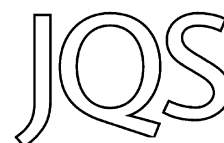


Long-term dynamics of fire refuges in boreal mixedwood forests



SAMIRA OUARMIM,^{1,2*} HUGO ASSELIN,¹ CHRISTELLE HÉLY,^{2,3} YVES BERGERON^{1,4} and ADAM A. ALI^{1,2}

¹Chaire industrielle CRSNG-UQAT-UQÀM en aménagement forestier durable, Université du Québec en Abitibi-Témiscamingue, 445 Boulevard de l'Université, Rouyn-Noranda, Canada J9X 5E4

²Centre de Bio-Archéologie et d'Ecologie (UMR5059 CNRS), Université Montpellier 2, Institut de Botanique, Montpellier, France

³Paléoenvironnements et Chronoécologie (PALECO EPHE), École Pratique des Hautes Études, Institut de Botanique, Montpellier, France

⁴Centre d'étude de la forêt, Université du Québec à Montréal, Montréal, Canada

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ABSTRACT: Burned areas in boreal mixedwood forests usually include tree patches that partially or entirely escaped fire. Some of these post-fire residual stands – called fire refuges – can escape several consecutive fires due to particular microsite conditions. Despite their potential importance as biodiversity hotspots, the long-term forest dynamics of fire refuges is unknown. High-resolution analysis of plant macroremains retrieved from forest organic matter profiles sampled in five fire refuges allowed us to describe up to 8000 years of forest dynamics. Our results display the importance of local conditions in forest dynamics. Wildfire was probably prevented by high moisture, as indicated by the presence of aquatic taxa and moisture-tolerant tree species. Lack of stand-replacing fire, coupled with organic matter accumulation, favored the millennial persistence of late-successional tree species. Shifts from spruce/larch dominance to fir/cedar dominance were noted at different occasions during the Holocene, probably resulting from endogenous processes. Copyright © 2014 John Wiley & Sons, Ltd.

KEYWORDS: boreal mixedwood forest; fire refuges; local conditions; long-term forest dynamics; moisture.

Introduction

Ecosystem-based forest management aims at preserving biodiversity and forest functions by reproducing the spatiotemporal patterns created by natural disturbances (Bergeron *et al.*, 2002; Gauthier *et al.*, 2008). Wildfire is one of the main natural disturbances shaping boreal forest landscapes (Zackrisson, 1977; Payette, 1992) and burned areas usually include tree patches that partially or entirely escaped fire – called post-fire residual stands (Gluck and Rempel, 1996; Burton *et al.*, 2008). Some of those post-fire residual stands – called fire refuges – can escape two or more consecutive fires and might remain unburned for up to several thousand years due to particular microsite conditions (S Ouarmim, AA Ali, H Asselin, C Hély and Y Bergeron, unpublished data). Many boreal forest attributes are related to the time elapsed since the last fire, including tree species composition, stand structure, abundance of woody debris and thickness of the soil organic matter layer (Hély *et al.*, 2000; Cyr *et al.*, 2009). Long-term ecological continuity in fire refuges could provide habitat for species associated with older successional stages (Selva, 2003; Rivas Plata *et al.*, 2008), as was observed in several Fennoscandian swamp forests (Zackrisson, 1977; Esseen *et al.*, 1992; Segerström, 1997; Hörnberg *et al.*, 1998). Despite their potential importance as biodiversity hotspots, the long-term forest dynamics of fire refuges has yet to be documented (Segerström, 1997), and such stands have so far been largely ignored in conservation policies in North American boreal forests (Cyr *et al.*, 2005; Gauthier *et al.*, 2008).

Following wildfire in the Eastern Canadian boreal mixedwood forest, there generally is a gradual change over time from stands dominated by shade-intolerant species (mostly broadleaved species but also pines on drier sites) to shade-tolerant species (mostly conifer species). Stand dynamics can broadly be divided into three stages: (i) the post-fire stage

dominated by broad-leaved tree species, such as trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*); (ii) the development of a mixedwood stand as coniferous species reach the canopy, such as balsam fir (*Abies balsamea*), eastern white cedar (*Thuja occidentalis*) and white spruce (*Picea glauca*); and (iii) the decline of broad-leaved species and the shift to dominance by coniferous species, some being characteristic of old-growth stands, such as eastern white cedar (Bergeron, 2000). The third stage is generally reached 150–200 years after a stand-replacing fire (Bergeron and Dubuc, 1989; Bergeron, 2000) and it is generally assumed that gap dynamics maintain the stand in a relative steady state until the next fire (Kneeshaw and Gauthier, 2003).

The species that currently characterize the Eastern Canadian boreal mixedwood forest have been present on the territory for several millennia (Richard, 1980). During periods characterized by high fire frequencies (e.g. early and late Holocene) and low fire frequencies (e.g. middle Holocene), landscapes have typically been dominated by species adapted to fire [e.g. jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*)] or not (e.g. balsam fir and eastern white cedar), respectively (Bergeron, 1998).

The long-term vegetation dynamics of boreal and temperate forests are mostly controlled by wildfire (Bergeron *et al.*, 2004). However, stand dynamics in the prolonged absence of fire (e.g. from several centuries to millennia) remain to be documented. The main objective of this study was to describe long-term vegetation history in fire refuges of the Eastern Canadian boreal mixedwood forest using high-resolution sedimentary records of plant macroremains.

Materials and methods

Study area

The study area is located within the Lake Duparquet Research and Teaching Forest (Fig. 1), in the Eastern Canadian boreal

*Correspondence: S. Ouarmim, ¹Chaire industrielle, as above.
E-mail: samira.ouarmim@uqat.ca

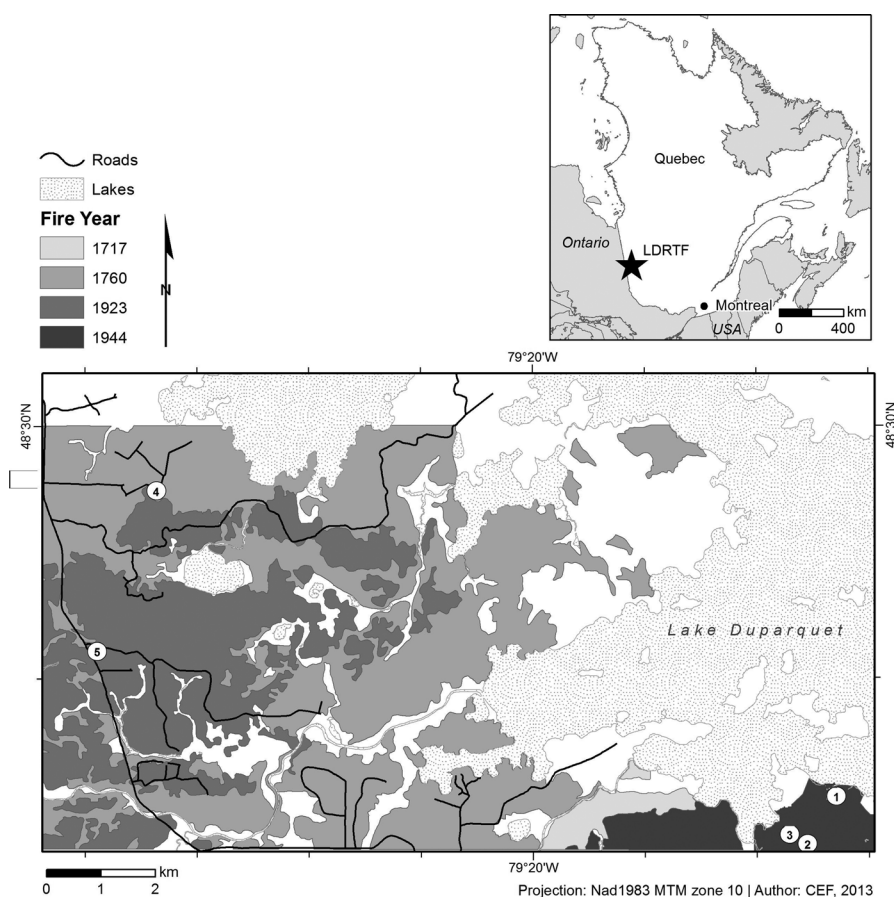


Figure 1. Location of the studied fire refuges in the Eastern Canadian boreal mixedwood forest (Lake Duparquet Research and Teaching Forest): (1) Georges, (2) Venteux, (3) Cadeau, (4) Barrage, (5) Monsabrais. Areas burned by the 1717, 1760, 1923 and 1944 fires are shown in different shades of grey.

mixedwood forest characterized by balsam fir, paper birch, white spruce, trembling aspen and eastern white cedar as the main tree species (Dansereau and Bergeron, 1993; Bergeron, 2000). Geomorphology is characterized by the presence of a massive clay deposit left by pro-glacial lakes Barlow and Ojibway (Vincent and Hardy, 1977). The climate is cold temperate with a mean annual temperature of 0.7 °C and mean annual precipitation of 889.8 mm (Environment Canada, 2011). The closest meteorological station is located at La Sarre, 42 km north of the study area.

In the Eastern Canadian mixedwood boreal forests, the two principal causes of natural disturbances, wildfire and spruce budworm [*Choristoneura fumiferana* (Clem.)], have been widely studied (e.g. Dansereau and Bergeron, 1993; Morin *et al.*, 1993). The fire cycle for the Lake Duparquet area has been estimated at 63 years before 1870 and more than 99 years afterwards (Bergeron, 1991). Spruce budworm outbreaks followed a 30-year cycle during the 20th century (Morin *et al.*, 1993), and the 1972–1987 outbreak resulted in the death of most of the mature balsam fir trees (Bergeron *et al.*, 1995).

Site selection and sampling

Typical post-fire succession in the Eastern Canadian boreal mixedwood forest involves a gradual change from pioneering stands dominated by broad-leaved tree species (trembling aspen and paper birch), to mid-successional mixed stands, and to late-successional coniferous stands dominated by balsam fir and eastern white cedar (Bergeron, 2000). Post-fire residual stands were thus distinguished from the surrounding forest matrix based on forest structure and composition retrieved from ecoforestry maps. Thirteen accessible post-fire residual stands were identified in areas where the last known

fire occurred in 1944 or 1923, depending on site location (Dansereau and Bergeron, 1993), and the second-to-last fire occurred in 1717 or 1760. These stands were coniferous old-growth forest patches (with balsam fir or eastern white cedar) embedded in a matrix of younger deciduous forests (with trembling aspen or paper birch) (Fig. 2).

Long-term fire reconstruction based on macroscopic soil charcoal analyses revealed that eight stands currently are fire refuges, or have been refuges in the past, before burning during an exceptionally severe fire (S Ouarmim, AA Ali, H Asselin, C Hély and Y Bergeron, unpublished data). The other stands only escaped the most recent fire, and thus displayed shorter ecological continuity (S Ouarmim, AA Ali, H Asselin, C Hély and Y Bergeron, unpublished data). From the eight fire refuges, the five sites with the thickest organic matter accumulation (>50 cm, Monsabrais, Cadeau, Georges, Barrage and Venteux; see Table 1) were selected to maximize the potential for paleoecological analysis (Fig. 1). A Russian corer was used to sample one complete organic matter profile (i.e. down to the mineral soil) in a micro-depression located in the center of each refuge.

Laboratory analyses

A previous analysis of macroscopic charcoal was carried out to detect fire events (S Ouarmim, AA Ali, H Asselin, C Hély and Y Bergeron, unpublished data). To reconstruct forest dynamics, contiguous 0.5-cm-thick slices were cut from the sampled organic matter profiles. A 1-cm³ subsample was retrieved from each slice and gently wet sieved through a 0.25-mm mesh. Plant macroremains (twigs, seeds, needles, leaves and macroscopic charcoal) from each subsample were sorted and counted under a dissecting microscope. Knowing that the production of macroremains differs among species,



Figure 2. Transition between a fire refuge (right) dominated by eastern white cedar and the surrounding matrix (left) dominated by paper birch. This figure is available in colour online at wileyonlinelibrary.com.

for each taxon, counts per level were divided by the maximum value recorded, resulting in data having a maximum range between zero and 1. Radiocarbon dating (^{14}C) by accelerator mass spectrometry (AMS) was conducted on 17 plant macroremain samples by Beta Analytic, Inc. (Miami, FL, USA), Poznan Radiocarbon Laboratory (Poznan, Poland) and Laboratoire de mesure du Carbone 14 (LMC14) (Paris, France). All ^{14}C age determinations were converted to calendar years before present (cal a BP; present = 1950AD) using version 6.1 of the Calib software (Stuiver and Reimer, 2005), and reported as intercepts with 2 sigma ranges (Table 2). Sudden leaps in ^{14}C ages observed at Monsabrais between 720 and 5695 cal a BP, at Georges between 1185 and 4890 cal a BP, and at Cadeau between 540 and 2180 cal a BP (Table 2) were interpreted as sedimentary hiatuses, i.e. loss of organic matter, probably due to combustion during severe fire events (Ali *et al.*, 2008). The TILIA and CONISS programs were used, respectively, to plot macroremains data and to identify vegetation periods by cluster analysis (Grimm, 1987).

Results

The same four taxa dominated tree assemblages at all sites during the Holocene, although their respective abundances varied with time: eastern larch (*Larix laricina*), spruce (black and/or white), balsam fir and eastern white cedar. The presence of sedimentary hiatuses prevented a complete Holocene history to be reconstructed at all sites. Nevertheless, each of the three main periods of the Holocene (i.e. early, middle and late) was recorded at least at one site.

Early Holocene (ca. 8090–5000 cal a BP)

At site Monsabrais, the early Holocene can be subdivided into three periods (Fig. 3A). The first period corresponds to an aquatic environment (between 8090 and 7695 years)

characterized by relatively high percentages of aquatic taxa, including macrofossils of algae (*Chara*, blue-green algae), *Potamogeton* sp., *Typha* sp. and punctual presence of herbaceous species, predominantly *Carex* sp. and *Rumex* sp. Abundance of tree taxa was very low during this period. The second period corresponds to the afforestation process, with the arrival of eastern larch ca. 7695 cal a BP, and spruce ca. 7055 cal a BP. Even though balsam fir and eastern white cedar established soon after spruce ca. 6965 cal a BP, larch and spruce remained dominant until ca. 6750 cal a BP. The third period records a major dominance shift, from spruce/larch to fir/cedar. Nevertheless, spruce abundance increased again at the end of the third period (between ca. 6250 and 5770 cal a BP) coincident with a decrease of fir and cedar.

At site Cadeau (Fig. 3B) the beginning of the first period was assigned to the early Holocene. Plant assemblages were dominated by larch, spruce and cedar, and their relative abundance fluctuated through time. Fir was not as dominant here as it was at the Monsabrais site.

Mid-Holocene (ca. 5000–3000 cal a BP)

Sites Monsabrais and Georges presented sedimentary hiatuses for the mid-Holocene period (Fig. 3A and C). At site Cadeau, the start of the mid-Holocene (period 1) was characterized by the continuation of the larch–spruce–cedar period (fir abundance remained low) (Fig. 3B). Then, starting from ca. 3325 cal a BP (period 2), the abundance of tree taxa was considerably lower and mostly dominated by spruce. This decrease in local tree abundance coincided with a slight increase in charcoal concentration.

Late Holocene (ca. 3000–0 cal a BP)

At sites Cadeau (periods 3 and 4) and Monsabrais (period 4), all tree species abundances were very low in the late Holocene, compared with the earlier periods (Fig. 3A and B).

Table 1. Characteristics of the five sampled fire refuges.

| Site name | Site number (as in Fig. 1) | Dominant species | Stand density (trees ha ⁻¹) | Organic matter thickness (cm) | Number of <i>in situ</i> fires |
|------------|-------------------------------|---------------------------|--|----------------------------------|-----------------------------------|
| Georges | 1 | <i>Abies balsamea</i> | 3373 | 49 | 2 |
| Venteux | 2 | <i>Thuja occidentalis</i> | 1211 | 50.5 | 1 |
| Cadeau | 3 | <i>Thuja occidentalis</i> | 2354 | 98 | 2 |
| Barrage | 4 | <i>Thuja occidentalis</i> | 1271 | 59 | 1 |
| Monsabrais | 5 | <i>Abies balsamea</i> | 1551 | 149 | 1 |

Table 2. Radiocarbon dates obtained from macroremains sampled in organic matter profiles from the five studied fire refuges.

| Site and sample depth (cm) | ¹⁴ C age (a BP) | Cal a BP (Median probability) | Reference |
|----------------------------|----------------------------|-------------------------------|------------|
| Monsabrais | | | |
| 24.5–25 | 810 ± 30 | 720 | SacA 25579 |
| 50–50.5 | 4975 ± 45 | 5695 | SacA 25578 |
| 75–75.5 | 5790 ± 45 | 6590 | SacA 25577 |
| 100–100.5 | 6090 ± 45 | 6960 | SacA 25576 |
| 124.5–125.5 | 6275 ± 45 | 7210 | SacA 25575 |
| 148–149 | 7265 ± 50 | 8090 | SacA 25574 |
| Cadeau | | | |
| 10–10.5 | 530 ± 30 | 540 | Beta318903 |
| 25.5–26 | 2160 ± 35 | 2180 | Poz43088 |
| 50–50.5 | 2820 ± 35 | 2925 | Poz43087 |
| 75–75.5 | 3695 ± 35 | 4035 | Poz43086 |
| 97–98 | 5470 ± 40 | 6275 | Poz43085 |
| Georges | | | |
| 14–14.5 | 140 ± 30 | 140 | Beta318904 |
| 30–30.5 | 1240 ± 30 | 1185 | Beta318905 |
| 47–47.5 | 4325 ± 35 | 4890 | Poz43091 |
| Barrage | | | |
| 29–29.5 | 260 ± 30 | 305 | Beta321197 |
| 57–57.5 | 900 ± 30 | 825 | Poz43090 |
| Venteux | | | |
| 50–50.5 | 800 ± 30 | 715 | Poz43089 |

Although eastern white cedar is currently present at the Monsabrais site, no macroremains of this species were found in the topmost part of the organic matter profile. Similarly, no fir or spruce macroremains were recorded in the topmost part of the Cadeau profile, despite these species being currently present at the site.

At site Georges, two fires occurred during the late Holocene (Fig. 3C), causing sedimentary hiatuses that complicated data interpretations. Consequently, we have limited our interpretation to the last 20 cm, which could be divided into two periods. A post-fire cohort dominated by spruce and larch dominated the stand between 160 and 60 cal a BP, before a rapid shift towards fir/cedar, which still dominate the stand today.

At site Barrage, the late Holocene period can be subdivided into five periods (Fig. 3D). The first was dominated by aquatic taxa with some balsam fir from the bottom of the sequence, ca. 825 cal a BP. The second period started at ca. 750 cal a BP with a dominance shift from aquatic taxa to fir and spruce. The third one, from ca. 280 to 160 cal a BP, was dominated by larch, although fir and spruce remained present. The fourth period, from 160 to 80 cal a BP, showed a sharp decrease of larch, whereas fir and spruce abundances remained high. Then, dominance shifted to fir/cedar in the last period, from 80 cal a BP to the present.

At site Venteux (Fig. 3E), the late Holocene can be subdivided into three periods. The first period was characterized by low abundances of eastern white cedar and balsam fir. Then, between ca. 590 and 200 cal a BP, the second period showed the co-occurrence of spruce, larch and fir. A fire prompted the switch from the second to the third period, characterized by the dominance of balsam fir and eastern white cedar.

Discussion

Four tree taxa were present in various abundances throughout the Holocene at all sites: eastern white cedar, spruce, balsam fir and eastern larch. These species are fire-sensitive (except

white spruce) and common in lowland sites, bogs and hydric sites (Eyre, 1980; Bergeron and Dubuc, 1989; Burns and Honkala, 1990). The occurrence of these species near or at the bottom of the profiles indicates that organic matter accumulation is not only attributable to time since fire (Heinselman, 1973) or climate (Charman, 2002), but also to endogenic factors, especially hydrological conditions (Payette, 2001). The accumulation of organic matter at a site is influenced by allogenic and autogenic factors, which reduce soil temperature, rate of organic matter decomposition, microbial activity, thickness of the aerated soil layer and nutrient availability (Taylor *et al.*, 1989; Payette, 2001). Two different processes could explain the initiation of organic matter accumulation in this study: (i) terrestrialization at sites Monsabrais and Barrage, as shown by the presence of aquatic taxa at the bottom of the sequences; and (ii) paludification at sites Venteux, Cadeau and Georges, explained by the absence of aquatic taxa at the bottom of the sequences (Gorham, 1957; Payette, 2001).

Successional pathways

The early Holocene composition at the Monsabrais site, dominated by aquatic and herbaceous taxa, probably corresponds to a eutrophic pond community with floating aquatic macrophytes, surrounded by an emergent shore-marsh (Kuhry *et al.*, 1993). The creation of this pond could have resulted from the infilling of a relictual lake following the retreat of post-glacial lake Ojibway ca. 8200 cal a BP (Vincent and Hardy, 1977). The aquatic community was progressively replaced by a forest community (spruce and larch) as eutrophication continued. The spruce/larch association is currently observed in peatlands, or in wet, lowland sites (Rudolf, 1966; Rowe, 1972).

A period dominated by aquatic taxa was also recorded in the late Holocene at site Barrage. Here, this could be explained by a flash flood as tree taxa were present concurrently, which excludes the possibility of the site having been a lake or a pond progressively colonized by trees through eutrophication. Flash floods were previously recorded in other boreal sites (Payette and Delwaide, 2004; Asselin and Payette, 2006; Ali *et al.*, 2008). Alternatively, the site could have been subject to periods of exceptionally wet conditions, flooding parts of the forested area (Dennerle *et al.*, 2008).

All sites, except Cadeau, recorded a dominance shift from spruce/larch to fir/cedar. However, the shifts occurred at different periods, thus excluding a regional climatic forcing and pointing instead to internal processes. Spruce and larch are considered pioneer species on humid, organic sites (Tilton, 1977; Eyre, 1980; Harvey *et al.*, 2002), and larch is generally the first tree species to invade filled-lake bogs (Elliott, 1979). The spruce/larch period varied in duration from 100 years at site Georges to 305 years at sites Venteux and Monsabrais. These differences in residence time could be related to differential proximity of balsam fir and eastern white cedar seed sources (Asselin *et al.*, 2001).

Although particular local conditions explained the initiation of forest succession, their effect decreased with time elapsed since disturbance, allowing for directional succession to take place and for late-successional species to establish (Bergeron and Dubuc, 1989; De Grandpré *et al.*, 1993). The association of eastern white cedar and balsam fir can be found on richer hydric soils and on mesic to subhydric sites (Harvey *et al.*, 2002). This is evidence that conditions remained somewhat wet in fire refuges, even several hundred years after the initiation of organic matter accumulation.

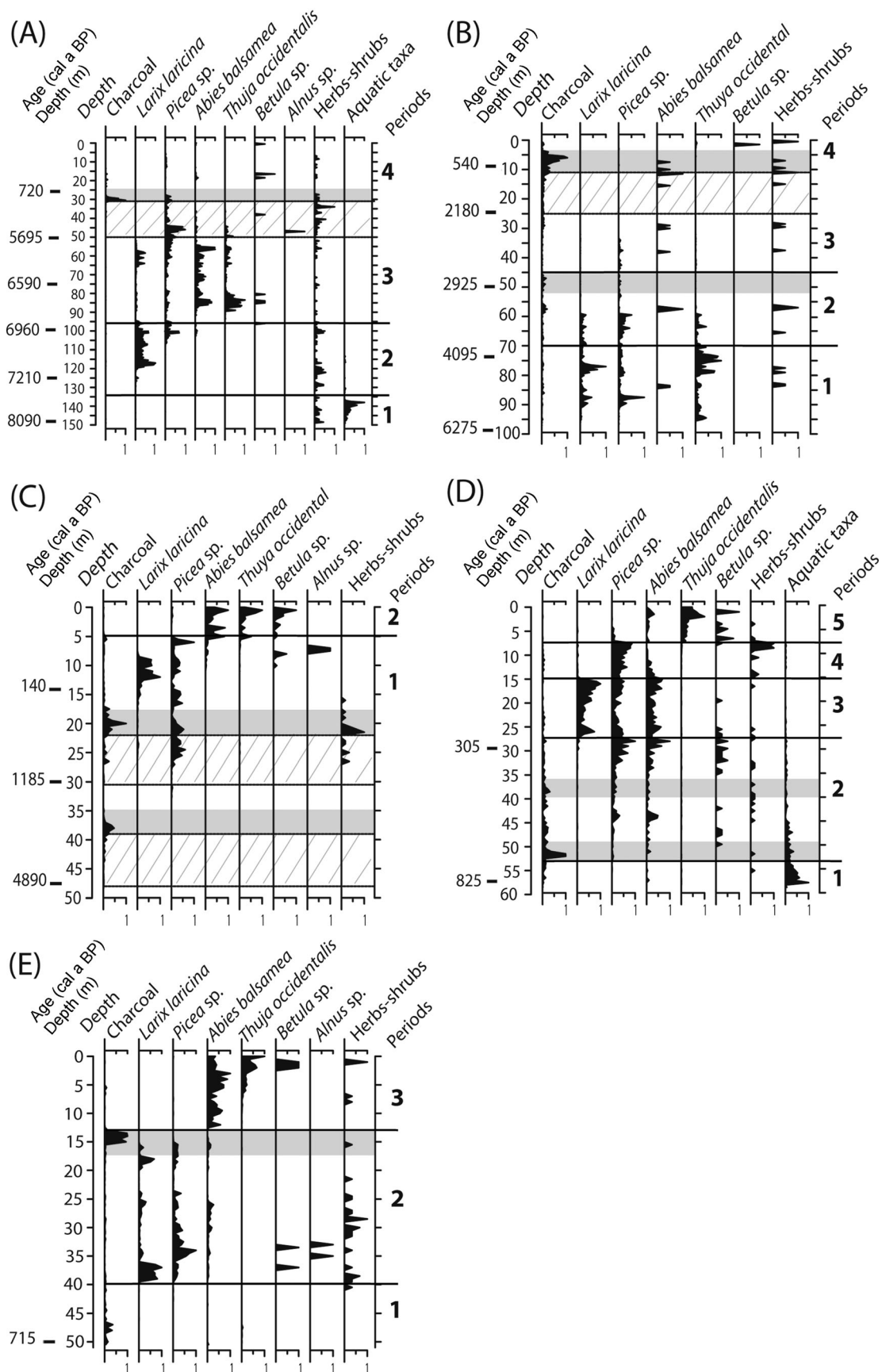


Figure 3. Charcoal and plant macroremain records (rescaled between 0 and 1) for sites Monsabrais (A), Cadeau (B), Georges (C), Barrage (D), and Venteux (E). Horizontal lines separate the periods identified by cluster analysis. Grey bars indicate *in situ* fire events and hatched bars indicate sedimentary hiatuses.

Nevertheless, the dominance shift from spruce/larch to fir/cedar could indicate a lowering of the water table (Bergeron *et al.*, 1983). The fir/cedar period can last up to 1680 years (site Monsabrais).

The low abundance of balsam fir at site Cadeau is hard to explain, although the nearby presence of black ash (*Fraxinus nigra*) and alder (*Alnus* sp.) (seen during fieldwork but not recorded in the organic matter profile) suggests a possible role of periodical flooding (Denneker *et al.*, 2008). The other coniferous species (larch, spruce, cedar) would sustain such stress, but not balsam fir (Ahlgren and Hansen, 1957).

Some species were not recorded in the topmost organic sediments, although they are currently present at the sites: cedar at Monsabrais, as well as fir and spruce at Cadeau. Macroremains are deposited a short distance (<20 m) from their origin (Bhiry and Filion, 2001), and thus species that were not dominant at the sites could have been missed if they were not present within a few tens of meters of the sampling point.

Post-fire succession

Sediment charcoal records (S Ouarmim, AA Ali, H Asselin, C Hély and Y Bergeron, unpublished data) indicated that sites Monsabrais and Venteux each burned once during the Holocene, whereas sites Cadeau, Barrage and Georges recorded two fire events (Table 1; Fig. 3). Some of these fire events were probably quite severe, as they created sedimentary hiatuses in the records. Such high-severity fires would be needed to burn fire refuges, that usually escape fire due to humid soil conditions (S Ouarmim, AA Ali, H Asselin, C Hély and Y Bergeron, unpublished data).

Different assemblages of tree species were recorded following fire: spruce/larch (Georges), spruce/fir (Barrage, Monsabrais), cedar/spruce (Cadeau) and fir/cedar (Venteux). Larch or spruce (black spruce) can establish after fire on hydric soils (Harvey *et al.*, 2002), but the presence of fir and cedar in early successional stages is more surprising. The low occurrence of broad-leaved species in early successional stages is also unusual in boreal mixedwood forests (Harvey and Bergeron, 1989; Bergeron and Charron, 1994; Bergeron, 2000) and could be explained by the thick humus layer preventing the recruitment of trembling aspen and paper birch (Lavertu *et al.*, 1994), coupled with low occurrence of fire disturbances through the post-fire residual stands. Proximity of coniferous seed sources is important, as seeds of balsam fir, white spruce and eastern white cedar are generally dispersed <100 m from parent trees (Asselin *et al.*, 2001).

Conclusions

Post-fire forest dynamics in fire refuges does not appear to follow the traditional successional pathway observed in boreal mixedwood forests. Humid site conditions favor species associated with moist areas like eastern larch, and a thick organic matter layer prevents the establishment of early successional broad-leaved species. In humid forest ecosystems, variations in water supply play an important role in determining ecosystem structure and function (Schoor and Matson, 2001). The characteristics of the studied sites are not only less prone to fire, but they also favor the long-term persistence of late-successional tree species. Such ecological continuity might be crucial for species closely associated with old-growth forests (Harper *et al.*, 2003), especially for species with low dispersal capacity (Martikainen *et al.*, 2000; Gandhi *et al.*, 2004). Fire refuges have conservation value as ecosystem types and they should thus be protected to meet the objectives of biodiversity maintenance central to ecosystem-based forest management.

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