AN ABSTRACT OF THE DISSERTATION OF

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Aerial photographs and field sampling were used to compare aspen (*Populus tremuloides*) age structure and stand conditions on elk winter range in the northern Yellowstone ecosystem. The elk winter ranges studied were the northern range in Yellowstone National Park (YNP) and the Gallatin National Forest and the Sunlight/Crandall elk winter range in the Shoshone National Forest.

I found significant differences when comparing aspen stands inside and outside of YNP borders. The aspen stands in the Gallatin and Sunlight/Crandall areas had a greater incidence of tall aspen suckers and stems in the 1-4, 5-9, and 10-19 cm DBH classes. Aspen stems within YNP had a significantly higher percentage of stems

with high levels of bark damage (>66% of bark surface damaged on the lowest 3 m of stem) than aspen stems in stands in the Gallatin or Sunlight/Crandall.

An aspen age structure was developed using 598 increment cores. The aspen age structure in YNP was significantly different than the age structures of the Gallatin and Sunlight/Crandall elk winter ranges. The Gallatin and Sunlight/Crandall areas did not have significant differences in their age structures. The greatest differences between YNP and the National Forest areas was in the younger age classes, measured as aspen stems originating between 1920-1989.

Within YNP, I found that the aspen age structure, size class distribution, incidence of tall suckers, and the percentage of browsed suckers of the scree habitat type was significantly different than the xeric and mesic habitat types. Scree forms a "natural exclosure" where ungulate browsing is reduced.

Aspen stands have successfully recruited new stems into their overstories in all habitat types from 1880-1989 on the Sunlight/Crandall elk winter range and the Gallatin's portion of the northern range. Within YNP, aspen stands successfully recruited new overstory stems between 1860-1929 in all habitat types. Since 1930, YNP aspen have successfully recruited overstory stems mostly in scree habitat type stands and other areas of reduced browsing pressure. I discussed several potential ecological factors impacting aspen overstory recruitment and conclude that changes in ungulate browsing patterns best explains the spatial and temporal pattern I observed.

Aspen Age Structure and Stand Conditions on Elk Winter Range in the Northern Yellowstone Ecosystem

By

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CHAPTER 1. INTRODUCTION

Yellowstone National Park's (YNP) northern ungulate winter range has seen a steady decline of overstory aspen recruitment and canopy coverage in the last century (Houston, 1982; Kay, 1990; Meagher and Houston, 1998, Ripple and Larsen, 2000). This decline is not confined to YNP, but has been documented throughout western North America (Krebill, 1972, Bartos and Campbell, 1998; Kay, 1997; White et al., 1998). Aspen in western North America reproduces principally by vegetative means, producing suckers from clones that may be thousands of years old (Barnes, 1966; Jelinski and Cheliak, 1992; Mitton and Grant, 1996). Successful aspen reproduction from seed is uncommon, so the maintenance of aspen in western landscapes is dependent on the continued viability of existing aspen clones (Jelinski and Cheliak, 1992; Kay, 1997).

There has been considerable debate over the processes contributing to aspen decline in the YNP area during the last century. Tyers (1981) provides a useful summary of historical views and policies regarding aspen on the northern range, both in YNP and in the Gallatin National Forest. Many early- to mid-20th century scientists and YNP managers attributed aspen decline principally to overbrowsing by ungulates, primarily Rocky Mountain Elk (*Cervus elaphus*) (Skinner, 1928; Rush, 1932; Grimm, 1939, Barmore, 1965). The YNP elk population was manipulated by "direct reduction" (live-trapping and killing) by YNP personnel from 1930–1968, but the manipulation of elk numbers had little or no documented effect on aspen overstory regeneration success (Tyers, 1981; Huff and Varley, 1998). Since the 1970s, several alternative explanations regarding aspen decline have been proposed. Some researchers have hypothesized that changes in northern range vegetation, including aspen, may be related to the lengthening of the interval between fires due suppression by European-Americans (Houston, 1973, Singer et al., 1998). Another hypothesis is that the warmer and dryer climatic conditions of the 20th century created suboptimal conditions for aspen overstory recruitment (Houston 1982; Singer et al., 1998; Meagher and Houston, 1998). This alteration of climate has been hypothesized as possibly influencing aspen's production of certain chemical compounds that discourage grazing of suckers by herbivores (Despain, 1990; YNP, 1997). Kay (1994, 1998) attributes aspen decline on the northern range principally to the removal of Native American influences, including the deliberate setting of fires and exploitation of elk, a preferred food choice. Ripple and Larsen (2000) hypothesized that an alteration of trophic cascades interactions between mammalian predators, elk, and aspen may have changed elk movement and feeding behaviors sufficiently for browsing to suppress aspen overstory recruitment on the northern range. Several authors have proposed that an interaction of several of the above factors may best explain the failure of aspen to regenerate overstory stems for most of the 20th century (Romme et al., 1995; YNP, 1997; Meagher and Houston, 1998).

Aspen has also declined in other national parks of western North America. Several studies have looked at aspen overstory regeneration in elk wintering areas of Colorado's Rocky Mountain National Park (Olmstead, 1977; Baker et al., 1997; Suzuki et al., 1998). These studies all concluded that ungulate browsing was the principal causative factor inhibiting successful regeneration of the aspen overstory. White et al. (1998) studied the status of aspen in the Banff, Jasper, Yoho, and Kootenay complex of national parks in the Canadian Rocky Mountains. The decline of aspen in these Canadian parks was attributed principally to the elimination of Native American land management practices, including frequent burning and native exploitation of elk through hunting.

Within the Greater Yellowstone Ecosystem (GYE), several studies have looked at the status of aspen. In the southern portion of the GYE, Krebill (1974) investigated aspen regeneration in the Gros Ventre elk winter range. Also in the Gros Ventre, experiments were conducted to test the response of aspen to prescribed fire (Krebill, 1972; Bartos and Mueggler, 1981) and small-scale clearcuts (Dieni et al., 2000). Hessl (2000) collected 700+ aspen increment cores and developed a comprehensive age-structure analysis for the Jackson/Gros Ventre area. Aspen on the northern range within YNP also has a long history of study, often in conjunction with the effects of wildlife such as beaver and elk. Warren (1926) conducted one of the earliest studies of YNP aspen in conjunction with his research into the beaver (*Castor canadensis*). He photographed trees, measured aspen stem diameters, and documented beaver utilization of aspen stands in riparian zones located in the Tower area of YNP. Annual reports prepared by YNP rangers Grimm (1933–1947) and Kittams (1948–1958) included discussion regarding aspen decline on YNP's portion of the northern range, along with management recommendations (Houston, 1982). Houston (1982) includes extensive discussion of aspen and other vegetation change in his study of elk on the northern range. The 1988 Yellowstone-area fires led to new research on the response of aspen to wildfire, both in existing clones and seedling establishment (Kay, 1993; Kay and Wagner, 1996; Romme et al., 1995, Romme et al., 1997).

The status of aspen on the national forest lands surrounding the northern range has not been as extensively studied. Approximately 35% of the northern elk winter range lies in the Gallatin National Forest, north of the YNP boundary (Lemke et al., 1998). Rush (1932, p. 42) included discussion of the vegetation on the Gallatin's portion of the northern range, stating that the elk winter range outside YNP was "overgrazed range in 1914 and by 1926 hardly enough forage existed to give hopes of this range ever recovering without extensive artificial reseeding." Tyers (1981) included a discussion of aspen and the condition of vegetation on the Gallatin's portion of the northern range in his history of the northern range. St. John (1995) studied ungulate impacts (both cattle and elk) on aspen stands on the Gallatin's portion of the northern range, concluding that the stands were likely to continue to decline, given current management policies.

No published studies were found regarding the status of aspen in the Sunlight and Crandall basins. Hyde (1964) and Hyde and Beetle (1964) described heavy browsing pressure on aspen from elk and moose in a 1964 range survey. Several small-scale clearcuts were done in the early 1980s to attempt to rejuvenate aspen stands and stimulate sucker production (King, personal communication).

The purpose of this dissertation research was to compare the condition of aspen stands on YNP's northern elk winter range with adjoining areas in the Gallatin and Shoshone National Forests. These areas outside YNP include the northern range on the Gallatin National Forest and the Sunlight and Crandall basins in the Shoshone National Forest. The study combined change detection of aspen canopy using 1950s–1990s aerial photographs, field measurements in aspen stands, and an age-structure analysis based on increment cores. No comprehensive landscape-scale analysis of aspen recruitment success encompassing areas both inside and outside of YNP borders has previously been conducted.

My examination of the status of aspen on the northern and Sunlight/Crandall elk winter ranges involved several major components, described in the following two chapters of this dissertation. The first was to develop a comprehensive inventory of aspen stands on the northern and Sunlight/Crandall study areas through aerial photograph interpretation of color infrared (CIR) aerial photographs. From that inventory I chose a stratified random sample and eventually collected data from 248 sites on the northern and Sunlight/Crandall elk winter ranges. My research combined change detection using matched sets of aerial photographs and field measurements of aspen stands, including the collection of 598 aspen increment cores to develop the first comprehensive aspen age structure in the northern Yellowstone area. Chapters 2 and 3 are manuscripts, which describe the background, methodologies, results, and interpretations of these efforts. In chapter 4, I interpreted my results in the context of the historical circumstances and ecological processes that may explain the pattern of aspen regeneration that I discovered.

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CHAPTER 2

ASPEN AGE STRUCTURE IN THE NORTHERN YELLOWSTONE ECOSYSTEM: USA

Abstract

An age-structure analysis of aspen (*Populus tremuloides*) was conducted on elk winter range in the northern Yellowstone area, collecting increment cores from aspen stands in Yellowstone National Park (YNP), and the Gallatin and Shoshone National Forests. The goal was to compare the aspen age structure for the YNP portion of the northern range with aspen age structures developed for the Gallatin National Forest portion of the northern range and the Sunlight/Crandall elk winter range in the Shoshone National Forest. I collected increment cores in three different diameter-at-breast-height (DBH) size classes, 5–9 cm DBH, 10–19 cm DBH, and >20 cm DBH. Cores were collected from three aspen habitat types (xeric, mesic, and scree), and a special effort was made to collect increment cores from the relatively rare scree habitat type within YNP.

For the three areas, 598 aspen increment cores were successfully dated. I dated 273 cores from 63 stands in the Gallatin, 189 cores from 51 stands in the Sunlight/Crandall basins, and 38 cores from 9 scree habitat type stands within YNP. I compared the resultant age structures with the YNP northern range age structure developed by Ripple and Larsen (2000), using 98 cores from 57 stands. The age structure of aspen in YNP was significantly different than the age structures of aspen in either the Gallatin or Sunlight/Crandall areas (p-values < 0.001). The Gallatin and Sunlight/Crandall age structures were not significantly different (p-value = 0.288). The greatest differences between YNP and the National Forest areas were in the younger age classes, measured as the period between 1920–1989. Only 6% of YNP aspen

stands contained stems that originated between 1920–1989, while 87% and 84% of the stands in the Gallatin and Sunlight/Crandall areas, respectively, contained stems from that period. The scree habitat type forms a "natural exclosure" where browsing pressure is reduced on aspen. Within YNP, the age structure of aspen in the scree habitat type was significantly different than the mesic and xeric sites that were available to ungulate browsing (p-value < 0.001). Aspen stems originating after 1920 dominated the scree stands, while trees originating between 1870 and 1920 dominated the non-scree stands.

I observed that aspen stands have successfully recruited new stems into their overstories in all habitat types from 1880–1989 in elk winter range on National Forest areas surrounding YNP. Within YNP, aspen stands successfully recruited new overstory stems between 1860 and 1929 in all habitat types. Since 1930, YNP aspen have successfully recruited overstory stems mostly in scree habitat type stands and other areas of reduced browsing pressure. I concluded that changes in ungulate browsing patterns best explain the spatial and temporal pattern I observed.

Introduction

On Yellowstone National Park's (YNP) northern range, the failure of existing aspen (*Populus tremuloides*) clones to regenerate replacement overstory stems has been documented since the 1920s (Warren, 1926; Rush, 1932; Grimm, 1939; Barmore, 1965; Kay, 1990; Romme et al., 1995; Houston, 1982; Meagher and Houston, 1998). The decline of overstory aspen is of concern since it is a unique and important species in YNP and the Greater Yellowstone Ecosystem (GYE). It is one of the few upland deciduous tree species present in the YNP area and ranks among the highest cover types for aboveground net primary productivity in the area (Hansen et al., 2000). Aspen forests are important for biodiversity, supporting a variety of plant associations as well as greater bird species richness and total abundance than the surrounding conifer forests (Winternitz, 1980; Turchi et al., 1995; Dieni and Anderson, 1997). Declines in aspen patch size decreased both the richness and abundance of bird species in a study conducted in Saskatchewan (Johns, 1993).

On YNP's northern range, much of the debate has centered on the possible reasons why aspen has failed to regenerate its overstory. Several early- to mid-20th century scientists attributed the failure of aspen to regenerate overstory stems to overbrowsing by ungulates, especially Rocky Mountain elk (*Cervus elephus*) (Skinner, 1928; Rush, 1932; Grimm, 1939; Barmore, 1965). Since the 1970s, several alternative hypotheses have been proposed. These include the lengthening of the interval between fires (Houston, 1973; Singer et. al, 1998), a trend toward a warmer, drier climatic regime (Meagher and Houston, 1998; Singer et. al, 1998), the removal of

Native American environmental influences, including the deliberate setting of fires and overexploitation of elk populations (Kay, 1994, 1998), and the alteration of trophic cascades relationships among predators, elk, and aspen (Ripple and Larsen, 2000, Ripple et al., in press). Several authors have proposed that an interaction of several of the above factors may best explain the failure of aspen to regenerate overstory stems in the 20th century (Romme et. al, 1995; Meagher and Houston, 1998; YNP, 1997).

Aspen reproduces principally by vegetative means, where root suckers develop from clones thought to be thousands of years old (Barnes, 1966; Mitton and Grant, 1996). Successful aspen reproduction from seed is infrequent, so the maintenance of these existing self-regenerating clones is critical to the continued presence of aspen in YNP and other western landscapes (Barnes, 1966; Jilinski and Cheliak, 1992; Mitton and Grant, 1996). Although the ecological processes that drive aspen regeneration success are not fully understood, there is consensus that there has been little aspen overstory recruitment in YNP for the previous 80 years (1920–2000) and that the aerial coverage of overstory aspen has declined. Houston (1982) estimated a decline of 40–60% in YNP aspen canopy coverage in the 20th century, while Kay and Wagner (1996) estimated the loss at 95% since 1872, when the park was established.

The northern range is located in the valleys of the Yellowstone, Lamar, and Gardiner Rivers. The boundary designation for YNP splits the northern elk winter range in two, a portion of it inside YNP and a portion of it outside in what is now a mixture of private land and the Gallatin National Forest (established in 1899). Most of the aspen research on the northern range has focused on conditions within YNP and the status of aspen in the Gallatin has not been as intensively studied. Kay (1990) conducted a limited aspen age-structure comparison between YNP and the Eagle Creek area of the Gallatin National Forest, finding younger aspen stems in the Gallatin than in YNP. St. John (1995) conducted a study of ungulate impacts on aspen on the Gallatin's portion of the northern range, concluding that current levels of ungulate use (cattle and elk) have resulted in the deterioration of aspen clones. East of YNP, aspen also occur in the Sunlight/Crandall elk wintering area in the Shoshone National Forest. There are no published studies dedicated to the status of aspen in the Sunlight/Crandall area, but Hyde and Beetle (1964) noted that aspen suckers were heavily browsed and overstory stems had been high-lined by elk in the Sunlight Basin during the early 1960s. Internal Forest Service documents also indicate that several Sunlight/Crandall area aspen stands had been cut or burned in 1980–1981, in an attempt to stimulate sucker production in decadent aspen stands (King, personal communication).

The goal of this study was to use aspen increment cores to develop and compare aspen age structures for elk winter ranges inside and outside of YNP boundaries. For YNP's northern range, I used an aspen age structure developed by Ripple and Larsen (2000). I selected two areas of elk winter range in close proximity to YNP's northern range and compared their aspen age structures with those of YNP. These two areas were the northern range in the Gallatin National Forest and the Sunlight/Crandall elk winter range in the Shoshone National Forest (Figure 2.1).

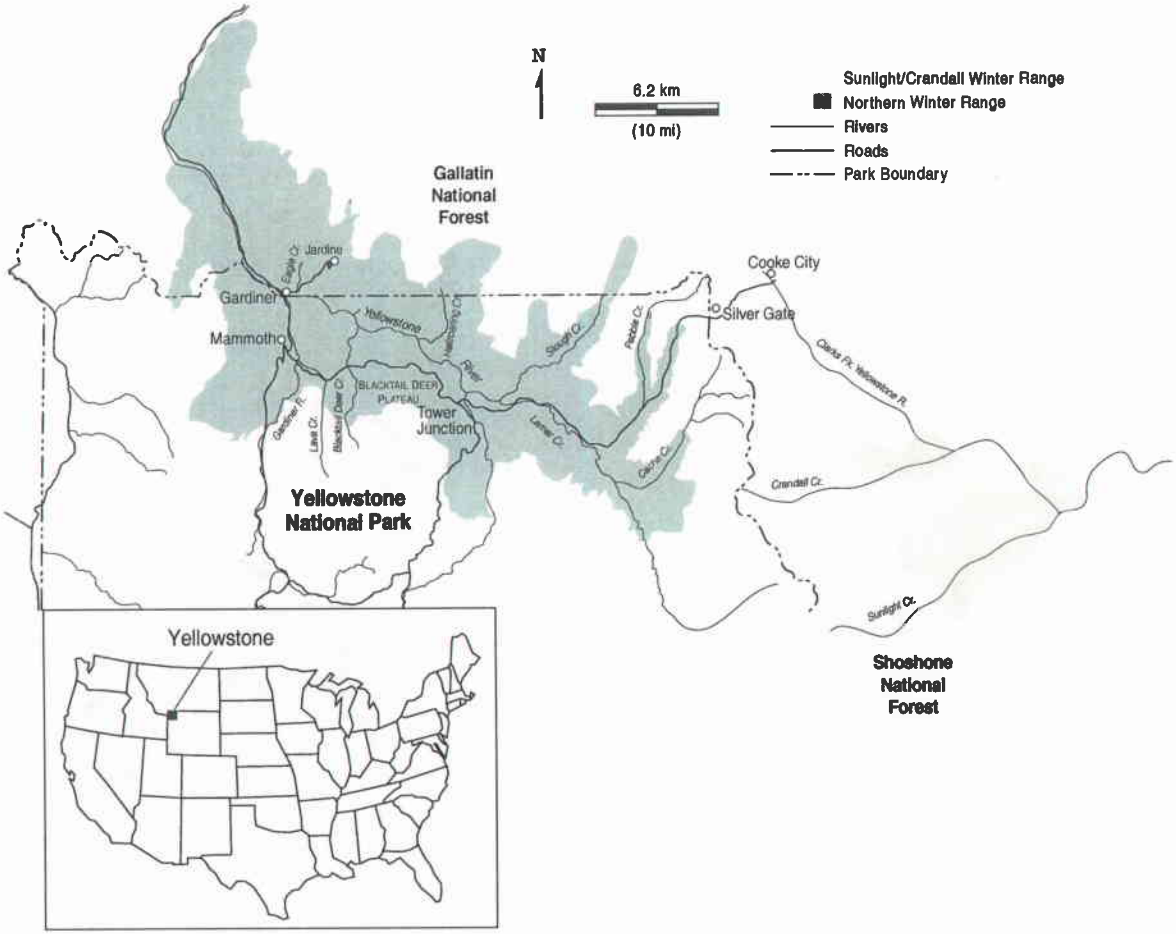

Figure 2.1. Study area map showing the elk winter ranges considered in this study. Yellowstone National Park and the Gallatin National Forest each administer a portion of the northern range. The Sunlight/Crandall elk winter range is east of YNP and is part of the Shoshone National Forest.

The objectives of this study were the following:

1.) To determine whether there were significant differences in the aspen age structure between YNP's portion of the northern elk winter range and the Gallatin's portion of the northern range.

2.) To determine whether there were significant differences in the aspen age structure between YNP's portion of the northern elk winter range and the Sunlight/Crandall elk winter range in the Shoshone National Forest.

3.) Interpret any differences in aspen age structures in terms of ecological and/or anthropogenic processes.

To fulfill these objectives, aspen increment cores were collected from areas of the northern range in YNP and the Gallatin National Forest, as well as from the Sunlight/Crandall basins. I dated the increment cores and then compared the age structure of YNP aspen stands with aspen stands in the Gallatin and Sunlight/Crandall areas. I also compared the habitat type, elevation, and aspect of aspen stands to test whether these site variables could explain any observed differences in overstory recruitment success.

Ripple and Larsen (2000) developed the most comprehensive YNP northern range aspen study to date. They concluded that the current YNP northern range aspen overstory originated primarily between 1860 and 1930, with essentially no overstory regeneration since that period on sites available to ungulate browsing. The only other published aspen age structure for YNP's northern range was developed by Romme et al. (1995), and they sampled only canopy-dominant trees. Warren (1926) collected 31 aspen increment cores from a restricted geographic area (near YNP's Camp Roosevelt) in 1921–1922. However, his objective in collecting these cores was to establish an age-diameter growth relationship, not to provide a comprehensive age-structure analysis of aspen on the northern range. In the southern portion of the Greater Yellowstone Ecosystem, several studies have used increment cores to develop aspen stand age structures (Krebill, 1972; Gruell and Loope, 1974; Hessl, 2000).

Yellowstone National Park was established in 1872 as the world's first national park. East of YNP, the Shoshone National Forest was established in 1891 as the first U.S. National Forest. The first permanent European-American settlers arrived in the Yellowstone region in 1868 (Haines, 1977). The "market hunting" era in and around YNP occurred between approximately 1872–1886; this led to large reductions in wildlife, as large animals were shot for their hides and their carcasses were poisoned to eliminate predators such as the gray wolf (*Canis lupus*) (Schullery and Whittlesley, 1992). In terms of its effect on aspen, the market hunting era is thought to have reduced browsing pressure enough to allow a large cohort of aspen overstory stems to be established on the northern range (Romme et al., 1995; Meagher and Houston, 1998).

Elk and other wildlife gradually recovered as the market hunting era closed. Although limited stock grazing was allowed within YNP borders during the early years after park establishment, land-use practices inside and outside of the park diverged as lands outside the YNP boundary were settled and stock grazing became the dominant land use (Rush, 1932). As the need for additional elk winter range was recognized, remaining federal lands on the northern range in the Gallatin National Forest were withdrawn from further human settlement in 1926, and cattle grazing was reduced

(Rush, 1932). Over the course of the 20th century, additional lands in the Gallatin National Forest have been removed from cattle grazing and are managed by the U.S. Forest Service as elk winter range (Lemke et al., 1998). Regulated elk hunting has been legal outside YNP boundaries for most of the 20th century, including a late-season hunt conducted during the month of January.

Study Areas

The study areas include portions of YNP, the Gallatin National Forest, and the Shoshone National Forest. In YNP and the Gallatin, the study area was the northern range, which lies in the valleys of the Yellowstone, Lamar, and Gardiner Rivers (Figure 2.1). The northern range is the wintering area for the largest elk herd in the GYE and consists of steppe, with islands of conifer and aspen intermixed, and with more continuous conifer forests above 2000 m. The northern range occupies an area of approximately 153,000 ha, with approximately 65% within YNP and 35% in the Gallatin National Forest (Lemke et al., 1998). Livestock grazing allotments occur on some portions of the Gallatin National Forest considered in this study although private lands within the National Forest matrix were not included.

The portion of the Shoshone National Forest included in this study was the Sunlight and Crandall Creek basins, which are both tributaries of the Clarks Fork of the Yellowstone River. The boundaries of the Sunlight/Crandall study area correspond to the critical elk winter range boundary established by the Wyoming Department of Game and Fish. Private lands were eliminated from consideration, but livestock grazing allotments exist on portions of the National Forest land in this area.

Aspen occurs in small patches within a steppe matrix in this area, similar to its landscape pattern on the northern range.

The climate of the Yellowstone area is characterized by cold winters and short, cool summers. Aspen occur in areas of the western U.S. that receive at least 38 cm of precipitation annually (Jones and DeByle, 1985) and the northern Yellowstone area is near this lower limit. On YNP's portion of the northern range, Mammoth Hot Springs averages 38.71 cm/year, while Tower (elevation = 1910 m) averages 42.95 cm/year (Western Regional Climate Center, 2000). Aspen stands on the Gallatin's portion of the northern range are within the same elevational range as those in YNP and receive comparable amounts of precipitation, since precipitation is strongly correlated with elevation in this mountainous area (Dirks and Martner, 1982). At the Crandall Creek weather station (elevation = 1968 m), annual precipitation averages 37.15 cm (Western Regional Climate Center, 2000).

Methods

In YNP and the Sunlight/Crandall basins, a set of color infrared (CIR) aerial photographs was used to inventory existing aspen stands and select a random sample. These photographs were taken in September 1988 at a scale of 1:24,000. CIR photographs were used due to the simplicity in which aspen (white crowns in the late fall CIR photographs) could be differentiated from conifers (red crowns in CIR). All aerial photograph interpretation was done with a scanning stereoscope, and sufficient detail was present in the CIR photographs to discern individual aspen crowns in poorly stocked stands. A 1.0 cm x 1.5 cm (240 m x 360 m cell size) rectangular grid was placed on each aerial photograph, and each cell was identified as either containing or not containing aspen. The sample was then stratified to include only those grid cells identified as containing aspen. From the stratified sample, a random selection was made of 100 grid cells in YNP and 55 cells from the Sunlight/Crandall basins. These cells comprised the sample for collecting the increment cores.

The 1988 CIR flight did not provide complete 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. Grids were placed over the aerial photographs and an aspen inventory was conducted using the same methods as described for YNP and the Sunlight/Crandall basins. A random sample of 75 cells containing aspen was chosen from the Gallatin National Forest inventory.

In the field, aspen increment cores were collected in one randomly selected aspen stand lying within each chosen grid cell. To capture the range of aspen ages within the stands, I attempted to obtain two cores from each of three diameter-at-breast-height (DBH) classes, 5–9 cm DBH, 10–19 cm DBH, and trees >20 cm DBH. Many aspen in the >20 cm DBH class had heart rots, and a maximum of nine trees were sampled for increment cores in each stand. Cores were drilled at a height of 1 m above the ground, and the calculated ages were not adjusted for coring height. The elevation, aspect, and slope were recorded for each sampled stand.

After drying, the cores were mounted on wooden trays and the annual growth rings were counted by using a dissecting microscope and standard dendrochronological procedures (Stokes and Smiley, 1968). I determined the aspen ages by counting the growth rings of each increment core twice and taking the mean.

A second individual conducted a blind recount of the YNP cores to derive an error estimate. The recount resulted in a mean difference of 4.06 years (SD = 5.11, n = 91) between estimated ages. I collected two increment cores from a single tree to derive a further estimate of accuracy in my aspen ages (n = 14 trees). The mean difference between these pairs of cores was 3.57 years (SD = 2.29 years). Cross dating was attempted, but was not successful due to the complacency in the ring widths. The distributions of aspen ages were skewed, so I used the Kruskal-Wallis (KW) test to compare median ages and the Kolmogorov-Smirnov (KS) test to determine whether the age distributions differed among the three study areas (Ramsey and Schafer, 1997).

To further assess the temporal pattern of aspen origination dates, I calculated the percentage of stands containing stems that originated in four time periods, reflecting different eras in YNP area history. The pre-1870 period represents the era before YNP establishment. The 1870–1899 era encompasses the market hunting era and early years of YNP establishment. Hunting was legal within YNP until 1883, a portion of this period (Haines, 1977). Within YNP from 1900–1919, there were significant efforts undertaken to eradicate predators while completely protecting the ungulate populations. The period from 1920–1998 represents the current era of low levels of aspen overstory recruitment on YNP's northern range. I also calculated the percentage of stands in mesic and xeric habitat types containing aspen stems that originated in each of the four time periods to assess the influence of site on successful overstory recruitment.

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 in the following manner:

1.) Xeric sites. The understory of these aspen stands included grasses, such as Idaho fescue (*Festuca idahoensis*), 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 sites. This aspen habitat type contained sites with moist to saturated soil conditions, including midslope benches, riparian areas, and wet meadows. A mixture of grasses and tall forbs characterized this habitat type. Timothy (*Phleum pratense*) was a dominant grass 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 characterized these sites. The understory was typified by sparse vegetation and thin soils in a rock substrate (St. John, 1995). Xeric conditions predominated in scree aspen stands.

In addition to my random sample, I collected increment cores in all aspen stands of the scree habitat type that were encountered during the course of the field work in YNP. These scree stands are a relatively rare habitat type and are valuable for comparative purposes, since the scree forms a "natural exclosure" where ungulate browsing levels are typically low. The KS test was used to determine whether the distribution of aspen ages in YNP was different in the scree habitat type than in the non-scree mesic and xeric habitat type stands.

Climatic variation was inferred from two dendroclimate indices prepared by Stockton (1973). For the northern range in both YNP and the Gallatin, the Gardiner dendroclimate index was used (Stockton, 1973). For the Sunlight/Crandall area, the Dead Indian Hill dendroclimate index was used (Stockton, 1973). Poisson log regression (Ramsey and Shafer, 1997) was used to analyze the relationship between 5-year averages for the dendroclimatic indices (independent variable) and aspen origination dates (dependent variable). The purpose of this analysis was to test whether climatic fluctuations (as measured by the dendroclimate indices) were related to the incidence of aspen origination. Five-year averages were developed from the dendroclimate indices and regressed against the sum total of aspen originating during these same 5-year periods. The regression was conducted separately for each of the three areas. Precipitation data from Mammoth Hot Springs and Tower within YNP were also compared with aspen origination dates using Poisson log regression.

Results

Of the 210 aspen stands sampled, 180 stands yielded at least one readable increment core that could have an origin date assigned to it. Of the 30 stands in which usable cores could not be obtained, 27 were in YNP, and 3 were in the Sunlight/Crandall basins. In total, 598 increment cores were successfully dated. Ripple and Larsen (2000) published the results from YNP's portion of the northern range, where 98 cores were dated from 57 aspen stands. In the Gallatin, 273 cores were dated from 63 stands. In the Sunlight/Crandall basins, 189 cores were dated from 51 aspen stands. An additional 38 increment cores were obtained from 9 scree habitat type stands in YNP.

Figures 2.2–2.4 show the aspen age structure (in 5-year periods) derived from the increment cores. Figure 2.2 shows the age distribution of aspen on YNP's northern range. Ninety-five percent of the cores collected on YNP's northern range originated before 1920, with 1885–1889 being the peak 5-year period of aspen stem origination. The temporal pattern of aspen origination was more continuous on the Gallatin's portion of the northern range, with aspen origination dates in every 5-year period from 1865–1989 (Figure 2.3). The Sunlight/Crandall basins also exhibited a continuous pattern of aspen origination, with stems originating during every 5-year period between 1880–1989 (Figure 2.4). I did not collect increment cores for any trees <5 cm DBH, so the period 1990–1998 was not represented in my graphs.

Table 2.1 compares the mean and median ages of aspen stems in the three areas. The median aspen age was significantly higher in YNP than in the Gallatin or Sunlight (KW p-values < 0.001) areas. The median ages were not different when comparing the Gallatin and Sunlight/Crandall study areas (KW p-value = 0.788). The distribution of aspen ages in YNP was also significantly different from either of the other two areas (KS p-values < 0.001). However, the age distributions in the Gallatin and Sunlight/Crandall areas were not significantly different (KS p-value = 0.288).

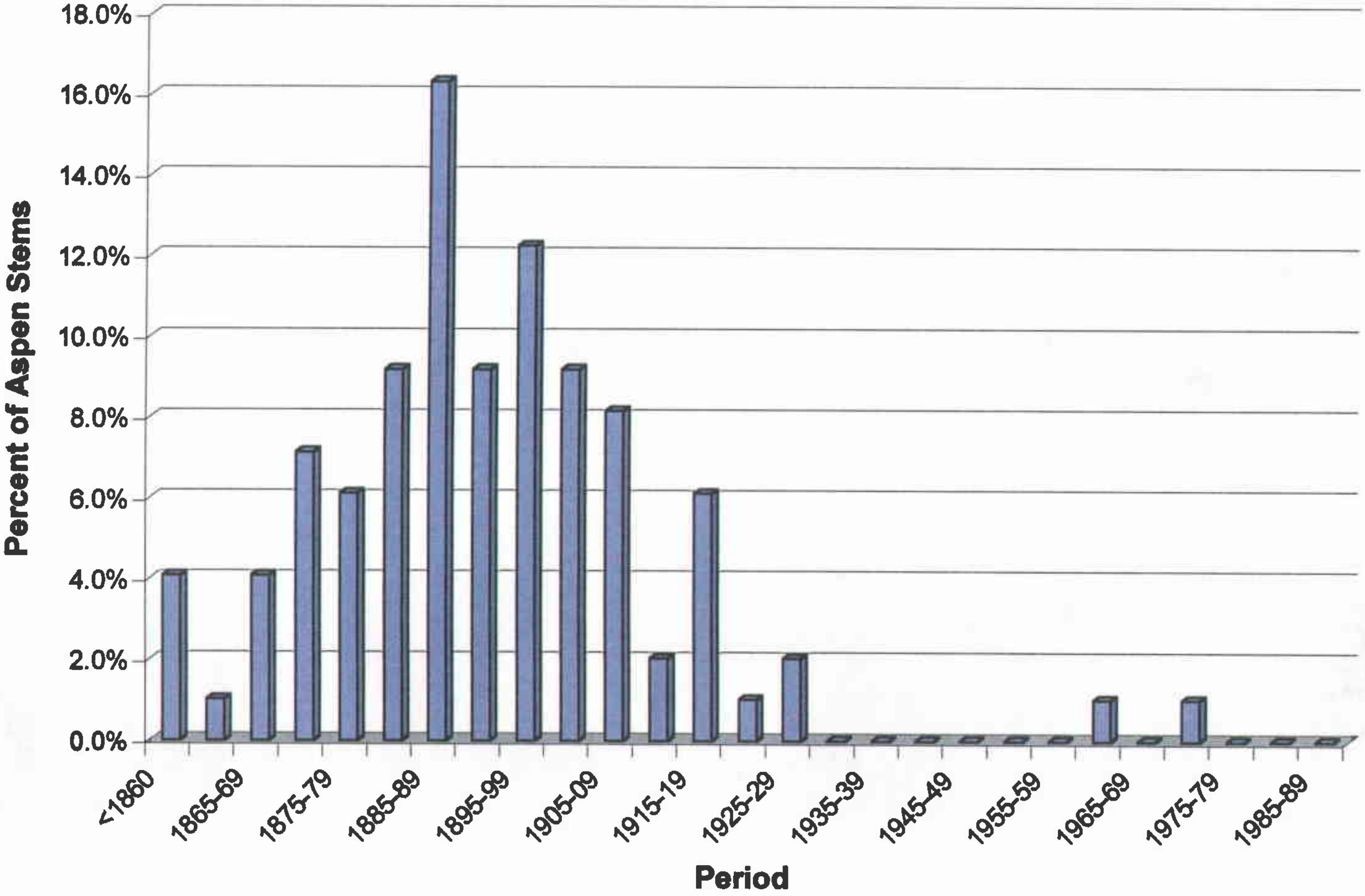

Figure 2.2. The percentage of 1998 aspen overstory stems established during 5-year periods on YNP's northern range (n=98 from 57 aspen stands, Source: Ripple and Larsen, 2000).

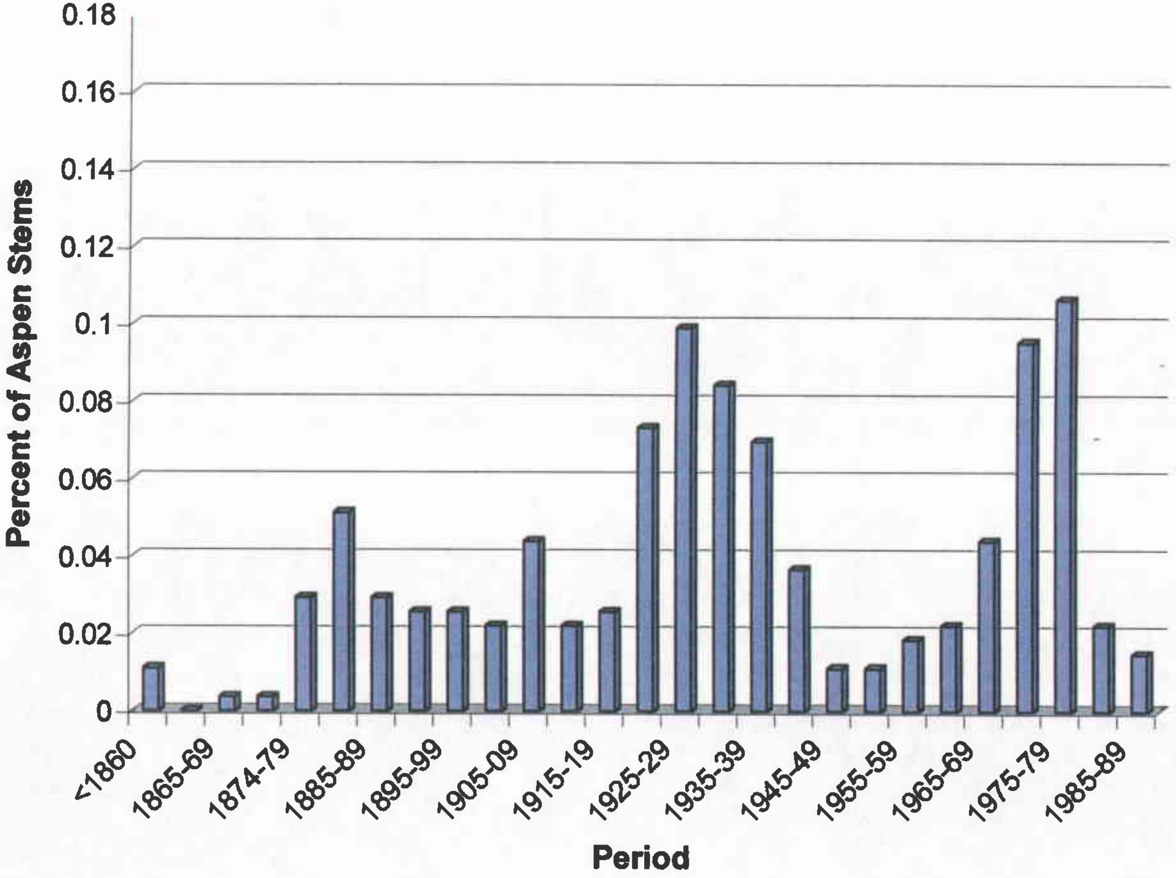

Figure 2.3. The percentage of 1998 aspen overstory stems established during 5-year periods on the Gallatin National Forest's portion of the northern range (n=273 from 63 aspen stands).

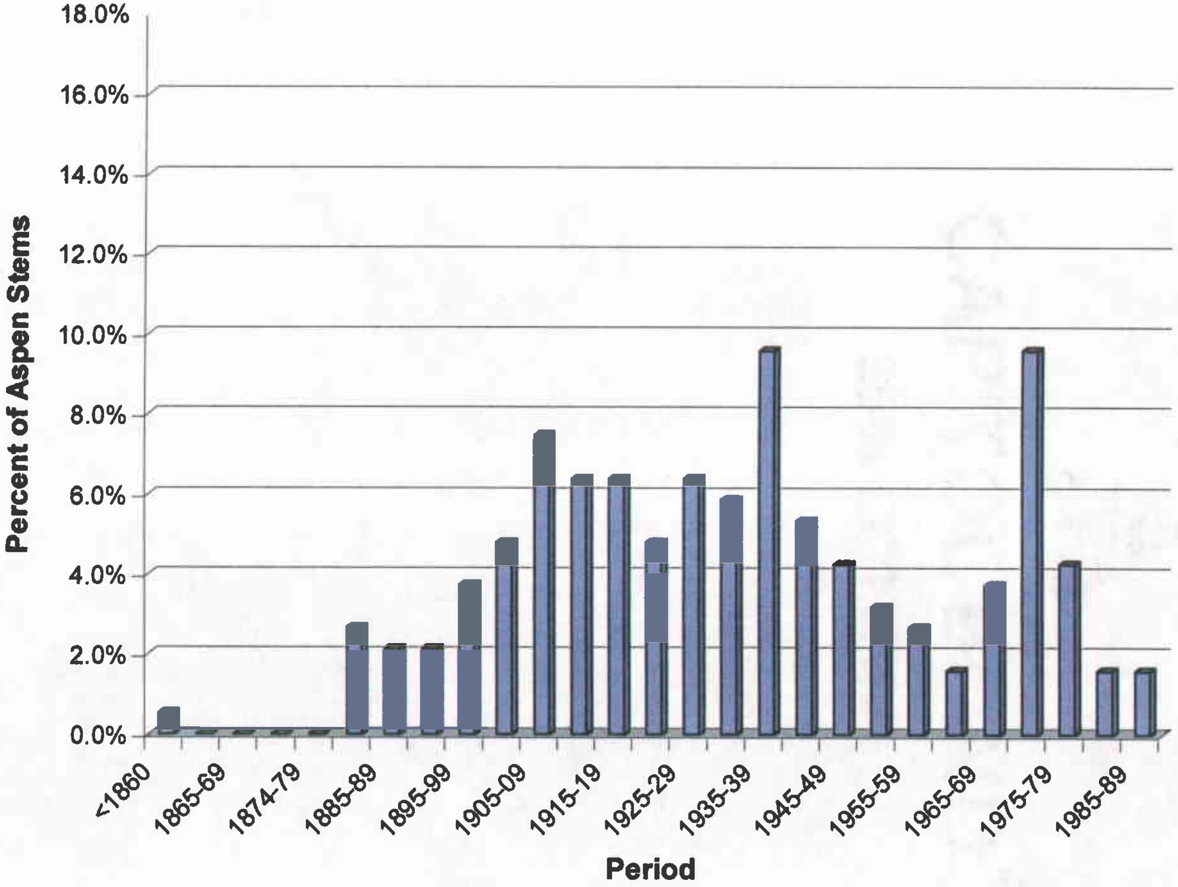

Figure 2.4. The percentage of 1998 aspen overstory stems established during 5-year periods on the Sunlight/Crandall elk winter range, Shoshone National Forest, Wyoming (n=189 from 51 aspen stands).

Table 2.1. A comparison of aspen ages on selected elk winter ranges in the northern portion of the Greater Yellowstone Ecosystem.

Study area	n	Mean aspen age	SD aspen age	Median aspen age
YNP	98	106.1	20.9	107.0
Gallatin	273	64.3	27.6	66.5
Sunlight/Crandall	187	64.4	27.6	64.3

I also analyzed aspen stem origination at the stand level over four time periods (pre-1870, 1870–1899, 1900–1919, 1920–1998). The percentage of stands with stems originating in these periods is shown in Table 2.2. When comparing YNP stands to the other areas, the largest differences were in the period of 1920–1998. In YNP, only 6% of aspen stands contained stems originating between 1920–1998, while the percentages in the Gallatin and Sunlight/Crandall areas were 87% and 84%, respectively (Table 2.2). I also stratified my samples by habitat type to analyze whether mesic or xeric type stands differed in their ability to produce overstory stems. At the stand level, I did not find a consistent pattern of aspen overstory recruitment based on habitat type.

Within YNP, I collected 38 increment cores from nine scree habitat-type aspen stands. The age distributions of these aspen are given in Figure 2.5. The KS test was used to compare the age distributions of the YNP scree aspen stands with the YNP non-scree xeric and mesic stands. The age distributions of the aspen in the scree

Table 2.2. The percentage of aspen stands with stems originating in 4 time periods from 1870–1989. Since aspen stands may have multiple age classes, the percentages add up to more than 100%.

			Percentage of aspen stands with stems originating by period			
Study area	Aspen stands sampled	n	pre-1870	1870–1899	1900–1919	1920–1998
YNP	All	57	13	83	38	6
Gallatin	All	63	5	51	32	87
Sunlight/Crandall	All	51	2	27	39	84
YNP	Mesic habitat type	29	11	79	36	4
	Xeric habitat type	25	16	88	40	8
Gallatin	Mesic habitat type	34	0	50	21	88
	Xeric habitat type	29	10	52	45	86
Sunlight/Crandall	Mesic habitat type	29	0	41	48	72
	Xeric habitat type	22	5	9	27	100

stands differed significantly from those of the non-scree stands, with the age distributions in the scree stands containing trees originating mostly after 1920 (p-value < 0.001).

Using Poisson log regression, there was not a significant relationship between aspen origination and climatic fluctuations as measured by the dendroclimate indices (YNP p-value = 0.369, Gallatin p-value = 0.400, Sunlight/Crandall p-value = 0.195). Poisson log regression was also used to test the relationship between 5-year averages of precipitation and aspen origination on the northern range. I did not find a significant

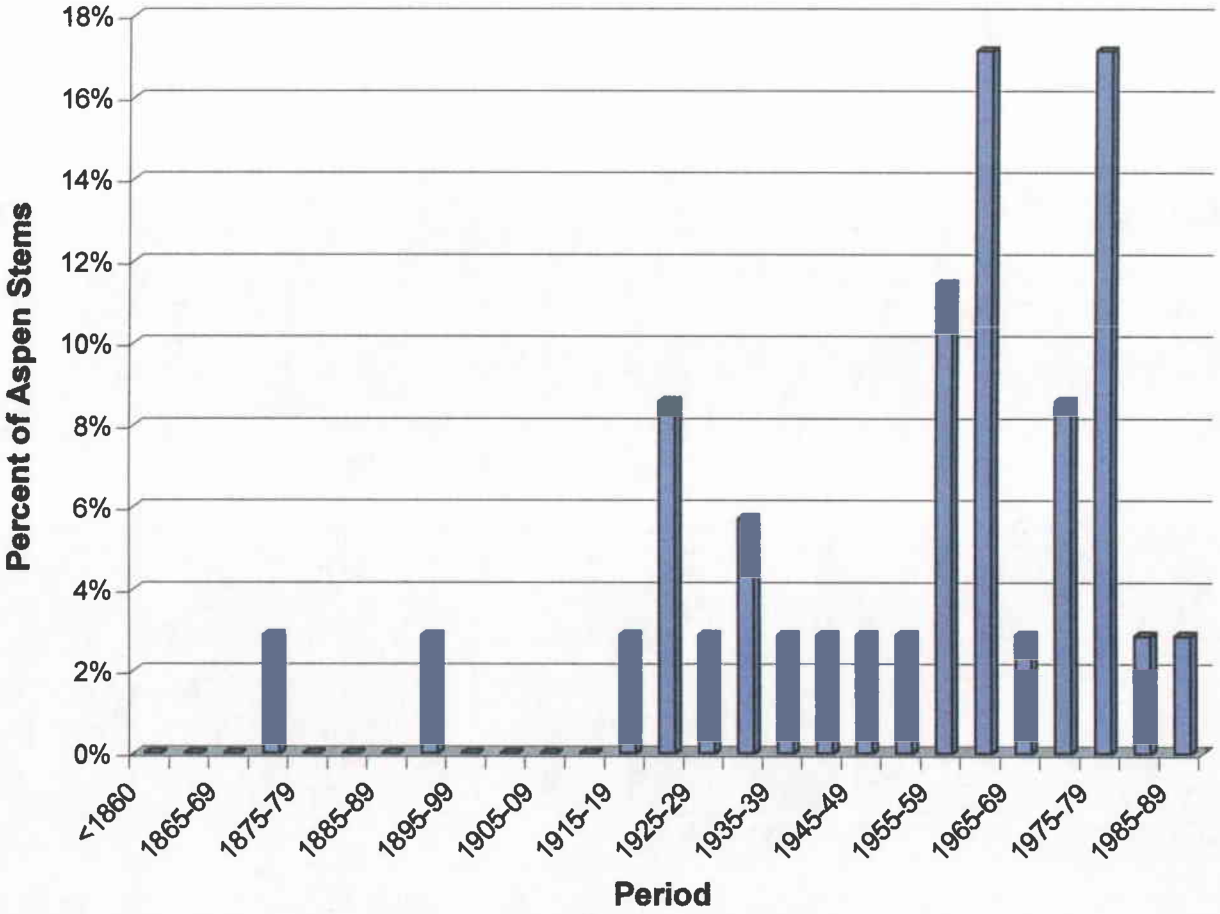

Figure 2.5. The percentage of 1998 aspen overstory stems established during 5-year periods in the scree habitat type on YNP's portion of the northern range (n=38 from 9 scree habitat type aspen stands)

relationship between precipitation fluctuations and aspen origination on the northern range, either in YNP or in the Gallatin (p-values > 0.512).

Discussion

Aspen stands outside YNP differ in several important respects from those in YNP. Aspen in the Gallatin and the Sunlight/Crandall basins exhibited a more continuous pattern of overstory recruitment than in YNP, especially for the period of 1920–1989 (Figures 2.2–2.4). In the Gallatin and Sunlight/Crandall areas, I documented aspen overstory recruitment success during every 5-year period from 1880–1989. In contrast, aspen overstory recruitment essentially ceased on YNP's portion of the northern range after the 1920s, except in scree habitat types (Figure 2.5) and other areas protected from ungulate browsing (Grimm, 1939; Barmore, 1965; Kay, 1990; Romme et al., 1995, Ripple and Larsen, 2000). In YNP only 6% of the randomly selected stands contained overstory stems originating between 1920 and 1989; in the Gallatin the percentage was 87%, and in the Sunlight/Crandall basins it was 84% (Table 2.2). Suzuki et al. (1998) found a similar pattern in Rocky Mountain National Park (RMNP), Colorado, and in the surrounding Roosevelt National Forest (RNF). They studied aspen stands on elk winter range inside and outside of RMNP boundaries and concluded that higher percentages of aspen stands were regenerating in RNF than in RMNP.

Warren (1926) photographed and described a multi-aged aspen overstory that existed along several riparian corridors on the northern range of YNP in 1921–1922. Using increment cores and the aspen diameters supplied by Warren (1926), Ripple and

Larsen (2000) developed a regression equation predicting that the 1920s-era aspen overstory consisted of trees originating from the mid-to-late 1700s to the 1920s. In addition to Warren (1926), other compilations of historic photographs also show evidence of several size classes of aspen evident on the northern range in the late 1800s to early 1900s (Houston, 1982; Kay, 1990; Meagher and Houston, 1998). These photographs also suggest a wider span of origination dates than 1870–1900. I therefore conclude that the successful recruitment of aspen overstory stems has been occurring from at least the late-1700s to the present on elk winter ranges in the northern Yellowstone area, although overstory recruitment within YNP is currently restricted to sites of low ungulate browsing pressure.

Using 5-year averages, I did not find a significant relationship between precipitation levels (measured at Mammoth Hot Springs, YNP) and aspen origination dates on the northern range. Similarly, there was not a significant relationship between the dendroclimate indices and aspen origination dates on any of the elk winter range areas I considered. In the Gros Ventre Valley south of YNP, Hessl (2000) also concluded that there appeared to be only a weak relationship between aspen origination and a local (Uhl Hill) dendroclimate index. Baker et al. (1997) concluded that the temporal pattern of aspen origination corresponded weakly, or not at all, with climatic and hydrologic variables in a study conducted on elk winter range in Colorado's Rocky Mountain National Park.

Aspen can tolerate severe cold, but may not tolerate arid or semiarid conditions well (Jones et al., 1985) and trends toward a more arid climate have been proposed as an explanation for vegetation change on the northern range (Houston, 1982; YNP, 1977; Singer et al., 1998). At the stand level, the spatial pattern I observed was not consistent with a lack of moisture being a significant variable in predicting aspen overstory recruitment success. If moisture stress were affecting aspen recruitment, I would expect that mesic sites such as riparian areas or wet meadows would produce greater numbers of overstory stems over time. In YNP I observed the opposite, where the greatest recruitment success occurred in the scree habitat type, which are xeric sites with thin, rocky soils (Figures 2.2 and 2.5). On the National Forest areas surrounding YNP, I found that aspen successfully recruited overstory stems on both mesic and xeric habitat types (Table 2.2). Based on my observations, I conclude that habitat type and the climatic variation expressed in the dendroclimate indices and annual precipitation cannot explain the pattern of aspen overstory recruitment in the winter ranges I studied in the northern Yellowstone area.

Houston (1973) estimated a historic fire interval of 20–25 years on the northern range, an interval that has been altered by European-American fire-suppression efforts beginning in the late 1800s. Fire can stimulate high levels of sucker production in aspen clones for 1–3 years afterward, with mean densities of 38,000 suckers/ha recorded on the northern range after the 1988 fires (Romme, 1995). However, the 1988 fires have not led to a cohort of aspen reaching tree size on YNP's portion of the northern range (Romme et al., 1995). On the Gallatin's portion of the northern range, the best 20th-century periods of aspen overstory recruitment (1925–1929, 1970–1974, and 1975–1979, Figure 2.3) were not associated with major fire events (Houston, 1973, 1982).

In the Sunlight/Crandall area there were at least two major fires in the 20th century, the 1935 Crandall/Closed Creek fire, and the 1988 Willow Mist fire (Dawson, personal communication, 2001). In the Crandall Basin, 28% (11 of 39 cores) of the sampled aspen originated between 1935 and 1939, and this cohort of aspen may be the result of the 1935 Crandall fire (Figure 2.4). However, there are very little data available on elk populations in the Sunlight/Crandall area in the 1930s, and browsing levels during this period are unknown. Estimates developed by the Wyoming Game and Fish Department for the Clarks Fork elk herd indicate that the herd grew from approximately 1,800 elk in 1949 to 5,000 for 1985–95, so the elk population in the Sunlight/Crandall area may have been smaller in the 1930s than it is currently (Emmerich, unpublished data, 2000). The Willow Mist fire of 1988 burned large areas in the Sunlight Basin but did not burn extensively in areas occupied by aspen, and my data do not show a large cohort of aspen developing from this fire. Fire also would appear to be unrelated to the large cohort of aspen I dated to the period 1970–1974, since no large fires occurred in the Sunlight/Crandall basins during that decade (Dawson, personal communication, 2001). My data were substantially in agreement with other studies that have concluded that aspen can recruit new overstory stems in the absence of wildfire (Kay, 1990; Baker, 1997; Suzuki, 1998; Hessl, 2000).

On YNP's portion of the northern range between 1920–1998, the aspen stands most successful in recruiting new overstory stems were located in scree habitat types, fenced exclosures, and jackstraw piles (Kay, 1990; Ripple and Larsen, 2001). All of these areas are at least partially protected from browsing, and this pattern of aspen overstory recruitment is consistent with ungulate browsing being the major factor limiting aspen growth in YNP. In contrast, my aspen increment cores from the Gallatin and the Sunlight/Crandall elk winter ranges document continuous aspen overstory recruitment in all habitat types between 1920–1998, which brings us to a consideration of why aspen has been more successful recruiting overstory stems outside YNP than inside. I hypothesize that the observed differences in the aspen age structures inside and outside of YNP has been principally due to predation risk effects affecting the movement and behavior of elk. Predation risk effects describe a trade-off in foraging strategy where elk may avoid certain areas to reduce their chances of being killed by human or animal predators (Lima and Dill, 1990; Schmitz et al., 1997). Historically, both Native American and other mammalian predators pursued elk throughout the area, and there has long been debate over possible changes in elk migration and behavior due to anthropogenic changes on the northern range. Early changes to the northern range outside of YNP included European-American settlement, unrestricted grazing of livestock (until 1926), and the establishment of the "firing line" just north of the YNP border, where hunters would gather and shoot elk immediately after they crossed the YNP boundary (Rush, 1932; Murie, 1947; Haines, 1977). Within YNP, 1895–1930 was the era of complete protection of elk, when wolves were eliminated as a source of predation (by 1926), human hunting was not allowed, and elk populations were rising (Houston, 1982; Singer and Mack, 1999). The lack of forage due to overgrazing outside YNP coupled with the "firing line" style of hunting and associated differential risk of predation inside/outside of YNP boundaries may have influenced both elk movements and behavior, since elk have been shown to change their migration patterns and behavior in the presence of predation (Boyce, 1989). Outside YNP, lower elk densities along with foraging strategies influenced by the risk of predation may have led to different browsing patterns and increased aspen overstory recruitment in the Gallatin and Sunlight/Crandall elk winter ranges. After 1930, the "direct reduction" (killing and live-trapping) program of elk management began in YNP (Singer and Mack, 1999). The failure of aspen to recruit overstory stems within YNP during this period (1930–68) has long puzzled scientists. Craighead et al. (1972) and Houston (1982) studied the effects of direct reduction on elk distributions and concluded that this program had disproportionately reduced the migratory segment of the herd, which may help explain why the direct reduction program had little or no effect on aspen overstory recruitment within YNP and may have actually assisted aspen recruitment outside of YNP by reducing browsing pressure. In the Gallatin National Forest, St. John (1995) concluded that aspen stands <500 m from roads were less impacted by ungulates than those further away, suggesting a foraging behavioral adjustment to avoid human contact and possible predation. Suzuki et al. (1998) suggested that management strategies to disperse elk might help alleviate local aspen declines in the RMNP area.

On elk winter ranges in the northern GYE, aspen have had greater success recruiting overstory stems in national forest areas outside of YNP borders. However, recent events in the GYE may again alter the behavior and browsing patterns of ungulates on the northern and Sunlight/Crandall elk winter ranges. Historically, predators may have affected elk behavior and movement sufficiently to allow for regeneration of aspen overstories at sites with high levels of predation risk. Wolves were reintroduced into YNP in 1995 and may be affecting the differential risk of predation and elk browsing patterns inside and outside of YNP borders. Ripple et al. (2000, in press) have recently begun a long-term study using permanent aspen plots to further study predation risk effects on elk browsing patterns and the trophic cascades relationship between wolves, elk, and aspen in the YNP area. Initial results of their study indicate that elk may be avoiding areas of high wolf presence on the northern range. Cooperative efforts to purchase additional elk winter range north of YNP within the Gallatin National Forest matrix have also been undertaken in recent years. Between 1976 and 1998, greater numbers of elk have migrated out of YNP during the winter months and have more than doubled the area they occupy in the Gallatin National Forest during the winter months (Lemke et al., 1998). This increase in the density and area occupied by elk on the Gallatin's portion of the northern range may also affect future spatial patterns of browsing and aspen overstory recruitment. Additional research into elk behavioral and browsing patterns in the presence of predators and aspen reproduction at the landscape or ecosystem scale is needed, and is especially urgent in the national forest areas surrounding YNP.

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CHAPTER 3

ASPEN STAND CONDITIONS ON ELK WINTER RANGES IN THE NORTHERN YELLOWSTONE ECOSYSTEM

Abstract

I compared aspen (*Populus tremuloides*) stand conditions on Yellowstone National Park's (YNP) northern range with stands in the Gallatin National Forest and in the Sunlight/Crandall basins of the Shoshone National Forest. All three of these areas are winter range for Rocky Mountain Elk (*Cervus elaphus*). I used 210 matched pairs of aerial photographs from 1958 and 1995 (1954 and 1992 in YNP) to analyze the change in aspen and conifer canopy coverage. All three areas had a loss of aspen canopy coverage in the 1958(54) to 1995(92) period. The aspen canopy in YNP had the greatest proportional decline from its 1950s level (–38.6%) of the areas studied. Conifer canopy coverage in YNP did not expand as much as in the Gallatin and Sunlight/Crandall elk winter range areas from 1958(54) to 1995(92).

I also established 2 x 30 m transects and collected field data for all 210 sites analyzed with the aerial photographs. I measured aspen sucker density, the percentage of browsed aspen suckers, aspen and conifer overstory density, and the diameter at breast height (DBH) of all overstory stems. I did not find significant differences in sucker densities or the percentage of browsed suckers in aspen stands inside and outside of YNP boundaries. Aspen stands outside YNP had a significantly higher percentage of stands with tall suckers (>100 cm), as well as a significantly higher percentage of aspen stands with overstory stems in the 1–4, 5–9, and 10–19 cm DBH categories. Conifer encroachment was greater in the Sunlight/Crandall basins than on the northern range in either YNP or the Gallatin. Aspen stems in YNP exhibited a

significantly higher level of bark scarring (caused by ungulate browsing) than the Gallatin or Sunlight/Crandall areas.

Elevation and aspect were recorded for each stand. Stand elevation and aspect were poor indicators of the presence of tall suckers and/or small DBH aspen stems. Aspen stands were also classified into three general habitat types, xeric, mesic, and scree. Aspen stands in the Gallatin and Sunlight/Crandall areas were successful in regenerating overstory stems in each DBH class in all of the habitat types. In YNP, the scree habitat type stands were the most successful in producing young aspen stems in the 1–4 cm, 5–9 cm, and 10–19 cm DBH categories. The scree forms a natural exclosure and illustrates that aspen stands have successfully recruited overstory stems on YNP's northern range under recent climatic and fire regime conditions when given partial protection from browsing. At a landscape scale, I concluded that the Gallatin and Sunlight/Crandall areas contained a greater diversity of aspen overstory DBH size classes in their canopies than in YNP. Aspen successfully regenerated overstory stems outside YNP on sites of comparable elevation, aspect, moisture availability, habitat type, and fire history to sites within the park. Climate fluctuation, fire suppression, or succession to conifers cannot adequately explain the spatial pattern of aspen overstory recruitment I observed. Ungulate browsing provides the most plausible explanation for the pattern of stand conditions, with tall suckers and cohorts of small DBH stems present in stands outside the park, but absent on comparable sites within YNP.

Introduction

Quaking aspen (*Populus tremuloides*) is an adaptable species that is the most widely distributed tree in North America. On the northern and Sunlight/Crandall elk winter ranges, the reduction of aspen overstory stems and biomass has concerned scientists and managers since the 1920s (Skinner, 1926; Warren, 1926; Grimm, 1939; Hyde and Beetle, 1964; Barmore, 1965; Kay, 1990). The northern range covers approximately 152,000 ha, with 65% of the area within Yellowstone National Park (YNP) and the remainder within the Gallatin National Forest (Lemke et al., 1998). Aspen is not a dominant cover type on YNP's northern range and occupies approximately 1% of the land area of the park. Aspen also occurs as a minor cover type in the Sunlight/Crandall elk winter range lying east of YNP in the Shoshone National Forest. Despite its limited distribution, aspen is considered ecologically significant, since it is one of the most productive cover types in the Greater Yellowstone Ecosystem (GYE) and is one of the few deciduous species in the area (Hansen et al., 2000). It provides habitat for numerous bird species, supports a variety of plant associations, and is used as browse by several ungulate species (Dieni and Anderson, 1997; St. John, 1995).

Aspen reproduces both sexually and asexually (DeByle and Winokur, 1985). Asexual or vegetative reproduction dominates in the western United States, where aspen suckers are produced from meristems developed in the root systems of existing clones (Schier et al., 1985). Individual aspen stems may live up to 200 years, but some of the clones are thought to be thousands of years old (Barnes, 1966, Mitton and

Grant, 1996). In YNP, >95% of the current aspen overstory consists of trees > 80 years (Ripple and Larsen, 2000); however, 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) to 95% (Kay and Wagner, 1996). In some YNP aspen clones, the overstory has been completely eliminated and the clones are currently persisting in a shrub form with suckers <1 m tall (Despain, 1990). The long-term persistence of these aspen clones in shrub form is unknown. The loss of aspen canopy and reduction in stand size is significant since at least 88 species of birds use aspen habitats in Wyoming (Dieni and Anderson, 1997). Reductions in stand size were significantly correlated with reduced bird species richness in aspen stands in Saskatchewan (Johns, 1993).

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; Kay, 1990; Krebill, 1972; Bartos, 1994; Romme et al., 1995). In the northern Yellowstone area, elk browsing on aspen occurs primarily in winter and takes two principal forms. Elk will repeatedly browse the leaders and twigs of aspen suckers and prevent their escapement to sapling or tree form (Figure 3.1). Elk also eat the bark of mature trees, leaving the black-scarred bark characteristic of aspen on YNP's northern range today (Figure 3.2). Kay (1990) and Kay and Wagner (1994) analyzed photographs taken in YNP during the late 1800s, and found little or no evidence of

Figure 3.1. A photograph of a browsed sucker taken near Hellroaring Creek trailhead, Yellowstone National Park.

Figure 3.2. Photograph illustrating the bark scarring of aspen caused by ungulate browsing. Taken near Mammoth Hot Springs, Yellowstone National Park.

aspen bark scarring during that period. This stripping of bark allows entry to pathogens and an increased incidence of disease and mortality in aspen stems (Hinds, 1985).

Kay (1994) has proposed that in the pre-European-American era, heavy predation by Native American hunters kept the elk population low enough to allow for aspen recruitment in the Yellowstone area. Unfavorable 20th-century climatic conditions for aspen recruitment has also been proposed as a cause of aspen decline in YNP and elsewhere in western North America (Houston, 1982; Romme et al., 1995; Meagher and Houston, 1998). Suppression of wildfire may also play a role in aspen decline (Houston, 1973; Bartos and Campbell, 1998). Romme et al. (1995) suggested that aspen overstory recruitment on YNP's northern range was influenced by an interaction of fire, climatic variation, and elk abundance. Ripple and Larsen (2000, Ripple et al., in press) proposed that a trophic cascades relationship involving mammalian predators, elk, and aspen may be a major factor affecting aspen overstory recruitment, where mammalian predation may have affected elk browsing patterns sufficiently to allow some aspen stands to recruit tree-sized stems.

Whether the inability of YNP aspen to regenerate overstory stems since the 1920s represents a departure from natural conditions or simply reflects the episodic nature of aspen regeneration in a centuries old pattern is uncertain. Meagher and Houston (1998) hypothesized that the current YNP aspen overstory may be a departure from a natural condition of little or no tree-sized aspen on the northern range. They suggested that the aspen occurring on the northern range currently are an artifact of the "market hunting" era (1872~1883) when animal populations were hunted to low levels and browsing pressure was minimal. Market hunting, coupled with favorable climatic conditions and the occurrence of wildfires may have created an unusual opportunity for a large cohort of aspen to grow to tree size during the late 1800s. Conversely, Ripple and Larsen (2000) concluded that aspen on YNP's northern range had recruited overstory stems successfully from the mid-to-late 1700s to the 1920s, but has had little success since that time.

Aspen stands on elk winter range near YNP's portion of the northern range have not been as extensively studied or compared to YNP stand conditions. Kay (1990) compared aspen overstory recruitment in the Eagle Creek drainage of the Gallatin National Forest with YNP, concluding that Eagle Creek stands had lower sucker densities but a greater diversity of overstory 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 concluded 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. In the Sunlight/Crandall elk winter range, I am aware of no studies devoted to the status of aspen. Hyde (1964) and Hyde and Beetle (1964) discussed the condition of aspen stands in the early 1960s, noting that the existing stems were highlined by elk browsing and suckers were being browsed heavily enough to prevent new cohorts of stems from joining the overstory. Several aspen stands were cut in the Sunlight/Crandall area in 1981–82 in an attempt to stimulate suckering and stand rejuvenation (King, personal communication).

Management of wild ungulates differs between YNP and the surrounding National Forests. Regulated hunting is legal on national forest lands in the area, but was banned in YNP in 1883, although a significant amount of poaching continued in the park for several years thereafter (Haines, 1977). The early years of the 20th century were a period of complete protection and periodic supplemental winter feeding of wild ungulates in YNP. The northern range elk herd grew until it was thought to be necessary to cull animals and reduce the size of the herd. Periodic elk herd reductions took place between 1935 and 1968 and included both live trapping and shooting by YNP personnel (Houston, 1982; Huff and Varley, 1999; Wright, 1998). Since 1968, elk have been protected from human predation within YNP boundaries under the natural regulation policy. Houston (1982) summarized estimates of the northern range elk herd size, hunter harvests outside YNP, and park service removals for the period of 1923–1979. Lemke et al. (1998) summarized elk population size and hunter harvest levels outside YNP for the period of 1975–1997.

I designed a remote sensing and field-based study to compare aspen stand conditions on YNP's northern range to contiguous national forest areas adjoining the park to the north and east. The objectives of my study were the following:

1.) Use matched sets of aerial photographs to determine the extent of aspen and conifer canopy change for the period of 1954–1992 (YNP's northern range) and 1958–1995 (Gallatin's northern range and the Sunlight/Crandall basins in the Shoshone National Forest).

2.) Use field-collected data to determine whether there were significant differences in the condition of aspen stands inside and outside of YNP borders and interpret any differences in terms of ecological processes.

Variables used to assess and compare the condition of aspen stands included the density of aspen suckers, the percentage of browsed suckers, the density and size class distribution of the aspen overstory, the extent of bark damage to aspen stems, and the degree of conifer encroachment in aspen stands. Ancillary information including elevation, aspect, and aspen habitat type were also collected to control for differences based on site character.

Methods

Study Area

The study area included portions of YNP, the Gallatin National Forest, and the Shoshone National Forest. These areas were selected since they all contain aspen, are in close geographic proximity to YNP's northern range, have similar climatic patterns, and are elk winter range. Only national park or national forest lands were included in the study; all private lands were omitted. Livestock grazing allotments occur on a portion of the national forest lands selected.

In YNP and the Gallatin, the study area was the northern range, which lies in the valleys of the Yellowstone, Lamar, and Gardiner Rivers (Figure 3.3). The northern range is the wintering area for the largest elk herd in YNP, called the "northern herd." Houston (1982) defined the northern elk winter range as an area of 100,000 ha lying within YNP and the Gallatin National Forest, as far north as Dome Mountain. Using GIS technology, a more recent estimate of the size of the northern elk winter range was 152,663 ha (Lemke et al., 1998). Much of this increase was due to elk expanding their winter range to the north of Dome Mountain, beginning in the winter of 1988–1989. The boundaries of the Sunlight/Crandall study area corresponded to the critical elk winter-range boundary established by the Wyoming Department of Game and Fish.

Northern range vegetation consists of steppe rangelands dominated by sagebrush (primarily Big Sagebrush, *Artemisia tridentate*) and grassland interspersed with small stands of conifer (primarily Douglas-fir, *Pseudotsuga menziesii*) and aspen (Houston, 1982). The climate is characterized by cold winters and short, cool summers. The northern and Sunlight/Crandall elk winter ranges are near the lower limit of precipitation (38 cm annually) required by aspen in the western United States (Jones and DeByle, 1985). The Crandall Creek weather station (elevation = 1968 m) averages 37.84 cm of precipitation/year, while the Tower weather station (YNP, elevation = 1910 m) averages 42.95 cm per year (Western Regional Climate Center, 2000) and the Lamar weather station (YNP, elevation = 1972 m) averages 37.15 cm/year (Dirks and Martner, 1982).

Sample Selection

In YNP and the Sunlight/Crandall basins, a set of color infrared (CIR) aerial photographs was used to inventory existing aspen stands and select a random sample. These photographs were taken in September 1988 at a scale of 1:24,000. CIR

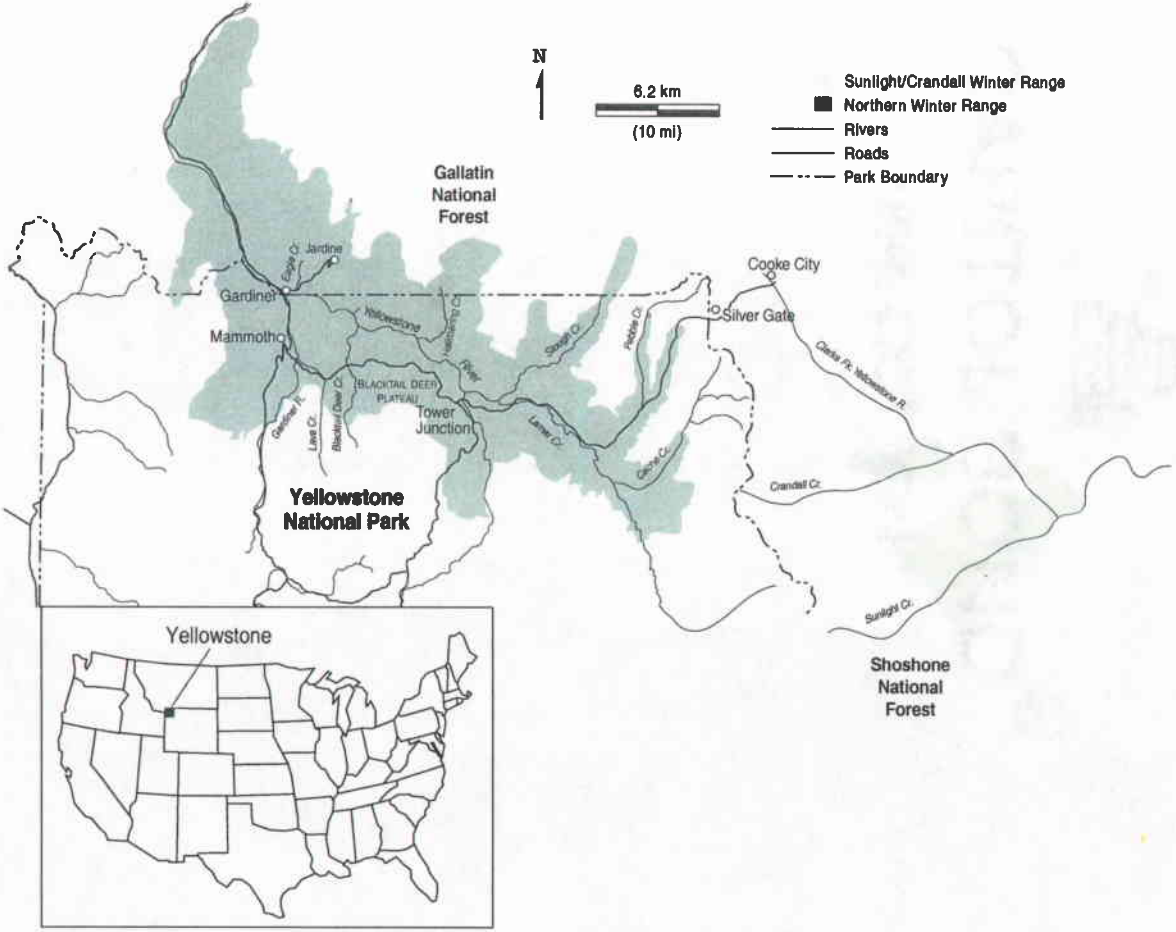

Figure 3.3. Study area map. A portion of the northern elk winter range lies within YNP and a portion lies within the Gallatin National Forest. The Sunlight/Crandall elk winter range lies east of YNP in the Shoshone National Forest.

photographs were used due to the simplicity with which aspen (white crowns in the late fall CIR photographs) could be differentiated from conifers (red crowns in CIR). All aerial photograph interpretation was done using a scanning stereoscope and sufficient detail was present in the CIR photographs to discern individual aspen crowns in poorly stocked stands. A 1.0 cm x 1.5 cm (240 m x 360 m cell size) rectangular grid was placed on each aerial photograph and each cell was identified as either containing or not containing aspen. The sample was then stratified to include only those grid cells identified as containing aspen. From the stratified sample, a random selection was made of 100 grid cells in YNP and 55 cells each from Sunlight/Crandall basins. These cells 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. Grids were placed over the aerial photographs and an aspen inventory was conducted using the same methods as described for YNP and the Shoshone National Forest. A random sample of 75 cells containing aspen was chosen from the Gallatin National Forest stratified sample.

Remote Sensing Analysis

For the remote sensing analysis, historic (1950s) aerial photographs were paired with recent (1990s) aerial photographs of the same sites to analyze change in aspen and conifer canopy coverage over time. An inventory of existing aerial photography in the study area was conducted, recognizing that the National Forests and YNP have not historically collected aerial photography at the same time or for the same purposes. The goal was to select sets of aerial photographs that provided complete coverage for the two National Forests and YNP and were as closely matched in time and scale as possible. In YNP, a set of 1954 black and white aerial photographs were paired with a 1992 natural-color set, providing a span of 38 years. In the Shoshone and Gallatin National Forests, 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 for the change detection analysis, a historic (1954/1958) and recent set (1992/1995) for YNP, the Gallatin National Forest, and the Sunlight/Crandall basins.

Each of the 285 randomly selected grid cells was located on both the historic and recent aerial photographs. For the 1992/1995 aerial photographs, a 35mm camera and a photographic copy stand were used to make a stereo pair of copy negatives of the chosen grid cells from which 1:7000 scale color enlargements were obtained. Sets of 9 x 9 inch black and white negatives were obtained for the 1954/1958 photographs. Using a 4 x 5 inch photographic enlarger, a set of stereo black and white enlargements matching the 1992/1995 prints was obtained. Figure 3.4 illustrates a matched set of 1954 and 1992 aerial photo plots located in the Lamar River valley in YNP.

A 9 x 18 dot grid (162 total dots) was placed over each 1:7000 enlargement. Using a scanning stereoscope and the dot grid, vegetation cover was counted as conifer, aspen, or steppe. The percentage of aspen and conifer canopy coverage per grid cell was calculated for each of the two time periods. Changes in mean canopy coverage were compared between the three areas for the period 1954(58) to 1992(95).

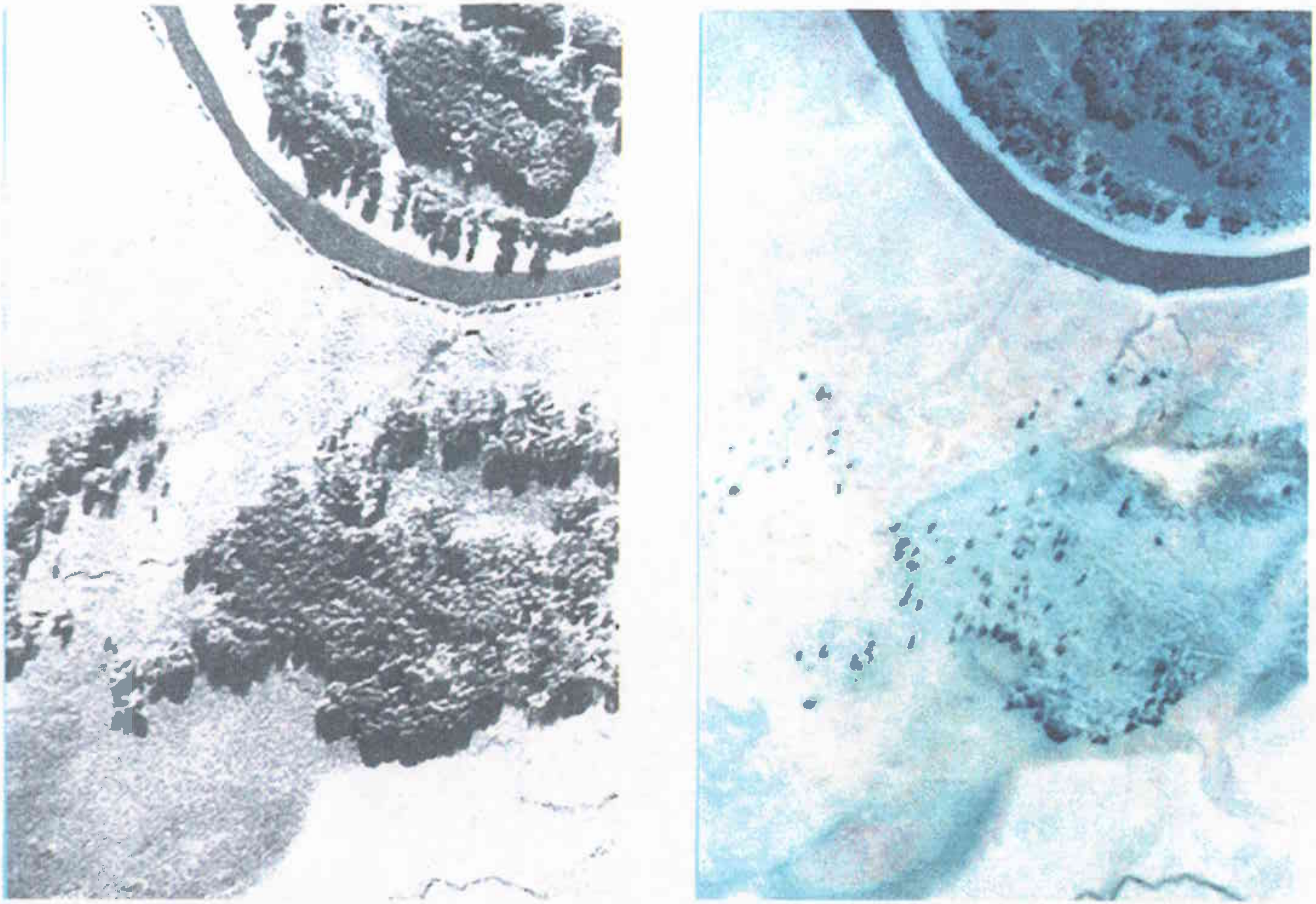

Figure 3.4. 1954-1992 comparison of an aspen stand occurring in a riparian area near the Lamar River in YNP. On the 1992 (color) photograph, dead aspen boles are clearly visible on the ground as white lines. This area did not burn in the interval 1954-1992.

Canopy coverage change in 1992(95) was also calculated as a proportion of the base year of 1954(58).

Field Methods

Each of the aspen grid cells analyzed in the remote sensing portion of the study were also sampled in the field. Additionally, transects were conducted in all the aspen stands located in scree habitats that were found in YNP during the course of field work. For the field measurements, one 2 x 30-m belt transect was located in an aspen stand at each of the sites. A stand was defined as a group of aspen trees all within 30 m of its cohorts. If the 240 x 360-m grid cell contained more than one aspen stand, the stands were numbered and a random selection of a single stand was made. A random cardinal start direction was chosen and the transect ran from the large-stem aspen (>5 cm DBH) standing furthest in that direction in towards the centroid of the aspen stand.

The following measurements were made in each of the field belt transects:

1.) The total number of suckers, and whether they were browsed, unbrowsed, or dead. A sucker was defined as an aspen ≤ 200 cm in height. The heights of all suckers > 100 cm were measured and recorded. Aspen suckers often occurred in clumps of two or more. These clumps were counted as a single sucker since only one of the sprouts would be likely to survive to tree form.

2.) The species and DBH of all overstory trees in the belt transect were recorded. An overstory aspen was defined as a stem >200 cm. Each stem was classified as living, standing dead, or dead and lying on the ground. Additionally, the degree of bark damage on all aspen overstory stems was recorded. Bark damage was defined as the black, corky bark scarring caused by ungulates and voles chewing on aspen bark (Figure 3.2). The aspen stems were visually inspected up the first 3 m of the trunk 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.) A Global Positioning System (GPS) was used to determine the UTM coordinates and elevation of the site. Additionally, the aspect, slope, evidence of fire, and the presence of any barriers to browsing were recorded. Browsing barriers included scree, boulders, roads, cliffs, or jackstrawed conifers.

The field-collected data was tested for skewness and kurtosis. Analysis of variance (ANOVA) was used to analyze differences among the three study areas when the data were normally distributed. Transformations were performed on data sets containing skewed distributions. If the data were still non-normally distributed after transformation, the Kruskal-Wallis (KW) test was used on the original data. DBH class, the presence of tall suckers (>100 cm) and bark scarring were collected as categorical data. Pearson's χ^2 test was used to analyze differences between the three areas for the categorical data (Johnson and Bhattacharyya, 1986). Overstory aspen were categorized into four DBH categories (1–4 cm, 5–9 cm, 10–19 cm, >20cm DBH). The degree of bark scarring was estimated as low (<33%), medium (33%–66%), or high (>66%). *Statgraphics* software was used to perform the statistical analysis.

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, delineated by understory vegetation, site wetness, and topography were as follows:

1.) Xeric sites. The understory of these aspen stands included grasses such as Idaho fescue (*Festuca idahoensis*), 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 sites. This aspen habitat type contained sites with moist to saturated soil conditions. A mixture of grasses and tall forbs characterized this habitat type. Timothy (*Phleum pratense*) was a dominant grass 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* sp.) mixed with timothy and forbs.

3.) Scree sites. An aspen community growing on scree slopes characterized these sites. The understory was typified by sparse vegetation and thin soils in a rock substrate (St. John, 1995). Xeric conditions predominated in scree aspen stands.

Scree forms a natural barrier to browsing; I compared aspen stands in the scree habitat type with the unprotected xeric and mesic sites in YNP. Sucker density/ha, the percentage of browsed suckers, and aspen overstory density/ha were compared using the Mann-Whitney test. The occurrence of tall suckers and the overstory DBH class structure were compared using Pearson's χ^2 test.

Results

Remote Sensing

I analyzed 210 of the 230 randomly chosen sites. The reasons for eliminating sites included misclassification in aerial photography (either cottonwood (*Populus* spp.), willow (*Salix* spp.), or burnt conifer being classified as aspen), site location on private land, or access problems due to crossing private land. My sample included 93 sites in YNP, 63 sites in the Gallatin, and 54 sites in the Sunlight/Crandall basins.

An example of the change detection process using the 1954–1992 aerial photographs is shown in Figure 3.4. The mean change in aspen canopy is shown as a percentage of the 240 x 360 m grid cells (Table 3.1). The mean area of aspen canopy coverage is shown in two ways, as an absolute figure and as a proportion of the 1954(58) canopy. In absolute terms, all areas declined less than 4% in aspen canopy coverage during the 1954(58)–1992(95) period. YNP showed the greatest loss of aspen canopy when taken as a proportion of its 1954 canopy, falling from a mean 1954 value of 7.41% canopy coverage (per 240 x 360 m cell) to 4.55% in 1992, a proportional decline of –38.6%. The Gallatin and Sunlight/Crandall areas had smaller proportional levels of decline (–22.73% and –22.74%, respectively) in their aspen canopies.

Conifer canopy coverage expanded more in the Gallatin and Sunlight/Crandall areas than in YNP (Table 3.1). These results were strongly influenced by the pattern of

Study Area	n	Mean canopy coverage per 240x360m cell (%)	SD (%)	Min	Max (%)	Mean canopy area change 1995-1958 (YNP 1954-1992) (%)	SD for canopy change 1995-1958 (YNP 1954-1992) (%)	Canopy coverage change as a proportion of 1958 canopy coverage (1995-1958)/1958 (%)
ASPEN								
Gallatin 1995	63	10.47	8.81	0	37.65	–3.08	7.24	–22.73
Gallatin 1958	63	13.55	11.67	0	45.65			
Sunlight/Crandall 1995	46	4.45	6.11	0	19.75	–1.31	2.88	–22.74
Sunlight/Crandall 1958	46	5.76	7.07	0	25.31			
YNP 1992	93	4.55	4.83	0	30.25	–2.90	4.69	–38.60
YNP 1958	93	7.41	7.01	0	33.33			
CONIFER								
Gallatin 1995	63	19.34	18.94	0	67.28	3.72	6.16	23.84
Gallatin 1958	63	15.62	17.57	0	62.35			
Sunlight/Crandall 1995	46	26.44	22.43	0	75.31	4.01	8.85	17.88
Sunlight/Crandall 1958	46	22.43	18.31	0	69.14			
YNP 1992	93	14.05	13.39	0	64.81	0.27	6.22	1.98
YNP 1958	93	13.78	14.21	0	69.75			

Table 3.1. Summary of mean changes in aspen and conifer canopy in the Clarks Fork, 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.

the 1988 fires, which burned a more extensive area in the YNP study area than in the Gallatin or Sunlight/Crandall.

Field Results —Aspen Suckers

Field transects were conducted for all 210 sites analyzed in the canopy change portion of the study. An additional 12 transects were completed in scree aspen habitat-type stands located in YNP.

There was not a significant difference among any of the study areas in the density of aspen suckers/ha (Table 3.2, p-value = 0.940). Aspen sucker densities in all areas were highly variable, ranging from 0–29,000/ha. The percentage of browsed suckers was high in all areas, and the KW test indicated that there was not a significant difference among the three study areas (p-value = 0.179).

The Gallatin and Sunlight/Crandall areas had higher percentages of aspen stands with tall suckers (>100 cm) than did YNP stands. On the northern range within YNP, tall suckers occurred in 10.8% of the stands, compared with 31.5% and 54.0% in the Sunlight/Crandall and Gallatin areas, respectively. Using Pearson's χ^2 test, YNP's percentage of stands with tall suckers was significantly less than stands in the other areas (p-value < 0.001); 2.5% of the total suckers measured in YNP exceeded 100 cm, compared with 10.0% and 5.0% in the Gallatin and Sunlight/Crandall areas, respectively.

Table 3.2. Summary of aspen stand field data

Variable	n	Mean	SD	Min	Max	Median	Kruskal-Wallis p-value	Homo-geneous groups
Aspen sucker density								
Gallatin	63	3846.56	3846.00	0.0	16500.0	2666.7		
Sunlight/Crandall	54	4577.16	5835.60	0.0	29000.0	2833.3		
YNP	93	3593.19	3593.00	0.0	19166.0	2166.7	0.940	G,S,Y*
Aspen suckers – percent browsed								
Gallatin	59	80%	23%	0%	100%	87%		
Sunlight/Crandall	48	82%	21%	0%	100%	82%		
YNP	83	87%	18%	0%	100%	90%	0.179	G,S,Y*
Aspen overstory density/ha								
Gallatin	63	1190.48	753.05	166.7	3500.0	1000.0		
Sunlight/Crandall	54	938.27	484.81	166.7	2166.7	833.3		
YNP	93	645.16	440.43	166.7	2666.7	500.0	<0.001	G,S*
Aspen overstory density >20cm DBH/ha								
Gallatin	63	515.87	369.92	0.0	1666.7	500.0		
Sunlight/Crandall	54	453.70	364.02	0.0	1666.7	416.7		G,Y*
YNP	93	627.24	425.91	166.7	2500.0	500.0	0.026	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%	0.648	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%	<0.001	G,Y*

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

Field Results —Aspen Overstory

Overstory aspen were grouped into four DBH categories: 1–4 cm, 5–9 cm, 10–19 cm, and >20 cm. The greatest differences inside and outside of YNP occurred in the 1–4 cm, 5–9 cm, and 10–19 cm DBH categories, where the YNP stands were poorly represented compared with the Gallatin and Sunlight/Crandall (Figure 3.5) areas. No sampled 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. The χ^2 test indicated significant differences in the DBH distributions of the three areas, with YNP differing from the Gallatin and Sunlight/Crandall areas (p-value <0. 001).

Overstory aspen density in YNP was significantly different (lower) than the other two study areas (Table 3.2, KW $p < 0.001$). This difference was due to YNP's lack of aspen stems in the 1–4, 5–9, and 10–19 DBH size classes (Figure 3.5).

The ratio of standing dead aspen to total aspen stems was similar in all areas, ranging from 27% in the Gallatin to 34% in the Clarks Fork area, but the differences were not significant (Table 3.2, p-value = 0.648).

Conifer encroachment into aspen stands was measured as the ratio 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 overstory than did those in the Sunlight/Crandall basins (Table 3.2). Aspen stands in YNP and the Gallatin averaged 12.0% (SD = 22%) and 17% (SD = 22%) of their overstories in conifer, while the Sunlight/Crandall area averaged 39% (SD = 29%)

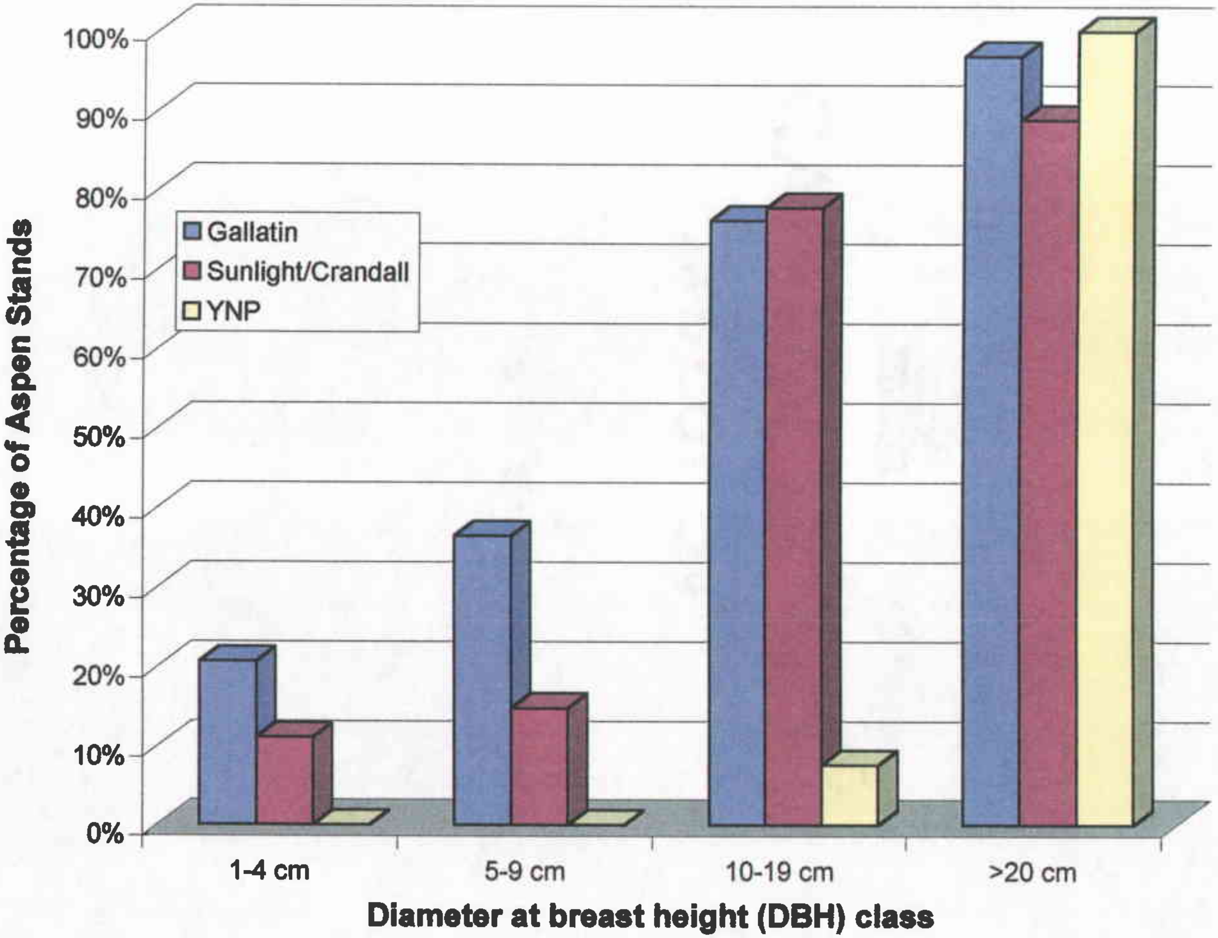

Figure 3.5. The percentage of aspen stands containing stems in 4 diameter-at-breast height (DBH) classes. Since aspen stands may contain more than one size class, the percentages may add up to more than 100%.

The level of bark scarring on aspen in YNP was significantly different (greater) than on aspen in the Gallatin or Sunlight/Crandall areas (p-value < 0.001). None of the measured aspen overstory stems in YNP (n=364) had low (<33%) or medium (33%–66%) levels of bark scarring (Figure 3.6).

Field Results —Elevation, Aspect, and Habitat Type

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 3 ranges (<2000 m, 2000–2199 m, and >2200 m) and each area was tested separately to see if sucker densities, overstory stem densities, the incidence of tall suckers, and DBH class distribution were influenced by elevation. Using the KW test, no significant difference was found in either sucker or overstory densities (p > 0.163 for all areas). Tall suckers and smaller DBH classes were found in all elevational ranges in the Gallatin and Sunlight/Crandall basins. Yellowstone National Park lacked 1–4 and 4–9 cm overstory stems in all the elevational ranges.

The greatest percentage of aspen stands sampled in the Sunlight/Crandall and Gallatin areas had south aspects, while in YNP north aspects were most common. Using the KW test, stem densities were not found to differ based on aspect in any of the three areas (p > 0.240 for all areas). In the Sunlight/Crandall area, tall suckers and all the DBH classes were present in all aspect classes. In the Gallatin area, there were no 1–4 cm DBH stems in north aspect aspen stands (n = 5 north aspect aspen stands), but all other aspects contained stands with tall suckers and stems in all the DBH classes. In YNP there were no 1–4 cm and 5–9 cm DBH stems found in any

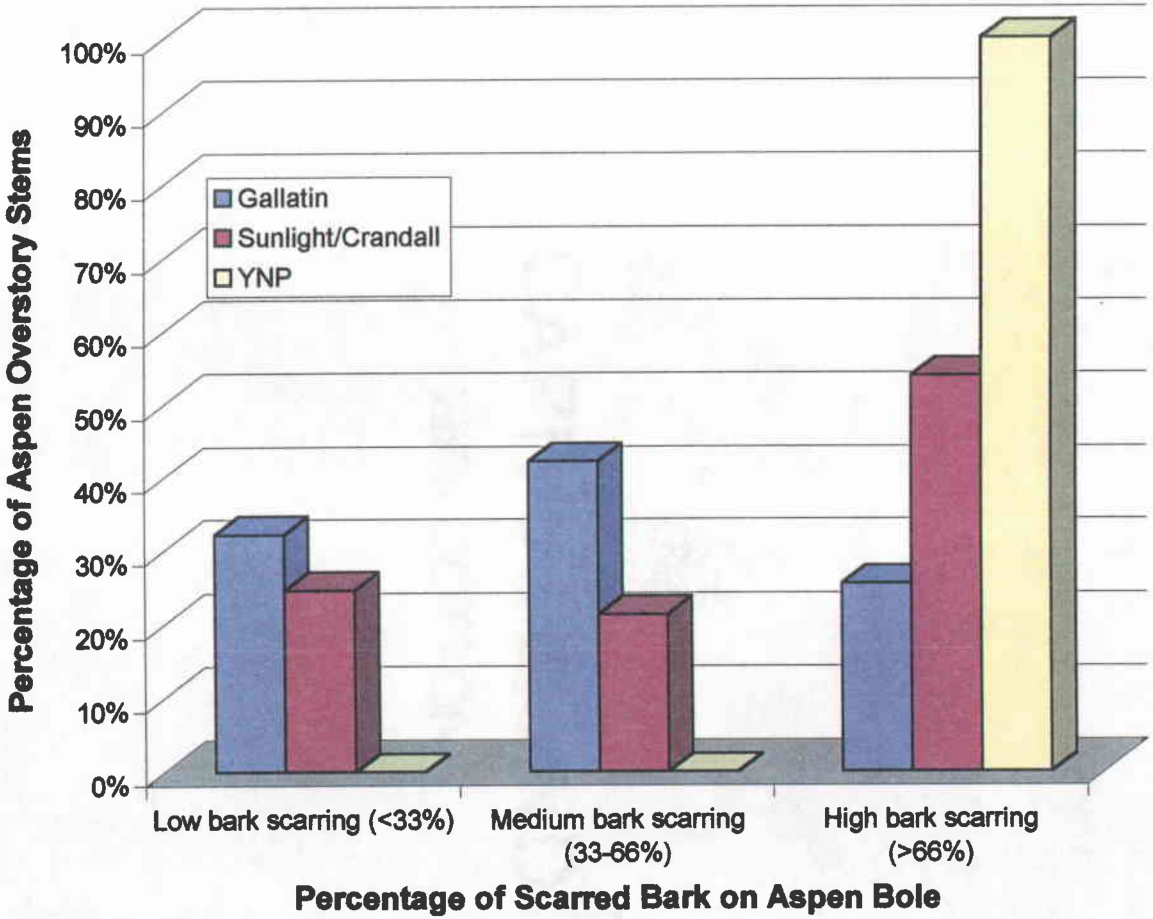

Figure 3.6. The percentage of aspen stems in 3 bark-scarring categories. The stems were inspected from ground level to 3 m up the bole. Low bark damage means that less than 33% of the bark area in the first 3 m consisted of the black, corky bark caused by ungulate browsing. Medium damage means that between 33-66% of the bark area was black, corky and damaged. High damage represents a >66% level of the black, corky, and damaged bark.

non-scree aspen transects, regardless of aspect. Aspen stems in the 10–19 cm and > 20 cm DBH classes were distributed among all four aspect classes.

YNP had 46 sites in the xeric habitat type and 47 sites in the mesic. The Sunlight/Crandall basins had 24 in the xeric and 23 in the mesic habitat type. The Gallatin contained 27 xeric and 36 mesic aspen stands. Mean overstory aspen stem and sucker densities were higher in mesic habitat type stands than in the xeric stands, but only in YNP were the differences even marginally significant ($p = 0.091$ for overstory density, $p = 0.023$ for sucker density in YNP).

Field Results —Scree vs. Non-scree Habitat-Type Stands within YNP

The 12 scree habitat type stands in YNP differed from the YNP non-scree (xeric and mesic) habitat types in several respects. The mean sucker density (805.56/ha, SD = 1786.4) in the scree stands was lower than in the non-scree habitat types (3593.19/ha, SD = 3804.0, p-value < 0.001). The scree stands contained a significantly lower percentage of browsed suckers than the other habitat types in YNP (Mann-Whitney p-value = 0.003). The incidence of tall suckers (> 100 cm) was significantly higher in the scree stands, occurring in 58% of the stands sampled as opposed to 10.8% in YNP non-scree habitat types ($p < 0.001$). The size class distribution was significantly different between the YNP scree habitat type stands and the non-scree types ($p < 0.001$), with the most significant differences in the smaller DBH categories (Figure 3.7). 75% of the scree stands contained aspen stems in the 1–4 cm DBH category (0% in YNP non-scree stands), 75% contained stems between 5–

9 cm DBH (0% in YNP non-scree stands), and 58% contained stems between 10–19 DBH (8% in YNP non-scree stands).

Discussion

Aspen stands on the northern range in the Gallatin National Forest and in the Sunlight/Crandall basin were more variable than were those in YNP, containing higher percentages of stands with tall suckers, smaller and younger DBH stems in their overstory, and lesser proportions of aspen canopy loss since the 1950s.

One hypothesis is that warmer and dryer climatic conditions during the 20th century may be a significant factor in the failure of aspen to recruit new overstory stems on the northern range (Huff and Varley, 1999; Meagher and Houston, 1998; YNP 1997). The pattern of aspen stand conditions I observed does not support that hypothesis. On a landscape scale, I observed in the Gallatin that tall suckers and small DBH, younger stems existed in aspen stands of similar elevation, aspect, and mean annual precipitation to those in YNP that had not produced any new overstory stems since the 1920s. Aspen stands in the Sunlight/Crandall basins have also been more successful in producing tall suckers and multiple DBH/age classes of stems in the 20th century than stands on YNP's northern range, despite having a lower mean level of annual precipitation (Western Regional Climate Center, 2000).

At the scale of the individual stand, aspen on the northern and Sunlight/Crandall elk winter ranges occur on a variety of site conditions, from the dry, thin soils of the scree habitat type to deeper alluvial soils in riparian and wet meadow sites. If variables such as moisture availability were significantly influencing aspen

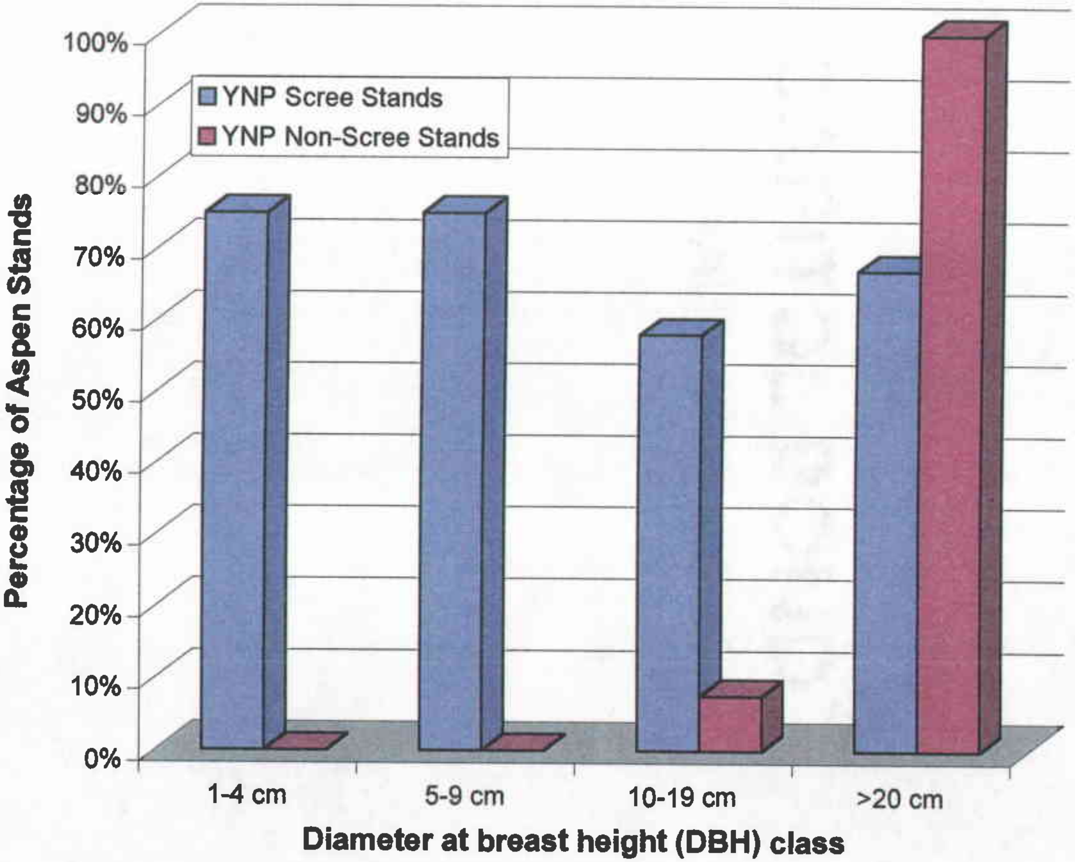

Figure 3.7. A comparison of the scree habitat aspen stands with non-scree stands (xeric and mesic habitat types) on the northern range in YNP. The bars represent the percentage of aspen stands containing stems in 4 DBH classes. Scree stands differ from the other habitat types (xeric and mesic) because the scree forms a natural barrier to ungulate browsing. This partial protection from browsing has allowed the scree habitat type stands to develop a more varied distribution of overstory stem DBH sizes than in non-protected stands.

overstory recruitment, one might expect a continuum of overstory regenerative success, correlated with site moisture and soil quality. However, I observed that the aspen stands most successful in producing new cohorts of overstory stems in YNP from 1920–98 occurred on the scree habitat type, characterized by xeric conditions and thin, rocky soils. Additionally, I found that aspen stands in the Gallatin and Sunlight/Crandall have produced small DBH, younger age classes on all habitat types, not just the sites of reduced browsing pressure. When comparing sites of comparable moisture availability, elevation, and aspect inside and outside of YNP borders, I conclude that the pattern of aspen overstory recruitment I observed is inconsistent with warmer and more arid conditions being significant factors in limiting aspen overstory recruitment for the period 1920–1998.

Fire has been shown to stimulate sucker production for several years post-burn 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 suckers/ha in six aspen stands burned in the 1988 Yellowstone fires, much higher than the densities I measured (Table 3.2). By 1991, Romme et al. (1995) noted a decline in sucker density in burned aspen stands and by 1997/98, my data showed no difference in mean sucker density in stands burned or unburned in the 1988 Yellowstone area fires. The 1988 fire season also helped create environmental conditions leading to a significant aspen seedling establishment within YNP, with mean densities as high as 142,695/ha in the Yancey's Hole region of YNP (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 5.39 cm DBH and my sample did not record any trees in YNP within the 1–9 cm DBH range, except on sites protected from browsing. In agreement with Kay (1993) and Romme et al. (1995), I found no evidence that the 1988 fires has or will lead to an episode of aspen overstory recruitment in YNP, except on a few sites protected from browsing. Further, the Gallatin and Sunlight/Crandall areas have similar histories of fire suppression as YNP, and fire cannot explain the spatial pattern of aspen stands with smaller DBH, younger age class trees outside of YNP boundaries.

The encroachment of conifers into aspen stands is related to the fire return interval. Bartos and Campbell (1998) outlined risk factors for aspen stands, one of which was conifers exceeding 25% of the total stem count. After a century of fire suppression, only 12% (YNP) to 17% (Gallatin) of northern range aspen stands exceeded 25% of the stem count in conifers, so conifers are not an immediate threat to dominate and eventually replace aspen 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 basins were more heavily invaded by conifers, with 59% of sampled aspen stands having more than 25% of the total stem count in conifers. However, many of these conifers are <3 m tall, so the conversion of aspen sites to conifer is not imminent, although continued monitoring is important.

Evidence of ungulate browsing was high in all four areas, ranging from mean levels of 78% of sampled aspen suckers in the Gallatin National Forest to 87% in YNP. Ungulates appear to browse nearly all available aspen suckers without discrimination. Most of the ungulate browsing on aspen occurs in the winter and the unbrowsed suckers I observed in YNP consisted primarily of first year suckers that ungulates had not yet had the opportunity to utilize. Virtually all northern range aspen suckers > 1 year exhibited the hedged branch structure that occurs when the leader of the sucker is browsed.

Although there was no significant difference in mean browsing pressure on aspen suckers among the study areas, there was evidence that ungulates may utilize aspen stands in YNP more intensively than those in the Gallatin and Sunlight/Crandall areas. YNP aspen stems had significantly higher levels of bark scarring than stems in the National Forest areas ($p < 0.001$). The absence of tall suckers also provides evidence that browsing levels may be more intensive in YNP than in the surrounding National Forest areas. On good sites, aspen suckers may grow more than one meter per year (Jones and Schier, 1985) and tall suckers provide a cohort of potential replacement overstory aspen stems for a stand. However, repeated ungulate browsing suppresses sucker heights and prevents suckers from obtaining heights > 1m. In YNP, only 11% of the sites contained tall suckers, compared with 31% in the Sunlight/Crandall basins and 54% in the Gallatin area.

The stand conditions in the YNP scree habitat aspen most closely resembled stands outside YNP in their ability to produce tall suckers and small DBH aspen stems. Within YNP, the percentage of browsed suckers and the degree of bark damage to overstory stems was much lower in the scree habitat type than in the other habitat types, indicating less intensive browsing pressure. The scree stands contained much higher percentages of tall suckers and stems in the 1–4 and 5–9 cm DBH class. These results were consistent with St. John's (1995) findings in a study conducted on the Gallatin National Forest. The scree aspen stands, along with the fenced exclosures, road ditches, and jackstraw piles were the areas where small DBH aspen stems were most commonly observed on YNP's portion of the northern range. These scree stands represent a natural condition in which browsing pressure is reduced and illustrate that YNP northern range aspen have produced a cohort of replacement overstory stems in the mid to latter 20th century on xeric sites in areas of reduced browsing pressure.

Although aspen canopy coverage has declined both inside and outside of YNP, aspen stands in the Gallatin and Sunlight/Crandall areas have produced significantly higher percentages of tall suckers and younger, smaller DBH trees than stands within YNP on sites of comparable elevation, aspect, moisture availability, and fire history. Aspen stands outside YNP also have significantly lower levels of bark damage to stems due to ungulate browsing. Within YNP, the scree habitat stands have produced significantly higher percentages of tall suckers and younger, smaller DBH trees than xeric and mesic sites available to ungulate browsing. These results suggest that elk browsing has been the principal factor in suppressing the recruitment of aspen overstory stems within YNP from the 1920s to 1998, rather than fire suppression or a trend toward more arid climatic conditions.

Much of the focus of previous research has been on the number of elk browsing on aspen, but I hypothesize that the differences in aspen stand conditions may be related to predation risk effects on elk behavior and movement, rather than strictly on elk densities. Predation risk effects describe a trade-off in foraging strategy where elk may avoid or spend less time in certain areas to reduce their chances of predation from humans or other mammalian predators (Lima and Dill, 1990; Schmitz et al., 1997).

Historically, both Native American and other mammalian predators preyed on elk throughout the area and there has been much debate on the impact of the YNP boundary line on elk movement and behavior (Skinner, 1928; Houston, 1982). Regulated hunting for elk has been legal in the Gallatin and Shoshone National Forests for most of the 20th century, while hunting was banned in YNP in 1883, and wolf predation was eliminated from the Yellowstone area by the 1920s (Weaver, 1978; Houston, 1982). However, YNP was managed under the "direct reduction" policy from 1930–1968, where the size of the elk herd within YNP was controlled by live-trapping and killing to stay within established population targets.

The failure of aspen to recruit overstory stems while the size of the elk herd was reduced within YNP has long puzzled scientists. Craighead et al. (1972) and Houston (1982) studied the effects of the direct reduction policy and concluded that it had disproportionately reduced the migratory segment of the herd, and perhaps disproportionately reduced browsing pressure on aspen outside of YNP. Increased numbers of elk have migrated out of YNP since 1988–1989 and hunter harvest levels have increased, although the overall effect of hunting on the total population of the northern elk herd has not been great (Lemke et al., 1998; Schafer, 2000). Other studies have shown that elk modify their behavior in the presence of predation, avoiding or minimizing contact with human and/or animal predators (Thompson and Henderson, 1998; Millspaugh et al., 2000). In the Gallatin's portion of the northern range, St. John (1995) concluded that aspen stands < 500 m from roads were less impacted by ungulates than were those further away, suggesting a foraging behavioral adjustment to avoid contact with humans.

To test my hypothesis that predation risk effects may allow some aspen stands to recruit overstory stems under the current levels of high ungulate density within YNP, I have recently begun a long-term trophic cascades study within YNP (Ripple and Larsen, 2000; Ripple et al., in press). My objective is to study whether elk may avoid areas of high wolf presence on YNP's northern range, allowing aspen to recruit smaller DBH, younger stems in those areas. Initial results indicate that elk may be avoiding areas of high wolf presence on the northern range but it is still uncertain whether this pattern will ultimately result in new aspen stems being recruited into the overstory.

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CHAPTER 4. CONCLUSIONS

This is the first comprehensive study of aspen stand conditions and age structure over the entire northern range, both within YNP and on the Gallatin National Forest. Additionally, this is the first ecosystem-scale study to compare the status of aspen on the northern elk winter range with the nearby Sunlight/Crandall elk winter range. I sought to accomplish four tasks in undertaking this dissertation research: 1) To compare the aspen age structure on YNP's northern range with the aspen age structure on elk winter range on contiguous and nearby elk winter range outside of YNP borders. 2) To compare current aspen stand conditions on elk winter range inside and outside of YNP borders. 3) To compare aspen and conifer canopy change from the 1950s to 1998. 4) To determine the relative influence of various ecological factors to explain the spatial and temporal patterns I discovered.

Aspen stands on the northern and Sunlight/Crandall elk winter ranges occur in a variety of environmental settings. This heterogeneity can make comparisons difficult between geographic areas so I collected data as to the elevation, aspect, and general habitat type of all the aspen stands I sampled. That allowed us to compare aspen stands of similar elevational ranges, aspects, and habitat types across the northern range and in the Sunlight/Crandall elk winter range. Based on my extensive sampling of aspen throughout these elk winter ranges in the northern GYE, I conclude that there has not been an ecosystem-scale failure of aspen to recruit new overstory stems from the 1920s to 1998. Aspen stands on the Gallatin's portion of the northern range and in the Sunlight/Crandall basins are heterogeneous, with decadent stands interspersed with stands containing significant percentages of stems in younger and smaller DBH classes. Only on YNP's portion of the northern range has there been a systematic failure of aspen to recruit new stems from the 1920s to 1998, and this has occurred only in areas that are available to browsing.

My data suggests that climatic fluctuations (as measured by the dendroclimate indices) were not responsible for the pattern of aspen overstory recruitment I observed. In the National Forest areas, I found aspen stands with tall suckers and younger, small DBH trees occurred in both the xeric and mesic habitat types. Within YNP, I found that the scree habitat type, characterized by poor soils and xeric conditions, were the most successful at producing tall suckers and replacement overstory aspen stems. Aspen stands in all three areas occurred in comparable elevational zones, aspects, habitat types, and precipitation levels and the pattern of stand conditions I observed inside and outside of YNP cannot be adequately explained by regional climatic fluctuations.

I found evidence that wildfire may have affected aspen stand conditions in the Crandall Creek area, where 28% of the increment cores collected were dated to within 5 years of the 1935 Crandall/Closed Creek fire. Jones and DeByle (1985) provide examples of even-aged aspen stands in the western U.S. that have been dated to large fire events. Other studies in the GYE have shown that fire will stimulate the production of suckers in aspen clones in the western U.S. (Bartos and Mueggler, 1981; Romme et al., 1995). However, studies in the GYE have also shown that the increased sucker production following fire does not always result in a new cohort of aspen reaching tree height, often due to ungulates browsing all the available suckers (Bartos, 1994; Romme, 1995). The reintroduction of fire back into the GYE must therefore be viewed with caution in respect to its effect on aspen. Following fire, aspen suckers must be given sufficient protection from browsing pressure for suckers to escape to tree height.

Comparing differences in browsing pressure, the occurrence of tall suckers, and the aspen age structure in the scree habitats with the unprotected xeric and mesic sites within YNP leads us to conclude that ungulate browsing is the major ecological process shaping the pattern of aspen stand conditions I observed. Fewer ungulates can browse in these scree stands because of their difficulty of access. However, ungulate density by itself does not explain the inside/outside YNP differences in aspen stands I observed. Historical events such as the "firing line" along the YNP border and the possibility that the "direct reduction" era disproportionately reduced the migratory segment of the northern elk herd were factors that may have contributed to the pattern of aspen stand conditions on the northern range. I hypothesize that differences in elk behaviors due to a differential risk of predation inside and outside of YNP borders may be a significant factor in the development of younger smaller DBH stems in the Gallatin and Sunlight/Crandall areas.

The reintroduction of wolves to YNP's northern range provides a unique opportunity to study the effects that these predators may have on ungulate behavior and browsing patterns. I have recently initiated a long-term study of the trophic cascades relationship between wolves, elk, and aspen on YNP's northern range. My goal is to measure whether the presence of wolves can sufficiently modify elk movements and feeding behaviors to provide areas of refugia on the northern range where aspen stems may be able to recruit new overstory stems. I hope that this dissertation research encourages other researchers to initiate landscape-scale ecological research projects in the GYE.

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APPENDIX

APPENDIX. ASPEN PLOT LOCATIONS

Yellowstone National Park Aspen Plots

Plot designator	n	UTM North	UTM East	Elevation (m)	Aspect
10-44-A5	1	no data	no data		Flat
10-46-F4	2	4979553	519164	2463	South
10-46-I8	3	4976275	517489	2291	South
11-45-D2	4	4979105	519585	2271	North
11-46-B2	5	4975363	522742	2362	South
11-49-G7	6	4976811	521007	2291	North
11-49-G8	7	4981331	522396	2047	East
11-51-AA2	8	4980989	522415	1986	West
11-51-AA5	9	4986391	519219	1934	West
11-51-C8	10	4985821	518970	1729	West
11-51-D8	11	4984440	520418	2009	North
11-51-E8	12	4984197	520388	1942	West
12-90-I8	13	4984376	520863	2019	North
12-90-J9	14	4980816	527126	2030	East
12-90-L6	15	4980699	527270	2325	South
12-92-H11	16	4981597	527758	2302	North
12-92-J9	17	4983756	526551	2022	South
12-92-K10	18	4984221	527540	2044	Flat
13-36-F5	19	no data	no data	2049	North
13-36-G6	20	4976913	530714	2204	North
13-36-G9	21	4976685	531111	2206	East
13-36-H1	22	4975664	531714	2511	East
13-36-H7	23	no data	no data	2178	North
13-37-F5	24	4976271	531493	2041	East
13-38-AA10	25	4978579	530621	2300	East
14-27-AAAA6	26	4979714	528497	2127	East
14-27-B7	27	4974934	532111	2031	Flat
14-27-D7	28	4974409	533363	2300	East
14-27-F6	29	4974317	534893	2038	West
14-27-G7	30	4974857	535471	2200	North
14-27-I1	31	4974549	535864	2122	East

Yellowstone National Park Aspen Plots (Continued)

Plot designator	n	UTM North	UTM East	Elevation (m)	Aspect
15-27-A9	32	4976181	536048	2293	East
16-74-H4	33	4974596	536052	2002	West
16-76-E6	34	4978534	542903	1843	Flat
17-66-F0	35	4981562	541683	2549	North
17-67-D4	36	4979204	545642	2060	Flat
17-68-E6	37	4979174	544986	2572	South
21-57-AAA9	38	4981842	545111	2512	West
20-50-A4	39	4978128	558897	2033	East
20-50-B2	40	4970101	555522	2354	East
20-50-I1	41	4970688	555982	2281	West
20-51-G10	42	4970863	558865	2067	East
21-58-E5	43	4970625	559052	2104	East
21-57-AA8	44	4980953	562344	1964	West
13-38-B5	45	4978303	559195	2035	North
13-38-D12	46	4980213	529816	2265	East
13-38-E4	47	4981035	no data	2123	Flat
13-38-E9	48	4980267	530490	1991	East
13-38-E11	49	4980245	530048	2262	East
13-38-E12	50	4979998	529970	2289	East
13-39-B8	51	4982407	529327	2033	South
13-39-E6	52	no data	no data	1993	South
14-30-A7	53	4980332	532680	1925	North
14-32-C9	54	4985071	533234	1913	South
14-32-D7	55	4985720	533718	2096	East
15-28-B8	56	4977979	526118	2072	Flat
15-28-D1	57	4979688	536761	2080	North
15-28-G9	58	4977803	538083	2194	North
15-30-A12	59	4979898	536482	2074	North
15-30-C6	60	4981600	537545	2094	South
15-30-C12	61	4980323	537742	1948	North
15-30-F9	62	4980614	538694	2020	West
17-64-AA2	63	4975097	543130	2110	South
18-61-E4	64	4975383	549119	1985	South
18-61-H1	65	4976198	550214	2039	Flat

Yellowstone National Park Aspen Plots (Continued)

Plot designator	n	UTM North	UTM East	Elevation (m)	Aspect
18-62-F5	66	4977240	549696	2224	South
19-59-J7	67	4972502	552444	1911	North
19-59-K7	68	4972672	552947	1909	North
19-59-K8	69	4972352	552575	2028	North
19-60-A7	70	4975737	549213	1912	South
19-60-E8	71	4975432	550776	1966	South
19-60-K1	72	4977275	553485	2045	South
19-60-K3	73	4976791	553385	2069	South
19-60-K4	74	4976449	553192	1916	Flat
19-60-L0	75	4977472	553462	1967	South
20-51-A3	76	4972458	556525	2081	North
20-52-A11	77	4972417	553970	2112	North
20-52-H5	78	4974107	556991	1960	South
20-52-L2	79	4975065	558260	2227	West
21-53-D6	80	4970320	561652	1992	South
21-53-F9	81	4969793	562556	2016	South
21-55-B8	82	4973273	560972	2154	North
21-55-B12	83	4972145	561086	2096	West
22-48-F1	84	4966166	566138	2172	West
22-48-G3	85	4965466	566604	2183	West
22-48-H6	86	4964667	566961	2078	South
22-48-J5	87	4965027	567727	1919	South
22-50-A10	88	4967159	563805	2085	Flat
22-50-F6	89	4968291	565953	1999	Flat
23-51-A5	90	4970606	567178	2128	South
23-52-A7	91	4971893	568193	2129	Flat
23-52-D0	92	4973818	569595	2141	South
23-52-C10	93	4971665	569437	2115	Flat

Gallatin National Forest Aspen Plots

Plot designator	n	Watershed	UTM North	UTM East	Elevation (m)	Aspect
1894-54-G3	1	Sphinx Creek	4999820	509454	2072	North
1894-55-C6	2		5000732	509009	1884	South
1894-55-D4	3		5001234	508743	1925	Flat
1894-55-D7	4		5000215	508684	2018	North
1994-76-E11	5	Bear Creek	4993958	529361	2037	East
1994-76-E12	6		4993753	529548	2271	South
1994-76-E9	7		4994073	529533	2143	North
1994-76-H12	8		4994113	530186	2271	Flat
594-160-A4	9	Cedar Creek	5008338	518338	2283	South
594-160-C7	10		5001150	518929	2132	East
594-160-D7	11		5001120	519311	2024	Flat
594-160-G4	12		5001517	519652	2248	South
594-163-A6	13		4997752	518321	2147	North
594-163-AA5	14		4997968	518065	2030	North
594-55-E5	15	Cinnabar Creek	4993707	511586	2259	East
594-61-G1	16	Joe Brown Creek	5003215	512090	2180	Flat
594-61-H3	17		5003220	512377	2172	South
594-62-I6	18		5003716	512307	2218	East
594-69-C6	19		5003567	512705	2146	East
594-69-D7	20		5003339	512916	2181	West
594-69-D9	21		5002867	512831	1956	South
594-93-B5	22	Slip-Slide	5002567	515682	2040	South
594-93-C4	23		5002692	515954	2139	West
594-93-F2	24		5002935	516553	2315	West
594-94-A4	25		5004259	515461	2177	South
594-94-A6	26		5004166	515441	2177	South
594-94-A7	27		5003812	515188	2120	West
594-94-AA3	28		5004527	515273	2181	West
594-94-B9	29		5003475	515285	2074	West
594-94-C2	30		5004800	515850	2131	South
594-94-D2	31		5004712	516034	2310	South
594-94-E4	32	Cinnabar Creek	4993707	511586	2157	East
594-94-F4	33		4993887	511734	2154	East

Gallatin National Forest Aspen Plots (Continued)

Plot designator	n	Watershed	UTM North	UTM East	Elevation (m)	Aspect
794-154-H5	34	Basset Creek	4995839	520029	2347	West
794-165-C4	35	Phelps Creek	4989325	523933	2123	South
794-165-G3	36	Eagle Creek	4989621	525051	2198	South
794-165-H1	37		4988613	525400	1930	Flat
794-165-H4	38		no data	no data	2025	Flat
794-166-C8	39		4989966	523979	2136	South
794-166-F7	40		4990297	524932	2239	West
794-166-G7	41		4989960	524974	2326	East
794-166-H1	42		4991139	525336	2187	East
794-166-H2	43	Eagle Creek	4991127	525251	2128	West
794-166-H6	44		4990335	525220	2190	West
794-167-D5	45		4990409	524128	2314	South
794-173-B7	46		4992165	526022	2513	South
794-173-B8	47		4991868	525987	2321	West
794-174-A2	48		4991581	525829	2267	East
794-174-F8	49		4990655	527006	2267	East
794-174-G5	50	Pole Creek	4991142	527354	2182	South
794-174-H3	51		4991475	527612	2196	East
794-174-H4	52		4991477	527670	2248	East
794-174-H5	53		4991151	527529	2265	East
794-175-C4	54	Eagle Creek	4989907	526289	2198	South
794-175-E1	55		4990524	526610	2255	South
794-195-E5	56	Little Trail Creek	4992641	521842	2396	East
794-196-D9	57		no data	no data	2664	South
794-196-G6	58		no data	no data	2676	South
894-36-A6	59	Tom Miner	4997006	494925	2250	South
894-36-B6	60		4996946	495186	2192	South
894-95-G1	61		4997700	494110	2314	South
894-95-G7	62		4996731	494134	2244	South
894-96-H1	63		4996536	494287	2255	East

Sunlight/Crandall Aspen Plots

Plot designator	n	Watershed	UTM North	UTM East	Elevation (m)	Aspect
1892-174-E1	1	Sunlight	4954445	621927	2072	West
1892-174-E2	2		4954776	622412	2148	Flat
1892-174-E3	3		4954888	622686	2196	North
1892-174-E4	4		4955283	623017	1971	East
32-10-F1	5	Crandall	4966530	604881	2041	South
32-10-F2	6		4966093	604847	2047	East
32-10-F3	7		4965988	604808	1996	East
32-10-G1	8		4966427	605445	2221	South
32-10-G2	9		4966328	605299	2161	South
32-11-A9	10		4967593	603728	2247	South
32-11-AA10	11		4966892	603116	2165	South
32-11-AA9	12		4967494	603451	2164	South
32-11-D10	13		4967219	605010	2240	West
32-11-D8	14		4967727	604854	2290	West
32-11-H12	15		4967009	606219	2079	South
33-1-H2	16	Sunlight	4950974	610000	2077	West
33-1-J3	17		4950540	610647	2072	Flat
34-1-B5	18		4952438	611530	2122	Flat
34-2-A4	19		4955043	611251	2323	North
34-2-B5	20		4954787	611323	2216	East
35-2-D7	21		4954546	615172	2083	North
35-2-E7	22		4954624	615517	2095	North
35-2-F5	23		4955004	615842	2088	Flat
35-2-F6	24		4954906	615995	2095	Flat
36-1-B11	25		4955768	no data	2063	North
36-1-B12	26		4955768	619473	2066	North
36-1-C2	27		4958281	619928	2067	East
36-1-C3	28		4957887	620083	2067	South
36-1-C4	29		4958000	620347	2108	South
36-1-D1	30		4958594	620165	2179	South
36-1-D2	31		4958497	620187	2066	South
36-1-D4	32		4958181	619970	2114	South
36-1-E2	33		4958230	620374	2096	South
36-1-E3	34		4958028	620561	1996	South
36-1-E4	35		4958042	620491	2084	South
36-1-E8	36		4956625	620756	1967	East
36-1-E9	37		4956506	620728	2001	North

Sunlight/Crandall Aspen Plots (Continued)

Plot designator	n	Watershed	UTM North	UTM East	Elevation (m)	Aspect
36-1-F2	38	Sunlight	4958485	620516	2182	South
36-1-F3	39		4958027	620994	2173	South
36-1-F4	40		4957913	620892	2048	West
36-1-F7	41		4956800	621090	2044	North
36-1-F9	42		4956676	621077	2018	North
36-1-G7	43		4956882	621693	1933	West
36-1-G8	44		4956757	621332	1931	West
36-1-H7	45		4956962	621738	2027	North
36-1-I7	46		4957072	622095	1950	North
33-9-D3	47	Clarks Fork	4969638	608413	2072	West
33-11-B10	48		4970898	607223	2024	South
33-11-C9	49		4970699	607741	2164	Flat
33-9-E1	50		no data	no data	2082	South
33-9-H0	51		no data	no data	2039	Flat
33-9-H1	52		no data	no data	1997	South
33-11-H11	53		no data	no data	2232	West
33-11-J13	54		no data	no data	2223	West