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Moose alter the rate but not the trajectory of forest canopy succession after low and high severity fire in Alaska

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A B S T R A C T

Mammalian herbivory on palatable trees affects tree growth, forest composition, and forest succession. Antecedent effects of herbivores can be identified through remnants of dead stems and altered tree morphology as well as changes in tree ring patterns and growth. Increases in fire severity, particularly surface fuel combustion, in the boreal forest of western North America can cause a shift in the successional trajectory from coniferous to deciduous dominated forests, which may alter plant–animal interactions. We measured height and tree ring growth of the two dominant canopy tree species, trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* (Mill.) BSP), in sites that experienced stand-replacing fire with deep versus shallow surface fuel combustion 20 years ago. We also classified individual trees into a category of browsing damage based on external features and morphology. We hypothesized the effects of browsing to be contingent on fire severity. Using linear mixed effect models, we investigated the main and interactive effects of fire severity and browsing intensity on aspen growth. We also developed tree ring chronologies to test for growth releases in aspen and black spruce.

Effects of moose browsing on aspen growth depended on fire severity (surface fuel combustion), with negative effects in high severity sites and no effects in low severity sites. Spruce growth showed no direct or indirect browsing effects, indicating moose have not altered the potential for spruce to reach the forest canopy. Aspen in severely burned sites showed abrupt growth releases in tree rings corresponding to changes in herbivore pressure and density. Height-growth projections indicated that moose slowed the rate of aspen growth and canopy dominance in severely burned areas by ten years, through repeated stunting of apical growth in aspen, without affecting the initial trajectory to an aspen-dominated canopy. Lightly burned areas, with their larger proportion of spruce biomass, slower aspen growth, and reduced browsing pressure during the first 20 years after fire, will likely provide accessible aspen forage until >50 years post-fire as sites return to spruce dominance. Heterogeneously burned forests could thus sustain high rates of available moose forage for a much longer period than previously reported. Our study highlights the importance of including fire severity when considering the impacts of large herbivores on tree growth and forest structure.

1. Introduction

Herbivores act as ecosystem engineers (Jones et al., 1994), with cumulative effects on the physical, chemical, and biological components of an ecosystem that can alter its structure and function (Kielland et al., 2006). Large mammals can impact forest structure and successional dynamics across temporal (years to decades) and spatial (tens of meters to kilometers) scales (Peterson et al., 1998). These impacts occur due to both direct and indirect effects of mammalian herbivores on the recruitment, survival, and growth of woody species. Direct effects often include browsing and consumption of biomass, with associated reductions in plant size (Chouinard and Filion, 2001), trampling (Schrama et al., 2013), and a decrease in plant reproduction by consuming flowers (Augustine and Frelich, 1998). These direct effects can alter animal–plant and plant–plant interactions, such as through changes to quality and quantity of food (Danell et al., 1994), and habitat modifications that affect vegetation structure and nutrient cycling (Rooney and Waller, 2003). Understanding the cumulative impacts of herbivores is a critical but complex element in predicting dynamic patterns of ecosystems in managed and unmanaged systems (Bailey and Whitham, 2002).

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Forest ecosystems across the globe are changing, and natural forest ecosystems appear particularly vulnerable to warming temperatures and altered natural disturbances (Allen et al., 2010). The vegetation composition of the boreal forest in Alaska has remained relatively stable for the past 6000 years; however, boreal forest vegetation is likely to change due to projected warming and associated changes in disturbance regimes (Chapin et al., 2010). Altered seedbeds from high severity fires have caused a shift from pre-fire mature black spruce (*Picea mariana* (Mill.) BSP) stands to early assemblages of deciduous broadleaf trees, such as Alaskan paper birch (*Betula neoalaskana* Sarg.) and trembling aspen (*Populus tremuloides* Michx.) (Johnstone et al., 2010). With these ecological shifts, deciduous trees may become increasingly dominant on the landscape (Mann et al., 2012). However, mammalian herbivores have the potential to alter successional pathways in forest ecosystems (Thompson et al., 1992) and may alter initial trajectories of deciduous dominance after high severity fires. Post-fire environmental conditions can influence tree growth and dominance (Bailey and Whitham, 2002) as well as species-specific strategies for response to potential herbivory (e.g., tolerance, escape, or resistance (Lindroth and St. Clair, 2013)). Aspen can use multiple strategies when responding to post-fire herbivory (Bailey and Whitham, 2002; Wan et al., 2014), and it is unclear whether these different strategies (particularly escaping herbivore pressure by growing quickly) will be affected by fire severity levels that affect aspen productivity in Alaska (Shenoy et al., 2011).

Historical impacts of mammalian herbivores can be detected through changes in tree architecture and/or tree ring growth. For example, browsed Sitka spruce (*Picea sitchensis* (Bong.)) on the Haida Gwaii islands off the coast of British Columbia, Canada, display two types of growth within an individual: stunted, wider growth when 'trapped' below the browsing height limit of local herbivores, and normal structure and shape once 'escaped' (Vila et al., 2003). Tree rings have been used to assess historical browsing through aging fraying scars from black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) (Vila et al., 2004) and measuring ring width patterns before and after herbivore introduction (Speed et al., 2011). Furthermore, growth releases often occur in trees that escape the negative effects of chronic disturbance (e.g., browsing by an animal, canopy gaps, insect outbreaks) (Bretfeld et al., 2015; Karlsson et al., 2004; Vila et al., 2003) or experience competitive release when neighbors are subject to stronger disturbance impacts. These approaches allow for characterization of browsing effects in a historical context and can enhance our understanding of plant–animal interactions.

Stand-replacing disturbances, such as fire, create even-aged tree cohorts that are optimal for studying the importance of ecological filters (disturbance, climate, competition, and herbivory) on stand development (Hansen et al., 2016; Turner, 2010). In interior Alaska, a stand-replacing fire (the Hajdukovich Creek burn) in 1994 created a landscape mosaic of low and high severity burn areas that varied in the level of surface fuel combustion (Michalek et al., 2000). Heterogeneity of surface fuel combustion within the burned area altered post-fire seedbeds and induced differential patterns of tree recruitment across the landscape (Johnstone and Kasischke, 2005). Initial effects on tree recruitment caused a divergence in successional trajectories of the forest canopy that have persisted into the second decade of post-fire growth (Shenoy et al., 2011). Aspen recruitment dominated severely burned sites in the 1994 burn (Johnstone and Kasischke, 2005), and the warmer soils at these sites fostered rapid aspen growth compared to low severity sites where aspen and black spruce co-dominated the regeneration (Shenoy et al., 2011). High severity sites continued to produce the highest amount of forage biomass 19 years post-fire, however the proportional removal of forage by moose (*Alces alces*) peaked 13 years post-fire and then declined (Brown et al., 2015; Lord, 2008). It remains unclear how the effects of initial disturbance and woody stem competition on post-fire establishment and community assembly (Johnstone and Kasischke, 2005; Shenoy et al., 2011) may be modified by mammalian herbivores that are themselves responsive to severity effects on forage availability.

The purpose of our study was to understand how herbivory by large mammals affects post-fire tree growth, and whether herbivory may influence differing pathways of succession triggered by fire severity. Specifically, we tested two hypotheses relating to herbivore effects: (1) herbivore impacts will be greatest in sites with the highest forage availability (severely burned areas), and (2) herbivore impacts on dominant forage species will lead indirectly to increased growth of less palatable species. Severely burned sites, compared to lightly burned, have promoted increased productivity of aspen (Shenoy et al., 2011) which should increase the success of escaping browse damage (e.g., Wan et al., 2014). However, in our study area aspen have been subject to increased moose browsing pressure in only severely burned sites (Brown et al., 2015; Lord, 2008). Thus, in severely burned sites, we predicted browsing damage would overcome the aspen escape strategy by slowing the rate of aspen growth, allowing non-palatable species, such as black spruce, to increase growth and potentially altering the rate or trajectory of canopy succession. We used external tree damage quantified in the field, growth rates below and above the browse limit, and growth patterns from tree rings to determine effects of browsing. From these results, we compared height-growth projections for aspen and black spruce growing in low and high severity sites, accounting for the effect of moose browsing on height growth. Our predictions of forest structure under different fire severity and browsing intensity scenarios provide information on duration of forage availability for moose and their influence on patterns of forest development.

2. Material and methods

2.1. Study area

We conducted our research in the 1994 Hajdukovich Creek burn, located in a flat, glacial outwash plain north of the Alaska Range mountains and approximately 35 km southeast of Delta Junction in interior Alaska (USA). The Hajdukovich Creek fire burned 8900 ha of black spruce forest between mid-June and late September 1994 (Michalek et al., 2000). Typical for interior Alaska, pre-fire vegetation was predominately black spruce with a few mixed stands of aspen and black spruce (Johnstone and Kasischke, 2005). Most of the spruce canopy was consumed by the fire, leading to 100% stand mortality. However, another metric of fire severity, the combustion of surface organic material (dead moss and undecomposed organic material), varied substantially across the burn due to variations in weather and soil thaw (Kasischke and Johnstone, 2005). Remote sensing classified 61% of the burn as low severity (little combustion of surface organic material), 6% as medium severity, and 33% as high severity (extensive combustion of up to 30 cm organic layer depth) (Kasischke and Johnstone, 2005; Michalek et al., 2000). Variations in fire severity affected seedbed quality and led to extensive recruitment and rapid growth of aspen in severely burned areas formerly dominated by black spruce (Johnstone and Kasischke, 2005; Shenoy et al., 2011). Aspen recruitment was principally from seed (Johnstone and Kasischke, 2005) as opposed to the clonal (asexual) reproduction that is common when aspen stands self-regenerate after fire (Barnes, 1966).

The Hajdukovich Creek burn is located in one of six subunits of Game Management Unit 20 (GMU 20D), which supported some of the highest moose densities in the state in the early 2000's due to