Natural Resources and Environmental Issues

Volume 16 *Shrublands: Wildlands and Wildlife Habitats*

Article 8

2011

Quaking Aspen Ecology on Forest Service Lands North of Yellowstone National Park

David S. Kimble

Daniel B. Tyers

Bok F. Sowell

Quaking Aspen Ecology on Forest Service Lands North of Yellowstone National Park

David S. Kimble[1], Daniel B. Tyers[2], and Bok F. Sowell[3]

ABSTRACT

Quaking aspen (Populus tremuloides) *occupy a small area in the northern Rocky Mountains, but are highly valued as wildlife habitat. Aspen stands in and around Yellowstone National Park commonly consist of few, large, mature overstory stems and numerous root suckers that do not grow above the browsing reach (≈ 2 m) of most wild ungulates. Our primary objective was to determine if the recruitment or density of aspen stems > 2 m tall had changed from 1991 to 2006 on a portion of the Gallatin National Forest. The same aspen stands were surveyed in 1991 and 2006 in the 560 km² study area (*n *= 316). Secondary objectives were to determine if aspen density was influenced by elk* (Cervus elaphus) *browsing, conifer establishment, and cattle (*Bos *spp.) grazing. Mean recruitment stem density did not change from 1991 to 2006 (*$P = 0.95$*). Density of stems > 2 m declined 12 percent from 1991 to 2006 (*$P = 0.04$*), which indicates that recruitment stems are not being produced at a sufficient rate to replace aging overstories. Areas with the greatest elk densities had the lowest recruitment stem densities and contributed the most to the decline. Although elk browsing seemed to play the largest role, conifer establishment and cattle grazing have also negatively impacted overstory recruitment in aspen stands. Even though elk numbers on the Northern Yellowstone Winter Range have declined since wolf reintroduction, aspen recruitment has not increased at the landscape level on the Gallatin National Forest.*

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 and primarily rely on root sprouts to replace aging stems for the species to persist in the Rocky Mountains (McDonough 1985). 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).

In: Wambolt, C.L. et al. comps. 2011. Proceedings – Shrublands: wildlands and wildlife habitats; 2008 June 17-19; Bozeman, MT. NREI, volume XVI. S.J. and Jessie E. Quinney Natural Resources Research Library, Logan, Utah, USA.

[1]David S. Kimble, South Dakota Department of Game, Fish & Parks, Rapid City, SD 3305 West South Street, Rapid City, SD david.kimble@state.sd.us

[2]Daniel B. Tyers, USDA Forest Service, Gardiner, MT

[3]Bok F. Sowell, Montana State University, Bozeman, MT

Where ungulate densities are high, browsing can suppress aspen sucker growth and prevent aspen clones from replacing older overstory stems with younger stems (Debyle 1985a). Aspen coverage on the Northern Yellowstone Winter Range (NYWR) has declined from 4 to 10 percent of the landscape near the beginning of the 20th century to 1 percent presently (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 (NRC 2002).

Apical dominance may impede regeneration when an aspen stand has many mature stems and auxins that suppress the growth of root sprouts are transported from the aboveground stems to the roots (Schier and others 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). Conifers are more shade tolerant than aspen and are generally associated aspen stands that have been undisturbed for many years. Eventually, conifers may invade aging aspen overstories (Jones and Schier 1985) and can suppress aspen growth (Brown and others 2006; Shepperd and others 2001).

Domestic cattle (*Bos* spp.) graze in aspen communities in some locations on the NYWR outside YNP. Domestic cattle will browse aspen and can suppress aspen growth or prevent stand regeneration under some conditions (Fitzgerald and Bailey 1984). Although elk browsing is generally accepted as the primary cause of aspen decline on the NYWR (NRC 2002), the cumulative effects of summer cattle browsing and winter wild ungulate browsing can result in decreased aspen recruitment (Kay and Bartos 2000).

St. John (1995) surveyed aspen clones or "stands" on the Gallatin National Forest (GNF) in 1990 and 1991—the largest study of its kind on the NYWR. Only 47 percent of aspen stands (n = 342) had recently grown any suckers above elk-browsing height and only 21 percent of stands had sufficient numbers of suckers escaping browsing for the overstories to remain stable or increase in density. Wolves (*Canis lupus*), a major predator of elk, were reintroduced into YNP in 1995 (Smith and others 2005). The NYWR elk herd decreased by ≈ 50 percent 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 appears to have allowed regeneration of willow (*Salix* spp.) and cottonwood (*Populus* spp.) on small scales at certain sites in YNP (Ripple and Beschta 2003; 2004; 2006). Browsing intensity has decreased and height of the tallest cohort of aspen suckers has increased in recent years in the Lamar Valley of the NYWR (Ripple and Beschta 2007). However, it is not known if growth of the 5 tallest suckers in the stand represent a true recovery relative to pre-wolf conditions. To date, published studies have not addressed changes in broad-scale aspen overstory regeneration since wolf reintroduction.

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; 3) conifer establishment in aspen stands influenced aspen density; and 4) cattle grazing influenced aspen density.

STUDY AREA

The study area was located in south-central Montana, primarily on the west unit of the Gardiner Ranger District (GRD), GNF and exclusive of the Absaroka-Beartooth Wilderness (figure 1). The southernmost portion of the study area abuts YNP. Mean annual precipitation in the Gardiner Basin at the southern end of the study area is 25 cm. 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).

Vegetation primarily consists of big sagebrush (*Artemisia tridentata* ssp.) and grassland (for example *Pseudoroegnaria spicata*; *Festuca idahoensis*) at lower elevations, some quaking aspen at forest-grassland boundaries and in riparian areas, Douglas-fir (*Pseudotsuga menziesii*) at mid-elevations, and lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii)*, and sub-alpine fir (*Abies lasiocarpa*) at higher elevations (Despain and others 1986). Aspen forests range from 1,571 m to 2,605 m in elevation and occupy ≈ 745 ha of the ≈ 560 km^2 study area (St. John 1995).

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.

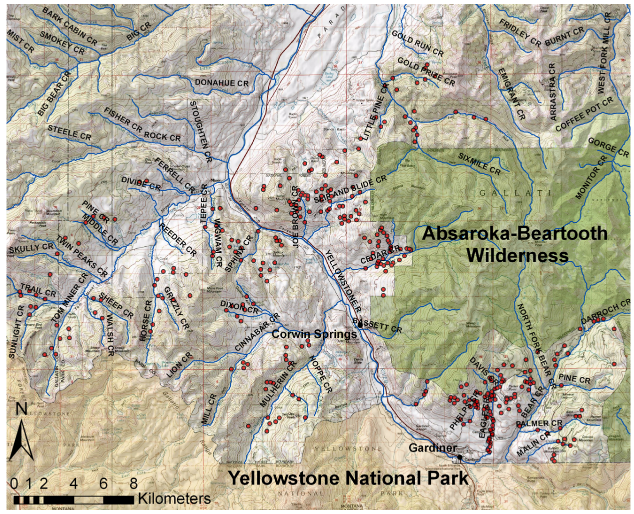

Figure 1—Sampled aspen stand locations on the study area.

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 (figure 2). East River, at ≈ 340 km^2, is the largest portion of the study area. Most of the East River unit is part of the NYWR (Lemke and others 1998). From 1989 to 1999, an average of 4.8 elk/km^2 were annually counted by aerial census in late winter on the East River unit. About 70 percent of elk migrating north of YNP and east of the Yellowstone River have spent the majority of the winter on the state-owned Dome Mountain Wildlife Management Area since 2000. From 2000 to 2006, late winter elk density on the East River unit averaged 2.4 elk/km² (NYCWWG 2005; Tom Lemke, MFWP, *unpublished data*).

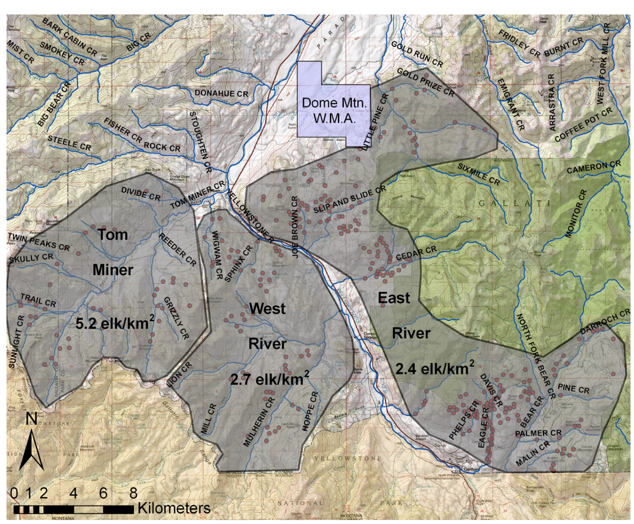

Figure 2—East River, West River, and Tom Miner subunits with different wintering elk densities.

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 (figure 2). The West River unit is also part of the NYWR (Lemke and others 1998). Average late-winter density of elk counted by aerial census was 1.9 elk/km^2 from 1989 to 1999 and 2.7 elk/km^2 from 2000 to 2006 (Tom Lemke, MFWP, *unpublished data*).

Tom Miner Basin occupies ≈ 100 km^2 (figure 2). Most of the basin bottom is private land, while Forest Service lands surround the basin at higher elevations. Tom Miner Basin is not part of the wintering range for the northern Yellowstone elk herd, but other local herds of elk winter there (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. Late winter elk density in Tom Miner Basin averaged 7.9 elk/km^2 from 1990 to 1999 and 5.2 elk/km^2 from 2000 to 2006 (Tom Lemke, MFWP, *unpublished data*). 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.

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 (Larsen and Ripple 2003). Elk density in scree stands was assumed to be 0 elk/km^2.

METHODS

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. Sampling methods were nearly identical to those employed by St. John (1995). After the aspen clone was relocated, the center of a 202.3 m² (1/20th 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 or number of mature aspen stems within the plot; and 3) the location most representative of the aspen stand. Each aspen stand was assigned a community type based on its associated vegetation. Aspen-conifer community types contained ≥ 10 percent canopy coverage of conifers in the stand (Mueggler 1988).

All live aspen stems within the plot were counted and categorized as sprouts (< 1 m tall), saplings (1 to 2 m tall), recruitment stems (≥ 2 m tall and < 5 cm diameter at breast height [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 to 2 m) have not grown beyond the reach of browsing elk, but are not being browsed to the depth of the winter snowpack (Romme and others 1995). Stems ≥ 2 m tall have grown beyond the height at which elk will browse the terminal leader (Kay 1985). 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). Not all recruitment stems will necessarily survive as a long term component of the aspen overstory, especially where elk populations are high (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

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 1 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. Therefore, the 24 burned or beaver-cut stands were excluded from analysis. A paired *t*-test was used to compare 1991 and 2006 aspen stand density to determine if recruitment and stems ≥ 2 m density had changed (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.

Secondary objectives were to determine if elk herbivory, conifer establishment, or cattle grazing in aspen stands influenced aspen density. Dependent variables analyzed were: sprout density, sapling density, recruitment stem density, and stems ≥ 2 m density. Paired *t*-tests were used to compare 1991 and 2006 recruitment and stems ≥ 2 m densities within cattle use categories. *F*-tests from the general linear model of analysis of variance were used to compare 2006 aspen densities in the elk use and conifer categories. The $y^{0.25}$ power transformation was used to correct nonnormality in the random errors of all dependent variables (Kuehl 1994). Differences were considered significant at $P \leq 0.10$. The SAS® 9.1 software program was used for all statistical analyses.

RESULTS AND DISCUSSION

Aspen Sustainability

Recruitment stem density did not change across the study area from 1991 to 2006. During this time, density of stems ≥ 2 m tall declined 12 percent (table 1). 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. About 20 percent 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, 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.

Table 1—Mean recruitment and stem ≥ 2 m 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)***	***Percent Change***	***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

[a] *P*-values based on paired *t*-tests.

Aspen canopy coverage in the Greater Yellowstone Ecosystem (GYE) declined 10 percent from 1956 to 2001 (Brown and others 2006). Aspen overstory density in our study area has declined a similar amount in less time (12 percent in 15 years). Aspen coverage is declining 0.2 percent annually on average in the GYE (Brown and others 2006), but aspen density in our study area is declining 0.8 percent annually. Remotely-sensed aspen canopy coverage (Brown and others 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 percent annually from 1958 to 1995 on the GNF portion of the NYWR within our general study area (Larsen and Ripple 2005). Our 0.8 percent annual loss in overstory density is comparable to Larsen and Ripple’s (2005) 0.6 percent annual canopy loss. Therefore, the 4-fold difference in rate of canopy loss on the GYE (Brown and others 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 and others 2006). Compared to the average aspen stand in surrounding areas in Montana and Wyoming (Brown and others 2006), our 12 percent decline in density in 15 years is severe.

Aspen overstory density has declined 2.5 percent per year on the Gros Ventre elk winter range in western Wyoming (Hart and Hart 2001). Stems ≥ 2 m density declined less than 1 percent annually from 1991 to 2006 on our study area. Differences are likely attributable to an older overstory (Krebill 1972) and higher elk density (≈ 10 elk/km²) (Kilpatrick and Abendroth 2001) on the Gros Ventre winter range than in our study area.

Elk Browsing

Because elk browsing is the major 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 hunting pressures on elk differ: East River, West River, and Tom Miner. In addition, aspen stands in scree communities largely unimpacted by elk.

Current stem densities were compared in each of the 4 elk use categories (table 2). Sprout (< 1 m tall) density is lowest in scree stands, probably because of the poor growing conditions on the dry, rocky substrate in scree communities. The highest recruitment stem and stem ≥ 2 m density is in scree stands (table 2). Absence of elk browsing enhances the ability of aspen stems in scree communities to grow above 2 m (Larsen and Ripple 2005). The greater density of overstory stems in scree stands is even more striking considering 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.

Sprout densities do not differ among Tom Miner Basin, the West River unit, and the East River unit. Sapling, recruitment stem, and stem ≥ 2 m densities are greater in the East River unit than Tom Miner Basin or the West River unit (table 2). 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 > 2 500 suckers (stems < 1.4 m tall) / ha had the potential to successfully replace the overstory.

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 prevents root suckers from growing above 1 m elsewhere on the NYWR (Romme and others 1995). Elk browsing is probably more effectively preventing sprouts from increasing in height in the West River unit and Tom Miner Basin than in the East River unit. Elk impacts on recruitment are likely more severe in Tom Miner Basin simply because elk density is higher (White and others 2003).

Table 2—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]

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

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 (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 in 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 and others 2001; White and others 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.

Conifer Establishment

Conifers often colonize aspen stands that have not recently burned and could reduce aspen regeneration. Aspen stands were divided into 2 groups with and without ≥ 10 percent conifer coverage in the stand. Sprout density does not differ in aspen stands with and without ≥ 10 percent conifer canopy coverage. Density of saplings, recruitment stems, and stems ≥ 2 m is approximately 2 times greater in stands with < 10 percent conifer canopy coverage than in stands with ≥ 10 percent conifer canopy coverage (table 3). Browsing seems to more effectively prevent sucker growth above 1 m in stands with conifers than in stands without conifers. Mean sprout density in aspen stands with ≥ 10 percent conifer coverage is still sufficiently high to replace the overstory (Mueggler 1989) and does not differ from mean sprout density in stands with < 10 percent conifer coverage. Because extensive root suckering occurs even in late-seral aspen stands that have been colonized by conifers, the theory of apical dominance preventing the initiation of root suckers (Schier and others 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 and others 2001), 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. The presence of a conifer canopy appears to exacerbate the effects of browsing ungulates.

Table 3—Mean sprout, sapling, recruitment stem, and stem ≥ 2 m densities in stands with and without ≥ 10 percent conifer coverage on the Gallatin National Forest.

	Conifers ≥ 10% Canopy Coverage (n = 173)	***Conifers < 10% Canopy Coverage (n =143)***	***P*[a]**
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

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

Table 4—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	Percent Change	P^a
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

[a]*P*-values based on paired *t*-tests.

Cattle Grazing

Cattle graze in summer and early fall in some aspen stands on the study area. We compared aspen density 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. 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, recruitment stem density increased more than 3-fold in stands where cattle grazing ended between 1991 and 2006 (table 4).

Even though stocking densities on Forest Service allotments are low (3 to 7 ha/animal unit month), the removal of cattle seems to have allowed more suckers to grow above 2 m. 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. However, increases in recruitment did not occur in every stand where cattle were removed. In fact, 54 percent of stands where cattle were removed still grew no recruitment stems. 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.

CONCLUSIONS

Overstory aspen 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 densities are apparently not sustainable on a landscape 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 560 km² study area since 1991. 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.

Aspen recruitment may have failed to increase in response to reduced wintering elk numbers in the East River unit for two likely reasons: First, more time could be required for aspen suckers "released" from browsing pressure to grow above browsing height. The number of wintering elk in the East River unit did not decline appreciably until 2000. If aspen sucker heights had been suppressed to 20 to 30 cm as in YNP (Romme and others 1995), it could take 6 years for completely unbrowsed suckers to reach 2 m in height (McColley 2007). 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.

Conifer establishment and cattle grazing in aspen stands also browsed by elk appear to more effectively suppress aspen recruitment than elk browsing alone. Nonetheless, elk browsing seems to be the primary cause of aspen decline, as evidenced by high aspen recruitment and overstory densities in scree communities.

MANAGEMENT IMPLICATIONS

Management may need to change if present aspen overstory densities are to be maintained on this portion of the GNF. Increased hunter harvest of elk, removal of conifers, or removal of cattle might accomplish this goal. 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. 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. 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. Cutting the conifers but leaving the aspen overstory is a "safer" strategy for stands that could receive high elk use. Removal of cattle from Forest Service allotments would promote recruitment in some areas. However, the interaction of conifers slowing sucker growth and continued elk browsing will probably prevent a detectable response in some aspen stands.

REFERENCES

Bartos, D.L., Mueggler, W.F. 1981. Early succession in aspen communities following fire in western Wyoming. Journal of Range Management 34:315-318.

Brown, K., Hansen, A.J., Keane, R.E., Graumlich, L.J. 2006. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. Landscape Ecology 21: 933-951.

Debyle, N.V. 1985a. Animal Impacts. *In*: Debyle, N. eds. Aspen: ecology and management in the western United States. GTr-RM-119., Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station. 283p.

Debyle, N.V. 1985b. Wildlife. *In*: Debyle, N. eds. Aspen: ecology and management in the western United States. GTR-RM-119, Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station. 283p.

Debyle, N.V., Winokur, R.P. 1985. Introduction. *In*: Debyle, N. eds. Aspen: ecology and management in the western United States. GTR-RM-119. Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station. 283p.

Despain, D.G., Houston, D.B., Meagher, M., Schullery, P. 1986. Wildlife in transition—man and nature on Yellowstone's northern range. Boulder, CO: Roberts Rinehart, Inc. 142p.

Fitzgerald, R.D., Bailey A.W. 1984. Control of aspen regrowth by grazing with cattle. Journal of Range Management 37:156-158.

Hart, J.H., Hart, D.L. 2001. Interaction among cervids, fungi, and aspen in northwest Wyoming. *In*: Shepperd, W.D. et al. eds. Sustaining aspen in western landscapes: symposium proceedings; 13-15 June 2000; Grand Junction, CO. Proceedings RMRS-P-18. Fort Collins, CO: USDA, Forest Service, Rocky Mountain Research Station. 460p.

Houston, D.B. 1982. The Northern Yellowstone Elk; Ecology and Management. New York, NY: Macmillan. 474p.

Jones, J.R., Schier, G.A. 1985. Growth. *In*: Debyle, N. eds. Aspen: ecology and management in the western United States. GTR-RM-119., Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station. 283p.

Kay, C.E. 1985. Aspen reproduction in the Yellowstone Park-Jackson Hole area and its relationship to the natural regulation of ungulates. *In:* Workman, G. ed. Western elk management: a symposium. Utah State University. Logan, UT. 213p.

Kay, C.E., Bartos, D.L. 2000. Ungulate herbivory on Utah aspen: assessment long exclosures. Journal of Range Management 53:145-153.

Keigley, R.B., Frisina, M.R. 2005. Aspen height, stem-girth and survivorship in area of high ungulate use. *In*: Frisina, M and S Knapp eds. Statewide browse evaluation project report number two. Montana Fish, Wildlife, and Parks. 110p.

Kilpatrick, S., Abendroth, D. 2001. Aspen response to prescribed fire and wild ungulate herbivory. *In*: Shepperd, W. et al. eds. Sustaining aspen in western landscapes: 13-15 June 2000; Grand Junction, CO. Proceedings RMRS-P-18. Rocky Mountain Research Station. 460p.

Krebill, R.G. 1972. Mortality of aspen on the Gros Ventre elk winter range. Research Paper INT-129. Ogden, UT: USDA, Forest Service, Intermountain Forest and Range Experiment Station. 16p.

Kuehl, R.O. 1994. Statistical principles of research design and analysis. Belmont, CA: Duxbury Press. 686p.

Larsen, E.J., Ripple, W.J. 2003. Aspen age structure in the northern Yellowstone ecosystem. Forest Ecology and Management 179:469-482.

Larsen, E.J., Ripple, W.J. 2005. Aspen stand conditions on elk winter ranges in the northern Yellowstone ecosystem. Natural Areas Journal 25:326-338.

Laundre, J.W., Hernandez, L., Altendorf, K.B. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, Canadian Journal of Zoology 79:1401-1409.

Lemke, T.O., Mack, J.A., Houston, D.B. 1998. Winter range expansion by northern Yellowstone elk herd. Intermountain Journal of Sciences 4:1-9.

McClave, J.T., Dietrich II, F.H. 1985. Statistics; Third Edition. San Francisco, CA: Dellen. 823p.

McColley, S.D. 2007. Restoring riparian aspen stands with beaver on the Northern Yellowstone Winter Range [thesis]. Bozeman, MT: Montana State University. 67p.

McDonough, W.T. 1985. Sexual reproduction, seeds, and seedlings. *In*: Debyle, N. and R. Winokur eds. Aspen: ecology and management in the western United States. Gen.Tech.Rep.RM-119., Fort Collins, CO: USDA, Rocky Mountain Forest and Range Experiment Station. 283p.

Mueggler, W.F. 1988. Aspen community types of the Intermountain Region. General Technical Report INT-250. Ogden, UT: USDA, Forest Service, Intermountain Forest and Range Research Station 135 p.

Mueggler, W.F. 1989. Age distribution and reproduction of intermountain aspen stands. Western Journal of Applied Forestry 4:41-45.

NYCWWG (Northern Yellowstone Cooperative Wildlife Working Group). 2005. 2005 Annual Report.

NRC (National Research Council). 2002. Ecological dynamics on Yellowstone's northern range. Wash., D.C.: National Academies Press. 180p.

Ripple, W.J., Beschta, R.L. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184: 299-313.

Ripple, W.J., Beschta, R.L. 2004. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of southwestern Montana, USA. Forest Ecology and Management 200: 161-181.

Ripple, W.J., Beschta, R.L. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management 230:96-106.

Ripple, W.J., Beschta, R.L. 2007. Restoring Yellowstone's aspen with wolves. Biological Conservation 138:514-519.

Ripple, W.J., Larsen, E.J. 2000. Historic aspen recruitment, elk, and wolves northern Yellowstone National Park. Biological Conservation 95: 361-370.

Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S. 1995. Aspen, elk, and fire in northern Yellowstone National Park. Ecology 76: 2097-2106.

Schier, G.A., Jones, J.R., Winokur, R.P. 1985. Vegetative Regeneration. *In*: Debyle, N. and R. Winokur eds. Aspen: ecology and management in the western United States. Gen Tech Rep RM-119., Fort Collins, CO: Forest Service, Rocky Mountain Forest and Range Experiment Station. 283p.

Shepperd, W.D., Bartos, D.L., Mata, S.A. 2001. Above- and below-ground effects of aspen clonal regeneration and succession to conifers. Canadian Journal of Forest Research 31: 739-745.

Smith, D.W., Stahler, D.R., Guernsey; D.S. 2005. Yellowstone Wolf Project: Annual Report, 2004. Yellowstone Center for Resources YCR-2005-02., Yellowstone National Park, Wyoming: USDI, National Park Service, Yellowstone Center for Resources. 18p.

St. John, R.A.1995. Aspen stand recruitment and ungulate impacts: Gardiner Ranger District [thesis]. Missoula: The University of Montana. 92p.

Wagner, F.H. 2006. Yellowstone's destabilized ecosystem: elk effects, science, and policy conflict. New York, Oxford University Press. 371p.

Western Regional Climate Center. 2007. Gardiner, MT and Jardine, MT climate summaries. Available at: http://www.wrcc. dri.edu/summary/ climsmmt.html.Accessed January 17, 2007.

White, C.A., Feller, M.C., Bayley, S. 2003. Predation risk and the functional response of elk-aspen herbivory. Forest Ecology and Management 181: 77-97.