Quaternary Science Reviews 30 (2011) 867–875

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Shifting zonal patterns of the southern boreal forest in eastern Canada associated with changing fire regime during the Holocene

Guillaume de Lafontaine*, Serge Payette

NSERC Northern Research Chair, Centre d'études nordiques, Département de Biologie, Université Laval, 1045 av. de la Médecine, Québec (QC), Canada, G1V 0A6

ARTICLE INFO

Article history:
Received 4 October 2010
Received in revised form
23 December 2010
Accepted 12 January 2011
Available online 5 February 2011

Keywords:
^{14}C AMS dating
Abies balsamea
Boreal biome
Eastern North America
Fire disturbance
Macrofossil analysis
Mineral soil charcoal
Picea mariana
Vegetation zones

ABSTRACT

This research aims at uncovering the stand-scale Holocene fire history of balsam fir forest stands from two bioclimatic zones of the boreal forest and assessing the existence of a sub-continental shift in past fire activity that could have triggered a change in the Holocene zonal pattern. In eastern Canada, the extant closed-crown boreal forest corresponds to two ecological regions separated along 49°N, the northern black spruce zone and the southern balsam fir zone. We sampled balsam fir stands from the southern fir zone ($n = 7$) and among the northernmost patches of fir forest located far beyond the fir zone boundary, into the spruce zone ($n = 6$). Macrofossil analysis of charcoal in mineral soils was used to reconstruct both the stand-scale and regional Holocene fire histories. Data were interpreted in the context of published palaeoecological evidence. Stands of the balsam fir zone were submitted to recurrent fire disturbances between *c.* 9000 and 5000 cal. yr B.P. Local fire histories suggested that four sites within the fir zone escaped fire during the Holocene. Such fire protected sites allowed the continuous maintenance of the balsam fir forest in the southern boreal landscape. Stands of the spruce zone have been affected by recurrent fires from 5000 cal. yr B.P. to present. Local fire histories indicated that no site escaped fire in this zone. Published palaeoecological data suggested that balsam fir migrated to its current northern limit sometime between 7300 and 6200 cal. yr B.P. A change of the fire regime 5000 years ago caused the regional decline of an historical northern balsam fir forest and its replacement by black spruce forest. The consequence was a sub-continental reshuffling of the fir and spruce zones within the closed-crown boreal forest. The macrofossil analysis of charcoal in mineral soils was instrumental to the reconstruction of stand-scale Holocene fire history at sites where no other *in situ* fire proxies were available.

1. Introduction

The circumboreal biome is subdivided into three extensive vegetation zones from south to north: the closed-crown forest, the open forest and the forest-tundra, respectively (Hare and Ritchie, 1972). These vegetation zones represent different plant communities as a function of climate (Larsen, 1980). Davis (1981) suggested climate change prevailing during the late Wisconsinan–early Holocene (*c.* 25,000–6500 cal. yr B.P.) as the ultimate cause for the post-glacial spread of tree species. However, rate of tree migration and geographic range of tree species were not always in equilibrium with climate as the post-glacial spread of species relied on propagules availability and establishment capacity of seedlings competing with other species already occupying favourable sites (Davis, 1981).

Heinselman (1981) outlined the instrumental role played by wildfires in structuring forest communities in the boreal biome. Consequently, Payette (1992) developed a model which states that the structure of vegetation zones, distribution of forest communities and presence/absence of tree species in different areas of the boreal landscape during the Holocene was a direct consequence of fire disturbance. The geographic range of a species has two major components, the distribution boundaries and the relative abundance of individuals within the range (Lomolino et al., 2006). The current range boundaries of a boreal tree species would correspond to its maximum Holocene expansion, driven by climate, whereas regional abundance within its range would be associated with prevailing disturbance regime (Payette, 1993).

The divergent community model of Payette (1992) suggests that more than a single 'climax' community type (alternative stable

* Corresponding author. Present address: INRA, UMR BIOGECO 1202, 69 Route d'Arcachon, 33610, Cestas, France. Tel.: +33 5 57 12 28 25; fax: +33 5 57 12 28 81.
E-mail addresses: gdelafon@pierroton.inra.fr, guillaume.de-lafontaine.1@ulaval.ca (G. de Lafontaine).

0277-3791/$ – see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.quascirev.2011.01.002

states) can theoretically exist on a given site (May, 1977; Scheffer et al., 2001). The shift from one community type to another may be due to regeneration failure during secondary succession after a disturbance or a series of compounded disturbances (Paine et al., 1998; Payette et al., 2000). At the sub-continental scale, such community transformations over the landscape may affect the geographic range of species and modify the zonal patterns of dominant vegetation assemblages. Empirical examples of the model were recently assessed in different vegetation zones of the boreal forest in eastern North America. Forest opening of the forest-tundra zone was caused by increased fire activity over the landscape starting *c.* 3200 cal. yr B.P. (Asselin and Payette, 2005). Lichen woodland patches located in moist, fire protected depressions are the remains of a forest cover more extensive prior to the change of the fire regime (Payette et al., 2001). The southernmost lichen woodland stands are located within the closed-crown forest zone and originate from post-fire regeneration failures beginning *c.* 1400 cal. yr B.P. (Jasinski and Payette, 2005). Here forest opening, triggered by wildfire activity, is currently ongoing all over the closed-crown forest zone at a faster pace over the last 100 years (Girard et al., 2008, 2009). Correspondingly, the northernmost closed-crown forest patches within the adjacent open forest zone are old-growth stands which escaped fire over the last centuries up to several millennia (Pollock and Payette, 2010). Such marginal stands are remnants of a once more extensive closed-crown forest zone which expanded further north prior to its transformation into lichen woodland zone caused by wildfire (Pollock and Payette, 2010). These empirical examples from the northern boreal landscape describe a general biogeographical pattern consistent with the divergent community model. Each vegetation zone is characterized by a dominant forest type (e.g. the open forest zone is characterized by lichen woodland). The relative abundance of each forest type throughout the landscape may be described by a normal distribution according to the latitude (Payette, 1992; Timoney et al., 1993). The greatest relative abundance (the mode of the latitudinal normal distribution) of a given forest type lies in the geographical centre of its corresponding vegetation zone and declines towards the northern and southern boundaries of the zone. The disjunct northernmost stands (northern tail of the normal distribution) are residual stands which have escaped the current fire regime (Payette, 1992; Payette et al., 2001) whereas the southernmost stands (southern tail of the normal distribution) originate from recent forest transformations caused by the disturbance (fire) regime (Payette et al., 2000).

In eastern North America, the closed-crown forest corresponds to two ecological regions roughly divided at 49°N (Lafond, 1964; Grandtner, 1966; Fig. 1). South of 49°N, the moist balsam fir (*Abies balsamea* (L.) Mill.) forest zone (fir zone, thereafter) is a mixed forest dominated by balsam fir along with white spruce (*Picea glauca* (Moench) Voss.) and white birch (*Betula papyrifera* Marsh.) as companion species. North of 49°N, the black spruce (*Picea mariana* (Mill.) B.S.P.) forest zone (spruce zone, thereafter) is dominated by extensive tracts of closed-crown black spruce forest 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), suggesting fire as a major force accounting for the distinctiveness of the fir zone and spruce zone.

The northernmost patches of fir forest are located beyond the fir zone boundary, into the spruce zone up to the southern edge of the open forest zone (Fig. 1). These disjunct stands are distributed in the moist subalpine belt of three high-elevated plateaus (*c.* 1000 m above sea level [a.s.l.]) in central Québec, *c.* 300–500 km north of the fir zone. Under the hypothesis that the fir zone conforms to the divergent community model, subalpine balsam fir stands isolated in a matrix of lowland black spruce forests could be the remnants of a past northern expansion of the fir zone. The regional decline of such extensive northern fir forests in the lowlands and their replacement by extant spruce forests could be a consequence of a change in the fire regime favouring fire-prone species (black spruce and jack pine) over fire intolerant species (balsam fir and white spruce). Indeed, stands of the spruce and the fir zones are currently characterized by two distinct fire regimes, with a greater fire activity in the spruce zone compared to that of the fir zone (de Lafontaine and Payette, 2010). However, a direct comparison of the long term (i.e. Holocene) fire histories between the two zones has never been done.

We hypothesize that a period of low fire activity prevailed in the past to allow the northern expansion of fire intolerant plant assemblages (i.e. balsam fir forest flora). This expansion probably occurred sometime in the past prior to the establishment and development of the current fire regime favouring black spruce forests in the northern closed-crown forest (de Lafontaine and Payette, 2010). The first objective of this investigation is to uncover the local (i.e. stand scale) Holocene fire history of extant, old-growth balsam fir stands located in the fir zone and the spruce zone. The second objective is to assess the existence of a sub-continental

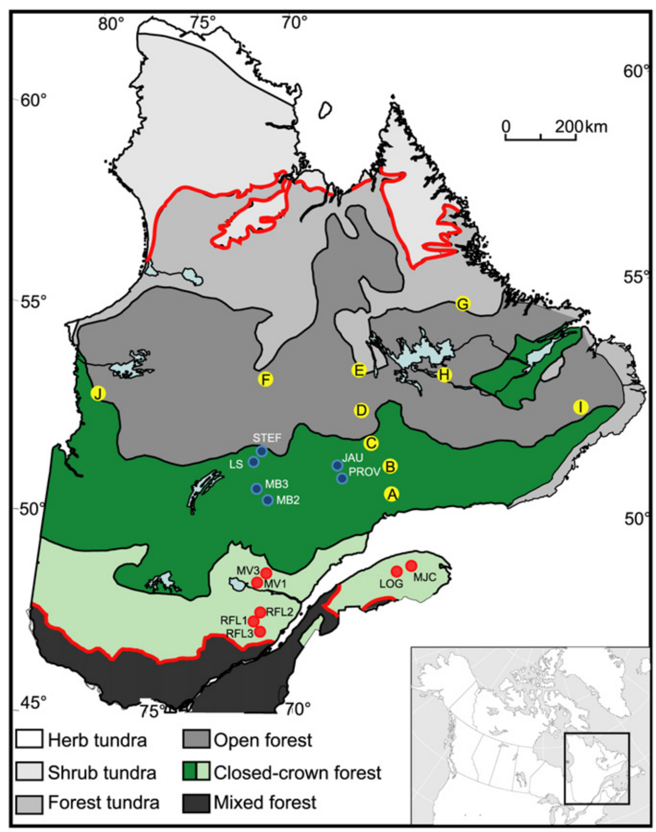

Fig. 1. Location of sampled sites. The main bioclimatic zones of Québec are represented; the zones corresponding to the boreal biome are between the two red lines. Note that the closed-crown forest is roughly subdivided along 49°N in two ecological regions represented by different shades of green; paler green represents the balsam fir zone whereas darker green represents the black spruce zone. Red dots ($n = 7$) show study sites in the balsam fir zone and blue dots ($n = 6$) study sites within the black spruce zone. Yellow circles indicate the sampling location of the published palaeoecological data discussed in the present study (A–E: King (1986); F: Richard et al. (1982); G: Lamb (1985); H: Morrison (1970); I: Lamb (1980); Engstrom and Hansen (1985); J: Arsenault and Sirois (2004)). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

shift of fire activity that could have triggered a change in the zonal pattern (as suggested by the divergent community model), and if so, to determine when during the Holocene. We interpreted our fire history data in the context of published palaeoecological evidence (pollen and macrofossil) showing the historical presence of balsam fir in the extant spruce zone in order to reconstruct the early Holocene history of the two zones of the closed-crown forest. To achieve our goals, macrofossil analysis of charcoal in mineral soils (Talon et al., 2005) was used to evaluate *in situ* Holocene fire history of balsam fir stands of the fir zone and the spruce zone.

2. Methods

2.1. Study sites

Thirteen old-growth balsam fir stands (plots: 50 m × 10 m or 50 m × 20 m) were sampled in 2006, 2007 and 2008. Sites were distributed across the closed-crown boreal forest (Fig. 1, see Appendix A). Seven sites were located in the southern fir zone, whereas six other sites were equally distributed on three high plateaus (i.e. 2 sites per plateau) of the northern spruce zone. The Forêt Montmorency weather station (47°19′N, 71°09′W, 640 m a.s.l.) located in the centre of the fir zone indicates average annual temperature of 0.3 °C and average annual total precipitation of 1600 mm with 40% falling as snow. The average growing season above 0 °C is 132 days and totals 1028 growing degree-days >5 °C. The Bonnard weather station (50°43′N, 71°03′W, 506 m a.s.l.) located in the centre of the spruce zone indicates average annual temperature of −1.8 °C and average annual total precipitation of 950 mm with 32% falling as snow. The average growing season above 0 °C is 134 days and totals 971 growing degree-days >5 °C. Average climatic data are based on the period between 1971 and 2000 (www.climate.weatheroffice.ec.gc.ca). Common species were typical of the balsam fir forest: *A. balsamea*, *P. glauca* and *B. papyrifera* (trees); *Alnus viridis* ssp. *crispa* (Aiton) Pursh, *Amelanchier bartamiana* (Taush) M. Roem. and *Ribes glandulosum* Graue (shrubs); *Clintonia borealis* (Aiton) Raf., *Coptis trifolia* (L.) Salisb., *Cornus canadensis* L., *Oxalis montana* Raf., *Solidago macrophylla* Pursh. and *Trientalis borealis* Raf. (herbs); *Gymnocarpium dryopteris* (L.) Newman (fern); *Dicranum* sp., *Pleurozium schreberi* (Brid.) Mitt. and *Sphagnum* sp. (mosses) (de Lafontaine and Payette, 2010).

2.2. Charcoal extraction

Charcoal analysis was based on the sampling of 25 soil cores in 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 such 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 formed and deposited *in situ*, and not transported from another location. Even charcoal as small as 0.5 mm is 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, weighed, 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 (Schweingruber, 1978, 1990; Schoch et al., 2004). Because site STEF had considerable amount of charcoal (1154 particles), identification was limited to particles ≥5 mg.

2.3. Radiocarbon dates

At each site, at least 12 charcoal particles extracted from the mineral 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, spatial distribution of the 25 soil cores and randomness. Other radiocarbon dates ($n \geq 3$ dates per site) were added to the dataset 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, Canada) and Keck Carbon Cycle AMS Facility (University of California, Irvine, CA, USA) 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).

2.4. 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 (Lafortune et al., 2006; Sanborn et al., 2006; Fesenmyer and Christensen, 2010). 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 error' is additive to the radiometric error and implies that 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). Thus, it may add a significant error that must be acknowledged and handled in sites with infrequent fires and long-lived trees as in humid, coastal forests of the western US and Canada (Gavin, 2001; Gavin et al., 2003). However, in sites experiencing more frequent fires with short-lived trees and fast decaying wood as in the eastern closed-crown boreal forest, the radiocarbon dates of charcoal approximate the actual dates of fire (Filion, 1984; Talon et al., 2005).

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 (Soberón and Llorente, 1993; Colwell and Coddington, 1994). 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

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

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.

A regional fire history was computed for each bioclimatic zone. This was done by pooling the radiocarbon dates from all sites within each zone and running the cumulative probabilities analysis (Meyer et al., 1992). A visual comparison of the regional fire histories allowed the identification of contrasted periods of fire activity between the balsam fir stands of both the spruce zone and the fir zone.

2.5. Published palaeoecological data

The genus *Abies* is underrepresented in fossil pollen assemblages owing to poor pollen dispersal and perhaps low production whereas *Picea* is well represented throughout its range (Richard, 1993; Jackson et al., 1997). Consequently, the existence of historical extensive balsam fir forests in the current spruce zone might have been overlooked in early interpretations made by palynologists because pollen analysis of the boreal forest was probably skewed towards better represented taxa. The North America Pollen Database (http://www.ncdc.noaa.gov/paleo/napd.html) was searched for pollen diagrams from central Québec and adjacent Labrador. We analyzed the available palaeoecological data (pollen diagrams and macrofossils) with a special focus on the genus *Abies* in order to find evidence of the past plant assemblage associated with balsam fir. For each published pollen diagram, we computed an age/depth model using calibrated radiocarbon dates. An assessment of the time period of balsam fir presence in the area was made from these models. We considered balsam fir to be present in the region surrounding a coring site whenever traces of *Abies* pollen were found in successive pollen samples along the core. We did not consider cores with occasional *Abies* pollen grains because we interpreted them as long distance dispersal originating from extra-regional source. For a given diagram, we defined the time period of regional fir presence as the interval between a sudden increase in *Abies* pollen count and its decrease. During this diagnostic period, the fir pollen percentages were above the average value for the entire core.

3. Results

3.1. Charcoal abundance

Among the seven sites sampled in the southern fir zone, charcoal was found at the organic/mineral soil interface in only one site (RFL2). A small amount of charcoal particles buried in the mineral soil (1–25 particles) of three sites (RFL1, RFL2 and RFL3; Fig. 2) was also found. No charcoal was recorded in the soils of the other four sites of the fir zone (Fig. 2). In contrast, charcoal was found at the organic/mineral soil interface at all six sites sampled in the northern spruce zone. A large amount of charcoal particles buried in mineral soil (106–1154 particles) of all the sites was also recorded (Fig. 2).

3.2. Stand-scale fire histories in the fir zone

At site RFL3, 13 radiocarbon dates corresponded to 7 fire events between 9170 and 5600 cal. yr B.P. (Fig 3A; see Appendix B). The accumulation curve indicated that the radiocarbon dataset may have missed a single fire event (Fig. 3B; see Appendix C). Botanically identified charcoal particles ($n = 13$) were either *Abies*, *Picea* or *Betula* ($n = 9$, 3, and 1, respectively; Fig. 2). At RFL2, a total of 16 radiocarbon dates corresponded to 11 fire events (Fig. 3C; Appendix B). The extrapolation indicated that sampling might have missed up

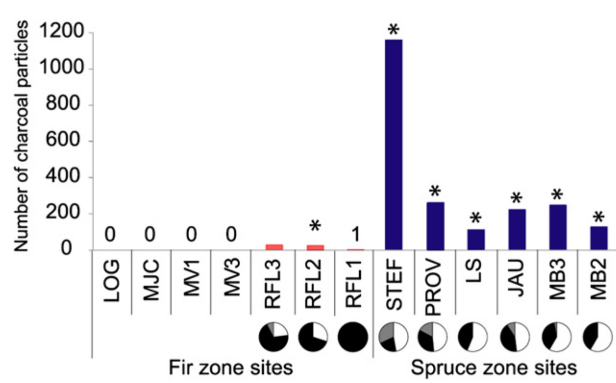

Fig. 2. Number of charcoal particles extracted from the mineral soil at each site (25 mineral soil cores [750 cm^3]) and pie-charts expressing the relative abundances of macrofossil charcoal taxonomic identifications (white, black and grey indicate percent *Picea*, *Abies* and *Betula*, respectively). '*' indicates that charcoal was found at the organic/mineral soil interface.

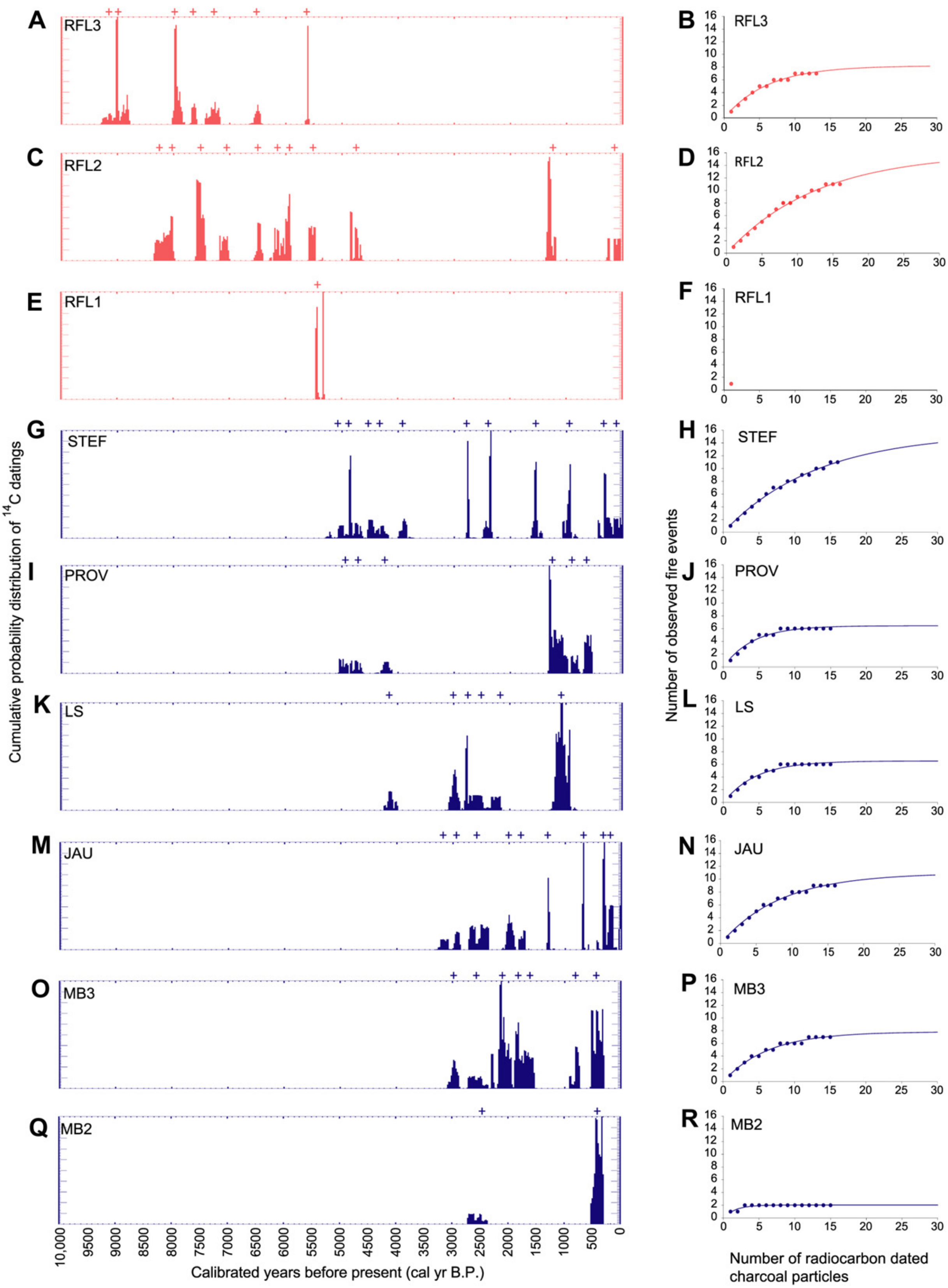

Fig. 3. Stand-scale fire histories. Sites from the fir zone are red colored and sites from the spruce zone are blue colored. Left panels: the histograms represent cumulated probability of the calibrated ^{14}C dates. '+' indicates different calibrated ^{14}C dates. Right panels: accumulation curves of the number of fire events recorded based on calibrated ^{14}C dated charcoal particles. Extrapolation curves were fitted using an asymptotic, negative exponential function. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

to 5 fire events (Fig. 3D; Appendix C). Ten identified charcoal particles were either *Abies* or *Picea* ($n = 7$ and 3, respectively; Fig. 2). At this site, two periods of contrasted fire activity are recognized (Fig. 3C). The first period (increased fire activity) was revealed by the charcoal particles buried in the mineral soil which recorded 9 fires between 8260 and 4730 cal. yr B.P. The second period (lower fire activity) was identified by charcoal particles located at the base of the organic horizon (i.e. deposited on the mineral soil surface), which recorded 2 fire events (1290 cal. yr B.P. and 95 cal. yr B.P.) over the last 4800 years. At site RFL1, only one charcoal (identified as *Abies*) was found buried in the mineral soil indicating a single fire event during the Holocene at 5430 cal. yr B.P. (Fig. 3E, F; Appendices B and C). At the four sites of the fir zone where no charcoal was found, the basal organic matter indicates a minimum period without fire of several thousand years at MV3 (5145 cal. yr B.P.), MJC (4120 cal. yr B.P.), LOG (3500 cal. yr B.P.), and more than 1300 years at MV1 (1375 cal. yr B.P.) (Appendix B).

3.3. Stand-scale fire histories in the spruce zone

At site STEF, 16 radiocarbon dates corresponded to 11 fire events between 4970 and 225 cal. yr B.P. indicating a fire-return interval of 430 yr (Fig. 3G; Appendix B). The extrapolation curve suggested that sampling may have missed up to 4 fire events (Fig. 3H; Appendix C). A total of 125 charcoal particles were identified as *Abies*, *Picea*, and *Betula* ($n = 26$, 59, and 40, respectively; Fig. 2). At this site, *Abies* charcoal was radiocarbon dated at 4970 cal. yr B.P. This is a direct evidence that genus *Abies* was already present on this northernmost site prior to the first fire event (Appendix B). At PROV, the 15 radiocarbon dates recorded 6 fire events between 4930 and 615 cal. yr B.P. corresponding to a 720-yr fire-return interval (Fig. 3I; Appendix B). The accumulation curve indicates that we identified all the fire events expected by the extrapolation (Fig. 3J; Appendix C). The 64 identified charcoal particles were *Abies*, *Picea*, or *Betula* ($n = 22$, 31, and 11, respectively; Fig. 2). *Abies* charcoal was radiocarbon dated at 4930 cal. yr. B.P., once again indicating early fir presence on this site (Appendix B). At site LS, 6 fire events occurring between 4115 and 940 cal. yr B.P. were identified using 15 radiocarbon charcoal dates (Fig. 3K; Appendix B). The fire-return interval on this site is thus 530 yr. Our sampling recorded all the fire events expected by the extrapolation (Fig. 3L; Appendix C). A total of 16 botanically identified charcoal particles were either *Abies* or *Picea* ($n = 7$ and 9, respectively; Fig. 2). At site JAU, 16 radiocarbon dates identified 9 fire events between 3160 and 190 cal. yr B.P. corresponding to a 330-yr fire-return interval (Fig. 3M; Appendix B). The accumulation curve indicated that sampling may have missed a single fire event (Fig. 3N; Appendix C). Taxonomic identification of the 54 charcoal particles revealed the presence of *Abies*, *Picea*, and *Betula* ($n = 23$, 26, and 5, respectively; Fig. 2). At MB3, 7 fire events occurring between 2980 and 390 cal. yr B.P. were identified based on 15 radiocarbon charcoal dates (Fig. 3O; Appendix B) indicating a fire-return interval of 370 yr. Our sampling identified all the fire events expected by the extrapolation (Fig. 3P; Appendix C). Charcoal particles were identified ($n = 36$) as *Abies*, *Picea*, or *Betula* ($n = 14$, 21, and 1, respectively; Fig. 2). Finally, 15 radiocarbon dates recorded 2 fire events throughout the Holocene at site MB2 (Fig. 3Q). The first one dated 2490 cal. yr B.P. and the last one centered around 430 cal. yr B.P. (Fig. 3Q; Appendix B). The fire-return interval is thus 1030 yr on this site. The extrapolation curve clearly indicates that sampling recorded all the fire events at this site (Fig. 3R; Appendix C). Botanically identified charcoal ($n = 36$) was either *Abies* or *Picea* ($n = 15$ and 21, respectively; Fig. 2).

3.4. Comparison of regional fire histories

The regional fire histories show a neat shift in fire activity around 5000–4700 cal. yr B.P. (Fig. 4). A period of fire activity was identified between 9200 and 4700 cal. yr B.P. in the fir zone, followed by a long period of decreased fire activity until today. In contrast, from 5000 cal. yr B.P. to present, balsam fir stands of the spruce zone were subjected to recurrent fires, with an average fire-return interval of 570 yr.

3.5. Published palaeoecological data

King (1986) provided a series of 5 pollen diagrams along a south to north transect located *c.* 300 km east of the high plateaus of the spruce zone (Fig. 1 points A–E). From south to north, the pollen diagrams showed high abundance of *Abies* from 7600 to 6200 cal. yr B.P (Fig. 1 point A), 7300 to 6500 cal. yr B.P. (Fig. 1 point B), 6200 to 4250 cal. yr B.P. (Fig. 1 point C), 5900 to 3000 cal. yr B.P. (Fig. 1 point D) and 5350 to 3900 cal. yr B.P. (Fig. 1 point E), respectively. All these pollen diagrams (King, 1986) show a characteristic increase in *Picea* pollen contemporary to the *Abies* decline. Pollen diagrams from the Caniapiscau area (Fig. 1 point F) record the presence of balsam fir between 5600 and 4000 cal. yr B.P. (Richard et al., 1982). A pollen diagram from Gravel Ridge, Labrador (Fig. 1 point G) indicated high fir abundance between 5800 and 4400 cal. yr B.P., followed by an increase in black spruce pollen (Lamb, 1985). Pollen diagrams from Churchill Falls, central Labrador (Fig. 1 point H), showed a peak of *Abies* pollen starting at 6000 cal. yr B.P., followed by a sudden decrease and replacement by black spruce pollen (Morrison, 1970). Pollen diagrams from southeast Labrador (Fig. 1 point I) recorded the presence of balsam fir from 8800 to 6500 cal. yr B.P. (Engstrom and Hansen, 1985) and 7400 to 6200 cal. yr B.P. (Lamb, 1980), subsequently replaced by black spruce. Finally, balsam fir remains dated between 5120 and 4690 cal. yr B.P. (Fig. 1 point J) were found buried under an extant jack pine and black spruce stand (Arsenault and Sirois, 2004).

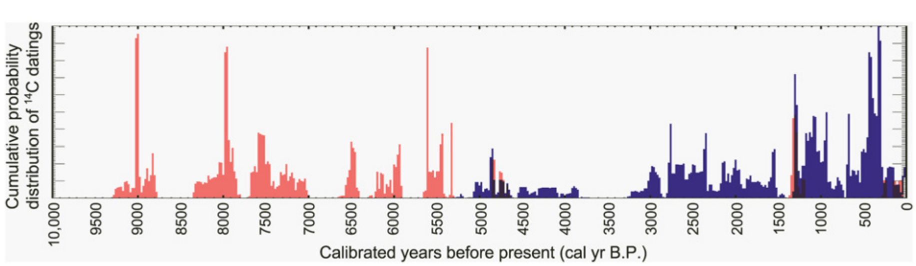

Fig. 4. Regional fire histories. The histograms represent cumulated probability of the calibrated ^{14}C dates. Data from the fir zone are colored red whereas those of the spruce zone are colored blue. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

4. Discussion

Charcoal analysis from mineral soils used in this study is a method based on direct fire evidence to reconstruct long-term fire history at the stand scale. No other fire proxies are available at the stand scale in the boreal forest to reconstruct fire history at the Holocene time scale. The local resolution of fire events was useful to differentiate between sites having charcoal with sites without charcoal among the same region. Of the 7 sites of the fir zone, 3 sites had charcoal particles indicating past fire activity whereas the mineral soil of 4 sites had no charcoal. Absence of large charcoal fragments must be more carefully interpreted in comparison to charcoal occurrences (Ohlson and Tryterud, 2000). A combination of small amount of fire fuel, fuel that produced no charcoal (e.g. mosses or grasses), low fire intensity and/or lack of burial by tree uprooting may explain the absence of charcoal in a mineral soil core despite the occurrence of a fire. However, in our study, the soil of each stand was thoroughly searched for charcoal particles using 25 cores per site. 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 up to more than 9170 years old at other sites of the boreal zone (this study). In this study, we therefore interpret an absence of charcoal in sites of the fir zone as an absence of local (i.e. stand scale) fire during the Holocene. Thanks to macrofossil analysis, charcoal particles were found buried in the mineral soil at two sites where no charcoal particles were recovered at the base of the organic horizon. At these old-growth stands, there was no *in situ* evidence of past fire events from any other known ecological proxies (e.g. charcoal in the organic matter, fire scars).

Pollen data of two forest hollows in the southern part of the fir zone (located $<$ 10 km west of site RFL1) indicated that balsam fir forest in this area date back to 9500 cal. yr B.P. (Colpron-Tremblay and Lavoie, 2010). Our stand-scale fire histories in the fir zone showed that 3 out of the 7 sampled sites were affected by wildfires whereas the other 4 sites were not. It is likely that balsam fir thus continuously maintained itself at some sites within the zone which escaped fire throughout the Holocene. Safe sites similar to those identified from our data were probably distributed throughout the fir zone. Such sites may have served as seed sources allowing successful post-fire regeneration of areas of the fir zone which burned repeatedly during early Holocene. This mechanism would explain the continuous presence of the fir forest in the southern boreal forest zone over the last 10 thousand years. In contrast, all the sampled sites of the spruce zone were disturbed by recurrent fires. Despite the fact that balsam fir is fire-intolerant, balsam fir forests are still growing in the subalpine belt of this zone. Due to orographic effects caused by contrasted topography associated with the high plateaus, subalpine fir forests are growing in more humid conditions than lowland forests. As a result, the average 570-yr fire-return interval in the subalpine belt of this area is two to five time longer than in the regional lowlands (115 yr [Parisien and Sirois, 2003], 130 yr [Cogbill, 1985] and 270 yr [Bouchard et al., 2008]). The longer fire interval of the subalpine belt is sufficient to maintain residual balsam fir stands at high elevation whereas the greater fire frequency in lowlands of the spruce zone probably excluded balsam fir while promoting black spruce. One could argue that the moist climatic conditions of the high plateaus might be favourable to balsam fir growth and persistence while at the same time being inhibitive to fire. This interpretation would imply that climate per se and not fire is directly regulating the distribution of these southern boreal plant assemblages. However, de Lafontaine and Payette (2010) have shown that, in the absence of fire, harsh high altitude climate has inhibitory effects on balsam fir which limits the species capacity to dominate stands at high elevation. It is therefore notable that isolated balsam fir stands at their northernmost limit are exclusively found at high elevation, in a subalpine environment where climatic conditions approach the ones limiting to the species. The absence of balsam fir stands in the lowlands, where the climate is less rigorous but where fire is more frequent, exemplifies how natural disturbances (wildfire) are instrumental to the distribution of boreal plant assemblages.

Taxonomic charcoal identification revealed that Holocene forest composition was limited to only three genera (*Abies*, *Picea* and *Betula*). By 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 are found in the area), we infer that the forest composition at all sites remained somewhat typical of the balsam fir forest flora during the Holocene. Of the sites where charcoal was found, many were close to reaching the asymptote of the accumulation curve indicating that the number of observed fire events roughly corresponds to the number of expected fire events based on the extrapolation. The exceptions are RFL2 in the fir zone and STEF in the spruce zone. Interestingly, these two sites border areas frequently disturbed by fire. Site RFL2 is located on the leeward side of the Laurentian Plateau, 6 km west of the Parc des Grands-Jardins (PGJ). This area harbours the southernmost lichen woodland stands which formed when post-fire regeneration failed to reconstruct the original closed-crown forest stands (Payette et al., 2000). Site RFL2 was disturbed by a number of wildfires which also burned the nearby PGJ. This is the case for fire occurring at 1290 cal. yr B.P. which was already documented in the PGJ where it was at the origin of the transformation of a closed-crown forest to a lichen woodland 13 km east of RFL2 (Jasinski and Payette, 2005). The other recent fire (95 cal. yr B.P.) recorded at RFL2 site was contemporaneous to the construction of the road between Québec City and Saguenay in the 1870s (Brousseau, 1926) and was thus probably of human origin. Site STEF is the northernmost sampled site located immediately south of the lichen woodland zone where wildfires are most frequent (fire return interval = 100 yr [Payette et al., 1989]). Only at these two sites located near areas with high fire occurrence did the number of observed fire events was significantly lower than the expected number of fire events based on the asymptote of the extrapolated accumulation curves. This implies that in order to obtain the complete local fire histories, more ^{14}C dates must be processed for sites RFL2 and STEF. However, it also indicates that the macrofossil analysis of charcoal in mineral soils is a reliable method to reconstruct stand-scale Holocene fire histories.

Data from the two regional fire histories outlined a neat subcontinental shift of fire activity from the fir zone to the spruce zone at *c.* 5000 cal. yr B.P. Stands of the fir zone were influenced by recurrent fires during four millennia (between *c.* 9000 and 5000 cal. yr B.P.), whereas fire disturbance which is still ongoing today in the spruce zone (de Lafontaine and Payette, 2010) dates back to five millennia. This shift of fire activity between the two zones roughly concurs with that found in previous studies reconstructing the long-term fire history of the southern boreal forest based on charcoal deposition in lacustrine sediments. Carcaillet and Richard (2000) found greater charcoal accumulation in lake sediments of the southern boreal forest (Lac Madeleine) between *c.* 8500 and 6000 cal. yr B.P. while charcoal accumulation in the spruce zone (Lac Desautels) was higher between *c.* 3500 and 1000 cal. yr B.P. Asnong and Richard (2003) also found greater charcoal influx between 10,500 and 6500 cal. yr B.P. in the sediments of two lakes from the balsam fir zone (eastern Québec). These studies yield slightly different results than ours due to the use of different methods (regional to local microfossil analysis of charcoal [from $\geq$12.5 to $\geq$160 μm] deposited in lacustrine sediments vs stand scale macrofossil analysis of charcoal [$\geq$2 mm] in mineral soils) in different study areas (there might be important site specific differences as exemplified by our stand-scale analysis). Nevertheless, both methods roughly uncovered the same two epochs/regions with increased fire activity. A period of greater fire activity is recorded in the balsam fir zone during the early to mid Holocene and a shift towards increased fire activity in the spruce zone occurred during the mid to late Holocene. Our data indicate that this shift in fire activity occurred at 5000 cal. yr B.P. in Québec-Labrador peninsula. This transition would thus be a direct response to the end of the Holocene climatic optimum and the onset of the neo-glacial.

According to deglaciation data, sites of the spruce zone were entirely free of ice sometime between 7800 and 7450 cal. yr B.P. (Dyke, 2004). This leaves a conservative 2450-year window after the melting of glacier ice during which there was probably only a few or no fire disturbances. The ecological conditions prevailing during this period were probably favourable for the northward expansion of the floral assemblage associated with balsam fir. Indeed, we found *Abies* charcoal dating back to the beginning of the fire activity in the spruce zone, a direct evidence indicating balsam fir presence in the area before 5000 cal. yr B.P. According to published pollen data, *Abies* post-glacial northern migration might have reached the regional lowlands surrounding the high plateaus of central Québec (Fig. 1 points B and C) sometime between 7300 and 6200 cal. yr B.P. (King, 1986). In all published pollen diagrams from the spruce zone, the decrease in *Abies* pollen was contemporary to an increase in *Picea*. This exemplifies the zonal transition from the historical expansion of balsam fir forests to the current extensive black spruce forests among the northern closed-crown boreal landscape. Climate change of the late Wisconsinian was the proximal cause for the post-glacial expansion of species (Davis, 1981). This study demonstrates how the zonation of the closed-crown boreal forest at the sub-continental scale since the neo-glacial was the direct consequence of the natural disturbances and not the climate per se. Climate cooling, driven inexorably by the Milankovitch cycles, was the ultimate cause for the change in the fire regime at 5000 cal. yr B.P. However, this shift of the fire activity directly caused the regional decline of balsam fir forests in the lowlands and their replacement by today's black spruce forest forests. This exemplifies how climate change has both direct and indirect effects accounting for the abundance of species within the boundaries of its climatic envelope.

5. Conclusions

Macrofossil analysis of charcoal in mineral soils was used to uncover *in situ* Holocene fire histories at the stand scale where no other known long-term fire proxies are available. The balsam fir forest probably maintained itself in the fir zone throughout the Holocene (Colpron-Tremblay and Lavoie, 2010). Even though the region was submitted to recurrent fires between 9000 and 5000 cal. yr B.P., stand-scale fire histories suggest that several sites within the fir zone escaped fire during the Holocene. Such safe sites probably served as seed sources allowing the regional maintenance of the fir forest through the period of recurrent fires. The spruce zone has been submitted to recurrent fires over the last 5000 years. Such a shift in the regional fire activity initiated a major restructuring of the fir and spruce zones. Increased regional fire activity caused the decline of the northern balsam fir forests in the lowlands and their replacement by extant black spruce forest stands.

Previous studies using other proxies (community ecology, molecular ecology) did suggest the scenario of a northern balsam fir forest expansion/retraction. First, de Lafontaine and Payette (2010) indicated that the northernmost balsam fir stands share structural and compositional attributes with stands of the fir zone, suggesting that subalpine stands could indeed originate from plant assemblages of the fir zone. Second, a study of chloroplast DNA variations of white spruce (a species closely associated with the balsam fir forest flora) suggested that populations located in the disjunct subalpine stands of central Québec were submitted to a genetic bottleneck. This genetic signal was caused by a demographic decline indicating the global collapse of the balsam fir floral assemblages in this region (de Lafontaine et al., 2010). These studies were the first to suggest the hypothesis that the fir zone once expanded north, up to latitudes corresponding to the northern part of extant spruce zone. Not only did the macrofossil analysis of charcoal in mineral soils, corroborate this expansion/retraction scenario, but it also explained the mechanism and provided a rigorous dating of this biogeographical process.

Fire is the major structuring agent of the boreal biome (Heinselman, 1981). The current zonation of the boreal landscape into closed-crown forest, open forest, and forest tundra was triggered by fire disturbances which opened the landscape during the Holocene (Payette, 1992). The decline of balsam fir forests in the lowlands and their replacement by black spruce forests in the northern part of the closed-crown boreal zone was somewhat hidden because direct field evidence is lacking (e.g. wood charcoal remains in a tundra is a direct field evidence of deforestation). However, from the divergent community model (Payette, 1992) which was empirically tested in the other boreal forest zones we suggested a hypothesis to explain the biogeographical origin of the northernmost disjunct balsam fir stands. Macrofossil analysis of charcoal in mineral soils allowed us to test our hypothesis by linking the balsam fir-black spruce zonal transition among the northern closed-crown boreal forest with a proximal causal process, i.e., a shift in the Holocene fire regime dated five millennia ago.

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. This work was supported by a NSERC research grant to S.P. and Alexander Graham Bell Canada Graduate Scholarship to G.dL.

Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.quascirev.2011.01.002.

References

Arsenault, D., Sirois, L., 2004. The millennial dynamics of a boreal forest stand from buried trees. Journal of Ecology 92, 490–504.
Asnong, H., Richard, P.H., 2003. La végétation et le climat postglaciaires du centre et de l'est de la Gaspésie, au Québec. Géographie Physique et Quaternaire 57, 37–63.
Asselin, H., Payette, S., 2005. Late Holocene opening of the forest tundra landscape in northern Québec, Canada. Global Ecology and Biogeography 14, 307–313.
Bouchard, M., Pothier, D., Gauthier, S., 2008. Fire return intervals and tree species succession in the North Shore region of eastern Québec. Canadian Journal of Forest Research 38, 1621–1633.
Brousseau, D., 1926. Report on the exploration of Montmorency crown lands, in the province of Québec for Anglo-Canadian. Pulp and Paper Mills, Ltd., Québec, Canada.
Carcaillet, C., 2001. Are Holocene wood-charcoal fragments stratified in alpine and subalpine soils? Evidence from the Alps based on AMS ^{14}C dates. The Holocene 11, 231–242.
Carcaillet, C., Richard, P.H., 2000. Holocene changes in seasonal precipitation highlighted by fire incidence in eastern Canada. Climate Dynamics 16, 549–559.
Cogbill, C.V., 1985. Dynamics of the boreal forests of the Laurentian Highlands, Canada. Canadian Journal of Forest Research 15, 252–261.

Colpron-Tremblay, J., Lavoie, M., 2010. Long-term stand-scale dynamics of a boreal mixed forest in Québec, Canada. Review of Palaeobotany and Palynology 161, 43–58.

Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of The Royal Society B 345, 101–118.

Davis, M.B., 1981. Quaternary history and the stability of forest communities. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession: Concepts and Applications. Springer-Verlag, New York, NY, pp. 132–153.

de Lafontaine, G., Payette, S., 2010. The origin and dynamics of subalpine white spruce and balsam fir stands in boreal eastern North America. Ecosystems 13, 932–947.

de Lafontaine, G., Turgeon, J., Payette, S., 2010. Phylogeography of white spruce (*Picea glauca*) in eastern North America reveals contrasting ecological trajectories. Journal of Biogeography 37, 741–751.

Dyke, A.S., 2004. An outline of North American deglaciation with emphasis on central and northern Canada. In: Ehlers, J., Gibbard, P.L. (Eds.), Quaternary Glaciations – Extent and Chronology, Part II. Elsevier B.V., Amsterdam, The Netherlands, pp. 373–424.

Engstrom, D.R., Hansen, B.C.S., 1985. Postglacial vegetational change and soil development in southeastern Labrador as inferred from pollen and chemical stratigraphy. Canadian Journal of Botany 63, 543–561.

Fesenmyer, K.A., Christensen, N.L., 2010. Reconstructing Holocene fire history in a southern Appalachian forest using soil charcoal. Ecology 91, 662–670.

Filion, L., 1984. A relationship between dunes, fire and climate recorded in the Holocene deposits of Quebec. Nature 309, 543–546.

Gavin, D.G., 2001. Estimation of inbuilt age in radiocarbon ages of soil charcoal for fire history studies. Radiocarbon 43, 27–44.

Gavin, D.G., Brubaker, L., Lertzman, K., 2003. Holocene fire history of a coastal temperate rain forest based on soil charcoal radiocarbon dates. Ecology 84, 186–201.

Girard, F., Payette, S., Gagnon, R., 2008. Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. Journal of Biogeography 35, 529–537.

Girard, F., Payette, S., Gagnon, R., 2009. Origin of the lichen-spruce woodland in the closed-crown forest zone of eastern Canada. Global Ecology and Biogeography 18, 291–303.

Grandtner, M.M., 1966. La végétation forestière du Québec méridional. Les Presses de l'Université Laval, Québec, Canada.

Hare, F.K., Ritchie, J.C., 1972. The boreal bioclimates. Geographical Review 62, 333–365.

Heinselman, M.L., 1981. Fire and succession in the conifer forests of northern North America. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession: Concepts and Application. Springer-Verlag, New York, NY, pp. 374–406.

Higuera, P.E., Sprugel, D.G., Brubaker, L.B., 2005. Reconstructing fire regimes with charcoal from small-hollow sediments: a calibration with tree-ring records of fire. The Holocene 15, 238–251.

Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T., Tosi, J.A., 1971. Forest Environments in Tropical Life Zones. Pergamon Press, Oxford, UK.

Jackson, S.T., Overpeck, J.T., Webb III, T., Keattch, S.E., Anderson, K.H., 1997. Mapped plant-macrofossil and pollen records of late quaternary vegetation change in Eastern North America. Quaternary Science Reviews 16, 1–70.

Jasinski, J.P.P., Payette, S., 2005. The creation of alternative stable states in the southern boreal forest, Québec, Canada. Ecological Monographs 75, 561–583.

King, G.A., 1986. Deglaciation and vegetation history of western Labrador and adjacent Quebec. Ph.D. Thesis, University of Minnesota, Minneapolis, MN.

Lafond, A., 1964. Classification écologique des forêts par la végétation: application à la province de Québec. Faculté d'Arpentage et de Génie forestier, Université Laval, Québec, Canada.

Lafortune, V., Filion, L., Hétu, B., 2006. Impacts of Holocene climatic variations on alluvial fan activity below snowpatches in subarctic Québec. Geomorphology 76, 375–391.

Lamb, H.F., 1980. Late Quaternary vegetational history of southeastern Labrador. Arctic and Alpine Research 12, 117–135.

Lamb, H.F., 1985. Palynological evidence for postglacial change in the position of tree limit in Labrador. Ecological Monographs 55, 241–258.

Larsen, J.A., 1980. The Boreal Ecosystem. Academic Press, New York, NY.

Lomolino, M.V., Riddle, B.R., Brown, J.H., 2006. Biogeography, third ed. Sinauer Associates, Sunderland, MA.

May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269, 471–477.

Meyer, G.A., Wells, S.G., Balling Jr., R.C., Jull, A.J.T., 1992. Response of alluvial systems to fire and climate change in Yellowstone National Park. Nature 357, 147–150.

Morrison, A., 1970. Pollen diagrams from interior Labrador. Canadian Journal of Botany 48, 1957–1975.

Ohlson, M., Tryterud, E., 2000. Interpretation of the charcoal record in forest soils: forest fires and their production and deposition of macroscopic charcoal. The Holocene 10, 519–525.

Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compounded perturbations yield ecological surprises. Ecosystems 1, 535–545.

Parisien, M.-A., Sirois, L., 2003. Distribution and dynamics of tree species across a fire frequency gradient in the James Bay region of Quebec. Canadian Journal of Forest Research 33, 243–256.

Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, UK, pp. 144–169.

Payette, S., 1993. The range limit of boreal tree species in Québec-Labrador: an ecological and palaeoecological interpretation. Review of Palaeobotany and Palynology 79, 7–30.

Payette, S., Morneau, C., Sirois, L., Desponts, M., 1989. Recent fire history of the northern Québec biomes. Ecology 70, 656–673.

Payette, S., Bhiry, N., Delwaide, A., Simard, M., 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce-moss forest. Canadian Journal of Forest Research 30, 288–305.

Payette, S., Fortin, M.-J., Gamache, I., 2001. The subarctic forest-tundra: the structure of a biome in a changing climate. Bioscience 51, 709–718.

Pollock, S.L., Payette, S., 2010. Stability in the patterns of long-term development and growth of the Canadian spruce-moss forest. Journal of Biogeography 37, 1684–1697.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Bertrand, C.J.H., et al., 2004. IntCal04 terrestrial radiocarbon age calibration, 26–0 ka BP. Radiocarbon 46, 1029–1058.

Richard, P.H., 1993. Origine et dynamique postglaciaire de la forêt mixte au Québec. Review of Palaeobotany and Palynology 79, 31–68.

Richard, P.H., Larouche, A., Bouchard, M.A., 1982. Âge de la déglaciation finale et histoire postglaciaire de la végétation dans la partie centrale du Nouveau-Québec. Géographie Physique et Quaternaire 36, 63–90.

Rowe, J.S., Scotter, G.W., 1973. Fire in the boreal forest. Quaternary Research 3, 444–464.

Soberón, M.J., Llorente, B.J., 1993. The use of species accumulation functions for the prediction of species richness. Conservation Biology 7, 480–488.

Sanborn, P., Geertsema, M., Jull, A.J.T., Hawkes, B., 2006. Soil and sedimentary charcoal evidence for Holocene forest fires in an inland temperate rainforest, east-central British Columbia, Canada. The Holocene 16, 415–427.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.

Schoch, W., Heller, I., Schweingruber, F.H., Kienast, F., 2004. Wood anatomy of central European species. Available from: www.woodanatomy.ch.

Schweingruber, F.H., 1978. Microscopic Wood Anatomy. Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Zürich, Switzerland.

Schweingruber, F.H., 1990. Anatomy of European Woods. Swiss Federal Institute for Forest, Snow and Landscape Research. Verlag Paul Haupt, Bern, Switzerland.

Stuiver, M., Reimer, P.J., Reimer, R.W., 2005. CALIB 5.0. [WWW program and documentation]. http://calib.qub.ac.uk/calib/.

Talon, B., Payette, S., Filion, L., Delwaide, A., 2005. Reconstruction of the long-term fire history of an old-growth deciduous forest in Southern Québec, Canada, from charred wood in mineral soils. Quaternary Research 64, 36–43.

Thinon, M., 1992. L'analyse pédoanthracologique:aspects méthodologiques et applications. Ph.D. Thesis, Université Paul Cézanne, Aix-Marseille, France.

Timoney, K.P., La roi, G.H., Dale, M.R.T., 1993. Subarctic forest-tundra vegetation gradients: the sigmoid wave hypothesis. Journal of Vegetation Science 4, 387–394.