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Elevated Rocky Mountain elk numbers prevent positive effects of fire on quaking aspen (*Populus tremuloides*) recruitment

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ABSTRACT

Quaking aspen (*Populus tremuloides*) is the most widespread tree species in North America and has supported a unique ecosystem for tens of thousands of years, yet is currently threatened by dramatic loss and possible local extinctions. While multiple factors such as climate change and fire suppression are thought to contribute to aspen's decline, increased browsing by elk (*Cervus elaphus*), which have experienced dramatic population increases in the last ~80 years, may severely inhibit aspen growth and regeneration. Fires are known to favor aspen recovery, but in the last several decades the spatial scale and intensity of wildfires has greatly increased, with poorly understood ramifications for aspen growth. Here, focusing on the 2000 Cerro Grande fire in central New Mexico – one of the earliest fires described as a "mega-fire" - we use three methods to examine the impact of elk browsing on aspen regeneration after a mega-fire. First, we use an exclosure experiment to show that aspen growing in the absence of elk were 3× taller than trees growing in the presence of elk. Further, aspen that were both protected from elk and experienced burning were 8.5× taller than unburned trees growing in the presence of elk, suggesting that the combination of release from herbivores and stimulation from fire creates the largest aspen growth rates. Second, using surveys at the landscape level, we found a correlation between elk browsing intensity and aspen height, such that where elk browsing was highest, aspen were shortest. This relationship between elk browsing intensity and aspen height was stronger in burned ($r = -0.53$) compared to unburned ($r = -0.24$) areas. Third, in conjunction with the landscape-level surveys, we identified possible natural refugia, microsites containing downed logs, shrubs etc. that may inhibit elk browsing by physically blocking aspen from elk or by impeding elk's ability to move through the forest patch. We did not find any consistent patterns between refuge elements and aspen size or canopy cover suggesting that natural refugia are not aiding in aspen recruitment and that *all* young aspen were susceptible to browsing. In much of their normal range, aspen are not growing to large size classes, which threatens the future of this iconic species and calls into question the ability of ecosystems to recover from mega-fires. Our results highlight the importance of considering multiple interacting factors (i.e. fire and increased elk browsing) when considering aspen management and regeneration.

1. Introduction

Despite the fact that it is the most widespread tree species in North America (Worrall et al., 2013), aspen (*Populus tremuloides*) is declining in much of its historic range. In some areas, aspen cover has decreased between 60–90% since European settlement (Kay, 1990, 1997; Kulakowski et al., 2013; Schier, 1975). Two potentially counter-acting factors, fire regimes and increased browsing by elk (*Cervus elaphus*), can strongly influence aspen recruitment; that is, the ability of young aspen to grow tall enough to avoid ungulate herbivory and eventually reproduce. Understanding the roles of these factors may help predict the future fate of aspen. Interestingly, fire regimes and patterns of elk browsing have dramatically changed in the American West during the last 100–150 years (e.g. Allen, 1996, 2004; Allen et al., 1995; Attiwill and Binkley, 2013; Sydoriak et al., 2000; Truett, 1996). North central New Mexico provides a useful case study of the changing fire and elk browsing regimes. Allen et al. (1995) describe the fire

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regime of recent centuries and most notably a strong change in fire frequency after the turn of the 20th century. Prior to the 20th century mixed conifer forests were shaped by fires, most of which were low intensity ground fires, although patchy, small crown fires did occur. Euro-American settlement in the early 1900s brought about active fire suppression (Sydoriak et al., 2000). The consequent build up of fuel loads combined with a changing climate that favors more extreme fire behavior has helped promote the "mega-fires" – fires of large areal extent, often with high intensity and resistance to control – seen in the much of the Western USA during the last few decades (Attiwill and Binkley, 2013; Stephens et al., 2014; Williams, 2013). For example, in the last ~45 years, the American West has experienced a fivefold increase in the number of fires greater than 100 km^2.

Because aspen recruitment is largely dependent on fire to create openings in the forest canopy, the change in fire regimes has altered, and will continue to alter patterns of aspen recruitment and age structure (Quinn and Wu, 2001). Aspen tend to regenerate profusely after wildfire (Bartos and Mueggler, 1981). For example, in an extensive study in burned and unburned areas of Yellowstone National Park, Turner et al. (2003) found as many as ~46,000 aspen seedlings/ha growing in burned areas, yet they found no aspen seedlings growing in unburned areas. In another study, Bartos and Mueggler (1981) documented a doubling of aspen shoot densities after a prescribed burn. In light of these data, the period of fire suppression is thought to have contributed to a lack of aspen recruitment in the early 20th century (Hessl, 2002). Thus it would be reasonable to hypothesize that recent mega-fires could potentially be a boon for aspen recruitment due to the large affected area. However, another factor, herbivory from elk, could dampen if not completely offset any positive effects of mega-fire on aspen recruitment.

Due to their dramatic increase in population size in the last ~100 years, elk may be one of the largest barriers to aspen recruitment in the Southwest. According to archaeological and paleontological records, Merriam's Elk (*C. canadensis merriami*) was likely a minor species (<3% of large mammals) in the Southwest US before Euro-American settlement (Allen, 1996, 2004; Truett, 1996). Mexican gray wolves (*Canis lupus baileyi*) and grizzly bears (*Ursus arctos*) inhabited the area until extinction in the 1930s (Allen, 2004; Beschta and Ripple, 2010), and likely played some role in reducing elk numbers. Another predator, the cougar (*Puma concolor*), has been the target of eradication efforts throughout the 20th century but has persisted in low numbers (Allen, 2004). Although the elimination of these predators was likely beneficial for elk, human hunting pressure and limited surface water were probably greater constraints (Rosenstock et al., 1999; Truett, 1996). In fact hunting pressure drove Southwest populations of elk to extinction in the early 1900s (Truett, 1996; Allen, 2004). Starting in the 1910s and continuing through the 1950s a different elk subspecies, Rocky Mountain Elk (*C. elaphus nelsoni*) were then (re-) introduced to the Southwest, from stock originating in Yellowstone National Park, (Allen, 2004; Leopold, 1918; Truett, 1996). For example, in 1948, 28 elk were introduced to the Jemez Mountains in and around Bandelier National Monument. By 1961, the population was estimated to be 200. Since then, the population grew exponentially and by 1992 the population was estimated at 7000 elk.

Bandelier National Monument in northern New Mexico offers a unique opportunity to examine the response of aspen forests to mega-fires in the presence of elk. First, in only the last 20 years, several mega-fires, such as the Dome Fire (1996), the Cerro Grande Fire (2000) and the Las Conchas Fire (2011), have burned the vast majority of high elevation forests in Bandelier and surrounding Santa Fe National Forest (Fig. 1). At its time, the Cerro Grande fire was the largest fire in New Mexico's recorded history. Secondly, it is thought that elk were historically rare or absent from Bandelier, but since human introduction, have grown to high numbers (Allen, 1996; Truett, 1996).

The aims of this paper are to examine the possible interactive effects of mega-fires and elk herbivory on aspen recruitment and to provide managers with information on how to protect and promote aspen forests through time.

We use three methods to examine the possible impact of elk and mega-fire on a southwestern population of aspen. First, we used exclosures to experimentally test the effect of elk on young aspen height. Second, conducting surveys over ~50 km^2, we examined the relationship between elk browsing intensity early on during post-fire recovery and subsequent height of young aspen. Third, working across the same ~50 km^2, we used a targeted search to examine possible refuge sites (i.e. microsites with downed logs, shrubs etc.) where aspen may be naturally protected from elk herbivory.

2. Methods

2.1. Elk Exclosures

We established five elk exclosures in areas of mixed conifer forests to track the influence of elk herbivory on aspen recovery. Each exclosure was 60 m × 60 m, and paired with an unfenced control plot with a 20 m buffer area between the treatment and control. One pair of plots burned in the 2000 Cerro Grande fire. For each of the five exclosures and their controls, we counted the total number of aspen shoots organized by height classes. We used a system of height classes which included 0.5 m increments from 0 to 2 m, 1 m increments from 2 to 7 m, and a class for trees >7 m. Exclosures were surveyed in 2001, 2002, 2005 and 2006.

To examine the potential effects of elk on aspen sprouting and growth, we compared the unburned exclosure to control sites using repeated measures ANOVA. For each of the four pairs of plots, a mean height was calculated by summing the products of the mid point of the height class × the proportion of trees in the height class. Since the blocking factor was insignificant in initial analyses it was excluded from future analyses. Thus, the final model included exclosure, time and their interaction as explanatory factors and number of shoots and height as the two response variables.

We used the burned pair of plots to explore possible effects of mega-fire on the number of aspen shoots and the height of those shoots in the presence and absence of elk. It is important to note that only one pair of plots burned. Thus, we did not replicate the effects of fire and cannot make definitive conclusions based on this data set (Hurlbert, 1984). Nonetheless, these plots represent a rare opportunity to monitor aspen recruitment after a large-scale wildfire in the presence and absence of elk. To examine the potential influence of fire on the number of aspen shoots, we created a contingency table that included the mean number of aspen shoots from the unburned plots (in and out of the exclosures) and the number of shoots from the burned plots (in and out of the burned exclosure). To examine height differences in the last year of the surveys, we compared the mean number of trees in each height class in the unburned exclosures to the number of trees in each height class in the burned exclosure. We used the fisher.test function in R (version 3.1.0) for these analyses (R core team, 2014).

2.2. Landscape-level surveys

We conducted landscape-level surveys in order to look for patterns among site characteristics, elk browsing and aspen height. We surveyed a ~50 km^2 area which included the northern-most portion of Bandelier National Monument and the surrounding