

Fire Interval Effects on Successional Trajectory in Boreal Forests of Northwest Canada

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ABSTRACT

Although succession may follow multiple pathways in a given environment, the causes of such variation are often elusive. This paper describes how changes in fire interval mediate successional trajectory in conifer-dominated boreal forests of northwestern Canada. Tree densities were measured 5 and 19 years after fire in permanent plots and related to pre-fire vegetation, site and fire characteristics. In stands that were greater than 75 years of age when they burned, recruitment density of conifers was significantly correlated with pre-fire species basal area, supporting the expectation of stand self-replacement as the most common successional pathway in these forests. In contrast, stands that were under 25 years of age at the time of burning had significantly reduced conifer recruitment, but showed no change in recruitment of trembling aspen (*Populus tremuloides*). As a result, young-burned stands had a much higher proba-

bility of regenerating to deciduous dominance than mature-burned stands, despite the dominance of both groups by spruce (*Picea mariana* and *Picea glauca*) and pine (*Pinus contorta*) before the fire. Once initiated, deciduous-dominated stands may be maintained across subsequent fire cycles through mechanisms such as low on-site availability of conifer seed, competition with the aspen canopy, and rapid asexual regeneration of aspen after fire. We suggest that climate-related increases in fire frequency could trigger more frequent shifts from conifer to deciduous-dominated successional trajectories in the future, with consequent effects on multiple ecosystem processes.

Key words: alternative community states; disturbance effects; fire return interval; *Pinus contorta*; *Picea mariana*; *Populus tremuloides*; postfire regeneration; successional trajectory.

INTRODUCTION

Variations in disturbance regime play a central role in determining patterns of ecosystem response and landscape legacies left by disturbance (Foster and others 1998; Turner and others 2003). In particular, nonlinear responses to changes in disturbance regime may cause rapid changes in forest structure (Paine and others 1998; Frelich and Reich 1999).

Once a shift has occurred, associated changes in processes such as nutrient cycling, trophic dynamics, and species regeneration may stabilize the community in an alternative stable state that differs substantially from the original system (Scheffer and others 2001).

In the boreal forest, stand composition is strongly influenced by interactions between species regeneration strategy and longevity, and the frequency and type of disturbance (Suffling 1995; Bergeron 2000). In the western boreal zone of North America, most tree individuals establish immediately after fire. Mean fire return intervals are short enough that many stands are likely to burn while the ori-

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ginal colonizers are still dominant in the canopy (Payette 1992; Outsell and Johnson 2002). Consequently, post-fire regeneration is a key process regulating forest composition. Boreal trees in western Canada show a variety of regeneration strategies related to disturbance. This includes cone serotiny and the development of aerial seed banks (*Pinus* spp. and *Picea marianda*), seed masting (*Picea glauca*) and asexual re-sprouting from roots and stumps (*Populus* spp. and *Betula* spp.; Zasada and others 1992). Patterns of forest cover in the boreal zone have been shown to strongly reflect the interactions between disturbance frequency and species regenerative potential (Payette 1992; Suffling 1995; Payette and others 2000).

The climate in the boreal forest is currently warming as rapidly as any place on Earth (Serreze and others 2000), and fire frequency is expected to increase in many areas (Flannigan and others 1998; Stocks and others 1998). The twofold increase in annual area burned in western North America in the last 40 years is probably linked to climate warming (Kasischke and Stocks 2000). Could this large change in disturbance regime trigger shifts in successional trajectories that would influence the composition of boreal forest? This study addresses that question by documenting the consequences of natural variations in fire interval patterns of stand regeneration in northwestern Canada, and exploring the implications of altered regeneration for community succession trajectories.

METHODS

Study area

The data for this study were collected from a series of permanent plots established in 1983 to monitor the long-term recovery of boreal forest vegetation after fire (Oswald and Brown 1990; Johnstone and others 2004). Plots were established in burn scars of three wildfires that occurred between mid-June and mid-August, 1982 on both sides of the Yukon/British Columbia border near Watson Lake, Yukon Territory, Canada (60°N, 128°W). Two of the fires were lightning-initiated and reached sizes of 182,000 ha (Fireside) and 8,000 ha (Tom Creek), and a third was human-caused and reached a size of 1,200 ha (Lower Post). Sampling intensity was relative to fire size, and 18, 11, and 5 plots were established in the Fireside, Tom Creek, and Lower Post burns, respectively (not including three original plots destroyed by road development).

Sample plots were located in road-accessible areas (>50 m distant from the road right-of-way).

The plots were selected to include a range in soil types, topography, and pre-fire vegetation characteristics. Pre-fire vegetation in the study area was dominated primarily by black spruce (*Picea mariana*) and lodgepole pine (*Pinus contorta* var. *latifolia*), with occasional stands of white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). More detailed descriptions of the fires and pre-fire vegetation can be found in Oswald and Brown (1990).

Field Measurements

Each plot consisted of a 10 × 10 m sampling area, divided into four 5 × 5 m subsections. Physical and pre-fire stand conditions in each plot were measured in the year after the fires (Oswald and Brown 1990). Physical measurements included slope angle, aspect, position on slope, and geomorphic landform type (Luttmerding and others 1990). Soil pits were dug in each plot, and soils were classified into a soil type based on the Canadian soil classification system (Agriculture Canada 1987). The upper portion of the mineral soil was assigned to a soil texture class using the 'texture-by-feel' method (Luttmerding and others 1990). Site elevation was estimated from topographic maps. Soil burn severity was also estimated from the percentage of exposed organic soil and depths of the ash layer and residual organic layer (Oswald and Brown 1990). Most plots were located out of visible range of unburned stands, and the distance to the nearest unburned stands was not measured.

All sites were categorized into different pre-fire age classes in 1983, and these ages were verified against observations of the size distributions of pre-fire deadwood made in 2001. Stands that had burned within 2–3 decades prior to the 1982 fire were identified based on the small basal diameters (3–7 cm) of the residual deadwood. Historical records of fire occurrence confirmed the presence of a 1959 fire within the Lower Post area and a 1965 fire in the Fireside area (Oswald and Brown 1990). Two plots in the Fireside burn appear to have experienced incomplete mortality in the 1965 burn, and retained 3–4 live stems/plot until 1982. These stands were grouped with others that burned in the 1959 or 1965 fires into a 'young-burned' class with pre-fire stand ages under 25 years. The remaining plots in the study had been classed as having pre-fire stand ages of 100 years or more (Oswald and Brown 1990). Basal diameters in these plots ranged from 4–41 cm, with a median of 11 cm.

We quality-checked a sub-set of the pre-fire age estimates in 2001 by counting rings on 1–4 basal tree disks in ten stands (Table 1). We were limited in the number of stem discs we sampled because of time constraints and the high incidence of stem rot or beetle holes in the 20 year-old wood. Tree ring counts on three small-diameter stems and a fire scar on one large-diameter stem from two plots in the Fireside burn (Table 1) were consistent with the estimate that young-burned stands in this area originated following the 1965 fire (Oswald and Brown 1990). Ring counts in the remaining stands produced estimates of stand ages that ranged from 75 to 135 years (Table 1). Plot 19 had the smallest mean stem diameter of the mature-burned stands in the study (7.6 cm), with a stand age estimate of 80 years. In general, the age estimates for mature-burned stands from Oswald and Brown's (1990) classification support the assessment of mature stand ages, although with a lower age cut-off of 75 rather than 100 years. Age classifications from Oswald and Brown (1990) were used for the remaining stands and all plots in the study fell into fire interval classes of either young- (pre-fire age < 25 years) or mature-burned stands (pre-fire age \geq 75 years). We used these classes in our analysis, rather than treating fire interval as a continuous variable, because the sampled stands fell into two discrete groups that would have differed substantially in within-stand availability of conifer seeds (see Discussion).

Pre-fire forest composition was characterized in terms of the dominant and sub-dominant tree species within the general area of a plot, based on the identification of partially burned tree stems. In some plots, coarse woody material was completely consumed by the fire and the dominant tree species were estimated from surrounding, more lightly burned stands or from pre-existing records (Oswald and Brown 1990). In 2001 we measured basal diameters of all pre-fire canopy trees in order to quantify the pre-fire basal area density of each tree species. The high level of fuel consumption in stands with small pre-fire trees meant that we were only able to consistently obtain basal diameter measurements for mature-burned stands.

Species identifications of burned stems were based on bark, branch and cone morphology. Black and white spruce were pooled because of the difficulty in differentiating between these species when cones were not present. On average, $70 \pm 4\%$ (± 1 SE) of the pre-fire trees were conclusively identified. Where we encountered conifer individuals of uncertain identity, we randomly assigned individuals to pine or spruce categories

according to the known proportions of the species in the plot.

Pre-fire stand dominance classes were derived from the listings of dominant and sub-dominant species recorded immediately after fire (E. Oswald and B. Brown, unpublished data; Figure 1). These estimates were compared with patterns of species dominance derived from pre-fire species basal area (estimated from basal diameter measurements) in mature stands. Stand dominance recorded by Oswald and Brown for the mature-burned stands used in our analyses were generally consistent with the relative basal area occupied by each species in the same plots (Figure 1). On the basis of this correspondence, we used the original post-fire estimates of dominant and sub-dominant species to estimated patterns of pre-fire composition in young-burned stands (Figure 1). For the two stands that were only lightly burned in 1965 (sites 20 and 22), we were able to obtain basal area measurements, and used those data to estimate pre-fire composition.

Repeated measurements of tree species density were made in the plots during the two decades after fire (Oswald and Brown 1990; Johnstone and others 2004). In this study, we used seedling count data from 5 years post-fire (Oswald and Brown 1990) to represent initial post-fire tree recruitment, and counts from 19 years post-fire to represent established stand composition (Johnstone and others 2004). All tree seedlings were identified to species, except for black and white spruce, which were difficult to distinguish in small seedlings. These species were pooled in our analysis, but we estimate that over 75% of the spruce seedlings examined in 2001 were black spruce, based on the presence of red hairs on one-year-old twigs (Cody 1996).

Statistical Analysis

Young-burned stands were uniformly located on Brunisol-type soils, while mature-burned stands occurred on a mixture of Brunisols, Regosols and Gleysols. Because differences in soil type are likely to cause substantial differences in physical site or vegetation factors (Agriculture Canada 1987), we excluded sites located on Regosols ($n = 2$) and Gleysols ($n = 4$) from our analysis of fire interval effects. We removed two additional plots that were persistent outliers in our analyses, one that represented the only mature aspen stand sampled in the study and another where all the regenerating pine seedlings (0.4 seedlings/m² in 1987) appeared to have been killed by snowshoe hare (*Lepus americanus*) herbivory between 5 and 10 years after

Table 1. Details of Tree Ring Samples Obtained From Pre-fire Deadwood in Sub-set of Ten Stands

Plot	Species	Mean Stem Diameter (cm)	Ring Counts	Estimated Stand Age
22	Pine	15.0 [†]	81, 123(15)*	15
24	Pine	5.5 [‡]	16, 17, 19	20
18	Spruce	9.1	79, 82, 86	85
19	Spruce	7.6	74, 74, 76, 80	80
21	Pine	12.4	96, 96, 107, 104	110
25	Pine	13.8	80, 82, 82	80
27	Aspen	31.3	105	105
30	Pine	19.1	92, 92, 94	95
33	Pine	22.0	71, 75	75
48	Spruce	12.0	125, 125, 129, 137	135

Mean stem diameter is based on all measured stems of that species in the plot. Ring counts were used to provide an approximate estimate of the stand age, based on fire scars or the age of the oldest trees, and without cross-dating of samples.

*Tree with a fire scar at approximately 15 years from the outer cambium.

[†]Only the two large diameter stems in the plot were sampled.

[‡]Only small diameter stems were sampled.

fire. The sites used in our analysis ($n = 28$) represent stands on Brunisol soil types that were dominated by conifers or mixed conifer/deciduous prior to the 1982 fire. Our analyses were conducted on 13 young-burned and 15 mature-burned plots.

All of our statistical analyses were performed in SAS v.8.02 (SAS Institute, Cary, NC). Our analyses addressed three main issues: (a) relations between pre-fire and post-fire forest composition in mature-burned stands, (b) relations between environmental variations and fire interval, and (c) comparison of environmental and fire interval effects on species regeneration. We first calculated the correlations between species pre-fire basal area density (cm^2/m^2 ; Greene and Johnson 1999) and post-fire stem density to assess the degree of autocorrelation between pre-fire and post-fire stand composition. This analysis used rank-transformed, Spearman correlation coefficients (r_s) to account for problems with heteroscedasticity (Conover 1999) and was performed on data from mature-burned stands only.

We used simple correlation (Pearson correlation coefficients, r_p) to assess relations between environmental variables and the occurrence of the two fire interval classes. Candidate variables were slope angle, aspect, elevation, drainage, and soil texture. Slope aspect data was first translated into ordinal scale by giving north-facing slopes a value of -1 , south-facing slopes a value of $+1$, and level, east- or west-facing slopes a value of 0 . Intermediate aspects were given intermediate values (for example, NE = -0.5). Site drainage data consisted of four classes ranging from very rapid to moderate drainage, and soil texture consisted of four classes ranging in coarseness from sand to silt loam. We were unable to derive an ordinal ranking for

geomorphic terrain origin, and did not include this factor in our analyses. Other measured environmental variables, such as slope position, showed little variation among sites and were not considered further.

The third stage of our analysis examined stand regeneration patterns across fire interval classes. We tested for differences in patterns of tree regeneration between young- and mature-burned stands using a multivariate analysis of variance (MANOVA) of log-transformed, post-fire densities of spruce, pine, and aspen, followed by separate ANOVA tests on each species (Scheiner 1993). We then used a combination of correlation analysis and linear model comparisons to estimate whether observed differences in post-fire tree density were due to direct effects of fire interval length or indirect effects of co-varying environmental factors. Partial correlation coefficients were used to estimate the relationship between fire interval class and stem density while controlling for the environmental variable that was most strongly correlated with the interval classes. Because multiple, weakly-correlated environmental variables may have accounted for the observed age effects, we also used multiple linear regression to construct two alternative models to predict post-fire species densities. One model type included age and environmental effects as variables in the model, and the other included only environmental effects. For each species, the best model within each class was selected based on the lowest corrected value of the Akaike Information Criteria (AIC_c ; Anderson and others 2000). The relative AIC weights of the two best models were compared to determine if the inclusion of age substantially improved the fit of the model.

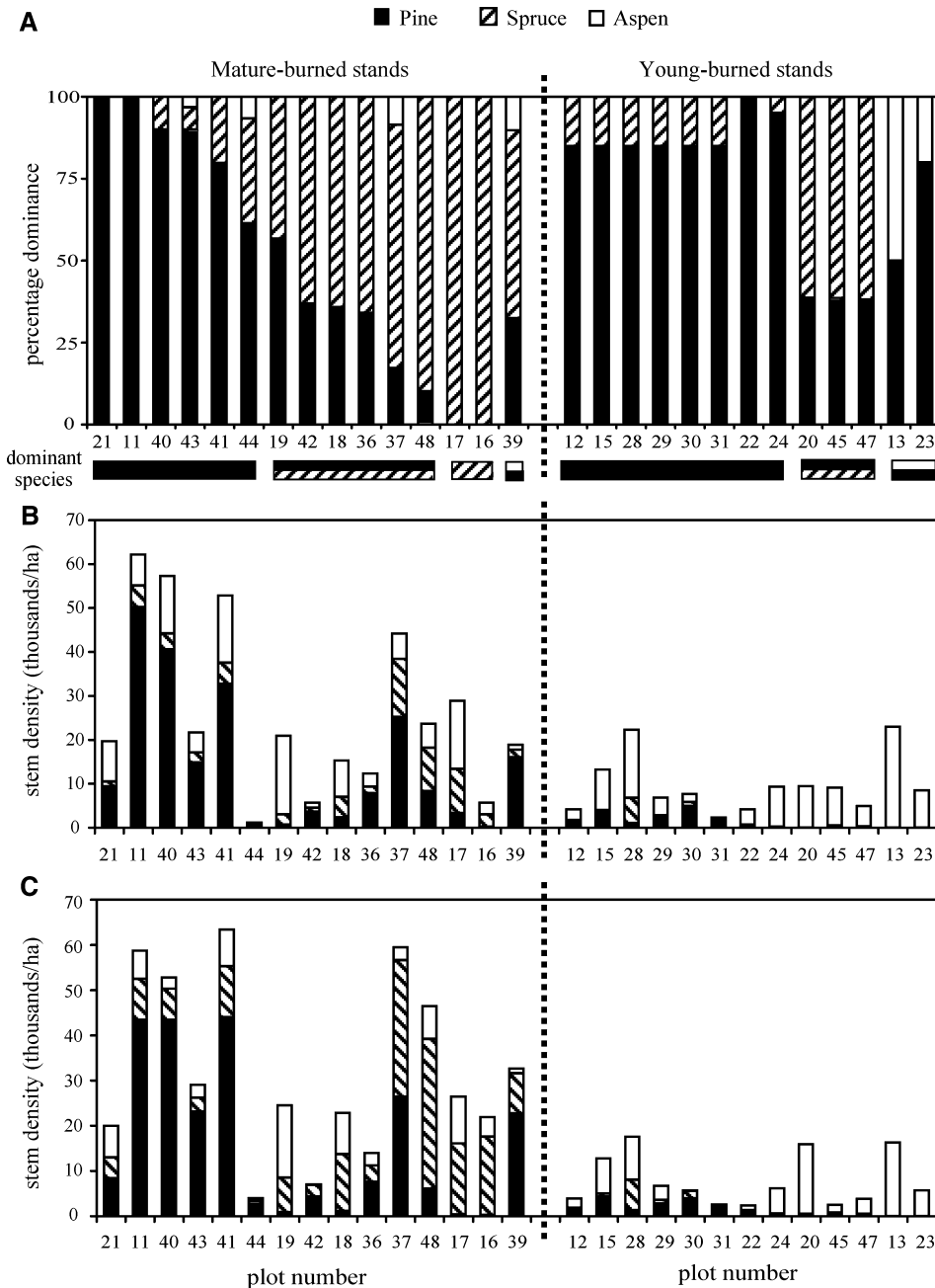


Figure 1. Forest stand composition estimated for before **A** and after **B** and **C** the 1982 fires for 28 study plots. The original plot numbers (Oswald and Brown 1990) are given on the *x*-axis, grouped into mature-burned and young-burned stands. In each panel, *filled*, *hatched*, and *open bars* represent lodgepole pine, spruce, and aspen, respectively. **A** Relative species dominance (%) for the pre-fire stands was calculated from measurements of species basal area for mature-burned stands and two young-burned plots (22 and 24). Relative dominance in the remaining young-burned stands was estimated from records of the dominant and sub-dominant species recorded in 1983 (Oswald and Brown 1990) and illustrated as *filled horizontal bars* below the corresponding plots. **B** and **C** Measurements of stem density by species (1,000 ha⁻¹) show patterns of post-fire species composition measured in 1987 **B** and 2001 **C**, 5 and 19 years after fire.

RESULTS

Post-fire densities of spruce and pine measured 19 years after fire were significantly correlated with pre-fire species basal area in mature-burned stands ($r_s = 0.60$ and 0.61 , $P = 0.017$ and 0.016 , respectively, $n = 15$). Aspen regeneration density was not correlated with pre-fire aspen basal area or with the presence or absence of aspen in the pre-fire stand ($P > 0.1$). Only 4 of 15 mature-burned stands in this analysis had aspen present in the sample plot prior to the fire; two additional sites had pre-fire aspen within 10 m of the plot borders. Post-fire aspen

recruits, in contrast, were found in all of the sampled plots.

Across the 28 stands in this study, young-burned stands tended to occur on sites with high rates of soil drainage ($r_p = 0.45$, $P = 0.01$; Figure 2). Both soil texture and elevation were significantly correlated with soil drainage ($r_p = -0.44$ and -0.50 , $P = 0.02$ and 0.006 , respectively), indicating a potentially complex influence of landscape configuration on observed patterns of fire occurrence.

The length of the previous fire return interval had a strong impact on post-fire regeneration patterns.

Stands that burned at a young age had significantly lower seedling densities than mature-burned stands, regardless of whether seedlings were measured 5 (MANOVA $F_{3,24} = 11.74$, $P < 0001$) or 19 years after fire (MANOVA $F_{3,24} = 15.54$, $P < 0001$; Figure 3). The substantial decrease in total seedling numbers in young-burned stands was largely accounted for by severe reductions in numbers of regenerating spruce and pine (ANOVA $F = 45.08$ and 13.96 , $P < 0.0001$ and 0.0009 , respectively; Figure 3). In contrast, aspen stem densities were unaffected by return interval (ANOVA $F = 0.08$, $P = 0.77$). Although species responses to differences in fire interval were similar between years 5 and 19, absolute seedling densities varied between the two census dates (Figure 1). Differences in seedling counts between dates are associated with continued recruitment and delayed recognition of conifer seedlings between years 5 and 10, and the initiation of pine and aspen thinning between years 10 and 19 (Johnstone and others 2004).

Variations in species responses to the difference in fire interval class resulted in different patterns of post-fire stand composition between the two classes (Figure 1). By 19 years after fire, most young-burned stands (11 of 13) were composed of over 40% deciduous seedlings, and five stands were more than 75% deciduous-dominated. In contrast, only 3 of 15 mature-burned stands developed stands with close to 40% deciduous trees, and no stands regenerated to deciduous dominance. These differences in post-fire composition appear to be unrelated to patterns of pre-fire composition, which indicate that conifers dominated the majority of both young- and mature-burned sites prior to the 1982 fire (Figure 1).

Using partial correlation to statistically control for the effects of covariance in site drainage, we found a persistent and significant effect of fire interval on post-fire spruce and pine densities (partial $r_p = 0.70$ and 0.60 , $P = 0.0001$ and 0.001 , respectively, $n = 28$). As with the simple correlation analysis, however, post-fire aspen density was uncorrelated with stand age at burning (partial $r_p = 0.06$, $P = 0.074$, $n = 28$). Likewise, our comparison of multiple regression models indicated that models with stand age provided a substantially better fit to the regeneration data for spruce and pine, but not aspen, compared to models using only environmental data (Table 2).

DISCUSSION

Patterns of post-fire recruitment at our mature-burned sites support previous observations that

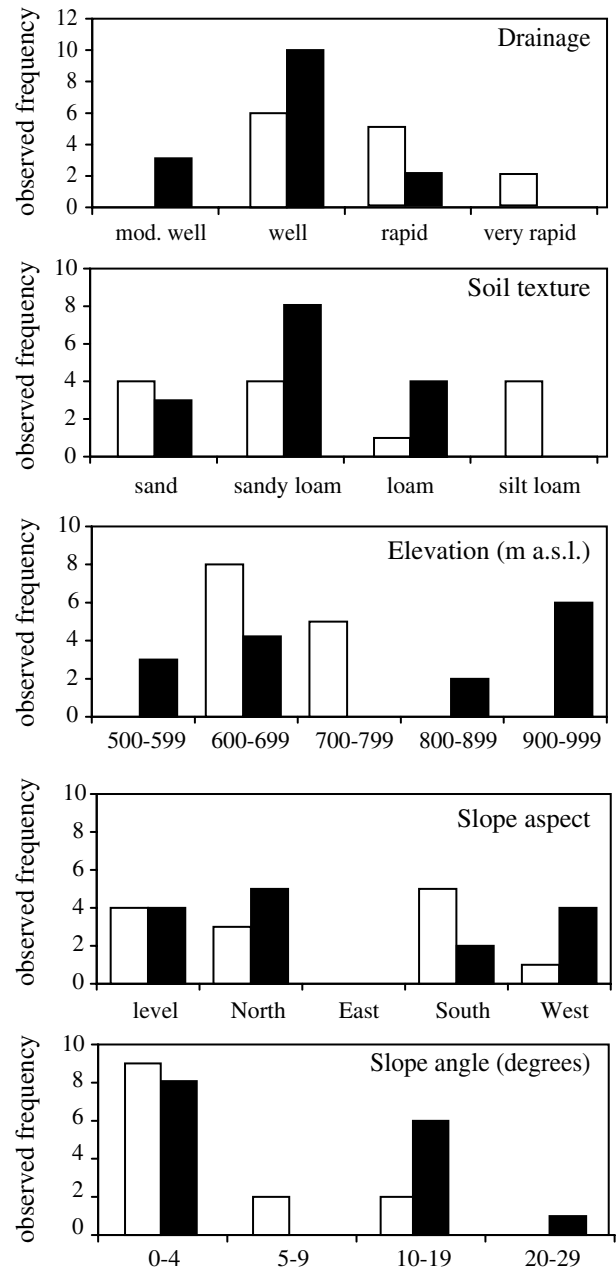


Figure 2. Frequency histograms showing the distribution of stands in two fire interval classes for environmental factors of site drainage, soil texture (ordered from coarse to fine), site elevation in meters above sea level (m a.s.l.), slope aspect, and slope angle in degrees. Distributions are shown separately for young-burned (light bars, $n = 13$) and mature-burned (dark bars, $n = 15$) classes.

stand regeneration in boreal forests is strongly linked to pre-fire composition and frequently leads to stand self-replacement (Viereck 1973; Greene and Johnson 1999). However, our data also show a divergence between pre-fire and post-fire species composition that appears to depend on fire return

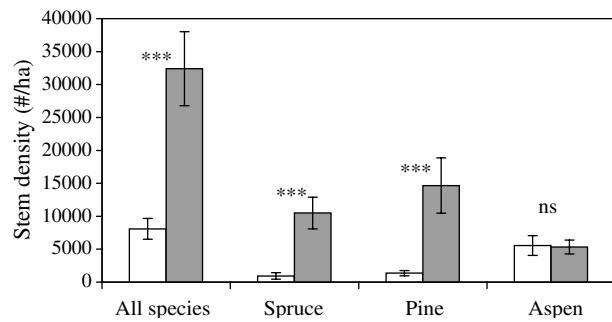


Figure 3. Patterns of tree stem density (stems per ha) measured 19 years after fire in stands that burned after a fire interval of less than 25 years (*light bars*, $n = 13$) or more than 75 years (*dark bars*, $n = 15$). Mean densities (± 1 SE) are shown for the total across all species, and individual components of spruce, lodgepole pine, and aspen. *Symbols* indicate the significance of differences between means in the two fire interval classes (*** $P < 0.001$; *ns* $P > 0.05$).

interval. Forest stands that burned at a young age (<30 years) had very low levels of post-fire conifer regeneration, despite being dominated by conifers before the fire. In contrast, aspen regeneration was insensitive to variations in fire frequency and, as a result, many of the young-burned stands switched to deciduous dominance after burning. Variations in environmental factors were unable to account for the effects of stand age on regeneration patterns, suggesting that changes in fire return interval were directly responsible for the altered succession trajectories.

Many of the young-burned stands in our study occurred preferentially at well-drained sites, indicating that components of a landscape influence susceptibility to a short fire interval or other change in fire regime (Larsen 1997). In addition, local climate and environmental conditions are likely to influence how ecosystems respond to changes in fire disturbance. At the forest-tundra boundary in eastern Canada, forest degradation is triggered by unusual fire events that interact with climatic stresses on conifer seed production and lead to failures of post-fire regeneration (Payette and others 2001). In the southern boreal zone, sparsely-treed lichen woodlands have been shown to originate from fires that follow severe outbreaks of insect defoliators that reduce conifer seed availability (Payette and others 2000). Despite the differences in forest community types, these examples and our results together support a general hypothesis that changes in post-fire regeneration potential are a key mechanism generating divergent trajectories of post-fire succession in boreal forests (Payette 1992).

Differences in species responses to fire interval length can be attributed to differences in basic life history characteristics (Suffling 1995). The decline in conifer recruitment associated with a short fire interval appears to be a consequence of both a strong dependence on local seed rain for recruitment and low seed production rates among young trees. Both black spruce and lodgepole pine store seeds in serotinous cones and rely heavily on local seed rain for post-fire regeneration (Lotan and Perry 1983; Greene and Johnson 1999). Although pine and spruce may initiate seed production within 20–30 years after fire (Burns and Honkala 1990), low rates of seed production and cone serotiny among juveniles limit the development of aerial seed banks (Burns and Honkala 1990; Zasada and others 1992).

In contrast to the conifers, deciduous species such as trembling aspen have regeneration strategies that capitalize on asexual re-sprouting from roots or stumps, and long-distance transport of small, wind-blown seeds (Zasada and others 1992). Asexual regeneration of aspen can occur after only 1 year of growth (Zasada and others 1992), indicating that there would be little effect of a shortened fire return interval on re-sprout capacity. Because we observed substantial aspen regeneration at sites where there were no pre-fire aspen stems in the plot or surrounding locality, we hypothesize that seed regeneration played a large role in aspen recruitment at many of our sites. Whether aspen recruitment occurs by seed or sprouting, variations in fire interval are likely to have little effect because of the lack of local age effects on aspen propagule availability.

Patterns of burn severity were confounded with differences in fire return interval in this study, making it difficult to assess the role played by burn severity in the observed responses. In mature-burned stands, sites with high burn severity tended to have higher densities of regenerating pine and aspen, and lower densities of spruce (Johnstone 2003). In young-burned stands, the small stature of young trees probably increased crown fire severity and the likelihood of cone and seed damage during the fire. In addition, high levels of soil burn severity and mineral soil exposure in young-burned stands may have enhanced the potential for establishment of deciduous seedlings from off-site seed sources (Johnstone and Chapin 2005, *in press*). In this fashion, where increased levels of burn severity are associated with shorter fire return intervals, severity effects may tend to reinforce the direct effects of fire interval on species regeneration patterns.

Table 2. Summary of Best-fit Multiple Regression Models to Predict Post-fire Regeneration Density of Spruce, Pine, and Aspen ($n = 28$).

Predicand	Model Class	Model Variables	R^2	AIC_c	w_j
Ln (Spruce Density)	With age	Age (+)	0.63	7.29	1.00
	Without Age	Aspect (-)	0.12	31.85	0.00
Ln (Pine Density)	With Age	Age (+) Elevation (+)	0.55	18.58	0.96
	Without Age	Texture (-) Elevation (+)	0.43	24.88	0.04
Ln (Aspen Density)	With Age	Age (+) Elevation (-) Aspect (-)	0.34	4.31	0.29
	Without Age	Elevation (-) Aspect (-)	0.32	2.49	0.71

Models have been split into those that include and those that exclude age as a predictor variable, and the best model in each class was selected to minimize AIC_c . Candidate environmental variables were site drainage, soil texture, elevation, slope, and aspect. A plus or negative sign beside a model variable indicates the direction of effect on regeneration density. For each species, the better of the two models is shown in bold. AIC weights (w_j) provide an indication of the relative likelihood of the two models, given the data (Anderson and others 2000).

Fire effects on early regeneration patterns are likely to have important implications for future stand development, as seedlings that regenerate immediately after fire usually dominate the canopies of mature stands (Yarrington and Yarrington 1975; Johnson and others 1994; Lavoie and Sirois 1998; Gutsell and Johnson 2002). At our sites, most tree establishment occurred within 5 years and few new seedlings were observed more than 10 years after fire (Johnstone and others 2004). Consequently, fire interval effects were rapidly apparent in the post-fire community and have persisted through two decades of early tree canopy development. This pattern is consistent with demographic analyses showing that once the initial phase of establishment is over, the pathway of succession is largely set until species-specific canopy mortality begins to occur (Johnson and others 1994; Bergeron 2000; Gutsell and Johnson 2002).

In mixed conifer-deciduous stands, the shorter life spans and lesser shade tolerance of deciduous species generally leads to increasing conifer dominance over time (Bergeron 2000; Outsell and Johnson 2002). This pattern appears to be occurring in many of our mature-burned stands, as aspen densities have generally decreased between years 5 and 19 post-fire. However, when conifers are absent or infrequent in the regenerating stand, deciduous species can maintain stand dominance through asexual regeneration in forest gaps (Gumming and others 2000). In approximately half of the young-burned stands in this study, aspen

canopy dominance is unlikely to be replaced by conifers because of the very low abundance of understory pine or spruce seedlings. Delayed establishment of conifers, which could alter the succession trajectory of a deciduous stand, is hindered by low seed availability (Greene and Johnson 2000), poor establishment success in the canopy understory (Simard and others 1998; Purdy and others 2002), and the relatively short fire cycle in many boreal forests (Mann and Plug 1999).

Average fire return intervals in boreal spruce and pine forests of western North America are frequently estimated in the range of 50–150 years (Payette 1992; Larsen 1997). Thus, the fire-free periods experienced by the mature-burned stands in this study (75–150 years) appear to represent normal fire frequencies for the region. In contrast, fire return intervals of less than 30 years, as experienced by our young-burned stands, appear to be unusual disturbance events. For example, an estimated 6% of the area burned in the 1980's and 1990's in Yukon Territory overlapped with fire scars from the three preceding decades (D. Milne, personal communication based on Yukon fire history data). However, future changes in fire frequency that occur in response to climate warming (Flannigan and others 1998; Stocks and others 1998) and/or declining availability of funds for fire suppression are likely to increase the frequency of burn overlap. Areas with dry macro-or micro-climate or coarse-textured soils may be particularly susceptible to more frequent fire (Larsen 1997).

The resulting changes in fire interval may directly influence landscape responses by altering patterns of forest regeneration and causing shifts between deciduous- and conifer-dominated succession trajectories (for example, Suffling 1995; Frelich and Reich 1999; Dale and others 2001). Because deciduous and conifer communities differ in many attributes of ecosystem function, such as land-atmosphere energy exchange (Chapin and others 2000), carbon turnover (Hobbie and others 2000), and plant regeneration pathways (Mann and Plug 1999), changes in the relative dominance of these community types may have important impacts on long-term ecosystem responses to climate change.

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