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Changes in fire regime explain the Holocene rise and fall of *Abies balsamea* in the coniferous forests of western Québec, Canada

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Abstract: The coniferous boreal forest of northeastern North America is characterized by large and severe fire events and dominated by black spruce (*Picea mariana*), with scattered patches of balsam fir (*Abies balsamea*), a species otherwise predominant in the more southern mixedwood boreal forests, characterized by smaller and less severe fire events. Because balsam fir is a late-successional species ill-adapted to fire, this study aimed at determining if the scattered balsam-fir patches found in the coniferous forest were relics of a former fire regime characterized by less frequent and/or severe conflagrations. Fire and vegetation history were assessed for a coniferous forest site through analyses of charcoal, pollen and plant macroremains preserved in lake sediments, peat and hydromorphic forest soil. Pollen and macroremains analyses show that black spruce dominated the local vegetation since deglaciation (*c*. 8000 cal. yr BP). Balsam fir was abundant around the site during the warm and humid summers of the Hypsithermal (between *c*. 7000 and 3500 cal. yr BP), before gradually declining during the cool and dry Neoglacial, which was characterized by increased fire frequency and severity. Scattered balsam fir patches in the coniferous forest result from the fragmentation of formerly larger populations and are presently in disequilibrium with climate.

Key words: *Abies balsamea,* biogeography, boreal forest, climate change, fire history, fire regimes, population ecology, palaeoecology, Canada, Holocene.

Introduction

Fire is a key ecological factor shaping global vegetation at different scales of space and time (Bond *et al*., 2005), particularly in boreal forests (Johnson, 1992; Payette, 1992; Niklasson and Granström, 2000; Lindbladh *et al*., 2003; Bergeron *et al*., 2004). In Canadian boreal forests, fire regimes have changed several times during the Holocene in response to climate variations (Payette and Gagnon, 1985; Filion *et al*., 1991; Carcaillet and Richard, 2000; Lynch *et al*., 2004a; Hallett and Hills, 2006), inducing vegetation transformations at the landscape scale (Asselin and Payette, 2005a; Jasinski and Payette, 2005; Asselin *et al*., 2006). Moreover, vegetation shifts toward communities dominated by fire-adapted species might act on fire regimes by feedbacks through changes in plant flammability, fuel load or landscape connectivity (Clark *et al*., 2001; Rupp *et al*., 2002; Hu *et al*., 2006). Understanding climate–fire–vegetation interactions is thus important for sustainable forest management (Bergeron *et al*., 1998) and biodiversity conservation (Willis and Birks, 2006), especially as model outputs predict that the current global warming will induce an increase in fire frequencies and areas burned in Canada, with potential environmental and economical consequences (Flannigan *et al*., 2005; Schumacher and Bugmann, 2006).

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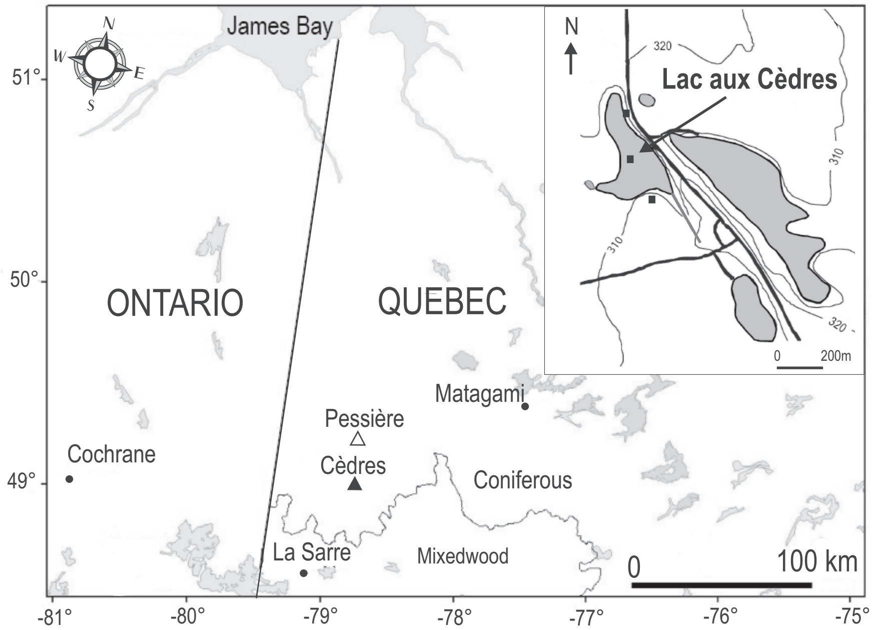

Figure 1 Location of the study site (solid triangle) in the coniferous boreal forest. A nearby site (Lac à la Pessière) is also shown (open triangle). The inset shows the location of the three sampling points (solid squares) in the vicinity of Lac aux Cèdres: in the southern peatland, in the lake and in the northern forest

In the boreal zone of Québec, the ecological processes controlling the transition between the southern mixedwood forest dominated by balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.) and white spruce (*Picea glauca* (Moench) Voss.), and the northern coniferous forest dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) are only partly understood. This transition occurs at *c*. 49°N in western Québec (Figure 1). According to Bergeron *et al*. (2004), the present-day transition between these two boreal zones is controlled by fire size and severity. Mixedwood forests are characterized by smaller and less severe fire events, compared to coniferous forests, where fires are larger and more severe (Hély *et al*., 2001). Large and severe fires induce high tree mortality, hence disadvantaging mixedwood forest species, which generally need survivor seed trees to reinvade burned areas (Asselin *et al*., 2001; Bergeron *et al*., 2004; Albani *et al*., 2005). In mixedwood forests, abundance of deciduous species and landscape fragmentation by large lakes contribute to reduce fire size and severity. Within this ecozone, the abundance of mature balsam fir trees increases with time since fire (Bergeron, 2000), suggesting that shorter fire intervals might also disadvantage balsam fir, to the benefit of pioneer species such as black spruce, jack pine (*Pinus banksiana* Lamb.), paper birch and trembling aspen (*Populus tremuloides* Michx.).

Balsam fir is locally abundant in coniferous forests, forming isolated patches up to 54°N (Payette, 1993; Sirois, 1997). The acid soils of the coniferous forest, resulting from slow decomposition of organic matter, could partly explain the northward decrease in abundance of balsam fir, a species usually associated with mesic sites (Bergeron and Dubuc, 1989; Gauthier *et al*., 2000). However, balsam fir fails to occupy all potentially suitable (mesic) sites in the coniferous forest (Messaoud *et al*., 2007a). Moreover, the gradual northward decrease of the growing season temperature was shown to negatively affect the capacity of balsam fir to produce viable seeds (Messaoud *et al*., 2007b). Nevertheless, climatic conditions, soil properties and topography together explain only 33% of the present-day distribution of balsam fir at the landscape scale (Messaoud *et al*., 2007a). Competition between black spruce and balsam fir during postglacial colonization, coupled with changes in fire regimes, could also explain the present-day distribution of balsam fir in the coniferous forest. In the Abitibi-Témiscamingue region of western Québec, postglacial colonization occurred rapidly after the retreat of proglacial lake Ojibway *c*. 8400 cal. yr BP and involved all the tree species presently found in the area (Richard, 1980; Liu, 1990; Carcaillet *et al*., 2001a). Since 7000 cal. BP, balsam fir and black spruce respectively dominate the mixedwood and coniferous forests (Garalla and Gajewski, 1992; Gajewski *et al*., 1996; Carcaillet *et al*., 2001a). According to Liu (1990), present-day balsam fir stands of the coniferous forest are remnants of formerly larger populations and would thus result from the fragmentation of those initial populations. The decline of balsam fir in the coniferous forest could be related to the climatic shift characterizing the beginning of the Neoglacial period, with the establishment of cooler and drier summers (Carcaillet and Richard, 2000), coincident with an increase in fire frequency in the coniferous forest *c*. 3000 cal. yr BP (Carcaillet *et al*., 2001a). Fire is more important than climate to explain the distribution limit of some species (Flannigan and Bergeron, 1998; Rupp *et al*., 2000; Asselin *et al*., 2003). Thus one could argue that fire regime is the main ecological forcing controlling the occurrence and abundance of balsam fir stands in the coniferous forest, although the long-term ecological mechanisms involved remain to be fully understood. In Europe, studies focusing on the dynamics of *Abies alba*, a vicarious fir species, attested that fires were responsible for the decline of this species during the mid Holocene (Tinner *et al*., 2000; Keller *et al*., 2002; Wick and Möhl, 2006; Colombaroli *et al*., 2007). The same scenario could explain the present-day scattered distribution of balsam fir in the coniferous Canadian boreal forest.

This study aimed to determine if the distribution pattern of balsam fir in the coniferous forest could result from past changes in fire regimes. Balsam fir is a late-successional species ill-adapted to fire, so its establishment in the coniferous forest should have occurred at times when fires were less frequent or severe, and a shift to more frequent or more severe fires might be responsible for the fragmentation of balsam fir populations in the coniferous forest, leading to the present-day distribution characterized by scattered patches in a matrix otherwise dominated by black spruce. To maximize reconstruction accuracy, our analyses were based on three different proxies (pollen, plant macroremains and charcoal fragments) sampled in three different sedimentary archives from the same site (lake sediments, peat and hydromorphic forest soil).

Material and methods

Study area

The present-day climate in the area is continental with cold winters and warm summers. According to data from the closest weather station (La Sarre, 60 km southward; Figure 1), the mean annual temperature is 0.8 ± 1.0°C and the annual precipitation range is between 800 and 900 mm, with 25% falling as snow. The sampling site is located in the vicinity of a 4 ha kettle lake (Lac aux Cèdres, 49°20′45″N; 79°12′30″W; Figure 1). The vegetation around Lac aux Cèdres is dominated by black spruce, along with jack pine. Scattered balsam fir and eastern white cedar (*Thuja occidentalis* L.) individuals grow along the southern and eastern lakeshores. *Alnus incana* (L.) Moench is the dominant tall shrub, and the understorey is mostly composed of *Sphagnum fuscum* (Schimp.) Klinggr, *Pleurozium schreberii* (Brid) Mitt., *Rhododendron groenlandicum* (Oeder) Kron and Judd, *Kalmia angustifolia* L., *Vaccinium angustifolium* Ait., *Gaultheria hispidula* (L.) Muhl., and *Cornus canadensis* L.

The postglacial fire history of the area inferred from charcoal preserved within the sediments of a lake located 20 km north of Lac aux Cèdres (Lac à la Pessière; Figure 1) displays short fire-free intervals before 7300 cal. BP and long fire-free intervals during the mid Holocene (between 7300 and 3300 cal. yr BP). The late Holocene is divided into two phases: the first (3300–1300 cal. yr BP) is characterized by short fire-free intervals, and the second (1300–0 cal. yr BP) by longer fire-free intervals (Carcaillet *et al*., 2001a). Since the end of the ‘Little Ice Age’ (*c*. 100 BP) fire frequencies are decreasing regionally (Bergeron *et al*., 2004) in response to increased summer moisture associated with global warming (Bergeron and Archambault, 1993; Girardin *et al*., 2006).

Sampling

Lac aux Cèdres has a maximum water depth of 16 m and a surface area of *c*. 4 ha. Sediments were extracted from the deepest part of the lake with a Mackereth sampler equipped with a 6 m long tube (Mackereth, 1958). A Kajak-Brinkhurst (KB) gravity (Glew, 1991) corer was used to collect the uppermost sediment. Peat sediments were sampled on the southern shore of the lake with a Russian corer (Jowsey, 1966), whereas a 35 cm thick hydromorphic soil profile was collected on the northeastern shore with a Wardenaar corer (Wardenaar, 1987). All profiles were sliced into continuous 1 cm thick subsamples for analysis of pollen, charcoal or macroremains.

Sediment dating

Chronologies were based on ^{14}C dates calibrated against dendrochronological years with version 5.0.1 of the CALIB program (Stuiver and Reimer, 1993), based on the IntCal04 data set (Reimer *et al*., 2004), and reported as intercepts with 2 sigma ranges. Because the lacustrine sediments were poor in plant macroremains, eight conventional ^{14}C dates were carried out on bulk sediments. Six AMS ^{14}C dates were obtained from plant macroremains and charcoal fragments from the peat, and four from the hydromorphic forest soil.

Pollen, charcoal and macroremains analyses

Lake sediments

For charcoal analysis, 1 cm^3 was used for each subsample. The subsamples were soaked in a 3% $(NaPO_3)_6$ deflocculating solution for a minimum of two days before wet-sieving through a 160 μm mesh. The remaining particles were bleached in a 10% sodium hypochlorite (NaOCl) solution to help distinguish charcoal from dark organic matter. Charcoal fragments larger than 160 μm were assumed to have been produced by fire events <500 m from the lakeshore (Lynch *et al*., 2004b; Higuera *et al*., 2005). The surface area of each charcoal fragment was estimated under a dissecting microscope (40×) with an ocular grid with 400 squares, each measuring 0.0144 mm^2 (Carcaillet *et al*., 2001b). Charcoal fragments were then grouped in ten exponentially increasing size-classes. Total charcoal surface area was calculated for each sample by first multiplying the number of fragments of each size class by its median surface area, and then by adding the values obtained for all size classes. Charcoal measurements are reported both as charcoal area concentration (mm^2/cm^3) and as charcoal accumulation rates (CHAR, mm^2/cm^2 per yr).

For pollen and spore analyses, 1 cm^3 subsamples were collected at each 16 cm and processed following the procedure proposed by Faegri and Iversen (1989). A known number of exotic pollen grains (*Eucalyptus*) were added to the samples to allow estimation of pollen concentrations. Samples were soaked in a 10% hot KOH solution and sieved through a 700 μm mesh. Carbonates, silicates and most of the organic matter were removed with 10% HCl, 48% HF and acetolysis, respectively. A minimum of 500 grains were counted per sample.

Peat

The peat subsamples were first boiled in a $(NaPO_3)_6$ solution before wet sieving through a series of meshes (2.00, 1.00, 0.50 and 0.25 mm). Only charcoal fragments > 0.5 mm in diameter – corresponding to local fire events (Clark *et al*., 1998; Ohlson and Tryterud, 2000; Lynch *et al*., 2004b; Higuera *et al*., 2005) – were used to calculate charcoal concentrations (mg/cm^3). Small hollows and peatlands are less suitable for precise detection of fire events and to establish fire chronologies, because they mostly record high-severity fires and sometimes fail to record up to half of the moderate- to low-severity fires (Niklasson *et al*., 2002; Higuera *et al*., 2005). The variability in fire recording is mostly related to the pattern of burned areas and to the distance between charcoal source area and deposition site (Higuera *et al*., 2005). The deposition of charcoal fragments produced by older fires, that had a long period of sequestration in the catchment area, can indicate false fire events. Each charcoal peak may represent a local fire event and the highest peaks can correspond to more severe fire events or to events that occurred closer to the deposition site (Clark *et al*., 1996; Daniels *et al*., 2005; Higuera *et al*., 2005).

The other plant remains collected in the peat profile (needles, twigs, seeds, cone scales, etc.) were identified by comparison with reference collections and specialized atlases (Young and Young, 1994; Crow and Hellquist, 2000a,b).

Hydromorphic forest soil

Only macrocharcoal fragments (> 0.5 mm) were analysed following the same method used for the peat profile. Charcoal fragments preserved in forest soils result from fires that burned the local woody vegetation and their identification could provide helpful information on pre-fire plant composition (Jacquiot *et al*., 1973; Carcaillet and Brun, 2000; Asselin and Payette, 2005b; Talon *et al*., 2005). Taxonomic identification was achieved on the largest fragments (> 1 mm) using distinctive anatomical characters observed under an episcopic microscope (200×, 500×, 1000×). A reference collection of charred wood, as well as wood anatomy atlases (eg, Schweingruber, 1990), were used to help identification.

Table 1 Radiocarbon dates obtained from the lake sediments, the peat, and the hydromorphic forest soil

Profile and level (cm)	Material	Dating	Age BP	Cal. BP (2σ)	Reference
Lake					
6–14 (M)	gyttja	conventional	3850 ± 90[a]	4260 (3990–4520)	Beta142349
18–24 (M)	gyttja	conventional	3790 ± 130[a]	4160 (3780–4530)	Beta140340
43–49 (KB)	gyttja	conventional	4730 ± 90[a]	5400 (5150–5650)	Beta142348
106–111 (M)	gyttja	conventional	3390 ± 80	3650 (3450–3840)	Beta140341
237–242 (M)	gyttja	conventional	4260 ± 80	4790 (4540–5040)	Beta140342
376–381 (M)	gyttja	conventional	5420 ± 80	6200 (5990–6400)	Beta140343
479–484 (M)	gyttja	conventional	6150 ± 90	7030 (6800–7260)	Beta140344
566.5–572.5 (M)	gyttja	conventional	6290 ± 160	7150 (6800–7490)	Beta140345
Peat					
8–9	macroremains	AMS	1335 ± 25[b]	1240 (1180–1300)	Poz14577
24–25	macroremains	AMS	410 ± 30	420 (320–520)	Poz16507
43–44	macroremains	AMS	4990 ± 40	5710 (5660–5840)	Poz14578
57–58	macroremains	AMS	5040 ± 40	5780 (5660–5900)	Poz16508
75–76	macroremains	AMS	7200 ± 40	8000 (7960–8030)	Poz14579
100–101	macroremains	AMS	7240 ± 50	8090 (8000–8170)	Poz14580
Hydromorphic forest soil					
10–11	charcoal	AMS	160 ± 30	140 (0–286)	Poz15208
19–20	charcoal	AMS	1775 ± 30	1710 (1610–1810)	Poz15209
24–25	charcoal	AMS	2045 ± 30	1970 (1930–2010)	Poz16509
33–34	charcoal	AMS	6970 ± 40	7820 (7700–7930)	Poz15210

Dates were calibrated using the Calib 5.0.1 program (Stuiver and Reimer, 1993) and rounded to the nearest 10 years.
M, Mackereth; KB, Kajak-Brinkhurst.
[a]Detrital peat (not used).
[b]Contaminated by runoff of extralocal, older sediments (not used).

Estimation of fire-free intervals

The numerical analysis of the lake charcoal series followed the method proposed by Gavin *et al*. (2006). Charcoal accumulation rates (CHAR) were divided into background and peak components with a tricube function with a time window of 500 years (CHARSTER program, version 0.8.3; Gavin, 2006). Different window values (between 200 and 1000 years) did not significantly change the output results. The background component represents long-term variation in overall CHAR magnitude resulting from changes in vegetation composition, fire regime and mechanisms of charcoal transport and deposition (Gavin *et al*., 2006). The peak component corresponds to the difference between CHAR and background and represents charcoal produced by single or closely successive fires (herein referred to as 'fire events'). Local fire events were inferred from the peak component by modelling the frequency distribution of the peak component as a mixture of overlapping Gaussian distributions using the CLUSTER program (Bouman, 2001). After being converted into equal 10 yr time intervals (based

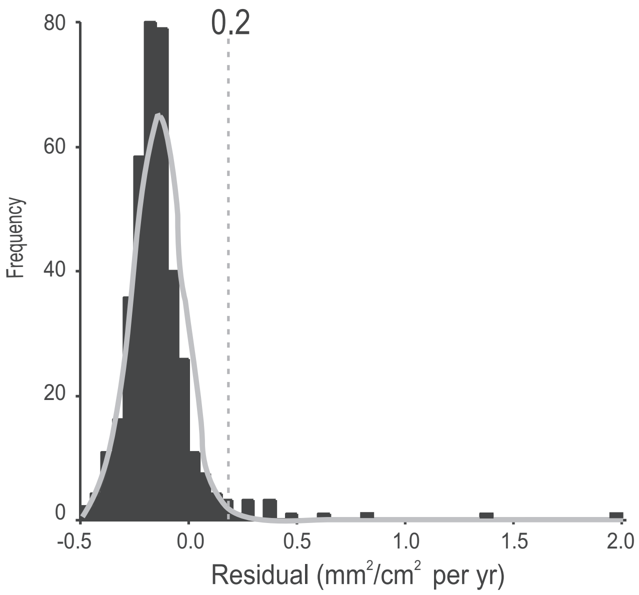

Figure 2 Gaussian model fitted to the peak component of the CHAR record. The vertical dashed line indicates the threshold (0.2 mm²/cm² per yr) selected to indicate local fire events

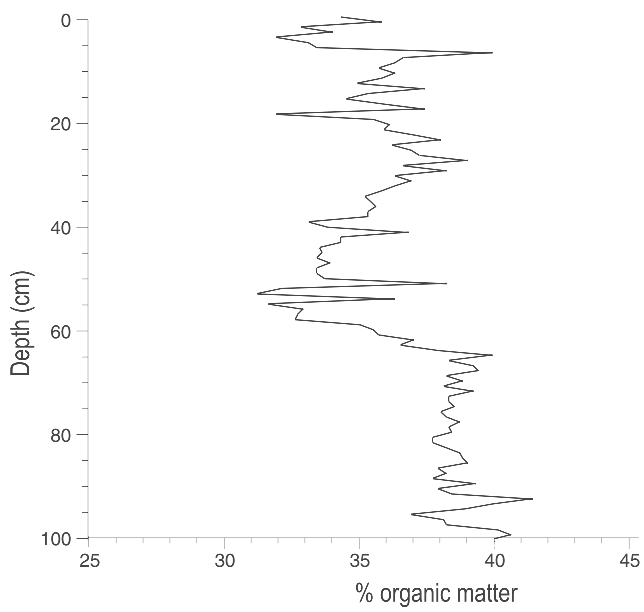

Figure 3 Percent organic matter in the lake sediment core as determined by loss-on-ignition analysis

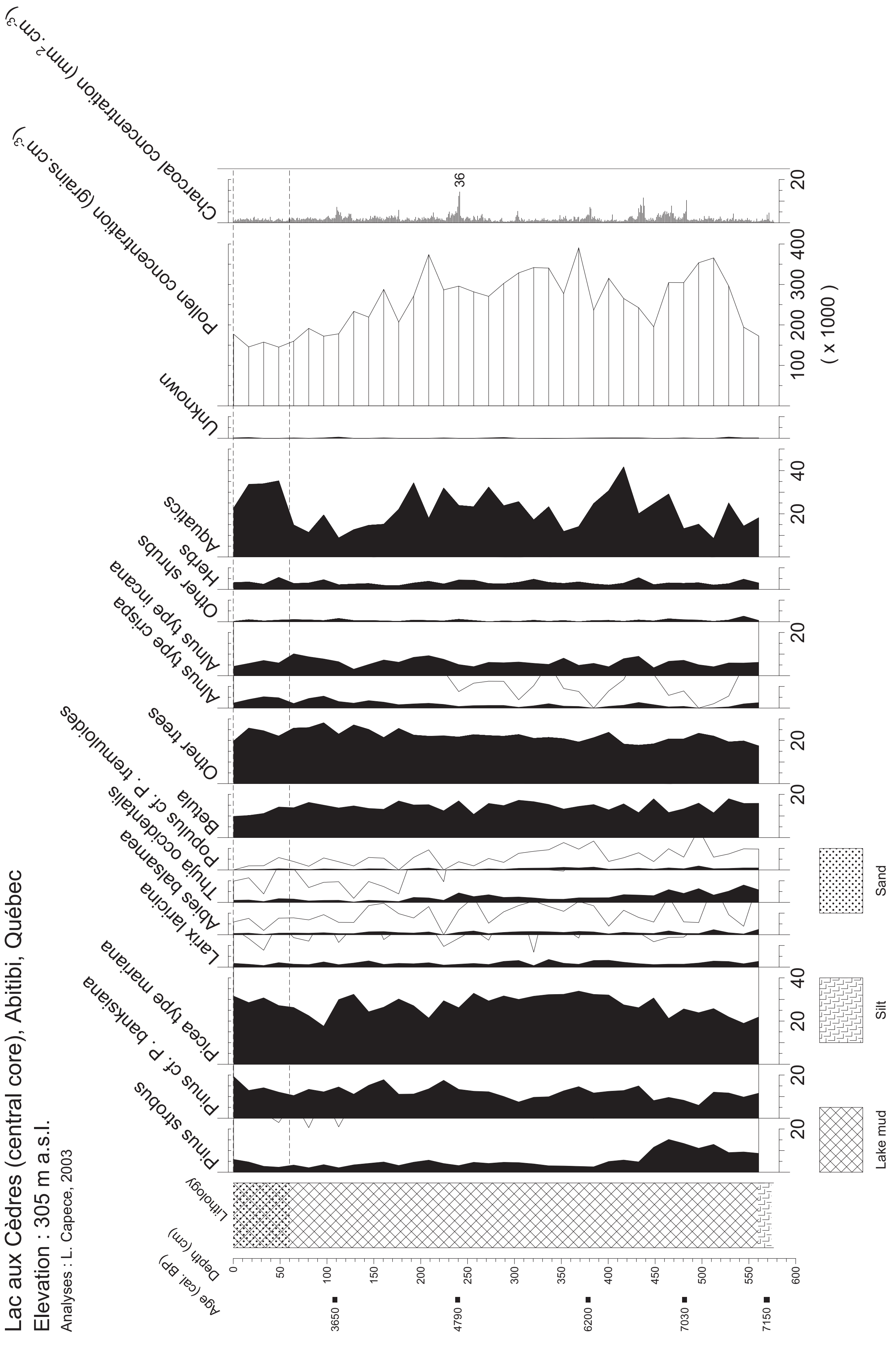

Figure 4 Summary pollen percentage diagram for the lake-sediment core. 10× exaggerations are shown (thin line) for under-represented pollen types. Charcoal concentration is also shown. The horizontal dashed line represents the start of detrital peat

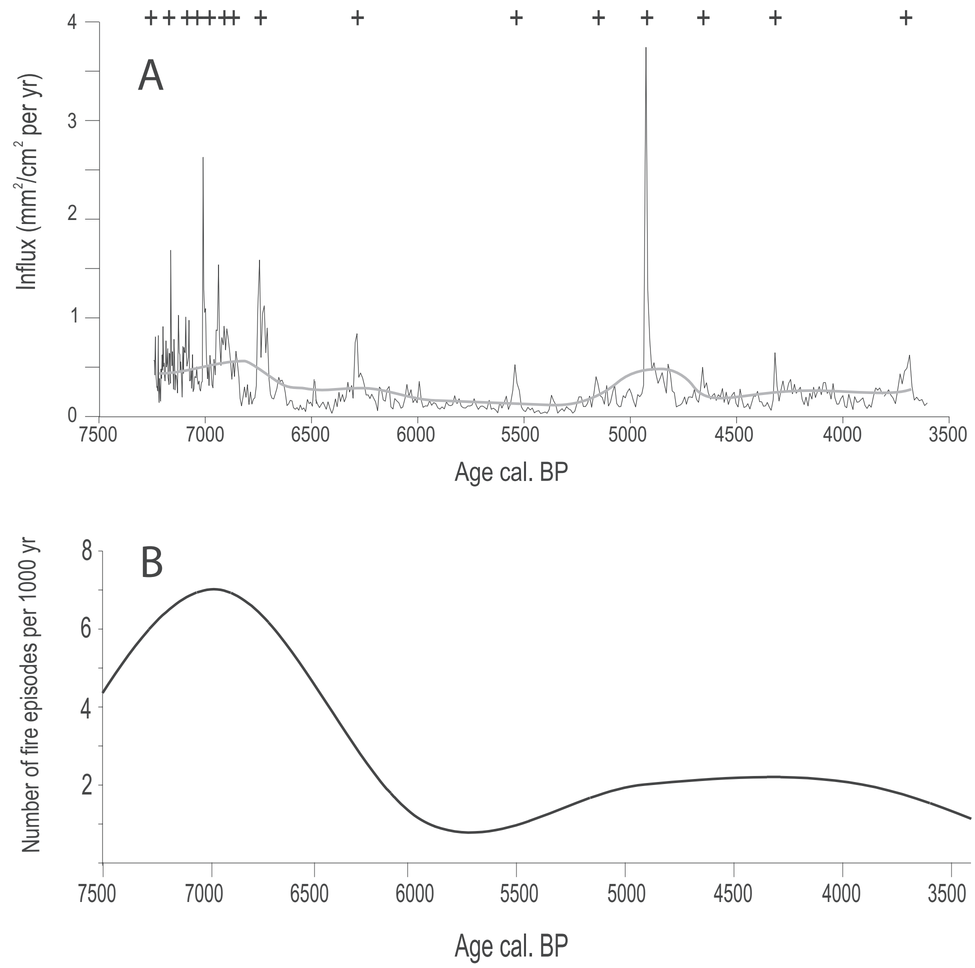

Figure 5 (A) Charcoal accumulation rate (CHAR) plotted against time for the lake sediment core, showing inferred fire events (+). The grey line represents background noise. (B) Fire events per 1000 years reconstructed with a smoothed tricube function with a 800 yr moving window

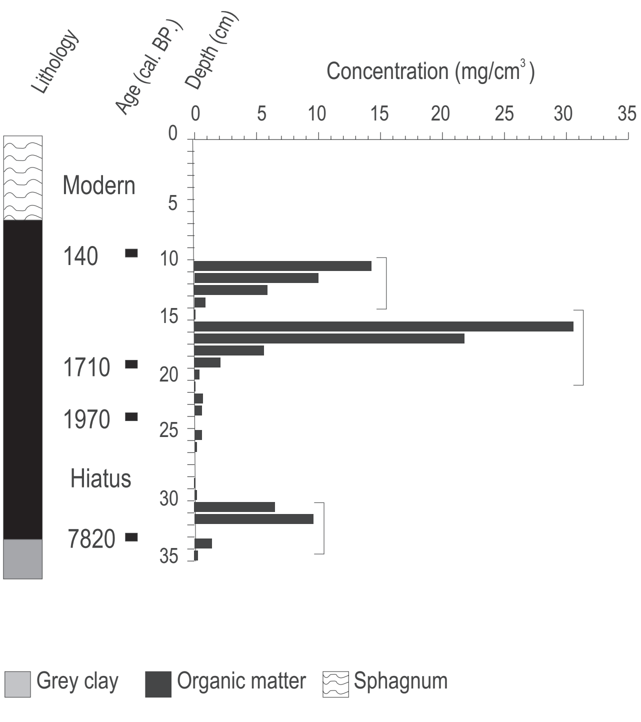

Figure 6 Charcoal concentration (mg/cm^3) according to depth (cm) in the hydromorphic forest soil. Brackets indicate detected fire events

on the mean sedimentation rate) to remove biases caused by changes in sedimentation rate, the peak component of the CHAR record was composed of two overlapping Gaussian distributions: (1) a small number of high values related to local fires, and (2) a large number of low values corresponding to regional fire events, analytical noise or redeposition of charcoal fragments sequestered during a long period of time in the catchment area (Gavin *et al*., 2006). The upper end of the distribution of high values may be considered the upper limit of noise-related values (Higuera, 2006), and thus the value of 0.2 mm^2/cm^2 per yr was selected as the final threshold (Figure 2). Each CHAR peak above the threshold was considered a local fire event, and the fire-free interval corresponds to the number of years between two adjacent peaks. Then, the number of fire events per 1000 years was obtained by smoothing event frequencies with a tricube function with a 800 yr moving window. This procedure allowed characterizing secular trends in fire-free interval.

Results

Dating and age–depth models

Inspection of the ^{14}C dates obtained from the lake sediments, the peat and the forest soil showed some discrepancies that needed to be explained before proceeding further with data analysis (Table 1). The topmost three dates from the lake core were apparently too old, whereas sedimentation hiatuses were clearly visible in the peat and

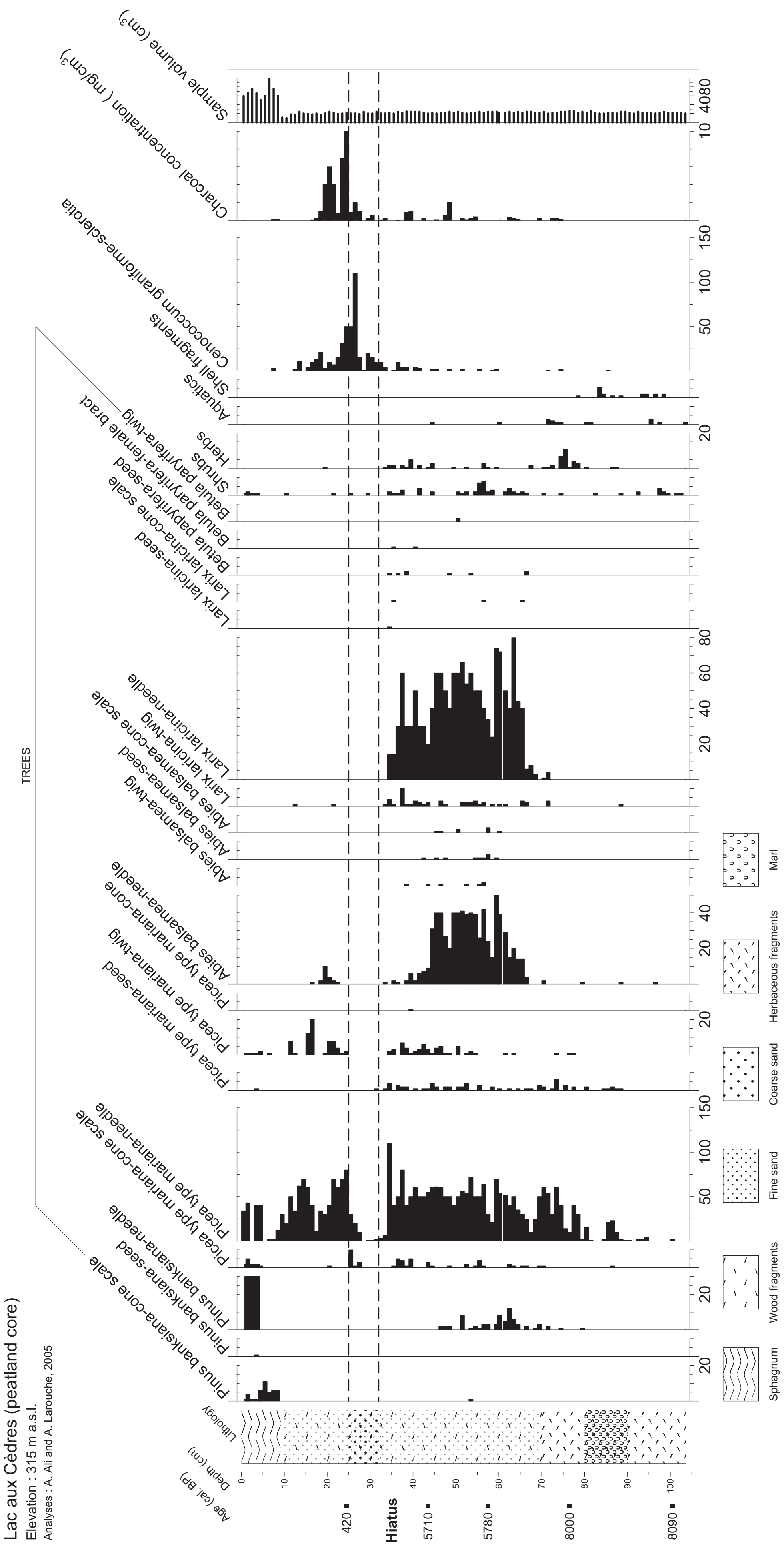

Figure 7 Summary macrofossil diagram (counts) for the peatland core. The horizontal dashed lines indicate the coarse sand deposit

soil profiles. The only hypothesis that could simultaneously explain all dating peculiarities was that a major flood occurred at some time in the watershed, resulting in a rapid rise of the lake level and erosion of some peat and forest humus from the shores and deposition in the lake. Lakes, ponds and peatlands from subarctic Québec were shown to have been affected by major floods in the past (Payette and Delwaide, 2004; Asselin and Payette, 2006). The uppermost acceptable date obtained from the lake sediments is 3650 cal. yr BP, yielding a minimum age for the flood, for dates obtained below the hiatuses in the peatland (5710 cal. yr BP) and in the forest soil (7820 cal. yr BP) are older. Humus and peat accumulation resumed by 1970 and 420 cal. yr BP, respectively. Thus the putative flood occurred sometime between 3650 and 1970 cal. yr BP. A thick (12 cm) layer of coarse sand was deposited in the peatland between the peat levels dated at 5710 and 420 cal. yr BP (see Figure 7). This lends support to the flooding hypothesis, as the peatland was cored next to a small inlet connecting a nearby esker with Lac aux Cèdres (Figure 1). The flood would have greatly increased the power of the small stream, enabling it to discharge over the peatland a massive amount of sand eroded from the nearby esker. The near absence of macrofossils in the sand layer supports rapid deposition. Sand was also transported to the lake, as evidenced by a sharp decrease in organic matter percentage starting at *c*. 65 cm (Figure 3). Sand was not found in the forest soil sequence as it is located on the other side of the lake (see Figure 6). The peatland site was transformed into a well-drained forest site for some time after the flood because of the deposition of the thick sand layer. This is evidenced by the presence of *Cenococcum graniforme* sclerotia, a mycorrhizal fungus indicating dry conditions (Akema and Futai, 2005) at the contact between sand and peat. Furthermore, this well-drained forest was likely more prone to fire ignition than a peatland, as evidenced by high charcoal concentration values at the contact between sand and peat. The organic-matter turnover was probably too rapid to allow humus accumulation, until peat accumulation resumed 420 cal. BP, probably in response to increased water levels in recent centuries (Payette and Delwaide, 2004). Finally, a problematic date was obtained from the base of the topmost *Sphagnum* layer in the peatland (1240 cal. yr BP). This date was deemed too old and thus rejected for two reasons: (1) a similar *Sphagnum* layer found at the top of the hydromorphic forest soil sequence dates at most from 140 cal. yr BP, and (2) the presence of jack pine macroremains in the peatland *Sphagnum* layer (while the species does not grow in the peatland) suggests that erosion (resulting from wind or runoff) from a nearby esker (where jack pine can presently be found) might have brought jack pine macroremains as well as older material (from a palaeosol?) to the peatland.

Because of the above-mentioned dating peculiarities, no attempt was made to correlate the Mackereth and KB lake cores, and analyses were only conducted on the Mackereth core, acknowledging that a few centimetres of the topmost sediments were lost during sampling. Furthermore, no age–depth model could be established for the peat and hydromorphic forest soil sequences, as well as for the topmost part of the lake sequence. Consequently, diagrams are shown with a depth rather than age scale, and concentrations are shown instead of influx, except for the lower part of the lake core.

Fire-history reconstruction

Lake-charcoal concentration displayed high values and high variability between 7150 and 3650 cal. yr BP (Figure 4), and low values and low variability thereafter. Low charcoal-concentration values and variability for the upper part of the lake core can be explained by the presence of detrital peat that was homogenized by mixing. The charcoal accumulation rate was calculated for the reliable portion of the lake core (7150–3650 cal. yr BP), allowing in turn calculation of fire frequency (number of fire events per 1000 years), that showed a sharp decrease between early and mid Holocene (Figure 5).

The pattern of charcoal concentration from the soil profile allows at least three fire events to be distinguished, one after 7820 cal. yr BP and two between 1710 and 140 cal. yr BP (Figure 6). Each of those events represents *c*. 300–400 years of sediment accumulation and might thus well correspond to more than one fire closely spaced in time.

Six fire events were recorded in the peatland for the period spanning *c*. 8100–5500 cal. BP, whereas four fire events were recorded between *c*. 500 cal. yr BP and the present (Figure 7). This equates to fire frequencies of 2–3 and 8 fires per 1000 years for the mid and late Holocene, respectively.

The information provided by the lake sediments, the peat and the forest soil suggest that fire frequency was relatively high during the early Holocene and low during the mid Holocene. Fire frequency rose in the late Holocene, although it is hard to determine if the values reached were as high as, or higher than, those of the early Holocene, considering the taphonomical differences between the three repositories (lake sediments, peat and forest humus). Registered charcoal peaks are smaller in the mid than in the late Holocene both in the peatland and in the forest (Figures 6 and 7).

Vegetation history

Although balsam fir has been present at the site since the beginning of the Holocene, black spruce pollen grains dominate the assemblages in all levels since at least 7150 cal. yr BP (Figure 4).

The peat-macrofossil diagram indicates that at *c*. 8000 cal. yr BP most remains belonged to black spruce (needles and seeds), with few remains of balsam fir (needles), tamarack (*Larix laricina* (Du Roi) Koch; needles) and paper birch (twigs) (Figure 7). Around 6000 cal. yr BP (65–60 cm) the assemblages are dominated by remains of black spruce, tamarack and balsam fir (needles, seeds, cone scales and twigs), suggesting that these three conifers were present in the local vegetation. Jack pine was also present at this time, although to a lesser extent. The recent part of the macrofossil sequence (after *c*. 500 cal. yr BP) is characterized by black spruce and jack pine remains (needles, twigs and cone scales), and these two species dominate the vegetation around the lake today. Taxonomic identifications achieved on charcoal frag-

Table 2 Taxonomic identification of charcoal fragments (> 1 mm) recovered from the hydromorphic forest soil

Taxa	Depth (cm)						
	33–34	18–19	17–18	16–17	15–16	12–13	10–11
Larix/Picea	6	13	26	38	52	18	16
Abies balsamea	0	4	1	3	0	0	0
Other gymnosperms	0	4	7	2	8	6	9
Ericaceae	0	1	0	3	1	0	0
Total	6	19	37	46	61	24	25

ments from the hydromorphic forest soil revealed that balsam fir was present in the northern part of the lake catchment until *c*. 1000 cal. yr BP (Table 2).

Discussion

Pollen analyses from the lake sediments indicate that balsam fir was continuously present around the lake in a vegetation otherwise largely dominated by black spruce, even taking into account the fact that balsam fir abundance is generally underestimated in palynological reconstructions of palaeovegetation (Richard, 1993). Black spruce predominance during the entire Holocene is consistent with other regional pollen studies carried out in the coniferous forest of Québec (Garalla and Gajewski, 1992; Gajewski *et al*., 1996; Carcaillet *et al*., 2001a).

Balsam fir established around Lac aux Cèdres during the mid Holocene, corresponding to the so-called Hypsithermal period (Terasmae and Anderson, 1970) characterized in eastern North America by warm and humid summers, causing lower fire frequencies because of decreased ignition (Carcaillet and Richard, 2000). High growing-season humidity is confirmed by high peat-accumulation rates recorded between *c*. 6000 and 5000 cal. yr BP in the peatland (Figure 7). The peatland and hydromorphic forest soil were probably frequently water-saturated during this period and thus less susceptible to fire. Hence only a few fires could have reached the peatland and lakeshore forest, and they must have been of low severity, as attested by the low charcoal peaks recorded during this period (Clark *et al*., 1996; Daniels *et al*., 2005). Decreased fire frequencies during the mid Holocene thus favoured late-successional species such as balsam fir and eastern white cedar.

The last 3500 years correspond to the return of high fire frequencies around Lac aux Cèdres. Furthermore, the high charcoal peaks recorded in the peatland and forest soil after the catastrophic flood could either indicate severe fire events during which great amounts of biomass were consumed (Clark *et al*., 1996; Daniels *et al*., 2005) or fires occurring very close to the site (Asselin and Payette, 2005b; Higuera *et al*., 2005). In any case, this lends support to the assertion that increased fire frequency and probably severity is responsible for the decreased abundance of balsam fir in the vicinity of Lac aux Cèdres, and likely more generally in the northern coniferous forest. Balsam fir is not adapted to recurrent and severe fires and thus part of the species decline in the coniferous forest could be attributed to the late-Holocene rise in fire frequency and severity linked to the establishment of the Neoglacial period, characterized by cooler and drier summers (Carcaillet and Richard, 2000). A nearby site located *c.* 20 km north of Lac aux Cèdres (Lac à la Pessière; Figure 1) also recorded increased fire frequencies during the late Holocene (Carcaillet *et al*., 2001a). Balsam fir is presently in disequilibrium with climate north of 49°N (Messaoud *et al*., 2007a), and individuals growing in the coniferous forest produce fewer viable seeds (Messaoud *et al*., 2007b). Hence, whenever a balsam fir stand is destroyed by fire, surviving seed trees do not suffice to regenerate the stand, and black spruce takes over.

Conclusion

The Holocene rise and fall of balsam fir in the coniferous forest of northeastern North America was likely linked to changes in climate and fire regime. The first balsam fir populations established in the coniferous forest during the warm and humid Hypsithermal period *c*. 7000 cal. yr BP, ie, when fire intensity and severity were low. The climate deterioration of the Neoglacial period toward cooler and drier summers since *c*. 3000 cal. yr BP favoured more frequent and severe fires, leading to the gradual demise of balsam fir in the coniferous forest. Most of the relic balsam fir stands are now confined to firebreaks such as lakeshores and peatlands.

The current climate warming could potentially be positive for balsam fir in the coniferous forest through an increase in viable seed production (Messaoud *et al*., 2007b). However, this positive climatic effect could be cancelled by the expected (although slight) increase in fire frequency and severity in response to climate warming (Flannigan *et al*., 2005; Bergeron *et al*., 2006), and thus balsam fir decline in the coniferous forest might continue in the future.

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