

Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce–moss forest

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Abstract: The lichen woodland is one of the most important forest ecosystems in North America, dominating the central part of the boreal forest. The southernmost lichen woodland is paradoxically in the heart of the southern boreal forest. This distribution prompted this study aiming to identify the factors responsible for the inception and development of the lichen woodland at its southern range limit in eastern Canada. We tested the hypothesis that the southern lichen–spruce woodland is a regressive, post-fire type of the spruce–moss forest. We studied adjacent lichen–spruce and spruce–moss stands growing under similar soil conditions. We reconstructed the recent history of spruce–moss forest transformation to lichen woodland using tree size, tree ring patterns, and macrofossil analysis of organic soil. All the plant macrofossils buried in the unburned organic mat below the charcoal layer of the last fire corresponded to a feather-moss forest assemblage and included head capsules of the spruce budworm (*Choristoneura fumiferana* (Clem.)) or European spruce sawfly (*Gilpinia hercyniae* Hartig.). The impact of combined insect and fire disturbances translates into a dramatic decrease in post-fire tree regeneration of the forest inducing the shift to lichen woodland. The inception of the southern lichen woodland highlights the fragility of the spruce–moss forest even in the core area of the southern commercial boreal forest.

Résumé : La pessière à lichens est une des plus importantes formations végétales d'Amérique du Nord, qui occupe la partie centrale et septentrionale de la forêt boréale. La limite méridionale de la pessière à lichens se situe au coeur de la forêt boréale commerciale. Nous avons testé l'hypothèse voulant que la pessière à lichens méridionale provienne de la régression post-incendiaire de la pessière à mousses. Nous avons sélectionné des pessières à lichens et des pessières à mousses poussant côte à côte, sous des conditions édaphiques similaires. Nous avons procédé à une analyse rétrospective afin de reconstituer les événements responsables de la transformation de la pessière à mousses en pessière à lichens. Les assemblages macrofossiles des sédiments organiques localisés sous la couche de charbons de bois montrent que la forêt pré-incendiaire était, dans les trois cas étudiés, une pessière à mousses. Les macrorestes étaient représentés principalement par des mousses hypnacées et des fragments d'épinette noire, ainsi que des capsules céphaliques de la tordeuse des bourgeons de l'épinette ou du diprion européen de l'épinette. La transformation de la pessière à mousses en pessière à lichens semble attribuable à l'incidence de deux perturbations en rafale, c'est-à-dire le passage d'un feu dans une pessière à mousses affectée par une infestation d'insectes défoliateurs. Nos données soulignent la fragilité écosystémique de la pessière à mousses, au coeur même de la forêt boréale commerciale.

Introduction

The lichen woodland is one of the most widespread forest ecosystems in North America (Hare 1959; Hare and Ritchie 1972; Larsen 1980; Rowe 1972, 1984; Payette 1992) covering approximately 1×10^6 km². It is predominantly distributed across the Canadian Precambrian Shield, with only sporadic occurrences westward in Alaska (Christiansen 1988; Viereck et al. 1992). The structure of the lichen woodland is rather simple with two dominant strata, i.e., sparse trees (mainly black spruce (*Picea mariana* (Mill.) BSP) several metres apart (generally 10–40% cover) and large expanses of fruticose lichens of the genus *Cladonia* and

Cladonia in eastern Canada (Payette 1992) and *Stereocaulon* in western Canada (Johnson 1981; Rowe 1984), interspersed by ericoid shrubs (*Vaccinium*, *Kalmia*, *Ledum*) and dwarf birch (*Betula glandulosa* Michx.) (Johnson and Rowe 1975; Maikawa and Kershaw 1976; Bradley et al. 1982; Morneau and Payette 1989). The lichen woodland is the zonal vegetation filling the central part of the boreal forest biome, north and south of the closed-crown spruce forest and the forest tundra, respectively (Hare 1950, 1959; Hare and Ritchie 1972; Rowe 1972; Payette 1992). The lichen woodland is a typical nutrient-poor forest thriving on acidic, well-drained, moraine-derived soils and granitic outcrops (Clayden and Bouchard 1983; Moore 1980, 1981; Rowe 1984; Payette 1992) composed of post-fire seral communities (Maikawa and Kershaw 1976; Johnson 1981; Auclair 1983; Rowe 1984; Payette and Morneau 1993) tightly tuned to a recurrent pattern of fire activity at the site scale.

Rowe (1984) briefly reviewed current hypotheses explaining the open structure of the North American lichen woodland,

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including radiation deficits (Vowinckel et al. 1975), nutrient deficits (Moore 1981), low soil temperature (Hustich 1951; Lucarotti 1976), allelopathic effects (Brown and Mikola 1974; Cowles 1982), and fire disturbance (Maikawa and Kershaw 1976; Kershaw 1977) promoting tree regeneration mostly at the time of the burn (Morneau and Payette 1989; Riverin and Gagnon 1996). Whether the lichen woodland zone consists of a shifting mosaic of all-aged, self-perpetuating open stands because of repetitive fire remains unknown, at least for several parts of the boreal forest. According to Maikawa and Kershaw (1976) and Kershaw (1977, 1978), the open structure of the lichen woodland results from low post-fire tree regeneration, and without fire disturbance it will undergo stand succession to closed-crown forest. Alternatively, another hypothesis considers the lichen woodland of the forest-tundra as a self-perpetuating open forest, with a relatively stable, low tree density even in a fire-free environment (Payette and Morneau 1993). The varying distribution of the lichen woodland, occupying a large array of landforms in the central part of the boreal forest and also northward in the forest tundra (Payette and Morneau 1993) and southward in the spruce-moss forest (Lambert and Maycock 1968; Clayden and Bouchard 1983; Payette 1992; Riverin and Gagnon 1996), suggests that its inception and long-term development are likely triggered by one or several independent factors causing the same poor tree regeneration.

At its southern range limit, the lichen woodland forms discrete, open forest patches within the closed-crown spruce-moss forest (Payette 1992; Bergeron 1996; Riverin and Gagnon 1996; Sirois 1996). The woodland patches are predominantly located on coarse and dry podzolic soils of low nutrient status and are considered edaphic climax (Lambert and Maycock 1968). The fate of the southern lichen woodland seems to be closely associated with recurrent fires, exacerbated by dry and mesic deposits on which they are growing today. Another viewpoint is to consider the southernmost lichen woodland as a regressive forest type of the spruce-moss forest resulting from deleterious fires significantly reducing post-fire tree regeneration (Payette 1992). Whether the southern lichen woodland is a cold, fire-induced forest ecosystem like the northern lichen woodland has been so far open to debate. Is the southern lichen woodland the last "subarctic" forest to develop azonally within the matrix of closed-crown, feather-moss forests? This is unlikely when one considers that the southern lichen woodland is growing in the same sites and at the same altitude as the spruce-moss forest within the "warm" boreal forest zone (with an annual temperature averaging 0°C). Consequently, temperature deficits and other cold-related factors may be questioned as primary controlling factors. Indeed, the functioning of the northernmost and southernmost lichen woodlands, at both ends of the broad boreal forest spectrum, are probably initiated and maintained by different environmental factors.

In this paper our objective is to identify the factors responsible for the inception of the lichen woodland at its southern range limit within the spruce-moss forest of the southern boreal forest zone. Asking the question of the azonal position of the southern lichen woodland readily provides the answer of the inception of this forest as a natural process of shifting forest canopies and associated understory vegetation, presently occurring under modern site condi-

tions. To meet this objective we have looked at the spatial coexistence of the contrasting lichen woodland and closed-crown forest stands growing under similar soil conditions, throughout the vegetation mosaic of the southern boreal forest zone. Three sites showing the spatial coexistence of both forest types were selected and analyzed in detail for the identification of the likely causal factors of shifting forest ecosystems. We used a retrospective analysis of the adjacent open and closed stands including population size and age, tree ring patterns, and macrofossil analysis of the organic soil horizons developed prior to and after the last fire to have occurred at each site. We have hypothesized that the shifting of spruce-moss forest to lichen woodland is initiated by catastrophic disturbances, based on the assumption (Payette 1992) that the southern lichen woodland is a regressive type of the spruce-moss forest induced by complex fire-mediated factors.

Study area

The southernmost lichen woodland stands in eastern Canada are located in the Parc des Grands-Jardins (PGJ), on the Charlevoix Highlands, 120 km northeast of Québec, near the transition to the mixed forest (Bergeron 1996). The PGJ (mean altitude of 600–800 m asl) is adjacent to the Réserve faunique des Laurentides (RFL), which forms an elevated plateau to the west and the northwest (mean altitude of 800–900 m asl, with several summits >1000 m) with abundant precipitation (>1500 mm/year). The massive RFL captures air humidity coming from westerly cyclonic air masses passing over the highlands, thus creating a large rain-shadow, which causes drier weather conditions to the east in the PGJ area (1000 mm/year). As a result, both areas are welded in a complex climatic (moisture) gradient at the regional scale with corresponding forest communities and ecological regimes (Payette 1997). Although at a higher altitude, the moist RFL area harbors dense spruce-moss forests favourable to logging operations, while the drier PGJ area is a mosaic of closed-crown forests and open forests less suited for tree harvesting. At a mean altitude of 700–800 m, lichen woodland stands are occupying the driest sites, particularly on fluvio-glacial deposits of the Malbaie River watershed, but also mesic, glacial-drift sites in close association with spruce-moss stands. The mean annual temperatures of both areas are similar at around 0°C (PGJ) and –0.5°C (RFL); the warmest month (July) in PGJ and RFL averages 14–15°C (Boisclair 1990). In the RFL area, white birch (*Betula papyrifera* Marsh.) – balsam fir (*Abies balsamea* (L.) Mill.) stands colonize mesic sites at an altitude <800 m, while balsam fir – black spruce forests occupy similar sites at an altitude >800 m (Grandtner 1966). The main disturbance factors affecting RFL forests are logging and spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks. Fire is apparently one of the most important disturbance factor in the PGJ area, although logging was conspicuous before the creation of the park in 1981. During this century, 80 km² of forest has burned, i.e., 26% of the total area of PGJ (310 km²), including 64 km² of closed-crown forests and 16 km² of lichen woodland stands (Payette 1997). The total area occupied by lichen woodland stands in PGJ is about 28 km². Based on an extensive field survey supplemented by an interpretation of air photos taken in 1950, 1964, 1981, and 1996, respectively, about 5 km² of spruce-moss forest reverted to lichen woodland during the same period.

Methods

Three different sites showing the spatial coexistence of lichen woodland and spruce-moss forest on well-drained podzolic soils

were selected for this study: the Lac Carré site (LC site), the Lac à la Bouillie site (LB site), and the Lac à l'Empêche site (LL site), situated at the edge of PGJ. The three sites were affected by a fire during this century: in 1939 at LC (fire-scar dated, this study), 1918 at LB (fire-scar dated, this study), and 1915 at LL (fire-scar dated, Dion 1986). The LC site was studied in greater detail than the two other sites, which were used as additional examples showing the process of forest reversion.

The LC site is located just north of Lac Carré (47°42'30"N, 70°48'W, 760 m asl) on the southern and eastern sides of a mesic, deep moraine-covered hill. It is occupied by two contrasting black spruce forests growing on the same soil surface: a spruce–moss forest located outside the burned area, and a lichen woodland regenerated after the 1939 fire. A 2500-m² quadrat (125 m × 20 m) was positioned at random along the 1939 fire line and included both unburned vegetation (20% of the quadrat surface: spruce–moss forest) and burned vegetation (80% of the quadrat surface: 74% of lichen woodland surrounding an untouched patch of the spruce–moss forest). The vegetation cover of both forests was surveyed using the line-intercept method (Mueller-Dombois and Ellenberg 1974); in each forest 20 lines 1 m long were used for the recording of plant species, with the first line being chosen at random and the others positioned in a systematic fashion at 1-m intervals. Each plant species touching the line was recorded in 10 cm long segments, totalling 10 segments per line. Thus, the survey in each forest was based on 200 measurements used for the calculation of species relative frequency averaged from the 200 segments.

In the lichen woodland, all adult trees, saplings, seedlings, and layers (>5 cm diameter at root collar) were mapped, using an infrared theodolite (Leica T1010, 0.0005-m precision). Because of the dense tree cover in the spruce–moss forest, mapping was done with a metric tape using the coordinates of a grid of small plots. The diameter at stem base was measured for all individuals. Tree height was evaluated with the theodolite when the stem apex was visible from the eight stations used; otherwise, it was measured with a telescopic perch (0.5-cm precision). All black spruce clones were delineated and mapped, and layers <5 cm diameter at root collar were recorded. The nature of the seedbed (mineral soil or organic horizon) of 55 stems (i.e., the largest stems based on basal diameter) established in the burned part of the quadrat was identified from the position of the root collar.

All trees >5 cm diameter at 30 cm above the ground were cored at this level with a Pressler probe, and smaller stems were sectioned at the root collar. Tree-ring cores (one core per tree) were processed at the laboratory, fixed on wood frames, finely sanded, and dated. Annual ring widths were measured under a binocular microscope at 40× with a Velmex micrometer (±0.002 mm) interfaced with a computer to record the data. Individual cores were cross-dated using skeleton plots and checked with the COFECHA program (Holmes 1983) to ensure proper dating of the samples. Indexed black spruce series were built to detrend tree growth according to age. The ring-width series were standardized with a horizontal line fit corresponding to mean ring width. Because the influence of insect defoliators was suspected and identified elsewhere in PGJ (M. Simard, in preparation), we used a low-pass filter (9 years) to remove the yearly variations (high frequency) from the black spruce chronologies based on 19 trees in the spruce–moss forest and 5 surviving trees in the lichen woodland to eliminate the yearly growth variations likely obscuring the influence of insect defoliations (Swetnam et al. 1985). A jack pine (*Pinus banksiana* Lamb.) chronology was also built from 21 trees (50 radii) sampled in three different post-fire sites (fire age ranging from 76 years to more than 100 years) of the PGJ. Jack pine was used as a non-host tree species relative to spruce budworm infestations likely damaging black spruce trees of the PGJ. Most sampled trees were selected at random from a mixed jack pine – black spruce stand established after fire in 1921. The oldest sampled trees were

the largest jack pine growing in a lichen–spruce woodland established after a fire during the 19th century. Individual cores were cross-dated with the same procedure used for black spruce. The indexed chronology was constructed using an exponential fit for old jack pine series and a straight curve with a negative slope for younger jack pine series. A low-pass filter (9 years) was also applied to the jack pine chronology for a comparison with the black spruce chronologies.

All the stems and trunks burned during the 1939 fire were exhumed, mapped (using the infrared theodolite), and measured for stem length (based on the mapped stem tips) and stem base width. Wood fragments were removed from each burned stem for species identification of balsam fir and spruce, in particular, using anatomical characters of the xylem (Panshin and de Zeeuw 1980). However, no microscopic analysis of the wood samples was done to distinguish spruce from eastern larch (*Larix laricina* (Du Roi) K. Koch). According to the general growth form of the burned stems, we assumed that eastern larch was rare in the site before 1939.

We measured the thickness of the organic horizon in the lichen woodland, on both sides of the charcoal layer associated with the 1939 fire, along a 125-m transect parallel to the quadrat at an interval of 1.25 m ($n = 68$ measurements). Moreover, along the same transect, at 6-m intervals, 18 soil cores (10 cm × 10 cm × 8.5 cm on average) from the surface to the uppermost mineral horizon, were used for macrofossil analysis. A 1 cm thick slice of the organic layer on both sides of the charcoal layer (made of all-sized charcoal fragments) was examined in all the cores for species identification of plant and insect remains. Also, two soil cores were analyzed in more detail, using contiguous slices 0.5 cm thick on each side of the charcoal layer, from the Ae horizon to the surface, to study the stratigraphy of insect remains in finer resolution. A 12 m long soil trench crossing the spruce–moss forest – lichen woodland border and divided in two equal parts (6 m long each) was also used for macrofossil, stratigraphical, and pedological purposes. Plant and insect macrofossils were sampled every 1 m using contiguous 1-cm slices from the base to the top of the organic horizon. The processing of soil cores and sorting, extraction, and identification of macrofossils were done according to Bhiry and Filion (1996a). The volume of each sample (60–100 cm³) was measured by water displacement. The preparation included a known volume of organic material boiled for 3 min in a water solution with a few drops of 5% NaOH added and then washed gently with water in sieves of 2.0, 1.0, 0.5, and 0.25 mesh, respectively. When necessary, a few drops of HCl were added to lighten macrofossils and facilitate the identification of plant remains. The macrofossils were picked out, identified, and counted using a stereomicroscope at 4× and 40×. Mosses were identified under a compound microscope at 40× and 1000×. Comparisons of fossil insect head capsules were made with modern larvae using scanning electron microphotography. In each sample, macrofossils (plants and insects) were converted to numbers per 100 cm³. Soils were described in the field following guidelines of the Canadian Soil Survey Committee (1978). Samples of Ae and B horizons of the unburned spruce–moss forest and the post-fire lichen woodland at each site (LC, LB, LL) were extracted for analytical procedures in the laboratory (sieving and sedimentation tube). Twelve samples were analyzed for grain size and parameters (mean, standard deviation, skewness, kurtosis) were calculated using particle sizing systems (PSS) according to the method of statistical moments (Syvitski 1991).

The sampling scheme at LB site was roughly similar to that at LC site. The site (47°43'10"N, 70°56'30"W, 800 m asl) is a well-drained, moraine-covered hill burned in 1918. Two contrasting black spruce forests are currently growing on the same soil surface, i.e., a spruce–moss forest established both inside and outside the burned area and a lichen–moss woodland that established itself after the 1918 fire. A 2400-m² (30 m × 80 m) quadrat was positioned at random and included the burned and unburned spruce–moss

Table 1. Relative frequency (%) of plant species at the Lac Carré site.

Species	Spruce–moss forest (%)	Lichen woodland (%)
<i>Kalmia angustifolia</i>	21.9	23.0
<i>Ledum groenlandicum</i>	23.4	12.7
<i>Vaccinium angustifolium</i>	8.6	12.8
<i>Lycopodium sabinaefolium</i>		0.7
<i>Lycopodium complanatum</i>		1.2
<i>Limnaea borealis</i>	0.3	
<i>Geocaulon lividum</i>		0.1
<i>Amelanchier</i> sp.		0.4
<i>Chiogenes hispidula</i>	0.4	
<i>Melampyrum lineare</i>		0.1
<i>Salix humilis</i>	0.6	0.7
<i>Picea mariana</i>	5.0	
<i>Cladina mitis</i>		13.2
<i>Cladina stellaris</i>		4.1
<i>Cladina rangiferina</i>	0.7	19.4
<i>Cladonia crispata</i>		0.4
<i>Cladonia gonecha</i>		0.3
<i>Cladonia uncialis</i>		0.9
<i>Peltigera canina</i>		0.4
<i>Pleurozium schreberi</i>	22.2	8.6
<i>Dicranum</i> sp.	4.8	0.9
<i>Ptilidium ciliare</i>	6.2	
<i>Ptilium crista-castrensis</i>	0.4	
<i>Hylocomium splendens</i>	1.3	
<i>Sphagnum girgensohnii</i>	3.0	
<i>Sphagnum nemoreum</i>	0.9	

forest (27% of the quadrat surface) and the post-fire lichen–moss woodland (73% of the quadrat surface). We used the same techniques as in LC site for determining the size and age structures of the lichen–moss woodland. An indexed tree-ring curve was built using 15 trees that survived the 1918 fire at the edge of the burned area. Mapping and measurement of tree stems of the prefire stand were not possible, because they were too decomposed. The thickness of the organic horizon on both sides of the 1918 charcoal layer in the burned part of the quadrat was measured at 10-m intervals along a 100-m transect ($n = 20$). Macrofossils were recovered from 1 cm thick organic samples above and below the 1918 charcoal layer, using six soil cores (10 cm \times 10 cm) taken at 10-m intervals along the transect within the lichen–moss woodland.

The southernmost lichen woodland is at LL site (47°42'30"N, 70°36'20"W, 780 m asl), where it occurs along with a spruce–moss forest growing on well-drained, fluvio-glacial deposits. In the lichen woodland, most stems of the pre-fire stand, i.e., before 1915, were completely decomposed. Therefore, only macrofossil data were considered in the analysis based on the sampling of nine organic soil cores (10 cm \times 10 cm) as in LB site, i.e., six cores in the lichen woodland. In each core, 1 cm thick organic samples on both sides of the 1915 charcoal layer were analyzed. The thickness of the organic horizon on both sides of the 1915 charcoal layer was measured at 10-m intervals along a 100-m transect ($n = 24$).

Results

Soil conditions

Well-drained podzolic soils developed on morainic and fluvio-glacial deposits in both unburned and burned areas of

the three sites. Each soil profile consisted of normal podzolic sequences of LFH, Ae, B, and C horizons. The average solum thickness varied between 20–40 cm (LC, LL) and 40–50 cm (LB). Ae horizons are composed of 10–20% gravel, 70–75% sand, and 10–15% silt (<63), and B horizons consisted of 20–25% gravel, 65–70% sand, and 5–15% silt. Grain-size parameters indicate similar Ae and B textural characteristics among all soils of the three sites. The mean textural class varied between 1.47 and 2.60 corresponding to weakly sorted fine to medium sand. The soil texture of Ae and B horizons display a bimodal mixture of medium to fine sand with gravel.

LC site

The vegetation of LC site is dominated by fruticose lichens and ericoid shrubs in the lichen woodland and by several moss and shrub species in the spruce–moss forest (Table 1). In the lichen woodland, the dominant lichen species are *Cladina rangiferina*, *Cladina mitis*, and *Cladina stellaris*. Among the shrub species, *Kalmia angustifolia*, *Vaccinium angustifolium*, and *Ledum groenlandicum* Oed. are prominent. Dwarf birch was not observed at the site, although this species is widespread in most lichen woodlands stands of PGJ. *Pleurozium schreberi* forms small circular carpets in the lichen woodland, particularly near the base of trees and around spruce clones. In the spruce–moss stand, this species is clearly dominating, accompanied by other forest mosses (*Hylocomium splendens*, *Dicranum* and *Ptilium crista-castrensis*) and the liverwort, *Ptilidium ciliare*. The only fruticose lichen distributed throughout the forest floor is *Cladina rangiferina* forming scattered, small clumps. *Ledum groenlandicum*, *K. angustifolia*, and *V. angustifolium* are the main understory shrubs.

Stand structure

The difference in number and distribution of all surveyed tree stems in the burned part of the quadrat, at the time of sampling (1997) and after the 1939 fire, is striking (Figs. 1a–1c). In 1939, there were at least 194 mature trees (937 stems/ha), whereas only 63 adult trees (304 stems/ha) were recorded in 1997, a drop of 67% of the initial stock (Table 2). A more dramatic reduction (84%) was observed for basal area, from 45 m² in 1939 to 7.3 m² in 1997. According to wood anatomy and stem growth forms, all the trees burned in 1939 were apparently black spruce. The number of adult stems and basal area of the burned forest in 1939 are less than that of the unburned spruce–moss forest in 1997 (Table 2), a difference likely attributable to the absence of smaller stems not recorded in the survey of the 1939 stand.

The size structure of the 1939 forest is significantly different from that of the post-fire stand ($D_{0.05}$, Kolmogorov–Smirnov (K–S) test), with a mean diameter at the collar of 16.2 and 11.4 cm, respectively (Fig. 2a). Larger trees were growing on the site before the fire, and the number of large trees was relatively high. Size distribution suggests that the 1939 forest was an old-growth stand (inverse-J trend, stems <10 cm went probably unnoticed because of greater decay of small-sized stems) that regenerated from fire several hundred years ago. Tree height in the 1939 and 1997 stands is significantly different ($D_{0.05}$, K–S test), in particular for the lowest class

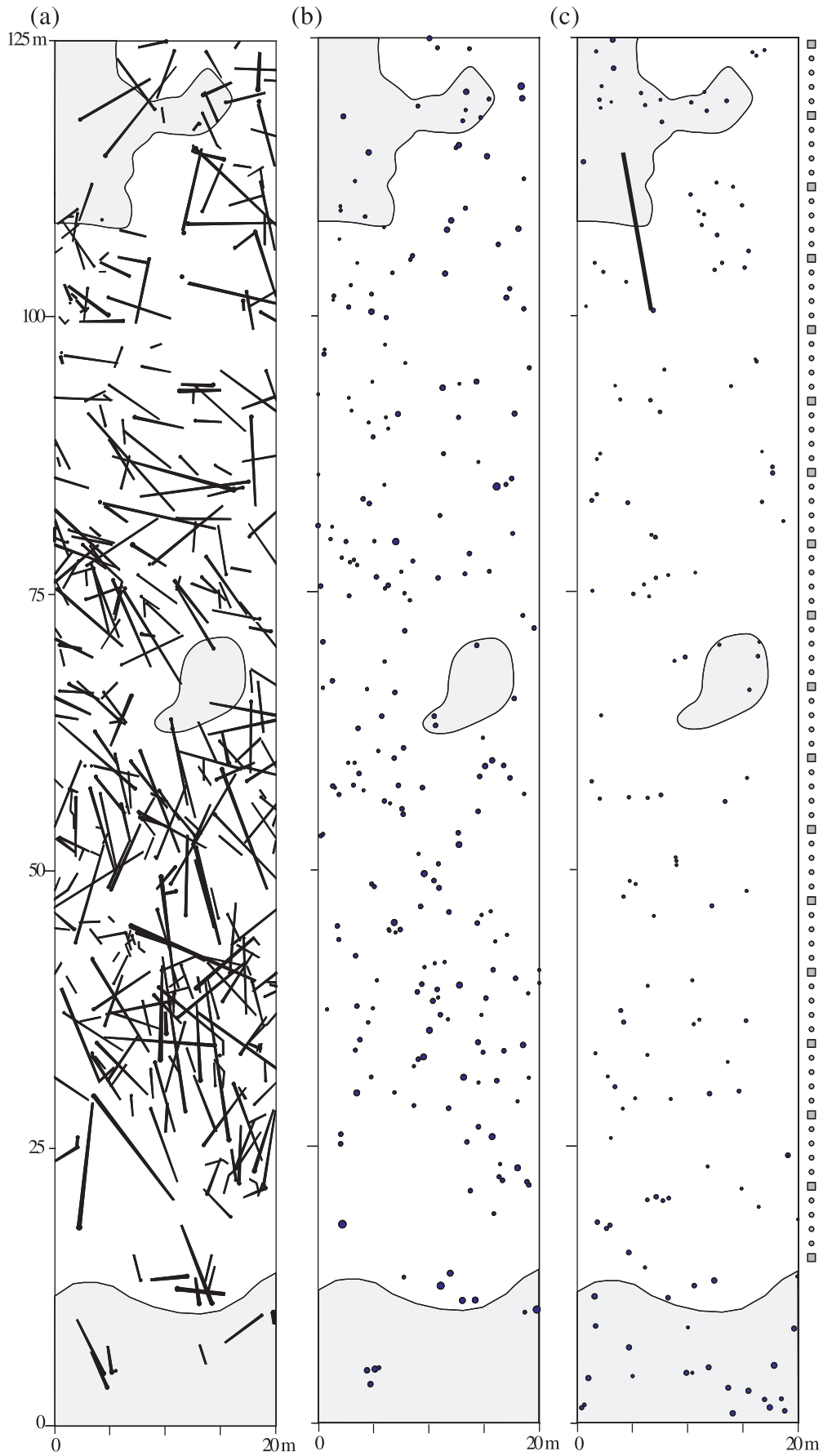
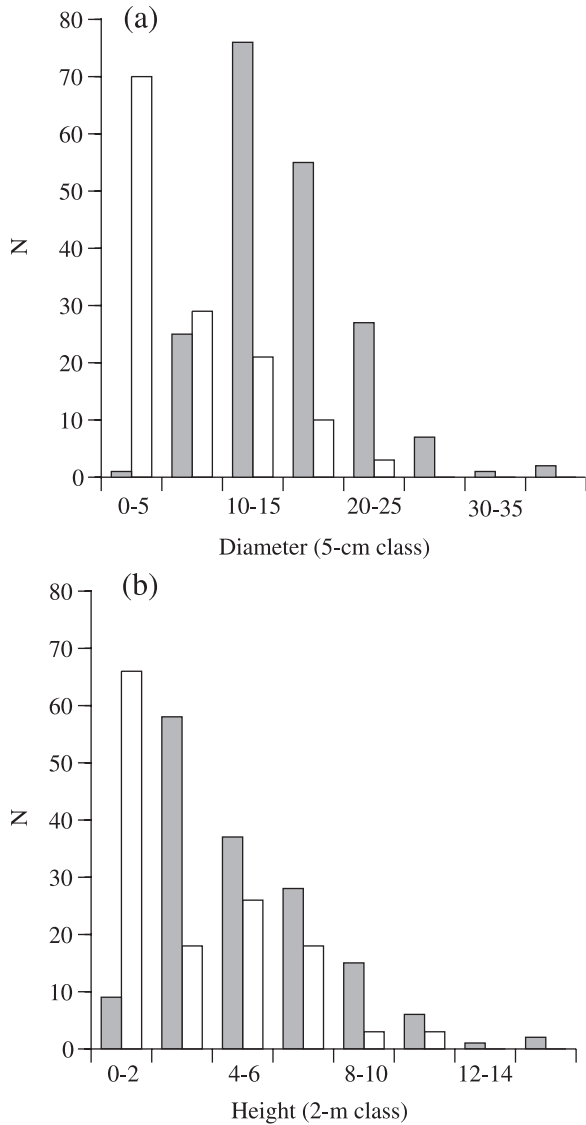


Fig. 1. The Lac Carré quadrat (125 m × 20 m). Shaded, unburned area; open, burned area. (a) Distribution and length of tree stems burned during the 1939 fire. (b) Position of all tree stems burned during the 1939 fire. Dot size corresponds to size of basal stem diameter (not to scale). (c) Position of all tree stems regenerated after the 1939 fire. Dot size corresponds to size of basal stem diameter (not at scale). Solid stripe, soil trench. Shaded squares outside the quadrat correspond to soil cores sampled at 6-m intervals.

Fig. 2. Size structure of forest trees burned in 1939 (shaded bar) and the post-fire lichen woodland (open bar) (a) Basal stem diameter distribution. (b) Stem height distribution.



of the 1939 stand (Fig. 2b). Trees at least 15 m high were growing in the 1939 stand. Both distributions of tree height and tree diameter in the 1997 stand are roughly similar, which suggests a common relationship with tree age.

The post-fire regeneration window of black spruce covered the entire period since 1939 (Fig. 3, grey bars). Five-year classes were used to plot the age data, because ring counts were made at 30 cm above the ground for all trees >5 cm diameter at the root collar. This is based on the time lapse deduced from the regression between age at sampling height and age at the root collar (real age), i.e., 8 ± 2 years

Fig. 3. Post-fire seedling establishment at the Lac Carré site (shaded bar) and the Lac à la Bouillie site (open bar).

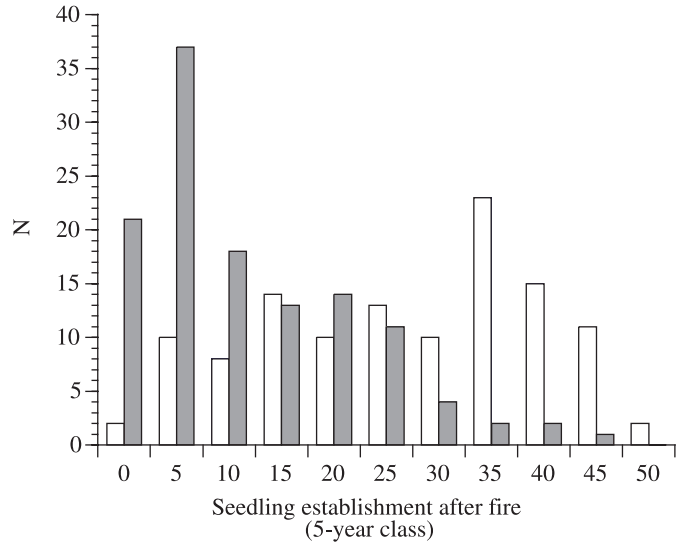


Table 2. Number and basal area of tree stems in the burned (1939) and unburned (1997) areas of the Lac Carré site.

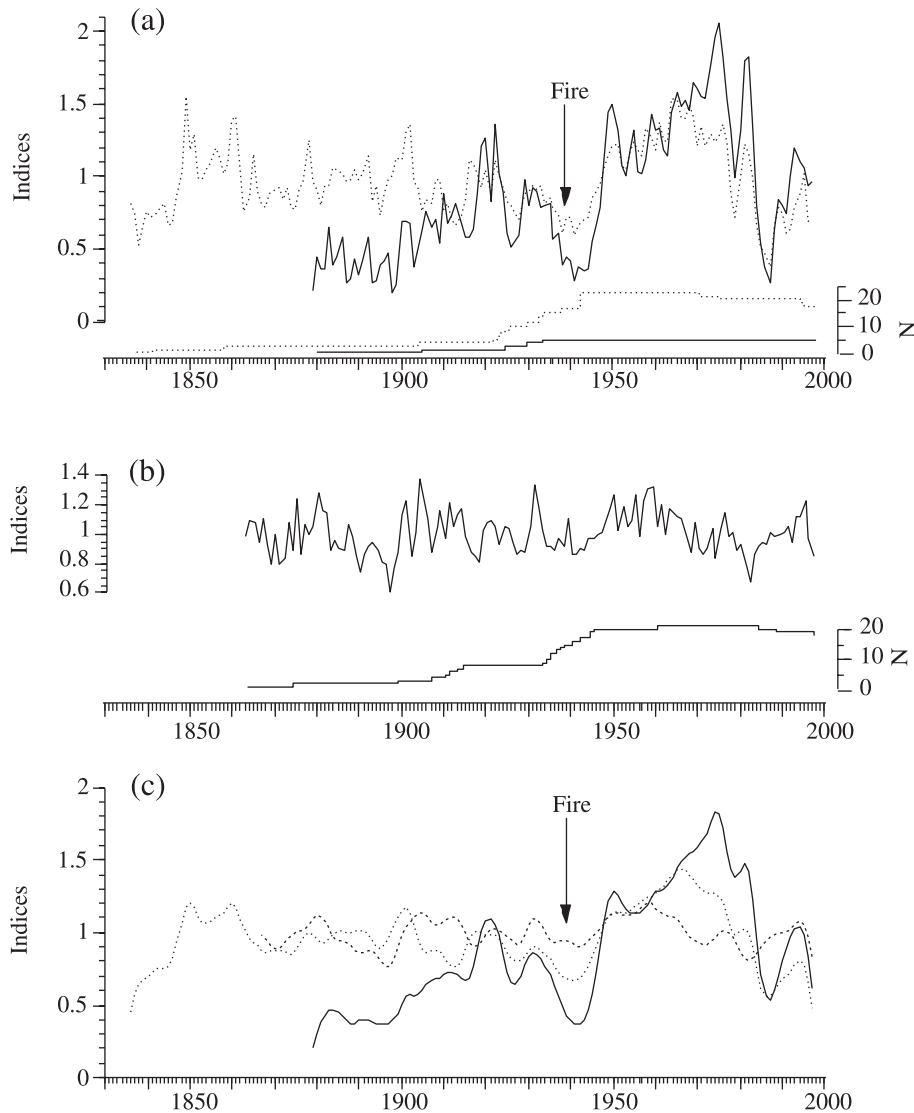
	Burned area	Unburned area
Trees 1939	194	—
Basal area (m ²)	44.90	—
Mean distance (m)	3.87	—
Stems/ha	937	—
Trees 1997 (>5 cm)	63	55
Basal area (m ²)	7.26	15.79
Mean distance (m)	5.45	—
Stems/ha	304	1279
Layers (>5 cm)	51	178
Basal area (m ²)	2.64	11.87
Area (m ²)	2070	430

(mean ± SD). The dating of basal stems <5 cm diameter at the root collar provided an accurate age, because the sections were taken above the first root at the junction with the collar. Among the 55 selected stems growing either on mineral or organic seedbeds, the oldest spruce established preferentially on mineral soil, whereas younger spruce were on organic seedbeds (chi-square, $p = 0.0065$).

Tree-ring series

The two black spruce tree-ring series from the spruce–moss forest and the lichen woodland (Fig. 4a) show similar short-term (high-frequency) variations and are significantly correlated ($r = 0.653$, $p < 0.01$). Both series include one

Fig. 4. (a) Indexed tree-ring series of black spruce at the Lac Carré site. (b) Indexed tree-ring series of jack pine in the Parc des Grands-Jardins. (c) Filtered tree-ring series of black spruce at the Lac Carré site and jack pine in the Parc des Grands-Jardins. Solid line, spruce surviving until the 1939 fire; dotted line, spruce from the unburned area; broken line, jack pine. In Figs. 4a and 4b, the number of sampled cores is indicated below the tree-ring curves.



minor but significant decline in the 1920s and two major growth declines during the late 1930s – early 1940s and in the mid-1980s (index = 0.5), following a short but sharp drop in 1978 and 1979. The growth trend before 1920 cannot be documented properly because of the small number of tree-ring cores. Overall, the major growth trends of the two filtered tree-ring series are similar with coincident highs and lows. The 1939 fire occurred during a period of growth depression. The jack pine tree-ring chronology is rather complacent with only two short growth reductions in the 1890s and early 1980s (Fig. 4b). Although of low amplitude, jack pine growth trend is coincident with that of black spruce during several parts of this century, for instance between the 1920s and the 1960s and in the 1990s (Fig. 4c).

Macrofossil analysis

Soil cores: The mean thickness of the organic horizons above (2.3 ± 2.6 cm) and beneath (6.3 ± 3.6 cm) the 1939

charcoal layer are quite different. According to the position of both burned and post-fire shoots of the dominant shrubs (*Kalmia*, *Ledum*, and *Vaccinium*) and thickness of the organic horizon below the charcoal layer, the 1939 fire was not severe, scorching superficially the top of the ground vegetation. At several sampling sites, the dense lichen carpet rests directly on the 1939 charcoal layer.

In all the 18 soil cores, plant macrofossils buried in the organic horizon (1-cm slice) below the 1939 charcoal layer are dominated by bryophytes (mostly *Pleurozium* and *Ptilidium ciliare*) and black spruce. No lichen remains were recorded. Eastern larch needles were identified in two cores (Table 3). This plant assemblage contrasts with the macrofossils located just above the charcoal layer where mosses were recorded in four cores among which only one core (LC30) was from the lichen woodland. Also, black spruce remains are less abundant, and larch needles were identified in only one core. The formation of the thin organic horizon

above the charcoal layer is probably due to the scarcity of mosses and dominance of lichens, which do not produce a thick mat.

Because three categories of black spruce needles were identified in the soil cores, i.e., normal-size, small-size, and egg-scarred needles, we compared the size and surface of small- and normal-size needles above and below the charcoal layer and on one living tree using 100 needles selected at random in each case. Needles from the living tree and above the charcoal layer were similar in size (needles from living tree: 6.37 ± 1.98 mm long, 1.11 ± 0.24 mm wide, 9.59 ± 2.24 mm² area vs. needles above the charcoal layer: 6.16 ± 1.41 mm long, 1.27 ± 0.30 mm wide, 9.60 ± 2.82 mm²), whereas needles from the small-size category below the charcoal layer were considerably smaller (4.17 ± 1.28 mm long, 0.79 ± 0.27 mm wide, 4.09 ± 1.83 mm²). Compared with needles above the charcoal layer (88% normal needles vs. 12% small needles), a greater number of small-size needles relative to normal-size needles was counted in 15 of the 18 samples below the charcoal layer (25% normal needles vs. 75% small needles) (Table 4). Also, 5–20% of all the needles in the organic slice below the charcoal layer were egg-scarred needles. Several well-preserved head capsules of the spruce budworm and scattered head capsules of the European spruce sawfly (*Gilpinia hercyniae* Hartig.) and a fairly large number of head capsule fragments were recorded below the charcoal layer in all the 18 cores. Egg-scarred needles at this level likely corresponded to oviposition sites of the European spruce sawfly. Similarly, a large proportion of small-size needles may be associated with spruce budworm activity.

Soil trench: Nine organic horizons along the soil trench were analyzed in more detail from the base to the top, using a continuous sequence of 1-cm slices (Fig. 5). Three (Nos. 13, 18, and 22) of the nine samples were from the unburned spruce–moss forest. The shift from a spruce–moss assemblage to a spruce–lichen assemblage associated with the burn is apparent and similar to that observed in the previous soil cores. Spruce needles are more concentrated near the charcoal layer, whereas moss remains extend well below towards the base of the organic horizons. The continuous sequence at each sampling site provides a finer picture of plant–insect co-occurrences. Indeed, all the samples below the charcoal layer show the same pattern of association between small-sized needles and egg-scarred needles with head capsules of the spruce budworm and the European spruce sawfly. In the unburned part of the soil trench the stratigraphical position of the 1939 fire is clearly outlined by a layer of head capsules of the spruce budworm and the European spruce sawfly. Above the stratigraphical position of the 1939 event, another layer of head capsules is apparent. Scattered head capsules of both insects are also present deeper in the soil well below the 1939 layer.

Macrofossil remains of insect defoliators extracted from the organic soils below and above the 1939 charcoal layer likely coincide with the major growth depressions depicted in the two tree-ring series. In addition, we selected two soil cores among the 18 soil cores (Table 4) of the transect for a finer resolution analysis of insect remains using contiguous 0.5-cm slices, from the base to the top of the organic horizon

(Table 5). Egg-scarred needles are associated with the rare head capsules of the European spruce sawfly just below the charcoal layer, whereas most small-size needles co-occur with head capsules of the spruce budworm at some distance below the charcoal layer. Fragments of head capsules recorded in practically all the sampled slices also suggest a continuous occupation of the site by unknown insect defoliators, although both spruce budworm and spruce sawfly are the likely candidates according to their stratigraphical position.

LB site

Stand structure

The size structure of the post-fire stand is similar to that of the unburned stand (Fig. 6). Balsam fir and eastern larch occur only as seedlings or saplings in the burned area, whereas adult trees of both species are present in the unburned part of the quadrat. Given the sampled area, the basal area and number of trees per hectare are 50% less in the lichen–moss stand than in the spruce–moss stand (Table 6).

As in LC site, the post-fire regeneration window of black spruce spanned a long period since the fire of 1918 (Fig. 3, open bars). Five-year classes were also used to plot the age data. The average difference between age at sampling height (30 cm) and age at the root collar was 8 ± 4 years. Basal stems <5 cm diameter at the root collar were dated accurately with the wood sections being sampled just above the first root near the collar.

Tree-ring series

A tree-ring series was constructed using spruce trees of the unburned spruce–moss forest (Fig. 7a). The series shows several major growth declines, i.e., during the 1910s, the late 1930s to the mid-1940s, and in the mid-1980s, following a sharp drop in 1978 and 1979; a short but abrupt drop occurred in the early 1950s. A sustained declining growth trend, apparent from the mid-19th century to the early 20th century and climaxing in the 1910s, was likely caused by suppressed growth conditions. The 1918 fire occurred during a period of growth depression, which was characterized by several incomplete rings in the studied wood sections in the years just preceding the fire event. The jack pine series also shows a minor growth reduction at this time (Fig. 7b) but slightly delayed relative to black spruce as shown in the two filtered series (Fig. 7c).

Macrofossil analysis

The organic horizons above (8.0 ± 4.3 cm) and below (9.5 ± 3.9 cm) the 1918 charcoal layer are thicker than in LC site because of moister conditions associated with the geographical position of LB site at the westernmost limit of lichen woodland near the RFL. As in LB site, burned and post-fire shoots of the dominant shrubs (*Kalmia* and *Ledum*) and thickness of the organic horizon below the charcoal layer suggest that the 1918 fire was not severe. Lichens and mosses rest directly on the 1918 charcoal layer.

In the six soil cores analyzed, plant macrofossils buried in the organic horizon (1-cm thick) below the 1918 charcoal layer are dominated by mosses and liverworts (mostly *Pleurozium* and *Ptilidium*) and black spruce (Table 3). This plant assemblage contrasts with the macrofossils located just above the charcoal layer where mosses and black spruce

Table 3. Number of plant macrofossils above and below the charcoal line in soil cores from the Lac Carré, Lac à la Bouillie, and Lac à l'Empêche sites.

	1 cm above charcoal line								1 cm below charcoal line			
	Spruce remains				Mosses				Spruce remains			
	Cones	Scales	Seeds	Needles	<i>Larix laricina</i>	<i>Pleurozium schreberi</i>	<i>Polytrichum</i> sp.	Others	Cones	Scales	Seeds	Needles
Lac Carré												
LC1	—	—	—	—	—	—	—	—	—	2	—	18
LC5	—	—	—	—	—	—	—	—	1	3	1	25
LC10	—	1	—	7	—	—	—	—	—	5	2	23
LC15	—	—	—	13	10	—	—	—	—	2	1	45
LC20	—	1	—	17	—	—	—	—	1	3	—	39
LC25	—	1	—	11	—	—	—	—	—	2	2	43
LC30	—	—	—	8	—	62	—	—	—	3	1	55
LC35	—	—	—	5	—	—	—	—	—	—	—	15
LC40	—	—	—	14	—	—	—	—	—	3	—	29
LC45	—	—	—	11	—	—	—	—	—	—	2	19
LC50	—	—	—	—	—	—	—	—	—	2	—	23
LC55	—	—	—	24	—	—	—	—	—	—	—	36
LC60	—	3	1	34	—	—	—	—	1	7	3	45
LC65	—	—	—	—	—	—	—	—	—	—	2	37
LC70	—	—	—	—	—	—	—	—	—	—	—	24
LC75	—	4	1	43	—	—	—	—	—	3	1	54
LC80	—	—	—	—	—	—	—	—	—	1	1	38
LC85	—	—	—	—	—	—	—	—	—	1	1	57
Lac à la Bouillie												
LB13	—	—	—	9	—	20	—	—	1	5	4	17
LB17	—	—	1	6	—	15	—	—	1	4	2	13
LB21	—	2	—	5	—	16	—	1	—	7	2	11
LB25	—	—	1	4	—	14	2	—	—	5	3	17
LB29	—	—	—	6	—	13	3	—	1	4	1	15
LB 33	—	—	1	9	—	26	1	1	—	6	3	21
Lac à l'Empêche												
LL 1	—	—	—	2	—	2	—	—	—	2	—	4
LL 5	—	3	—	3	—	—	—	—	—	1	1	6
LL 9	—	—	1	2	—	2	—	—	1	—	—	12
LL 13	—	2	—	3	—	—	—	—	2	1	—	14
LL 17	—	—	—	—	—	—	—	—	—	1	1	15
LL 21	—	—	—	1	—	1	—	—	—	3	1	10

*Plants at the ground surface in decreasing order of abundance from 1 to 5 and p (presence); l, lichens; k, *Kalmia angustifolia*; v, *Vaccinium angustifolium*; ld, *Ledum groenlandicum*; ps, *Pleurozium schreberi*; s, *Salix humilis*; e, *Picea mariana*; py, *Polytrichum* sp.; m, moss.

remains are less abundant. Compared with needles above the charcoal layer (97% normal needles vs. 3% small needles), small-size needles below the charcoal layer are conspicuous in most cores with the same proportion as in LC site (23% normal needles vs. 77% small needles) (Table 4). Also, egg-scarred needles are far less abundant in LB site, with one and three needles recorded in two cores, respectively. Several head capsules of the spruce budworm and a fairly large number of head capsule fragments were recorded below and above the charcoal layer.

LL site

Thickness of the organic horizons above (3.7 ± 1.7 cm) and below (5.6 ± 2.6 cm) the 1915 charcoal layer is similar to that of LC site. As in the other sites, burned and post-fire shoots of the dominant shrubs (*Kalmia* and *Ledum*) and

thickness of the organic horizon below the charcoal layer suggest that the 1915 fire was not severe. Lichens grow directly on the 1915 charcoal layer.

In the six soil cores examined, the organic layer below the 1915 charcoal layer is more decomposed than that of LC and LB sites. However, relatively well-preserved plant macrofossils were recorded in the organic horizon (1 cm thick) below the 1915 charcoal layer, again dominated by mosses (mostly *Pleurozium* and *Dicranum*) and black spruce fragments (Table 3). The macrofossil assemblage is different from that above the charcoal layer, where mosses and black spruce remains are less conspicuous. Compared with needles above the charcoal layer (90% normal needles vs. 10% small needles), small-size needles below the charcoal layer are in greater number than normal-size needles, having the largest proportion among the three studied sites (13% normal needles

Table 3 (concluded).

1 cm below charcoal line							Present vegetation*					
<i>Larix laricina</i>	Mosses and liverworts						1	2	3	4	5	p
	<i>Pleurozium schreberi</i>	<i>Polytrichum</i> sp.	<i>Ptilidium ciliare</i>	<i>Dicranum polysetum</i>	<i>Dicranum undulatum</i>	Others						
—	64	—	—	—	—	7	l	k				
—	50	—	12	—	—	—	l	k	m			
—	11	—	—	—	—	—	l					
55	4	—	1	—	—	—	k	m	l	ld	v	
13	—	—	—	—	—	—	k	l				v
—	13	1	3	—	—	—	l	k				
—	90	—	49	—	—	—	m	l	k			v
—	—	—	—	—	—	—	l	k				v
—	9	—	—	—	—	1	l	m	k			ld
—	—	—	—	—	—	—	l	v	k			ld
—	—	—	—	—	—	—	l	m	s	v	ld	ld
—	—	—	—	—	—	—	l	v				
—	12	1	6	—	—	—	l	m	k	v		
—	—	—	—	—	—	—	l	v	e			k
—	—	—	—	—	—	—	l	v	k			
—	—	—	—	—	—	—	e	l	k			
—	4	1	1	—	—	—	l	v	k			
—	21	—	10	—	—	—	l	m	k			v
—	13	—	12	—	—	—	e	ps	py			
—	65	2	35	—	—	4	l	ps	ld			
—	31	—	11	—	—	—	ld	l	ps			
—	45	3	19	—	—	3	ps	l	ld			
—	29	—	24	—	—	6	l	ld				
—	32	—	22	—	—	—	l	ps	ld			
—	15	—	—	3	1	—	l	ps	ld	k	e	
—	21	—	—	2	—	—	py	k				
—	14	—	—	—	—	—	l	ps	k			
—	19	1	—	5	—	—	l	ps	k			
—	17	—	—	2	1	—	ps	l	k	ox		
—	8	—	—	3	—	—	ps	pt	k	e		

vs. 87% small needles) (Table 4). No egg-scarred needles were found in any of the organic samples below and above the charcoal layer. Only head capsules of the spruce budworm were identified below the charcoal layer, along with a large number of head capsule fragments.

Discussion

In this study, we have used complementary ecological and paleoecological techniques, such as tree population, tree-ring, and macrofossil data, to document the inception of the southern lichen woodland. The three sites studied are genuine, young lichen woodlands derived from the degradation of mature spruce–moss stands caused by allogenic disturbances (insect outbreaks and forest fires) common to the bo-

real biota and damaging the forest trees in a systematic fashion during a short time period.

According to stand (LC site) and macrofossil data, the three sites were formerly spruce–moss stands, until fire decimated the three forests in 1915, 1918, and 1939, respectively. At the time of the burn, the black spruce stands were affected by insect defoliators, i.e., the spruce budworm with the European spruce sawfly co-occurring at least at one of the three sites. During the 20th century, three major outbreaks of the spruce budworm have been reported in the nearby RFL area, i.e., in the 1910s, 1940s, and 1970s, respectively (Blais 1983). The finding of head capsules of the spruce budworm associated with numerous small-size needles just below the 1915 charcoal layer at LL site outlines the combined, negative impact of the 1910s' outbreak of this species and fire (Table 4). A similar finding at LB site also showed the

Table 4. Number of spruce needles and head capsules of spruce budworm and European spruce sawfly above (first value) and below (second value) the charcoal layer in soil cores from the Lac Carré, Lac à la Bouillie, and Lake à l'Empêche sites.

Sample No.	Spruce needles			Head capsules		
	Normal	Small	Egg scarred	<i>Gilpinia hercyniae</i>	<i>Choristoneura fumiferana</i>	Fragments
Lac Carré						
LC 1	0/7	0/8	0/3	—	1/7	10/15
LC 5	0/16	0/6	0/3	—	0/6	12/7
LC10	6/15	1/7	0/1	0/1	0/8	7/6
LC 15	10/11	3/31	0/3	—	0/5	14/11
LC 20	12/2	4/33	1/4	0/1	1/4	12/13
LC 25	11/3	0/35	0/5	—	0/7	17/25
LC 30	7/4	1/39	0/12	—	1/7	80/17
LC 35	4/2	1/12	0/1	—	1/8	11/12
LC 40	12/4	2/23	0/2	0/1	0/7	12/14
LC 45	11/1	0/16	0/2	—	0/5	16/21
LC 50	0/4	0/16	0/3	—	1/9	11/15
LC 55	21/12	2/20	1/4	—	0/8	13/14
LC 60	30/6	3/36	1/3	—	0/5	14/21
LC 65	0/5	0/29	0/3	0/1	0/4	20/19
LC 70	0/4	0/17	0/3	0/1	0/4	21/17
LC 75	41/10	2/39	0/5	—	1/7	9/11
LC 80	0/23	0/10	0/5	—	1/7	7/12
LC 85	0/29	0/21	0/7	—	0/4	17/21
Lac à la Bouillie						
LB13	9/2	0/14	0/1	—	0/2	9/11
LB17	6/3	0/10	—	—	0/2	15/13
LB21	5/2	0/9	—	—	1/3	11/12
LB25	3/2	1/15	0/3	—	0/1	13/15
LB29	6/6	0/9	—	—	0/2	17/13
LB 33	9/6	0/14	—	—	1/3	12/11
Lac à l'Empêche						
LL 1	2/0	0/4	—	—	—	13/15
LL 5	3/1	0/5	—	—	0/2	15/11
LL 9	2/2	0/10	—	—	0/1	8/12
LL 13	2/2	1/12	—	—	—	11/13
LL 17	0/1	0/14	—	—	1/2	9/11
LL 21	1/2	0/8	—	—	—	15/17

presence of another insect defoliator, the spruce sawfly, as evidenced by four egg-scarred needles below the 1918 charcoal layer, during the first major spruce budworm outbreak across the RFL area of this century (Blais 1983). The tree-ring series at this site also recorded the outbreak and another infestation of this species in the mid-1940s. The last infestation at this site dates back to 1978 and 1979, then interrupted until 1984–1985 when it lasted for 4 or 5 years (Figs. 4 and 7; M. Simard, in preparation). Furthermore, the co-occurrence of head capsules of the spruce budworm and small spruce needles in the organic soil above the charcoal layer in LB and LL sites are probably contemporaneous with the last outbreaks of the 1940s and 1980s.

The most detailed evidence for a shift of the spruce–moss forest to the lichen woodland comes from LC site, where the remains of the burned trees leaning on the lichen-covered ground clearly indicate the former presence of a dense forest. According to size data, the forest was an old-growth stand most favourable to insect attacks (Bauce et al. 1994).

The co-occurrences of the spruce budworm and the European spruce sawfly in the organic beds below the 1939 charcoal layer is interesting in the context of the spruce budworm outbreaks identified during this century in the RFL area (Blais 1983) and in the nearby Lac Saint-Jean area (Morin and Laprise 1990; Morin 1994). When fire occurred at this site in 1939, a major European spruce sawfly infestation was already in action in the PGJ area (Department of Agriculture 1939; Gobeil 1939; Lambert and Genest 1940; Lambert 1941), whereas no spruce budworm infestation was yet reported for this period, except the one recorded after the fire event in the mid-1940s (Blais 1983; Morin and Laprise 1990; Morin 1994). Because of this suite of infestation events, it was then necessary to sort out the respective influence of the European spruce sawfly and the spruce budworm on the forest. That is why we analyzed in more detail two soil cores with contiguous 0.5-cm organic slices (Table 5). Although the spruce budworm was present in the site during the 1939 fire, it is likely that it had reached an infestation

Fig. 5. Distribution and abundance of plant and insect macrofossils along the soil trench at Lac Carré site. Number above the soil trench in Fig. 5a and the macrofossil diagram in Fig. 5b refer to sampling cores. (a) Distribution and depth of organic (shaded to solid) and mineral (Ae and B) horizons and boulders (hatched). (b) Distribution of macrofossils according to depth of organic horizons. Black bar: spruce needles. Shaded bar: leaves and leafy stems of bryophytes. Broken line shows the 1939 charcoal layer. Asterisks show head capsules of the spruce budworm. Solid circles show head capsules of the European spruce sawfly.

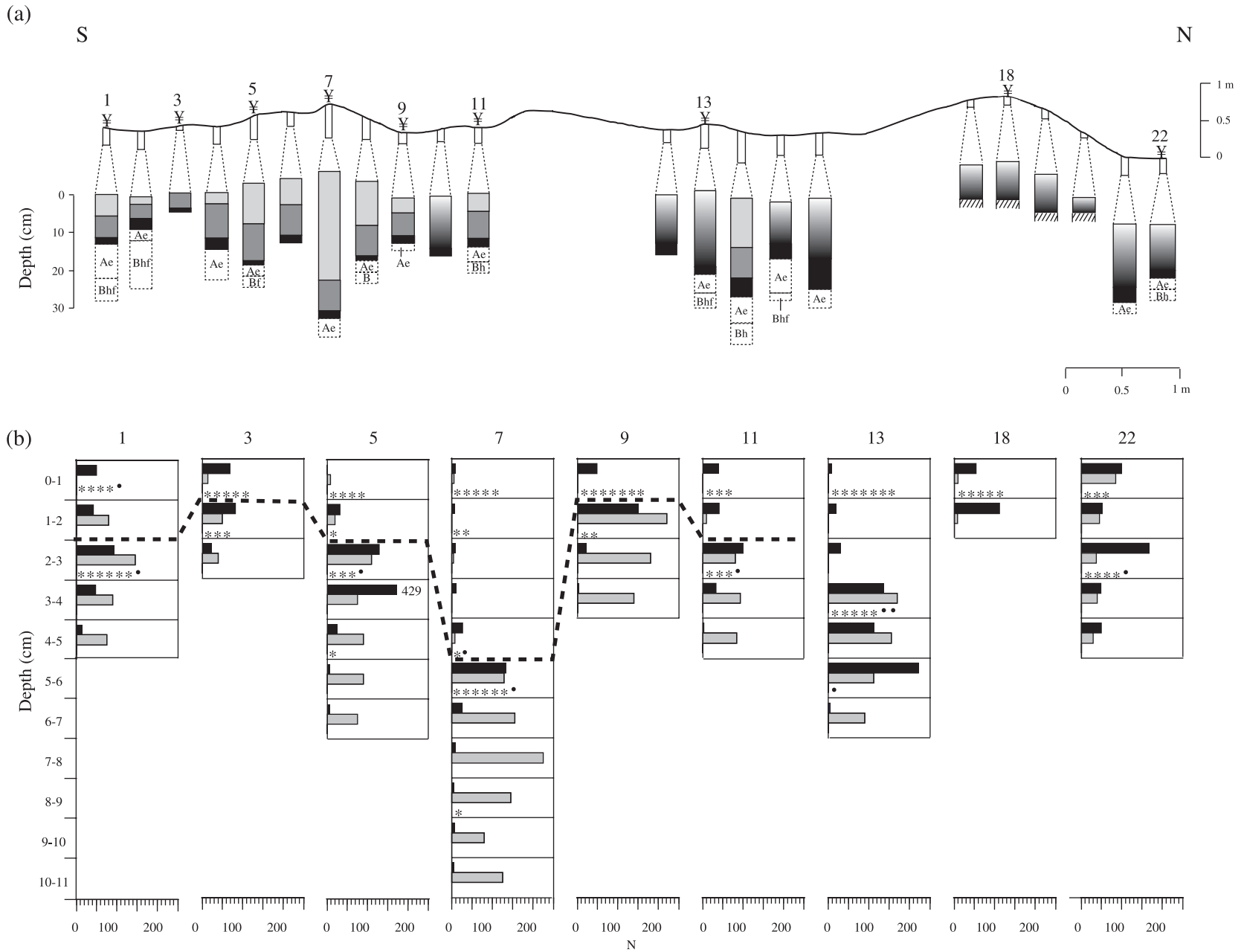


Table 5. Number of spruce needles and head capsules of spruce budworm and European spruce sawfly in contiguous 0.5-cm organic slices in cores 2 and 37 from the Lac Carré site.

(A) LC2 sample (total depth 5 cm)						
Depth (cm)	Spruce (needles)			Head capsules		
	Normal	Small	Egg scarred	<i>Gilpinia hercyniae</i>	<i>Choristoneura fumiferana</i>	Fragments
0–0.5	5	4	0	0	7	10
0.5–1.0	13	4	1	0	0	9
1939 charcoal line						
1.0–1.5	6	5	17	1	0	12
1.5–2.0	7	13	5	0	1	10
2.0–2.5	3	19	2	0	5	11
2.5–3.0	7	2	0	0	0	7
3.5–4.0	9	0	0	0	1	13
4.0–4.5	8	1	0	0	0	9
4.5–5.0	Charcoal – mineral soil					
(B) LC37 sample (total depth 4.5 cm)						
Depth (cm)	Spruce (needles)			Head capsules		
	Normal	Small	Egg scarred	<i>Gilpinia hercyniae</i>	<i>Choristoneura fumiferana</i>	Fragments
0–0.5	7	3	0	0	4	10
1939 charcoal line						
0.5–1.0	4	11	17	0	1	9
1.0–1.5	7	14	5	1	0	12
1.5–2.0	4	17	1	0	1	10
2.0–2.5	2	9	1	0	3	11
2.5–3.0	7	1	0	0	0	7
3.5–4.0	5	2	0	0	0	
4.0–4.5	3	0	0	0	0	9
4.5–5.0	Charcoal–mineral soil					

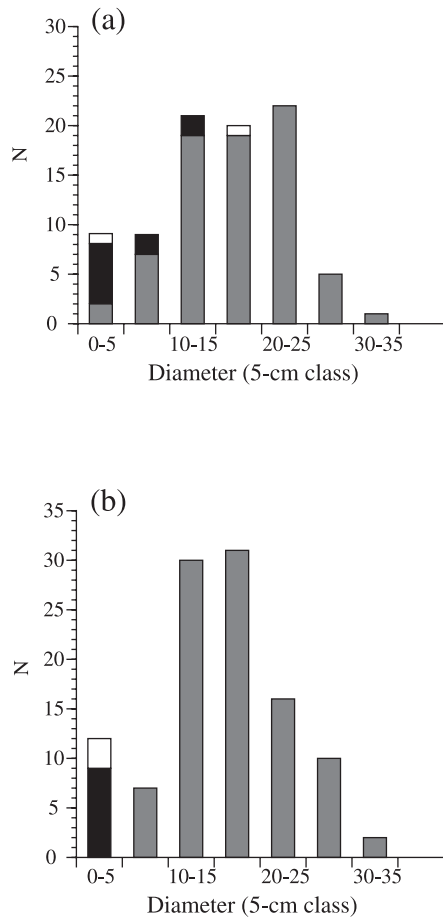
level earlier than that of the European spruce sawfly in the late 1930s (see also the insect surveys of Department of Agriculture 1939; Gobeil 1939; Lambert and Genest 1940; Lambert 1941). Accordingly, it is probable that the forest was first damaged by a spruce budworm infestation in the 1920s (as deduced from depressed growth in the tree-ring series (Fig. 4) or even earlier. As a result, the European spruce sawfly may have invaded the site and damaged the forest, which was already suffering from a recent budworm attack.

The double impact of insect and fire disturbances on the spruce–moss forest resulted in heavily reduced post-fire tree regeneration, as shown for LC and LB sites. At the time of the burn, the insect-damaged spruce trees likely had few viable seeds, thus explaining the lower recruitment. Schooley (1980) reported that virtually all flowers of black spruce are eaten by the spruce budworm even when this species is at a low population density. The heavy feeding on the reproductive buds is apparently due to the fact that black spruce needles and vegetative buds are less favourable food sites. In addition, as observed in spruce stands damaged by the recent spruce budworm infestation (middle to late 1980s) in the PGJ, other insect species are currently preying on cones and seeds of standing, dead, and moribund tree stems, thus reducing dramatically the seed pool and the regeneration potential of the forest (S. Payette, A. Delwaide, and M. Simard, unpub-

lished data). Thus, it seems likely that the shift to lichen woodland is due primarily to the reduced seed pool of black spruce caused by the feeding of spruce budworm. Although fire was not severe enough to create more favourable seedbeds, post-fire regeneration would have been also drastically altered even with better germination conditions.

Despite the reduced seed rain in burned sites, the regeneration window was not restricted to the first years after the fire event (Fig. 3). Spruce establishment has been rather continuous since fire, probably because of dispersal from seed-bearing trees surrounding the burned sites. At least 50% of all post-fire spruce established on the lichen mat, with the primary root and collar above the mineral soil. This pattern of seedling establishment, quite common in several sites across the boreal forest, contrasts with recent arguments for a strictly narrow regeneration window in post-fire stands (Des Rochers and Gagnon 1997). Continuous seedling establishment on the lichen carpet is widespread not only in the North American spruce woodlands. Steijlen et al. (1995) showed that lichen (*Cladonia*) dominated vegetation was a better seedbed for Scots pine (*Pinus sylvestris* L.) establishment than feather-moss (*Pleurozium schreberi*) seedbed, because of moisture deficits, allelopathic influence, and nutrient availability. A similar moisture stress induced by feather-moss carpets may also affect black spruce seedlings (Jeglum 1979). Increasing thickness of the organic horizon

Fig. 6. Lac à la Bouillie site. (a) Basal stem diameter distribution of the unburned stand. (b) Basal stem diameter distribution of the post-fire stand. Shaded bar, black spruce; open bar, eastern larch; solid bar, balsam fir.



has generally inhibitory effects on post-fire seedling establishment (Thomas and Wein 1985; St-Pierre et al. 1992; Sirois 1993).

Low precipitation and warmer temperatures during the 1910s and the 1940s were generally associated with outbreaks of the spruce budworm in eastern Canada (Greenbank 1956), which contrast with conditions favourable to outbreaks of the western spruce budworm in western United States (Swetnam and Lynch 1993). In eastern Canada, insect outbreaks and fire ignition are often synchronized during dry years. It is possible that the coincident growth trend of jack pine and black spruce (Figs. 4 and 7) between the 1920s and the 1960s and in the 1990s may be attributable to similar climatic (dry conditions) and biotic (spruce budworm) stresses. Although a non-host species, jack pine trees may be affected to a minor degree by the spruce budworm (Martineau 1985).

Insect outbreaks and fire are totally independent events, but case studies on combined disturbances are necessary to evaluate the impact of individual and cumulative catastrophic events on forest composition. As pointed by Stocks (1987), Pech (1993), and McCullough et al. (1998), the interactions between insects and fire in the dynamics of the boreal forest need to be assessed in more detail. Whether

Table 6. Number and basal area of tree stems in the burned (1918) and unburned (1997) areas of the Lac à la Bouillie site.

	Burned area		Unburned area	
	N	Basal area (m ²)	N	Basal area (m ²)
Trees only				
Black spruce	96	25.6	85	22.3
Larch	0	—	1	0.21
Balsam fir	1	0.01	4	0.25
Total	97	25.7	90	22.8
Stems/ha	564		1317	
Trees + layers (>5 cm)				
Black spruce	281	44.6	408	59.2
Larch	0	—	1	0.21
Balsam fir	1	0.07	4	0.55
Total	282	44.7	413	59.9
Stems/ha	1642		6061	
Total area (m ²)		1750		650

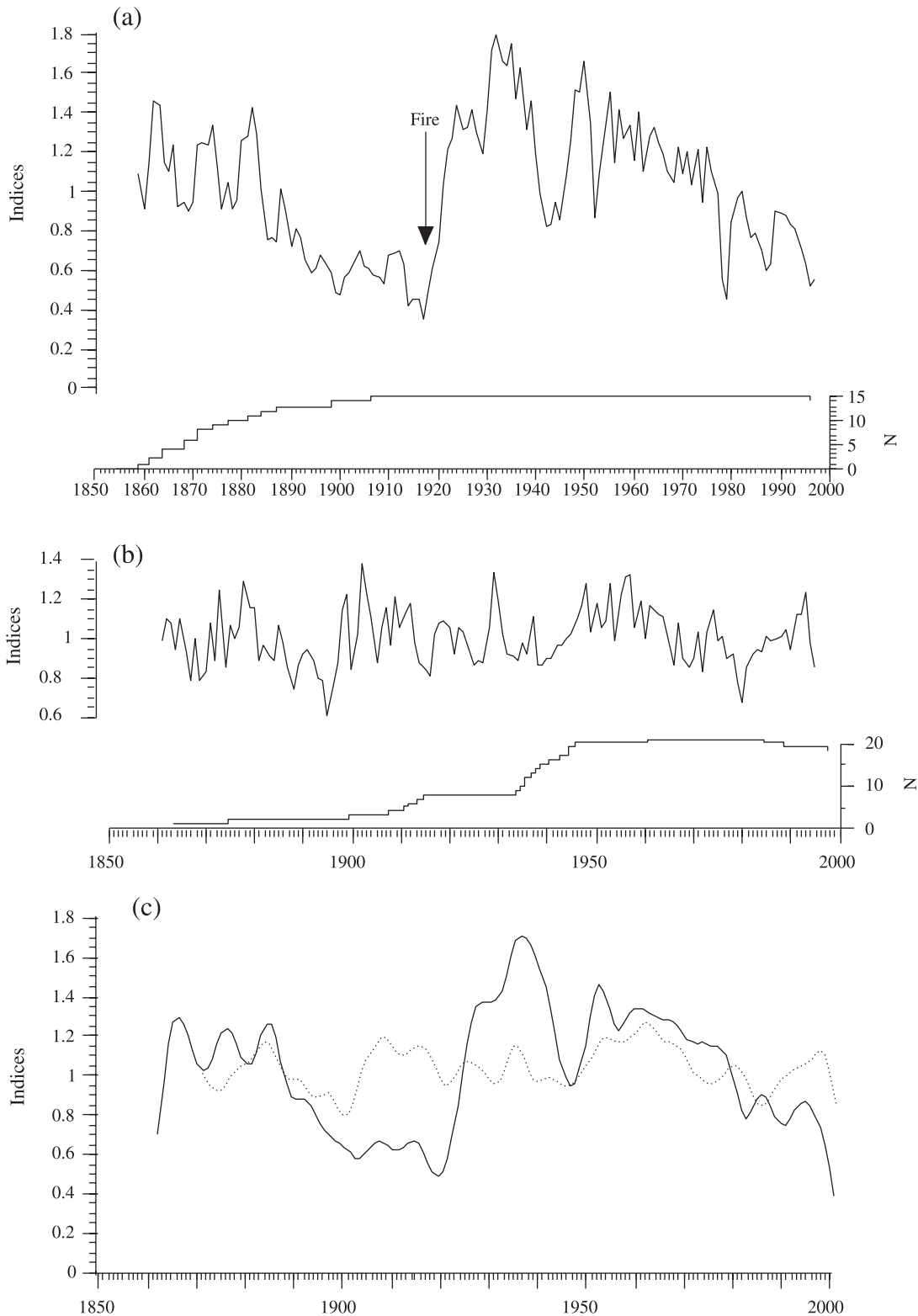
damaged forests by spruce budworm are facilitating fire ignition or not is an important question (Stocks 1987; Pech 1993) given the fact that both disturbances often occur under similar climatic conditions. However, in the study area, insect-damaged stands are not necessarily conducive to fire ignition because the ground vegetation is not drier than that of undamaged stands nearby. For instance, the most recent burn to occur in the PGJ started in late May 1999 at a riparian site not affected by the spruce budworm but spread readily across healthy and insect-damaged forests depending on local weather conditions (wind speed, etc). As a matter of fact, a recent survey showed that the LC site has been destroyed by this fire, thus pushing the lichen woodland to another regeneration stress. Indeed, the hazard of lightning strike distribution is virtually independent of vegetation types and stand age (Van Wagner 1978; Johnson and Van Wagner 1985; Johnson and Gutsell 1994).

Conclusions

Hadley and Veblen (1993) showed that outbreak severity may be the result of large forests burned simultaneously and entering developmental stages susceptible to insect outbreak. Here, in contrast, we have shown the impact of a deadly combination of disturbances: that of outbreak conditions predisposing the damaged forest to post-fire decimation. The timing of such combined disturbances was possibly common in the history of the southern boreal forest. However, long tree-ring series and macrofossil analysis are needed to evaluate the extent in time and space of the cumulative impact of such combined insect- and fire-damaged events.

Several theoretical and practical implications arise from this study on the origin and development of the lichen woodland in the southern boreal forest zone of eastern Canada. The breakdown of the spruce-moss forest as documented here is another illustration of the important role played by insect defoliators in the fate of whole forest ecosystems or individual tree species in this century and during the Holocene. One of the most striking examples of the impact of

Fig. 7. (a) Indexed tree-ring series of black spruce from the unburned forest at the Lac à la Bouillie site. (b) Indexed tree-ring series of jack pine in the Parc des Grands-Jardins. (c) Filtered tree-ring series of black spruce (solid line) from the unburned forest at the Lac à la Bouillie site and of jack pine (broken line) in the Parc des Grands-Jardins. In Figs. 7a and 7b, the number of sampled cores is indicated below the two tree-ring curves.



successive insect outbreaks is the decline of eastern hemlock (*Tsuga canadensis* (L.) Carr.) in southern Quebec during the mid-Holocene (Bhiry and Filion 1996a, 1996b).

Although its magnitude in time and space is not yet fully appreciated (P. Jasinski, in preparation), the shift from closed forest to woodland across the southern boreal forest

also suggests a declining density of black spruce at least in recent times.

Forest, tree-ring, and macrofossil data provided direct evidence for the degradation of the spruce–moss forest to lichen woodland under a regime of successive catastrophic disturbances associated with insect outbreaks and fire. This confirms that the southernmost lichen woodland in eastern Canada is a regressive type of the spruce–moss forest ecosystem and is not related to the temperature-stressed factors that influence the subarctic lichen woodland throughout the high-latitude Canadian boreal forest. The three stands studied are regressive because of the reduced spruce density allowing the development of a lichen carpet. These stands are incipient lichen woodlands compared with most lichen woodlands of the PGJ based on stand composition. The incipient woodlands are devoid of dwarf birch, a shrub species common to the other mature lichen woodlands. It is likely that future fire disturbances will maintain the open structure of the woodlands and will allow with time the invasion and establishment of dwarf birch. Indeed, more than one fire is necessary for the spread and development of dwarf birch populations. Such repetitive fires, as observed at the LC site, which burned again in 1999, are positive factors for the maintenance and further botanical development of the “typical” lichen woodland. This is not to say that all lichen woodlands at their southernmost limit originated from the same combination of disturbance factors. Further research is required to identify other lethal combinations, for example, short intervals between fires. An extension of our results is the likeliness of the inception of subalpine stands on the Charlevoix Highlands, near the LL site, forming regressive types of black spruce – balsam fir – white birch forests that may have experienced similar catastrophic disturbances.

The apparent fragility of the lichen woodland within the southern boreal zone mirrors the inability or weak resilience of the spruce–moss forest, and more particularly black spruce, in the wake of successive disturbances. An important point to consider in future studies is if the spatial pattern and extent of coexisting spruce–moss forest and lichen woodland in the southern boreal zone are a direct regeneration response of black spruce, over the last decades and centuries, associated with individual and successive insect and fire disturbances. Alternatively, the ecological succession from lichen woodland to spruce–moss forest is a natural process which certainly can be envisioned, considering the regeneration potential of black spruce in the southern boreal zone. However, the evidence for such a reversion is not available at this time.

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