

Reconstructing the recent dynamics of mires using a multitechnique approach

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Summary

1 The recent vegetation dynamics of 16 ombrotrophic mires in southern Québec (Canada) was studied through palaeoecological (dendrochronology, plant macrofossil and pollen analyses) and historical (aerial photograph analyses) techniques.

2 Plant macrofossil analyses show that prior to European colonization (*c.* 1800), mires were predominately open environments dominated by *Sphagnum* mosses. Many sites subsequently became forested with little or no *Sphagnum*.

3 Aerial photograph analyses indicate that widespread forest expansion occurred in all mires between 1948 and 1995. The percentage of the total mire area occupied by forest increased from 22.5 to 56.5%, an overall gain of 137 ha of forest habitat.

4 A dry climatic period during the first part of the 20th century, drainage resulting from human activities, and fire events, seem to be the main causal factors of vegetation changes.

5 Forest expansion is expected to cause profound changes in bog ecosystems, such as altering hydrological conditions and organic accumulation processes, and to be detrimental to regional biodiversity and the carbon balance.

6 Overall, this study highlights the need to incorporate multiple approaches in reconstructing the vegetation dynamics of an ecosystem, and in determining causal factors of vegetation change.

Key-words: anthropogenic disturbance, fire, forest expansion, historical ecology, mires

Journal of Ecology (2003) **91**, 1008–1021

Introduction

The vegetation dynamics of mires, defined as changes in vegetation structure and species composition over time (Smith & Huston 1989), is a slow process compared with vegetation dynamics occurring in terrestrial ecosystems (Klinger 1996; Gunnarsson *et al.* 2002). The most obvious change observed in mires is the transition from the minerotrophic (vegetation dominated by sedges and brown mosses) to the ombrotrophic (vegetation dominated by *Sphagnum* species) stage, a transition occurring over several thousand years (Svensson 1988; Kuhry *et al.* 1993; Hu & Davis 1995; Hughes & Dumayne-Peaty 2002). Mire dynamics is influenced by autogenic (e.g. peat accumulation processes) and allogenic (e.g. climate) factors (Payette

1988). Vegetation in ombrotrophic mires (bogs) is particularly sensitive to climate as bogs receive their water and nutrient supply from atmospheric precipitation. Several palaeoecological studies have reported vegetation modifications in response to climate change (Barber 1981; Winkler 1988; Mauquoy & Barber 1999a, 1999b; Ellis & Tallis 2000; Lavoie & Richard 2000). For example, the recurrent decline of *Sphagnum imbricatum* in several bogs of the British Isles, and its replacement by other *Sphagnum* species, have been attributed to an increase in climatic and mire surface wetness (Mauquoy & Barber 1999b; Ellis & Tallis 2000).

World-wide, mires are subjected to expanding industrial (peat extraction, tree plantation) and agricultural activities, especially in Europe, in the northern United States and in southern Canada (Moore 2002). As a result, the recent vegetation dynamics of many mires is now mainly influenced by anthropogenic activities, which may have an impact on bog species composition over very short time periods. For example, in a bog in northern England, a significant decrease in true ombrotrophic species was observed within only 30 years, and was

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attributed to land-use changes in the vicinity of the mire, as well as the cessation of traditional land management, such as grazing and burning (Chapman & Rose 1991). In a bog in southern Germany, a major increase in the area dominated by *Pinus sylvestris* and *Betula pubescens* woodlands occurred between 1962 and 1992 in response to anthropogenic drainage (Frankl & Schmeidl 2000). Pine colonization and expansion during the last 200 years in a bog in the Jura Mountains (Switzerland) was also linked to drainage (Freléchoux *et al.* 2000). On the other hand, pristine mires may also experience major changes in response to diffuse human pollution. For example, both the decrease of *Sphagnum* abundance and the expansion of vascular plants within seemingly untouched European mires have been related to an increase of atmospheric nitrogen deposition (Berendse *et al.* 2001; Gunnarsson *et al.* 2002).

In southern Québec (Canada), mires are often isolated within an agricultural landscape, and most are threatened by agriculture, forestry and peat mining activities. A recent study conducted in undisturbed remnants of mined bogs of the Bas-Saint-Laurent region (Fig. 1a) showed that major forest expansion

occurred during the last 50 years (Pellerin & Lavoie 2000). Is this phenomenon widespread in mires of the region? Which factor(s) is (are) responsible for the forest expansion? To answer these questions, the recent history of the vegetation structure of several bogs was reconstructed using a unique combination of palaeoecological (dendrochronology, plant macrofossil and pollen analyses) and historical (aerial photograph analyses) techniques. Historical data were also integrated in a geographical information system (GIS). In this paper, we hypothesized that fires and peat drainage resulting from human activities were the main factors responsible for vegetation changes.

STUDY AREA AND SITES

The study area (176 km²) is a narrow (< 12 km wide), low-altitude (< 170 m above sea level) agricultural plain located between the municipalities of Rivière-du-Loup and L'Isle-Verte in the Bas-Saint-Laurent region, southern Québec, Canada (Fig. 1a). The region was deglaciated about 12 000 years BP, but was then submerged by the Goldthwait Sea (Dionne 1977). The vegetation cover was established about 9500 years BP, shortly after marine regression, and the modern vegetation developed around 8000 years BP (Richard *et al.* 1992). On mesic and xeric sites, vegetation is characterized by *Acer saccharum* Marsh., *Betula alleghaniensis* Britt. and *Abies balsamea* (L.) Mill. forests (Grondin 1996). Ombrotrophic mires are common in wet depressions and are located at the transition between the geographical range of semi-forested and maritime non-forested bogs (Glaser & Janssens 1986).

The colonization of the study area began around 1680 near Rivière-du-Loup (Morin 1993a), but only a few settlers established before 1800 (Morin 1993b). Between 1800 and 1830, agricultural activities expanded, and about one-third of the study area was cleared for cultivation (Bouchette 1832). The remaining forest cover was then rapidly logged, such that by 1870 most of the land was used for agriculture (Fortin 1993a). Until recently, mires were one of the last ecosystems undisturbed by human activities (Fortin 1993b). Nevertheless, between 1929 and 2000, 62% of the total area covered by bogs (4829 ha) was disturbed, mainly by peat mining, logging and farming activities (Pellerin 2003). Historical data on drainage activities within the study area are non-existent. Nevertheless, a close examination of the oldest aerial photographs (1929) revealed that most of the drainage network present outside bogs today was already in place 70 years ago. However, other aerial photographs taken between 1960 and 1980 showed that many drainage ditches have been straightened, probably indicating an improvement of land drainage efficiency.

Sixteen undisturbed bogs ranging in size from 1.5 to 157.7 ha (Fig. 1b, Table 1) are located within the study area. Six of them are remnants of bogs mined for the production of horticultural peat (BDB, CAC, MIC,

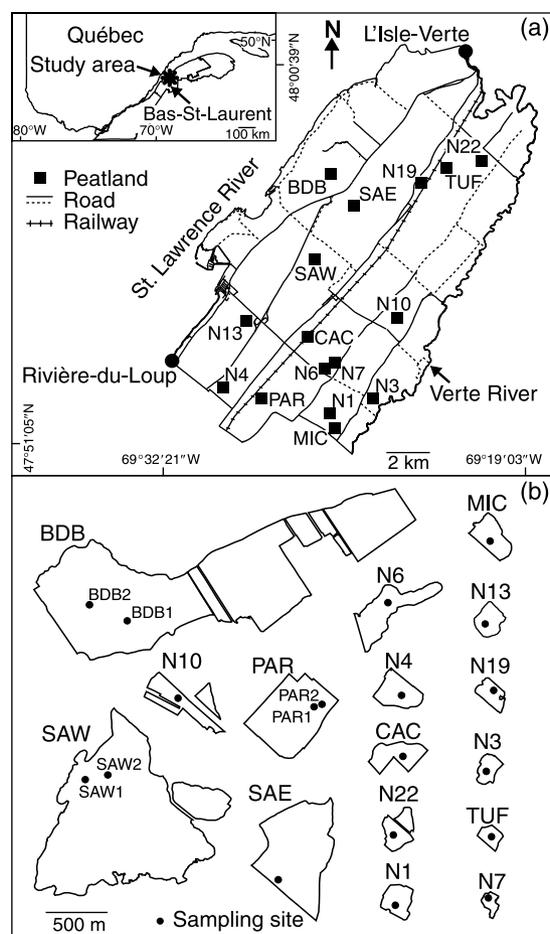


Fig. 1 (a) Location of the study area, Bas-Saint-Laurent region, southern Québec (Canada), and spatial distribution of the studied mires. (b) Shape and relative area of the 16 studied mires, and location of the 19 sampling sites.

Table 1 Characteristics of the 16 studied mires, Bas-Saint-Laurent region, southern Québec

Site	Area (ha)	Peat thickness (cm)		Forest cover (%)		
		Mean	Min.–Max.	1948	1995	Variation
BDB	157.7	203	44–298	42.5	67.5	+25.0
CAC	5.7	212	100–260	11.1	82.1	+71.0
MIC	4.3	101	29–260	79.2	95.2	+16.0
N1	4.6	162	51–256	85.4	90.4	+5.0
N3	2.6	121	22–169	24.1	46.7	+22.6
N4	7.4	126	34–198	0.0	30.8	+30.8
N6	10.9	141	43–207	26.5	46.5	+20.0
N7	1.5	125	24–172	17.0	100.0	+83.0
N10	10.5	101	23–231	2.5	62.1	+59.6
N13	4.3	74	20–94	33.5	80.5	+47.0
N19	3.5	97	56–121	28.7	76.1	+47.4
N22	5.1	210	120–261	38.3	62.5	+24.2
PAR	32.4	231	66–460	4.9	81.2	+76.3
SAE	35.7	93	34–205	12.2	50.5	+38.3
SAW	115.1	170	22–389	1.1	32.8	+31.7
TUF	2.4	205	131–262	2.5	43.3	+40.8
All sites	403.7	162	20–460	22.5	56.5	+34.0

PAR, SAE, TUF). A mosaic of open and forested patches characterizes the vegetation cover of the mires. Dominant tree species include *Picea mariana* (Mill.) B.S.P., *Pinus banksiana* Lamb. and *Larix laricina* (Du Roi) K. Koch. Ericaceous shrubs (mainly *Chamaedaphne calyculata* (L.) Moench, *Kalmia angustifolia* L., *Ledum groenlandicum* Oeder and *Vaccinium angustifolium* Ait.) are widespread in all bogs. The ground layer of open patches is covered by *Sphagnum* mosses (mainly *S. capillifolium* (Ehrh.), *S. fuscum* (Schimp.) Klinggr., *S. magellanicum* Brid. and *S. rubellum* Wils.), whereas *Pleurozium schreberi* (Brid.) Mitt. dominates the ground layer of forested sites (S. Pellerin, unpublished data).

Methods

FIELD SAMPLING

To select sampling sites, the vegetation cover of the 16 bogs was surveyed during the summers of 1998 and 1999. The most recent (1995) aerial photograph (1 : 15 000) covering each bog was digitized, registered in space, and corrected to limit geometrical distortions using Geographic Transformer software (Blue Marble Geographics, Gardiner, Maine, USA). Corrected photographs were imported in a GIS, MapInfo Professional (MapInfo Corporation, New York, USA). In the GIS, a grid of sampling stations located 50-m apart (bog area < 100 ha) or 100-m apart (bog area > 100 ha) was superimposed on each mire. The latitude and longitude of each station ($n = 1005$) were obtained with the GIS, and then located in the field using a global positioning system. For each station, we visually described the vegetation cover (dominant species, vegetation structure) and identified each tree stem selected with a factor 2 metric wedge prism (Bitterlich 1984). We also meas-

ured the thickness of the peat deposit using an iron rod driven into the soil (Table 1) and noted if there was any woodcutting evidence or fire scars on trees. For bogs smaller than 20 ha, one sampling site was located in the dominant vegetation type, whereas two sampling sites were selected for larger sites, i.e. one in an open environment and the other in a nearby forested environment. SAE bog (36 ha) was sampled only once because its vegetation cover was homogeneous throughout. All sampling sites were located at a minimum of 20 m from any disturbance (drainage ditch, peat mining, woodcutting). Nineteen sampling sites were selected (Fig. 1b).

Within each sampling site, a 400-m² quadrat (20 × 20 m) was delineated. All tree stems located inside the quadrat were identified and numbered. A cross section of a maximum of 75 stems (randomly selected) was taken using an increment borer as close as possible to the collar. In order to reconstruct the recent vegetation dynamics of all sites, a peat monolith (15 × 15 cm wide, 20–60 cm deep) was extracted at the centre of each quadrat for plant macrofossil analyses. Furthermore, one peat core covering the entire organic deposit was extracted from seven mires for pollen analyses using a side-wall peat corer (Jowsey 1966). Cores were only taken at small sites (< 11 ha) to maximize the local and extra-local (*c.* 500 m) pollen representation (Jacobson & Bradshaw 1981). Three cores (MIC, N7 and N19) were taken in a forested environment, and four cores (N3, N4, N6 and N22) in an open environment. Pollen analyses were used to determine which horizon in the peat deposit corresponded to the beginning of noticeable human activities (farming) in the study area, i.e. *c.* 1800 (Bouchette 1832; Morin 1993b). In pollen diagrams, this event is characterized by an increase in pollen percentages of ruderal or cultivated taxa such as *Ambrosia*, *Rumex* and *Poaceae* spp. (Foster *et al.* 1992; Russell

et al. 1993). This increase was used as a chronological marker.

DENDROCHRONOLOGICAL, PLANT MACROFOSSIL AND POLLEN ANALYSES

Tree cores were dried, finely sanded, and the annual growth rings were counted under a low-power (50×) binocular microscope. Only cores that reached or barely missed the pith were used to construct the age structure of tree stands. For plant macrofossil analyses, subsamples of 100 cm³ were taken between 0 and 2, 2–4, 4–6 and 6–10 cm (depths below the soil surface), and subsequently by contiguous 5-cm-thick slices along the peat monolith. Subsamples were washed through a series of sieves (2, 1 and 0.5 mm meshes), and the remaining fractions were air-dried to prevent fungal contamination. Macroscopic remains (vascular plants, mosses, liverworts and charcoal pieces) were sorted under a low-power (50×) binocular microscope. When macrofossil remains of a particular taxon were too numerous to be easily counted ($n > 200$), 0.5 g of the subsample was extracted. Fossil pieces were then counted, and the total number of pieces was estimated from the total dry weight of the subsample. For pollen analyses, cores were subsampled (1 cm³) at every 2.5 cm for the upper 50 cm of the core, and then at every 5 cm until the mineral deposit was reached. Subsamples were treated following the procedure of Faegri & Iversen (1989). At least 500 pollen grains of terrestrial vascular plants (pollen sum) were counted per sample using a light microscope (400×).

AERIAL PHOTOGRAPH ANALYSES

The recent evolution of the forest cover of each bog was analysed using 13 series of aerial photographs taken in 1948, 1961, 1963, 1970, 1973, 1974, 1978, 1979, 1983, 1986, 1990, 1991 and 1995, and the EASI/PACE digital image processing software (PCI Geomatics, Richmond Hill, Canada). Each photograph was digitized, registered in space and corrected to limit geometrical distortions. A supervised classification approach with a maximum likelihood classifier was used (Campbell 1996). On aerial photographs the forested vegetation could easily be distinguished from open vegetation (i.e. with only small or no trees) and hence these two vegetation types were used to classify the photographs. Each photograph was classified separately to minimize between-image differences in brightness and contrast, and a mask for each bog was created to restrict the analysis to the area of interest. For each photograph, the area covered by each vegetation type and the percentage of accurate pixel classification was obtained.

No long-term record of water table level was available for any of the 16 sites studied. However, numerous drainage ditches have been dug in mires during the last 50 years. To reconstruct the potential impact of these

ditches on the water level of each bog, we used the series of corrected aerial photographs (1948–95) covering the study area. All corrected photographs were integrated into the GIS and every visible drainage ditch located inside or bordering the bogs was numerized. A grid of points located 30-m apart was then superimposed on each bog. Thirty points were randomly chosen, the distance separating each point to the nearest drainage ditch was measured, and the percentage of points located less than 45 m from a ditch was calculated. This value of 45 m was chosen because it is the maximum mid-point distance between two drainage ditches recommended by forest engineers in Québec's bogs. Below this distance, a drainage ditch has an impact on the water level of peaty soils important enough to improve tree growth (Prévost *et al.* 2001). This is a conservative value as most of the drying effect associated with a drainage ditch in bogs usually occurs within 25 m (Hillman 1992; Rothwell *et al.* 1996).

FIRE DATING AND RECONSTRUCTION OF THE CLIMATE RECORD

No fire scar was found in any of the 16 bogs, but numerous charcoal layers were detected in the peat monoliths. Interviews were conducted with the landowners of each site to determine the year of the most recent fire event. When no information was available, the depth of the charcoal layer was compared with that of the pollen chronological marker (*c.* 1800), and the year of the fire event was estimated by linear interpolation. To detect whether climate could have had an influence on the recent evolution of bog vegetation structure, we carefully examined the climatic data available (1913–95) from the La Pocatière meteorological station, located 60 km south-west of the study area (Environment Canada, unpublished data). Only annual precipitation data are presented in this study.

Results

POLLEN CHRONOLOGICAL MARKER

An abrupt increase in *Ambrosia*, *Rumex* and *Poaceae* spp. pollen percentages is noticeable in the upper part of each pollen diagram (Fig. 2). This rise is located between 12.5 and 15 cm (depth below the surface) in cores extracted under forest cover (MIC, N7 and N19), and between 22.5 and 25 cm in three of the four cores extracted from open areas (N4, N6 and N22). The increase is located deeper (42.5 cm) in the N3 peat profile because the acrotelm (oxygenated upper layer of peat with living *Sphagnum* stems) was thicker at this site (30 cm at N3 vs. 20 cm at N4, N6 and N22). Consequently, we used 15 cm as the maximum depth of the horizon corresponding to *c.* 1800 for all forest sites, 25 cm for all open sites with an acrotelm thinner than 30 cm, and 42.5 cm for all open sites with an acrotelm thicker than 30 cm.

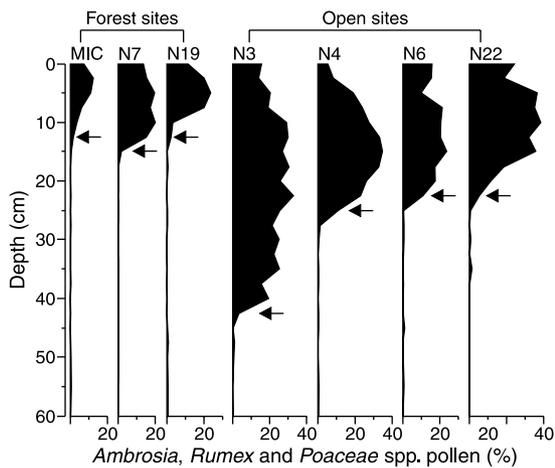


Fig. 2 Diagrams of the percentage of *Ambrosia*, *Rumex* and *Poaceae* spp. pollen (all taxa considered) contained at different peat depths for three forested and four open mires of the Bas-Saint-Laurent region, southern Québec. Diagrams are truncated at 60 cm (depth below the ground surface). Arrows indicate the beginning of noticeable farming activities in the study area (c. 1800).

RECENT VEGETATION HISTORY RECONSTRUCTED USING PLANT MACROFOSSILS

All sites except BDB2, N13 and SAW2 have a macrofossil record extending back before the beginning of noticeable farming activities in the region (Fig. 3). Plant macrofossil analyses show that before c. 1800, only N6 was not characterized by an open environment dominated by *Sphagnum* mosses. Nine of the open sites subsequently became forested, and the rise of *Picea mariana*, *Larix laricina* and/or *Pinus banksiana* macrofossils in the upper peat layers coincided with the disappearance of *Sphagnum* remains at five of these (CAC, N1, N7, PAR1 and SAW1). This phenomenon was not detectable within peat monoliths extracted from MIC, N13 and N19, but the *Sphagnum* cover of these sites was consistently lower than 20% in 1998 and 1999 (S. Pellerin, unpublished data). At BDB1, the *Sphagnum* cover was higher than 80% in 1999, although the site was densely covered by *Picea mariana*. At CAC, PAR1 and SAW1, the increase in tree remains (mainly *Pinus banksiana*) occurred just above the most recent charcoal layer. Remains of the forest moss *Pleurozium schreberi* became more abundant in the surface layer of all forest sites (except CAC and N13). Sites that are still characterized by an open vegetation structure have not recently undergone major vegetation changes. However, the remains of some mosses (*Polytrichum strictum* Brid. and *Pohlia nutans* (Hedw.) Lindb.), liverwort (*Mylia anomala* (Hook.) S. Gray) and trees were more abundant in the upper peat layers. Finally, ericaceous shrubs remains increased in the upper peat layers of most sites.

RECENT VEGETATION HISTORY RECONSTRUCTED USING AERIAL PHOTOGRAPHS

The chronological sequence of aerial photographs indicates that a widespread forest expansion phenomenon occurred in all mires between 1948 and 1995 (Table 1, Figs 4 and 5). During the 47-year period, the percentage of the total mire area occupied by forest increased from 22.5 to 56.5%, which represents an overall gain of 137 ha of forest habitat (Table 1). Forest expansion per site ranges from 5 to 83%. *Picea mariana* (70% of the trees sampled with the prism), *Pinus banksiana* (14%) and *Larix laricina* (10%) accounted for most of the increase in the forest cover.

The forest expansion trend detected on aerial photographs differed between bogs (Fig. 5). At some sites, the forest expansion was gradual from 1948 (BDB, CAC, N3, N7, N19, N22, SAE, SAW), while at others, forest cover increase was initiated at the beginning of the 1960s (N13, TUF) or 1970s (N4, N10). Forest expansion at PAR occurred mainly between 1948 and 1961, and between 1979 and 1995, whereas a dense forest cover already characterized the vegetation cover at MIC and N1 in 1948.

RECENT VEGETATION HISTORY RECONSTRUCTED USING TREE RINGS

The age structure of tree populations was only reconstructed at sampling sites where at least 10 individuals of the same species were sampled (Fig. 6). At BDB1, MIC, N1 and N22, tree stand establishment occurred from c. 1880–1890 until c. 1960. At N3, N7, N19, SAE, SAW2 and BDB2, tree stand establishment occurred mainly from 1915 to 1935–65. At CAC the first tree became established in 1927, but most individuals appeared between 1945 and 1949. At N6 *Picea mariana* establishment occurred mostly from 1940 to 1975. At PAR1 and SAW1, the first *Pinus banksiana* individual appeared in 1943, and a massive establishment of trees occurred 2 years later. At N13 most *Larix laricina* individuals appeared between 1960 and 1970.

DRAINAGE, FIRE AND CLIMATE HISTORY

The potential influence of drainage ditches increased at all sites between 1948 and 1995 (Fig. 5). During the 47-year period, the increase of the percentage of points located < 45 m from a ditch ranged from 3 to 87%. In most bogs, the intensification of drainage activities occurred before 1975. In 1995, the percentage of points located < 45 m from a ditch was > 50% at CAC, N10, N19 and TUF, and between 40 and 50% at N1, N7 and N22.

At least one fire event had occurred since the beginning of noticeable farming activities in the study area (c. 1800) in 11 of the 16 studied bogs (Fig. 3). Seven fires occurred after 1900. Interviews indicated that at N10, the most recent fire occurred in 1942, and prior to

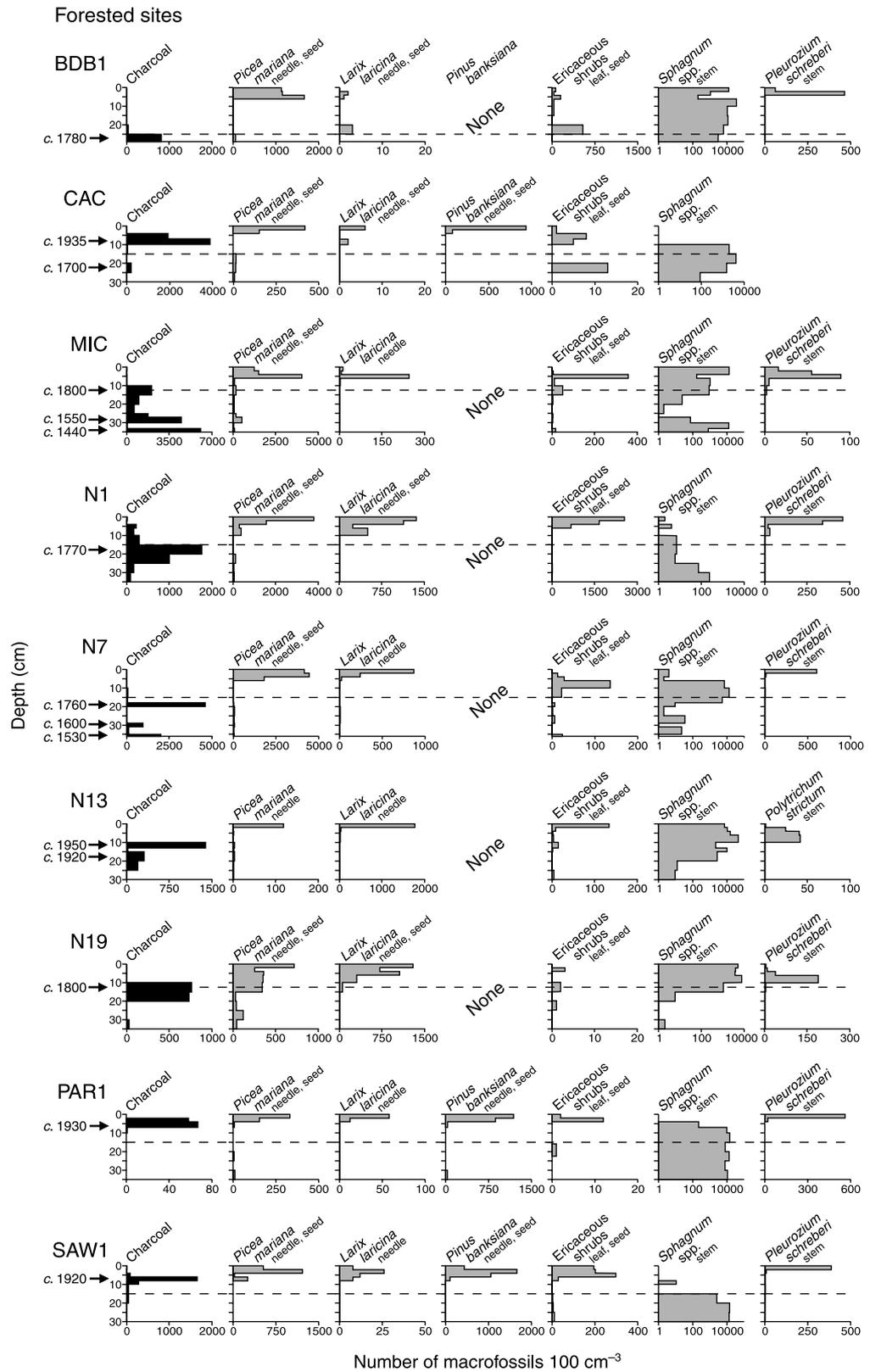


Fig. 3 Macrofossil diagrams of surface peat layers extracted from mires of the Bas-Saint-Laurent region, southern Québec (selected taxa only). The scale varies according to species and sites; note the logarithmic scale for *Sphagnum* spp. Estimated dates of fire events (charcoal layers) are indicated. Dotted lines indicate the approximate position of the peat layers corresponding to the beginning of noticeable farming activities in the study area (c. 1800).

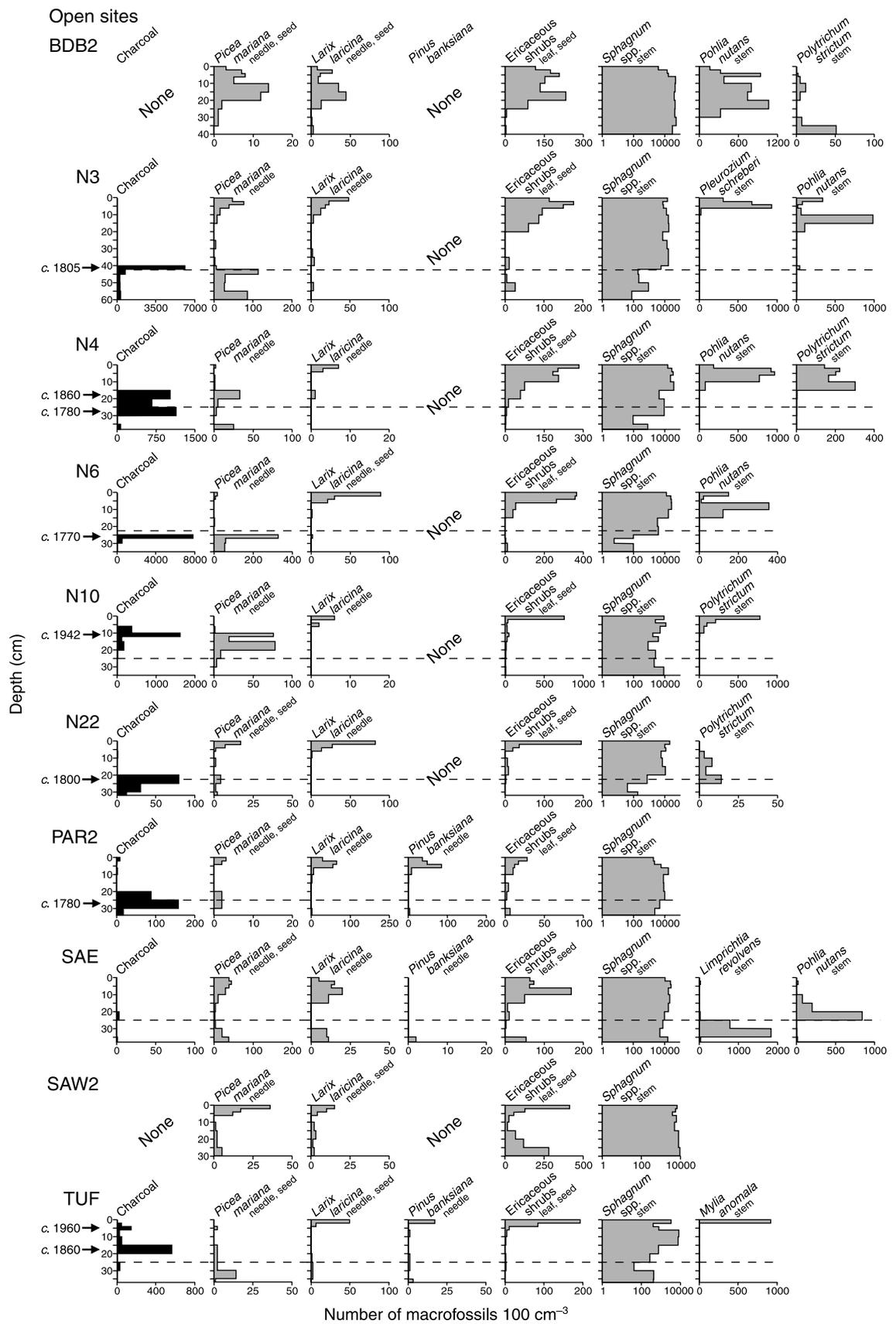


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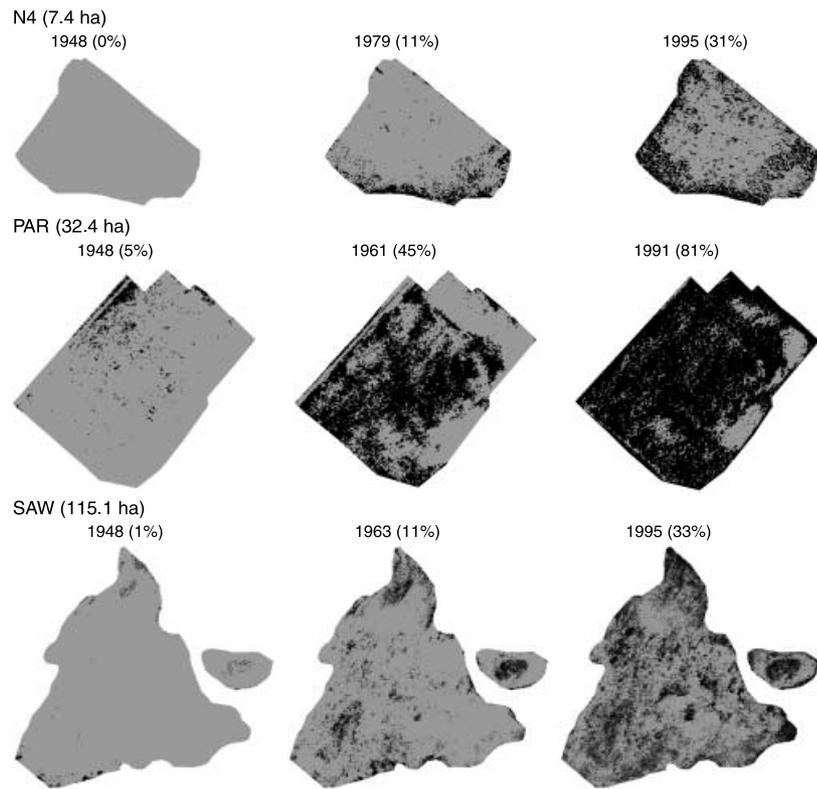


Fig. 4 Spatiotemporal evolution of the forest cover (black areas) of N4, PAR and SAW mires, Bas-Saint-Laurent, southern Québec, reconstructed using aerial photographs. Percentage of the mire area covered by forest is indicated for each year.

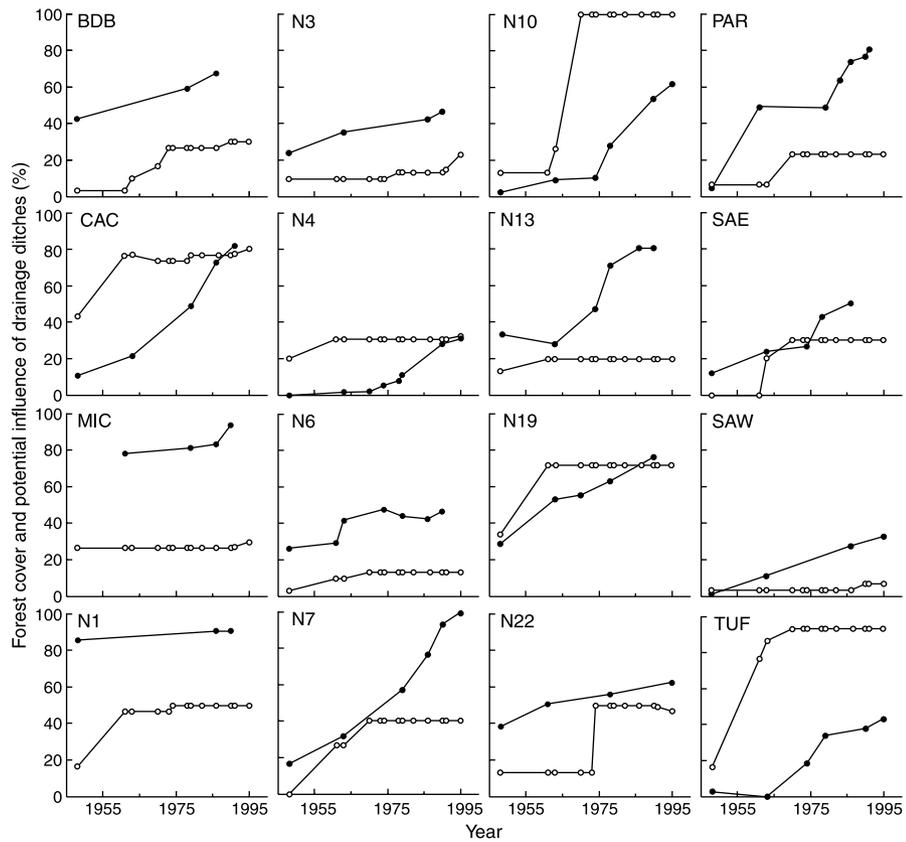


Fig. 5 Evolution of the forest cover (closed circle; percentage of the total area covered by forest) and of the potential influence of drainage ditches (open circle; percentage of the sampling points located less than 45 m from a ditch) in 16 mires of the Bas-Saint-Laurent region, southern Québec. Forest cover data are presented only for years with an accurate pixel classification percentage higher than 90%.

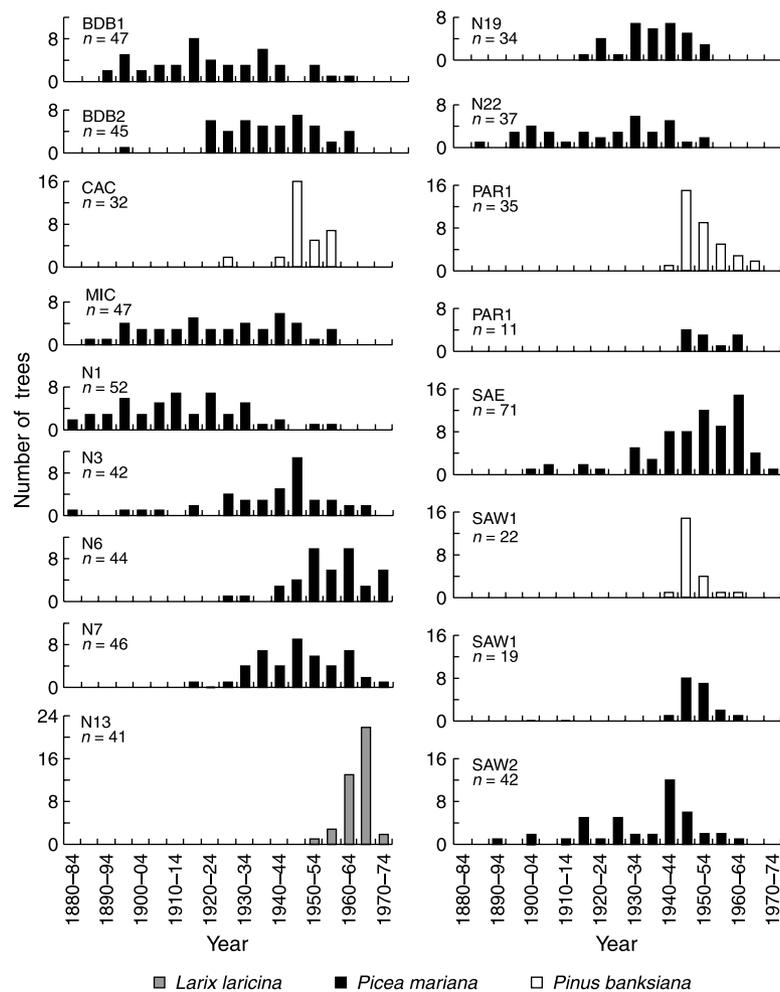


Fig. 6 Age structure (5-year classes) of tree stands from mires of the Bas-Saint-Laurent region, southern Québec.

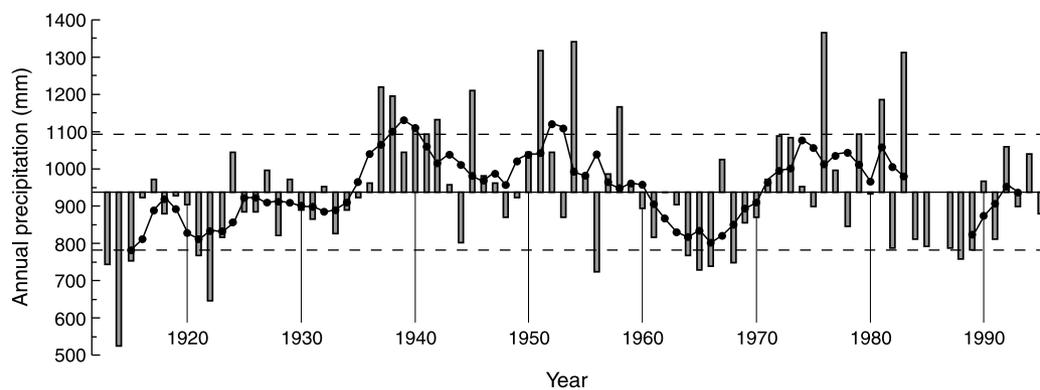


Fig. 7 Reconstruction of the climatic anomalies between 1913 and 1995 at La Pocatière meteorological station, Bas-Saint-Laurent region, southern Québec. Horizontal lines: mean value (1913–95). Vertical bars: precipitation. Dotted lines: standard deviation. Solid line: 5-year running mean. Missing value: 1986.

1940 at SAW. The cause of the fires was unknown for all but one of the study sites; a human accidentally ignited the fire at SAW.

While the climate at La Pocatière from 1913 to 1995 was characterized by dry and wet periods, no long-term

trend in the precipitation record is noticeable (Fig. 7). Drier-than-average climatic periods were recorded from 1913 to 1935, in the 1960s and in the 1980s. Wetter-than-average periods occurred around 1940, at the beginning of the 1950s and during the 1970s.

Discussion

RECENT VEGETATION DYNAMICS OF MIREs

Our study shows that mires of the Bas-Saint-Laurent region are dynamic ecosystems where vegetation communities have experienced substantial changes over a very short time period. Palaeoecological analyses strongly suggest that the vegetation structure of several mires shifted from open and *Sphagnum*-dominated to forested and *Sphagnum*-poor after c. 1800. Aerial photograph analyses also indicate that a major increase in the forest cover occurred in most bogs within the study area over the last few decades. The percentage of the total mire area covered by woodlands had more than doubled (from 22.5 to 56.5%) between 1948 and 1995. However, dendrochronological data indicate that this phenomenon was initiated earlier, as most tree stands established before 1950; saplings have to reach a minimum height before being detectable on aerial photographs (Cameron *et al.* 2000).

The recent shift from a *Sphagnum*-dominated to a forested vegetation structure that was observed in mires of the Bas-Saint-Laurent region is not necessarily an unusual event in the Holocene history of bogs. In Europe, several palaeoecological studies have shown that during some periods of the Holocene epoch, ombrotrophic mires were covered by pine forests (Birks 1975; McNally & Doyle 1984; Bridge *et al.* 1990; Gear & Huntley 1991; Pilcher *et al.* 1995). In the study area, macrofossil analyses conducted in the BDB and PAR bogs, which covered the last 8900 years, also showed that forest episodes dominated by *Picea mariana* occurred during short (200–300 years) periods of their ombrogenic history (Lavoie *et al.* 2001; Pellerin & Lavoie 2003). More recently, forest expansion resulting from anthropogenic activities has been documented in European bogs (Åberg 1992; Frankl & Schmeidl 2000; Freléchoux *et al.* 2000) and minerotrophic mires of North America (Jacobson *et al.* 1991; Bunting *et al.* 1998). However, to our knowledge, our study is the only one clearly demonstrating recent and widespread forest expansion in North American bogs.

CAUSES OF FOREST EXPANSION

The examination of causal factors of the recent forest expansion in bogs of the Bas-Saint-Laurent region follows the approach proposed by Ritchie (1985) and MacDonald (1993) for palaeoecological studies, and is derived from the methodological falsification approach of Popper (1965). According to Popper (1965), when a hypothesis is proposed, any evidence that would force its abandonment must be clearly spelt out; a hypothesis is thus accepted or rejected instead of proven or disproven. Four hypotheses (or causal factors) have been examined to explain the recent forest expansion: (i) anthropogenic drainage; (ii) recent fire events; (iii) dry climatic period; and (iv) natural succession.

Drainage

Recent forest expansion in ombrotrophic mires is often associated with human activities (Frankl & Schmeidl 2000; Freléchoux *et al.* 2000). Drainage lowers the water table, which improves the aeration of the upper peat layers and increases soil temperature and nutrient availability (Hillman 1992; Pakarinen 1994; Paavilainen & Päivänen 1995; Silins & Rothwell 1999). Such changes in edaphic conditions facilitate the survival and growth of trees in mires (Lees 1972; Lieffers & Rothwell 1986; Laine *et al.* 1995; Macdonald & Yin 1999). Peat surface dryness and increasing tree stand shading may also lead to the disappearance of *Sphagnum* mosses and their replacement with forest mosses like *Pleurozium schreberi* (Laine & Vanha-Majamaa 1992; Laine *et al.* 1995).

Are the Bas-Saint-Laurent bogs affected by drainage resulting from human activities? There is little doubt that their hydrology has been altered (Van Seters & Price 2001) as most mires are either mined and/or dissected by drainage ditches. However, the potential influence of drainage ditches was not the same in all mires. If the evolution of the potential influence of drainage ditches parallels the expansion of the forest cover or if an increase in the potential influence of drainage ditches occurs before a rise in the forest cover, the hypothesis that forest expansion was caused by anthropogenic drainage cannot be rejected. Otherwise, although drainage may have contributed to increasing the forest cover of a mire, it cannot be accepted as a triggering factor. Such a link cannot be rejected for CAC, N7, N10, N19 and TUF (Fig. 5) and peripheral drainage may also have contributed to the forest cover increase at N4. This small site is completely surrounded by agricultural lands, and forest expansion mainly occurred at the margins, where drainage ditches are located (Fig. 4). For all other sites, it is unlikely that anthropogenic drainage triggered the forest expansion phenomenon.

Fire

Macrofossil analyses showed that forest expansion occurred at CAC, PAR1 and SAW1 following the most recent fire. This phenomenon is unusual because fire usually has few long-term impacts on the vegetation structure of ombrotrophic mires (Jasieniuk & Johnson 1982; Foster & Glaser 1986; Kuhry 1994). Furthermore, fire generally helps to maintain a treeless environment in bogs, as it kills any trees that do establish, thus maintaining a higher water table and favouring the growth of *Sphagnum* mosses (Damman 1977; Chambers 1997). Tree seedlings established in a *Sphagnum*-dominated environment have little chance of survival because they are rapidly overgrown by *Sphagnum* species (Ohlson & Zackrisson 1992; Gunnarsson & Rydin 1998; Ohlson *et al.* 2001).

On the other hand, fires can trigger forest expansion by eliminating the *Sphagnum* mat and spreading the

seeds of tree species that are well adapted to post-fire regeneration, such as pines (Lewis & Dowding 1926; Yefremova & Yefremov 1996; Pellerin & Lavoie 2003). The presence of charred needles of *Pinus banksiana* in the most recent charcoal layer of CAC, PAR1 and SAW1 indicates that this tree species was growing on these sites when fires occurred. Pellerin & Lavoie (2003) suggested that in the Bas-Saint-Laurent region, frequent fires occurring during the 20th century have contributed to the emergence of large pine stands in mires. This phenomenon may have been facilitated by a drier-than-average climatic period during the first part of the 20th century, i.e. before 1935. Drying of mire surface due to low-rainfall years, or anthropogenic drainage, makes them more susceptible to fire (Cypert 1961; Wein 1983; Tallis 1987; Pitkanen *et al.* 1999). This phenomenon can facilitate the encroachment of invasive species (McDade 2000) and modify species composition (Maltby *et al.* 1990). Thus, the hypothesis of a link between fire and forest cover cannot be rejected for CAC, PAR1 and SAW1.

Climate

In Europe, tree colonization in mires during the Holocene epoch has usually been ascribed to warmer and/or drier climatic periods (Birks 1975; Bridge *et al.* 1990; Gear & Huntley 1991; Pilcher *et al.* 1995). Dry climatic conditions, like drainage activities, lower the water table, which facilitates the survival and growth of many tree species in waterlogged ecosystems. Coincidence between tree establishment and drier-than-average climatic periods or synchronous forest expansion in all bogs, irrespective of their area, peat deposit thickness or the intensity of anthropogenic disturbance, would suggest a regional climatic control (Payette 1988).

To establish a link between climate and tree establishment for BDB1, MIC, N1 and N22, a longer climate record (i.e. covering the last part of the 19th century and the first part of the 20th century) would have been necessary, as tree establishment was initiated before 1913. Tree establishment was initiated at BDB2, N3, N7, N19, SAE and SAW2 during a long drier-than-average period extending from *c.* 1913–35. At N13, tree establishment occurred during the 1960s, i.e. during a shorter dry period. Tree establishment at CAC, N6, PAR1 and SAW1 was, however, initiated between 1940 and 1950, i.e. during a relatively wet period. However, tree ring counts at ground level usually underestimate the year of tree establishment in bogs because of the presence of missing or partially formed growth rings, and because the real tree collar is often buried in the peat (DesRochers & Gagnon 1997; Parent *et al.* 2000). For instance, the underestimation can be as great as 19 years for *Picea mariana* (DesRochers & Gagnon 1997). Consequently, it is likely that most tree stands, including those from CAC, N6, PAR1 and SAW1, became established earlier, i.e. mainly during the 1913–35 period. Additional sampling of 254 trees at PAR (C.

Lavoie, unpublished data) revealed that some individuals are older (1925–40; cored at breast height) than those sampled at PAR1 site, supporting this assertion.

While precipitation was only slightly lower than average during most of the 1913–35 period, even a slight (a few centimetres) lowering of the water table can promote tree colonization in bogs (Frankl & Schmeidl 2000; Freléchoux *et al.* 2000). A very dry climatic period would be detrimental to tree survival and growth, because trees growing on organic soils have root systems that are mainly confined to the unsaturated surface peat layers (Liefers & Rothwell 1987). A major lowering of the water table exposes trees, especially seedlings, to water stress (Dang & Liefers 1989; Malmer *et al.* 1994; Gunnarsson & Rydin 1998) and negates any benefits generated by low ground water levels (Pepin *et al.* 2002).

Whatever the exact role of the 1913–35 dry period, the fact that forest expansion occurred in all mires, including large sites (> 100 ha) with little disturbance (e.g. SAW and BDB), and that this phenomenon occurred almost simultaneously in all bogs, strongly suggests that an external factor, such as climate, initiated or contributed to forest expansion in the Bas-Saint-Laurent mires. A link between climate and the recent expansion of the forest cover cannot therefore be rejected for any site.

Natural succession

It might be suggested that the recent forest expansion was the result of a natural vegetation succession phenomenon, from open bog towards a woodland climax. However, this hypothesis seems improbable because the phenomenon occurred very rapidly. Succession in mires rarely shows major changes on a decadal scale, mainly because *Sphagnum* bogs are dominated by very stable vegetation communities (Backéus 1972; Klingner 1996; Gunnarsson *et al.* 2000; Ohlson *et al.* 2001). Moreover, the fact that forest expansion occurred in all sites during the last century, despite the fact that peat deposition did not begin at the same time and they are therefore probably not at the same successional stage (Lortie 1983; Lavoie *et al.* 2001; Van Seters & Price 2002; Pellerin & Lavoie 2003), strongly suggests that there is no link between the expansion of forest cover and natural succession.

Conclusion

Our study shows that the forest expansion observed in ombrotrophic mires of the Bas-Saint-Laurent region is a recent phenomenon, that probably results from the complex interaction of several factors, of which climate, drainage resulting from human activities and recent fire events predominate. It is also probable that the isolation of the mires within an agricultural plain helped forest expansion, but this impact is assumed to be restricted to the bog margins where drainage ditches are located. On the other hand, as the Bas-Saint-Laurent region is still virtually unaffected by air pollution,

and atmospheric loading of sulphur and nitrogen is lower than critical loads (Ouimet *et al.* 2001), it seems improbable that the forest expansion within mires was a response to airborne pollutants. Our study shows that even ecosystems, such as mires, which are known to be resistant to disturbances may undergo rapid and major changes when they are subjected to multiple disturbances, and especially to human influences.

Whatever the causes of the recent forest expansion in the Bas-Saint-Laurent mires, this phenomenon is expected to cause profound changes in bog ecosystems, such as altering hydrological conditions (Ohlson *et al.* 2001). For instance, trees decrease the amount of water stored in the soil by intercepting rainfall, withdrawing water from peat, and increasing evapotranspiration rates (Anderson *et al.* 2000; Frankl & Schmeidl 2000; Van Seters & Price 2001). Furthermore, the disappearance of *Sphagnum* may disrupt peat accumulation and carbon sequestration rates because it is the principal plant involved in the accumulation process, and because *Sphagnum* carpets decay more slowly than vascular plant remains (Coulson & Butterfield 1978; Bartsch & Moore 1985; Malmer *et al.* 1994). Finally, the loss of large areas of open bogs is also problematic for the preservation of regional biodiversity. The richness and diversity of plants (especially mosses), insects and birds are usually higher in open bogs than in forest bogs (Smith & Charman 1988; Calmé & Desrochers 1999; Pellerin & Lavoie 2000; Lavoie 2001), especially in the Bas-Saint-Laurent region (D. Lachance, unpublished data).

Overall, this work highlights the need to incorporate multiple approaches in historical studies in order to reconstruct the vegetation dynamics of an ecosystem, and to determine causal factors of vegetation changes. For example, although macrofossil and pollen analyses provided continuous long-term records of the changes in the composition of bog plant communities, they were of limited value when evaluating the extent of forest expansion. Aerial photograph analyses gave more information about the spatial distribution of the phenomenon, but were limited by the gap between the real beginning of forest expansion and its photographic evidence. Dendrochronological analyses filled this gap by providing more accurate information about tree stand establishment. Together these techniques provide a far more complete analysis than any single technique in isolation.

Acknowledgements

This research was financially supported (grants to C.L.) by the Natural Sciences and Engineering Research Council of Canada (NSERC). The Fonds pour la Formation de chercheurs et l'aide à la recherche du Québec (FCAR) and NSERC provided doctoral scholarships to S.P. We are grateful to Premier Horticulture and all private landowners for allowing us to work in their mires. Pollen analyses were conducted

at the Harvard Forest with the support of D.R. Foster. We thank G. Létourneau for his help with aerial photograph classification. We also thank N. Bhiry, M. Garneau, R. Gauthier, A.C. Larouche and C. Roy for their help with macrofossil and moss identification, J. Bussièrès, C. Huot, D. Lachance, K. Marcoux, A. Saint-Louis and C. Zimmermann for field and laboratory assistance, and M. Lavoie, D.R. Foster and two anonymous reviewers for helpful comments on earlier drafts of the manuscript.

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Received 11 December 2002
revision accepted 22 July 2003