Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest[1]

Jill F. Johnstone and Eric S. Kasischke

Abstract: This study tested whether variations in soil burn severity (soil organic layer consumption) influenced patterns of early postfire plant regeneration in a black spruce (*Picea mariana* (Mill.) BSP) forest in interior Alaska. Variations in burn severity were related to measurements of postfire tree seedling establishment and cover of plant growth forms observed 7–8 years after fire. Black spruce and trembling aspen (*Populus tremuloides* Michx.) showed significant and opposite responses of seedling density to changes in soil burn severity. Positive correlations between burn severity and aspen density and individual seedling biomass led to an increase of over three orders of magnitude in aspen standing biomass (aboveground, g/m^2) from the least to most severely burned sites. Variations in aspen productivity and consequent effects on litter production and seedbed quality possibly explain the observed negative response of black spruce density to increasing burn severity. Variations in the cover of several plant growth forms were also strongly correlated with patterns of soil burn severity. Regenerating plant communities in low-severity sites had a greater cover of evergreen shrubs and graminoids, while high-severity sites had increased cover of aspen and acrocarpous mosses. Observations of regeneration patterns in the burn are largely consistent with experimental studies of severity effects and suggest that variations in soil burn severity can have a strong influence on landscape patterns of postfire forest recovery. In this case, increases in burn severity have shifted successional trajectories away from simple conifer self-replacement towards a trajectory of mixed conifer and deciduous dominance.

Résumé : Cette étude visait à déterminer l'influence de la sévérité du brûlage du sol (couche organique consumée par le feu) sur les patrons de régénération de la végétation immédiatement après un feu dans une forêt d'épinette noire (*Picea mariana* (Mill.) BSP) du centre de l'Alaska. Les variations de la sévérité du brûlage ont été reliées à des mesures d'établissement de semis d'arbres après le feu et à la couverture de différents types végétaux observée de 7 à 8 ans après le feu. Les semis d'épinette noire et de peuplier faux-tremble (*Populus tremuloides* Michx.) ont réagi de façon significative mais contraire aux variations de la sévérité du brûlage du sol. Des corrélations positives entre la sévérité du brûlage et la densité du peuplier et la biomasse individuelle des semis font en sorte que la biomasse aérienne de peuplier (g/m^2) des stations les plus sévèrement brûlées est plus de 1000 fois supérieure à celle des stations les moins sévèrement brûlées. Les variations dans la productivité du peuplier et ses effets sur la production de litière et la qualité des lits de germination sont possiblement responsables de la réaction négative des semis d'épinette noire à l'augmentation de la sévérité du brûlage. Le couvert de plusieurs types de végétation a aussi été fortement corrélé à la sévérité du brûlage. Les communautés végétales qui se régénéraient dans les stations faiblement brûlées étaient dominées par des arbustes à feuilles persistantes et par des graminées alors que les stations sévèrement brûlées étaient surtout recouvertes de peuplier et de mousses acrocarpes. Ces observations au sujet des patrons de régénération dans le brûlis corroborent en grande partie les résultats d'études expérimentales sur les effets de la sévérité des feux et suggèrent que les variations de la sévérité du brûlage du sol peuvent avoir une influence déterminante sur les patrons de régénération à l'échelle du paysage. Dans notre cas, l'augmentation de la sévérité du brûlage a modifié la trajectoire de la succession de la végétation qui est passée du simple remplacement des conifères par d'autres conifères vers la formation de peuplements mélangés avec des conifères dominés par les feuillus.

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Introduction

Fire is the most common natural disturbance and initiator of secondary succession in the boreal forest. Research on postfire succession in boreal ecosystems has been successful in documenting several common patterns and pathways of forest succession (Van Cleve and Viereck 1981; Payette 1992; Bergeron 2000; Lampainen et al. 2004). However, our understanding of the flexibility and variation in these successional pathways is poor, and this constrains our ability to predict community change (Chapin et al. 2005). For example, postfire succession in moist black spruce (*Picea mariana* (Mill.) BSP) forests of Alaska is expected to follow a simple pattern of spruce self-replacement that involves relatively few intervening changes in plant community composition (Van Cleve and Viereck 1981; Van Cleve et al. 1991). This constrained pattern of spruce-to-spruce succession is driven by local site conditions and plant–soil interactions that favour the accumulation of organic soils, low soil temperatures, and slow nutrient cycling (Van Cleve et al. 1991). Such conditions favour the conservative growth strategy of black spruce and inhibit the establishment and growth of deciduous species. Nevertheless, field observations indicate that even in "typical" black spruce forests, succession trajectories can shift to include codominance with deciduous trees (Viereck 1983; Landhausser and Wein 1993; Kasischke et al. 2000; Fastie et al. 2003). Understanding the factors that control these variations in succession is critical to predicting long-term changes in forest composition.

Changes in disturbance regime may influence succession patterns through effects on physical site conditions, legacies left by the predisturbance community, and spatial effects on factors such as seed availability and animal herbivory (Turner 1989; Greene et al. 2004). In moist parts of the boreal forest where thick soil organic layers accumulate (Van Cleve and Viereck 1981; Rapalee et al. 1998), variations in fuel conditions and fire weather can generate large variations in the level of organic matter combustion (Dyrness and Norum 1983; Van Wagner 1983; Miyanishi and Johnson 2002). The amount of organic layer combustion, or soil burn severity, may, in turn, interact with legacies of the prefire community to affect patterns of postfire regeneration (Schimmel and Granström 1996; Turner et al. 1999; Greene et al. 2004). Variations in the level of organic layer combustion have been shown to strongly influence rates of tree seedling establishment (Chrosciewicz 1974; Zasada et al. 1983; Charron and Greene 2002; Greene et al. 2004; Johnstone and Chapin 2005) and the relative success of different plant regeneration strategies (Schimmel and Granström 1996; Johnstone and Chapin 2005). However, much of the research on severity effects has been conducted at the plot (square metre) scale, and additional data are needed to determine whether and how the effects observed at this small scale are likely to influence stand or landscape patterns of vegetation succession (e.g., Turner et al. 1999). This question is particularly relevant with respect to soil burn severity, where small (square metre) variations in organic layer combustion (Dyrness and Norum 1983; Miyanishi and Johnson 2002) are often nested within a larger mosaic of landscape variation (Turner et al. 2003; Greene et al. 2004).

We studied a wildfire of variable severity to assess how natural variations in soil burn severity influenced stand-level patterns of succession in a black spruce forest landscape in interior Alaska, USA. Information from remote sensing (Michalek et al. 2000) and stratified field observations were used to correlate variations in burn severity with patterns of postfire forest regeneration. We compared our estimates of burn severity effects with expectations derived from plot-level studies to assess how well small-scale effects appeared to predict stand-level patterns of postfire regeneration. In particular, we tested hypotheses that increases in soil burn severity should lead to (1) increases in postfire tree seedling density and aboveground biomass, (2) increases in the relative establishment success of deciduous versus conifer seedlings, and (3) shifts in plant community composition from predominantly resprouters to predominantly seed establishers. Results of the study have provided information on the role of fire in driving variations in succession patterns across forest landscapes.

Materials and methods

Study area

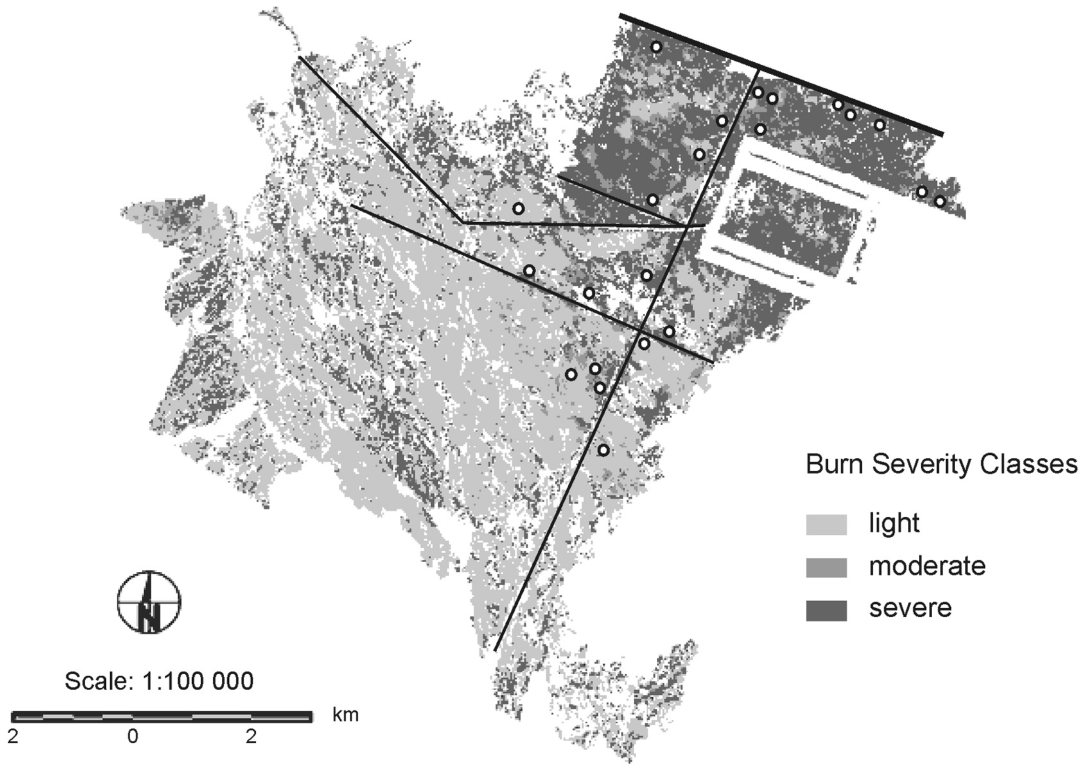
The study area was located on a broad glacial outwash plain in central Alaska, situated north of the Alaska Range and approximately 35 km east of the town of Delta Junction. Sampling focused on an 8900-ha area of boreal forest in the vicinity of Hajdukovich Creek that burned from 14 June to early September in 1994 (the HC94 burn; Fig. 1). The fire initiated along the extreme western edge of the burn boundary, slowly spread to the north, east, and south during July, and reached the northeast portion of the burn in early August (Michalek et al. 2000). The Alaska Fire Service calculated burning conditions during the fire using the Canadian Fire Weather Index System and weather data from Delta Junction (Alaska Fire Service, unpublished data). Burning conditions in June and most of July were characterized by low values of the Drought Code (DC, range 275–400) and Buildup Index (BUI, range 20–70) and by moderate fire weather (mean daily Fire Weather Index (FWI) = 4.6, SD = 15.5). Continued dry weather in late July and August resulted in the development of extreme DC during the first 3 weeks of August (DC range 460 to >600), increases in the BUI (range 80–130), and more severe fire weather (mean daily FWI = 25.6, SD = 8.0). Areas burned during this period (the northeast portion of the burn) generally experienced higher levels of soil burn severity (Fig. 1).

The prefire forest in the HC94 burn area was dominated by open- to closed-canopy black spruce, with occasional stands of trembling aspen (*Populus tremuloides* Michx.) in areas of coarse soils (Kasischke et al. 2000). White spruce (*Picea glauca* (Moench) Voss s.l.) was not abundant in the burned area and was largely restricted to mixtures with aspen. Soils in the burn were composed of silt loams on top of gravel or sandy outwash and till layers, with an overlying layer of organic soil up to 30 cm thick. Much of the area is underlain by near-surface permafrost (<2 m below the soil surface). A more detailed description of the soils and physiographic setting is given in Kasischke and Johnstone (2005).

Field observations

A total of 22 sites within the HC94 burn were sampled for prefire stand composition, soil characteristics, and postfire

Fig. 1. A map of the HC94 burn, showing burn severity classes (light, moderate, and severe) derived from Landsat imagery (modified from Michalek et al. 2000). Sample sites are shown as black and white circles. Thin black lines indicate the network of dirt trails used to access the area; a thick black line at the northeastern edge of the burn indicates the Alaska Highway. The white rectangular insert in the burn image is an area that had been artificially cleared.



seedling establishment. We used two sources of satellite information to aid us in site selection. The first was a map with three burn severity categories (light, moderate, and severe) generated from a supervised classification of a Landsat Thematic Mapper image collected in September 1995 (Fig. 1; see Michalek et al. (2000) for details). The second was a vegetation recovery map showing surface "greenness" estimated from the normalized-difference vegetation index and calculated from a July 2000 IKONOS satellite image with 4-m resolution. The sites used in this study were selected in a stratified-random fashion to cover the full spectrum of burn severity and vegetation cover indicated by the satellite images for the forested portions of the burn. Because of logistical constraints, sample sites were restricted to road- and trail-accessible areas (Fig. 1). Tree mortality in the sampled stands ranged from 90% to 100%. All sites were located over 100 m from an unburned forest edge. Field measurements were made in early August 2001 (4 stands) and July 2002 (18 stands).

At each site, vegetation and soil measurements were collected along parallel, 2 m × 50 m belt transects (100 m^2, n = 5) positioned at random distances from each other within the bounds of a visually homogeneous, 50 m × 50 m area (0.25 ha). The sampling layout was established by walking into an area of visually homogeneous vegetation, setting a 50-m baseline of random orientation, and then laying out five sampling transects oriented perpendicular to the baseline. One of the sampling transects was always established at the baseline midpoint (25 m), and two transects were established on each side of the midpoint at random distances along the baseline.

Satellite-based classifications of burn severity were confirmed on the ground by assigning each site to a soil burn severity class (light, moderate, or severe) based on qualitative estimates of mineral soil exposure (Michalek et al. 2000). Measurements of organic-layer depths at 5-m intervals along each 50-m transect (11 points per transect, n = 55 per site) provided a more quantitative estimate of soil burn severity. At each point, the depth of the different organic soil layers (dead moss, char, fibric organic material, humic organic material) was measured from a 20 cm × 20 cm square core removed with a flat-bladed shovel. Samples of the organic layer were collected for measurements of bulk density from one randomly selected core on each transect (n = 5). These samples were obtained by cutting the core down to a 10 cm × 10 cm block that was separated into its component layers of dead moss, fibric organic material, humic organic material, and the upper mineral soil. The depth of each layer was recorded in the field to the nearest 0.5 cm. Samples were returned to the laboratory, dried for 48 h at 60 °C, and weighed to estimate soil bulk density (g dry mass/cm^3). Mineral soil characteristics were described from a single soil pit dug to approximately 50 cm. Data on soil texture and stratigraphy were used to develop an estimated drainage index for the sites (Table 1). Classes in the drainage index were defined as follows: (1) poorest drainage: shallow active layer (permafrost at <50 cm) or only fine soils within the upper 50 cm; (2) coarse soil layers (gravel or cobble) at depths of 30–

Table 1. Summary of site-level data on soil burn severity, prefire stand characteristics, and postfire seedling regeneration.

						Spruce				Aspen			
Site No.	Soil burn severity class	Organic layer depth (cm)	Surface bulk density (g/cm^3)	Prefire stand age (years)	Drainage class (1 = low)	Prefire basal area (m^2/ha)	Postfire density (stems/m^2)	Seedling biomass (g/seedling)	Total biomass (g/m^2)	Prefire basal area (m^2/ha)	Postfire density (stems/m^2)	Seedling biomass (g/seedling)	Total biomass (g/m^2)
1	Severe	0.8	0.57	120	3	33.2	0.3	2.7	0.4	0	1.5	264.0	448.0
2	Severe	1.6	0.62	85	3	4.5	0.1	1.7	0.1	19.3	6.3	25.8	218.7
3	Light	14.3	0.19	230	2	10.9	1.1	2.0	4.0	0	0.0	4.8	0.6
4	Light	11.4	0.26	120	1	28.7	6.7	0.5	1.3	0.5	5.1	0.5	1.2
5	Light	9.4	0.23	85	3	29.5	2.5	3.6	5.2	0	2.1	5.8	29.9
6	Severe	1.7	0.52	120	3	23.3	0.7	0.4	0.3	0	1.5	82.2	189.0
7	Severe	2.8	0.42	120	2	24.7	0.8	0.2	0.2	0	4.0	7.5	30.5
8	Light	6.5	0.20	85	2	35.0	1.7	0.2	0.4	0	0.8	3.8	4.5
9	Severe	1.1	0.47	85	4	6.5	0.8	0.8	1.2	26.6	5.9	10.2	86.0
10	Moderate	7.3	0.29	230	4	13.8	0.4	0.7	0.4	0	2.5	19.2	57.8
11	Severe	1.2	0.78	230	3	24.3	0.3	0.3	0.1	0	3.9	93.4	466.0
12	Light	11.2	0.23	280	4	18.8	7.2	0.4	3.4	0.3	2.1	2.4	4.9
13	Moderate	5.6	0.49	280	3	22.6	1.4	0.1	0.2	0	6.7	33.8	194.8
14*	Light	26.6	0.16	85	1	5.7	0.3	0.0	0.0	0	0.1	na	0.0
15	Severe	4.0	0.41	120	2	29.8	5.9	0.2	2.8	0.4	6.0	3.6	46.1
16	Light	5.4	0.31	120	3	32.4	0.2	0.4	0.0	0	0.8	14.0	18.7
17	Severe	1.4	0.55	120	3	25.3	0.4	0.3	0.1	0	1.6	117.2	189.5
18	Moderate	3.9	0.59	120	2	15.5	1.5	0.8	2.6	0	7.1	2.3	22.1
101†	Severe	0.4	0.50	120	2	20.7	0.6	—	—	0	2.4	—	—
102†	Severe	2.0	0.43	230	1	15.0	0.4	—	—	0	1.7	—	—
103†	Light	19.1	0.10	200	2	27.5	2.7	—	—	0	0.5	—	—
104†	Severe	2.0	0.49	120	3	23.7	0.6	—	—	0	2.5	—	—

Note: Except for severity class and stand age, values are site means. Data are provided for the two most common tree species, black spruce (*Picea mariana*) and aspen (*Populus tremuloides*).
*Dominated by tussock vegetation and not included in the statistical analyses.
†Sites 101–104 were measured in 2001. Seedling biomass data are not available for these sites.

50 cm; (3) coarse soil layers at depths of 10–30 cm; (4) most rapid drainage: coarse materials dominate the soil profile.

Information on the prefire vegetation community was obtained by recording the composition and basal diameters (centimetres) of standing or fallen prefire trees (>1.5 m tall) rooted within the 2-m belt transects. Species determinations of dead trees were based on cone, bark, and branching morphology. Trees that were dead at the time of the fire, determined from evidence of deep charring on the bole, were not included in the measurements.

Tree ring counts from 10–12 trees provided an estimate of stand age prior to burning. Trees were systematically sampled along the baseline or central sampling transects at regular intervals (both transects were sampled when tree densities were low). Ring counts were obtained from tree stem disks, or occasionally increment cores, sampled 15–20 cm above the upper roots or soil surface, and just above the swollen portion of the trunk base. The samples were sanded and measured under a binocular microscope. Trees (mostly black spruce) were assumed to have grown for a minimum of 5 years before reaching the height of the tree-ring sample (J.F. Johnstone, personal observation). Minimum stand age or time since fire was estimated from the ages of the oldest trees in the stand. Stands with age estimates that differed by less than 10 years were assumed to have been initiated by the same fire.

Postfire tree seedling density was measured by counting live seedlings or saplings of each tree species within the 2-m belt transects. Black spruce and trembling aspen were the dominant species, but we also occasionally encountered individuals of paper birch (*Betula papyrifera* Marsh., up to 8% of seedlings) and Alaskan larch (*Larix laricina* (Du Roi) K. Koch), less than 0.1% of seedlings). Because of difficulties in differentiating young seedlings of black and white spruce, it is possible that some of the black spruce seedling counts included misidentified white spruce. However, we are confident the majority of spruce seedlings were black spruce, as white spruce had very low prefire abundance in the burn area and most sites were far (>2 km) from an unburned white spruce seed source.

Basal diameters of regenerating black spruce and aspen stems were measured within randomly selected 10-m^2 subsections of the 100-m^2 sampling transects, for all sites sampled in 2002 (n = 18). These data were translated into estimates of abovegound biomass using allometric equations (Table 1). To develop the allometric equations, basal diameters of black spruce (n = 25) and aspen (n = 39) seedlings were measured in the field, and the aboveground portions of the seedlings were clipped at the ground surface. Each sample was separated into woody and green biomass in the laboratory, dried in an oven at 40 °C for 48 h, and weighed to obtain aboveground dry mass (grams). Allometric equations to predict aboveground biomass (grams) from basal diameter (millimetres) for each species were fitted using linear regression of log-transformed diameter and biomass data (Wagner and Ter-Mikaelian 1999). Field measurements of basal diameter from each site were then translated into aboveground biomass using the allometric equations along with a correction factor to account for back transformation of log data (Sprugel 1983). Mean aboveground biomass per square metre was calculated as the sum of estimated biomass divided by the sample area.

Measurements of visual percent cover of the major plant growth forms (mosses, graminoids, herbs, and woody shrubs) provided an assessment of the postfire composition of the plant community at each site. Cover classes were assigned using a semi-logarithmic cover scale with 10 classes of percent cover ranging from 0% to 100% (classes (%): 0, 1, 2–3, 3–5, 5–10, 10–20, 20–35, 35–50, 50–75, 75–100). Cover estimates were based on a visual survey of a 10 m radius area within the center of each sample area. Woody shrubs were separated into willow (*Salix* spp.) and non-willow groups. Cover of aspen and cover of spruce were also estimated separately. Spruce cover was limited to <3% at all sites, and consequently this species was not included in the plant community analysis. Plant cover data were collected for 17 stands sampled in 2002.

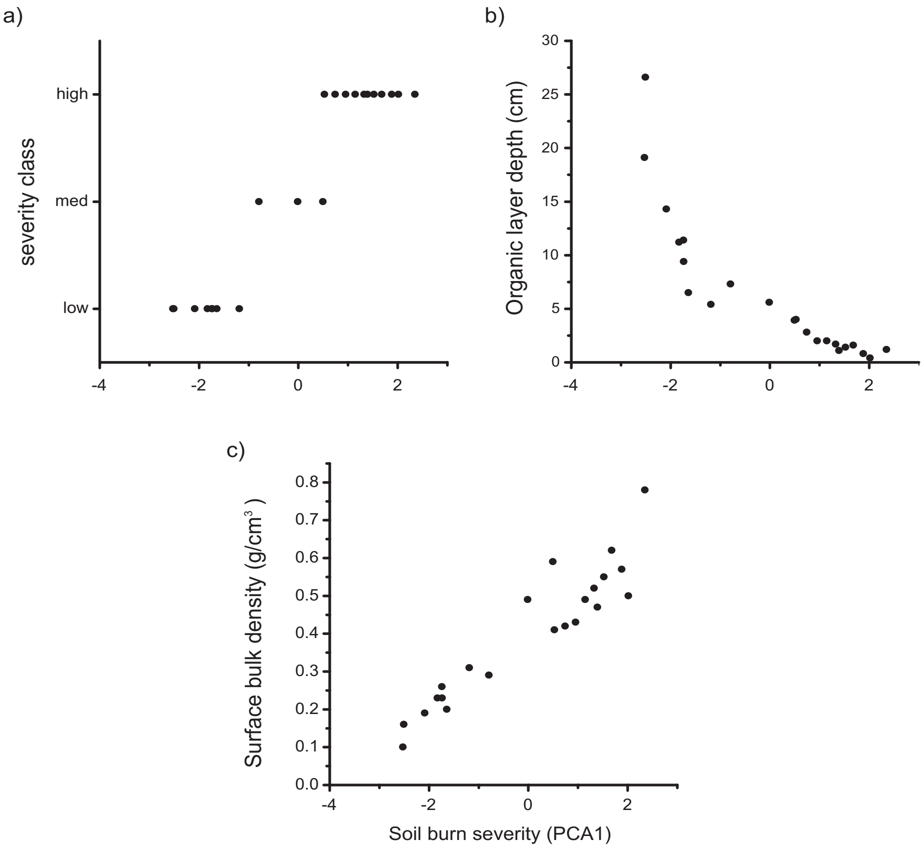
Data analysis

Data collected from the individual transects within a stand were averaged or summed to provide five subsample replicates, from which stand means were calculated and used in subsequent analyses (Table 1). Data collected from a single stand (site 14) characterized by tussock vegetation (primarily *Eriophorum vaginatum* L.), near-surface permafrost, and unusually thick organic soils were consistent outliers in the analysis of seedling density and biomass patterns (Table 1). This data point is shown in our summary figures and tables but was not included in the statistical analyses of regeneration patterns. Because of variations in the types of data collected at each site, final sample sizes for the analyses were n = 21 for seedling density, n = 17 for seedling biomass, and n = 16 for vegetation cover. Measurements made at four sites in 2001 could not be systematically differentiated from the 2002 measurements, and both data sets were included in our analysis.

Principal components analysis (PCA) provided a means to collapse information contained in multiple, intercorrelated variables into a single eigenvector that could be used in univariate analyses. PCA eigenvectors were extracted from the soil data set to represent overall variations in soil burn severity, and from the vegetation cover data to represent variations in plant community composition.

Simple correlation analyses provided an assessment of relationships between different variables measured in the study. A suite of multivariate regression models were also fitted to the seedling data sets to (1) assess our ability to predict observed patterns in tree seedling densities and standing biomass from measured variables, and (2) to compare the support for models based on soil burn severity and prefire species basal area density (Greene and Johnson 1999; Greene et al. 2004) with alternative models that included other site factors. Candidate independent variables for the alternative models included prefire and environmental site factors, as well as postfire aspen variables for the black spruce models. The "best" models for each dependent variable were selected based on Akaike Information Criteria (AIC) values. AIC weights were used to assess the relative support for the different models based on the data (Anderson et al. 2000). Prior to analysis, postfire stem density and biomass values were log transformed to account for negative skew in the distributions of these variables. The analyses were performed

Fig. 2. Correlations of measured soil variables with a single principle components eigenvector (PCA1) used to represent overall variations in soil burn severity. Positive weightings on the PCA axis indicate high levels of burn severity, and negative weightings indicate low burn severity. The PCA eigenvector was calculated directly from the three soil variables shown on the *y* axes: (*a*) severity class, (*b*) total organic layer depth (cm), and (*c*) bulk density (g dry soil/cm^3) of the upper 5 cm of surface soil.



using SAS version 8.2 (copyright SAS Institute Inc., Cary, N.C.).

Results

Site characteristics

The majority (20 of 22) of the stands we sampled in the HC94 burn were dominated by black spruce before they burned, sometimes with a few stems (≤1%) of white spruce (three stands) or aspen (three stands). The remaining two sampled stands were dominated by aspen when they burned and included up to 5% of white spruce. These prefire aspen stands occurred in areas with coarse cobble and gravel soils near the ground surface (drainage classes 3 and 4). Soils in the black spruce stands were dominated by fine-textured silt and silt loams, although several sites had gravel or cobble layers alternating with silt in the upper mineral soil.

Ages of individual trees estimated from ring counts ranged from 60 to 280 years. Many stands showed a clustering of tree ages, suggesting that the trees had established following a stand-replacing fire. The variation in tree ages within a stand increased with stand age, ranging from a mean coefficient of variation of 9% for stands under 100 years in age to 21% for stands estimated to be over 200 years, as would be expected given the accumulated errors associated with aging old stands (DesRochers and Gagnon 1997; Peters et al. 2002). The tree-ring data indicated two fires had occurred in the sample area over the past 200 years, one around 1910 (initiating 5 of 22 stands) and another around 1875 (initiating 10 of 22 stands). Seven of the sampled stands had mean tree ages over 200 years and are likely to have burned in the mid to late 1700s (Table 1). The two prefire stands dominated by aspen originated in the most recent burn. Aspen stems were also present at low densities in two mid-aged stands and in one stand in the oldest age-class. Prefire spruce densities showed no significant correlation with stand age (r = –0.29, $p > 0.1$). Stand age was also uncorrelated with mean organic layer depths measured after the fire ($r < 0.3$, $p > 0.1$).

Postfire organic layer depths varied substantially among stands, ranging from near zero to over 20 cm in depth (Table 1). Variations in postfire organic layer depths were consistent with classifications of sites as high, medium, or low burn severity based on satellite observations (Fig. 2). Variations in total organic layer depth were correlated with depths of the fibric and humic components of the organic layer and with surface bulk density. Mean bulk density within the near-surface soil was lowest for surface organic layers (dead moss and fibric layers, mean (±SD) 0.31 ± 0.16 g/cm^3, n = 65) and higher for the humic organic layer (0.47 ± 0.21 g/cm^3, n = 60) and upper mineral soil (0.52 ± 0.19 g/cm^3, n = 15). Both shallow and deep organic layers in the study area showed signs of aolian silt deposition, such as residual surface silt veneers, observable particles within the organic layers, and varved layers of silt and organic soil near the mineral soil –

Table 2. Allometric equations for the prediction of aboveground biomass (grams dry mass) from measurements of basal diameter for spruce and aspen seedlings.

	Black spruce	Trembling aspen
n	25	39
Diameter range (mm)	0.6–8.2	1.8–55.6
Biomass range (g)	0.01–32.1	0.15–2120
Equation	ln(biomass) = –4.304 + 3.271 ln(diameter)	ln(biomass) = –3.183 + 2.828 ln(diameter)
Correction factor	1.103	1.022
r^2	0.97	0.99
p value	<0.0001	<0.0001

organic layer interface. Aolian deposition is likely to account for the unusually high estimates of organic layer bulk density obtained in this study.

A PCA of total organic layer depth, bulk density, and severity class was used to generate a single index of soil burn severity, estimated by the first PCA eigenvector (Fig. 2). This eigenvector captured 90% of the variance in the severity-related soil properties and was used in subsequent analyses to represent overall variations in soil burn severity among the sampled sites. Variations in the burn severity index were not significantly related to prefire species stem density, basal area, or the site drainage index ($r < 0.3$, $p > 0.1$).

Postfire regeneration patterns

Postfire seedling densities were uncorrelated with prefire tree densities for all species ($r = 0.3$, $p > 0.1$). Mean density of black spruce was 0.8 trees/m^2 (maximum 1.6) before the fire and 1.7 seedlings/m^2 (maximum 7.2) after the fire. Aspen stems, which were absent from the majority of prefire stands, established in most stands after the burn and reached postfire densities equivalent to those of black spruce (mean of 3.0 and maximum of 6.0 seedlings/m^2). Postfire seedling densities were poorly correlated with prefire species basal area ($r = 0.34$ and 0.30 for black spruce and aspen, respectively, $p > 0.1$), a factor that has been previously used as an index of postfire seed or propagule availability (Greene and Johnson 1999; Greene et al. 2004).

Allometric equations relating seedling basal diameter to total aboveground biomass indicated that seedling biomass could be well predicted from diameter measurements (Table 2). Across stands, mean predicted biomass of seedlings (g dry mass/individual) was uncorrelated with seedling density of the same species ($r < 0.1$, $p > 0.1$ for aspen and spruce). However, postfire spruce density was significantly and negatively correlated with aboveground aspen biomass represented on a per individual ($r = –0.74$, $p = 0.001$) or per square metre basis ($r = –0.61$, $p = 0.01$).

Seedling responses to variations in soil burn severity differed in strength and direction between spruce and aspen (Fig. 3). Postfire densities of spruce decreased with increases in burn severity ($r = –0.61$, $p = 0.004$), while aspen density increased with severity ($r = 0.49$, $p = 0.02$). Mean biomass of individual spruce seedlings was largely insensitive to severity level ($r = 0.07$, $p = 0.8$), but severity effects on spruce density were reflected in a negative correlation between total spruce biomass (g/m^2) and burn severity ($r = 0.47$, $p = 0.06$). In contrast, aspen biomass increased with increasing burn severity, both on a per individual ($r = 0.71$, $p = 0.002$) and per square metre ($r = 0.87$, $p < 0.0001$) basis. Values for the two prefire aspen stands included in our study fit well within the overall relationships observed for the largely spruce-dominated sites in the data set (Table 1).

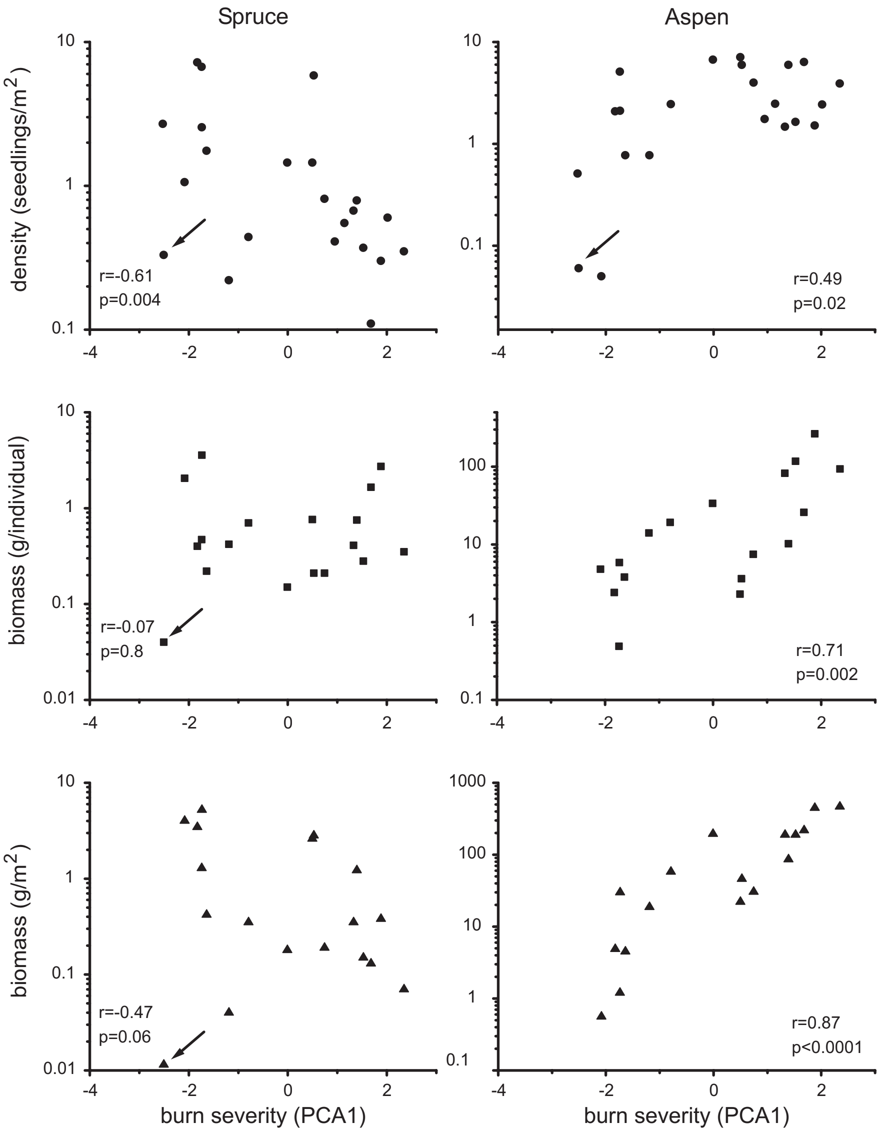
A comparison of models predicting postfire seedling densities and aboveground standing biomass (g/m^2) indicated that spruce regeneration was most strongly related to aspen biomass, while aspen density and biomass were most strongly related to burn severity (Table 3). There was little support for prefire species basal area as a direct predictor of postfire regeneration, although this variable was included in the best-fit multivariate models predicting black spruce density and aspen standing biomass. In the case of black spruce, over half the variance in seedling densities was explained by aspen seedling biomass (g/individual), and this increased to 70% with the inclusion of prefire spruce basal area and stand age in the model (Table 3). Aspen seedling densities were less predictable from the site data, although there was some support for aspen basal area or site drainage as explanatory variables of potential importance. Aspen standing biomass, on the other hand, was well predicted ($R^2 > 0.75$) by burn severity alone or in combination with prefire aspen basal area and site drainage (Table 3).

PCA of the vegetation cover data generated a first eigenvector that captured 52% of the variance and distinguished changes in community composition caused by inverse patterns of aspen and moss cover versus non-willow woody shrubs and graminoids (Fig. 4). Variations in postfire plant community composition represented by this eigenvector were strongly correlated with patterns of burn severity ($r = –0.89$, $p < 0.001$; Fig. 5) and unrelated to site factors of stand age, site drainage, prefire spruce density, or spruce basal area ($r < 0.3$, $p > 0.2$). Areas of high burn severity generally supported communities that were dominated by a high cover of aspen and small acrocarpous mosses (mainly *Ceratadon pupureus* (Hedw.) Brid. and *Pohlia nutans* (Hedw.) Lindb.). As burn severity decreased, communities were increasingly dominated by graminoids (primarily *Calamagrostis lapponica* (Wahlenb.) Hartm.) and non-willow woody shrubs (dominated by *Ledum palustre* L. s.l., *Vaccinium* spp., and *Rosa acicularis* Lindl. s.l.). A second eigenvector accounted for 21% of the variance in plant cover and represented changes in cover of willows (*Salix* spp.) and herbs. This eigenvector was uncorrelated with burn severity or other measured site factors ($p > 0.1$).

Discussion

Several lines of evidence suggest that the large variations in postfire organic layer depths observed within the HC94

Fig. 3. Seedling density (seedlings/m^2, n = 21), aboveground seedling biomass (g/individual, n = 17), and total standing biomass (g/m^2, n = 17) of black spruce and aspen in relation to the soil burn severity index (PCA1). Positive values on the x axis indicate high levels of burn severity, and negative values indicate low burn severity. Note the y axes are shown on log scales. Arrows indicate the location of the tussock-dominated stand that was not included in the correlation analyses.



burn arose from variations in fire behaviour, rather than from differences in prefire conditions. Prefire vegetation maps derived from 1992 Landsat imagery show that the sampled portions of the HC94 fire were located within a continuous matrix of medium–high density black spruce forest with small, scattered patches (<10%) of deciduous forest (Michalek et al. 2000). Measurements of adventitious roots on dead black spruce within the burn suggest mean prefire organic layer depths of over 25 cm in severely burned stands (Kasischke and Johnstone 2005). These values correspond closely with mean depths of 25–30 cm measured in adjacent, unburned spruce stands (Kasischke and Johnstone 2005). In addition, many of the severely burned stands show no upper fibric layer, while the lightly burned stands show fibric layers of variable depth above humic layers similar in depth to those in unburned stands (J.F. Johnstone, unpublished data). This pattern is consistent with the process of organic layer combustion proceeding from the surface layers downward. Finally, spatial patterns in postburn organic layer depths were consistently related to seasonal changes in burn characteristics (Michalek et al. 2000) and soil drainage associated with permafrost thaw (Kasischke and Johnstone 2005). This suggests that seasonal changes in fuel conditions and fire behaviour were a primary factor affecting patterns of soil burn severity (Kasischke and Johnstone 2005). Together, these data indicate that the spruce forests of the HC94 burn were characterized by widespread, deep (>20 cm) organic layers before the fire and that postfire variations in organic layer depths arose as a consequence of altered fire behaviour. The relatively uniform prefire conditions and large variability in soil burn severity within the HC94 burn thus provide an excellent "natural experiment" to evaluate fire effects on postfire revegetation processes.

Variations in postfire organic layer depths clearly influenced stand-level patterns of postfire tree recruitment and growth in the HC94 burn. Trembling aspen showed signifi-

Table 3. Comparison of models that predict postfire density (stems/m^2) and standing aboveground biomass (g dry mass/m^2) of black spruce and aspen.

Dependent variable	Model type	Independent variables	R^2	AIC_c	w_i
Black spruce					
Density	Burn severity	Severity (–)	0.32	–25.24	0.01
	Prefire composition	Spruce BA (+)	0.06	–19.62	0.00
	Severity and composition	Severity (–), spruce BA (+)	0.34	–23.53	0.00
	Best univariate model	Aspen seedling biomass (–)	0.55	–32.06	0.25
	Best multivariate model	Aspen seedling biomass (–), spruce BA (+), stand age (+)	0.70	–34.25	0.74
Biomass/m^2	Burn severity	Severity (–)	0.22	–15.44	0.11
	Prefire composition	Spruce BA (+)	0.02	–11.51	0.02
	Severity and composition	Severity (–), spruce BA (+)	0.28	–14.36	0.07
	Best univariate model	Aspen seedling biomass (–)	0.38	–19.40	0.81
Aspen					
Density	Burn severity	Severity (+)	0.24	–32.03	0.50
	Prefire composition	Aspen BA (–)	0.09	–28.42	0.08
	Severity and composition	Severity (+), aspen BA (–)	0.27	–30.63	0.25
	Best multivariate model	Severity (+), drainage (+)	0.24	–29.86	0.17
Biomass/m^2	Burn severity	Severity (+)	0.76	–30.08	0.04
	Prefire composition	Aspen BA (–)	0.05	–6.68	0.00
	Severity and composition	Severity (+), aspen BA (–)	0.77	–28.28	0.02
	Best multivariate model	Severity (+), aspen BA (–), drainage (+)	0.88	–36.35	0.94

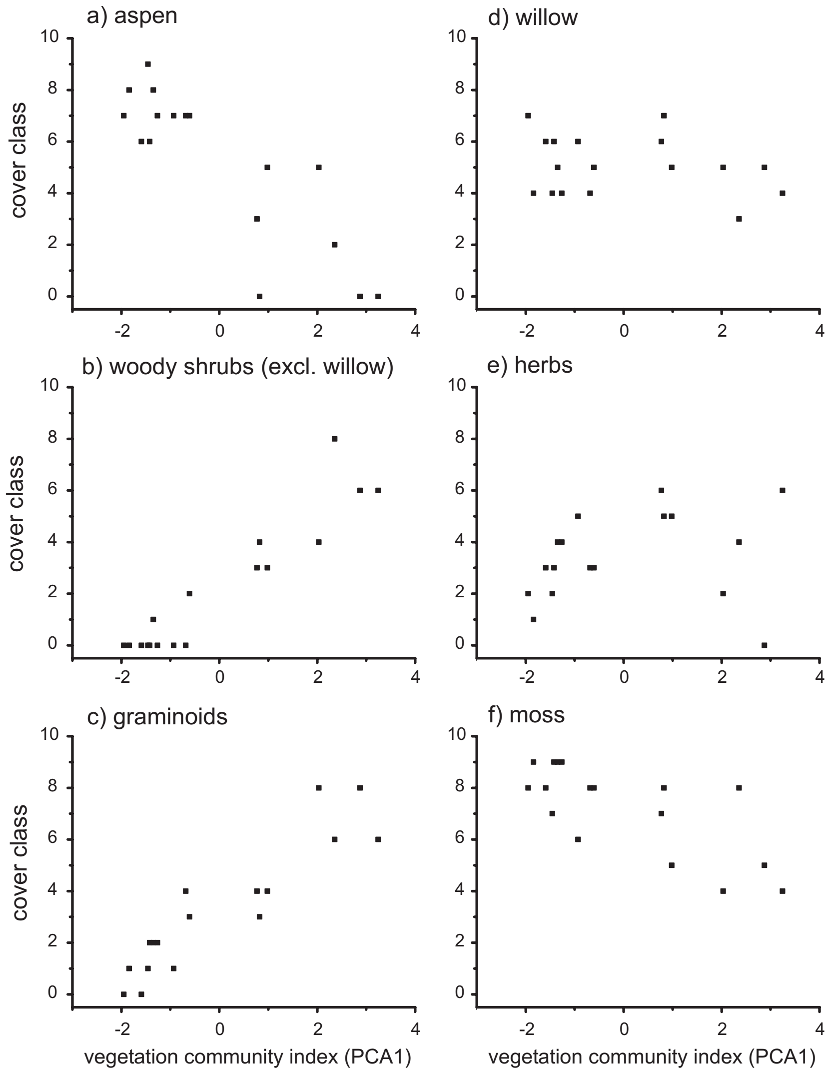
Note: Candidate models specifically included those based on burn severity (PCA1) and prefire species basal area (BA) (Greene and Johnson 1999; Greene et al. 2004), as well as alternative models that included other site factors. Positive and negative signs in parentheses following names of the independent variables indicate the direction of effect on the dependent variables. The "best" model was selected as that with the smallest corrected Akaike Information Criteria (AIC_c) value. Relative support for the models is given by the AIC weights (w_i). Seedling data (dependent variables) were log transformed before fitting the models.

cant increases in density and aboveground seedling biomass with increased burn severity, a pattern consistent with plot-level observations of increased seedling germination, growth, and survival on severely burned substrates (Chrosciewicz 1974; Zasada et al. 1983; Charron and Greene 2002; Greene et al. 2004; Johnstone and Chapin 2005). However, we also observed an unexpected decrease in black spruce density with severity. Postfire spruce densities were largely unrelated to prefire spruce basal area, and high levels of canopy burn severity were experienced by all stands, making it unlikely that variations in the size of aerial seed banks or abscission rates (Greene and Johnson 1999; Greene et al. 2004) controlled the observed variations in spruce regeneration. Likewise, although low levels of moisture availability have been implicated in other instances of negative severity effects (Johnstone and Chapin 2005), we found no evidence of moisture effects in our study. Instead, we hypothesize that black spruce responded negatively to burn severity in the HC94 burn because of an indirect effect caused by interactions with aspen.

Within the HC94 burn, seedling densities of black spruce were most strongly correlated with aspen biomass, a factor that was, in turn, strongly and positively correlated with soil burn severity. A negative correlation between black spruce and burn severity may have arisen if variations in aspen productivity (associated with severely burned sites) influenced spruce regeneration through some competitive effect. Correlations between aspen productivity and spruce density but not spruce seedling biomass suggest that aspen competitive effects would have been focused on early spruce germination and survival, rather than on later growth. One way in which aspen growth may have affected spruce establishment is through increased rates of litter accumulation and consequent negative effects on seedbed quality and conifer seedling survivorship (Simard et al. 1998, 2003; Purdy et al. 2002). Field experiments at a nearby site in Alaska have demonstrated the potential for high levels of aspen cover (and associated litter production) to significantly reduce conifer seedling establishment within a few years after fire (Johnstone 2005). We hypothesize that high rates of growth of individual aspen seedlings created localized areas of heavy litterfall and low spruce recruitment and led to an overall reduction in spruce seedling densities. This hypothesis highlights the potential for both direct and indirect effects to be important in driving species responses to burn severity.

The wide extent of aspen establishment we observed within the HC94 burn was surprising given the very low abundance of prefire aspen and the expectation that aspen is largely dependent on resprouting for recruitment (Peterson and Peterson 1992; Greene and Johnson 1999). Only 5 of the 22 stands we sampled had prefire individuals of aspen within the sample plot or in the visible surroundings (within ~10 m of the plot boundary). Data on prefire tree composition and adventitious root depths (Kasischke and Johnstone 2005) indicate that many stands with postfire aspen were dominated before the fire by mature, closed-canopied black spruce with

Fig. 4. Cover class estimates (see Materials and methods for details) of individual growth forms plotted against the first eigenvector (PCA1) from a principal components analysis of the full set of cover data. The resulting vegetation community index shows strong positive loadings on graminoid and non-willow woody shrub cover, and negative loadings on aspen and moss cover.

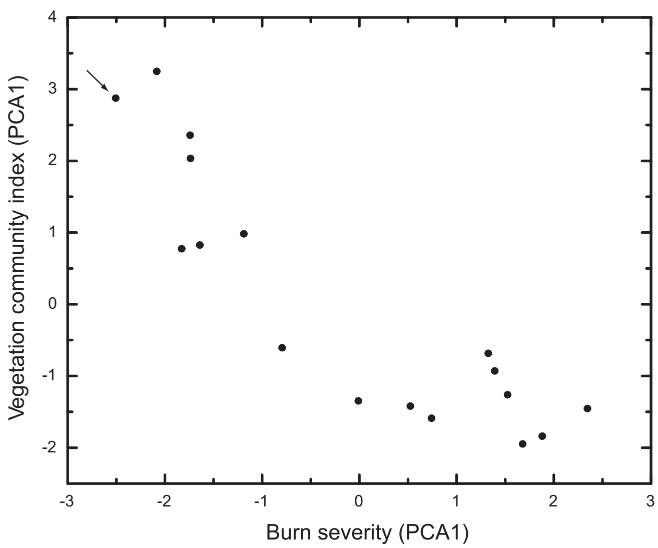


thick organic layers. These conditions are unlikely to have supported live aspen trees for many decades. Scattered test excavations of aspen at these sites also showed no evidence of root suckering (J.F. Johnstone, personal observation), although it is possible that root connections may have disintegrated in the 7–8 years after fire.

We suggest that the simplest explanation for the presence of aspen seedlings in prefire spruce stands within the HC94 burn is that they arose from seed dispersed from unburned stands. Other postfire studies have provided evidence of widespread aspen recruitment from seed (Turner et al. 2003; Johnstone et al. 2004). Together, these studies suggest that sexual regeneration of aspen may be more common than previously supposed. Aspen densities were much more strongly correlated with burn severity than with prefire aspen basal area, indicating that resprout potential (Greene and Johnson 1999; Greene et al. 2004) was relatively unimportant in controlling patterns of aspen recruitment in this burn. Indeed, levels of aspen establishment and growth in severely burned stands of black spruce were equivalent or greater than those observed in the two prefire aspen stands with the potential for extensive asexual regeneration.

Patterns of vegetation cover in the HC94 burn also showed a strong influence of soil burn severity on plant community composition. Areas of low severity were dominated by ericaceous shrubs and rhizomatous graminoids, groups characterized by a high potential for asexual regeneration by sprouting (Rowe 1983). In contrast, severely burned areas showed an increase in cover of acrocarpous mosses, probably as a result of increased exposure of mineral soil that favoured spore colonization and rapid growth. Experimental studies have shown that increases in burn severity can destroy the buried shoot and bud banks, which provide the meristems necessary for asexual regeneration (Schimmel and Granström 1996). At the same time, removal of porous layers of unburned organic material at the soil surface provides a more stable moisture supply that favours recruitment from dispersed propagules such as seeds or spores (Johnstone and Chapin 2005). In the HC94 burn, increases in burn severity appear to have caused a shift from vegetation communities

Fig. 5. Vegetation community index (first eigenvector of a principal component analysis (PCA) on plant cover) plotted against the soil burn severity index (first eigenvector of a PCA on soil variables). Scales on both axes are unitless. Positive values on the *y* axis represent increased cover of graminoids and non-willow woody shrubs, and negative values indicate increased aspen and moss cover. Positive and negative values on the *x* axis respectively indicate high and low levels of soil burn severity. A single arrow indicates the tussock-dominated stand that was excluded from the correlation analysis.



dominated by resprouting evergreen shrubs and graminoids to communities dominated by sexually regenerating aspen and acrocarpous mosses. The lack of response observed by other groups, such as willows and herbs, may have arisen from a higher diversity of regeneration modes utilized by plants in these groups. For example, regenerating willows in the study area showed both clumped and single-stemmed growth habits, indicating the occurrence of both sexual and asexual regeneration.

Conclusions

Observations of stand-level regeneration patterns within the HC94 burn are partially consistent with results of plot-based studies showing that increases in soil burn severity lead to increases in seedling establishment and growth, particularly for deciduous species (reviewed in Johnstone and Chapin 2005). Likewise, observed patterns of vegetation cover are consistent with an expected increase in sexual regeneration versus resprouting in more severely burned habitats (Rowe 1983; Schimmel and Granström 1996). However, we are aware of no study of soil burn severity in moist boreal forests that would have predicted a decrease in density of black spruce with increasing severity. The correlation structure of the data suggests this pattern may be attributed to indirect effects of aspen growth on spruce establishment, thus indicating the potential importance of species interactions in mediating processes of postfire regeneration.

This study provides evidence for a strong link between variations in soil burn severity and patterns of early plant regeneration in the HC94 burn. Given the importance of early plant establishment to subsequent stand development (e.g., Gutsell and Johnson 2002; Johnstone et al. 2004), we suggest that these changes indicate important effects on successional trajectories. Although the data in this study are limited to a single burn and thus suffer from a lack of regional replication, observations from the HC94 burn provide at least an initial assessment of the potential effects of soil burn severity on forest succession. Stands that experienced low soil burn severity showed a "typical" pattern of postfire recovery, with black spruce constituting the primary recolonizing tree species and understory regeneration dominated by shrubs and graminoids on organic soils (Van Cleve and Viereck 1981; Van Cleve et al. 1991; Chapin et al. 2005). Severely burned stands showed an altered pattern, with high densities of aspen seedlings, an extensive deciduous canopy, and an understory dominated by small mosses on exposed mineral soils.

Whether the effects of burn severity are translated to later stages of succession will be determined by the degree to which these early changes influence biophysical processes and subsequent patterns of species mortality (Bergeron 2000). At severely burned sites, a reestablishment of pleurocarpous (feather) mosses, thickening of the organic layer, and cooling of the soil would favour high rates of aspen mortality and a return to evergreen dominance (Viereck 1983). However, a rapid return to cold, spruce-dominated forests may be hindered by fire-induced changes in these processes. Decreases in organic layer thickness caused by increases in burn severity are likely to warm soil temperatures, increase the thickness of the active layer, and improve soil drainage (Kasischke and Johnstone 2005). In addition, higher rates of evapotranspiration associated with increased aspen cover may further enhance the process of soil warming and drying (Chapin et al. 2000). At the same time, on-going production of deciduous litter may restrict the establishment and growth of pleurocarpous mosses (Bonan and Korzuhin 1989). Depending on the strength of these biophysical feedbacks, aspen-dominated or mixed aspen–spruce communities could be maintained for long periods even in these formerly black spruce dominated forests. Given the relatively short fire cycles of 50–150 years estimated for Alaska black spruce forests (Yarie 1981; Viereck 1983), many of these stands may well be in a deciduous or mixedwood phase when they burn again. Thus, impacts of burn severity on forest recovery in the current disturbance cycle could generate a new legacy of prefire vegetation to influence the next round of succession.

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