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

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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.

1. 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) and vegetation recovery (Kasischke and Johnstone, 2005). 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).

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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 our 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. Materials and methods

2.1. 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 Hadjukovich 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).

2.2. 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 and Kasischke, 2005; Kasischke and 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

Table 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 + 2.496 ln(basal diameter)	0.94	<0.001
Picea mariana	65	0.06–1.86	ln(biomass) = 3.841 + 2.816 ln(basal diameter)	0.93	<0.001

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 × 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 × 30 m belt transects (total sampling area = 180 m^2). Basal diameters of aspen and spruce stems were measured in three 10 m × 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 × 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 × 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. *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).

3. 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. 1b). In contrast, aspen biomass accounted for over 90% of total aboveground tree biomass at sites with shallow organic layers (<4 cm; Fig. 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. 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). 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. 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

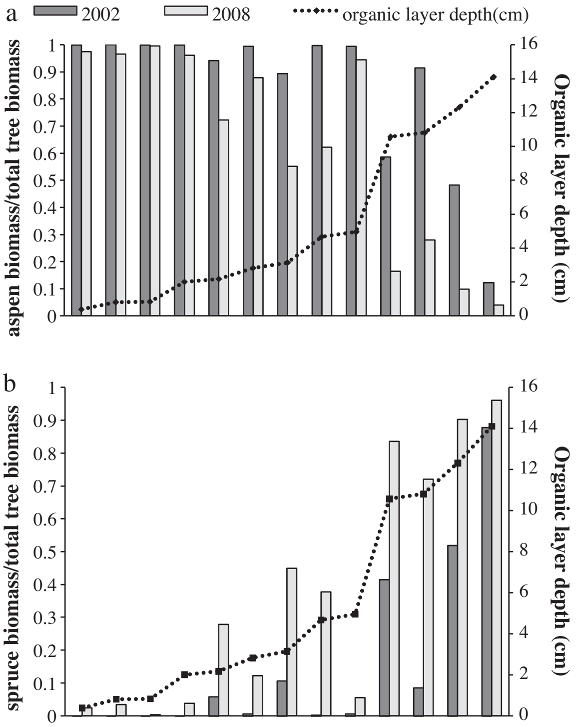

Fig. 1. Biomass of (a) aspen and (b) spruce, expressed as a proportion of total tree biomass in plots sampled in 2002 and 2008. The dotted line represents average organic layer depth (cm) measured in 2008.

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. 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. 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. 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 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 3). In contrast, changes in aspen biomass, as well as average individual biomass, were negatively correlated with 2002 spruce stem density (Table 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. 4, Table 4). Specifically, stem density of aspen was negatively correlated with organic layer depth in the 1987,1994 and 1999 burns (Fig. 4a), while aspen biomass was negatively correlated with organic layer depth in all four burns (Fig. 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. 4e). In contrast to aspen, stem density of spruce was positively correlated with organic layer depth in the 1987 and 1994 burns (Fig. 4b). Aboveground biomass (g/m^2) of spruce was also positively correlated with organic layer depth in the 1994 burn (Fig. 4d), while average individual biomass was uncorrelated with organic layer depth in all four burns (Fig. 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. 5).

4. 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. 5). The effects of organic layer depth on stem density and biomass were negative or neutral 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. 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; Johnstone

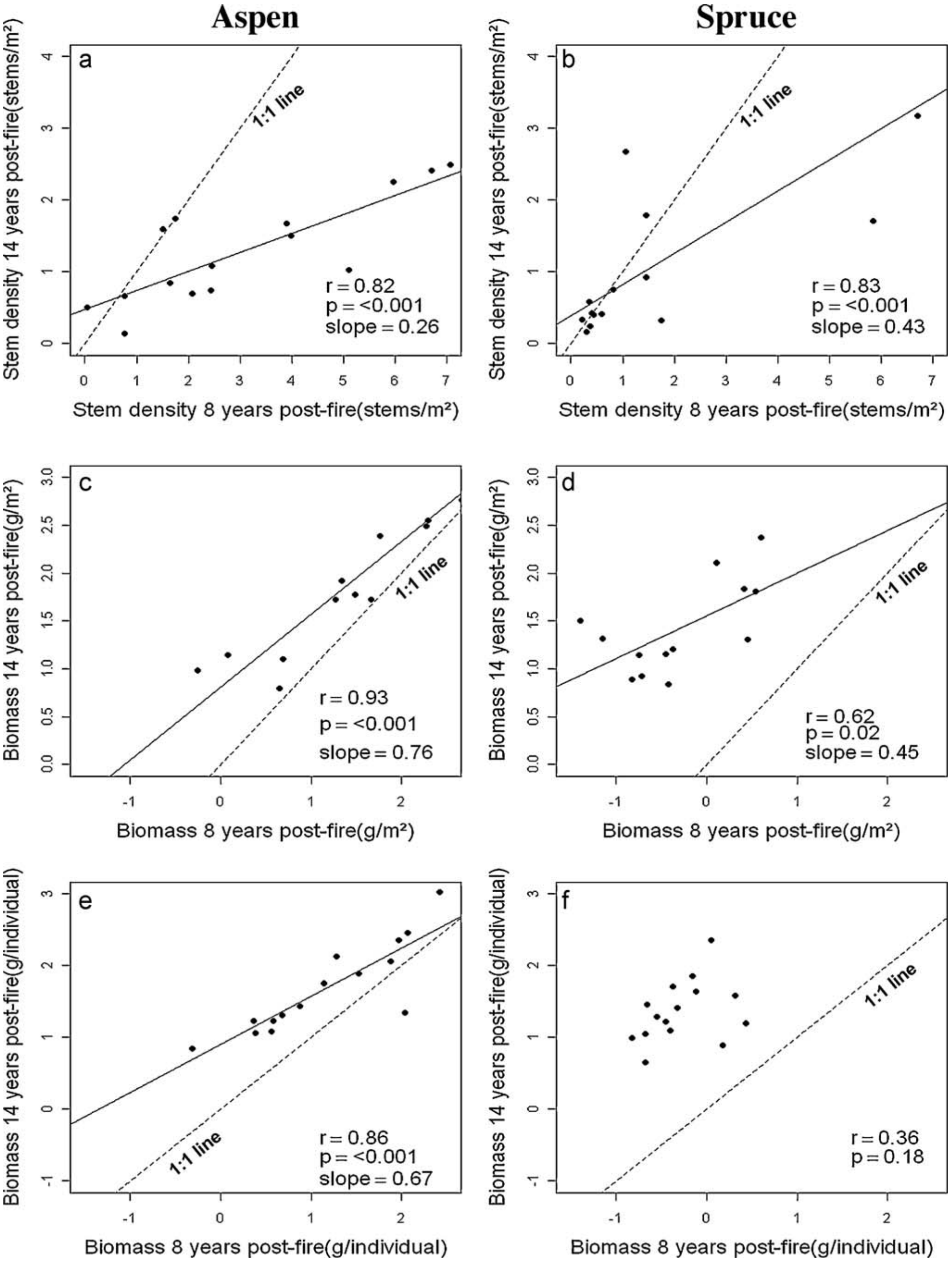

Fig. 2. Scatterplots of stem density (stems/m^2), biomass (g/m^2) and average individual biomass (g/individual) recorded in the same plots 8 years post-fire versus that recorded 14 years post-fire for aspen (a,c,e) and spruce (b,d,f) in the 1994 burn. Biomass values have been log$_{10}$ transformed ($n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

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

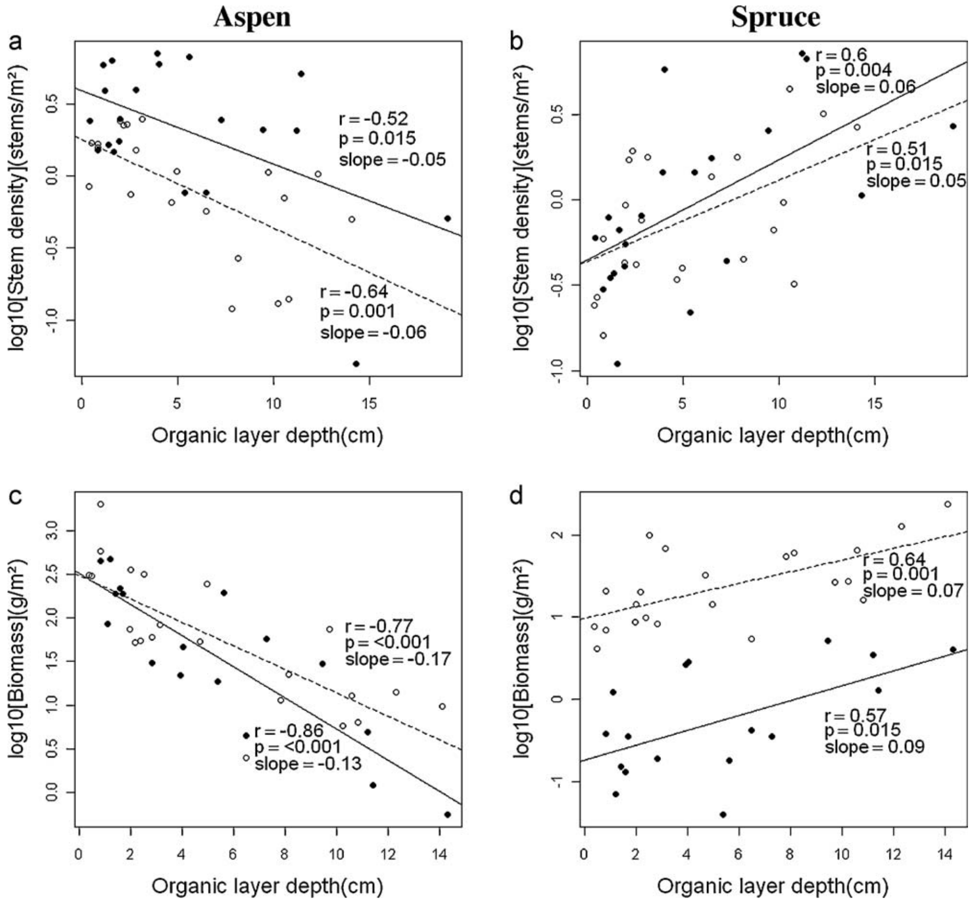

Fig. 3. Log-linear correlations between organic layer depth (cm) and (a) aspen stem density ($\log_{10}$stems/m^2), (b) spruce stem density ($\log_{10}$stems/m^2), (c) aspen biomass ($\log_{10}$ g/m^2), and (d) spruce biomass ($\log_{10}$ g/m^2), in the 1994 burn. Filled circles represent measurements 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).

Table 2

ANCOVA comparison of the relationship between organic layer depth (cm) and stem density (stems/m^2), and organic layer depth and aboveground biomass (g/m^2) 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)

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 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. 3, 4 and 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, 2007; Johnstone et al., 2010a). This study shows that these initial effects persist through the first 1–2 decades of succession and demonstrate that

Table 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 $\alpha = 0.05$ 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

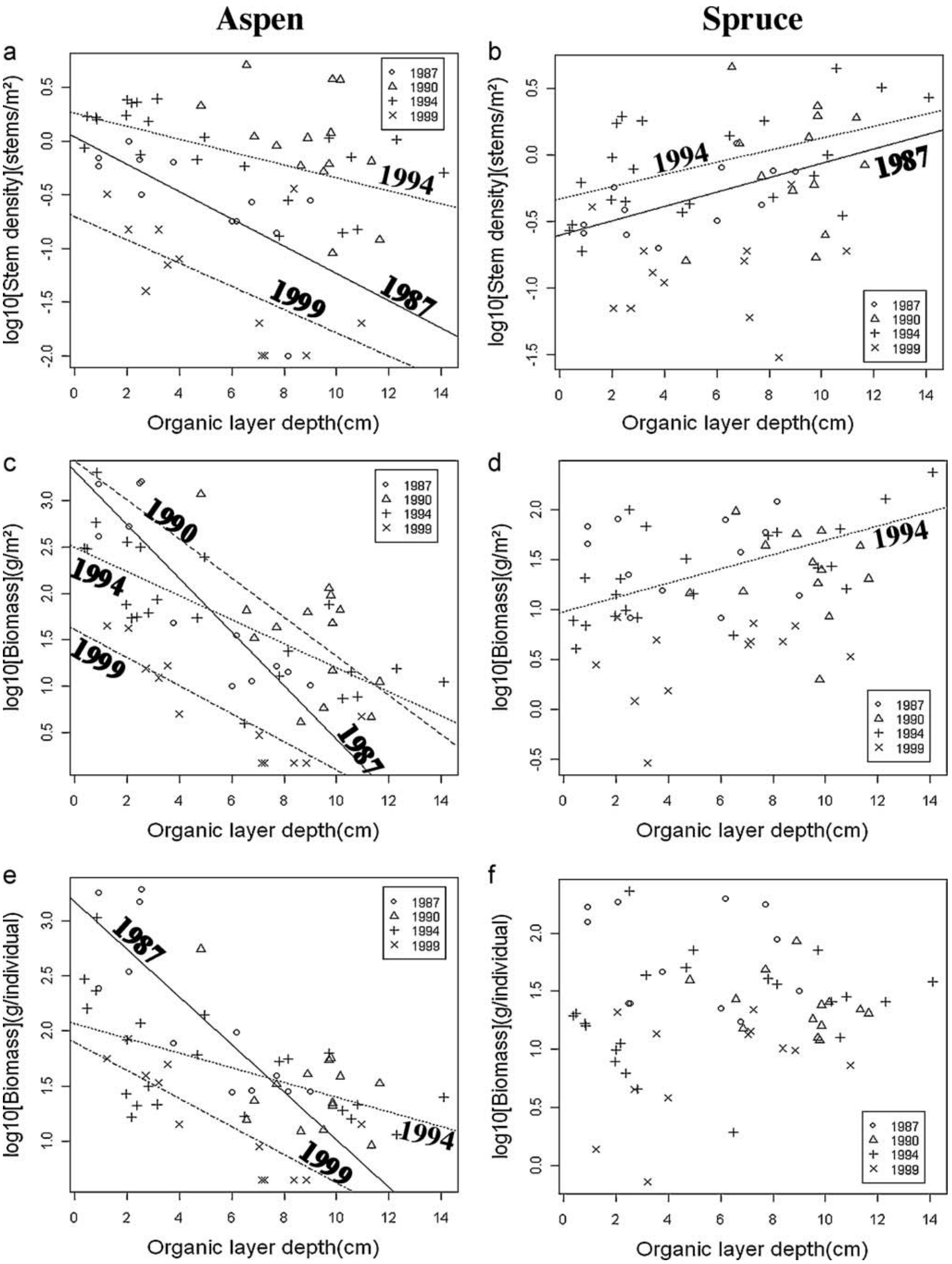

Fig. 4. Linear correlations between organic layer depth (cm) and (a) aspen stem density ($\log_{10}$stems/m^2), (b) spruce stem density ($\log_{10}$stems/m^2), (c) aspen biomass ($\log_{10}$g/m^2), (d) spruce biomass ($\log_{10}$g/m^2), (e) aspen mean biomass ($\log_{10}$g) per individual, and (f) spruce mean biomass ($\log_{10}$g) per individual in the 1987, 1990, 1994 and 1999 burns.

Table 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 text. Slopes and standard errors (SE) of significant correlations are shown.

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

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, higher sensible heat flux, and warmer surface temperatures (Bonan et al., 1992). In contrast, deciduous forests

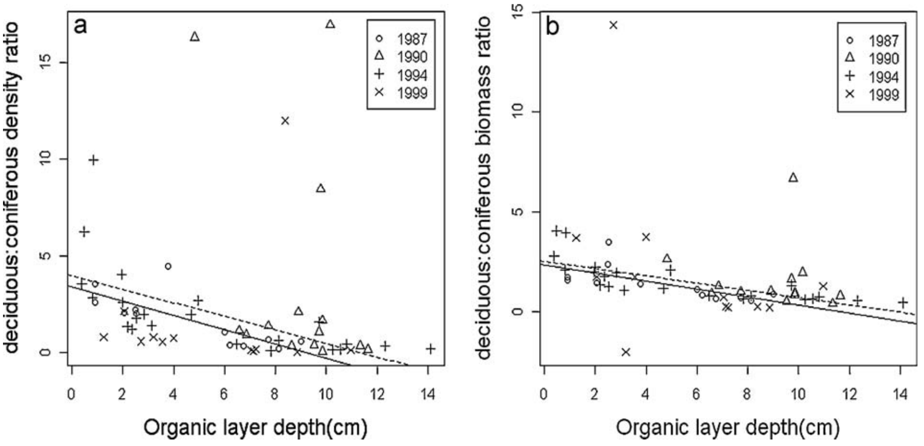

Fig. 5. Scatterplots showing relationships between organic layer depth (cm) and deciduous:coniferous ratios of (a) $\log_{10}$stem density and (b) $\log_{10}$biomass in four areas of black spruce forest that burned in 1987, 1990, 1994, and 1999. Significant linear correlations are indicated by lines 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 ($r = -0.76$, $p < 0.001$).

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 dominated 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 indicated 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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