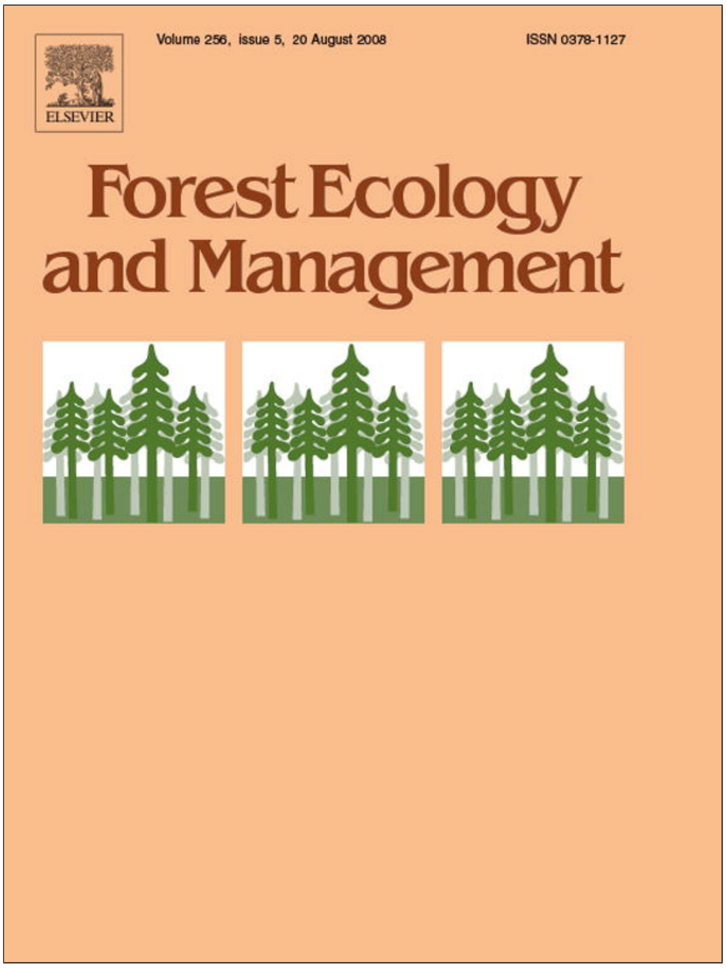

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Recoupling fire and aspen recruitment after wolf reintroduction in Yellowstone National Park, USA

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ABSTRACT

We report on the recent growth of upland aspen (*Populus tremuloides* Michx.) thickets in northwestern Yellowstone National Park, USA following wolf (*Canis lupus* L.) reintroduction in 1995. We compared aspen growth patterns in an area burned by the 1988 fires to aspen growth patterns in an adjacent unburned area. Elk (*Cervus elaphus* L.) are the principal ungulates that use this area to meet foraging needs. Within a 2 m × 6 m belt transect established in each aspen thicket, we measured aspen densities and recorded annual browsing and height information on the three tallest post-1988 aspen stems. We found greater densities ($p < 0.01$) in the burned area relative to the unburned area. A decline in the percentage of stems browsed in the burned area began in 1997, with no measured browsing occurring since 2001. In contrast, the percentage of stems browsed in the unburned area began declining in 2002, with 41% of stems still being browsed in 2004. We hypothesize that the combined effect of fire and a subsequent decrease in herbivory following wolf reintroduction facilitated aspen growth. We further propose that, in addition to any changes in elk density in recent years, a recoupling of fire with increased predation risk from wolves may create a positive feedback loop that improves aspen recruitment.

1. Introduction

Annual herbivory by wild or domestic ungulates can prevent aspen (*Populus tremuloides* Michx.) from growing above an upper browse level. For ungulates such as elk (*Cervus elaphus* L.), this height is approximately 200–250 cm (Romme et al., 1995; Keigley et al., 2002). Where such herbivory persists over a period of many years and overstory trees die of disease or other causes, the likelihood of sustaining aspen stands into the future becomes low. Thus, in areas of the Rocky Mountains frequented by ungulates, long-term browsing may represent a major factor contributing to the decline of aspen and other palatable plant species (Bartos, 1994; Romme et al., 1995; Baker et al., 1997; White et al., 1998; Ripple and Larsen, 2001).

While aspen stem densities can greatly increase following fire, primarily through sprouting, in western Wyoming Bartos (1994) found post-fire stem densities returning to pre-fire levels within 12 years due to high levels of wild-ungulate herbivory. Similarly, Romme et al. (1995) and Turner et al. (2003) documented overall suppression and mortality of post-fire aspen stems largely as a consequence of wild-ungulate herbivory in the northern range of Yellowstone National Park. In effect, annually intense herbivory "uncoupled" the expected increase in both aspen densities and recruitment following fire (Hessl and Graumlich, 2002; Beschta and Ripple, 2007) where recruitment is defined as the growth of suckers/seedlings into tall saplings or trees.

Although Bartos (1994) and Romme et al. (1995) reported both a decline in post-fire aspen densities and a lack of new aspen recruitment as a consequence of herbivory, those studies were conducted in wolf-free (*Canis lupus* L.) environments. In Canada, White et al. (2003) found that the risk of predation from human hunters and/or wolves caused the relationship between aspen, fire, and elk herbivory to vary (a behaviorally mediated effect). Specifically, they documented a positive relationship between predation risk and aspen densities illustrating factors other than a numerical decline in elk (a density-mediated effect) affected aspen growth in their study area. After seven decades of wolf absence in Yellowstone National Park, both a decline in elk numbers and changes in elk behavior have been documented following the reintroduction of wolves (Laundré et al., 2001; Childress and Lung, 2003; Gude et al., 2006). While elk densities may change as a direct response to predation, concurrent changes in elk behavior (e.g., changes in foraging and movement patterns) may also contribute to locally reduced elk densities.

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Given that wolves had been absent in Yellowstone National Park from the mid-1920s to 1995 (Smith, 1998), the objective of this study was to assess differences in patterns of aspen growth between paired burned and unburned areas following wolf reintroduction. To our knowledge, the occurrence of upland aspen seedlings or root sprouts attaining >200–250 cm in height outside of refugia (e.g., exclosures and jack-strawed tree boles) has not been documented within the park for several decades although such heights have been recently reported for riparian aspen in Yellowstone's northern range (Ripple and Beschta, 2007).

1.1. Study area

Our research was located on the northwest edge of the park, approximately 15 km north of West Yellowstone. The study area of ~3 km^2 is characterized by gentle, undulating topography (mean elevation of study area = 2083 m, standard deviation [S.D.] = 8 m; mean slope = 7%, S.D. = 5%) and scattered forests of lodgepole pine (*Pinus contorta*). Douglas-fir (*Pseudotsuga menziesii*) was present in low numbers. Our study area contained mostly pure aspen stands with minimal conifer presence inside any stand. Aspen understories were primarily composed of grasses and forbs.

Hunting occurs adjacent to the park boundary and two elk feedgrounds, located on private land within ~8 km of the study area, were open since at least the 1970s until approximately 1995 (Pils, personal communication). While the study area is used year-round by elk, greatest use occurs in the spring/early summer and late fall/early winter (Pils, personal communication). Winter use of the area by elk declines during years of deep snowpack. Information on specific elk numbers is currently not collected in or near the study area.

2. Methods

The study extent was subdivided into two areas: (1) an unburned portion with an aspen overstory (aspen boles >5 cm in diameter at breast height) present and (2) a portion burned during the 1988 Yellowstone fires and characterized by a near absence of overstory aspen. Both areas were initially identified from a burn-severity map for the 1988 Yellowstone fires, but were further defined from field observations of charcoal and residual overstory tree presence. We assumed pre-fire stand compositions to be mostly pure aspen although there likely was some conifer present in the understory and/or overstory.

To minimize potential edge effects due to changes in fire severity, a 250-m buffer was positioned between the two areas, with an additional 100 m buffer between the unburned area and the park boundary. We used the generic term "stem" to describe any aspen sucker or seedling originating after the 1988 fires. We searched for groups of stems, or thickets, in both the burned and unburned area. Thickets were typically small in size and thus we oriented a 2 m × 6 m belt transect from a thicket's edge toward its centroid for comparisons between the unburned and burned areas. For circular thickets, we randomly determined where transects began. Elliptical thickets had a major axis at least twice as long as the minor axis. For elliptical thickets, we randomly placed our belt transect in the middle third of the thicket, perpendicular to the major axis. Each thicket was >15 m from any other thicket.

We measured plant architecture, an approach that examines plant growth form to determine annual browsing and height history (Keigley et al., 2003; Ripple and Beschta, 2007), using the terminal leader of the three tallest aspen stems within each transect. When the terminal leader of an aspen stem is browsed, a branch off the main stem typically becomes the new terminal leader. Because of this tendency, the growth form of a browsed aspen stem has a zig-zag pattern. We used this pattern to record annual occurrence/absence of browsing and annual stem height for a minimum of six and a maximum of 10 previous years. We also extracted an increment core ~20 cm above the base of each measured aspen in both unburned and burned areas to determine stem age. Following Stokes and Smiley (1968), aspen cores were air-dried, mounted, and sanded to aid in counting growth rings using a dissecting binocular microscope.

Because predation risk may cause elk to browse thicket edges but not thicket interiors (White et al., 2003), we measured the tallest stem in each meter of transect length to determine if stems closer to thicket edges were shorter than stems further from thicket edges. We tallied the total number of stems within each belt transect to calculate stem density. In addition to annual height growth and browsing patterns, we used plant architecture information to determine whether a stem was within the normal reach of elk the last year that it was browsed. We assumed weather and browsing opportunities were similar for both portions of the study area.

We used two-sample *t*-test with unequal variances to determine if differences in aspen densities and growth patterns were present between the two areas. Before conducting *t*-test, stem densities, 2004 stem heights, and the height when each stem was last browsed were log-transformed to better meet the assumptions of normality. We also conducted a linear regression to determine if there was a significant relationship between stem height with distance along transects.

3. Results

We located 23 aspen thickets in the burned area and 21 aspen thickets in the unburned area. A pulse of new aspen stems followed the 1988 fires in the burned area with another pulse of stems peaking in 1996–1998 in the unburned area (Fig. 1). Aspen stem densities were more than three times greater in the burned area compared to the unburned area (Table 1 and Fig. 2). While differences in stem heights between areas have been present since at least 1995 and can in part be attributed to differences in stem ages, heights in the burned area have increased at a faster rate then stem heights in the unburned area (Fig. 3b). In 2004, unbrowsed aspen stems in the burned area had significantly greater mean annual height growth than unbrowsed stems in the unburned area (Table 1).

There were no differences in stem heights within transects of the burned and unburned areas (unburned: $F_{5,85} = 0.21$, p-value = 0.91; burned: $F_{5,128} = 1.76$, p-value = 0.13) indicating elk

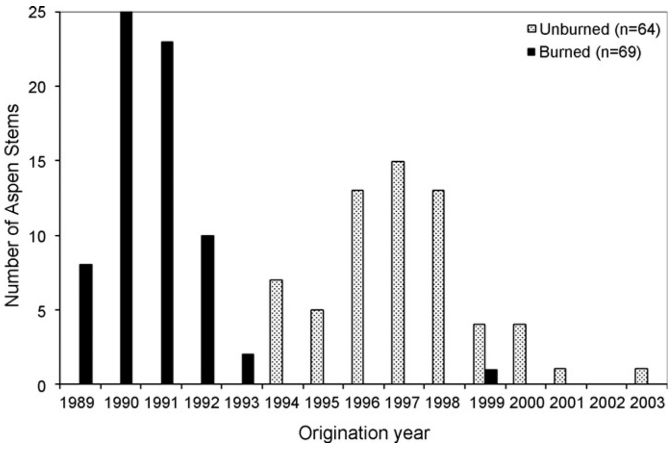

Fig. 1. Origination dates of aspen stems in unburned and burned areas. The burned area resulted from the 1988 Yellowstone fires.

Table 1
Aspen characteristics between the burned and unburned areas

Variable	Unburned area	Burned area	*t*-Statistic	Degrees of freedom	*p*-Value
	Mean (95% CL)	Mean (95% CL)			
Density of stems originating after the 1988 fires (per ha)[a]	8118 (6616, 9960)	28344 (23931, 33571)	9.82	22	<0.01
Height (cm) when stems were last browsed[a,b]	71 (63, 80)	114 (105, 124)	−6.92	22	<0.01
Stem height in 2004 (cm)[a]	88 (77, 101)	330 (294, 370)	15.62	22	<0.01
Annual height growth of unbrowsed stems in 2004 (cm)	20 (15, 26)	47 (42, 52)	8.12	22	<0.01

[a] The mean and the 95% confidence limits (CL) for the mean were back-transformed from log space.

[b] The height at which stems were last browsed was used to determine if measured aspen stems stopped being browsed within the reach of elk (200–250 cm).

were not preferentially browsing stems closer to thicket edges. The last year any of the measured stems in the burned area were browsed was in 2001, whereas 27 of 66 stems (41%) in the unburned area were browsed in 2004 (Fig. 3). All measured stems were within the reach of elk the last year they were browsed; aspen were last browsed between 102 and 133 cm in the burned area and between 29 and 158 cm in height in the unburned area. Browsing levels on aspen stems in the burned area declined from nearly 100% in 1995 to zero in 2002. In contrast, herbivory levels in the unburned area remained ≥73% between 1995 and 2002 (Fig. 3a).

4. Discussion

While exploratory, our discussion examines different mechanisms that could explain the variation in aspen recruitment observed both in space and through time.

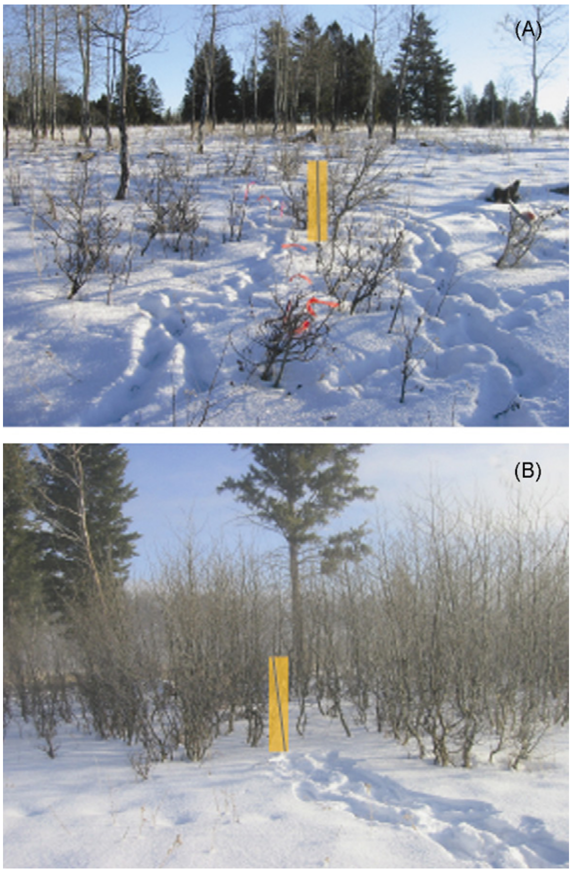

Fig. 2. Aspen thickets in northwestern Yellowstone National Park: (A) a short thicket in the unburned area and (B) a tall thicket in the burned area. The bar in each picture approximates 1 m in height.

4.1. Weather patterns

Since burned and unburned sites were in close proximity to each other and in relatively flat topography, we have no reason to suspect significant differences in local weather patterns might be factors in this study. Potential weather or other site differences also seem unlikely because all stems were equally browsed during 1995 and 1996, before browsing patterns diverged coincident with wolf reintroduction.

4.2. Fire

Aspen densities in the burned area were similar to those reported in the aspen literature (DeByle and Winokur, 1985; Bartos, 1994; Romme et al., 1995; Bailey and Whitham, 2002), and likely related to a release from apical dominance following the removal of overstory trees by fire and the associated increase in plant resources (Frey et al., 2003). Increased height growth in the burned area may have been due, in part, to less overstory presence,

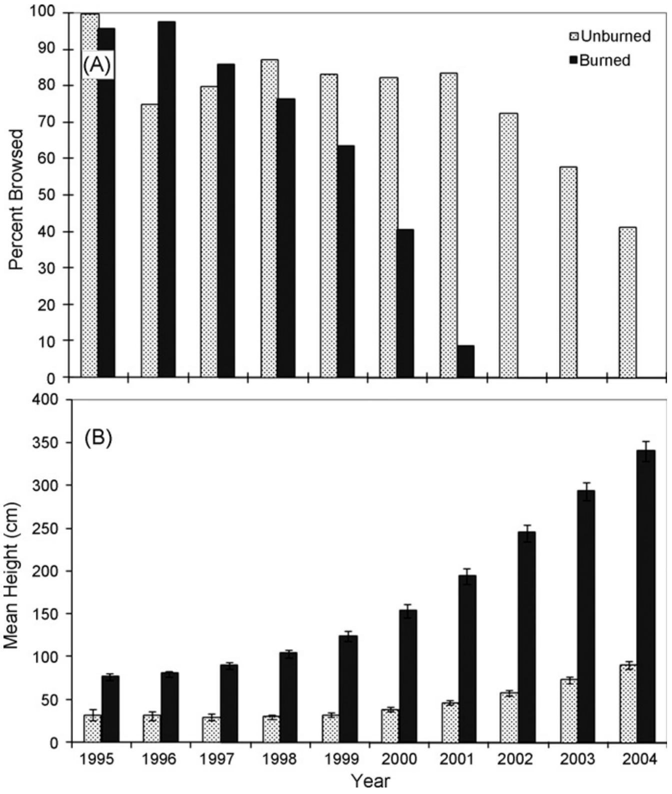

Fig. 3. (A) Percentage of measured aspen stems browsed and (B) mean annual heights (±standard errors) for burned and unburned areas of northeastern Yellowstone National Park. November 2005 height data was excluded because those stems had not been exposed to a full year of browsing at the time of measurement.

greater carbohydrate reserves, and less shade than those stems in the unburned area (Table 1).

Although fire severity may help explain patterns of aspen densities between burned and unburned areas, fire does not explain elk browsing patterns. While Romme et al. (1995) considered YNP to be marginal habitat for aspen and therefore did not necessarily expect many tall aspen, the authors nonetheless concluded elk browsed aspen sprouts 2 and 3 years after the 1988 fires regardless of aspen densities or fire severity. Based on 95% territory estimates, the current study area has been part of known wolf pack territories for every year between 1995 and 2004 except for 1997 and 1999 (Phillips and Smith, 1997; Smith, 1998; Smith et al., 1999, 2000, 2001; Smith and Guernsey, 2002; Smith et al., 2003, 2004, 2005). While suppression of young aspen from herbivory has been reported where wolves were absent (Bartos, 1994; Romme et al., 1995), the current study and White et al. (2003) found a patchy occurrence of tall and dense thickets of aspen after fire disturbance in the presence of wolves.

4.3. Changes in elk densities

Although elk densities in the study area may have changed over the past 10 years, census data was unavailable within or adjacent to the study area. Based on optimal foraging theory (Lima and Dill, 1990), herbivores in a predator-poor environment should spend more time in areas with high-energy gain and minimal search effort. Such an expectation is consistent with the ~100% stems browsed in 1995 and 1996 in the burned area (Fig. 3). Yet the percentage of stems browsed in the burned area following 1996 declined even though the stems were within the reach of elk (Table 1) and browsing opportunities were equivalent between burned and unburned areas. Such a finding is inconsistent with optimal foraging theory in a predator-free environment.

From the perspective of young aspen stems, there could be "safety in numbers" in an herbivore-rich system. With a relatively high density of stems, perhaps there is a greater likelihood some stems would escape herbivory. Conversely, assuming browsing opportunities in both areas were similar, it would have been more energetically efficient to browse in the burned area thus enabling the relatively dispersed stems in the unburned area to escape repeated herbivory. Neither the safety in numbers nor the dispersed stems escaping herbivory suppositions are consistent with the data presented in this paper, nor that of Romme et al. (1995) and Bartos (1994). Therefore, while elk densities may have changed, such changes in and of themselves are unlikely explanations for differences in herbivory between the measured burned and unburned areas.

4.4. Predation risk

Our results indicate elk browsed both areas at high levels in 1995 and 1996 after which they preferentially browsed the unburned area coinciding with wolf reintroduction (Fig. 3a). A change in preferential browsing is consistent with optimal foraging theory in a predator rich environment. With reduced predator detection and maneuverability through tall and dense aspen thickets, ungulate risk from predation increases (Lima, 1992; Ripple and Beschta, 2004) resulting in thicket avoidance by elk and creating a potential feedback mechanism that enables stems to grow taller.

In areas with a high risk of predation, White et al. (2003) noted an inverse relationship between predation risk and the number of elk pellets in dense thickets. They suggested dense thickets might increase aspen fitness in predator-rich environments, whereas the same thickets in herbivore-rich situations could be detrimentally impacted. Their suggestion is consistent with our observation of suppressed aspen growth in burned thickets in 1995 and 1996, an herbivore-rich situation, followed by a decline in browsing after wolf reintroduction (increased predator richness and predation risk). The occurrence of a predation risk effect is also consistent with changes in elk vigilance levels and habitat preferences following wolf reintroduction in Yellowstone National Park (Laundré et al., 2001; Childress and Lung, 2003; Wolff and Van Horn, 2003; Creel et al., 2005; Fortin et al., 2005). Furthermore, Halofsky and Ripple (2008) found greater female elk vigilance near escape impediments such as down woody debris, a common feature in burned forests. Bergman et al. (2006) noted more wolf-killed elk in YNP near hard edges such as those between burned and open forests. Thus, there is mounting evidence of changes in elk foraging and movement patterns in predator presence as well as differences in wolf-kill success with variations in landscape structures.

4.5. Aspen, fire, and wolves—a recoupling hypothesis

Given the documented shifts in elk behavior and movement patterns since wolf reintroduction (Laundré et al., 2001; Childress and Lung 2003; Fortin et al., 2005; Hebblewhite et al., 2005; Mao et al., 2005), we suggest that greater densities and rates of growth for young aspen stems in burned areas are due to a loss of apical dominance and shade as a result of fire in conjunction with reduced browsing. This reduction in browsing, in turn, may be associated with lower elk densities (density mediated) and/or perceived predation risk (behaviorally mediated). The perceived risk from predation associated with relatively dense thickets and/or dead wood in burned areas might impede elk escape from predators and/or create difficulties for elk to detect predators. As a result, we postulate elk are less likely to approach and browse thickets, specifically in burned areas, which allows for increased aspen height growth, and hence further avoidance by elk. Overall, our results suggest a correlation between wolf reintroduction and reduced browsing pressure on aspen within the study area, although we cannot document a causal effect between wolves and aspen. Together with the regenerative effects of fire, aspen recruitment may be facilitated by the presence of top predators.

5. Conclusion

For park managers, these results confirm additional aspen recruitment within Yellowstone National Park is now occurring outside of exclosures and jack-straw piles. Whether this response is a precursor to a more general improvement in recruitment will remain uncertain without further monitoring through time. These results also suggest that using fire as a strategy to increase aspen numbers and recruitment in areas of high elk herbivory is unlikely to occur without wolves. In wolf-free environments, restoration of aspen with prescribed fire could have greater success if information on both ungulate densities and distributions are incorporated into management plans.

Broadly, our results suggest aspen numbers and recruitment can be affected by multiple processes including top-down influences from large predators, pulse (fire) vs. chronic (herbivory in a wolf-free environment) disturbances, and bottom-up influences resulting from fire such as changes to apical dominance and shading. More specifically, our data indicate a potential relationship among fire and reduced herbivory in the presence of wolves, a combination that allows for increased thicket density and height growth of aspen stems. Although changes in herbivory may have in part resulted from density-mediated effects, our results are also consistent with expected changes associated with a behaviorally mediated trophic cascade. Thus, the recoupling of fire disturbances with the effects of wolves may again facilitate upland aspen recruitment that has been missing for many decades.

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