Plant Ecol (2013) 214:587–596
DOI 10.1007/s11258-013-0191-0

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

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Received: 14 September 2012 / Accepted: 27 February 2013 / Published online: 10 March 2013

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.

Keywords Fire severity · Boreal forest · Soil nitrogen · Plant nitrogen uptake · Succession

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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 5 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 those 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). 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.

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 8,900 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 (*Hylocomium splendens, Pleurozium schreberi,* and *Aulacomnium* spp.). 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 × 100 m sites within the 1994 burn, encompassing a range of organic layer depths (from 0 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 × 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 deep × 6 cm diameter soil core at the North West corner of each quadrat, for determination of soil pH. We measured organic layer depth (cm) on a 20 × 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 (2 cm below the forest floor surface) and the mineral layer (2 cm below the organic–mineral interface). In severely burned sites, probes were inserted horizontally at 2 cm 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 and 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 (organic layer), and

2 cm below the organic–mineral soil interface (mineral layer) in one severely and one lightly burned site. Two moisture sensors were inserted at 2 cm below the soil surface (moisture values recorded by these two sensors were averaged), and one was inserted at 2 cm below the organic–mineral soil interface. One temperature sensor was inserted at 2 cm below the soil surface, and one was inserted at 2 cm below the organic–mineral soil interface. Note that in the severely burned sites, most "organic" samples were in the mineral soil layer (2 cm below the forest floor surface) as the organic layer had been completely combusted in the fire.

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/$\sim$400 cm^3) and aboveground biomass ($n = 20$ for each species). We harvested the aboveground (shoot) biomass, and collected four 15 cm deep $\times$ 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 five aspen and five 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 nine aliquots, injected through nine uniformly distributed holes in a circular Lexan™ 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 $\times$ 6 cm diameter soil core 12 h later. Soil cores were brought to the lab on ice and processed the same day. All fine roots (diameter $\leq$2 mm) of the aspen or spruce plant were picked out from each core, washed with 0.5 M KCl, dried at 60 °C for 24 h, 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 $\delta^{15}N$ 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 1 M 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} $month^{-1}$.

Table 1 Characteristics of sites representing lightly and severely burned areas within the 1994 burn ($n = 10$ plots per site)

Severity	Organic layer depth (cm)	Soil nitrogen concentration (μg 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)	1,303.2 (467.9)	120.78 (41.6)	5.0 (1.5)	375.3 (225.7)	22.64 (7.98)

In the case of soil nitrogen concentration, $n = 5$. Values indicate mean (SE)

Table 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

The dried and ground ^{15}N enriched plant roots were analyzed for $\delta^{15}N$ 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

$$\delta^{15}N = \left[\left(R_{sample} - R_{standard}\right)/R_{standard}\right] \times 10^3, \quad (1)$$

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 (μg N g^{-1} root h^{-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 (μg N g^{-1}root h^{-1}) to obtain total N uptake on an area basis (μg N m^{-2} h^{-1}).

Temperature and moisture values were averaged across the months June–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).

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). The organic layer or top 2 cm 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). 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. 1; Table 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 ($t = -0.43$; $p = 0.68$).

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^- versus 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. 2). While both aspen and spruce took up significantly more NO_3^- per gram root in severely burned than in lightly burned sites,

Table 3 Mean soil temperature and moisture measured over the 2010 growing season in lightly and severely burned sites within the 1994 burn

Soil layer		Severity		*t*	*p*
		Light	Severe		
Temperature (°C)	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

Values indicate mean (SE)

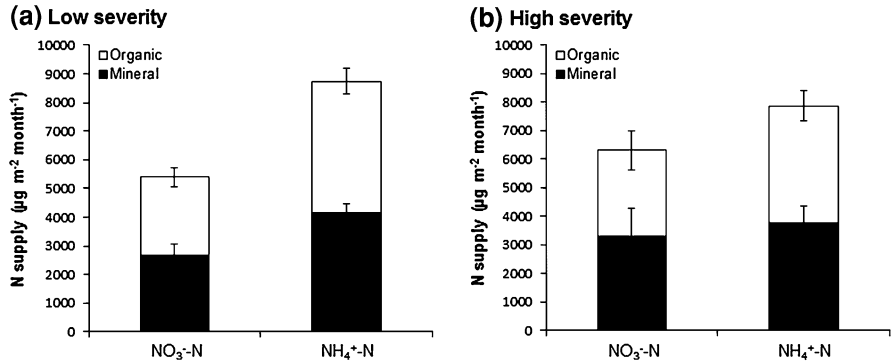

Fig. 1 Inorganic nitrogen supply rates (µg m^{-2} $month^{-1}$) measured using ion exchange probes in **a** low severity ($n = 8$) and **b** high severity ($n = 4$) sites. Nitrogen supply was measured in the mineral and organic soil layers separately. Values were averaged across 2 month long burial periods.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

there was no significant difference between aspen and spruce across fire severity (Table 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 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. 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), 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 1). Thus, the interaction of species × N form preferences was magnified at the stand level, reflecting differences in the effects of fire severity on total biomass of the two species.

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^- versus 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

Table 4 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

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

Significant *p* values are indicated in bold

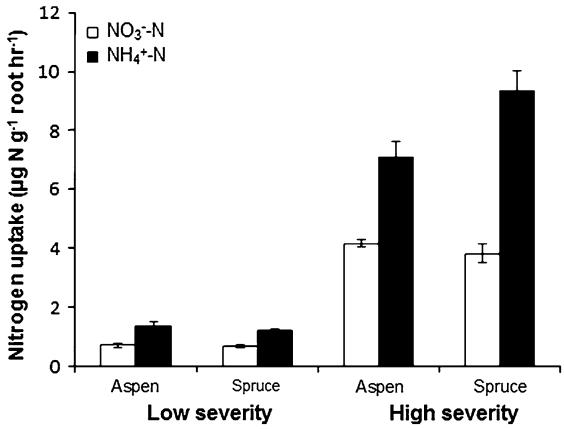

Fig. 2 Inorganic N uptake rates ($\mu g\ N\ g^{-1}$root h^{-1}) measured using ^{15}N labeled NO_3^- and NH_4^+ over a 24 h period during August 2010. *Bars* indicate mean ± SE ($n = 5$)

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 (e.g., soil moisture, pH, and organic matter content) 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 toward 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

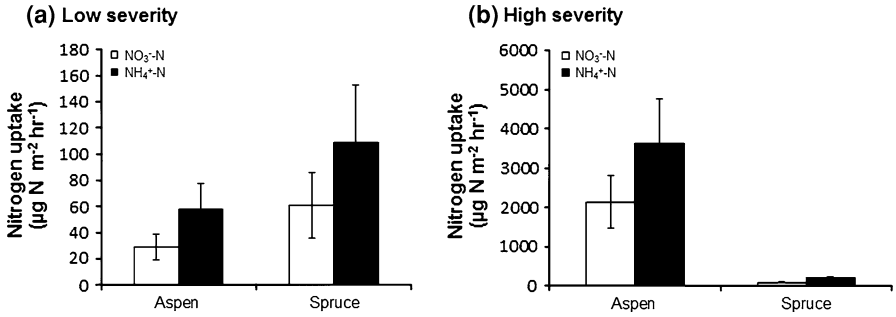

Fig. 3 Total inorganic N uptake rates for aspen and spruce expressed on an area basis (µg N m^{-2} h^{-1}) in **a** low severity ($n = 8$) and **b** high severity sites ($n = 4$). Note axis maxima are different in each case. *Bars* indicate mean ± SE

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 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^+ versus NO_3^- in the field was much smaller (2×) than that observed under laboratory conditions (10×) (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 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.

Acknowledgments This research was funded by National Aeronautics and Space Administration (NASA grant number NNG04GR24G), Bonanza Creek Long-Term Ecological Research Program, and a University of Alaska Fairbanks Center for Global Change Student Research Grant. We thank Roger W. Ruess for his editorial comments, and Benjamin Cook and Cassidy Phillips for field assistance.

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