

# Fire Severity and Long-term Ecosystem Biomass Dynamics in Coniferous Boreal Forests of Eastern Canada

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## ABSTRACT

The objective of this study was to characterize the effects of soil burn severity and initial tree composition on long-term forest floor dynamics and ecosystem biomass partitioning within the *Picea mariana* [Mill.] BSP-feathermoss bioclimatic domain of northwestern Quebec. Changes in forest floor organic matter and ecosystem biomass partitioning were evaluated along a 2,355-year chronosequence of extant stands. Dendroecological and paleoecological methods were used to determine the time since the last fire, the soil burn severity of the last fire (high vs. low severity), and the post-fire tree composition of each stand (*P. mariana* vs. *Pinus banksiana* Lamb). In this paper, soil burn severity refers to the thickness of the organic matter layer accumulated above the mineral soil that was not burned by the last fire. In stands originating from high severity fires, the post-fire dominance by *Pinus banksiana* or *P. mariana* had little effect on the change in forest floor thickness and tree biomass. In contrast, stands established after low severity fires accumulated during the first century after fire 73% thicker forest floors and produced 50% less tree biomass than stands established after high severity fires. Standing tree biomass increased until approximately 100 years after high severity fires, and

then decreased at a logarithmic rate in the millennial absence of fire. Forest floor thickness also showed a rapid initial accumulation rate, and continued to increase in the millennial absence of fire at a much slower rate. However, because forest floor density increased through time, the overall rate of increase in forest floor biomass ( $58 \text{ g m}^{-2} \text{ y}^{-1}$ ) remained constant for numerous centuries after fire (700 years). Although young stands (< 200 years) have more than 60% of ecosystem biomass locked-up in living biomass, older stands (> 200 years) sequester the majority (> 80%) of it in their forest floor. The results from this study illustrate that, under similar edaphic conditions, a single gradient related to time since disturbance is insufficient to account for the full spectrum of ecosystem biomass dynamics occurring in eastern boreal forests and highlights the importance of considering soil burn severity. Although fire severity induces diverging ecosystem biomass dynamics in the short term, the extended absence of fire brings about a convergence in terms of ecosystem biomass accumulation and partitioning.

**Key words:** fire disturbance; forest succession; soil burn severity; forest floor organic matter; biomass partitioning; biomass accumulation; ecological convergence; chronosequence; black spruce (*Picea mariana*); jack pine (*Pinus banksiana*).

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## INTRODUCTION

Boreal forests play an important role in the global carbon cycle therefore many studies have tried to understand how global climate change may affect boreal forest dynamics (for example, Kasischke and others 1995; Kurz and Apps 1999). In boreal forest ecosystems, carbon is stored in two main pools: living tree biomass and the forest floor organic matter accumulated above the mineral soil (Gower and others 1997; O'Connell and others 2003; Wang and others 2003). The accumulation of organic carbon and the distribution of this carbon among these pools is however not homogeneous among and within boreal landscapes (Gower and others 1997, 2001; Yu and others 2002; Bhatti and others 2002; Swanson and others 2000). Understanding the factors responsible for this variability is of critical importance if we are to properly estimate the role of boreal forests in current and future global carbon cycling.

In the boreal forest, fire is the main disturbance that terminates/initiates secondary succession and redistributes biomass between the forest floor and living trees (O'Neill and others 2002, Wardle and others 1997, 2003). Relatively short fire cycles (< 100 years) predominate in the western and central portions of the North-American boreal biome (Johnson 1992). However, studies in the eastern portion of this biome, which is under the influence of a humid maritime climate, have documented much longer current fire cycles (> 300 years; Foster 1983; Bergeron and others 2004a; Cyr and others 2005). Longer fire cycles may increase the prevalence of low severity fires that do not fully consume the thick and dense forest floor organic matter that accumulates during long fire-free periods (Foster 1985; Simon and Schwab 2005). To date, most biomass accumulation studies have been undertaken in the western and central portions of the boreal forest and as a result researchers have concentrated their efforts on the effects of high severity fires at relatively short time scales (0–150 years) (for example, Kurtz and Apps 1999; Wang and others 2003; Gower and others 1997). Because old stands (> 150 years) and low severity fires can predominate in some eastern boreal landscapes (Foster 1985; Simon and Schwab 2005; Bergeron and others 2004b), to properly estimate the role of these forests in the global carbon cycle, we need to understand how fire severity influences biomass sequestration as succession proceeds in the extended absence of fire (> 150 years).

Fire cycles vary spatially (for example, Amiro and others 2001) and temporally (Bergeron and others

2001) across the boreal zone and changes in fire frequency may result in changes in the frequency of successional pathways co-occurring under similar edaphic conditions (Johnstone and Chapin 2005; LeGoff and Sirois 2004; Parisien and Sirois 2003; Larocque and others 2000). Within eastern boreal landscapes, short fire intervals favor species that reach sexual maturity quickly such as *Pinus banksiana* Lamb. to the detriment of slower-maturing species such as *P. mariana* [Mill.] BSP (Lecomte and Bergeron 2005; Harper and others 2002). On the other hand, long fire intervals will tend to favor longer-lived species or species that are able to regenerate in the absence of fire such as *P. mariana* and unlike *Pinus banksiana* (Lecomte and Bergeron 2005; Harper and others 2002). Given that *Pinus banksiana* is a fast-growing early successional species and that it produces a higher quality litter (lower C:N ratio) than *P. mariana* (Preston and others 2002), initial tree composition may influence ecosystem biomass accumulation and partitioning. As global climate change will certainly influence fire frequency (Kasischke and others 2001; Flannigan and others 2001), understanding how global climate change may influence biomass sequestration in the eastern boreal necessitates an understanding on how biomass sequestration differs along multiple successional pathways co-occurring under similar edaphic conditions.

In this paper, we report on the effects of the initial tree composition and fire severity on long-term forest floor dynamics and ecosystem biomass partitioning in coniferous stands on fine-textured deposits. We refer to fire severity exclusively as the effects of fire on the organic matter accumulated above the mineral soil (quantity of duff burned/unburned sensu Miyaniishi and Johnson 2002) as opposed to the effects of fire on the canopy (% trees killed; sensu Greene and others 2004). We hypothesized that among-stand diversity in forest floor thickness and biomass partitioning can be explained by the initial post-fire stand conditions and by processes operating in the absence of fire at the stand scale. Given that short-term studies indicate that fire severity affects seed germination (Chrosiewicz 1974, 1976; Zasada and others 1983), subsequent tree growth (Zasada and others 1987) and soil temperature and nutrient availability (Van Cleve and Viereck 1981; Van Cleve and Dyrness 1983), we hypothesize that low severity fires will depress tree biomass production and result in altered biomass partitioning as compared to high severity fires. Due to the higher quality litter and faster growth of *Pinus banksiana* as compared to *Pinus mariana*, we hypothesize that the post-fire

stand dominance by *P. banksiana* may increase decomposition rates and consequently reduce forest floor thickness and increase the amount of biomass accumulated in living trees.

## METHODS

### Study Area

The study area is part of the Lake Matagami Lowland ecological region, within the *P. mariana*—feathermoss bioclimatic domain (Robitaille and Saucier 1998). This area is located within the Clay Belt of northeastern Ontario and northwestern Quebec, a physiographic unit composed primarily of clay deposits left by pro-glacial Lake Ojibway (Veillette 1994). Although 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°C and 0.7°C with an average of 906 and 890 mm of precipitation annually (Environment Canada 2005). Although agricultural settlement south of the study area began in the middle of the 1930s, intensive logging of this area only began in the late 1970s. Most of the region is covered by structurally diverse coniferous forests dominated either by *P. mariana* or *Pinus banksiana* (Harper and others 2002) with a forest floor dominated either by *Sphagnum spp.* or *Pleurozium schreberi* (Boudreault and others 2002). Occasional deciduous stands (*Populus tremuloides* Michx. and *Betula papyrifera* Marsh.) are dispersed across the landscape. Fire is the main disturbance that terminates and initiates secondary successions. Fire cycle length has increased from 101 years before 1850, to 135 years between 1850 and 1920, to 398 years since 1920; mean stand age is 148 years (Bergeron and others 2004b). Compared to regions further east and south, the spruce budworm, *Choristoneura fumiferana* (Clem.), has a markedly reduced impact in this area. Both historical patterns of budworm defoliation (Boulet and others 1996; Gray and others 2000) and tree-ring reconstructions (M. Simard and others unpublished data) show that spruce budworm has a negligible impact in these black spruce-dominated forests.

### Data Sets

To investigate the role of fire severity and initial composition on forest floor organic matter accumulation and ecosystem biomass partitioning, three data sets were used. The first data set (214 stands) is a compilation of forest inventory plots

measured by the Quebec Ministry of Natural Resources (QMNR) in 1996. The second data set (48 stands) represents a chronosequence survey that was undertaken between 2000 and 2003, and is representative of stands from the landscape survey with a bias towards coniferous stands on fine-textured deposits. The final data set (eight stands) is a survey of forest floor organic matter that was undertaken in 2003 among a representative subset of *P. mariana* stands from the chronosequence survey.

### QMNR Landscape Survey

Because the QMNR inventories the forest for forestry purposes, forest stands on slopes greater than 40% and with a canopy shorter than 7 m were not sampled. In the study area, 214 circular plots of 400 m<sup>2</sup> were sampled. In each plot, every tree with a diameter at breast height (dbh) larger than 10 cm was identified to species and tabulated in 2-cm diameter classes, whereas trees with dbh less than 10 cm were sampled in a concentric subplot of 40 m<sup>2</sup>. In each plot, the age at breast height of three dominant stems was determined from increment cores. Slope quantification, mineral soil classification and the measurement of the thickness of the forest floor (*L*, *F* and *H* horizons) were done on site (Saucier 1994). By overlaying fire reconstruction maps (Bergeron and others 2004a) onto the forest inventory, a date since last fire was assigned to every forest stand, and was further validated using the oldest age determined for the three dominant trees per stand. The fire reconstruction maps were developed by dating fire scars and post-fire tree cohorts, and by using archives and aerial photographs for recent fires (see Bergeron and others 2004a for further details).

### Chronosequence Survey

*Site Selection and Tree Sampling.* Within the area covered by the QMNR survey, we visited all the burned areas that were located less than 2 km from a road. In all, 43 distinct fires of different ages were sampled. In each fire, the density and composition (*P. mariana* vs. *Pinus banksiana*) of the post-fire tree cohort was estimated based on current and/or deadwood tree composition. When different post-fire densities and compositions were observed within the same fire, several stands were sampled. Each stand had to be on fine-textured mineral deposits, on a slight incline and free of any sign of anthropogenic disturbance. In a representative 10 m × 10 m quadrat, the height and dbh of all live and dead stems larger than 2 m in height were

measured for each tree species. 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 post-fire) was assessed with the presence/absence of charcoal.

**Soil Analyses and Topography.** To insure that all sites were comparable with respect to soil texture, two mineral soil samples were taken at the center of each quadrat: one at the surface and another at a depth of 1 m. The samples were air dried and analyzed for texture (Bouyoucos hydrometer method; McKeague 1976), and then the results from the two horizons were averaged to obtain the percentage of sand, silt and clay of the mineral soil per site.

As in general the Clay Belt's topography may be considered flat, slight variations in topography, which can be masked by peat accumulation, may determine the moisture regime of stands. A theodolite was therefore used to characterize the topography of the mineral soil surrounding each stand by noting the relative heights of points positioned every 10 m along four 50 m transects each starting at the center of the quadrat and passing through one of the four corners. For each transect, we calculated the slope of the mineral soil. Transects with slopes that were not significant ( $P > 0.05$ ) were given a value of 0. 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 (that is, one transect of 100 m). If the slopes were of the same sign, we summed these slopes to obtain a negative slope value (depression) and 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.

**Stand Age Determination.** Stand age (fire year) for the youngest stands (< 100 years old) was determined from a stand initiation map (Bergeron and others 2004a) and was validated by counting rings from cross-sections taken at the base of dominant trees. In older stands, stand age was obtained by carefully dating cross-sections taken at the base of live and dead dominant trees. Cross-sections were finely sanded and crossdated using a frost-ring chronology under a dissecting microscope at 40× magnification. Crossdating was verified using the program COFECHA (Holmes 1983). In stands where the oldest tree was more than 200 years of age, and where no fire scars or pioneer species (*Pinus banksiana*) were found, samples of carbonized plant remains from the uppermost charcoal layer of the forest floor were sent to Iso-

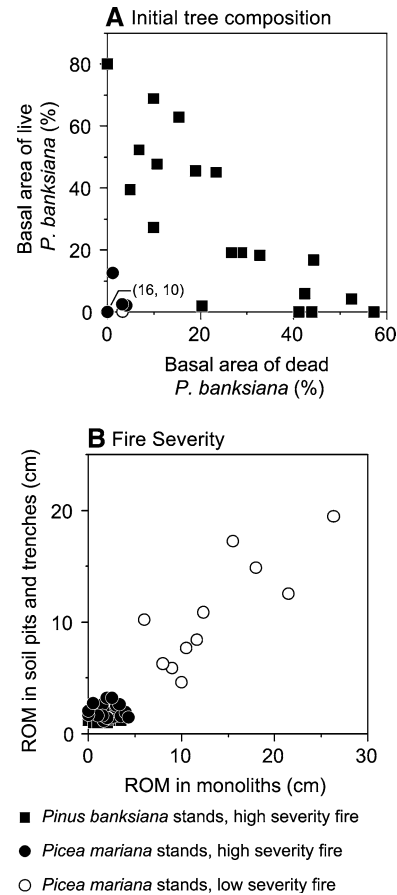
Trace Laboratories (Toronto, Canada) for AMS (Accelerator Mass Spectrometry) radiocarbon dating. The radiocarbon years were calibrated in calendar years using INTCAL98 (Stuiver and others 1998) (see <http://www.springerlink.com> Appendix A). Radiocarbon datings from a parallel study (Cyr and others 2005) undertaken in two of the oldest stands (> 250 years) are also shown (<http://www.springerlink.com> Appendix A). In this study however the authors dated the organic matter located just above the uppermost charcoal layer within the forest floor profile. This may account for the younger dates this study obtained as compared to our radiocarbon dates from carbonized material. Nonetheless, as the radiocarbon dates of humus predate the age of the oldest tree present, we used the dates obtained from carbonized plant remains.

**Fire Severity.** At each stand, the severity of the last fire was qualified based on the average thickness of duff that was not consumed by the last fire, that is, the residual organic matter (ROM). Ideally soil burn severity is quantified as the amount of organic matter consumed (sensu Miyanishi and Johnson 2002). Nonetheless, 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 (for example, Nguyen-Xuan and others 2000). The thickness of the ROM was measured with two methods: by meticulous laboratory analysis of a few forest floor profiles per site, and by careful in situ observations of charcoal layers within numerous pits and trenches dug into the forest floor. At each site, between two and four, 10 cm × 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 sections. Subsamples of 50 cm<sup>3</sup> were deflocculated 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 observed microscopically at 40× magnification. Individual plant remains were identified by type (cone scales, leaf fragments, seeds, and so on) and to species, genus or family depending on extent of decomposition. The relative abundance of each plant remain type was then quantified (0–12.5%, 12.5–25%, 25–50%, 50–75%, 75–100%). Charcoal fragments were extracted, dried and then weighed. The mineral soil/organic matter interface of each monolith was established where the mineral soil represented less than 25% of the particles retained in the 2 mm mesh. The thickness of the residual organic matter was calculated as the number of

1 cm layers above the mineral soil but under the last layer deposited to contain more than 0.001 g of charcoal.

In the younger black spruce sites (< 200 years), 2.25 m trenches were dug about 20 cm into the mineral soil. At every 15 cm along the trench, the depth of the uppermost charcoal layer and of the mineral soil were noted, so that the thickness of the residual organic matter (ROM) and of the organic matter accumulated since the last fire (post-fire forest floor thickness) could be calculated as well as the total thickness of the forest floor (*L*, *F*, and *H* horizons; post-fire forest floor thickness and ROM thickness combined). Additionally, in each *Pinus banksiana* and *P. mariana* stand, respectively, ten and fifteen 25 cm × 25 cm pits were dug into the mineral soil every 2 m along two or three 10-m transects. For each pit, the same measurements were noted as done for the trenches.

**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 A <http://www.springerlink.com>, Table 1). Furthermore, we are confident that the paleoecological methods used in this study (exhumation and identification of dead wood, careful quantification of plant macroremains and charcoals found in numerous organic matter profiles per site) 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 (Figure 1A, B). Because of this, we classified all stands in one of two categories of stand composition (dominance by *Pinus banksiana* or *P. mariana*, based on the relative basal area of living and dead trees), and in one of two categories of soil burn severity (high severity fire = thin residual organic matter layer; low severity fire = thick residual organic matter layer). Because no stands that were dominated by *Pinus 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 *Pinus banksiana* established after a high severity fire.



**Figure 1.** Classification of stands based on initial tree composition (**A**) and fire severity (**B**). **A** Basal area of live versus dead *Pinus banksiana* stems relative to total stand basal area (all species, live and dead stems). Numbers in parentheses represent the number of data superposed at coordinates (0,0) for *Picea mariana* high severity stands, and *P. mariana* low severity stands, respectively. **B** Mean thickness of residual organic matter (ROM) obtained in the field versus from detailed laboratory charcoal analysis.

According to the basal area of live and dead trees, 19 of the 48 sampled stands were dominated by *Pinus banksiana* after fire (Figure 1A). For the remaining 29 sites, as no significant traces of any other tree species except for *P. mariana* were found among the deadwood or among macro-remains within forest floor profiles described above (Appendix A, <http://www.springerlink.com>), these sites were all classified as being dominated by *P. mariana* after fire.

Sites were classified as either originating 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 severe burns in the boreal forest has shown that coniferous post-fire seed germina-

tion was significantly impacted when residual organic matter approached 5 cm (D. Greene, unpublished data). We used this ecologically significant threshold (5 cm) to classify soil burn severity. Among the stands sampled, 11 of the 29 *P. mariana* stands were established after the passage of an LS fire (Figure 1B).

## Forest Floor Survey

To quantify forest floor biomass accumulation, a subset of 8 HS fire stands were selected among the 29 black spruce-dominated stands. The stands were chosen according to their accessibility and age, so that they still represented a chronosequence spanning numerous decades (> 700 years). At each site, five pits were dug at 4-m intervals along a randomly placed 20-m transect. In each pit, a 10 cm × 10 cm × 5 cm sample of organic matter was retrieved at a depth of 10 cm below the surface (upper forest floor organic matter) and another immediately above the charcoal layer of the last fire (lower forest floor organic matter). When total forest floor thickness was less than 15 cm thick, only one sample was taken and identified as the upper forest floor organic matter. Each sample was delicately cut out from the pits and brought back to laboratory in rigid containers to avoid altering its volume. We removed roots from a subsample, which was trimmed to fit inside an open container of known volume, then dried and weighted to calculate its density. Organic matter density for each site was calculated by first averaging the density of the upper and lower horizons for each pit, and then by calculating the mean density of the five pits. The mean organic matter density data per site were then coupled to the forest floor thickness data to calculate forest floor organic matter biomass per site on an areal basis.

## Statistical Analyses

**QMNR Data Set.** Given the fact that *P. mariana* replaces *Pinus banksiana* when the fire interval exceeds 100 years (Harper and others 2002) and that we have no information on the composition of deadwood in the stands sampled by the QMNR, we only used stands less than 100 years old from this data set (102 stands). We checked for differences in slope and stand age, and compared the forest floor thickness and stand basal area of the two composition types using a *t*-test, or a modified *t*-test when their variance was not equal. Fire severity was not tested with this dataset because the QMNR does not qualify the severity of the last fire during its inventory. The response variables that were

investigated are stand basal area and total forest floor thickness. The independent variable was stand composition (categorical variable: *P. mariana*- and *Pinus banksiana*-dominated stands).

**Chronosequence Data Set.** The chronosequence database, that spanned different time scales depending on fire severity and initial composition (*Pinus banksiana* HS fires: 45–229 years, *P. mariana* LS fires: 38–169 years, and *P. mariana* HS fires: 52–2,355 years), was analyzed at two distinct time scales: medium term (< 250 years) and long term (> 250 years). The medium-term scale (< 250 years), allowed us to assess the effects of both fire severity and initial composition on ecosystem biomass dynamics, and to compare these results to those obtained with the QMNR data set. The long-term scale (250–2,500 years) allowed us to evaluate how *P. mariana* stands established after HS fires changed in the extended absence of fire.

Topography (slope index) and soil variables (percent sand, silt, and clay) were not used in the chronosequence analyses because they were uncorrelated ( $\alpha = 0.05$ ) to both the response variables (tree biomass, total forest floor thickness and post-fire forest floor thickness) and the predictor variables (stand age, fire severity, and initial composition) (Table 1). This is probably a result of the general homogeneity of the landscape with respect to soil texture and slope, and of our homogeneous selection of stands.

Total oven-dry tree biomass was estimated from the dbh of living trees greater than 2 m in height in the quadrats using allometric equations developed for the province (Ouellet 1983). Forest floor thickness was analyzed both as the total thickness (from the mineral soil to the surface; total forest floor thickness) and as the portion that has accumulated since the last fire, that is, excluding the residual organic matter (from the uppermost charcoal layer to the surface; post-fire forest floor thickness). At the medium-term scale, the response variables (tree biomass, total forest floor thickness, post-fire forest floor thickness) were analyzed in a backward regression analysis with a linear model design (proc GLM, SAS/STAT statistical package version 8.0) using a combination of a continuous predictor variable (time since last fire; "TSF") and categorical predictor variables (initial stand composition, "COMP" and fire severity, "SEV"). Quadratic effects and interactions were included with the predictor variables in the initial model, but were removed when they were not significant ( $\alpha = 0.1$ ). Because the design was incomplete (that is, no *P. banksiana* stands originating from a LS fire), we excluded SEV \* COMP interaction terms.

**Table 1.** Spearman (Fire Severity and Initial Composition) and Pearson (All Other Variables) Correlations between the Environmental Variables, and the Response and Predictor Variables using the Chronosequence Dataset ( $n = 48$ )

	Environmental variables			
	Sand (%)	Silt (%)	Clay (%)	Slope index (°)
Response variables				
Total forest floor thickness	-0.03	-0.12	0.10	-0.04
Post-fire forest floor thickness	0.01	-0.09	0.05	-0.12
Tree biomass	0.08	-0.07	0.00	-0.17
Predictor variables				
Time since fire	-0.08	-0.08	0.10	0.12
Fire severity	-0.23	-0.07	0.10	0.28
Initial composition	-0.12	0.12	-0.04	0.26

*Total forest floor thickness comprises both post-fire and residual forest floor organic matter.  
For all correlations  $P > 0.05$ .*

Among the 48 chronosequence stands, there were 4 pairs of young (< 100 years) *P. mariana* stands with each pair originating from the same fire event but differing with respect to the local severity of the last fire. These pairs were used to test the short-term (< 100 years) effects of fire severity on forest floor thickness and tree biomass using paired *t*-tests.

The effects of the extended absence of fire (> 250 years) on forest floor organic matter characteristics and biomass partitioning were assessed with linear regression (proc GLM, SAS/STAT statistical package version 8.0) following appropriate transformation of the predictor variable (time since fire) to meet the assumptions of homoskedasticity and normality of residuals. For the forest floor survey data set, response variables were upper and lower forest floor density, forest floor biomass, and total ecosystem biomass (tree + forest floor biomass). All statistical analyses were performed with SAS/STAT statistical package (version 8.0).

## RESULTS

### QMNR Landscape Survey

The comparison of stand characteristics of young (< 100 years) *P. mariana* and *Pinus banksiana*-dominated stands on fine-textured deposits within the QMNR database indicated that *Pinus banksiana* stands were more productive (tree basal area) and accumulated significantly thinner forest floors than *P. mariana* stands (Figure 2). The age and slope index of *Pinus banksiana* and *P. mariana* stands were not significantly different ( $t = 0.61$ ,  $P = 0.54$  and  $t = 1.32$ ,  $P = 0.19$  respectively; data not shown otherwise).

### Chronosequence Survey

When the severity of the last fire was taken into account, as was the case in the chronosequence survey, no significant differences were observed between the composition types with respect to standing tree biomass and forest floor thickness in high severity (HS) fires (Table 2, Figure 3). On the other hand, soil burn severity significantly affected standing tree biomass, total forest floor thickness, and post-fire forest floor thickness in black spruce-dominated stands (Table 2, Figure 3). In the absence of fire, tree biomass peaked in stands established after HS fires at a higher value ( $17 \text{ kg m}^{-2}$ ) and at an earlier time (79 years) than stands established after low severity (LS) fires ( $8.8 \text{ kg m}^{-2}$ , 128 years; Figure 3A). Although the change in tree biomass was significantly affected by fire severity (SEV \* TSF interaction, Table 2), the amount of tree biomass in black spruce-dominated stands converged a few centuries after fire, regardless of fire severity (Figure 3A). Stands established after LS fires not only had a consistently thicker forest floor than stands established after HS fires (Figure 3B), but they also accumulated forest floor organic matter at a quicker rate (SEV \* TSF interaction, Table 2, Figure 3C).

The analysis of the paired HS and LS sites, with each pair originating from the same fire, demonstrated similar results; LS stands accumulated, since the last fire, a 73% thicker forest floor and 50% less tree biomass than the stands established after HS fires (Table 3). No significant difference was observed ( $P > 0.2$ ) between the paired sites with respect to soil topography and texture (data not shown).

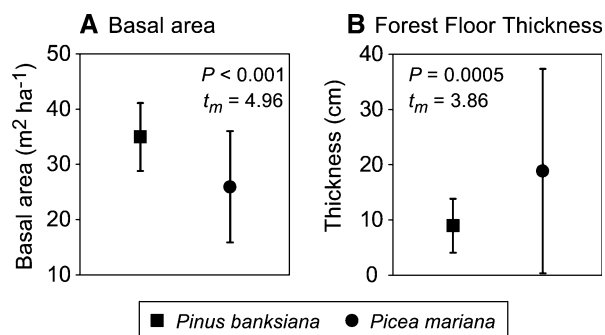


Figure 2. Basal area (A) and total forest floor thickness (B) of the two composition types [*Pinus banksiana* ( $n = 18$ ) and *P. mariana* ( $n = 84$ )] from the QMNR database. Error bars are standard deviations.

After an initial burst and subsequent significant drop, tree biomass of *P. mariana* stands established after HS fires continued to decrease in the millennial absence of fire but at a much reduced rate (Figure 4A). Similarly, forest floor thickness, which increased significantly during the first couple of centuries, continued to increase in the long term but at a much slower rate (Figure 4B). Interestingly, forest floor thickness and standing tree biomass values for old stands (> 250 years) established after HS fires are similar to that of much younger stands (< 150 years) established after LS fires (Figure 4).

### Forest Floor Survey

Forest floor characteristics significantly changed in the extended absence of fire and the upper and lower horizons within forest floor profiles changed differently (Figure 5A). Although the density of the lower forest floor layer significantly increased in the absence of fire, it slightly decreased in the upper forest floor layer. Consequently, although the accumulation of the forest floor organic matter measured as thickness appeared to slow down a few centuries after fire (Figure 4B), forest floor biomass increased linearly at a rate of  $58 \text{ g m}^{-2} \text{ y}^{-1}$  for numerous centuries after fire (Figure 5B). Total biomass (tree + forest floor pools) remained more or less constant for a few centuries after fire to subsequently increase exponentially (Figure 5B). Although ecosystem biomass may not have changed during the first few centuries after fire, the partitioning of this biomass among the tree and forest floor pools was significantly affected during this period (Figure 5B). Biomass in young stands was primarily (> 60%) locked-up in the tree pool, whereas it progressively became locked-up in the forest floor pool (> 80%) as succession proceeded.

## DISCUSSION

### Initial Tree Composition

With the QMNR database, under similar abiotic conditions, *Pinus banksiana* stands appeared to accumulate less organic matter and produce more standing tree basal area than *P. mariana* stands. However, when the stand characteristics were compared between *P. mariana* and *Pinus banksiana* stands under similar abiotic conditions and after fires of comparable severity (chronosequence dataset), no significant difference in forest floor thickness or standing tree biomass emerged between the stand composition types. However, fire severity had significant effects on biomass dynamics, with *P. mariana* stands established after LS fires showing thicker forest floors and lower standing tree biomass than stands established after HS fires. We therefore suggest that the apparent differences observed between stand composition types using the QMNR database is a result of the restriction of *Pinus banksiana*'s regeneration to sites with little ROM (HS fires) and the lack of qualification of fire severity during this inventory. Studies probing the short-term effects of residual organic matter (ROM) on post-fire regeneration have demonstrated that coniferous tree regeneration is negatively affected by an increase in the ROM thickness (Zasada and others 1983). However, *P. mariana* regeneration appears to be less affected than *Pinus banksiana*'s regeneration (Chrosiewicz 1974, 1976; Jøglum 1979). The rarity of *Pinus banksiana* stands established after LS fires may also be a consequence of low post-fire seed availability, as some have suggested that LS fires are a result of long fire intervals that permit an excessive accumulation of forest floor humus (Foster 1985) and a replacement of *Pinus banksiana* by *P. mariana* after the first post-fire century (Lesieur and others 2002; Lecomte and Bergeron 2005). These results, and the erroneous conclusions we would have drawn with the QMNR database, are a testimony to the importance of qualifying the severity of the last fire to understand the full range of ecosystem processes occurring in the boreal forest.

These results contradict our hypothesis and previous reports, which stated that organic matter accumulation above the mineral soil is reduced whereas tree biomass production is enhanced in *Pinus banksiana* stands as compared to *P. mariana* stands (for example, Gower and others 1997; Yu and others 2002; Miyanishi and Johnson 2002). As the severity of the last fire has rarely been taken into account in previous work in the boreal forest,



**Table 2.** Results of Linear Modeling for Tree Biomass and Total and Post-fire Forest Floor Thickness using the Medium Term (< 250 years;  $n = 42$ ) Chronosequence Dataset

Response variables	Source	F	P
Tree biomass (kg m <sup>-2</sup> ) $R^2 = 0.58$	Initial composition (COMP)	–	N.S.
	Fire severity (SEV)	15.01	<b>&lt; 0.0001</b>
	Time since fire (TSF)	3.49	<u>0.070</u>
	COMP * TSF	–	N.S.
	SEV * TSF	2.89	0.098
	TSF * TSF	4.72	<u><b>0.036</b></u>
Total forest floor thickness (cm) $R^2 = 0.74$	Initial composition (COMP)	–	N.S.
	Fire severity (SEV)	93.54	<b>&lt; 0.0001</b>
	Time since fire (TSF)	35.40	<b>&lt; 0.0001</b>
	COMP * TSF	–	N.S.
	SEV * TSF	–	N.S.
	TSF * TSF	–	N.S.
Post-fire forest floor thickness (cm) $R^2 = 0.74$	Initial composition (COMP)	–	N.S.
	Fire severity (SEV)	1.69	0.201
	Time since fire (TSF)	63.87	<b>&lt; 0.0001</b>
	COMP * TSF	–	N.S.
	SEV * TSF	3.51	<u>0.069</u>
	TSF * TSF	–	N.S.

Total forest floor thickness comprises both post-fire and residual forest floor organic matter. Effects significant at the 0.05 and 0.10 level are in boldface and underlined, respectively. N.S., not significant.

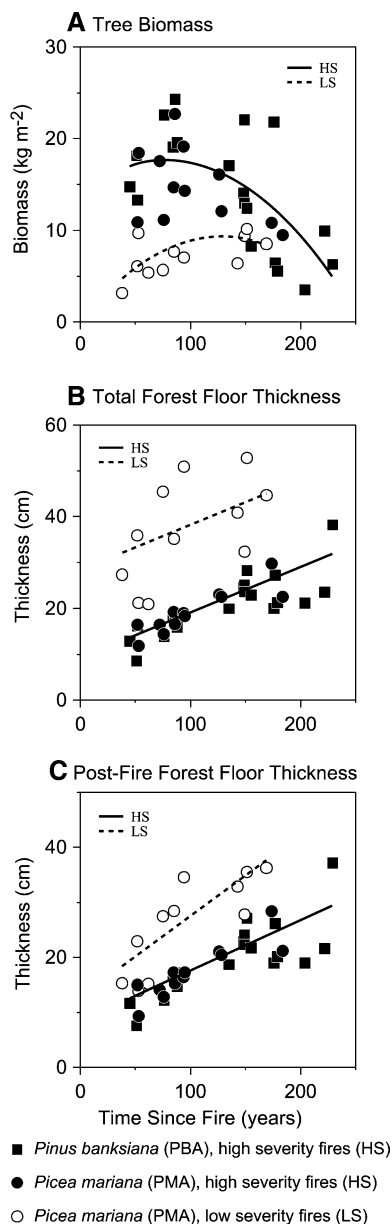
these earlier reports may not have controlled sufficiently for fire severity and/or edaphic conditions. We postulate that under similar post-fire abiotic conditions, *P. mariana* stands may be as productive as *Pinus banksiana* stands, which reflects *P. mariana*'s plasticity with respect to its ability to grow as an early successional fast-growing species and as a late successional slow-growing species (Dix and Swan 1971). Furthermore, although we assumed black spruce litter decomposed at a slower rate than pine litter because of high litter C:N ratio and lignin content (Preston and others 2000), recent work over a 6-year period indicates that *P. mariana* needles may actually decompose as fast as *Pinus banksiana* needles despite having a higher lignin:N ratio (Trofymow and others 2002). In the end, the physiological plasticity of *P. mariana* and the slight differences in litter decomposition rates of the two species are probably the main reason we did not observe a difference in forest floor thickness and tree biomass dynamics between the composition types.

### Extended Absence of Fire

As succession proceeds after HS fires, forest floors not only become thicker, but also denser because of compaction and humification of lower horizons. Although the accumulation rate of organic matter,

measured as thickness, appears to slow down a few centuries after fire, it actually remains constant for numerous centuries after fire when expressed as dry biomass. Concurrently, after a peak in tree biomass a few decades after fire (80 years after HS fires), tree biomass declined rapidly during the following century and at a much reduced rate afterwards. Consequently, biomass partitioning is clearly regulated by the prolonged absence of fire. As succession proceeds, forest ecosystem biomass is progressively bound up in belowground biomass, whereas young stands have proportionately more biomass bound up in living trees. That the older stands contained much higher belowground biomass levels than younger ones supports the notion that wild fire is of critical importance in reversing forest floor biomass lock-up in boreal forest ecosystems (Wardle and others 1997; O'Neill and others 2002; Van Cleve and Viereck 1981; Heinselman 1981).

One intriguing aspect of our data is that since forest floor biomass accumulation occurs whenever decomposition rates are outpaced by the rate of detritus production, how can boreal forest floors continually accumulate biomass for numerous centuries after fire with an apparent drop in standing tree biomass and hence tree productivity? Although some have demonstrated that bryophytes and understory shrub species can represent a sig-



**Figure 3.** **A** Standing tree biomass, **B** total forest floor thickness and **C** post-fire forest floor thickness in relation to time since the last fire, using the medium term chronosequence dataset. Each symbol represents a stand ( $n = 42$ ).

nificant portion of annual biomass production (Chapin 1983; O'Connell and others 2003), it is unlikely that they could compensate for the dramatic loss in tree productivity we observe in the Clay Belt. An explanation may be that decomposition rates decline through time, hence maintaining forest floor biomass accumulation constant although biomass production decreases.

Although there is little change in tree composition along the black spruce chronosequence, the bryophyte community shows a succession from

a feathermoss-dominated community (primarily *Pleurozium schreberi*) to one that is dominated by *Sphagnum* species (Boudreault and others 2002; Lecomte and others 2005), as others have reported in eastern North American boreal forests (Foster 1985; Taylor and others 1997). The presence of *Sphagnum* spp. have been shown to change water balance (Klenk 2001), lower soil temperatures (Van Cleve and Viereck 1981), reduce litter quality and consequently reduce decomposition rates (Zoltai and others 1998). Alternatively, the decrease in decomposition rates may be due to a positive feedback effect where the accumulation of forest floor humus, by dampening soil temperatures (Heinselman 1963; Swanson and others 2000; Klenk 2001; Fenton and others 2006), simply lowers decomposition rates which maintains forest floor accumulation rates constant as tree productivity decreases.

The forest floor organic matter accumulation rates we report for *P. mariana* forests on the Clay Belt ( $58 \text{ g m}^{-2} \text{ y}^{-1}$ ) are closer to accumulation rates in North-American peatlands (bogs and fens) (Gorham and others 2003) than those reported for boreal forests (for example, Wardle and others 2003). Gorham and colleagues (2003) compared peat accumulations rates in 32 sites from Alaska to Newfoundland and reported long-term rates that ranged from  $16$  to  $80 \text{ g m}^{-2} \text{ y}^{-1}$  with a median rate of  $47 \text{ g m}^{-2} \text{ y}^{-1}$  and a mean rate of  $50 \text{ g m}^{-2} \text{ y}^{-1}$ . Depending on the methods used to calculate accumulation rates, the authors reported rates between  $54.6$  and  $62.2 \text{ g m}^{-2} \text{ y}^{-1}$  for a peatland site located near our study area (Lac Parent, Quebec  $48^\circ 47' \text{N}$ ,  $77^\circ 10' \text{W}$ ). The close agreement between these completely independent estimates of forest floor accumulation rates suggests that our chronosequence method of calculating peat accumulation in forested landscapes is valid.

The rate of carbon storage in the forest floor within the boreal zone of Sweden was estimated at about  $5 \text{ g C m}^{-2} \text{ y}^{-1}$  (Wardle and others 2003). Assuming that forest floor biomass is on average 40 to 50% carbon in black spruce forests (Wang and others 2003; M. Simard, unpublished data) the reported rate of carbon accumulation in the forest floor organic matter for the Clay Belt would be close to five times higher than those reported for the boreal forest of Sweden. The higher rate of biomass accumulation and lock-up in the Clay Belt may be due to different ground cover compositions and to the underlying clay mineral soil. The gradual invasion of *Sphagnum* species over the course of succession in the Clay Belt may enhance the primary production of mosses or decrease decomposition, resulting in higher accumulation of organic

**Table 3.** Paired *t*-tests for Mean ( $\pm$  SD) Total and Post-fire Forest Floor Thickness, and Tree Biomass with four Pairs of *Picea mariana* Stands which Originated from the Same Fire but Differed with respect to Fire Severity

Response variables	High severity	Low severity	<i>P</i>
Tree biomass (kg m <sup>-2</sup> )	15.4 (3.8)	7.6 (1.5)	<b>0.01</b>
Total forest floor thickness (cm)	16.5 (3.4)	35.7 (12.1)	<b>0.03</b>
Post-fire forest floor thickness (cm)	14.4 (3.6)	24.9 (8.8)	<b>0.04</b>

Data from the chronosequence survey.

Total forest floor thickness comprises both post-fire and residual forest floor organic matter.

Significant effects at ( $P < 0.05$ ) are given in bold.

matter compared to forest floors that lack these species, such as in Wardle and others (2003). The appearance of fast-growing *Sphagnum* species might in turn be favored by the underlying clay mineral soil that retains more water than the moranic deposits of the Swedish study.

### Fire Severity and Convergence

This study suggests that LS fires hamper the production of tree biomass, but enhance the accumulation of forest floor organic matter and thus influence ecosystem biomass partitioning. The similarity in thickness of forest floor organic matter and standing tree biomass between very old stands (> 250 years) established after HS fires and the relatively young stands (< 150 years) established after LS suggests that LS fires do not fully reverse the biomass lock-up in forest floor organic matter observed in this landscape.

Although long-term studies on the effects of fire severity on stand development are lacking, there are several studies at shorter time scales that might shed light on the processes that may be responsible for the significant differences observed between severity types. Partially burned residual organic matter has been shown to be a poor regeneration seedbed for most boreal tree species, reducing germination, early survivorship, and growth, compared to mineral or thin humus seedbeds (Chrosiewicz 1974, 1976; Zasada and others 1983, 1987; Charron and Greene 2002; Brais and others 2000). Furthermore, LS fires tend to favor understory species that possess an abundant buried propagule bank within the forest floor (Rydgren and others 2004; Schimmel and Granstrom 1996) notably the peat mosses (*Sphagnum* spp.) with their extraordinary ability to resprout from tissues deeply buried in the humus layer (Clymo and Duckett 1986; Dyrness and Norum 1983). The high cover of *Sphagnum* spp. after LS fires may have further depressed tree biomass production because tree growth is negatively affected

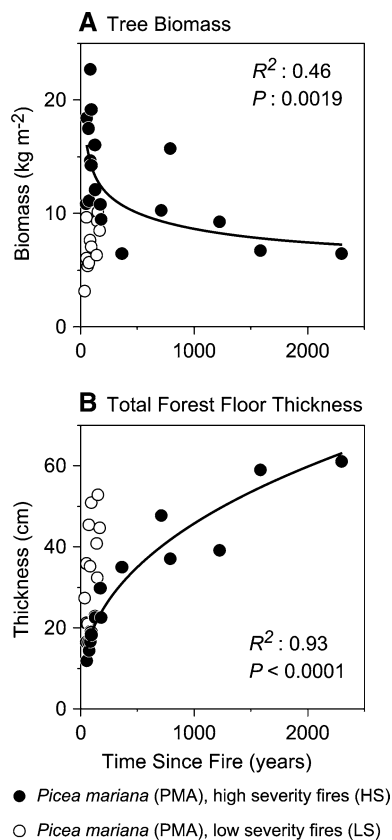
by increases in the thickness of peat derived from *Sphagnum* spp. (Heinselman 1963). Because deep forest floors and *Sphagnum* spp. may reduce decomposition rates, we postulate that these conditions, characteristic of young stands established after LS fires, are the main reasons forest floor biomass accumulation was enhanced and tree biomass was depressed after LS fires.

Our results demonstrate that in the short term, fire severity induces a divergence in ecosystem biomass accumulation rate and relative partitioning among carbon pools. Nonetheless, the continual accumulation of organic matter and the drop in tree biomass observed after HS fires suggests that ecosystems, with respect to biomass dynamics, may converge in the extended absence of fire as noted for other ecosystem attributes in coniferous forest (Kashian and others 2005; Lecomte and Bergeron 2005).

### CONCLUSION

This study demonstrates that *P. mariana* ecosystems established after HS fires continually accumulate biomass for numerous centuries after fire (> 700 years). After HS fires, ecosystem biomass partitioning was greatly altered as succession proceeded. Young stands had predominantly more biomass in living tree tissue whereas older stands had the majority of ecosystem biomass locked-up in forest floor organic matter. The post-fire dominance of *Pinus banksiana* had little effect on tree biomass production or forest floor thickness as compared to *P. mariana* stands. On the other hand, fire severity significantly impacted tree productivity and forest floor thickness. The passage of LS fires favored the accumulation of thicker forest floors but lower standing tree biomass than HS fires, and therefore soil-burn severity significantly influenced ecosystem biomass partitioning.

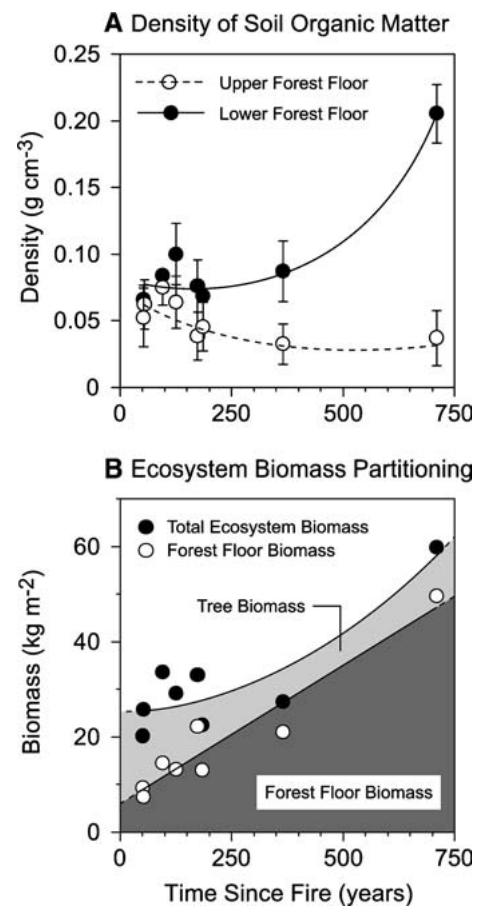
These findings, combined with the observed reduction in fire frequency since the end of the 'Little Ice Age' in the Clay Belt (approximately



**Figure 4.** **A** Standing tree biomass and **B** total forest floor thickness with time since fire using the long-term chronosequence dataset. The regression equation between time since fire (TSF) and tree biomass ( $BIOM_{TREE}$ ) is  $\log BIOM_{TREE} = -0.209 \log TSF + 1.56$ , and between time since fire (TSF) and total forest floor thickness ( $THCK_{FF}$ ) is  $\log THCK_{FF} = 0.384 \log TSF + 0.509$ .

1850; Bergeron and others 2001), may have induced a significant amount of carbon sequestration within forest floors of coniferous stands on the northern Clay Belt. If current global climate change continues to induce even longer fire cycles in the eastern boreal forest (Flannigan and others 2001), the boreal forest on the Clay Belt of northwestern Quebec may continue to act as a significant carbon sink in the future. The results from this study illustrate that the effects of long fire-free periods and fire burn severity should be accounted for in eastern boreal forest carbon inventories and models.

These results also indicate that an increase in forest floor thickness may negatively impact tree productivity. This has led some, including ourselves (Fenton and others 2005), to suggest that to increase or maintain stand yield, forest managers in the Clay Belt should favor silvicultural approaches that remove a significant portion of the forest floor accumulated above the mineral soil (scarification, controlled burning). These approaches appear to



**Figure 5.** **A** Changes in density ( $\pm$  standard deviation) of the forest floor in the upper and lower horizons. The regression equation between time since fire (TSF) and the density of the upper forest floor horizon ( $DENS_{UFF}$ ) is  $\log DENS_{UFF} = 0.00000151 TSF^2 - 0.00159 TSF - 1.12$ , and between time since fire (TSF) and the density of the lower forest floor horizon ( $DENS_{LFF}$ ) is  $\log DENS_{LFF} = 0.00000151 TSF^2 - 0.000508 TSF - 1.09$  ( $R^2 = 0.64$ ,  $P < 0.0001$  for the full model). **B** Total forest floor biomass and total ecosystem biomass (tree + forest floor) using the forest floor organic matter data set. The regression equation between time since fire (TSF) and total forest floor biomass ( $BIOM_{FF}$ ) is  $BIOM_{FF} = 0.0581 TSF + 6.03$  ( $R^2 = 0.92$ ,  $P = 0.0002$ ), and between time since fire (TSF) and total ecosystem biomass ( $BIOM_{ECO}$ ) is  $BIOM_{ECO} = 0.0000651 TSF^2 + 25.5$  ( $R^2 = 0.82$ ,  $P = 0.0021$ ).

make economic sense from a wood fiber production perspective. Nonetheless, from a climate change point of view, these approaches may prove very costly by releasing considerable amounts of carbon that have been sequestered in forest floor organic matter for centuries or even millennia. Careful studies should be undertaken to understand how current and alternative silvicultural practices might impact long-term carbon sequestration in the eastern boreal forest.

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**APPENDIX**  
**Appendix A.** Site Characteristics of Stands from the Chronosequence Survey

Site <sup>1</sup>	Initial composition <sup>2</sup>	<i>Pinus banksiana</i> basal area <sup>3</sup> (%)	Abundance of <i>Pinus banksiana</i> macroremains <sup>4</sup> (%)	Fire severity <sup>5</sup>	Residual OM <sup>6</sup>	Oldest tree <sup>7</sup>	Stand age			Mineral soil			Slope index (°) <sup>10</sup>
							Calibrated <sup>14</sup> C age (charcoal) <sup>8</sup>	Calibrated <sup>14</sup> C age (humus) <sup>9</sup>	Sand (%)	Silt (%)	Clay (%)		
30	Pine	80.0	88.5	High	1.2	45	-	-	1.5	22.0	76.5	1.0	
54	Pine	78.4	92.5	High	1.0	51	-	-	0.0	12.7	87.3	1.9	
61	Pine	78.8	77.1	High	1.5	51	-	-	6.5	21.5	72.0	5.1	
36	Pine	59.1	63.2	High	1.6	76	-	-	1.0	23.6	75.4	0.6	
38	Pine	37.2	75.2	High	1.6	84	-	-	0.0	9.0	91.0	0.7	
23	Pine	44.4	63.1	High	1.3	86	-	-	3.5	26.9	69.7	1.4	
57	Pine	58.4	57.2	High	1.2	88	-	-	13.0	45.5	41.5	1.2	
29	Pine	64.6	44.3	High	1.2	135	-	-	19.9	30.8	49.3	1.2	
69	Pine	43.9	40.7	High	1.1	139	-	-	2.0	34.3	63.7	1.9	
66	Pine	48.0	36.4	High	1.7	149	-	-	12.5	25.0	62.5	8.7	
73	Pine	68.4	27.9	High	1.3	149	-	-	26.0	25.0	49.0	1.5	
40	Pine	61.2	28.6	High	1.1	151	-	-	25.5	27.5	47.0	2.4	
49	Pine	48.4	35.7	High	1.2	155	-	-	14.0	63.0	23.0	2.1	
94	Pine	51.2	36.0	High	1.0	176	-	-	6.0	24.5	69.5	5.1	
83	Pine	56.8	61.7	High	1.0	177	-	-	4.0	20.0	76.0	1.0	
79	Pine	45.8	16.0	High	1.1	179	-	-	2.4	29.0	68.6	0.0	
65	Pine	57.3	8.8	High	2.1	204	-	-	14.0	32.5	53.5	0.8	
64	Pine	41.1	2.6	High	1.9	222	-	-	0.0	38.4	61.6	3.9	
67	Pine	22.3	0	High	1.0	229	-	-	0.0	28.6	71.4	1.4	
62*	Spruce	0.0	0.0	High	1.4	52	-	-	2.0	23.4	74.6	10.5	
4*	Spruce	0.0	0.0	High	2.5	53	-	-	0.0	38.1	61.9	2.5	
59	Spruce	13.7	11.7	High	2.3	72	-	-	13.0	22.5	64.5	1.7	
15	Spruce	6.1	30.3	High	1.5	76	-	-	10.3	27.9	61.8	-4.6	
2*	Spruce	0.0	0.0	High	1.9	84	-	-	0.0	21.0	79.0	0.6	
56	Spruce	0.0	0.0	High	1.3	86	-	-	13.5	28.5	58.0	0.8	
12	Spruce	0.0	0.0	High	1.1	95	-	-	0.0	20.9	79.1	2.1	
55*	Spruce	0.2	22.2	High	2.5	94	-	-	14.5	30.0	55.5	0.9	
18	Spruce	0.0	0.0	High	2.0	126	-	-	15.0	18.0	67.0	1.8	
75	Spruce	0.0	0.0	High	2.0	128	-	-	3.4	24.5	72.1	-1.3	
8	Spruce	0.0	0.0	High	1.4	174	-	-	9.0	25.5	65.5	1.4	
95	Spruce	0.0	0.0	High	1.3	184	-	-	3.0	26.0	71.0	1.7	
9	Spruce	0.0	0.0	High	1.5	215	1,225	-	11.5	23.5	65.0	1.6	
7	Spruce	0.0	0.0	High	1.7	217	790	-	7.5	27.0	65.5	1.1	
50	Spruce	0.0	0.0	High	2.0	222	365	-	19.0	27.0	54.0	1.3	

## Appendix A. Continued

Site <sup>1</sup>	Initial composition <sup>2</sup>	<i>Pinus banksiana</i> basal area <sup>3</sup> (%)	Abundance of <i>Pinus banksiana</i> macroremains <sup>4</sup> (%)	Fire severity <sup>5</sup>	Residual OM <sup>6</sup>	Oldest tree <sup>7</sup>	Stand age			Mineral soil		
							Calibrated <sup>14</sup> C age (charcoal) <sup>8</sup>	Calibrated <sup>14</sup> C age (humus) <sup>9</sup>	Sand (%)	Silt (%)	Clay (%)	Slope index (°) <sup>10</sup>
6	Spruce	0.0	0.0	High	3.2	280	710	555	1.0	22.7	76.4	0.4
16	Spruce	0.0	0.0	High	2.7	286	1,585	705	10.0	18.0	72.0	0.5
20	Spruce	0.0	0.0	High	3.2	353	2,355	-	5.9	22.8	71.3	1.9
11	Spruce	0.0	0.0	Low	12.0	38	-	-	21.0	29.5	49.5	1.1
74*	Spruce	0.0	0.0	Low	13.0	52	-	-	6.0	26.5	67.5	1.3
53*	Spruce	0.0	0.0	Low	7.3	53	-	-	20.0	31.0	49.0	0.6
58	Spruce	0.0	0.0	Low	5.8	62	-	-	23.0	30.5	46.5	2.1
78	Spruce	0.0	0.0	Low	17.9	75	-	-	17.0	28.0	55.0	0.6
60*	Spruce	0.0	17.6	Low	6.7	84	-	-	9.0	15.0	76.0	1.2
3*	Spruce	0.0	0.0	Low	16.2	94	-	-	1.9	16.0	82.0	0.0
68	Spruce	3.2	4.9	Low	4.6	139	-	-	1.0	22.7	76.4	0.8
63	Spruce	0.0	0.0	Low	7.9	143	-	-	2.0	18.5	79.5	0.8
17	Spruce	0.0	0.0	Low	17.3	151	-	-	17.5	33.0	49.5	0.8
5	Spruce	0.0	0.0	Low	8.4	169	-	-	13.9	47.6	38.5	0.3

<sup>1</sup>Sites in boldface were part of the organic matter survey and those with an asterisk are the paired sites originating after the same fire but differing with respect to fire severity.

<sup>2</sup>Initial stand composition determined from the composition of dead and live trees as well as plant remains in forest floor profiles (see Methods).

<sup>3</sup>Includes both live and dead stems greater than 2 m in height.

<sup>4</sup>Abundance of *P. banksiana* macroremains in forest floor profiles relative to all tree macroremains found in the last fire (see Methods).

<sup>5</sup>Fire severity determined from the thickness of the residual organic matter (see Methods).

<sup>6</sup>Thickness of the residual organic matter, that is, the organic matter that was not burned by the last fire.

<sup>7</sup>Stand age determined from tree-ring analysis. Stands where the post-fire cohort of trees was not found were given a minimum age and were radiocarbon dated.

<sup>8</sup>Radiocarbon datings obtained from humus accumulated just above the uppermost charcoal layer (from Cyr and others 2005).

<sup>9</sup>Radiocarbon datings obtained from humus accumulated just above the uppermost charcoal layer (from Cyr and others 2005).

<sup>10</sup>Slope Index integrates slope incline and landform shape, and can assume positive (mounds or regular slopes) or negative values (depressions) (see Methods).