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Impact of fire on long-term vegetation dynamics of ombrotrophic peatlands in northwestern Québec, Canada

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ABSTRACT

A 7000-year record of local fire history was reconstructed from three ombrotrophic peatlands in the James Bay lowlands (northwestern Québec, Canada) using a high-resolution analysis of macroscopic charcoal (long axis ≥ 0.5 mm). The impact of fire on vegetation changes was evaluated using detailed analysis of plant macrofossils. Compared to upland boreal forest, fire incidence in these *Sphagnum*-dominated bogs is rather low. Past fire occurrence seems to have been controlled primarily by internal processes associated with local hydroseral succession. Size of the peatland basin and distance from the well-drained forest soils also appear to be factors controlling fire occurrence. The impact of peatland fires on long-term vegetation succession appears negligible except in a forested bog, where it initiated the replacement of *Sphagnum* by mosses. In some circumstances, fire caused marked changes in the bryophyte assemblages over many decades. However, ombrotrophic peatland vegetation is generally resilient to surface fire.

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Introduction

In the boreal and subarctic regions of northern Canada, peatlands cover an estimated area of 1.1×10^6 km^2, equivalent to about 12% of the total land area (Tarnocai et al., 2005). Although they are a common physiographic feature of the northern landscape, fire impact on the long-term dynamics of *Sphagnum* bogs remains poorly documented and understood compared to upland coniferous forests. Peatlands have often been considered as fuel breaks because of their high moisture content and scarcity of forest cover (Hörnberg et al., 1998; Hellberg et al., 2004). In a long-term perspective, peatlands may act as fire-free refugia for fire-sensitive coniferous species such as *Larix laricina* (eastern larch) in string fens of northwestern Québec (Busque and Arsenault, 2005) and *Picea abies* (Norway spruce) in swamp-forests of Sweden (Hörnberg et al., 1995). However, fire has been a dominant disturbance in western Canadian peatlands, affecting an average area of 1850 km^2 each year over the last 50 yr (Turetsky et al., 2004). In the James Bay lowlands (northwestern Québec), as well as in western boreal Canada, many ombrotrophic peatlands are characterized by the presence of charred stumps at the soil surface and/or charred layers in the peat deposit (Kuhry, 1994; Thibault and Payette, 2009), indicating that the surface vegetation was burned in the past.

Within boreal continental bogs, a fire-free interval of 1150 yr has been estimated in western Canada (Saskatchewan and Alberta) (Kuhry, 1994) and of 880 yr in the south of the James Bay Lowlands (van Bellen et al., 2011). Longer fire-free intervals have been reported from temperate and oceanic ombrotrophic peatlands. In southern Québec, a fire-free interval of 2000–2500 yr has been calculated for a set of ombrotrophic peatlands (Lavoie and Pellerin, 2007), whereas on Anticosti Island in the Gulf of St. Lawrence only one local fire occurred in a peat bog during the last 4000 yr (Lavoie et al., 2009).

Few studies have assessed the impact of fire on the long-term dynamics of peatlands. The combustion of peatland vegetation and peat deposits can have significant impacts on permafrost development (Couillard and Payette, 1985; Robinson and Moore, 2000), on microtopographic development such as hummocks and hollows (Benscoter and Wieder, 2003; Benscoter et al., 2005), and on long-term carbon accumulation (Zoltai et al., 1998; Pitkänen et al., 1999; Robinson and Moore, 2000; Turetsky et al., 2002; Wieder et al., 2009). However, fires usually have a minor long-term influence on vegetation succession in ombrotrophic peatlands. *Sphagnum* tends to recover rapidly (few decades) after the disturbance (Jasieniuk and Johnson, 1982; Kuhry, 1994; Pellerin and Lavoie, 2003; Benscoter, 2006).

The main objective of the present study is to determine the role of fire in the long-term development of three peat bogs located at their northernmost range limit in northwestern Québec (James Bay area; Fig. 1). Specifically, this study aims *i*) to reconstruct the fire history of these peatlands since their origin, and *ii*) to determine the impact of fire on local-scale vegetation dynamics. To do so, we have used a

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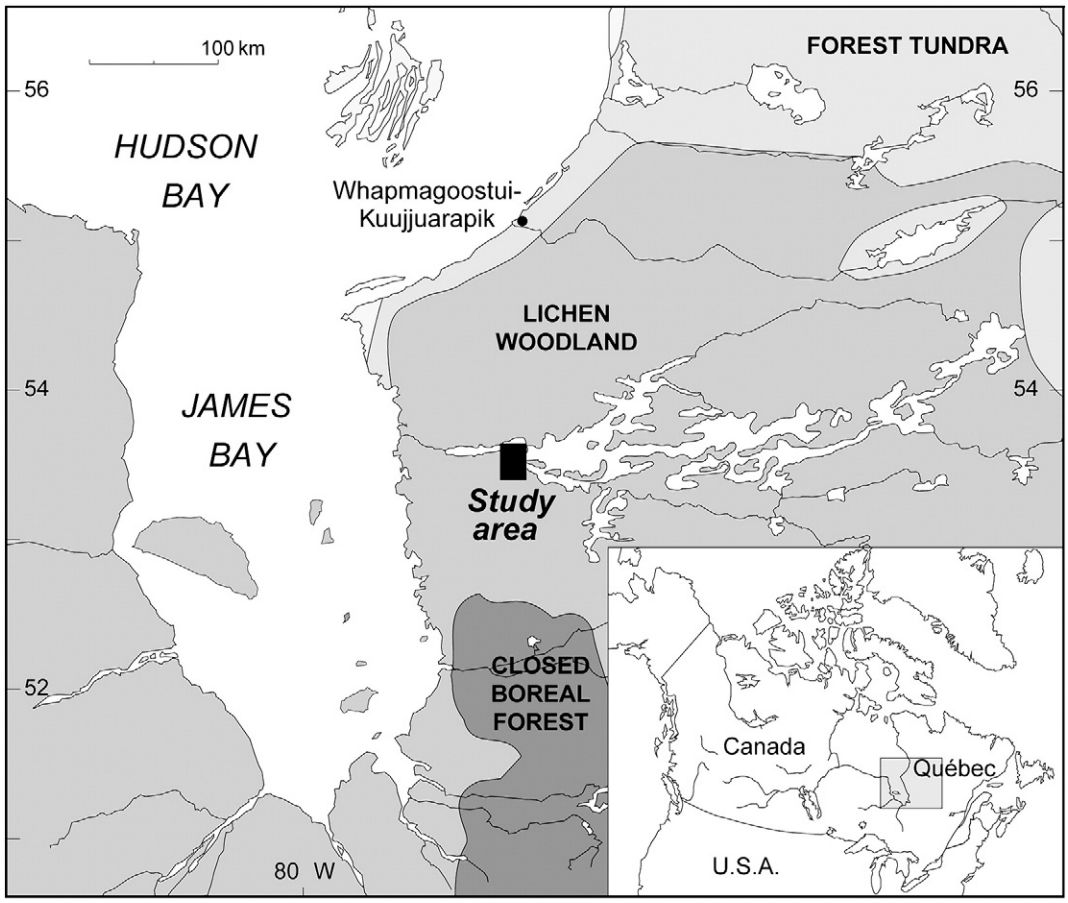

Figure 1. Map of northwestern Québec showing the location of the study area.

high-resolution paleoecological analysis of peat sequences based on macrocharcoal and plant macrofossil pieces. We hypothesize that these ombrotrophic peatlands are resilient to fire, and that local vegetation communities should return to pre-disturbance conditions within a short period of time.

Study area and sites

The study area is located in the boreal forest of northwestern Québec, 100 km east of James Bay (Fig. 1). The region is part of the Precambrian Canadian Shield, composed of granite and gneiss. Altitudes range between 150 and 200 m asl. Low plateaus are covered by tills and fluvio-glacial sands, whereas marine clay deposits are located in depressed lowlands. The region was deglaciated around 8000 cal yr BP (Dyke and Prest, 1987) and submerged by marine waters (Tyrrell Sea transgression) until 7200 cal yr BP (Hardy, 1977). Present-day climate is subarctic-continental with a mean annual temperature of −3.1°C. July is the warmest month of the year (mean 13.7°C) and January the coldest (mean −23.2°C). Annual precipitation totals 650 mm, of which 40% falls as snow (Environment Canada, 2010; La Grande Rivière A weather station).

The regional vegetation cover on well-drained sites is mainly composed of open coniferous forests corresponding to the lichen woodland zone (Fig. 1). *Picea mariana* (black spruce; semi-serotinous cones) and *Pinus banksiana* (jack pine; serotinous cones) are the dominant tree species; these conifers are well-adapted to natural regeneration following the fire (Johnson, 1992). *P. mariana* is found in a wide range of habitats, especially in moderately to poorly drained areas. *P. banksiana* is dominant on well-drained sites with shallow deposits frequently affected by fire, whereas *L. laricina* is abundant in minerotrophic peatlands and floodplains. Other tree species are distributed sporadically across the landscape and include *Populus tremuloides* (trembling aspen), *Populus balsamifera* (balsam poplar), *Betula papyrifera* (paper birch) and *Abies balsamea* (balsam fir). Fire is a recurrent disturbance in lichen woodlands. The fire rotation in the upland forests is estimated to be about 100–110 yr (Payette et al., 1989; Couturier and St-Martin, 1990; Parisien and Sirois, 2003). Peatlands are a major component of the landscape in the James Bay lowlands where they form large complexes covering about 20–30% of the land area (Arseneault and Sirois, 2004). The study area corresponds to the northern range limit of ombrotrophic peatlands in northwestern Québec (Payette, 2001a).

Three ombrotrophic peatlands were selected for this study. Radisson peatland is located 8 km southeast of the village of Radisson (53°43.47′N, 77°42.18′W). It is a small semi-forested bog (diameter ~200 m) colonized by *P. mariana* and *L. laricina* (Fig. 2). Airport I and Airport II peatlands are located 3 km northwest of La Grande Airport (53°39.22′N, 77°43.50′W) and 10 km southwest of Radisson peatland. Airport I peatland (Fig. 2) is a treeless bog with a dense ericaceous shrub cover dominated by *Chamaedaphne calyculata* and *Rhododendron groenlandicum* on hummocks, whereas lichens and *Carex* spp. are growing in hollows. Airport II peatland is located 200 m east of Airport I peatland (53°39.23′N, 77°43.40′W). It is also an open bog characterized by a microtopography of hummocks and hollows. Ombrotrophic heath communities (e.g., *R. groenlandicum*, *Vaccinium oxycoccos*, *Vaccinium myrtilloides*, *Vaccinium uliginosum*, *Andromeda glaucophylla*) are distributed on hummocks whereas hollows are dominated by lichens (*Cladonia rangiferina*, *mitis*, *stellaris*) and mosses (*Polytrichum strictum*, *Dicranum undulatum*). *P. mariana*, *L. laricina* and *P. banksiana* trees are found sporadically across the peatland, their abundance increasing at the peatland margin. Airport I and II peatlands were both affected by a large fire as evidenced by

Figure 2. Pictures of the coring sites in the small forested peatland (Radisson) (left) and in the large open peatland (Airport I) (right).

the presence of several charred stumps and fire scars on trees. This fire occurred in the early summer of AD 1941 (SOPFEU, 2004) during a period of warm and dry conditions. It spread through several minerotrophic peatlands in the area (Busque and Arsenault, 2005).

Methods

Field sampling

At each study site, peat thickness was measured and peat stratigraphy was described at 50-m intervals along a series of transects, distributed evenly throughout the peatlands, using a metal probe and a modified Russian peat corer (Jowsey, 1966). In each peatland, a peat core was collected from the optimal sampling location (i.e., maximum *Sphagnum*-peat thickness and most numerous visible charcoal layers in stratigraphy). The three coring sites are located at different distances from the well-drained forest soils (Radisson: 50 m; Airport II: 200 m; Airport II: 400 m) which enabled evaluation of whether this is a factor controlling fire occurrence. Peat sediments were wrapped in plastic and aluminum foil for transport to the laboratory and stored at 4°C.

Radiocarbon dating and the age–depth model

Eighteen samples were AMS radiocarbon dated at the Radiocarbon Laboratory of Université Laval and at the Keck Laboratory (University of California, Irvine) (Table 1). The fire chronology is based on radiocarbon dates from macroscopic charcoal particles (10 samples). In

Table 1
Radiocarbon dates.

Site	Depth (cm)	Laboratory number	Age (^{14}C yr BP)	1σ range (cal yr BP)	Calibrated age (cal yr BP)	Material dated
Radisson	13–14	ULA-610 UCIAMS-47291	195 ± 20	150–174	160	Charcoal
	51–53	ULA-507 UCIAMS-42574	735 ± 15	670–681	680	Charcoal
	76–77	ULA-508 UCIAMS-42575	1600 ± 20	1418–1466	1440	Charcoal
	110–111	ULA-288 UCIAMS-35052	2820 ± 15	2921–2950	2940	*Sphagnum*-peat
	119–121	ULA-497 UCIAMS-41209	3365 ± 20	3582–3634	3610	Charcoal
	178–179	ULA-279 UCIAMS-35049	5375 ± 15	6183–6211	6200	Bulk Peat
Airport I	2–3	ULA-586 UCIAMS-45701	Modern	Modern	0	*Sphagnum*-peat
	20–21	ULA-611 UCIAMS-47292	855 ± 25	734–781	760	*Sphagnum*-peat
	31–32	ULA-509 UCIAMS-42576	2340 ± 20	2343–2352	2350	Charcoal
	38–39	ULA-498 UCIAMS-41210	2390 ± 20	2410–2439	2430	Charcoal
	170–171	ULA-280 UCIAMS-35050	4705 ± 15	5330–5377	5350	Bulk peat
	256–257	ULA-281 UCIAMS-35051	5915 ± 20	6716–6751	6730	Bulk peat
Airport II	4–5	ULA-591 UCIAMS-45704	Modern	Modern	0	Charcoal
	37–39	ULA-510 UCIAMS-42577	1515 ± 15	1377–1408	1390	Charcoal
	55–56	ULA-506 UCIAMS-41213	3085 ± 30	3319–3359	3340	Charcoal
	61–62	ULA-499 UCIAMS-41211	3055 ± 20	3281–3333	3310	Charcoal
	115–116	ULA-431 UCIAMS-39574	3920 ± 15	4299–4326	4310	Bulk peat
	167–168	ULA-430 UCIAMS-39573	5215 ± 20	5964–5989	5980	Bulk peat

order to limit a potential error due to inbuilt age in radiocarbon ages (Gavin, 2001), we only selected charcoal derived from ericaceous shrubs (i.e., short-lived species). Other radiocarbon dates (8 samples) were carried out on the basal peat and on the stratigraphic transitions. Radiocarbon dates (^{14}C yr BP) were calibrated (cal yr BP) using the CALIB 5.0 program (Stuiver and Reimer, 1993). Calibrated dates were rounded to the nearest 10 yr using 1-sigma cal age ranges. All dates reported are expressed in calendar years before present.

Net vertical peat accumulation rates (PARs; mm yr^{-1}) were calculated by linear interpolation between calibrated dates using the midpoint of the 1-sigma calibrated age ranges. Linear interpolation assumes that changes in peat accumulation occur at the depth of the dates. In the context of the present study, it is the most appropriate age–depth model since radiocarbon dates were placed at the fire horizons and at the stratigraphic transitions where it is expected that accumulation rates change.

Charcoal analysis

In the laboratory, peat sequences were sliced into contiguous 1-cm-thick subsamples. For the three cores, a 1-cm interval was used for macroscopic charcoal analysis within the *Sphagnum*-dominated peat, and a 2-cm interval was used for the underlying portion of the cores corresponding to the minerotrophic peat (e.g., herbaceous and moss-dominated peat). A modified version of the procedure of Hörnberg et al. (1995) was used to reconstruct local fire history. For each level, a subsample of 1 cm^3 was soaked in a potassium hydroxide (KOH) solution (5%) for 24 h, then sieved through a 0.425-mm mesh screen. The remaining particles were bleached in a sodium hypochlorite (NaClO) solution (10%) to distinguish charcoal from dark organic matter. Charcoal particles were counted in a petri dish using a stereomicroscope at 16 to 40× magnification. Only macroscopic (longest axis ≥ 0.5 mm) charcoal fragments were counted, as that size class represents the occurrence of local and nearby fires (Hörnberg et al., 1995; Ohlson and Tryterud, 2000). In each sample (1 cm^3), all the macrocharcoal fragments were picked from the petri dish, placed in weighing boats and oven-dried overnight (±50°C). The mass of charcoal (anthracomass) was determined for each sample using an electronic balance. Data are expressed as charcoal accumulation rates (CHAR; particles cm^{-2} yr^{-1}) and anthracomass (mg cm^{-3}). The identification of local fires was based on the following criteria: distinct peaks in the macrocharcoal values (anthracomass and CHAR), diversity and abundance of charred plant remains (e.g., leaves and stems of bryophytes, conifer needles, leaves and roots of ericaceous species). Although some macroscopic charcoal fragments in the peat stratigraphy may be derived from upland forest fires, the identified charred layers can usually be attributed confidently to local burning because they correspond to distinct changes in the macrofossil records. For each site, the fire-free interval during the bog stage was calculated by dividing the age of the fen–bog transition by the number of identified fire events occurring since the beginning of this period.

Plant macrofossil analysis

In laboratory, the stratigraphy of each peat core was described by evaluating the peat composition within 1-cm^3 subsamples every centimeter along the cores. To reconstruct the local pre- and post-fire vegetation assemblages, a more detailed plant macrofossil analysis was conducted 2 cm below and up to 10 cm above each charred layer (except for the most recent horizons corresponding to the AD 1941 fire). The interval used for macrofossil analysis above charred layers varied from 1 to 2 cm depending on the temporal resolution between contiguous samples. For each level, subsamples of 5 cm^3 of sediments were prepared according to the procedure of Bhiry and Filion (2001). Macrofossils were separated from the organic matrix by boiling the material for about 3 min in a 5% KOH solution for deflocculation. The material was then wet-sieved through 0.425- and 0.180-mm mesh screens. Remains of vascular plants and bryophytes were identified and counted in a petri dish using a stereomicroscope at 4 to 40× magnification. The volume percentages of the main botanical groups (*Sphagnum*, mosses, Cyperaceae, wood remains, roots and rootlets, leaf fragments) were calculated using a gridded petri dish and dividing the area covered by each macrofossil type by the total sample area. The other plant macroremain types (e.g., seeds, conifer needles, sclerotia of *Cenococcum*) were counted and are expressed in concentrations (number per sample of 5 cm^3). References used for plant remains identification were Montgomery (1977) and Lévesque et al. (1988) for vascular species, Ireland (1982) for bryophytes, and the plant-macrofossil reference collection of the Centre d'études Nordiques (Université Laval). Macrofossil diagrams were constructed using Palaeo Data Plotter 1.0 software (Juggins, 2002). Botanical nomenclature follows Marie-Victorin (1995) for vascular plants, Crum and Anderson (1981) for mosses, and Vitt and Andrus (1977) for *Sphagnum*.

Results

Radisson peatland (RAD)

At the RAD sampling point, organic sediments are 176 cm thick and overlie coarse fluvio-glacial sand (Fig. 3). The onset of peat accumulation was dated to 6200 cal yr BP (Fig. 3 and Table 1). The basal part of the core (177–166 cm), dominated by sedges and brown mosses, is overlain by an herbaceous peat (166–124 cm) interspersed by several wood layers. The remaining uppermost section of the peat sequence (124–0 cm) is dominated by *Sphagnum* remains. Net PARs ranged from 0.15 to 0.32 mm yr^{-1} between 6200 and 680 cal yr BP

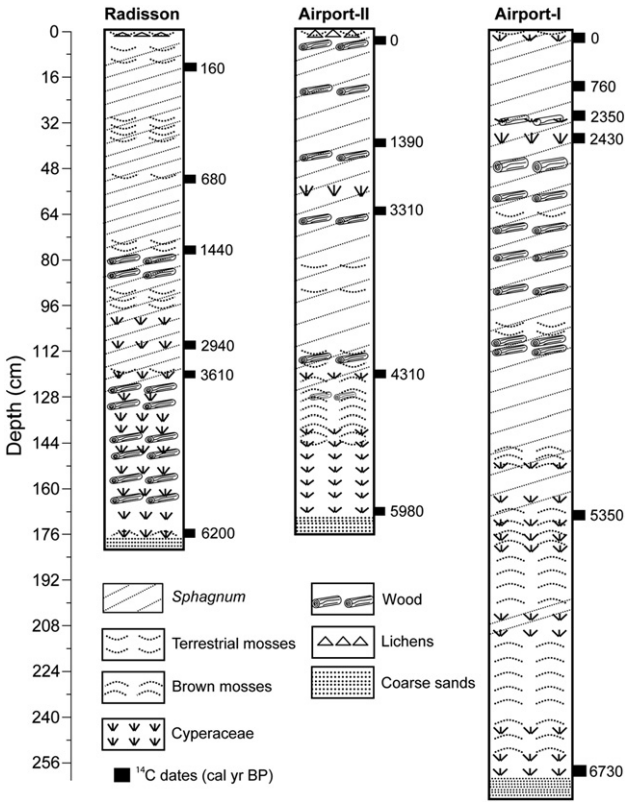

Figure 3. Stratigraphy, radiocarbon dates and net peat accumulation rates of the three studied cores.

(178–52 cm) and increased subsequently (0.75–0.80 mm yr^{-1}) in the upper 52 cm of the core (680 cal yr BP to present) (Fig. 4).

Nine fire events, labeled RAD-1 to RAD-9, were identified based on charcoal and charred botanical remains (Figs. 5 and 6). All charcoal layers were identified within the *Sphagnum*-dominated portion of the core, after the onset of ombrotrophic conditions dated to ca. 3980 cal yr BP. No macroscopic charcoal layer was found within the Cyperaceae-dominated portion of the core (178–124 cm; 6200–3980 cal yr BP). This suggests that the prevailing wet surface conditions during the minerotrophic developmental stage of the peatland prevented fire from spreading to the coring location. A series of macrocharcoal layers with high contents of charred macroremains is found directly after the onset of ombrotrophic conditions (124–105 cm) (Fig. 6). Two distinct levels were radiocarbon dated within this series and yielded different ages (119–121 cm; 3610 cal yr BP, and 110–111 cm; 2940 cal yr BP) suggesting that they represent distinct fire events. Although charcoal horizons between 3745 and 2720 cal yr BP are not clearly distinguishable, the charred macroremains assemblages (Fig. 6) and the macrocharcoal peaks (Fig. 5) suggest that it could represent four distinct fire events (RAD-1 to RAD-4 dated 3610, ca. 3340, ca. 3080, and 2940 cal yr BP, respectively). Subsequently, five fire events were recorded during the last 2500 yr; RAD-5 to RAD-9 dated to ca. 2280, 1440, 680, ca. 520, and 160 cal yr BP, respectively. According to the radiocarbon dates and the age–depth model, the fire-free interval during the ombrotrophic stage of RAD peatland was estimated to be 440 yr.

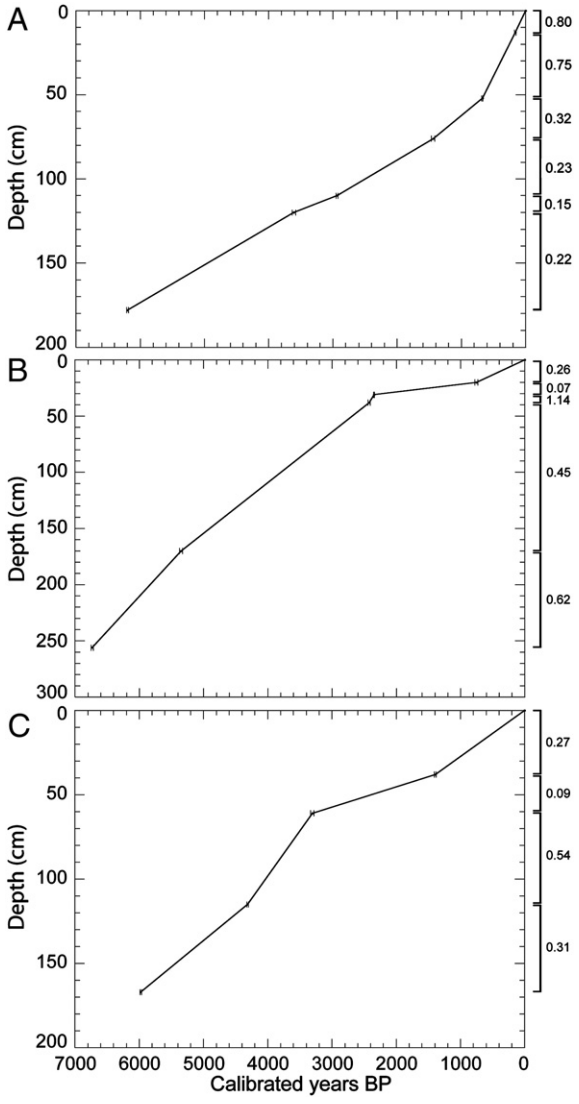

Figure 4. Age–depth models (solid black line) with error bars (1σ confidence intervals) illustrating the peat accumulation rates. (A) Radisson, (B) Airport 1, (C) Airport 2.

The fire events RAD-1 to RAD-4 were not associated with significant changes in the local floristic composition (Fig. 6). Only a decrease in *Sphagnum* sp. abundance associated with an increase in ligneous fragments is noted between the RAD-2 and RAD-3 fire events. However, the very low peat accumulation rate (0.15 mm yr^{-1}) between 3610 and 2940 cal yr BP suggests that the post-fire macrofossil record may have been lost by combustion. Within RAD-1 to RAD-4 charcoal layers, ligneous fragments and charred conifer needles and ericaceous leaves are very abundant. This suggests that fire propagation to the coring location was facilitated by a dense shrub cover along with *P. mariana* and *L. laricina*. Repeated burning of conifer trees and ericaceous shrubs may have maintained wet conditions locally by reducing evapotranspiration, thus favoring the maintenance of Cyperaceae (Fig. 6). The RAD-5 to RAD-9 fire events resulted in the replacement of *Sphagnum* sp. by terrestrial mosses. The post-fire plant-macrofossil assemblages were composed of *P. strictum*, *Dicranum* sp. and *Pohlia nutans*. Remains of *P. schreberi* and *Mylia anomala* were also found above RAD-5. All these post-fire bryophytes are associated with relatively dry surface conditions in ombrotrophic peatlands (Crum and Anderson, 1981). In some cases, the fire-induced shifts in moss assemblages persisted for several centuries. According to our chronological framework, the average time since fire for *Sphagnum* recovery during the bog stage was 200 yr, ranging from 80 yr (RAD-7) to 440 yr (RAD-5). Most fire events at RAD peatland produced highly diversified macroscopic charred remains such as needles (*P. mariana*, *L. laricina*) and leaves (Ericaceae, *Sphagnum* and mosses) (Fig. 6), providing strong evidence that fires have consumed the aboveground biomass locally.

Airport I peatland (AIR-I)

A 260-cm-thick peat core was collected at AIR-1 peatland (Fig. 3). Onset of peat accumulation began at 6730 cal yr BP over fluvio-glacial sands. The organic matrix of the basal part of the core (257–240 cm) is a mixture of brown moss and Cyperaceae remains. Brown moss-dominated peat accumulated between 240 and 180 cm, interbedded with a 9-cm-thick mixed herbaceous-*Sphagnum* layer (214–205 cm). Between 180 and 164 cm, the organic matrix is composed of Cyperaceae and brown moss remains. The upper part of the core (164–0 cm) consists of *Sphagnum*-dominated peat containing several wood layers. The net PARs range from 0.07 to 1.14 mm yr^{-1} (Fig. 4).

At least four distinct local fires, labeled AI-1 to AI-4, occurred during the ombrotrophic developmental stage, which started ca. 4780 cal yr BP. According to macrocharcoal values and radiocarbon dates (Fig. 5), the first three fires (AI-1 to AI-3) occurred within a short period of time: ca. 2740 cal yr BP (AI-1; 52 cm), 2430 cal yr BP (AI-2; 38 cm) and 2350 cal yr BP (AI-3; 31 cm). Given the inherent uncertainties in radiocarbon dating or a possible downward transport of macrocharcoal in the peat profile, charred layers AI-2 (2430 cal yr BP) and AI-3 (2350 cal yr BP) could represent the same fire event. However, based on distinctive macrocharcoal peaks and charred macroremains assemblages (Figs. 5 and 7), we attribute the layers to different fire events. Following these two fire events, peat accumulation rates slowed down notably between 2350 and 760 cal yr BP (0.07 mm yr^{-1}). The uppermost charred layer (AI-4; 2–3 cm) was characterized by a high anthracomass (44.2 mg cm^{-3}) (Fig. 5) and is attributed to the fire that spread in the peatland in AD 1941 (SOPFEU, 2004). Following this fire, peat accumulation ceased as a lichen cover developed locally, indicating that *Sphagnum* failed to recover over the last 70 yr. The fire-free interval for the ombrotrophic portion of the peat profile was estimated to be 1200 yr.

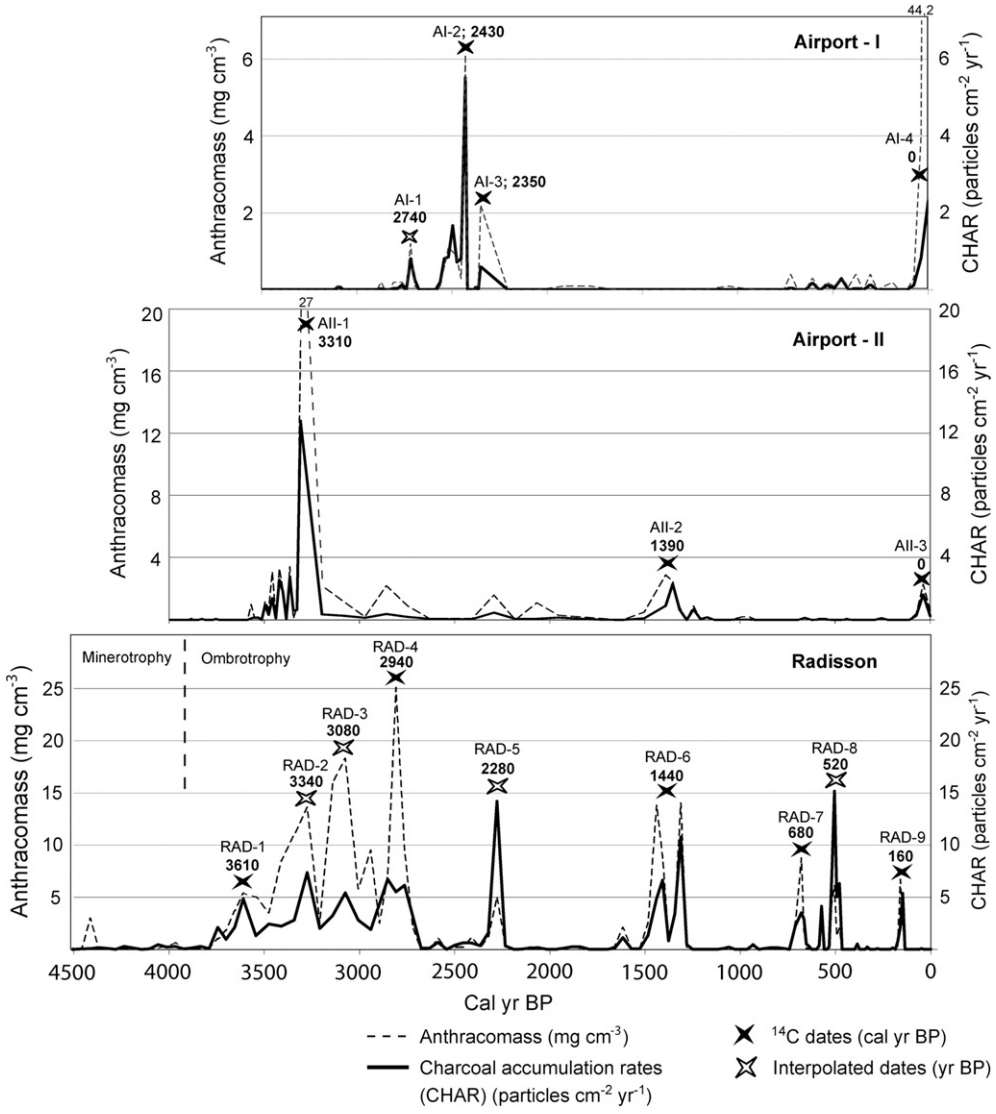

Figure 5. Charcoal accumulation rates, anthracomass and the reconstructed fire chronologies of the three study sites.

The plant-macrofossil records show that fires AI-1 to AI-3 had a minor impact on vegetation succession. *Sphagnum* remained abundant after the fire events (Fig. 7) and only few remains of *P. nutans* and *M. anomala* were found above the charred layer A1-I. *Carex* abundance increased before the second fire event (A1-2) likely indicating increased wetness of the bog surface. Charred conifer needles are abundant in every charred layer suggesting that trees likely contributed to fire propagation at the coring location. Conifer needles of both *L. laricina* and *P. mariana* are particularly abundant below AI-3. The disappearance of needles from the macrofossil assemblages above AI-3 (31 cm; 2350 cal yr BP) suggests the clearance of conifer trees by fire. According to the age–depth model, recovery of conifer trees occurred about 600 yr after the fire (27 cm; ca. 1770 cal yr BP).

The lack of post-fire changes in the bryophyte assemblages above A1-1 to A1-3 suggests that these fires have been relatively light or that they only have affected conifer trees nearby without destroying the peat deposit locally. This interpretation is supported by the relatively low CHAR (6 particles $cm^{-2}\,yr^{-1}$) and anthracomass values ($\leq$6 mg cm^{-3}) as well as the lower diversity of the charred plant macroremains.

Airport II peatland (AIR-II)

At AIR-II peatland, basal organic sediments accumulated over fluvio-glacial sands, and the peat deposit was 168 cm thick at the coring site (Fig. 3). Basal peat was dated to 5980 cal yr BP. The bottommost portion of the core (168–140 cm), composed of Cyperaceae remains, is overlain by brown moss peat interspersed by wood remains and sedges (140–123 cm). A mixture of wood, sedges and mosses is found between 123 and 108 cm and is overlain by a *Sphagnum*-dominated peat layer with wood from 108 cm to the surface. Net PARs vary from 0.09 to 0.54 mm yr^{-1} throughout the peat profile (Fig. 4).

Three fire events, labeled AII-1 to AII-3, were identified within the ombrotrophic stage of the peatland after 4300 cal yr BP (Fig. 5). The first two charred layers were radiocarbon dated to 3310 cal yr BP (61–55 cm) and 1390 cal yr BP (39–38 cm) (Fig. 8). We attribute the uppermost charcoal layer (4–5 cm) to the AD 1941 fire (AII-3). The oldest charred layer (AII-1; 61–55 cm) contains a large volume of charred remains ($\geq$75%) and a high anthracomass (maximum of 27 mg cm^{-3}) (Figs. 5 and 8). Macrocharcoal particles were radiocarbon-dated within the upper and lowermost levels of the charred layer (61 and 55 cm) and provided similar calibrated ages (3310 and 3340 cal yr BP) (Table 1). Consequently, this 6-cm-thick layer likely represents a single fire event (AII-I; 3310 cal yr BP). Nonetheless, the fire was followed by a major decrease in PAR value (0.09 mm yr^{-1}) between AII-1 and AII-2. This could indicate that fire, by modifying local growth conditions (e.g., tree removal), affected peat accumulation subsequently. It is also possible that the AII-2 fire

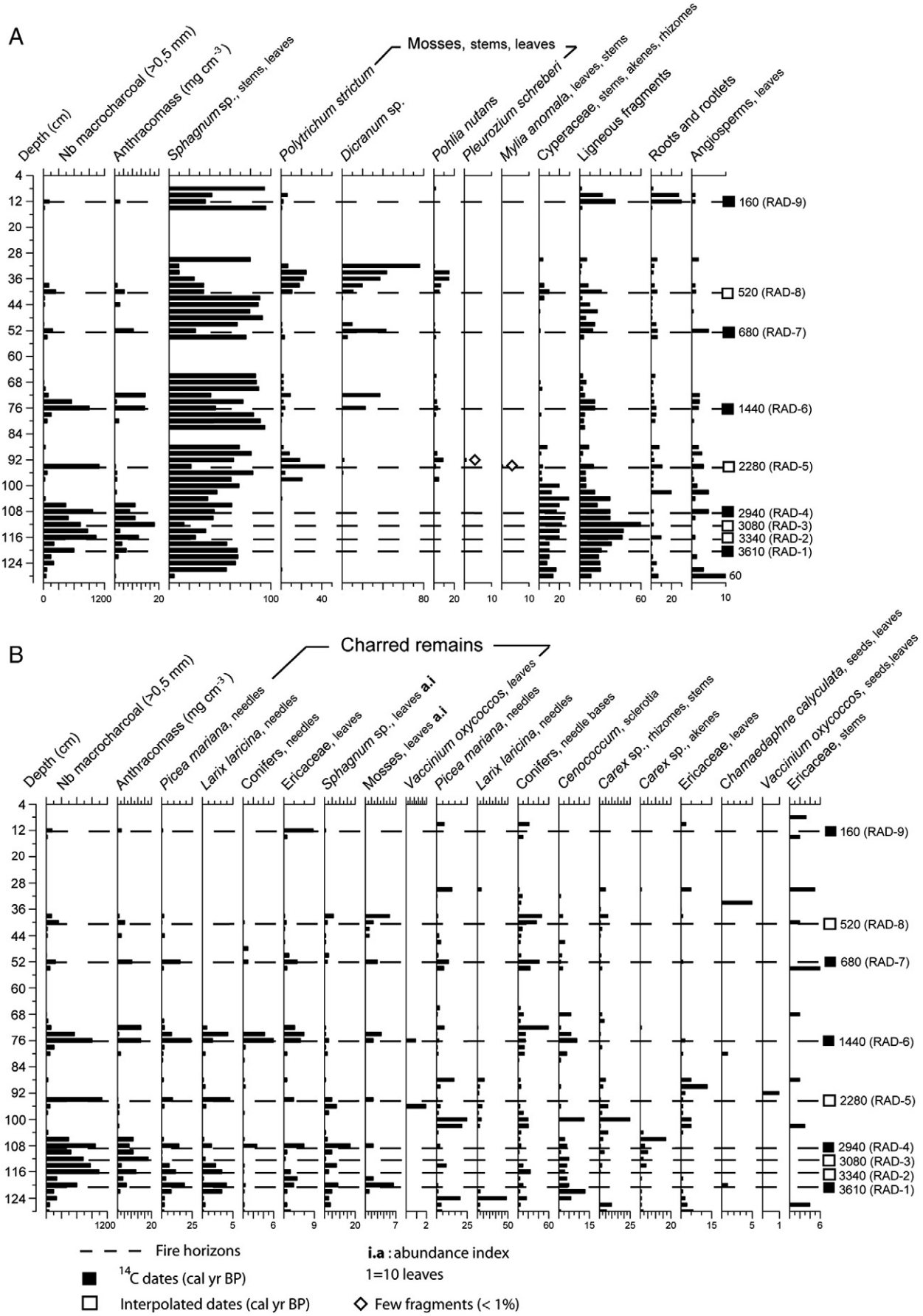

Figure 6. Macrofossil diagrams of Radisson peatland. Results are expressed in A) volume percentages (5-cm^{-3} samples) and B) concentrations (number of pieces per 5 cm^{-3}). The scales are not constant.

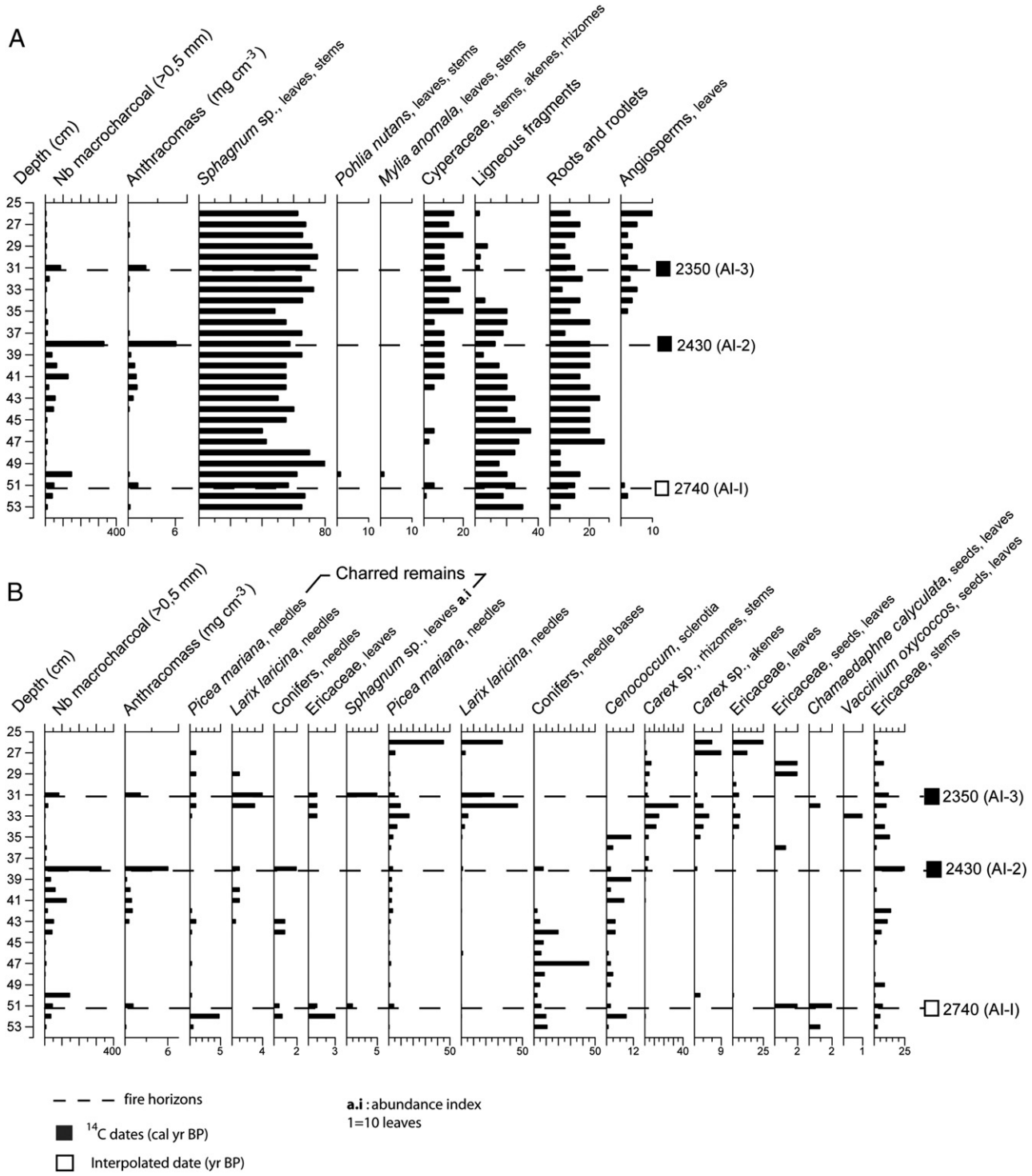

Figure 7. Macrofossil diagrams of Airport I peatland. Results are expressed in A) volume percentages (5-cm^{-3} samples) and B) concentrations (number of pieces per 5 cm^{-3}). The scales are not constant.

created a hiatus in the peat sequence. The fire-free interval during the bog phase at AIR-2 peatland was estimated at 1440 yr.

The AII-1 and AII-2 fire events had a limited impact on the local vegetation cover. Ligneous fragments and *P. mariana* needles are abundant beneath the charred layers indicating its local presence before the fire event. The charcoal layers contain charred *P. mariana* needles and abundant ligneous fragments, roots, and rootlets, along with sclerotia of *Cenococcum graniforme*, a mycorrhiza that develops in association with shrubs in well-drained sites (Jackson and Mason, 1984). The fires produced high amounts of macrocharcoal pieces (Figs. 5 and 8) probably owing to the local presence of *P. mariana*. The macrofossil diagrams (Fig. 8) show an increase in *Sphagnum* abundance after the first fire (AII-1) following a decrease in the abundance of ligneous fragments. This probably results from the removal of the woody biomass (ericaceous shrubs and conifers) by fire. The second fire (AII-2) likely burned the vegetation of a hollow where sedges (*Carex* spp.) were abundant. The only noticeable impact of the fires on the non-vascular communities is the appearance of *Dicranum* sp. above AII-1 and *P. strictum* and lichens above AII-2.

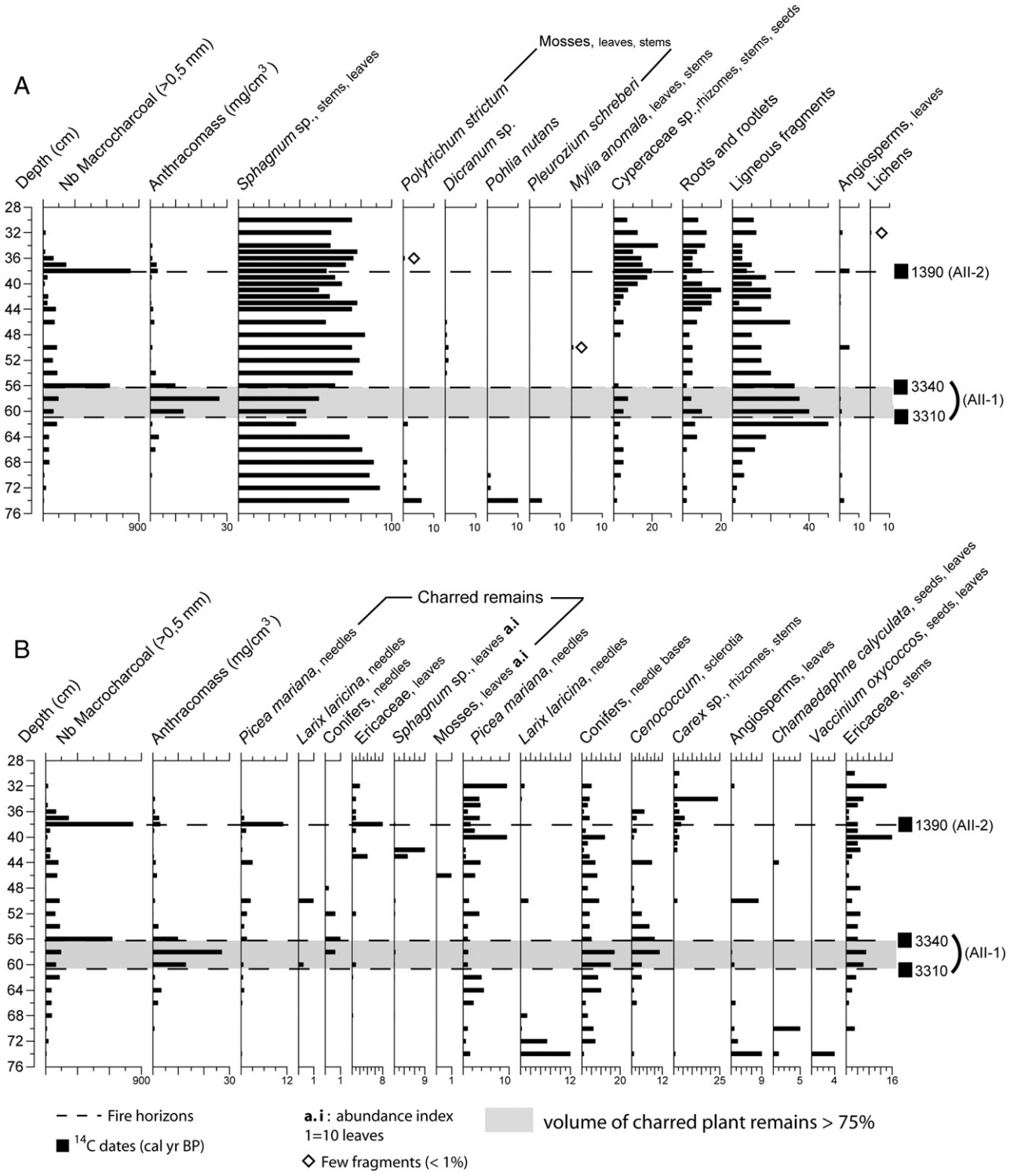

Figure 8. Macrofossil diagrams of Airport II peatland. Results are expressed in A) volume percentages (5-cm^{-3} samples) and B) concentrations (number of pieces per 5 cm^{-3}). The scales are not constant.

Discussion

Long-term fire dynamics in peatlands

In the three studied peatlands, fire events occurred after the onset of ombrotrophic conditions. The absence of fire during the minerotrophic stage corroborates the observations of previous studies suggesting that fire disturbance is excluded from *Carex*-dominated peatlands because of high water tables and low wood fuel loads (Kuhry, 1994; Zoltai et al., 1998; Hellberg et al., 2004; Busque and Arsenault, 2005; Ohlson et al., 2006; Arlen-Pouliot, 2009). Most charred layers reported from boreal and temperate peatlands in Canada (e.g., Kuhry, 1994; Lavoie and Pellerin, 2007; Lavoie et al., 2009) and in northern Europe (e.g., Ohlson et al., 2006; Valirenta et al., 2007) were found in *Sphagnum*-peat (i.e., during the ombrotrophic stage). However, the absence of macroscopic charcoal in minerotrophic peat must be interpreted with caution given that charcoal-based fire detection in sediments depends on fire severity (Higuera et al., 2005) and vegetation composition

Table 2
Characteristics of the coring sites and of the macroscopic charcoal records.

Sites	Core length (cm)	Basal age (cal yr BP)	Peatland area (ha)	Distance (m) from the forest margin	Fire events (nb)	Mean macrocharcoal pieces/fire	Mean anthracomass (mg cm^{-3})/fire	Fire-free interval (bog stage) (yr)
Radisson	179	6200	4	50	9	734	28.5	440
Airport II	168	5980	50	200	3	764	54.3	1400
Airport I	257	6730	50	400	4	153	16.8	1200

(Pitkänen et al., 2003). Hence, light fires occurring in relatively wet environments may not be recorded in the peat sequences. The abundance of Cyperaceae remains below and within some charcoal layers (e.g., AI-2, AI-3 and AII-2) suggests that fires have burned plants growing in relatively wet biotopes (probably hollows).

Past fire occurrence in the studied peatlands was primarily under the control of autogenic factors (e.g., peat build-up and vegetation succession). The hydroseral succession from fen to bog resulting in a decreased surface wetness allows the development of a dense woody biomass which facilitates fire propagation. In the three studied sites, the local presence of conifer trees during the bog phase was probably instrumental for the spread of fire since charred needles of *P. mariana* and *L. laricina* were found under and within most charred layers.

Upland forest fires generally stop at peatland margins and are less likely to reach the central parts of large open bogs because the tree density tends to decrease from the edges to the central sections. As a result, in a long-term perspective, the edges of large peatlands burn more often than their central parts (Foster and Glaser, 1986; Pitkänen et al., 2001; Robichaud and Bégin, 2009). The size of peatland basin is thus a factor controlling fire propagation in peatlands. Ohlson et al. (2006) have shown that over long time scales (i.e., Holocene), the central parts of small forested peatlands in Norway (~2 ha) can burn as often as the edges.

The distance of the sampling points from the forested mineral soils seems to have been a factor controlling local fire regime in our studied sites. Radisson peatland is characterized by a significantly shorter fire-free interval during the bog stage compared to Airport I and II peatlands (Table 2). The smaller area of this forested peatland (~4 ha) and its proximity to mineral soils probably allowed the long-term residence of conifer trees, thus increasing fire susceptibility and fire severity. Fires produced significantly greater amounts of macroscopic charcoal at RAD and AIR-II sites compared to the AIR-I coring point, which is located farther from the well-drained forest soils (Table 2). This could suggest that more severe fires occurred at these coring locations because of the higher density of heath shrubs and conifers (i.e., greater aboveground biomass). However, this finding must be interpreted carefully considering the unpredictable relationship between charcoal abundance and fire severity (Higuera et al., 2005). It is difficult to interpret past fire severity accurately from our macrocharcoal records because the amount of charcoal produced by fire depends on the type and quantity of biomass (dead and living) consumed. Our study shows that the amount of macroscopic charcoal pieces produced by fires is directly influenced by the abundance of the ligneous fragments.

Past fire occurrence in peatlands and paleoclimatic conditions during the Holocene

It has been suggested in previous studies that past climate changes have driven the long-term fire dynamics of peatlands. In boreal western and central Canada, Kuhry (1994) and Camill et al. (2009) suggested that a change toward warmer and drier conditions during the Hypsithermal (between ca. 8000–6000 cal yr BP) was responsible for an increased fire frequency in peatlands. Our results suggest that the long-term fire dynamics of the studied peatlands was primarily controlled by local vegetation succession. However, there is evidence that fire propagation in bogs of the James Bay lowlands has been facilitated by a climate-mediated change in surface wetness during the late Holocene. All fire events recorded in the studied peatlands and in a bog located nearby (Godbout, 2002) occurred after 3600 cal yr BP. In northwestern Québec, a change toward drier and colder conditions after 3500 cal yr BP was documented by an increase in fire-induced aeolian activity (Filion, 1984; Filion et al., 1991), a fire-mediated opening of the boreal forest (e.g., Payette and Gagnon, 1985; Gajewski et al., 1993), and permafrost growth in peatlands (Payette, 2001b). In a peat bog located 1 km south of the AIR I and II sites, a gradual decrease in peat accumulation rates associated with decreasing surface wetness was recorded between 4500 and 1500 cal yr BP (Beaulieu-Audy et al., 2009). In the Eastmain area, 150 km south of Radisson, many episodes of very dry surface conditions were also recorded in bogs after 3000 cal yr BP (Loisel and Garneau, 2010; van Bellen et al., 2011).

The interpretation of a link between paleoclimate and fire occurrence in peatlands should be taken with caution when using a single core per site because the macrofossil records in these environments are individualistic (Ohlson et al., 2006). Despite their proximity (200 m apart), Airport I and II sites have contrasting fire history, and only the most recent fire of AD 1941 (AI-4 and AII-3) has been recorded in both sites. These results corroborate previous studies showing the high spatial variability of fire propagation in peatlands (Hörnberg et al., 1998; Turetsky and Wieder, 2001; Ohlson et al., 2006) resulting in distinct macroscopic charcoal records even between closely spaced sites.

Are peatland vegetation communities resilient to fire?

It was previously recognized that fires have usually only minor long-term impacts on the dynamics of bog vegetation (Kuhry, 1994). This is mainly because fires in peatlands are generally superficial owing to the high moisture conditions. High-severity fires have rarely been observed in pristine peatlands except in subarctic permafrost bogs that had previously experienced major water-table drawdown (Zoltai et al., 1998). Previous studies have shown that deep peat fires can transform hummocks into hollows (e.g., Benscoter et al., 2005). There is no evidence of such changes in our macrofossil records, suggesting that most fires only burnt the aboveground biomass without destroying the peat deposit.

At RAD peatland, the shift from *Sphagnum* to moss assemblages was associated with local fires during the ombrotrophic stage. *P. strictum*, a common pioneer species in recently burned peat bogs of the James Bay area (Thibault and Payette, 2009), was the dominant bryophyte species in the post-fire assemblages. This moss is well-adapted to harsh microclimatic conditions and provides a buffer effect against frost heaving in bare peat surfaces (Groeneveld and Rochefort, 2005). *P. strictum* and other companion mosses located above the charred layers, (i.e., *Dicranum* sp., *P. nutans*, and *P. schreberi*) were also found in post-fire assemblages of boreal and subarctic bogs elsewhere in Canada (Jasieniuk and Johnson, 1982; Kuhry, 1994; Pellerin and Lavoie, 2003; Paitre, 2008; Robichaud and Bégin, 2009). The post-fire proliferation of these mosses, which are indicative of relatively dry surface conditions, suggests that peat combustion reinitiated

vegetation succession without affecting local hydrology. Once established, mosses may have facilitated the recovery of late-successional species like *Sphagnum* and ericaceous shrubs. Fire-induced moss changes were usually short-lived, although in some cases (RAD peatland), mosses were present locally for several hundred years (up to 400 yr) after fire. This contrasts with previous studies showing *Sphagnum* recovery within a few decades (~40 yr) after fire (e.g., Jasieniuk and Johnson, 1982; Kuhry, 1994; Pellerin and Lavoie, 2003). However, peat bog vegetation is generally resilient to fire. Low fire incidence and fire severity in large open bogs may allow the long-term self-perpetuation of plant communities in the absence of other major disturbances. This is the case for *L. laricina*, a fire-sensitive species that persisted in these peatlands in the absence of severe fire, supporting the idea that these ecosystems may act as fire-free refugia (Busque and Arsenault, 2005). This contrasts with the surrounding forest stands where vegetation diversity and successional processes are primarily driven by recurrent fires (Morneau and Payette, 1989).

Although fires had only minor impacts on local vegetation communities in Airport I and II sites, peat accumulation slowed down markedly during the late Holocene period following the fire events dated at 3310 and 2350 cal yr BP (Fig. 4). These particularly low rates of peat accumulation may reflect the absence of post-fire vegetation regeneration or may reveal the loss of peat by combustion in the following fires. It has been shown that fires in bogs of the James Bay area result in the dominance of lichen communities, which slow down the post-fire successional stages (Thibault and Payette, 2009). At AIR-I and AIR-II, peat accumulation ceased following the last fire (AD 1941) and *Sphagnum* communities have not yet recovered. In the central parts of the large bogs (AIR-I and AIR-II), fire could be responsible for the reduced peat accumulation during the late Holocene. In these more exposed environments, the removal of shrubs and conifers can have considerable effects on the thermal regime of the peat surface due to a major change in snow conditions. In the absence of successful post-fire regeneration by pioneer mosses, *Sphagnum* may have failed to recover under these harsh microclimatic conditions and have been replaced by lichens, which significantly slowed peat accumulation.

Conclusion

The role of fire in local-scale vegetation dynamics of three ombrotrophic peatlands in northwestern Québec was evaluated based on high-resolution analyses of macroscopic charcoal and plant remains. Fire propagation to the sites seemed mainly controlled by local autogenic processes, in particular the hydroseral succession from fen to bog associated with a decreasing surface wetness. The distance from the present-day forest margins and the local presence of conifer trees may also have controlled fire susceptibility and fire intensity. Our data confirm that plant communities of ombrotrophic peatlands are resilient to fire. Most fire horizons reveal low-intensity fires that have not consumed the peat deposit hence allowing the rapid recovery of conifers and ericaceous shrubs. Although some fires have resulted in the replacement of *Sphagnum* by terrestrial mosses, they have not caused major ecological changes in these peatlands. However, there is evidence that fires have slowed down peat accumulation in the most exposed sites during the late Holocene. Further research should attempt to determine how past climate changes have affected fire frequencies in peatlands, notably by evaluating the interaction between climate, hydrology and fire occurrence using many replicates from distinct sites.

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