ÉCOSCIENCE

10 (2): 247-257 (2003)

Recent expansion of jack pine in peatlands of southeastern Québec: A paleoecological study[1]

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Abstract: Jack pine (*Pinus banksiana*) colonization and expansion in ombrotrophic peatlands of the Bas-Saint-Laurent region, southeastern Québec, was analyzed using macrofossil and dendrochronological analyses. During the last 80 years, and mainly between 1920 and 1945, several open peatlands dominated by *Sphagnum* species were invaded by jack pine following a fire event. This phenomenon appears to have no precedent over the last 8,900 years, at least in one of the study sites. Fires triggered the expansion by eliminating the *Sphagnum* mat and spreading thousands of pine seeds released by a few individuals. While fires contributed to the expansion of pines in bogs, this phenomenon may have been facilitated by a drier-than-average climatic period during the first part of the 20th century. The fact that dense jack pine stands are now growing on thick organic deposits indicates that this species has a wider ecological tolerance than previously known and/or that the Bas-Saint-Laurent peatlands have recently undergone major ecological and hydrological changes favouring the growth of non-bog species.
Keywords: fire, jack pine, peatland, *Pinus banksiana*, vegetation dynamics, Québec.

Résumé : Nous avons analysé les patrons de colonisation et d'expansion du Pin gris (*Pinus banksiana*) dans les tourbières du Bas-Saint-Laurent (sud-est du Québec) à l'aide d'analyses macrofossiles et dendrochronologiques. Au cours des 80 dernières années, et principalement entre 1920 et 1945, plusieurs tourbières ouvertes dominées par les sphaignes ont été envahies par le Pin gris à la suite d'un feu. Il s'agirait d'un événement sans précédent au cours des 8900 dernières années, du moins dans l'un des sites à l'étude. Le feu a favorisé l'expansion du Pin gris en éliminant le tapis de sphaignes et en permettant la dissémination des graines de pin. Une période climatique plus sèche que la normale au début du XXe siècle a pu faciliter le phénomène. La présence de peuplements denses de Pin gris sur dépôt organique épais indique que cette espèce peut coloniser un éventail plus large d'habitats ou encore que les tourbières du Bas-Saint-Laurent ont subi récemment d'importants changements écologiques et hydrologiques favorisant la croissance d'espèces que l'on ne trouve pas habituellement dans les tourbières.
Mots-clés : dynamique de la végétation, feu, Pin gris, *Pinus banksiana*, Québec, tourbière.

Nomenclature: Anderson, Crum & Buck, 1990; Kartesz, 1994; Marie-Victorin, 1995.

Introduction

The distribution of jack pine (*Pinus banksiana*) in Canada roughly corresponds to the area occupied by the fire-prone boreal forest (Rudolph & Laidly, 1990). Its range extends from Nova Scotia to Alberta, and north to the Mackenzie River valley in the Northwest Territories (Majcen, Gagnon & Benzie, 1980; Farrar, 1996). Jack pine is well adapted to postfire regeneration because its serotinous cones enclose a large number of seeds, which are released after intense fire events (Beaufait, 1960; Cayford, Chrosciewicz & Sims, 1967; Rowe & Scotter, 1973; Cayford & McRae, 1983). Fire eliminates competitors and prepares a suitable seedbed by burning the organic soil layer and exposing mineral soil (Critchfield, 1985; Thomas & Wein, 1985; Chrosciewicz, 1990). Jack pine is primarily found on podzolic soils (Cayford, Chrosciewicz & Sims, 1967). It grows best on well-drained loamy sands, but it is also found on very dry sandy or gravely soils (Kenkel, 1986; Rudolph & Laidly, 1990). This tree species grows poorly on waterlogged organic soils (Janssen, 1967; Rudolph & Laidly, 1990). However, recent vegetation surveys conducted in the Bas-Saint-Laurent region, southeastern Québec (Figure 1), have shown that dense jack pine stands (60 to 100% dominance) are widespread in ombrotrophic peatlands (Pellerin, Lachance & Lavoie, unpubl. data).

The presence of dense jack pine stands in ombrotrophic peatlands appears to be unusual, at least in Québec. Few botanists have mentioned its occurrence in such ecosystems (Lafond & Ladouceur, 1968; Gauthier & Grandtner, 1975; Lallier, 2000; Muller, 2001). Furthermore, neither paleoecological analyses conducted in the present range of the species in Québec (Garneau, 1987; Lavoie, Zimmermann & Pellerin, 2001; Muller, 2001) nor those conducted in its previous range (Larouche, 1979; Lavoie, Larouche & Richard, 1995; Lavoie & Richard, 2000a,b) have revealed a historical presence of jack pine stands in peatlands.

In this study, the historical pattern of jack pine colonization was analyzed in the peatlands of the Bas-Saint-Laurent region. Our objectives were to reconstruct the history of jack pine stands in peatlands and to determine which factors could have favoured their establishment and expansion. To achieve our objectives, we studied nine jack pine stands in six peatlands using plant macrofossil and dendrochronological analyses. We hypothesized that (*i*) the establishment of jack pine in the peatlands of the

[1]Rec. 2002-05-30; acc. 2002-10-15.
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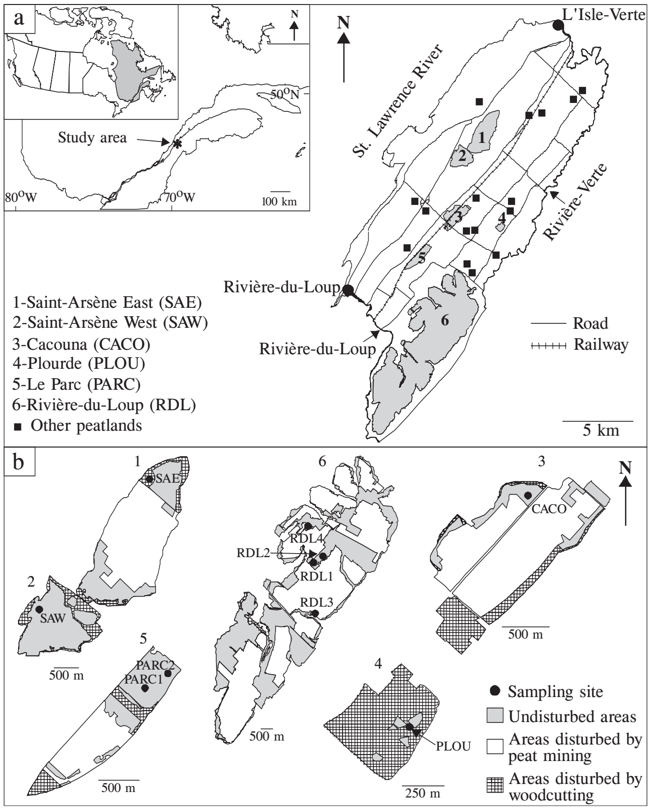


FIGURE 1. a) Location of ombrotrophic peatlands in the study area, Bas-Saint-Laurent region, southeastern Québec; b) Location of jack pine sampling stations and spatial distribution of anthropogenic disturbances in bogs studied.

Bas-Saint-Laurent region is a recent phenomenon (less than 100 years); (*ii*) fire accelerated the jack pine invasion process; and (*iii*) peat drainage induced by human activities facilitated the establishment and survival of jack pine.

Methods

STUDY AREA

The study area is a narrow (12 km), low-elevation (< 170 m) strip of sand, silt, and clay surficial marine deposits (Fulton, 1995) located between the settlements of Rivière-du-Loup and L'Isle-Verte in the Bas-Saint-Laurent region, southeastern Québec, Canada (Figure 1a). It is an agricultural plain (245 km^2) bordered on the northwest by the St. Lawrence River and on the southeast by the Rivière Verte. 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 9,500 years BP, shortly after marine regression, and the modern vegetation developed after 8,000 years BP (Richard, Larouche & Lortie, 1992). On mesic and xeric sites, modern vegetation is characterized by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and balsam fir (*Abies balsamea*) forests (Grondin, 1996). Jack pine typically occurs as isolated clumps on open rocky sites (Blouin, 1970; Garneau, 1984). Large ombrotrophic peatlands are common in wet depressions and are dominated by black spruce (*Picea mariana*), ericaceous shrubs, and *Sphagnum* species (Gauthier & Grandtner, 1975).

The original forest cover of the study area was almost completely cleared during the 19th century. Until recently, peatlands were one of the last ecosystems undisturbed by human activities (Fortin, 1993). Nevertheless, between 1930 and 2000, 62% of the total area covered by bogs (4,829 ha) was reclaimed (Pellerin, unpubl. data). Peat extraction for horticultural use (84% of the disturbed area), logging (9%), and farming (4%) were the main anthropogenic activities in these peatlands.

The regional climate is wet and continental. Data from the meteorological station of Saint-Arsène, located in the study area, indicate that the mean annual temperature is 3°C. January is the coldest month (mean temperature: -12°C) and July, the warmest month (mean temperature: 18°C). The mean annual precipitation is 924 mm, 27% of which falls as snow (Environnement Canada, 1993).

FIELD SAMPLING

To locate jack pine stands, we surveyed tree populations of all bogs (n=22) of the study area (Figure 1a). The most recent (1995) aerial photograph (1:15,000) covering each peatland was digitized, registered in space, and corrected to limit geometrical distortions using Geographic Transformer™ software (Blue Marble Geographics, Gardiner, Maine, U.S.A.). Corrected photographs were integrated in the geographic information system MapInfo Professional™ (MapInfo Corporation, Troy, New York, U.S.A.). The area of each peatland was delineated, and a grid of sampling stations located 50 m apart was then superimposed on the peatland polygon. The latitude and longitude of each sampling station were obtained with the geographic information system. Stations were located in the field during the summer of 1999 using a global positioning system. For each station, we visually described the vegetation (dominant tree species, vegetation structure, tree density) and noted whether there was any evidence of woodcutting or fire scars on the trees. For the large Rivière-du-Loup peatland (3,375 ha), we used a detailed vegetation cover map (Gauthier, 1967) to locate jack pine stands.

We identified twelve large jack pine stands within nine peatlands. Three stands were rejected for sampling because they were too severely damaged by forestry practices. Therefore, we sampled nine stands located within six different peatlands (Table I and Figure 1b). The total area of individual peatlands ranged from 23 to 3,375 ha, but their undisturbed areas were much smaller, ranging from 1 to 1,250 ha (Figure 1b). Le Parc bog (PARC) was mined for the production of horticultural peat between 1962 and 1967, and Cacouna bog (CACO) from 1942 to 1975 and from 1983 to 1989, while the Rivière-du-Loup (RDL) and Saint-Arsène East (SAE) sites have been mined since 1939 and 1959, respectively (Lavoie & Saint-Louis, 1999). However, in the Rivière-du-Loup bog, only a small area located south of the RDL3 stand was mined before 1960. The mining activities near the three other stands began between 1961 and 1963 (Desaulniers, 2000). Logging was the main activity damaging Plourde (PLOU)

TABLE I. Characteristics of jack pine stands in bogs of the Bas-Saint-Laurent region, southeastern Québec. RDL, Rivière-du-Loup; PLOU, Plourde; PARC, Le Parc; SAE, Saint-Arsène East; SAW, Saint-Arsène West; CACO, Cacouna.

Site	Longitude (N)	Latitude (W)	Altitude (m)	Beginning of peat mining	Mean peat thickness (cm ± SD; n = 9)	Basal area (m^{-2} ha)	Density (stems ha^{-1})
RDL1	47°49'19″	69°28'34″	100	1939	179 ± 20	33.5	2000
RDL2	47°49'42″	69°28'12″	100	1939	242 ± 28	25.3	1125
RDL3	47°48'11″	69°28'38″	102	1939	101 ± 33	47.7	1575
RDL4	47°50'06″	69°28'41″	98	1939	272 ± 19	26.0	3275
PLOU	47°53'14″	69°24'31″	140		186 ± 28	39.3	2350
PARC1	47°52'21″	69°28'48″	72	1962	378 ± 19	25.6	2300
PARC2	47°52'25″	69°28'37″	72	1962	176 ± 34	26.4	2350
SAE	47°57'22″	69°25'20″	50	1959	209 ± 20	7.5	1450
SAW	47°56'02″	69°27'02″	54		272 ± 10	8.4	1450
CACO	47°54'16″	69°27'27″	82	1942	207 ± 28	75.1	1825

and Saint-Arsène West (SAW) bogs between 1932 and 1948 and between 1970 and 1986, respectively.

A 400-m^2 quadrat was delineated inside each jack pine stand (Le Parc bog was sampled in two different locations). We visually described the vegetation cover (tree species, presence of dead trees), counted all living jack pine individuals located inside the quadrat, and measured their diameter at breast height (DBH). We cored a maximum of 50 stems (randomly chosen) as close as possible to the collar using an increment borer. DBH values were used to calculate the basal area occupied by jack pine.

At each sampling station, peat thickness was estimated using an iron rod driven into the soil every 10 m along three transects (20 m long, 10 m apart). A peat monolith (15 cm × 15 cm wide, 20 cm to 35 cm deep) was extracted at the centre of each quadrat in order to reconstruct the recent history of jack pine stands using plant macrofossil analyses. In addition, to obtain a longer historical perspective on the presence of jack pine in peatlands, a peat core (394 cm long) was extracted from Le Parc bog (near PARC1 sampling station) using a side-wall peat corer (Jowsey, 1966). Le Parc bog was selected because it supports the largest jack pine stand and has the thickest peat deposit.

DENDROCHRONOLOGICAL ANALYSES

Tree cores were dried and finely sanded, and the tree rings were counted under a low-power (50x) binocular microscope. On the cores without pith, we estimated the distance separating the innermost ring to the pith by fitting a circular template on the innermost ring and determining the diameter of the circle that best fitted the curvature of that ring (Conkey, Keifer & Lloyd, 1995). We then estimated the number of missing rings using an age-diameter relationship established with cores having pith. Only cores with the pith present or with fewer than five estimated missing rings were used to construct the age structure of each stand.

PLANT MACROFOSSIL ANALYSES

Surface peat monoliths were subsampled (100 cm^3) at the 0-2 cm, 2-4 cm, 4-6 cm, and 6-10 cm levels (depths below the soil surface) and subsequently by contiguous 5-cm-thick slices along the peat section. Macrofossil analyses of the Le Parc peat core were conducted on 2-cm segments for the upper 20-cm section and then on 2.5-cm segments along the core. Subsamples were washed through a series of sieves (2-mm, 1-mm, and 0.5-mm meshes), and the remaining fractions were air-dried to prevent fungal contamination (Wohlfarth *et al.,* 1998). Macroscopic remains (vascular plant, moss, and charcoal pieces) were sorted under a low-power (50x) 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 weight of the subsample (Lavoie & Payette, 1995). Accelerator mass spectrometry dating was carried out on plant material extracted from subsamples 240-242.5 cm (fen-bog transition) and 390-394 cm (basal peat sample) of the Le Parc peat core.

RECENT FIRE AND CLIMATE HISTORY

No fire scar was found; recent fire events were detected by charcoal layers located less than 10 cm below the soil surface. Interviews were conducted with the owners of each site to estimate the year of the most recent fire event. In order to detect whether the climate could have had an influence on jack pine establishment in bogs, we carefully examined the climatic data available (1913-1995) from the La Pocatière meteorological station, located 60 km southwest of the Rivière-du-Loup bog (Environnement Canada, unpubl. data). Data from Saint-Arsène station were not used because the record was much shorter and incomplete. Only annual precipitation data are presented in this analysis.

Results

CHARACTERISTICS OF JACK PINE STANDS

The basal area and the density of jack pine stems varied greatly among the stands (Table I). The basal area ranged from 7.5 to 75.1 m^2 ha^{-1} and the pine density from 1,125 to 3,275 stems ha^{-1}. No jack pine seedling or sapling (a tree smaller than 1.3 m) was found. The mean thickness of the peat deposit differed largely between sites (101-378 cm).

AGE STRUCTURE OF JACK PINE STANDS

All pine stands were less than 80 years old. At Rivière-du-Loup bog, the first jack pines established between 1921 and 1944 (Figure 2). At RDL3, more than 80% of individuals appeared between 1945 and 1949. At

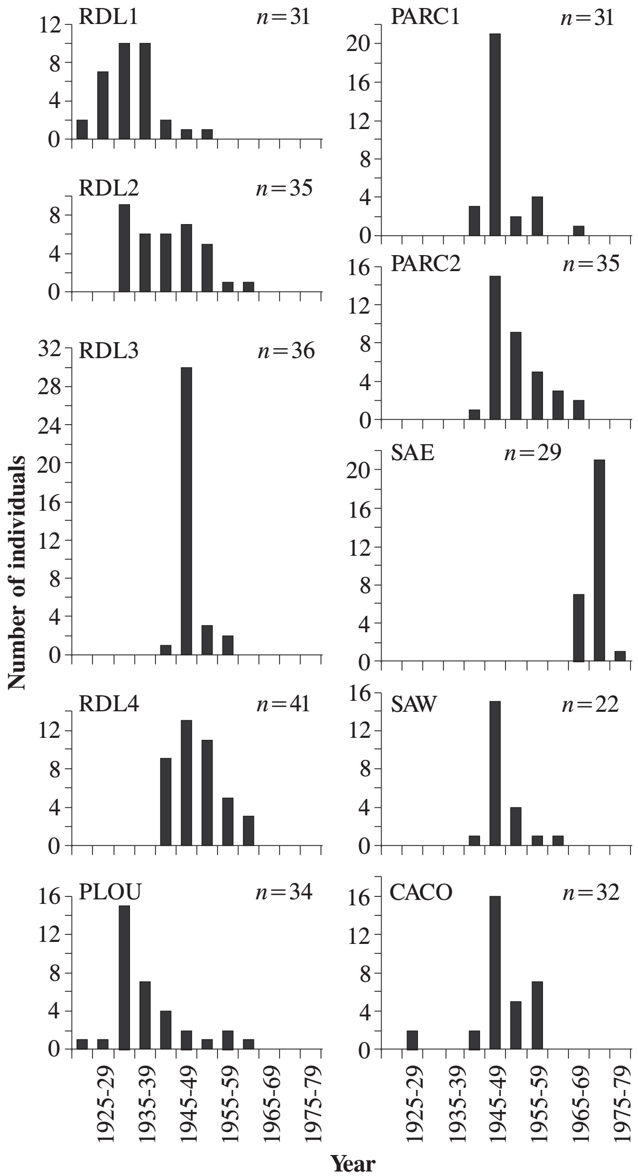


FIGURE 2. Age structure (5-year classes) of jack pine stands in bogs of the Bas-Saint-Laurent region, southeastern Québec. RDL, Rivière-du-Loup; PLOU, Plourde; PARC, Le Parc; SAE, Saint-Arsène East; SAW, Saint-Arsène West; CACO, Cacouna.

PLOU, the first pine established in 1924, followed by a massive recruitment six years later. At Le Parc bog, the first individuals established in 1943 and 1944. In both stands, a massive establishment occurred less than two years later. The SAE stand, where most of the trees established between 1967 and 1974, is the youngest stand. At SAW, while the first tree established in 1943, most individuals established between 1945 and 1949. At CACO, the first pine established in 1927, but most individuals established between 1945 and 1949.

PLANT MACROFOSSIL ANALYSES

Plant macrofossil analyses showed that a similar pattern of vegetation change recently occurred at each study site (Figure 3). Black spruce and especially jack pine macrofossils are much more abundant above than below the most recent charcoal layer: 98.6% of pine macrofossils were recovered above the charcoal layer. At RDL2, RDL3, RDL4, and SAW we found charred needles of jack pine in the most recent charcoal layer, indicating that there was at least one jack pine at those sites when fire events occurred. The sites hold few or no *Sphagnum* remains above the most recent charcoal layer. The decrease of *Sphagnum* macrofossils was not detected at PARC1 because the organic material was too decomposed to allow *Sphagnum* stems to be counted. The forest mosses *Pleurozium schreberi* (RDL2, RDL4, PLOU, PARC1, PARC2, SAW), *Ptilium crista-castrensis* (SAW) and *Rhytidiadelphus triquetrus* (RDL1) were more abundant above than below the most recent charcoal layer. An increase in the number of macrofossils of ericaceous shrub species (*Kalmia angustifolia*, *Ledum groenlandicum*, *Rhododendron canadense*, *Vaccinium angustifolium*) was also found in the postfire environment at most sites. Leatherleaf (*Chamaedaphne calyculata*), a shade-intolerant species (Marie-Victorin, 1995), disappeared in the upper layers of the peat deposits at RDL1, RDL3, PLOU, SAE, and SAW. Interviews indicated that at PLOU and SAW peatlands, the most recent fire occurred around 1930 and 1940, respectively. The cause of the fires was unknown for all but one of the study sites: at SAW it was accidentally ignited by humans.

Peat accumulation at Le Parc bog initiated *ca* 8,890 years BP (Figure 4). Changes in the species composition in the peat profile indicate two main developmental stages. During Stage I, local conditions were minerotrophic, and the peat was mainly composed of remains of Cyperaceae, tamarack (*Larix laricina*), and *Drepanocladus aduncus*. At least three fire events occurred during this stage. The transition between Stage I and Stage II (6,610 years BP) is characterized by an increase of *Sphagnum* remains and a decrease of Cyperaceae and tamarack macrofossils. Local conditions became ombrotrophic. Stage II was subdivided into three substages: Substage IIa, dominated by black spruce and *Sphagnum* remains; Substage IIb, characterized by the scarcity of black spruce remains; and Substage IIc, characterized by a major increase of jack pine, black spruce, and *Pleurozium schreberi* remains, just above the most recent charcoal layer. Although occasionally present in some subsamples of macrofossil substages I, IIa, and IIb, jack pine remains were very rare below the most recent charcoal layer.

CLIMATE HISTORY

While the climate of the La Pocatière area during the last 80 years was characterized by dry and wet periods, no long-term trends in the precipitation record were noticeable (Figure 5). Drier-than-average climatic periods were recorded from 1913 to 1935, in the 1960s, and in the 1980s. Wetter periods occurred around 1940, at the beginning of the 1950s, and during the 1970s. The establishment of jack pine at RDL1, RDL2, PLOU, and SAE occurred during drier climatic periods (1913-1935 and 1960-1970), while at RDL3, RDL4, PARC1, PARC2, SAW, and CACO, the establishment coincided with a wetter climatic period (beginning of 1940s).

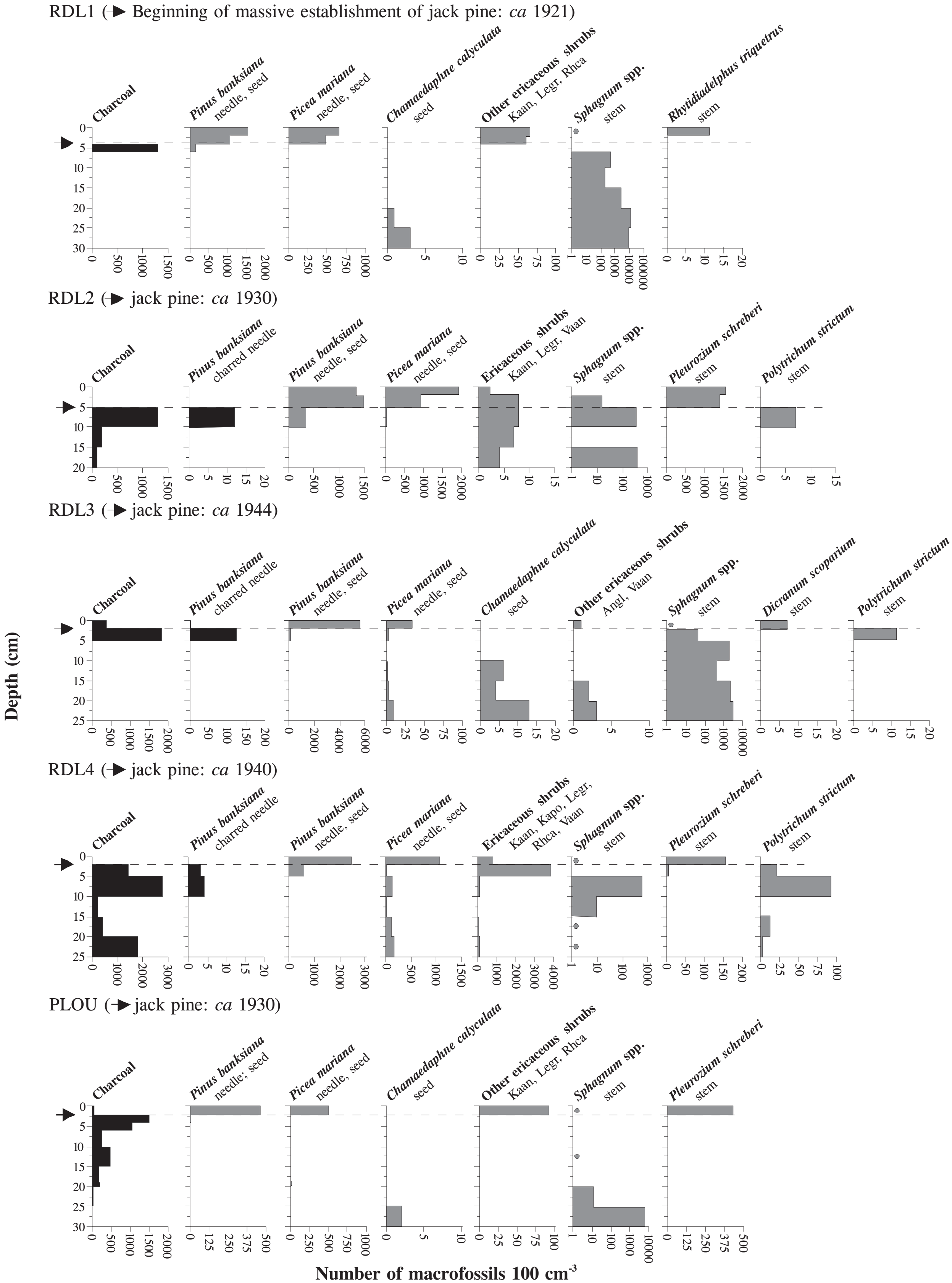
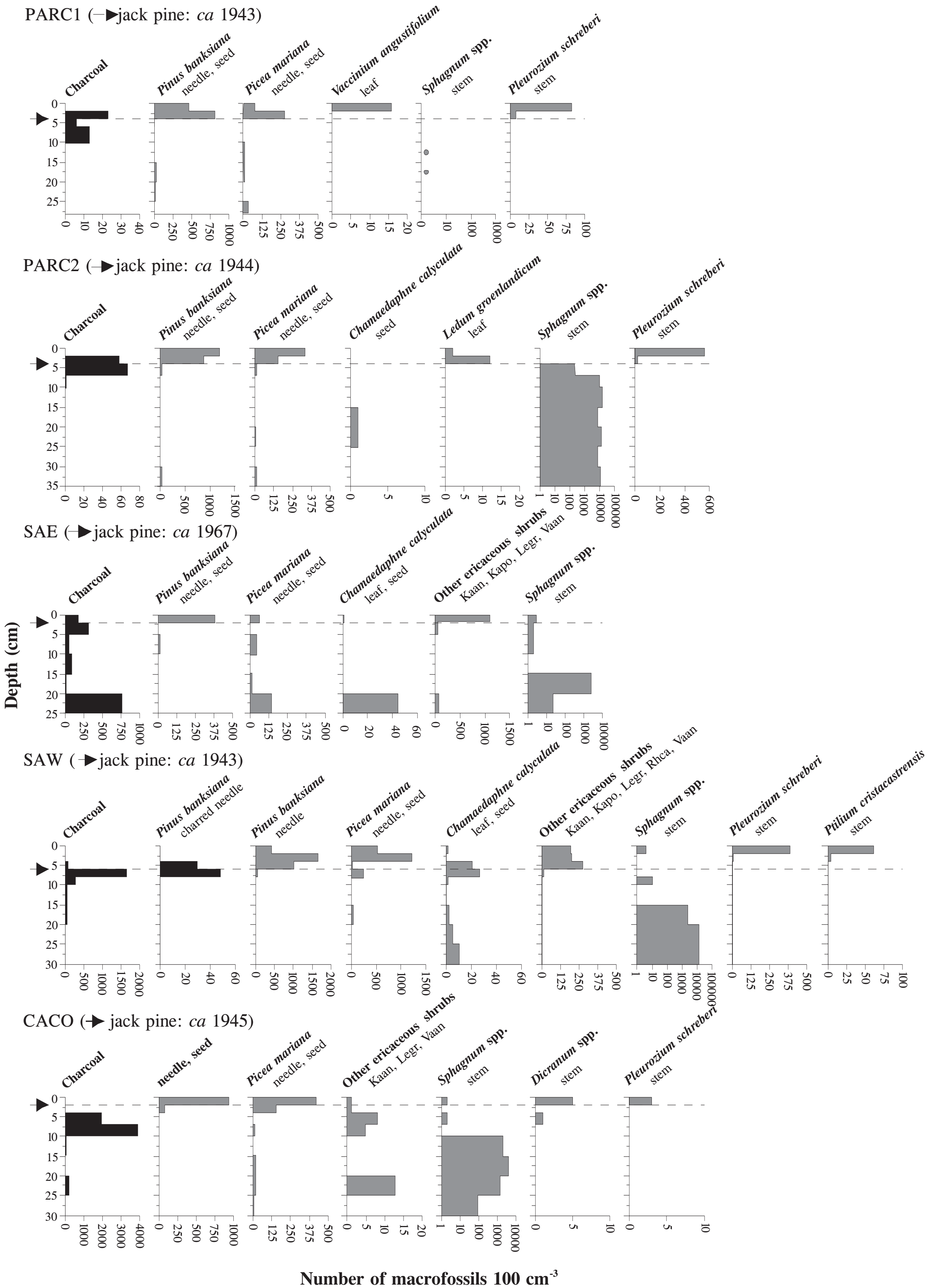


FIGURE 3. Macrofossil diagrams (selected taxa) from jack pine stands in bogs of the Bas-Saint-Laurent region, southeastern Québec. Angl, *Andromeda glaucophylla*; Kaan, *Kalmia angustifolia*; Kapo, *Kalmia polifolia*; Legr, *Ledum groenlandicum*; Vaan, *Vaccinium angustifolium*. Macrofossil pieces: linear scale, except for *Sphagnum* (logarithmic scale); •, one piece only. Arrow and dotted line indicate the beginning of the massive establishment of jack pine during the 20th century. See Figure 2 for site name's code.



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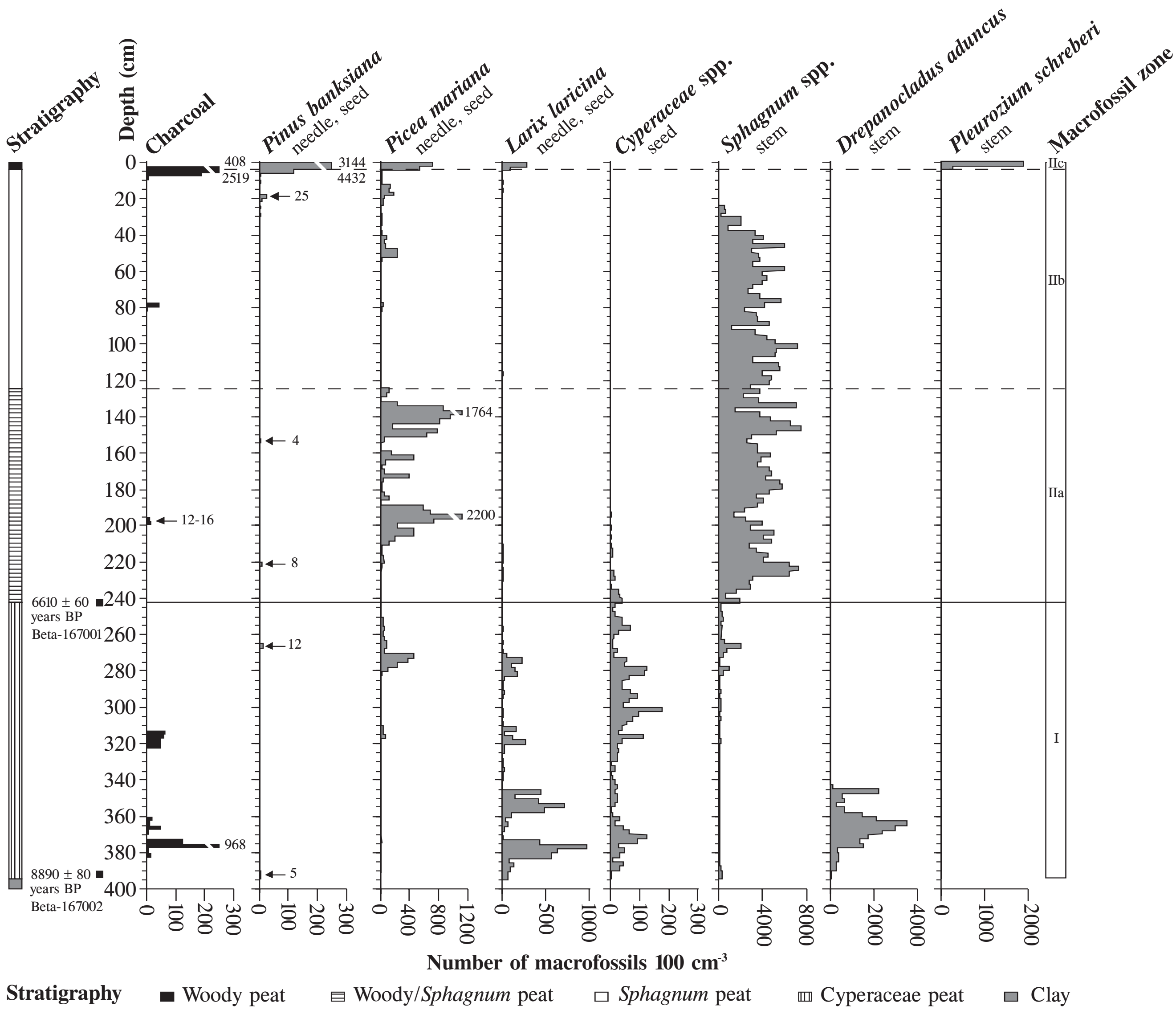

FIGURE 4. Macrofossil diagram (selected taxa) of the Le Parc bog, Bas-Saint-Laurent region, southeastern Québec.

Discussion

JACK PINE STAND CHARACTERISTICS AND ESTABLISHMENT

Compared to other jack pine populations located in the southern (Conkey, Keifer & Lloyd, 1995), central (Béland & Bergeron, 1993), and northern (Desponts & Payette, 1992) part of the species range in eastern North America, the jack pine stands of the Bas-Saint-Laurent peatlands are rather dense with a high basal area. The establishment of large jack pine stands in ombrotrophic peatlands of the Bas-Saint-Laurent region is a recent phenomenon, initiated during the 20th century. Macrofossil and dendrochronological analyses showed that during the last 80 years, and mainly between 1920 and 1945, open peatlands dominated by *Sphagnum* species were invaded by jack pine following the most recent fire event. A close examination of aerial photographs taken in 1929 supports this interpretation, since no evidence of a dense forest cover was detectable at the location of sampling stations. The presence of a dense jack pine stand appears to be a unique event in the *ca* 8,900-year history of the Le Parc bog. However, the presence of charred pine needles in several peat sections indicates that some jack pine individuals were growing in the peatlands when these fires occurred, suggesting that the present-day population originated from seeds released by a few individuals.

CAUSES OF THE RECENT JACK PINE EXPANSION

FIRE

Our macrofossil data indicate that jack pine invaded the bogs following the most recent fire that burned these ecosystems. Several studies have shown that fire has usually few long-term impacts on the vegetation and habitat structure of ombrotrophic peatlands (Damman, 1977; Jasieniuk & Johnson, 1982; Foster & Glaser, 1986; Kuhry, 1994; Lavoie, Zimmermann & Pellerin, 2001). In Canada, the most important change reported in a bog after a fire event is a slight increase in the cover of some mosses (*e.g., Polytrichum strictum*) and ericaceous shrubs (Jasienuk & Johnson, 1982; Foster & Glaser, 1986;

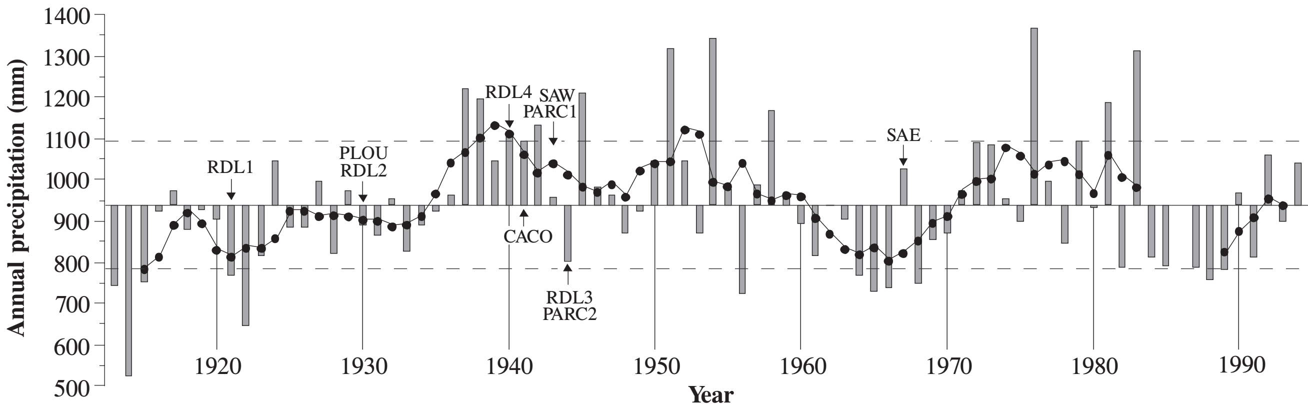

FIGURE 5. Reconstruction of climatic anomalies at La Pocatière meteorological station, southeastern Québec, between 1913 and 1995. Horizontal line: mean value (1913-1995). Dotted lines: standard deviation. Vertical bars: precipitation value. Solid line: five-year running mean. Missing values: 1986. The approximate year of establishment of jack pine stands is indicated by arrows.

Kuhry, 1994). Although fires are not essential to maintain a treeless environment in ombrotrophic peatlands (Klinger, 1996), fires in bogs kill trees, which results in a higher water table favouring the growth of *Sphagnum* mosses (Damman, 1977; Chambers, 1997). Tree seedlings established in a *Sphagnum*-dominated environment have little chance of surviving because they are rapidly overgrown by *Sphagnum* mosses (Gauthier, 1980; Ohlson & Zackrisson, 1992; Gunnarsson & Rydin, 1998, Ohlson *et al.,* 2001). Although fires have certainly accelerated the afforestation process in the Bas-Saint-Laurent peatlands by facilitating the spread of jack pine seeds and preparing a seedbed favourable for seed germination and seedling establishment, it is unlikely that fire alone can explain the recent jack pine expansion. For instance, in the Le Parc bog several fires were recorded during its 8,900-year history, but none, except the most recent one, was followed by a massive establishment of jack pine.

DRAINAGE

In Europe and North America, the recent afforestation of peatlands is often associated with human activities (Jacobson, Almquist-Jacobson & Winne, 1991; Bunting *et al.,* 1998; Frankl & Schmeidl, 2000; Freléchoux *et al.,* 2000). For example, Freléchoux *et al.* (2000) linked the recent development of pinewoods in bogs of the Jura Mountains (Switzerland) to drainage associated with the peat-cutting industry. 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; Silins & Rothwell, 1999). Those changes in edaphic conditions facilitate the survival and the growth of trees in peatlands (Lees, 1972; Lieffers & Rothwell, 1986; Macdonald & Yin, 1999).

Are the Bas-Saint-Laurent peatlands affected by drainage resulting from human activities? There is little doubt that their hydrology has been altered (Van Seters & Price, 2001), since most bogs are either mined or crossed by drainage ditches. However, peat mining activities, which are responsible for the development of drainage ditch networks in most of the bogs studied, started after the beginning of the pine invasion at RDL1, RDL2, RDL4, PARC1, and PARC2. At CACO, the establishment of the pine stand occurred at approximately the same time as the beginning of mining activities, but the drainage ditches present at that time were located far from the stand studied in this paper. Furthermore, the SAW and PLOU sites have never been mined. In 1929 and 1948 (years corresponding to the oldest aerial photographs in the study area), all study sites were located 70 to 500 m from the closest drainage ditch. Since most of the drying effect associated with a drainage ditch occurs within 25 m (Hillman, 1992; Rothwell, Silins & Hillman, 1996; Prévost, Belleau & Plamondon, 1997; Silins & Rothwell, 1999), drainage ditches should have had only a minor impact on the hydrology of the study sites when jack pine established (before 1945 at all sites, except SAE).

CLIMATE

In Europe, Scots pine (*Pinus sylvestris*) colonization in peatlands during the Holocene epoch was ascribed to warmer and/or drier climatic periods (Birks, 1975; Pears, 1975; Bridge, Haggart & Lowe, 1990; Gear & Huntley, 1991; Pilcher *et al.,* 1995). Dry climatic conditions lowered the water table and enabled pine seedlings to colonize peat surfaces. Pine colonization usually stopped after bog-surface moisture increased (Chambers, 1997).

The relationship between pine colonization and climate is unclear in the Bas-Saint-Laurent region. Some stands established during drier periods, while others established during wetter periods. However, it should be noted that eight of the nine pine stands established before 1945, thus during or just after a long climatic period (from *ca* 1913 to 1935) with precipitation lower than average. Furthermore, tree ring counts at ground level usually underestimate the year of establishment of the tree stands due to missing or partially formed growth rings, and because the real tree collars are often buried in the peat or misidentified (DesRochers & Gagnon, 1997; Parent, Morin & Messier, 2000). Consequently, it is likely that the establishment of the five pine stands estimated to have occurred between 1940 and 1944 actually occurred earlier, *i.e.,* during the 1913-1935 climatic period. Additional sampling of 254 trees at Le Parc bog (Lavoie, unpubl. data) revealed that some jack pines are older (1925-1940: cored at breast height) than those sampled in PARC1 and PARC2 quadrats, supporting this assertion.

Although we have no historical data on the hydrology of the Bas-Saint-Laurent peatlands, it is possible that a long-term water input deficit (1913-1935) may have dried the peat surface, thereby simultaneously impeding postfire re-establishment of a thick *Sphagnum* mat and favouring the survival of pine seedlings. While precipitation was only slightly lower than average during most of the 1913-1935 period, even a slight (a few centimetres) lowering of the water table can promote pine colonization in bogs (Frankl & Schmeidl, 2000; Freléchoux *et al.,* 2000). A very dry climatic period would be detrimental to pine survival and growth, because trees growing on organic soils have root systems that are mainly confined to the unsaturated surface peat layers (Lieffers & Rothwell, 1987). A major lowering of the water table exposes trees, especially seedlings, to water stress (Dang & Lieffers, 1989; Malmer, Svensson & Wallén, 1994; Gunnarsson & Rydin, 1998) and negates any benefits generated by low groundwater levels (Pepin, Plamondon & Britel, 2002).

Conclusion

The jack pine expansion in the ombrotrophic peatlands of the Bas-Saint-Laurent region is a recent phenomenon (< 100 years), possibly unique in the last 8,900 years. Fires triggered the expansion by eliminating the *Sphagnum* mat and spreading thousands of pine seeds released by a few individuals. During the last two centuries, fire probably occurred more frequently in the Bas-Saint-Laurent peatlands than during the remainder of the Holocene epoch. Pollen and macrofossil analyses of 17 peatlands located in the study area indicate that at least one fire has occurred at thirteen sites since the beginning of European settlement (*ca* 1800), seven of which occurred after 1900. Fires ignited by humans have burned three Bas-Saint-Laurent bogs since 1992 (Pellerin, unpubl. data). Yet, frequent fires appear to be unusual, since fire intervals calculated for the Bas-Saint-Laurent peatlands range from 760 to 2,500 years (Bois-des-Bel bog: Lavoie, Zimmermann & Pellerin, 2001; Le Parc bog: this study). Therefore, we suggest that recent fires indicate an increasing human influence on peatland ecosystems and have contributed to the emergence of large pine stands.

While fires contributed to the expansion of pines in bogs, this phenomenon may have been facilitated by a drier-than-average climatic period during the first part of the 20th century. This period might have been dry enough to inhibit *Sphagnum* growth and allow the establishment of dense jack pine stands after fire and yet not sufficiently dry to cause water stress on pine seedlings. Whereas other similar climatic periods may have occurred in the Bas-Saint-Laurent region during the Holocene, the rarity of fires would have prevented the establishment of pines. Furthermore, drainage induced by human activities during the last decades has probably further facilitated the growth of pines already established.

The fact that dense jack pine stands are now growing on thick organic deposits indicates that this species has a wider ecological tolerance than previously known and/or that the Bas-Saint-Laurent peatlands have undergone major ecological and hydrological changes favouring the growth of non-bog species. Whatever the causes of the recent expansion of jack pine in the Bas-Saint-Laurent peatlands, this phenomenon is expected to cause profound changes in bog ecosystems, such as altering hydrological conditions and increasing the above-ground accumulation of litter (Ohlson *et al.,* 2001).

Acknowledgements

This research was financially supported (grants to C. Lavoie) 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 fellowships to S. Pellerin. We are grateful to Premier Horticulture for allowing us to work in Rivière-du-Loup and Saint-Arsène peatlands. We thank M. Garneau and C. Roy for their help with macrofossil and moss identification, J. Bussières, N. Hamel, C. Huot, D. Lachance, K. Marcoux, A. Saint-Louis, and C. Zimmermann for field and laboratory assistance and D. Arseneault, R. Anderson, C. Carcaillet, M. Lavoie, L. Sirois, and an anonymous reviewer for comments on an earlier draft.

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