins have similar vegetation patterns to the northern range.

Remote Sensing Methods – measuring changes in aspen canopy coverage

In YNP and the Sunlight/Crandall basins, a post-fire October 1988 set of color infrared (CIR) aerial photographs (1:24,000) and a scanning stereoscope were used to identify aspen stands. A 1.0-cm x 1.5-cm (240-m x 360-m ground resolution) rectangular grid was placed on each aerial photograph and grid cells were identified as either containing or not containing aspen. The sample was then stratified to include only those grid cells (sites) containing aspen and a random selection of 100 sites in YNP and 55 sites in the Sunlight/Crandall basin area was made. Of the initially chosen sites, several were dropped from consideration due to misclassification of cottonwood or burnt conifer as aspen. We eventually used 93 sites in YNP and 54 in the Sunlight/Crandall areas and these sites comprised the sample for both the remote sensing and field portions of the study.

The 1988 CIR flight did not provide extensive coverage in the Gallatin's portion of the northern range. Therefore, a 1995 set of 1:24,000 scale natural color aerial photographs was used to inventory aspen in the Gallatin. The photographs were taken in late summer. An aspen inventory

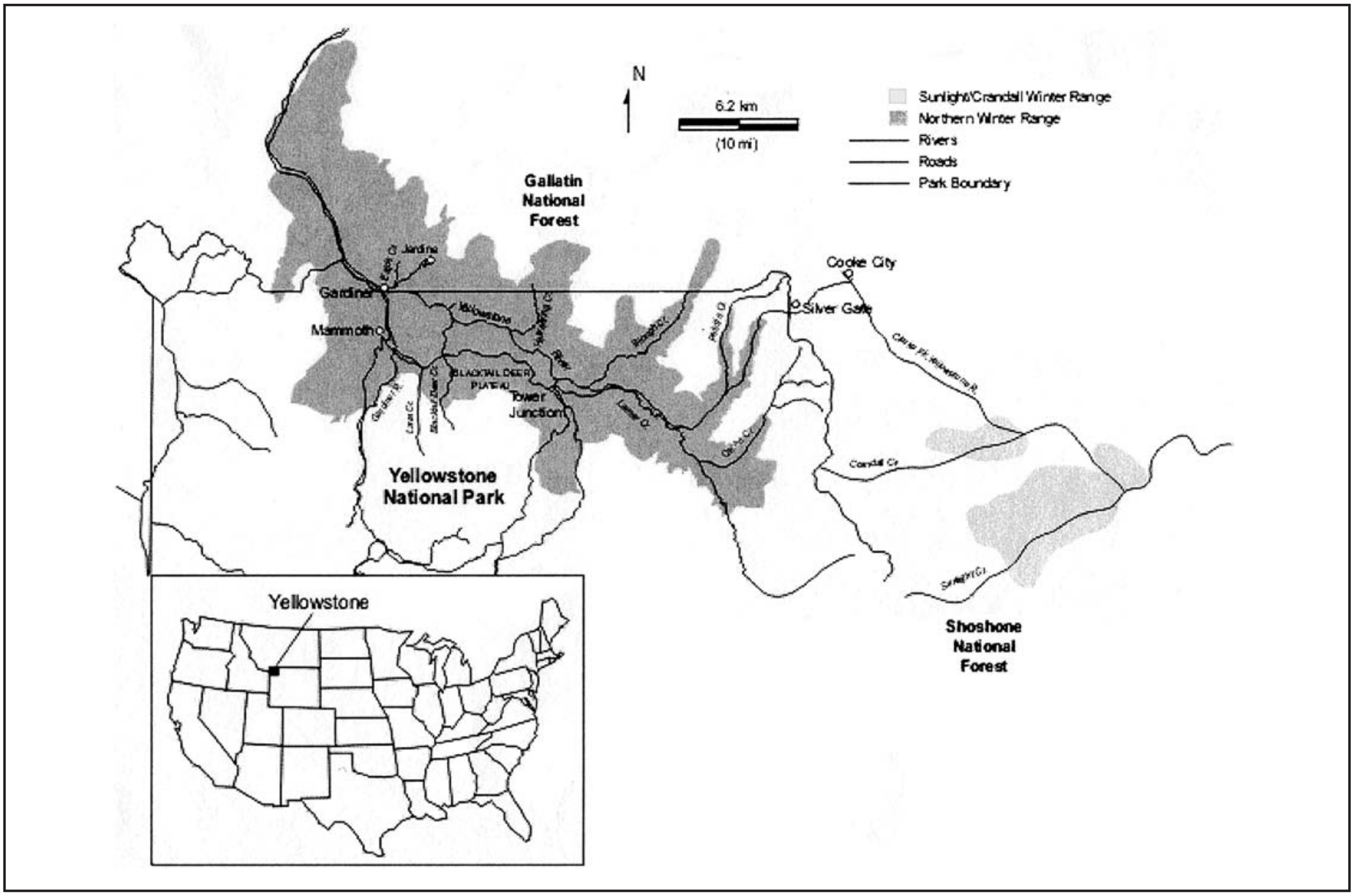

Figure 1. Study area map. The northern elk winter range encompasses portions of both Yellowstone National Park and the Gallatin National Forest in Wyoming and Montana. The Sunlight/Crandall elk winter range is contained within the Shoshone National Forest, Wyoming.

was conducted using the same methods as described for YNP, and a random selection of 75 sites containing aspen was chosen from the stratified sample. Twelve of the 75 sites were dropped due to misclassification or access problems (private land); therefore, 63 sites were used in the Gallatin National Forest.

Historic aerial photographs were paired with the recent aerial photographs of the same sites to analyze change in aspen and conifer canopy coverage over time. For YNP, a set of 1954 black and white aerial photographs was paired with a 1992 natural color set, providing a span of 38 years. In the Gallatin and Sunlight/Crandall, sets of 1958 black and white photographs were paired with 1995 natural color photographs, a span of 37 years. Therefore, six sets of aerial photographs were used to analyze changes in canopy coverage, a historic (1954/58) and recent (1992/95) set for YNP, the Gallatin, and the Sunlight/Crandall. All the aerial photographs analyzed were originally acquired between August and early October in the full leaf-on period.

The 210 sites were located on each set (historic and recent) of aerial photographs. For the 1992/95 aerial photographs, 1:5000 scale color enlargements of the sites were created from copy negatives. Using the 1954/58 negatives and a photographic enlarger, we created a set of stereo black and white 1:5000 scale enlargements matching the 1992/95 prints. Figure 2 illustrates a matched photo set and the canopy decline in an YNP aspen stand between 1954 and 1992. A scanning stereoscope and dot grid were used to classify ground cover vegetation as aspen, conifer, or steppe. The percentage of aspen and conifer canopy coverage per site was calculated for each of the two time periods. Aerial photo enlargements were not geometrically corrected since the variable percent canopy coverage is scale independent. Changes in mean canopy coverage of aspen and conifer were compared for the period 1954(58) to 1992(95). Change in canopy coverage was also calculated as a proportion of the 1954(58) cover, the base year.

Field methods – measuring variation in aspen stand structure

Each of the sites analyzed with aerial photographs was also sampled in the field. Additionally, transects were conducted in all the aspen stands located in scree habitats found in YNP during the course of fieldwork. For the field measurements, one 2-m x 30-m belt transect was located in an aspen stand at each of the 210 sites. An aspen stand was defined as a group of trees in which each tree was no more than 30 m from another tree or group of

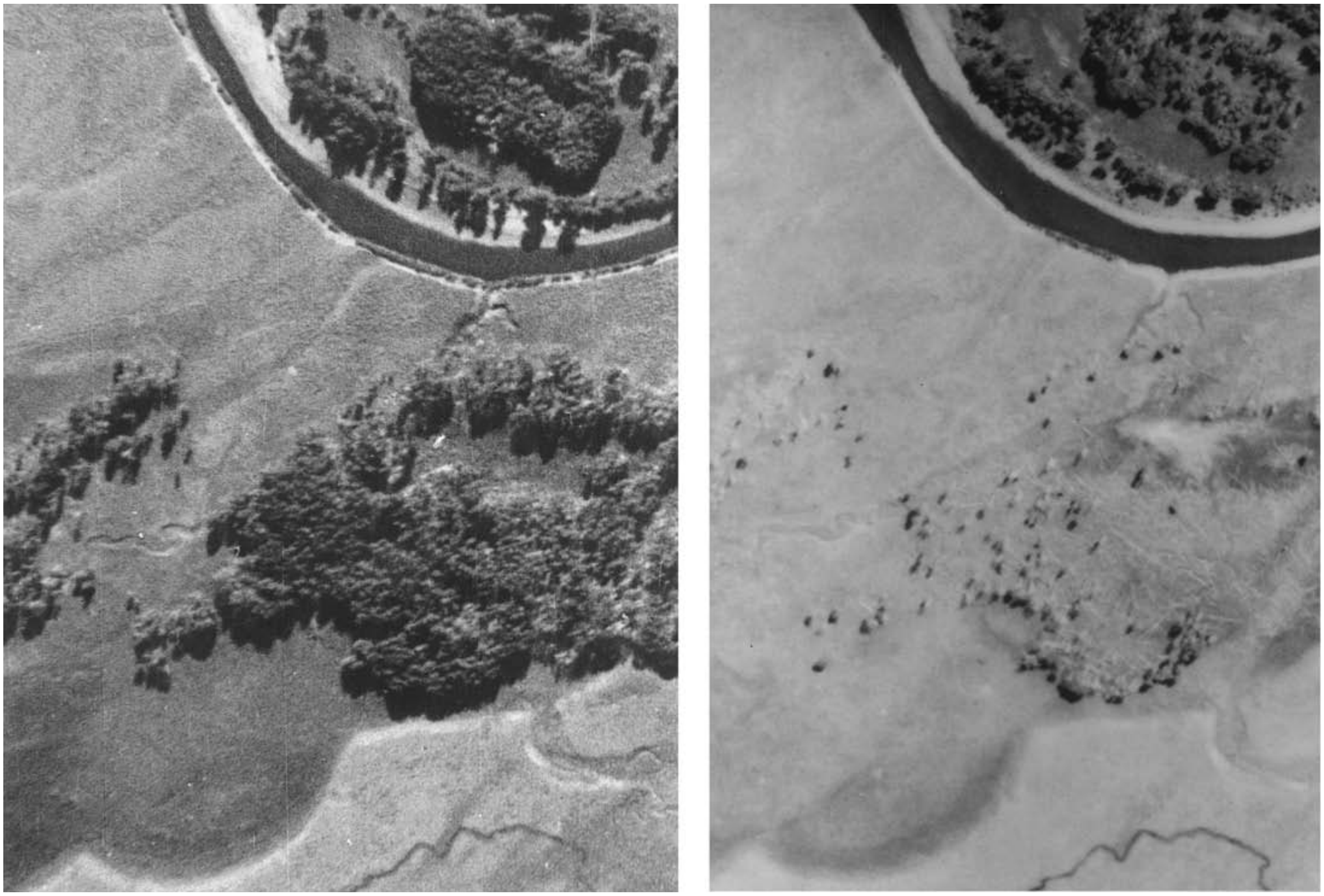

Figure 2. A 1954-1992 comparison of an aspen stand in a riparian area near the Lamar River in YNP. On the 1992 photograph, dead aspen boles are clearly visible on the ground as white lines. This area did not burn in the interval 1954-92..

trees within the stand. If the site contained multiple aspen stands, a single stand was randomly selected for the belt transect. A random cardinal start direction was chosen, and the transect originated from the large-stem aspen (> 5 cm dbh) furthest in that direction. From the "start tree," the transect ran towards the centroid of the aspen stand. All transects were 30 m, even if that required us to extend the transect beyond the opposite edge of an irregularly shaped stand.

The following measurements were made in the 2-m x 30-m belt transects:

1.) Ramets: A ramet was defined as an aspen < 200 cm in height. Total number, condition (browsed, unbrowsed, or dead), and height of "tall" ramets (> 100 cm) were recorded. Since aspen ramets often occurred in clumps of two or more, these clumps were counted as a single ramet because only one of the sprouts would be likely to survive to tree form. Browsed ramets were defined as a ramet whose leader or tallest auxiliary shoot had been removed.
2.) Overstory trees: Species, diameter at breast height (dbh), and condition (living, standing dead, or dead on the ground) of all overstory trees was recorded. Overstory trees were defined as stems > 200 cm in height. For aspen, the degree of bark damage was also measured. Bark damage was defined as the black corky bark scarring caused by ungulates and rodents chewing on aspen bark. The lower 2 m of the tree trunk was visually inspected, and bark scarring was categorized as high (> 66% of bark was scarred), medium (33%-66% was scarred), and low (< 33% of bark was scarred).
3.) Site character: A Global Positioning System (GPS) unit was used to determine the UTM coordinates and elevation of the site. Additionally, aspect, slope, topographic position, evidence of fire, and presence of any barriers to browsing were recorded. Browsing barriers included scree, boulders, roads, cliffs, or coarse woody debris, such as fallen conifers.

Three generalized habitat types were used to describe possible differences in aspen growth due to site quality (Despain 1990, St. John 1995). The habitat types were delineated by understory vegetation, site wetness, and topography as follows:

1.) Xeric upland steppe. The understory

of these aspen stands included grasses such as Idaho fescue *(Festuca idahoenis)*, bluebunch wheatgrass *(Agropyron spicatum)*, bearded wheatgrass *(Agropyron caninum)*, and the forb yarrow *(Achillea millefolium).* These stands often included or were surrounded by big sagebrush (*Artemisia tridentata).* The soils of this habitat type were derived from andesite and sedimentary tills and were generally dry.

2.) Mesic upland steppe/wet meadow/riparian. This aspen habitat type contains sites with moist to saturated soil conditions. A mixture of grasses and tall forbs characterized this habitat type. Timothy grass *(Phleum pratense)* was a dominant type in the understory of these stands, with Idaho fescue and bearded wheatgrass also present. Forbs included yarrow and goldenrod *(Solidago missouriensis).* Aspen stands in wet meadows and riparian areas also included various types of sedges *(Carex* spp.*)* mixed with timothy and forbs.

3.) Scree stands. An aspen community growing on scree slopes characterizes these sites. The understory is typified by sparse vegetation and thin soils in a rock substrate (St. John 1995).

The variables aspen ramet density/ha, percentage of browsed ramets (% ramets browsed), aspen overstory density/ha, aspen overstory density >20 cm dbh/ha, dead aspen, and conifer density were tested for skewness and kurtosis. The square root transformation was applied on the ramet density, percentage of browsed ramets, and overstory density data to achieve normality. ANOVA was used to analyze differences among the three study areas when the data were normally distributed. If the data were still non-normally distributed after the square root transformation, the Kruskal-Wallis (K-W) test was used on the original data. Three of the variables were collected as categorical data: dbh class, presence of tall ramets (>100 cm), and bark scarring. Overstory aspen were placed into four dbh categories (1-4 cm, 5-9 cm, 10-19 cm, and > 20 cm dbh). Stands containing tall ramets were placed into two categories (present or absent), and the bark scarring contained three categories. Pearson's χ^2 test was used to analyze differences among the three areas for the categorical data (Johnson and Bhattacharyya 1986).

A review of previous studies and preliminary field observations indicated that smaller diameter aspen stems would be uncommon or absent within YNP. We therefore made a special effort to measure all scree habitat type aspen stands we found within YNP to test whether natural barriers to browsing would allow the establishment of younger, smaller diameter overstory stems. We compared aspen stands in the scree habitat type with the unprotected xeric and mesic sites in YNP. Ramet density/ha, browsing intensity, and aspen overstory density/ha were compared using the Mann-Whitney test. The occurrence of tall ramets and the overstory dbh class structure were compared using Pearson's χ^2 test.

We used climate data from by the Western Regional Climate Center to compare winter precipitation and snow depths in our study areas. We used data for Mammoth Hot Springs, Tower, and the Lamar Ranger station to represent YNP winter conditions. The Jardine, Montana, climate records were used to represent the Gallatin, and the Crandall Creek station was used to represent the Sunlight/Crandall winter conditions.

Northern range winter elk densities were calculated based on aerial surveys conducted by YNP and Montana Fish, Wildlife, and Parks. Elk census information has not been systematically collected in the Sunlight/Crandall area, so we used trend data provided by the Wyoming Department of Game and Fish. Hunter harvest levels were also compared between the northern range and Sunlight/Crandall.

RESULTS

Changes in aspen canopy coverage 1950s-1990s

Of the 230 randomly chosen sites, 210 were analyzed (93 sites in YNP, 63 sites in the Gallatin, and 54 sites in the Sunlight/Crandall basins). The other 20 sites were eliminated because of misclassification in aerial photography (either cottonwood *(Populus angustifolia, Populus trichocarpa)*, willow *(Salix* spp.*)*, or burnt conifer erroneously identified as aspen on the aerial photographs), site location on private land, or access problems due to crossing private land. The mean area of aspen canopy coverage in all areas declined between 1954 (58)-1992 (95) (Table 1). YNP showed the greatest loss of aspen canopy when taken as a proportion of its 1954 canopy, falling from a mean 1954 value of 7.4% canopy coverage (per 240-m x 360-m cell) to 4.6% in 1992, a proportional decline of 38.6%. The Gallatin and Sunlight/Crandall areas had smaller proportional levels of decline (-22.7% in both cases) in aspen canopy.

Variation in aspen stand structure

Belt transects were completed for all 210 sites considered in the remote sensing analysis. An additional 12 belt transects were conducted in scree aspen habitat-type stands located within YNP.

The density of aspen ramets in non-scree habitat types varied from a mean value of 3593/ha (SD=3593) in YNP, 3847/ha (SD=3846) in the Gallatin, and 4577/ha (SD=5835) in the Sunlight/Crandall (Table 2) although there was not a significant difference among any of the study areas (K-W p = 0.94). Aspen ramet densities in all areas were highly variable, ranging from 0-29,000/ha. The percentage of browsed ramets was high in all areas, ranging from 87% (SD=18%) in YNP, 78% (SD=27%) in the Gallatin, and 82% (SD=26%) in the Sunlight/Crandall (Table 2). However, the K-W test indicated that there was not a significant difference among the medians in the three study areas (p = 0.18).

The Gallatin and Sunlight/Crandall areas had higher percentages of aspen stands with tall ramets (> 100 cm) than did YNP stands. On the northern range within YNP, tall ramets occurred in 10.8% of the stands, compared with 54.0% and 31.5% in the Gallatin and Sunlight/Crandall respectively. Using the χ^2 test, YNP's percentage of stands with tall ramets was signifi-

Table 1. Summary of mean changes in aspen and conifer canopy in the Gallatin, Sunlight/Crandall and YNP areas. Mean canopy coverage refers to the mean percentage of the 240 x 360 m cell covered by that cover type. Mean canopy area change is calculated by subtracting the mean canopy coverage in 1958 (1954 in YNP) from the mean canopy coverage in 1995 (1992 in YNP). Proportional change is a normalized figure where the mean canopy area change is divided by the mean canopy coverage in 1958 (1954 in YNP) to express the 1995(92) coverage as a proportion of 1958(54) coverage.

		Canopy coverage per 240m x 360m cell				Change in canopy area from 1958 to 1995 (from 1954 to 1992 for YNP)		
Study Area	n	Mean (%)	SD (%)	Min	Max (%)	Mean (%)	SD (%)	Percentage of 1958 (or 1954) coverage (%)
ASPEN								
Gallatin 1995	63	10.5	8.8	0	37.7	-3.1	7.2	-22.7
Gallatin 1958	63	13.6	11.7	0	45.7			
Sunlight/Crandall 1995	54	4.5	6.1	0	19.8	-1.3	2.9	-22.7
Sunlight/Crandall 1958	54	5.8	7.1	0	25.3			
YNP 1992	93	4.6	4.8	0	30.3	-2.9	4.7	-38.6
YNP 1958	93	7.4	7.0	0	33.3			
CONIFER								
Gallatin 1995	63	19.3	18.9	0	67.3	3.7	6.2	23.8
Gallatin 1958	63	15.6	17.6	0	62.4			
Sunlight/Crandall 1995	54	26.4	22.4	0	75.3	4	8.9	17.9
Sunlight/Crandall 1958	54	22.4	18.3	0	69.1			
YNP 1992	93	14.0	13.4	0	64.8	0.3	6.2	1.9
YNP 1958	93	13.8	14.2	0	69.8			

cantly less than stands in the other areas ($p < 0.01$). In terms of the total number of ramets counted, 2.5% of the ramets measured in YNP exceeded 100 cm, compared with 10.0% and 5.0% in the Gallatin and Sunlight/Crandall respectively.

Aspen stands in YNP had a significantly different dbh distribution of overstory aspen stems than the National Forest areas (χ^2 test, $p<0.01$). None of the non-scree YNP aspen stands (n=93) contained stems in the 1-4 cm and 5-9 cm dbh classes, and only 8% (7/93) of the stands contained stems in the 10-19 cm dbh class (Figure 3).

The lowest density of live aspen overstory stems amongst the three areas was found in YNP, which had a mean density of 645 stems/ha (SD=440), compared with 1190 (SD=753) in the Gallatin and 938 (SD=485) in the Sunlight/Crandall (Table 2). Overstory aspen density in YNP was significantly different from the other study areas (K-W test, $p < 0.01$). This difference was due to YNP's lack of aspen stems in the 1-4 cm, 5-9 cm, and 10-19 cm dbh size classes (Figure 3). However, YNP did have the highest density of stems/ha in the largest diameter class (> 20 cm dbh). The percentage of standing dead aspen to total aspen stems was similar in all areas, ranging from 27% in the Gallatin to 31% in the Sunlight/Crandall area, but the differences were not significant (Table 2, p=0.65).

The encroachment of conifer into aspen stands was measured as the percentage of conifers present to the sum of aspen and conifer stems (live stems only). Aspen stands in YNP and the Gallatin had lower percentages of conifers in their overstories than the Sunlight/Crandall area (Table 2). Aspen stands in YNP and the Gallatin averaged 12% (SD=22%) and 17% (SD=22%) of their overstories in conifer, while the Sunlight/Crandall study area averaged 39% (SD=29%). Significant differences in bark scarring were found among the three areas (Figure 4, χ^2 test, $p < 0.01$). YNP's results deviated furthest from the expected values, since none of the measured aspen overstory stems (n=364) had low or medium levels of bark scarring.

The 12 scree habitat stands in YNP differed from the YNP non-scree habitat types in several respects. The mean ramet density (806/ha, SD=1786) was lower in the scree stands than in the non-scree habitat types (3593/ha, SD = 3804). The scree stands contained a significantly lower percentage of browsed ramets than the other habitat types in YNP (Mann-Whitney test, $p < 0.01$). Tall ramets (> 100 cm) occurred in 58% of the scree stands sampled as opposed to 11% in non-scree habitat types (Mann-Whitney test, $p < 0.01$). The size class distribution was significantly different as well ($p < 0.01$), with the largest differences in the smaller dbh categories (Figure 5). Of the YNP scree stands, 75% contained small

Table 2. Summary of aspen stand field data.

Variable	n	Mean	SD	Min	Max	Median	Kruskal-Wallis p-value	Homogeneous groups
Aspen sucker density								
Gallatin	63	3846.6	3846	0	16500	2666.7		
Sunlight/Crandall	54	4577.2	5835.6	0	29000	2833.3		
YNP	93	3593.2	3593	0	19166	2166.7	0.94	G,S,Y*
Aspen suckers – percent browsed								
Gallatin	63	80%	23%	0%	100%	87%		
Sunlight/Crandall	54	82%	21%	0%	100%	82%		
YNP	93	87%	18%	0%	100%	90%	0.18	G,S,Y*
Aspen overstory density/ha								
Gallatin	63	1190.5	753.1	166.7	3500	1000		
Sunlight/Crandall	54	938.3	484.8	166.7	2166.7	833.3		
YNP	93	645.2	440.4	166.7	2666.7	500	<0.01	G,S*
Aspen overstory density >20cm dbh/ha								
Gallatin	63	515.9	369.9	0	1666.7	500		
Sunlight/Crandall	54	453.7	364	0	1666.7	416.7		G,Y*
YNP	93	627.2	425.9	166.7	2500	500	0.03	G,S*
Dead aspen as a percentage of total aspen stems								
Gallatin	63	27%	21%	0%	90%	25%		
Sunlight/Crandall	54	31%	23%	0%	85%	33%		
YNP	93	28%	24%	0%	75%	25%	0.65	G,S,Y*
Conifer stems as a percentage of total aspen and conifer stems								
Gallatin	63	17%	22%	0%	78%	0%		
Sunlight/Crandall	54	39%	29%	0%	94%	36%		
YNP	93	12%	22%	0%	80%	0%	<0.01	G,Y*

* G = Gallatin, S = Sunlight/Crandall, Y = Yellowstone National Park.

aspen stems in the 1-4 cm dbh category (0% in non-scree), 75% contained stems in the 5-9 cm category (0% in non-scree), and 58% contained stems in the 10-19 dbh category (8% in non-scree).

Mean plot elevations were 2111 m in YNP, 2197 m in the Gallatin, and 2098 m in the Sunlight/Crandall basins. Aspen stands were placed in three groups (< 2000 m, 2000-2199 m, and > 2200 m) and each study area was tested separately to see if ramet densities, overstory stem densities, incidence of tall ramets, and dbh class distribution were influenced by elevation. No significant differences were found in the incidence of tall ramets (K-W test, $p > 0.10$ for all cases) or the densities of ramets or overstory stems (K-W test, $p > 0.16$ for all cases) based on elevation. Similarly, aspect was not found to significantly affect the densities, heights, or dbh of either ramets or overstory stems.

YNP had 46 sites in the xeric habitat type and 47 sites in the mesic. The Gallatin contained 27 xeric and 36 mesic sites; while the Sunlight/Crandall basins had 24 xeric and 23 mesic habitat type stands. Mean overstory aspen stem and ramet densities were higher in mesic habitat type stands but only in YNP were the differences even marginally significant ($p = 0.09$ for overstory density, $p=0.02$ for ramet density in YNP).

Table 3 compares precipitation totals, snowfall, and snow depth for weather stations in each of our study areas during the winter months. Mammoth Hot Springs was the lowest elevation area we considered and had the lowest snowfall

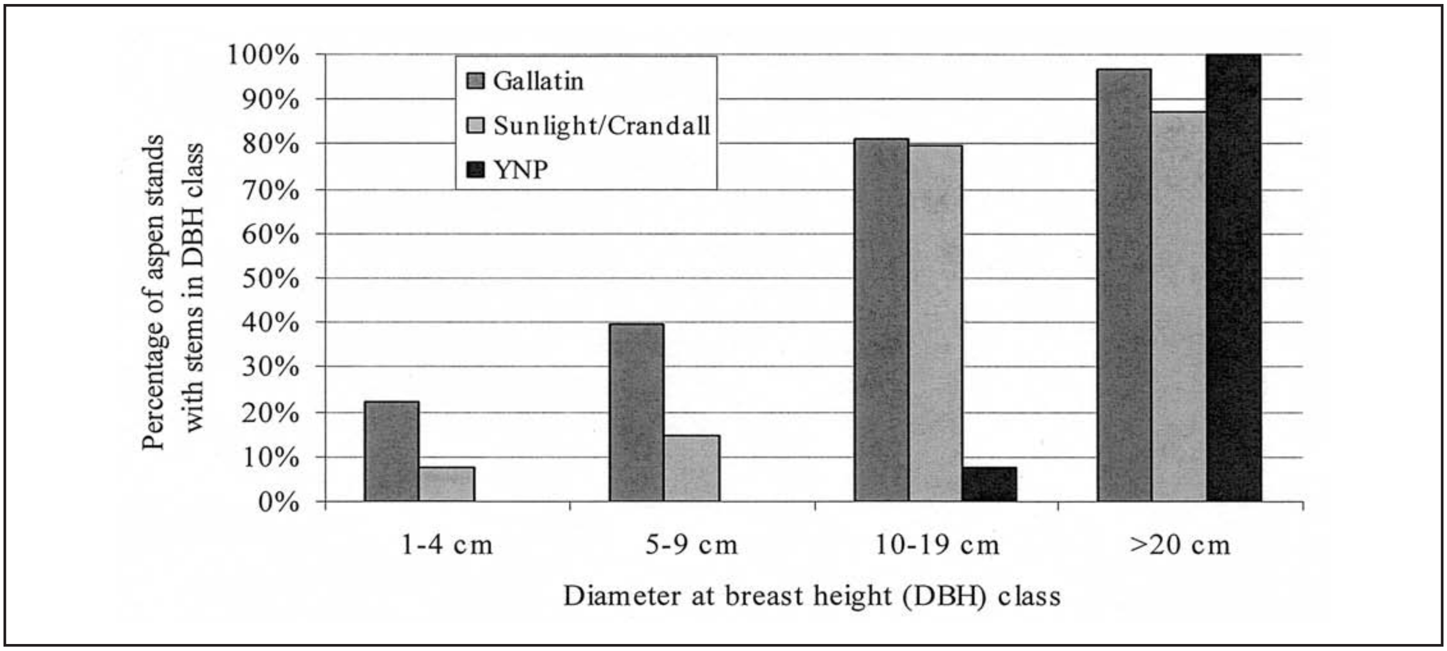

Figure 3. The percentage of aspen stands containing stems in four dbh classes. None of the YNP transects contained aspen in the 1-4 or 5-9 cm dbh classes.

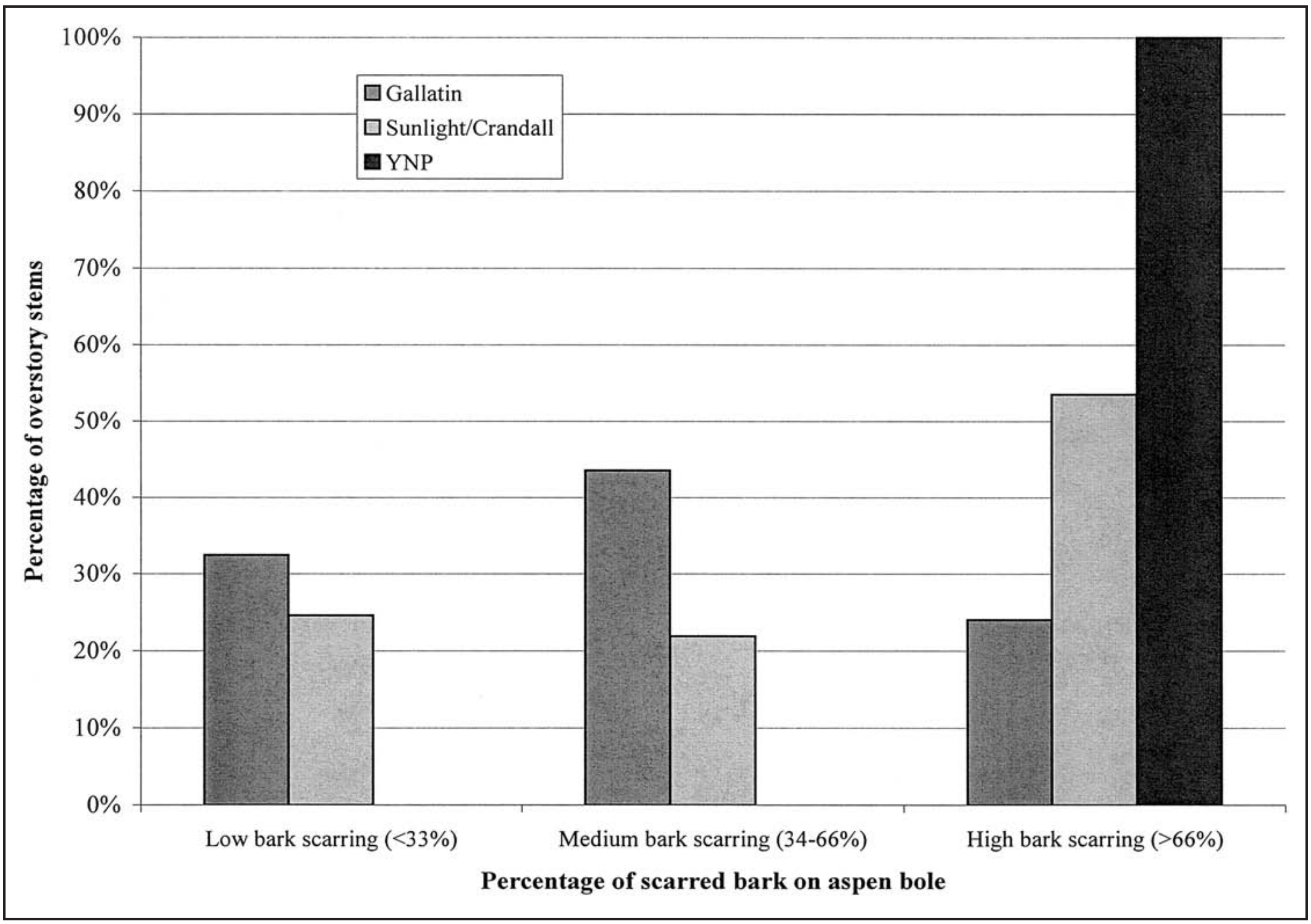

Figure 4. The percentage of aspen stems in three bark scarring categories. The stems were inspected from ground level to 2 m up the bole.

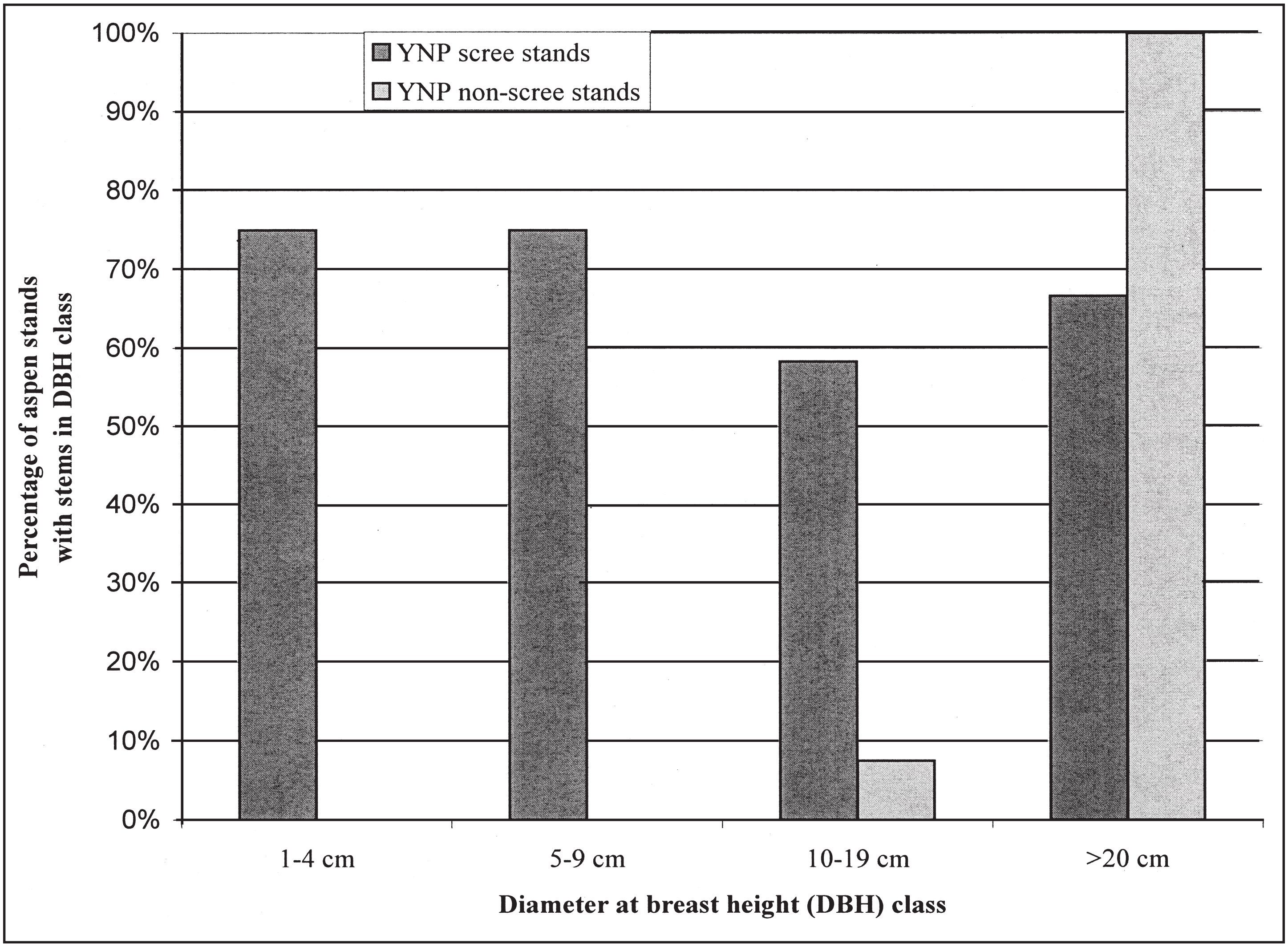

Figure 5. A comparison of scree and non-scree habitat aspen stands on the northern range in YNP. The bars represent the percentage of stands containing aspen stems in four dbh classes. None of the YNP's non-scree transects contained aspen in the 1-4 or 5-9 cm dbh classes.

and depth totals.

Elk densities on the winter ranges vary temporally and geographically. An aerial census of northern range elk had been conducted in early winter (December-January) over the entire northern range. Lemke et al. (1998) provided detail on the methods of conducting the aerial elk census. Based on the data for 1989-99, YNP has averaged densities of 12 elk/km^2 (range 8.0-17.9 elk/km^2). The Gallatin's portion of the northern range averaged 7.6 elk/km^2, with a range of 2.8-14.4 elk/km^2 (Lemke 2004). However, elk continue to move throughout the winter, and areas of the Gallatin north of Dome Mountain that may have few elk present in December and January may have 2000-3000 elk present in March (Lemke, pers. comm.). Aerial elk census data has not been systematically collected in the Sunlight/Crandall areas, but a limited amount of trend data collected by the Wyoming Department of Game and Fish suggests the density of elk wintering in the Sunlight/Crandall area is < 7 elk/km^2 (Emmerich, pers. comm.). Hunter harvest levels in the Clarks Fork of the Yellowstone River Basin (which includes the Sunlight and Crandall Creek areas) average less than 50% of those in the Gallatin's portion of the northern range for the period 1983-96 (Figure 6).

DISCUSSION

The absence of aspen overstory recruitment in areas accessible to ungulate browsing reported for YNP's northern range during the 20th century (Barmore 1965, Kay 1990, Romme et al. 1995, Ripple and Larsen 2000) is not typical for the aspen stands we measured in the adjoining National Forests. Aspen stands in the Gallatin and Sunlight/Crandall are more variable than those in YNP, containing higher percentages of stands with tall ramets, younger and smaller dbh stems, and with less proportional loss of aspen canopy since the 1950's. Our results were similar to those reported by Suzuki et al. in Rocky Mountain National Park (RMNP) and the adjacent Roosevelt National Forest in Colorado. Suzuki et al. (1999) reported lower aspen regeneration in the Estes Valley area of RMNP, where > 90% of the elk in RMNP spend their winters. Similar to our results, they also reported much more robust aspen regeneration in elk winter range located on the Roosevelt National Forest than within RMNP.

Browsing by ungulates, especially elk, appears to be a significant factor in explaining the patterns we observed. Although there was no significant difference in the percentage of browsed ramets among the study areas, there was evidence that ungulates used aspen stands in the surrounding National Forests less intensively than in YNP. The degree of bark scarring was significantly less in the National Forest aspen stands than in YNP, suggesting less intensive browsing (Figure 4). The lower density of tall ramets (> 100 cm) in YNP aspen stands also suggests that browsing levels may be more intensive in YNP than in the surrounding National Forest areas. Aspen stands in the Gallatin and Sunlight/Crandall areas were three to five times more likely to contain tall ramets than stands within

Table 3. Mean precipitation, snowfall, and snow depth at weather stations within the northern range and the Sunlight/Crandall basins.

Average Total Snowfall (cm)	Station Elevation (m)	Period of Record	Dec.	Jan.	Feb.	Mar.	Apr.	Annual
Yellowstone National Park								
Mammoth Hot Springs	1900	1948-2004	33.3	36.6	24.9	32.5	14.8	180.3
Tower Falls	1911	1948-2004	51.6	55.1	35.1	34.5	20.8	245.1
Lamar	1973	1948-1977	44.5	53.8	39.9	34.3	21.3	242.3
Gallatin National Forest								
Jardine	1967	1951-1976	50	56.9	49	41.9	29.8	280.2
Shoshone National Forest								
Crandall	2031	1948-2004	32.3	48.8	37.6	36.8	22.3	220.5

Average Snow Depth (cm)	Station Elevation (m)	Period of Record	Dec.	Jan.	Feb.	Mar.	Apr.	Annual
Yellowstone National Park								
Mammoth Hot Springs	1900	1948-2004	12.7	20.3	20.3	15.2	2.5	5.1
Tower Falls	1911	1948-2004	25.4	43.2	50.8	48.3	15	15.2
Lamar	1973	1948-1977	15.2	30.5	38.1	35.6	10	12.7
Gallatin National Forest								
Jardine	1967	1951-1976	25.4	43.2	53.3	40.6	12.5	15.2
Shoshone National Forest								
Crandall	2031	1948-2004	17.8	40.6	50.8	43.2	10	12.7

Average Total Precipitation (cm)	Station Elevation (m)	Period of Record	Dec.	Jan.	Feb.	Mar.	Apr.	Annual
Yellowstone National Park								
Mammoth Hot Springs	1900	1948-2004	2.5	2.7	1.8	2.7	3	38
Tower Falls	1911	1948-2004	3.3	3.4	2.3	2.7	3	42.2
Lamar	1973	1948-1997	2.2	2.5	1.7	1.7	2.3	34.4
Gallatin National Forest								
Jardine	1967	1951-1976	3.9	4	2.9	2.4	3.4	44.5
Shoshone National Forest								
Crandall	2031	1948-2004	3.1	4.2	2.9	3	2.9	37.8

YNP. Winter elk densities appear to have been lower on winter range outside YNP during the 1980s-90s (and probably before that also). This difference in elk densities between YNP and the National Forest areas may have influenced total foraging pressure on aspen. In addition, the migration to winter range outside the park is a gradual process over the course in the fall/winter, and the season of intense aspen browsing may therefore be shorter in the National Forest areas.

Comparing habitat types within YNP, we found that aspen stands located in areas that have natural barriers to browsing (scree stands) had much lower percentages of browsed ramets, a greater incidence of tall ramets, and a multiple size/age class aspen overstory. These results were consistent with St. John's (1995) findings for scree aspen stands in the Gallatin National Forest. These aspen stands, along with stands protected by fenced exclosures, road ditches, and coarse woody debris, were the only areas on YNP's portion of the northern range where 1-4 cm and 5-9 cm dbh class aspen stems were observed. This illustrates that YNP northern range aspen stands have been able to produce a cohort of replacement overstory stems since the 1920s in areas where browsing pressure has been reduced. These results were also consistent with those reported by Suzuki et al. (1999).

Aspen overstory regeneration has occurred

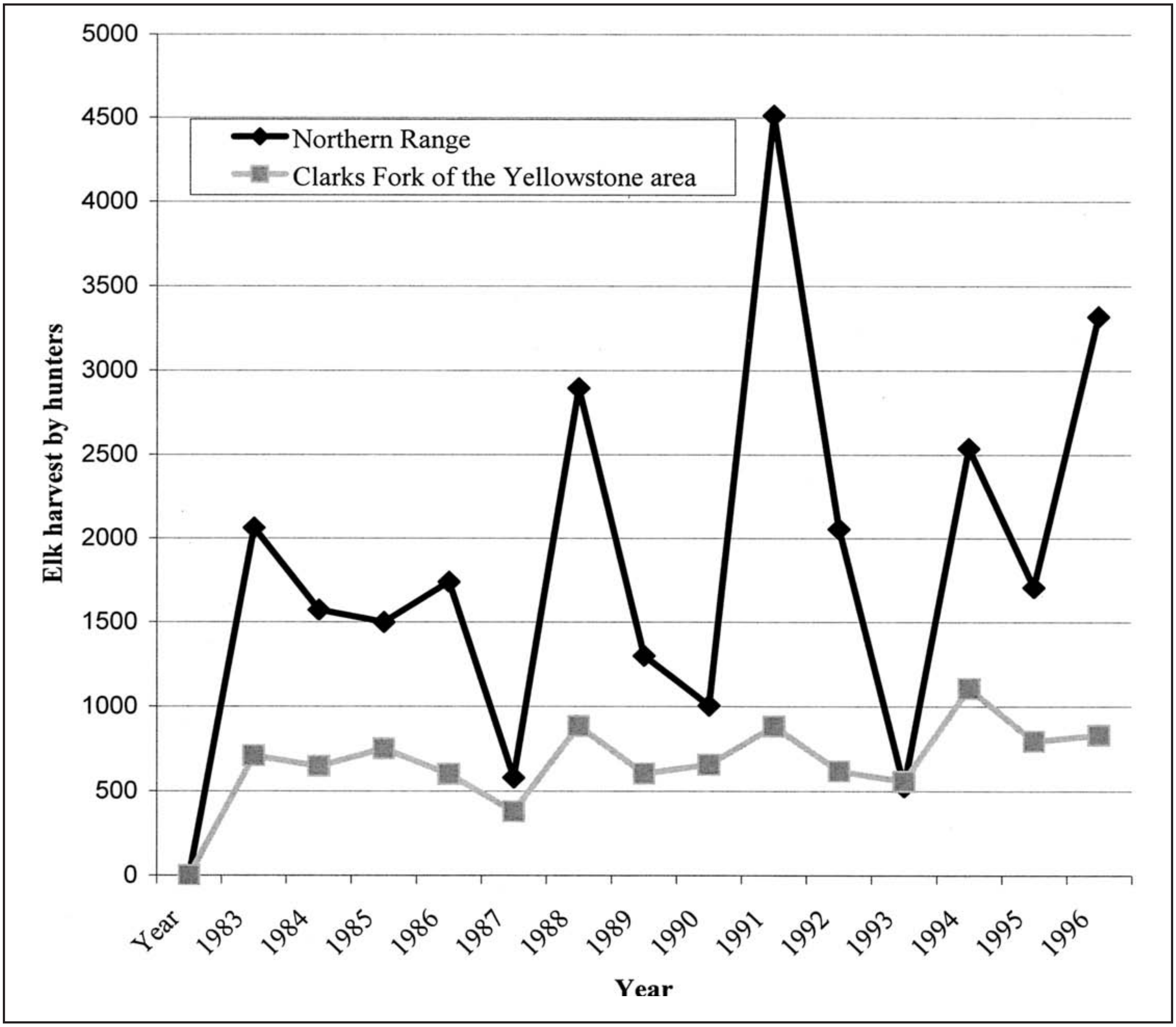

Figure 6. Elk harvests on the northern range of the Gallatin National Forest and in the Clarks Fork of the Yellowstone River area of the Shoshone National Forest. The Sunlight/Crandall study area is within the Clarks Fork of the Yellowstone basin. Source: Montana Fish, Wildlife, and Parks and the Wyoming Department of Game and Fish.

on elk winter range outside YNP on sites of comparable habitat type, elevation, and aspect to many sites within YNP. Since aspen canopy has declined in all three areas, we cannot conclude that aspen overstory recruitment in the areas surrounding YNP is as vigorous as it may have been historically; but since the 1920s, it clearly has been more robust than within YNP.

Available evidence from prior studies lends little support to the hypothesis that unfavorable climatic conditions during the 20th century has been a significant factor in the failure of aspen to recruit new overstory stems in the northern Yellowstone area (National Research Council 2002, Larsen and Ripple 2003). The northern range and the Sunlight/Crandall basin are both influenced by the same macroclimatic regime, characterized by wet summers and dry winters (Despain 1987, Whitlock and Bartlein 1993). Snowfall and snow depths are not significantly different in the three elk wintering areas considered. At a finer scale, aspen occur on a variety of habitat types in the area. In the Gallatin and Sunlight/Crandall, the occurrence of tall ramets and small diameter replacement overstory stems was not restricted to the cooler and moister conditions associated with northern aspects or higher elevations. Aspen stands in the Gallatin portion of the northern range have produced small diameter, young age classes of aspen on sites comparable in elevation, aspect, and habitat type to many aspen sites within YNP.

Fire has been shown to stimulate ramet production for several years after burns in YNP and elsewhere (Bartos and Mueggler 1981, Bartos 1994, Romme et al. 1995). In 1990, Romme et al. (1995) measured a mean density of 38,000 ramets/ha in six aspen stands burned in the 1988 Yellowstone fires, a higher density than any we measured (Table 2). By 1991, Romme et al. (1995) noted a decline in ramet densities in burned aspen stands, and by 1997/98, our data found no difference among mean ramet densities in stands burned or not burned in the 1988 YNP fires. The 1988 fire season also helped create environmental conditions leading to significant aspen seedling establishment within YNP, with mean seedling densities as high as 142,695/ha in the Yancey's Hole region of the northern range (Kay 1993). Using a linear regression equation for aspen growth in northern range riparian areas (Ripple and Larsen 2000), the predicted dbh for aspen established in the 1988 fires (on riparian sites) is 5.4 cm. The 1988 fires affected YNP's portion of the northern range more than our other study areas, yet we found no aspen in the 1-9 cm dbh range in YNP, except on sites protected from browsing. In agreement with Kay (1993) and Romme et al. (1995), we found no evidence that the 1988 fires have led to an episode of aspen overstory recruitment in YNP's northern range, except on a few sites protected from browsing. Aspen stands on the Gallatin's portion of the northern range were not severely affected by the 1988 fires yet contained a much higher incidence of small diameter stems (Figure 3).

The encroachment of conifers into aspen stands may be related to the fire return interval. Bartos and Campbell (1998) outlined risk factors for aspen stands, one of which was the presence of conifers in excess of 25% of the total stem count. However, even after a century of fire suppression, only 12% (YNP) to 17% (Gallatin) of northern range aspen stands have a conifer stem count greater than 25%. Thus, there is not an immediate landscape scale threat that conifers will dominate and replace northern range aspen stands via successional processes. The loss of canopy coverage and the inability of YNP aspen clones to regenerate their overstory under current conditions indicate that conversion of historic aspen sites to sage dominated shrub communities is a more likely scenario. Aspen stands in the Sunlight/Crandall areas have been more heavily invaded by conifers, with 59% of sampled aspen stands having more than 25% of the total stem count in conifers. Most of these conifers are < 3 m tall, so the conversion of aspen sites to conifer is not imminent, although continued monitoring will be important.

We are currently testing the hypothesis that changes at two scales may have affected the movement and browsing patterns of the northern elk herd and help explain the spatial patterns of aspen regeneration that we observed. At one scale, human hunting pressures and land use changes outside of YNP may have led to truncated elk migration patterns and an increased likelihood of ungulates wintering on YNP's portion of the northern range (Larsen and Ripple 2001). This may have altered browsing patterns and intensity sufficiently outside YNP borders to allow the aspen overstory regeneration we observed in the Gallatin and Sunlight/Crandall areas. Within the park, a lack of predation on elk (sport hunting and/or wolves) may have contributed to high elk browsing pressure and the poor regeneration success for aspen (Ripple and Larsen 2000, Ripple and Beschta 2004). The 1995 reintroduction of the wolf *(Canis lupus)* provides a unique opportunity to observe whether reestablished predators can influence elk herbivory on aspen via a trophic cascade effect. A recent YNP study concluded that the possibility of encounters with wolves led elk to decrease their habitat preference for aspen stands (Fortin et al. 2005). Our study provides valuable base-line information on aspen stand condition at the time of wolf reintroduction, and continued monitoring of the stands will test whether wolf reintroduction can change elk foraging behavior sufficiently to allow aspen ramets to escape browsing and form new cohorts of overstory stems. Additional research on aspen dynamics and possible linkages with wolves and elk should offer a more comprehensive understanding of this ecosystem and its individual components.

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