ROLE OF FIRE SEVERITY IN CONTROLLING PATTERNS OF STAND DOMINANCE FOLLOWING WILDFIRE IN BOREAL FORESTS

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Abstract

Global trends of climate warming have been particularly pronounced in northern latitudes, and have been linked to an intensification of the fire regime in arctic and boreal ecosystems. Increases in fire frequency, extent, and severity that have been observed over the past several decades are expected to continue under a warming climate. Severe fires can drastically reduce or remove the deep organic layers that accumulate in mature black spruce forests. Extensive studies in the boreal forests of interior Alaska and Canada have shown that parts of the landscape that undergo severe burning provide favorable seedbeds for the recruitment of deciduous tree seedlings, and thereby reduce the relative abundance of coniferous seedling recruitment in these areas shortly after fire. The persistence of deciduous species such as aspen beyond the seedling recruitment and establishment stage is as yet relatively unknown. To address this knowledge gap, I asked the question: is increased deciduous recruitment observed in severely burned areas transient, or does it result in persistent changes in stand composition later in succession? I examined changes in relative dominance patterns of aspen and black spruce that had occurred between 8 and 14 years post-fire along an organic layer depth gradient within a single burn. I found that patterns of relative species dominance established shortly after fire persisted into the second decade of succession, resulting in productive aspen-dominated stands in severely burned areas with shallow organic layers, and black spruce dominated stands in lightly burned areas with deep organic layers. These patterns of stand dominance in relation to post-fire organic layer depth were also observed in several other burns in the region. Therefore, deep burning fires are likely to result in a persistent shift from black spruce to aspen dominance in severely burned parts of the boreal forest. In order to understand how variation in organic layer depth is driving these alternate successional pathways, I measured nutrient uptake rates of aspen and spruce in severely and lightly burned sites within a single burn. I also examined relationships between post-fire organic layer depth and a suite of soil variables, and evaluated the relative importance of these soil variables in explaining variation in stand level aspen biomass, spruce biomass, and the relative dominance of aspen vs. spruce. I found that variations in post-fire organic layer depth result in contrasting soil environments, with soils in shallow organic layer sites being warmer, drier, and more alkaline than soils in deep organic layer sites. Variations in aspen biomass and aspen: spruce biomass were largely being driven by substrate conditions, whereas stand level spruce biomass was less sensitive to these same variations in soil conditions. Nutrient uptake rates of both aspen and spruce were higher in severely burned areas with shallow organic layers, but the differences between species were magnified by stand biomass patterns in relation to post-fire organic layer depth. My results suggest that the positive effects of soil conditions associated with mineral soil substrates extend well beyond the initial seedling recruitment phase, and may continue to influence aspen growth rates into the second decade of succession resulting in the differential patterns of biomass accumulation and stand dominance in relation to post-fire organic layer depth. With the predicted increase in fire severity and shortening of the fire cycle, the proportion of aspen dominated stands on the landscape is likely to increase, which will incur substantial changes in ecosystem function (e.g., land-atmosphere energy exchange, C and N storage, nutrient cycling, net primary productivity, and wildlife habitat quality) compared to the current forests dominated by conifers.

Table of Contents

Page

List of Figures

List of Tables

List of Appendices

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Chapter 1.

General Introduction

In recent decades, an intensification of the fire regime (in particular the more frequent occurrence of large severe fires) has been observed concomitantly with climate change in northern boreal forests (Kasischke and Turetsky 2006, Kasischke et al. 2010, Calef et al. 2015). Changes in the thickness of the soil organic layer remaining following fire have been linked to a shift in forest canopy dominance from coniferous to deciduous species in severely burned parts of the boreal forest (Johnstone and Kasischke 2005, Johnstone et al. 2010). Canopy composition in northern boreal forests is important as this biome covers a vast land surface, has strong impacts on global climate-feedbacks and stores large amounts of carbon in vegetation and soils (Chapin et al. 2000). Black spruce (*Picea mariana*) forests are the dominant forest type in the boreal region of interior Alaska. The alternative canopy species that dominate some forest stands are white spruce (*Picea glauca*), and deciduous trees such as paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). Black spruce and deciduous forests fundamentally differ with respect to productivity, and their effects on land-atmosphere energy exchange, nutrient cycling and ecosystem carbon storage. For instance, black spruce forests absorb more incoming radiation thereby decreasing the land surface albedo and warming the land surface (Bonan et al. 1992). Deciduous forests on the other hand increase the land surface albedo over 2-fold compared to coniferous forests (Chapin et al. 2000, Baldocchi et al. 2000), and have much higher rates of evapotranspiration thereby resulting in a net cooling effect on climate (Randerson et al. 2006). Black spruce forests accumulate deep organic layers due to the recalcitrant nature of the litter and low soil temperatures that impede decomposition (Van Cleve et al. 1983). Deciduous forests tend not to accumulate deep organic layers due to warmer soil temperatures and high decomposability of the leaf litter, and thereby store less carbon in their soils than black spruce forests (Gower et al. 1997, Alexander and Mack 2015). Carbon storage and land-atmosphere energy exchange at high latitudes are both crucial components of climate feedbacks that may result in a net cooling or warming of the atmosphere. Because black spruce and deciduous forests have sharply contrasting effects on both of these processes, the species identity of the dominant canopy cover on the landscape is of critical importance in studies of ecosystem responses to climate change at northern latitudes.

Canopy composition and tree productivity in boreal forests of interior Alaska are tightly linked to landscape characteristics (e.g. slope, aspect and drainage) and associated soil conditions. For instance, north-facing slopes receive limited insolation, have cold, poorly drained soils with underlying permafrost, and are largely occupied by black spruce stands with a moss understory (Viereck et al. 1983, Van Cleve et al. 1991). South facing aspects on the other hand have warmer soils, are well drained, and tend to be occupied by deciduous trees and white spruce (Viereck et al. 1983). Fire is an inseparable component of boreal forest dynamics (Lynch et al. 2002), and the fire return interval has historically been 40 – 200 years in many parts of these forests (Yarie 1981, Dyrness et al. 1986). Hence in addition to landscape controls, fire history plays a major role in shaping the distribution of stand types and ages on the landscape. Black spruce stands typically follow a post-fire successional trajectory of self-replacement in which the pre-fire stand dominant replaces itself shortly after fire (Van Cleve et al. 1983, Fastie et al. 2003). Alternatively these stands may follow a successional sequence from shrubs to deciduous trees to black spruce dominance over a period of about 100 years (Black and Bliss 1978, Chapin et al. 2006). The boreal forest landscape in interior Alaska is therefore a mosaic of canopy types that are typically determined by landscape characteristics and fire history.

Climate warming over the past several decades and associated changes in weather patterns have been linked to an intensification of fire regimes (increased fire frequency, longer fire seasons, greater area burned and increased fire severity) in the western United States (Westerling et al. 2006, Kasischke et al. 2010), in northern boreal forests (Stocks et al. 1998, Kasischke and Turetsky 2006, Soja et al. 2007, Krawchuk et al. 2009*a*, Kasischke et al. 2010), and on a global scale (Krawchuk et al. 2009*b*, Moritz et al. 2012). Fires in interior Alaska are usually stand-replacing due to the high flammability of black spruce (Rupp et al. 2002), whereas combustion of the surface organic layer is variable (Kasischke et al. 2000, Miyanishi and Johnson 2002, Kane et al. 2007). Increased fire activity (area burned, lengthened fire season and increased fire severity) in this region is resulting in the surface organic layer being combusted to greater depths (Turetsky et al. 2011), exposing the underlying mineral soil in severely burned areas. This increase in organic layer consumption has been linked to increased occurrence of deciduous regeneration on the landscape (Johnstone and Kasischke 2005, Johnstone et al. 2010, Beck et al. 2011), and could lead to a prolonged shift in vegetation dominance in parts of the boreal forest.

There is abundant evidence that mineral soil seedbeds are preferable to thick organic layer mats for the germination and establishment of many boreal tree species (Chrosciewicz 1974, Zasada et al. 1983, Charron and Greene 2002, Greene et al. 2004, Jayen et al. 2006, Johnstone and Chapin 2006). The removal of the porous organic layer by fire lifts moisture constraints on germination and seedling growth, as well as physical constraints to the growth of emerging germinants (Charron and Greene 2002, Johnstone and Chapin 2006). Variations in the depth of the residual organic layer remaining after fire have been linked to patterns of post-fire seedling recruitment, with high levels of deciduous seedlings recruiting and establishing in severely burned areas with shallow organic layers, and black spruce dominating the post-fire seedling cohort in sites with deep organic layers (Johnstone and Kasischke 2005, Johnstone and Chapin 2006, Greene et al. 2007). Most studies that have examined patterns of vegetation composition following fire have focused on the seedling recruitment and establishment stage that occurs during the initial phase of post-fire succession (e.g. Charron and Greene 2002, Johnstone and Chapin 2006, Kemball et al. 2006). Although it is well established that post-fire organic layer depth influences patterns of species dominance at the recruitment stage, little is known about whether these patterns persist and impact stand composition and productivity later on in succession. In particular, a gap remains in our understanding of whether effects of post-fire organic layer depth are limited to the initial impacts on seedbed quality, or if changes in soil conditions resulting from variations in organic layer depth continue to impact tree growth, canopy composition and productivity over the course of succession.

The overarching goal of my dissertation research is to understand how variation in post-fire organic layer depth influences stand dominance and productivity in early successional forests. In particular I attempt to uncover the main drivers of the observed patterns of aspen stand dominance in severely burned sites versus black spruce dominance in lightly burned sites (Fig.1.1). I conducted this research in the 1994 Hajdukovich Creek burn in interior Alaska. This burn was ideal for the study because 1) the pre-fire vegetation was dominated by black spruce, 2) topography within the burn was relatively uniform, 3) the mineral soil layer consisted predominantly of silt loam overlying sand and gravel deposits, 4) there were large variations in post-fire residual organic layer depth (Kasischke and Johnstone 2005), and 5) studies conducted in this burn in 2002 revealed striking variation in deciduous vs. coniferous seedling dominance in relation to organic layer depth (Johnstone and Kasischke 2005).

In Chapter 2 I examine changes in density and biomass of the dominant canopy species (black spruce and aspen) during the first two decades of succession in the 1994 Hadjukovich Creek burn. I compared patterns of species composition observed 8 years following fire (Johnstone and Kasischke 2005) to measurements taken 14 years post-fire in the same sites, in order to assess whether effects of post-fire organic layer depth on seedling recruitment persist and impact stand productivity later in succession. I then explored whether the relationships between organic layer depth and vegetation composition and density observed in the Hadjukovich Creek burn consistently occurred in other burned black spruce stands in the region. In Chapter 3 I examine effects of fire severity on nutrient supply and inorganic nitrogen uptake rates of aspen and spruce in severely versus lightly burned sites in the Hajdukovich Creek burn. I tested the hypothesis that higher inorganic nitrogen supply rates in severely burned sites and greater nitrogen uptake rates of aspen give it an advantage over spruce, thereby contributing to aspen dominance in these sites. In Chapter 4 I compared the physiological performance of aspen and black spruce in sites with shallow vs. deep organic layers. I went on to investigate the relationships between post-fire organic layer depth and soil environmental conditions (temperature, moisture, pH, decomposition potential and total inorganic nitrogen). To better understand the drivers of the opposing stand dominance patterns in relation to fire severity, I evaluated the relative importance of these soil parameters, and stand density on aspen and spruce biomass, and the relative stand dominance of aspen versus spruce in the second decade of succession.

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1.2 Figures

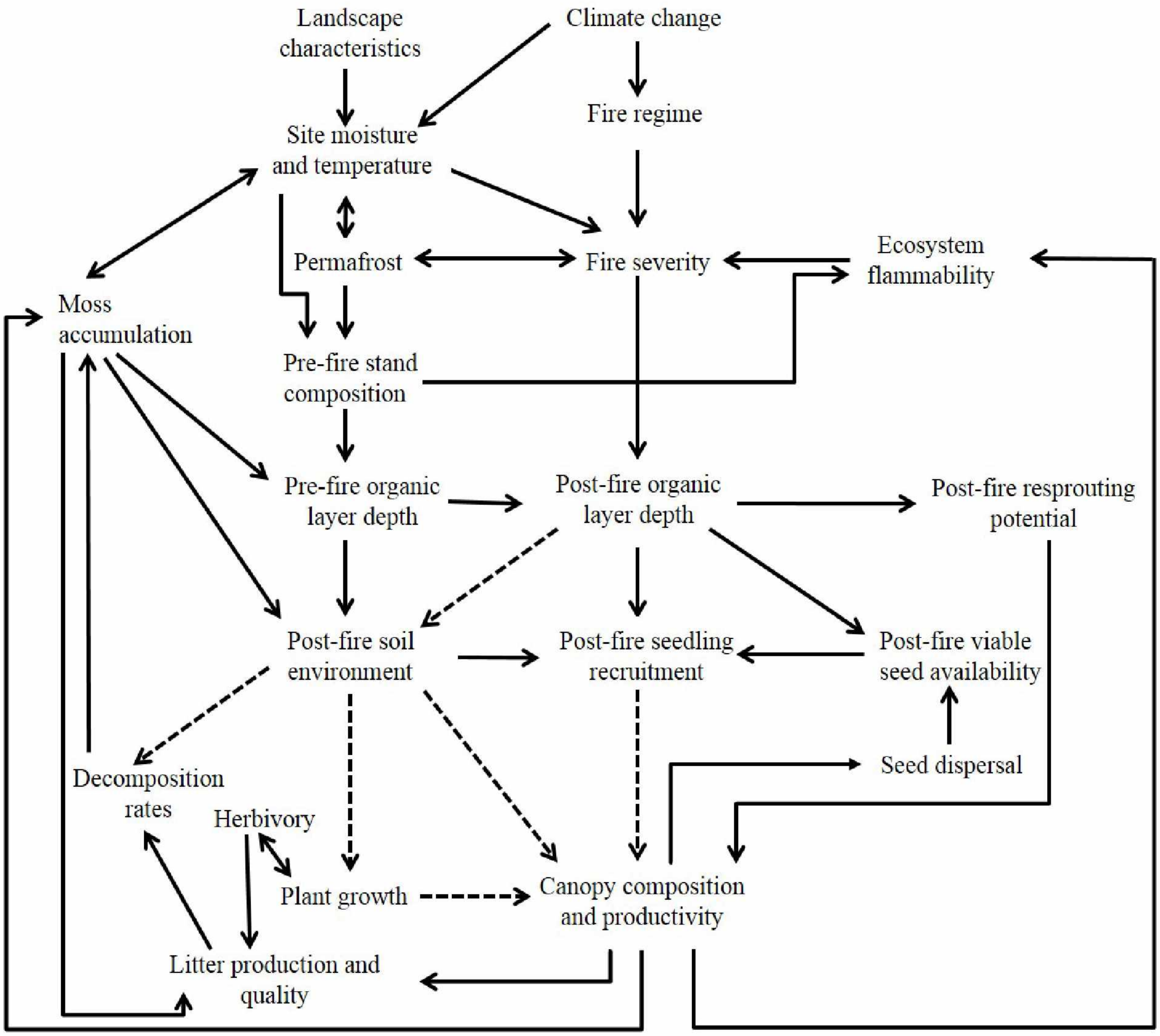

Fig.1.1 Schematic representation of the contextual basis for the research. Broken arrows indicate the linkages addressed in this dissertation.

Chapter 2.

Persistent effects of fire severity on early successional forests in interior Alaska[1]

2.1 Abstract

There has been a recent increase in the frequency and extent of wildfires in interior Alaska, and this trend is predicted to continue under a warming climate. Although less well documented, corresponding increases in fire severity are expected. Previous research from boreal forests in Alaska and western Canada indicate that severe fire promotes the recruitment of deciduous tree species and decreases the relative abundance of black spruce (*Picea mariana*) immediately after fire. Here we extend these observations by (1) examining changes in patterns of aspen and spruce density and biomass that occurred during the first two decades of post-fire succession, and (2) comparing patterns of tree composition in relation to variations in post-fire organic layer depth in four burned black spruce forests in interior Alaska after 10-20 years of succession. We found that initial effects of fire severity on recruitment and establishment of aspen and black spruce were maintained by subsequent effects of organic layer depth and initial plant biomass on plant growth during post-fire succession. The proportional contribution of aspen (*Populus tremuloides*) to total stand biomass remained above 90% during the first and second decades of succession in severely burned sites, while in lightly burned sites the proportional contribution of aspen was reduced due to a 40-fold increase in spruce biomass in these sites. Relationships between organic layer depth and stem density and biomass were consistently negative for aspen, and positive or neutral for black spruce in all four burns. Our results suggest that initial effects of post-fire organic layer depths on deciduous recruitment are likely to translate into a prolonged phase of deciduous dominance during post-fire succession in severely burned stands. This shift in vegetation distribution has important implications for climate-albedo feedbacks, future fire regime, wildlife habitat quality and natural resources for indigenous subsistence activities in interior Alaska.

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[1] Shenoy, A., Johnstone, J.F., Kasischke, E.S., Kielland, K., 2011. Persistent effects of fire severity on early successional forests in interior Alaska. For. Ecol. Manag. 261, 381-390.

2.2 Introduction

Black spruce (*Picea mariana*) forests are the most common forest type of interior Alaska (Van Cleve et al. 1983). Wildfire, being the primary driver of secondary succession in these forests, plays a major role in shaping forest structure and composition (Chapin et al. 2006). Black spruce stands typically follow a post-fire successional trajectory of self-replacement, in which the pre-fire stand dominant replaces itself shortly after fire (Van Cleve et al. 1983). Alternatively, these stands may succeed to an early phase of deciduous tree dominance that may transition back to black spruce about 100 years following fire (Chapin et al. 2006) or be maintained as a deciduous-dominated stand until the next fire (Cumming et al. 2000). Recent observations of increased frequency and extent of fires in interior Alaska (Kasischke and Turetsky 2006, Kasischke et al. 2010) are projected to continue under a warming climate (Flannigan et al. 2005).Statistical relationships between fire size and severity suggest that increases in fire extent are likely to be associated with increases in fire severity, or biomass consumption (Duffy et al. 2007). Fire consumption of the surface organic layer is an important dimension of fire severity in black spruce forests as the total depth of burning influences carbon loss through combustion (Kasischke et al. 2005), and the depth of the residual organic layer affects post-fire processes such as permafrost thaw (Yoshikawa et al. 2003, Kasischke and Johnstone 2005) and vegetation recovery. Although a number of factors control the burning of the surface organic layer in boreal forests, fuel moisture content is a key constraint on combustion (Miyanishi and Johnson 2002). Spatial variations in the moisture content of surface fuels are influenced by site drainage and topography (Harden et al. 2006, Kane et al. 2007) and the species composition and bulk density of the surface fuels (Miyanishi and Johnson 2002, Shetler et al. 2008). These spatial factors interact with annual and seasonal variations in weather and soil thaw depth to influence the patterns of soil organic layer consumption within a particular fire (Wein 1983, Kasischke and Johnstone 2005).

It is well established that mineral soil seedbeds exposed by severe surface fire are favorable for the germination and establishment of a number of boreal tree species (e.g. Chrosciewicz 1974, Zasada et al. 1983, Charron and Greene 2002, Johnstone and Chapin 2006, Greene et al. 2007). Shallow organic layers also support greater above ground tree biomass than deep organic layers (Lecomte et al. 2006). In particular, fire severity is strongly linked to the relative dominance of deciduous versus coniferous species as there is a strong positive relationship between the depth of the residual organic layer and recruitment of small-seeded deciduous trees such as aspen (*Populus tremuloides*) (Johnstone and Kasischke 2005, Johnstone and Chapin 2006, Greene et al. 2007). Initial patterns of species composition and densities established during the first few years of post-fire succession are maintained through decades of stand development (Gutsell and Johnson 2002, Fastie et al. 2003, Johnstone et al. 2004). Therefore, the influence of fire severity on recruitment and establishment is likely to be a critical process in determining later forest composition. Shifts in forest composition from dominance by conifers such as black spruce to deciduous trees are likely to be of regional importance because of effects on land-atmosphere energy exchange (Bonan et al. 1992), nutrient cycling and plant productivity (Chapin 2003, Diaz et al. 2004), and wildlife habitat use (Nelson et al. 2008). Consequently, it is important to understand the mechanisms that favor and maintain deciduous versus coniferous dominated successional trajectories in boreal forests.

Most studies that have investigated patterns of vegetation development in relation to fire severity have focused on the seedling recruitment and establishment phase, during the first few years of post-fire succession (e.g. Charron and Greene 2002, Kemball et al. 2006, Johnstone and Chapin 2006, Johnstone et al. 2010a). A gap remains in our understanding of whether the effects of fire severity on boreal forest communities are solely driven by the response of seedling recruitment to variations in organic layer depths, or are also shaped by subsequent effects of fire on soil conditions that affect the growth of established individuals. Moreover, it is not yet known whether initial effects of post-fire soil organic layer depths on seedling density and biomass will be manifested in patterns of stand productivity for several decades after fire. The maintenance of initial fire severity effects through succession could lead to the development of alternate, persistent cycles of succession at a site. For instance, if deciduous dominance in severely burned parts of the landscape is sustained until the next stand-replacing fire, asexual regeneration is likely to result in the rapid recovery of deciduous dominance after fire (McIntire et al. 2005). Thus, stable deciduous-dominated stands could develop as an alternate stable state triggered by the drastic reduction of organic mat thickness by fire in stands previously dominated by black spruce, rather than merely as a transient stage in succession (Scheffer et al. 2001). Such a shift in canopy species dominance from coniferous to deciduous over large areas and for a prolonged period of time would have a significant impact on ecosystem structure and function in boreal forests (Chapin et al. 2000, Chambers and Chapin 2003).

In this study we examined changes in the density and biomass of canopy species during early succession within a single 1994 burn in black spruce forest and related these patterns to variations in fire severity, as indicated by post-fire organic layer depths. The 1994 burn occurred in an area of relatively homogenous topography and pre-fire stand composition, but produced great variation in post-fire organic layer depths and vegetation regrowth (Johnstone and Kasischke 2005). To expand out inference beyond the 1994 burn, we examined soil and vegetation relationships in three other burns within the same region, in an attempt to answer the following questions: (1) do the effects of organic layer depth on post-fire species recruitment and establishment persist beyond the initial seedling recruitment phase of succession and impact stand productivity? (2) Are the patterns observed in the 1994 burn representative of other burns in the region, or do they appear to be dependent on specific site conditions?

2.3 Materials and Methods

2.3.1 Study site description

This research was conducted in burned black spruce stands located near the towns of Delta Junction (63°50'N, 145°40'W) and Tok Junction (61°21'N, 142°54'W) of interior Alaska. The study region consists of a relatively flat glacial outwash plain lying between the Alaska Range to the south, and the Tanana River to the north. The climate in the study region is continental, with an average annual temperature of -2.3°C, and monthly average temperatures ranging from -19°C in January to 16°C in July (Big Delta, AK for 1971-2000, Shulski and Wendler 2007). Average annual precipitation is about 28.6 cm, most of which is received during the months May to September. Our sampling was focused in four burns – the 1987 Granite Creek burn, the 1994 Hajdukovich Creek burn, and the 1999 Donnelly Flats burn, all located in the Delta Junction study area, and the 1990 Tok burn. The 1987 fire burned 20,000 ha during the period late May to early June in 1987. The 1999 fire burned approximately 8000 ha during two weeks in June 1999 (Harden et al. 2006). The 1994 fire burned 8900 ha during the months June-September 1994 (Michalek et al. 2000). The 1990 burn was the result of a series of fires that burned 40,000 hectares during the months of July and August 1990 (Bourgeau-Chavez et al.

2007). The pre-fire stands in all the burns studied here were dominated by black spruce with a few interspersed patches of trembling aspen and white spruce (*Picea glauca*).

Soils in the Delta Junction study area consisted predominantly of silt loam overlying sand and gravel deposits, with some areas having a layer of stream-deposited cobble on top of the silt (Johnstone and Kasischke 2005). Unburned stands adjacent to the 1987 and 1994 burns had organic layers which were 20-25 cm deep, and were dominated by feather moss. They both had well established permafrost, with active layers 20-50 cm below the organic layer (Kasischke and Johnstone 2005). The 1999 burn occurred in an area with more complex geomorphology. The southern portion of the 1999 burn occurred on a flat plain that formed as a result of alluvial outwash. The northern portion of the burn was located on a gradually undulating till plain formed during the retreat of the Gerstle glacier; the soils of this site contained unsorted gravel till, were extremely well drained and were permafrost-free. The 1990 burn area was underlain by permafrost, and the soils were fine-textured silt and clay lying on top of coarser-grained sand and gravel (O'Neill et al. 2002).

2.3.2 Field measurements

Field measurements were carried out during the months June-August of 2008. Within each of the four burns, sampling sites were selected so as to encompass a range of residual organic layer depths. Sampling in each burn included sites with residual organic layer depths of >8 cm, 4 – 8 cm, and <4 cm. In the 1990 burn, sampling did not include sites which had <4 cm organic layer depth, as these were not encountered. Twelve sites were sampled in the 1987 burn, 22 in the 1994 burn, 14 in the 1990 burn and 12 in the 1999 burn. In the 1994 burn, 15 of the 22 plots had been previously sampled in 2002 (Johnstone & Kasischke 2005, Kasischke & Johnstone 2005). These plots were re-located using GPS coordinates and sampled in order to compare aspen and spruce stem densities and biomass recorded 8 years following fire (Johnstone and Kasischke 2005) to that observed 14 years following fire. The 7 additional plots sampled in the 1994 burn, and the plots sampled in the 1987, 1994 and 1999 burns were located in large patches of pre-fire black spruce which characterized different organic layer depth categories.

Field sampling procedures followed methods laid out in Johnstone and Kasischke (2005). At each site, a visually homogenous area of approximately 30 m x 30 m was selected for sampling that was at least 10 m away from a foot trail (created by human or animal trampling), and at least 100 m away from a dirt or paved road. From the center of the homogenous area, a randomly oriented 30 m baseline transect was established. Three 30 m transects were then established perpendicular to and at random distances along the baseline transect. Each of the three transects was centered on the baseline transect. The minimum distance separating two transects was 4 m. All vegetation and soil sampling occurred along these three transects.

In each site we counted aspen and black spruce stems along the three 2 m x 30 m belt transects (total sampling area = 180 m^2). Basal diameters of aspen and spruce stems were measured in three 10 m x 1 m plots, each established at a random distance and side of each belt transect (n = 3/site for a sampling area of 30 m^2). In cases where fewer than 10 stems of aspen or spruce were encountered in these sub-plots, a random sample of stem diameters was obtained from elsewhere within the vicinity of the plot, and the diameters were recorded. We estimated stem density, basal area and composition of the pre-fire stand by measuring the basal diameter (cm) of all standing and fallen dead stems that were greater than 1.5 m tall, and rooted within three 2 m x 30 m belt transects. Soil organic layer depth measurements were made every 5 m along each of the three transects (for a total of 21 sampling points in each site). At each of the sampling points a 20 cm x 20 cm cube of surface organic layer was extracted with a flat-bladed shovel, and the thickness of the organic layer (cm) was measured after removing accumulated leaf litter or any green moss from the soil surface.

Basal diameter measurements on live aspen and spruce stems were converted to biomass estimates using allometric equations. Allometric equations were based on data from Johnstone and Kasischke (2005) and extended using additional data collected at three sites within the 1994 burn that represented shallow, intermediate or deep organic layer depths. At these sites, the nearest aspen and spruce stems were collected every 5 m along a 50 m randomly oriented transect. The above-ground portion of each individual was collected after measuring the basal diameter and plant height. The aspen and spruce stems were placed in bags and returned to the lab. Aboveground plant parts were dried to a constant weight and weighed to obtain dry biomass (g) (Table 1).

2.3.3 Data analysis

Values of organic layer depth were averaged over the 21 sampling points in each site to obtain a single value representing mean organic layer depth for each site. Stem counts of aspen and spruce from the three belt transects in each site were summed and then divided by the total area sampled to estimate the number of stems/m^2. Paired sample t-tests were used to assess significant differences in stem density and biomass between 2002 and 2008. In comparing measurements of stem density and biomass taken 8 years post-fire, change in biomass and in stem density were calculated as the difference between the measurement taken in 2008 and that taken in 2002 at the same site. An analysis of covariance (ANCOVA) was used to assess differences in slopes between the 2002 and 2008 organic layer depth-density and organic layer depth-biomass relationships. Allometric equations were applied using linear regression to estimate ln-transformed aboveground biomass (g) from basal diameter (cm) measurements of spruce and aspen. Biomass values for individual aspen and spruce measured in the 3 sub-plots at each site were then summed and divided by the total area sampled (30 m^2) to estimate biomass as g/m^2. Pearson's product-moment correlation estimated simple correlations between organic layer depth and stem density and biomass. Since stem density and biomass values were positively skewed, $\log_{10}$ transformed values were used in all analyses. To deal with zero values for density and biomass encountered in the data, the smallest value in the data set was added to all the values in the data set to allow log transformation. Biomass values were missing for aspen and spruce in two of the 15 plots that were re-sampled in the 1994 burn. All data analyses were performed using R (R Development Core Team, 2008).

2.4 Results

Patterns of density and biomass change at sites measured in 2002 and 2008 from the 1994 burn differed between aspen and spruce. For aspen, stem density decreased by about 60% ($t = 2.6$, $p = 0.02$) from 2002 to 2008, while biomass per unit area increased by 176.8 g/m^2 on average ($t = -4.6$, $p < 0.001$). For spruce, there was no significant change in stem density ($t = 1.54$, $p = 0.14$), but aboveground biomass per unit area increased by 47.8 g/m^2 on average ($t = -11.7$, $p < 0.001$). Spruce accounted for over 50% of total aboveground tree biomass only at sites with thick organic layers (>8 cm depth; Fig. 2.1b). In contrast, aspen biomass accounted for over 90% of total aboveground tree biomass at sites with shallow organic layers (<4 cm; Fig.2.1a). In sites which had <4 cm organic layer depth, there was no significant change in the proportional contribution of aspen to total stand biomass ($t = 2.31$, $p = 0.06$). In sites which had >4 cm organic layer depth there was a significant decrease in aspen contribution ($t = 3.58$, $p = 0.016$), and a concomitant increase in the spruce contribution to total stand biomass in these sites (Fig.2.1).

Most of the repeated measurements of the 1994 burn sites also indicated that earlier differences observed across severity levels in species densities and biomass were maintained in 2008. Measures of stem density and biomass in 2008 were strongly correlated with 2002 measurements for both aspen and spruce (Fig.2.2). Average individual biomass (g/individual) of aspen measured in 2008 was closely correlated with average individual biomass measured in 2002 ($r = 0.86$, $p < 0.001$), while in the case of spruce there was no correlation between the two (Fig.2.2e, f). Change in aspen stem density from 2002 to 2008 occurred independently of organic layer depth, but changes in aboveground biomass of aspen and spruce (g/m^2) between 2002 and 2008 were correlated with organic layer depth ($r = -0.7$, $p = 0.004$ for aspen and $r = 0.67$, $p = 0.005$ for spruce). However, changes in aspen and spruce biomass were also positively correlated with biomass of each species measured in 2002 (referred to from here on as "initial biomass") ($r = 0.76$, $p = 0.002$ for aspen, and $r = 0.59$, $p = 0.03$ for spruce). A partial correlation analysis between organic layer depth and change in biomass, in which variance associated with initial biomass was controlled for, revealed that there was no significant correlation between organic layer depth and change in biomass of aspen (partial $r = 0.15$, $p = 0.62$). However, spruce biomass change was positively associated with organic layer depth (partial $r = 0.65$, $p = 0.015$) even when initial biomass was controlled for. Similarly, change in average individual size of aspen was significantly correlated with organic layer depth ($r = -0.63$, $p = 0.02$) as well as with initial size ($r = 0.91$, $p < 0.001$), but the partial correlation between organic layer depth and change in average individual size was insignificant (partial $r = 0.17$, $p = 0.57$) when initial size was controlled for. Change in average individual biomass from 2002 to 2008 for spruce was uncorrelated with both organic layer depth ($r = 0.32$, $p = 0.28$) and initial size ($r = 0.48$, $p = 0.08$). When initial biomass was controlled for, the partial correlation between organic layer depth and change in average individual biomass was not significant (partial $r = 0.26$, $p = 0.39$).

Fourteen years following fire, in the 1994 burn, aspen stem density and biomass were negatively correlated with residual organic layer depth ($r = -0.64$, $p = 0.001$ and $r = -0.86$, $p < 0.001$ respectively; Fig. 2.3a,c). In contrast, black spruce stem density and biomass were positively correlated ($r = 0.51$, $p = 0.015$ and $r = 0.64$, $p = 0.001$ respectively) with organic layer depth (Fig.2.3b, d). Analysis of covariance indicated similar slopes (Table 2) of relationships between organic layer depth and density and biomass between 2002 and 2008 in the case of both aspen and spruce (Fig.2.3, Table 2). Change in aspen stem density from 2002 to 2008 displayed a strong negative relationship to 2002 aspen stem density such that there was the greatest proportional reduction in aspen stem density at sites that had the highest 2002 aspen densities (Table 2.3). Thus, repeat measurements in the 1994 burn indicated that patterns of aspen stem density in the second decade after fire remained significantly linked to variations in residual organic layer depths, despite density-dependent thinning of aspen stems over time. Initial densities of potentially competing tree species did not appear to affect changes in density over time, as change in aspen density from 2002 to 2008 was unrelated to spruce density in 2002 (Table 2.3). In contrast, changes in aspen biomass, as well as average individual biomass, were negatively correlated with 2002 spruce stem density (Table 2.3). Aboveground biomass on an area basis was positively correlated with stem density in the case of both aspen ($r = 0.57$, $p = 0.005$) and spruce ($r = 0.55$, $p = 0.008$), while average individual mass was not significantly correlated with stem density in either case (data not shown).

Relationships between residual organic layer depth and early successional stand composition appeared to be consistent across several recent burns in interior Alaska. In all four burns, sites which had shallow organic layer depths (<4 cm) had significantly higher aspen biomass than sites with deep organic layers, regardless of pre-fire spruce basal area (data not shown). The direction of organic layer depth effects on stem density and biomass were negative or neutral in the case of aspen, and positive or neutral in the case of spruce (Fig.2.4, Table 2.4). Specifically, stem density of aspen was negatively correlated with organic layer depth in the 1987,1994 and 1999 burns (Fig.2.4a), while aspen biomass was negatively correlated with organic layer depth in all four burns (Fig. 2.4c). Average individual biomass of aspen was also negatively correlated with organic layer depth in the 1987, 1994 and 1999 burns, but not in the 1990 burn (Fig.2.4e). In contrast to aspen, stem density of spruce was positively correlated with organic layer depth in the 1987 and 1994 burns (Fig.2.4b). Aboveground biomass (g/m^2) of spruce was also positively correlated with organic layer depth in the 1994 burn (Fig.2.4d), while average individual biomass was uncorrelated with organic layer depth in all four burns (Fig.2.4f). Density and biomass ratios of aspen versus spruce were negatively correlated with organic layer depth in the 1987 and 1994 burns, indicating that aspen consistently dominated sites with shallow organic layer depths in those burns (Fig.2.5).

2.5 Discussion

Our results show that variations in fire severity leave a legacy of post-fire changes in forest composition that persist for at least two decades after fire. Moreover, evidence from this study suggests that the initial positive effects of severe burning and shallow post-fire organic layer depth on deciduous recruitment are likely to translate into a prolonged phase of deciduous dominance during post-fire succession. There was a strong correlation between organic layer depth and the relative dominance of deciduous and coniferous species (Fig.2.5). The effects of organic layer depth on stem density and biomass were negative in the case of aspen, and positive or neutral in the case of spruce. Our data from multiple burns spanning 9-21 years post-fire indicate that the effects of organic layer depth on forest recovery can persist for several decades after fire. Our results suggest that early successional canopy dominance in these post-fire spruce stands is strongly determined by the legacy effect of initial growth and establishment of aspen, and by continued effects of organic layer depth on spruce growth. Aspen biomass comprised the majority of total tree biomass in severely burned sites from 2002 to 2008, but was reduced relative to spruce biomass in sites that were lightly burned and had thick residual organic layers (Fig.2.1). This indicates that divergent successional trajectories (aspen-dominated versus spruce-dominated) are developing at the two ends of the fire severity gradient represented by shallow versus deep post-fire soil organic layers. These observations strongly suggest that variations in fire severity on the landscape could exert a strong control over future species composition and stand productivity in boreal forests.

We found that the patterns of canopy species composition and density in the second decade of post-fire succession mirrored patterns of recruitment and establishment that were observed during the first decade following fire in the 1994 burn (Fig.2.2; Johnstone and Kasischke 2005). This result is consistent with previous findings that stand composition in boreal forests is largely determined during the first few years following disturbance (Gutsell and

Johnson 2002, Johnstone et al. 2004). Long-term (20-30 years post-fire) observations of stem densities made in the SE Yukon and interior Alaska, have shown that aspen stem density peaked within the first 10 years following fire and experienced substantial mortality during the second decade following fire, while spruce stem density remained stable or continued to increase (Johnstone et al. 2004). Similarly, we observed substantial declines in aspen stem density between 8 and 14 years following fire and no significant change in spruce density over the same time period. These observations suggest that aspen and spruce stem densities have already peaked in these early successional stands, and that established dominance hierarchies are likely to be maintained for several decades (Lavoie and Sirois 1998, Johnstone et al. 2004). The fire return interval in black spruce forests is typically 80-120 years (Johnstone et al. 2010b), and aspen individuals can survive for over 100 years (Cumming et al. 2000, Fastie et al. 2003). Since fire frequency and area burned in boreal forests is predicted to increase under a warming climate (Flannigan et al. 2005, Balshi et al. 2009), the likelihood of spruce replacing aspen in severely burned stands before the next stand-replacing fire is proportionately reduced.

Our results indicate that the accumulation of stand biomass proceeds differently in the case of aspen versus spruce during the first two decades of post-fire succession. For instance, spruce experienced no significant change in stem density from 2002 to 2008, while there was a 40-fold increase in biomass. In contrast, aspen stems underwent density-dependent thinning, but only experienced a 2-fold increase in biomass. This indicates that increase in size of aspen individuals was compensated for by decreases in density, but in the case of spruce substantial growth occurred without a concomitant decline in stem density.

Change in aspen stem density from 2002 to 2008 was strongly correlated with initial aspen stem density, but uncorrelated with the initial density of spruce. This pattern is consistent with the interpretation that natural self-thinning in aspen is primarily driven by intra specific rather than interspecific competition for resources (e.g. Johnstone et al. 2004). Nevertheless, increases in aspen biomass (mean plot level biomass as well as mean biomass per individual) were greater in sites with low initial levels of spruce stem density (Table 3). This observation is perhaps best explained by the fact that low spruce densities occurred in plots with shallower organic layers, where aspen growth was greatest. Studies investigating the ecophysiological factors and mechanisms that drive the sharply contrasting tree species abundances in lightly versus severely burned sites would be crucial to furthering our understanding of post-fire vegetation dynamics in boreal forests. For instance, aspen fine root biomass has been found to be strongly correlated with stand basal area, while in the case of conifers, root biomass does not match basal area (Bauhus and Messier 1999). In addition, aspen has been found to produce high fine root biomass and high root length density even in conifer-dominated areas, and overall soil exploitation is higher in mixed (deciduous-coniferous) forests than in pure coniferous stands (Bauhus and Messier 1999). Avoidance of competition for soil resources could in part explain the higher density and biomass of black spruce in lightly burned sites where organic soils are thick and aspen density and biomass are low (Figs.2.3, 2.4 and 2.5). Consistent effects of organic layer depth on post-fire canopy species composition and densities, were observed in the 1987, 1990, 1994 and 1999 burns and suggest that variations in organic layer depth are a key mechanism determining vegetation composition in boreal forests within a given fire cycle. The results observed here are consistent with observations of differential recruitment and growth of conifers and deciduous trees with respect to organic layer depth in the first few years after fire (Johnstone and Chapin 2006, Greene et al. 2004, Greene et al. 2007, Johnstone et al. 2010a). This study shows that these initial effects persist through the first 1-2 decades of succession and demonstrate that sites starting from similar pre-fire conditions in terms of species composition and topography can be set on different post-fire successional trajectories (deciduous-dominated or spruce-dominated) in response to variations in depth of burning. The occupation of sites that represent the two ends of the fire severity spectrum (severely burned versus lightly burned) by plant functional types which differ dramatically in their physiological strategy (Lambers and Poorter 1992), productivity (Van Cleve et al. 1983), functional effects on ecosystem processes (e.g. Chapin 2003), and flammability (Cumming 2001, Rupp et al. 2002) presents a striking dichotomy in successional trajectories occurring simultaneously on the post-fire landscape.

The unique environmental conditions created by severe burning combined with resident vegetation effects on surface albedo, ground thermal regimes and edaphic properties are likely to affect local and regional climate. A switch in stand dominance from successional cycles dominated by coniferous forest (black spruce) to those with prolonged phases of deciduous dominance may have significant impacts on local and regional climate via vegetation feedback effects on land-atmosphere energy exchanges. Land-atmosphere energy exchanges are controlled by evapotranspiration, albedo, and surface roughness, each of which is determined in large part by leaf area, biomass and canopy architecture of the dominant resident vegetation (Chapin et al.

1996). Since aspen and spruce differ widely with respect to each of these traits, long lasting post-fire vegetation conversion from spruce to aspen over large areal extents will alter land-atmosphere energy exchange. For instance, spruce dominated forests have a low surface albedo, resulting in higher sensible heat flux, and warmer surface temperatures (Bonan et al. 1992). In contrast, deciduous forests increase the land surface albedo two fold compared to coniferous forests (Baldocchi et al. 2000) and have higher rates of evapotranspiration (Chapin et al. 2000), thereby reducing sensible heat flux, and resulting in a net cooling effect on climate (Betts and Ball 1997, Randerson et al. 2006). Therefore, in severely burned stands, the preponderance of deciduous vegetation would increase surface albedo and evapotranspiration, resulting in a net cooling effect on the atmosphere (Baldocchi et al. 2000, Randerson et al. 2006). Deciduous trees and black spruce also differ with respect to key functional traits such as relative growth rate, leaf area index, and leaf litter quality (Lavorel and Garnier 2002, Diaz et al. 2004) which directly influence ecosystem properties such as stand productivity, decomposition rates and nutrient availability (Chapin 2003, Diaz et al. 2004). Vegetation effects on soil processes can also result in long term climatic feedbacks. For instance, aspen dominated stands are characterized by high quality leaf litter, high decomposition and mineralization rates, and maintenance of a thin litter layer, while spruce dominated stands have a thick organic mat and moss layer that insulates the mineral soil (Johnstone et al. 2010b). The absence of the organic mat and moss layer in deciduous stands results in increased soil thermal conductivity, deepening of the active layer and gradual degradation of permafrost and the release of soil carbon to the atmosphere (Osterkamp and Romanovsky 1999, Yoshikawa et al. 2003, Schuur et al. 2008). The reinforcement of warmer soil temperatures, melting of permafrost, and increase in nutrient availability by the effects of deciduous vegetation on soil processes may perpetuate the survival and persistence of deciduous canopy species in post-fire successional stands (Johnstone et al. 2010b).

The conversion of stands from black spruce to aspen driven by variations in fire severity may have cascading effects for animal populations and human subsistence resources. Moose are one of the main subsistence resources in interior Alaska (Scott et al. 2001), and their populations are managed to optimize sustainable harvest densities (Boertje et al. 2009). Forage availability is an important factor in determining moose demography (Van Ballenberghe and Ballard 1998, Boertje et al. 2007), and consequently could be important in driving population densities. Deciduous stands present higher quality forage than do coniferous stands, and have been found to support higher moose population densities than mature conifer stands (Spencer and Hakala 1964, Cederlund and Okarma 1988). Moose population densities in turn influence vegetation dynamics during succession, via the effects of herbivory on early successional plant growth and on biogeochemical processes (Kielland and Bryant 1998, Persson et al. 2007), making them important ecosystem engineers in the boreal forest. For instance, in the Delta Junction region, where fire frequency and area burned has increased over the past few decades, moose densities have been increasing at an average annual rate of ten per cent over the past decade (Dubois 2008). Moreover, areas which were severely burned were found to support high browse production and higher rates of browse removal compared to areas which were lightly burned (Lord 2007).

Since the frequency of high fire years and land area burned are predicted to increase (Flannigan et al. 2005, Balshi et al. 2009) concomitantly with fire severity (Duffy et al. 2007) under a warming climate, the extent of deciduous dominance on the landscape is likely to increase. Sites that previously maintained stable cycles of black spruce self-replacement following low-severity fires have the potential to switch to alternative states dominated by deciduous trees as the fire regime changes. Our findings show that variations in fire severity, as indicted by residual organic layer depths, in areas of relatively uniform topography and pre-fire stand composition can drive the formation and persistence of forest stands undergoing different successional trajectories. How the coniferous and deciduous stands in this landscape mosaic interact with each other in terms of propagule dispersal, and their effects on fire behavior, as well as how the dominant canopy species respond to further modifications of the mosaic by future fires will play a large role in determining the extent of future change in species dominance in the Alaskan boreal landscape.

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2.8 Figures

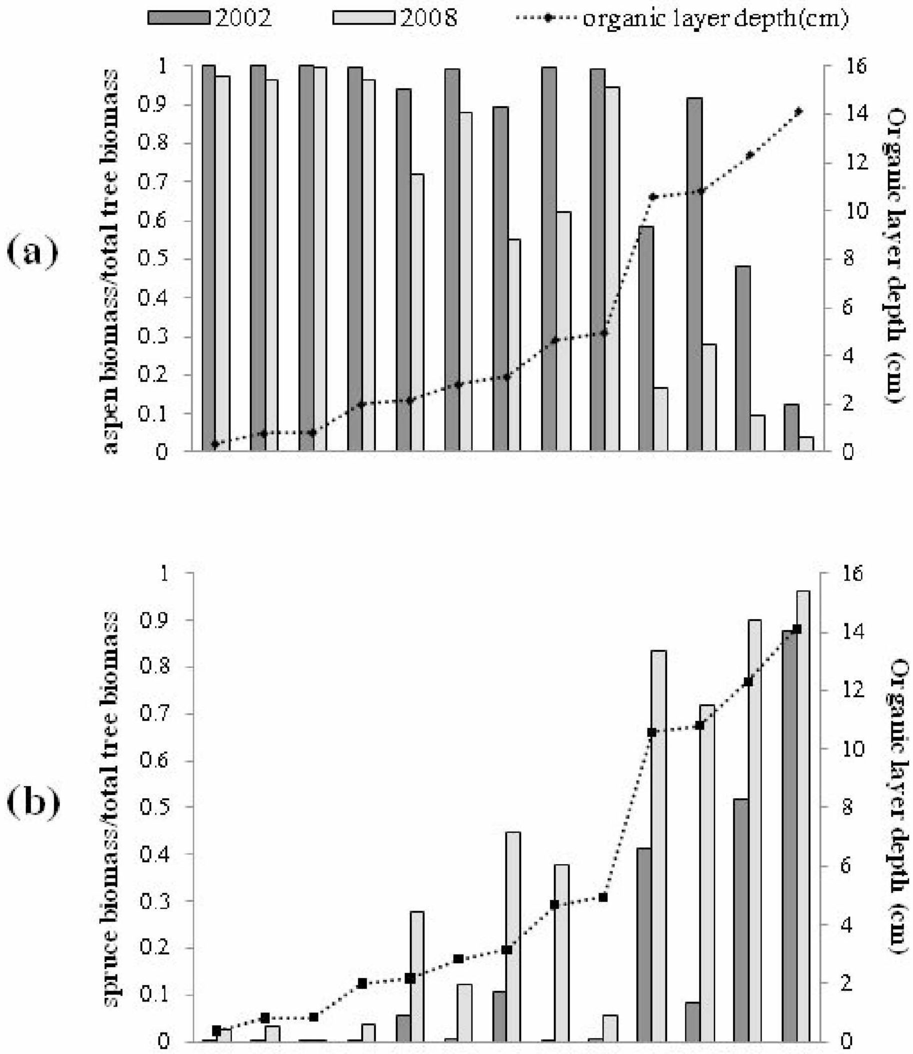

Fig.2.1 Biomass of (a) aspen and (b) spruce, expressed as a proportion of total tree biomass in plots sampled in 2002 and 2008. The dotted line represents average organic layer depth (cm) measured in 2008.

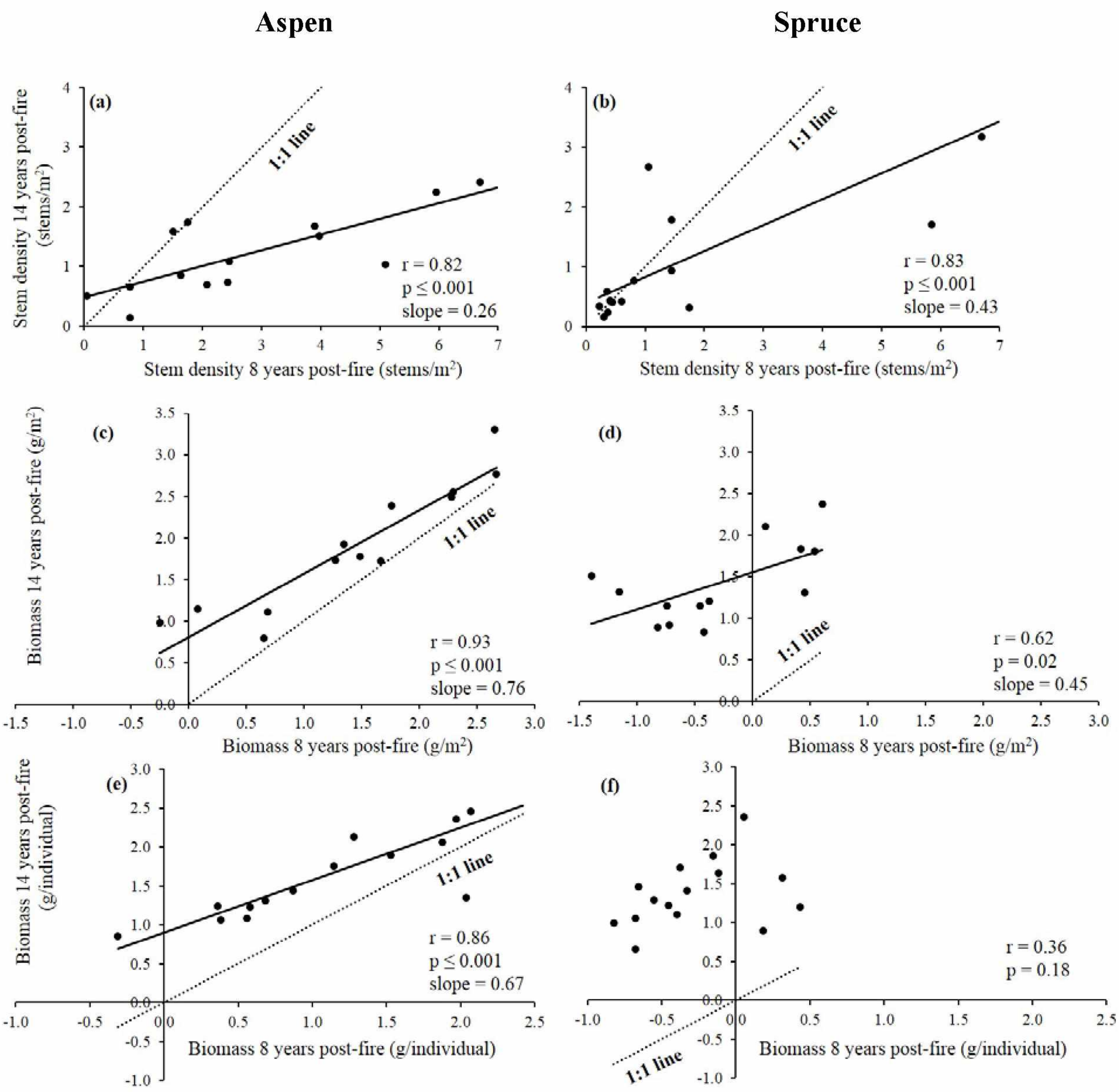

Fig.2.2 Scatterplots of stem density (stems/m^2), biomass (g/m^2) and average individual biomass (g/individual) recorded in the same plots 8 years and 14 years post-fire for aspen (a,c,e) and spruce (b,d,f) in the 1994 burn. Biomass values have been $\log_{10}$ transformed (n=15 for stem density and average individual biomass, n=13 for biomass). The dashed line represents the 1:1 relationship in each case.

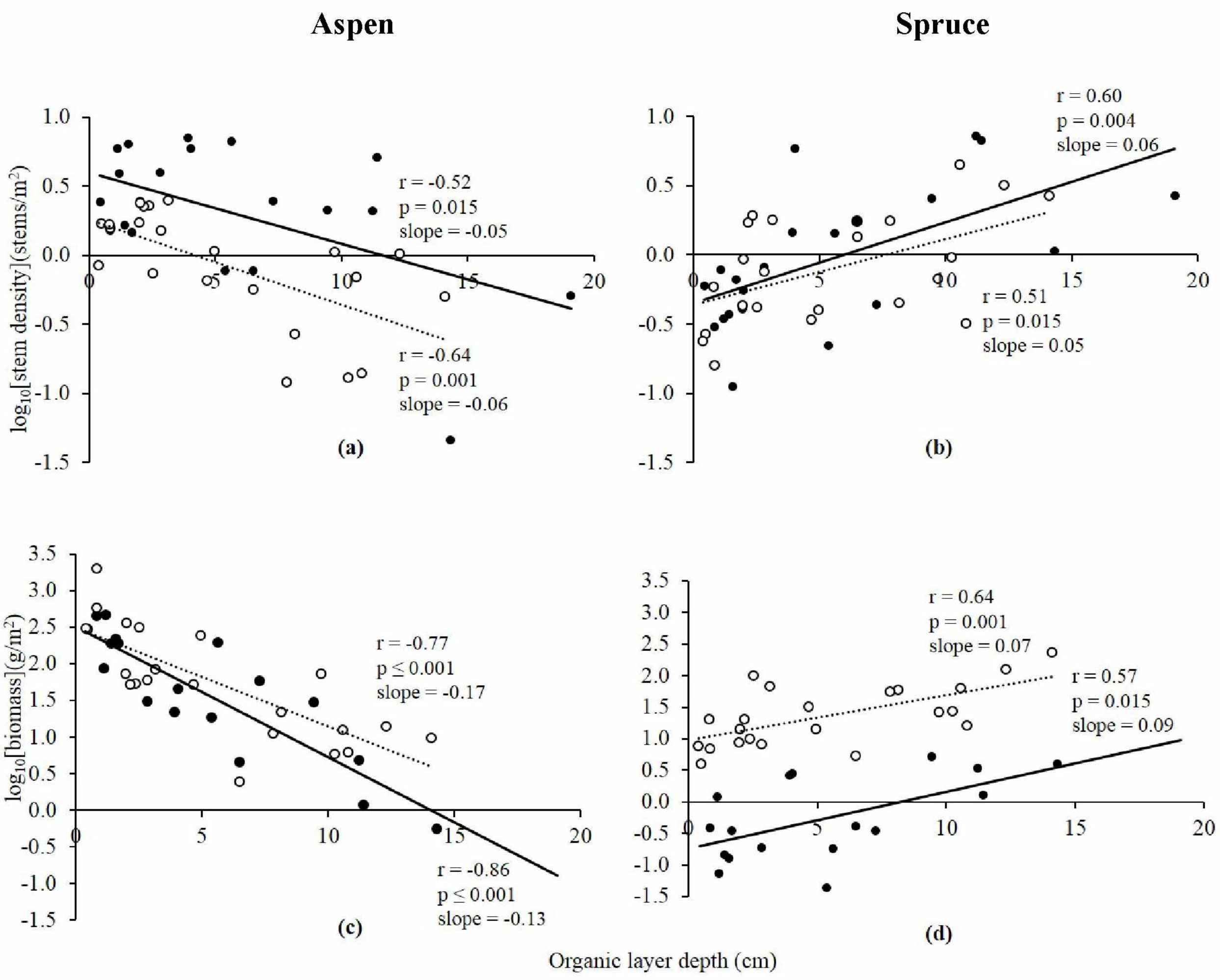

Fig.2.3 Organic layer depth-vegetation relationships 8 and 14 years post-fire. Log-linear correlations between organic layer depth (cm) and (a) aspen stem density (log$_{10}$stems/m^2), (b) spruce stem density (log$_{10}$stems/m^2), (c) aspen biomass (log$_{10}$ g/m^2), and (d) spruce biomass (log$_{10}$ g/m^2), in the 1994 burn. Filled circles represent measurements made 8 years post-fire, while open circles represent 14 years post-fire (n=21 for 2002 stem density, n=17 for 2002 biomass, and n=22 for stem density and biomass for 2008).

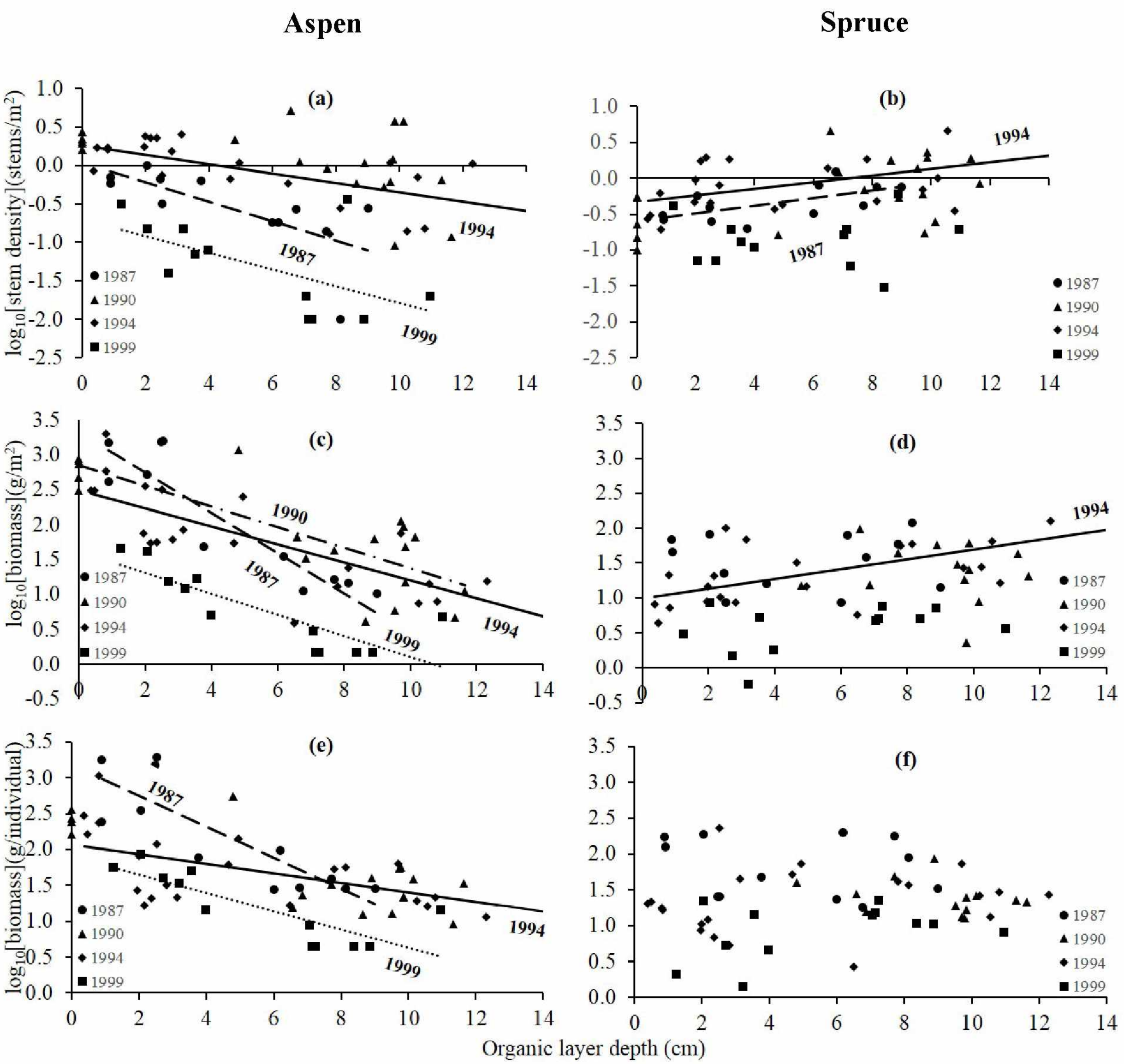

Fig.2.4 Organic layer depth- vegetation relationships in multiple burns. Linear correlations between organic layer depth (cm) and (a) aspen stem density (log$_{10}$stems/m^2), (b) spruce stem density (log$_{10}$stems/m^2), (c) aspen biomass (log$_{10}$g/m^2), (d) spruce biomass (log$_{10}$g/m^2), (e) aspen mean biomass (log$_{10}$g) per individual, and (f) spruce mean biomass (log$_{10}$g) per individual in the 1987, 1990, 1994 and 1999 burns.

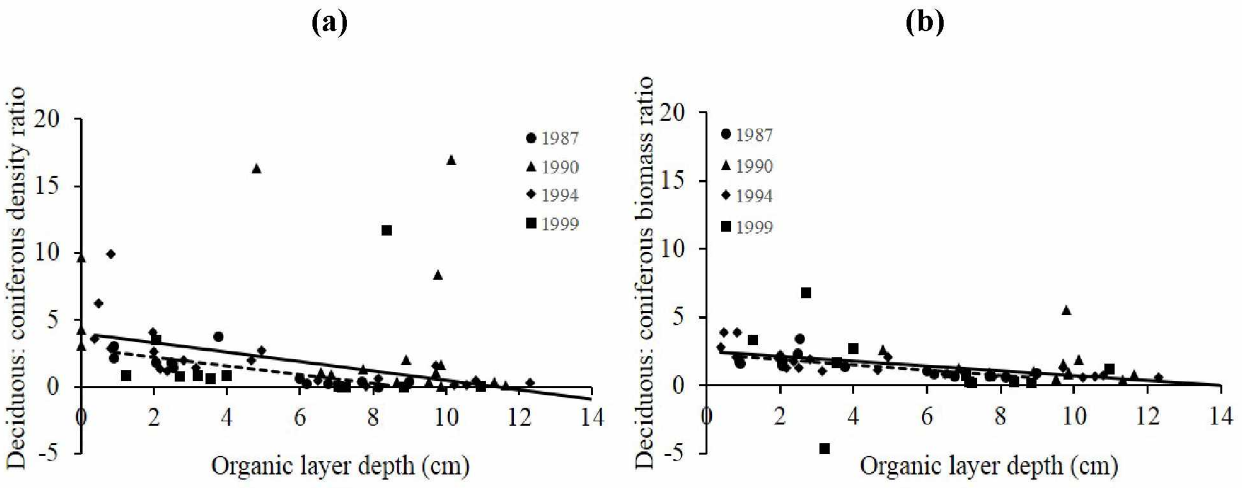

Fig.2.5 Scatterplots showing relationships between organic layer depth (cm) and deciduous : coniferous ratios of (a) $\log_{10}$stem density and (b) $\log_{10}$biomass in four areas of black spruce forest that burned in 1987, 1990, 1994, and 1999. Significant linear correlations are indicated by lines in panels (a) for 1987 (r=-0.79, p=0.003) and 1994 (r=-0.65, p=0.001) and (b) for 1987 (r=-0.69, p=0.01) and 1994 (r=-0.76, p<0.001).

2.9 Tables

Table 2.1 Summary of allometric equations used to convert basal diameter (cm) of aspen and spruce to total aboveground biomass (g).

Species	Total no. of stems	Basal diameter range (cm)	Linear regression equation	R^2	p
Populus tremuloides	107	0.1-12	ln(biomass)=3.426+2.496ln(basal diameter)	0.94	<0.001
Picea mariana	65	0.06-1.86	ln(biomass)=3.841+2.816ln(basal diameter)	0.93	<0.001

Table 2.2 ANCOVA comparison of the relationship between organic layer depth (cm) and stem density, and organic layer depth and aboveground biomass for aspen and spruce 8 years post-fire (2002) and 14 years post-fire (2008) in the 1994 burn.

Species	*F*	*p*	*df*	*Slope(SE)*
Aspen				
Stem density	0.168	0.68	1,39	**2002**: -0.05 *(0.02)* **2008**: -0.06 *(0.016)*
Aboveground biomass	1.367	0.25	1,35	**2002**: -0.18 *(0.03)* **2008**: -0.13 *(0.025)*
Spruce				
Stem density	0.194	0.66	1,39	**2002**: 0.06 *(0.017)* **2008**: 0.05 *(0.018)*
Aboveground biomass	0.289	0.59	1,35	**2002**: 0.09 *(0.03)* **2008**: 0.07 *(0.02)*

Table 2.3 Summary of linear regression relationships between aspen and spruce initial stem densities (measured in 2002) and changes in stem density (for aspen only), plot-level average biomass, and average individual biomass from 2002 to 2008 for aspen and spruce. Significance was evaluated at α=0.05 level. Significant p-values are indicated by bold text.

Response variable/direction of change (+/-) from 2002 to 2008	***Predictor variable (stems/m^2)***	***R^2***	***p***
Change in aspen density (stems/m^2) (-)	Aspen stem density in 2002	**0.93**	**<0.001**
Change in aspen density (stems/m^2) (-)	Spruce stem density in 2002	0.1	0.12
Change in aspen biomass (g/m^2) (+)	Aspen stem density in 2002	-0.07	0.74
Change in spruce biomass (g/m^2) (+)	Aspen stem density in 2002	-0.09	0.98
Change in aspen biomass (g/m^2) (+)	Spruce stem density in 2002	**0.24**	**0.05**
Change in spruce biomass(g/m^2) (+)	Spruce stem density in 2002	0.11	0.14
Change in aspen biomass (g/individual) (+)	Aspen stem density in 2002	0.01	0.31
Change in spruce biomass(g/individual) (+)	Aspen stem density in 2002	-0.03	0.45
Change in aspen biomass (g/individual) (+)	Spruce stem density in 2002	**0.42**	**0.007**
Change in spruce biomass(g/individual) (+)	Spruce stem density in 2002	-0.04	0.5

Table 2.4 Linear correlations between organic layer depth and stem density ($\log_{10}$ stems/m^2), biomass ($\log_{10}$g/m^2) and average individual biomass ($\log_{10}$g/individual) for aspen and spruce in the 1987, 1990, 1994 and 1999 burns. Significant linear correlations are indicated by bold, italicized text. Slopes and standard errors (SE) of significant correlations are shown.

Species	***Burn***	***r***	***p***	***Slope (SE)***
	1987			
Aspen ***(df=10)***	Stem density (stems/m^2)	**-0.69**	0.01	-0.127 (*0.04*)
	Biomass (g/m^2)	**-0.9**	<0.001	-0.297 (*0.04*)
	Biomass (g/individual)	**-0.85**	<0.001	-0.225 (*0.04*)
Spruce ***(df=10)***	Stem density (stems/m^2)	**0.64**	0.02	0.057 (*0.02*)
	Biomass (g/m^2)	0.017	0.95	-
	Biomass (g/individual)	-0.18	0.56	-
	1990			
Aspen ***(df=12)***	Stem density (stems/m^2)	-0.47	0.08	-
	Biomass (g/m^2)	**-0.58**	0.03	-0.22 (*0.08*)
	Biomass (g/individual)	-0.47	0.08	-
Spruce ***(df=11)***	Stem density (stems/m^2)	0.14	0.64	-
	Biomass (g/m^2)	-0.1	0.72	-
	Biomass (g/individual)	-0.33	0.25	-
	1994			
Aspen ***(df=20)***	Stem density (stems/m^2)	**-0.64**	0.001	-0.06 (*0.016*)
	Biomass (g/m^2)	**-0.79**	<0.001	-0.13 (*0.02*)
	Biomass (g/individual)	**-0.57**	0.005	-0.07 (*0.02*)
Spruce ***(df=20)***	Stem density (stems/m^2)	**0.51**	0.015	0.05 (*0.018*)
	Biomass (g/m^2)	**0.64**	0.001	0.07 (*0.019*)
	Biomass (g/individual)	0.22	0.3	-
	1999			
Aspen ***(df=10)***	Stem density (stems/m^2)	**-0.58**	0.047	-0.1 (*0.05*)
	Biomass (g/m^2)	**-0.83**	<0.001	-0.15 (*0.03*)
	Biomass (g/individual)	**-0.81**	0.001	-0.13 (*0.03*)
Spruce ***(df=10)***	Stem density (stems/m^2)	0.03	0.92	-
	Biomass (g/m^2)	0.37	0.22	-
	Biomass (g/individual)	0.43	0.16	-

Chapter 3.

Effects of fire severity on plant nutrient uptake reinforce alternate pathways of succession in boreal forests[2]

3.1 Abstract

Fire activity in the North American boreal region is projected to increase under a warming climate and trigger changes in vegetation composition. In black spruce forests of interior Alaska, fire severity impacts residual organic layer depth which is strongly linked to the relative dominance of deciduous versus coniferous trees in early succession. These alternate successional pathways may be reinforced by biogeochemical processes that affect the relative ability of deciduous versus coniferous trees to acquire limiting nutrients. To test this hypothesis, we examined changes in soil inorganic nitrogen (N) supply and in situ ^{15}N root uptake by aspen (*Populus tremuloides*) and black spruce *(Picea mariana)* saplings regenerating in lightly and severely burned sites, 16 years following fire. Fire severity did not impact the composition or magnitude of N supply, and nitrate represented nearly 40% of total N supply. Both aspen and spruce took up more N in severely burned than in lightly burned sites. Spruce exhibited only a moderately lower rate of nitrate uptake, and a higher ammonium uptake rate than aspen in severely burned sites. At the stand level, differences in species nutrient uptake were magnified, with aspen taking up nearly an order-of-magnitude more N per m^2 in severely burned than in lightly burned sites. We suggest that differences in nutrient sinks (biomass) established early in succession, and effects of post-fire organic layer depth on nutrient uptake, are key mechanisms reinforcing the opposing stand dominance patterns that have developed in response to variations in organic layer depth.

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[2] Shenoy A, Kielland K, Johnstone JF (2013) Effects of fire severity on plant nutrient uptake reinforce alternate pathways of succession in boreal forests. Plant Ecol 214: 587-596

3.2 Introduction

Wildfire is the primary initiator of secondary succession in many boreal forests, and fire characteristics subsequently shape ecosystem structure and function. In black spruce-dominated forests the depth of the soil organic layer remaining following fire varies as a function of fire severity, or surface fuel consumption, and pre-fire organic layer depth (Boby et al. 2010). Post-fire organic layer depth is strongly linked to the relative dominance of deciduous tree seedlings such as *Populus tremuloides* (aspen) versus coniferous species such as *Picea mariana* (black spruce). High rates of deciduous recruitment have been found to occur in severely burned areas that have little or no organic layer remaining, and black spruce self-replacement takes place in lightly burned areas that have deep organic layers (Johnstone and Kasischke 2005; Johnstone and Chapin 2006; Greene et al. 2007). These initial patterns of seedling recruitment that arise from the effects of fire severity on post-fire organic layer depths are sustained for at least two decades following fire (Shenoy et al. 2011), and are predicted to result in long-term shifts in stand dominance (Johnstone et al. 2010; Beck et al. 2011). Although the demographic processes initiating this switch to deciduous dominance following severe burning are well studied, the biogeochemical underpinnings of the observed relationship between fire severity and plant functional type dominance have yet to be investigated. Since aboveground productivity in boreal forests is strongly nitrogen limited (Van Cleve et al. 1983), effects of fire severity (measured here as post-fire organic layer depth) on nitrogen availability could influence patterns of post-fire stand dominance.

Fire affects ecosystem nutrient stocks and plant nutrient availability in a myriad of ways. Although fire results in large losses of N through volatilization and leaching (Raison et al. 1985), post-fire increases in available soil N have been documented in a variety of ecosystems (e.g. Dyrness et al. 1989; Smithwick et al. 2005; Turner et al. 2007). Rapid mineralization of organic matter following fire results in increased ammonium (NH_4^+) and nitrate (NO_3^-) (Wan et al. 2001). Moreover, increased post-fire soil pH and temperature have been found to accelerate nitrification rates in boreal forest soils (Neary et al. 1999; Smithwick et al. 2005). The amount of organic matter combusted by fire may affect the magnitude of increase in available soil inorganic N (Covington and Sackett 1992), with severely burned soils being likely to have higher NO_3^- concentrations than lightly burned soils. Studies that have directly measured post-fire nutrient availability in coniferous ecosystems (e.g. Dyrness et al. 1989; Harden et al. 2004; Smithwick et al. 2005; Turner et al. 2007) have focused on the first five years following fire, although chronosequence studies have shown that post-fire soil N stocks may increase (Yermakov and Rothstein 2006) or decrease (Smithwick et al. 2009) over time in mature stands. Inorganic N increases generally decline with time since fire (e.g. Turner et al. 2007), although there is evidence suggesting that the fire fertilization effect may persist into later succession in boreal forests (Pare et al. 1993; Harden et al. 2003). Little is known about the longevity of fire effects on soil N, especially during the first few decades following fire. However, because aspen and spruce stem densities peak at one and two decades, respectively, following fire (Johnstone et al. 2004), this time period represents a critical window during which successional pathways are established. Addressing the potential role played by fire-driven changes to nutrient availability in determining the relative success of deciduous or coniferous canopy species will increase our understanding of mechanisms shaping successional trajectories in boreal forests.

Fast-growing deciduous species like aspen have higher nutrient uptake capacity than slow-growing conifers like black spruce (Lambers and Poorter 1992). Furthermore, there is evidence that coniferous and deciduous species differ in their capacity to take up and process different forms of inorganic N (Kronzucker et al. 1997; Min et al. 2000). For instance, late successional conifers such as white spruce (*Picea glauca*) exhibit much greater root uptake of NH_4^+ than NO_3^- when both are present in equimolar concentrations (Kronzucker et al. 1997). In contrast, root nitrate reductase activity and rate of NO_3^- influx into aspen roots were much higher than for lodgepole pine (Min et al. 1998). These inherent physiological differences between deciduous and coniferous species, may affect species' relative success in post-disturbance environments that are expected to be high in NO_3^- (severely burned), compared to environments in which NH_4^+ may be the dominant form of inorganic N (lightly burned). While several investigators have assessed N uptake of boreal tree seedlings in laboratory studies (Chapin et al. 1986; Kronzucker et al. 1997; Min et al. 2000), few have measured N uptake in the field, with some notable exceptions (Persson et al. 2003; Nordin et al. 2004; Kielland et al. 2006; McFarland et al. 2010). Moreover, although white spruce is well studied, whether black spruce similarly exhibits a preference for NH_4^+ and a limited capacity for NO_3^- uptake, is unknown.

Our objective was to provide a biogeochemical perspective on the dramatic increase in aspen biomass relative to black spruce in severely burned sites (organic layer depths of 0 – 4 cm) compared to lightly burned sites (organic layer depths >8 cm) (Shenoy et al. 2011). We hypothesized that 1) soil NO_3^- supply would be higher in severely burned sites and (2) since conifers have been shown to have a reduced physiological capacity for NO_3^- uptake, aspen will display greater NO_3^- uptake rates than black spruce in severely burned sites. We conducted our study in 16 year-old burned black spruce stands in interior Alaska. Variations in post-fire organic layer depth within this burn have resulted in aspen-dominated stands in areas with shallow organic layers, and black spruce self-replacement in areas with deep organic layers (Johnstone and Kasischke 2005; Shenoy et al. 2011). We examined soil inorganic N supply rates in relation to fire severity, measured *in situ* uptake of ^{15}N-labeled NH_4^+ and NO_3^- by aspen and black spruce saplings, and compared species responses in relation to fire severity. If soils in severely burned parts of these early successional forests are indeed high NO_3^- environments relative to lightly burned stands, and if black spruce roots exhibit a reduced capacity to take up NO_3^- relative to NH_4^+, this could in part explain the shift from spruce to aspen dominance in parts of the boreal forest which undergo severe burning. Here we examine the interaction between wildfire-driven effects on soil nutrient status and potential physiological preferences of dominant canopy species in shaping alternate post-fire successional trajectories in boreal forests.

3.3 Methods

This research was conducted in the Hajdukovich Creek burn, located near the town of Delta Junction (63°50'N, 145°40'W) in interior Alaska. The fire burned 8900 ha during June-September 1994. The pre-fire vegetation was dominated by black spruce with a few interspersed patches of trembling aspen and white spruce. The study region consists of a relatively flat glacial outwash plain lying between the Alaska Range to the south, and the Tanana River to the north. The climate is continental, with an average annual temperature of −2.3°C, and monthly average temperatures ranging from −19°C in January to 16°C in July (Big Delta, AK for 1971–2000, Shulski and Wendler 2007). Average annual precipitation is approximately 28.6 cm, most of which is received as rain during May to September. Soils in the study area consist predominantly of silt loam overlying sand and gravel deposits, with some areas having a layer of stream-deposited cobble on top of the silt (Johnstone and Kasischke 2005). Unburned stands adjacent to the 1994 burn had 20 – 25 cm deep organic layers, and ground layers dominated by feather moss.

They had well established permafrost, with active layer depths 20 – 50 cm below the organic layer (Kasischke and Johnstone 2005).

In 2009 we established fifteen 50 m X 100 m sites within the 1994 burn, encompassing a range of organic layer depths (from 0 cm to > 8 cm) (Shenoy et al. 2011). Sampling at each site was carried out along a randomly oriented 50 m long transect. Ten sampling points were located at random distances along the transect, on a random side, and at a random distance (up to 50 m) from the transect line. At each sampling point, we estimated density and biomass of aspen and spruce stems in 1 m x 1 m quadrats (n = 10). We counted all aspen and spruce stems in the quadrat to obtain stem density per m^2, and measured the basal diameter (cm) of each stem. Basal diameter measurements were converted to biomass (g) estimates using allometric equations presented in Shenoy et al. (2011).

We collected a 15 cm x 6 cm soil core at the North West corner of each quadrat, for determination of soil pH. We measured organic layer depth (cm) on a 20 cm x 20 cm block of soil excavated 1-2 m away from the quadrat, after removing surface leaf litter. We then buried ion-exchange membranes in the excavated pit and replaced the soil block. We inserted anion and cation exchange probes (Plant Root Simulator™ probes, Western Ag Innovations, Saskatoon, SK) horizontally into the organic layer (2cm below the forest floor surface) and the mineral layer (2cm below the mineral-organic interface). In severely burned sites probes were inserted horizontally at 2cm below the surface, and at 15 cm depth. The depth of probe burial was standardized across sites to account for the fact that in severely burned areas the organic layer was usually between 0-2 cm deep, while in lightly burned areas the organic layer was usually >8 cm deep. Probes were buried in early July 2009 and collected a month later, and the process repeated to obtain NO_3^- and NH_4^+ supply rates over the period July-August and August-September 2009. N supply rates were averaged across these two time periods. We measured soil temperature and moisture in the mineral and organic layers continuously over the *2010* growing season using ECH20 data loggers (Decagon Devices, Inc. Pullman, WA). Temperature and moisture sensors were inserted horizontally in the soil at 2 cm below the soil surface, and 2 cm below the organic-mineral soil interface in one severely and one lightly burned site.

We collected the nearest individual stem of aspen and spruce every 5 m along a 50 m transect in one severely and one lightly burned site to develop allometric relationships between root biomass (g/~ 400 cm^3)and aboveground biomass (n = 20 for each species). We harvested the aboveground (shoot) biomass, and collected four 15 cm deep x 6 cm diameter soil cores beneath the canopy diameter of each plant for estimation of root biomass. We picked roots (diameter > 2 mm) of either aspen or spruce from the soil cores and pooled them. Roots and shoots were dried at 60°C and weighed to obtain root biomass (g per volume soil; values were averaged across the four cores) and shoot biomass (g per individual).

For the ^{15}N uptake study, we sampled 5 aspen and 5 spruce saplings in a severely burned and a lightly burned site within the 1994 burn during August 2010. The two sites differed significantly with respect to average organic layer depth, and stem density and biomass of spruce and aspen (Table 1). We set up a randomly oriented 50 m transect in each site and assigned treatments to the nearest aspen and spruce saplings at random distances along the transect. We injected 98% enriched ^{15}N labeled solutions of NH_4^+ and NO_3^- into the soil within 4 cm of each sampled sapling. Each treatment consisted of 9 aliquots, injected through 9 uniformly distributed holes in a circular Lexan^{TM} injection grid whose diameter corresponded to the diameter of the soil corer (McFarland et al. 2002). Labeled solutions were injected evenly across soil depths of 0-15 cm. Each aliquot had a volume of 2 ml, with concentrations of 4.48 µg N/2 ml as $(NH_4)_2SO_4$ and 2.94 µg N/2 ml as KNO_3, reflecting the relative concentrations of NH_4^+ and NO_3^- in the soil. We injected each sampled plant with a total of 40.32 µg/dose of NH_4^+ and 26.46 µg/dose of NO_3^- which represented 1-15% of the background concentrations of NH_4^+ and NO_3^- at the time of the experiment. We marked the center of the injection zone with a flag, and retrieved the 15 cm deep x 6 cm diameter soil core 12 hours later. Soil cores were brought to the lab on ice, and processed the same day. All fine roots (diameter ≤ 2mm) of the aspen or spruce plant were picked out from each core, washed with 0.5M KCl, dried at 60° C for 24 hours, and ground using a ball mill. Roots from the plants used to develop allometric relationships between aboveground biomass and root biomass, were used as control roots, and analyzed for natural abundance δ^{15}N using the same procedures as for the ^{15}N enriched roots.

Lab analysis: The ion-exchange probes were brought to the lab on ice, washed with deionized water, and shipped to Western Ag Innovations, Saskatoon, SK for analysis of 1M KCl extractable NO_3^- and NH_4^+. N supply data were calculated on the basis of surface area of the ion-exchange membrane and expressed as µg N m^{-2} $month^{-1}$.

The dried and ground ^{15}N enriched plant roots were analyzed for δ^{15}N using a continuous-flow isotope ratio mass spectrometer with an instrument precision of <0.2 ‰. Soil pH was determined electrometrically, in water extracts following standard procedures (Robertson et al. 1999).

Root $\delta^{15}N$ was obtained using the formula

$\delta^{15}N = [(R_{sample} - R_{standard})/R_{standard}] * 10^3$,

where R_{sample} is the isotopic ratio $^{15}N/^{14}N$, and $R_{standard}$ is the atmospheric value (Peterson and Fry 1987).Total ^{15}N uptake ($\mu g\ N\ g^{-1}$ root hr^{-1}) was calculated by subtracting the atom% ^{15}N of the unlabeled control roots from each labeled sample. Mass of ^{15}N in excess of background was then calculated by multiplying the atom% at excess values by the mass of N in the sample. We scaled uptake to the available N pool by dividing the amount of ^{15}N absorbed by dilution of the label by the available soil N pool (^{15}N dose applied/ soil N pool) of the soil volume sampled (Kielland et al. 2006; Averill and Finzi 2011).

We developed allometric equations which estimated linear relationships between aboveground biomass (g) and root biomass (g) (Table 2). Due to two missing values, and one outlying shoot weight value in the case of aspen, and one missing value and two high outlying root weight values in the case of spruce, three data points were not included in the regression in each case, reducing the sample size to 17 for each species. Aboveground biomass (g m^{-2}) values (Shenoy et al. 2011) were used to estimate root biomass on an area basis (g m^{-2}), and these values were multiplied by N uptake values ($\mu g\ N\ g^{-1}$root hr^{-1}) to obtain total N uptake on an area basis ($\mu g\ N\ m^{-2}\ hr^{-1}$).

Temperature and moisture values were averaged across the months June to September in 2010. We tested for significant differences in temperature and moisture between lightly and severely burned sites using Welch's two-sample t-test. N supply rates and ^{15}N uptake rates were analyzed using two-way ANOVA, with fire severity and soil layer as fixed effects in the former, and fire severity and species as fixed effects in the latter. Tukey Honestly Significant Difference test was used for post-hoc comparisons of means. All statistical analyses were performed using R (R Development Core Team 2011).

3.4 Results

Measurements of soil characteristics 16 years after fire showed mixed effects of fire severity on soil conditions. There was a non-significant trend for soils to be warmer in severely burned than in lightly burned sites in organic as well as mineral layers (Table 3.3). The organic layer or top 2cm of soil was significantly drier in severely burned sites than in lightly burned sites, whereas moisture in the mineral layer was similar across sites (Table 3.3). Soils were more acidic in lightly burned (average pH 5.4 ± 0.03) than in severely burned sites (average pH 6.2 ± 0.14). Supply rates of NO_3^- and NH_4^+ showed no significant differences between severely and lightly burned sites or between organic and mineral layers (Fig.3.1; Table 3.4). NH_4^+ supply rates were significantly greater than NO_3^- supply rates in lightly burned sites in organic ($t = -2.87$; $p = 0.01$) and mineral layers ($t = -2.524$; $p = 0.02$), whereas NO_3^- and NH_4^+ supply rates were similar in severely burned sites in organic ($t = -1.21$; $p = 0.27$) and mineral layers ($t = -0.43$; $p = 0.68$). Note that in severely burned sites most "organic" samples were in the mineral soil layer (2cm below the forest floor surface) as the organic layer had been completely combusted in the fire.

Fire severity had a strong impact on specific N uptake rates (µg N g^{-1}root) of both aspen and spruce, but differences between species in uptake of NO_3^- vs. NH_4^+ were slight. Both aspen and spruce took up significantly more NH_4^+ than NO_3^- per gram root regardless of fire severity (Fig.3.2). While both aspen and spruce took up significantly more NO_3^- per gram root in severely burned than in lightly burned sites, there was no significant difference between aspen and spruce across fire severity (Table 3.4). In contrast to NO_3^- uptake, specific NH_4^+ uptake differed significantly between species, and between sites, with a significant interaction between effects of species and severity (Table 3.4). Spruce took up significantly more NH_4^+ per gram root than aspen in severely burned sites ($p = 0.009$), but uptake rates were similar in lightly burned sites ($p = 0.99$). Both aspen and spruce took up significantly more NH_4^+ per gram root in severely burned than in lightly burned sites (Fig.3.2).

At the stand level, black spruce took up significantly more NO_3^- and NH_4^+ on a per unit area basis than aspen in lightly burned sites ($p<0.001$; Fig.3.3), while aspen took up 30 times more NO_3^- and 20 times more NH_4^+ than spruce in severely burned sites ($p<0.001$). These differences in stand-level uptake between species reflect the large differences in relative species biomass between stands of different severity levels (Table 3.1). Thus, the interaction of species x

N form preferences was magnified at the stand level, reflecting differences in the effects of fire severity on total biomass of the two species.

3.5 Discussion

We found that site-level differences in fire severity and post-fire organic layer depths did not change the relative contribution of NO_3^- vs. NH_4^+ to soil N supply by the second decade of succession. However, NO_3^- supply was surprisingly high 16 years following fire compared to other studies in interior Alaska (Van Cleve et al. 1983; Kielland et al. 2006). We found unexpected similarities in physiological responses of spruce and aspen to site differences in fire severity. This result contrasts with previous research demonstrating that closely related species, such as white spruce, not only exhibit a preference for NH_4^+ over NO_3^-, but also have a limited physiological capacity to acquire and process NO_3^- (Kronzucker et al. 1997). Our results suggest that while the initial effects of fire severity and post-fire organic layer depth on seedling recruitment and establishment are critical in shaping alternate trajectories of post-fire canopy composition (Johnstone and Kasischke 2005), subsequent stand level variations in nutrient uptake play a role in perpetuating patterns set early in succession. We suggest that variations in edaphic conditions created by burning combined with differences in density and biomass of aspen and spruce established early in succession are more important than inherent physiological preferences of the dominant tree species in maintaining alternate trajectories of post-fire canopy composition.

Effective N supply rates to plants are controlled by both the concentration of soil inorganic N and diffusion and mass flow through the soil, which in turn are controlled by factors such as soil buffering capacity, moisture content, and porosity (Barber 1995). In lightly burned sites, total N pools could be expected to be higher than in severely burned sites, due to the greater quantity of organic material remaining following fire. However, it appears that this factor was offset in the Hajdukovich Creek burn by greater diffusive capacity of mineral soil (due to greater bulk density and moisture content), resulting in similar inorganic N supply rates.

Our finding that NO_3^- represented approximately 40% of total inorganic N supply regardless of fire severity is noteworthy, since soils in boreal forests typically exhibit low soil

NO_3^- concentrations and low nitrification rates (Van Cleve et al. 1983; Kielland et al. 2006). Studies of post-fire N pools and availability have found that increases in available N following fire are transient, and decline within a few years following fire (Wan et al. 2001; Smithwick et al. 2005; Turner et al. 2007). Here we report relatively high NO_3^- supply rates occurring almost two decades following fire, in an ecosystem that has been shown to be dominated by NH_4^+ and organic N (Van Cleve et al. 1983; Kielland et al. 2006). Since severely burned soils were more alkaline than lightly burned soils, we might expect a shift towards greater dominance of bacteria relative to fungi (Flanagan and Van Cleve 1983), resulting in greater nitrification potentials in these sites. We found negligible effects of fire severity on NO_3^- and NH_4^+ supply rates, and both aspen and spruce absorbed more NH_4^+ than NO_3^- regardless of fire severity. These differences are reflected in the tendency for greater availability of NH_4^+ compared to NO_3^- in both severely and lightly burned sites, and is consistent with the expectation that supply and uptake in conifer forest soils are dominated by organic N and NH_4^+ rather than NO_3^- (Van Cleve et al. 1983).

Both aspen and spruce exhibited significantly higher specific uptake rates of both NH_4^+ and NO_3^- in severely burned compared to lightly burned sites. This could have been facilitated by higher soil temperatures in severely burned sites (Van Cleve et al. 1983; Bassirirad 2000). More importantly, we suggest that increased N uptake in severely burned sites is better explained by changes in soil physico-chemical characteristics which resulted in increased ion diffusion rates. Since the bulk of fine root biomass occurs in the top 15 cm of soil in boreal forests (Strong and La Roi 1983; Finer et al. 1997), variation in post-fire organic layer depth results in a shift in the soil environment to which the majority of fine roots are exposed. In severely burned sites, fine roots are located entirely in the mineral soil layer, whereas in lightly burned sites, the bulk of root biomass would be in the organic layer. High porosity of the unburned organic layer leads to large differences in bulk density (0.21 ± 0.02 g/cm^3 vs. 0.52 ± 0.03 g/cm^3 in mineral soils; Johnstone and Kasischke 2005), potentially increasing diffusion distances between nutrient ions and root surfaces in lightly burned versus severely burned sites. This is particularly relevant in the case of NO_3^- supply and uptake, as it is highly mobile in soil solution compared to NH_4^+ (Chapin 1980, Barber 1995).

Whereas NH_4^+ appears to be proportionally more important to N nutrition of black spruce, our results indicate that this species has a substantial capacity for NO_3^- uptake in the field. In addition our results show that the difference in specific uptake rates of NH_4^+ vs. NO_3^- in the field were much smaller (2X) than those observed under laboratory conditions (10X) (Chapin et al. 1986; Kronzucker et al. 1997; Min et al. 2000). Though we have no independent data to verify the conjecture that these observational dissimilarities reflect the difference between potential and realized uptake rates, it seems plausible that edaphic controls over ion movement would favor the acquisition of NO_3^- over NH_4^+ in the field since the diffusion coefficient of NO_3^- in soil is much higher than that of NH_4^+ (Barber 1995). In contrast to this, Kronzucker et al. (1997) showed in a laboratory study that white spruce is an NH_4^+ specialist and exhibits a limited physiological capacity to acquire NO_3^-, which may explain its failure to establish and compete with more nitrophilic species in high NO_3^- post-disturbance environments (Kronzucker et al. 1997). However, field uptake studies have shown that the capacity of *Picea abies* (Norway spruce) to acquire NO_3^- does not differ from its capacity to absorb other sources of nitrogen (Persson et al. 2003). It is worth noting that within a given fire severity, black spruce and aspen do not differ widely in specific uptake of NO_3^- or NH_4^+, suggesting that both species are considerably plastic in their response to the varied soil conditions associated with two ends of the fire severity spectrum. This physiological plasticity regarding uptake of different N forms may be adaptive in N-limiting soils (Kielland et al. 2006).

Because this study was conducted 16 years following fire, it is relevant to discuss our observations in light of successional changes that have taken place since these stands burned, particularly with reference to the effects of the developing vegetation. In essence, in the second decade of post-fire succession in this burn, severely burned sites had converted from pre-fire black spruce to aspen stands, while lightly burned sites remained black spruce stands (Shenoy et al. 2011). After the seedling establishment phase sets up initial differences in species relative density (Johnstone and Kasischke 2005), subsequent plant-soil feedbacks may play a role in perpetuating the relative dominance of each species in contrasting soil environments. For instance, aboveground biomass of aspen was nearly 20 fold greater in severely burned compared to lightly burned sites, while spruce biomass in severely and lightly burned sites was similar (Table 3.1). In aspen-dominated sites, higher leaf litter quality and warmer soil temperatures would favor faster decomposition rates and greater available N. Calculations of N stocks with respect to N uptake in these stands suggest that uptake of NH_4^+ and NO_3^- represent a small fraction of soil solution pools (<1%) in lightly burned sites, while NO_3^- uptake was approximately equal to NO_3^- availability in severely burned sites (data not shown). However, we do not have actual production or turnover rates of soil inorganic N. Aspen leaf litter suppresses moss colonization and growth (Startsev et al. 2008), thereby preventing the accumulation of a deep organic layer, and facilitating the growth and persistence of aspen in these sites. In addition to initiating changes in canopy composition, fire severity initiates changes in the understory vegetation, with an increase in grasses and forbs, and loss of evergreen shrubs, mosses and lichen species in severely burned sites, while predominantly coniferous species, ericaceous shrubs, and feather moss are maintained in lightly burned sites (Johnstone and Kasischke 2005; Bernhardt et al. 2011). These differences in vegetation composition can impact plant-soil feedbacks (Legare et al. 2005), and affect nutrient cycling at the stand level. For instance, deciduous stands in interior Alaska display higher nutrient uptake, requirement, and return, and faster forest floor turnover rates than coniferous stands (Van Cleve et al. 1983). Thus, the high N uptake rates we observed in severely burned relative to lightly burned stands may be driven in part by high nutrient requirement of the dominant vegetation. Our results show that effects of fire severity on plant nutrient uptake rates, and differences between species nutrient uptake are magnified at the stand level. We conclude that effects of fire severity on an important aspect of plant physiology (nutrient uptake) are likely to be manifested at the stand level through its effects on species biomass.

3.6 Acknowledgements

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3.8 Figures

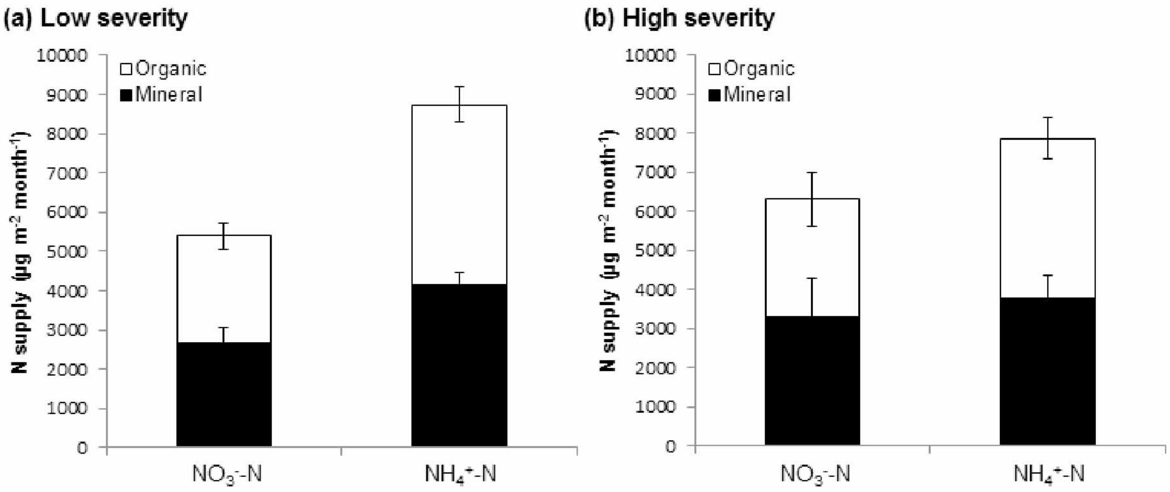

Fig. 3.1 Inorganic nitrogen supply rates (µg m^{-2} month^{-1}) measured using ion exchange probes in (a) low severity (n = 8) and (b) high severity (n = 4) sites. Nitrogen supply was measured in the mineral and organic soil layers separately. Values were averaged across two month long burial periods. Bars indicate mean ± SE.

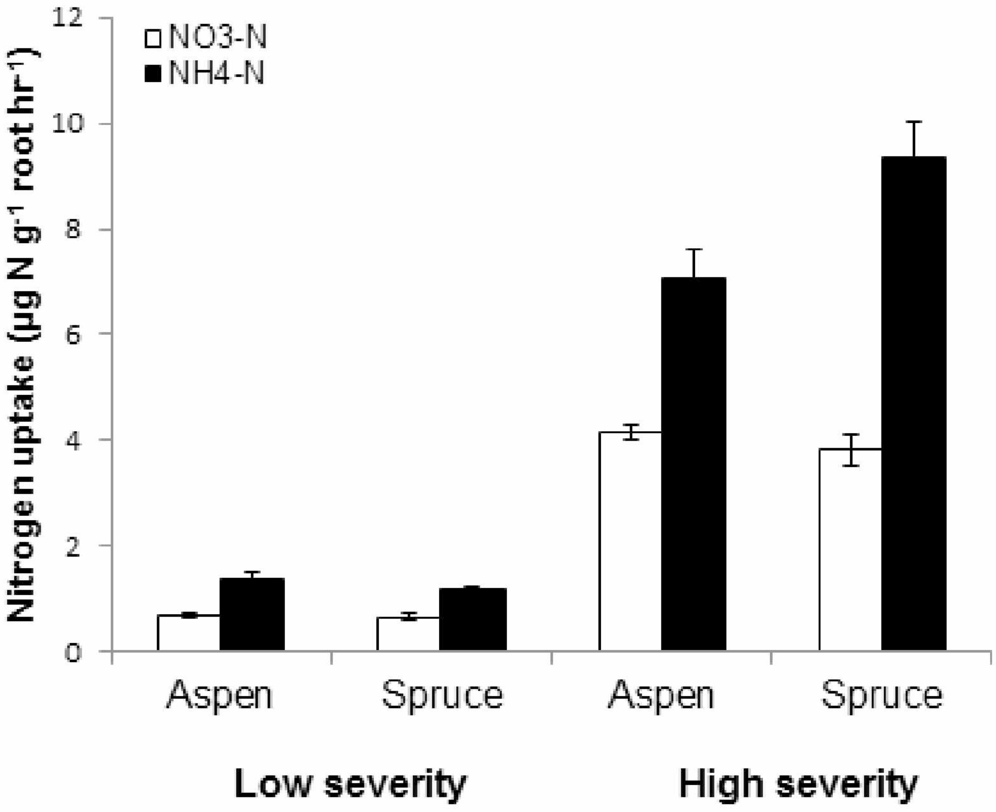

Fig. 3.2 Inorganic N uptake rates (µg N g^{-1}root hr^{-1}) in aspen and spruce measured using ^{15}N labeled NO_3^- and NH_4^+ over a 24 hour period during August 2010. Bars indicate mean ± SE (n = 5).

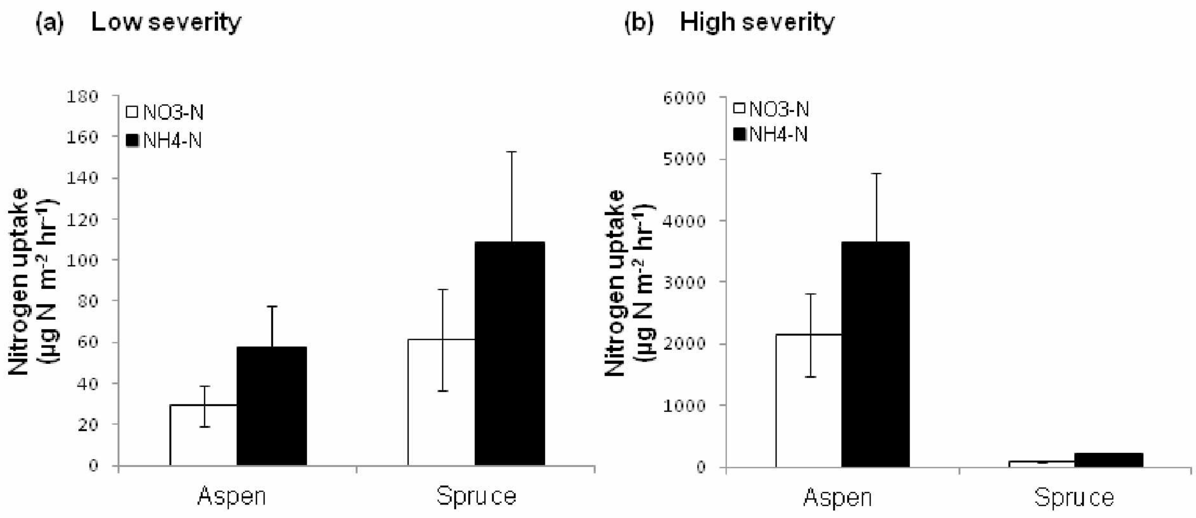

Fig. 3.3 Total inorganic N uptake rates for aspen and spruce expressed on an area basis (µg N m^{-2} hr^{-1}) in (a) low severity (n = 8) and (b) high severity sites (n = 4). Note axis maxima are different in each case. Bars indicate mean ± SE.

3.9 Tables

Table 3.1 Characteristics of sites representing lightly and severely burned areas within the 1994 burn (n = 10 plots per site). In the case of soil nitrogen concentration, n = 5. Values indicate mean (SE).

Severity	*Organic layer depth (cm)*	*Soil nitrogen concentration ($\mu g\ g^{-1}$ soil)*		***Aspen***			***Spruce***		
		NH_4^+	*NO_3^-*	*Stem density (# m^{-2})*	*Aboveground Biomass (g m^{-2})*	*Root biomass (g m^{-2})*	*Stem density (# m^{-2})*	*Aboveground Biomass (g m^{-2})*	*Root biomass (g m^{-2})*
Light	14 *(0.6)*	2.7 *(0.16)*	0.1 *(0.07)*	1.2 *(0.5)*	6.8 *(5.5)*	0.92 *(0.7)*	9.8 *(2.5)*	342.2 *(159.6)*	17.75 *(6.5)*
Severe	0.6 *(0.2)*	4.3 *(1.3)*	0.24 *(0.04)*	3.3 *(0.68)*	1303.2 *(467.9)*	120.78 *(41.6)*	5.0 *(1.5)*	375.3 *(225.7)*	22.64 *(7.98)*

Table 3.2 Summary of allometric equations used to estimate root biomass (g/ volume soil) of aspen and spruce from aboveground (shoot) biomass (g).

Species	n	Shoot biomass range (g)	Linear regression equation	R^2	p
Populus tremuloides	17	2.7 - 80	root mass = 0.8036 + 0.088 (shoot mass)	0.5	0.001
Picea mariana	17	1.7 - 210.5	root mass = 1.2656 + 0.033 (shoot mass)	0.69	<0.001

Table 3.3 Mean soil temperature and moisture measured over the 2010 growing season in lightly and severely burned sites within the 1994 burn. Values indicate mean (SE).

	Soil layer	***Severity*** *Light*	*Severe*	*t*	*p*
Temperature (ºC)	Organic	8.7*(1.4)*	10.3*(1.6)*	-0.75	0.48
	Mineral	7.9*(0.9)*	9*(1.1)*	-0.68	0.5
Moisture (%VWC)	Organic	0.29*(0.004)*	0.25*(0.008)*	4.7	0.007
	Mineral	0.32*(0.005)*	0.29*(0.01)*	1.8	0.15

Table 3.4 Effects of fire severity on N supply and uptake. Summary of results of two-way ANOVAs to test the effects of fire severity (high vs. low) and soil layer (mineral vs. organic) on N supply, or severity and species (black spruce vs. aspen) on N uptake, expressed on a per g root or per unit area basis. Significant p-values are indicated in bold.

Parameter		*F*	*p*
NH_4^+ supply (μg m^{-2} month^{-1})	Severity	0.67	0.42
	Layer	0.57	0.46
	Severity x Layer	0.01	0.9
NO_3^- supply (μg m^{-2} month^{-1})	Severity	0.59	0.45
	Layer	0.002	0.96
	Severity x Layer	0.09	0.76
NH_4^+ uptake (μg N g^{-1} root hr^{-1})	Species	5.85	**0.028**
	Severity	251.67	**<0.001**
	Species x Severity	7.85	**0.013**
NO_3^- uptake (μg N g^{-1} root hr^{-1})	Species	1.1	0.3
	Severity	389.54	**<0.001**
	Species x Severity	0.93	0.35
NH_4^+ uptake (μg N m^{-2} hr^{-1})	Species	9.37	**0.006**
	Severity	22.85	**<0.001**
	Species X Severity	20.5	**<0.001**
NO_3^- uptake (μg N m^{-2} hr^{-1})	Species	9.7	**0.005**
	Severity	22.26	**<0.001**
	Species x Severity	21.32	**<0.001**

Chapter 4.

Drivers of early stand dominance in burned black spruce forests[3]

4.1 Abstract

In recent decades increases in fire frequency, extent, and severity have been observed concomitantly with climate change in northern boreal forests. On parts of the landscape where severe burning occurs, the thick organic mats that are characteristic of mature black spruce stands may be completely combusted, resulting in exposure of the underlying mineral soil. Changes in post-fire residual organic layer depth have been linked to a shift in canopy dominance from coniferous (predominantly black spruce) to deciduous (predominantly aspen) tree species, and severely burned sites have been shown to support greater tree productivity than lightly burned sites in the second decade of succession. In this study I examined how variations in post-fire organic layer depth impact growth rates and physiological attributes of aspen and black spruce, and soil environment 15 years following fire. I then explored the relative importance of soil-based and stand density-based predictors of stand level aspen biomass, black spruce biomass, and the relative dominance of aspen vs. black spruce during post-fire succession. I found that aspen growth rates were 20 fold higher in shallow organic layer compared to deep organic layer sites, and that black spruce exhibited the opposite response to post-fire organic layer depth, but of a much lesser magnitude (2 fold). While aspen and black spruce did not exhibit discernible physiological adjustments (root : shoot biomass distribution, C : N ratio, specific N absorption rate) in a shallow organic layer site compared to a deep organic layer site, foliage of both aspen and black spruce were enriched in ^{15}N and depleted in ^{13}C in the shallow organic layer site. Variations in post-fire organic layer depth impacted soil temperature, moisture and pH such that soils in shallow organic layer sites were warmer, drier, and more alkaline than soils in deep organic layer sites. The large variations in stand level aspen biomass and relative dominance of aspen versus black spruce were best predicted by substrate conditions (organic layer depth, soil temperature, soil moisture, and soil pH). On the other hand, black spruce biomass was far less sensitive to the same variations in soil environment in relation to post-fire organic layer depth. My results demonstrate that patterns of stand biomass are largely being

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[3] Shenoy, A., Johnstone, J.F., Kielland, K. 2016. Drivers of early stand dominance in burned black spruce forests: In preparation for submission to Ecosystems

driven by substrate conditions rather than by inter specific competition in the second decade of post-fire succession.

4.2 Introduction

In northern boreal forests wildfire is a major agent of ecological disturbance and a key driver of secondary succession (Chapin et al. 2006). Climate warming is expected to increase fire activity on a global scale (Flannigan et al. 2009, Moritz et al. 2012). At northern latitudes, where the effects of climate warming have been especially pronounced, increases in fire frequency, severity, and extent have been observed in recent decades (Kasischke and Turetsky 2006, Soja et al. 2007, Kasischke et al. 2010, Calef et al. 2015). Boreal forests typically accumulate deep organic layers that are slow to decompose and are a major storehouse of carbon and nutrients. Changes in the thickness of the organic layer remaining following fire have been linked to a shift in boreal forest composition from coniferous (black spruce) to deciduous (aspen) canopy dominance (Johnstone and Kasischke 2005, Johnstone et al. 2010a). Whereas this shift in canopy dominance is controlled by the change in seedbed quality brought about by partial or complete combustion of the organic layer (Johnstone and Chapin 2006, Greene et al. 2007), the mechanisms by which post-fire organic layer depth impacts the soil environment and tree growth are as yet to be resolved.

Changes in canopy composition are particularly important in boreal forests due to the vast spatial extent of intact forest cover and the sharply contrasting effects of the alternate canopy dominants on ecosystem function and land-atmosphere feedbacks (Bonan et al. 1992). For instance, black spruce-dominated forests have low surface albedo and high sensible heat flux resulting in warming of surface temperatures (Bonan et al. 1992). In contrast, deciduous canopies increase the land surface albedo, and have high evapotranspiration rates, thereby reducing sensible heat flux and resulting in a net cooling effect on climate (Randerson et al. 2006). Deciduous trees and black spruce also differ with respect to key functional traits (Lavorel and Garnier 2002) that directly influence ecosystem properties such as stand productivity, decomposition rates, and nutrient availability (Chapin 2003, Diaz et al. 2004). Moreover, black spruce and deciduous forests differ strongly in their impacts on the fate of soil organic carbon (Laganiere et al. 2011), ecosystem carbon storage (Bond-Lamberty et al. 2007, Alexander and Mack 2015), and nutrient cycling (Melvin et al. 2015). Therefore, a shift from coniferous to deciduous dominance in boreal forests could impact the direction of climate feedbacks and influence ecosystem function.

The extent to which the organic layer is combusted during a fire is a key factor controlling the conditions under which post-fire seedlings recruit. Studies have shown that the mineral soil layer which is exposed after severe burning presents a higher quality seedbed for seedling recruitment in comparison to organic seedbeds (Zasada et al. 1983, Johnstone and Chapin 2006, Jayen et al. 2006, Greene et al. 2007). Moreover, patterns of recruitment and establishment set early in succession have been found to persist for decades in boreal forests (Fastie et al. 2003, Johnstone et al. 2004). Post-fire organic layer depth is positively related to black spruce density and biomass, and negatively related to aspen density and biomass (Johnstone and Kasischke 2005, Shenoy et al. 2011). Hence black spruce stands typically undergo self-replacement following light burning, whereas severely burned black spruce stands are likely to undergo conversion to deciduous-dominated forests during post-fire succession in interior Alaska (Johnstone et al. 2010a, Shenoy et al. 2011).

Although we know that post-fire organic layer depth affects the early dominance of black spruce vs. deciduous species, we still know little about *how* organic layer depth influences stand dominance via its effects on the post-fire soil environment and tree growth. Fire not only alters soil organic layer depths and seedbed quality, but also modifies the soil environment by removing vegetation, reducing microbial biomass (Dooley and Treseder 2012), depositing ash and charcoal in the forest floor (Zackrisson et al. 1996, Wardle et al. 1998), increasing soil temperature and pH (Van Cleve and Dyrness 1983), rapidly mineralizing organic material, and increasing inorganic nitrogen availability (Harden et al. 2004, Certini 2005). The severity of burning determines the magnitude of these changes (Zackrisson et al. 1996, Johnston and Elliott 1998, Choromanska and Deluca 2002, Harden et al. 2004). Residual organic layer depth is a key control on soil moisture and temperature during post-fire succession in boreal forests (Kasischke and Johnstone 2005). A study in Ponderosa pine forests showed that the increase in inorganic nitrogen availability following burning was positively correlated to the amount of forest floor burned (Covington and Sackett 1992). Increases in nitrogen availability have been found to wane with time since fire in some cases (Smithwick et al. 2005, Turner et al. 2007) or persist later into succession in boreal forests (Pare et al. 1993, Harden et al. 2003). Tree growth in boreal forests is strongly limited by soil temperature and nitrogen availability (Van Cleve et al. 1983). Nitrogen availability in turn is influenced by the soil physical environment (soil temperature, moisture, and pH) and rates of litter decomposition (Facelli and Pickett 1991, Attiwill and Adams 1993).

Therefore, changes in these soil parameters as a result of variation in post-fire organic layer depth could impact growth rate, physiological attributes (such as allocation to belowground vs. aboveground biomass), and productivity of canopy trees during post-fire succession.

Changes in the availability of resources such as light, water and nutrients have also been shown to result in changes in plant allocation to below or aboveground tissues in order to facilitate capture of the limiting resource in a given environment (Grime 1979, Garnier 1991, Poorter and Nagel 2000, Shipley and Meziane 2002). Moreover, evergreen vs. deciduous species have been found to have inherently different capabilities for expansion of root systems, uptake and assimilation of nutrients, and morphological plasticity under varying resource conditions (Aerts et al. 1991, Aerts 1995). Because variation in fire severity results in changes in the environment to which regenerating plants are exposed during post-fire succession, deciduous and evergreen seedlings may shift allocation to roots vs. shoots in response to these altered resource levels. The differential capacity of aspen or black spruce to adapt to the environmental conditions associated with the two ends of the fire severity spectrum could contribute to the observed patterns of species dominance.

I conducted this study 15 years following fire in stands that were black spruce-dominated prior to burning. I investigated how post-fire organic layer depth (1) alters the soil physical and chemical environment, (2) impacts root : shoot biomass distribution, whole plant C : N ratios (an indication of nutrient use efficiency), specific N absorption rate (amount of N absorbed per unit root biomass), and foliar ^{15}N and ^{13}C isotope discrimination, and (3) influences growth rate of aspen and spruce differentially. I then investigated the relationship between a suite of soil variables and stand level aspen biomass, spruce biomass, and the relative dominance of aspen vs. black spruce in burned stands. In doing so, I aimed to elucidate a mechanism by which alternate successional trajectories develop at two ends of the fire severity gradient, ranging from lightly burned sites with low aspen density and biomass to severely burned sites where stand biomass is dominated by aspen in the second decade of succession.

4.3 Methods

4.3.1 Study site description

I conducted this study in the Hajdukovich Creek burn, located near the town of Delta Junction (63°50'N, 145°40'W) in interior Alaska. The fire burned 8900 ha during the months of June-September 1994. The pre-fire vegetation was dominated by black spruce with a few interspersed patches of trembling aspen and white spruce (Johnstone and Kasischke 2005). The study region consists of a relatively flat outwash plain lying between the Alaska Range to the south, and the Tanana River to the north. The climate in this region is continental, with an average annual temperature of −2.3°C, and monthly average temperatures ranging from −19°C in January to 16°C in July (Big Delta, AK for 1971–2000, Shulski and Wendler 2007). Average annual precipitation is 286 mm, most of which is received as rain during the months May to September. Soils in the study area consist predominantly of silt loam overlying sand and gravel deposits, with some areas having a layer of stream-deposited cobble on top of the silt (Johnstone and Kasischke 2005). Unburned stands adjacent to the 1994 burn had 20 – 25 cm deep organic layers, ground layers dominated by feather moss, and well-established permafrost (Kasischke and Johnstone 2005).

4.3.2 Field measurements

In July 2009 I established fifteen 50 x 100 m sites within the 1994 burn that encompassed a gradient of post-fire organic layer depths ranging from 0 cm to 14 cm. Sampling in each site was carried out along a randomly oriented 50 m long baseline transect. In each site ten sampling points (n = 150 sampling points across the 15 sites) were located at random distances along the baseline transect, on a random side, and at a random distance (up to 50 m) from the transect line. At each sampling point I took a suite of vegetation and soil measurements.

4.3.3 Vegetation measurements

At each of the sampling points (n = 150), I measured the basal diameter (cm) of all aspen and spruce stems in 1 m x 1 m quadrats. Stem density was expressed as number of stems per m^2 of each species. Basal diameter measurements were converted to total aboveground biomass (g) estimates using allometric equations presented in Shenoy et al. (2011). Biomass values of individual aspen and black spruce (hereafter, spruce) were summed and divided by the total sampling area (10 m^2) to estimate aboveground biomass as g m^{-2}.

I collected 5 basal discs of each species in 6 severely burned sites and 5 lightly burned sites. In sites where aspen and spruce stems were almost all below breast height (1.37 m), basal discs were not collected. In each site I felled regenerating aspen (n = 5) and spruce (n = 5) individuals that were taller than breast height and within ~5 m of the baseline transect. Saplings or trees were felled just above the root swelling with either a handsaw or chainsaw.

4.3.4 Soil measurements

I collected a soil core (15 cm depth x 6 cm diameter) at the North West corner of each 1 m x 1 m quadrat, for determination of gravimetric soil moisture, soil pH and inorganic nitrogen concentration. The soil cores were frozen until lab analysis. I measured total organic layer depth (cm) on a 20 cm x 20 cm block of soil excavated 1-2 m away from the quadrat with a flat bladed shovel, after removing leaf litter from the surface. Mineral soil temperature (°C) and volumetric moisture (%) were then measured in the same soil pit using a hand held digital thermometer and Campbell Scientific Hydro-sensor, respectively. Temperature and moisture were both measured horizontally at a depth of 15cm. In plots where organic layer depth was greater than 15 cm (this occurred in 10 out of the 150 plots), the measurements were taken at 2 cm below the organic-mineral soil interface. The resulting depth at which temperature and moisture measurements were taken ranged from 15 cm to 22 cm across all sites. These measurements were made over two-week periods in July and August 2009, and averaged across these two months. From here on this measure of mineral soil moisture will be referred to as $\text{moisture}_{\text{vwc}}$. I inserted anion and cation exchange probes (Plant Root Simulator^{TM} probes, Western Ag Innovations, Saskatoon, SK) in the organic and mineral layers in the excavated pit in which soil moisture and temperature measurements were taken. Details of probe burial are described in Shenoy et al. (2013). Probes were buried in early July 2009 and collected a month later, and the process repeated to obtain NO_3^- and NH_4^+ supply rates over the period July – August and August – September 2009. N supply rates were averaged over these two time periods. I placed a sheet of Whatman #5 filter paper (standardized substrate) enclosed in a 0.5 mm mesh bag in the litter layer in each plot in order to measure decomposition potential. The weight of the substrate was measured prior to burial and collected and weighed two years later in August 2011. Mesh trays measuring 0.5 m x

0.5 m were placed in 6 randomly assigned plots within a subset of sites (4 shallow organic layer and 4 deep organic layer sites) for collection of litterfall over the 2010 growing season. The litter trays were deployed in July 2010 and collected in early October of the same year after litterfall had occurred.

In August 2014, I measured soil temperature at 5 cm depth increments from the soil surface to a depth of 35 cm in 3 deep organic layer sites and 3 shallow organic layer sites (3 plots per site). Soil temperature was not measured at 35 cm depth in shallow organic layer sites due to rockiness. For the same reason, temperature measurements at 30 cm depth were obtained at 2 of the 3 shallow organic layer sites. Temperature was measured horizontally with a hand-held probe over the course of 5 hours on the same day. Locations of the three soil pits were selected randomly from the 10 established plots within each site (n = 3 sites x 3 plots).

4.3.5 Whole plant measurements

During the 2010 growing season I collected the shoots and sampled the root systems of 10 aspen and spruce individuals in one severely burned and one lightly burned site each for biomass distribution and physiology measurements. I collected the nearest individual of aspen and spruce every 5 m along a 50 m transect in each site. In each case I harvested the aboveground (shoot) biomass, and collected four 15 cm deep x 6 cm diameter soil cores beneath the canopy diameter of each plant for estimation of root biomass. I picked roots of either aspen or spruce from the soil cores and pooled them. Roots and shoots were dried at 60°C and weighed to obtain root biomass (g per volume soil; values were averaged across the four cores) and shoot biomass (g per individual).

4.3.6 Laboratory analysis

In the lab, the soil cores were thawed and then separated into organic and mineral layers (when an organic layer was present), each of which was homogenized. A subsample of approximately 10 g was set aside for gravimetric moisture analysis. These samples were dried in a drying oven at 105°C until they reached constant weight, and the difference between initial and final weight was recorded. Gravimetric moisture (hereafter $\text{moisture}_{\text{grav}}$) was calculated as the percentage of water in the soil sample. I obtained soil samples for extraction from the mineral and organic layers of each core separately. I extracted approximately 10g of fresh soil in 75ml of

2M KCl (Robertson et al. 1999). Extracts were filtered through Whatman #5 filter paper and analyzed for NH_4^+ and NO_3^- by flow injection colorimetry using a Lachat autoanalyzer (Keeney and Nelson 1982). NH_4^+ and NO_3^- values were expressed as $\mu g\ N\ g^{-1}$ soil, and summed to obtain total inorganic nitrogen. Soil pH was determined electrometrically in water extracts following standard procedures (Robertson et al. 1999). The cation and anion exchange probes were brought to the lab on ice, rinsed with deionized water, and shipped to Western Ag Innovation, Saskatoon, SK for analysis of 1 M KCl extractable NH_4^+ and NO_3^- . N supply data were calculated on the basis of the surface area of the ion-exchange membrane (10 cm^2) and expressed as $\mu g\ N\ m^{-2}$ 30 $days^{-1}$. I dried the standardized decomposition substrates to constant weight at 60°C, and then weighed them. I calculated the weight loss (%) over the two year burial period as an index of decomposition potential.

Whole plant tissues (leaves, stems and roots) were ground using a Wiley mill after the dry weight was recorded. Tissues were then pulverized using a ball mill to ensure complete homogenization of the samples. The ground tissue samples were then analyzed for C and N concentration (%), $\delta^{15}N$ and $\delta^{13}C$ using a continuous-flow isotope ratio mass spectrometer with an instrument precision of <0.2‰ at the University of Alaska Fairbanks Stable Isotope Facility. Leaf litter samples that were collected in shallow organic layer and deep organic layer sites were first weighed to obtain litter mass (g), and then analyzed for C and N concentration (%) by the same method.

I air-dried basal discs of aspen and spruce and then sanded them with a belt sander using progressively finer grades of sandpaper (ranging from 50 to 220 grit) until the ring boundaries were clearly visible. I measured ring widths using a Velmex sliding stage at 0.001 mm resolution. The mean series intercorrelation calculated in the program COFECHA (Grissino-Mayer et al. 1992) was 0.34 for aspen and 0.46 for spruce.

4.3.7 Data analysis

4.3.7a Data averaging and calculations

All of the soil variables and vegetation density and biomass values were averaged across the 10 plots within each of the 15 sites to obtain the site level average. These values (n = 15) were used for all correlation analyses estimating relationships between organic layer depth and soil variables, and between soil variables and the deciduous : coniferous biomass ratio. Due to missing values for some of the variables in the data set, the resulting number of plots was 132. Since stem density and biomass values were positively skewed, $\log_{10}$ transformed values were used in all analyses. To deal with zero values for density and biomass encountered in the data, the smallest value in the data set was added to all the values in the data set to allow $\log_{10}$ transformation prior to analysis. Individual plot data ($n = 132$) were used in the principal components analysis of the explanatory variables. For whole-plant analysis, values for individual plants ($n = 10$) sampled from 1 severely burned and 1 lightly burned site were used as replicates.

Because each soil core contained varying proportions of organic and mineral soil depending on organic layer depth, volumetric moisture content of the soil in a core of dimensions 15 cm deep x 6 cm diameter was calculated in two steps. First, the mass (g) of organic material in the core was calculated as the product of organic layer volume and bulk density (BD), using published bulk density values measured in the 1994 burn (Johnstone and Kasischke 2005). The average surface bulk density reported in the preceding paper for severely burned plots (BD = 0.52 ± 0.03 g cm^{-3}) was used in mineral layer calculations, and the average surface bulk density reported for lightly burned plots (BD = 0.22 ± 0.02 g cm^{-3}) was used for organic layer calculations. $Moisture_{grav}$ measurements of organic layer samples were then used to estimate the moisture content of the organic portion of each soil core. Similarly, the mass of mineral soil in each core was determined and percent moisture (v/v) measurements from the mineral soil layer ($moisture_{vwc}$) were used to estimate the moisture content of the mineral portion of the core. The moisture contents of each layer thus calculated were summed and then expressed as a percentage of total soil mass in the core. This quantity is from here on referred to as soil moisture content (%). Inorganic nitrogen pools were calculated by multiplying NO_3^- and NH_4^+ concentrations ($\mu g\ g^{-1}$) in the organic and mineral soil by the mass (g) of organic material and mineral soil in each core respectively. Total inorganic N ($NO_3^-+NH_4^+$) in the core thus obtained was expressed as g N m^{-2} (to a depth of 15 cm) using the surface area of the soil core. Specific N absorption rate was calculated by dividing total plant N content (mg) by root biomass (g) (Schlesinger et al. 1989).

For the tree ring analysis ($n = 11$), ring increment measurements for 2-3 radii per disc were averaged. Cumulative distance to the center was calculated starting from the outer most ring to obtain the radius for each year of growth. Basal area increment (mm^2) was calculated for a given year of growth using the formula:

$$3.142 * (radius_y^2 - radius_{y-1}^2)$$

where y is the year of growth in question and y-1 is the preceding year of growth (Fritts 1971). Annual basal area increment was averaged across all the trees of a given species in a site to obtain an annual site level average.

Natural abundance of ^{15}N and ^{13}C were expressed in per mil (‰) deviation from the international standards:

$$\delta^{15}N \text{ or } \delta^{13}C = (R_{sample}/\ R_{standard} - 1) * 1000$$

where R in each case is $^{15}N/^{14}N$ or $^{13}C/^{12}C$. The standards for N and C were atmospheric nitrogen and Pee Dee Belemnite respectively (Peterson and Fry 1987).

4.3.7b Statistical analysis

I used t-tests to detect significant differences ($\alpha = 0.05$) in basal area increment between shallow organic layer and deep organic layer sites ($n = 15$). I analyzed plant physiological data (root : shoot ratio, C : N ratio, specific N absorption rate, foliage $\delta^{15}N$, and $\delta^{13}C$) using two-way Analysis of Variance with species and severity as categorical fixed effects ($n = 10$ individuals per treatment combination). There was some evidence of heteroscedasticity in the root : shoot ratio, C : N ratio, and $\delta^{13}C$ data. Therefore I performed a two-way ANOVA using the white.adjust command in the car package in R (Fox and Weisberg 2011). The white.adjust command applies the "hc3" correction (Long and Ervin 2000) to calculate heteroscedasticity-corrected covariance matrices. I conducted Tukey Honestly Significant Difference test for post-hoc comparisons of means, using the multcomp package in R (Hothorn et al. 2008). I used Pearson product-moment correlations to estimate bivariate relationships between organic layer depth and soil variables and between soil variables and deciduous : coniferous biomass ($n = 15$). An unpaired t-test was used to test significant difference in mean soil temperature measured at 15 cm depth between deep organic layer and shallow organic layer sites ($n = 3$; Appendix 4.B).

The relationships between a suite of soil variables (organic layer depth, soil moisture, soil temperature, soil pH, and inorganic N supply; Table 4.1) and the response variables (1) aspen biomass, (2) spruce biomass, and (3) aspen : spruce biomass (Table 4.2) were investigated. Many of the explanatory variables were highly correlated with one another (Table 4.3). Because multicollinearity exists among the explanatory variables, using Ordinary Least Squares regression techniques to model the response variable would result in biased parameter estimates that are difficult to interpret (Neter et al. 1990, Legendre and Legendre 1998, Graham 2003). A Principal Components Regression (PCR) approach was therefore implemented, as this technique produces stable and meaningful parameter estimates even when multicollinearity exists among the explanatory variables (Gunst and Mason 1980, Draper and Smith 1981, Graham 2003). In order to be able to compare the relative influence of each variable, I standardized the explanatory soil variables to z-scores (where z-score = value – mean/standard deviation). I carried out a Principal Components Analysis (PCA) on the standardized explanatory variables (n = 132) using the rda function in the package vegan in R (Borcard et al. 2011, Oksanen et al. 2015). The orthogonal principal components thus obtained are linear combinations of the original standardized variables, and account successively, for the most variation in the explanatory variables. The Kaiser-Guttman criterion (Guttman 1954) was applied to select interpretable principal components axes. Only those principal component axes whose eigenvalues (EV) were greater than the mean eigenvalue calculated across all axes were interpreted. Pearson's correlations between the principal component axes and the original variables were used to interpret the axes. Principal component scores for these axes were then used as independent explanatory variables in linear mixed effects models with random intercept, explaining the variation in $\log_{10}$aspen biomass (aspen biomass model), $\log_{10}$spruce biomass (spruce biomass model), and $\log_{10}$aspen biomass : $\log_{10}$spruce biomass (biomass ratio model). Because of the hierarchical nature of the data (132 plots were nested within 15 sites), "site" was introduced as a random effect in all the models. This approach accounts for the dependence among observations within a site (random effect), while examining the influence of the fixed effects on the response variable (Zuur et al. 2009). In order to assess whether the inclusion of aspen or spruce stem density (as an index of interspecific competition) improved the model (by decreasing model deviance), additional mixed models were assessed in which the explanatory variables included the PC scores as well as 1) stem density of the other species (eg. spruce density in the case of the aspen biomass model), and 2) stem density of both aspen and spruce. In the case of the ratio model, three additional models were assessed, which included the PC scores as well as 1) aspen density, 2) spruce density, and 3) stem density of both aspen and spruce as explanatory variables. To evaluate the relative support for each of the models, I used Akaike Information Criteria (AIC) model selection procedures (Burnham and Anderson 2002, Anderson 2008). AIC values (AIC) were calculated using the formula

$$AIC = -2\log L + 2K$$

Where K is the number of parameters, and logL is the log likelihood value. I used AIC weights (w_i) and model deviance (-2logL) to assess the relative support for each of the models given the data (Anderson 2008). All statistical analyses were performed using R (R Development Core Team 2012).

4.4 Results

4.4.1 Effects of post-fire organic layer depth on stand basal area increment

Post-fire organic layer depth had a large impact on aspen and spruce growth (Fig.4.1). Aspen basal area increment over the 10 year period (2000 – 2010) was on average 20 fold greater ($t = 8.98$, $p < 0.001$) in shallow organic layer sites (260.03 ± 28.77 mm^2 $year^{-1}$) than in deep organic layer sites (12.96 ± 2.23 mm^2 $year^{-1}$). By contrast spruce basal area increment over the same time period exhibited the opposite response to post-fire organic layer depth, with only slightly more than 2 fold greater ($t = -1.73$, $p = 0.1$) response in deep organic layer (38.1 ± 12.9 mm^2 $year^{-1}$) vs. shallow organic layer sites (15.59 ± 4.34 mm^2 $year^{-1}$).

4.4.2 Effects of post-fire organic layer depth on plant physiological attributes

Plant biomass distribution patterns: Aspen had higher root : shoot ratios than spruce regardless of site post-fire organic layer depth (Fig. 4.2a, Table 4.4). However, site organic layer depth did not affect root : shoot biomass distribution of either species (Fig. 4.2a). Spruce had greater whole plant C : N ratio than aspen in the shallow organic layer site, whereas there was no significant difference between aspen and spruce C : N ratio in the deep organic layer site (Fig. 4.2b, Table 4.4). Specific nitrogen absorption rate (SAR) did not vary significantly by species or site organic layer depth (Fig. 4.2c, Table 4.4).

Leaf litter mass was 3-fold higher in shallow organic layer sites compared to deep organic layer sites (Fig. 4.5). Leaf litter N content was 0.51 ± 0.08 g m^{-2} in shallow organic layer sites, and 0.21 ± 0.03 g m^{-2} in deep organic layer sites.

Foliage C and N isotope discrimination: Foliage from aspen growing in the deep organic layer site was significantly depleted in ^{15}N compared to those growing in the shallow organic layer site (Fig. 4.3a, Table 4.4). A similar pattern was observed in the case of spruce, with foliage in the deep organic layer site being more depleted in ^{15}N compared to foliage of plants growing in the shallow organic layer site, although this difference was not statistically significant. Furthermore, spruce foliage was significantly more depleted in ^{15}N than aspen foliage regardless of site organic layer depth (Fig. 4.3a, Table 4.4). In terms of δ^{13}C, aspen foliage was significantly depleted compared to spruce regardless of site organic layer depth (Fig. 4.3b, Table 4.4). Both aspen and spruce were significantly more depleted in ^{13}C in the shallow organic layer site compared to the deep organic layer site (Fig. 4.3b, Table 4.4).

4.4.3 Relationships between post-fire organic layer depth and soil variables

Organic layer depth was positively related to soil volumetric moisture content ($r = 0.85$, $p < 0.001$ Fig. 4.4a) and negatively related to mineral soil temperature ($r = -0.79$, $p < 0.001$; Fig. 4.4b). There was an increase in soil inorganic nitrogen pool (g m^{-2} to a depth of 15 cm) as organic layer depth increased ($r = 0.86$, $p < 0.001$; Fig.4.4d; Appendix 4.A); however, there was no significant relationship between organic layer depth and supply of inorganic N as measured with the ion-exchange probes in the organic or mineral soil layers ($p = 0.41$ and $p = 0.85$ respectively). Furthermore, I found a significant negative relationship between organic layer depth and soil pH ($r = -0.74$, $p = 0.002$; Fig. 4.4c). Site decomposition potential also showed a negative relationship with organic layer depth ($r = -0.67$, $p = 0.008$; Fig.4.4e).

4.4.4 Principal components regression and model selection

The PCA that was conducted on the explanatory (soil) variables revealed that PC1 accounted for 43% of the variability in the data (Fig.4.6). Organic layer depth and moisture were strongly positively correlated with PC1 ($r = 0.85$ and $r = 0.83$ respectively), whereas temperature and pH were negatively correlated with this axis ($r = -0.87$ and $r = -0.61$ respectively). PC2 accounted for approximately 20% of the variability in the data, and was positively correlated with TIN_{org} and TIN_{min} ($r = 0.59$ and $r = 0.83$ respectively; Fig.4.6). PC1 (EV = 2.59) and PC2 (EV = 1.20) were the only axes whose eigenvalues were greater than the average eigenvalue calculated across all 6 axes (average EV = 0.99). Therefore the scores for the first two PC axes were used as the predictor variables in the aspen biomass, spruce biomass, and biomass ratio models.

Based on AIC model weights, variation in aspen biomass was best explained by the model containing PC1 and PC2 ($w_i = 0.94$; Table 4.5).Variation in aspen biomass was significantly predicted by only PC1, and the response was negative (Table 4.5). The inclusion of neither spruce density alone (model 2; Table 4.5), nor aspen and spruce density (model 3; Table 4.5) as explanatory variables resulted in a decrease in model deviance relative to the model containing PC1 and PC2. Variation in spruce biomass was not predicted by any of the explanatory variables (Table 4.6). Variation in biomass ratio was best explained by the model containing PC1 and PC2 ($w_i = 0.65$; Table 4.7). PC1 was the only significant predictor of biomass ratio (Table 4.7). The inclusion of neither aspen density (model 2; Table 4.7), spruce density (model 3; Table 4.7) nor both species density (model 4; Table 4.7) as explanatory variables resulted in an improvement to the model (decrease in model deviance) relative to the model containing PC1 and PC2.

4.5 Discussion

Variation in post-fire organic layer depth results in a shift in the soil environment to which the majority of plant roots are exposed; roots experience relatively colder, wetter and more acidic conditions in deep organic layer sites, but warmer, drier, more alkaline conditions in shallow organic layer sites. I found that differences in organic layer depth have a large impact on aspen and spruce growth rates, with aspen exhibiting dramatically greater annual basal area increment in severely burned sites and spruce exhibiting the opposite pattern, albeit of a lower magnitude. Variations in aspen biomass and the relative dominance of aspen vs spruce were predicted by substrate conditions (organic layer depth, soil moisture, soil temperature, and soil pH), whereas spruce biomass was much less sensitive to the same variations in soil conditions. My findings highlight the role of post-fire organic layer depth in initiating a major shift in forest composition and productivity via its effects on plant growth and soil environmental conditions.

I found that post-fire organic layer depth has a positive impact on the growth rate (basal area increment per year) of spruce, but a negative impact on aspen growth. However, the effect of fire severity on growth (positive or negative) differed by an order-of-magnitude between the two species. These differences in growth rate clearly reflect the divergent patterns of stand dominance observed during the second decade of succession (albeit in trees that area taller than 1.37 m) at the two ends of the post-fire gradient in organic layer depth (Shenoy et al. 2011).

My results show that root biomass (biomass per unit volume of soil) relative to shoot biomass (total aboveground biomass) was higher in the case of aspen than spruce regardless of site organic layer depth. This finding is similar to results from a greenhouse study that found aspen had higher root : shoot ratio in comparison to black and white spruce (Peng and Dang 2003). The finding that spruce had greater whole plant C : N ratio (an indication of nutrient use efficiency) than aspen is not surprising. Slow-growing evergreen species which are adapted to low-nutrient availability, typically have long-lived foliage and are generally expected to have a high nutrient use efficiency in comparison to fast-growing species from productive habitats (Grime 1979, Vitousek 1982, Field and Mooney 1986, Aerts 1995, Aerts and Chapin 2000). Spruce foliage showed significantly depleted δ^{15}N values in comparison to aspen in the high severity site. This pattern could be indicative of greater dependence on ectomycorrhizal fungi for uptake of organic N in the case of spruce (Hobbie et al. 1999, Kielland et al. 2006, Craine et al. 2009), and uptake of inorganic N forms (that tend to be isotopically lighter than organic N forms from which they are derived) in the case of aspen (Nadelhoffer et al. 1994). A study conducted in black spruce forests in interior Alaska (Mayor et al. 2012) showed that stands with low foliar δ^{15}N values tended to have high dependence on ectomycorrhizal derived organic N (a scenario similar to our lightly burned black spruce-dominated stands), whereas stands that had higher foliar δ^{15}N values tended to have lower fungal biomass and higher NH_4^+ usage (a scenario similar to our severely burned aspen-dominated stands). Here I found that aspen foliage was significantly enriched in ^{15}N in the shallow organic layer site compared to the deep organic layer site. This pattern could be attributed in part to the depth at which aspen roots are accessing inorganic nitrogen – older soil nitrogen at deeper depths can be expected to be enriched relative to soil nitrogen that is closer to the soil surface (Garten 1993). Severe burning has been found to result in greater declines in ectomycorrhizal fungi populations than in low intensity burns (Dahlberg et al. 2001, Dahlberg 2002). Moreover, results from a study conducted in burned black spruce stands in this study region showed that ectomycorrhizal colonization could take >15 years to recover to pre-fire levels (Treseder et al. 2004). Therefore, it is possible that fungal biomass is reduced in severely burned sites resulting in an overall isotopic enrichment of the vegetation.

Aspen foliage had enriched $\delta^{13}C$ values compared to spruce in both the low severity and the high severity site, a pattern that is not consistent with the expectation that evergreen species like spruce should have higher $\delta^{13}C$ values due to inherently higher water use efficiency compared to deciduous species like aspen (Farquhar et al. 1989). Spruce foliage was significantly depleted in ^{13}C in shallow organic layer sites compared to deep organic layer sites. Results from an earlier study conducted in these stands showed that inorganic nitrogen uptake by aspen and spruce were significantly higher in severely burned sites compared to lightly burned sites (Shenoy et al. 2013). I suggest that in severely burned sites, increased N uptake results in increased photosynthesis and stomatal conductance, leading to depleted $\delta^{13}C$ values, and the opposite pattern in lightly burned sites could in part explain the enriched foliar $\delta^{13}C$ values of plants growing in these sites.

My findings show that conditions in the top 15 cm of soil, where the majority of plant roots occur in boreal forests (Finer et al. 1997, Ruess et al. 2006) are significantly impacted by variations in post-fire organic layer depth. Post-fire organic layer depth has a strong inverse relationship with mineral soil temperature, but a clear positive correlation with soil moisture, consistent with the findings of a previous study conducted in this burn (Kasischke and Johnstone 2005). Moreover, pH measurements taken in the top 15 cm of soil showed that severely burned sites with shallow organic layers were more alkaline in comparison to lightly burned sites with deep organic layers. Inorganic nitrogen pools in the top 15 cm of soil increased with increasing organic layer depth, perhaps due to the greater quantity of accumulated organic material in deep organic layer sites relative to shallow organic layer sites. However, rates of inorganic nitrogen supply in the organic and mineral soil layers were similar across sites. A recent study conducted in western Siberia across a latitudinal transect encompassing ecosystems from tundra to steppe, has shown that rates of nitrogen mineralization and nitrification are significantly higher in mineral than in organic soil horizons across ecosystems (Wild et al. 2015). It is possible that higher nitrogen mineralization and nitrification rates in mineral soils (predominant in shallow organic layer sites) offset the smaller inorganic nitrogen pools in these sites compared to lightly burned sites with deep organic layers, resulting in similar inorganic nitrogen supply rates across the post-fire organic layer depth gradient.

Decomposition potential was higher in shallow organic layer sites than in deep organic layer sites (Fig.4.4e). Studies in Canadian boreal forests revealed that decomposition rates were 5-10 times slower in deep organic layer soils compared to shallow organic layer soils (Trumbore and Harden 1997). A study that examined biotic and abiotic factors influencing decomposition along a gradient of aspen abundance in boreal forests in eastern Canada showed that decomposition rates of standard substrates were higher in stands with a greater aspen component due to associated increases in the soil macrofaunal community (Laganiere et al. 2009). I found that litter nitrogen content was over 2-fold higher, and litter mass almost 3-fold higher in sites with shallow organic layers compared to deep organic layer sites (Fig. 4.5). There is a large body of evidence that shows decomposition rates are strongly driven by soil environment and substrate quality of leaf litter (Aerts 1997, Cornelissen 1996). Plant functional type is also an important driver of decomposition rates (Cornwell et al. 2008), through effects on litter chemistry as well as through species effects on soil microclimate, carbon availability, and nitrogen mineralization rates (Grime et al. 1996, Cornelissen et al. 1999, Perez-Harguindeguy et al. 2000, Eviner et al. 2006). Although I did not quantify decomposition rates of resident leaf litter in this study, I have shown that fire significantly impacts soil variables that in turn may impact the decomposition environment. This taken together with my finding that sites with higher decomposition potential also had greater litter nitrogen content is indicative of possible positive feedbacks between vegetation production, leaf litter quality, decomposition rate, and nutrient availability. Feedback loops of this nature (Johnstone et al. 2010b) are likely to contribute to the stability and persistence of deciduous stands that develop in severely burned parts of the boreal forest.

The principal component axis which accounted for the most variation among the environmental variables (PC1) represented a gradient in substrate conditions, ranging from deep organic layer depths and high soil moisture, to high soil temperature and alkaline soil pH. This axis largely represents the strong linkage of post-fire organic layer depth to soil moisture and temperature gradients (Kasischke and Johnstone 2005), with deep post-fire organic layers being associated with relatively colder, wetter, and more acidic conditions not favorable to aspen regeneration, and shallow organic layers being associated with warmer and drier conditions more suitable for aspen regeneration and growth. The second principal component axis (PC2) was related to soil nitrogen supply. Results of the linear mixed-effects models showed that PC1 was the only significant predictor of aspen biomass, and was negatively related with this response variable, indicating that increased biomass accumulation in aspen is associated with relatively warm, dry, alkaline soils and shallow organic layers. In interior Alaska aspen productivity tends to be favored in warm, well drained sites (Van Cleve et al. 1983, Van Cleve et al. 1991), and soil pH has been found to be positively related to both aspen height growth (Paré et al. 2001) and productivity (Pinno and Belanger 2011). Variation in spruce biomass however was not explained by any of the explanatory variables. Growth chamber experiments have shown that spruce growth exhibits lower sensitivity to temperature compared to many deciduous tree species (Landhausser et al. 1996, Landhausser et al. 2001). Furthermore, biomass accumulation in black spruce has been found to be less sensitive to changes in organic layer thickness in comparison to aspen (Gewehr et al. 2014). It seems plausible that the decrease in spruce biomass in shallow organic layer sites (compared to deep organic layer sites) may be due to competition for light with the fast growing aspen in these sites. However the results of this study suggest that variation in neither spruce nor aspen biomass were responsive to interspecific competition (as indicated by stem density of the other species). The relative dominance of aspen versus spruce (aspen : spruce biomass) was predicted by PC1, and was thus associated with the same conditions that are driving variation in aspen biomass.

A key finding of this study is that substrate conditions (organic layer depth, soil moisture, soil temperature, and soil pH) explained the most variation in aspen biomass, and the relative dominance of aspen versus spruce. The physical characteristics of organic and mineral substrates differ with respect to porosity, bulk density, hydraulic conductance, and thermal conductivity (Hinzman et al. 1991). All of these factors influence available soil moisture, stability of moisture supply, soil temperature, and tortuosity of the soil matrix to which plant roots are exposed. These in turn influence the effective soil volume available to plant roots for water and nutrient uptake, rates of fine root growth, and rates of nutrient supply and transport in the soil matrix (Barber 1995). It is well established that mineral soil seedbeds (predominant in severely burned sites) provide a more favorable environment for seedling recruitment and establishment compared to organic seedbeds (predominant in lightly burned sites) (Johnstone and Chapin 2006, Greene et al. 2007). Due to its high hydraulic conductivity the organic layer responds quickly to wetting and drying episodes (Hinzman et al. 1991) resulting in an unstable moisture supply for seedlings and consequent high rates of seedling mortality. Mineral soils on the other hand provide a far more stable moisture supply to seedlings owing to their lower porosity and hydraulic conductance. These characteristics of mineral versus organic substrates are likely to have played a large role in allowing post-fire aspen seedlings to achieve higher rates of survival and growth in severely burned mineral soil seedbeds compared to seedlings that established on lightly burned organic seedbeds during the initial phase of post fire succession. In addition to the negative relationship between post-fire organic layer depth and soil temperature, I also found that soil temperature decreased more rapidly with depth in deep organic layer sites compared to shallow organic layer sites (Appendix 4.B). For example, the temperature gradient (change in temperature/ change in depth) between 5 and 15 cm below the soil surface was 0.5 in lightly burned sites, and 0.2 in severely burned sites. At 15 cm depth, soil temperature in lightly burned sites ($5.9 \pm 0.4^{\circ}C$) was significantly lower than in severely burned sites ($9.3 \pm 0.2^{\circ}C$; $t = 7.9$, $p<0.01$; Appendix 4.B). Root growth in aspen and related deciduous tree species is inhibited at below $5^{\circ}C$ (Wan et al. 1999, Landhäusser et al. 2001, Landhäusser et al. 2003), and roots penetrate to greater depths in warm compared to cold soils (Tyron and Chapin 1983). Warmer soil temperatures also result in significantly higher rates of photosynthesis and whole-plant growth in aspen (King et al. 1999, Landhäusser et al. 2001). Moreover, root hydraulic conductance and rates of root water uptake decrease at lower soil temperatures in aspen (Wan et al. 2001), and cold soil temperatures appear to suppress aspen seedling growth to a greater extent than seedlings of coniferous tree species such as *Picea glauca* (Landhäusser et al. 2001, Landhäusser et al. 2003). Lastly, black spruce maintain higher root elongation rates in cold, wet soil compared to aspen and other deciduous tree species (Tyron and Chapin 1983). Thus, the warmer soil temperatures observed in severely burned sites with mineral soil substrates likely facilitated aspen to attain greater rates of water and nutrient uptake (Shenoy et al. 2013), thereby resulting in higher rates of aspen biomass accumulation in these sites. Therefore it is plausible that the large increase in aspen biomass associated with shallow organic layers may be due to a release from the negative effects of substrate conditions (in particular soil temperature) prevailing in sites with deep organic layers. The high aspen productivity observed in severely burned sites could be expected to result in higher water use and evapotranspiration rates, thereby leading to drier soils in these sites. This could explain the inverse relationship between aspen biomass and soil moisture observed 16 years following fire.

The greater rates of germination success and survival (Johnstone and Chapin 2006), and higher initial density and biomass (Johnstone and Kasischke 2005) of deciduous seedlings in severely burned sites compared to lightly burned sites shortly after fire translate into much higher stand level aspen biomass (14 fold) in severely burned sites compared to lightly burned sites in the second decade of succession. The magnitude by which spruce biomass differs between high and low severity sites is modest in comparison (7 fold), a result that reinforces findings from other studies which have shown that thick organic mats are more of an impediment to aspen seedling success and growth than it is for spruce (eg. Greene et al. 2007, Gewehr et al. 2014). Consequently, stand dominance (ratio of aspen : spruce biomass) patterns in the second decade of succession (Shenoy et al. 2011) are largely being driven by variations in aspen biomass in relation to organic layer depth. Here I have shown that growth rates (basal area increment averaged over a 10 year period) of aspen growing in severely burned sites were nearly 20 fold greater compared to aspen growing in lightly burned sites, whereas spruce growth rates were a little over 2 fold greater in lightly versus severely burned sites. Similar relationships between soil organic layer depth and aspen and spruce basal area increment have been reported in the Canadian boreal forest (Gewehr et al. 2014). These results suggest that the positive effects of soil conditions associated with mineral soil substrates extend well beyond the initial seedling recruitment phase, and may continue to influence aspen growth rates into the second decade of succession resulting in the differential patterns of biomass accumulation and stand dominance in relation to post-fire organic layer depth.

4.6 Acknowledgements

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4.8 Figures

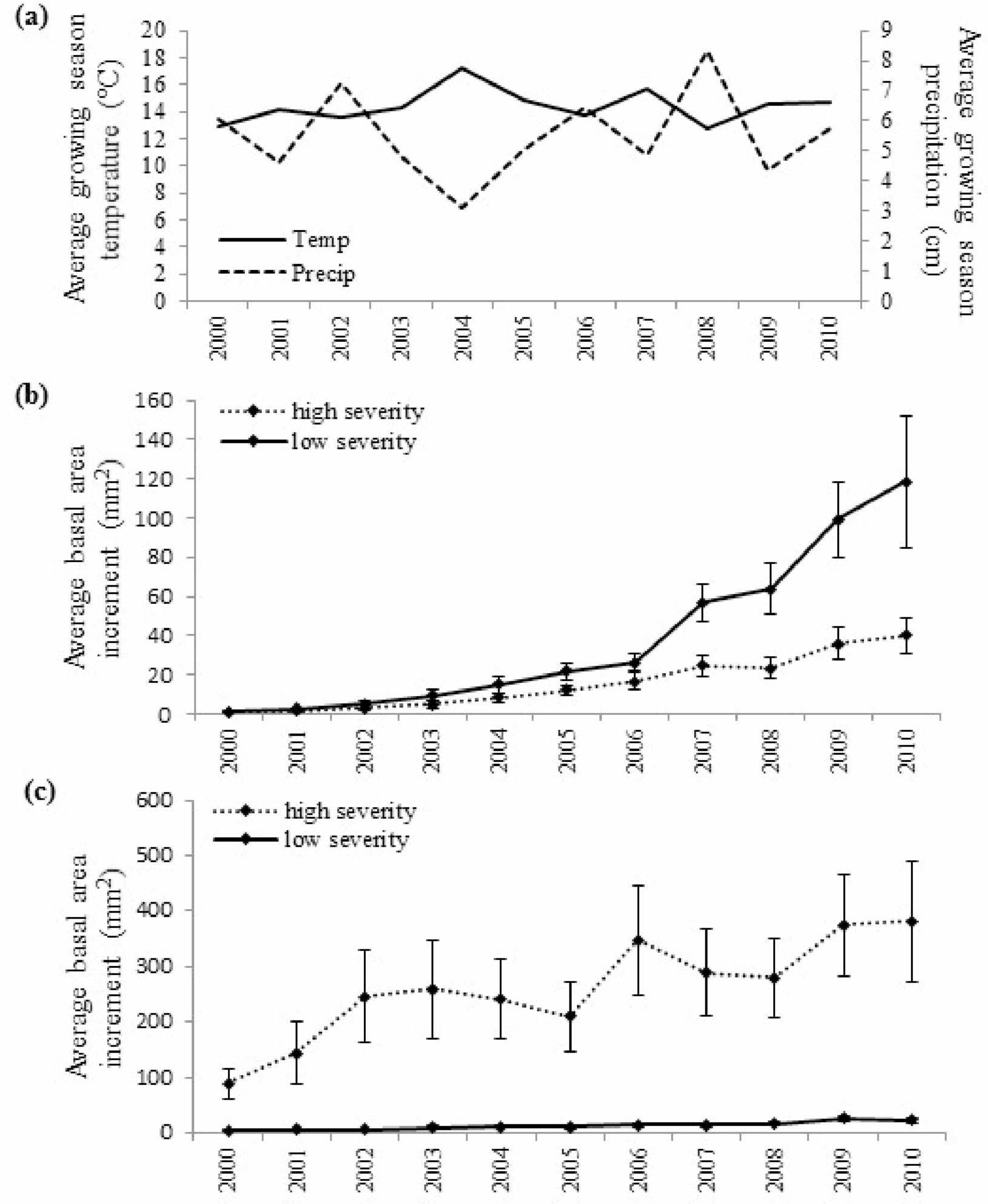


Fig.4.1 (a) Average growing season (June-August) temperature and precipitation over the period 2000-2010 in the Delta Junction region, (b) black spruce basal area increment (mm^2), and (c) aspen basal area increment in severely burned shallow organic layer sites (n = 5) and lightly burned deep organic layer sites (n = 6) over the period 2000-2010 in the Hajdukovich Creek burn (Mean ± SE).

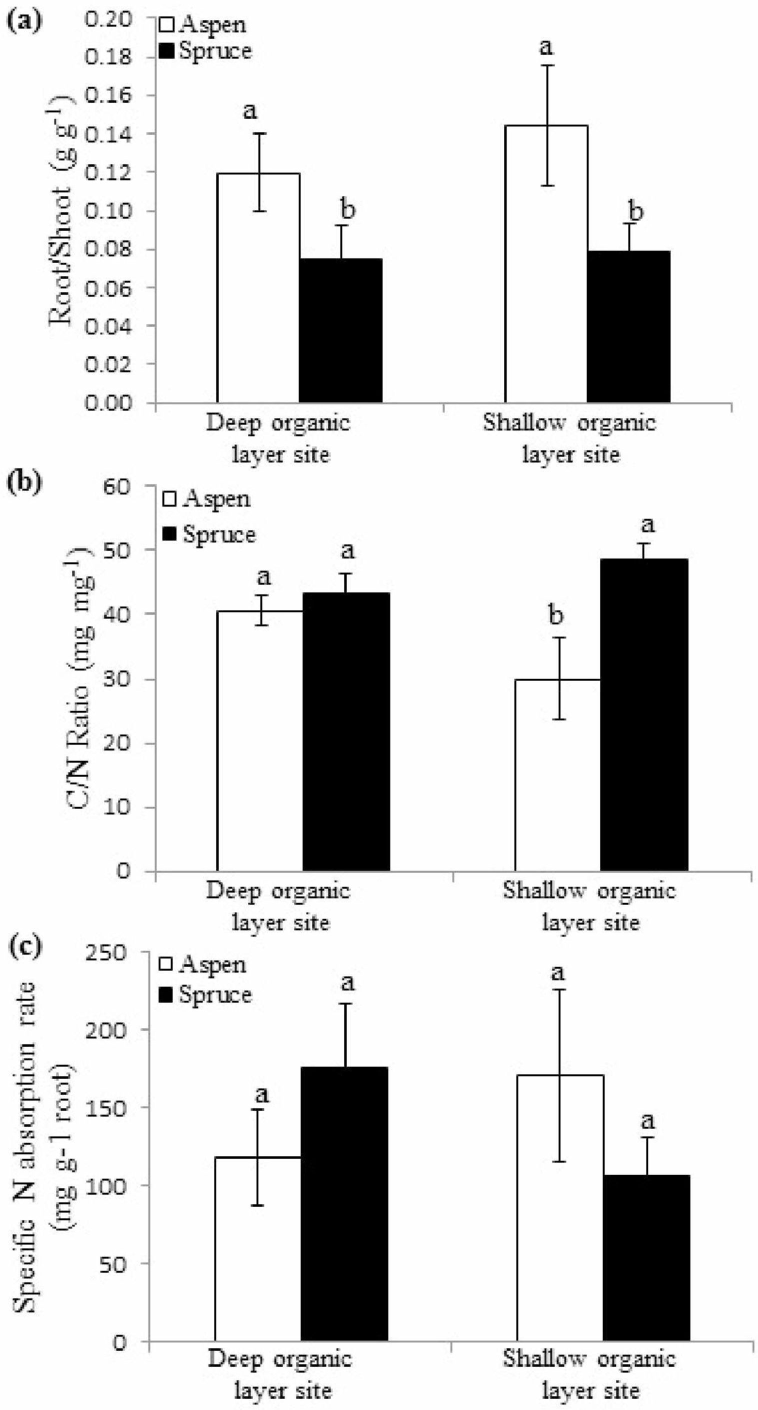


Fig.4.2 (a) Root : shoot ratios, (b) whole plant C : N ratios, and (c) specific N absorption rate measured on 10 aspen and 10 spruce individuals in one deep organic layer site and one shallow organic layer site within the 1994 Hadjukovich Creek burn (Mean ± S.E; n = 10). Means with the same letter are not significantly different ($\alpha=0.05$).

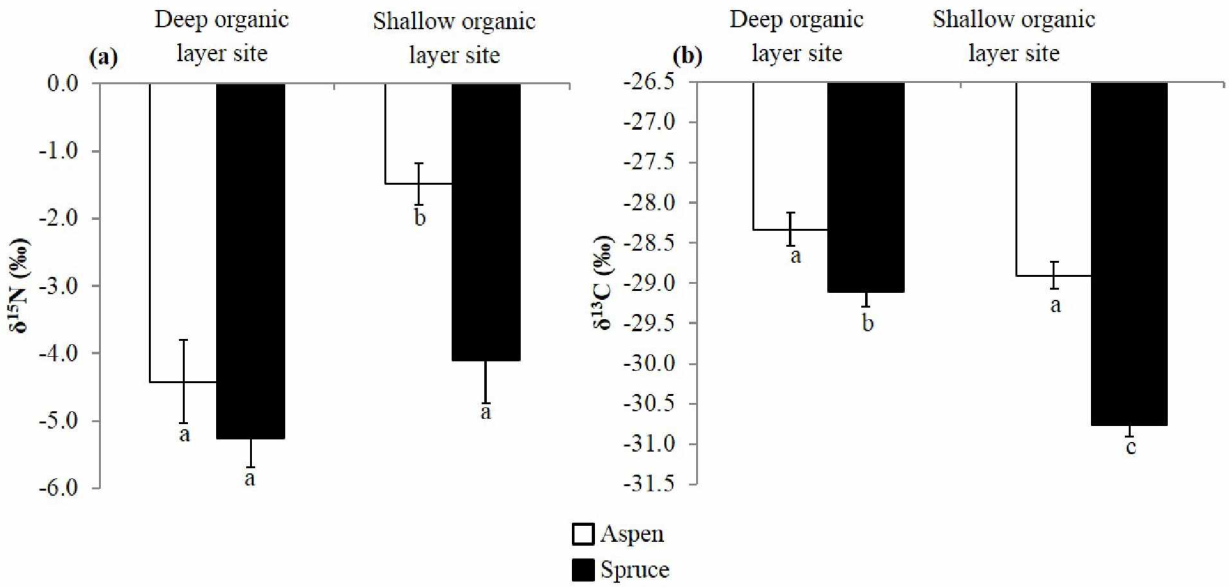


Fig.4.3 Foliar (a) $\delta^{15}N$ (‰), and (b) $\delta^{13}C$ (‰) of aspen and spruce in one deep organic layer and one shallow organic layer site within the 1994 Hadjukovich Creek burn (Mean ± S.E; n = 10). Means with the same letter are not significantly different (α=0.05).

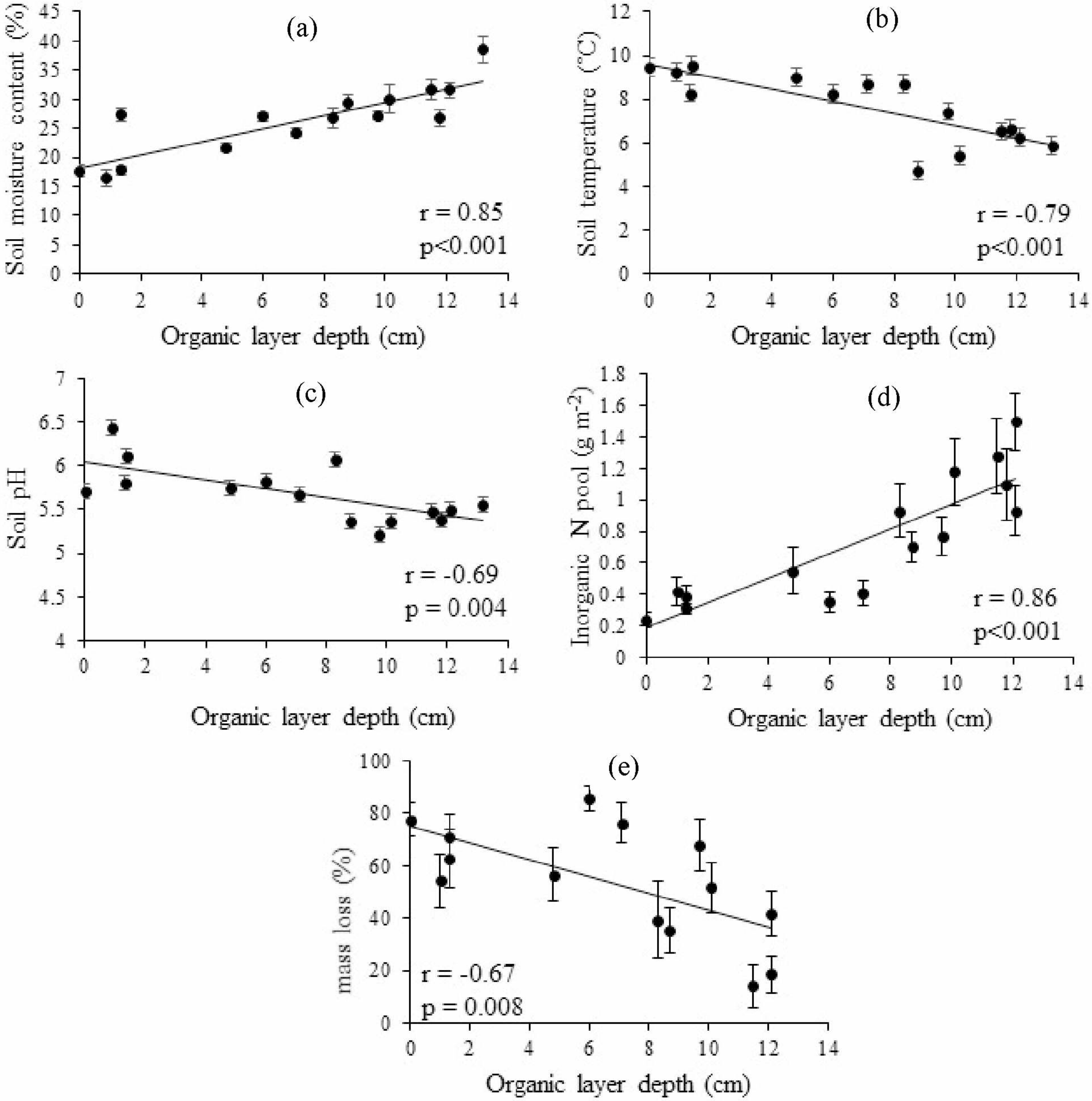


Fig.4.4 Bivariate relationships between post-fire organic layer depth and (a) soil moisture content (%) to a depth of 15 cm, (b) mineral soil temperature (°C) measured at 15 cm depth below the soil surface (c) soil pH, (d) total inorganic N pool (g m^{-2}) to a depth of 15 cm, and (e) mass loss of Whatman filter paper over a 2 year period (Mean ± S.E; n = 15).

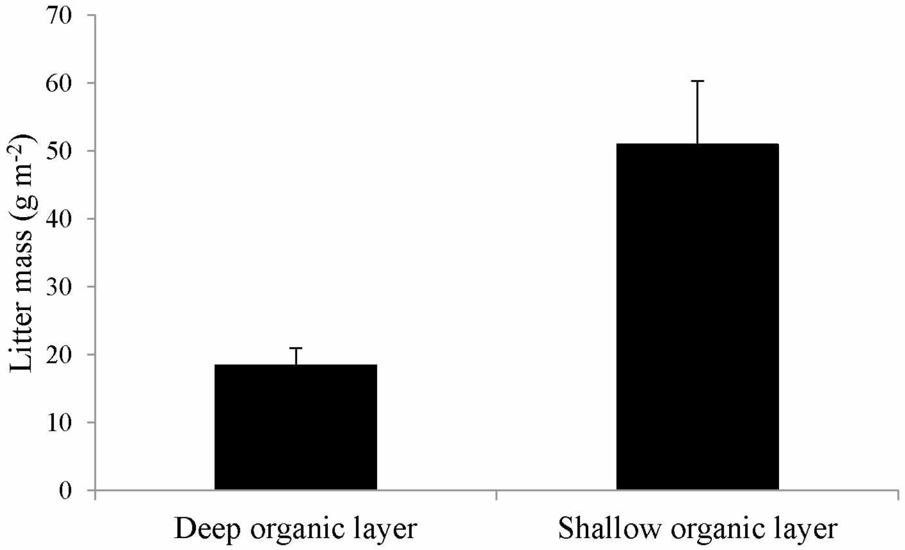


Fig.4.5 Leaf litter mass (g m^{-2}) in lightly burned (deep organic layer) versus severely burned (shallow organic layer) sites (Mean ± SE; n = 4).

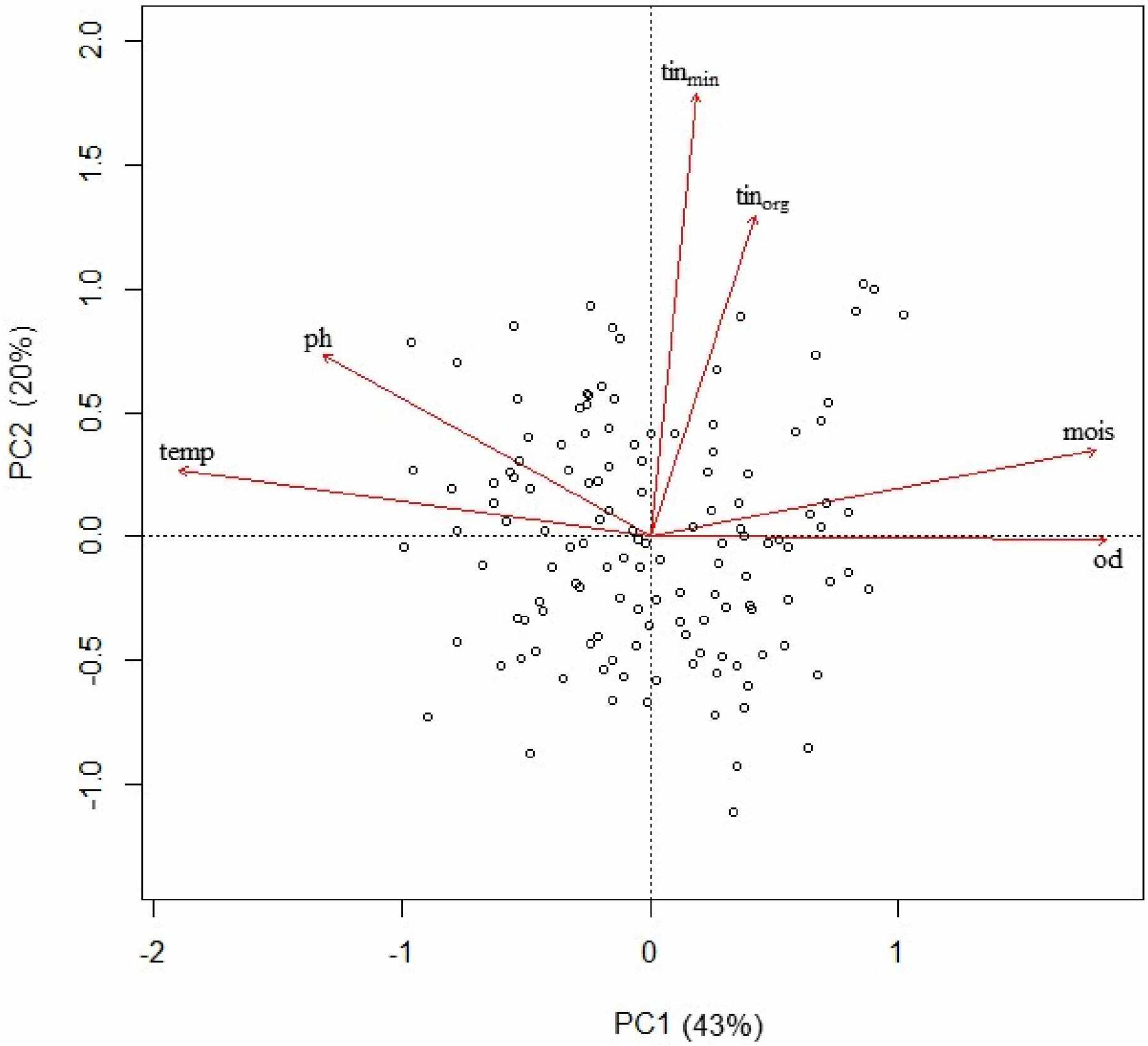


Fig.4.6 Principal components analysis (PCA) of soil variables: organic layer depth (od), soil moisture (mois), soil temperature (temp), soil pH (pH), total inorganic nitrogen supply in the organic (TIN_{org}) and mineral soil (TIN_{min}) layers. Angles between descriptors in the biplot reflect their correlations. If the angle between two vectors is small, this indicates that the two descriptors are strongly associated. A 90° angle between two vectors indicates that the descriptors are uncorrelated. The length of the vector represents the contribution of that variable.

4.9 Tables

Table 4.1 Site level averages (±1 S.E.; n = 10 plots per site) for the explanatory variables measured in 15 sites within the 1994 Hajdukovich Creek burn. Sites are arranged in order of increasing organic layer depth.

Site	Organic layer depth (cm)	Soil moisture (%)	Soil temperature (°C)	Soil pH	TIN supply – organic layer (µg N m^{-2} 30 days^{-1})	TIN supply – mineral layer (µg N m^{-2} 30 days^{-1})	Aspen stem density (log$_{10}$stems m^{-2})	Spruce stem density (log$_{10}$stems m^{-2})
1	0.00(0.00)	17.71(1.08)	9.49(0.29)	5.7(0.12)	3286 (870)	2121(384)	0.91(0.14)	0.36(0.15)
2	0.88(0.44)	16.46(1.57)	9.22(0.20)	6.43(0.21)	3225(224)	3838(318)	0.78(0.08)	0.51(0.14)
3	1.33(0.67)	27.41(1.11)	8.28(0.16)	5.80(0.12)	3744(316)	3756(389)	0.59(0.09)	0.56(0.14)
4	1.38(0.53)	17.83(0.69)	9.53(0.19)	6.11(0.25)	3925(313)	3963(247)	0.72(0.08)	0.46(0.13)
5	4.80(0.53)	21.75(0.71)	9.01(0.13)	5.74(0.14)	2230(367)	2270(330)	1.23(0.10)	0.88(0.18)
6	6.00(0.52)	26.96(0.82)	8.23(0.18)	5.83(0.11)	3110(464)	4440(419)	1.08(0.09)	1.23(0.11)
7	7.10(0.60)	24.25(0.67)	8.68(0.17)	5.67(0.07)	2570(510)	2820(350)	1.24(0.09)	1.19(0.14)
8	8.30(0.42)	26.89(1.74)	8.71(0.28)	6.07(0.14)	4150(601)	4010(319)	0.71(0.11)	0.36(0.11)
9	8.78(0.72)	29.48(1.32)	4.74(0.31)	5.37(0.15)	2278(568)	1900(296)	0.47(0.20)	0.97(0.15)
10	9.75(0.65)	27.16(0.80)	7.44(0.20)	5.22(0.10)	3200(426)	3300(514)	0.53(0.14)	0.65(0.17)
11	10.14(1.68)	29.99(2.43)	5.44(0.56)	5.37(0.04)	3914(611)	3629(656)	0.47(0.18)	0.64(0.16)
12	11.50(1.00)	31.68 (1.77)	6.53(0.17)	5.48(0.03)	3530(669)	2900(292)	0.14(0.06)	0.71(0.15)
13	11.80(1.34)	26.76 (1.55)	6.64(0.22)	5.38(0.11)	3150(361)	2710(281)	0.96(0.16)	1.54(0.10)
14	12.10(0.97)	31.53 (1.31)	6.28(0.62)	5.49(0.12)	4960(937)	4150(417)	0.45(0.11)	0.87(0.15)
15	13.17(1.49)	38.53 (2.31)	5.85(0.22)	5.56(0.05)	4000(642)	4783(516)	0.23(0.13)	0.85(0.13)

Table 4.2 Site level averages (± 1 S.E.; n = 10 plots per site) of the response variables measured in 15 sites sampled in the 1994 Hajdukovich Creek burn. Sites are arranged in order of increasing post-fire organic layer depth.

Site	**Aspen biomass (g m^{-2})**	**Spruce biomass (g m^{-2})**	**Aspen : spruce biomass ratio**
1	9780.7 (2899.5)	141.6 (42.6)	253.9 (134.5)
2	4563.9 (1756.3)	476.1 (150.0)	93.3 (78.8)
3	1303.1 (467.8)	375.3 (225.8)	154.6 (113.9)
4	7334.7 (1402.5)	225.4 (62.1)	45.2 (11.0)
5	453.8 (61.4)	185.9 (126.8)	27.6 (18.1)
6	547.1 (126.2)	172.2 (36.9)	8.1 (3.9)
7	483.7 (68.0)	94.6 (19.6)	8.9 (2.4)
8	1378.2 (174.8)	9537.6 (5687.9)	0.8 (0.2)
9	229.7 (74.0)	320.9 (75.4)	0.72 (0.2)
10	591.3 (109.6)	775.4 (202.8)	2.7 (1.2)
11	591.4 (322.9)	4028.2 (3443.8)	4.7 (3.9)
12	26.5 (11.0)	1445.7 (502.9)	0.17 (0.13)
13	210.9 (43.9)	884.3 (208.6)	0.3 (0.1)
14	6.8 (5.5)	342.2 (159.6)	0.03 (0.03)
15	319.2 (141.3)	644.4 (99.9)	0.6 (0.2)

Table 4.3 Summary of linear correlations among the explanatory variables (n = 15). Bold text indicates significant correlations at $\alpha = 0.05$.

	Organic layer depth	**moisture**	**temp**	**pH**	**tin$_{org}$**	**tin$_{min}$**	**Aspen density**	**Spruce density**
Organic layer depth	1.00	**0.85**	**-0.79**	**-0.69**	0.23	0.14	-0.47	0.47
moisture	-	1.00	**-0.81**	**-0.62**	0.33	0.32	**-0.63**	0.31
temperature	-	-	1.00	**0.74**	-0.12	0.02	**0.64**	-0.36
pH	-	-	-	1.00	0.08	0.33	0.33	-0.42
TIN$_{org}$	-	-	-	-	1.00	**0.70**	**-0.54**	-0.38
TIN$_{min}$	-	-	-	-	-	1.00	-0.29	-0.14
Aspen density	-	-	-	-	-	-	1.00	0.34
Spruce density	-	-	-	-	-	-	-	1.00

Table 4.4 Summary of two-way ANOVAs (n = 10 individuals) to test the site effects likely related to organic layer depth (shallow organic layer vs. deep organic layer) and species (aspen vs. spruce) on plant root: shoot ratios, whole plant C: N ratios, specific N absorption rate, foliage $\delta^{15}N$ and foliage $\delta^{13}C$. Root: shoot ratios were calculated as grams of root per unit volume of soil: total aboveground biomass. Significant p-values are indicated in bold.

Parameter		*F*	*p*
Root: shoot ratio (g g^{-1})	Species	5.501	**0.03**
	Site	0.208	0.65
	Species * Site	0.191	0.66
C: N ratio (mg mg^{-1})	Species	7.037	**0.01**
	Site	0.082	0.78
	Species * Site	2.947	0.10
Specific N absorption rate (mg N g^{-1} root)	Species	0.024	0.88
	Site	0.428	0.52
	Species * Site	2.122	0.15
Foliage $\delta^{15}N$ (‰)	Species	10.574	**0.002**
	Site	15.798	**<0.001**
	Species * Site	2.623	0.11
Foliage $\delta^{13}C$ (‰)	Species	68.935	**<0.001**
	Site OL depth	43.223	**<0.001**
	Species * Site OL depth	8.798	**0.005**

Table 4.5 Results of linear mixed models explaining variation in aspen biomass. The response variable was $\log_{10}$ transformed. Parameter estimates that are significant at $\alpha=0.05$ level are indicated in bold. The "best model" as indicated by Akaike's Information Criterion (AIC) scores is in bold text in each case. Model weights are indicated by w_i.

Response variable	**Model**	**Predictor variables**	**Estimate**	**Std. error**	**p-value**	**Model AIC**	**w_i**
aspen biomass	1	PC1	**-0.097**	0.014	<0.001	251.12	**0.94**
		PC2	0.005	0.023	0.83		
	2	PC1	**-0.097**	0.014	<0.001	256.99	0.05
		PC2	0.005	0.023	0.83		
		spruce density	0.002	0.057	0.97		
	3	PC1	**-0.091**	0.016	<0.001	261.62	0.01
		PC2	0.007	0.023	0.76		
		spruce density	-0.016	0.061	0.79		
		aspen density	0.065	0.068	0.34		

Table 4.6 Results of linear mixed models explaining variation in spruce biomass. The response variable was $\log_{10}$ transformed. Parameter estimates that are significant at $\alpha=0.05$ level are indicated in bold. The "best model" as indicated by Akaike's Information Criterion (AIC) scores is in bold text in each case. Model weights are indicated by w_i.

Response variable	**Model**	**Predictor variables**	**Estimate**	**Std. error**	**p-value**	**Model AIC**	**w_i**
spruce biomass	1	PC1	0.016	0.019	0.42	333.73	**0.92**
		PC2	0.056	0.032	0.08		
	2	PC1	0.015	0.021	0.47	338.72	0.08
		PC2	-0.057	0.032	0.08		
		aspen density	-0.006	0.089	0.94		
	3	PC1	-0.019	0.021	0.36	343.79	0.01
		PC2	0.056	0.032	0.08		
		aspen density	0.008	0.093	0.93		
		spruce density	-0.029	0.093	0.73		

Table 4.7 Results of linear mixed models explaining variation in aspen: spruce biomass (biomass ratio). The response variable was $\log_{10}$ transformed. Parameter estimates that are significant at $\alpha=0.05$ level are indicated in bold. The "best model" as indicated by Akaike's Information Criterion (AIC) scores is in bold text in each case. Model weights are indicated by w_i.

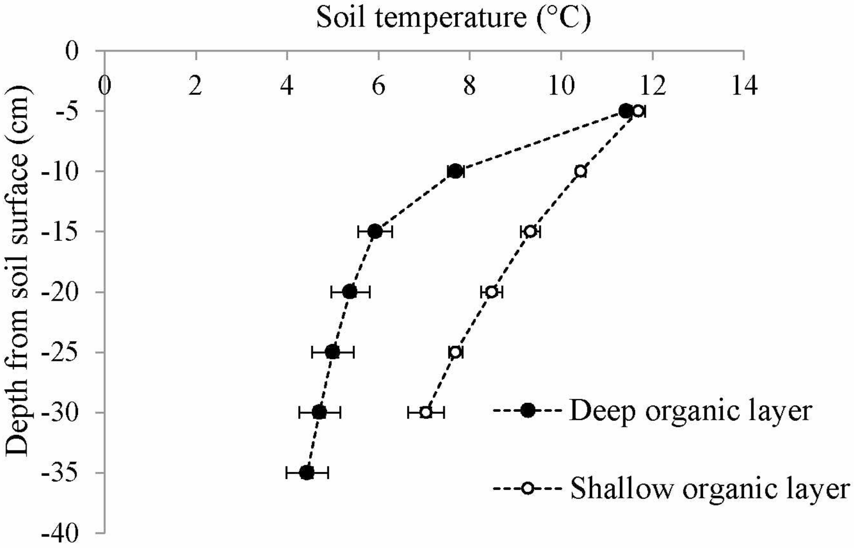
Response variable	**Model**	**Predictor variables**	**Estimate**	**Std. error**	**p-value**	**Model AIC**	**w_i**
biomass ratio	1	PC1	**-0.095**	0.016	<0.001	405.56	**0.65**
		PC2	-0.027	0.035	0.43		
	2	PC1	**-0.081**	0.018	<0.001	407.59	0.24
		PC2	-0.016	0.035	0.66		
		aspen density	0.171	0.105	0.11		
	3	PC1	**-0.096**	0.017	<0.001	410.41	0.06
		PC2	-0.027	0.036	0.45		
		spruce density	0.013	0.096	0.89		
	4	PC1	**-0.074**	0.021	<0.001	411.75	0.03
		PC2	-0.018	0.036	0.61		
		aspen density	0.208	0.118	0.08		
		spruce density	-0.073	0.107	0.49		

4.10 Appendices

Appendix 4.A Mineral soil temperature and moisture measured at 15 cm depth in July and August 2009. Sites are arranged in order of increasing organic layer depth.

Site	Temperature (°C) July	Temperature (°C) August	Moisture (%VWC) July	Moisture (%VWC) August
HC15	10.7	8.2	21.4	14.1
HC16	10.3	7.9	11.5	15.9
HC5	7.6	9.0	40.7	16.5
HC17	10.7	8.3	22.7	14.0
HC9	10.1	7.9	27.1	22.1
HC18	9.1	7.4	35.8	26.9
HC14	9.4	8.0	32.5	23.0
HC11	9.7	7.7	19.0	19.2
HC3	5.3	4.2	43.2	29.9
HC8	8.3	6.4	33.8	23.1
HC13	7.5	3.9	37.4	23.9
HC1	6.2	7.0	48.0	23.9
HC7	5.8	7.3	41.0	20.9
HC2	6.9	6.4	22.1	25.6
HC12	7.3	5.3	38.8	26.3

Appendix 4.B Temperature profiles measured in deep organic layer and shallow organic layer sites. Temperature was measured at 5 cm depth increments from the soil surface (Mean ± S.E.; n = 3).



Chapter 5.

General Conclusions

The intensification of the fire regime in North American boreal forests has resulted in an increased occurrence of large fire years and late-burning fires, and a decrease in the fire-free interval over the past several decades (Kasischke and Turetsky 2006, Kasischke et al. 2010). Moreover, an increase in fire severity (defined by combustion of the surface organic layer) has been observed in black spruce forests over the past decade (Turetsky et al. 2011). This trend in increased fire activity and changes in fire characteristics are expected to accelerate into the 21st century under a warming climate (Duffy et al. 2007, Balshi et al. 2009). Extensive studies in the boreal forests of interior Alaska (Van Cleve et al. 1983, Van Cleve and Yarie 1986) have shown that stand composition and productivity are under tight control by state factors (e.g. topography, climate, and time since disturbance). The ongoing and unprecedented increases in fire activity and in particular an increase in deep burning fires on the landscape are forcing us to assess how fire severity is changing patterns of canopy composition (Johnstone and Chapin 2006) and productivity (Mack et al. 2008), and possibly leading to long term shifts in vegetation composition on the landscape scale (Johnstone et al. 2010, Beck et al. 2011, Mann et al. 2012). In my dissertation I examined the impacts of post-fire organic layer depth on density and biomass patterns of dominant canopy species during the second decade of succession (Chapter 2), evaluated a potential nutrient-based mechanism for patterns of stand dominance in relation to fire severity (Chapter 3), and investigated potential drivers of stand dominance patterns in burned black spruce stands (Chapter 4).

My research has shown that initial patterns of post-fire seedling recruitment in relation to organic layer depth persist into the second decade of succession (Chapter 2). Severely burned sites were dominated by aspen, whereas lightly burned sites underwent self-replacement to black spruce. Furthermore, species dominance hierarchies established shortly after fire are reinforced rather than diminished over time, by the continued effects of post-fire organic layer depth on plant growth and biomass accumulation. Growth rates (annual basal area increment) of aspen and spruce respond in opposite directions and with differing magnitude to variations in organic layer depth. Aspen showed a 30-fold increase in basal area increment in severely burned compared to lightly burned sites, whereas spruce showed a 2-fold increase in basal area increment in lightly versus severely burned sites (Chapter 4). These differences in growth rates over the course of early succession in these stands have translated into large differences in relative stand level dominance (deciduous : coniferous biomass) at opposite ends of the organic layer depth gradient (Chapter 2). Aspen accounted for over 90% of total aboveground tree biomass in severely burned sites (<4 cm organic layer depth), whereas spruce accounted for over 50% of total aboveground tree biomass only at sites with thick organic layers (>8 cm organic layer depth) in the 1994 burn. Observations from multiple burns in the region spanning 9-21 years post-fire consistently showed that the effects of post-fire organic layer depth on patterns of aspen and spruce density and biomass can be maintained for several decades following fire (Chapter 2). These findings are consistent with previous studies that have shown that patterns of stand composition in boreal forests are largely determined during the first few years following disturbance (Johnstone et al. 2004). Furthermore these results indicate that increases in deep burning fires are likely to result in a persistent shift from black spruce to aspen dominance in severely burned parts of the boreal forest.

The soil conditions associated with lightly burned sites (relatively cold, wet, low pH, low decomposition potential) and severely burned sites (relatively warm, dry, high pH, high decomposition potential) reflect the conditions that would be expected in black spruce versus aspen stands respectively (Van Cleve et al. 1983). Therefore, variation in fire severity within a single burn in an area of uniform topography and pre-fire black spruce dominance throughout has resulted in contrasting soil environments that are supporting coniferous vs. deciduous stands in lightly versus severely burned areas in the second decade of succession. Because this study was conducted 16 years following fire, it is likely that effects of the dominant resident vegetation on soil processes are contributing to the contrasting soil conditions observed in lightly vs. severely burned sites. For instance, high evapotranspiration rates and water utilization by aspen stands in severely burned sites could be contributing to the drier soils observed in these sites. Total inorganic nitrogen pools increased with increasing organic layer depth (Chapter 4), likely due to the greater quantity of organic material remaining after fire in lightly compared to severely burned sites. It is also plausible that this pattern is in part due to the greater nutrient requirement (Gower et al. 2000) and N uptake rates of vegetation in severely compared to lightly burned sites; the greater utilization of N pools in severely burned sites could lead to proportionately more N being immobilized in vegetation biomass rather than in the soil.

The physiological performance of aspen and spruce tended to vary in similar ways in lightly versus severely burned sites. For instance, both aspen and spruce had increased specific root uptake rates of nitrate and ammonium in severely burned sites compared to lightly burned sites, even though the relative contribution of nitrate vs. ammonium to total inorganic nitrogen supply was similar across sites (Chapter 3). However, physiological performance in terms of distribution of aboveground vs. belowground tissues varied between species as expected, but did not vary significantly between the severely burned site and the lightly burned site that were sampled (Chapter 4). Whole plant nutrient use efficiency (C : N ratio) also differed between aspen and spruce but not across sites. Since the majority of fine root biomass occurs in the top 15 cm of soil (Finer et al. 1997, Ruess et al. 2006), variations in post-fire organic layer depth result in a shift in the soil environment to which the majority of fine roots are exposed. In severely burned sites, plant roots are almost entirely exposed to mineral soil, whereas in lightly burned sites the majority of plant roots are located in the organic layer. Differences in bulk density and porosity are likely to result in higher ion diffusion rates in mineral versus organic soils (Barber 1995), which could explain greater root uptake in aspen and spruce in severely burned sites. Moreover, soils in severely burned sites were warmer than in lightly burned sites, which could also have facilitated higher specific root uptake rates in both species (Van Cleve et al. 1983, Bassirirad 2000). In addition to edaphic factors, patterns of vegetation productivity and biomass that have developed during the course of post-fire succession in these stands, could also have contributed to the observed patterns of nitrogen uptake (Chapter 3). Aspen aboveground biomass in severely burned sites was 20-fold greater than in lightly burned sites. The greater nutrient demand by the resident vegetation in severely burned sites could in part explain the higher nitrogen uptake rates of aspen and spruce in these sites (Chapin 1980, Van Cleve et al. 1983). At the stand level, differences in nutrient uptake (on a per area basis) were magnified, with aspen taking up more than an order of magnitude more nitrogen in severely burned compared to lightly burned sites. The large differences in stand level nitrogen uptake between aspen and spruce in relation to fire severity are most likely to be driven by differences in root biomass between lightly and severely burned sites (Chapter 3). These results taken together suggest that the increased inorganic nitrogen uptake rates in severely burned sites are more likely to be due to the sharply contrasting edaphic conditions and species biomass patterns associated with lightly vs.

severely burned sites rather than to physiological changes exhibited by aspen and spruce in response to fire severity.

Evaluation of models predicting aspen biomass and stand dominance revealed that the observed variations in aspen biomass and the relative dominance of aspen vs. spruce are largely being driven by substrate conditions (soil organic layer depth, temperature, moisture, and pH) rather than interspecific competition (Chapter 4). On the other hand, spruce biomass was not well predicted by any of the measured variables. Studies have shown that spruce grows on a wider range of substrates and organic layer depths than aspen (Greene et al. 2007, Gewehr et al. 2014), which implies relatively less sensitivity to soil conditions. My finding that spruce growth rates differed by only 2 fold, and biomass 7 fold between lightly and severely burned sites (compared to much larger differences in the case of aspen; Chapter 4) reflects this. It is possible that other processes such as seed dispersal and availability of viable seed following fire may be relatively more important than soil conditions in shaping regeneration patterns of spruce in relation to fire severity. It should be noted that soil variables measured in only one growing season were used in evaluating relationships between soil environmental conditions and stand biomass patterns. Additional research pairing soil measurements and annual biomass accumulation across multiple growing seasons is required to definitively identify factors controlling plant growth rates in relation to post-fire organic layer depth. Analyses of growth responses to climate variability in aspen and black spruce in eastern Canadian boreal forests have shown that spruce growth was favored by cooler wetter conditions, whereas aspen growth was favored by warmer and drier conditions (Drobyshev et al. 2013), similar to the results reported here albeit on a different scale.

Herbivory is likely to be an important process shaping regeneration patterns and ratios of deciduous : coniferous biomass along fire severity gradients in these forests. In intermediate sites (4-8 cm organic layer depth) within the 1994 burn, extensive browse by moose and snowshoe hare on aspen stems was observed but not quantified. A previous study conducted within this burn showed that rates of production and removal of forage biomass were greater in severely burned compared to lightly burned areas (Lord 2008). However, rapid growth rates of aspen in severely burned sites (Chapter 4) may allow the vertical escape of aspen from herbivory during early succession. Successional trajectories in these intermediate sites is likely to be modulated by the impact of herbivory on soil chemistry and vegetation dynamics (Kielland and Bryant 1998), which could result in dominance by the less palatable and hence relatively more browse-resistant black spruce in these sites over time. Thus herbivory may provide a mechanism for the continued coexistence of aspen and black spruce sites on the landscape.

My results show that 16 years following fire, severely burned parts of these forests have essentially been converted to aspen stands, whereas lightly burned areas are dominated by black spruce and have low densities of aspen (Fig.5.1). In addition to changes in canopy dominance, the associated understory vegetation is also altered, with an increase in grasses, forbs and herbaceous species in severely burned sites, and ericaceous shrubs and feather moss dominating the understory in lightly burned sites (Johnstone and Kasischke 2005, Bernhardt et al. 2011). I found that severely burned stands had much higher litter mass in the understory than lightly burned sites. This taken together with my findings that soils were warmer and decomposition potential significantly higher in severely burned sites points towards greater decomposition rates in these sites. Moreover, aspen leaf litter has been shown to suppress moss colonization and growth (Startsev et al. 2008), and deciduous stands have been found to display higher nutrient uptake, requirement, and return, and faster forest floor turnover rates than coniferous stands (Van Cleve et al. 1983, Melvin et al. 2015).These findings suggest that it is unlikely that severely burned aspen-dominated stands will accumulate deeper organic layers over time. This would result in further warming of soils and deepening of the active layer. Such positive feedback loops between deciduous vegetation, litter quality, soil temperature, and decomposition rates are likely to perpetuate aspen presence in severely burned parts of the boreal forest. Since black spruce individuals may take 30 – 100 years to be able to produce viable seeds (Viglas et al. 2013), the predicted increase in fire frequency (Flannigan et al. 2009, Balshi et al. 2009) makes it unlikely that black spruce individuals growing in these stands will reach seed production age by the time these stands burn again**.** With an increase in large fire years and fire severity (Duffy et al. 2007, Turetsky et al. 2011), parts of the boreal landscape that once maintained black spruce dominance across multiple fire cycles are vulnerable to a switch in dominance to deciduous canopy species.

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5.2 Figures

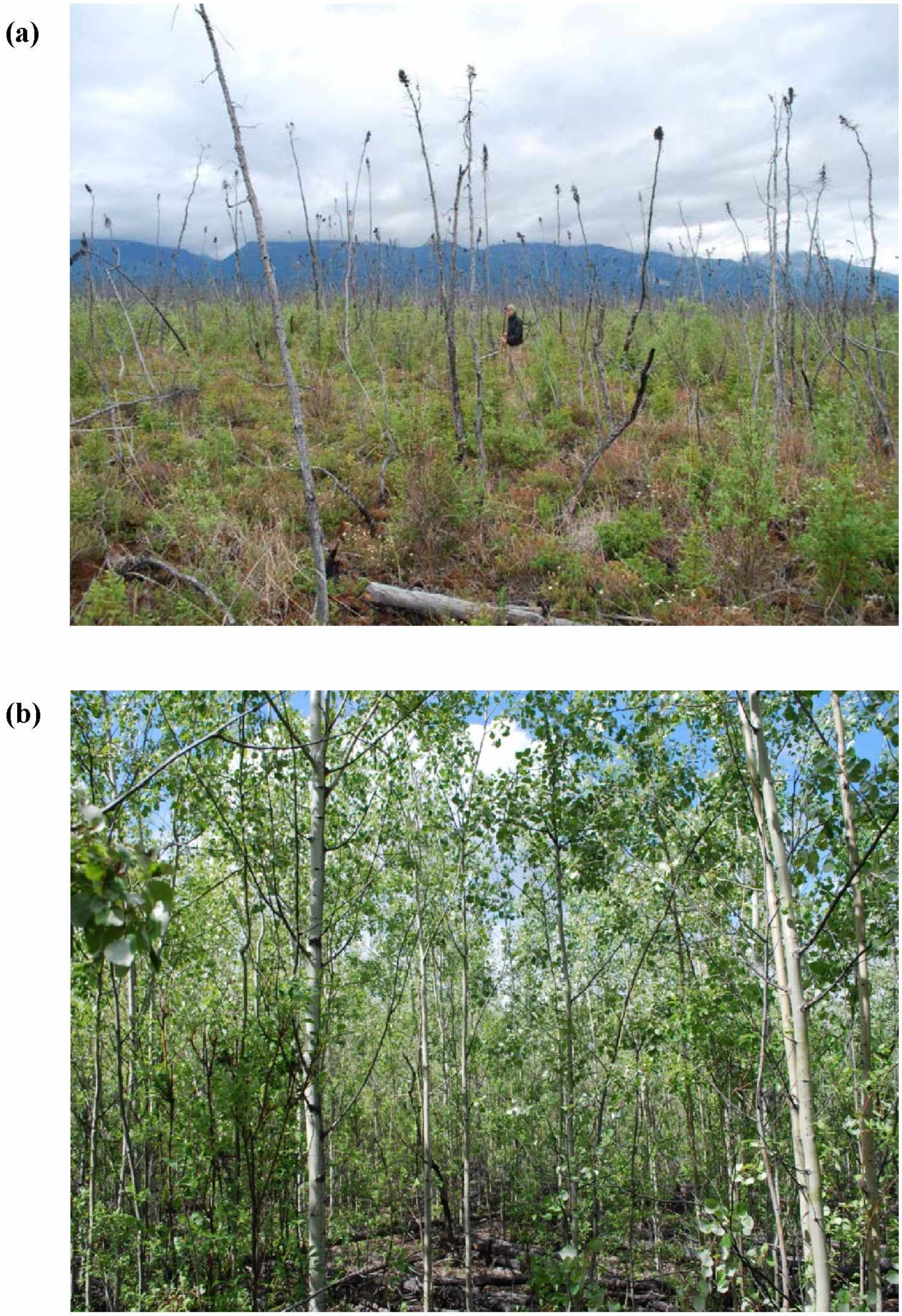

Fig.5.1 (a) Lightly burned site with deep organic layer and (b) severely burned site with shallow organic layer within the 1994 Hajdukovich Creek burn.