Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec, Canada¹

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Abstract: The effects of fire severity and initial post-fire tree composition on long-term stand structural development were investigated in the *Picea mariana*–feathermoss bioclimatic domain of northwestern Québec. Paleoecological methods were used to categorize the severity of the last fire (high or low) and initial tree composition (*Picea mariana versus Pinus banksiana*). Changes in stand structure were evaluated by quantifying stand structural attributes along three chronosequences. Except for accelerating stand break-up, the post-fire presence of *P. banksiana* (which is eventually replaced by *P. mariana*) had little effect on stand structural development. Fire severity had significant effects on the evolution of stand structural attributes, with low severity fires being particularly detrimental for stand productivity. Stands colonizing low severity fires were characterized by low post-fire tree recruitment and growth and remained open throughout succession. In contrast, after high severity fires, dense productive stands were rapidly established regardless of fire composition and gradually became open as succession proceeded. These results suggest that in the prolonged absence of fire, the different stand structural development pathways gradually converge regardless of the severity or initial composition. We argue that stand structural diversity within the coniferous boreal forest is a result of the severity of the last fire and of processes operating at the stand scale in the absence of fire.

Keywords: black spruce, chronosequence, Clay Belt, forest succession, jack pine, natural disturbances, *Pinus banksiana, Picea mariana,* residual soil organic matter, stand structure.

Résumé : Les effets de la sévérité du dernier feu et de la composition forestière initiale post-incendie sur le développement à long terme de la structure des peuplements ont été étudiés dans le domaine de la pessière noire à mousses de l'Ouest du Québec. Des méthodes paléoécologiques ont été utilisées afin de catégoriser la sévérité du dernier feu (forte *versus* faible) et la composition initiale (*Picea mariana versus Pinus banksiana*). Les changements dans la structure des peuplements ont été évalués en quantifiant les attributs de structure le long de trois chronoséquences. Si la présence après feu de *Pinus banksiana* (qui est éventuellement remplacé par *P. mariana*) a accéléré le bris des peuplements, elle a eu peu d'effets sur l'évolution de leur structure. Cependant, la sévérité du dernier feu a significativement influencé l'évolution des attributs structuraux des peuplements, les feux peu sévères étant particulièrement néfastes pour la productivité des peuplements. Les peuplements qui tirent leur origine d'un brûlis peu sévère sont caractérisés par une faible régénération, une faible croissance après feu et une canopée qui est maintenue ouverte tout au long de la succession. Après un feu sévère, peu importe la composition après feu, on observe au contraire une installation rapide d'un peuplement dense et productif qui s'ouvre graduellement en l'absence prolongée du feu. Ces résultats suggèrent donc que les différentes trajectoires de développement de la structure des peuplements convergent graduellement, et cela peu importe la sévérité du dernier feu ou la composition initiale. Nous avançons que la diversité dans la structure des peuplements au sein de la forêt boréale coniférienne est fonction de la sévérité du dernier feu et de processus opérant en l'absence du feu.

Mots-clés : ceinture d'argile, chronoséquence, épinette noire, matière organique résiduelle du sol, perturbations naturelles, *Picea mariana*, pin gris, *Pinus banksiana*, structure des peuplements, succession forestière.

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Introduction

Maintaining the diversity of forest structure types at the landscape scale is thought to be crucial for the conservation of species diversity (Lindenmayer & Franklin, 2002). Therefore, a better understanding of the factors influencing the structural development of forests is essential to achieve sustainable forest management. In boreal regions that are under the influence of short fire cycles (< 100 y), changes in tree composition or stand structure are rarely observed between two fire events (Johnson, 1992). In contrast, in the eastern boreal forest of North America, where the cool, humid maritime climate currently induces much longer fire cycles (> 300 y; Foster, 1985; Bergeron *et al.*, 2004a), forest succession and stand structural changes can occur (Groot & Horton, 1994; Bergeron, 2000; Harper *et al.*, 2002; 2005).

In the boreal forest, even under similar abiotic conditions, multiple successional trajectories in overstory tree composition can co-occur within a landscape (Harper *et al.*, 2002). This co-occurrence can be strongly linked to site-specific historical fire regimes (Payette, 1992; Johnstone & Chapin, 2006a). Short fire intervals tend to favour tree species that reach sexual maturity quickly, such as *Pinus banksiana*, whereas longer fire cycles tend to favour longer-lived species or species that are able to regenerate in the absence of fire such as *Picea mariana*. Long fire cycles also result in a high proportion of low severity fires that do not fully consume the thick forest floor that has accumulated during the long fire-free intervals (Foster, 1985; Simon & Schwab, 2005).

Studies undertaken in the Clay Belt of Ontario and Québec have shown that virtually all stands that have not burned in 200 y are open forests with discontinuous canopies (Boudreault et al., 2002; Harper et al., 2002). However, these studies have also demonstrated that the structural variability among stands is very high 50 y after fire, with only about half of the stands exhibiting > 60% canopy cover (Harper et al., 2002; Lecomte & Bergeron, 2005). These results suggest a high among-stand diversity in early post-fire stand structural development. In this study, we investigate the influence of fire severity and initial tree composition on stand structural development in the Clay Belt of Ontario and Québec. We refer to fire severity exclusively as the effects of fire on the accumulated soil organic matter (quantity of duff burned/quantity of duff unburned; sensu Miyanishi & Johnson, 2002) as opposed to the effects of fire on the canopy (% trees killed; sensu Greene et al., 2004).

We suggest that among-stand structural diversity in eastern boreal landscapes can be explained by processes operating at the stand scale in the absence of fire and also by initial post-fire stand conditions. Since mixed stands are composed of two species, with one shade tolerant and long lived (*Picea mariana*) and the other shade intolerant and short lived (*Pinus banksiana*), we hypothesize that the presence of *P. banksiana* will be associated with a two-layered vertical distribution of stems, whereas in the pure *P. mariana* stands, single-layered height structures will prevail. Furthermore, given that *P. banksiana* is a faster growing and shorter lived species than *P. mariana*, we hypothesize that the co-dominance of *P. banksiana* will result in a higher stand productivity but a premature and quicker rate of stand break-up. Although few studies have examined the longterm effects of fire severity on stand structural development, short-term studies indicate that post-fire tree germination and subsequent growth are negatively impacted by an increase in residual duff depth (Chrosciewicz, 1976; Zasada *et al.*, 1983; 1987; Charron & Greene, 2002). We thus hypothesize that stands evolving after low severity fires will be more open and will exhibit reduced tree productivity as compared to stands established after high severity fires.

Methods

STUDY AREA

The study area $(49^{\circ}00' - 50^{\circ}00' \text{ N}, 78^{\circ}30' - 80^{\circ}00' \text{ W})$ is located in the eastern North American coniferous boreal forest and is within the Picea mariana-feathermoss bioclimatic domain (Robitaille & Saucier, 1998). This area is on the Clay Belt of northeastern Ontario and northwestern Québec, a physiographic unit composed mostly of clay deposits left by pro-glacial Lake Ojibway (Veillette, 1994). While a few rocky outcrops are scattered across the landscape, the topography is generally flat. Average annual temperature (1971-2000) recorded at the closest weather station to the north (Matagami, 49° 46' N, 77° 49' W) and to the south (La Sarre, 48° 46' N, 79° 13' W) are respectively -0.7 and 0.7 °C with an average of 906 and 890 mm of precipitation annually (Environment Canada, 2005). The area is dominated by P. mariana, which tends to form monospecific, structurally diverse stands (Boudreault et al., 2002; Harper et al., 2002; 2005). Occasional deciduous- and pine-dominated stands are dispersed across the landscape. Fire is the main disturbance that terminates and initiates secondary succession. Fire cycle length has increased from 101 y before 1850 to 398 y since 1920; mean stand age is 148 y (Bergeron et al., 2004b). The spruce budworm (Choristoneura fumiferana) has a small impact in this area compared to regions further east and south. Both historical patterns of budworm defoliation (Boulet et al., 1996; Gray, Régnière & Boulet, 2000) and tree-ring reconstructions (M. Simard, N. Lecomte & Y. Bergeron, unpubl. data) show that spruce budworm is a negligible disturbance factor in these black spruce-dominated forests.

CHRONOSEQUENCE DATASET

SITE SELECTION AND TREE SAMPLING

During the summers of 2000–2002, using a stand initiation map developed for the northern part of the Clay Belt (Bergeron *et al.*, 2004b), we visited all the burned areas that were located < 2 km from a road. In all, 43 distinct fires of different age were sampled. In each fire, the density and composition of the post-fire tree cohort (*P. mariana versus P. banksiana*) was estimated based on live and/or dead tree composition. Within each fire, at least one representative $10- \times 10$ -m quadrat was placed for detailed dendroecological analysis. When variable post-fire density or composition was observed within the same fire, several quadrats were sampled. As a result, a total of 48 sites were sampled within 43 distinct fires. Each site had to be on fine-textured mineral deposits, on a slight incline, and free of any sign of anthropogenic disturbance. In each quadrat, for each tree species, the height and DBH (diameter at breast height) of all live and dead stems > 2 m in height were measured. Dead trees buried under the organic matter were exhumed, measured, and identified to species based on bark, branching, and wood morphology. Origin of dead stems (pre- or postfire) was assessed with the presence/absence of charcoal. Saplings (trees < 2 m in height) were sampled in a randomly selected sub-quadrat. As we attempted to sample roughly the same number of saplings as trees, the size of this subquadrat varied with the density of trees and saplings.

STAND AGE DETERMINATION

Stand age (fire year) for the youngest stands (< 100 y old) was determined from a stand initiation map (Bergeron et al., 2004b) and was validated by counting rings from cross-sections taken at the base of dominant trees (n = 3)to 20). In older stands, stand age was obtained by carefully dating cross-sections taken at the base of live and dead dominant trees (n = 3 to 20). Cross-sections were finely sanded and crossdated using a frost-ring chronology, under a dissecting microscope at 40x magnification. Crossdating was verified using the program COFECHA (Holmes, 1983). In stands where the oldest tree was older than 200 y, and where no fire scars or pioneer species (P. banksiana) were found, samples of carbonized plant remains found in the uppermost charcoal layer in the soil humus were sent to IsoTrace Laboratory (Toronto, Ontario) for AMS (accelerator mass spectrometry) radiocarbon dating. The radiocarbon years were calibrated in calendar years using INTCAL98 (Stuiver et al., 1998; Appendix I). Radiocarbon dates from a parallel study on two of the old stands (Cvr et al., 2005) are also shown (Appendix I). In this study, however, the authors dated the organic matter located just above the uppermost charcoal layer within the humus profile, which may account for the slightly younger dates obtained as compared to our radiocarbon dates from carbonized material. Nonetheless, since in both cases the age of humus predates the age of the oldest tree present in the stand, we have used the radiocarbon dates from carbonized plant remains.

Soil texture and topography

Although the mineral soil texture was hand-checked in situ, two mineral soil samples were taken at the centre of each quadrat, one at the surface and another are at a depth of 1 m. Soil texture was then determined with the Bouyoucos hydrometer method (McKeague, 1976). The mineral soil topography, which may be masked by peat accumulation, was assessed with a theodolite at each site along four 50-m transects starting at the centre of the quadrat and passing through separate corners. Significance of the slopes was assessed with simple linear regressions, and non-significant slopes (P > 0.05) were given a value of zero. If the slopes of transects going in opposite directions were of opposite signs, or if one or both of the slopes was null, we calculated the slope of the two transects combined (*i.e.*, one transect of 100 m). If the slopes were of the same sign, we summed these slopes to obtain a negative slope value (depression) or positive value (mound or incline) for the 100-m transect. The slope index used in this study is the mean of the slopes of the two 100-m transects (Appendix I).

FIRE SEVERITY

At each stand, the soil burn severity of the last fire was qualified as being either high (HS) or low (LS) based on the quantity of duff that was not consumed by the last fire (*i.e.*, the residual organic matter). Ideally, soil burn severity is quantified as the amount of organic matter consumed (sensu Miyanishi & Johnson, 2002). However, as it is impossible to know how much organic matter was present in the pre-fire stand, we have chosen to qualify fire severity as the amount of organic matter not consumed by the fire (sensu Nguyen-Xuan et al., 2000). The residual organic matter was measured with two methods: first, by detailed laboratory analysis of a few humus profiles per site and, second, by in situ observations of charcoal layers in numerous pits and trenches dug into the humus layer. At each site, between two and four, $10 - \times 10$ -cm monoliths of the organic layer were cut down to the mineral soil with a Wardenaar sampler. The monoliths were frozen and then sliced into 1-cm-thick sections. Subsamples of 50 cm³ were defloculated in a 2% NaOH solution for 24 h at 60 °C before a gentle manual water spray was used to sieve the samples through a 2 mm mesh. Samples were then bleached in a 10-20% HCl solution and identified microscopically at 40x magnification. The percentage of mineral soil was estimated, and charcoal fragments were extracted, dried, and then weighed. The mineral soil/organic matter interface for each monolith was established where the mineral soil represented less than 25% of the particles retained in the 2-mm mesh. The depth of the residual organic matter was calculated as the number of 1-cm-thick layers above the mineral soil but under the last charcoal layer deposited.

In the younger black spruce sites (< 150 y), 2.25-m trenches were dug about 20 cm into the mineral soil. At every 15 cm along the trenches, the depth of the uppermost charcoal layer and of the mineral soil were noted so that the thickness of the residual organic matter could be calculated. Additionally, in each *P. banksiana* and *P. mariana* stand, respectively 10 and 15, 25- \times 25-cm pits were dug into the mineral soil every 2 m along two or three randomly chosen 10-m transects. For each pit, the same measurements as for the trenches were done.

SITE CLASSIFICATION

The substitution of time by space (chronosequence approach) to understand long-term stand dynamics has been widely used but also extensively criticized. The main potential drawback of using a chronosequence approach is the possibility of selecting stands that differ with respect to their biophysical site characteristics and/or initial conditions after the stand-replacing disturbance. We carefully selected and characterized the biophysical conditions of stands to reduce variability in surficial deposit and slope (Appendix I). Furthermore, we are confident that the paleological methods used in this study (exhumation and identification of dead wood, careful quantification of charcoal found in numerous organic matter profiles per site) have allowed us to obtain a good estimation of initial stand conditions (depth of residual organic matter and initial tree composition). The tree composition and residual organic matter data showed a strong bimodal distribution (Appendix I). Because of this, we classified all stands into one of two categories of stand composition (dominance by *P. banksiana* or *P. mariana*, based on the relative basal area of living and dead trees) and into one of two categories of fire severity (high severity fire = thin residual organic matter layer; low severity fire = thick residual organic matter layer). Because no stands that were dominated by *P. banksiana* showed a thick residual organic matter layer (= low severity fire), this classification resulted in three distinct chronosequences: *P. mariana* established after a low severity fire, *P. mariana* established after a high severity fire, and *P. banksiana* established after a high severity fire.

According to the basal area of live and dead trees, 19 of the 48 sampled stands were dominated by *Pinus banksiana* after fire (Appendix I). For the remaining 29 sites, as no significant traces of any other tree species except for *Picea mariana* were found among the deadwood or among macro-remains within forest floor profiles described above (Appendix I), these sites were all classified as being dominated by *P. mariana* after fire.

Sites were classified as originating either from a high severity (HS) or low severity (LS) fire based on the average thickness of the residual organic matter obtained from both the monoliths and the pits/trenches. A study of seven burns in the boreal forest has demonstrated that coniferous post-fire seed germination was significantly impacted when residual organic matter approached 5 cm (Greene, 2004). We used this ecologically significant threshold (4 cm) to classify soil burn severity. Among the stands sampled, 11 of the 29 *P. mariana* stands were established after the passage of a LS fire (Appendix I).

Statistical analyses

To obtain an integrated representation of the forest structure and to evaluate the factors responsible for the variation in forest structure, a canonical correspondence analysis (CCA) was computed using the program CANOCO Version 4 (ter Braak & Smilauer, 1999). The "pseudo-species" variables used were the relative number of stems in five height classes of live trees (2–4 m, 4–8 m, 8–12 m, 12–16 m, and > 16 m) and three DBH classes of dead trees (< 10 cm, 10–15 cm, and > 15 cm). The continuous environmental variables (mineral soil clay content, slope index, and time since fire [TSF]) and categorical variables (fire severity and initial stand composition) were loaded by forward selection. Significance of each variable was computed using a Monte Carlo test ($\alpha = 0.05$).

We used regression analyses to assess the changes in forest structure with TSF and to test the effects of fire severity and initial composition. The following stand structural attributes were used: 1) basal area of live trees (height > 2 m), 2) basal area of large live trees (DBH > 10 cm), 3) density of saplings (height < 2 m), 4) basal area of large dead trees (DBH > 10 cm), 5) mean tree height (stems > 2 m), and 6) coefficient of variation of tree height (stems > 2 m). Since the CCA showed that slope index and soil texture were not significant in explaining stand structure, we have not included them in these analyses. As the chronosequences, based on initial composition and fire severity, spanned different time scales (*P. banksiana* high severity: 45–229 y, P. mariana low severity: 38-169 y, and P. mariana high severity: 51-2355 y), we have analyzed the data at two distinct time scales: medium term (< 250 y) and long term (> 250 y). The medium-term scale (< 250 y) was used to assess the effects of both fire severity and initial composition on stand structural development, while the long-term time scale (> 250 y) allowed us to evaluate how P. mariana stands established after high severity fires evolved in the extended absence of fire. Medium-term effects were assessed with a General Linear Model design (PROC GLM, SAS Institute, 2000) with a combination of a continuous predictor variable (TSF) and categorical predictor variables (initial stand composition and fire severity). When predictor variables or their interactions were non-significant (P > 0.05) they were removed from the models. The quantitative effects of the extended absence of fire (> 250 y) on structural development were assessed with simple linear regression following appropriate transformation of the independent variable (TSF). The significance level ($\alpha = 0.05$) for both medium-term and long-term regressions was lowered to $\alpha = 0.025$ for the variables basal area of live trees and basal area of large live trees as these datasets were partly similar.

To assess if fire severity and initial composition influenced post-fire stand density and self-thinning, an analysis of variance was computed using only the younger stands (< 100 y). Since the two-way ANOVA design was incomplete (*i.e.*, no *P. banksiana* stands originating from a low severity fire), the specific effect of each independent variable was tested using planned comparisons. As previous work in the boreal forest has demonstrated that coniferous post-fire regeneration is limited to the first 5-10 y following fire (Gutsell & Johnson, 2002; Johnstone et al., 2004), we estimated initial post-fire density as the total number of stems (live and dead) > 2 m in height and the degree of self-thinning as the number of small dead stems (DBH < 10 cm). Among the 48 chronosequence stands, there were four pairs of young (< 100 y) *P. mariana* stands, with each pair originating from the same fire but differing with respect to the severity of the last fire. These pairs were used to further test the effects of fire severity on initial stand densities and productivity using paired *t*-tests. For this comparison, three productivity variables were computed based on the mean height of the three, five, or 10 tallest *P. mariana* stems.

Results

ORDINATION TRENDS

The canonical correspondence analysis showed that 1) the canonical axes 1 and 2 explained respectively 10% and 8% of the variance in stand structural characteristics (data not shown) and 2) fire severity explained 8% of the variation, time since fire 5%, and initial composition 4% (Table I). The environmental variables mineral soil clay content and slope index did not significantly ($\alpha = 0.05$) explain any more of the among-stand structural variability.

The ordination diagram showed that 1) fire severity was negatively correlated with axis 1 and positively correlated with axis 2, 2) time since fire was positively correlated with both axes, and 3) initial stand composition was positively correlated with axis 2 (Figure 1a). The position

TABLE I. Summary statistics of the canonical correspondence analysis (CCA) using the chronosequence dataset with a forward selection of environmental variables. Boldface *P*-values are significant at the 0.05 level.

Variable	% of variance explained	F	Р	
Fire severity	8	5.66	0.005	
Time since fire	5	3.07	0.015	
Initial tree composition	4	3.21	0.02	
Mineral soil texture	2	1.09	0.32	
Slope index	1	0.67	0.60	

of the pseudo-species centroids indicated that high proportions of large live stems (L4 and L5) and small dead stems (D1) were characteristic of stands established after high severity (HS) fires. Small live stems (L1, L2), positioned on the opposite side of the severity centroid, were prevalent in stands originating from low severity (LS) fires. The position of large dead stems (D2 and D3) suggested that they were associated with old stands originating from HS fires and/or a post-fire dominance of *Pinus banksiana*. Finally, the position of intermediate live stems (L3) indicated that they were important in young stands regardless of fire severity.

The successional vectors, which connect the mean ordination score of each age-class from youngest to oldest for each chronosequence, revealed two major trends. First, the length of the HS fire vectors connecting the youngest age class (< 100 y) to the intermediate age class (100–200 y) suggested that the post-fire dominance of *P. banksiana*, while not affecting the direction of structural development, may have accelerated the rate of succession (compare solid and dashed vectors in Figure 1b). Second, while fire severity induced diverging short-term structural development pathways, the prolonged absence of fire brought about a convergence of *Picea mariana* stand structure regardless of fire severity (compare dashed and dotted vectors in Figure 1b).

MEDIUM-TERM EFFECTS OF STAND COMPOSITION AND FIRE SEVERITY

The presence of *Pinus banksiana* after HS fires did not affect post-fire stand densities (7600 versus 9517 stems·ha⁻¹; P = 0.20) or the degree of self-thinning as measured by the number of small dead stems (2329 versus 3625 stems·ha⁻¹; P = 0.06; data not shown otherwise). On the other hand, *Picea mariana* stands established after LS fires had significantly lower initial stand densities (6071 versus 9517 stems·ha⁻¹; P = 0.03) and experienced less self-thinning (328 versus 3625 dead stems·ha⁻¹; P < 0.0001; data not shown otherwise) than HS fires.

The post-fire dominance of *P. banksiana* had little effect on the evolution of forest structure (Table II). After HS fires, stand basal area and mean stem height decreased as the variability in stem height increased with the continued absence of fire (Figure 2). Canopy closure, as measured by the number of large live stems, peaked at 103 y and subsequently dropped significantly (Figure 2b), while the density of saplings increased (Figure 2c). Since the basal area of large dead stems increased at a faster rate when *P. banksiana* dominated the initial composition (Figure 2d), the post-fire dominance of *P. banksiana* appeared to accelerate stand break-up. In contrast, stands originating from LS fires initially showed low basal area of live trees and low mean tree height that both increased with time. Although LS fire



FIGURE 1. Canonical correspondence analysis of stand structure (relative abundance of stems represented by eight pseudo-species based on status and stem size classes) using the chronosequence dataset. a) Pseudo-species (closed circles) and environmental variables (open squares for categorical variables, vector for the continuous variable). b) Successional vectors connecting the mean value of each age-class (<100 y, 100–200 y, and > 200 y), from the youngest to the oldest, in the three chronosequences (PBA, *Pinus banksiana*; PMA, *Picea mariana*; HS, high severity fire; LS, low severity fire). Pseudo-species codes for live stems are L1 (height 2–4 m), L2 (4–8 m), L3 (8–12 m), L4 (12–16 m), and L5 (> 16 m) and for dead stems, D1 (DBH < 10 cm), D2 (10–15 cm), and D3 (> 15 cm). Environmental variables are as follows: TSF, time since last fire; SEV, centroid of stands originating from a high severity fire; COMP, centroid of *Pinus banksiana*-dominated stands.

stands showed lower basal area (Figures 2a & b), fire severity did not significantly affect stand break-up as measured by the number of large dead stems (Table II; Figure 2d). While fire severity had a significant short-term effect on forest structural development (Table II; Figure 2), the different structural development pathways caused by fire severity converged after 150-200 y (Figure 2).

Stand height development after HS fires was characterized by a rapid establishment of a dense stand dominated by tall stems, which gradually evolved into an open stand dominated by short stems (Figure 3). There was no difference between the mean height structure of *P. banksiana* and *P. mariana* stands originating from HS fires (Kolmogorov-Smirnov two-sided test, $\alpha = 0.05$). In contrast, stands estab-

Variable	Source	F	Р
Basal area, live trees	Initial composition (COMP)	-	ns
$R^2 = 0.58$	Fire severity (SEV)	25.15	< 0.0001
P < 0.0001	Time since fire (TSF)	2.81	0.1019
	COMP * TSF	_	ns
	SEV * TSF	7.67	0.0086
	TSF * TSF	-	ns
Basal area, large live trees	Initial composition (COMP)	_	ns
$R^2 = 0.54$	Fire severity (SEV)	30.89	< 0.0001
P < 0.0001	Time since fire (TSF)	7.73	0.0084
	COMP * TSF	-	ns
	SEV * TSF	-	ns
	TSF * TSF	11.77	0.0015
Basal area, large dead trees	Initial composition (COMP)	0.74	0.3946
$R^2 = 0.51$	Fire severity (SEV)	-	ns
<i>P</i> < 0.0001	Time since fire (TSF)	72.83	< 0.0001
	COMP * TSF	8.44	0.0061
	SEV * TSF	-	ns
	TSF * TSF	-	ns
Density, saplings	Initial composition (COMP)	-	ns
$R^2 = 0.28$	Fire severity (SEV)	9.18	0.0044
P = 0.0058	Time since fire (TSF)	0.34	0.5624
	COMP * TSF	-	ns
	SEV * TSF	6.09	0.0182
	TSF * TSF	-	ns
Mean tree height	Initial composition (COMP)	-	ns
$R^2 = 0.45$	Fire severity (SEV)	19.81	< 0.0001
<i>P</i> < 0.0001	Time since fire (TSF)	0.39	0.5378
	COMP * TSF	-	ns
	SEV * TSF	8.89	0.005
	TSF * TSF	-	ns
CV mean tree height	Initial composition (COMP)	-	ns
$R^2 = 0.26$	Fire severity (SEV)	-	ns
P = 0.0006	Time since fire (TSF)	14.00	0.006
	COMP * TSF	-	ns
	SEV * TSF	-	ns
	TSF * TSF	-	ns

TABLE II. Results of the general linear models relating initial tree composition, fire severity, and time since fire to stand structural attributes using the medium term (< 250 y) chronosequence dataset (n = 42 stands).

ns = non-significant (α = 0.05, except for Basal area, live trees and Basal area, large live trees, where the significance level was corrected (α = 0.025); see Methods).

Boldface P-values are significant at the 0.05 level.

lished after LS fires evolved from an initially open structure with few tall stems to one that is relatively more closed, while still maintaining a high proportion of short stems. Stands established after LS fires thus showed in the first century after fire a height structure that was significantly ($\alpha = 0.05$) different from that of stands established after HS fire; that difference was no longer visible in stands aged between 100 and 200 y old (Figure 3).

The comparison of the four paired *P. mariana* stands confirmed that LS fires resulted in lower initial tree densities as compared to high severity fires (Table III). When the mean height of only the three tallest trees was considered, no difference in height was observed between severity types. However, as the number of trees increased, a difference in tree height emerged, mostly caused by a lower mean tree height in stands established after LS fires (Table III). Although the use of multiple tests on mostly the same subset of trees hinders the strict interpretation of *P*-values, this trend suggests that the effects of fire severity on stand productivity are a result of both a lower post-fire recruitment and a subsequent higher variability in within-stand stem height growth after LS fires.

EXTENDED ABSENCE OF FIRE AND STAND STRUCTURAL DEVELOPMENT

The structural evolution of stands established after HS fires continued in the extended absence of fire (> 250 y), but at a much reduced rate (Figure 4). In comparison with the evolution observed during the first few centuries after fire (Figure 2), the changes occurring after 250 y appeared to be minimal (Figure 4). Interestingly, stand characteristics of old *P. mariana* stands established after HS fires resembled those of relatively young stands established after LS fires (Figure 4).

Discussion

INITIAL COMPOSITION

Initial post-fire tree composition had little influence on forest structural development. Although we hypothesized



FIGURE 2. Evolution of stand structural attributes with time since the last fire at a medium-term timescale (≤ 250 y). Coefficients of determination and probability levels are in Table II.

that the co-dominance of *Pinus banksiana* would affect within-stand stem height distribution, we observed no difference between the two composition types (Table II; Figures 2 and 3). This may reflect the plasticity of *P. mariana* with respect to its ability to grow as an early successional fastgrowing species and as a late successional shade-tolerant species (Dix & Swan, 1971). Similarly, there was no difference in post-fire density or stand basal area between stand composition types (Figure 2; Table II). This suggests that under similar post-fire abiotic conditions, *P. mariana* stands may be as productive as *P. banksiana* co-dominated stands.

While there appeared to be little difference in the timing of stand break-up between the two composition types (Figure 2b; Table II), *P. banksiana* stands seemed to have broken up at a quicker rate than *P. mariana*-dominated stands (Figure 2d). This may have been due to the shorter longevity of *P. banksiana* or to species-specific pathogens like the Swaine jack pine sawfly (*Neodiprion swainei*) or the jack pine budworm (*Choristoneura pinus pinus*) (Martineau,



FIGURE 3. Height structure of stands (lines) in *Pinus banksiana* (PBA)dominated stands originating from high severity (HS) fires (upper row), *Picea mariana* (PMA)-dominated stands originating from high severity fires (middle row), and *P. mariana* stands established after low severity (LS) fires (bottom row). The left column of graphs represents stands younger than 100 y, the middle column, stands aged between 100 and 200 y, and the right column, stands older than 200 y. Each line represents a stand. Height classes: 2 = 2-4 m, 4 = 4-8 m, 8 = 8-12 m, 12 = 12-16 m, $16 \ge$ 16 m. Number of stands is indicated. Groups of stands showing a different letter within the same column have a significantly ($\alpha = 0.05$) different mean frequency distribution (two-sided Kolmogorov–Smirnov test).

1984). Stand reconstruction studies could clarify the timing, rate, and causes of stand break-up in the coniferous boreal forest of the Clay Belt.

FIRE SEVERITY

Fire severity, defined as the thickness of the unburned soil organic matter, had a determinant influence on the

TABLE III. Results of the paired *t*-tests for total density and mean height of four pairs of young (< 100 y) *Picea mariana* stands that originated after the same fire but differed with respect to the severity of the last fire.

Variable	High severity	Low severity	Р
Total density (trees ha ⁻¹)	9825	7075	0.04
Mean height of 3 tallest trees (m)	13.42	11.70	0.11
Mean height of 5 tallest trees (m)	13.25	10.90	0.07
Mean height of 10 tallest trees (m)	13.00	9.93	0.03

Total density comprises all stems (live and dead) that were > 2 m in height.

structural development of the Clay Belt's forests. Most structural attributes evolved differently along the LS and HS fire chronosequences (TSF \times fire severity interaction), and the large initial differences between severity types (HS versus LS) eventually disappeared as the forest structure converged. This convergence may account for the small explanatory power of the CCA (Figure 1), which considered only primary effects. Picea mariana-dominated stands established after LS fires were less productive (lower stand basal area) than those established after HS fires. This loss in productivity appears to have been due to both a lower initial recruitment and a lower growth rate of trees. Our results corroborate other studies that have shown that recruitment of most coniferous boreal species is inversely related to the amount of organic matter remaining after fire (Chrosciewicz, 1976; Johnstone & Chapins, 2006b). It is hypothesized that residual duff, by altering seedbed physical and chemical properties, makes microsites less suitable for seed germination and/or seedling survival (Zasada et al., 1983; Foster, 1985; Charron & Greene, 2002). However, since post-fire regeneration not only depends on seedbed suitability but also on the number of seeds available for recolonization (Sirois & Payette, 1991; Payette et al., 2000), we cannot rule out that differences in seed availability between severity types could have been an additional factor that contributed to reduced post-fire regeneration.

The comparison of same-age stands from different fire severity types showed that site productivity was similar when only the three tallest trees were compared (a method commonly used in forest growth and yield inventories). A difference emerged, however, when additional trees were used, suggesting that a lower number of trees had optimal growing conditions in LS stands. This could be explained by the heterogeneity of post-fire seedbeds. High severity fires completely consume the forest floor, providing to the next generation of trees a relatively homogeneous environment composed mostly of favourable microsites for seed germination and seedling growth. On the other hand, LS fires create a heterogeneous post-fire environment composed of few microsites favourable for seed germination and seedling growth and a high frequency of poor microsites. This heterogeneity of microsites has a major influence on growth variation and size inequality in P. mariana stands (Macdonald & Yin, 1999). We postulate that the depressed productivity observed after LS fires is a consequence of the heterogeneity of microsites in these sites. Additionally, LS fires favour species that resprout after fire, notably competing shrubs such as Ledum groenlandicum and members of the Sphagnaceae (Dyrness & Norum, 1983; Purdon, Brais & Bergeron, 2004; Lecomte et al., 2005), both of which are known to degrade



FIGURE 4. Long-term evolution (> 250 y) of stand structural attributes in *Picea mariana*-dominated stands established after high severity fires.

growing conditions for trees (Heinselman, 1963; Inderjit & Mallik, 1996). Of equal importance for understanding the reduced productivity associated with LS fires may be the openness of these stands, which increases the prevalence of frost events in late spring or early summer and may further hinder tree growth (Langvall & Örlander, 2001).

In sum, stand structural development during the first century after fire can be described as being affected by a series of positive feedback loops, which either favour or impede tree growth. Stand structure after HS fires is characterized by a high initial tree density that results in complete canopy closure, which in turn shades out competing vegetation and decreases the probability of growing-season frost events. On the other hand, stand structure after LS fires is characterized by a low initial tree regeneration and an abundant cover of shade-intolerant shrubs (*Kalmia, Ledum*) known to impede tree growth. The high cover of these competing species in LS fires (Lecomte *et al.*, 2005) might delay canopy closure and thus increase their own chance of survival and the prevalence of late spring/early summer frost events.

CONVERGENCE AND LONG-TERM STABILITY OF THE CLOSED CONIFEROUS BOREAL FOREST

In the Clay Belt, a diversity of structural development pathways are present, and the initial conditions (mostly fire severity) are important in determining the direction and rate of succession (Figure 5). Although fire severity induces diverging pathways of stand structural development in the short term, the prolonged absence of fire leads to a convergence of stand structure (Figure 5), as has been documented in other fire-dominated landscapes (Kashian, Turner & Romme, 2005; Kashian et al., 2005). In the Clay Belt, the mechanism driving this convergence of forest structure may be paludification, *i.e.*, the accumulation of soil organic matter, which is prevalent in the study area (Taylor, Carleton & Adams, 1987; Boudreault et al., 2002). Paludification, by lowering soil temperatures and nutrient availability, significantly reduces stand productivity (Heinselman, 1963; Van Cleve & Viereck, 1981). Therefore, in the prolonged absence of fire, all stands become paludified, averaging out post-fire differences in conditions caused by fire severity. This leads to a convergence in tree growth conditions and stand structural attributes regardless of initial tree composition or the severity of the last fire.

Previous studies have demonstrated that the fire cycle in the Clay Belt has been increasing since the end of the Little Ice Age (*ca.* 1850) (Bergeron *et al.*, 2004b) and is predicted to continue to increase under current global climate change projections (Flannigan *et al.*, 2001). Given the structural development pathways described in this study (Figure 5), the continued decrease in fire frequency may have a detrimental effect on the long-term stability of the closed coniferous boreal forest. Long fire intervals may increase the probability of low post-fire densities because old stands with low basal area possibly produce fewer seeds (Black & Bliss, 1980; Sirois, 2000; Greene et al., 2004) and accumulate excessive amounts of organic matter (Foster, 1985; Boudreault et al., 2002) that are unlikely to be consumed completely by fire. Thus, long fire cycles possibly reduce both the seed source and the post-fire availability of favourable seedbeds. In the end, if the fire regime becomes characterized by a lower fire frequency, the fires may also show reduced severity, which in the long run would reduce the proportion of dense productive stands in the landscape. Current provincial guidelines that only prescribe careful logging approaches that do not remove the soil organic layer (and are thus similar to the effects of LS fires) may also give rise to a loss in stand productivity and stand structural diversity within this landscape, especially on fine-textured deposits. In order to maintain both landscape stand productivity and stand diversity, future silvicultural approaches should include the removal of the soil organic matter to favour the establishment of dense productive stands similar to those established after HS fires. Our results suggest that the monitoring and manipulation of early seedling densities and microsite growth conditions should provide useful tools for the management of boreal stands in the Clay Belt.

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Time since last fire (y)

FIGURE 5. Conceptualized development pathways of stand structure in the Clay Belt of northwestern Québec. Stand structural diversity in this landscape is a function of the severity of the last fire (vertical vector) and the time elapsed since the last fire (horizontal vector). After high severity fires, the composition of the dense initial stands can vary between a complete dominance of *Picea mariana* to a co-dominance with *Pinus banksiana*. Eventually, all stands converge towards an open structured *P. mariana*-dominated stand after *ca*. 200 y.

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Literature cited

- Anderson, L. E., H. A. Crum & W. R. Buck, 1990. List of the mosses of North America north of Mexico. Bryologist, 93: 448–449.
- Bergeron, Y., 2000. Species and stand dynamics in the mixed-woods of Québec's southern boreal forest. Ecology, 81: 1500–1516.
- Bergeron, Y., M. Flannigan, S. Gauthier, A. Leduc & P. Lefort, 2004a. Past, current and future fire frequency in the Canadian boreal forest: Implications for sustainable forest management. Ambio, 33: 356–360.
- Bergeron, Y., S. Gauthier, M. Flannigan & V. Kafka, 2004b. Fire regimes at the transition between mixedwoods and coniferous boreal forests in northwestern Québec. Ecology, 85: 1916–1932.
- Black, R. A. & L. C. Bliss, 1980. Reproductive ecology of *Picea mariana*, at tree line near Inuvik, Northwest Territories, Canada. Ecological Monographs, 50: 331–354.
- Boudreault, C., Y. Bergeron, S. Gauthier & P. Drapeau, 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. Canadian Journal of Forest Research, 32: 1080–1093.
- Boulet, B., M. Chabot, L. Dorais, A. Dupont & R. Gagnon, 1996. Entomologie forestière. Pages 1008–1043 in J. Bérard & M. Côté (eds.). Manuel de Foresterie. Les Presses de l'Université Laval, Sainte-Foy, Québec.
- Charron, I. & D. F. Greene, 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. Canadian Journal of Forest Research, 32: 1607–1615.
- Chrosciewicz, Z., 1976. Burning for black spruce regeneration on a lowland cutover site in south-eastern Manitoba. Canadian Journal of Forest Research, 6: 179–186.
- Cyr, D., Y. Bergeron, S. Gauthier & A. C. Larouche, 2005. Are the old-growth forests of the Clay Belt part of a fire-regulated mosaic? Canadian Journal of Forest Research, 35: 65–73.
- Dix, R. L. & J. M. A. Swan, 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Canadian Journal of Botany, 49: 657–676.
- Dyrness, C. T. & R. A. Norum, 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. Canadian Journal of Forest Research, 13: 879–893.
- Environment Canada, 2005. Canadian Climate Normals 1971-2000. [Online] URL: http://www.climate.weatheroffice.ec.gc.ca
- Flannigan, M. D., I. Campbell, B. M. Wotton, C. Carcaillet, P. Richard & Y. Bergeron, 2001. Future fire in Canada's boreal forest: Paleoecology results and general circulation model – regional climate model simulations. Canadian Journal of Forest Research, 31: 854–864.
- Foster, D., 1985. Vegetation development following fire in *Picea* mariana (black spruce)–*Pleurozium* forests of south-eastern Labrador, Canada. Journal of Ecology, 73: 517–534.
- Gray, D. R., J. Régnière & B. Boulet, 2000. Analysis and use of historical patterns of spruce budworm defoliation to forecast outbreak patterns in Québec. Forest Ecology and Management, 127: 217–231.

- Greene, D. F., 2004. A survey of post-fire seedbeds from seven fires in Canada. Presentation given at the 5th International Conference on Disturbance Dynamics in Boreal Forests. Dubna, Russia. August 1–5.
- Greene, D. F., J. Noel, Y. Bergeron, M. Rousseau & S. Gauthier, 2004. Recruitment of *Picea mariana*, *Pinus banksiana* and *Populus tremuloides* across a burn severity gradient following fire in the southern boreal forest of Québec. Canadian Journal of Forest Research, 34: 1845–1857.
- Groot, A. & B. J. Horton, 1994. Age and size structure of natural and second growth peatland *Picea mariana* stands. Canadian Journal of Forest Research, 24: 225–233.
- Gutsell, S. & E. A. Johnson, 2002. Accurately ageing trees and examining their height-growth rates: Implications for interpreting forest dynamics. Journal of Ecology, 90: 153–166.
- Harper, K. A., Y. Bergeron, S. Gauthier & P. Drapeau, 2002. Postfire development of canopy structure and composition in black spruce forests of Abitibi, Québec: A landscape scale study. Silva Fennica, 36: 249–263.
- Harper, K. A., Y. Bergeron, P. Drapeau, S. Gauthier & L. De Grandpré, 2005. Structural development following fire in black spruce boreal forest. Forest Ecology and Management, 206: 293–306.
- Heinselman, M. L., 1963. Forest sites, bog processes, and peatland types, in the Glacial Lake Agassiz Region, Minnesota. Ecological Monographs, 33: 327–374.
- Holmes, R. L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin, 43: 69–78.
- Inderjit & A. U. Mallik, 1996. Growth and physiological responses of black spruce (*Picea mariana*) to sites dominated by *Ledum* groenlandicum. Journal of Chemical Ecology, 22: 575–585.
- Johnson, E. A., 1992. Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. Cambridge University Press, Cambridge.
- Johnstone, J. F. & F. S. Chapin III, 2006a. Fire interval effects on successional trajectory in boreal forests of Northwest Canada. Ecosystems, 9: 268-277.
- Johnstone, J. F. & F. S. Chapin III, 2006b. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems, 9:14-31.
- Johnstone, J. F., F. S. Chapin III, F. Foote, S. Kemmett, K. Price & L. Viereck, 2004. Decadal observations of tree regeneration following fire in boreal forests. Canadian Journal of Forest Research, 34: 267–273.
- Kashian, D. M., M. G. Turner & W. H. Romme, 2005. Variability in leaf area and stemwood increment along a 300-year lodgepole pine chronosequence. Ecosystems, 8: 48–61.
- Kashian, D, M., M. G. Turner, W. H. Romme & C. G. Lorimer, 2005. Variability and convergence in stand structural development in a fire-dominated subalpine landscape. Ecology, 86: 643–654.
- Langvall, O. & G. Örlander, 2001. Effects of pine shelterwoods on microclimate and frost damage to Norway spruce seedlings. Canadian Journal of Forest Research, 31: 155–164.
- Lecomte, N., M. Simard, Y. Bergeron, A. Larouche, H. Asnong & P. J. H. Richard, 2005. Effects of fire severity and initial tree composition on understorey vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data. Journal of Vegetation Science, 16: 665-674.
- Lecomte, N. & Y. Bergeron, 2005. Successional pathways on different surficial deposits in the coniferous boreal forest of the Québec Clay-Belt. Canadian Journal of Forest Research, 8: 1984-1995.

- Lindenmayer, D. B. & J. F. Franklin, 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Washington, DC.
- Macdonald, S. E. & F. Yin, 1999. Factors influencing size inequality in peatland black spruce and tamarack: Evidence from post drainage release growth. Journal of Ecology, 87: 404–412.
- Marie-Victorin, 1995. Flore Laurentienne. 3^e édition. Les presses de l'Université de Montréal, Montréal, Québec.
- Martineau, R., 1984. Insects Harmful to Forest Trees. Forestry Technical Report 32. Multiscience Publications Limited and Canadian Forestry Service, Ottawa, Ontario.
- McKeague, J. A., 1976. Manual on Soil Sampling and Methods of Analysis. Canadian Society of Soil Sciences, Ottawa, Ontario.
- Miyanishi, K. & E. A. Johnson, 2002. Process and patterns of duff consumption in the mixedwood boreal forest. Canadian Journal of Forest Research, 32: 1285–1295.
- Nguyen-Xuan, T., Y. Bergeron, D. Simard, J. W. Fyles & D. Paré, 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Québec: A wildfire *versus* logging comparison. Canadian Journal of Forest Research, 30: 1353–1364.
- Payette, S., 1992. Fire as a controlling process in the North American boreal forest. Pages 144–169 in H. H. Shugart, R. Leemans & G. B. Bonan (eds.). A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge.
- Payette, S., N. Bhiry, A. Delwaide & M. Simard, 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: The catastrophic impact of insect defoliators and fire on the spruce-moss forest. Canadian Journal of Forest Research, 30: 288–305.
- Poole, R. W. & P. Gentili (eds.), 1996-97. Nomina Insecta Nearctica: A Check List of the Insects of North America. Vol. 1-4. Entomological Information Services, Rockville, Maryland. [Online] URL: http://www.nearctica.com/nomina/main.htm
- Purdon, M., S. Brais & Y. Bergeron, 2004. Initial response of understorey vegetation to fire severity and salvage-logging in the southern boreal forest of Québec. Applied Vegetation Science, 7: 49–60.

- Robitaille, A. & J.-P. Saucier, 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Ste-Foy, Québec.
- SAS Institute, 2000. SAS/STAT User's Guide, v. 8.2. SAS Publishing, Cary, North Carolina.
- Simon, N. P. P. & F. E. Schwab, 2005. Plant community structure after wildfire in the subarctic forests of western Labrador. Journal of Applied Northern Forestry, 22: 229-235.
- Sirois, L., 2000. Spatiotemporal variation in black spruce cone and seed crops along a boreal forest–tree line transect. Canadian Journal of Forest Research, 30: 900–909.
- Sirois, L. & S. Payette, 1991. Reduced postfire tree regeneration along a boreal forest–forest–tundra transect in northern Québec. Ecology, 72: 619–627.
- Stuiver, M., P. J. Reimer, E. Bard, J. W. Beck, G. S. Burr, K. A. Hughen, B. Kromer, G. McCormac, J. van der Plicht & M. Spurk, 1998. Intcal98 radiocarbon age calibration. Radiocarbon, 40: 1041–1083.
- Taylor, S. J., T. J. Carleton & P. Adams, 1987. Understory vegetation change in a chronosequence. Vegetatio, 73: 63–72.
- ter Braak, C. J. F. & P. Šmilauer, 1999. Canoco Reference Manual and User Guide to Canoco for Windows: Software for Canonical Community Ordination Version 4. Microcomputer power, Ithaca, New York.
- Van Cleve, K. & L. A. Viereck, 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. Pages 185–211 in D. C. West, H. H. Shugart & D. B. Botkin (eds.). Forest Succession: Concepts and Application. Springer-Verlag, New York, New York.
- Veillette, J. J., 1994. Evolution and paleohydrology of glacial lakes Barlow and Ojibway. Quaternary Science Reviews, 13: 945–971.
- Zasada, J. C., R. A. Norum, R. M. Van Veldhuizen & C. E. Teutsch, 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. Canadian Journal of Forest Research, 13: 903–913.
- Zasada, J. C., R. A. Norum, C. E. Teutsch & R. Densmore, 1987. Survival and growth of planted black spruce, alder, aspen and willow after fire on black spruce/feather moss sites in interior Alaska. Forestry Chronicle, 63: 84–88.

APPENDIX I. Characteristics of the chronosequence survey stands.

	Pinus			Stand age (y)		Mineral soil					
	Initial	banksiana	Eiro	Desidual OM5	Oldaat	Calibrated 14C	Calibrated 14C	Sand	C:1+	Class	Clana
a'. 1		(%)	Fire	Residual ONIS	Oldest			Sand	5111	Clay	Slope
Site	composition ²	basal area	severity	(cm)	tree	age (charcoal)'	age (numus) ^o	(%)	(%)	(%)	index'
30	Pine	80.0	High	1.2	45	-	-	1.5	22.0	76.5	1.0
54	Pine	78.4	High	1.0	51	-	-	0.0	12.7	87.3	1.9
61	Pine	78.8	High	1.5	51	-	-	6.5	21.5	72.0	5.1
36	Pine	59.1	High	1.6	76	-	-	1.0	23.6	75.4	0.6
38	Pine	37.2	High	1.6	84	-	-	0.0	9.0	91.0	0.7
23	Pine	44.4	High	1.3	86	-	-	3.5	26.9	69.7	1.4
57	Pine	58.4	High	1.2	88	-	-	13.0	45.5	41.5	1.2
29	Pine	64.6	High	1.2	135	-	-	19.9	30.8	49.3	1.2
69	Pine	43.9	High	1.1	139	-	-	2.0	34.3	63.7	1.9
66	Pine	48.0	High	1.7	149	-	-	12.5	25.0	62.5	8.7
73	Pine	68.4	High	1.3	149	-	-	26.0	25.0	49.0	1.5
40	Pine	61.2	High	1.1	151	-	-	25.5	27.5	47.0	2.4
49	Pine	48.4	High	1.2	155	-	-	14.0	63.0	23.0	2.1
94	Pine	51.2	High	1.0	176	-	-	6.0	24.5	69.5	5.1
83	Pine	56.8	High	1.0	177	-	-	4.0	20.0	76.0	1.0
/9	Pine	45.8	High	1.1	1/9	-	-	2.4	29.0	68.6	0.0
65	Pine	57.3	High	2.1	204	-	-	14.0	32.5	53.5	0.8
64	Pine	41.1	High	1.9	222	-	-	0.0	38.4	61.6	3.9
67	Pine	22.3	High	1.0	229	-	-	0.0	28.6	/1.4	1.4
02	Spruce	0.0	High	1.4	52	-	-	2.0	23.4	/4.6	10.5
U4 50	Spruce	0.0	High	2.5	23 72	-	-	0.0	38.1	64.5	2.5
39 15	Spruce	13.7	High	2.5	76	-	-	10.2	22.3	61.0	1./
13	Spruce	0.1	High	1.3	/0	-	-	10.5	27.9	70.0	-4.0
56	Spruce	0.0	High	1.9	04 86	-	-	12.5	21.0	79.0 58.0	0.0
12	Spruce	0.0	High	1.3	05	-	-	13.5	20.5	58.0 70.1	0.8
55	Spruce	0.0	High	2.5	95	-	-	14.5	20.9	79.1 55.5	2.1
18	Spruce	0.2	High	2.5	126	-	-	14.5	18.0	67.0	1.8
75	Spruce	0.0	High	2.0	120	-	-	3.4	24.5	72.1	1.0
08	Spruce	0.0	High	2.0	120	-	-	9.4	24.5	65.5	-1.3
95	Spruce	0.0	High	13	18/			3.0	25.5	71.0	1.7
09	Spruce	0.0	High	1.5	215	1225		11.5	23.5	65.0	1.7
07	Spruce	0.0	High	1.5	213	790	_	7.5	27.0	65.5	1.0
50	Spruce	0.0	High	2.0	227	365	_	19.0	27.0	54.0	13
06	Spruce	0.0	High	3.2	280	710	555	1.0	22.7	76.4	0.4
16	Spruce	0.0	High	2.7	286	1585	705	10.0	18.0	72.0	0.5
20	Spruce	0.0	High	3.2	353	2355	-	5.9	22.8	71.3	1.9
11	Spruce	0.0	Low	12.0	38		-	21.0	29.5	49.5	1.1
74	Spruce	0.0	Low	13.0	52	-	-	6.0	26.5	67.5	1.3
53	Spruce	0.0	Low	7.3	53	-	-	20.0	31.0	49.0	0.6
58	Spruce	0.0	Low	5.8	62	-	-	23.0	30.5	46.5	2.1
78	Spruce	0.0	Low	17.9	75	-	-	17.0	28.0	55.0	0.6
60	Spruce	0.0	Low	6.7	84	-	-	9.0	15.0	76.0	1.2
03	Spruce	0.0	Low	16.2	94	-	-	1.9	16.0	82.0	0.0
68	Spruce	3.2	Low	4.6	139	-	-	1.0	22.7	76.4	0.8
63	Spruce	0.0	Low	7.9	143	-	-	2.0	18.5	79.5	0.8
17	Spruce	0.0	Low	17.3	151	-	-	17.5	33.0	49.5	0.8
05	Spruce	0.0	Low	8.4	169	-	-	13.9	47.6	38.5	0.3

¹ Sites in **boldface** are the paired sites originating from the same fire but differing with respect to fire severity.

² Initial stand composition determined from the composition of dead and live trees (see Methods).

³ Includes both live and dead stems > 2 m in height.

⁴ Fire severity determined from the thickness of the residual organic matter (see Methods).

⁵ Thickness of the residual organic matter, *i.e.*, the organic matter that was not burned by the last fire, located between the mineral horizon and the uppermost charcoal layer.

⁶ Stand age determined from tree-ring analysis. Stands where the postfire cohort of trees was not found were given a minimum age and were radiocarbon dated.

⁷ Radiocarbon dates obtained for carbonized plant remains (see Methods).

⁸ Radiocarbon dates obtained for humus accumulated just above uppermost charcoal layer (from Cyr et al., 2005).

⁹ Slope index integrates slope incline and landform shape and can assume positive (mounds or regular slopes) and negative values (depressions) (see Methods).