QUAKING ASPEN (*Populus tremuloides*) ECOLOGY ON FOREST SERVICE LANDS NORTH OF YELLOWSTONE NATIONAL PARK

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Animal and Range Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2007

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of a thesis submitted by

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

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David S. Kimble

April 2007

ACKNOWLEDGEMENTS

I would like to thank my wife, Karen, my faithful field assistant who hiked with me to hundreds of remote aspen stands. The U.S. Forest Service in Gardiner, Montana funded this research. Gerry Bennett, Dick Ohman, and Jim Wood have contributed significantly to the funding of wildlife habitat projects on the Gardiner Ranger District. Dan Tyers, U.S.F.S., came up with the idea for this project and assisted me in numerous ways throughout the project. Rob St. John provided early guidance and completed the 1991 aspen survey, without which this project would not exist. I would like to thank my advisor, Bok Sowell, for working with me through all stages of writing this thesis. Committee members Mike Frisina and Carl Wambolt provided valuable insight. I would also like to thank other F.S. personnel who assisted in data collection: Heidi Bergsjo, Ken Britton, Kasper Engelhardt, Kat Hickman, Gitske Houge, Matt Latini, Sam McColley, Leah Spurlin, Kristine Ulvund, Sarah Wallace, and Jeremy Zimmer. Tom Lemke, Montana Fish, Wildlife, and Parks, provided me with valuable elk population data. Patrick Hoppe and Chauntelle Rock gave me information on F.S. cattle allotment stocking. Walt Allen, U.S.F.S. gave me history of the privately-owned Cedar Creek drainage. Finally, I would like to thank the Royal Teton Ranch, Stermitz Ranch, B-Bar Ranch, Hubbard's Yellowstone Lodge, Grizzly Creek Ranch, and Shooting Star Ranch for allowing me to pass through their land to access F.S. land parcels.

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ABSTRACT

The primary objective of this study was to determine if quaking aspen (*Populus tremuloides*) density and recruitment changed on the Gallatin National Forest north of Yellowstone National Park from 1991 to 2006. Three-hundred sixteen aspen stands were surveyed on the 560 km² study area. Secondary objectives were to determine if aspen density and recruitment were influenced by elk (*Cervus elaphus*) browsing, conifer establishment, and cattle (*Bos* spp.) grazing.

A 202.3 m² circular plot was established within each stand. All aspen stems within each plot were categorized into size classes: sprouts (< 1 m), saplings (1-2 m), recruitment stems (> 2 m and < 5 cm diameter at breast height), and mature stems (> 2 m and > 5 cm diameter at breast height). Recruitment stems and mature stems have grown above the height at which elk generally browse. Recruitment stems have attained this height in the past 10-15 years. Therefore, important measures of aspen stand sustainability are changes in recruitment stem density and density of all stems > 2 m tall across the study area. Individual stands were further categorized as sustainable if the number of stems > 2 m remained stable or increased from 1991 to 2006.

Sixty-three percent of stands are not recruiting sufficient numbers of stems to replace aging overstories. Mean recruitment stem density across the study area did not change from 1991 to 2006. Stems > 2 m density is the most meaningful measure of aspen sustainability at the landscape level. Mean stems > 2 m density declined 12% from 1991 to 2006. The average annual loss of stems > 2 m is four times the rate of canopy cover loss in surrounding areas in Montana and Wyoming.

Areas with the greatest elk densities had the lowest recruitment stem densities, which indicates that elk herbivory was the primary reason for the 12% decline in stems > 2 m density. Conifer establishment and cattle grazing in aspen stands also contributed to this decline. Even though elk numbers on the Northern Yellowstone Winter Range have declined since wolf reintroduction, aspen recruitment has not increased at the landscape level.

CHAPTER 1

INTRODUCTION

Quaking aspen (*Populus tremuloides*) occupy a small area in the northern Rocky Mountains, but stand out as the only upland, deciduous tree species in much of the West (Debyle and Winokur 1985). Aspen are clonal species and primarily rely on root sprouts to replace aging stems for the species to persist in the Rocky Mountains (McDonough 1985; Schier et al. 1985). Aspen forests may support a diverse understory of shrubs, forbs, and grasses that are high quality forage for herbivores (Mueggler 1988; St. John 1995). Although aspen forests make up a small percentage of vegetative cover in the Rocky Mountains, they commonly support more species and greater numbers of wildlife than associated conifer habitats (DeByle 1985b). Wild ungulates such as moose (*Alces alces*), Rocky Mountain elk (*Cervus elaphus*), and deer (*Odocoileus spp.*) selectively browse aspen suckers in winter because they are palatable and available above the snow (Houston 1982; DeByle 1985b).

Where ungulate densities are high, browsing can suppress aspen sucker growth and prevent aspen clones from replacing older overstory stems with younger stems (Olmsted 1979; Debyle 1985a). Aspen coverage on the Northern Yellowstone Winter Range (NYWR) has declined from 4-10% of the landscape near the beginning of the 20th century to 1% presently (Houston 1982; Ripple et al. 2001; Wagner 2006). The NYWR is the wintering ground for Yellowstone National Park's (YNP) largest elk herd and consists of low- to mid-elevation areas in the Lamar, Yellowstone, and Gardner River

drainages inside and outside YNP (Houston 1982). Although other factors may play a role, the primary cause of aspen decline on the NYWR is browsing of suckers by wintering elk (Romme et al. 2001; NRC 2002; Wagner 2006).

St. John (1995) surveyed quaking aspen clones or "stands" on the Gallatin National Forest (GNF) in 1990 and 1991—the largest study of its kind on the NYWR. Only 21% of aspen stands had sufficient numbers of suckers escaping browsing for the stands to remain stable or increase in density. Ungulate impacts were lower and overstory stem recruitment was more frequent in aspen stands in scree communities or near roads. Elk are excluded from scree communities by steep slopes and rocky substrate and often avoid roads due to human activities. In addition, overstory recruitment was less frequent in aspen stands in cattle allotments than in stands not grazed by cattle (St. John 1995).

Wolves (*Canis lupus*), a major predator of elk, were reintroduced into YNP in 1995 (Smith et al. 2005). The NYWR elk herd decreased by ≈ 50% from 1995 to 2004 (NYCWWG 2005) and some researchers hypothesized that wolf predation could relieve elk browsing pressure such that aspen overstories could regenerate (Ripple and Larsen 2000). A wolf-elk-browse plant trophic cascade may have occurred on small scales at certain sites in YNP (Ripple et al. 2001, Ripple and Beschta 2003; 2004; 2005; 2006). To date, published studies have not addressed changes in broad-scale aspen overstory regeneration since wolf reintroduction.

GNF managers are concerned about aspen habitats. Some GNF goals and objectives are: to "provide habitat for viable populations of all indigenous wildlife

species", to "maintain or improve the forage resource", and to emphasize "management of special and unique wildlife habitats", of which aspen habitats area are a listed priority (GNF 1987). In response to these mandates, the GNF sponsored the original 1991 aspen inventory with the intent of repeating it to gain a longer temporal perspective on local aspen condition and trend. With these data, GNF managers would be equipped to prepare a site-specific aspen management plan (Dan Tyers, USFS, *personal communication*).

This study repeated the 1991 aspen survey on the GNF portion of the NYWR (St. John 1995). Objectives were to determine if: 1) aspen overstory density and recruitment decreased, increased, or was stable from 1991 to 2006; 2) elk herbivory influenced aspen density or recruitment; 3) conifer establishment in aspen stands influenced aspen density or recruitment; and 4) cattle grazing in aspen stands influenced aspen density or recruitment.

CHAPTER 2

LITERATURE REVIEW

Aspen Ecology

Quaking aspen grow at mid-elevations (1 525-2 300 m) on both riparian and upland sites on the NYWR (Houston 1982). They are limited by moisture due to accelerated evapotranspiration at low elevations and by length of growing season at upper elevations (Mueggler 1988).

Aspen are clonal tree species that grow in clumps of root-connected stems referred to as "stands". A stand originates from one genetically unique individual and increases in size via asexual reproduction when roots sprout new clone stems called ramets (Jones and Debyle 1985a). Aspen in the Rocky Mountains rarely reproduce sexually (Kay 1993). Although mature aspen produce large amounts of seed, the exacting requirements for seeds to germinate and survive are infrequently met. To survive, aspen seeds need to land on a mineral surface that is moist, yet well-drained, and in an area with moderate temperatures and little competition from other plants (McDonough 1985).

Few ramets in the Rocky Mountains live beyond 120 years, but aspen clones can survive indefinitely by resprouting (Mueggler 1989). When an aspen stand has many mature stems, auxins that suppress the growth of root sprouts or "suckers" are transported from the aboveground ramets to the roots. This is referred to as apical dominance (Schier et al. 1985). A disturbance such as fire or beaver cutting that kills the aboveground stems

can end apical dominance in the clone, usually results in abundant production of root suckers in subsequent years, and may allow large numbers of suckers to eventually grow to tree size (Bartos and Mueggler 1981; Jones and DeByle 1985b). Disturbance could be a requirement for successful regeneration in some aspen clones (Loope and Gruell 1973; Mueggler 1988). Late-seral conifers are more shade tolerant than aspen, may invade aging aspen overstories (Jones and Schier 1985; Mueggler 1988), and can suppress aspen growth (Shepperd et al. 2001; Brown et al. 2006). However, aspen are not always early-seral species and can exist in stable or near-stable communities. These stands are characterized by an uneven age distribution of aspen stems, lack an uneven aged conifer understory (Mueggler 1985; 1989), and could comprise between one-half and two-thirds of aspen stands on the NYWR (Kay 1990).

Importance of Aspen

Quaking aspen have been long-recognized as an important ecosystem component in the northern Rocky Mountains. Although they only make up a small percentage of the area's vegetative cover, aspen have always stood out as the only upland, deciduous tree species in much of the Rocky Mountains (Debyle and Winokur 1985).

The sporadic distribution of aspen communities in the northern Rocky Mountains may actually serve to underscore their benefits to wildlife (St. John 1995). On average, aspen habitats have more species of wildlife and greater numbers of wildlife than associated conifer habitats (DeByle 1985b), only surpassed for total biodiversity in the Rocky Mountains by riparian plant communities (White et al. 1998). Wild ungulates

regularly seek out young aspen as a preferred browse species (DeByle 1985a). Elk, moose, rabbits (*Sylvilagus spp.*) and hares (*Lepus spp.*), mice and voles (*Microtus spp.*), and porcupines (*Erethizon spp.*) are all known to feed on the bark of young and mature aspen (Debyle 1985b). Ruffed grouse (*Bonasa umbellus*) feed on aspen buds in the winter and beaver (*Castor canadensis)* depend on aspen as a food source and as dam material (Debyle 1985b, 1985c). Black bears (*Ursus americanus*) even climb aspen trees in the spring to eat catkins, young leaves, and buds (Debyle 1985b). Some cavity nesting birds prefer to nest in aspen rather than associated conifers and have lower nest mortality in aspen forests than other forest types (Debyle 1985b, Struempf et al. 2001).

Due to their relatively open canopy, aspen forests commonly support a diverse understory of shrubs, forbs, and grasses that provide high quality forage for livestock as well as wildlife (Mueggler 1988; St. John 1995). Aspen may be key players in water quality due to their common association with riparian areas (Sampson 1919; St. John 1995) and are less flammable than conifers, sometimes serving as naturally occurring firebreaks (Debyle and Winokur 1985).

Aspen and Ungulates

Browsing by wild ungulates can compromise an aspen stand's ability to replace its older overstory stems with younger stems (Olmsted 1979; Debyle 1985a). Elk are the primary browser of aspen on the NYWR and woody plants can make up 40% of elk diets during severe winters (Houston 1982; Kay 1985). Most aspen stems that have grown above 2 m will survive elk browsing of the twigs and could eventually become part of the

aspen overstory (Kay 1985). However, elk gnawing of aspen bark and fungal pathogens associated with this injury can kill a large proportion of stems < 10-15 cm diameter at breast height (dbh) where elk populations are high (Krebill 1972; Keigley and Frisina 2005). Stems > 2 m tall and < 5 cm dbh have attained this height in the past 10-15 years on the NYWR, while stems > 5 cm dbh represent earlier periods of recruitment in the stand (Kay 1985; 1990). Kay (1985) suggested that the ratio of aspen stems > 2 m in height and < 5 cm dbh to stems > 2 m in height and > 5 cm dbh must be ≥ 1.0 if an aspen stand is to remain stable or increase in size or density.

Domestic cattle (*Bos* spp.) will browse aspen and can suppress aspen growth or prevent stand regeneration under some conditions (Sampson 1919; Fitzgerald and Bailey 1984; Dockrill et al. 2004). Cattle generally forage on aspen foliage during a relatively short period of time in late-summer after herbaceous plants have begun to cure, but before aspen leaf-fall (Sampson 1919; USFS 1937; Fitzgerald et al. 1986). Most published negative cattle impacts on aspen regeneration have been documented where cattle have been stocked at high rates and experimentally "forced" into aspen stands (Fitzgerald and Bailey 1984; Fitzgerald et al. 1986; Dockrill et al. 2004). However, the cumulative effects of summer cattle browsing and winter wild ungulate browsing of aspen can result in decreased aspen recruitment (St. John 1995; Kay and Bartos 2000), even when cattle are given free choice of forage.

Aspen Decline in the West

Bartos (2001) estimated that quaking aspen coverage has declined by ≈ 60% across the West since Euro-American settlement. Others have suggested that landscape-scale aspen decline has been overestimated (Suzuki et al. 1999; Brown et al. 2006). Brown et al. (2006) reported a ≈ 10% aspen decline from 1956 to 2001 in the Greater Yellowstone Ecosystem. However, aspen coverage and density in the Rocky Mountains have declined at faster rates where wild ungulate populations, mainly elk, are high (White et al. 1998; Brown et al. 2006). Historic photos show young aspen stands with no evidence of bark stripping or browsing prior to 1910 in 6 major Rocky Mountain national parks of the United States and Canada. Later, researchers in all the national parks documented aspen decline as elk herds grew (White et al. 1998). Elk were extirpated by hunting and absent from Rocky Mountain National Park (RMNP), Colorado prior to their 1915 reintroduction. Rocky Mountain National Park employed an aggressive elk reduction program in the 1940's, 1950's, and 1960's after range managers concluded the elk population was too large. Aspen stands on winter range inside RMNP only regenerated prior to the late-1930's and from 1950-1970, precisely when the elk population was low (Olmsted 1979; Baker et al. 1997). However, aspen regenerated more frequently outside RMNP on winter range where elk densities were lower (Suzuki et al. 1999). Aspen stands regenerated on elk winter range near Grand Teton National Park, Wyoming during 3 time periods when elk populations were low or moderate, but otherwise have seldom regenerated since Euro-American settlement (Hessl and Graumlich 2002). Inside Grand Teton National Park, aspen declined in the presence of

heavy elk browsing from 1966-1977 (Weinstein 1979). From 1930-1970, no aspen suckers grew beyond browse height on the Gros Ventre elk winter range of the Teton National Forest, Wyoming (Krebill 1972).

Aspen and the Northern Yellowstone Winter Range

The NYWR consists of low- to mid-elevation portions of the Lamar, Yellowstone, and Gardner River drainages in Montana and Wyoming (Houston 1982). The 152,663 ha northern range is the wintering ground for YNP's largest elk herd (Houston 1982; Lemke et al. 1998). Sixty-five percent of the NYWR is located inside YNP and 35% is composed of federal, state, and private lands north of YNP (Lemke et al. 1998). The NYWR is occupied by several large herbivores including elk, mule deer (*Odocoileus hemionus*), bison (*Bison bison*), moose, pronghorn antelope (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*) and large carnivores including wolves, mountain lions (*Puma concolor*), black bears, and grizzly bears (*Ursus arctos horribilis*) (Houston 1982). Due to its abundance of wildlife and its association with the United States' first national park, the NYWR has been well-studied by scientists for nearly 100 years.

Aspen currently cover 1% of the NYWR, but probably occupied 4-10% of the same area prior to YNP establishment in 1872 (Houston 1982; Ripple et al. 2001; Wagner 2006). Mature aspen stems reaching senescence have not been replaced by younger stems growing above browse height. In 1998, only 5% of 57 aspen stands sampled on the NYWR inside YNP had overstory stems that had originated since 1921

(Ripple and Larsen 2000). Kay (1990) and Romme et al. (1995) reported similar findings for aspen stands on the NYWR inside YNP. Aspen stands have also declined where elk density is lower on the NYWR outside YNP, but generally contain at least some overstory stems that have originated since 1920 (Larsen and Ripple 2003; 2005).

Concern about the decline of woody browse plants in northern YNP first became prevalent among range scientists in the 1920's and 1930's. Aspen, black cottonwood (*Populus trichocarpa*), narrowleaf cottonwood (*Populus angustafolia*), and willow (*Salix* spp.) were decreasing in coverage area or failing to recruit new stems to tree height (Houston 1982; Keigley 1997; Ripple and Larsen 2000; Beschta 2003, Ripple and Beschta 2004). Most biologists and range scientists attributed this decline to excessive browsing of young stems by the wintering elk herd. They believed that YNP was hosting a high number of wintering elk because human settlement in the valleys outside YNP prevented elk migration to former winter ranges (Tyers 1981; YNP 1997; Wagner 2006). From 1923 to 1968, elk were live-trapped and relocated or shot inside YNP to reduce the NYWR elk herd to a "healthier" level. Elk numbers declined; a low of 3 172 elk were counted by aerial census in 1968 (YNP 1997). Despite the reduction in elk numbers, new aspen stems did not join the forest overstory inside YNP while the elk population was low (Romme et al. 1995; Ripple and Larsen 2000). However, some aspen stands in the Eagle Creek drainage of the NYWR (north of YNP on the GNF) did regenerate overstory stems (Kay 1990). Based on hunter harvest data from the area, Kay (1990) stated that few elk migrated out of the YNP during the time of elk reductions, temporarily relieving the aspen from browsing. Inside YNP, 3 new cottonwood stands were established on

Soda Butte Creek in 1968, 1977, and 1985. Architecture of the stands indicated that browsing increased sometime between 1968 and 1977, which corresponds to the NYWR elk herd population increase following the cessation of artificial controls (Keigley 1997). Aspen inside YNP may have failed to respond while the elk population was smaller because the elk herd was still large enough to severely browse aspen. Or, disturbances such as fire or beaver cutting to stimulate new ramet sprouting may have needed to occur at the same time as the low elk population. Also, elk numbers may not have been reduced long enough for aspen to recover or aspen clones' capacity to rebound may have been suppressed by years of heavy browsing (Tyers 1981; Wagner 2006).

Due to public resistance to killing elk and change in National Park Service policy, YNP halted efforts to artificially reduce the northern Yellowstone elk herd in 1969 (YNP 1997; Wagner 2006). Park Service scientists hypothesized that elk browsing was not the major cause of aspen decline (Houston 1982; Despain et al. 1986).

National Park Service scientists believed that aspen in the Yellowstone ecosystem were primarily an early-seral stage species and were being replaced by conifers due to wildfire suppression inside YNP for the previous 80 years (Houston 1973; Houston 1982; Despain et al. 1986). Using scars on Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta* var. *latifolia*), Houston (1973) concluded that fire burned along the forest and shrub-steppe ecotone where aspen are typically found every 20-25 years prior to YNP's fire suppression efforts. Widespread fires in YNP in the summer of 1988 burned 22% of the NYWR and provided a test for the hypothesis that aspen would regenerate after a return to a natural fire regime (Romme et al. 1995). The fires burned

many mature aspen stands, root suckers sprouted prolifically the following year (Romme et al. 1995), and new seedlings were established (Kay 1993; Romme et al. 2005). Some seedlings have persisted and may eventually form new clones. But by 1991, all aspen seedlings at Yancey's Hole on the NYWR had been repeatedly browsed (Kay 1993). By 2000, none of the seedlings sampled in central YNP had attained a 1 m height and 85-88% showed evidence of ungulate browsing (Romme et al. 2005). By 1991, root sucker densities and heights in burned existing clones were similar to sucker heights and densities in unburned clones (Romme et al. 1995). Similarly, root suckers in aspen stands on elk winter range in the Bridger-Teton National Forest northeast of Jackson, Wyoming were only 0.5 m tall on average 12 years after prescribed fire burned the stands (Bartos et al. 1994). Bartos et al. (1994) attributed post-fire aspen stands' failure to recruit new stems into the overstory to heavy elk browsing. Aspen stands in the same area regenerated overstory stems where elk use was low, regardless of whether or not they had burned (Kay 2001a).

After aspen failed to regenerate following the 1988 fires, some scientists suggested that a warmer and drier climate could play a major role in the decline of aspen coverage on the NYWR (Romme et al. 1995; YNP 1997). However, there has been no significant downward trend in precipitation in the past 100 years (NRC 2002) and a relationship between aspen overstory establishment and climatic fluctuation on the NYWR has not been found (Larsen and Ripple 2003). In addition, successful aspen regeneration on xeric scree slopes inaccessible to ungulates (St. John 1995; Larsen and

Ripple 2003) and inside all aspen exclosures on the NYWR (Kay 2001b; NRC 2002) suggests that climate change has not played a major role in aspen decline.

Meanwhile, researchers continued to find evidence that elk browsing was the primary cause of the decline of woody browse plants on the NYWR (NRC 2002). Aspen stands recruited new overstory stems more successfully on winter ranges outside YNP where elk densities were lower. At the same time, conifer colonization of aspen stands was comparable inside and outside YNP (Kay 1985; Larsen and Ripple 2005). Similarly, uneven aged cottonwood stands have grown at La Duke Spring and Devil's Slide on the Yellowstone River on the NYWR north of YNP (Beschta 2005). Elk have likely avoided these areas because of human activity on a nearby highway. Very little recruitment of cottonwoods has occurred since about 1920 along the Lamar River and Soda Butte Creek in YNP where elk use is greater, despite the regular occurrence of floods needed to establish cottonwood seedlings. Seedlings and root suckers have been abundant in YNP, but are almost always < 1 m tall and are browsed every winter (Keigley 1997; Beschta 2003; Beschta 2005).

Gardiner Ranger District Aspen Survey: 1991

In 1991, St. John (1995) completed the largest known quantitative sampling of aspen on the NYWR. He located and mapped 1 146 separate aspen clones present on the west side of the Gardiner Ranger District (GRD) of the GNF and randomly sampled 342 stands. St. John established a circular plot ≈ 200 m² at a representative location in each of the 342 stands that were sampled. Every aspen stem > 2 m in height within the plot

was counted as a recruitment stem (< 5 cm dbh) or a nonrecruitment stem (> 5 cm dbh). Most aspen stems that have grown beyond 2 m will survive elk browsing of the twigs and could eventually become part of the aspen overstory (Kay 1985). Stems > 2 m tall and < 5 cm dbh have attained this height in the past ≈ 10 years, while stems > 5 cm dbh represent earlier periods of recruitment in the stand (Kay 1985; 1990). Although not unequivocally accurate locally, these metrics have become common convention for characterizing aspen stands. St. John also qualitatively assessed ungulate impacts to aspen stems within each clone. Impacts assessed were scars on aspen boles caused by bark chewing/stripping and hedged growth forms of root suckers caused by repeated browsing.

Only 21% of aspen stands St. John assessed had sufficient numbers of recruitment stems for the stands to remain stable or increase in density according to Kay's (1985) criterion. The presence of recruitment stems was associated with less severe ungulate impacts. Aspen stands in scree communities or < 500 m from roads had less severe bark stripping and bole scarring on stems and more recruitment stems than stands not in scree communities or > 500 m from roads. Stands in scree communities are inaccessible to elk and elk avoid roads due to human presence during hunting season (St. John 1995). A higher proportion of aspen stands not grazed by cattle were recruiting new stems into the overstory than stands on cattle allotment land. The cumulative impacts of winter wild ungulate use and summer to early-fall cattle grazing on aspen regeneration were greater than the impact of wild ungulate browsing alone (St. John 1995).

Wolf Reintroduction

By the winter of 1993-1994, 19 045 elk were counted by aerial census on the NYWR (NYCWWG 2005). In 1995 and 1996, 31 wolves were reintroduced into YNP. They had been extirpated from the Yellowstone ecosystem since the 1920's due to predator control programs (Smith et al. 2005). Soon after the reintroductions, some scientists hypothesized that the presence of wolves could affect aspen and other woody browse species through a trophic cascade (Ripple and Larsen 2000). Trophic cascades can occur when a predator affects its prey's numbers or behavior and those effects produce changes in the vegetation the prey feeds on (Ripple et al. 2001). Wolves apparently influence elk use of aspen stands on several winter ranges in the Rocky Mountains in Alberta (White et al. 2003). Evidence suggests a wolf-elk-aspen trophic cascade occurred in Banff National Park, Alberta after wolves recolonized the area in the 1980's (Hebblewhite et al. 2005).

A viable wolf population in YNP was established almost immediately following the reintroductions. By the end of 2004, at least 84 wolves in 7 packs lived on the NYWR inside YNP (Smith et al. 2005). Wolves dispersed to areas outside YNP as well. The home ranges of at least 38 wolves overlapped portions of our study area at the end of 2004 (Smith et al. 2005; USFWS 2005). As expected, wolves preyed upon elk. Wolves occupying the NYWR killed an estimated 1.8 elk per wolf per 30 days from 1995-2000 and 1.1 elk per wolf per 30 days from 2001-2004 (Smith et al. 2005). Wolf activity inside and outside YNP impacted the northern Yellowstone elk herd that browses aspen on our study area.

Following the reintroduction of wolves, the northern Yellowstone elk herd population steadily decreased from ≈ 19 000 elk in 1994 to an average of ≈ 9 000 elk counted in the aerial censuses of 2003, 2004, and 2005. An average of ≈ 5 500 elk migrated north of YNP in the winter from 1989 to 1999, but only ≈ 3 900 migrated north of YNP from 2000 to 2005 (NYCWWG 2005). Despite this decline in elk numbers, there is no definitive evidence that reduced browsing pressure from the smaller elk herd has allowed aspen coverage or recruitment to increase inside or outside YNP on a landscape scale.

The presence of wolves has changed the behavior of elk in YNP (Laundre et al. 2001; Fortin et al. 2005). Female elk have sacrificed foraging effort to spend more time being vigilant for predators in areas of YNP colonized by wolves than in areas not colonized by wolves (Laundre et al. 2001). Yellowstone elk have also changed winter range habitat preferences in the presence of wolves (Fortin et al. 2005; Mao et al. 2005). Elk spend less time in aspen stands and more time in conifer forest in areas frequently used by wolves than in areas infrequently used by wolves (Fortin et al. 2005). Also, NYWR elk inside YNP have more frequently selected open habitats during winter since wolf reintroduction than prior to wolf reintroduction (Mao et al. 2005).

In some situations, this change in elk behavior seems to have produced a change in the aspen, cottonwood, or willow in the Yellowstone area. Elk use of riparian aspen stands on the NYWR inside YNP appears lower and sucker heights are greater in aspen stands with high wolf use than in stands with low wolf use (Ripple et al. 2001).

However, wolf activity did not seem to influence elk use or aspen growth in upland aspen stands (Ripple et al. 2001).

Cottonwoods appear to be recruiting new saplings above elk browsing height (2-4 m tall) in 3 locations on lower Soda Butte Creek and the Lamar River in YNP (Ripple and Beschta 2003). These stands were browsed less than nearby stands and existed on river point bars and an island with nearby impediments to an elk's escape from wolves.

Willows on the NYWR and the Gallatin winter range northwest of YNP may have responded to decreased elk use as a result of increased wolf activity (Ripple and Beschta 2004; Ripple and Beschta 2006). Annual browsing has decreased and willow heights have increased on some sites since wolves have colonized the area. Willow height increases were especially pronounced where visibility was restricted or there were impediments to an elk's escape from wolves. However, only willows growing in valley-bottoms increased in height. Heights of willows growing in the uplands have not changed since wolf colonization (Ripple and Beschta 2004; Ripple and Beschta 2006). Willows at Crystal Creek near its confluence with the Lamar River have increased in height and appear to be "sheltering" aspen suckers growing among the willows (Ripple and Beschta 2005).

The hypothesized wolf-elk-browse plant trophic cascade seems to have occurred on small scales at certain sites in YNP (Ripple et al. 2001, Ripple and Beschta 2003; 2004; 2005; 2006). To date, published studies have not addressed landscape-wide changes in aspen overstory regeneration on the NYWR since wolf reintroduction. The 1991 GRD aspen survey (St. John 1995) has provided a unique opportunity for NYWR

investigators to compare aspen conditions shortly before wolf reintroduction with present conditions. The current status of quaking aspen on the GRD was compared to 1991 and addressed the question: Has aspen regeneration on the NYWR responded similarly since wolf reintroduction in 316 stands on a 560 km² scale as on small scales in YNP? The primary objective of this study was to determine if aspen density or recruitment changed since 1991. Secondary objectives were to determine if aspen density or recruitment were influenced by elk browsing, conifer establishment, or cattle grazing in aspen stands.

CHAPTER 3

METHODS

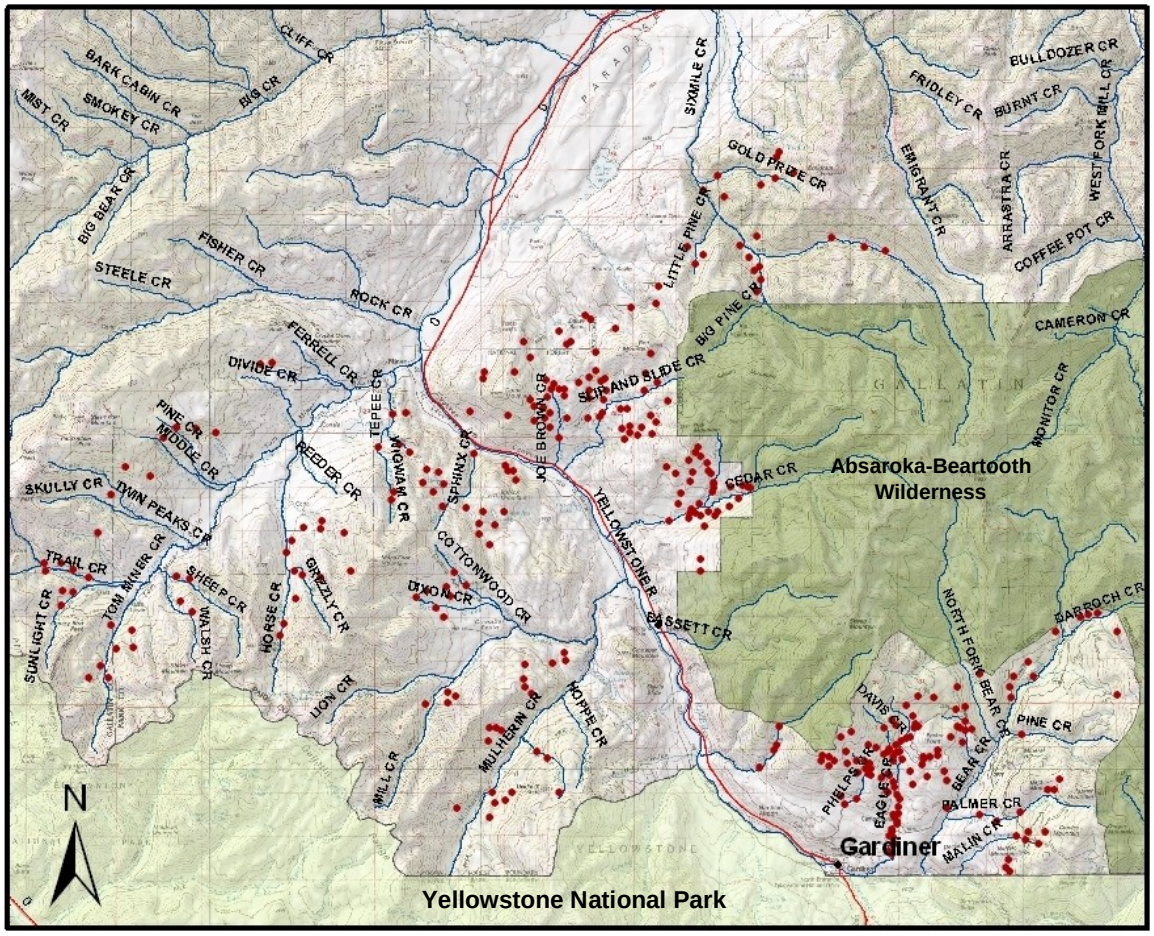
General Study Area

This study area was located in south-central Montana, primarily on the west unit of the GRD, GNF and exclusive of the Absaroka-Beartooth Wilderness (Fig 1.). Aspen occupy ≈ 745 ha of the ≈ 56 000 ha study area (St. John 1995). The northernmost portion of the study area is within the Sixmile Creek drainage of the Livingston Ranger District (LRD), GNF. The southernmost portion of the study area abuts YNP. The study area consists of three biologically dissimilar geographic regions where elk migration patterns, population trends, and human hunting pressures differ. The study area is separated into the East River, West River, and Tom Miner Basin regions to determine if aspen density or recruitment is influenced by elk herbivory.

Climate is similar in the 3 regions of the study area. Mean annual precipitation in the Gardiner Basin at the southern end of the study area is 25 cm. Peak precipitation falls in May and June; the two months account for 25-30% of annual precipitation. Mean minimum temperature in January is -10°C and mean maximum temperature in July is 30°C. Elevation in the town of Gardiner is 1 618 m. Precipitation increases and temperature decreases as elevation increases in the study area. Elevation in Jardine, Montana is 1 966 m and mean annual precipitation is 45 cm (Western Regional Climate Center 2007).

Soils in the East River and West River portions of the study area are mainly argic or typic cryoborolls or argiborolls of the order mollisol with a glacial drift substratum. Soils in Tom Miner Basin are primarily mollic cryoboralfs of the order alfisol with a glacial drift substratum. Soils on higher mountains in the study area are mainly cryochrepts of the order inceptisol with a volcanic substratum (NRCS 2007).

Figure 1. Aspen stand locations on the study area.



Vegetation primarily consists of big sagebrush (*Artemisia tridentata* ssp. *vaseyana; A. t.* ssp. *wyomingensis; A. t.* ssp. *tridentata*) and grassland (*Pseudoroegnaria spicata*; *Festuca idahoensis*) at lower elevations, some quaking aspen at forest-grassland

boundaries and in riparian areas, Douglas-fir at mid-elevations, and lodgepole pine, Engelmann spruce (*Picea engelmannii)*, and sub-alpine fir (*Abies lasiocarpa*) at higher elevations (Despain et al. 1986). Vegetation in Tom Miner Basin and the East and West River units is similar. However, Tom Miner Basin is characterized by more mesic plant communities (i.e. subalpine fir/Engelmann spruce) at lower elevations than the East and West River units. Aspen forests range from 1 571 m to 2 605 m in elevation on the study area.

Elk are the most prevalent ungulate species in the study area that browse aspen (Houston 1982; NYCWWG 2005). Mule deer, white-tailed deer (*Odocoileus virginianus*), and moose inhabit the study area and will browse aspen. Most wild ungulate browsing on aspen occurs in winter, as wildlife typically eat more succulent grasses and forbs in summer (Debyle 1985a). Approximately 2 000 mule deer winter on the NYWR, mostly north of YNP (NYCWWG 2005). However, the impact of deer on aspen is probably minor, since they typically winter below elevations where aspen grow and consume less forage than elk (Houston 1982; Debyle 1985a). Moose consume large quantities of forage and winter at elevations at and above where aspen grows. However, only ≈ 200 moose live on the entire NYWR (YNP 1997). Bighorn sheep, bison, and pronghorn antelope inhabit parts of study area, but do not commonly browse aspen (Houston 1982).

Beaver were reintroduced to Eagle Creek in 1991. Beaver from 2-3 colonies have cut aspen overstory in Eagle Creek since 1991 (Dan Tyers, GRD, *personal*

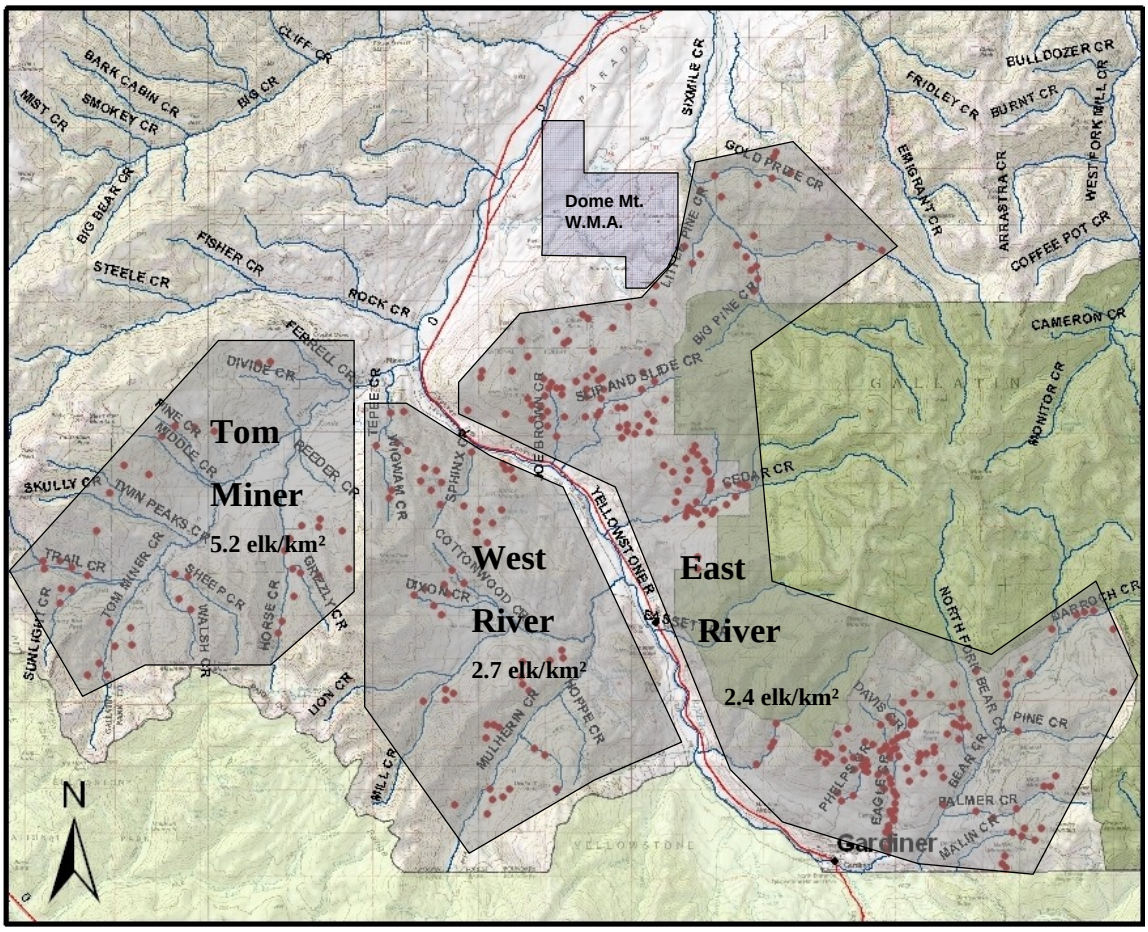
communication). Transient beavers have impacted aspen on lower reaches of Phelps Creek and Mulherin Creek since 1991.

Cattle grazing in the study area has declined throughout the past 20-30 years. In the 1970's, 3 621 AUMs were grazed by cattle in 14 allotments on the GRD. By 1995, 2 867 AUMs were grazed by cattle and 11 allotments used (St. John 1995). In 2006, 6 cattle allotments on the GRD were in use in 2006 and 1 788 animal unit months (AUMs) were grazed (Patrick Hoppe, GRD, *personal communication*). Two cattle allotments were occupied in the Sixmile Creek drainage of the LRD in 1991. By 2006, one allotment in the Sixmile Creek drainage was occupied (Chauntelle Rock, LRD, *personal communication*).

East River

The East River unit is separated from Tom Miner Basin and the West River unit by the Yellowstone River, private residences and agricultural lands in the river valley, and a major highway (Fig. 2). The East River, at ≈ 340 km^2, is the largest portion of the study area. The Bear Creek, Eagle Creek, Phelps Creek, Little Trail Creek, Cedar Creek, Slip and Slide Creek, Joe Brown Creek, and Sixmile Creek drainages subdivide the East River unit.

Figure 2. East River, West River, and Tom Miner subunits with different wintering elk densities.



Migration patterns, population trends, and human hunting pressures on elk in the East River portion differ from the West River and Tom Miner Basin portions of the study area. Most of the East River unit is part of the NYWR (Lemke et al. 1998). Gold Prize Creek and the North Fork of Sixmile Creek are part of the Sixmile Creek drainage, but are not considered part of the NYWR (Lemke et al. 1998). However, wintering elk commonly browsed in accessible (non-scree) aspen stands in these drainages, so the areas

were considered part of the East River unit due to their geographic proximity to the NYWR.

Since 1976, elk on the East River unit have been subject to human hunting pressure in winter during the Gardiner Late Elk Hunt. Hunting pressure on elk has declined in recent years. Annual elk harvest permits have declined from 2 882 in 2000 to 148 permits in 2006 (NYCWWG 2005).

From 1989 to 1999, an average of 3 640 elk were annually counted by aerial census in late winter after the January hunting season on the NYWR north of YNP and east of the Yellowstone River. During this time, ≈ 55% of elk spent the majority of the winter north of Dome Mountain (NYCWWG 2005; Tom Lemke, MFWP, *unpublished data*). Elk that winter north of Dome Mountain pass through the East River portion of the study area, but are largely transient in this area (Tom Lemke, MFWP, *personal communication*). The number of elk wintering on the state-owned Dome Mountain Wildlife Management area, which is outside the study area, is approximately equal to the number of elk that annually winter north of Dome Mountain (Frisina 2005; NYCWWG 2005). Therefore, an average of 1 640 elk spent the majority of the winter on the East River portion of the study area from 1989 to 1999. Elk that migrate north of Dome Mountain and elk harvested earlier in the winter use the area to varying degrees, so 1 640 is a conservative estimate of total wintering elk numbers.

From 2000 to 2006, an average of 2 700 elk were annually counted by aerial census in late winter after the January hunting season on the NYWR north of YNP and east of the Yellowstone River (Tom Lemke, Montana Fish, Wildlife, and Parks [MFWP],

unpublished data). About 70% of elk north of YNP and east of the Yellowstone River have spent the majority of the winter north of Dome Mountain since 2000 (NYCWWG 2005; Tom Lemke, MFWP, *unpublished data*). Therefore, an average of 810 elk spent the majority of the winter on the East River portion of the study area from 2000 to 2006. Late winter elk density on the East River unit has averaged 2.4 elk/km² since 2000. Average wintering elk density on the East River unit from 2000 to 2006 was 50% less than from 1989 to 1999.

Cattle have been removed from the East River unit since 1991 in 1 allotment on the LRD and 1 previously privately owned drainage (St. John 1995; Chauntelle Rock, LRD, *personal communication*; Patrick Hoppe, GRD, *personal communication*). Most of the Cedar Creek drainage was privately owned and grazed by cattle until 1991. Cattle grazing was not continued after the Forest Service acquired the land in 1991 (Walt Allen, GNF, *personal communication*). In 2006, 1 allotment on the GRD and 1 allotment on the LRD in the East River unit were grazed by cattle (Chauntelle Rock, LRD, *personal communication*; Patrick Hoppe, GRD, *personal communication*).

West River

The West River portion of the study area occupies ≈ 120 km^2 and is separated from Tom Miner Basin by a hydrologic divide of 2 900 m mountains in the south and private residences and agricultural land in the north (Fig. 2). Unlike the East River unit, extensive private landholdings are interspersed with Forest Service lands throughout much of the West River unit. The Mulherin Creek and Sphinx Creek drainages subdivide

the West River unit. The Wigwam and Tepee Creek drainages, the easternmost portion of the Tom Miner drainage, were included in the West River unit because of their proximity to Sphinx Creek and because there was no apparent impediment to elk movement between the drainages.

Migration patterns, population trends, and human hunting pressures on elk in the West River portion differ from the East River and Tom Miner Basin portions of the study area. The West River unit is part of the NYWR (Lemke et al. 1998) and the Gardiner Late Elk Hunt area (NYCWWG 2005). From 2000 to 2006, an average of 320 elk were annually counted by aerial census in late winter after the January hunting season on the NYWR north of YNP and west of the Yellowstone River (Tom Lemke, MFWP, *unpublished data*). Therefore, late winter elk density on the West River unit has averaged 2.7 elk/km^2 since 2000. Since the aerial census does not include elk harvested in January, this is a conservative estimate of total winter elk density. From 1989 to 1999, an average of 230 elk were counted in late winter on the West River unit (Tom Lemke, MFWP, *unpublished data*). Average wintering elk density on the West River unit from 2000 to 2006 was 40% more than from 1989 to 1999. Current elk densities on the East and West River units are similar. It is important to note that elk numbers are declining in the East River unit, but increasing in the West River unit. The elk population trend could affect the ability of aspen clones to grow new stems above browsing height.

Cattle have been removed from parts of the West River unit since 1991. Seven allotments in the West River unit were grazed by cattle in 1991 (St. John 1995). But by

2006, only 3 allotments were still occupied (Patrick Hoppe, GRD, *personal communication*).

Tom Miner Basin

The Tom Miner Basin portion of the study area occupies ≈ 100 km^2 (Fig. 2). Most of the basin bottom is private land, while Forest Service lands surround the basin at higher elevations. Tom Miner Basin is subdivided into several smaller creek drainages, all of which flow into Tom Miner Creek.

Migration patterns, population trends, and human hunting pressures on elk in Tom Miner Basin differ from the East River and West River portions of the study area. Tom Miner Basin is not part of the wintering range for the northern Yellowstone elk herd, but other local herds of elk winter in this portion of the study area (Lemke et al. 1998; Tom Lemke, MFWP, *unpublished data*). The number of elk wintering in Tom Miner Basin since 1990 has been highly variable. A high of ≈ 1 470 elk were censused in late winter in 1996 and a low of 190 elk were censused in 2004. From 2000 to 2006, an average of 520 elk were counted in late winter in Tom Miner Basin (Tom Lemke, MFWP, *unpublished data*). Unlike the East and West River units, there is no winter elk hunting season in Tom Miner Basin. Late winter elk density in Tom Miner Basin has averaged 5.2 elk/km^2 since 2000. From 1990 to 1999, an average of 790 elk were counted in late winter in Tom Miner Basin (Tom Lemke, MFWP, *unpublished data*). Average wintering elk density in Tom Miner Basin from 2000 to 2006 was 35% less than from 1989 to 1999. Despite the decline in density, average wintering elk density in Tom Miner Basin has exceeded elk density in the East and West River units since 1990.

There has been a minor decrease in cattle grazing in Tom Miner Basin since 1991. Three allotments in Tom Miner Basin were grazed by cattle in 1991 (St John 1995). Two of these were still occupied in 2006 (Patrick Hoppe, GRD, *personal communication*).

Sampling Methods

Using a combination of marked topographical maps and photographic slides taken in 1991, 342 aspen clones that St. John (1995) sampled in 1991 were revisited in 2005 and 2006. Sampling methods were nearly identical to those employed by St. John (1995). After the aspen clone was relocated, the center of a 202.3 m^2 ($1/20^{th}$ ac) circular plot was staked within the aspen stand. The location of the plot within the stand depended upon, in ranking order: 1) where it appeared St. John's plot was located according to the photographic slide from 1991; 2) St. John's site description and site determinants such as slope, aspect, species of vegetation within the plot, or number of mature aspen stems in the plot; and 3) the location most representative of the aspen stand. Slope and aspect at the center of the plot were measured with a compass. Elevation and Universal Transverse Mercator coordinates were measured with a Geographic Positioning System unit. Observers recorded whether or not the aspen stand containing the plot had burned or been cut by beaver since 1991. Each aspen stand was assigned a community type based on its associated vegetation. Aspen stands that were not adequately classified in Mueggler's (1988) "Aspen Community Types of the Intermountain Region" were classified by St. John's (1995) "Additional Aspen Community Types on the GRD". Aspen-conifer community types contained ≥ 10%

canopy coverage of conifers in the stand. Canopy coverage was visually estimated (Anderson 1986).

Next, the circular plot (radius ≈ 8.02 m) was divided into quadrants with tape measures. All live aspen stems within the plot were counted and categorized as sprouts (< 1 m tall), saplings (1-2 m tall), recruitment stems (≥ 2 m tall and < 5 cm dbh), or mature stems (≥ 2 m tall and > 5 cm dbh). Stems were categorized by height to determine if the terminal leader had grown beyond the reach of browsing elk. Saplings (1-2 m) have not grown beyond the reach of browsing elk, but are not being browsed to the depth of the winter snowpack (Romme 1995). Stems ≥ 2 m tall have grown beyond the height at which elk will browse the terminal leader (Kay 1985). Stems ≥ 2 m tall were categorized by diameter to determine the relative age of stems that had grown beyond the reach of browsing elk. Stems ≥ 2 m tall and < 5 cm dbh theoretically have attained this height in recent years, while stems > 5 cm dbh represent earlier periods of recruitment in the stand (Kay 1985). Kay (1985) suggested that the ratio of the number of recruitment stems to the number of mature stems must be ≥ 1.0 if an aspen stand is to remain stable or increase in size or density.

Kay's criterion is a conservative estimate of aspen stand sustainability and is useful when the observer does not have the benefit of previous aspen stem density data. However, the recruitment ratio of a stand can be misleading. If many older (mature) stems in a stand die, the number of recruitment stems needs only to remain constant for the recruitment ratio to increase. Also, if many stems in a stand grow beyond 5 cm dbh, the recruitment ratio of the stand will decrease—even if overall density of the stand in

increasing. A better criterion for aspen stand sustainability is: the total number of live aspen stems that have grown above browsing height (2 m) must remain stable or increase over time. This criterion more reliably estimates if aspen stands are recruiting new stems in sufficient densities to maintain the current overstory. This criterion was used to estimate individual aspen stand sustainability in our study.

Recruitment stem densities and frequencies are useful indices to compare the relative success of aspen stand regeneration at different times and in different areas. However, not all recruitment stems will necessarily survive as a long term component of the aspen overstory. Even after the terminal leader of an aspen stem has grown beyond browsing height, elk gnawing of aspen bark and fungal pathogens associated with this injury can kill a large proportion of stems < 10-15 cm dbh where elk populations are high (Krebill 1972; Keigley and Frisina 2005). Nevertheless, this fact does not invalidate the use of recruitment stems as an index. Even if only a small proportion of recruitment stems survive to reach mature size, stands with many recruitment stems can be considered more successful at regenerating than stands with very few or no recruitment stems.

Data Analyses

The experimental unit for all analyses was the circular plot—1 for each aspen stand sampled. Dependent variables analyzed were: sprout density, sapling density, presence of recruitment stems, recruitment stem density, and stems ≥ 2 m density. Random errors were independent of each other and homogeneous among treatments, but

were not normally distributed around the mean (Kuehl 1994). The Box and Cox method was used to choose a power transformation that would correct nonnormality in the random errors (Kuehl 1994). The $y^{0.25}$ power transformation was used on density of stems ≥ 2 m tall, recruitment stem density, sapling density, and sprout density. The power transformation improved the normal probability plots, but errors of some of the dependent variables still did not pass the Kolmogorov-Smirnov test ($\alpha = 0.05$) for normality (Kutner et al. 2005). However, *t*-tests and *F*-tests can be used on data with non-normal distributions when sample size is large (> 30 per treatment) and the risk of committing a Type I error is similar to the risk associated with normal distributions (Boneau 1960; Oaten 1995; Senoglu and Tiku 2001; Devore and Peck 2005). *F*-tests were conducted on the power transformed dependent variables to reduce the probability of committing a Type II error (Senoglu and Tiku 2001). Differences were considered significant at $P \leq 0.10$. The SAS® 9.1 software program was used for all statistical analyses.

The first objective was to determine if aspen overstory density and recruitment on the study area changed from 1991 to 2006. Three-hundred forty-one of the 342 stands St. John sampled in 1991 were relocated and sampled in 2006. Aspen stem density data was unavailable for one stand St. John sampled. Twenty-four aspen stands sampled in the study area were burned or cut by beaver after 1991. Comparisons of aspen mortality and recruitment at different times and in different areas should be made among stands with similar disturbance regimes if differences are to be attributed to aspen stem senescence or ungulate impacts. Insufficient time has passed for overstories to regenerate at some

burned or cut sites, while others may be failing to regenerate an overstory because of intense ungulate browsing, as in YNP after the 1988 fires (Romme et al. 1995). It is too early to predict the ultimate fates of these stands. Therefore, the 24 burned or beaver-cut stands are excluded from analysis (APPENDIX A).

In the remaining 316 stands, Pearson's χ^2 test was used to analyze differences in the proportion of stands with recruitment and with sufficient recruitment to meet Kay's criterion in 1991 and 2006 (McClave and Dietrich 1985). Although I do not believe Kay's criterion is an accurate estimate of aspen stand sustainability, it was used by St. John (1995) and is used to compare 1991 and 2006 recruitment success. A paired *t*-test was used to compare 1991 aspen stand density with 2006 aspen stand density to determine if recruitment and stems ≥ 2 m density had changed from 1991 to 2006 (McClave and Dietrich 1985). Sprout and sapling density data was not available for 1991, so all 1991 to 2006 comparisons were made only among ≥ 2 m size classes.

The second objective was to determine if aspen density and recruitment was influenced by elk herbivory. Twenty-four stands that were cut by beavers or burned since 1991 were excluded from analysis to remove the confounding factor of different disturbances. Four paired *t*-tests were used to compare 1991 density with 2006 density in Tom Miner Basin (5.2 elk/km²), West River unit (2.7 elk/km²), East River unit (2.4 elk/km²), and scree communities (0 elk/km²) to determine if aspen density had changed in each area where elk density differed. Pearson's χ^2 test was used to analyze differences in the current proportion of stands with recruitment in the 4 categories. Current aspen

densities in the 4 elk density categories were compared using $y^{0.25}$ transformed values and the general linear model (GLM) of analysis of variance (ANOVA).

The third objective was to determine if conifer establishment in aspen stands influenced aspen density and recruitment. All 316 stands lacking major overstory disturbance were categorized based on whether or not conifer canopy coverage exceeded 10%. Two paired *t*-tests were used to compare 1991 density with 2006 density in stands with or without ≥ 10% conifer coverage. Pearson's χ^2 test was used to analyze differences in the proportion of stands with recruitment where conifer canopy coverage was < 10% or ≥ 10%. Aspen densities in stands with and without ≥ 10% conifer coverage were compared using $y^{0.25}$ transformed values and the GLM procedure of ANOVA.

The fourth objective was to determine if cattle grazing in aspen stands influenced aspen density and recruitment. Two-hundred ninety-three undisturbed stands were categorized as: 1) Grazed by cattle from 1991 to 2006; 2) Cattle removed between 1991 and 2006; or 3) Not grazed by cattle from 1991 to 2006. Twenty-three stands in scree communities were excluded from analysis because neither cattle nor wild ungulates typically forage in scree communities. Aspen stands in cattle allotments on slopes steeper than 25° were categorized as not grazed because cattle use is "very minor" on such steep slopes (Mackie 1970). Three paired *t*-tests were used to compare 1991 density with 2006 density in the 3 cattle grazing categories. Pearson's χ^2 test was used to analyze differences in the proportion of stands with recruitment in the 3 cattle grazing

categories. Aspen densities in the 3 cattle grazing categories were compared using $y^{0.25}$ transformed values and the GLM procedure of ANOVA.

CHAPTER 4

RESULTS AND DISCUSSION

Aspen Sustainability

The first objective was to evaluate the current status of aspen on the study area relative to 1991. The sample of 340 aspen stands, randomly selected by St. John (1995), comprises about 25% of stands present in the study area. Twenty-four burned or beaver-cut stands were excluded from analysis so that differences could be attributed to aspen senescence or ungulate impacts. Mean recruitment stem density did not change and mean density of total stems ≥ 2 m tall declined 12% from 1991 to 2006 (Table 1).

Table 1. Mean recruitment and stem ≥ 2m densities for undisturbed aspen stands on the entire study area sampled in 1991 and 2006 on the Gallatin National Forest.

	1991 (*n*=316)	2006 (*n*=316)	Δ%	*P*
Recruitment stems ≥ 2 m and < 5 cm dbh / ha	467.2	463.2	--	0.95
Stems ≥ 2 m / ha (total overstory)	1 257.6	1 106.3	-12%	0.04

P-values based on paired *t*-tests.

Individual aspen stands in the study area were also categorized based on recruitment success and stand sustainability. The proportion of plots with a presence of recruitment stems and the proportion of plots with recruitment ratios ≥ 1.0 has not changed from 1991 to 2006 (Table 2). Recruitment success of aspen stands has not changed by these measures from 1991 to 2006. By my measure of aspen stand sustainability, 118 of the 316 undisturbed stands on this study area can sustain overstory

densities under current conditions (Table 2). Therefore, 63% of individual aspen stands in this study area are in a state of decline and cannot sustain current overstory densities.

Table 2. Proportion of plots with a presence of recruitment stems (≥ 2 m tall and < 5 cm dbh) and recruitment ratios ≥ 1.0 in 1991 and 2006, and stands that can sustain current overstory densities on the Gallatin National Forest.

	1991 (*n*=316)	2006 (*n*=316)	*P*
Proportion of plots with ≥ 1 recruitment stem	50%	55%	0.20
Proportion of plots with recruitment ratio ≥ 1.0 (# recruitment stems / # mature stems)	21%	26%	0.13
Proportion of aspen stands that are sustainable (2006 overstory stems – 1991 overstory stems ≥ 0)	--	37%	--

P-values based on Pearson's χ^2 tests.

Mean stem density from all stands averaged across the entire study area is the most meaningful measure of aspen sustainability on the landscape scale (Table 1). Because stems ≥ 2 m have grown above the reach of browsing elk (Kay 1985), a change in density of stems ≥ 2 m largely reflects change in the total aspen overstory. Recruitment stems (≥ 2 m tall and < 5 cm dbh) have likely grown above the reach of browsing elk within the last 10-15 years on NYWR (Kay 1990; Ripple and Larsen 2000). Density of the recruitment stem segment of the overstory is an important measure of recent overstory replacement. However, the change in total overstory (stems ≥ 2 m) density is a better measure of whether or not recruitment has been sufficient to maintain the aspen overstory on the landscape. Individual aspen stands can also be categorized as sustainable or unsustainable. However, the categorization of individual aspen stands does not inform us of the status of the aspen habitat type on the whole. Aspen

recruitment in individual stands is episodic. Many individual aspen stands in an area could be declining in density at any given time while average aspen density in that area remains stable or increases. For this reason, stems ≥ 2 m density averaged across the entire study area is used throughout this discussion as the most reliable indicator of aspen sustainability on the landscape scale.

While I believe that stems ≥ 2 m density averaged across the entire area is the most meaningful indicator of landscape-wide aspen sustainability, it is nonetheless informative to know how many stands are successfully recruiting sufficient numbers of new stems to maintain current overstory densities (Table 2). Plots with a presence (1 or more) of recruitment stems represent stands where at least some ramets have recently grown beyond the height at which elk typically browse aspen. These plots occur in stands with at least minimal recruitment success. The presence of at least 1 recruitment stem is certainly not a reliable indicator of sustainability of the entire aspen stand over time. However, the presence of recruitment stems is indicative of less severe ungulate impacts than occur in stands with no recruitment stems. Also, aspen stands with minimal recruitment success may sustain at least some overstory over time and may not decline as quickly as stands with no recruitment. Presence of recruitment stems is one index to compare recruitment success over time and in different areas.

Plots with recruitment ratios ≥ 1.0 have sufficient numbers of recruitment stems to meet Kay's (1985) criterion for stand sustainability. Aspen stands where the number of recruitment stems (≥ 2 m tall and < 5 cm dbh) equals or exceeds the number of mature stems (≥ 2 m tall and < 5 cm dbh) are theoretically stable or increasing in density (Kay

1985). Because Kay's criterion is a ratio (# recruitment stems / # mature stems), it is not an accurate measure of changes in density that might occur in individual aspen stands. For example, mortality of mature stems will increase the recruitment ratio and diameter growth of recruitment stems into mature stems will decrease the recruitment ratio. Although I do not believe Kay's criterion is an accurate estimate of aspen stand sustainability, it was used by St. John (1995) and is useful to compare 1991 and 2006 recruitment success.

Kay's (1985) criterion is a conservative estimate of aspen stand sustainability and is useful for categorizing individual stands when the observer does not have the benefit of previous aspen density data. However, a better measure of individual aspen stand sustainability is: the total number of live aspen stems that have grown above browsing height (2 m) must remain stable or increase over time. This criterion was used to estimate individual aspen stand sustainability in our study.

Mortality of all stems that have grown above browsing height is greater than recruitment of new stems to this height in the average aspen stand in the study area (Table 1). The decline in total density of stems ≥ 2 m tall from 1991 to 2006 is due to increased mortality of older stems, not decreased replacement with recruitment stems. About 20% of aspen overstory stems on the GNF portion of the NYWR were established before 1900 (Larsen and Ripple 2003), are nearing the end of their average maximum lifespan of 120 years (Mueggler 1989), and can be expected to deteriorate rapidly (Mueggler 1989). As aging overstory stems die at a faster rate, they must also be

replaced with recruitment stems at a faster rate if aspen stands in this study area are to remain stable or increase in density.

Aspen canopy coverage in the Greater Yellowstone Ecosystem (GYE) declined 10% from 1956 to 2001 (Brown et al. 2006). Aspen overstory density in our study area has declined a similar amount in less time (12% in 15 years). Aspen coverage is declining 0.2% annually on average in the GYE (Brown et al. 2006), but aspen density in our study area is declining 0.8% annually. Remotely-sensed aspen canopy coverage (Brown et al. 2006) and aspen density perhaps cannot be directly compared. As aspen stems senesce, it is likely that aspen stand density will decline before stand peripheries are significantly reduced. However, aspen canopy coverage has declined 0.6% annually from 1958 to 1995 on the GNF portion of the NYWR in the same general area as our study area (Larsen and Ripple 2005). Our 0.8% annual loss in overstory density is comparable to Larsen and Ripple's (2005) 0.6% annual canopy loss. Therefore, the 4-fold difference in rate of canopy loss on the GYE (Brown et al. 2006) and overstory density loss on our study area is still notable. Most aspen stands in the GYE are not located on heavily used ungulate winter ranges and are not in an accelerated state of decline (Brown et al. 2006). Compared to the average aspen stand in surrounding areas in Montana and Wyoming (Brown et al. 2006), our 12% decline in density in 15 years is severe.

Elk Browsing

Because elk browsing is the usually the greatest influence on aspen stand regeneration in this area (NRC 2002), we can better understand aspen sustainability by separating the study area into 3 distinct regions where elk migration patterns, elk population trends, and human hunting pressures on elk are different. Most elk in the East and West River units migrate north from YNP, while Tom Miner Basin is wintering range for other local elk herds. Late-winter elk density in the East River unit has declined from 4.8 elk/km^2 in the 1990s to 2.4 elk/km^2 since 2000. Elk density in the West River unit has increased from 1.8 elk/km^2 in the 1990s to 2.7 elk/km^2 since 2000. Elk density in Tom Miner Basin has decreased from 7.9 elk/km^2 in the 1990s to 5.2 elk/km^2 since 2000 (Tom Lemke, MFWP, *unpublished data*). Elk have been hunted in the winter in the East and West River units since 1976, but not in Tom Miner Basin (NYCWWG 2005).

Twenty-three aspen stands located in scree communities are distributed across the study area. Aspen stands in scree communities are largely inaccessible to wild ungulates because of steep slope and rocky substrate, and can be viewed as "natural" ungulate exclosures (St. John 1995; Larsen and Ripple 2003). Elk density in scree stands was assumed to be 0 elk/km^2. Similar to a control in an experiment, scree stands characterize how aspen stands might respond in the absence of browsing.

Table 3. Mean density of recruitment stems and stems ≥ 2 m in scree communities, East River unit, West River unit, and Tom Miner Basin on the Gallatin National Forest in 1991 and 2006.

		1991	2006	Δ%	*P*
Scree 0 elk/km² (*n*=23)	Recruitment stems / ha	958.3	876.7	--	0.74
	Stems ≥ 2 m / ha (total overstory)	1 510.6	1 566.4	--	0.84
East River 2.4 elk/km² (*n*=203)	Recruitment stems / ha	482.5	530.2	--	0.60
	Stems ≥ 2 m / ha (total overstory)	1 383.3	1 254.5	--	0.19
West River 2.7 elk/km² (*n*=50)	Recruitment stems / ha	30.6	182.9	+498%	0.01
	Stems ≥ 2 m / ha (total overstory)	680.0	563.4	-17%	0.09
Tom Miner 5.2 elk/km² (*n*=40)	Recruitment stems / ha	652.4	236.0	-64%	0.07
	Stems ≥ 2 m / ha (total overstory)	1 196.0	768.5	-36%	0.03

P-values based on paired *t*-tests.

The influence of elk browsing was examined by determining if mean aspen recruitment stem and stems ≥ 2 m density changed from 1991 to 2006 in each of the 3 study subunits and in scree communities. Mean density of recruitment stems or stems ≥ 2 m did not change from 1991 to 2006 in scree communities or the East River unit. Mean recruitment stem density increased in the West River unit from 1991 to 2006 (Table 3). Nevertheless, recruitment was still insufficient to replace the overstory such that total density of stems ≥ 2 m decreased 17% in the West River unit. Mean recruitment stem density declined 64% and stems ≥ 2 m declined 36% in Tom Miner Basin (Table 3).

Overstory aspen density did not change from 1991 to 2006 in scree communities, probably because elk browsing in the stands did not change. Because scree stands have

an uneven aged distribution of stems (Larsen and Ripple 2005), one can expect similar rates of old stem senescence and new stem recruitment in the future. Even though elk density in the East River unit declined 50% from the 1990s to the 2000s, recruitment stem and total stems ≥ 2 m densities remained stable.

Aspen stands are also declining on the NYWR inside YNP (Kay 1990; Romme et al. 1995; Ripple and Larsen 2000) and on other winter ranges in the western US (Baker et al. 1997; Hessl and Graumlich 2002). Declining aspen stands are typical on winter ranges in the Rocky Mountains where elk density is high (White et al. 1998).

Most of the 12% overall decline of aspen ≥ 2 m on the study area (Table 1) can be attributed to the 36% decline in Tom Miner Basin and the 17% decline in the West River unit, since aspen densities in the East River unit and scree communities did not change (Table 3). While mean recruitment stem density has remained stable and increased on the East River and West River units, respectively, it has declined ≈ 400 stems/ha in Tom Miner Basin (Table 3). Elk browsing appears to be preventing aspen suckers from growing above browsing height, as evidenced by the high recruitment densities in scree stands. Apparently, young aspen stems in Tom Miner Basin have successfully grown above 2 m less frequently in recent years than in years preceding St. John's 1991 survey (Table 3). Although elk density has decreased 35% since the 1990s, Tom Miner Basin has still had the highest average elk density of the 3 study subunits for the past 15 years. Lower pre-1990 wintering elk numbers in Tom Miner Basin could have allowed the recruitment stems that St. John observed in 1991 to grow. Browsing impacts on aspen

are generally greater where elk density is high (White et al. 2003) and elk density may need to be < 3 elk/km² for browsing impacts to be noticeably reduced (Mao et al. 2005).

Preventing root suckers from reaching 2 m may not be the only way that elk have contributed to aspen decline in Tom Miner Basin. More than 10 elk/km² wintered in Tom Miner Basin during a 3-year surge in elk numbers that began in 1994 (Tom Lemke, MFWP, *unpublished data*). Stems that had recently grown above browsing height may have been killed by elk gnawing and stripping the bark (Keigley and Frisina 2005). Elk killed the majority of aspen stems that were ≈ 3.7 m tall 3 years after an exclosure fence was removed in Arizona (Rolf 2001). Aspen stems that have grown above 2 m are not "safe" from all elk impacts. Many of the recruitment stems observed by St. John (1995) in Tom Miner Basin in 1991 (652 stems/ha; Table 3) probably died rather than grew to > 5 cm dbh.

Recruitment stem density increased in the West River unit, despite the fact that elk density increased 40% from the 1990s to the 2000s. Increases in aspen recruitment were likely able to occur in the West River unit because elk density is still relatively low (< 3 elk/km²), even after the increase in elk numbers. However, expectations of a future rebound of aspen in this area should be tempered. Total stem ≥ 2 m density has still decreased, even though recruitment stem density has increased. The increased recruitment rate in the West River unit is apparently being accompanied by an increased mortality rate of mature stems ≥ 2 m tall. Also, the increase in recruitment stems only occurred in a small number of stands in the West River unit. Elk browsing has still prevented growth of any recruitment stems in 37 of the 50 stands in the West River unit.

Table 4. Proportion of plots with a presence of recruitment stems, with recruitment ratios ≥ 1.0 in 2006, and stands that can sustain current overstory densities in scree communities, East River unit, West River unit, and Tom Miner Basin on the Gallatin National Forest.

	Scree 0 elk/km² (n=23)	East River 2.4 elk/km² (n=203)	West River 2.7 elk/km² (n=50)	Tom Miner 5.2 elk/km² (n=40)
Proportion of plots with ≥ 1 recruitment stem	91%[a]	61%[b]	26%[c]	40%[c]
Proportion of plots with recruitment ratio ≥ 1.0 (# recruitment stems / # mature stems)	65%[a]	27%[b]	16%[c]	13%[c]
Proportion of aspen stands that are sustainable (2006 overstory stems – 1991 overstory stems ≥ 0)	57%[a]	40%[b]	22%[c]	33%[b]

Different superscripts represent means that differ ($P \leq 0.10$) based on Pearson's χ^2 test.
Comparisons made in rows.

We can also examine the influence of elk browsing on aspen density and recruitment by comparing current conditions in areas with different current elk densities and in scree communities where elk do not browse. We can compare proportions of individual stands that meet our criteria for recruitment success (Table 4). The largest proportions of stands with a presence of recruitment stems, stands that meet Kay's criterion, and stands that can sustain current overstory densities are in scree stands—where elk do not browse. A greater proportion of stands have at least minimal recruitment success, meet Kay's criterion, and can sustain current overstory densities in the East River unit than in the West River unit or Tom Miner Basin (Table 4). Individual stands are more commonly growing new stems above browsing height in the East River unit, probably because wintering elk numbers are lowest in this subunit and are declining.

Even though total stems ≥ 2 m density of scree stands across the landscape did not change from 1991 to 2006 (Table 3), 35% and 43% of scree stands did not meet Kay's or my criteria for sustainability, respectively. This fact highlights the inadequacy of using individual aspen stand assessments to examine aspen sustainability on the landscape. Clearly, the current aspen overstory averaged across all scree stands is sustainable. Mean stems ≥ 2 m density did not change from 1991 to 2006 (Table 3). Any number of individual aspen stands could be declining in density at any given time. In scree stands, self-thinning of dense growth of stems ≥ 2 m is probably the cause of individual stand declines (Schier et al. 1985). Where aspen is sustainable on the landscape, losses in individual stand density are compensated for by increases in density in other stands. The most meaningful indicator of aspen overstory sustainability on the landscape is density averaged across many stands (Table 3).

Table 5. Mean sprout, sapling, recruitment stem, and stem ≥ 2 m densities in 2006 in scree communities, East River unit, West River unit, and Tom Miner Basin, Gallatin National Forest.

	Scree 0 elk/km² (*n*=23)	East River 2.4 elk/km² (*n*=203)	West River 2.7 elk/km² (*n*=50)	Tom Miner 5.2 elk/km² (*n*=40)
Sprouts < 1 m / ha	1 315.0[a]	4 181.8[b]	4 475.6[b]	3 974.7[b]
Saplings 1-2 m / ha	855.2[a]	1 946.7[b]	918.2[a]	1 287.4[a]
Recruitment stems ≥ 2 m and < 5 cm dbh / ha	876.7[a]	530.2[b]	182.9[c]	236.0[c]
Stems ≥ 2 m / ha (total overstory)	1 566.4[a]	1 254.5[b]	563.4[c]	768.5[c]

Different superscripts represent means that differ ($P \leq 0.10$) based on ANOVA contrasts. Comparisons made in rows.

We can also examine elk browsing impacts on aspen by comparing current stem densities averaged across all aspen stands in each of the 4 elk use categories (Table 5). Mean sprout (< 1 m tall) density is lowest in scree stands, probably because of the dry, rocky conditions in scree communities. Sapling (1-2 m) density in scree stands is also lower than in East River and Tom Miner Basin, which is also probably due to the poor growing conditions in scree stands. The highest recruitment stem and stem ≥ 2 m density is in scree stands (Table 5).

Absence of elk browsing enhances the ability of aspen stems in scree communities to grow above 2 m. The greater density of overstory stems in scree stands is even more striking in light of the low numbers of root sprouts produced in scree stands. A large fraction of root sprouts produced in scree stands apparently survive to grow above 2 m, or the stems ≥ 2 m density would not be as high as it is. Scree stands on the NYWR inside YNP exhibit similar characteristics as scree stands in our study area (Larsen and Ripple 2005). Scree stands in our study area and YNP grow new stems above 2 m more frequently than nonscree stands. Larsen and Ripple (2005) found that 9 (75%) of 12 scree stands in YNP contained at least 1 recruitment stem inside a 60 m² plot (202.3 m² plot was used in our study). No plots in 93 non-scree stands in YNP contained recruitment stems, likely due to intense elk browsing where aspen is accessible (Larsen and Ripple 2005).

Mean densities of sprouts do not differ among Tom Miner Basin, the West River unit, and the East River unit. Sapling density, recruitment stem density, and total stem ≥ 2 m density are greater in the East River unit than Tom Miner Basin or the West River

unit (Table 5). Because sprout densities do not differ among Tom Miner, West River, and East River aspen stands, the ability of stands in the 3 areas to produce root suckers appears similar. Mueggler (1989) estimated that aspen stands with > 2500 suckers (stems < 1.4 m tall) / ha had the potential to successfully replace the overstory. The average sprout densities for aspen stands in each of the 3 areas exceed this number. However, densities of stems in size classes > 1 m are lower in the West River unit and Tom Miner Basin than in the East River unit. Elk browsing can prevent root suckers from growing above 1 m elsewhere in the GYE (Bartos and Mueggler 1981; Romme et al. 1995). Elk browsing is probably preventing sprouts in the West River unit and Tom Miner Basin from increasing in height more effectively than in the East River unit. Elk impacts on recruitment are likely more severe in Tom Miner Basin simply because elk density is higher.

The reasons for different densities of stems > 1 m in the East and West River unit may be more complex than simple differences in elk densities. Elk density was higher in the East River unit than the West River unit for most of the 1990s and has only been slightly lower in the 2000s (2.4 elk/km² vs 2.7 elk/km²). The elk populations' different risks of predation in the two areas could account for the different stem densities. Elk have been hunted by humans in the winter in the East and West River units since 1976 (NYCWWG 2005). However, public hunting access to Forest Service land in the West River unit is limited because of interspersed private landholdings. The greater hunting disturbance may have caused elk to browse aspen stands less efficiently (Laundre et al. 2001; Ripple et al. 2001; White et al. 2003) in the East River unit than the West River

unit. Also, the population trend of the elk herd could be more important in preventing sapling and recruitment stem growth than elk densities. The decreasing elk numbers on the East River unit may have created conditions more favorable for the escape of new suckers above browsing height than the increasing elk numbers on the West River unit.

Aspen mortality was examined in a study similar to ours on the Gros Ventre elk winter range in western Wyoming (Hart and Hart 2001). Eighty-five circular plots established where elk browsing was common in 1970 were resampled in 1985 and 1999 (Krebill 1972; Hart and Hart 2001). From 1970 to 1999, average annual mortality of stems > 2.5 cm dbh was 2.5% (Hart and Hart 2001). For comparison, aspen stems 2 m tall and 2.5 cm dbh are of similar size (*personal observation*). Density of aspen stems ≥ 2 m tall declined 2.3% and 1.1% per year on average from 1991 to 2006 in Tom Miner Basin and the West River unit, respectively. Density of stems ≥ 2 m is stable in the East River unit and scree communities (Table 3). Aspen overstory density is declining more quickly in aspen stands on the Gros Ventre winter range commonly used by elk than in our study area. This is probably due to the fact that overstory aspen stems are generally older (Krebill 1972) and elk density (≈ 10 elk/km²) is higher (Kilpatrick and Abendroth 2001) in the Gros Ventre drainage than in our study area.

Aspen stands in our study area recruit new stems above elk browsing height more successfully than on the NYWR inside YNP (Ripple and Larsen 2000). Over half (55%) of aspen stands on our study area have had at least minimal recruitment success in the past 10-15 years (Table 2). This contrasts with the NYWR inside YNP in 1998, where no stems above browsing height and < 10 dbh (< 20 years old) were located in 57 aspen

stands (Ripple and Larsen 2000). Aspen stands have recruited new overstory stems more successfully outside YNP on the GNF elk winter range and the Sunlight/Crandall elk winter range than inside YNP for the past 80 years (Larsen and Ripple 2003; 2005). The difference in the success of aspen regeneration outside and inside YNP is likely due to a history of lower elk densities and less intense browsing outside YNP than inside YNP (Larsen and Ripple 2005). A similar pattern is found in RMNP, Colorado, where aspen regenerate more frequently on elk winter range outside the Park than inside (Suzuki et al. 1999).

Trophic Cascades: Large Scale vs. Small Scale

After their reintroduction in 1995, researchers hypothesized that wolves could reduce the NYWR elk population such that aspen regeneration would increase (Ripple and Larsen 2000). However, an overall increase in aspen overstory replacement has not occurred over our entire 560 km² study area since 1991 (Table 1). At this point, it does not appear that a wolf-elk-aspen trophic cascade has allowed aspen recruitment to increase at the landscape level on the GNF north of YNP.

On the smaller scale of the elk use subunits (East River = 340 km²; West River = 120 km²; Tom Miner = 100 km²), aspen recruitment was unchanged in East River, increased in West River, and decreased in Tom Miner (Table 3). At first glance, it might appear that a trophic cascade has allowed aspen overstories to regenerate on the West River unit. However, a further examination of the data reveals that aspen recruitment density in the West River is still the lowest of the 3 subunits (Table 4) and that

recruitment is not sufficient to maintain current overstory densities (Table 3). Also, elk numbers increased recently in the West River unit, so it is unlikely that wolves caused the minor response in aspen we observed. Lethal effects of wolves on elk may have contributed to the 50% decline in elk numbers on the East River unit. A greater presence of human settlements in the West River unit and Tom Miner Basin may have reduced wolf predation on these elk herd segments. Aspen overstory density and recruitment has largely remained stable in the East River unit. Meanwhile, overstory density has declined in Tom Miner Basin and the West River unit (Table 3). The reduction in the NYWR elk population on the East River unit may have prevented a further decline in aspen density that would have occurred if the population had remained stable. If the definition of a wolf-elk-aspen trophic cascade is broadened from "allowing aspen recruitment to increase" to "allowing total overstory density to remain stable", one could argue there is evidence of a trophic cascade in the East River unit.

Smaller-scale increases in cottonwood and willow heights have occurred in some areas of YNP since wolf reintroduction (Ripple and Beschta 2003; 2004). Willow response was observed along ≈ 3 km stream reaches in the Gallatin winter range, while cottonwood response was observed at 3 specific sites inside 120 m² belt transects near the Lamar River and Soda Butte Creek. Aspen sucker height increases were observed on a larger scale (800 km²) in the Lamar and upper Yellowstone River drainages inside YNP, but only occurred in riparian aspen stands (Ripple et al. 2001). Our study area could be divided into 21 separate creek drainages ≈ 8-20 km² in size. Mean recruitment stem density increased from 1991 to 2006 in 8 of the 21 smaller drainages. For example,

recruitment density increased 5-fold in the North Fork of Bear Creek area—an area frequented by wolves (Dan Tyers, USFS, *personal communication*). Depending on the size and location of the area chosen, small-scale evidence can support or fail to support the hypothesis that wolf effects on elk have relieved browsing pressure and allowed browse species such as aspen, willow, or cottonwood to recruit new stems above browsing height. Evidence of aspen release in one or a few drainages cannot be extrapolated to the larger landscape. Although aspen recruitment did increase in some drainages on our study area, aspen recruitment did not increase at the landscape level.

Conifer Establishment

Conifers often colonize aspen stands that have not recently burned and could reduce aspen regeneration on this study area. In order to examine the effects of conifers on aspen density and recruitment, 316 stands lacking major overstory disturbance between 1991 and 2006 were divided into 2 groups with and without ≥ 10% conifer coverage in the stand. Conifer canopy coverage was ≥ 10% in 164 (52%) undisturbed aspen stands in 1991. In 2006, conifer canopy coverage was ≥ 10% in 173 (55%) stands. The proportion of stands with ≥ 10% conifer coverage was not different in 1991 and 2006 ($P = 0.47$). Even in the absence of major disturbance, the proportion of aspen stands where conifers occupy ≥ 10% of the stand has not changed in 15 years. Conifer establishment in aspen stands in this area has been slow.

Table 6. Mean density of recruitment stems and stems ≥ 2 m in stands with and without ≥ 10% conifer coverage in 1991 and 2006 on the Gallatin National Forest.

		1991	2006	Δ%	*P*
Conifers ≥ 10% canopy coverage (*n*=173)	Recruitment stems / ha	267.1	292.5	--	0.69
	Stems ≥ 2 m / ha (total overstory)	834.7	731.0	-12%	0.10
Conifers < 10% canopy coverage (*n*=143)	Recruitment stems / ha	709.2	669.8	--	0.76
	Stems ≥ 2 m / ha (total overstory)	1 769.1	1 560.4	--	0.14

P-values based on paired *t*-tests.

Recruitment stem density did not change from 1991 to 2006 in stands with or without ≥ 10% conifer canopy coverage. Stems ≥ 2 m density declined in stands with ≥ 10% conifer coverage, but did not change in stands with < 10% conifer coverage (Table 6). Because conifer establishment is often associated with late-seral aspen stands, overstory stems in stands colonized by conifers are probably older, on average, than overstories in stands that do not contain conifers. Overstories in stands with ≥ 10% conifer presence have senesced more rapidly than recruitment stems can replace them in the past 15 years. On average, aspen stands not colonized by conifers have been more stable (Table 6).

Table 7. Proportion of plots with a presence of recruitment stems, with recruitment ratios ≥ 1.0, and stands that can sustain current overstory densities with and without ≥ 10% conifer coverage on the Gallatin National Forest.

	Conifers ≥ 10% canopy coverage (*n*=173)	Conifers < 10% canopy coverage (*n*=143)	*P*
Proportion of plots with ≥ 1 recruitment stem	44%	68%	0.0001
Proportion of plots with recruitment ratio ≥ 1.0 (# recruitment stems / # mature stems)	20%	34%	0.01
Proportion of aspen stands that are sustainable (2006 overstory stems – 1991 overstory stems ≥ 0)	36%	39%	0.54

P-values based on Pearson's χ^2 tests.

Recruitment stems are present in a larger proportion of stands with < 10% conifer coverage than stands with ≥ 10% conifer coverage (Table 7). A larger proportion of aspen stands with < 10% conifer coverage within the stand grow at least minimal numbers of new stems above 2 m than stands where conifer canopy coverage exceeds 10%. Nevertheless, about one-third of aspen stands without significant conifer presence still grow no stems above 2 m. Ungulate browsing prevents even minimal recruitment in some aspen stands in this area, even if conifers have not colonized the stand. A greater proportion of individual stands without 10% conifers recruit successfully by Kay's criterion than stands with 10% conifers (Table 7). A similar proportion of stands with and without 10% conifers can sustain current overstory densities (Table 7). However, conifer colonized aspen stands may already have lower overstory densities that can be sustained. This can be examined by comparing current aspen densities averaged across all stands with and without ≥ 10% conifer coverage.

Table 8. Mean sprout, sapling, recruitment stem, and stem ≥ 2 m densities in stands with and without ≥ 10% conifer coverage on the Gallatin National Forest.

	Conifers ≥ 10% canopy coverage (*n*=173)	Conifers < 10% canopy coverage (*n*=143)	*P*
Sprouts < 1 m / ha	3 934.8	4 064.3	0.44
Saplings 1-2 m / ha	1 142.7	2 199.8	0.004
Recruitment stems ≥ 2 m and < 5 cm dbh / ha	292.5	669.8	0.0001
Stems ≥ 2 m / ha (total overstory)	731.0	1 560.4	0.0001

P-values based on the *F*-test from ANOVA.

Mean sprout density does not differ in aspen stands with and without ≥ 10% conifer canopy coverage (Table 8). Mean density of saplings, recruitment stems, and stems ≥ 2 m is approximately 2 times greater in stands with < 10% conifer canopy coverage than in stands with ≥ 10% conifer canopy coverage.

Mean density of all size classes of aspen stems taller than 1 m is significantly less in stands with ≥ 10% conifer coverage than in stands with < 10% conifer coverage on this study area. Clearly, browsing more effectively prevents sucker growth above 1 m in stands with conifers than in stands without conifers. However, mean sprout density in aspen stands with ≥ 10% conifer coverage is still sufficiently high to replace the overstory (Mueggler 1989) and is not different from mean sprout density in stands with < 10% conifer coverage. Because extensive root suckering occurs even in late-seral aspen stands that have been colonized by conifers, the classic theory of apical dominance preventing the initiation of root suckers (Schier et al. 1985) does not seem to apply to

most stands in this study area. In Utah, aspen stands inside ungulate exclosures regenerate overstory stems even if they are colonized by conifers (Kay and Bartos 2000).

Aspen grow more slowly in the shade of conifers (Shepperd et al. 2001; Brown et al. 2006), which probably plays a larger role in the failure of conifer-colonized stands of this study area to produce recruitment stems than decreased numbers of suckers. Where sucker growth is slow, less frequent browsing is required to prevent growth above 2 m than where growth is faster. Also, aspen stands colonized by conifers could be more attractive to wintering elk than stands where conifers have not established because they simultaneously provide forage, thermal cover, hiding cover, and lower snow depths. In summary, ungulate browsing, not apical dominance or conifer establishment appears to be the cause of the failure of aspen stems to grow above browsing height in this study area. The presence of a conifer canopy appears to exacerbate the effects of browsing ungulates.

Cattle Grazing

Cattle graze in summer and early fall in some aspen stands on the study area. In order to examine the effects of cattle grazing on aspen regeneration, we compared density and frequency of recruitment in stands where cattle grazed from 1991 to 2006, cattle grazing ended between 1991 and 2006, and cattle did not graze from 1991 to 2006. Twenty-three scree communities were excluded from analysis because they were not used by wild ungulates or cattle. Two-hundred ninety-three stands were unimpacted by major overstory disturbance and located in non-scree communities in 2006. In 1991, 165 aspen stands were located on active Forest Service cattle allotments. One-hundred

twenty-eight stands were not grazed by cattle because they were located on non-allotment land or on slopes steeper than 25° (Mackie 1970). In 2006, 104 stands were on active cattle allotments and 189 stands were not grazed by cattle. Sixty-one aspen stands that were grazed by cattle in 1991 were no longer being grazed in 2006.

Table 9. Mean density of recruitment stems and stems ≥ 2 m in 1991 and 2006 on the Gallatin National Forest where cattle grazed from 1991 to 2006, grazing ended between 1991 and 2006, or cattle did not graze from 1991 to 2006.

		1991	2006	Δ%	*P*
Grazed 1991 to 2006 (*n*=104)	Recruitment stems / ha	384.4	279.4	--	0.31
	Stems ≥ 2 m / ha (total overstory)	1 055.4	776.5	-26%	0.003
Grazed 1991, not 2006 (*n*=61)	Recruitment stems / ha	151.5	520.9	+244%	0.01
	Stems ≥ 2 m / ha (total overstory)	836.9	1026.5	--	0.15
Not grazed 1991 to 2006 (*n*=128)	Recruitment stems / ha	596.5	510.8	--	0.48
	Stems ≥ 2 m / ha (total overstory)	1 576.8	1 329.7	-16%	0.08

P-values based on paired *t*-tests.

The effects of cattle grazing on aspen recruitment were examined by comparing 1991 densities to 2006 densities in the 3 cattle use categories (Table 9). Mean recruitment stem density did not change in stands where cattle grazed from 1991 to 2006 or in stands not grazed from 1991 to 2006. However, mean recruitment stem density increased more than 3-fold in stands where cattle grazing ended between 1991 and 2006 (Table 9). Total stem ≥ 2 m density decreased 26% in stands where cattle continued to graze and decreased 16% in stands with no cattle grazing in the past 15 years (Table 9).

Total density of stems ≥ 2 m tall is declining in stands where the status of cattle grazing has not changed in the past 15 years. This finding is consistent with my results which indicated that aspen stands in this study area, on average, are declining (Table 1). Total density of stems ≥ 2 m is not declining in stands where cattle have been removed, primarily because recruitment stem density has increased from 1991 to 2006. Even though stocking densities on Forest Service allotments are low (3-7 ha/AUM), the removal of cattle stimulated more suckers to grow above 2 m in this study area. Because many aspen stands in the study area are heavily browsed by elk (St. John 1995), even light stocking of cattle seems to negatively impact recruitment. Also, 31 of the 61 stands where cattle were removed were located in the Cedar Creek drainage, which was privately owned until 1991. Previous cattle stocking rates in this drainage are not known, but it is likely that they were higher than stocking rates on Forest Service allotments in 1991. Cattle impacts in this drainage may have been more severe in 1991, so an aspen recruitment increase after the removal of cattle may have been even more likely to occur in Cedar Creek than in the Forest Service allotments.

The removal of cattle resulted in increased mean recruitment stem density, but increases in recruitment did not occur in every stand where cattle were removed. In fact, 54% of stands where cattle were removed still grew no recruitment stems. Cattle grazing ended in 1991, 1995, 2001, or 2005 in stands across the study area. An aspen sprout that is completely protected from browsing could grow above 2 m in about 6 years in this study area (Sam McColley, *unpublished data*), so insufficient time may have passed for aspen to grow above 2 m since the removal of cattle from some stands. Since conifer

establishment and elk browsing are also associated with the failure to produce recruitment stems in this area, it is likely these factors must be limited if recruitment stem production is to increase after the removal of cattle.

Table 10. Proportion of plots with a presence of recruitment stems, with recruitment ratios ≥ 1.0, and stands that can sustain current overstory densities on the Gallatin National Forest where cattle grazed from 1991 to 2006, grazing ended between 1991 and 2006, or cattle did not graze from 1991 to 2006.

	Grazed 1991 to 2006 (*n*=104)	Grazed 1991, not 2006 (*n*=61)	Not grazed 1991 to 2006 (*n*=128)
Proportion of plots with ≥ 1 recruitment stem	43%[a]	46%[a]	62%[b]
Proportion of plots with recruitment ratio ≥ 1.0 (# recruitment stems / # mature stems)	20%[a]	25%[a]	25%[a]
Proportion of aspen stands that are sustainable (2006 overstory stems – 1991 overstory stems ≥ 0)	27%[a]	51%[b]	36%[a]

Different superscripts represent means that differ ($P \leq 0.10$) based on Pearson's χ^2 test.
Comparisons made in rows.

The proportion of stands with a presence of recruitment stems is greater in stands with no of cattle grazing in the past 15 years, whether cattle have continued to graze or have been removed since 1991 (Table 10). Similar proportions of individual stands meet Kay's criterion, regardless of cattle grazing status. Because Kay's criterion is a ratio (# recruitment stems / # mature stems), it is not sensitive to all changes in density that might occur in individual aspen stands. The largest proportion of individual stands that are sustainable by my criteria are stands where cattle grazing ended between 1991 and 2006. Mean recruitment stem density has increased since 1991 in stands where cattle have been

removed (Table 9). Overstory densities in some stands where cattle have been removed are actually increasing and are therefore considered sustainable (Table 10).

Table 11. Mean sprout, sapling, recruitment stem, and stem ≥ 2 m densities on the Gallatin National Forest where cattle grazed from 1991 to 2006, grazing ended between 1991 and 2006, or cattle did not graze from 1991 to 2006.

	Grazed 1991 to 2006 (*n*=104)	Grazed 1991, not 2006 (*n*=61)	Not grazed 1991 to 2006 (*n*=128)
Sprouts < 1 m / ha	4 150.0[a]	4 001.5[a]	4 343.7[a]
Saplings 1-2 m / ha	1 450.8[ab]	1 361.9[a]	2 020.5[b]
Recruitment stems ≥ 2 m and < 5 cm dbh / ha	279.4[a*]	520.9[ab*]	510.8[b*]
Stems ≥ 2 m / ha (total overstory)	776.5[a]	1 026.5[a]	1 329.7[b]

Different superscripts represent means that differ ($P \leq 0.10$) based on ANOVA contrasts. Comparisons made in rows.
*Actual $y^{0.25}$ transformed means are 1.97, 2.27, and 2.78, respectively.

Current density of total stems ≥ 2 m is greater in stands with no cattle grazing in the past 15 years than in stands that have been grazed in the past 15 years, whether cattle have continued to graze or have been removed since 1991 (Table 11). Most stands not grazed in 15 years have never been grazed by cattle or have not been grazed for about 70 years (St. John 1995). Cattle appear to have played a historic role in limiting aspen growth above 2 m on the study area. Cattle may forage extensively on aspen leaves and twigs in late summer and early fall after herbaceous forage has cured (USFS 1937). Late-season browsing seems to make aspen suckers more susceptible to frost injury (Krebill 1972; Fitzgerald and Bailey 1984).

Mean density of saplings and sprouts far exceeds the 2 500 suckers / ha required to sustain most stands (Mueggler 1989), regardless of cattle grazing status. Even if

browsing or subsequent frost damage kills suckers, most aspen stands on the study area are quick to resprout new root suckers the following spring such that total density does not decrease. Aspen stands that are grazed by cattle fail to grow new stems above 2 m because height growth of suckers is suppressed by browsing, not because the aspen clones are unable to produce sufficient numbers of root suckers.

I emphasize that these results show the cumulative impacts of cattle and elk browsing, not the impacts of cattle alone. No ramets have grown above 2 m inside the plots of 49 (38%) of the 128 stands ungrazed by cattle in the past 15 years (Table 10). Only half (26 stands) of these stands were also colonized by conifers. This fact indicates that wild ungulate browsing alone can completely suppress overstory recruitment in some stands on the study area. This commonly occurs inside YNP (Kay 1985).

These results concur with the results from an assessment of aspen density in Utah inside specialized exclosures where deer and elk browsed but cattle were excluded and outside exclosures were deer, elk, and cattle foraged (Kay and Bartos 2000). Mean densities of sapling and sprouts (stems < 2 m tall) were did not differ and were high enough to replace the overstory inside and outside the exclosures (Kay and Bartos 2000). However, recruitment stem density was 150% greater inside exclosures that excluded cattle but allowed deer and elk to browse than outside exclosures where cattle, deer, and elk browsed (Kay and Bartos 2000). Similarly, sprout and sapling density in our study area is not lower in stands where cattle and elk browse, but recruitment stem density is lower.

St. John (1995) reported that 28% of aspen stands on the study area not grazed by cattle and 12% of stands grazed by cattle had recruitment ratios ≥ 1.0 (# recruitment stems > 2 m/# mature stems > 2 m). The higher recruitment density (Table 11) and greater proportion of stands with recruitment (Table 10) in 2006 in stands ungrazed by cattle than in stands currently grazed by cattle corroborate St. John's (1995) finding that cattle grazing negatively impacts aspen recruitment in this area.

CHAPTER 5

CONCLUSIONS

Sixty-three percent of individual aspen stands on the study area are not recruiting sufficient numbers of stems above 2 m to replace aging overstories. Total stems ≥ 2 m have decreased from 1991 to 2006 in these stands. However, mean recruitment stem and stems ≥ 2 m density are more meaningful measures of aspen sustainability at the landscape level. Mean recruitment of new overstory aspen stems did not change on the study area from 1991 to 2006. During this same time, mean density of total overstory (≥ 2 m tall) aspen stems has declined 12%. Overstory stems are dying more rapidly than they are being replaced in the average stand on the study area. Although NYWR elk numbers have declined since 1991, aspen recruitment has not increased and current overstory aspen densities are apparently not sustainable at the landscape level.

I believe aspen recruitment on the overall study area may have failed to increase in response to reduced wintering elk numbers for two reasons: First, more time could be required for aspen suckers "released" from browsing pressure to grow above browsing height. Aspen did not show dramatic change inside an exclosure on the Gallatin winter range until more than 18 years after the exclosure was built (Kay 2001b). The number of elk wintering north of YNP on our study area did not decline appreciably until 2000. Aspen suckers completely protected from browsing grow about 30 cm per year on the NYWR (Sam McColley, *unpublished data*). If aspen sucker heights had been suppressed to 20-30 cm as in YNP (Romme et al. 1995), it could take 6 years for completely

unbrowsed suckers to reach 2 m in height. Second, elk numbers could still be too high for aspen regeneration to increase. Because aspen are highly preferred forage in winter and occupy such a small proportion of the landscape (Houston 1982), low densities of elk may continue to suppress recruitment.

Aspen overstory densities have not declined uniformly across the study area from 1991 to 2006. Mean density of stems ≥ 2 m decreased 36% in Tom Miner Basin and 17% in the West River unit, accounting for most of the observed decline in aspen on the whole study area. Density of stems ≥ 2 m in the East River unit did not change, likely because elk density is lower than in West River unit and Tom Miner Basin and has decreased 50% since the 1990s. Current recruitment stem densities are lowest in the West River unit and Tom Miner Basin—the subunits with the highest elk densities. Elk herbivory appears to be the primary cause of aspen decline at the landscape level on our study area.

Conifer establishment in aspen stands has also contributed to this decline, especially in the West River unit and Tom Miner Basin where conifers are present in the majority of stands. Conifer canopies generally impede aspen recruitment by slowing sucker growth and exacerbating the effects of browsing, not by preventing the initiation of root sprouts. Cattle grazing in aspen stands has also contributed to aspen overstory decline, especially in Tom Miner Basin where most aspen stands are currently grazed by cattle. The cumulative impacts of winter elk browsing and late-summer cattle browsing on aspen suckers prevents growth above 2 m more effectively than the impact of elk browsing alone.

Aspen recruitment increased from 1991 to 2006 in 8 of 21 smaller (8-20 km²) creek drainages on our study area, even though aspen recruitment did not increase across the larger landscape (560 km²) of our entire study area. Depending on which specific drainage is chosen, evidence from a single drainage can support or fail to support the hypothesis that aspen recruitment has increased since wolf reintroduction. Others have examined even smaller areas and suggested that a wolf-elk-browse plant trophic cascade may have occurred on a landscape scale (Ripple and Beschta 2003; 2004). Evidence of aspen release in one or a few drainages cannot be extrapolated to the larger landscape. Aspen recruitment has not increased at the landscape level on the Gallatin National Forest since wolf reintroduction.

CHAPTER 6

MANAGEMENT IMPLICATIONS

Management on the GNF will need to change if the current aspen resource is to be maintained. One hundred ninety-eight of 316 stands (63%) are losing overstory stems more quickly than they are being replaced. However, individual aspen stands are highly variable. The change in overstory densities averaged across many aspen stands is more informative for managers to know which general areas are losing aspen coverage. Even though some management actions must occur on a stand-by-stand basis, the following recommendations are intended to allow managers to prioritize management actions and choose appropriate management actions for larger landscapes. Aspen overstory density has remained relatively stable in the East River portion of the study area, but has declined in the West River portion and Tom Miner Basin. Because elk population dynamics, conifer establishment in aspen stands, and cattle grazing differ in these 3 areas, management prescriptions to promote aspen will be suggested separately for each area.

If the goal is to maintain present densities of aspen, no management action needs to be taken under current conditions in the East River unit. Conifers could eventually hinder aspen recruitment in this area, but conifer colonization in our study area is slow. If wintering elk numbers in the East River do not increase, managers can expect overstory aspen density to remain stable for another 15 years.

Management may need to change if present aspen overstory densities are to be maintained in the West River unit. Increased hunter harvest of elk, removal of conifers,

or removal of cattle might accomplish this goal in the West River unit. Gardiner Late Hunt elk harvests have been drastically reduced in recent years in Montana Hunting District 313 (East and West River units, roughly) in response to declining numbers of elk migrating north from YNP. However, wintering elk numbers in the West River unit have increased since the 1990s. Hunting regulations could be changed so that elk harvest west of the Yellowstone River could increase, while harvest east of the Yellowstone River could remain low. Conifers occupy a majority of stands in the West River unit. Cutting conifers out of the canopy of aspen stands could increase aspen recruitment by increasing solar radiation and growth rates of aspen suckers. It is not necessary to cut or burn the aspen canopy to promote suckering in most stands in this area. Mean sucker densities are sufficiently high to replace aspen overstories (Mueggler 1989), even in stands colonized by conifers. Cutting the conifers but leaving the aspen overstory is a "safer" strategy for stands that could receive high elk use. If elk browsing is intense enough to prevent aspen recruitment even after the treatment, the overstory of the stand will still be present. This management does not run the risk of hastening the demise of a stand, as occurred in several beaver-cut stands sampled in Eagle Creek and 2 burned stands on Deckard Flats in the Bear Creek drainage. Removal of cattle grazing could promote aspen recruitment in the West River unit, as occurred between 1991 and 2006. However, the interaction of conifers slowing sucker growth and continued elk browsing will probably prevent a detectable response in some aspen stands.

Management must also change in Tom Miner Basin if present aspen overstory densities are to be maintained. Increased hunter harvest of elk is the most likely means to

accomplish the goal of maintaining aspen overstory density in Tom Miner Basin. Because of the higher elk density in Tom Miner Basin, it is unlikely that removal of conifers or cattle alone would increase aspen overstory recruitment in most stands at current elk densities.

If a management goal is to *increase* aspen overstory density in the study area, there is no better time than the present to attempt management actions. The 2006-2007 northern Yellowstone elk count of 6 738 elk is the lowest count in decades (NYCWWG 2007). Removing conifers and/or cattle would probably be successful in some stands in the East and West River units if elk densities remain low (< 3 elk/km^2). There is a high probability that removing cattle from Joe Brown and Slip and Slide Creek drainages in the East River unit would increase aspen recruitment in many stands. This occurred after the removal of cattle in Cedar Creek, the adjacent drainage to the south.

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APPENDIX A:

BURNED AND BEAVER-CUT ASPEN STANDS

Nine aspen stands on the study area were burned by four separate fires in 1994, 2000, and 2001. Mean density of stems ≥ 2 m and recruitment stems declined 80-90% in burned stands from 1991 to 2006 (Table 12). Two stands burned in 1994 did not recruit new stems above browsing height after fire. Fire has hastened the demise of these stands where elk use is high, as has occurred in YNP (Romme 1995) and near Jackson Hole, Wyoming (Kay 2001a). Two stands in the Sixmile Creek drainage disappeared from the site following fire in 2000. Since these stands were not located in an area with severe browsing pressure, fire appeared to kill above- and below-ground parts of these clones. It is too early to know with certainty if other stands burned in 2000 and 2001 will regenerate new overstories. About 45 000 suckers (< 2 m)/ha have sprouted in 2 aspen stands near the top of Dome Mountain that burned in 2001. These stands receive little wintering elk use and probably will regenerate.

Table 12. Mean density of recruitment stems and stems ≥ 2 m for 9 aspen stands burned on the Gallatin National Forest between 1991 and 2006.

		1991	2006	Δ%	*P*
Burned aspen stands (*n*=9)	Recruitment stems / ha	834.7	109.8	-87%	0.08
	Stems ≥ 2 m / ha (total overstory)	1 658.4	225.1	-86%	0.03

Fifteen aspen stands in 3 creek drainages were fully or partially cut by beavers since 1991. Thirteen stands were located in the Eagle Creek drainage and two stands were in the lower reaches of the Phelps Creek and Mulherin Creek drainages. Mean density of stems ≥ 2 m tall in beaver-cut stands declined 55% from 1991 to 2006. Mean recruitment stem density was highly variable among stands (Table 13). The average

beaver-cut stand in Eagle Creek has not recruited overstory stems to replace the previous overstory that existed prior to cutting. Insufficient time for regrowth may have passed since cutting in some stands, but heavy elk browsing is probably preventing overstory regeneration in most beaver-cut stands. Two stands that were partially cut by beavers recruited new stems such that 2006 density of stems > 2 m is actually greater than 1991 density. Both of these stands are near the Jardine road and the Eagle Creek campground, so elk may avoid the area due to human activities.

Table 13. Mean density of recruitment stems and stem ≥ 2 m for 15 aspen stands cut by beavers on the Gallatin National Forest between 1991 and 2006.

		1991	2006	Δ%	*P*
Beaver-cut aspen stands (*n*=15)	Recruitment stems / ha	1 317.9	642.5	--	0.13
	Stems ≥ 2 m / ha (total overstory)	2 560.0	1 156.5	-55%	0.01