

Response of boreal plant communities to variations in previous fire-free interval

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Abstract. The present study used overlapping burn scars from natural wildfires to examine the effects of changes in the fire-free interval on early successional plant communities in boreal forests of central Yukon Territory, Canada. Data on plant community composition and residual organic material were collected in the first decade of post-fire regeneration in two study areas with recent fire overlap. Sites with a shorter fire-free interval had reduced loads of deadwood and shallower organic layers after the most recent fire. Multivariate analysis of species cover indicated that sites in and out of the burn overlap zones also supported distinct plant communities. Differences in the plant communities were associated with a greater abundance of woody deciduous species, such as *Populus tremuloides*, *Salix* spp., and *Shepherdia canadensis*, at sites that had recently re-burned. Sites that burned after a longer interval had higher moss cover and greater abundance of *Picea mariana*, *Calamagrostis canadensis*, and *Ribes glandulosum* in one study area, and *Epilobium angustifolium* in the second area. Ordinations of species cover indicated that plant community patterns were most strongly associated with gradients related to fire history and topography. In general, shorter fire-free intervals reduced pools of residual plant material and favored dominance of resprouting, woody deciduous species.

Additional keywords: boreal forest; coarse woody debris; fire frequency; non-metric multidimensional scaling ordination; plant functional types; post-fire regeneration; regeneration traits; Yukon Territory.

Introduction

Changes in fire frequency have been predicted for many areas of boreal forest under future climate warming scenarios (Stocks *et al.* 1998; Flannigan *et al.* 2005). Fire is a dominant disturbance agent in boreal forests and geographic variations in fire regime are strongly reflected in plant community composition and structure (Heinselman 1981; Johnson 1992). Consequently, we can expect changes to fire regimes caused by climate change to have important effects on modern plant communities. Knowledge of plant life history traits provides a strong theoretical basis for predicting changes in plant species abundance in response to altered disturbance (Rowe 1983; McIntyre *et al.* 1999; Pausas *et al.* 2004). However, the inherent difficulties associated with experimental manipulations of fire regime means that there remains little empirical information that is suitable for testing these predictions. Comparisons between geographic regions with different disturbance regimes are almost inevitably confounded with other environmental gradients. Paleoecological investigations have provided valuable information on how changes in disturbance regime over time are correlated with vegetation shifts, but

it is often difficult to separate interacting effects of changing climate, disturbance, and vegetation composition (e.g. Carcaillet *et al.* 2001). Thus, there remains a need for other types of observations that can be used to assess vegetation community responses to altered disturbance.

The present study uses overlapping burn scars as a 'natural experiment' to explore the effects of a shift in fire return interval on regenerating plant communities in boreal forests. Zones of fire overlap provide an opportunity to compare local-scale responses of the plant community between adjacent areas in the same successional stage that differ in the length of the previous fire-free interval (Fig. 1). Restriction of comparisons to samples from within a single burn that lie within and outside the overlap zone helps minimize the potential for results to be confounded by spatial or successional changes in other environmental factors. Previous work using overlapping burn scars (Delitti *et al.* 2005; Johnstone and Chapin 2006a) or recurring insect and fire disturbances (Payette *et al.* 2000; Jasinski and Payette 2005) has demonstrated strong effects of increased disturbance frequency on patterns of tree recruitment and subsequent forest recovery.

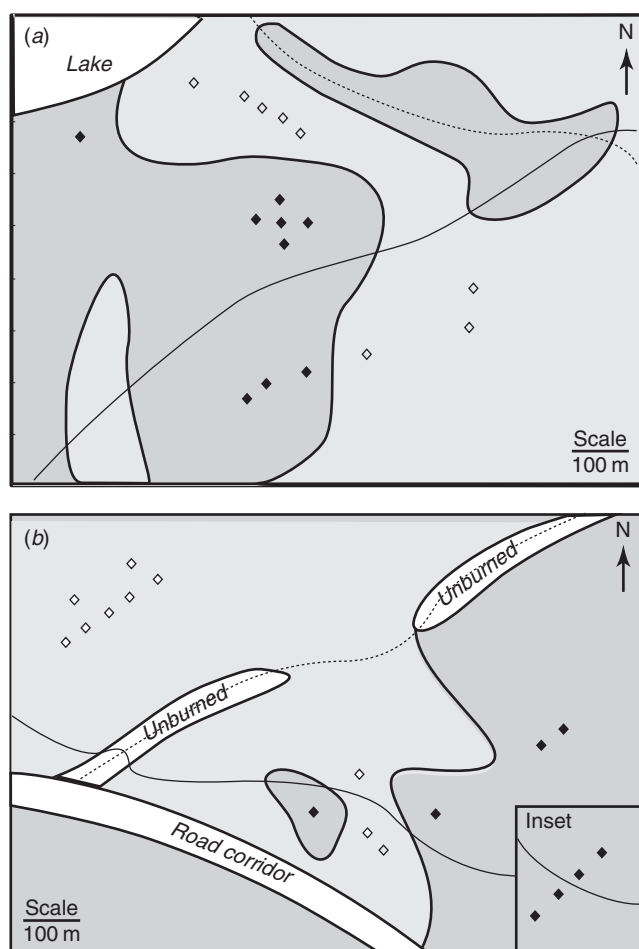


Fig. 1. Site maps of field sample plots in relation to overlapping burn scars at (a) Pelly and (b) Braeburn study areas. The different grey tones indicate differences in the length of the previous fire-free interval, with darker areas having a fire-free interval of ≥ 80 years, and lighter areas having a fire-free interval of ≤ 50 years. All grey areas were burned by recent fires in the 1990s. Sample points are shown as filled (long fire-free interval) or open (short fire-free interval) diamonds. Streams are indicated on the maps by thin dotted lines, and thin solid lines indicate 100-m contour intervals. An inset in the Braeburn map (b) shows the relative positioning of four sample plots located 2 km from the main sample area.

However, there is still little information on the responses of non-tree plants or other ecosystem components to variations in disturbance frequency in boreal forests (however, see Delitti *et al.* 2005).

The current study presents information on plant community responses to differences in the length of the previous fire-free interval at two study areas located in *Picea* (spruce)-dominated boreal forests of south-central Yukon Territory, Canada. Patterns of plant species abundance were compared between burn overlap zones within a study area to assess the effects of a change in fire-free interval on post-fire vegetation composition. Comparison of regeneration traits of plant

species that differed in abundances between zones provided an assessment of the degree to which plant responses were associated with general life history traits. Pools of post-fire residual deadwood and surface organic material were also contrasted across fire interval zones to evaluate how changes in fire frequency may affect long-term storage and turnover of dead plant material.

Methods

Field sampling

Study areas were located in natural forested areas of south-central Yukon Territory, Canada, that had experienced successive fire disturbance within the past half-century. Fire perimeters recorded in the Yukon Fire History database (Yukon Territorial Government, unpublished data) since 1946 were used to identify areas of successive fire disturbance caused by overlapping burn scars. Although the Fire History database identified over 200 000 ha of potential fire overlap, much of this area was located in wilderness areas difficult to access for research. Initial selection identified 10 potential overlap areas over 1000 ha in size that had feasible access from roads or rivers. Air photos of these areas were then inspected to confirm the fire history record and several sites without evidence of overlapping fire scars were discarded. The two most accessible sites were selected for study.

One study area was located adjacent to the Alaska Highway ~ 10 km south of Pelly, Yukon ($62^{\circ}42'N$ $136^{\circ}40'W$). Sample plots were accessed by canoe from Rock Island Lake (*T'he N'du*) on the south side of the highway. The area was documented as having been initially burned in 1969, and the southern edge burned again in 1995. Climate records from nearby Pelly indicate daily mean temperatures of $-27.5^{\circ}C$ in January and $15.5^{\circ}C$ in July, with an average of 31 cm of precipitation per year (Environment Canada 2006). Local climate conditions in the lowland plots sampled near the lake were generally cool and moist with near-surface permafrost (seasonal thaw < 1.5 m). Plots sampled along the north- and west-facing hillslope provided more well-drained conditions, and did not show evidence of permafrost. Prior to burning, forests in the area were dominated by *Picea mariana* (black spruce), with co-dominance of *Populus tremuloides* (trembling aspen) and occasional *Betula neoalaskana* (Alaskan paper birch) in young stands.

A second study area was located 10 km south-east of Braeburn Lake and ~ 80 km north of Whitehorse, Yukon, and was accessible from the Alaska Highway ($61^{\circ}25'N$ $135^{\circ}42'W$). This area had burned most recently in 1998 in a fire that overlapped on its northern edge with another fire scar from 1958. The area was characterized by daily mean temperatures of $-21.2^{\circ}C$ in January and $13.6^{\circ}C$ in July, with an average of 28 cm of precipitation per year, based on climate records from Braeburn Lake (Environment Canada 2006). The largely

south- and west-facing slopes of the sample area provided relatively warm and dry conditions during summer. Forests in the area were dominated before the 1998 fire primarily by *Picea glauca* (white spruce), with co-dominance of *Populus tremuloides* in young stands.

Sampling took place within recently burned forests and was stratified into two zones of differing fire-free interval. One zone was located in areas where the previous fire-free interval was short and burned stands were composed of small, immature trees. The other zone was located in areas with a long fire-free interval, where burned stands were composed of mature trees (Fig. 1). Within each zone, eight to ten circular, 7-m diameter plots were established randomly or systematically along transects at distances of 50 m and with a random starting point. An effort was made to sample areas of similar slope and aspect between fire interval zones within a study area. Sampling was constrained to ensure that plots were located at least 30 m from the edge of burned stands in a different fire interval zone, and greater than 100 m from any patches of unburned forest. Sample points were excluded if they fell within areas that had been incompletely burned in recent fires. In order to obtain sufficient samples that were not disturbed by recent post-fire logging at the Braeburn area, four mature-burned plots were established on a comparable hillslope sequence located 2 km away. These sites were located in an area of similar slope, aspect, soils, and pre-fire forest composition as mature sites located directly adjacent to the overlap zone, but were unaffected by logging disturbance.

Field sampling for vegetation cover occurred at peak growing season in mid-July 2004, 6 and 9 years after burning for sites at Braeburn and Pelly, respectively. In each plot, post-fire vegetation cover (visual percentage cover within a quadrat) was measured by the same observer in four 1-m² quadrats that were systematically positioned 3 m from the plot center in four compass directions. This area of sub-sampling consistently captured most of the species present in the larger sample plot; rare species present in the plot but not observed in the quadrats were assigned a plot cover value of 0.1%. Percentage cover was estimated separately for all plant species or plant groups (*Salix* and small mosses) within a quadrat, and for surface cover types of dead plant litter, wood, or bare soil. Total cover in a quadrat ranged from 100 to 160% owing to vegetation overlap. Voucher specimens were collected as needed to verify species of uncertain identity. Species nomenclature followed Cody (1996).

Composition and basal stem diameter (measured 15 cm above ground, or directly above the swollen root collar) of all standing and fallen tree stems from the pre-fire community were measured in the 7-m radius plot (153.8 m²). All sampled stands experienced 100% stand mortality in the previous fire.

The depth of the post-fire soil organic layer was measured at eight points per plot from soil plugs excavated with a flat-bladed shovel. A soil pit was dug to 50 cm depth to assess soil texture in the near-surface soil profile, using the

'texture-by-feel' method (Luttmerding *et al.* 1990). Slope, aspect, elevation, and location coordinates were recorded at each plot, along with distance of the plot to the nearest burn edge. An index of the relative amount of solar energy received at each plot (insolation) based on slope and aspect (e.g. Bennie *et al.* 2006) was calculated as

$$I = \cos(S) \times \cos(L - 23) - \sin(S) \times \cos(A) \times \sin(L - 23),$$

where I is the insolation index, based on the potential solar radiation received on 21 June, and S is slope angle in degrees, A is slope aspect in degrees, and L is degrees North latitude, adjusted to the solstice sun position (offset by 23°).

Tree ring samples, in the form of stem disks or cores, provided independent estimates of pre-fire stand age and the length of the preceding fire interval. Stem samples were taken from just above the swelling of the root collar for four or eight pre-fire trees per plot, depending on whether the stem size distribution appeared uni- or multi-modal (total tree samples = 182). After sanding, tree rings were counted under a binocular microscope to estimate minimum tree age. Stem samples were not cross-dated, as minimum tree ages provided sufficient data to estimate the approximate length of the previous fire-free interval. Histograms of stem ages were plotted to identify periods of high tree recruitment likely to indicate stand-replacing fire (Gutsell and Johnson 2002). To compensate for ageing error associated with missing rings or uncounted years between the root collar and stem sample (DesRochers and Gagnon 1997; Peters *et al.* 2002), the minimum age of a fire event was estimated as the age of the oldest tree associated with a peak in tree recruitment (estimated in 5-year increments to avoid false precision). This efficacy of this approach was assessed using tree-ring data from young-burned stands at Braeburn, where a known fire return interval of 40 years was compared with an observed peak in tree ages at 35 years and a maximum observed stem age of 38 years (Table 1).

Data analysis

Data analysis focused on a categorical comparison between burn overlap zones within a study area. However, information on tree ages collected during the study revealed in some cases a gradient in actual fire-free intervals within a zone (Table 1). Where appropriate, analyses with measured fire-free intervals were used to supplement the categorical analysis of the original study design. Analyses were performed separately for the two study areas, as differences in characteristics such as local climate, time-since-burning, and species composition permitted only general and qualitative comparisons between areas.

Species abundance in each sample plot was summarized as an average of percentage cover measured across the four quadrats in a plot. There were two groups of species, *Salix* (willow) shrubs, and a group of small acrocarpus mosses

Table 1. Fire history estimated from tree-ring counts and the associated number of sample plots in stands with a short or long fire-free interval for the Pelly and Braeburn study areas

Study area	Fire-free interval class	No. plots	Previous stand recruitment peak (years)		Estimated length of previous fire-free interval (years)
			Mean	Maximum	
Pelly (hillslope)	Short	3	20	22	26 ^A
	Long	3	90	100	100
Pelly (lowland)	Short	5	38	43	45
	Long	6	200 ^B	212	215
Braeburn	Short	10	34	38	40 ^A
	Long	2	65	79	80
		2	140	150	150
		4	235	252	250

^AExact fire-free interval confirmed in historical fire record. ^BStands in this class showed a bimodal age distribution, with a second peak in ring counts at 140 (maximum 160) years.

(dominated by *Ceratodon purpureus*, often intermixed with other small mosses such as *Pohlia nutans* and *Leptobryum pyriforme*) that were difficult to conclusively identify because of the frequent absence of reproductive structures. In order to avoid spurious patterns caused by incorrect or inconsistent identification, these groups were identified as functional groups of *Salix* spp. and *Ceratodon*-type moss for analysis. Woody shrubs in the *Salix* group share a common ability to resprout from belowground stems or roots, and small acrocarpous mosses such as *Ceratodon*, *Pohlia*, and *Leptobryum* are often rapid colonizers after disturbance. Vascular plant litter, defined as attached and unattached dead biomass of recognizable origin, was included as a third functional group.

Rare species that were observed in only one or two plots in a study area were deleted from the dataset. This procedure reduces the variance and noise in the dataset, while still permitting a robust assessment of community responses to environmental gradients (McCune and Grace 2002). Iterative trials with the Braeburn dataset indicated that deletion of rare species did not have noticeable effects on ordination results until species occurring in four or fewer plots were deleted. All cover data were square-root transformed prior to analysis to reduce skew and kurtosis. Cover data were not standardized within a species; consequently, abundant species likely had stronger effects on the ordination results than rare species. This approach was chosen to allow the analyses to reflect patterns in community structure (primarily affected by dominant species) as well as composition.

Categorical effects of burn zone on residual organic material (organic layer depth and deadwood basal area) were tested using single-factor ANOVA on square-root transformed data. A two-factor ANOVA that included blocking by topographic position was applied to organic layer depths at Pelly because of large differences in drainage and moisture conditions between hillslope and lowland sites. ANOVA calculations were performed with SAS version 8.02 (SAS Institute 2001).

Differences in community composition between burn overlap zones were tested with multi-response permutation procedures (MRPP) calculated with Sørensen (city-block) distances between sample plots, which represent the shared abundances of species proportional to their total abundance (McCune and Grace 2002). The MRPP procedure uses repeated shufflings of the distance matrix to test the hypothesis of no difference between two groups of community data, and thus provides a non-parametric significance test of group differences (McCune and Grace 2002). Where the MRPP test rejected the null hypothesis ($\alpha = 0.05$), I used indicator species analysis to identify species that consistently differed in their abundance between groups (Dufrêne and Legendre 1997). Indicator values were calculated from the relative abundance and frequency of species in each group (Dufrêne and Legendre 1997). All multivariate analyses of the vegetation data were performed with PC-ORD version 4 (McCune and Mefford 1999).

Ordination of sample plots based on species cover data was calculated using non-metric multidimensional scaling (NMS), an iterative procedure that minimizes the stress in a multi-dimensional distance matrix. This ordination approach has been recommended for ecological analyses, in part because it produces robust and interpretable results when relationships among variables are non-linear (McCune and Grace 2002). NMS calculations for both datasets were performed using Sørensen distances, random starting configurations, and 40 runs with the real data. The optimal number of dimensions was assessed using a Monte Carlo procedure in which stress reductions in runs with real data were compared with stress obtained from 50 runs with randomized data. Stability of the final solution was assessed by comparing stress *v.* iteration number to ensure stress levels had reached a stable plateau in later iterations. The ordination solution was then rotated to align one of the axes with the fire frequency gradient by maximizing the correlation between the axis scores and fire return interval. Post-hoc

estimates of the amount of variation in the original dataset represented by each axis were generated by regressions of Sørensen distances in the ordinated data against Euclidian distances in the original data (McCune and Grace 2002). Correlations between environmental gradients and ordination axes were used to assess which of the measured environmental gradients had the strongest effect on plant community composition. I used linear correlation coefficients (Pearson's r) to avoid problems with tied values for ordinal variables and because results were qualitatively similar to ranked correlation statistics (Kendall's tau). Candidate environmental variables included fire return interval (years), elevation, soil texture class (from fine silty clay to coarse sand), slope, relative insolation, residual organic layer depth (cm), and distance to unburned stands. Joint-plot overlays were used to indicate the environmental variables most strongly related to the distribution of sample units on the ordination axes. A threshold correlation of $r = 0.5$ was used for inclusion of variables in the joint plot. Ordination scores were also correlated with the total cover of different plant functional types (deciduous trees and shrubs, evergreen trees and shrubs, forbs, graminoids, lichens, moss, litter, bare soil, and total live vegetation).

Results

Fire history

Stand age estimates from tree ring counts generally corroborated the presence of the historical fires recorded in the Yukon Fire History database. However, the mapping accuracy of perimeters from older historical fires was relatively poor and consequently did not represent the true spatial arrangement of fire histories and overlap zones on the ground. At the Pelly site, tree ring samples from lowland, young-burned stands indicated that a portion of the area mapped as the 1969 fire actually burned in an undocumented, earlier fire dating from around 1950 (Table 1). At the Braeburn site, a large portion of the area mapped as having burned in both 1958 and 1998 showed no evidence of having burned in the earlier fire. The amount of overlap between the two burns was much smaller than was mapped and was restricted to a narrow (1–2 km wide) band along the north edge of the 1998 burn scar. Actual fire perimeters of both recent and older fires included numerous patches of partially burned or unburned forests that resulted in a complex mosaic of fire history that was poorly represented by fire history maps.

Tree ring samples from mature-burned stands at Pelly indicated that previous stand-replacing fires had occurred ~100 years earlier at three hillslope sites and 215 years earlier at six lowland sites (Table 1). At Braeburn, mature-burned stands were estimated to have originated from fires occurring 80, 150, and 250 years before the recent fire in 1998. Tree ages sampled from mature-burned stands at both sites were generally unimodal and showed clear peaks in tree ages that

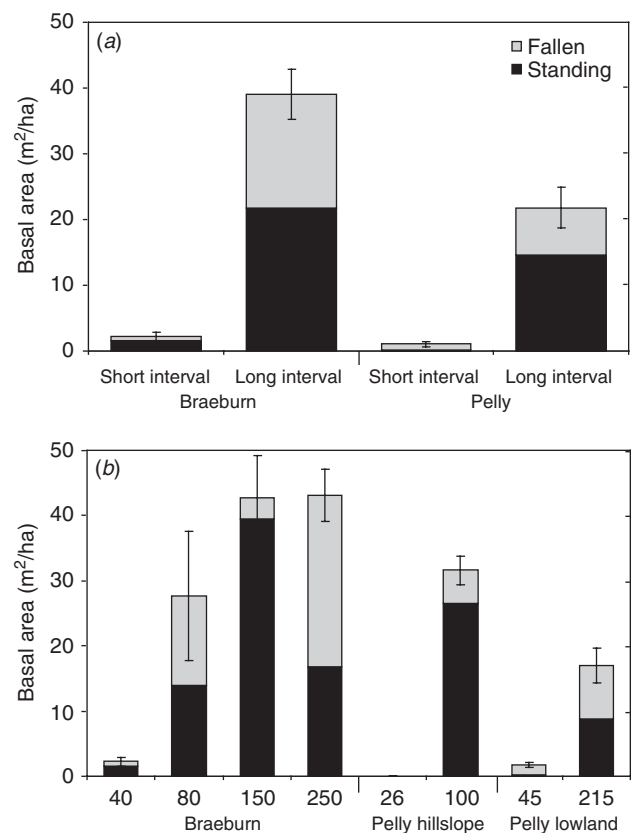


Fig. 2. Mean basal area density (m²/ha) of fallen (grey) and standing (black) deadwood measured after the most recent fire in stands with a short (≤ 50 years) or long (≥ 80 years) fire-free interval at Braeburn and Pelly (a). Sample classes in (b) are further subdivided by stand age at burning (both areas) and hillslope position (Pelly). Error bars indicate s.e. of standing plus fallen basal area.

were interpreted to represent recruitment following stand-replacement fire. An exception to this pattern was apparent at the lowland plots at Pelly, where two peaks were present, one around 210 years and a second around 140 years before the more recent fire. The presence of the second peak suggested the occurrence of an intermediate fire with only partial stand mortality. This set of stands all contained multiple stems from the older age cohort, and dates of the older recruitment pulse were used to represent the interval between stand-replacing fires (Table 1).

Residual plant biomass

Burn zones differed substantially in the amount of residual organic material that remained after the most recent fire. Both sites showed large and significant reductions in the basal area of post-fire deadwood found in stands with short v. long fire-free intervals (Pelly $F = 58.2$, $P < 0.0001$; Braeburn $F = 67.5$, $P < 0.0001$; Fig. 2a). When sample plots were further divided by observed fire intervals or topographic position, residual deadwood remained substantially lower in

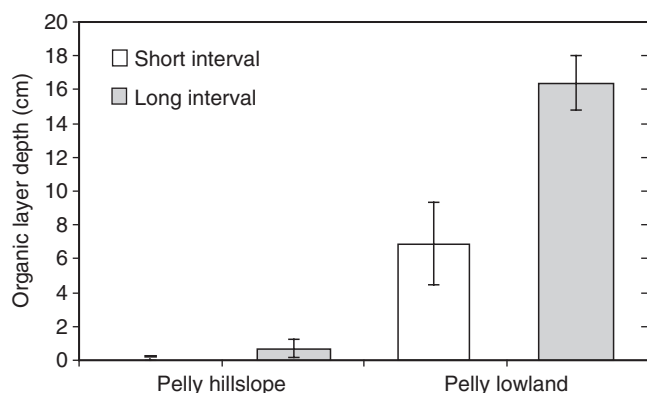


Fig. 3. Post-fire depth (cm) of the soil organic layer (mean \pm s.e.) in stands with a short (white) or long (grey) fire-free interval at hillslope and lowland sites at Pelly.

stands with a fire-free interval under 50 years compared to stands with an interval of 80 years or longer (Fig. 2b). Closely recurring fire events in the short-interval stands resulted in the loss of most of the large-diameter deadwood that would have been generated by an earlier fire in mature forest, as well as consumption of many small-diameter stems recruited during the intervening fire-free period. Because basal area was measured on intact stems and is directly proportional to stem volume (Bond-Lamberty *et al.* 2002a), the observed decrease in basal area (Fig. 2) represents a dramatic reduction in the volume of coarse woody debris present in young-burned stands. All stands showed a mixture of standing and fallen deadwood, without clear differences in the proportions of these classes across site groups.

In addition to fire interval effects on deadwood, sites at Pelly also showed a substantial decrease in the depth of the surface organic layer in young-burned stands (Fig. 3). Organic layers at Pelly were deeper at lowland compared to hillslope sites (block effect $F = 36.85$, $P < 0.0001$), but were significantly lower in stands with a short fire-free interval within each topographic position (interval effect $F = 10.4$, $P = 0.007$; interaction $P > 0.1$). At Braeburn, all but four sites with the longest fire return interval experienced complete combustion of the forest organic layer, and differences in organic layer depths were not tested.

Vegetation composition at Pelly

The plant cover dataset for Pelly consisted of 29 species or groups observed in at least three of 17 sample units. Nine species were deleted from the dataset because they were observed at only one (three species) or two (six species) sites. The most widespread and dominant plants were *Ceratodon*-type moss (cover range 20–75%), *Salix* spp. (0.1–35%), and *Equisetum scirpoides* (scouring rush; 0–30%). Species richness and Shannon's diversity, calculated from non-transformed data and including rare species, were

estimated across the four cover quadrats in each sampled plot and averaged 14.6 and 1.5, respectively.

Plant community composition at Pelly differed significantly between stands that burned after short *v.* long fire-free intervals (MRPP chance-corrected within-group agreement = 0.166, $t = -4.26$, $P = 0.0015$). Between-plot variance was larger within the long-interval group (average distance = 0.49) than the short-interval group (average distance = 0.33), indicating increased heterogeneity of species composition across sites outside the burn overlap zone. Eleven species were identified as being associated with one or the other of the two burn groups (Table 2). Plots with a short fire-free interval generally showed an increased abundance of *Populus tremuloides*, *Salix* spp., *Ledum groenlandicum* (Labrador tea), and plant litter, and the only occurrences of *Shepherdia canadensis* (soapberry) and *Astragalus bodinii* (vetch). Stands that burned after a long fire-free interval were associated with greater cover of *Picea mariana* and *Ceratodon*-type moss, and more frequent observations of *Ribes hudsonianum* (northern black currant), *Calamagrostis canadensis* (Canadian bluejoint grass), and the moss *Aulacomnium palustre*. *P. tremuloides* was the best predictor of group membership for young-burned stands (75% of perfect prediction) and *P. mariana* was the best predictor for mature-burned stands (67% of perfect prediction).

Ordination of the Pelly vegetation data resulted in a three-dimensional solution that captured 88% of the variation in the original dataset. The NMS ordination used 80 iterations to produce a solution with a final stress of 7.9 and instability of 0.00001. Axes 1 and 2 in the ordination represented 37 and 39%, respectively, of the variation in species composition. The arrangement of sample units on these axes showed a clear distinction between plots located inside and outside the burn overlap zone (Fig. 4a). Axis 1 represented the main gradient of fire effects and was positively correlated with the length of the fire-free interval and depth of the organic layer (Fig. 4a; Table 3). Individual species that showed the strongest correlations with Axis 1 were largely the same as those selected in the indicator species analysis, and included *P. tremuloides* ($r = -0.83$), plant litter ($r = 0.82$), *Salix* spp. ($r = -0.80$), and *C. canadensis* ($r = 0.65$). In general, the highest cover values of deciduous trees and shrubs, plant litter, and total vegetation were associated with low values on Axis 1 (Table 3).

Axis 2 in the Pelly ordination represented a gradient in topographical effects, and was negatively correlated with slope and elevation, and positively correlated with relative insolation (Fig. 4a; Table 3). High values on Axis 2 were associated with high total forb cover, and low moss cover (Table 3). Species strongly correlated with Axis 2 were *Epilobium angustifolium* (fireweed; $r = -0.93$) and *E. scirpoides* ($r = 0.87$). A third axis (data not shown) represented 12% of the variation in the dataset and showed moderate correlations with fire return interval (Table 3). This axis was most

Table 2. Indicator species associated with a short or long fire-free interval at the Pelly and Braeburn study areas

Species	No. observations		Indicator value ^A		Indicator <i>P</i> -value ^B
	Short interval	Long interval	Short interval	Long interval	
Pelly study area ^C					
	(<i>n</i> = 8)	(<i>n</i> = 9)			
<i>Populus tremuloides</i>	8	6	74.8		0.012
<i>Picea mariana</i>	6	9		67.1	0.058
<i>Salix</i> spp.	8	9	60.5		0.088
Plant litter	8	9	57.8		0.027
<i>Calamagrostis canadensis</i>	1	6		57.5	0.026
<i>Ribes hudsonianum</i>	0	5		55.6	0.025
<i>Ceratadon</i> -type moss	8	9		54.7	0.028
<i>Aulacomnium palustre</i>	1	5		51.8	0.056
<i>Shepherdia canadensis</i>	4	0	50.0		0.040
<i>Ledum groenlandicum</i>	5	2	49.1		0.092
<i>Astragalus bodinii</i>	3	0	37.5		0.068
Braeburn study area ^D					
	(<i>n</i> = 10)	(<i>n</i> = 8)			
<i>Shepherdia canadensis</i>	9	1	88.9		0.002
<i>Ceratadon</i> -type moss	10	8		70.8	0.001
<i>Populus tremuloides</i>	10	3	71.5		0.016
<i>Epilobium angustifolium</i>	10	8		69.3	0.001
<i>Salix</i> spp.	10	8	68.5		0.013
<i>Linnea borealis</i>	7	4	63.2		0.056
Plant litter	10	8		55.1	0.054
<i>Ledum groenlandicum</i>	0	3		37.5	0.056
<i>Peltigera canina</i>	0	3		37.5	0.056
<i>Polytrichum juniperinum</i>	0	3		37.5	0.058

^AIndicates the percentage of perfect indication for a given group, based on species abundance and frequency.

^BA threshold of $P < 0.1$ was used to identify significant indicators. *P*-values were determined from 1000 Monte Carlo iterations of the original dataset. ^CSpecies present in the sample set but not selected as significant indicators included: *Arctostaphylos rubra*, *Arctostaphylos uva-ursi*, *Aster sibirica*, *Betula papyrifera*, *Calamagrostis lapponica*, *Carex concinna*, *Epilobium angustifolium*, *Equisetum scirpoides*, *Lupinus arcticus*, *Marchantia polymorpha*, *Orthilia secunda*, *Peltigera canina*, *Pinus contorta*, *Polytrichum juniperinum*, *Populus balsamifera*, *Rosa acicularis*, *Solidago simplex*, and *Vaccinium vitis-idaea*. ^DSpecies present in the sample set but not selected as significant indicators included: *Achillea millefolium*, *Calamagrostis lapponica*, *Equisetum scirpoides*, *Orthilia secunda*, *Picea glauca*, *Populus balsamifera*, *Rosa acicularis*, *Solidago simplex*, and *Taraxacum officinalis*.

strongly related to species cover of *Aster borealis* ($r = 0.74$) and *L. groenlandicum* ($r = 0.68$).

Vegetation composition at Braeburn

The vegetation dataset for Braeburn consisted of 19 species or groups observed across three or more of the 18 sample units. Nine species that were observed at only one (six species) or two (three species) sites were deleted from the dataset. The most widespread and dominant plants were *Ceratadon*-type moss (cover range 1–79%), *Salix* spp. (0.1–30%), and *E. angustifolium* (0.1–26%). Species richness and Shannon's diversity averaged 9.8 and 1.4, respectively.

Plant community composition at the Braeburn sites was significantly different between stands that burned after a short v. long fire-free interval (MRPP chance-corrected within-group agreement = 0.347, $t = -8.9$, $P < 0.0001$). Unlike Pelly, between-plot variance in species composition was greater in the burn overlap zone (average distance = 0.44)

compared to outside the zone of recent fire overlap (average distance = 0.185). Ten species were identified as being associated with one or the other of the burn groups (Table 2). Similar to the Pelly site, plots with a short fire-free interval showed increased abundance of *P. tremuloides*, *Salix* spp., and *S. canadensis*, as well as increased cover of *Linnea borealis* (twin-flower). Plots with a longer fire-free interval were associated with increased cover of *E. angustifolium* and *Ceratadon*-type moss, and included the only observations of *L. groenlandicum*, the moss *Polytrichum juniperinum*, and the lichen *Peltigera canina*. Higher amounts of plant litter were also associated with mature-burned stands. *S. canadensis* was the strongest indicator of young-burned stands (89% of perfect indication) and *Ceratadon*-type moss was the best indicator of mature-burned stands (90% of perfect indication).

Ordination of the Braeburn vegetation dataset resulted in a two-dimensional solution that captured an estimated 90% of the variation in the original dataset. The NMS ordination

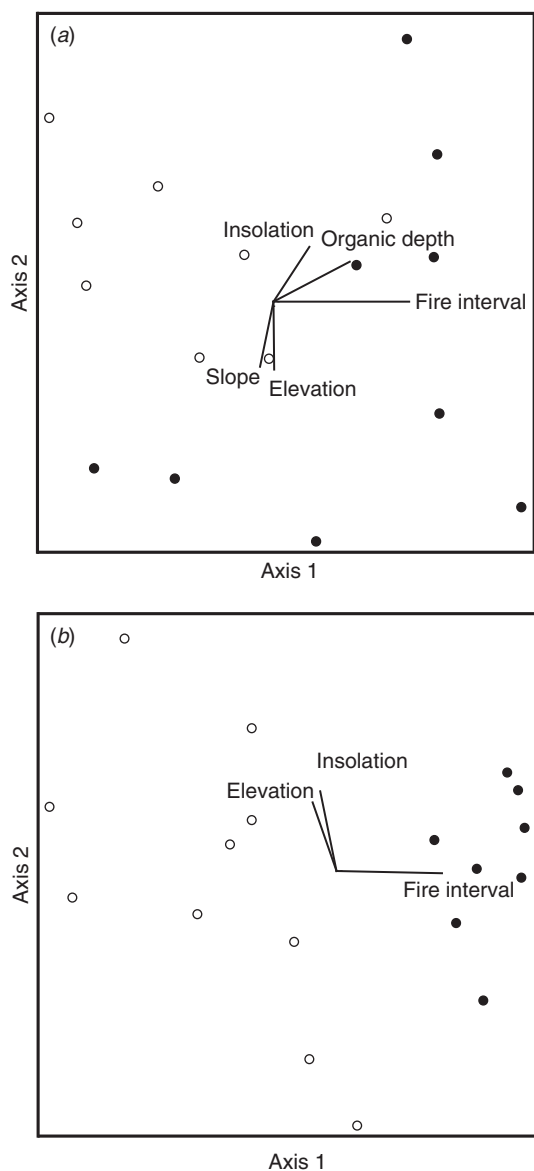


Fig. 4. Joint-plot of non-metric multidimensional scaling ordination of species cover shown with correlated environmental gradients for (a) Pelly, and (b) Braeburn study areas. Scores for sample units in stands with short (○) or long (●) fire-free intervals are plotted on Axes 1 and 2 of the ordination, which represent 37 and 39% of the variation in species cover, respectively. Correlations ($r \geq 0.5$) of environmental variables with ordination axes are indicated by line vectors, where line length is proportional to correlation strength.

used 42 iterations to produce a solution with a final stress of 10.5 and instability of 0.00001. The first axis in the ordination represented 65% of the variation in species composition, with an additional 24% represented by the second orthogonal axis. Plotting of the sample units on Axes 1 and 2 showed a clear distinction between groups with a short v. long fire-free interval (Fig. 4b). Axis 1 in the ordination was strongly correlated with fire return interval (Fig. 4b; Table 3). As would be expected, many of the species selected in the

indicator species analysis for the burn zone groups were correlated with Axis 1, such as *Ceratodon*-type moss ($r = 0.94$), *E. angustifolium* ($r = 0.86$), and *Salix* spp. ($r = -0.64$). High values of Axis 1 were associated with high total plant cover, plant litter, and forb and moss cover. Low values on Axis 1 were associated with higher cover of bare soil and deciduous trees and shrubs (Table 3). Similar to the Pelly dataset, Axis 2 represented a topographical gradient and was positively correlated with elevation and relative insolation (Table 3). The two species most strongly correlated with Axis 2 were *E. scirpoides* ($r = -0.75$) and *Populus balsamifera* (balsam poplar; $r = -0.68$).

Discussion

The present study provides evidence that variations in fire frequency, exemplified by the length of the previous fire-free interval, can have strong effects on patterns of early post-fire community composition and ecosystem pools of residual plant material. Analysis of early successional plant communities showed a clear divergence between sites in adjacent locations that burned after a short (<50 years) v. long (80–250 years) fire-free interval. Within a study area, variations in community composition were more strongly correlated with fire interval than other measured environmental gradients, such as soil texture, relative insolation, and elevation. In the community ordinations, fire interval effects were largely orthogonal to the primary environmental gradients (Fig. 4), supporting the use of burn overlap scars as a ‘natural experiment’ to assess effects of variation in fire return time on regenerating plant communities. In the absence of differences in fire history, we would expect that patterns of plant community composition and residual organic material would be driven by the key environmental gradients identified in the ordinations, such as elevation and insolation. The overriding effects of the preceding fire-free interval apparent in the present study indicate that variations in fire history can be an important factor that interacts with environmental gradients to shape local patterns of plant community structure in boreal forests.

Fire effects on plant communities are hypothesized to be mediated by the interaction between fire regime and plant regeneration or life history strategies (Rowe 1983; Pausas *et al.* 2004). Previous authors have identified disturbance-related plant functional types that differentiate between species on the basis of regeneration strategies, shade tolerance, or other life history traits (Rowe 1983; Lavorel and Garnier 2002; Pausas and Lavorel 2003). These traits are hypothesized to interact with patterns of fire severity and frequency to generate predictable responses of vegetation to disturbance. For example, short fire-free intervals may reduce the frequency of late-successional or slow-maturing species by pre-empting the time needed for propagule accumulation (Jasinski and Payette 2005; Johnstone and Chapin 2006a).

Table 3. Pearson correlation coefficients indicating relations between ordination axes and environmental variables or vegetation functional groups at the Pelly and Braeburn study areas

Stronger correlations ($r > 0.5$) are shown in bold font

Variable	Pelly correlations			Braeburn correlations	
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2
Environmental variables					
Fire interval	0.74	-0.02	-0.47	0.66	-0.09
Slope	-0.23	-0.51	0.34	-0.13	0.25
Elevation	-0.09	-0.52	0.46	-0.32	0.53
Distance to unburned	-0.16	0.22	0.36	-0.24	-0.06
Insolation index	0.56	0.40	-0.29	-0.26	0.57
Organic layer depth	0.38	0.47	-0.29	0.36	-0.28
Soil texture rank	-0.45	-0.34	0.29	0.18	-0.12
Plant functional types					
Deciduous trees/shrubs	-0.77	0.28	-0.40	-0.56	0.43
Evergreen trees/shrubs	0.36	-0.12	-0.11	-0.34	-0.22
Forbs	0.03	0.67	0.26	0.90	-0.03
Graminoids	0.48	-0.27	0.02	0.31	-0.13
Lichen	-0.57	0.00	-0.28	0.35	-0.15
Moss	0.52	-0.62	-0.01	0.86	-0.07
Plant litter	-0.80	-0.03	-0.23	0.51	0.34
Total vegetation cover	-0.55	-0.18	-0.41	0.84	0.14
Bare soil	0.26	0.28	0.02	-0.89	-0.15

High levels of surface burn severity that reduce propagule banks in the soil organic layer and create a favorable mineral seedbed have been shown to favor seed-dispersing species over species regenerating from the seedbank (Schimmel and Granström 1996; Wang and Kemball 2005). Species that regenerate by resprouting are predicted to be favored by fire return intervals that do not exceed the lifespan of the species (Rowe 1983; Suffling 1995), and fire severities that are sufficient to remove aboveground biomass but not kill belowground buds (Rowe 1983; Schimmel and Granström 1996).

Life history traits of the species identified as indicators of short or long fire-free intervals in the present study show some support for the application of functional types to predicting plant responses to variations in fire return interval (Table 4). For example, four of six species identified as indicators of short fire-free intervals were woody shrubs that regenerate by resprouting from roots in mineral soil. Similarly, several species that regenerate from roots in organic soil were identified as indicators of mature-burned stands, presumably in response to increased organic layer depths in those stands. Both fire frequency and severity (particularly organic layer consumption) are likely to interact with plant traits to influence the post-fire regeneration response. The successional status and habitat preferences of a species will influence whether it is likely to be present prior to a fire, whereas survival of belowground buds will be influenced by the depth and combustion of the organic layer (Schimmel and Granström 1996). In the present study, several early- to

mid-successional species with resprouting ability, such as *Populus tremuloides*, *Salix* spp., and *Shepherdia canadensis*, were most abundant in short-interval stands, where their roots were located in mineral or dense humic soil exposed after the recent previous fire. Other resprouting species, such as *Ledum groenlandicum*, *Ribes hudsonianum*, and *Calamagrostis canadensis*, showed an association with stands burned after a long fire-free interval. These species are not specifically late successional, but are generally found in more mesic conditions common in late successional stands and may have been rooted in surficial organic layers vulnerable to burning. Interestingly, *L. groenlandicum* was identified as an indicator of a short fire-free interval at Pelly and a long fire-free interval at Braeburn. This pattern may be related to a preference for more open, sunny habitat on the relatively cool organic soils at Pelly, combined with a low capacity to regenerate in the absence of a residual organic layer in the young-burned sites at Braeburn.

Modes of seed regeneration showed less differentiation between the two plant indicator groups, although species with wind-dispersed propagules, including several mosses, appear to have been more common in mature-burned stands. This pattern contrasts with an expected increase of seed-dispersing species on severely burned soils (Wang and Kemball 2005; Johnstone and Chapin 2006b) that were more common after a short fire-free interval. However, colonizing species in the present study may have been sensitive to the apparently more severe microclimate conditions found in young-burned stands, associated with a decrease in

Table 4. Plant regeneration and life history traits for species identified as indicators of short or long fire-free intervals, following the hierarchical framework presented by Pausas and Lavorel (2003)

Information on regeneration and life history traits were obtained from Beaudry *et al.* (1999), the Fire Effects Information Database (FEIS 2006) and personal observations. Common modes of regeneration for a species are indicated as follows: X = dominant mode of regeneration, x = alternative mode of regeneration, ? = suspected but unconfirmed mode of regeneration

Species	Fire interval group ^A	Regeneration traits			Dispersal capacity Wind-dispersed propagules	Life history traits	
		Individual persistence Resprout: mineral soil	Resprout: organic soil	Propagule persistence Seed/spore bank		Competitive capacity Shade tolerance	Succession stage ^B
<i>Aulacomnium palustre</i>	Long			?	X	Low	Later
<i>Calamagrostis canadensis</i>	Long	x	X		x	Variable	Early
<i>Epilobium angustifolium</i>	Long		X		X	Low	Early
<i>Peltigera canina</i>	Long			?	X	Variable	Mid?
<i>Picea mariana</i>	Long			X (aerial)		Moderate	Late
<i>Ceratodon-type moss</i>	Long				X	Low	Early
<i>Polytrichum juniperinum</i>	Long			?	X	Variable	Mid
<i>Ribes hudsonianum</i>	Long		X	x		Moderate	Late
<i>Ledum groenlandicum</i>	Long or short		X		x	Variable	All
<i>Astragalus bodinii</i>	Short			?	?	Low	Early
<i>Linnaea borealis</i>	Short	X			x	Variable	All
<i>Populus tremuloides</i>	Short	X			x	Low	Early-mid
<i>Salix</i> spp.	Short	X			X	Low-moderate	Early
<i>Shepherdia canadensis</i>	Short	X				Low-moderate	Early-mid

^AThe indicator is associated with: short (<50 years) or long (80–250 years) fire-free interval. ^BStage when species reaches maximum relative abundance (early, mid, or late). Uncertainty in assigning a successional stage is indicated by a question mark.

shade and shelter provided by deadwood (J. F. Johnstone, personal observation). Few responses of seedbank species were detected in the current study. However, the lower abundance of *Picea mariana* in stands with a short fire-free interval is likely associated with insufficient time for this species to develop a large seed reserve in serotinous cones (Johnstone and Chapin 2006a). In general, the plant responses observed here are consistent with forest modeling studies that predict an increase in resprouting deciduous trees and a decrease in serotinous conifers dependent on aerial seedbanks with increased fire frequency (Suffling 1995; de Groot *et al.* 2003; McIntire *et al.* 2005).

Plant species responses to altered fire regimes also have implications for ecosystem function (Chapin 2003). Increases in deciduous plant cover associated with a shorter fire interval (Table 3) may influence patterns of nutrient cycling, as this plant growth form generally exhibits high rates of litter production and quality, relative growth, and nutrient uptake (Chapin *et al.* 1996). In addition, changes in the abundance of woody species are likely to affect the habitat quality of species such as moose (*Alces alces*) or snowshoe hare (*Lepus americanus*) that depend heavily on these species for food (Bryant and Chapin 1986). Site-specific variations in the cover of plant functional types with respect to fire interval can be linked to local environmental conditions and also have implications for local ecosystem function. For example, shorter fire intervals in the context of the cool and moist conditions

at the Pelly sites appear to have had positive overall effects on plant productivity, as indicated by total vegetation cover and vascular plant litter (Table 3). In contrast, shorter fire intervals at the warmer and drier sites in the Braeburn area were associated with reduced plant productivity, and appear to have led to decreased establishment of herbaceous plants and cryptogams. Thus, although functional types may provide an initial hypothesis of fire effects on plant communities, local site context remains an important mediator of functional responses to fire and the resulting ecosystem consequences.

In addition to responses of live vegetation, results from the present study demonstrate a strong effect of a decrease in the fire-free interval on the retention of dead plant material across fire cycles. Stand-replacing fires in mature boreal forests generally produce large amounts of dead woody material, as trees are killed but stems are not consumed. Because decomposition rates are slow in northern forests, fire-killed wood can persist for many decades before it decomposes (Bond-Lamberty *et al.* 2002b). Standing wood is likely to decompose more slowly than fallen wood, and in Yukon forests, standing deadwood originating in a previous fire is often preserved in mature forests for well over a century (J. F. Johnstone, personal observation). Proportions of standing and fallen deadwood reported here for stands with a long fire-free interval indicate that fires in mature stands produce a mixture of standing and fallen wood that is likely to persist for long periods. Under a typical fire cycle, subsequent fires

in a mature forest burn away existing deadwood and generate a new crop of fire-killed stems. A short fire interval alters this cycle by consuming the previous deadwood load without replacing it, except for the presence of a few small stems or fire-charred stumps. The general absence of coarse woody debris following a short fire interval is likely to alter wildlife habitat quality (where deadwood may provide critical habitat for some species and form a structural impedance for others; e.g. Turner *et al.* 2003), ecosystem carbon storage (Amiro *et al.* 2001), and delayed colonization of plants dependent on establishment on rotting wood (e.g. Simard *et al.* 1998). Reductions in the depth of the soil organic layer that are associated with a short fire interval may have similar implications for animal habitat, carbon storage, and plant establishment.

What does the present study tell us about potential effects of increased fire frequency on boreal forests? At the most general level, the data presented here indicate that boreal plant communities are sensitive to large variations in the length of the fire-free interval, and that shorter fire intervals are likely to alter both the composition and structure of forest ecosystems. Vegetation responses are at least partially predictable from plant regeneration and life history characters, but need to be taken in context of local site conditions and available flora (e.g. Pausas *et al.* 2004). Deciduous woody plants that resprout from roots in the mineral soil appear to be the group most likely to be favored by shorter fire return intervals in the boreal forest. Increases in fire frequency may have the strongest direct effects on the accumulation and residence time of dead biomass pools such as fire-killed wood and the surface organic layer. Other effects of altered fire frequency on ecosystem processes, such as aboveground plant productivity, may vary in direction and magnitude depending on local environmental conditions.

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