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*The Holocene* 2012 22: 191 originally published online 1 September 2011
DOI: 10.1177/0959683611414931

Research paper

The Holocene
22(2) 191–201

DOI: 10.1177/0959683611414931
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# Long-term fire and forest history of subalpine balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) stands in eastern Canada inferred from soil charcoal analysis

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**Abstract**
The northernmost balsam fir forest in eastern Canada forms disjunct stands far beyond the extensive balsam fir forest zone of southern Canada. The northern balsam fir stands are distributed in the subalpine belt of high plateaus and coexist locally with white spruce stands. These subalpine stands contrast greatly with black spruce forest stands located in lowlands. Given that subalpine stands are remnants of an earlier northern expansion of the balsam fir forest, the main objective of this study is to assess whether white spruce stands are distinct communities having diverged from the balsam fir forest community earlier in the Holocene or if they rather correspond to a different stage of the chronosequence within the subalpine belt. Macrofossil analysis of charcoal in mineral soils was used to compare the stand-scale fire histories and taxonomic fossil composition of subalpine, old-growth balsam fir stands and white spruce stands. No significant differences of mean number of observed fires (mean = 6.35 fires per site), Holocene fire recurrence at the landscape scale and mean fire-return interval (mean = 580 years) were found between white spruce stands and balsam fir stands. The botanical composition of charcoal fragments from mineral soils showed that *Abies*, *Betula* and *Picea* were present throughout the fire period from 5600 cal. BP to present, and no difference was found in the fossil composition of the balsam fir and white spruce stands. No historical change in the botanical composition of charcoal from soils of both stand types was observed indicating that the initial floristic composition remained through the period of recurrent fires. Charcoal data suggest that white spruce stands are not divergent community types. Rather, the two community types are arranged along a chronosequence of different successional stages within the subalpine relict flora.

**Keywords**
$^{14}$C AMS dating, *Abies balsamea*, boreal forest, charcoal analysis, eastern North America, ecological succession, macrofossil analysis, mineral soil charcoal, *Picea glauca*

## Introduction

In eastern North America, the extensive balsam fir (*Abies balsamea* (L.) Mill.) forest corresponds to the southernmost boreal zone located between the mixed forest to the south, and the closed-crown spruce-moss boreal forest to the north (Grandtner, 1966; Rowe, 1972; Figure 1). The balsam fir forest is dominated by balsam fir whereas white spruce (*Picea glauca* (Moench.) Voss.) and white birch (*Betula papyrifera* Marsh.) are companion species. The adjacent spruce-moss zone is dominated by extensive tracts of closed-crown black spruce (*Picea mariana* (Mill.) B.S.P.) forest stands interspaced with monospecific stands of jack pine (*Pinus banksiana* Lamb.). Of all the widespread North American boreal tree species, white spruce and especially balsam fir are the least adapted to fire, whereas jack pine and black spruce are fire-adapted species (Rowe and Scotter, 1973). Wildfires constitute the primary disturbance in the spruce-moss zone whereas the balsam fir zone is not so much affected by recurrent fires (de Lafontaine and Payette, 2010). This suggests that fire disturbance is a major ecological forcing factor accounting for the distinctiveness of the two boreal zones. The northernmost balsam fir stands are distributed in the subalpine belt of three high plateaus (Monts Otish, Montagnes Blanches and Monts Groulx; *c*. 1000 m above sea level (a.s.l.)) 300 to 500 km north of the extensive balsam fir zone, well into the black spruce zone (Figure 1). The balsam fir stands coexist at the same elevation with other isolated, subalpine communities dominated by white spruce under the same environmental and climatic conditions. It has been hypothesized that the two subalpine forest assemblages are remnants of a past northern expansion of the balsam fir forest zone (de Lafontaine et al., 2010). Palynological data suggest that the balsam fir flora expanded to its extant northernmost limit sometime between 7500 and 6000 cal. BP (King, 1986). Charcoal data suggested that balsam fir stands were isolated in the subalpine belt of the high plateaus as a result of a change in the fire regime around 5000 cal. BP which caused the decline of the balsam fir flora and its zonal replacement by the spruce-moss forest in the lowlands (de Lafontaine and Payette, 2011). Whereas these paleoecological

Received 8 October 2010; revised manuscript accepted 8 May 2011

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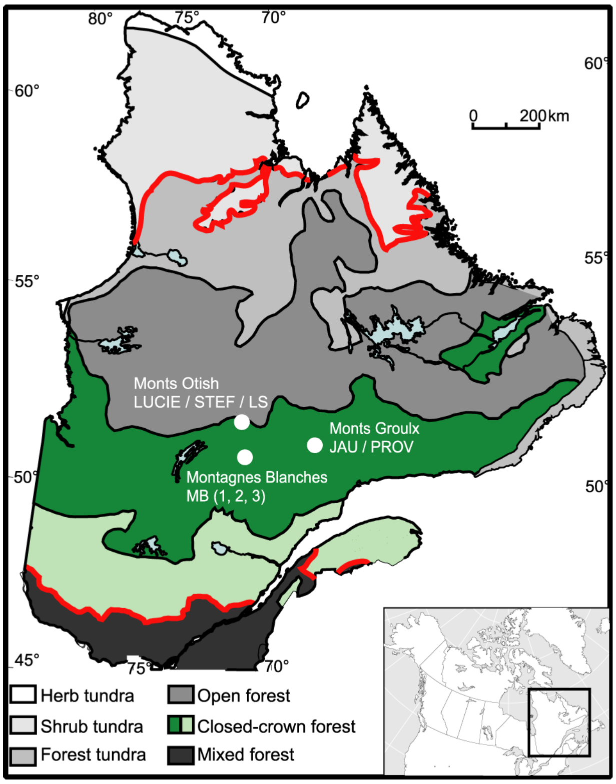


**Figure 1.** Location of sampled sites. The main bioclimatic zones of Québec are represented; the zones corresponding to the boreal biome are between the two red lines. Note that the closed-crown forest is roughly subdivided along 49°N in two ecological regions represented by different shades of green; the paler green represents the balsam fir zone whereas the darker green represents the black spruce zone. For interpretation of the references to color in this figure legend, the reader is referred to the online version of this paper

data accounted for the origin of the northernmost balsam fir stands, the origin of white spruce stands coexisting with balsam fir stands in the subalpine belt of the high plateaus remains unclear.

The local coexistence of white spruce and balsam fir stands on the northern high plateaus forms a mosaic of forest stands throughout the subalpine belt. White spruce stands could either have a long-lasting ecological history different from their co-occurring balsam fir stands or they could represent a postdisturbance successional stage within the residual balsam fir forest assemblage. Recent inferences based on forest stand structure and composition suggested that white spruce stands may be early seral communities of a post-fire chronosequence eventually converging towards late-successional balsam fir stands (de Lafontaine and Payette, 2010). However, the ecological status of white spruce stands within the subalpine belt was not addressed directly to evaluate the possibility of a long-term, steady-state, ecological differentiation between the two stand types. Indeed, the alternative explanation for the coexistence of contrasted stand types under the same climatic conditions is the long-lasting transformation of a stand type into a divergent, steady-state, stand type (Holling, 1973; Lewontin, 1969; May, 1977; Payette, 1992; Scheffer et al., 2001; Sutherland, 1974). This can occur after a change in the disturbance regime or after a series of compounded disturbances (Jasinski and Payette, 2005; Paine et al., 1998; Payette and Delwaide, 2003; Payette et al., 2000). Many empirical studies in different areas of the boreal forest have shown that historical changes in the disturbance (fire) regime were instrumental for such a community transformation. The process was observed in the forest tundra where former lichen woodland stands shifted into deforested tundra as a result of a postfire regeneration failure (Asselin and Payette, 2005; Payette and Gagnon, 1985; Payette et al., 2001). The transformation of former spruce-moss stands into lichen woodland in the closed-crown boreal forest was the outcome of compounded disturbances (fire and insect outbreaks) causing a regeneration failure which opened the stands (Girard et al., 2008; Jasinski and Payette, 2005; Payette and Delwaide, 2003; Payette et al., 2000).

The aim of this study is to compare the paleoecological records of northern subalpine white spruce and balsam fir stands in order to assess whether the two community types are divergent steady-states with contrasted long-term stand histories or if they represent different postdisturbance successional stages resulting from the ongoing disturbance regime within the residual balsam fir forest. If the two community types are divergent steady-states, the reconstruction of the botanical assemblages from fossil charcoal and the historical fire records should be different between the subalpine white spruce and balsam fir stands. They are considered divergent steady-states if a historical shift occurred in the community composition (i.e. a transition from one community type to another) associated with a change in the disturbance regime and if the contrasted community types persist through time. On the other hand, the stands are considered seral stages if the two community types are part of the same ecological dynamics within the subalpine belt. Macrofossil analysis of charcoal in mineral soils (Talon et al., 2005) was used to assess these two alternative scenarios by comparing in situ Holocene fire and community composition history of northern white spruce and balsam fir stands located in the subalpine belt of the high plateaus of the spruce-moss boreal zone.

## Materials and methods

This study was based on a data set comprising 12 old-growth subalpine stands, including six white spruce stands and six balsam fir stands (plot size: 50 m × 10 m or 50 m × 20 m) (Appendix 1). Data from the balsam fir stands were from a previous study (de Lafontaine and Payette, 2011) which specifically documented Holocene fire regimes of subalpine balsam fir stands from central Québec (this study) and extensive balsam fir stands located in the southern boreal zone of southern Québec. Data from subalpine balsam fir stands are used here in direct comparison with similar data from nearby, co-occurring white spruce stands in order to test a specific hypothesis regarding the past composition and disturbance history of subalpine balsam fir and white spruce stands. A total of four sites (two white spruce and two balsam fir stands) were sampled during growing seasons of 2006, 2007 and 2008 in each of the high elevated plateaus (Monts Otish, Montagnes Blanches and Monts Groulx; Figure 1). In this remote area, the nearest weather station is located *c*. 80 km southwest of the southernmost high plateau (Bonnard weather station: 50°43'N, 71°03'W, 506 m a.s.l.). The average annual temperature is −1.8°C, with July and January being the warmest (average 14.6°C) and coldest months (average −21°C), respectively. The average annual precipitation is 950 mm with 32% falling as snow. The growing season >0°C is 134 days. Average climatic data are based on the period between 1971 and 2000 available online from Environment Canada, Canada's National Climate Archives (www.climate.weatheroffice.ec.gc.ca). Common species in the white spruce stands are *Picea glauca* and *Abies balsamea* (trees); *Alnus viridis* ssp. *crispa* (Aiton) Pursh, *Betula glandulosa* Michx., and *Ribes glandulosum* Grauer (shrubs); *Calamagrostis canadensis* (Michx.) P. Beauv., *Clintonia borealis* (Aiton) Raf., *Coptis trifolia* (L.) Salisb., *Cornus canadensis* L., and *Solidago macrophylla* Pursh. (herbs). High abundance species in the balsam fir stands are *Abies balsamea* and *Picea glauca* (trees); *Vaccinium uliginosum* L. (shrub); *Clintonia borealis* (Aiton) Raf., *Coptis trifolia* (L.) Salisb., *Cornus canadensis* L., *Rubus chamaemorus* L., *Solidago macrophylla* Pursh., and *Trientalis borealis* (herbs).; *Gymnocarpium dryopteris* (L.) Newman (fern); *Dicranum* sp., *Pleurozium schreberi* (Brid.) Mitt., and *Ptilium crista-castrensis* (Hedw.) De Not. (mosses). A general comparison with published data on species composition of the boreal landscape (Desponts et al., 2004; Jurdant, 1959; La Roi, 1967; Pollock and Payette, 2010) suggests that the common flora of these stands is more typical of the southern balsam fir forest of the fir zone than that of the surrounding black spruce forest in the lowlands. A detailed ecological description of the study sites including species composition, stand structure and recent ecological dynamics is available in de Lafontaine and Payette (2010).

### *Charcoal extraction and botanical identification*

Charcoal analysis was based on the sampling of 25 soil cores at each site. Cores were sampled every 5 m along the plot perimeter (or at 10 m along the 20 m edges of 1000 m$^2$ plots) with a core in the middle of the plot. For each core, the organic topsoil was thoroughly examined in order to record any charcoal present in the organic layer. Because no such charcoal was found at any site, the organic topsoil was completely eliminated and charcoal particles were collected at the mineral soil surface, when present. At sites where no charcoal was found, basal organic matter (H horizon) was collected in order to obtain a minimum age of the stand without fire disturbance (all records from the organic/mineral interface were published in de Lafontaine and Payette, 2010). Next, a 10 cm long mineral soil core (750 cm$^3$) was extracted with a soil auger. Upon arrival at the laboratory, the mineral deposit of each core was immersed for 12 h in a solution of sodium hydroxide (NaOH 1%) to disperse soil aggregates. The material was then washed with water in sieves with mesh sizes of 4 mm and 2 mm. There is very little doubt that charcoal of that size (≥ 2 mm) was produced and deposited in situ, and not transported from extralocal source. Even charcoal as small as 0.5 mm are considered to be of local origin (Ohlson and Tryterud, 2000). Charcoal was extracted from the mineral fraction by flotation and manual sorting under a binocular microscope (Thinon, 1992). Charcoal particles were dried at room temperature, weighted, and particles (> 2.5 mg) were identified to the genus level based on wood anatomy under an optical microscope with the aid of a charred wood reference collection at the Centre d'Études Nordiques (Université Laval, Québec) and botanical keys (Schoch et al., 2004; Schweingruber, 1978, 1990). Because sites STEF and LUCIE had considerable amount of charcoal (1154 and 1503 particles, respectively), identification was limited to particles ≥ 5 mg.

### *Radiocarbon dates*

At each site, at least eight charcoal particles extracted from the soil cores were radiocarbon dated by the AMS (Accelerator Mass Spectrometry) technique. Selection of charcoal fragments to be dated was based on dry weight of the particles (> 3 mg), botanical identification (i.e. when possible, equal amount of *Abies* and *Picea* charcoal and at least one *Betula* particle), spatial distribution of the 25 soil cores and randomness. Other radiocarbon dates ($n \geq 3$ dates per site) were added to the data set either from charcoal collected at the organic/mineral soil interface or from basal organic matter (H horizon), in the absence of charcoal (data taken from de Lafontaine and Payette, 2010). Radiocarbon dating was performed at the Centre d'Études Nordiques (Université Laval, Québec) and Keck Carbon Cycle AMS Facility (University of California, Irvine) laboratories. The radiocarbon dates were calibrated using calibration dataset IntCal04.14c (Reimer et al., 2004) implemented in CALIB (version 5.0.1) software (Stuiver et al., 2005).

### *Reconstruction of fire histories*

At each site, the determination of fire events was based on the cumulative probabilities analysis (Meyer et al., 1992) using the 'sum probabilities' option in CALIB 5.0.1 (Stuiver et al., 2005) to plot the probability that a given event occurred at a particular time (Fesenmyer and Christensen, 2010; Lafortune et al., 2006; Sanborn et al., 2006). This method sums the probabilities of all dates and therefore takes into account the uncertainties inherent to radiocarbon dating. The main caveat with soil charcoal analysis is that the radiocarbon age of a charcoal fragment corresponds to the time when the wood that comprises charcoal was actually produced and not to the actual age of a fire event. Such 'inbuilt age error' is additive to the radiometric error and implies that, in some specific cases, radiocarbon age may be several centuries older than the actual date of the fire which produced charcoal. The inbuilt error depends on stand age structure and rate of wood decay (Gavin, 2001; Gavin et al., 2003) and by the prevailing fire regime itself (Higuera et al., 2005). In humid, coastal forests of the western US and Canada, large inbuilt age values (up to 670 yr) may add a significant error that must be acknowledged and handled (Gavin, 2001). However, such high inbuilt age values are specific to the North American coastal rainforest and should not necessarily be applied to other forest ecosystems. Indeed, these large inbuilt age values were found in very wet sites (annual precipitation: > 3500 mm) having long fire interval (mean time since fire: 740 to more than 4400 yr) and containing long-lived trees species (> 1000 yr) with slow decaying rate (> 1000 yr) (Gavin, 2001; Gavin et al., 2003). In sites experiencing more frequent fires with short-lived trees and fast decaying wood, as in the eastern closed-crown boreal forest (estimations of mean fire interval are all between 100 and 570 yr (Bouchard et al., 2008; Cogbill, 1985; de Lafontaine and Payette, 2011; Parisien and Sirois, 2003; Payette et al., 1989), mean tree longevity is *c.* 150 yr at our study sites (data not shown), mean wood decaying time is *c.* 60 yr after disturbance (Moroni, 2006)), the radiocarbon dates of charcoal should correctly approximate the actual dates of fire.

Charcoal particles were originally buried in mineral soil by tree uprooting. Their position in the soil profile was further reworked by subsequent uprooting events and biotic activity. As such, they are not stratified in soils (Carcaillet, 2001; Fesenmyer and Christensen, 2010) and one may argue that a random sampling of charcoal particles for radiocarbon dating does not reflect the actual fire history of a site. To address this issue, we computed asymptotic accumulation curves from our $^{14}C$ data to estimate by extrapolation the expected maximum number of fire events occurring at each site. The rationale for the asymptotic accumulation curve is similar to the 'species accumulation curve' or 'collector's curve', a plot of the cumulative number of species discovered, within a defined area, as a function of some measure of the sampling effort expended to find them (Colwell and Coddington, 1994; Soberón and Llorente, 1993). The collector's curve allows an estimate (by extrapolation) of the actual number of species in an area (thus estimating the number of species missed by the empirical sampling). In the context of inferring stand-scale fire histories, the asymptotic accumulation curves allowed us to estimate how many fire events were missed in each reconstruction of local fire history (i.e. the number of actual fire events not included in our sampling). The actual number of stand-scale fire events is a finite, discrete number; as is the actual number of species in a given area, whereas the number of radiocarbon date per site represents the sampling effort. To built the accumulation curves, we first plotted the number of recorded fire events ($F(n)$) as a function of the number of radiocarbon dated charcoal particles ($n$). We then extrapolated an expected number of fire events ($F_{max}$) by fitting an asymptotic, negative exponential function:

$$F(n) = F_{max}(1-e^{Kn}) \quad (1)$$

where $F_{max}$, the asymptote, is the estimated expected number of fire events at each site, and $K$ is a fitted constant that controls the shape of the accumulation curve (Holdridge et al., 1971; Soberón and Llorente, 1993). Equation parameters were calculated by using an online curve-fitting website (http://zunzun.com). An adjusted $F_{max}$ was obtained by removing the decimals in order to provide a finite, discrete number corresponding to the expected number of fire events. The difference between adjusted $F_{max}$ and the number of recorded fire events corresponds to an estimation of the number of fire events missed by our sampling.

It must be acknowledged that there are many estimators to model the 'collector's curve' (Colwell and Coddington, 1994). We found that the asymptotic, negative exponential function gave a more realistic number of fire events when compared with other estimators (data not shown). This was most obvious at sites where few fire events were recorded and empirical data quickly approached the asymptote, typically, other tested estimators overestimated the number of fire events. Yet, the accumulation curve remains an extrapolation procedure and should be interpreted as a relative appreciation of the completeness of our reconstructions of local fire history, not indicate the true number of fire events. The true number of fire events would be obtained by radiocarbon dating all charcoal particles on each site which is currently impracticable given the high cost of AMS radiocarbon dates.

Regional fire histories of balsam fir stands, white spruce stands, and central Québec subalpine stands were computed by pooling the radiocarbon dates from the six balsam fir stands, the six white spruce stands, and all 12 sampled stands, respectively. The cumulative probabilities analysis was run on each pooled data set (Meyer et al., 1992). We compared the parameters of the regional fire histories (number of fire events, period of active fire and fire-return interval) of the white spruce stands with those of the balsam fir stands. In this way, we were able to assess if contrasted Holocene fire regimes are an explanatory factor for the difference between balsam fir and white spruce forest communities.

### *Historical forest composition*

Holocene arboreal composition was inferred from botanically identified and radiocarbon-dated charcoal particles. The number of charcoal particles of each tree taxa in successive 500 cal. yr intervals between 6000 cal. BP to present was used to reconstruct past forest composition. These inferences were made for each site and then for all balsam fir stands taken as a group, for white spruce stands as another group, and for a last group including all subalpine stands. A visual comparison of the past arboreal compositions was made between balsam fir and white spruce stands to assess if the macrofossil assemblages of these communities differed during the Holocene.

## Results

### *Charcoal abundance and botanical identification*

Charcoal was found at the organic/mineral soil interface at all sites except one (PROV WSP). Charcoal particles were extracted from the mineral soil (1 to 1503 particles) at all sites (Table 1, Figure 2). A similar amount of charcoal particles was recovered from the white spruce and balsam fir stands (1992 and 2103 charcoal particles, respectively; averages of 332.0 and 350.5 particles per site are not different ($t$-test; $P = 0.950$)). The distribution of charcoal abundance across sites was similar for the group of white spruce and that of balsam fir stands (Figure 2). Each group had one site (both sites located in the Monts Otish) containing a large amount of charcoal (> 1000 particles) while the other sites contained relatively low to moderate amounts (between 1 and 261 particles). Botanically identified charcoal revealed that all subalpine forests contained *Abies* and *Picea* during the Holocene, as well as *Betula* at seven sites (Figure 2). Overall, the mean relative abundance of each taxa in the macrofossil charcoal assemblages was not significantly different between the group of white spruce stands with that of balsam fir stands (*Abies*: 26.4% in white spruce stands was not different from 37.2 % in balsam fir stands (*t*-test; $P = 0.073$); *Picea*: 59.2% in white spruce stands was not different from 52.5% in balsam fir stands (*t*-test; $P = 0.474$); *Betula*: 24.0% in white spruce stands was not different from 15.3% in balsam fir stands (*t*-test; $P = 0.506$)).

### Local fire histories of the white spruce stands

At site LUCIE, 17 radiocarbon dates corresponded to nine fire events between 5615 and 85 cal. BP indicating a fire-return interval of 614 yr (Figure 3a; Table 1; Appendix 2). The accumulation curve indicates that our sampling might have missed one fire event expected by the extrapolation (Figure 3b; Table 1). At LS WSP, the 11 radiocarbon dates recorded seven fire events between 3160 and 405 cal. BP corresponding to a 394 yr fire-return interval (Figure 3c; Table 1; Appendix 2). The extrapolation curve suggested that sampling might have missed two fire events (Figure 3d; Table 1). At site MB3 WSP, three fire events occurring between 3010 and 300 cal. BP were identified using 11 radiocarbon charcoal dates (Figure 3e; Appendix 2). The fire-return interval at this site was 903 yr (Table 1). All the fire events expected by the extrapolation were identified (Figure 3f; Table 1).

At site JAU WSP, 14 radiocarbon dates identified 11 fire events between 2545 and 50 cal. BP corresponding to a 227 yr fire-return interval (Figure 3g; Table 1; Appendix 2). The accumulation curve was far from reaching the asymptote and indicated that our sampling might have missed up to nine fire events (Figure 3h; Table 1). At MB1 WSP, 11 radiocarbon dates recorded four fire events between 2065 cal. BP and 290 cal. BP corresponding to a 444 yr fire return interval (Figure 3i; Appendix 2). The extrapolation curve indicates that sampling might have missed a single fire event at this site (Figure 3j; Table 1). Finally, at site PROV WSP, only one charcoal particle was found buried in the mineral soil (Figure 2). Although, it was too small for AMS dating (0.4 mg), the presence of this charcoal particle could indicate at least the occurrence of one fire event at this site. Radiocarbon dating of the basal organic matter indicated a stand age of at least 3350 cal. BP which gives a minimum time since fire disturbance (Appendix 2).

### Comparison of fire histories

Local fire histories of balsam fir stands are available in de Lafontaine and Payette (2011). A summary of these data including period of active fire regime, fire-return interval, number of observed and estimated fire events in each balsam fir stand is

**Table 1.** Parameters of the local fire histories

| Site name | Number of buried charcoal particles | Number of identified charcoal particles | Number of $^{14}C$ dates ($n$) | Number of observed fire ($F(n)$) | Fire period (cal. BP) | Fire-return interval (yr) | Accumulation curve (extrapolation of the fire history) | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Number of estimated fire ($F_{max}$) | Accumulation rate ($K$) | $R^2$ |
| *White spruce stands* | | | | | | | | | |
| LUCIE | 1503 | 224 | 17 | 9 | 5615–85 | 614 | 10.50 | 0.113 | 0.988 |
| LS WSP | 42 | 17 | 11 | 7 | 3160–405 | 394 | 9.64 | 0.117 | 0.983 |
| MB3 WSP | 150 | 37 | 11 | 3 | 3010–300 | 903 | 3.28 | 0.300 | 0.900 |
| JAU WSP | 189 | 65 | 14 | 11 | 2545–50 | 227 | 20.08 | 0.060 | 0.992 |
| MB1 WSP | 107 | 35 | 11 | 4 | 2065–290 | 444 | 5.25 | 0.155 | 0.938 |
| PROV WSP | 1 | 0 | 0 | – | before 3550 | – | – | – | – |
| *Balsam fir stands* | | | | | | | | | |
| STEF | 1154 | 174 | 16 | 11 | 4970–225 | 431 | 15.61 | 0.077 | 0.993 |
| PROV FIR | 261 | 80 | 15 | 6 | 4930–615 | 719 | 6.44 | 0.157 | 0.976 |
| LS FIR | 106 | 25 | 15 | 6 | 4115–940 | 529 | 6.52 | 0.221 | 0.971 |
| JAU FIR | 218 | 69 | 16 | 9 | 3160–190 | 330 | 10.94 | 0.119 | 0.989 |
| MB3 FIR | 242 | 47 | 15 | 7 | 2980–390 | 370 | 7.83 | 0.159 | 0.983 |
| MB2 FIR | 122 | 41 | 15 | 2 | 2490–430 | 1030 | 2.03 | 0.608 | 0.821 |

Fir stands data are from de Lafontaine and Payette, 2011.

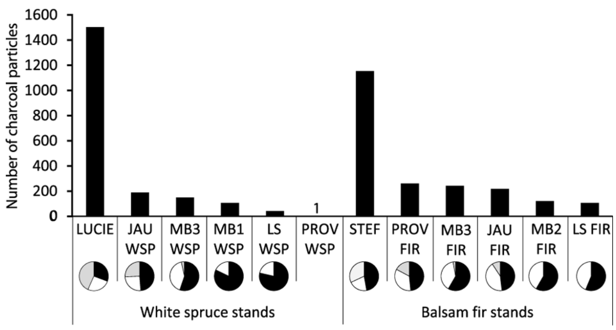


**Figure 2.** Number of charcoal particles extracted from the mineral soil at each site (25 mineral soil cores (750 cm$^3$)) and pie-charts expressing the relative abundances of macrofossil charcoal taxonomic identifications (black, white and grey indicate percent *Picea*, *Abies* and *Betula*, respectively)

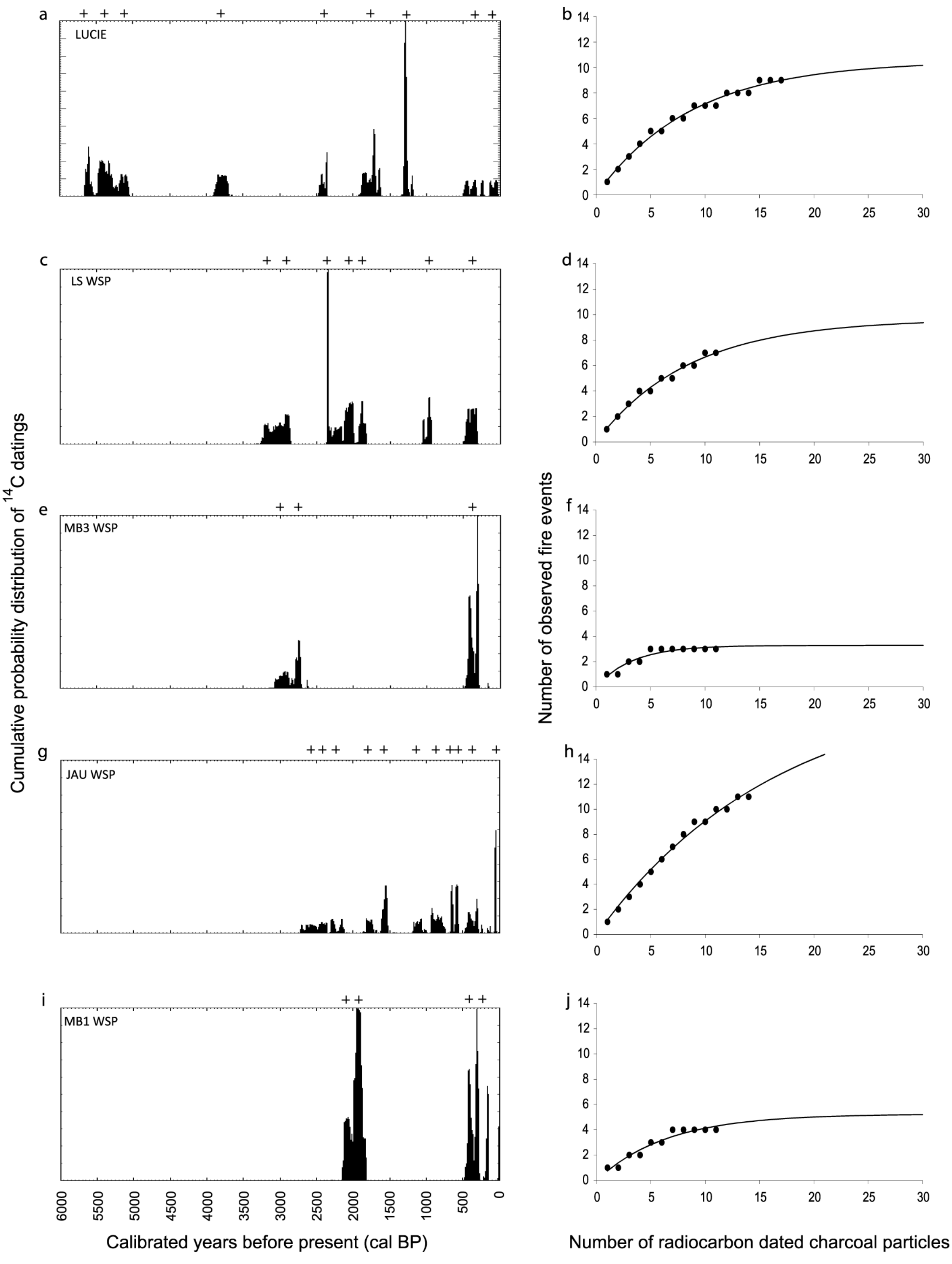


**Figure 3.** Stand-scale fire histories of the white spruce stands. Left panels: the histograms represent cumulated probability of the calibrated $^{14}C$ dates. + indicates different calibrated $^{14}C$ dates. Right panels: accumulation curves of the number of fire events recorded based on calibrated $^{14}C$ dated charcoal particles. Extrapolation curves were fitted using an asymptotic, negative exponential function

given in Table 1. Overall, the Holocene fire history of the balsam fir stands is not different to that of the white spruce stands. The number of observed fire events (3 to 11 fire events per site in white spruce stands and 2 to 11 events per site in balsam fir stands; means of 6.80 and 6.83 fires per site, respectively) are not different (*t*-test; $P = 0.987$). The periods of active fire regime in white spruce stands (regional fire period: 5600 cal. BP to 50 cal. BP) completely overlap with that of balsam fir stands (regional fire period: 4970 cal. BP to 190 cal. BP) (Figure 4), and all studied sites show evidence of at least one fire event by 2000 cal. BP. Fire-return intervals (227 to 903 yr in the white spruce stands and 330 to 1030 yr in the balsam fir stands; means of 516.4 and 568.2 yr, respectively) are not different (*t*-test; $P = 0.751$) (Table 1).

### *Macrofossil charcoal assemblages*

The stand-scale charcoal assemblages indicate that there was no shift in tree composition at any of the studied sites (Figure 5). Moreover, no apparent divergence was found in charcoal

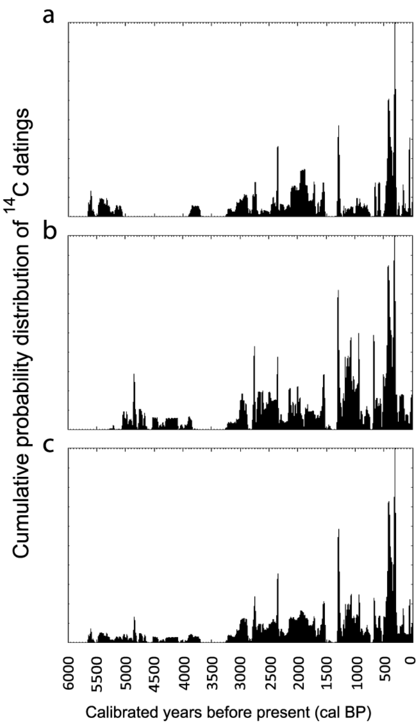


**Figure 4.** Regional fire histories of the white spruce stands (a), the balsam fir stands (b), and all subalpine stands (c). The histograms represent cumulated probability of the calibrated $^{14}C$ dates

composition between the group of white spruce stands and that of balsam fir stands over the Holocene (Figure 6a, b). Rather, the two arboreal taxa were present at the beginning and during the regional fire period and are still common in today's subalpine flora (Figure 6c).

## Discussion

The stand-scale resolution of fire events in the white spruce stands was useful to reconstruct the fire histories of these sites where no other Holocene fire proxies are available at the local scale. The accumulation curves at all sites but JAU WSP were close to the asymptote indicating that most of the Holocene fires were identified at these sites. At site JAU WSP, the accumulation curve was incomplete; consequently, the extrapolation of the expected number of fire events remains highly speculative. In this specific case, the accumulation curve merely indicates that more charcoal particles should be dated in order to obtain a more realistic extrapolation. Yet, a total of 11 Holocene fire events were correctly identified at JAU WSP and this substantial part of the stand-scale fire history can still be interpreted as is.

The fire history inferred by pooling together the 12 study sites suggests that the regional fire period began 5600 yr ago, and by 2000 cal. BP all white spruce stands had burned at least once. Our method was used previously to record stand fires up to more than 10 440 years old in an old-growth deciduous forest in southern Québec (Talon et al., 2005) and a regional fire history in the southern boreal up to more than 9170 years old (de Lafontaine and Payette, 2011). In this study, we thus interpret the lack of charcoal record earlier than 5600 yr across the 12 study sites as a period of low occurrence of regional fire. Regional fire records based on microcharcoal deposition in lacustrine sediments inferred a period of higher fire incidence in the spruce zone (Lac Desautels: 49°27'N; 73°15'W) between *c.* 3500 and 1000 cal. yr BP (Carcaillet and Richard, 2000). This study yielded different results to ours because of the use of different methods (regional microfossil analysis of charcoal (from ≥12.5 to ≥160 μm) deposited in lacustrine sediments versus stand-scale macrofossil analysis of charcoal (≥2 mm) in mineral soils), in different study areas (there might be important site-specific differences as exemplified by our stand-scale analysis). Nevertheless, our regional fire record completely overlaps with that of Carcaillet and Richard (2000) while providing direct field evidence that the period of increased fire activity in the spruce zone occurred *c.* 2000 yr earlier than inferred from the lacustrine sediments.

Overall, the fire history of white spruce stands (mean number of observed fires, period of recurrent fires, and mean fire-return interval) was not different from that of the coexisting balsam fir stands in the subalpine belt of the high plateaus. Botanical identification of macrofossil charcoal indicated that overall Holocene composition was similar in the two community types, that there was no shift in botanical composition at any studied stand, and that there was no long-lasting divergence in composition of the fossil record between white spruce and balsam fir stands. This similarity of the paleoecological records between the white spruce and balsam fir stands suggests that they originate from the same forest assemblage. Their differences result from ongoing ecological dynamics and are not the outcome of distinct historical ecological trajectories. These paleoecological data concur with previous ecological evidence (stand structure and species composition), suggesting that the two community-types are different successional stages among the subalpine forest assemblage (de Lafontaine and Payette, 2010).

Identification of macrofossil charcoal to genus indicated that a forest assemblage including genera *Abies, Picea*, and *Betula* was continuously maintained among these northern subalpine stands at least during the last 5600 cal. BP. Assuming that genus *Picea* corresponds to white spruce whereas genus *Betula* is white birch (genus *Abies* is obviously balsam fir because no other *Abies* species is found in the area), it is likely that forest stand composition in the subalpine belt of the high plateaus of central Québec remained somewhat similar to that of the extensive southern balsam fir forest flora (Grandtner, 1966). It has been suggested that white spruce stands are transient, early successional post-fire communities ultimately developing into balsam fir stands as time since the last fire increases (de Lafontaine and Payette, 2010). This makes sense given the current white spruce distribution in eastern North America. The species is typically a companion species occupying *c.* 10% of the canopy in the extensive forest dominated by balsam fir throughout the southern boreal zone (Jurdant, 1959; Lafond, 1964) whereas the white spruce-dominated stands are rather small, endemic and transient forest patches of successional origin. For example, pioneering white spruce stands are developing on the fast-rising coast of Hudson Bay (Caccianiga and Payette, 2006; Laliberté and Payette, 2008) and in protected valleys along the maritime coast of Labrador (Payette, 2007). Other transient white spruce stands are distributed on Anticosti Island in the Gulf of St Lawrence and are associated with herbivore disturbance (Potvin et al., 2003). Finally, pioneering white spruce stands are found on abandoned old-fields (Nienstaedt and Zasada, 1990). By contrast, balsam fir is the dominant, late successional species throughout the southernmost zone of the boreal forest (south of 49°N) (Grandtner, 1966).

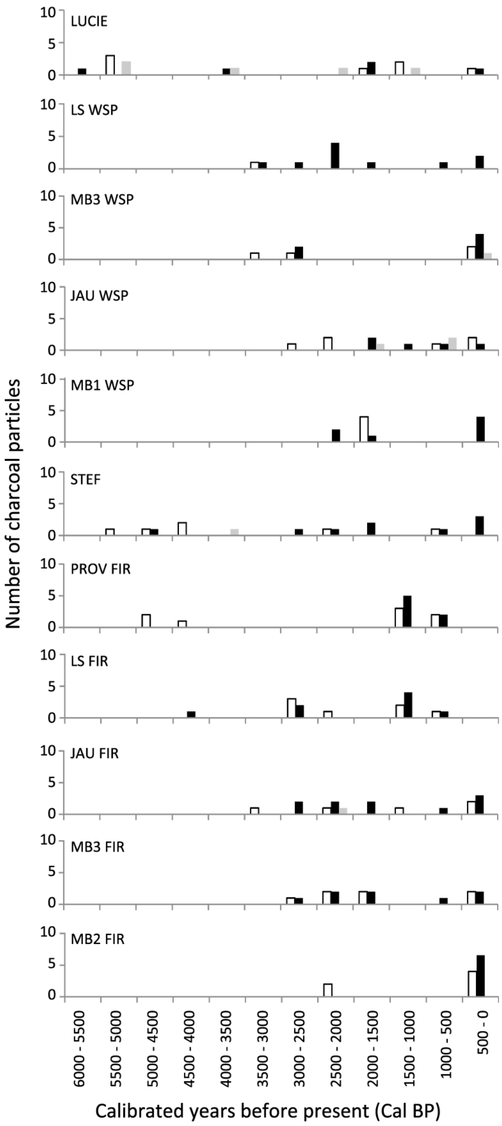


**Figure 5.** Stand-scale macrofossil charcoal assemblages. Black, white and grey bars indicate the number of *Picea*, *Abies*, and *Betula* charcoal particles recorded in each 500 cal. yr BP interval, respectively

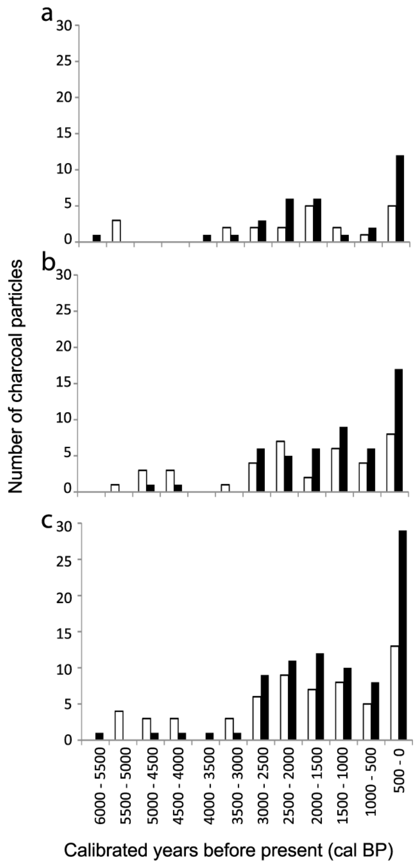


**Figure 6.** Regional macrofossil charcoal assemblages of the white spruce stands (a), the balsam fir stands (b), and all subalpine stands (c). Black and white bars indicate the number of *Picea* and *Abies* charcoal particles recorded in each 500 cal.yr BP interval, respectively

The similarity of the northern subalpine flora (both extant (de Lafontaine and Payette, 2010) and macrofossil (this study)) with that of the extensive southern boreal forest concur with other evidences suggesting that these flora were connected in the past and were subsequently isolated. Indeed, this hypothesis is also supported by the genetic signature showing evidence of a demographic decline (i.e. genetic bottleneck) across the subalpine white spruce stands (de Lafontaine et al., 2010). Palaeoecological data presented here indicate that subalpine white spruce stands were continually maintained as part of the ecological dynamics within the balsam fir flora of this area. Pollen diagrams from the lowlands surrounding the high plateaus also indicate a northern expansion of *Abies* prior to its replacement by *Picea* (probably black spruce) as a result of increased fire activity (de Lafontaine and Payette, 2011). It thus follows that the demographic decline of white spruce populations uncovered by genetic data was probably contemporary to the isolation of the northernmost balsam fir flora in the subalpine belt of the high plateaus.

## Conclusion

The paleoecological data presented here suggest that white spruce and balsam fir stands of the high plateaus of central Québec are not divergent community types originating from long-lasting distinct Holocene histories. The coexistence of the two community types is rather the outcome of an active successional dynamics among the northernmost balsam fir forest patches. In the subalpine belt of this area, fire is likely the most important stand disturbance initiating secondary succession in which white spruce is the pioneer species (de Lafontaine and Payette, 2010). Despite its fire intolerance, the balsam fir flora in this area has been resilient during the last 5600 yr period of recurrent fires. The orographic effect of the high plateaus of central Québec increases the atmospheric moisture, resulting in a relatively long mean fire-return interval (542 yr). The fire-intolerant forest assemblage was locally maintained as a mosaic of different successional stages, i.e. the coexistence of white spruce and balsam fir stands in the subalpine belt. Shorter fire intervals in the lowlands (between 100 and 270 yr (Bouchard et al., 2008; Cogbill, 1985; Parisien and Sirois, 2003; Payette et al., 1989)) likely resulted in the regional collapse of the northern balsam fir flora and its replacement by fire-prone black spruce assemblages (de Lafontaine and Payette, 2011; de Lafontaine et al., 2010). This process isolated the subalpine balsam fir flora from the extensive balsam fir forest located in the moister southern boreal landscape.

## Appendices

### Appendix 1

Location and details of sites sampled

| Location | Site name | Abbreviation | Latitude (°N) | Longitude (°W) | Altitude (m) | Aspect | Mean depth of organic-mineral interface (cm) |
|---|---|---|---|---|---|---|---|
| White spruce stands | Lac Shapiko | LS WSP | 52.431 | 70.548 | 925 | E | 10.0 ± 3.9 |
| | Mont Lucie | LUCIE | 52.332 | 71.079 | 890 | S | 13.0 ± 6.0 |
| | Montagnes Blanches 1 | MB1 WSP | 51.284 | 70.368 | 930 | E | 10.1 ± 3.2 |
| | Montagnes Blanches 3 | MB3 WSP | 51.315 | 70.518 | 801 | W | 12.9 ± 4.0 |
| | Mont Provencher | PROV WSP | 51.480 | 68.159 | 843 | W | 23.7 ± 10.0 |
| | Mont Jauffret | JAU WSP | 51.648 | 68.113 | 885 | W | 7.9 ± 2.5 |
| Balsam fir stands | Lac Shapiko | LS FIR | 52.396 | 70.550 | 907 | NW | 10.6 ± 3.4 |
| | Mont Stefansson | STEF | 52.691 | 70.502 | 817 | NW | 18.2 ± 4.4 |
| | Montagnes Blanches 2 | MB2 FIR | 51.290 | 70.401 | 849 | E | 9.8 ± 4.9 |
| | Montagnes Blanches 3 | MB3 FIR | 51.314 | 70.513 | 798 | E | 7.5 ± 3.0 |
| | Mont Provencher | PROV FIR | 51.472 | 68.181 | 684 | NW | 10.7 ± 5.4 |
| | Mont Jauffret | JAU FIR | 51.656 | 68.106 | 834 | W | 11.4 ± 4.2 |

### Appendix 2

Details of the 67 AMS radiocarbon dates

| Location (site) | Botanical charcoal identification | Laboratory number | Date ($^{14}$C yr BP) | Interval (cal. BP) | Probability |
|---|---|---|---|---|---|
| LUCIE | *Picea* | ULA-1367 | 4875 ± 25 | 5585–5648 | 1.000 |
| LUCIE | *Abies* | ULA-1341 | 4705 ± 25 | 5324–5416 | 0.589 |
| LUCIE | *Betula* | ULA-1343 | 4670 ± 25 | 5319–5468 | 1.000 |
| LUCIE | *Abies* | ULA-1342 | 4635 ± 25 | 5375–5461 | 0.792 |
| LUCIE | *Betula* | ULA-1368 | 4535 ± 25 | 5053–5189 | 0.686 |
| LUCIE | *Abies* | ULA-1369 | 4515 ± 25 | 5051–5192 | 0.676 |
| LUCIE | *Betula* | ULA-1364 | 3535 ± 25 | 3809–3892 | 0.532 |
| LUCIE | *Picea* | ULA-1366 | 3480 ± 20 | 3695–3829 | 1.000 |
| LUCIE | *Betula* | ULA-1376 | 2390 ± 15 | 2381–2460 | 0.641 |
| LUCIE | *Picea* | ULA-1365 | 1895 ± 25 | 1773–1896 | 0.960 |
| *LUCIE | *Abies* | ULA-1055 | 1795 ± 20 | 1692–1816 | 0.898 |
| LUCIE | *Picea* | ULA-1370 | 1785 ± 15 | 1690–1741 | 0.646 |
| LUCIE | *Abies* | ULA-1372 | 1370 ± 20 | 1275–1311 | 1.000 |
| LUCIE | *Betula* | ULA-1371 | 1335 ± 15 | 1261–1297 | 0.992 |
| *LUCIE | *Abies* | ULA-1053 | 1325 ± 20 | 1240–1296 | 0.868 |
| *LUCIE | *Picea* | ULA-1052 | 355 ± 20 | 318–394 | 0.507 |
| *LUCIE | *Abies* | ULA-1054 | 90 ± 20 | 31–138 | 0.723 |
| LS WSP | *Picea* | ULA-1318 | 2980 ± 20 | 3078–3241 | 1.000 |
| LS WSP | *Abies* | ULA-1289 | 2885 ± 20 | 2948–3078 | 0.996 |
| LS WSP | *Picea* | ULA-1292 | 2805 ± 15 | 2862–2952 | 1.000 |
| LS WSP | *Picea* | ULA-1286 | 2330 ± 20 | 2333–2355 | 1.000 |
| LS WSP | *Picea* | ULA-1291 | 2215 ± 20 | 2153–2278 | 0.834 |
| *LS WSP | *Picea* | ULA-1047 | 2085 ± 20 | 1997–2117 | 1.000 |
| LS WSP | *Picea* | ULA-1304 | 2080 ± 20 | 1995–2116 | 1.000 |
| LS WSP | *Picea* | ULA-1288 | 1930 ± 20 | 1825–1903 | 0.882 |
| LS WSP | *Picea* | ULA-1287 | 1070 ± 20 | 932–1005 | 0.819 |
| *LS WSP | *Picea* | ULA-1048 | 335 ± 20 | 313–467 | 1.000 |
| *LS WSP | *Picea* | ULA-1051 | 330 ± 20 | 346–463 | 0.794 |
| MB3 WSP | *Abies* | ULA-1322 | 2880 ± 20 | 2944–3077 | 0.998 |
| MB3 WSP | *Picea* | ULA-1300 | 2820 ± 15 | 2869–2960 | 1.000 |
| MB3 WSP | *Picea* | ULA-1321 | 2685 ± 20 | 2753–2799 | 0.789 |
| MB3 WSP | *Abies* | ULA-1299 | 2575 ± 20 | 2712–2751 | 0.958 |

*(Continued)*

**Appendix 2.** *(Continued)*

| Location (site) | Botanical charcoal identification | Laboratory number | Date ($^{14}$C yr BP) | Interval (cal. BP) | Probability |
|---|---|---|---|---|---|
| *MB3 WSP | *Abies* | ULA-1059 | 325 ± 20 | 347– 460 | 0.794 |
| MB3 WSP | *Picea* | ULA-1338 | 315 ± 15 | 350–437 | 0.783 |
| *MB3 WSP | *Betula* | ULA-1060 | 315 ± 20 | 349–456 | 0.787 |
| MB3 WSP | *Picea* | ULA-1319 | 300 ± 15 | 373–429 | 0.689 |
| *MB3 WSP | *Picea* | ULA-1050 | 290 ± 20 | 358–430 | 0.647 |
| MB3 WSP | *Abies* | ULA-1374 | 275 ± 15 | 291–317 | 0.733 |
| MB3 WSP | *Picea* | ULA-1320 | 260 ± 15 | 285–314 | 0.972 |
| JAU WSP | *Abies* | ULA-1375 | 2500 ± 15 | 2492–2601 | 0.671 |
| *JAU WSP | *Abies* | ULA-1062 | 2410 ± 20 | 2352–2488 | 0.959 |
| JAU WSP | *Abies* | ULA-1325 | 2175 ± 20 | 2231–2306 | 0.609 |
| JAU WSP | *Picea* | ULA-1323 | 1845 ± 15 | 1719–1823 | 1.000 |
| JAU WSP | *Picea* | ULA-1326 | 1670 ± 15 | 1531–1612 | 1.000 |
| JAU WSP | *Betula* | ULA-1340 | 1655 ± 20 | 1521–1611 | 1.000 |
| JAU WSP | *Picea* | ULA-1324 | 1175 ± 20 | 1055–1172 | 0.966 |
| JAU WSP | *Abies* | ULA-1327 | 970 ± 20 | 898–932 | 0.445 |
| JAU WSP | *Betula* | ULA-1363 | 895 ± 20 | 738–803 | 0.462 |
| JAU WSP | *Betula* | ULA-1328 | 640 ± 15 | 560–598 | 0.603 |
| JAU WSP | *Picea* | ULA-1339 | 635 ± 15 | 559–600 | 0.606 |
| *JAU WSP | *Picea* | ULA-1061 | 325 ± 20 | 347–460 | 0.794 |
| *JAU WSP | *Abies* | ULA-1063 | 270 ± 25 | 284–328 | 0.575 |
| JAU WSP | *Abies* | ULA-1329 | 50 ± 15 | 39–63 | 0.740 |
| MB1 WSP | *Picea* | ULA-1305 | 2100 ± 20 | 2001–2129 | 1.000 |
| *MB1 WSP | *Picea* | ULA-1057 | 2100 ± 20 | 2001–2129 | 1.000 |
| MB1 WSP | *Abies* | ULA-1298 | 2000 ± 15 | 1920–1992 | 0.913 |
| MB1 WSP | *Picea* | ULA-1294 | 1990 ± 20 | 1893–1990 | 1.000 |
| MB1 WSP | *Abies* | ULA-1297 | 1985 ± 15 | 1891–1953 | 0.809 |
| MB1 WSP | *Abies* | ULA-1296 | 1960 ± 20 | 1867–1950 | 0.973 |
| MB1 WSP | *Abies* | ULA-1295 | 1925 ± 20 | 1823–1902 | 0.927 |
| MB1 WSP | *Picea* | ULA-1293 | 310 ± 20 | 349–439 | 0.747 |
| *MB1 WSP | *Picea* | ULA-1058 | 305± 25 | 349–457 | 0.754 |
| *MB1 WSP | *Picea* | ULA-1056 | 270 ± 20 | 285–319 | 0.695 |
| MB1 WSP | *Picea* | ULA-1373 | 220 ± 20 | 272–304 | 0.446 |
| **PROV WSP* | – | *ULA-1025* | *3100 ± 20* | *3317–3376* | *0.687* |
| **PROV WSP* | – | *ULA-1026* | *2345 ± 20* | *2332–2364* | *0.985* |
| **PROV WSP* | – | *ULA-1027* | *2305 ± 20* | *2312–2352* | *0.993* |

*Indicates dates ($n$ = 19) already published by de Lafontaine and Payette (2010). Dates in italics ($n$ = 3) are from basal organic matter, indicating a minimum apparent stand age in the absence of radiocarbon dated soil charcoal.

## Acknowledgements

We wish to thank Catherine Plasse, Joannie Savard, and William H. Romme who helped us with field work as well as many others who helped us with macrofossil analysis in the laboratory.

## Funding

This work was supported by a NSERC research grant to S.P. (Northern research chair on disturbance ecology) and Alexander Graham Bell Canada Graduate Scholarship to G.dL.

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