

MAMMALIAN HERBIVORY SLOWS THE GROWTH OF BROADLEAF SPECIES
IN POST-FIRE, EARLY SUCCESSIONAL FORESTS IN INTERIOR ALASKA

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By

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ABSTRACT

Boreal forest vegetation is likely to change in response to warming and associated changes in disturbance regimes. Recently, high severity fires have caused a shift from pre-fire mature black spruce stands to early assemblages of broadleaf trees. However, interactions between plants and animals may modify the outcomes of early forest succession. Selective herbivory by mammalian herbivores can alter the relative dominance of forest canopy species and influence successional pathways. However, woody plants have evolved multiple strategies to maximize chances of survival and long-term fitness after herbivory. In this thesis, I explore the dynamics of moose-tree interactions and their consequences for early succession in boreal forests of interior Alaska. I assessed the interaction of moose browsing and fire severity on tree growth and canopy composition and found that moose slow the rate of trembling aspen growth, but only in severely burned areas. Black spruce showed no direct or indirect growth responses to moose browsing, indicating that moose browsing on aspen did not alter the initial trajectory to an aspen-dominated canopy within my study area. In lightly burned areas, moose may benefit from longer durations of forage availability and accelerate the development of a mixed spruce-aspen canopy. Alaskan paper birch is the other dominant broadleaf species colonizing early post-fire forests and I determined saplings' ability to tolerate simulated summer leaf stripping by moose. I found decreases in woody growth and carbon-based defenses while individual leaf area increased in response to simulated leaf stripping. My results are consistent with the carbon-nutrient balance hypothesis suggesting that the loss of growing points during leaf stripping decreased competition for nutrients, which were then available for leaf regrowth. Birch saplings have the potential to compensate for herbivory, but resilience of individuals will depend on the intensity, season, and frequency of herbivory. I set up long-term exclosures to test if mammalian herbivores can alter patterns of canopy succession in early post-fire sites that ranged in broadleaf dominance. Removal of natural moose herbivory inside exclosures led to species-specific responses after two years. Alaskan paper birch (dominant broadleaf species) grew larger when safe from herbivores while the opposite was true for black spruce. However, impacts of natural moose browsing on the dominant birch were insufficient to eliminate the competitive hierarchies that supported birch dominance of the canopy and suppressed growth of black spruce in the understory. I conclude that even with the negative impacts of moose on broadleaf species growth, their tolerance to

browse damage enables their persistence as the dominant canopy species after large and severe fires in the boreal forest of Alaska.

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CHAPTER 1: INTRODUCTION

1.1 Drivers of ecosystem change

Anthropogenic changes to climate, disturbances, and land use practices are rapidly altering ecosystems around the Earth. Changes in temperature and precipitation can influence the frequency, duration, extent, and intensity of natural and human-induced disturbances, such as fire, drought, and insect and pathogen outbreaks (Dale et al. 2001, Allen et al. 2010, Turner 2010, Hicke et al. 2012). These altered disturbance regimes can reduce our ability to predict successional pathways (Turner et al. 1998). As succession drives ecosystem recovery after disturbance, the processes governing vegetation succession are crucial to understand. Factors driving succession are complex, ranging from bottom up to top down controls, and occur across a range of spatial and temporal scales (Walker and Chapin 1987, Schmitz et al. 2006). In my thesis, I focus on the potential role of biotic factors in driving ecosystem change, specifically how mammalian herbivores shape boreal forest composition and succession.

Over the last century, temperatures in the circumpolar North have increased at an unprecedented rate. Climate change will have both direct and indirect impacts on the boreal forest. Warmer temperatures without a concomitant increase in precipitation will lead to drier conditions and reduced soil moisture; drier conditions may result in an increase in larger and more severe fires (Balshi et al. 2009). Fire is the dominant disturbance in the boreal forest ecosystem altering vegetation distribution and composition (Beck et al. 2011). Despite disturbance by fire, the vegetation composition of the boreal forest, specifically in Alaska, has remained relatively unchanged for the past 5000-6000 years (Lloyd et al. 2006, Chapin et al. 2010).

The function and composition of boreal forest vegetation are likely to change due to projected warming (Chapin et al. 2010). Changes in vegetation composition in interior Alaska are occurring due to, in part, the vulnerability of black spruce (*Picea mariana*) forests to changes in the fire regime (Kasischke et al. 2010). Sites across interior Alaska that experienced recent high severity fires have seen changes in post-fire vegetation with an increase in broadleaf dominance (Johnstone et al. 2010a). A switch from a coniferous-dominated forest to a broadleaf-dominated, or mixed forest, will have impacts on climate feedbacks, permafrost distribution, and wildlife populations and habitat. Broadleaf cover has a greater albedo than coniferous forests; accounting for an increase in broadleaf-dominated forests and the future fire regime, the greater albedo of early successional stands could result in a decrease in atmospheric heating (Euskirchen

et al. 2009, 2010). Broadleaf forests also differ in their abundance of moss cover, which is generally low until late-successional stages when coniferous trees dominate (Turetsky et al. 2010). Moss serves as a thermal buffer between the atmosphere, soils and permafrost (Turetsky et al. 2010); a decrease in moss cover may affect permafrost stability. Lastly, populations of wildlife rely on specific forest compositions for survival, therefore positive and/or negative effects may occur for wildlife depending on forage preference (Maier et al. 2005, Rupp et al. 2006).

Recent experimental work has shown that a single ecosystem can display both bottom up and top down controls (Schmitz et al. 2006). Bottom up controls, such as limiting supplies of nutrients and light to plants, are one of the driving forces behind succession and trophic structure (Lindeman 1942, Odum 1969). Top down effects of consumers can govern succession (Schmitz et al., 2006 and references within) thus biotic factors are important to consider as they can be a dominant influence on vegetation composition (Post and Pedersen 2008). For example, primary succession in the floodplains of interior Alaska has been altered through selective browsing by both moose (*Alces alces*) (Kielland and Bryant 1998, Butler and Kielland 2008) and snowshoe hares (*Lepus americanus*) (Olson and Kielland 2016). While bottom up controls on secondary successional patterns in upland boreal forests of Alaska are relatively well understood, top down controls are not. Initial community assembly 3-10 years post-fire is often hypothesized to be indicative of future canopy composition (Gutsell and Johnson 2002, Johnstone et al. 2004, 2010b, Peters et al. 2005). Saplings in areas that have burned in the last few decades are in the vulnerable stage of early succession damage from herbivores and rapid shifts in vegetation dominance are still possible. As such, interior Alaska is an ideal location to study how herbivores may alter the current emerging picture of changing succession (from coniferous-dominated to broadleaf-dominated) in the boreal forest.

1.2 Herbivores as ecosystem engineers

Herbivores act as ecosystem engineers by directly or indirectly altering resource availability through changes in the physical state of biotic or abiotic materials (Jones et al. 1994). Insect herbivores typically only consume a fraction of plant primary production; however, they can have effects on plant population dynamics (Abrahamson 1988) by reducing plant reproduction and growth, and increasing rates of mortality (Bergeron et al. 1995, Kaitaniemi et

al. 1999, Reinikainen et al. 2012). Similarly mammalian herbivores impact primary production, decomposition, and nutrient redistribution (Abrahamson 1988), thereby affecting plants at an individual, population, community and ecosystem level (Danell and Bergström 2002). Fluctuations in herbivore population size, in particular boreal mammalian herbivores (Elton 1924), can lead to strong direct and indirect top down effects that cascade through the ecosystem (Kielland et al. 2006, Rexstad and Kielland 2006).

Plants generally employ three defense strategies to deal with herbivory: tolerance, resistance, and escape (Karban and Baldwin 1997, Lindroth and St. Clair 2013). Tolerance is reflective of a plant's ability to maintain growth and reproduction after herbivory damage. Broadleaf species are often found to be more tolerant than conifers (Persson et al. 2007, Baraza et al. 2010, Piper and Fajardo 2014). Resistance is any plant trait (e.g., toxins, spikes) that decreases the herbivores' preference of the plant or the damage ensuing from herbivory. In some cases, resistance of the plant and herbivore tolerance have co-evolved (Bloom et al. 1985, Bryant et al. 1989, Mithöfer and Boland 2012). Escape is the ability of a plant, usually a tree, to reduce the duration the tree is vulnerable to herbivory damage through changes in architecture and/or phenology. Many factors, such as genetics, development, and environmental conditions, influence which defense mechanisms are used by plants (Lindroth and St. Clair 2013). For example, increased conifer abundance had a negative effect on the escape and resistance defenses of trembling aspen (*Populus tremuloides*) saplings (Calder et al. 2011) while extreme climatic events have increased resistance in trembling aspen leaves (St. Clair et al. 2009).

Even with defense strategies in place, mammalian herbivory can directly affect the growth and survival of woody species such as trees through browsing of leaves, stems, and twigs. Browsing will generally reduce growth and total biomass of an individual tree (White 2012). Repeated browsing suppresses vertical growth and changes tree architecture and morphology, generally resulting in excessive lateral branching (Danell et al. 1994). Normal tree growth generally resumes once a height free from herbivore damage is reached; however, the length of time to recover from damage also depends on the tree species and browsing tolerance (Vourc'h et al. 2002, Vila et al. 2003a, 2003b). Although trees can respond with compensatory or over-compensatory growth after damage (Stouter 2008, De Jager and Pastor 2010), when browsing pressure is high, even trees tolerant to browsing display negative growth responses (Champagne et al. 2012).

Over time, the vertical growth of trees can be suppressed so much that the stand structure of the forest is altered (Brandner et al. 1990, Chouinard and Filion 2001, 2005, Rooney and Waller 2003). These changes in stand structure are often due to differences in herbivore density as stand structure is most vulnerable to re-organization when browsing pressure is high (Tremblay et al. 2007, Gosse et al. 2011). High herbivore density and browsing pressure suppresses tree growth and results in a more open tree canopy (Snyder and Janke 1976, Thompson et al. 1992, Potvin et al. 2003). With an open canopy, the increased light reaching the forest floor can have positive effects on understory growth and tolerance to browse (McLaren 1996). On the other hand, herbivores can also change stand structure by decreasing the abundance of grasses, shrubs and small understory trees (Vila et al. 2004, Stroh et al. 2008), which has consequences for other organisms that rely on these habitats (Martin et al. 2010).

Changes in forest stand structure are often associated with changes in forest composition (Tanentzap et al. 2011, White 2012, Hidding et al. 2013). Generally, herbivores will target more palatable species when foraging. Over time, this selective browsing can change the dominant canopy species and overall forest composition. A common mechanism driving changes in forest composition is a shift in competitive dominance among tree species, often decreasing the ability of browsed species to access light (McInnes et al. 1992, Eschtruth and Battles 2009). For example, moose have caused the abundance of balsam fir (*Abies balsamea*) to decline on predator free islands in eastern North America and replaced by less palatable white spruce (*Picea glauca*) and black spruce (Thompson and Curran 1993, Chouinard and Filion 2005).

1.3 Herbivores in interior Alaska

Herbivory can potentially influence the rates and trajectories of both early- and mid-succession (Davidson 1993). For example, an accelerated rate of succession in Alaskan floodplains has been observed due to moose herbivory on woody species that dominate early succession (Kielland and Bryant 1998). When browsing is focused on early successional species, late successional species can dominant the forest canopy sooner than would be expected if herbivores were absent. Additionally, herbivores can increase nitrogen availability due to changes in nutrient cycling, which can alter the competitive ability of tree species (Butler and Kielland 2008). While the role of mammalian herbivores has been studied in the floodplains in interior Alaska (Walker et al. 1986, Kielland and Bryant 1998, Butler and Kielland 2008), few

studies have examined whether herbivores alter the increased dominance of broadleaf species in early post-fire upland forests.

Moose and snowshoe hare are dominant mammalian herbivores in the boreal forest and can impact tree growth and establishment, and thereby influence successional patterns (Thompson et al. 1992, Olnes and Kielland 2016). In Alaska, moose and snowshoe hare have overlapping diets with a preference for broadleaf trees and willows (*Salix* spp.) (Bryant and Kuropat 1980); snowshoe hares also feed on black spruce year-round (Wolff 1978). The summer diet of moose in Alaska consists of >60% willow in the summer, however the winter diet of moose comprises equal proportions of willow and *Betula* species (Van Ballenberghe and Miquelle 1989, Weixelman et al. 1998, Shipley 2010). Habitat use and selection by large mammals is strongly influenced by fire. In interior Alaska, high moose densities have been associated with fires that occurred within the previous 11-30 years (Maier et al. 2005); a mosaic of fire severity can increase the longevity of available moose habitat due to fire effects on species composition and growth rates (Kielland and Brown 2015). In my thesis I focus primarily on the influence of moose to determine their role in shaping community dynamics in post-fire upland forests.

To further our understanding of how herbivores shape forest succession and our ability to predict possible change in upland boreal forest in Alaska we need to consider a few important issues. In an extensive review of 82 studies on the effects of ungulates, Wisdom et al. (2006) highlighted key considerations that need to be addressed to better understand damage inflicted by ungulates. First, the context of succession needs to be considered as it can shape the possibility of herbivore impacts. Second, we need to consider selective feeding by animals. Third, we need to know precisely how long the negative effect of herbivory on tree growth and regeneration lasts. The duration a specific tree species remains suppressed between browsing events could in turn dictate whether or not the rate or trajectory of succession is affected (Wisdom et al. 2006).

With these considerations in mind, there are a few plausible scenarios of how mammalian herbivores may shape succession in upland boreal forests of interior Alaska. Fire in the boreal forest can vary in severity, with long-lasting effects on the ecosystem; for example, the amount of organic layer burned and exposed mineral soil will influence the post-fire vegetation composition (Johnstone and Chapin 2006). Regenerating vegetation will display different growth rates depending on fire severity (Shenoy et al. 2011), affecting the duration of vulnerability to

browsing (Lord 2008, Brown et al. 2015). Thus, fires of varying severity will create a heterogeneous landscape that will differ in its vulnerability to damage and change by herbivores. In a mixed broadleaf-conifer stand in Alaska, moose are likely to browse on broadleaf trees (Bryant and Kuropat 1980), which may speed up the rate of succession if conifers experience a competitive release and can occupy the canopy quicker. If snowshoe hares are browsing in the same mixed forest, broadleaf trees will escape browsing damage by hares more quickly than browsing by moose because the browsing height limit of snowshoe hare is lower compared to moose. The rate of succession could thus be slowed due to snowshoe hares browsing on conifers, which are often used by hares but avoided by moose (Wolff 1978, Bryant and Kuropat 1980). Thus, the interactive effects of multiple herbivores on species composition and succession is important to consider when predicting the consequences of herbivory for forest dynamics (Hester et al. 2000, Kuijper et al. 2008).

1.4 Dissertation objectives and structure

The overall objective of my thesis is to examine how mammalian herbivores alter tree growth in early successional post-fire forests. As mentioned above, fire severity can create a mosaic of plant communities that vary in growth rate and species dominance (Johnstone and Kasischke 2005, Shenoy et al. 2011). These changing successional contexts are likely to be drivers of how important herbivores will be in impacting succession. Using a 20-year old burn as a case study, I assess the impact of fire severity and moose browsing on the growth of trembling aspen and black spruce in interior Alaska (Chapter 2). The Hajdukovich Creek burn was a mosaic of low and high fire severities (with respect to surface fuel combustion) that led to varying post-fire regeneration patterns (Johnstone and Kasischke 2005). I measured height and tree ring growth, and antecedent browsing damage, of the two dominant canopy tree species in low and high fire severity sites. I tested for the main and interactive effects of fire severity and browsing intensity on tree growth as well as for growth releases in tree ring chronologies. I hypothesized that in severely burned sites, browsing damage would slow the rate of trembling aspen growth, allowing black spruce to increase in growth and potentially accelerating the rate of succession back to a canopy dominated by black spruce.

Broadleaf species typically employ a combination of defense strategies (tolerance, resistance, and escape) to lessen the impacts from herbivores. Generally herbivory results in a loss of biomass that causes trade-offs between growth, storage, and defense; woody plants thus show a continuum of responses, including under- and over-compensation to herbivory, which can be attributed to variations in the intensity and type of herbivory. I used an experimental approach to determine the effect of summer moose leaf stripping on growth and defense responses of Alaskan paper birch (*Betula neoalaskana*) during critical life stages of early post-fire succession (Chapter 3). I simulated summer leaf stripping by moose at different levels of intensity on saplings of Alaskan paper birch across varying post-fire site conditions in interior Alaska and measured responses of woody growth, canopy architecture, leaf size, and carbon-based defenses after one-year. I predicted growth and defense trade-offs to occur; specifically, based on the carbon-nutrient balance hypothesis (Bryant and Reichardt 1992), the removal of leaves would cause a decrease in leaf and shoot growth due to increased competition for nutrients, while C-based defenses would increase. Furthermore, I anticipated natural winter browsing and local competition would affect the ability of birch saplings to respond to leaf stripping.

Herbivores can shift species composition and rates of succession through selective browsing of palatable species. These impacts are likely to occur when saplings are most vulnerable to damage and mortality due to browsing. Thus, I established a long-term experiment aimed at assessing how the presence of herbivores impacts succession in post-fire forests (Chapter 4). I erected six exclosures and paired control plots at post-fire sites that were at a critical stage to be influenced by herbivores. Inside exclosure and control plots, I measured the growth of trembling aspen, Alaskan paper birch, and black spruce saplings for two years. Based on palatability, I expected broadleaf species (aspen and birch) to benefit from the exclusion of herbivores (specifically moose) and grow relatively larger than individuals vulnerable to natural browsing in the control plots. I also expected that removal of moose herbivory on broadleaf species inside exclosures would lead to decreased spruce growth, with implications for the rate of canopy succession.

I conclude my thesis by highlighting my main findings and discussing the impact of mammalian herbivores in upland boreal forests of interior Alaska compared to other boreal and temperate forests (Chapter 5). Based on my findings, I predict where mammalian herbivores will

have the greatest potential to alter successional patterns and what this means for the future of the changing boreal forest in interior Alaska.

1.5 References

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CHAPTER 2: MOOSE ALTER THE RATE BUT NOT THE TRAJECTORY OF FOREST CANOPY SUCCESSION AFTER LOW AND HIGH SEVERITY FIRE IN ALASKA

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For this publication I was the lead in developing the concept of the study, collecting and analyzing data, and writing the paper. Jill Johnstone contributed to the concept and writing of the publication.

2.1 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).

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) (Vila et al. 2003, Karlsson et al. 2004, Bretfeld et al. 2015) 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 (Turner 2010, Hansen et al. 2016). 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 (Lord 2008, Brown et al. 2015). 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 (Lord 2008, Brown et al. 2015). 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.

2.2 Material and methods

2.2.1 *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) (Michalek et al. 2000, Kasischke and Johnstone 2005). 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 wildfires and predator control (1.78 moose/km² in 2006 (DuBois 2010); moose density in Alaska ranges from 0.01–1.93 moose/km²). However, aerial surveys in GMU 20D estimated that moose populations subsequently decreased during 2007–2009 (DuBois, 2010).

2.2.2 Sampling design and field work

In the summer of 2014, we sampled 12 previously established sites (Figure 2.1, Table A2.1) in the Hajdukovich Creek burn that experienced low (n = 6) and high (n = 6) fire severity, resulting in different forest composition (Johnstone and Kasischke, 2005). Study site selection took advantage of previous research documenting fire severity, environmental conditions, and post-fire plant recruitment (Johnstone and Kasischke, 2005; Shenoy et al., 2011), as well as recent herbivore activity and habitat use (Brown et al. 2015). We selected all low severity sites that were most recently sampled (Brown et al. 2015), and randomly selected an equal number of high severity sites. All sites excluded pre-fire aspen stems to ensure aspen regeneration was from seed. All sites experienced a stand-replacing burn, were on flat terrain, and the primary factor driving initial (8-15 years post-fire) tree growth and composition was fire severity (Johnstone and Kasischke 2005, Shenoy et al. 2011). Detailed site data is available online in the Bonanza Creek Long-Term Ecological Research (LTER) data archive (Johnstone and Kasischke 2003).

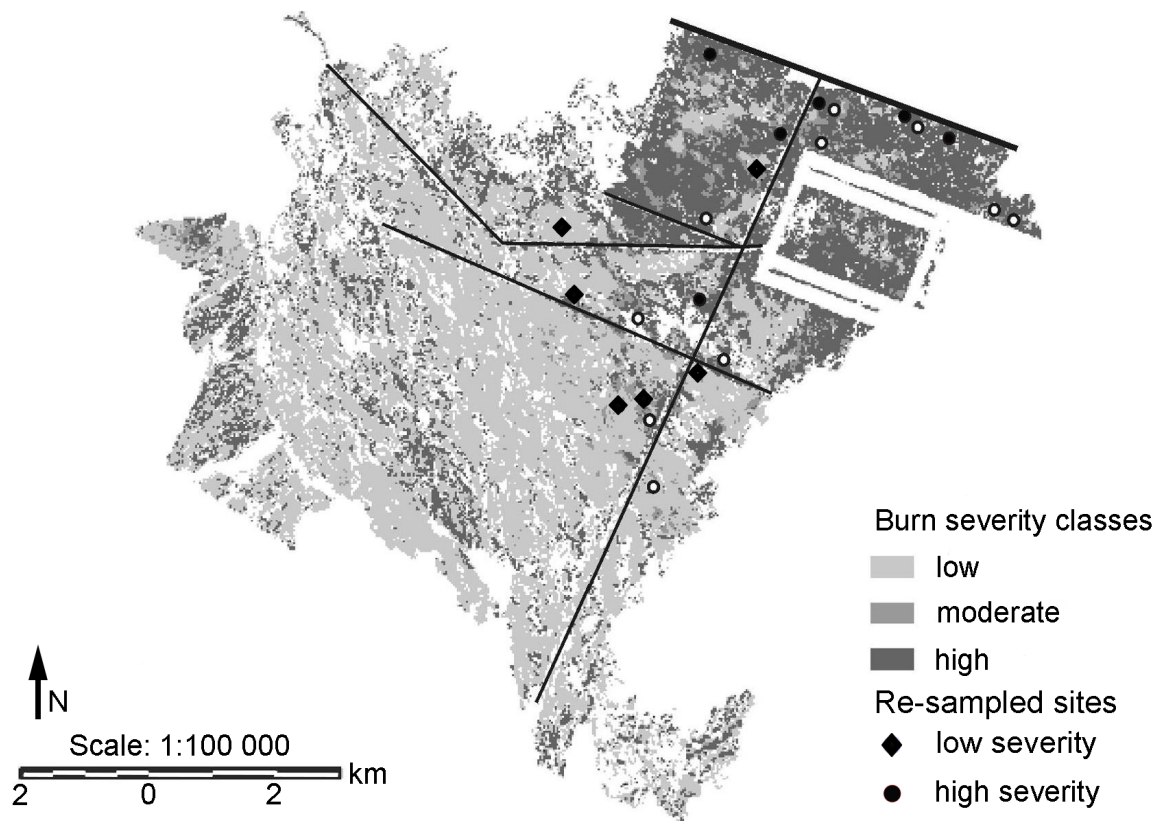


Figure 2.1. A map of the burn severity classes (light, moderate, high) after the 1994 Hajdukovich Creek burn (modified from Johnstone & Kasischke, 2005). Black symbols are sites re-sampled in 2014 in either low (diamonds) or high (circles) severity areas. Black and white circles are additional sites sampled in 2001/2002, not included in this study. Thin black lines represent dirt trails, while the thicker black line at the northern edge of the burn is the Alaska Highway. The white grid is a disturbed area that was non-forested prior to the fire.

At each site, we established a 30 m baseline transect through a homogeneous area with visually similar tree density and height. We then placed three 24 m transects perpendicular to the baseline transect at 0, 15, and 30 m (Figure A2.1). On each of these perpendicular transects, we established sampling points at the 0 m mark, and at 6 m intervals thereafter (i.e., 5 sampling points along each transect). At each sampling point, we identified the two closest individuals of black spruce or aspen ($n = 30$ individuals of each species, per site). For aspen, if the closest individual was short (< 25 cm), we pulled the individual out of the ground to check for evidence of the individual being a sucker (produced by recent asexual growth). Because one of our goals was to estimate how browsing has affected individuals that regenerated shortly after the fire, we included suckers ($n = 13$) in density measurements but measured and collected the next closest individual that established from seed.

We measured tree height and distance from the sampling point, and collected an intact basal disk from each individual. We examined each individual for bite marks, cut stems, and broken branches, and classified each individual into a browse category based on the presence, density, and growth of specific morphological features called twig clusters (Figure 2.2) (Keigley et al. 2003). Individuals were either classified as having zero evidence of browsing, light (one twig cluster, or up to five minor twig clusters that only contain one broken stem), or heavy (multiple twig clusters distributed along the stem below the browse limit). Only one aspen in all high severity sites experienced no past browsing, so we combined the ‘zero’ and ‘light’ browsing categories. We recorded the height of browse damage, and the type of herbivore when possible (browsing by snowshoe hares (*Lepus americanus*) was distinguished from moose browsing by stems cut cleanly at a 45° angle). The browse limit used for moose in Alaska is generally 3 m (Lord 2008, Seaton et al. 2011), therefore we also collected tree disks at the 3 m mark from all individuals (that were >3 m tall) to determine the age at which trees escaped browsing damage.

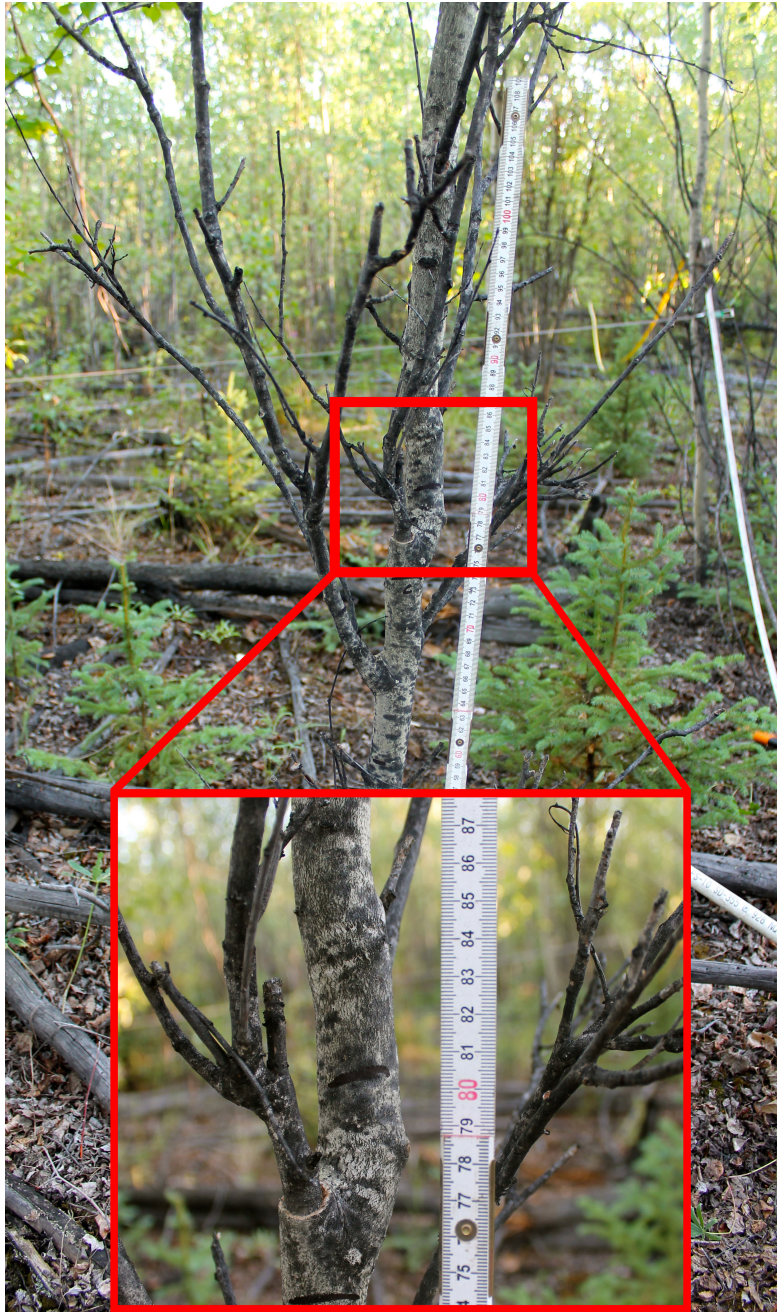


Figure 2.2 A heavily browsed aspen located in a high fire severity site in the Hajdukovich Creek burn. The inset is a close-up of the place where the original apical meristem was removed, generating a twig cluster, and causing apical dominance to switch to a new branch at a stem height of 77 cm.

2.2.3 Laboratory work

Aspen and black spruce stem disks were dried and sanded with increasingly fine sandpaper, up to a grit of 600, to accentuate visible rings. We scanned all disks and measured annual rings (resolution 0.001mm) on two radii per disk using WinDENDRO software version 2012 (Regent Instruments 2012). The year 2014 was not included in analyses, as the growing season was not finished; time series are from 1995 to 2013. All samples were visually cross-dated within sites using WinDENDRO.

Ring-width series were analyzed in R version 3.1.2 (R Development Core Team 2014) and the package ‘dplR’ version 1.6.3 (Bunn, 2008). We took the average of two measured radii per disk to obtain a raw ring width. Each raw ring width series was detrended and standardized (to produce dimensionless units known as ring width index) (Fritz and Swetnam 1989) using the modified negative exponential curve (Fritz 1976). The modified negative exponential curve attempts to fit a classic nonlinear model of biological growth; however, if a suitable nonlinear model cannot be fit (function is non-decreasing or some values are negative) then a linear model is used (Bunn 2008). Trees with growth trends that did not fit an exponential or linear model were excluded from the final chronology (see below for final sample sizes). We also calculated basal area increment (BAI) for each raw ring width series. BAI represents overall tree growth better than ring width (Husch et al. 2003) because it calculates the ring width area for each year, whereas ring width does not account for tree radius. For aspen, chronologies were built using detrended and standardized ring width and BAI measurements, and grouped for trees that experienced different browse intensities within low ($n = 39$ and 88) and high fire severity ($n = 34$ and 74 , for light and heavy browse, respectively). Spruce chronologies were also assembled for low ($n = 178$) and high ($n = 178$) fire severity. Autocorrelation in the final chronologies was removed using the prewhitened function. All chronologies met general chronology statistics (i.e., expressed population signal > 0.85) (Wigley et al. 1984).

2.2.4 Data analysis

All analyses were performed in R version 3.1.2 (R Development Core Team 2014) and reported means include ± 1 standard error. Sample units were individuals nested within site. All dependent variables were log-transformed to meet assumptions of normality and homoscedasticity. Spatial autocorrelation among sites was first assessed by calculating Moran’s I

using the ‘ape’ package (Paradis et al. 2004). We found no evidence of spatial autocorrelation (Table A2.2) but accounted for the nesting of individuals within sites by including site as a random effect in linear mixed effect models (LME) (Zuur et al. 2009). Thus, site was used as the sample unit ($n = 6$) for analyses; however, graphical representations vary from including individual subsample-level data to site-level data as noted below.

We used LME models, with the package ‘nlme’ (Pinheiro et al. 2016), to determine the effect of: fire severity and tree species on tree growth; fire severity and past browsing on aspen growth; and past browsing and 3 m threshold (below or above) on annual aspen height growth. Each model included an interaction between fixed effects and all within-level comparisons were examined by changing the reference levels for fixed effects. We considered browsing and fire severity as crossed effects, although they technically could be considered a split-plot design. We used this approach because fire behavior is a spatially contagious process and thus difficult to get spatially independent, random samples. Furthermore, previous work (Johnstone and Kasischke 2005) indicates that pre-fire conditions in low and high severity sites were comparable thus further supporting results of Moran I’s analyses, and justifying our decision to treat severity as a crossed design and include site as a random effect. The best random structure for each model was selected based on the lowest Akaike information criterion value and an F-test comparison (see Table A2.3 for model syntax).

To detect growth releases in tree ring chronologies, we used a radial-growth averaging criteria (Nowacki and Abrams 1997), which is based on the running mean: $\%GC = [(M2 - MI)/MI] \times 100$ where $\%GC$ is the percentage of growth change, MI is the average ring width growth over a preceding time period (e.g., ten years) including the target year, and $M2$ (excluding the target year) is the average ring width growth over the subsequent time period (e.g., ten years). Although a ten-year interval is common, shorter time periods have been used to investigate recent growth responses to insect outbreaks (Bretfeld et al. 2015). For our analyses, we used the ‘TRADER’ (Tree Ring Analysis of Disturbance Events in R) package (Altman et al. 2014). Our criteria to detect growth releases included a moderate threshold of growth change between 25–50%, a three year time period averaged for pre- and post-potential release, and a two year time period that must exceed the growth change (Altman et al. 2014). We tested for growth releases in all standardized detrended chronologies for both aspen and black spruce. Thus, hypothesis two was tested through examination of black spruce growth patterns associated with

time periods of aspen suppression and growth. Chronologies were also compared graphically and statistically, with the Gleichläufigkeit (G) coefficient (Schweingruber 1988), to measure the similarity in tree ring growth for different time periods between browse intensities.

We projected future patterns of height-growth in aspen and black spruce depending on fire severity and browse intensity using the following assumptions. We calculated the annual height growth by taking the height of each individual and dividing by basal age, and then projected the average time it would take to reach 3 m. This approach is conservative because it assumes growth rates of lightly and heavily browsed trees will continue at their current average rate, which could change if browsed again. We used the difference in growth rate between heavily and lightly browsed aspen in high severity sites (49.6% lower in heavily browsed) to project aspen height under high intensities of moose browsing, as a negative effect on aspen growth is expected to occur (see discussion), in low severity sites after 20 years post-fire. We used 3 m as the cut-off for our projections as aspen are then safe from moose browsing, and height growth becomes nonlinear as growth increases (Chen et al. 1998).

2.3 Results

2.3.1 Study site characteristics

Tree composition and growth varied among sites with different levels of fire severity. High severity sites supported higher densities of aspen than black spruce, whereas the opposite was true for low severity sites (Table 2.1). For tree height, we found a significant interaction between fire severity and tree species (Table A2.4). Aspen were twice as tall in high fire severity sites compared to low severity sites, while the opposite was found for black spruce (Table 2.1, A2.4). Aspen and black spruce were similar in height in low severity sites, whereas aspen was over five times taller than spruce in high severity sites. Average BAI of aspen and black spruce showed similar patterns as height.

Table 2.1. Trembling aspen and black spruce height (cm) (average \pm standard error), basal area increment (BAI) (mm^2/year), and density (individuals/ m^2) for low ($n = 6$) and high ($n = 6$) severity sites.

	Height (cm)	BAI (mm^2/year)	Density (individuals/ m^2)
<u>Aspen</u>			
Low Severity	126.47 \pm 11.98	8.22 \pm 0.74	1.11 \pm 0.62
High Severity	346.26 \pm 37.86	50.47 \pm 10.24	3.83 \pm 0.65
<u>Spruce</u>			
Low Severity	133.44 \pm 6.94	18.81 \pm 3.43	5.49 \pm 1.57
High Severity	61.39 \pm 6.78	3.79 \pm 0.78	1.48 \pm 0.32

2.3.2 *Effects of browsing*

Aspen and black spruce were browsed in low and high fire severity sites by moose and snowshoe hares. Aspen was heavily browsed in both fire severities (63% and 67% for high and low severity, respectively; Table 2.2). 94% of browsing on aspen was from moose, while the remaining individuals were browsed by snowshoe hare, or both moose and snowshoe hare. Moose browsing occurred at an average height on an aspen stem of 80.0 ± 13.9 cm and a maximum height of 261 cm. We found evidence of snowshoe hare browsing on spruce ($n = 46$; 360 total) with more occurrences in high severity than low severity sites. Due to the high intensity of past browsing on aspen, we focused our analyses on the effect of moose browsing on aspen growth.

Past browsing had different effects on aspen growth depending on fire severity (Table 2.2). With respect to aspen height and average BAI, we found a significant interaction between past browsing and fire severity (Table 2.3). In high severity fires, aspen that were heavily browsed were shorter and had a lower average BAI than those that experienced light browsing (Figure 2.3). In contrast, heavy browsing had no effect on aspen growth in low severity sites (Table 2.3).

Table 2.2. Summary of browsing intensity (number of individuals) on trembling aspen and its effects on height (cm) (average \pm standard error) and basal area increment (BAI) (mm^2/year) in low ($n = 6$) and high ($n = 6$) fire severity sites.

	Light Browse	Heavy Browse
<u>Low Severity</u>		
Individuals browsed (#)	59	121
Height (cm)	103.13 \pm 20.36	139.11 \pm 10.71
BAI (mm^2/year)	6.88 \pm 1.32	8.93 \pm 0.66
<u>High Severity</u>		
Individuals browsed (#)	66	114
Height (cm)	492.16 \pm 106.76	250.73 \pm 17.27
BAI (mm^2/year)	119.52 \pm 51.65	20.37 \pm 1.20

Table 2.3. Parameter estimates from linear mixed effect models (n = 6) of the effects of browsing (light and heavy) and fire severity (low and high) on aspen height (log transformed) and aspen average basal area increment (BAI) (log transformed) with a random intercept and slope for browsing effects within sites to account for site-specific responses of individual trees.

Height					
Within-level	Fixed effect	Estimate	Standard error	t-statistic	p-value
Light browse	Severity*	1.392	0.355	3.916	0.003
Heavy browse		0.536	0.106	5.064	<0.001
Low severity	Browse*	0.350	0.222	1.576	0.116
High severity		-0.505	0.228	-2.217	0.027
	Severity*Browse	-0.855	0.318	-2.687	0.008
Average BAI					
Light browse	Severity*	1.922	0.569	3.379	0.007
Heavy browse		0.600	0.155	3.873	0.003
Low severity	Browse*	0.384	0.348	1.104	0.270
High severity		-0.937	0.358	-2.617	0.009
	Severity*Browse	-1.322	0.499	-2.647	0.009

Note: *Reference levels were set to low severity and light browsing, thus fixed effects are comparing: high severity to low severity, within each level of browsing, and heavy browsing to light browsing, within each level of fire severity. The interaction term (Severity*Browse) has reference levels set to low severity and light browsing.

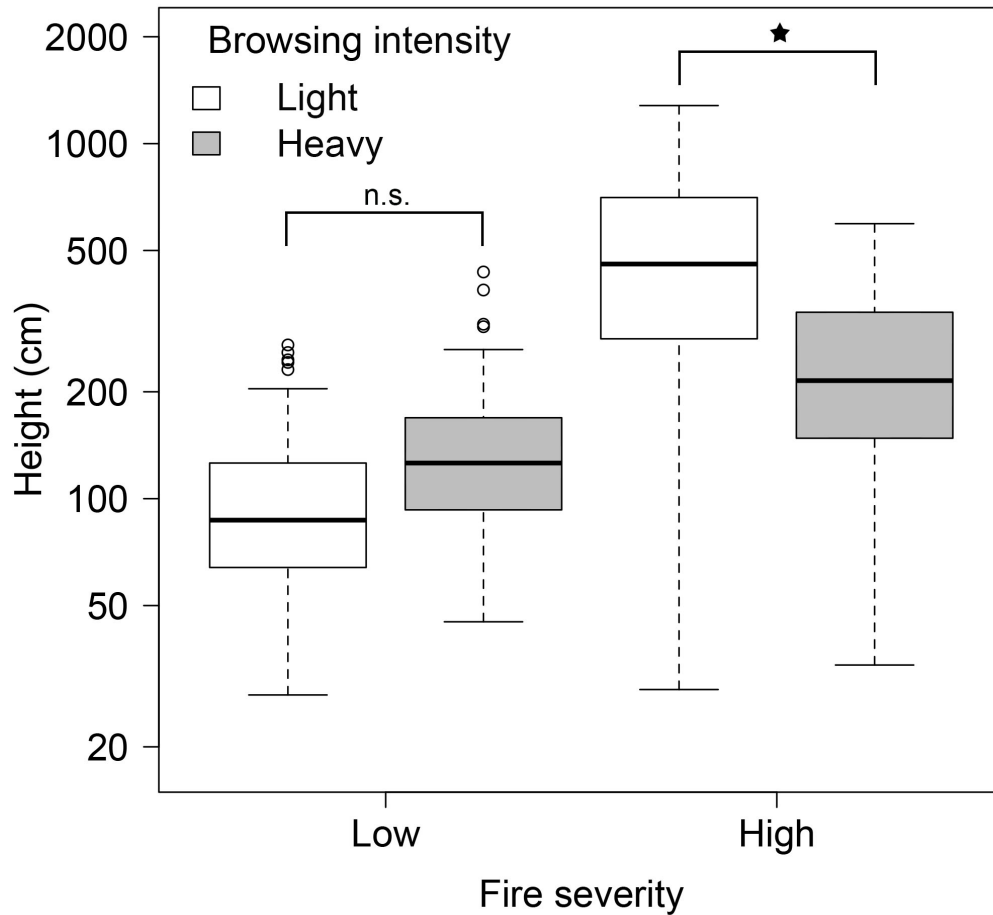


Figure 2.3. Height (cm) of trembling aspen in high ($n = 6$) and low ($n = 6$) severity sites that experienced light (white boxes) and heavy (grey boxes) browsing. Boxes encompass 25–75% quantiles of the data, while whiskers encompass 5–95%. The median is indicated by the black horizontal line, and outliers are shown as dots. Note the y axis is plotted on the natural log scale. Treatment effects can be assessed by comparing the white and grey boxes within a species; significant differences from a linear mixed effect model comparing the effect of browsing within fire severity levels are indicated by: * $P < 0.05$; n.s. $P > 0.05$ and details are given in table 2.3.

Of the 360 aspen trees we measured, 75 were over 3 m tall. All but one of the >3 m individuals were from high fire severity sites. The majority of these trees (61%) were lightly browsed. Lightly browsed trees reached 3 m in height before those that were heavily browsed (averaging 10.0 ± 1.3 and 13.2 ± 0.7 years for light and heavy browse, respectively). The shortest time to reach 3 m in height was 5 years post-fire. Height growth rate below and above 3 m differed between browsing intensities (Figure 2.4). Heavy browsing had a negative effect on annual height growth when individuals were below 3 m; there was no difference between browsing intensities once trees surpassed 3 m in height (Table 2.4).

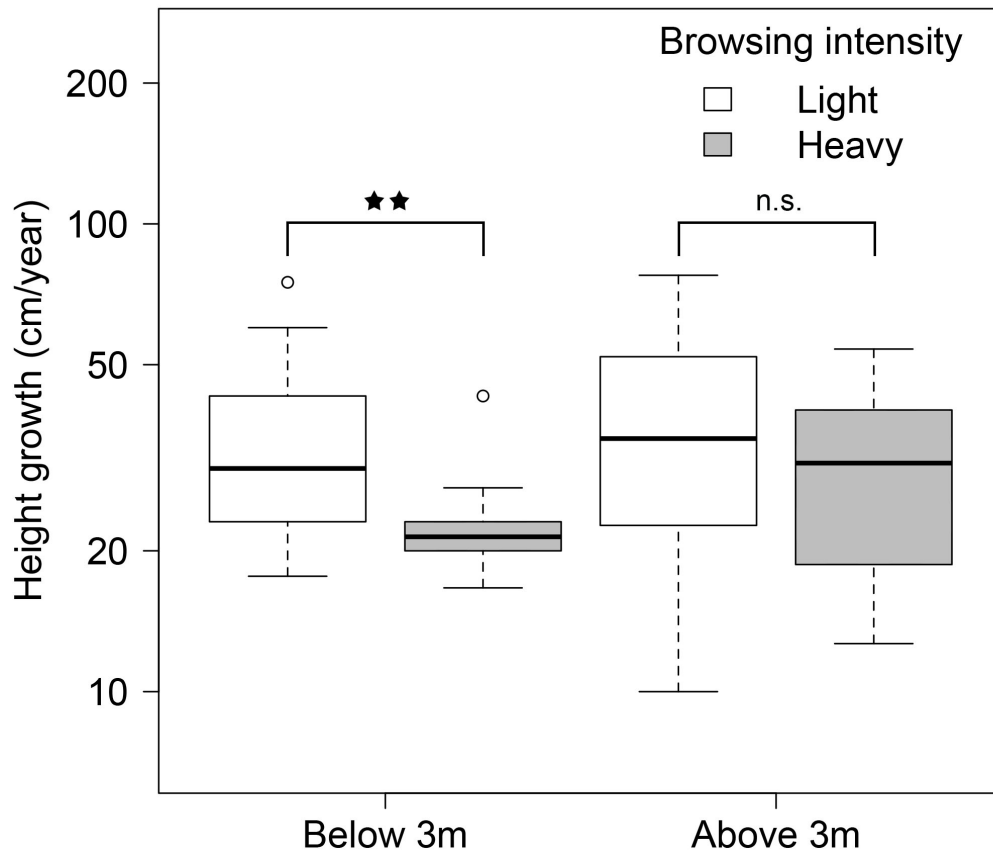


Figure 2.4. Aspen height growth (cm/year) below and above 3 m for individuals that were lightly (white boxes) and heavily (grey boxes) browsed; $n = 46$ and 29 for light and heavy browsing, respectively. Note the y axis is plotted on the natural log scale. Treatment effects can be assessed by comparing the white and grey boxes within a species; significant differences from a linear mixed effect model comparing the effect of browsing within the 3m height threshold levels are indicated by: $**P < 0.01$; n.s. $P > 0.05$ and details are given in table 2.4.

Table 2.4. Parameter estimates from linear mixed effect models of the effects of past browsing (light and heavy) and 3 m threshold (below and above) on annual height growth rate (log-transformed) with a random intercept for individual nested within site and random slopes for browse effects within sites.

Within-level	Fixed effect	Estimate	Standard error	t-statistic	p-value
Light browse	3m threshold*	-0.029	0.076	-0.377	0.707
Heavy browse		-0.212	0.096	-2.215	0.030
Below 3 m	Browse*	-0.406	0.146	-2.765	0.007
Above 3 m		-0.220	0.146	-1.509	0.136
	3m threshold*browse	-0.183	0.122	-1.500	0.138

Note: *Reference levels were set to above 3 m and light browse, thus fixed effects are comparing: annual height growth below 3 m to above 3 m, within levels of browse, and heavy browse to light browse, within levels of below or above 3 m. The interaction term (3 m threshold*Browse) has reference levels set to above 3 m and light browse.

2.3.3 *Tree ring chronologies*

Basal area index chronologies showed that aspen in low severity sites that established earlier were heavily browsed (Figure 2.5a). Visually, similar growth patterns were present for lightly and heavily browsed aspen in low fire severity sites (Figure 2.5c). Statistically, browsed aspen chronologies were moderately similar ($G = 58\%$). For low fire severity aspen chronologies, we did not detect any growth releases for either browse intensity. In high severity sites, lightly browsed aspen were consistently larger than heavily browsed trees (Figure 2.5b). Growth for both browse intensities was relatively slow from 1997 to 2007, however increased thereafter, particularly for lightly browsed trees. Lightly and heavily browsed aspen visually followed similar standardized ring width patterns, except between 2001 and 2005 (Figure 2.5d). Short divergent trends in chronologies can be indicative of different responses to browsing pressure and intensity (Chouinard and Filion 2001). Lightly browsed aspen experienced a small spike and decline in growth (2001–2005), whereas growth of heavily browsed aspen remained constant and relatively low. Overall, the two browsed chronologies in high fire severity were moderately similar ($G = 0.59\%$). When we separated out the divergent time period (time period 2001–2005, $G = 50\%$), we found that growth was more similar during the time periods exclusive of the divergent period (1995–2000 & 2006–2013, $G = 69\%$). In the high fire severity chronologies, a moderate growth release occurred in 2008 for aspen that were lightly browsed, and in 2009 for aspen that were heavily browsed (Figure 2.5d).

Growth of BAI in spruce was similar between low and high fire severities until 2000, when spruce in low severity sites grew at a faster rate (Figure 2.6). Standardized ring width growth was similar between fire severities for spruce. We detected no growth releases for spruce in either the low or high fire severity chronology.

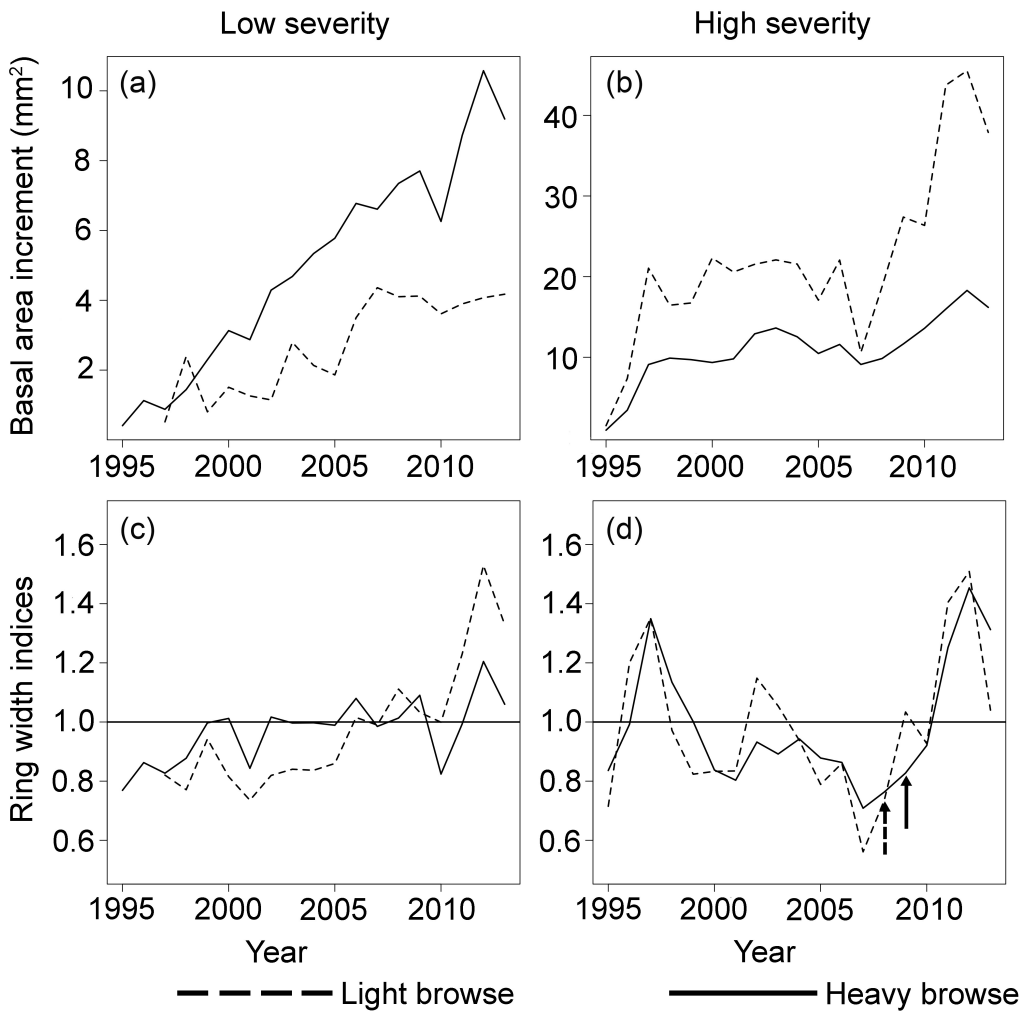


Figure 2.5. Aspen basal area increment (mm^2/year) and standardized ring width chronologies from 1995 to 2013. Chronologies for low (dashed line) and high (solid line) browsing intensities in both low (a, c) and high (b, d) fire severity sites are included. Ring width indices are standardized with a mean of 1.0, with the black horizontal line indicating when growth was below or above average. Growth releases, detected through growth-averaging, are indicated on the ring width index plots with arrows for either low (dashed arrow) or high browsed (solid arrow) chronologies. Note the difference in y-axis values for basal area increment.

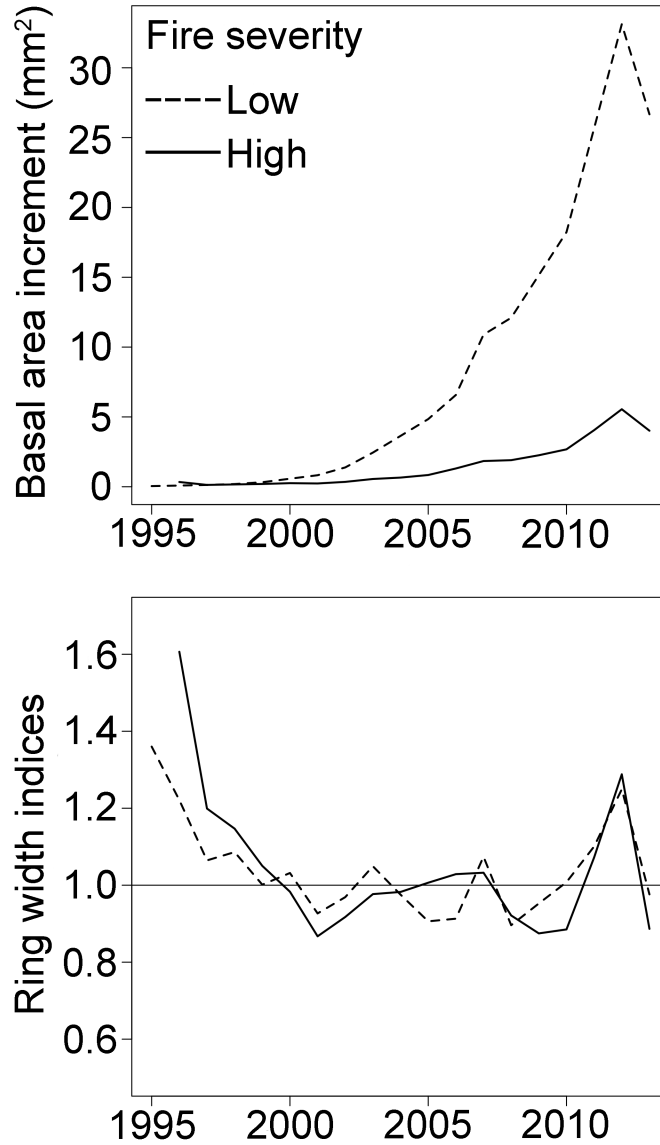


Figure 2.6. Black spruce basal area increment (mm²/year) and standardized ring width chronologies from 1995 to 2013. Chronologies for low (dashed line) and high (solid line) fire severities are included. Ring width indices are standardized with a mean of 1.0, with the black horizontal line indicating when growth was below or above average.

2.4 Discussion

Our results strongly suggest that moose are affecting the *rate* but not the *trajectory* of canopy dominance in these mixed aspen and black spruce forests. Initial effects of fire severity on post-fire tree regeneration and growth, which suggest an aspen-dominated trajectory in high severity sites (Johnstone and Kasischke 2005, Shenoy et al. 2011), provided large amounts of available moose forage (Lord 2008, Brown et al. 2015). Twenty years post-fire, moose had substantially reduced the rate of aspen growth in sites that burned severely during the Hajdukovich Creek fire. However, aspen at these sites have shown high tolerance to moose damage, with heavily browsed individuals approaching 3 m in height. We found no growth releases in black spruce at these sites, indicating that even high levels of moose browse have been insufficient to cause these sites to revert to the dominance of black spruce that was present prior to the fire. Moose browsing in low severity sites had no effect on aspen growth rate. Browsing in low severity sites has likely been relatively light, compared to high severity sites, and has yet to cause any negative effects to aspen growth. Reconstructed patterns of aspen and spruce growth indicate that herbivory by moose has slowed the development of aspen canopy dominance in severely burned sites, but has not affected the initial trajectories of succession at high and low severity sites. Nevertheless, variations in the severity of the Hajdukovich burn has persisted as heterogeneity in tree growth and moose herbivory and had consequences for the period of time that forage is available to moose within the burn.

In high fire severity areas, moose browsing negatively affected aspen height and basal growth rates as evinced by the occurrence of twig clusters, a slower height growth rate for heavily browsed aspen under 3 m, and tree ring chronologies that diverged between heavily and lightly browsed. This finding is supported across temperate and boreal forests where ungulates have been observed to suppress growth of browsed trees (Rooney and Waller 2003). Similarly, in Arizona, foraging by elk (*Cervus canadensis*) reduced aspen regeneration in high severity sites due to greater rates of browse damage compared to intermediate severity sites (Bailey and Whitham 2002). In contrary, in Utah, Wan et al., (2014) found lower browse damage on aspen in moderate and high severity sites due to successfully escaping herbivore pressure by growing at a faster rate. Heavily browsed aspen in our severely burned sites averaged half the height of lightly browsed individuals, and on average had yet to reach a height safe from moose browsing (>3 m) twenty years after fire (Table 2.2). Nevertheless, even under high browse pressure, aspen in high

severity sites were still four times taller than spruce and continue to dominate these sites. Of the suppressed individuals that reached 3 m in height, growth rates increased and were comparable to lightly browsed individuals (Figure 2.4). The high tolerance of aspen to browsing is likely supported through mechanisms such as the utilization of reserves stored in roots or stems, increased photosynthetic activity, or the activation of dormant meristems (Tiffin 2000).

Our results show that decreased browsing pressure can produce large increases in radial growth rates in both lightly and heavily browsed aspen in high fire severity sites. It is unlikely that growth releases were due to climatic conditions, as low and high severity sites are in close proximity to each other (Figure 2.1), but no growth releases were detected at low severity sites. The observed decrease in the local moose population from 2007–2009 (DuBois 2010) coincides with the growth releases. The proportional removal of forage by moose declined by 50% from 2007 to 2013 in high fire severity sites (Brown et al. 2015), indicating a decrease in the presence of moose at the time of the growth releases. Our results show that radial growth releases can be detected in aspen that are likely associated with a reduction in mammalian browse pressure, which is promising for future studies aiming to quantify historical effects of plant–mammal interactions.

In low severity sites, browsing had no apparent effect on aspen growth. We propose two explanations for this result: compensation and overall low browse intensity. It is plausible that moose may preferentially browse on larger individuals, increasing the chance of heavily browsed aspen being able to compensate for or adjust to the loss of tissue sufficiently to maintain similar growth rates to lightly browsed individuals (Hjálten et al. 1993). Furthermore, up until 19 years post-fire, low severity sites produced less available forage than high severity (Lord 2008, Brown et al. 2015), which likely translates to an overall lower browsing intensity in these sites. However, twenty years post-fire in low severity sites, aspen were still vulnerable to moose browsing (i.e., below 3 m in height; Table 2.2), which indicates that there will be impacts from moose over decades in heterogeneously burned areas.

Differences in rates of aspen growth and timing of browsing between fire severities could affect black spruce growth and presence. In severely burned areas, lightly browsed aspen dominated the lower canopy (3 m) as early as 11 years post-fire (Figure 2.7, Figure A2.2). Although moose have slowed the rate of aspen growth by 10 years in high severity areas, this did not translate into a detectable increase in black spruce growth (Figure 2.6). If we assume slow

black spruce growth under the dominant aspen canopy, likely due to light limitations, black spruce seedlings will be vulnerable to snowshoe hare browsing, which may further reduce their growth and/or presence in the understory (Wolff 1978). Twenty years post-fire, aspen and black spruce are similar in height in low severity areas, which suggests a co-dominant mature forest. Moose browsing could be important in these mixed areas by targeting aspen and shifting the competitive balance towards spruce, causing growth suppression for the shade intolerant aspen (Wright et al. 2000).

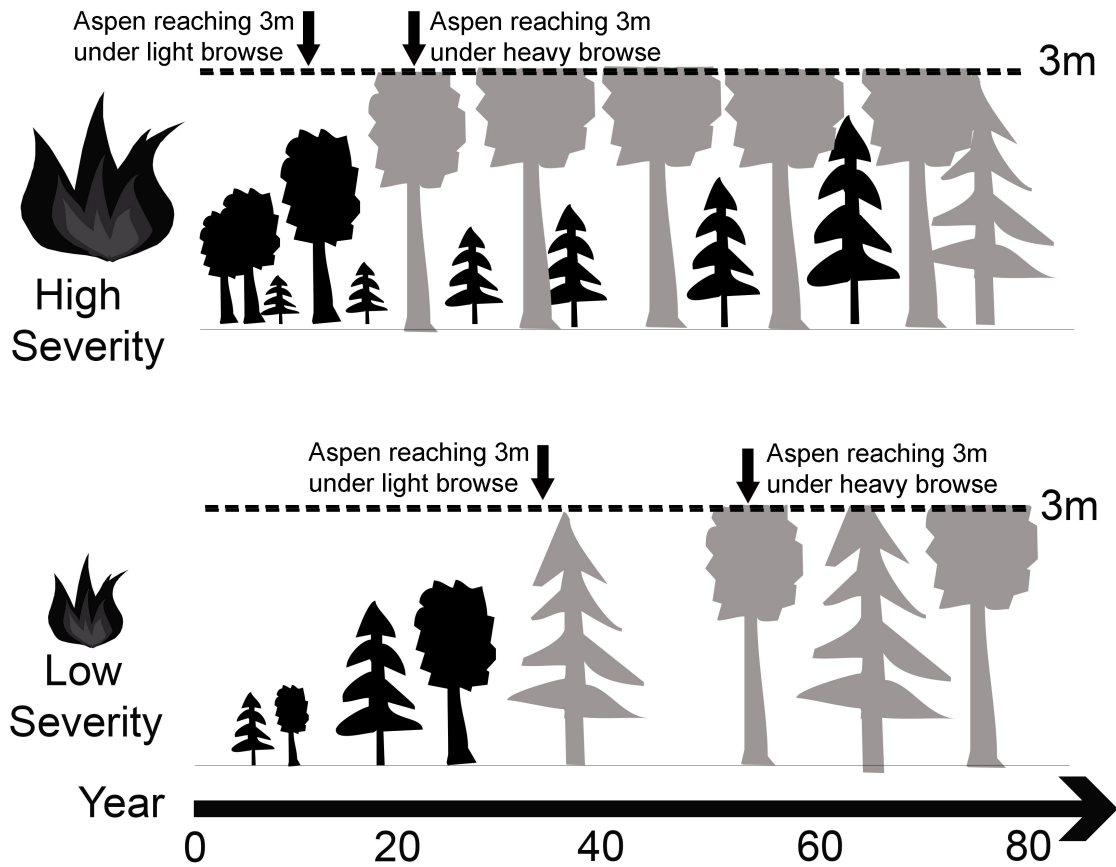


Figure 2.7. Projected height-growth of aspen and black spruce after high and low severity fires. Trees below 3 m are black whereas grey trees have surpassed the 3 m mark. Greyed out trees are based on a heavy browse intensity, and thus represent the maximum time aspen are available as forage for moose. Arrows indicate the time period in which aspen will escape browsing pressure, based on either light or heavy browse.

Similar to moose impacts on primary succession in the floodplains in Alaska (Kielland and Bryant 1998), we found that moose significantly affected the early stages of secondary succession by affecting the rate of aspen growth (Table 2.3). In contrast, in eastern North American boreal and temperate forests, large ungulates have altered forest successional trajectories (McInnes et al. 1992, Thompson et al. 1992, Rossell et al. 2005). For example, on Anticosti Island, Québec, an alternative successional trajectory of broadleaf-dominance, as opposed to *Picea* spp., was found only when white-tailed deer (*Odocoileus virginianus*) were excluded immediately after logging (Hidding et al. 2013). The high resilience and tolerance of aspen to browsing (Lindroth and St. Clair 2013), and lower densities of large herbivores (e.g., our study with 1.78 moose/km² compared to the study by Rossell et al., (2005) in Virginia, USA with 67 deer/km²) in our study area contribute to the differences between our results and those in eastern North American forests.

In interior Alaska, the highest density of moose is associated with areas that are 11–30 years post-fire, without consideration of fire severity (Weixelman et al. 1998, Maier et al. 2005). However, height-growth projections from our data illustrate that moose affect the time period of forage availability and forest structure differently in low and high fire severity patches (Figure 2.7). Within the Hajdukovich Creek burn, forage was available soon after fire (fast growth in high fire severity sites) and could remain until 54 years post-fire in low severity sites. In our study, 19 years after fire forage removal has diminished in high severity areas (Brown et al. 2015), moose are now spending their winters in low severity areas (Kielland and Brown 2015). Thus, the long time period of forage availability in low severity sites is attributed to an expected increase in intensity and effects of browsing twenty years after fire. However, these effects will also be contingent on the nutritional quality of forage, which could decrease as time since disturbance increases, in turn affecting moose fitness and browsing (Wam et al. 2016). Low and high fire severity patches will provide forage over different periods and lengths of time, thus predictions of optimal post-fire moose habitat should include variations in fire severity.

2.5 Conclusion

In high fire severity sites, moose browsing had direct negative effects on aspen growth, but had no associated indirect effects on spruce growth. Although moose browsing slowed aspen growth in severely burned areas, aspen still dominated the canopy, demonstrating high tolerance

to browsing. Extrapolation of herbivory effects from high to low fire severity suggests that moose effects on aspen growth in low severity burns may hasten the recovery of black spruce canopy dominance, but such effects were not yet apparent 20 years after fire. Heterogeneous patterns of fire severity can play an important role in maintaining variations in post-fire succession and sustaining high rates of available moose forage for a much longer period than previously reported.

2.6 References

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CHAPTER 3: ALASKAN PAPER BIRCH SAPLINGS REDUCE WOODY GROWTH
AND CARBON-BASED DEFENSES AFTER SIMULATED LEAF STRIPPING

3.1 Introduction

Plants have evolved multiple strategies to avoid damage from vertebrate herbivores. Tolerance (ability to compensate after damage), resistance (ability to prevent or reduce herbivory), and escape (rapid growth into herbivore-free space) are three common strategies employed by woody plants to deal with herbivores (Karban and Baldwin 1997). Although fast-growing deciduous tree species generally utilize an escape strategy (Allcock and Hik 2004, Dantas and Pausas 2013, Lindroth and St. Clair 2013), rapid growth may not be a viable mechanism to escape herbivore damage in nutrient poor areas (Bryant et al. 1983). Thus, chemical defenses against herbivory (i.e., resistance strategy) have evolved in numerous plant species (Mithöfer and Boland 2012). Woody plants have a finite amount of resources to allocate carbon to growth, storage and chemical defense at the same time. Herein lies the challenge for woody plants experiencing herbivory: where to best invest resources to maximize chances of survival and long-term fitness. The consequences of these responses in resource allocation go beyond just the impact on an individual species, but also create the potential for herbivory events at key life stages to alter patterns of plant community development. Therefore, understanding plant responses to herbivory is a central element to understanding how herbivores may shape biotic communities.

Carbon (C) is a vital building block for many aspects of plant growth and defense. C allocation in plants is complex as it involves multiple pathways and is strongly dependent on factors such as plant growth form, ontogeny, environmental conditions, and past disturbances (Chapin et al. 1990). Herbivores alter the availability of C and nutrients to a plant by removing biomass, but the impact of these effects often depends on the intensity of herbivory. For example, increasing intensity of browsing shifted *Betula glandulosa* Michx. regrowth ability from compensation to under-compensation, likely due to plasticity in shoot production at lower levels of browsing (Champagne et al. 2012).

Timing (i.e., during dormant or active growing period) and type (e.g., what tissues are removed) of herbivory are also particularly important in temperate and boreal forests. For example, moose (*Alces alces*) browse dormant shoots in winter through consumption of woody biomass (twigs) and in the summer by leaf stripping and sometimes removal of the apical bud (Miquelle 1983, Bergström and Danell 1995, Wam and Hjeljord 2010). Moose avoid current annual shoots in the summer as they are low in nutrients and high in chemical defenses (Bryant

and Kuropat 1980). In general, boreal deciduous plants respond to moose winter browsing with compensatory growth due to the removal of apical dominance, which reduces competition among remaining growing points for mineral nutrients (Bergström and Danell 1987). This leads to a decrease in vertical growth due to sprouting or lateral growth (Danell et al. 1994). In these situations, individual (Stouter 2008) and total (De Jager and Pastor 2010) shoot biomass is often higher compared to unbrowsed individuals. In contrast, deciduous trees generally do not show compensatory growth responses after summer browsing; however, responses of leaf nutrient concentrations and leaf size vary (Danell et al. 1994). In addition, plant responses to herbivore damage can be altered by the surrounding vegetation (Hjálten et al. 1993), likely through competition for light (Millett et al. 2006).

The carbon-nutrient balance hypothesis (CNBH) has been posed to account for the variability in woody plant responses to herbivory across gradients in resource availability (Pahlsson 1992, Mutikainen et al. 2000, Hikosaka et al. 2005, Månsson et al. 2009). The CNBH predicts that when nutrients are limiting, growth is depressed more than photosynthesis, resulting in an excess of C that can be allocated to build C-based secondary metabolites that do not require the limiting nutrients (Bryant et al. 1983). In contrast, during periods of light limitations (i.e., shading), both photosynthesis and growth are C-limited and concentration of nutrients in leaves and shoots tend to accumulate (Bryant et al. 1992). The type of herbivory also alters these growth and chemical responses. For example, when vertebrate herbivores browse the stems of woody plants, competition for nutrients among remaining shoots is reduced, which increases concentrations of nutrients available to support regrowth, thereby decreasing allocation to secondary C-based metabolites (Bryant and Reichardt 1992). Alternatively, severe defoliation, such as by insects, removes leaves and the high concentrations of nutrients they contain, causing plant growth to become progressively more nutrient- than C-limited. This results in a surplus of carbohydrates that can be used for C-based secondary metabolites (Bryant and Reichardt 1992). I am interested in testing the nuances of the CNBH when both meristems (growing points) and leaves (nutrient pools) are removed and/or damaged, especially in areas where alterations to plant growth could have ramifications for the plant and soil community.

My main objective was to understand how Alaskan paper birch (*Betula neoalaskana* Sarg.) responds to simulated moose leaf stripping in an early post-fire boreal upland environment. I had two specific objectives: first to identify at what intensity of leaf stripping

saplings start to show a response, and whether the shape of the response is linear or nonlinear. I predicted that low intensity leaf stripping would not affect an individual's carbon-nutrient balance, thus shoot and leaf growth and C-based secondary metabolite production would be comparable to that of control individuals (e.g., compensation). At high leaf stripping intensities I expected saplings to respond similarly to insect defoliation under the CNBH. Specifically, the removal of leaves would cause a decrease in leaf and shoot growth due to increased competition for nutrients among remaining growing points, thereby increasing C-based secondary metabolites. I used linear mixed effect models to test the response of shoot, leaf, and C-based defense responses to leaf stripping intensity and to identify potential nonlinearities in plant response. Secondly, I used a structural equation model (SEM) to incorporate the influence of natural winter browsing and local woody basal area on responses of birch saplings to leaf stripping. If previous winter browsing causes larger regrowth and leaves in the following year (Bergström and Danell 1987, Stouter 2008), then I expected that natural occurrences of previous browsing should increase resource acquisition and ability of a sapling to compensate for damage caused by summer leaf stripping. Furthermore, if saplings in these young, post-fire stands are competing for light, I predicted that local woody basal area should be negatively related to growth and C-based secondary metabolites because of shading effects on photosynthesis and consequent declines in carbohydrate concentrations. My study tests the CNBH and improves our understanding of how Alaskan paper birch responds to herbivory during critical life stages of early post-fire succession.

3.2 Methods

3.2.1 Study area

My study area is approximately 50 km northeast of Fairbanks, Alaska along the Steese highway (~65.142889 °N, 147.470556 °W). Although the dominant mature forest in the area is composed of black spruce (*Picea mariana* (Mill.) BSP), many areas are dominated by deciduous trees, primarily trembling aspen (*Populus tremuloides* Michx.) and Alaskan paper birch. The Boundary Fire along the Steese highway burned almost 218,000 hectares of this landscape in 2004. Within these burns deciduous species have regenerated, primarily in severely burned areas (Johnstone et al. 2010). This switch from coniferous to deciduous stands in early post-fire succession suggests mature deciduous stands will increase in dominance across the landscape

(Mann et al. 2012). However, young deciduous species are important forage for mammalian herbivores and moose are able to slow the rate of deciduous dominance and growth by 10 years in interior Alaska (Conway and Johnstone 2017). Thus the potential of mammalian herbivores to alter tree growth is an important consideration in this system. Local moose density in the study area peaked in 2009 with 0.85 moose/km² and has since decreased to 0.58 moose/km² in 2013 (Alaska Department of Fish and Game 2014).

3.2.2 Study species and experimental design

I started my experiment when saplings of Alaskan paper birch were within moose browsing range (50 cm to 3 m in height) (Danell and Ericson 1986, Weixelman et al. 1998, Seaton et al. 2011). Alaskan paper birch have both short and long shoots allowing for high plasticity in growth; short shoots grow a few millimeters and are specialized for leaf display while long shoots have elongated internodes, with alternating leaves that contribute to crown expansion (Maillette 1982). Moose browse long shoots of birch species in winter through consumption of woody biomass (twigs) and in the summer by leaf stripping and sometimes removal of the terminal bud (Miquelle 1983, Bergström and Danell 1995, Wam and Hjeljord 2010). Alaskan paper birch are chemically defended by a C-based metabolite (a triterpenoid, papyriferic acid) which is a deterrent to mammalian herbivores (Reichardt et al. 1984, Bryant et al. 1987). Papyriferic acid is found in the resin excreted by external glands visible on current year long shoots (Lapinjoki et al. 1991, Raatikainen et al. 1992). Palatability of Alaskan paper birch and mammalian preference is strongly and negatively correlated with the number of resin glands (Rousi et al. 1991, Laitinen et al. 2002); thus density of resin glands has been used as a proxy for defense (Stevens et al. 2016). Compared to mature Alaskan paper birch, juveniles are more vulnerable to browsing damage, and winter browsing by mammals has selected for a chemical defense over time (Bryant et al. 2014). However, mature Alaskan paper birch also produce adventitious shoots high in resin content after severe winter hare browsing, demonstrating a flexibility with respect to chemical defenses (Bryant 1981).

In mid-July 2014, I established six sites within the Poker Flats Research Range and Caribou Poker Creek Research Watershed, along the Steese Highway. Sites were located near long-term sites established one year after the 2004 burn to investigate post-fire regeneration across fire severity gradients (Johnstone et al., 2010). At each site I selected a homogeneous area

with Alaskan paper birch saplings of similar size, and established a sampling grid by laying out six parallel transects that were 27 m in length and three m apart. Along each transect I sampled ten points at three m intervals, selecting the closest Alaskan paper birch sapling to each point for measurement. A total of 360 birch saplings were measured. Due to logistical restraints, I was unable to protect individuals from herbivore damage during the winter after my leaf stripping treatment however I do not think this influenced my results (see section 3.3.1).

3.2.3 Field measurements and treatment

Before the leaf stripping treatment was applied I measured multiple attributes of each sapling, which I divided into two categories (woody and architecture). I recorded height, basal diameter, and the total number of current year short and long shoots (woody growth category) (Table 3.1). Architectural measurements included canopy width (width included two measurements: the largest width and the width perpendicular to that measurement) and depth (from the first long shoot on the stem to the top of the tree). Final canopy width was averaged between the two measurements. I characterized the intensity of past natural winter herbivory by counting all shoots that had been browsed or broken by moose or snowshoe hare. Lastly, I measured the basal diameter of all woody species in a square 4 m² plot surrounding each individual sapling as a surrogate for local competition intensity.

Table 3.1. Pre-treatment means (± 1 standard error; n = 6 sites) for birch woody and leaf variables.

Woody variables	Mean
Height (cm)	145.48 \pm 12.62
Basal (mm)	16.60 \pm 1.32
Short shoots (#)	101.34 \pm 17.76
Long shoots (#)	27.33 \pm 5.03
Crown width (cm)	53.33 \pm 5.07
Crown depth (cm)	109.50 \pm 12.90
Leaf variables	
Average leaf area (cm ²)	11.82 \pm 0.91
Specific leaf area (cm ² /g)	138.90 \pm 0.32

Note: Woody variables included 60 Alaskan paper birch saplings within each site, whereas leaf variables included only 50 (control trees were not destructively sampled for pre-treatment leaf measurements)

The intensity of leaf stripping treatments (0, 20, 40, 60, 80, 100% of long shoots stripped) was randomly assigned to each tree at a site (ten saplings per treatment category). I identified which long shoots would be stripped and collected up to ten intact leaves (third leaf from the terminal bud, when possible) that were brought to the laboratory for further processing. Thus, pre-treatment leaf measurements were only taken for saplings subjected to the leaf stripping treatment (not from controls (0% stripped)).

Leaf stripping was done by hand and only once per shoot. Instead of evenly stripping long shoots distributed along the entire stem, I mimicked natural moose browsing (Figure 3.1a) by first stripping long shoots at the top of an individual that were easily accessible and worked my way down the stem, as needed (Figure 3.1b, c). All stripped biomass (including all leaves and any buds, bark, or resin) was brought to the laboratory for processing. My design allowed me to apply a proportional categorical leaf stripping treatment to each individual, and also have a continuous measure of biomass removed for analyses.

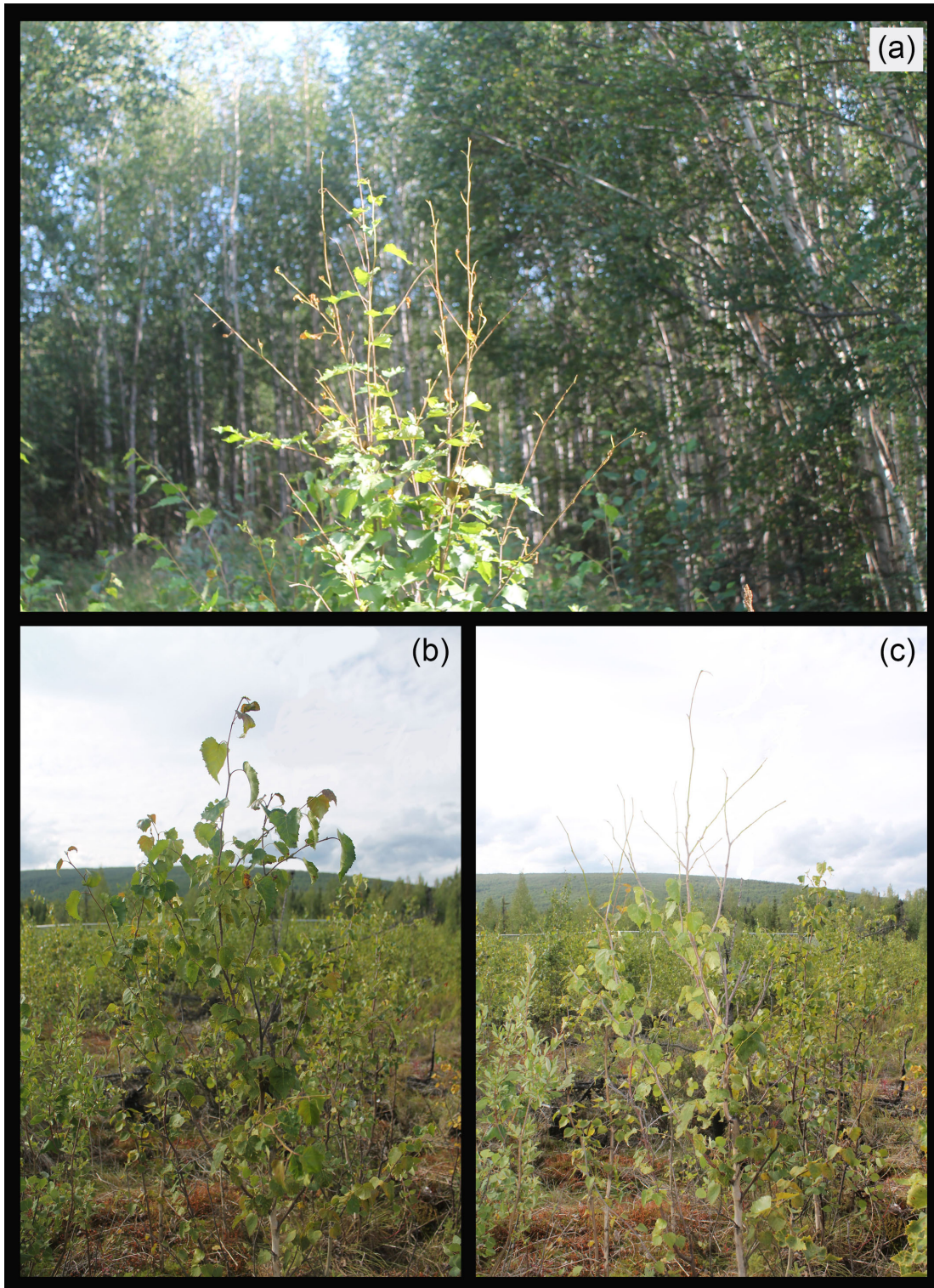


Figure 3.1. Alaskan paper birch sapling that was naturally leaf stripped by moose (a). Tagged saplings (b) before simulated leaf stripping and (c) after 100% leaf stripping of long shoots.

I re-measured woody and architectural variables for each tagged sapling one year later and collected up to ten long shoot leaves from each tree, including the control, for processing described below. In addition, I recorded the number of 2015 winter browse marks, which were clearly distinguishable from previous winter browsing measured in 2014. Lastly, I collected up to five current annual long shoots from each individual to quantify resin gland density (C-based defense category).

3.2.4 Laboratory work

Laboratory work consisted of weighing and measuring leaves, and counting resin glands on long shoots. All leaves collected were scanned fresh at a resolution of 400 dpi, and images were processed using WinFolia (Regent Instruments Inc., 2012) to calculate total leaf area. Leaves were dried for 48 hours at 30 °C, and specific leaf area (SLA) was calculated by dividing total leaf area (cm²) by total leaf dry weight (grams). Long shoots collected for resin gland counts were scanned fresh in colour at 600 dpi, and scanned images were imported into Adobe Photoshop CS6 for analysis. I counted all resin glands on a standard area of each twig (two cm length, ~three mm width). For consistency, resin glands were counted on the stem between the second and third most recent leaf. To avoid observer bias, I had another individual independently count resin glands on a subset of images (n = 100) and found no difference between the two counts ($t_{(100)} = 0.894$, $p = 0.373$).

3.2.5 Data analysis

All analyses were performed in R version 3.3.1 (R Development Core Team 2014). First, I used linear mixed effect models (LME) within the ‘nlme’ package in R (Pinheiro et al. 2016) to determine the effect of local woody basal area, past browsing, and their interaction on pre-treatment woody, architectural, and leaf measurements; I also examined these effects on the number of resin glands on control saplings (ten saplings per site). I accounted for the effect of site in the random term of each model.

I accounted for the effect of tree size on the amount of leaf stripped biomass by calculating the total proportion of leaf biomass removed using allometric equations. Allometric equations were developed from unpublished data for samples of six-year old Alaskan paper birch saplings (n = 53) that were planted after the 2004 burn along the Steese highway. The height

range of planted Alaskan paper birch saplings (range = 17.5 – 321 cm; mean = 113.45 cm) is comparable to naturally grown saplings in my study (range = 45 – 320 cm; mean = 145.48 cm). From these relationships (See equation 1 below; R^2 of 0.95), I estimated the amount of new biomass for each sapling in my study and then calculated the proportion (%) I removed.

$$\text{Current Annual Growth} = -2.4316300 + 1.8373055 * \log(\text{Basal Diameter}) + 0.7721064 * \log(\text{Height}) \quad (\text{Eq. 3.1})$$

I addressed my first objective (linear or quadratic response) using LME models. I used both the Akaike Information Criterion (AIC) and F-test model comparisons in my model selection for each response variable. The model with the lower AIC was chosen, however if the two models had AIC values within 2 (Burnham et al. 2011), the simpler (linear) model was chosen. Woody and architectural response variables were investigated using the proportional change between pre- and post-treatment measurements. Leaf measurements and defense responses were represented by the values measured in the year after treatment. I was not able to collect ten long shoot leaves for each individual thus total leaf area and weight were divided by number of leaves for an average value that was used in analyses. When necessary, response variables (long shoots, leaf area and resin glands) were log-transformed to meet assumptions of normality and heteroscedasticity.

Linear mixed effect models with treatment (proportional amount of leaf biomass removed) as a fixed effect were constructed for each response variable to determine the most appropriate random effect (Zuur et al. 2009). Random effects were either a random intercept of site, or a random intercept and slope for treatment effects within sites. Including just a random intercept for site was the best structure for all models (consistently lower AIC compared to model with more complex random structure). Thus, site was used as the sample unit ($n = 6$) for analyses; however, graphical representations vary from including individual subsample-level data to site-level data as noted below. To determine how the response of Alaskan paper birch varied depending on the intensity of leaf stripping I compared linear and quadratic models. Significant relationships, with one standard error, were plotted using the ‘stat_smooth’ function within the ‘ggplot2’ package (Wickham 2009).

I used structural equation models (SEMs) (Grace 2006) to investigate the trade-offs between Alaskan paper birch growth and defense production after simulated summer moose browsing (objective 2). SEMs are capable of testing a network of causal hypotheses that are developed *a priori* based on scientific evidence and ecological knowledge (Grace 2006, Grace et al. 2012). To avoid over-fitting the hypothetical model, I only used one response variable, measured in 2015, from each of my four categories: woody, architecture, leaf, defense. For consistency, final measurements after treatment (i.e., not proportional change for woody and architectural categories) were used for all four variables. Number of long shoots represented woody growth as long shoots contribute to the overall growth of paper birch and are consumed by moose in summer and winter. I used crown depth for the architectural response as it encompasses height ($r = 0.94$) and is correlated with crown width ($r = 0.84$). I used average individual leaf area for leaf growth, as leaf area and weight were highly correlated ($r = 0.93$).

I expected my leaf stripping treatment to influence all four response variables and be consistent with the CNBH based on insect defoliation (Figure 3.2). I hypothesized the effect of increasing local woody basal area would have an overall negative effect on woody, leaf and C-based defense response to leaf stripping due to increased competition for light (Figure 3.2). Height at the start of the experiment was expected to have a direct positive effect on woody, architecture and leaf responses (Chapin et al. 2016). Since past browsing was positively related to pre-treatment woody, architecture and leaf measurements (see section 3.3.1), I expected previously browsed individuals to be better equipped to tolerate leaf stripping damage (Figure 3.2). I also anticipated a negative interaction between woody basal area and past winter browsing; as competition for light becomes increasingly stronger, the effect of past browsing would be dampened.

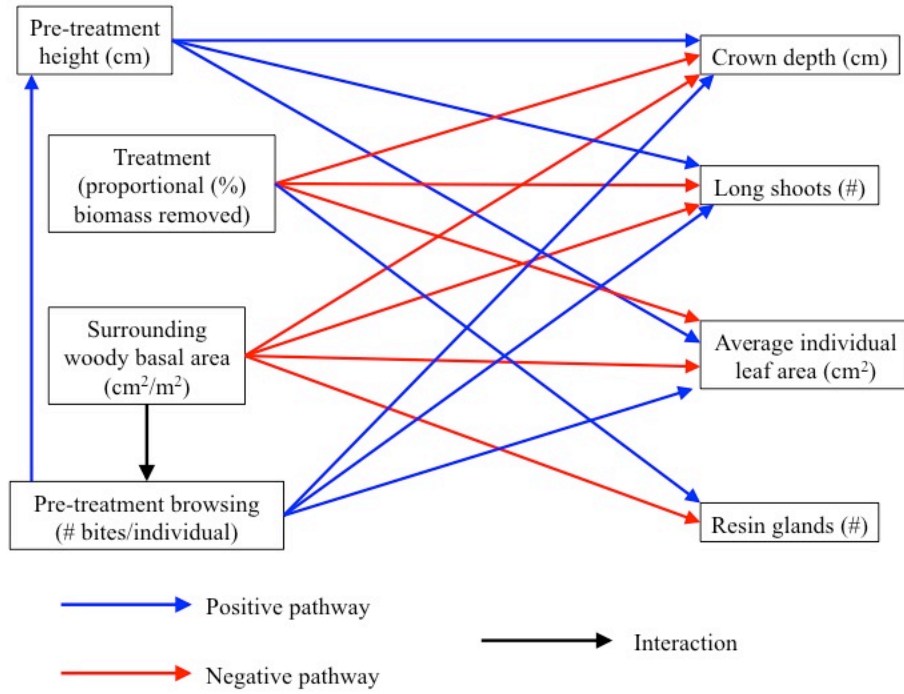


Figure 3.2. Hypothetical *a priori* structural equation model for paper birch response to treatment and biotic effects. Expected positive (blue arrows), negative (red arrows) pathways, and interactions (black arrow) between variables are denoted.

Prior to fitting the SEM, I examined and tested all bivariate relationships for linearity. Once all variables were log-transformed, relationships were linear and thus appropriate for use in the SEM. Models were fit using the ‘lavaan’ package in R with bootstrapping of 1000 iterations to account for any remaining non-normal distributions (Rosseel 2012). First, I removed any non-significant ($P > 0.05$) pathways from the initial hypothetical model. Modification indices (MIs) were then used to identify any important missing pathways that I did not include in the original model. Additional pathways were added one at a time, based on highest MI values, and whether they made ecological sense (Grace et al. 2012). I continued adding plausible pathways until the SEM had a good fit based on a chi-square test (P values > 0.05), Root Mean Square Error of Approximation (RMSEA; value close to zero), and the Comparative Fit Index (CFI; values greater than 0.90) (Grace et al. 2012, Sandom et al. 2013).

My SEM model did not incorporate the hierarchical structure of my study design, with individuals nested within site. I compared my SEM results to LME models to ensure my approach was not biased and still provided robust parameter estimates (e.g., Chapin et al., 2016). I ran LME models for each response variable, with fixed effects based on the significant pathways found in the SEM, and site as the random effect.

3.3 Results

3.3.1 Site characteristics and effects on pre-treatment variables

Total woody basal area (including Alaskan paper birch, trembling aspen, black spruce, and all *Salix* spp.) differed by up to 6-fold among sites (Table 3.2). Basal area of birch saplings varied from 28% (site BF84) to 83% (site BF86) of total woody basal area. A 6-fold difference between sites was also present for average biomass estimates of birch saplings (Table 3.2). Past herbivory also varied across sites, with the smallest amount in the site with the lowest basal area and biomass of birch saplings. In total, 33 tagged saplings were browsed in the 2015 winter; however, browsing was evenly distributed across leaf stripping categories ($\chi^2(5, N=33) = 9.36$, $p = 0.10$).

Local woody basal area and past winter browsing had positive relationships with pre-treatment height, basal diameter, crown depth, and SLA (Table 3.3). Birch saplings that were previously browsed also had greater leaf weight, leaf area, and crown width, and a greater number of long shoots. Only one model had a significant interaction (Table 3.3); as local woody

basal area increased, past browsing had a more positive effect on the number of short shoots. Resin gland density of control saplings in 2015 was not affected by either woody basal area or past browsing (Table 3.3).

Table 3.2. Plant productivity and pre-treatment winter herbivory at each site (n = 60).

Site	Total woody basal area (cm ² /m ²)	Birch basal area (cm ² /m ²)	Average individual birch biomass (g)	Pre-treatment winter herbivory (% individual birch browsed)
BF72	7.06 ± 0.62	4.45 ± 0.51	121.39 ± 15.65	26.67%
BF76	11.12 ± 1.04	5.77 ± 0.78	189.68 ± 32.61	30.00%
BF77	14.68 ± 0.83	9.66 ± 0.68	135.46 ± 20.27	71.67%
BF81	18.11 ± 0.82	13.41 ± 0.79	94.74 ± 8.25	26.67%
BF84	3.40 ± 0.31	0.97 ± 0.18	29.58 ± 3.68	10.00%
BF86	12.63 ± 0.77	10.47 ± 0.69	79.32 ± 9.44	21.67%

Table 3.3. Parameter estimates from linear mixed effect models, with a random intercept of site (n = 6), of woody basal area (BA) and past browsing effects on pre-treatment measurements on Alaskan paper birch saplings.

Response	Fixed effect	Value	Standard error	t-value	p-value
Growth responses					
Height	Woody BA	19.408	3.091	6.279	<0.001
	Past browsing	3.980	0.913	4.358	<0.001
	BA*Browsing	-0.770	0.753	-1.023	0.307
Basal ^a	Woody BA	0.074	0.028	2.656	0.008
	Past browsing	0.070	0.008	8.373	<0.001
	BA*Browsing	0.005	0.007	0.771	0.441
Short shoots ^a	Woody BA	-0.011	0.052	-0.213	0.832
	Past browsing	0.082	0.015	5.309	<0.001
	BA*Browsing	0.033	0.013	2.561	0.011
Long shoots ^a	Woody BA	0.094	0.060	1.583	0.114
	Past browsing	0.074	0.018	4.162	<0.001
	BA*Browsing	0.015	0.015	0.996	0.320
Architectural responses					
Crown depth ^a	Woody BA	0.131	0.027	4.842	<0.001
	Past browsing	0.034	0.008	4.238	<0.001
	BA*Browsing	-0.007	0.007	-0.986	0.325
Crown width ^a	Woody BA	0.055	0.029	1.911	0.057
	Past browsing	0.063	0.009	7.333	<0.001
	BA*Browsing	0.004	0.007	0.580	0.562
Leaf responses					
Leaf area	Woody BA	0.618	0.341	1.813	0.071
	Past browsing	0.460	0.096	4.809	<0.001
	BA*Browsing	0.162	0.086	1.879	0.061
Leaf weight	Woody BA	0.003	0.002	1.376	0.170
	Past browsing	0.002	<0.001	3.642	<0.001
	BA*Browsing	<0.001	<0.001	1.440	0.151
Specific leaf area	Woody BA	2.505	1.092	2.293	0.022
	Past browsing	1.007	0.323	3.120	0.002
	BA*Browsing	-0.045	0.267	-0.168	0.867
Defense responses					
Resin glands	Woody BA	1.240	2.636	0.470	0.640
	Past browsing	-1.560	1.189	-1.312	0.196
	BA*Browsing	0.865	0.651	1.330	0.190

Note: ^a Response variables were log-transformed to meet assumptions of normality.

3.3.2 *Linear and non-linear responses to leaf-stripping*

Simulated leaf stripping had generally negative effects on woody and architectural growth responses, except for the positive response of basal diameter (Figure 3.3). As the proportion of leaf biomass removed increased, birch saplings put on fewer short shoots and reduced crown width (Figure 3.3c, e). Quadratic relationships were found for change in height, crown depth, and number of long shoots (Table A3.1). Individuals put on fewer long shoots and reduced in crown depth and height size at smaller proportions of leaf biomass removed; however, as the treatment intensity increased (~50% removed), the relationship plateaued and became slightly positive. However, note that sample size decreases quite substantially when the treatment was >50% of biomass removed hence the wide confidence intervals observed.

Conversely to woody growth responses, individual leaf area increased with increasing amounts of leaf biomass removed (Figure 3.4). However this relationship began to decrease at high levels of leaf biomass removed. Individual leaf weight followed a similar response as leaf area, and was marginally significant (Table A3.1) and specific leaf area showed no relationship to biomass removed. Similar to woody responses, as leaf biomass removed increased, saplings had lower densities of resin glands (Figure 3.4d).

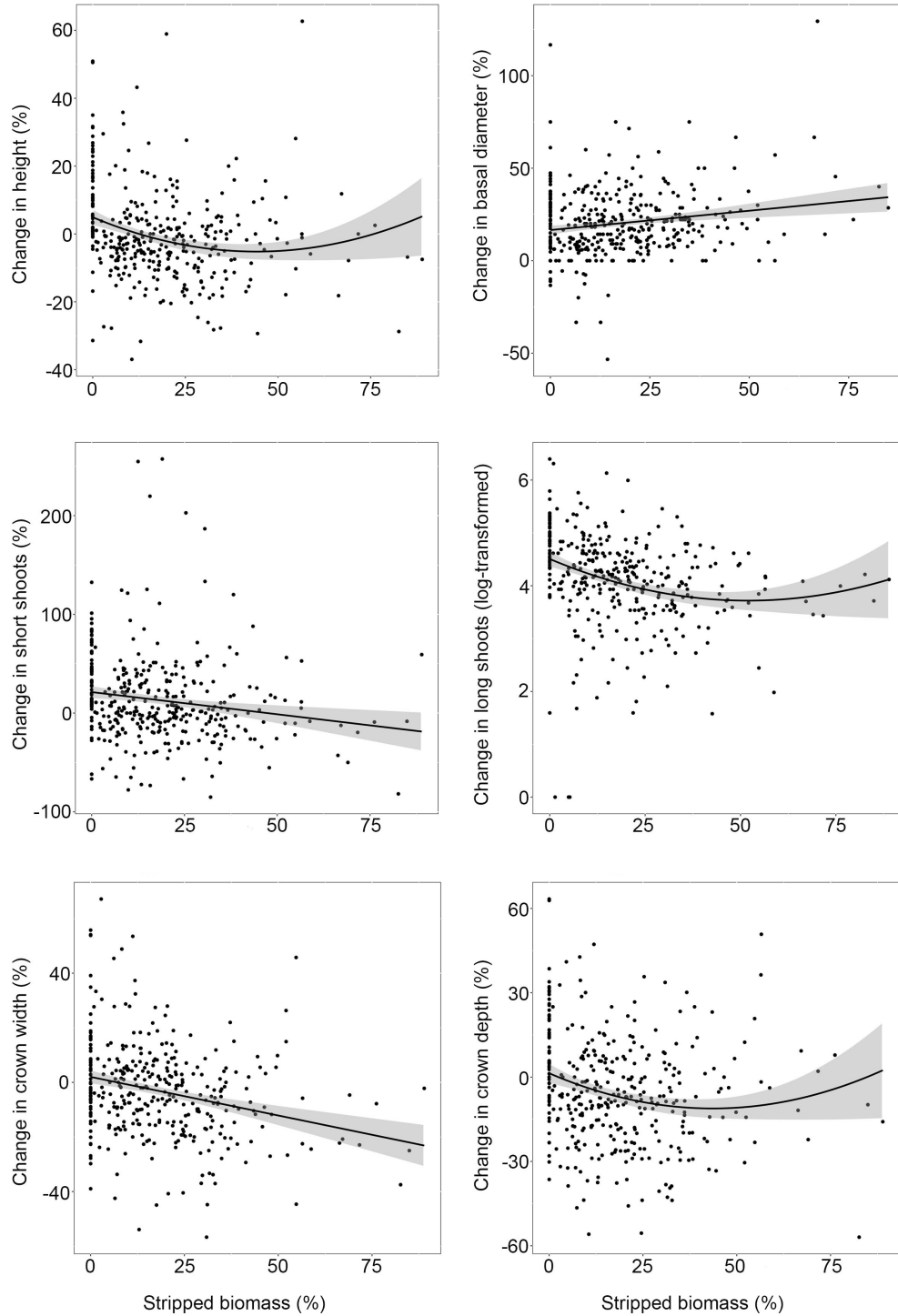


Figure 3.3. Bivariate relationships between the leaf stripping treatment and woody response variables. Points represent individual Alaskan paper birch saplings ($n = 360$). Black lines, with standard error grey shading, represent significant relationships. Note the different y-axes scales.

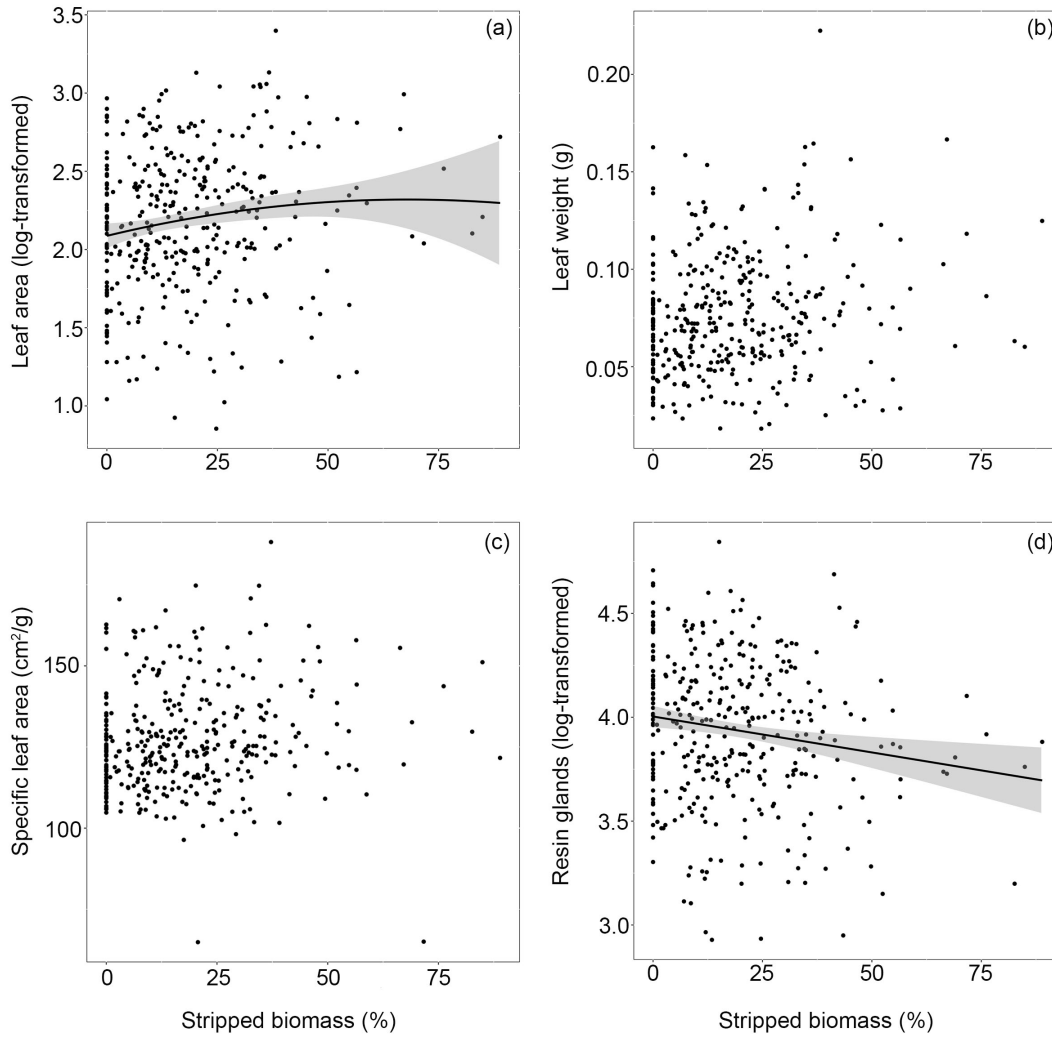


Figure 3.4. Bivariate relationships between the leaf stripping treatment and leaf and resin gland variables. Points represent individual Alaskan paper birch saplings ($n = 360$). Black lines, with standard error grey shading, represent significant relationships. Note the different y-axes scales.

3.3.3 Structural equation model

My initial hypothetical model (Figure 3.2) was inconsistent with the data ($p(\chi^2) < 0.05$); however, after removing non-significant pathways and including ecologically meaningful pathways, a good model fit was achieved ($p(\chi^2) = 0.935$, CFI = 1.00, RMSEA < 0.001, n = 343) (Table A3.2). Alaskan paper birch response to leaf stripping was comparable to results from bivariate LME models as woody growth (crown depth and number of long-shoots) and defense (resin gland density) were negatively affected, while average leaf area increased after treatment (Figure 3.5). Woody, architectural, and leaf responses were all positively related to pre-treatment height. Only one significant interaction between woody basal area and past herbivory remained in the final SEM. As woody basal area increased, the magnitude of the positive effect of past herbivory on number of long shoots increased (Table A3.2). In total the model explained 53% of the variation in number of long shoots. The SEM explained 76% of the variation in crown depth, which also included positive effects of past winter herbivory. In contrast, past winter herbivory had a negative effect on resin gland density.

LME models were in general agreement to SEM results, however the more conservative LME approach indicated some pathways included in the SEM were not statistically significant (Table 3.4). For example, leaf area was not affected by local woody basal area and only marginally ($p = 0.069$) affected by the leaf stripping treatment. Similarly, in the LME model, pre-treatment height no longer had an effect on resin gland density. When no past browsing occurred, woody basal area decreased the number of long shoots; however, similar to the SEM results, past browsing progressively increased the number of long shoots as woody basal area increased (Table 3.4).

Table 3.4. Parameter estimates from linear mixed effect models (n = 6) of each log-transformed response variable for comparison to results of the structural equation model.

Response	Explanatory	Estimate	Std. Error	t-value	p-value
Long shoots	Treatment	-0.009	0.002	-3.679	<0.001
	Pre-treatment height	0.012	<0.001	13.309	<0.001
	Past browsing	0.087	0.016	5.508	<0.001
	Woody BA	-0.214	0.054	-3.947	<0.001
	BA*Browsing	0.034	0.013	2.650	0.008
Crown depth	Treatment	-0.003	<0.001	-3.891	<0.001
	Pre-treatment height	0.008	<0.001	23.432	<0.001
	Past browsing	0.018	0.005	3.405	<0.001
	Woody BA	-0.026	0.018	-1.459	0.146
Leaf area	Treatment	0.002	0.001	1.825	0.069
	Pre-treatment height	0.003	<0.001	6.104	<0.001
	Woody BA	-0.013	0.025	-0.542	0.588
Resin glands	Treatment	-0.004	0.001	-3.252	0.001
	Pre-treatment height	<0.001	<0.001	-0.124	0.901
	Past browsing	-0.021	0.007	-3.162	0.002

Note: Woody basal area was mean-centered (as the values of woody basal area were all greater than zero) for meaningful interpretation when the interaction between woody basal area and past browsing was included.

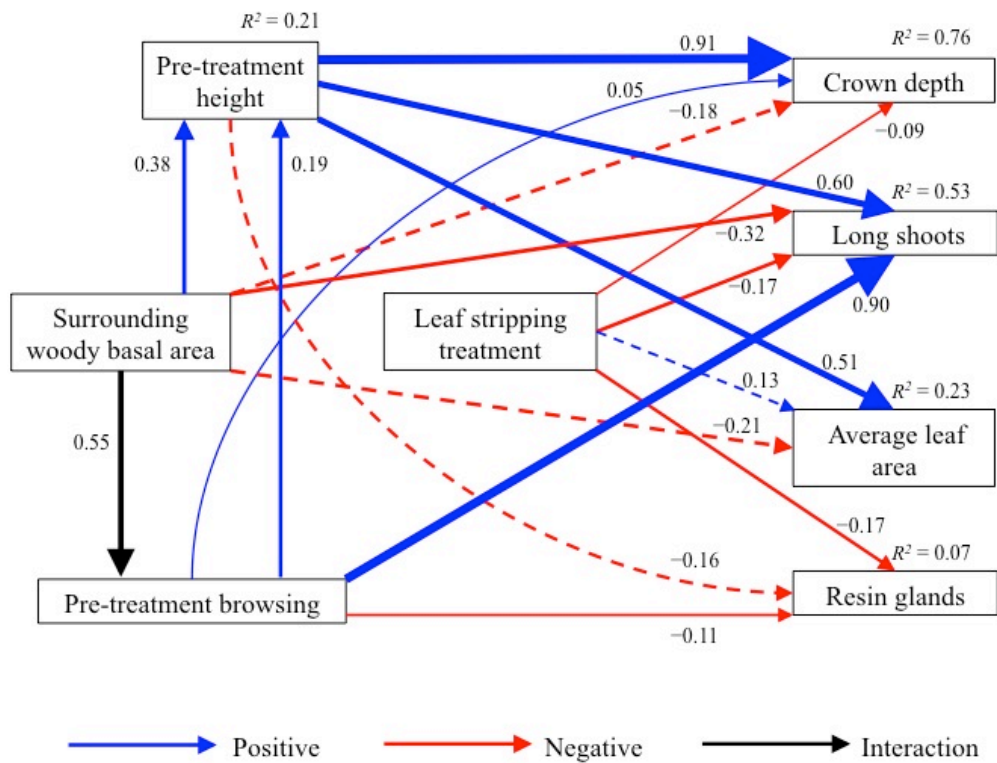


Figure 3.5. Final SEM pathways fit for paper birch responses to leaf stripping treatment and biotic factors. Solid lines represent significant pathways from both the SEM and linear mixed-effect (LME) results. Dashed lines are significant pathways only in the SEM model, which does not account for individuals nested within sites. Blue lines represent positive pathways, while red lines are negative pathways. One significant interaction was found between surrounding woody basal area and pre-treatment browsing for long shoots (black line). Standardized prediction coefficients from the SEM model are included and the magnitude of effects indicated by the width of the arrow. R^2 values are included for all response variable pathways.

3.4 Discussion

My results demonstrate that Alaskan paper birch does not respond to leaf stripping in a manner consistent with the carbon-nutrient balance hypothesis for insect defoliation, as I had hypothesized. I found decreases in woody growth and C-based secondary metabolites while average area per leaf increased, suggesting leaf stripping acts to remove competition for nutrients among remaining shoots (Bryant and Reichardt 1992). Results from my structural equation model emphasize the importance of year-round herbivory as the cumulative effects of summer and winter browsing can initiate the same (e.g., decrease in resin glands) or opposing (e.g., negative and positive in long shoots, respectively) aboveground plant responses. Furthermore, the influence of surrounding vegetation was complex and highlights the potential interactive effects of competition and browsing.

My approach of using a continuous treatment proved beneficial in identifying potential non-linear responses of Alaskan paper birch saplings, but low sample sizes at the highest level of biomass removal makes interpretation tentative. Calculating the proportion of leaf biomass removed by the leaf stripping treatment accounted for inherent differences in tree size and architecture encountered in natural field settings. Mammalian winter browsing often has mixed effects on woody and architectural growth, with decreases in height but increases in shoot growth and lateral branching (Danell et al. 1994). In general, I found leaf stripping had a negative effect on woody and architectural paper birch responses (Figure 3.3), which has been found in previous studies of summer leaf stripping (Bergström and Danell 1995). My results also indicate that leaf stripping reduced the density of resin glands, suggesting an impaired carbon balance (Chapin et al. 1985). I assumed a decrease in resin gland density corresponds to an overall decrease in papyriferic acid concentrations as the two are highly correlated (Rousi et al. 1991, Laitinen et al. 2002). However, it is possible that the production of resin glands (containing C-based secondary metabolites) was a growth cost that competed with leaf production and decreased with the growth of other tissues in favour of nutrient-rich leaves. Thus the decrease I observed in C-based secondary metabolites due to leaf stripping is consistent with predicted outcomes from the CNBH when shoots are damaged by vertebrate browsing (Bryant and Reichardt 1992).

The optimal partitioning theory states that plants should allocate more biomass to the organ that acquires the most limiting resource (Bloom et al. 1985). My leaf stripping treatment

removed photosynthetic material halfway through the growing season, and thus likely reduced whole-plant photosynthetic rates (Zangerl et al. 2002, Schwachtje and Baldwin 2008). Alaskan paper birch saplings responded by allocating resources to increasing average leaf area the following year, at the expense of shoot and resin gland production (Figure 3.5). I found no changes in specific leaf area after leaf stripping, which suggests individuals are not responding by changing their photosynthetic rate and/or whole-plant performance (Poorter et al. 2009). At the minimum, I can conclude birch saplings still compensated for biomass loss through resource allocation to leaves. Although I did not quantify leaf N, increases in average leaf area could indicate an increase in total leaf N content and chlorophyll as this has been found in other birch species (Danell and Huss-Danell 1985, Danell et al. 1985). I suggest two possible mechanisms to explain regrowth in leaves after leaf stripping. First, in my study area vegetation productivity may not be N-limited. For example, negative effects of intense insect defoliation on leaf mass, area, and N content of Alaskan paper birch have been shown to be mitigated by N fertilization (Bryant et al. 1993). Second, the growing points (meristems) removed as a byproduct of leaf stripping decreased the development of new branches and was more detrimental than the loss of nutrients in leaves.

Because study sites varied in growth, density, and productivity of birch and other tree species, the measure of surrounding woody stem basal area encompasses both post-fire site productivity as well as competition. The positive relationship between woody stem basal area and multiple growth, architecture and leaf measurements prior to the treatment (Table 3.3) is likely reflective of site productivity influenced by fire severity. However, I found a negative relationship between woody basal area and long shoot production after leaf stripping (Table 3.4); this suggests the mechanism influencing sapling response was competition as capacity for regrowth has been found to decrease with competition in *Betula pubescens* Ehrh. (Hjálten et al. 1993). Further work should examine both above- and below-ground production after multiple years of leaf stripping to better understand resource allocation and whole plant response. The positive interaction between woody stem basal area and past browsing on long shoots could be due to increased resources aiding birch to increase production of long shoots in response to past browsing. It would be helpful to have direct measures of light, nutrient, and water, availability to tease out the underlying mechanism influencing birch response to leaf stripping under different environmental scenarios.

Summer leaf stripping and previous winter browsing were synergistic or had opposing effects on birch saplings, depending on which plant response variable was examined. Simulated leaf stripping and winter browsing both had negative effects on resin gland density. In contrast, birch that experienced past winter browsing had a positive relationship between browsing and both long shoot production and crown depth. However, it is possible that winter browsing is not driving the positive response in sapling growth but is simply a function of larger trees being browsed more frequently. The effect of moose browsing has been estimated to last from 2-4 years (Danell et al. 1994). Due to the nature of my design, I do not know the frequency of past herbivory; however, I estimate the intensity/frequency to be in the lower range of what birch saplings can tolerate. This is based on: 1) individuals' not displaying severely 'broomed' architecture (common after intense winter browsing), and 2) of the individuals that were browsed, the average proportion of shoots with bite marks was $12.9\% \pm 1.01$ SE (with a maximum of 50%). Given the similar and opposing effects of winter versus summer browsing on birch growth and defense, a study controlling for frequency and intensity of both types of herbivory would provide further insight into the possible range of plant responses to mammalian herbivores.

This study has focused on Alaskan paper birch responses to herbivory, however it is also important to put in context how these changes in plant growth and morphology can in turn affect the herbivore and plant community. A decrease in long shoot production after leaf stripping will decrease the amount of forage available to large herbivores, and perhaps temporarily protect that individual tree from further damage. However a decrease in resin gland density will increase the palatability of remaining long shoots. Furthermore, if an increase in leaf size translates to an increase in nutrients, birch saplings could be more vulnerable to repeated browsing, especially since moose prefer to re-browse new shoots (Danell et al. 1985, Stouter 2008). Leaf stripping did not cause any mortality in my study, which suggests Alaskan paper birch saplings can tolerate high levels of a single event of leaf stripping. With the high density and aboveground annual growth of Alaskan paper birch in the Boundary fire, it is unlikely that even increased damage due to moose re-browsing could alter patterns of succession after large and severe fires in interior Alaska.

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CHAPTER 4: SHORT-TERM TREE RESPONSES TO MAMMAL EXCLOSURES IN POST-FIRE UPLAND FORESTS OF INTERIOR ALASKA

4.1 Introduction

Fire is the dominant landscape-scale disturbance in the boreal forest. In recent decades, fires in the boreal forests of Alaska and Canada have increased in severity, size and frequency (Kasischke and Turetsky 2006, Balshi et al. 2009). More severe fires increase the loss of above- and below-ground organic material (Keeley 2009), exposing mineral soil that is a more suitable seedbed for recruitment of small-seeded, broadleaf tree species (Johnstone et al. 2010). Severe fires in interior Alaska are causing some black spruce (*Picea mariana* (Mill.) B.S.P.) forests to shift to dominance by broadleaf species such as trembling aspen (*Populus tremuloides* Michx.) and Alaskan paper birch (*Betula neoalaskana* Sarg.) during early succession (Johnstone et al. 2010). Landscape modeling predicts these switches from coniferous to broadleaf stands in early post-fire succession will increase the dominance of mature broadleaf stands across the Alaskan boreal forest (Mann et al. 2012). Large herbivores can act as ecosystem engineers, altering forest composition and successional patterns (Côté et al. 2004), and could modify the successional outcomes of fire-induced changes in the forest landscape. Thus, understanding the impacts of mammalian herbivores on early successional, broadleaf forests is crucial for predicting the long-term consequences of changes in fire and climate for Alaskan boreal forests.

Herbivory can be a major driver of change in forest structure and composition during early- and mid-succession once vegetation has established after a disturbance (Côté et al. 2004, Post and Pedersen 2008). Mammalian herbivory on leaves, stems, and twigs can have direct negative effects on tree growth that can lead to mortality (Côté et al. 2004, Wisdom et al. 2006). Stand structure can be altered through a reduction of tall, canopy trees (Chouinard and Filion 2001) or a decrease in tree biomass (McLaren 1996) and is most vulnerable to re-organization when herbivore pressure is high (Tremblay et al. 2007, Gosse et al. 2011). Large herbivores are often selective browsers; important factors determining their diet choice include palatability and nutritive value, as well as the density and frequency of occurrence of potential diet species (Wolff 1978, Bryant and Kuropat 1980). Species with higher relative growth rates often dominate early succession and are generally highly palatable to herbivores (Bryant and Kuropat 1980), which increases the potential for mammalian herbivory to shift composition towards late successional species.

Moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) are dominant vertebrate herbivores in boreal forests; herbivory by these species can impact tree growth and

establishment, and thereby influence successional patterns (Thompson et al. 1992, Olnes and Kielland 2016, Conway and Johnstone 2017). On floodplains of interior Alaska, moose and snowshoe hare have been found to alter species-specific patterns of tree recruitment and growth and accelerate the rate of primary succession (Kielland and Bryant 1998, Kielland et al. 2006, Chapin et al. 2016). The influence of mammalian herbivores in upland forests could be different than on the floodplains due to differences in successional dynamics, available forage, and habitat use. Successional dynamics can be substantially influenced by the abundance of biological legacies (Turner et al. 1998). Stronger biological legacies during secondary succession compared to primary succession could mean a faster pace of succession, and thus a shorter period where the system is vulnerable to the effects of herbivores. Moose and snowshoe hare have overlapping diets with a preference for broadleaf trees and willows (*Salix* spp.) (Bryant and Kuropat 1980). Snowshoe hares also feed on black spruce year-round, with almost 40% of their winter diet consisting of spruce needles (Wolff 1978). Fire influences habitat use and selection by large mammals, creating heterogeneity in forest composition and structure at both small and large spatial scales. In interior Alaska, high moose densities have been associated with fires that occurred within the previous 11-30 years (Maier et al. 2005); a mosaic of fire severity can increase the longevity of available moose habitat due to fire effects on species composition and growth rates (Kielland and Brown 2015, Conway and Johnstone 2017). The presence of adequate understory cover drives habitat quality of snowshoe hares (Carreker 1985) and dense black spruce forests in interior Alaska are associated with high densities and survival of snowshoe hares (Feierabend and Kielland 2015). As moose were the driving factor behind increasing the rate of succession on Alaskan floodplains (Kielland and Bryant 1998), determining their role in upland forests will further our understanding of how herbivores shape community dynamics.

My objective for this study was to establish a long-term experiment aimed at assessing how the exclusion of mammalian herbivores affects tree growth and mortality in early post-fire Alaskan boreal forests. Here, I evaluate the short-term responses of three dominant tree species to two years of protection from mammalian herbivores. I set-up six paired exclosure and control plots across a range of early post-fire vegetation composition and density in interior Alaska. Based on palatability, I expected broadleaf species (aspen and birch) to benefit from the exclusion of herbivores (specifically moose) and grow relatively larger than individuals vulnerable to natural browsing in the control plots. A positive response to mammalian exclusion

is expected even in the short-term as saplings can demonstrate growth releases shortly after herbivore damage ceases (Chouinard and Filion 2001, Motta 2003, Vila et al. 2003). In turn, I hypothesized black spruce growth would be lower inside the exclosures compared to control plots due to the increased competition with broadleaf species that were no longer subject to natural herbivory by moose or hare. This research provides information on the short-term responses of broadleaf species when free from mammal herbivory and contributes to our understanding of how large herbivores may drive successional patterns and change in Alaskan upland boreal forests.

4.2 Methods

4.2.1 Study area

Interior Alaska is characterized by a mosaic of boreal forest types, ranging from deciduous hardwood to conifer-dominated stands, that support populations of dominant herbivores such as moose and hare. The region is bounded by the Brooks Range mountains to the north and the Alaska Range to the south. Mean-annual temperatures at the Fairbanks International Airport, in the center of the region, average $-3.1\text{ }^{\circ}\text{C}$ over the period of record (1917-2000) (Hinzman et al. 2006). Precipitation is generally low and decreases from west to east, with a 50-year average for Fairbanks of 287 mm (Hinzman et al. 2006). Common tree species in interior Alaska are black spruce, white spruce (*Picea glauca* (Moench) Voss), trembling aspen, and Alaskan paper birch. Black spruce forests have dominated interior Alaska for ~ 5000 years with an approximate fire cycle of ~ 100 years (Yarie 1981, Lloyd et al. 2006). However, the once stable state of black spruce forests might be shifting, with increases in early dominance of broadleaf species after severe fires (Johnstone et al. 2010).

My study area is approximately 50 km northeast of Fairbanks, Alaska in an area along the Steese highway that experienced widespread burning of mature black spruce forests in 2004. Early regeneration was influenced by fire severity, from severely burned areas dominated by broadleaf species to pure black spruce regeneration in lightly burned areas (Johnstone et al. 2010). Moose densities have increased in interior Alaska since the 1990s, concurrent with fires creating suitable habitat (DuBois 2010). Local moose density in my study area (Game Management Unit 20A) peaked in 2009 with 0.85 moose/km^2 and has since decreased to 0.58 moose/km^2 in 2013 (Alaska Department of Fish and Game 2014). The snowshoe hare cycle last

peaked in interior Alaska between 2008 and 2010, and roadside counts in 2016 show a recent increase in snowshoe hare populations near Fairbanks (Merizon and Carroll 2016).

4.2.2 Experimental design

Long-term sites along the Steese Highway were established in 2005 to monitor patterns of tree establishment and vegetation succession in response to widespread fire in 2004 (Johnstone et al. 2010, Hollingsworth et al. 2013). In 2013, I established six pairs of plots near a subset of the long-term sites, with selection based on accessibility, the homogeneity of vegetation, and a range of broadleaf canopy dominance and relative growth rate. All sites were located within ~3 kilometers of each other. For reference, I used the same site nomenclature of the initial long-term site established through the Joint Fire Science Program. At each site, I established two plots approximately ten meters apart that measured 12.19 x 12.19 meters (40 x 40 feet) and were visually similar in vegetation composition and density. A one meter wide buffer was established around the inside edge of each plot where no measurements were taken. One plot was assigned the treatment (exclusion of large herbivores with a fenced enclosure) and the other a paired control (natural herbivory). Each enclosure was 1.82 m tall and constructed of chain-linked fence panels that prevented access by moose and hare throughout the year.

I measured density of potential canopy tree species (trembling aspen, Alaskan paper birch, and black spruce) as well as willows (*Salix* species) in 2013 in two randomly positioned, parallel belt transects (10 x 1 m) in each enclosure and control plot (Figure 4.1). Density was averaged between the two transects for each plot. I also permanently marked 20 individuals of each tree species to evaluate the impact of herbivory on tree growth and survival over time. In each plot (excluding site BF84), I established two randomly placed line transects spanning the length of the plot. The three closest individuals (one of each species) were then tagged at each one meter mark along the transect. Due to low density of saplings in BF84, I established four transects in each plot; saplings were selected at every two meter mark. I measured height, basal diameter, DBH (when present), and the presence/absence of any historical herbivore damage (winter 2013 and earlier) for each sapling.

In early June 2014 and 2015, I recorded any evidence (# of stems browsed) of herbivory on tagged individuals during the preceding winter. I installed two ThermoChron iButtons (Maxim Integrated Products, San Jose, CA, USA) ~10 cm below the organic layer surface in each plot

and recorded soil temperature for one full year beginning in August 2014. On June 17th 2015, I dug three soil pits in each plot and measured organic layer depth, soil pH, and soil moisture. *In situ* organic layer depth (including layers of dead moss and fibric and humic organic material) and soil pH (of mineral soil) was measured once per pit; soil pH was measured using a pH meter (Hanna Instruments) on a 1:1 dilution with de-ionized water (Roberston et al. 1999). Two soil moisture measurements were taken and averaged using a hand-held moisture probe (Hydro-Sense, Campbell Scientific, Edmonton, AB, Canada) inserted at a 45° angle into the upper 10 cm of mineral soil at each pit. In August of 2014 and 2015, I measured height, basal diameter, crown width (widest part of the crown and perpendicular to that), crown depth, and leaf length (of broadleaf trees) of all saplings. The average of both crown width measurements was used for analyses. The survival of each individual (live or dead) was recorded; for dead individuals, I noted any evidence relating to the cause of mortality (e.g., snowshoe hare browsing, broken apical meristem).

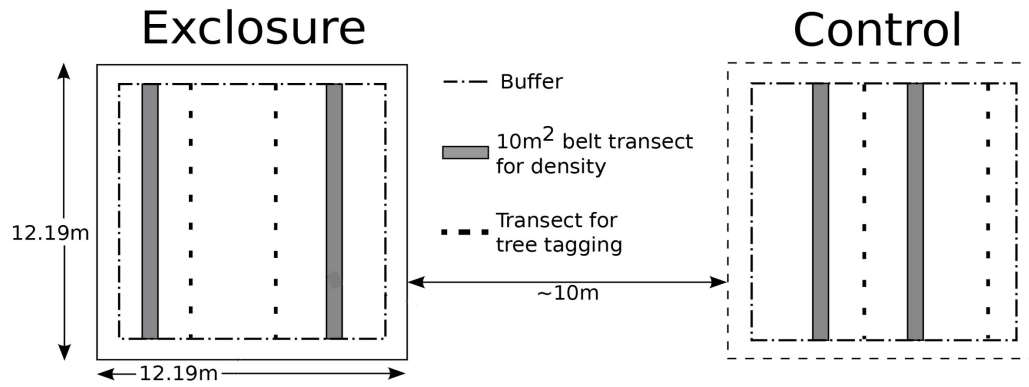


Figure 4.1. Experimental plot design at each site (n = 6) and photograph taken from the inside of an exclosure set-up at site BF72.

4.2.3 Statistical analyses

All analyses were performed using R version 3.3.3 (R Development Core Team 2014). I used linear mixed effect models in the ‘nlme’ package in R (Pinheiro et al. 2016) to determine the effect of exclosures on growth measurements of all three species. All growth response models included fixed effects of treatment (i.e., exclosure), with site as the random term. Thus, site was used as the sample unit ($n = 6$) for analyses; however, graphical representations vary from including individual subsample-level data to site-level data as noted below. I ran models for height, basal diameter, crown width, crown depth, and leaf length (only for broadleaf species). These growth measurements were transformed to represent the proportional change from either 2013 to 2015 (height and basal diameter) or 2014 to 2015 (crown width, depth and leaf length). Proportional change was used to account for differences in initial sapling size and, as an example for height, was calculated as: $2015 \text{ height} - 2013 \text{ height} / 2013 \text{ height} * 100$. Standard error (SE) measurements included in the text (sections 4.3.2 and 4.3.4) are at the site level ($n = 6$).

4.3 Results

4.3.1 Site characteristics

The six sites represent a range in post-fire environmental characteristics (Table 4.1). Organic layer depth was least at BF76, a south-facing site that also had the tallest trees. The thickest organic layer and coldest summer soil temperatures were at BF84, a moist, flat area in a toe-slope position dominated by tussocks that burned at a low severity. Although not statistically tested, soil characteristics were similar between paired control and exclosure plots (Table 4.1) with the exception of lower soil moisture measured in the exclosure in BF76 and BF81; these apparent differences are confounded with low replication due to hitting rocks.

4.3.2 Pre-treatment sapling height and density

Alaskan paper birch was the tallest sapling at all six sites (Table A4.1). Compared to black spruce, density of broadleaf species was higher and more variable across sites (Figure 4.2). Black spruce had the highest density at one site (BF84), with over 3 times greater densities than both broadleaf species (Table A4.2). Density of birch and aspen was similar; however, birch was the tallest species (Figure 4.2). Over half of the tagged aspen were below 50 cm and thus likely protected from moose damage by snow in winter (Figure 4.2). Average density of all *Salix*

species was half that of both broadleaf species ($4.55 /\text{m}^2 \pm 1.47$ (mean \pm SE)) and individuals were mostly single-stemmed and short ($\sim 50\text{cm}$) (personal observation).

Table 4.1. Environmental characteristics (mean \pm SE) of each plot in 2015.

Site	Plot	pH	Organic layer depth (cm)	Moisture ⁺	Summer soil temperature (°C) ^Ψ
BF72	Control	3.7 \pm 0.1	6.5 \pm 0.8	29.9 ^a	6.7
	Exclosure	3.2 \pm 0.1	9.0 \pm 3.0	29.6 ^a	7.2
BF76	Control	3.5 \pm 0.2	2.8 \pm 0.4	14.7 ^b	6.2
	Exclosure	3.2 \pm 0.0	5.0 \pm 1.3	3.0 ^c	7.3
BF77	Control	3.7 \pm 0.1	9.0 \pm 0.8	45.9 ^a	7.8
	Exclosure	3.7 \pm 0.1	8.7 \pm 0.4	40.7 ^a	7.4
BF81	Control	4.5 \pm 0.1	3.8 \pm 1.6	42.8 ^b	6.4
	Exclosure	4.4 \pm 0.2	3.7 \pm 0.6	25.9 ^c	7.4
BF84	Control	3.9 \pm 0.2	12.8 \pm 4.2	47.1 ^a	4.0
	Exclosure	4.0 \pm 0.1	16.8 \pm 1.0	47.1 ^a	4.8
BF86	Control	4.1 \pm 0.1	5.8 \pm 1.4	25.2 ^a	6.8
	Exclosure	4.3 \pm 0.1	8.5 \pm 1.2	25.8 ^a	7.4

Note:

+ Sample size for moisture varied from n = 3 (denoted by ^a), n = 2 (denoted by ^b), n = 1 (denoted by ^c) due to surrounding rocks in soil pits.

Ψ Summer soil temperatures are the average of growing season temperatures (May – August).

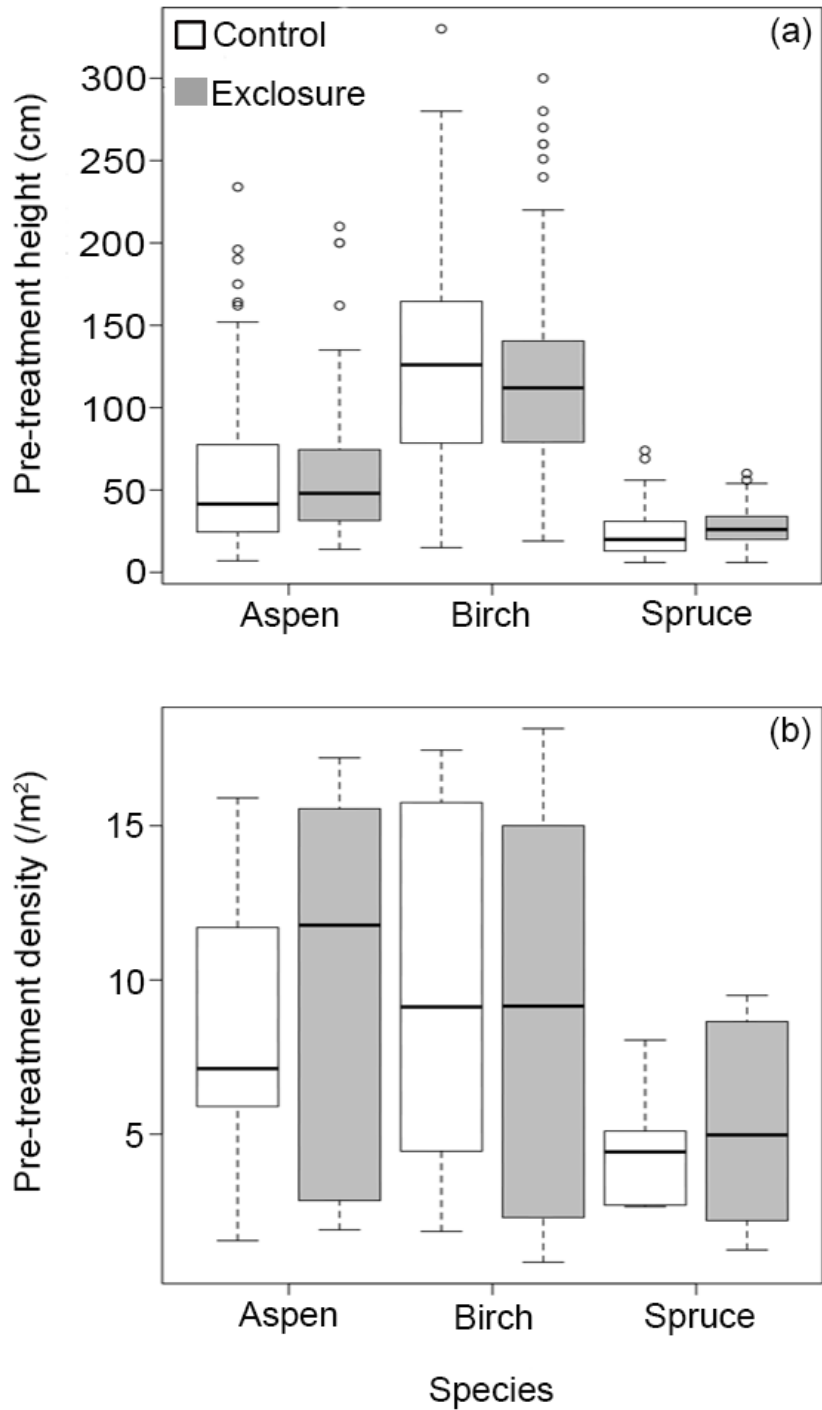


Figure 4.2. Pre-treatment height (a) and density (b) of each tree species in control (white) and exclosure (grey) plots. Pre-treatment height includes data from all tagged individuals ($n = 120$) where density is the average from two belt transects at each plot ($n = 6$). Boxes encompass 25-75% quantiles of the data, while whiskers encompass 5-95%. Outliers are shown as dots, and the median is indicated by the black horizontal line.

4.3.3 *Browsing on, and survival of, saplings*

Birch saplings experienced the highest occurrences of pre-treatment browsing compared to aspen and black spruce. Before exclosures were set-up, approximately double the number of birch saplings were browsed compared to aspen (Figure 4.3). I observed no browsing inside exclosures once they were set-up. Browsing on spruce was low, with only two individuals damaged prior to 2014 and one individual browsed in a control plot in 2015; all browsing on spruce was from snowshoe hares. Less than 10% of aspen individuals in control plots were browsed in the winters of 2014 and 2015. Whereas over 35% of birch saplings in control plots were browsed in the winter of 2014, but only ~10% were browsed during the 2015 winter (Figure 4.3). The majority (n = 195; 95%) of winter browsing was from moose.

Survivorship was high for all three species (Figure 4.4). Fewer aspen saplings survived in the control plots compared to exclosures (Figure 4.4); however, aspen mortality did occur in both control and exclosure plots. Of the aspen saplings that died, two individuals in control plots had been browsed the previous winter by a snowshoe hare. No birch saplings died within exclosure plots over the course of my experiment (Figure 4.4). A total of five birch in control plots died; two of the dead individuals had been browsed the past winter by a snowshoe hare. Lastly, one spruce sapling died during the study, in an exclosure.

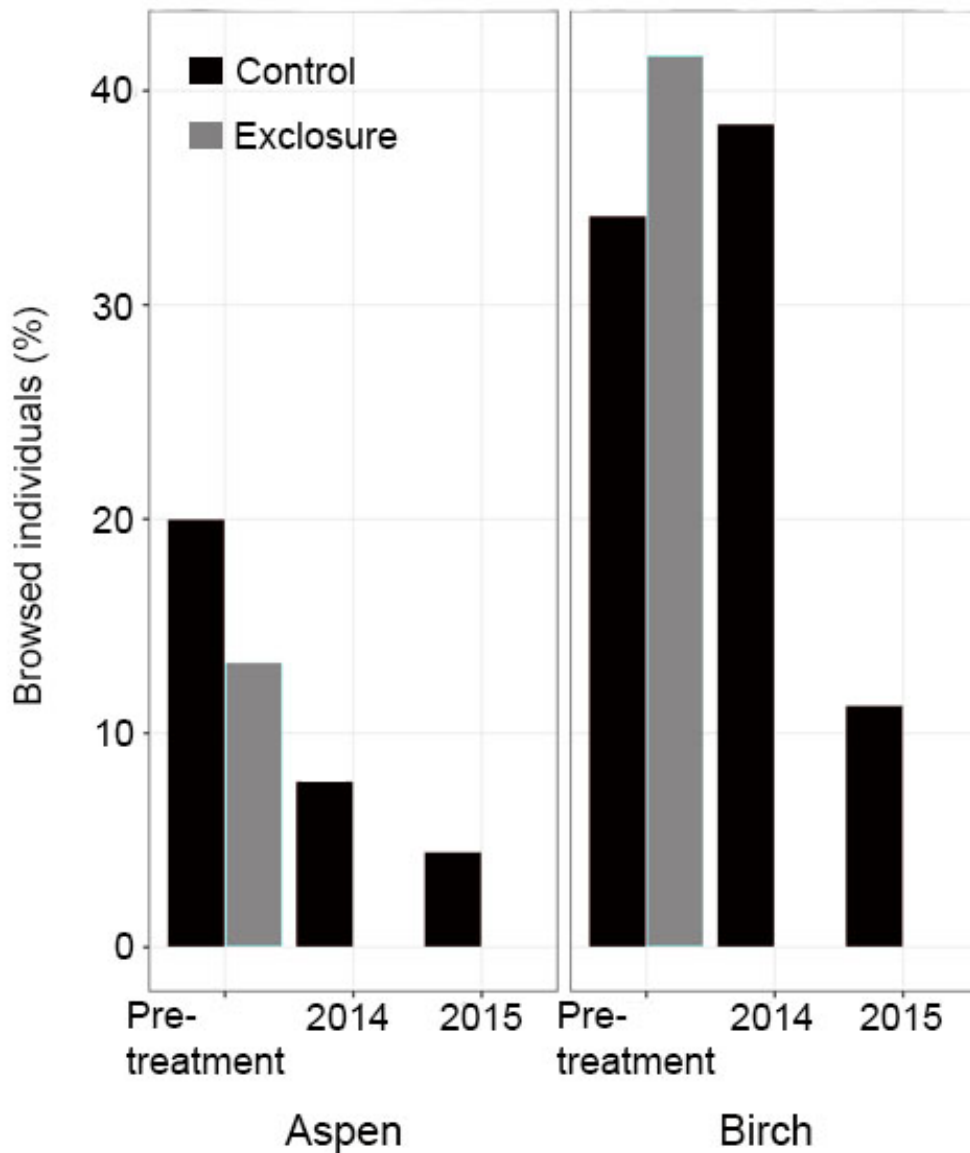


Figure 4.3. Cumulative total (%) of broadleaf saplings (across all sites) that experienced winter browsing (by either moose or snowshoe hare) in either control (n = 120) or exclosure plots (n = 120). Pre-treatment includes all evidence of browsing (2005 – 2013) before exclosures were erected. No evidence of browsing was observed inside the exclosures in 2014 or 2015.

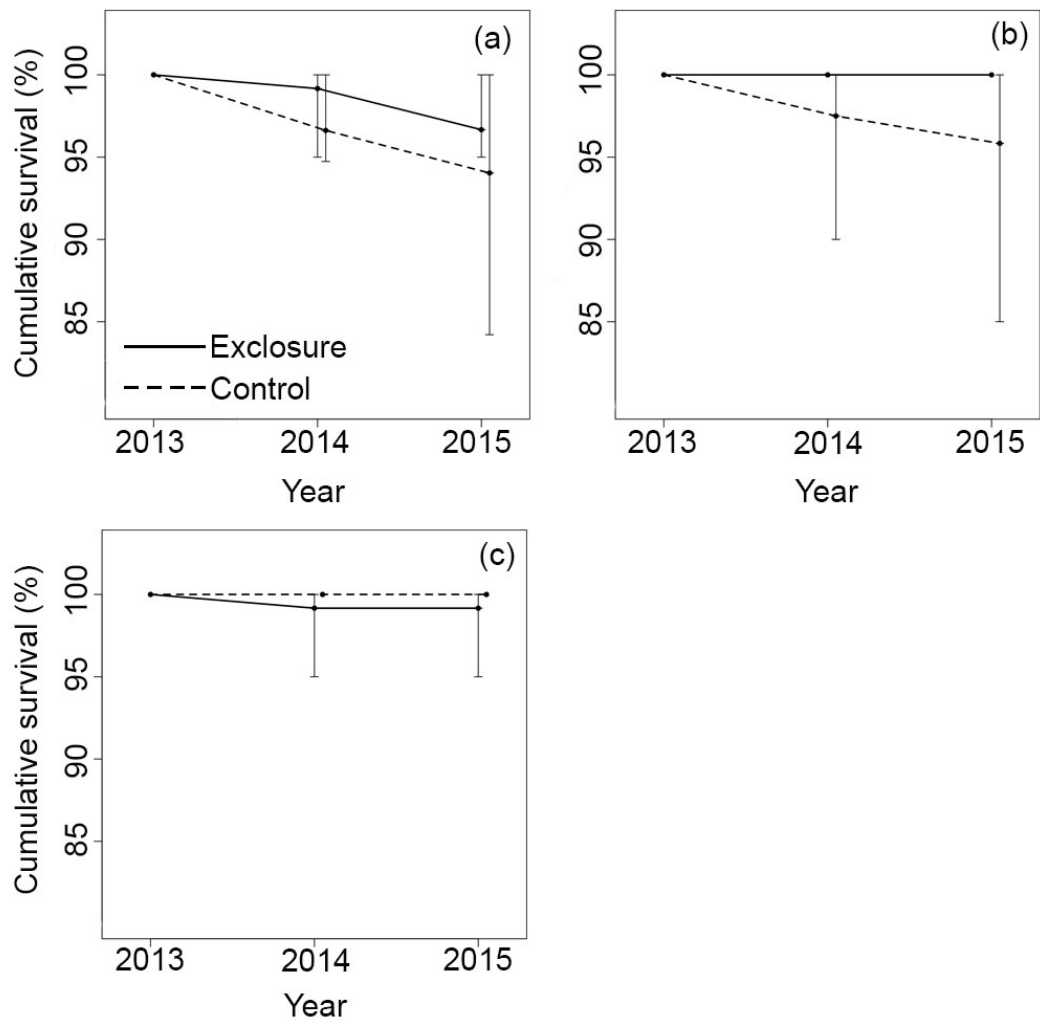


Figure 4.4. Cumulative survival (%) of aspen (a), birch (b), and spruce (c) in all control (dashed line) and exclosure (solid line) plots. Error bars represent the minimum and maximum of cumulative survival across sites (n = 6).

4.3.4 *Effect of mammalian exclusion*

Two years after set-up, exclosures had neutral, positive, or negative effects on proportional sapling growth (i.e., % of growth relative to initial growth measure), depending on the species (Figure 4.5). I found no effect of exclosures on aspen growth; however, aspen saplings had marginally smaller basal diameters inside exclosures (Table 4.2). Birch saplings were taller inside exclosures, where they grew by 42.1% (± 9.5 SE) compared to 27.2% in control plots (± 8.5) (Table 4.2). Inside the exclosures, birch saplings also had proportionally longer leaves compared to control plots (Table 4.2). In contrast, black spruce saplings increased growth over time more in the control plots than the exclosures. Black spruce height increased by 60.7% ± 18.9 in control plots compared to 38.7% ± 10.1 in the exclosures, and spruce stems grew 84.6% ± 10.3 thicker in controls while growing only 54.1% ± 6.6 thicker inside the exclosures (Table 4.2). None of the tree species showed significant changes in crown architecture in response to the exclosure treatment.

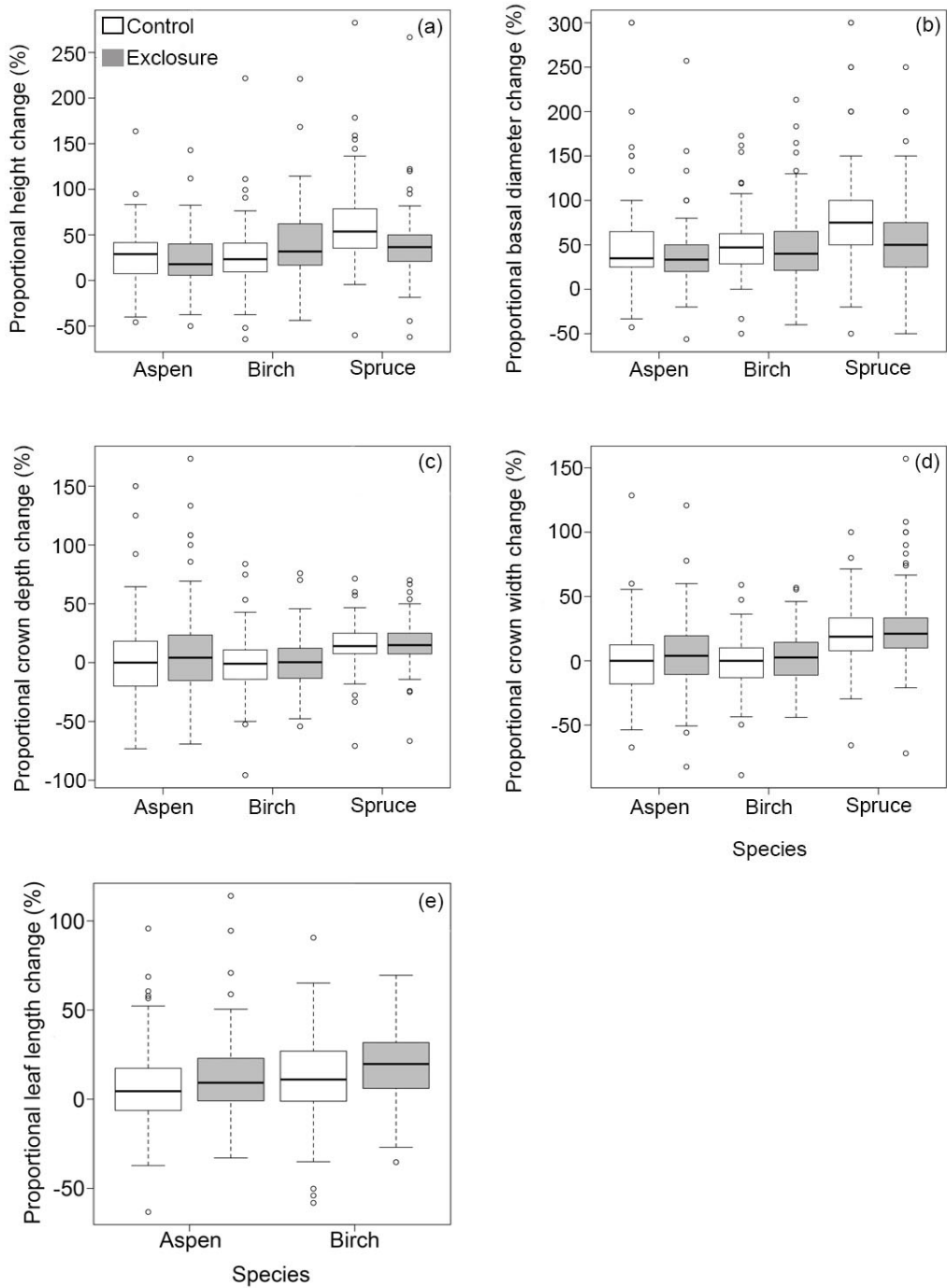


Figure 4.5. Proportional growth responses of trembling aspen, Alaskan paper birch, and black spruce in control (white) and exclosure (grey) plots ($n = 120$ per species). Proportional growth was calculated as the total growth divided by the initial growth measurement. For height and basal diameter total growth was from 2013 to 2015 and for crown and leaf measurements it was from 2014 to 2015. Treatment effects can be assessed by comparing the white and grey boxes within a species; statistical significance of treatment effects is given in Table 4.2.

Table 4.2. Parameter estimates from linear mixed effect models^ψ assessing the effect of the enclosure treatment on proportional growth response^φ of trembling aspen, Alaskan paper birch, and black spruce saplings.

Response variable	Value	Std. Error	t-value	P-value
Aspen				
Height	-3.346	3.833	-0.873	0.384
Basal diameter	-11.202	5.886	-1.903	0.058
Crown depth	6.278	4.776	1.314	0.190
Crown width	5.986	3.526	1.698	0.091
Leaf length	3.915	2.829	1.384	0.168
Birch				
Height	15.499	3.860	4.016	<0.001
Basal diameter	-0.126	4.443	-0.028	0.978
Crown depth	2.258	2.685	0.961	0.337
Crown width	4.394	2.505	1.754	0.081
Leaf length	7.373	2.420	3.047	0.003
Spruce				
Height	-21.961	4.762	-4.612	<0.001
Basal diameter	-30.468	7.140	-4.267	<0.001
Crown depth	0.427	2.258	0.189	0.850
Crown width	4.592	3.336	1.377	0.170

Note: ^ψ Linear mixed effect models were run using the ‘nlme’ package in R and the following code: lme(Response Variable ~ Treatment, random = ~1|Site)

^φ Proportional growth was calculated as: 2015 growth – 2013 growth/2013 growth * 100 for height and basal diameter, and 2015 growth – 2014 growth/2014 growth * 100 for crown and leaf measurements.

4.4 Discussion

Alaskan paper birch responded quickly to herbivore exclusion with increased height and leaf growth just two years after the exclosures were established. Moose were the dominant herbivore at all six sites with the majority (95%) of browsing damage coming from moose. Trembling aspen and Alaskan paper birch are both more palatable to moose than black spruce (Bryant and Kuropat 1980); however, only birch saplings benefited from being inside exclosures. Thus, palatability to herbivores was not the best predictor of responses to the exclosure treatment. Instead, the relative position of each tree species within the dominance hierarchy best predicted growth responses to herbivore exclusion. Birch and aspen were found in similar densities; however, birch was the tallest species and browsed the most before the study began. Thus, the order of positive, neutral and negative responses corresponds to species dominance and frequency of occurrence in my study area: birch, aspen, and black spruce, respectively.

In forests where moose are the predominant herbivore, the rate of succession has been both hastened or reversed due to damage by moose (Davidson 1993, Persson et al. 2005, McLaren et al. 2009). My study supports observational work (Conway and Johnstone 2017) that moose alter the rate of growth in Alaskan post-fire forests. Conway and Johnstone (2017) found that severe moose browsing can slow the rate of aspen height growth by 10 years, while no direct or indirect effects were observed on black spruce growth. The results presented here suggest an inverse relationship of broadleaf versus black spruce growth that is mediated by preferential herbivory on the dominant species. However, whole plant growth for black spruce could have been maintained within the exclosures as I did not measure belowground plant responses. Birch that have been released from herbivory inside exclosures could also be acquiring disproportionately more resources, primarily light, which decreases resource availability for understory conifers. For example, taller broadleaf trees in 11 year old boreal stands have negative effects on neighbouring conifers (Simard and Sachs 2004). Furthermore, I detected lower rates of black spruce height and basal diameter growth, but no differences in crown width inside and outside exclosures. White spruce has been reported to decrease in height, but not lateral growth (i.e., crown width) under increasing levels of shade (Sims et al. 1990). Direct measurements of light availability inside and outside exclosures would help tease out the underlying mechanism driving reduced aboveground black spruce growth under the birch canopy.

My study found increases in height occurred inside and outside the exclosures, with birch saplings growing ~15% taller (42 versus 27% inside and outside, respectively) after two years of herbivore protection. I used the average pre-experiment height of 123 cm and average proportional annual growth rate of 13 and 21%, for control and exclosure plots, respectively, to predict when birch will reach three meters in height (a safe height from moose (Lord 2008, Seaton et al. 2011)). Birch saplings inside exclosures are projected to reach three meters in height five years after being protected from herbivores. Birch saplings subjected to natural herbivory would take an additional three years to reach a safe height from moose. Presumably, once birch in control plots reach three meters, individuals would have comparable growth rates to individuals inside exclosures (Conway and Johnstone 2017). Thus, the difference of three years for birch in control plots to reach three meters does not seem substantial enough to affect canopy dominance of mature sites; this is until black spruce is considered. When birch in control plots are projected to be safe from herbivores (eight years after the start of my experiment), black spruce are estimated to be 60% of birch height (210 versus 338 cm for spruce and birch, respectively). Alternatively, after eight years inside exclosures black spruce will be less than 20% the size of birch. Although birch is likely to dominate the canopy of post-fire sites, moose could enable black spruce to more quickly reach a co-dominant status in a mixed broadleaf-conifer canopy. However, the growth and co-dominance of black spruce could also be influenced by snowshoe hares reinforcing broadleaf dominance while targeting black spruce (Olnes and Kielland 2016).

Long-term studies of forest growth and succession are crucial as short-term and long-term results can be contradictory (Chapin et al. 2016). The duration of my study did not allow for observations of larger ecosystem processes that can be altered with the presence of large herbivores due to direct and indirect effects (Persson et al. 2000). Selective browsing often results in a shift in the canopy composition towards increased dominance of unbrowsed species (McInnes et al. 1992, Kielland and Bryant 1998). I found lower survivorship rates in aspen and birch compared to spruce; however, survivorship was still high for all three species. It is possible that soil conditions were optimal for initial broadleaf establishment but could benefit black spruce shallow rooting growth in the long-term (LeBarron 1945). I have established 1x1 m sub-plots in all exclosure and control plots to further monitor changes in potential canopy composition. With a longer duration of mammalian exclusion, indirect impacts of herbivores on

ecosystem processes through trampling, defecation and urination (McKendrick et al. 1980, Persson et al. 2000, Rooney and Waller 2003), or an increase in the density of alder (Kielland et al. 2006) could become more apparent. For example, moose can depress soil N availability through trampling (Pastor et al. 1998), whereas the contribution of nutrients from feces and urine to plants and microbes could cause significant fertilization effects at small scales (Hobbs 1996). I did observe evidence of moose trampling in control plots as many birch saplings had broken branches. The presence of moose could potentially slow the rate of birch growth more than I estimated; however, the density of birch saplings is high enough that birch will still likely dominate the canopy in 10-20 years.

Alaskan paper birch, trembling aspen, and black spruce, the three tree species that could potentially dominate the forest canopy, responded to exclosures in a manner consistent with their relative biomass and density in these upland post-fire boreal forests. Birch was the most dominant species based on density and height before exclosures were erected and experienced the highest occurrence of past browsing. This is indicative of birch either being the preferred diet species for moose in the area or the total off-take of birch was simply a function of availability. Birch responded quickly to being safe from herbivores, and increased height at an annual rate of 8% more than individuals in control plots. Spruce aboveground growth was lower inside exclosures, potentially due to birch acquiring proportionally more resources. Herbivore activity may increase the rate at which black spruce saplings can grow and reach co-dominant status with broadleaf species in a mixed-wood forest, depending on whether they are browsed by snowshoe hares at some time before they reach hare escapement height (Olnes and Kielland 2016). Overall, these results suggest that the natural rate of moose browsing in control plots in these sites is unlikely to switch the projected canopy dominance of Alaskan paper birch in post-fire areas.

4.5 References

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CHAPTER 5: CONCLUSIONS

5.1 Synthesis of main results and directions for future work

Historically, upland black spruce (*Picea mariana*) stands followed self-replacement successional trajectories with forests recovering to a composition similar to the pre-fire vegetation (Viereck et al. 1983). Changes in the fire regime have stimulated increases in broadleaf recruitment at many sites, suggesting these stands may have shifted to a broadleaf-dominated successional trajectory (Johnstone et al. 2010). Moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) prefer to browse on early successional broadleaf species (Bryant and Kuropat 1980); a shift to more broadleaf-dominated stands could influence large herbivore foraging in interior Alaska. Mammalian browsing has affected successional rates and trajectories in other ecosystems, including the Canadian boreal forest (Bergerud and Manuel 1968, Chouinard and Filion 2005) and Alaskan floodplains (Kielland and Bryant 1998, Angell and Kielland 2009). By determining the response and tolerance of woody species to mammalian browse, we will enhance our ability to predict and understand successional dynamics in early post-fire forests of boreal Alaska.

The effects of herbivores observed in my research appear to be insufficient to alter the successional trajectory of sites with an initial dominance of broadleaf species (generally those that burned severely) resulting in a broadleaf-dominated mature canopy. Natural winter browsing from moose in 19 year-old forests has slowed the rate of vertical growth of trembling aspen (*Populus tremuloides*) saplings and trees in high severity sites by ~10 years (Chapter 2). Trembling aspen growth in low severity sites was not affected by moose browsing, due to a compensatory response or low levels of browsing pressure. I did not detect any direct or indirect effects of moose browsing on black spruce (Chapter 2) leading me to conclude that even in the face of herbivore damage, trembling aspen will eventually dominate the mature canopy in high severity sites.

I found species-specific responses to mammalian exclusion based on the dominance hierarchy and palatability of the three dominant saplings that I studied (Chapter 4). Trembling aspen height, basal diameter, crown size and leaf size were similar inside and outside of the exclosures. Alaskan paper birch (*Betula neoalaskana*), the dominant species at the study sites, increased annual height growth by 8% when safe from herbivores, compared to individuals outside the exclosure. Black spruce, the most unpalatable species of the three, was shorter and narrower inside exclosures. Unlike my observational work in Chapter 2, results from Chapter 4

suggest a possible shift in competitive ability and advantage when herbivores are excluded. I hypothesized the increase in vertical growth of Alaskan paper birch saplings allowed these individuals to acquire disproportionately more resources, primarily light (Simard and Sachs 2004), which negatively affected black spruce growth. Results suggest that Alaskan paper birch would dominate the mature canopy slightly faster (estimate of 3 years) if natural mammalian herbivory was absent in early post-fire sites (Chapter 4); however, I predict the tolerance and escape strategies that birch have displayed will enable their survival and eventual dominance under the current rates of herbivory following high severity fires.

Continued monitoring of tree growth in the sites where I erected exclosure and control plots would provide information on indirect effects of herbivores as well as capture multiple hare cycles, which could alter tree growth predictions. It is not uncommon to find different treatment effects when comparing short-term (5 years) and long-term (25 years) observations (Chapin et al. 2016). Although I hypothesized birch saplings disproportionately increased acquisition of light when protected from herbivory, it is possible that black spruce saplings aboveground growth decreased only because resources were allocated to belowground growth (Gower et al. 2001). Understanding the mechanism behind decreased spruce growth would allow us to better predict if the initial results I observed are going to be maintained in the long-term and/or would occur across a broader landscape. Episodes of high snowshoe hare density and browsing could further slow down Alaskan paper birch and/or decrease black spruce growth and co-dominance. Furthermore, monitoring nutrient cycling and litter fall inside and outside exclosures will be important as these factors can reinforce feedbacks (Kielland et al. 1997, Kielland and Bryant 1998).

I found under-compensation with regards to height, crown, and shoot growth, and carbon-based defense production of Alaskan paper birch one year after I simulated summer leaf stripping by moose (Chapter 3). These patterns suggest that both escape and resistance strategies were compromised by simulated herbivory. These results came as a surprise, as I expected birch saplings to have a surplus of carbohydrates due to the loss of nutrients in leaves and thus produce an increase of carbon-based defenses (Bryant and Reichardt 1992). My results suggest: 1) the loss of meristems needed to support development of new branches was more detrimental than the loss of leaves, and 2) resin gland production was outcompeted by leaf production, and in turn a decrease in C-based secondary metabolites occurred.

Future experimental work should explicitly study winter browsing by both moose and snowshoe hare to understand how the frequency and intensity of browsing may alter forest growth and community composition. I estimate the natural winter browsing I encountered at early successional sites (Chapters 3 and 4) was low to medium frequency and/or intensity. This estimate is based on my observation that few trees displayed a broomed architecture, a low proportion of total twigs were eaten on individuals (Chapter 3), and less than half the total proportion of individuals had evidence of browse (Chapter 4). Furthermore, the majority of winter browse that I encountered was from moose, and thus my study was unable to incorporate the effects of snowshoe hares in upland forests. Getting a better understanding of when trees are most vulnerable to herbivore effects of reduced growth, mortality, and thus shifts in forest composition can only be accomplished by studying all mammalian herbivores across a range of possible browse damage. Furthermore, I recommend that future work is focused on forest succession and composition in two areas that are most vulnerable to mammal damage: 1) early successional sites burned with low- to mid-severity that have comparable densities and growth of conifer and broadleaf species after fire, and 2) smaller high severity burn patches. Early successional areas that have comparably lower growth and density of broadleaf trees will be more sensitive to herbivore impacts; however, this vulnerability will depend on the interaction between strength of dominance hierarchies and the density of herbivores on the landscape. If herbivores are present during this vulnerable stage, there is the potential of mammalian herbivory to shift the competitive advantage towards black spruce to maintain either a co-dominant broadleaf-conifer or a conifer-dominated canopy. Similarly in smaller burn patches, vegetation dynamics has the potential to be controlled by high densities of mammalian herbivores as total food biomass will be lower in small patches.

5.2 Mammalian herbivory across ecosystems

The effect of mammalian herbivores in forested ecosystems is highly variable, likely due to: (1) the characteristics of the disturbance that initiated succession; (2) the herbivory regime (e.g., severity, frequency, season, and type of damage as well as the herbivore species and density); (3) the duration of the study (Wisdom et al. 2006). These three considerations translate into varying results in a tree's capacity to regrow and employ defense strategies following

browsing (Gill 1992). My three data chapters filled in key information that was missing about the importance of these three considerations in early post-fire forests of interior Alaska.

Furthermore, these three points contribute to my prediction that mammalian herbivores will not cause a change in successional trajectory and forest composition in upland forests that experienced large and severe fires in Alaska, unlike in many other forested ecosystems (Brandner et al. 1990, Thompson and Curran 1993, Côté et al. 2004, Hidding et al. 2013).

Mammalian herbivores in interior Alaska will have different effects on primary and secondary boreal forest succession. The role of mammalian herbivores on primary succession has been studied over decades on the floodplains of interior Alaska (Walker et al. 1986, Kielland and Bryant 1998, Ruess et al. 1998, Butler and Kielland 2008, Olnes and Kielland 2016). Moose accelerated the rate of succession in Alaskan floodplains because preferential browsing reduced growth and increased mortality of early successional willows (*Salix* spp.), which led to earlier dominance of mid-successional alder (*Alnus tenuifolia*) (Kielland and Bryant 1998, Butler and Kielland 2008). However, snowshoe hares have retarded succession in the same system by browsing on white spruce (*Picea glauca*) (Olnes and Kielland 2016), which typically dominates late successional forests on the floodplains (Mann et al. 1995). I found that upland Alaskan forests are impacted in a similar fashion, in that trembling aspen growth was slowed by 10 years (Chapter 2) when heavily browsed and Alaskan paper birch growth increased when safe from herbivores (Chapter 4). Although the rate of succession can be slowed during both primary and secondary succession, two main differences between canopy structure and the environment are present. First, strong biological legacies present during secondary succession could mean a faster pace of succession and a shorter time frame the system is vulnerable to herbivory. Second, fire can create a heterogeneous environment, even across small areas. Variations in fire severity has caused extreme differences in post-fire establishment and growth that can be maintained for close to two decades (Johnstone et al. 2010, Shenoy et al. 2011). Broadleaf densities in pre-fire black spruce stands that burned severely are high, growth is rapid (escape strategy) and heavily browsed individuals still persist (tolerance strategy) (Chapters 2 and 4).

There are many factors included under the herbivory regime category that are important drivers of tree response to browse damage. Trees that were browsed more frequently and severely had slower growth rates (Chapters 2 and 3). This is common across forested landscapes (Danell et al. 1994, Puettmann and Saunders 2001, Jones et al. 2009, Champagne et al. 2012) and

is often due to a depletion of carbohydrate reserves (Jameson 1963). The season that browsing occurs in will have varying consequences for a tree's ability to respond to damage in interior Alaska (Chapter 3). In general, I found Alaskan paper birch saplings responded positively to natural winter browsing and negatively to summer leaf stripping, which is similar to *Betula pendula* and *Betula pubescens* (Danell et al., 1994). My findings help to improve our predictive ability of how plants will respond to browsing damage; when frequency, severity and seasonality of browsing are accounted for, generalized predictions applicable across broad groups of trees (broadleaf versus coniferous) can be formed. Considering results from my thesis, I have provided predictions for different outcomes in pre-fire black spruce upland boreal Alaska based on fire severity (and the associated effects on broadleaf density and relative growth rate) and browsing intensity (Figure 5.1). High severity fires are expected to have mature forests dominated by broadleaf species; however, high browsing intensity will extend the length of time until dominance is reached (Figure 5.1). I predict a mixed broadleaf-conifer mature forest when browsing is intense after a low severity fire, with the potential of changing herbivore regimes increasing conifer dominance after low intensity browse as well (Figure 5.1).

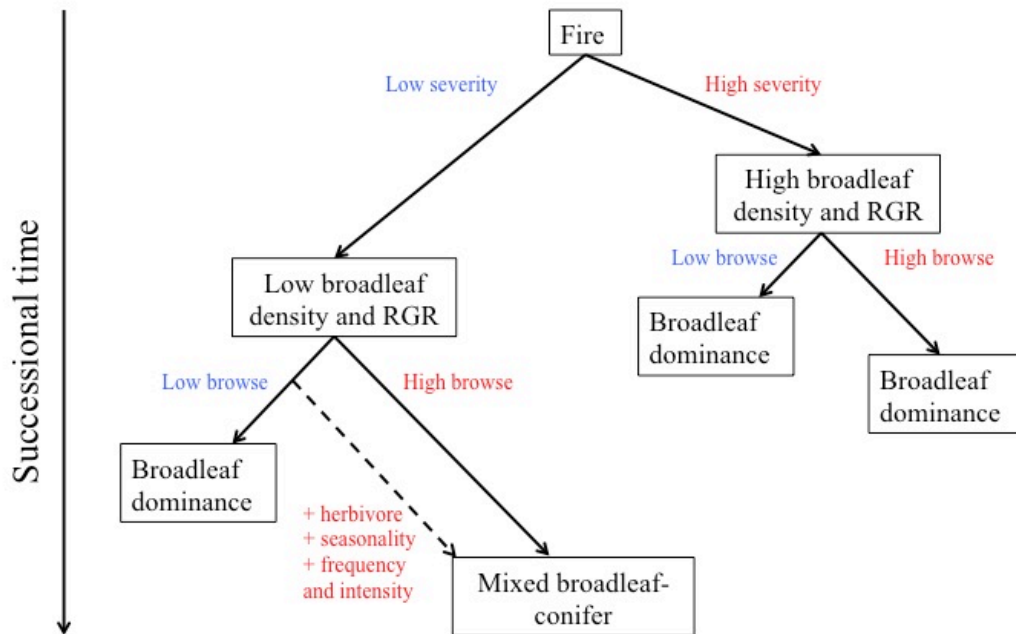


Figure 5.1 Predictions of how fire severity, initial forest composition, and herbivory intensity may interact to drive different outcomes of mature forest canopies in upland boreal forests of Alaska. Here I am predicting only for mature forests that were pre-fire black spruce dominated. Predictions of the effects of fire on the density and relative growth rate (RGR) of broadleaf species are based on previous work in boreal upland forests of interior Alaska (Johnstone and Kasischke 2005, Johnstone et al. 2010, Shenoy et al. 2011). Variations in herbivory intensity are associated with the intensity and frequency of moose browsing, which will vary with moose density on the landscape. Dashed lines indicate the potential for an alternate mature canopy, based on increases in species of herbivore, season of browse, and increases in both frequency and intensity. The length of time each of these four forests will reach a mature canopy is along the x-axis, with low severity fire and high browsing rates taking the longest time.

Forest succession happens over a long time-scale, from multiple decades to centuries and thus is difficult to study in a short time frame. However, long-term studies are vital to document changes in forest composition and succession; for example, Newfoundland (Bergerud and Manuel 1968, Thompson and Curran 1993, Gosse et al. 2011) and Isle Royale (Snyder and Janke 1976, Brandner et al. 1990, Pastor et al. 1993) both have extensive long-term data on the effects of moose on forest dynamics. Studies in Isle Royale and Newfoundland have focused on how moose have altered the composition and growth of two mature canopy species: balsam fir (*Abies balsamea*) and white spruce; balsam fir is preferred by moose (Brandner et al. 1990, Thompson and Curran 1993). In Newfoundland, predictions made in 1968 of an altered forest structure due to reduced balsam fir growth and survival and increased dominance of white spruce (Bergerud and Manuel 1968) were confirmed 27 years later (Thompson and Curran 1993). On Isle Royale, the growth of balsam fir saplings have been suppressed since moose populations peaked in the 1920s (Brandner et al. 1990). In interior Alaska, moose densities have been comparable to densities in Isle Royale and Newfoundland and yet I project that sites with initial high densities and growth rates of trembling aspen (i.e., high severity burns) (Johnstone et al. 2010, Shenoy et al. 2011) will have a mature canopy of aspen (Chapter 2). I hypothesize across interior Alaska that the higher growth rate and density of broadleaf saplings in severely burned areas (compared to black spruce) will be enough to maintain their dominance and growth into the mature canopy. Herbivores have the potential to further reinforce broadleaf dominance if browsing occurs on black spruce seedlings that are present in the understory. However, only with long-term research can this prediction be tested, hence the establishment of exclosures (Chapter 4).

5.3 Take-home messages

In this thesis, I examined how multiple-tree species respond to mammalian browsing and projected the future potential composition of post-fire forests. The results I have presented throughout this thesis provide baseline knowledge of how trees respond to herbivores across browsing intensities and seasons while considering a range of post-fire environments. Fire drives both initial community assembly and influences the role of herbivores in early- to mid-succession forests. Severely burned areas are an ideal environment for broadleaf trees to colonize and grow quickly; herbivores can slow down the relative growth rate of broadleaf saplings but

will not shift the mature canopy predicted from initial composition (Chapter 2 and 4). Saplings' defense strategies against herbivores are altered and impacted by the intensity and season of browse (Chapter 3). Leaf stripping during summer can be more detrimental than shoot browsing in winter and needs to be considered to understand the response of individuals to herbivore damage. The dominance hierarchy of the early post-fire environment will be essential in predicting if and where herbivores may have the largest potential to impact forest growth and succession (Chapter 4). I predict mammalian herbivores will have the largest impact in co-dominant broadleaf-conifer forests recovering from mid- to low-severity fires; future work should be focused in these vulnerable areas.

5.4 References

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APPENDIX 1: SUPPORTING INFORMATION FOR CHAPTER 2

Table A2.1. Site identification (n = 12) and residual organic layer depths (Johnstone and Kasischke, 2005) following the same nomenclature as historical site data archived online in the BNZ LTER database (<http://www.lter.uaf.edu/data/data-detail/id/100>)

Site ID	Fire severity class	Residual organic layer depth (cm)
94_3	Low	14.3
94_4	Low	11.4
94_7	High	2.8
94_8	Low	6.5
94_11	High	1.2
94_12	Low	11.2
94_15	High	4.0
94_16	Low	5.4
94_17	High	1.4
100	High	0.4
102	Low	19.1
103	High	2.0

Table A2.2. Results from Moran's I test for spatial autocorrelation in height and average basal area increment (BAI) among all sites, and just low and high severity sites.

Comparison	Variable	p-value
All sites	Height	0.134
	BAI	0.292
Low severity	Height	0.752
	BAI	0.214
High severity	Height	0.622
	BAI	0.113

Table A2.3. Random term syntax (using function ‘lme’, in package ‘nlme’ version 3.1-128, in R version 3.3.1) for the best fit model (based on lowest AIC).

Model	Random term syntax
Effect of fire severity and tree species on height and BAI	Random= $\sim 1 + \text{Species} \text{Site}$
Effect of fire severity and browsing on height and BAI of aspen	Random= $\sim 1 + \text{Browsing} \text{Site}$
Effect of 3m threshold and browsing on annual height growth	Random= $\sim 1 + \text{Browsing} \text{Site} / \text{Individual ID}$

Table A2.4. Parameter estimates from linear mixed effect models estimating the effects of species (aspen and spruce) and fire severity (low and high) on tree height (log transformed) and average basal area increment (BAI) (log transformed) with a random intercept and slope for species effects within sites.

Height					
Within-level	Fixed effects	Estimate	Standard error	t-statistic	p-value
Low severity	Species	0.005	0.152	0.035	0.973
High severity		1.646	0.152	10.826	<0.001
Aspen	Fire severity	0.873	0.158	5.520	<0.001
Spruce		-0.767	0.104	-7.350	<0.001
Species*severity		1.640	0.215	7.631	<0.001
Average BAI					
Low severity	Species	-0.348	0.218	-1.594	0.112
High severity		2.304	0.218	10.554	<0.001
Aspen	Fire severity	1.102	0.234	4.705	<0.001
Spruce		-1.550	0.204	-7.590	<0.001
Species*severity		2.652	0.309	8.591	<0.001

Note: *Reference levels were set to low severity and spruce, thus fixed effects are comparing: aspen to spruce, within each level of fire severity, and high severity to low severity, within each level of species. The interaction term (Species*severity) has reference levels set to low severity and black spruce.

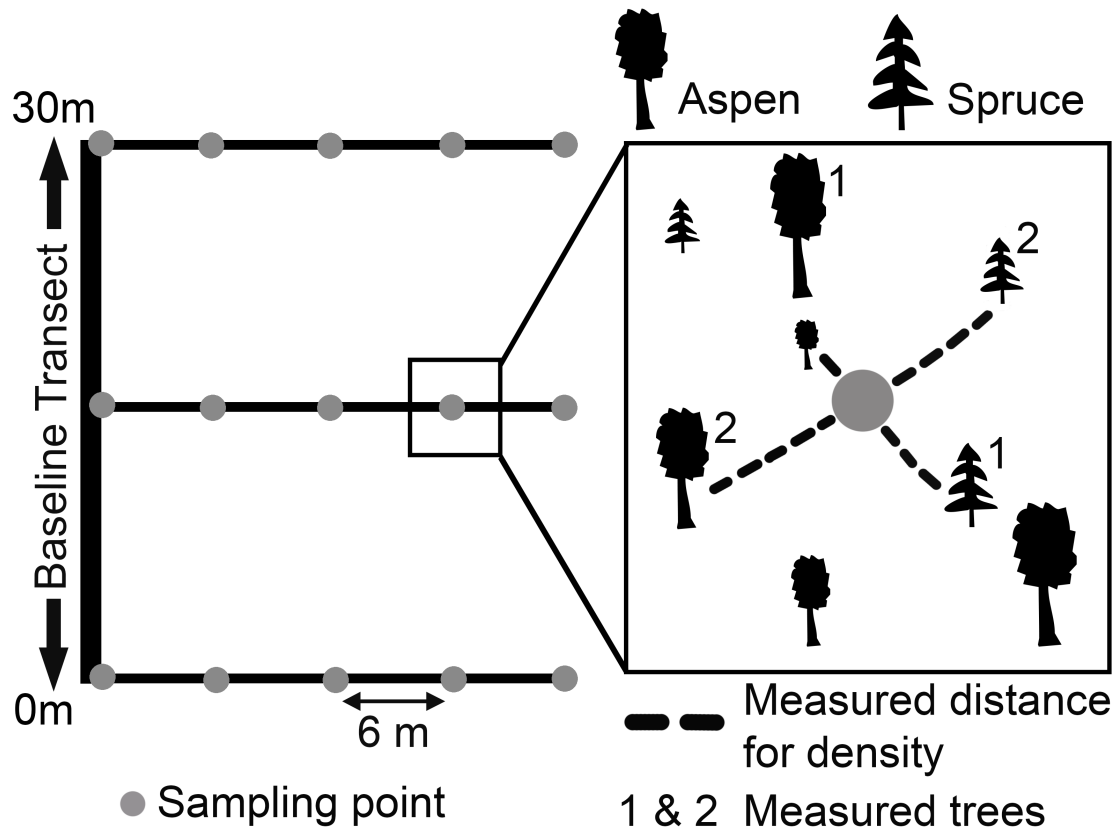


Figure A2.1. Field sampling design for each site ($n = 12$) sampled in the 1994 Hajdukovich Creek fire in interior Alaska. Five sampling points, 6 meters apart, were located on each parallel transect ($n = 3$) extending from the baseline transect. At each sampling point, we measured the distance (dashed line) to the two closest trembling aspen and black spruce. If either of the aspen appeared to arise from recent asexual spread, we collected measurements from the next closest aspen (1, 2). Measurements included height, diameter at breast height, and intensity of past browse. We also collected stem disks at the tree base and at 3 meters, when tree height was >3 m.

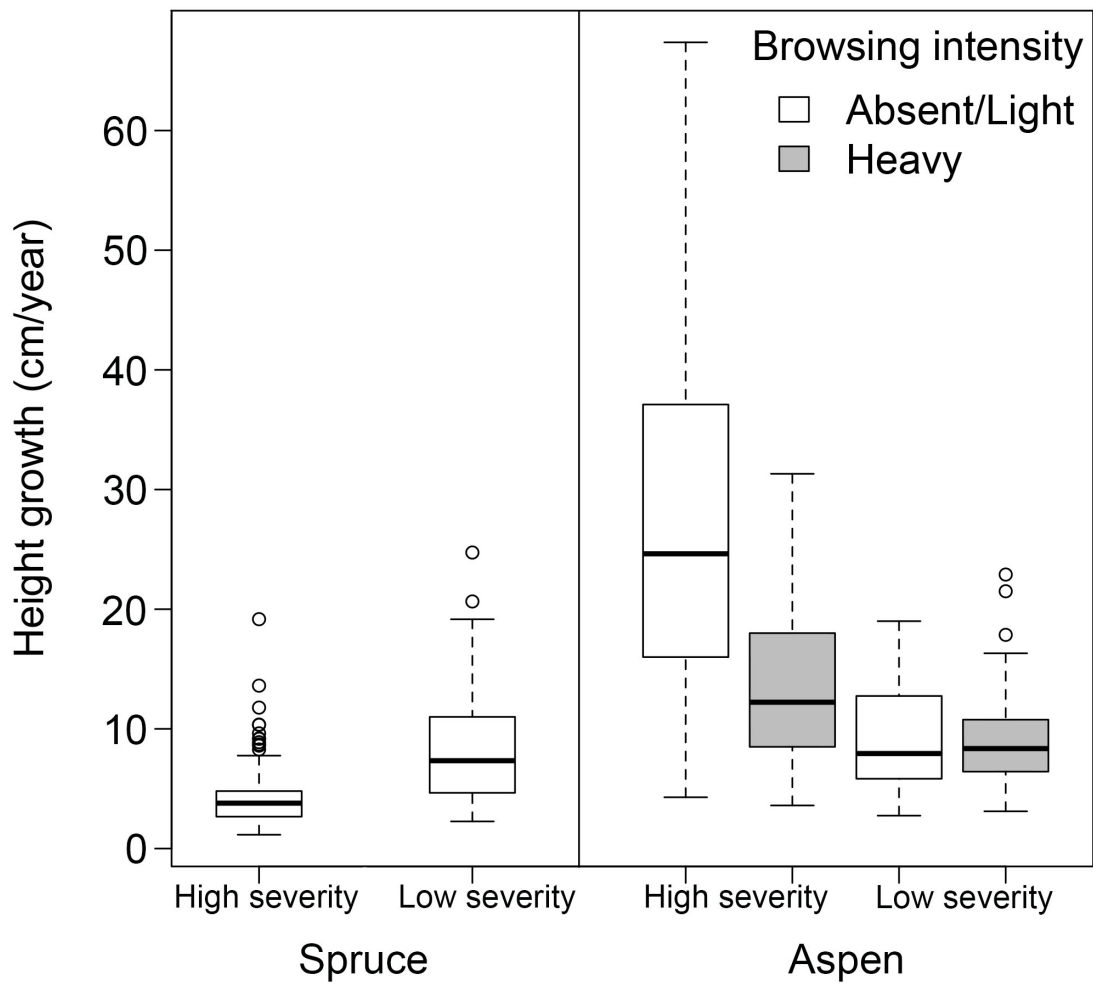


Figure A2.2. Average annual height growth (cm/year) for black spruce and lightly and heavily browsed aspen in low and high fire severity sites. Spruce never experienced heavy browsing intensity thus only growth rates for absent/light browsing are presented.

APPENDIX 2: SUPPORTING INFORMATION FOR CHAPTER 3

Table A3.1. Parameter estimates from linear mixed effect models^a, with a random intercept of site, of the leaf stripping treatment effect on response variables.

Response	Fixed effect	Value	Standard error	t-value	p-value
Growth responses					
Δ Height	Treatment	-71.245	12.469	-5.714	<0.001
	Treatment ²	36.022	12.052	2.989	0.003
Δ Basal	Treatment	0.173	0.060	2.861	0.005
Δ Short shoots	Treatment	-0.455	0.143	-3.182	0.002
Δ Long shoots ^b	Treatment	-4.806	0.829	-5.796	<0.001
	Treatment ²	2.281	0.804	2.837	0.005
Architectural responses					
Δ Crown depth	Treatment	-88.503	18.632	-4.750	<0.001
	Treatment ²	47.351	17.976	2.634	0.009
Δ Crown width	Treatment	-0.352	0.054	-6.545	<0.001
Leaf responses					
Leaf area ^b	Treatment	0.409	0.370	1.104	0.270
	Treatment ²	-0.844	0.357	-2.362	0.019
Leaf weight	Treatment	0.040	0.026	1.518	0.130
	Treatment ²	-0.048	0.025	-1.905	0.058
Specific leaf area	Treatment	0.061	0.050	1.235	0.218
Defense responses					
Resin glands ^b	Treatment	-0.003	0.001	-2.931	0.004

Note:

^a The 'nlme' package in R version 3.3.1 was used to run linear mixed effect models with the code: lme(Response variable ~ Treatment, random = ~1|Site)

^b Response variables were log-transformed to meet assumptions of normality.

Table A3.2. Results from the structural equation model investigating trade-offs between Alaskan paper birch growth and defense after leaf stripping.

Response	Explanatory	Estimate	Std. Error	z-value	p-value	Stand.
Long shoots	Treatment	-0.138	0.028	-4.895	<0.001	-0.172
	Pre-treatment height	1.663	0.123	13.529	<0.001	0.597
	Past browsing	1.269	0.377	3.366	0.001	0.895
	Woody BA	-0.367	0.049	-7.459	<0.001	-0.322
	BA*Browsing	0.144	0.069	2.088	0.037	0.548
Crown depth	Treatment	-0.037	0.012	-3.140	0.002	-0.092
	Pre-treatment height	1.299	0.041	31.458	<0.001	0.913
	Past browsing	0.037	0.018	2.081	0.037	0.052
	Woody BA	-0.106	0.018	-5.776	<0.001	-0.182
Leaf area	Treatment	0.044	0.017	2.652	0.008	0.125
	Pre-treatment height	0.632	0.063	10.031	<0.001	0.513
	Woody BA	-0.105	0.029	-3.601	<0.001	-0.208
Resin glands	Treatment	-0.047	0.014	-3.303	0.001	-0.168
	Pre-treatment height	-0.153	0.054	-2.824	0.005	-0.157
	Past browsing	-0.056	0.028	-1.987	0.047	-0.114
Pre-treatment height	Past browsing	0.095	0.020	4.633	<0.001	0.187
	Woody BA	0.157	0.022	7.188	<0.001	0.383

APPENDIX 3: SUPPORTING INFORMATION FOR CHAPTER 4

Table A4.1. Pre-treatment height of trembling aspen, Alaskan paper birch, and black spruce in each plot.

Site	Plot	Aspen pre-treatment height (cm)	Birch pre-treatment height (cm)	Spruce pre-treatment height (cm)
BF72	Control	61.5 ± 8.9	124.4 ± 8.0	15.2 ± 1.7
BF72	Exclosure	63.9 ± 9.2	111.3 ± 8.1	23.7 ± 2.8
BF76	Control	115.8 ± 12.3	196.8 ± 13.6	24.4 ± 3.7
BF76	Exclosure	103.4 ± 10.7	173.0 ± 14.9	28.7 ± 2.7
BF77	Control	62.6 ± 5.7	117.2 ± 8.1	23.5 ± 2.9
BF77	Exclosure	55.9 ± 5.9	103.6 ± 8.2	24.4 ± 2.8
BF81	Control	31.8 ± 3.6	124.7 ± 12.1	19.5 ± 2.5
BF81	Exclosure	39.7 ± 4.4	114.4 ± 11.3	25.5 ± 2.0
BF84	Control	26.0 ± 1.9	66.8 ± 7.4	26.7 ± 2.8
BF84	Exclosure	41.7 ± 4.4	77.5 ± 6.7	34.3 ± 2.7
BF86	Control	36.3 ± 6.3	134.0 ± 13.5	33.0 ± 3.3
BF86	Exclosure	45.2 ± 4.1	137.1 ± 12.8	31.9 ± 2.8

Table A4.2. Pre-treatment density of trembling aspen, Alaskan paper birch, and black spruce in each plot.

Site	Plot	Aspen density (/m ²)	Birch density (/m ²)	Spruce density (/m ²)
BF72	Control	5.90	5.75	2.70
BF72	Exclosure	2.85	3.35	1.25
BF76	Control	7.50	4.45	3.85
BF76	Exclosure	10.50	2.30	2.95
BF79	Control	15.90	15.75	2.65
BF79	Exclosure	17.20	18.15	2.20
BF82	Control	6.75	12.50	5.00
BF82	Exclosure	13.05	14.95	8.65
BF84	Control	1.55	1.85	5.10
BF84	Exclosure	1.90	0.85	7.00
BF86	Control	11.70	17.45	8.05
BF86	Exclosure	15.55	15.00	9.50