

# Effects of Soil Burn Severity on Post-Fire Tree Recruitment in Boreal Forest

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## ABSTRACT

Fire, which is the dominant disturbance in the boreal forest, creates substantial heterogeneity in soil burn severity at patch and landscape scales. We present results from five field experiments in Yukon Territory, Canada, and Alaska, USA that document the effects of soil burn severity on the germination and establishment of four common boreal trees: *Picea glauca*, *Picea mariana*, *Pinus contorta* subsp. *latifolia*, and *Populus tremuloides*. Burn severity had strong positive effects on seed germination and net seedling establishment after 3 years. Growth of transplanted seedlings was also significantly higher on severely burned soils. Our data and a synthesis of the literature indicated a consistent, steep decline in conifer establishment on organic soils at depths greater than 2.5 cm. A meta-analysis of seedling responses found no difference in the magnitude of severity effects on germination versus net establishment. There were, however,

significant differences in establishment but not germination responses among deciduous trees, spruce, and pine, suggesting that small-seeded species experience greater mortality on lightly burned, organic soils than large-seeded species. Together, our analyses indicate that variations in burn severity can influence multiple aspects of forest stand structure, by affecting the density and composition of tree seedlings that establish after fire. These effects are predicted to be most important in moderately-drained forest stands, where a high potential variability in soil burn severity is coupled with strong severity effects on tree recruitment.

**Key words:** ecosystem structure; disturbance regime; landscape pattern; *Picea mariana*; *Picea glauca*; *Pinus contorta*; *Populus tremuloides*; post-fire regeneration; soil organic layer.

## INTRODUCTION

Disturbance is an important driver of variation in community structure and composition in most ecosystems, so variations in disturbance characteristics, such as frequency, size, and severity, strongly affect ecosystem properties and processes (for example, Foster and others 1998). A clear under-

standing of the mechanisms and pathways of disturbance effects on ecosystems is therefore essential to interpret current ecosystem structure, to devise effective strategies of ecosystem management and restoration, and to predict ecosystem responses to future changes in disturbance regime.

In the boreal forest, fire is the dominant disturbance affecting stand structure and composition through its effects on patterns of mortality and regeneration (Van Cleve and others 1991; Johnson 1992; Payette 1992). Under the crown fire regimes common in the North American boreal forest (Johnson and others 1998), regeneration of the

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future tree canopy generally occurs shortly after fire (Johnson and Fryer 1989; Lavoie and Sirois 1998; Gutsell and Johnson 2002; Johnstone and others 2004). Burn characteristics that affect patterns of plant regeneration during this critical establishment period can thus exert a strong influence on future stand characteristics.

Burn severity, or the amount of organic material consumed by a fire (Rowe 1983), is a key component of the fire regime that influences patterns of post-fire regeneration. Variations in canopy burn severity have been shown to be an important driver of post-fire regeneration in many forest systems, especially those that experience variability in canopy mortality (for example, Pausas and others 2003; Choung and others 2004). In boreal forests, however, canopy mortality is often complete, whereas patterns of burn severity at the soil level can be highly variable (Dyrness and Norum 1983; Miyanishi and Johnson 2002). Soils in these forests generally accumulate organic material at the soil surface, which then burns to varying depths, depending, on the weather and characteristics of the fuel bed (Dyrness and Norum 1983; Miyanishi and Johnson 2002).

Soil burn severity influences both the availability of plant propagules (Rowe 1983; Schimmel and Granström 1996) and the physical properties of the post-fire soil (Dyrness and Norum 1983; Coyea 1988; Johnston and Elliott 1998). Multiple studies of boreal tree recruitment have reported an increase in seedling recruitment when combustion of surficial organic material exposed deeper mineral or organic soil layers (LeBarron 1945; Jarvis 1966; Chrosciewicz 1974; Clautice 1974; Zasada and others 1983; Zasada 1985; Weber and others 1987; Schimmel 1993; Herr and Duchesne 1995; Charron and Greene 2002). However, other studies have found negative or neutral effects of burn severity on recruitment (Keays 1987; Schimmel 1993; Sirois 1993; Duchesne and Sirois 1995). In general, little attention has been paid to variations in the direction and magnitude of severity effects across species or environmental conditions, although an understanding of such variation is critical for the extrapolation of severity effects beyond the bounds of individual studies. In addition, few studies (Schimmel 1993; Charron and Greene 2002) have separated seedling responses to severity into different components of germination, survival, and growth to provide a mechanistic understanding of severity effects on forest structure.

The objectives of this study were to combine new experimental data with existing published records

to develop a synthetic assessment of the effects of soil burn severity on patterns of stand regeneration in boreal forests. We used a series of replicated field experiments with four common tree species to test for severity effects on different stages of seedling recruitment across species and sites. We then combined these data with other published records to look for patterns in severity responses across different life history stages and among species groups. Data from these studies also provide information on how responses vary across environmental conditions, which we used as the basis for developing a conceptual model of variations in the strength and direction of severity effects across landscapes. Together these analyses provide information on the pathways by which burn severity affects boreal tree recruitment, the conditions under which these effects are likely to be important, and the role of species differences in contributing to fire effects on forest composition and structure.

## METHODS

### Field Experiments

*Study Area.* We established burn severity contrasts at five locations in four recently burned forests of interior Alaska, USA and central Yukon Territory, Canada (Table 1). At the time of burning, sites were dominated by mature stands of black or white spruce (*Picea mariana* and *P. glauca*, respectively). Sites were selected from road- or trail-accessible portions of a burn in areas of patchy organic layer consumption. At the start of the experiment, each of the study areas had burned within the preceding 1–2 growing seasons and was in the earliest stages of post-fire regeneration. Surviving trees were absent in the vicinity of sites at the CPRW, Delta, and Fox Lake burns, but there were patches of live trees within 100 m of the study site at the Campbell Highway burn.

*Experimental Design.* In June 2000, we established plots at each site to compare areas of intact organic layer (zones of low severity where a large portion of the fibric organic layer [upper duff] was not combusted) with severely-burned areas where the organic layer had been removed by smouldering combustion (complete consumption of fibric material and partial to full consumption of humic material [lower duff]). These treatments are referred to as 'organic' and 'severe' burn treatments, respectively, in this paper. We used slightly different experimental approaches at different sites (Table 1). At two sites (CPCRW and Fox Lake 'Experimental'), high and low severity treatments

**Table 1.** Summary of Study Site Characteristics

	CPCRW (Alaska) <sup>a</sup>	Delta (Alaska)	Campbell highway (Yukon)	Fox Lake, experimental (Yukon)	Fox Lake, natural (Yukon)
Location	65° 10' N 147° 31' W	63° 55' N 145° 44' W	62° 07' N 135° 17' W	61° 19' N 135° 36' W	61° 19' N 135° 36' W
Burn year and type	1999 experimental burn	1999 wildfire	1998 wildfire	1998 wildfire	1998 wildfire
Severity treatments	Organic severe	Organic severe mineral	Organic severe	Organic severe mineral	Organic severe ash
Manipulation	Manual burning	Natural contrasts (interspersed) and manual removal	Natural contrasts (contiguous areas)	Manual burning and removal	Natural contrasts (interspersed)
Experimental design	Circular plots two blocks $n = 6$	Circular plots one block $n = 6$	Rectangular plots three blocks $n = 9$	Circular plots two blocks $n = 6$	Rectangular plots two blocks $n = 6$
Pre-fire composition	Black spruce (100%)	Black spruce (80%) + white spruce (20%)	Black spruce (85%) + white spruce (12%) + lodgepole pine (3%)	White spruce (100%)	White spruce (100%)
Topography and soils	NE slope (3–8°), moderately-drained, silt loam over cobbles	Flat, well-drained, silt loam over cobbles	Shallow W slope (0–3°), moderately-drained, sandy loam	Flat, moderately-drained, silt clay loam	Flat, moderately-drained, silt clay loam

*Details of location, site conditions, and severity treatments are given for the five experimental sites in Alaska and Yukon Territory.*

*<sup>a</sup>Caribou and Poker Creeks Research Watershed (CPCRW) is a component of the Bonanza Creek LTER site, and was burned in a watershed-scale experimental burn.*

**Table 2.** Details of Species Seed and Transplant Applications

	Lodgepole pine	Black spruce	White spruce	Trembling aspen
Seed viability	86 ± 1% (9)	73 ± 5% (9)	81 ± 2% (5)	81 ± 1% (5)
Viable seeds sown (g/m <sup>2</sup> )	0.86	0.73	0.81	1.73
(seeds/m <sup>2</sup> )	282	559	316	17,060
Initial aboveground biomass (g) of transplants	0.70 ± 0.07 (8)	0.84 ± 0.12 (8)	0.98 ± 0.12 (8)	0.93 ± 0.17 (12)

Seed viability and the initial total aboveground biomass of seedling transplants are shown as means ± 1 SE (n). Sowing rates are expressed as the mass (g/m<sup>2</sup>) and number (seeds/m<sup>2</sup>) of viable seeds sown in a single application. Seeds were sown once for aspen and twice for pine and spruce, in plots with an individual area of 0.28 m<sup>2</sup>.

were randomly assigned to areas with an intact organic layer, and we manually burned the residual organic layer with a propane torch to establish burn-severity contrasts. At the remaining sites, we used natural variations in the depth of burn to establish burn-severity contrasts. Plots at Delta and Fox Lake Natural were established in spatially interspersed, small-scale (1–10 m<sup>2</sup>) patches of high and low burn severity. At the Campbell Highway site, patchiness in burn severity occurred at a larger scale (100 m<sup>2</sup>), and we established plots in adjacent areas of severely- or lightly-burned ground. Experimental blocks were used to account for variations in pre-fire tree density or soil conditions, with three or more replicates per block (Table 1). A third soil treatment was included at three sites to represent seedbed conditions where all organic material had been completely removed (Table 1). At Fox Lake Natural, this treatment was represented by an 'ash' treatment in which all surface organics, including fine roots and organic carbon in the upper mineral soil, had been completely consumed by the fire. At Delta and Fox Lake Experimental, we used a manual soil removal treatment, where the organic layer was 'peeled' off the plot by hand rather than burned.

The basic experimental unit at each site was a rectangular (0.75 × 3.25 m) or circular (1 m radius) plot split into five or six smaller subplots (each 0.28 m<sup>2</sup>; Table 1). Main plots were treated with a given burn severity level ( $n = 6$  or  $9$ ), and seedling treatments were randomly assigned to the subplots in a split-plot design. There were four seedling treatments corresponding to applications of four tree species common to the western boreal forest of North America: black spruce (BS), white spruce (WS), lodgepole pine (LP; *Pinus contorta* subsp. *latifolia*), and trembling aspen (TA; *Populus tremuloides*). The remaining 1–2 subplots were used to monitor natural seedling establishment.

Seeds of black spruce, white spruce, and lodgepole pine were sown into their respective subplots in late June and early September 2000. Aspen was seeded once, in June 2000, within 1–2 weeks of its

natural dispersal time. Seeds were broadcast by hand as evenly as possible over the ground surface. Seed provenances came from Delta (BS and TA), Tok (WS), and Whitehorse (LP). The conifer seed had been collected several years previously and stored below freezing (circa  $-10^{\circ}\text{C}$ ). Aspen seed was collected in early June 2000, dried at  $30^{\circ}\text{C}$ , and stored at  $4^{\circ}\text{C}$  after processing. Seed viability (Table 2) was tested in the laboratory in May (BS and LP) or September (all species) of 2000, using four or five replicate samples of approximately 100 seeds that were kept on moist filter paper in petri dishes for 2 (TA) or 20 days (conifers). Although similar weights of viable seed were used in the seedling treatments of each species, differences in seed size meant that the numbers of seeds applied differed among species (Table 2). Over 95% of the seedlings observed in the seeded plots germinated in 2000 and 2001. In plots with high germination rates, seedlings within a cohort were thinned once to a density of 15 seedlings per sub-plot ( $\sim 50$  seedlings/cohort/m<sup>2</sup>). Thinning occurred in June 2001 for the 2000 cohort and September 2001 for the 2001 cohort. Estimates of survivorship of the thinned seedlings were calculated from observed mortality of the remaining seedlings.

In June 2001, transplanted seedlings of the four species were added to the treated plots (three seedlings/sub-plot). To allow time for transplants to acclimatize to growing conditions in the field, growth measurements were made only for the second year after transplanting. The transplants were initially grown in a sterile peat and vermiculite potting mixture, in 4 × 10 cm standard forestry 'conetainers' for 4 months in a greenhouse at the University of Alaska Fairbanks. At the time of planting, the seedlings were the size of healthy, 2- or 3- year-old naturally occurring seedlings. Eight individuals of each species (12 for TA) were harvested prior to transplanting to estimate average starting biomass (Table 2). Seedlings were not transplanted at Fox Lake Natural or in mineral soil plots at Delta, and white spruce was not included in the transplants at Campbell Highway.

*Field Measurements.* All sub-plots were surveyed for established seedlings at the beginning, middle and end of each summer. Seedlings were individually marked with color-coded tags to identify the year in which they were first observed. Natural establishment rates were estimated from seedling counts in control plots. At peak season (mid-late July) in each year, visual estimates of species cover of naturally regenerating vegetation were made in a  $1 \times 1$  m or  $50 \times 50$  cm quadrat (for circular and rectangular plots, respectively) positioned in the center of each plot. At the end of the experiments in late August 2002, transplanted seedlings were harvested, sorted, dried (at  $60^\circ\text{C}$  for 48 h), and weighed to obtain current year, aboveground biomass.

Measurements of soil organic layer depths were made in 2001 and 2002 using a hand-held soil corer. Soil cores (5.4 cm diameter) were collected at all sites in July 2002 for laboratory analysis of moisture content and bulk density. The cores were separated into an organic layer portion and the upper 5 cm of mineral soil, which were weighed before and after drying at  $60^\circ\text{C}$  for 48 h. Bulk density ( $\text{g}/\text{cm}^3$ ) and volumetric water content ( $\text{cm}^3$  water/ $\text{cm}^3$  soil) for the upper 5 cm of soil were calculated as weighted averages of organic and mineral soil layers, based on depths measured in the field.

*Data Analysis.* We estimated the number of germinated seedlings as the sum of all new seedlings observed, established seedlings as the number of live seedlings at the end of the experiment, and seedling survival as the ratio of the two (established/germinated  $\times 100$ ). The contribution of seedlings from natural sources was estimated from counts in unseeded control plots. We were able to use counts of lodgepole pine, which had no local seed source at four sites, to estimate the spread of planted seeds beyond sub-plot boundaries. At these sites, the ratio of 'escaped' pine germinants relative to germinants in seeded plots averaged  $0.020 \pm 0.007$  (mean  $\pm$  SE,  $n = 11$ ). Using this ratio of escapement to correct our estimates of natural establishment of other species, we estimate that natural seedling establishment constituted rarely more than 1%, and never more than 7%, of the species counts obtained in seeded plots. Given the small size of this bias, we chose to perform our analyses directly on the field count data.

We analyzed data from our field trials as five independent experiments, except for data on seedling survival, where low sample sizes required pooling data across sites. We also combined data across sites to estimate the average weight of viable seed required to produce a live seedling on organic and severely burned soils. Data from Delta were

excluded from analyses where data were pooled across sites because of the few numbers of seedlings observed at that site. To test for treatment effects, we used analysis of variance (ANOVA), or multivariate analysis of variance (MANOVA) in the case where we measured more than one response variable. Experimental responses were analyzed following a split-plot design, where severity effects were tested against plot-level variation, and species effects were tested against the residual model variation (Cochran and Cox 1992). Severity and species effects were considered as fixed. Random effects of blocks were included where appropriate. We used rank transformations of the germination data because of frequent outliers (Conover 1999). Survival data were arcsine-transformed, and data on seed weight requirements for establishment were log-transformed. We performed our statistical analyses using SAS v.8.2 (SAS Institute, Cary, North Carolina).

## Synthesis of Severity Studies

Our data synthesis was focused on summarizing the effects of burn severity on patterns of tree seedling recruitment. We conducted a literature search for relevant studies using online databases (OCLC First Search, Online Computer Library Center, Dublin, OH, and ISI Web of Science, Thompson ISI, Stamford, CT), and by using citations from indexed papers to locate studies from non-indexed sources. We restricted our search to studies that (a) contained data on seedling recruitment of boreal trees or erect woody shrubs, (b) included at least two levels of burn severity, and (c) were published in English or French. One applicable study (Turner and others 1999) was excluded because data were collected at a site level, rather than the plot level we wished to examine. Our final synthesis incorporated data from our own experiments, plus 11 other studies (Jarvis 1966; Chrosciewicz 1974; Clautice 1974; Zasada and others 1983; Zasada 1985; Weber and others 1987; Schimmel 1993; Sirois 1993; Duchesne and Sirois 1995; Herr and Duchesne 1995; Charron and Greene 2002).

We synthesized data from these studies in two sets of analyses. The first examined variation in relative seedling establishment of conifers across gradients in post-fire organic layer depth, using data from four studies (this study, Chrosciewicz 1974; Zasada 1985; Weber and others 1987). Within each study, we defined a set of substrate classes based on reported measurements of average organic layer depth (Weber and others 1987) or

**Table 3.** Soil Characteristics of Burn Severity Treatments at the Five Sites

Site/treatment	<i>n</i>	Organic layer depth (cm)	Bulk density (g/cm <sup>3</sup> )	Volumetric moisture (cm <sup>3</sup> /cm <sup>3</sup> )	Manova test for overall treatment effect
CPCRW					
Organic	6	4.8 ± 0.8 <sup>a</sup>	0.19 ± 0.14 <sup>a</sup>	15.6 ± 3.5 <sup>a</sup>	<i>F</i> = 8.07 <sub>3,7</sub>
Severe	6	1.0 ± 0.1 <sup>b</sup>	0.45 ± 0.04 <sup>a</sup>	28.1 ± 3.0 <sup>b</sup>	<i>P</i> = 0.01
Delta					
Organic	6	7.9 ± 0.9 <sup>a</sup>	0.15 ± 0.02 <sup>a</sup>	13.0 ± 3.7 <sup>a</sup>	<i>F</i> = 27.21 <sub>3,8</sub>
Severe <sup>†</sup>	6	2.2 ± 0.1 <sup>b</sup>	0.38 ± 0.01 <sup>b</sup>	25.9 ± 5.9 <sup>a</sup>	<i>P</i> = 0.0002
Mineral	6	0.0 ± 0.0 <sup>c</sup>	n/a	n/a	
Campbell Hwy.					
Organic	9	4.3 ± 0.6 <sup>a</sup>	0.25 ± 0.05 <sup>a</sup>	10.4 ± 2.4 <sup>a</sup>	<i>F</i> = 14.68 <sub>3,12</sub>
Severe	9	0.7 ± 0.2 <sup>b</sup>	0.48 ± 0.04 <sup>b</sup>	27.2 ± 3.0 <sup>b</sup>	<i>P</i> = 0.0003
Fox Lake Experimental					
Organic	6	6.6 ± 1.0 <sup>a</sup>	0.17 ± 0.03 <sup>a</sup>	16.0 ± 1.3 <sup>a</sup>	<i>F</i> = 15.24 <sub>6,24</sub>
Severe	6	1.1 ± 0.1 <sup>b</sup>	0.38 ± 0.06 <sup>a</sup>	25.6 ± 3.2 <sup>b</sup>	<i>P</i> < 0.0001
Mineral	6	0.0 ± 0.0 <sup>b</sup>	0.93 ± 0.09 <sup>b</sup>	32.4 ± 1.8 <sup>b</sup>	
Fox Lake Natural					
Organic	6	9.0 ± 1.1 <sup>a</sup>	0.13 ± 0.02 <sup>a</sup>	13.9 ± 2.0 <sup>a</sup>	<i>F</i> = 11.96 <sub>6,24</sub>
Severe	6	1.5 ± 1.1 <sup>b</sup>	0.47 ± 0.08 <sup>b</sup>	21.4 ± 1.8 <sup>a</sup>	<i>P</i> < 0.0001
Ash	6	0.0 ± 0.0 <sup>b</sup>	0.69 ± 0.05 <sup>c</sup>	15.1 ± 3.5 <sup>a</sup>	

Values are means ± 1 SE. Bulk density and volumetric water content, sampled in mid-July, 2002, are presented as a weighted mean for the upper 5 cm of soil, using values measured separately for the organic layer and upper mineral soil. Values with different letters represent significant differences between treatments within a site (Tukey's multiple range test, *P* < 0.05).

<sup>†</sup> Surficial organic layers in the severe plots at Delta generally include a 1–2 cm veneer of aolian-deposited silt above a layer of buried organics or charcoal.

ranges in organic depth (this study, Chrosiewicz 1974; Zasada 1985). We assumed that seedling establishment was estimated across equal areas for each substrate class within a study or were standardized by the area surveyed, although this was not clearly stated in two of the studies (Chrosiewicz 1974; Zasada 1985). For each substrate class, we estimated the proportional seedling establishment ( $p_j$ ) as the observed establishment within class  $j$  divided by the summed establishment observed across all  $m$  classes in the study. Although the calculation of proportions accounted for differences in absolute seedling numbers across sites, direct comparisons among sites required us to correct for the fact that the proportions (summing to 100) were being divided across varying numbers of classes in each study. To do this, we calculated a establishment index ( $EI$ ), where

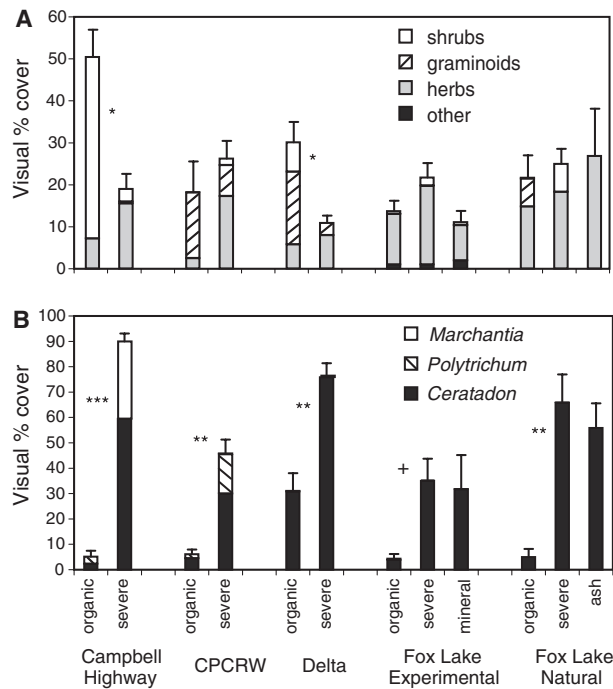
$$EI_j = p_j \times m$$

The resulting  $EI$  is a relative index where proportions have been weighted by the number of classes to allow direct comparison of establishment patterns across sites on the same axis scale.

In the second portion of our synthesis, we used meta-analysis techniques to test for effects of habitat type, recruitment stage and species type on the magnitude of seedling responses to variations in

post-fire organic layer depth. The metric of severity effects was based on a response ratio (RR; Hedges and others 1999) calculated as the ratio of seedlings observed on low and high severity substrates. We chose to put values from the organic treatment in the numerator, because of frequent observations of zero seedlings on organic substrates. Analyses were performed directly on the unweighted and untransformed RR values, because the distribution of values in the final dataset was small (between 0 and 1), not noticeably improved by transformation, and there was insufficient information on sample variances to calculate a weighted metric. Response ratios were calculated from data on seedling germination and establishment in the form of totals, averages, or proportions of sown seed, depending on information available. Comparisons that were based on fewer than ten seedlings were excluded. Each study provided a minimum of one sample for the meta-analysis. The responses of different species within a study were expected to be independent of each other and each species within an experiment was recorded as an individual sample. Likewise, studies that included data on more than one independent experiment contributed additional samples.

We used a hierarchical approach to estimate the effects of site conditions, recruitment stage, and species on burn severity responses. We first examined how variations in potential organic layer



**Figure 1.** Variations in natural vegetation cover across sites and burn severity levels. *Bar heights* indicate the average total cover ( $\pm 1$  SE) of (A) vascular plants, divided into components of woody shrubs, graminoids, flowering herbs, and other (mostly *Equisetum* spp.); and (B) bryophytes, divided into components of *Marchantia polymorpha*, *Polytrichum* spp., and *Ceratodon*-type (includes *Ceratodon purpureus* and other small mosses of similar morphology). Data are visual cover estimates made in year 3 of the experiments. Significant treatment effects on total vascular plant or moss cover are indicated with asterisks ( $^+P < 0.1$ ,  $*P < 0.01$ ,  $**P < 0.001$ ,  $***P < 0.0001$ ).

depth may have influenced severity responses by plotting RR against mean organic depth from the low severity treatments. To minimize variation associated with recruitment stage and species, data were plotted separately for germination and establishment stages and only conifer species were included. We then selected the most common habitat type (moist conifer forest) and estimated severity effect sizes across all species for the recruitment stages of germination and establishment separately. Within each recruitment stage, species differences in severity responses were then estimated by comparing severity effect sizes across groups of species. Three species groups were defined on the basis of average seed weights (Leadem and others 1997): (a) deciduous species (seeds  $< 1$  mg), (b) black and white spruce (seeds 1–2.5 mg), and (c) pines and large-seeded spruce (*Picea abies*; seeds 2.5–4 mg). We used bootstrapped 95% con-

fidence intervals calculated in the program Meta-Win (Rosenberg and others 2000) to assess whether severity responses differed significantly from 1 (no effect) or between groups.

## RESULTS

### Field Experiments

At all of our sites, burn severity treatments had a significant effect on post-fire soils (Table 3). Organic plots had thicker organic layers and lower bulk densities than severely burned plots (MANOVAs by site,  $P < 0.01$ ). The surficial material in the organic plots was generally composed of low-density, dead moss or fibric (partially-decomposed) organic material, while deeper burns in the severe plots increased the exposure of mineral soil or humic organic layers with higher bulk densities (Table 3). These differences in soil surface type and bulk density were frequently associated with lower levels of soil moisture at peak season 2002 in the organic soil plots (Table 3). Spot measurements taken at other dates during the 2000–2002 growing seasons (data not shown) also generally showed lower moisture content in the organic than in severely burned plots, except for short periods after precipitation events.

Patterns of natural revegetation measured in the third year of our experiments indicate both positive and negative responses to increased burn severity. Total cover of vascular plants decreased significantly with increased burn severity at two sites (Campbell Highway and Delta; ANOVAs by site,  $P < 0.005$ ), but showed no significant response at the remaining three sites (Figure 1). Among the vascular plants, herbs consistently responded positively to increased burn severity, while other growth forms showed neutral or variable responses. Moss cover also showed significant positive responses to burn severity at all sites (Figure 1). This effect was largely due to increases in the cover of small, monocarpus mosses (primarily *Ceratodon purpureus*).

Despite a wide variation in seedling numbers observed across sites, increased burn severity consistently enhanced seed germination (Figure 2; Table 4). Germination on manually exposed, mineral soil surfaces at Fox Lake Experimental and Delta was higher than on severely burned surfaces, indicating that the effects of a severe burn differed from direct soil removal. Significant species-by-severity interactions were observed at Campbell Highway and Fox Lake Experimental, where aspen showed a much stronger response of germination

**Table 4.** Results of Statistical Tests of Severity and Species Effects on Germination, for Two Types of Standardization Methods (by weight or number of viable seeds sown)

Site	Severity effect	Variable	Species effect	Severity * species interaction
Campbell highway	$F = 34.99_{2,15}$ $P < \mathbf{0.0001}$	Seedlings/ g viable seed	$F = 4.14$ $P = \mathbf{0.01}$	$F = 5.77$ $P = \mathbf{0.002}$
		Seedlings/100 seeds sown	$F = 5.81$ $P = \mathbf{0.002}$	$F = 3.12$ ns
CPCRW	$F = 6.53_{2,9}$ $P = \mathbf{0.017}$	Seedlings/ g viable seed	$F = 2.98$ ns	$F = 0.42$ ns
		Seedlings/100 seeds sown	$F = 8.03$ $P = \mathbf{0.0004}$	$F = 0.02$ ns
Fox lake experiment	$F = 10.15_{4,30}^*$ $P < \mathbf{0.0001}$	Seedlings/ g viable seed	$F = 13.13$ $P < \mathbf{0.0001}$	$F = 8.20$ $P < \mathbf{0.0001}$
		org vs. min + sev		
Fox lake natural	$F = 18.66_{2,14}$ $P = \mathbf{0.0001}$	Seedlings/100 seeds sown	$F = 42.97$ $P < \mathbf{0.0001}$	$F = 3.46$ $P = \mathbf{0.007}$
	$F = 5.56_{2,14}$ $P = \mathbf{0.02}$			
	$F = 3.35_{4,30}^*$ $P = \mathbf{0.018}$	Seedlings/ g viable seed	$F = 7.50$ $P = \mathbf{0.0004}$	$F = 0.44$ ns
	org vs. ash + sev			
Delta	$F = 10.05_{2,14}$ $P = \mathbf{0.002}$	Seedlings/100 seeds sown	$F = 21.44$ $P < \mathbf{0.0001}$	$F = 1.06$ ns
	$F = 0.80_{2,14}$ ns			
	$F = 6.00_{4,30}^*$ $P < \mathbf{0.001}$	Seedlings/ g viable seed	$F = 4.24$ $P = \mathbf{0.01}$	$F = 1.76$ ns
	org vs. min + sev			
	$F = 12.88_{2,14}$ $P = \mathbf{0.007}$	Seedlings/100 seeds sown	$F = 7.74$ $P = \mathbf{0.0003}$	$F = 2.13$ ns
	$F = 10.73_{2,14}$ $P = \mathbf{0.0015}$			

Severity effects were tested in a separate MANOVA for each site ( $\alpha = 0.05$ ), followed by orthogonal contrasts for sites with three treatment levels. Species and species  $\times$  severity effects were tested in separate univariate ANOVAs ( $\alpha = 0.05/2 = 0.025$ ). Significant effects are indicated in bold font. Data were rank-transformed prior to analysis. \*F-statistic is Pillai's Trace.

to severity than did the other species. Although aspen showed high rates of germination per gram of viable seed sown in severely burned plots at several sites (Figure 2), standardization of germination counts by seed number rather than weight greatly reduced these values, due to the low germination success of individual seeds. When standardized by seed number, black spruce or lodgepole pine showed the highest average germination across treatments and aspen the lowest (data not shown).

In addition to observations in seeded plots, there were sufficient densities of naturally-regenerating paper birch (*Betula papyrifera*) at CPCRW to test for severity effects on natural germination. Birch germination responded positively to increased burn severity, averaging  $15.6 \pm 5.5$  (mean  $\pm$  SE) seedlings/m<sup>2</sup> in severely burned plots and  $3.9 \pm 1.5$  seedlings/m<sup>2</sup> in organic plots (*t*-test on ranked data,  $t = 2.23$ ,  $P = 0.047$ ).

Burn severity had a weak or neutral effect on the survival of sown seedlings, with an estimated 10–20% decrease in survival for conifers in organic compared to severe treatments (Figure 3; ANOVA across sites,  $F_{1,25} = 3.56$ ,  $P = 0.07$ ). This test is, however, inherently confounded by differences in sample size that arose from differences in germination across treatments (Figure 3). Qualitative field observations indicate differences in the principle causes of mortality across severity levels, with seedling desiccation causing the majority of seedling deaths in organic treatments, whereas uprooting by needle ice and overgrowth by mosses was frequently the most common cause of death in the severe burn and manual soil removal treatments. Evidence of seedling mortality caused by herbivory was observed only at Campbell Highway, where several aspen stems showed evidence (diagonally clipped stems) of browsing by snowshoe hares (*Lepus americanus*).



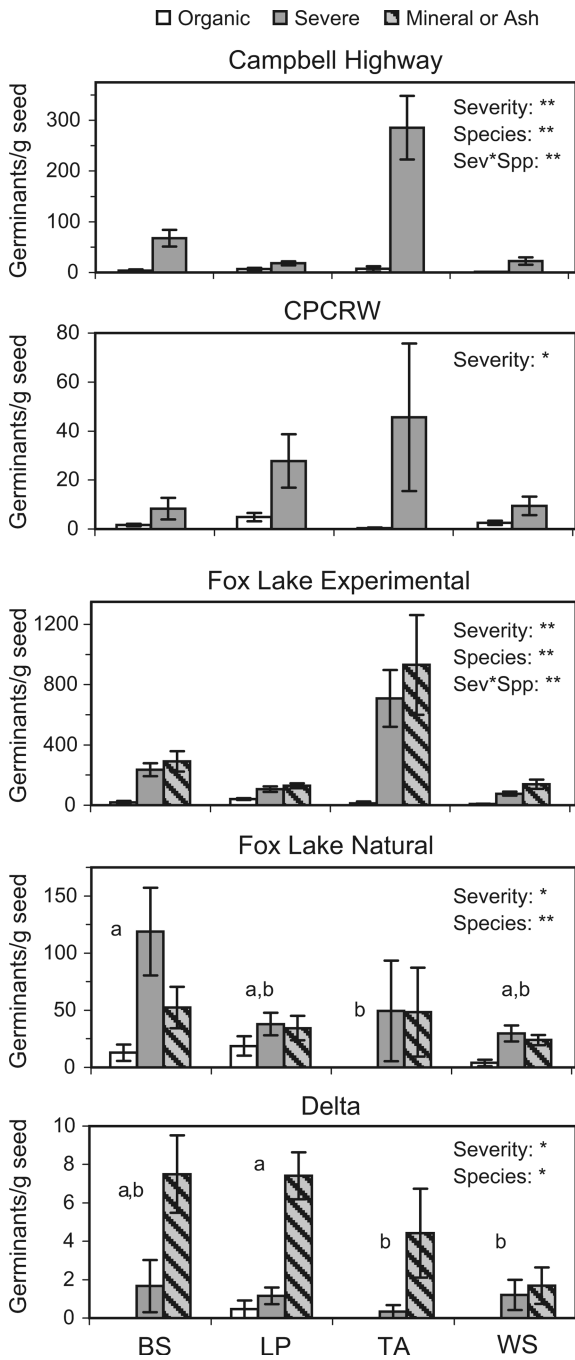


Figure 2. Numbers of germinating seeds (per g viable seeds sown) observed across severity treatments, species, and sites. Note the differences in y-axis scales. Significant treatment effects are indicated in the site panels (\* $P < 0.025$ , \*\* $P < 0.001$ ). Differences in overall species means (Tukey's multiple range test,  $P < 0.05$ ) are shown by different letters where species  $\times$  severity interactions were not significant. Tests were performed on rank-transformed data. Species codes are as follows: BS = black spruce, LP lodgepole pine, TA trembling aspen, and WS white spruce.

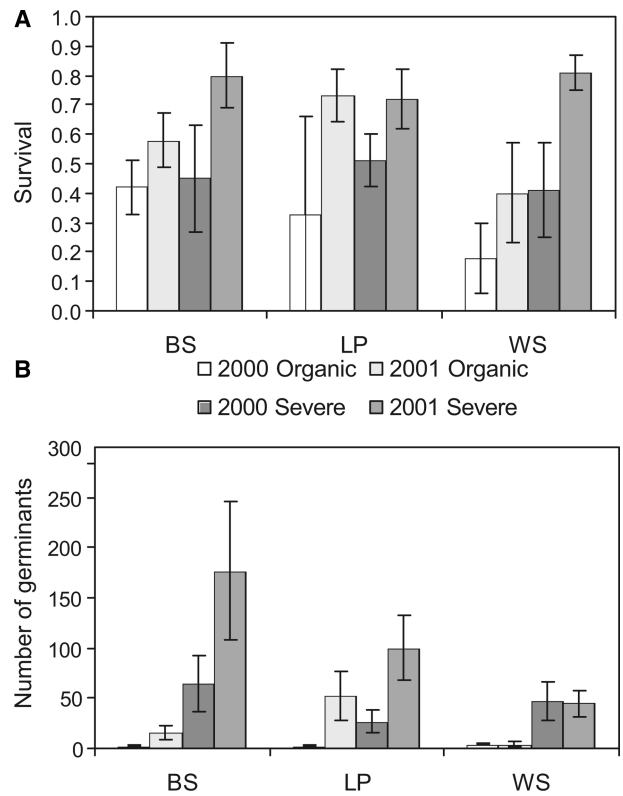
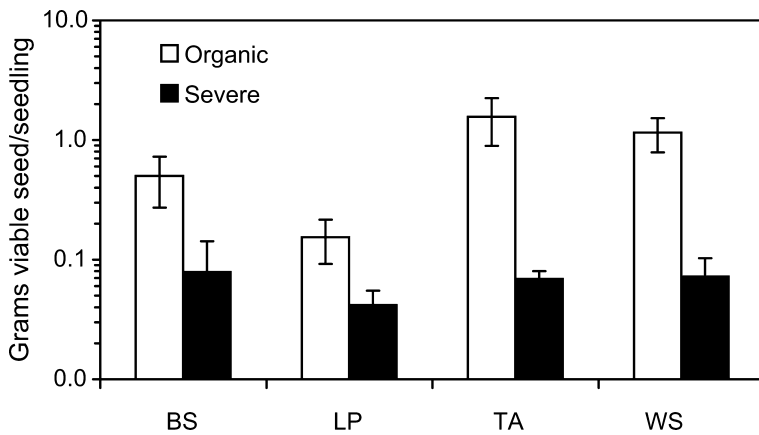


Figure 3. Survival (A) and sample sizes (B) of conifer germinants across treatments and cohorts. Survival (mean  $\pm 1$  SE) was estimated as the proportion of germinants surviving to the end of the experiment. Means and standard errors were calculated using a single value for each site, based on the sum of germinants across individual plots. Survival was estimated only from sites with 2 or more germinants ( $n = 2-4$ ), while sample sizes were calculated using data from all sites ( $n = 4$ ). Species codes are as follows: BS black spruce, LP lodgepole pine, and WS white spruce.

Seedling survival did not differ among the conifer species ( $F < 0.8$ ,  $P > 0.1$  for species main and interaction effects), but aspen survival in the severe treatment (mean  $0.16 \pm 0.07$  SE,  $n = 4$ ) was substantially lower than estimated for conifers in the same treatment (Figure 3). Sample sizes of aspen were too low to estimate survival in the organic treatment. Conifer survival also differed significantly among cohorts ( $F_{1,25} = 10.16$ ,  $P = 0.004$ ), with seedlings that germinated in 2000 having approximately 20–40% lower survival rates than those that germinated in 2001 (Figure 3). This difference was associated with a greater rate of first-year mortality for the 2000 cohort, which germinated late in the growing season.



**Figure 4.** Mass (g) of viable seed required to generate a single, 2-year-old live seedling of four species in severely burned and organic treatments. Values are means  $\pm$  1 SE, averaged across sites ( $n = 4$ , except for aspen in the organic treatment, where  $n = 3$ ). Observations from Delta have been excluded because of frequent zero counts. Data were log-transformed for analysis, and are plotted on a log scale. Species codes are as follows: *BS* black spruce, *LP* lodgepole pine, *TA* trembling aspen, and *WS* white spruce.

Patterns of net seedling establishment observed at the end of the experiment were generally similar to germination patterns (data not shown; refer to Figure 2 and Table 4). Low aspen survival increased the differences in establishment between aspen and the conifers, while the trend towards relatively high survival of lodgepole pine on organic substrates (Figure 3) led to a general pattern of reduced sensitivity of pine establishment to severity level compared to other species. Establishment patterns across sites showed that all species required more seed to produce a live, 2-year-old seedling on organic substrates compared to those that had been severely burned (Figure 4; ANOVA across sites, severity effect  $F_{1,31} = 44.5$ ,  $P < 0.0001$ ). Species differed in their overall seed weight requirements for establishment (species effect  $F_{3,31} = 4.5$ ,  $P = 0.01$ ), but did not significantly differ in their treatment responses (severity  $\times$  species interaction  $F_{3,31} = 1.5$ ,  $P = 0.25$ ). On average, it took 12-fold more grams of seed to produce a viable seedling on organic than on severely burned soils.

Transplanted seedlings of the four species all produced more aboveground biomass in 2002 in severe treatments compared to organic (ANOVAs by site, severity effects  $P < 0.01$ ), although aspen productivity was significantly lower than that of the conifer species (species effects  $P < 0.01$ ; Figure 5). Snowshoe hares preferentially browsed on aspen transplants in the severe burn treatment at Campbell Highway, which complicated the interpretation of aspen responses to the severity treatment.

At the plot level, seedling establishment of all species responded negatively to increases in organic layer depth, and above-average seedling counts were restricted to shallow organic layers less than approximately 2 cm thick (Figure 6). Of the four species, only lodgepole pine showed incidences of above-average establishment on organic layers

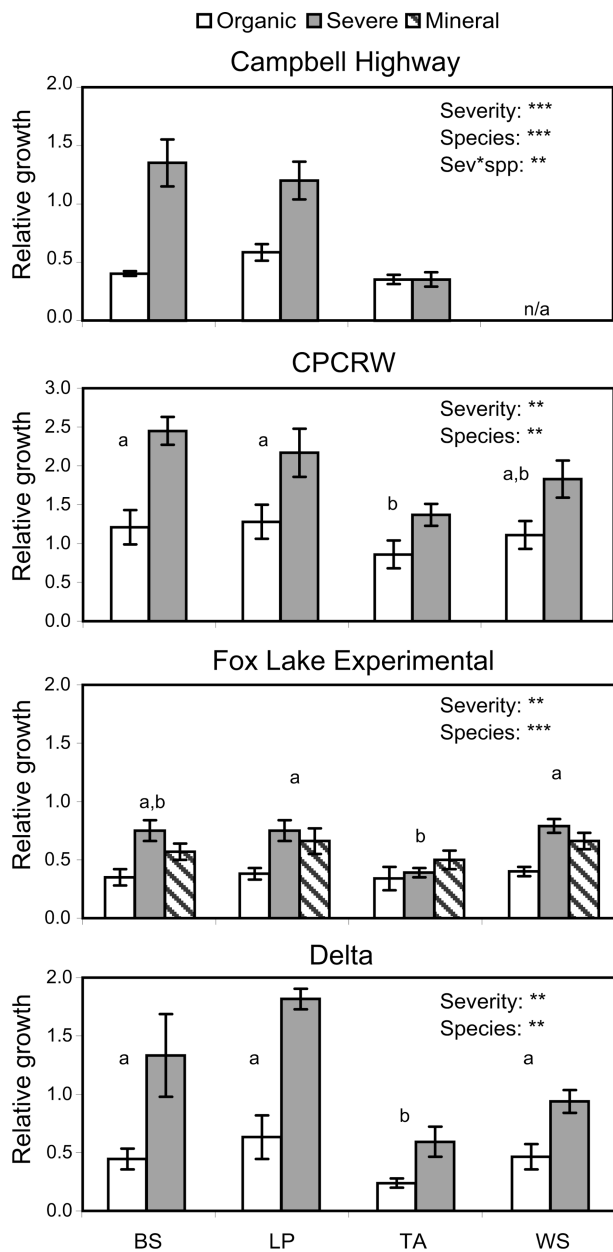
over 3 cm in depth. Plot-level data on transplant growth showed a similar but more gradual decrease in plant growth with increasing organic layer depth, also with the majority of above-average observations limited to soils with organic layer depths under 2–3 cm (Figure 7).

### Synthesis of Severity Effects

We found a high similarity in the shapes of individual seedling response curves when comparing observations from multiple studies of relative seedling establishment versus post-fire organic layer depth (Figure 8). All studies showed the highest seedling establishment on organic soils less than 2.5 cm in depth and a rapid decline in establishment on thicker organic soils. Many of the curves suggested a non-linear response of seedling establishment to variations in organic layer depth, with large changes in establishment across organic depths up to 3 cm, and little response to changes in depth over 4 cm (Figure 8).

The data collected for our meta-analysis of severity effects on seedling recruitment showed a large range across studies in seedling responses to severity treatments (Figure 9A and B). The type of severity response was correlated with habitat, with sites in lichen woodlands generally showing a positive or neutral response (response ratio  $> 1$ ) to increased post-fire organic layer depth, compared to largely negative responses (response ratio  $< 1$ ) observed in moist conifer forests (Figure 9). Sites in lichen woodlands had the shallowest post-fire organic layer depths and thus, the smallest potential variation in depth with severity level. Within the moist conifer forests, sites with thin organic mats also exhibited a greater range in severity responses than sites with thick organic layers.

The summary of severity responses in moist conifer forests indicated significant, 3- to 5-fold



**Figure 5.** Aboveground relative growth (g/g initial weight) of transplanted seedlings in 2002 across severity treatments, species, and sites. Values are means  $\pm$  1 SE. Significant treatment effects on transplant growth are indicated in the panel for each site (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.0001$ ). Differences in overall species means (Tukey's multiple range test,  $P < 0.05$ ) are shown only where the species  $\times$  severity interaction was not significant and are indicated by different letters above the bars for each species. Transplant data were not available for white spruce at Campbell Highway. Species codes are as follows: *BS* black spruce, *LP* lodgepole pine, *TA* trembling aspen, and *WS* white spruce.

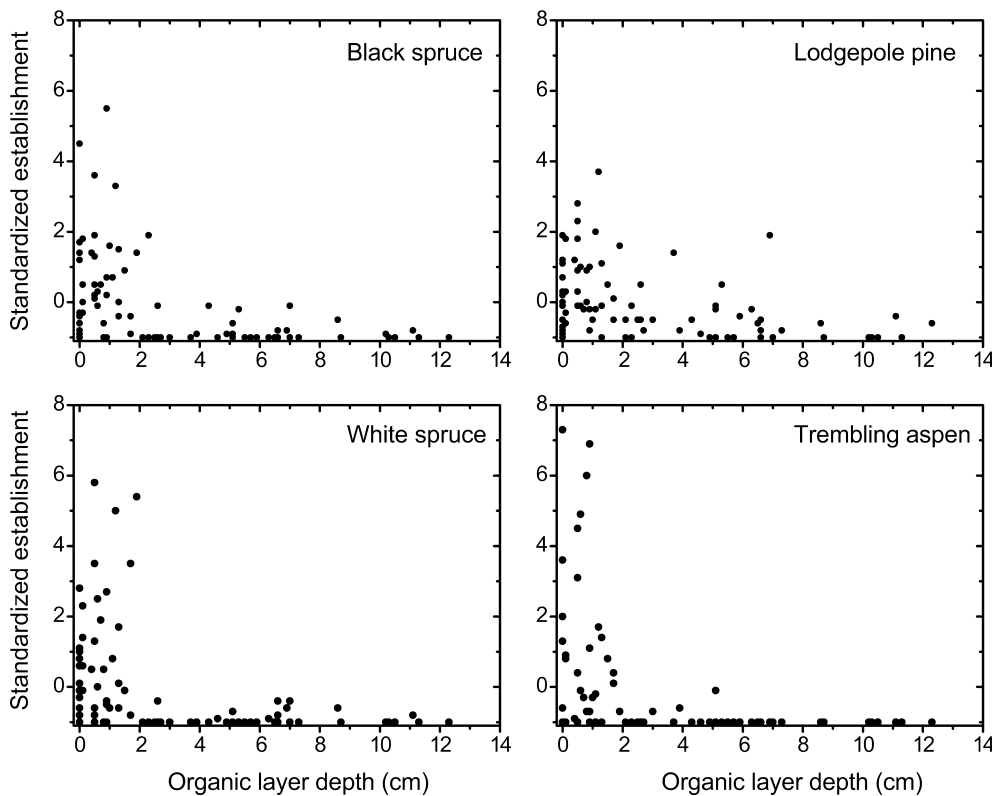
overall reductions (response ratio  $< 1$ ) in seed germination and seedling establishment in organic relative to severe burn treatments (Figure 9C). Germination and establishment effect sizes were similar in magnitude, indicating that germination effects were the primary factor driving severity effects on seedling recruitment. There were, however, significant differences in severity responses among species groups for seedling establishment but not germination, indicating the potential for additional impacts of burn severity to occur following germination. Differences in the relative size of severity effects on establishment among species groups corresponded to general differences in seed size, with deciduous, spruce, and pine groups showing high, intermediate, and low sensitivity, respectively (Figure 9C).

## DISCUSSION

### Patterns and Mechanisms of Severity Response

The data from our field experiments are similar to those of other studies of mesic boreal forests in demonstrating strong burn severity effects on patterns of tree seedling recruitment (Jarvis 1966; Chrosiewicz 1974; Clautice 1974; Zasada and others 1983; Weber and others 1987; Schimmel 1993; Charron and Greene 2002). The similarity that we observed in the relative responses across sites that differed by an order of magnitude in average establishment suggests that severity responses occur relative to the overall site potential rather than as an absolute response. Analysis of our plot-scale data also shows that reductions in organic layer depth appear to increase the range of variation in recruitment, but do not eliminate the potential for recruitment failures to occur in severely burned patches. Thus, increases in burn severity appear to stimulate recruitment primarily by relaxing constraints that occur on organic soils, increasing the potential range of outcomes possible within the bounds of the local site context.

This concept of recruitment 'release' on severely-burned soils is consistent with our observations of a non-linear threshold in seedling responses to organic layer depth. In low severity burns, incomplete combustion of moss or fibric layers leaves a dark, porous layer at the soil surface that is prone to large diurnal heat fluctuations and rapid drying of the soil surface (Coyea 1988; Duchesne and Sirois 1995; Table 3). Seed germination and early seedling survival on these surface layers are likely to be strongly limited by an unstable moisture supply



**Figure 6.** Plot-level variations in seedling establishment versus mean organic layer depth, by species. Seedling establishment has been standardized against the mean establishment rate for each site, such that positive values indicate above-average establishment, and negative values indicate below-average establishment for that species. Only data from burned treatments were included.

and frequent drought stress (Zasada and others 1983; Herr and Duchesne 1995; Charron and Greene 2002). On mineral soils, moisture availability is moderated by high thermal heat capacity and wicking from sub-surface layers, thus relieving this primary limitation on establishment. The amelioration of moisture stress is likely to be the primary cause of the frequent increases in seedling recruitment observed on severely burned substrates. Small patches of poor recruitment in severe burns may represent areas impacted by high moss competition or needle ice activity.

Other physical changes that are associated with increased burn severity can have widespread negative impacts on seedling recruitment that may only become detectable at very high levels of burn severity or in comparison to alternative methods of organic mat removal. In our study, the presence of negative severity effects is suggested by trends toward decreased seedling establishment on the most deeply burned soils at three of our sites (Figure 8) and increased germination and establishment in manual soil removal compared to severe burn treatments (Figure 2; Table 4). Other studies have documented negative effects of ash leachates on seedling establishment and growth (Keays 1987; Coyea 1988; Herr and Duchesne 1995) and reduced recruitment on water-repellent ash layers at the soil surface (Keays 1987). Layers of char at the

soil surface or within the mineral soil column (buried by aeolian mineral soil deposits) can reduce moisture availability at the soil surface even in severely burned patches. On drier sites, moisture stress may be frequent across all severity levels, diminishing the potential for positive seedling responses and allowing negative effects to dominate the severity response. At our Delta site, the presence of a buried char layer in severe patches appears to have constrained the positive response of seedling establishment to increased burn severity. Manual soil removal treatments at this site show a positive recruitment response to organic layer removal, although dry site conditions caused seedling densities in all treatments to remain low (Table 3 and Figure 2). Similarly, dry site conditions and negative effects of ash or hydrophobic soil layers have been implicated in observed negative seedling responses to increased burn severity in dry lichen woodland habitats (Figure 9; Keays 1987; Sirois 1993).

Studies of soil combustion in boreal forests have shown that variations in organic layer depth and moisture availability influence the potential for smouldering combustion to occur (Dyrness and Norum 1983; Miyanishi and Johnson 2002). Consequently, the probability of occurrence of a severe burn will be influenced by landscape context as well as variations in weather (Miyanishi and

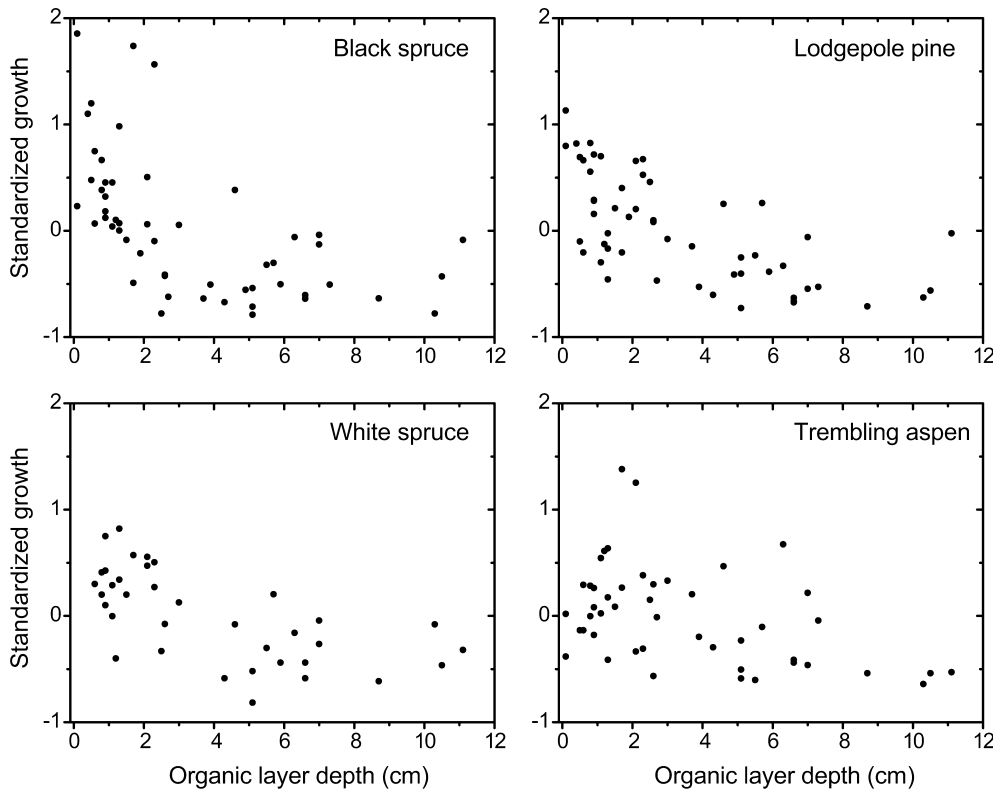


Figure 7. Plot-level variations in aboveground growth of transplanted seedlings in 2002 versus organic layer depth, by species. Transplant growth has been standardized against mean growth for each site, such that positive values indicate above-average growth, and negative values indicate below-average growth for that species. Only data from burned treatments were included.

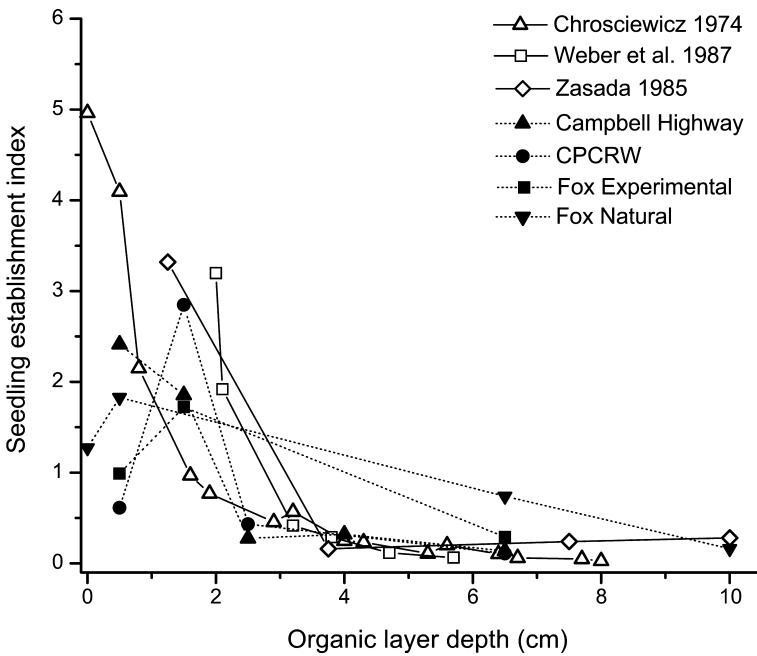
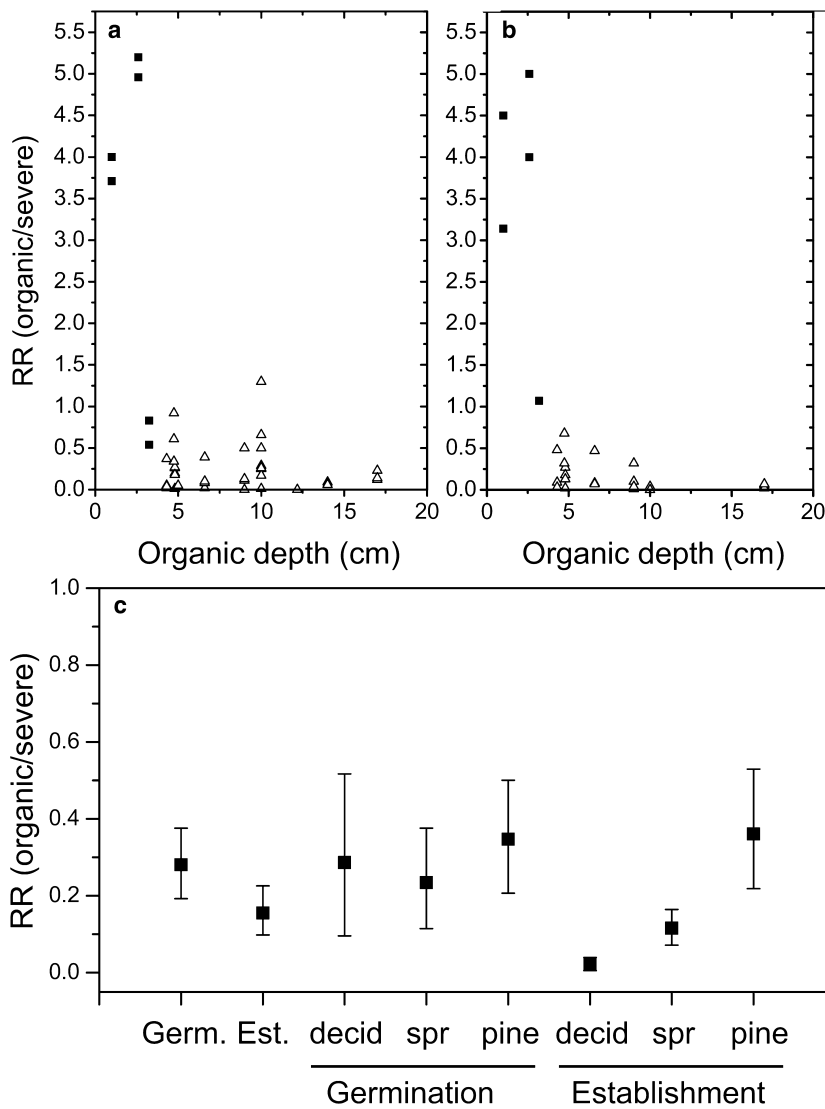


Figure 8. Patterns of conifer seedling establishment versus post-fire organic layer depth, summarized across studies. Data are shown in series for each study, using a seedling establishment index (see methods) to compare patterns among sites. Data are for *Pinus banksiana* (Chrosiewicz 1974; Weber and others 1987), *Picea glauca* (Zasada 1985), and the sum of *Picea glauca*, *P. mariana*, and *Pinus contorta* (filled symbols, by site from data in this study).

Johnson 2002). In addition, systematic variations observed among sites in seedling responses to burn severity suggest that landscape context may play a

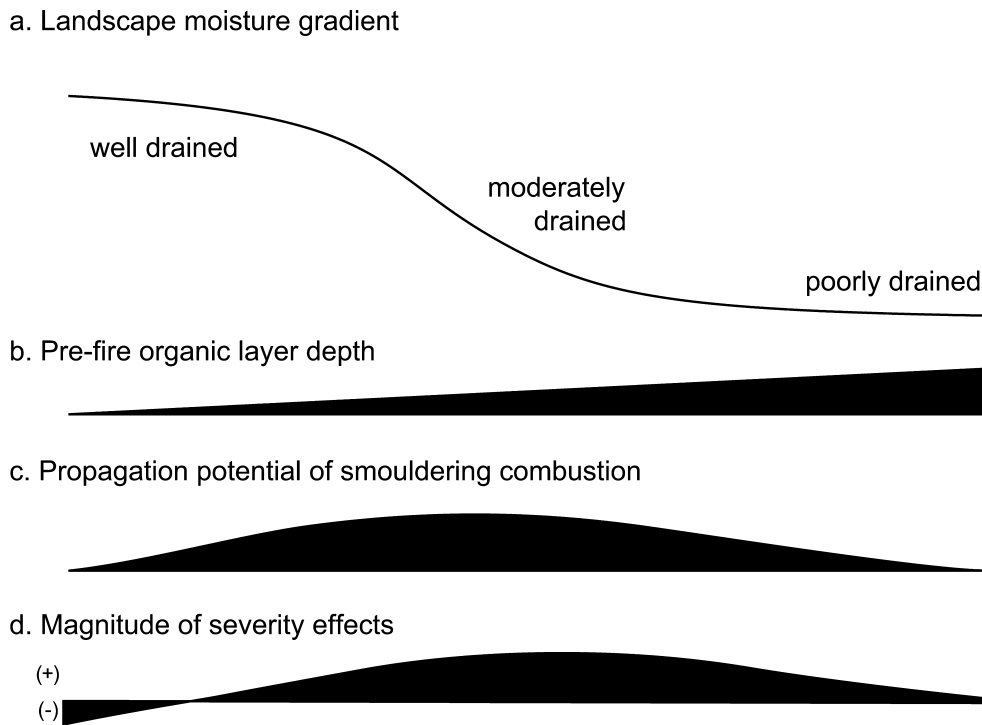
strong role in determining the direction and magnitude of severity effects on tree recruitment. In particular, we hypothesize that dry sites with



**Figure 9.** Effects of burn severity on seedling germination and establishment, summarized across studies. Effect sizes are estimated as a response ratio (RR), calculated as the ratio of seedlings observed on organic versus severely burned soils. Values above and below 1.0, respectively, indicate higher and lower seedling counts on low severity compared to high severity plots. The upper panels show conifer germination (**a**) and establishment (**b**) responses to severity plotted against the mean post-fire organic depth (cm) of the low severity treatments, for data from lichen woodlands (*filled squares*) and moist conifer forests (*open triangles*). Overall severity effects (**c**) in moist conifer forests are summarized for germination (Germ.) and establishment (Est.) and between species groups (decid, spr, and pine refer to deciduous, spruce, and pine species, respectively) within a given stage. *Whisker brackets* indicate bootstrapped 95% confidence intervals, and non-overlapping confidence intervals indicate significant differences between regeneration stages or species groups.

shallow organic layers and widespread moisture limitation are likely to experience small and largely negative effects of burn severity on recruitment (Figure 10). At very moist sites, the effects of burn severity are likely to be relatively unimportant, both because severe burns are rare in these habitats and moisture availability is frequently sufficient to permit seedling establishment even on organic substrates (for example, Black and Bliss 1980). At sites of intermediate drainage, however, there is the potential for large variations in burn severity and strong positive effects of severity on surface moisture availability and seedling establishment (Figure 10). Variations in burn severity can also have strong effects on soil thermal properties in zones of intermediate moisture status (Swanson 1996), creating the potential for altered patterns of burn severity to trigger a suite of changes in ecosystem processes at these sites.

Species may also differ in their responses to burn severity, but such variation has received relatively little attention or rigorous testing in the literature (however, see Zasada and others 1983). Nevertheless, our analysis of combined responses across multiple studies found that small-seeded, deciduous species showed significantly greater reductions in establishment potential on organic surfaces than black and white spruce, which in turn showed greater reductions than large-seeded pines and Norway spruce (Figure 9). These differences in severity responses among species were present in comparisons of establishment and not germination, indicating that the differences arose from interactive effects of species and burn severity on post-germination survival. Although such a pattern has not emerged in analyses of seedling survival presented here and elsewhere (Schimmel 1993; Charron and Greene 2002), we have, in truth, little



**Figure 10.** A hypothetical model illustrating the influence of landscape position on the magnitude of burn severity effects on tree recruitment. Landscape moisture gradients (**a**) influence the overall degree of moisture limitation at a site, as well as (**b**) rates of organic layer accumulation (Van Cleve and others 1991). Moisture and organic layer depth control (**c**) the probability of a severe burn occurring through smouldering combustion of the organic layer (Dyrness and Norum 1983; Miyanishi and Johnson 2002). As a result, positive severity effects on seedling recruitment (**d**) are predicted to be greatest at sites of intermediate drainage.

capacity to test for interactive effects of species and severity on survival, due to the scarcity of survival data and the problem of confounding sample sizes across severity treatments.

Despite current constraints on testing the mechanism behind this pattern, the differences among species groups observed in the meta-analysis appear biologically plausible and are consistent with species adaptations in seed size and drought tolerance. Species with small seeds have fewer reserves to support initial root growth and thus may have less access to stable moisture or nutrient supplies during early development. Variations in root morphology and leaf architecture will interact with seed size to influence early survival, such as early taproot elongation in pine providing access to a stable water supply and increased specific leaf area of deciduous species increasing transpiration water losses. Deciduous species appear to partially compensate for the poor survival of their small seeds by producing large numbers of seed. Although this strategy may permit high rates of seedling establishment per gram seed on severely burned surfaces, it does not

appear to overcome the marginal conditions for establishment on lightly burned surfaces (Figures 2, 6). Tradeoffs between seed size and seed number thus appear to be most important in contributing to species differences in recruitment ability on organic substrates.

### Soil Burn Severity as a Dynamic Driver of Forest Structure and Composition

Our results indicate that variations in burn severity have the greatest impact on seed germination, with relatively small and possibly species-specific effects on seedling survival (see also Charron and Greene 2002). Nevertheless, burn severity effects have been clearly detected over a decade after fire occurrence (Weber and others 1987) and may frequently persist to influence the structure and composition of mature stands. This persistence through time of burn severity effects is likely to be driven primarily by the temporal dynamics in boreal forest regeneration, where early post-fire recruits commonly form the major source of canopy trees in mature stands (Johnson and Fryer

1989; Gutsell and Johnson 2002). Although stand thinning may be initiated within two decades after establishment (Wurtz and Zasada 2001; Johnstone and others 2004), density-dependent mortality appears to be slow to compensate for large differences in initial recruitment (Lotan and Perry 1983; Arseneault 2001). Under the crowded conditions generated by increased recruitment in a high severity burn, initial patterns of increased growth may shift over time to decreased growth potential, due to competition or the loss of nutrients stored in the soil organic layer (Wurtz and Zasada 2001; Johnstone and others 2004). Severe burns are thus likely to generate dense stands with slow rates of individual tree growth and high canopy cover, restricting the potential for subsequent recruitment and leading to a narrow age distribution in the mature forest (Johnson and others 1994; Arseneault 2001). In contrast, stands that regenerate following a low-severity burn are likely to develop open-canopied forests that may provide increased opportunities for delayed seedling recruitment and the development of multi-aged stands (Foster 1985; Arseneault 2001).

At the scale of meters to kilometers, patchiness in burn severity can also generate spatial structure in the density and arrangement of established trees, promoting heterogeneity in stand structure across a landscape (Turner and others 2003). Severely burned areas are frequently distributed as patches of varying size and extent due to spatial effects of smouldering combustion, differences in local site conditions, and variations in weather at the time of burning (Dyrness and Norum 1983; Miyanishi and Johnson 2002; Turner and others 2003). At the stand scale, seedling densities should be most sensitive to the overall coverage of patches of different severity, while the arrangement of patches will influence spatial patterns of seedling distribution. In some cases, post-fire patterns of seedling recruitment may reflect patterns present before a fire occurred, as preferential deep burning around the bases of trees (Miyanishi and Johnson 2002), or mineral soil exposure in tree tip-ups (Clautice 1974) favors tree establishment in the same microsites occupied by pre-fire individuals. Severity effects on the spatial structure of vegetation may, in turn, generate spatial patterns in biogeochemical processes (Pastor and others 1999) and wildlife use (Turner and others 2003).

Finally, differences in the relative ability of species to establish on organic versus severely burned soils may influence patterns of forest composition in response to variations in fire severity. Deciduous species, in particular, appear to be highly con-

strained in their ability to establish on organic soils. When deciduous species are present in the pre-fire stand, their high capacity for asexual reproduction makes seed recruitment of little practical importance (Zasada and others 1992). However, when these species are absent from the pre-fire community, successful colonization will depend on seed recruitment, and therefore will be largely restricted to areas of high burn severity (for example, Kasischke and others 2000). In low-severity burns, the large quantities of seed required to produce a seedling will greatly favor recruitment by species that generate large amounts of seed rain after fire, namely, serotinous species such as black spruce and lodgepole or jack pine (*Pinus banksiana*). Invading species or species without an on-site propagule source, such as white spruce, are likely to have the greatest success when colonizing severe burns because of the increased recruitment potential of individual seeds. Changes in burn severity are likely to be most important at sites of intermediate moisture availability, where succession pathways may be strongly constrained following low severity burns, but become open to the potential for rapid change when a high-severity burn occurs.

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## REFERENCES

- Arseneault D. 2001. Impact of fire behavior on postfire forest development in a homogeneous boreal landscape. *Can J Forest Res* 31:1367-74.



- Black RA, Bliss LC. 1980. Reproductive ecology of *Picea mariana* (Mill.) Bsp., at tree line near inuvik, Northwest Territories, Canada. *Ecol Monogr* 50:331–54.
- Charron I, Greene DF. 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. *Can J Forest Res* 32:1607–15.
- Choung Y, Lee BC, Cho JH, Lee KS, Jang IS, Kim SH, Hong SK, Jung HC, Choung HL. 2004. Forest responses to the large-scale east coast fires in Korea. *Ecol Res* 19:43–54.
- Chrosiewicz Z. 1974. Evaluation of fire-produced seedbeds for jack pine regeneration in central Ontario. *Can J Forest Res* 4:455–7.
- Clautice SF. 1974. Spruce and birch germination on different seedbeds and aspects after fire in interior Alaska. MSc thesis, Fairbanks, AK, USA: University of Alaska Fairbanks.
- Cochran WG, Cox GM. 1992. Experimental designs. New York: Wiley, p 611.
- Conover WJ. 1999. Practical nonparametric statistics. New York: Wiley, p 584.
- Coyea MR. 1988. Factors affecting white spruce (*Picea glauca*) seed germination on burned forest litter. MSc thesis, Edmonton, Alberta: University of Alberta.
- Duchesne S, Sirois L. 1995. Phase initiale de régénération après feu des populations conifériennes subarctiques. *Can J Forest Res* 25:307–18.
- Dyrness CT, Norum RA. 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. *Can J Forest Res* 13:879–93.
- Foster DR. 1985. Vegetation development following fire in *Picea mariana* (black spruce) – *Pleurozium* forests of south-eastern Labrador, Canada. *J Ecol* 73:517–34.
- Foster DR, Knight DH, Franklin JF. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1:497–510.
- Gutsell S, Johnson EA. 2002. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. *J Ecol* 90:153–66.
- Hedges LV, Gurevitch J, Curtis PS. 1999. The meta-analysis of response ratios in ecology. *Ecology* 80:1150–6.
- Herr DG, Duchesne LC. 1995. Jack Pine (*Pinus banksiana*) seedling emergence is affected by organic horizon removal, ashes, soil, water and shade. *Water Air Soil Pollut* 82:147–54.
- Jarvis JM. 1966. Seeding white spruce, black spruce and jack pine on burned seedbeds in Manitoba. Canada Department of Forestry Report. No. 1166, Ottawa, Ontario.
- Johnson EA. 1992. Fire and vegetation dynamics. Studies from the North American Boreal Forest. Cambridge: Cambridge University Press, p 129.
- Johnson EA, Fryer GI. 1989. Population dynamics in lodgepole pine-engelmann spruce forests. *Ecology* 70:1335–45.
- Johnson EA, Miyanishi K, Kleb H. 1994. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta* – *Picea engelmannii* forest. *J Ecol* 82:923–31.
- Johnson EA, Miyanishi K, Weir JMH. 1998. Wildfires in the western Canadian boreal forest: landscape patterns and ecosystem management. *J Veg Sci* 9:603–10.
- Johnston M, Elliott J. 1998. The effect of fire severity on ash, and plant and soil nutrient levels following experimental burning in a boreal mixedwood stand. *Can J Soil Sci* 78:35–44.
- Johnstone JF, Chapin FSI, Foote J, Kemmett S, Price K, Viereck L. 2004. Decadal observations of tree regeneration following fire in boreal forests. *Can J Forest Res* 34:267–73.
- Kasischke ES, French NHF, O'Neill KP, Richter DD, Bourgeau-Chavez LL, Harrell PA. 2000. Influence of fire on long-term patterns of forest succession in Alaskan boreal forests. In: Kasischke ES, Stocks BJ, Eds. Fire, climate change, and carbon cycling in the boreal forest. Berlin Heidelberg. New York: Springer. p 214–38.
- Keays GM. 1987. Early post-fire succession following a severe fire in Wood Buffalo National Park, Northwest Territories. MSc thesis. Fredericton, New Brunswick: University of New Brunswick.
- Lavoie L, Sirois L. 1998. Vegetation changes caused by recent fires in the northern boreal forest of eastern Canada. *J Veg Sci* 9:483–92.
- Leadem CL, Gillies SL, Yearsley HK, Sit V, Spittlehouse DL, Burton PJ. 1997. Field studies of seed biology. Victoria (BC): British Columbia Ministry of Forests.
- LeBarron RK. 1945. Mineral soil is favorable seedbed for spruce and fir. Lake States Forest Experiment Station Technical Note 237, St. Paul, Minnesota.
- Lotan JE, Perry DA. 1983. Ecology and regeneration of lodgepole pine. Washington, DC: USDA forest service agriculture handbook no. 606.
- Miyanishi K, Johnson EA. 2002. Process and patterns of duff consumption in the mixedwood boreal forest. *Can J Forest Res* 32:1285–95.
- Pastor J, Cohen Y, Moen R. 1999. Generation of spatial patterns in boreal forest landscapes. *Ecosystems* 2:439–50.
- Pausas JG, Ouadah N, Ferran A, Gimeno T, Vallejo R. 2003. Fire severity and seedling establishment in *Pinus halepensis* woodlands, eastern Iberian Peninsula. *Plant Ecol* 169:205–13.
- Payette S. 1992. Fire as a controlling process in the North American boreal forest. In: Shugart HH, Leemans R, Bonan GB, Eds. A systems analysis of the global boreal forest. Cambridge: Cambridge University Press. p 144–69.
- Rosenberg MS, Adams DC, Gurevitch J. 2000. MetaWin, version 2.0. Sunderland (MA): Sinauer Associates, Inc.
- Rowe JS. 1983. Concepts of fire effects on plant individuals and species. In: Wein RW, MacLean DA, Eds. The role of fire in northern circumpolar ecosystems. Chichester: Wiley. p 135–54.
- Schimmel J. 1993. On fire: fire behavior, fuel succession and vegetation response to fire in the Swedish boreal forest. PhD thesis Umea, Sweden: Swedish University of Agricultural Sciences.
- Schimmel J, Granström A. 1996. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77:1436–50.
- Sirois L. 1993. Impact of fire on *Picea mariana* and *Pinus banksiana* seedlings in subarctic lichen woodlands. *J Veg Sci* 4:795–802.
- Swanson DK. 1996. Susceptibility of permafrost soils to deep thaw after forest fires in interior Alaska, USA, and some ecologic implications. *Arctic Alpine Res* 28:217–27.
- Turner MG, Romme WH, Gardner RH. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *Int J Wildland Fire* 9:21–36.
- Turner MG, Romme WH, Tinker DB. 2003. Surprises and lessons from the 1988 Yellowstone fires. *Front Ecol Environ* 1:351–8.

- Van Cleve K, Chapin FS III, Dryness CT, Viereck LA. 1991. Element cycling in taiga forest: state-factor control. *BioScience* 41:78–88.
- Weber MG, Hummel M, Van Wagner CE. 1987. Selected parameters of fire behavior and *Pinus banksiana* Lamb. regeneration in eastern Ontario. *Forestry Chron* 63:340–6.
- Wurtz TL, Zasada JC. 2001. An alternative to clear-cutting in the boreal forest of Alaska: a 27-year study of regeneration after shelterwood harvesting. *Can J Forest Res* 31:999–1011.
- Zasada J, Norum RA, Van Veldhuizen RM, Teutsch CE. 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. *Can J Forest Res* 13:903–13.
- Zasada JC. 1985. Production, dispersal, and germination of white spruce and paper birch and first-year seedling establishment after the Rosie Creek Fire. In: Juday GP, Dryness CT, Eds. Early results of the Rosie Creek fire research project, 1984. Fairbanks (AK): Agricultural and Forestry Experiment Station, University of Alaska Fairbanks. p 34–7.
- Zasada JC, Sharik TL, Nygren M. 1992. The reproductive process in boreal forest trees. In: Shugart HH, Leemans R, Bonan GB, Eds. A systems analysis of the global boreal forest. Cambridge: Cambridge University Press. p 85–125.