

Black spruce decline triggered by spruce budworm at the southern limit of lichen woodland in eastern Canada

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Abstract: Black spruce (*Picea mariana* (Mill.) BSP) is the dominant tree species of the southernmost (48°N) lichen woodlands in eastern Canada. Most spruce trees in mature lichen woodlands appear to be declining, as shown by the massive invasion of the epiphytic lichen *Bryoria* on dead branches of dying trees. A dendroecological study was undertaken to identify the main causal factors of the decline. A decline index based on the abundance of *Bryoria* on spruce trees was used to distinguish healthy from damaged lichen–spruce woodlands and to select sampling sites for tree-ring measurements. Three conifer species (black spruce, balsam fir (*Abies balsamea* (L.) Mill.), and jack pine (*Pinus banksiana* Lamb.)) were sampled to compare their growth patterns in time and space. In the late 1970s and mid-1980s, black spruce and balsam fir experienced sharp and synchronous radial-growth reductions, a high frequency of incomplete and missing rings, and mass mortality likely caused by spruce budworm (*Choristoneura fumiferana* (Clem.)) defoliation. Jack pine, a non-host species, showed no such trend. Because black spruce layers were spared, lichen woodlands will eventually regenerate unless fire occurs in the following years. Black spruce decline can thus be considered as a normal stage in the natural dynamics of the southern lichen woodlands.

Résumé : L'épinette noire (*Picea mariana* (Mill.) BSP) est l'espèce dominante des pessières à lichens les plus méridionales (48°N) dans l'est du Canada. La plupart des épinettes dans les pessières à lichens matures sont selon toute apparence en voie de dépérissement, ce qui se manifeste par l'invasion du lichen épiphyte *Bryoria* sur les branches mortes des arbres moribonds. Afin de déterminer les facteurs responsables du dépérissement, nous avons utilisé une approche dendroécologique. Un indice de dépérissement, calculé selon l'abondance de *Bryoria* sur les épinettes, a servi à distinguer les pessières à lichens saines et dépéries, puis à sélectionner les sites d'échantillonnage pour fins d'analyse dendrochronologique. Trois espèces conifériennes (épinette noire, sapin baumier (*Abies balsamea* (L.) Mill.) et pin gris (*Pinus banksiana* Lamb.)) ont été échantillonnées afin de comparer leur patron de croissance dans le temps et l'espace. Dans les années 1970 et 1980, l'épinette noire et le sapin baumier ont connu des chutes de croissance radiale abruptes et synchrones, une grande incidence de cerne incomplets et absents et une mortalité en masse, probablement causées par la défoliation de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)). Le pin gris, une espèce non hôte, ne montre pas une telle tendance. Puisque les marcottes des épinettes ont été épargnées, les pessières à lichens vont éventuellement se régénérer à moins qu'un incendie ne survienne dans les prochaines années. Le dépérissement de l'épinette noire peut donc être considéré comme un stade normal dans la dynamique naturelle des pessières à lichens méridionales.

Introduction

Low-latitude lichen woodlands are exceptional in that they are found far south of 52°N, which is the southern limit of continuous lichen woodlands in eastern Canada (Fig. 1). They are characterized by a low density of black spruce (*Picea mariana* (Mill.) BSP) trees (~25% cover), which grow on a continuous lichen mat (mainly *Cladina* spp.), in-

terspersed with ericaceous shrubs (*Ledum*, *Kalmia*, *Vaccinium*) and dwarf birch (*Betula glandulosa* Michx.). In these open stands, black spruce trees establish after wildfires and then reproduce through layering, forming dense, well-spaced clones. In northern Quebec, lichen woodlands occur in large expanses on well-drained sites separated by moist, forested stands in valleys. At its southernmost range limit, the lichen woodland forms small, discontinuous patches within the closed-crown boreal forest. The origin of several southern lichen woodlands has been recently investigated, and findings indicate that they likely result from the opening of closed-crown spruce forests caused by the combined impact of insect defoliators and fire (Payette et al. 2000).

The southernmost lichen woodlands in eastern Canada are located in the Parc des Grands-Jardins (PGJ) (48°N), which is surrounded by black spruce – balsam fir (*Abies balsamea* (L.) Mill.) forests (Fig. 1). Most lichen woodland stands in the PGJ have a large number of moribund and standing dead black spruce trees, bearing unusually high loads of the epiphytic lichen *Bryoria*, a phenomenon commonly called

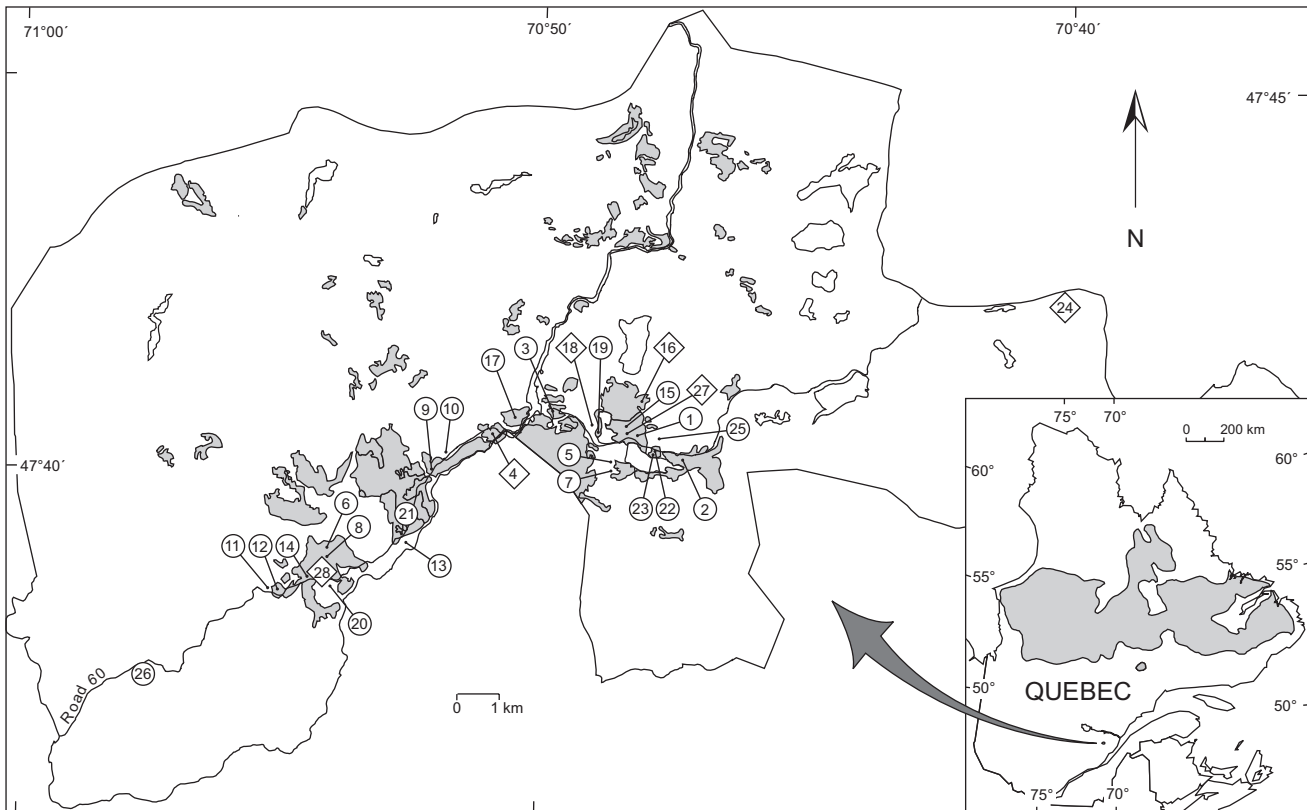
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Fig. 1. Distribution of lichen woodlands in the Parc des Grands-Jardins (gray area) and location of surveyed sites (numbers). The numbers inside diamonds are the sites sampled for chronologies. Inset map shows lichen woodlands in Quebec (gray area) and location of the study area.



black spruce decline, owing to its conspicuous character and widespread occurrence (Cyr 1998; Simard 2000). *Bryoria* is a common hair lichen that grows on boreal trees in Canada (Brodo and Hawksworth 1977; Goward 1998). Its biomass is generally proportional to stand age (Lang et al. 1980; Arseneau et al. 1997) and reaches a maximum at mid-tree height (Arseneau et al. 1997; Liu et al. 2000). However, in contrast to this pattern, several young spruce stands in the PGJ harbor unusually high loads of *Bryoria*, primarily in the upper crown of trees that were top-killed and subsequently developed new leaders. In the most damaged stands, several spruce trees are dead and completely covered with lichen. Black spruce seems to be the only species affected in the PGJ, as jack pine (*Pinus banksiana* Lamb.) trees growing among damaged black spruce stands do not harbor epiphytic lichens in measurable quantities. To our knowledge, this type of forest decline has not been observed elsewhere and has been studied only once before (Cyr 1998). Cyr (1998) subjected healthy and damaged spruce trees to experimental drought and demonstrated the sensitivity of declining trees to this stress without being able to establish causality between drought and decline.

The objective of this study is to identify the main causal factors of black spruce decline. We used a dendroecological approach, comparing tree-ring patterns of healthy and damaged spruce trees with those of unaffected species and taking into account stand age, associated vegetation, disturbance history, and soils. We hypothesized that spruce budworm (*Choristoneura fumiferana* (Clem.)) infestation was the primary factor responsible for the black spruce decline. The

tree-ring signature associated with infestations of defoliating insects is characteristic, i.e., the destruction of current-year (and sometimes old) needles induces abrupt and synchronous radial-growth depressions (MacLean 1985; Swetnam et al. 1985) that are proportional to the intensity and duration of defoliation (Piene and Little 1990). Several years of severe defoliation result in a high frequency of incomplete and missing rings (O'Neil 1963; Swetnam and Lynch 1989; Jardon et al. 1994b) and mass mortality (MacLean 1980; Lussier 1997; Filion et al. 1998).

To meet our objective, damaged stands were first surveyed to characterize the severity of the decline in relation to various ecological conditions (stand age, drainage, etc.). Survey data were then used to select sampling sites for tree-ring analysis. We chose sites that allowed us to isolate the effect of specific factors, including stand age, drainage, and species composition. Finally, we compared the radial growth of host (black spruce and balsam fir) and non-host (jack pine) species of the spruce budworm with weather and insect survey data.

Study area

The PGJ (47°40'N, 70°50'W) is located in the eastern part of the Laurentian Highlands (800–900 m altitude), 120 km northeast of Québec. Westerly air masses progressively unload their water content when passing over the highlands, thus creating a precipitation gradient between the Réserve Faunique des Laurentides (RFL) in the west (1500 mm/year, on average) and the PGJ in the east (1000 mm/year, on average). Mean annual temperature is similar in

both areas (0° to -0.5°C), as is the frost-free period, one of the shortest (51 days) in southern Quebec (Boisclair 1990).

The RFL area is dominated by the mixed conifer forest. Balsam fir – white birch (*Betula papyrifera* Marsh.) forests occupy low-altitude sites, whereas balsam fir – black spruce stands are typically found at an altitude >800 m. The forests of the RFL are subjected to two major disturbances: logging and spruce budworm outbreaks (Lachance et al. 1991). The spruce budworm is considered to be the most important insect pest in eastern North America (Armstrong and Ives 1995). Tree-ring analyses have been used to reconstruct the history of spruce budworm outbreaks in eastern Canada (Blais 1983; Morin 1994; Filion et al. 1998), particularly in the RFL area (Blais 1964, 1965; Lussier 1997). Three major spruce budworm outbreaks have occurred in eastern North America during the 20th century, with onsets in the 1910s, 1940s, and 1970s. The last outbreak occurred in the RFL area between 1974 and 1985 and was closely monitored using yearly aerial surveys of the defoliation and insect surveys in the field.

Unlike the RFL, fire is obviously one of the most important disturbance factor in the PGJ. Logging was also important between the 1950s and the 1970s, before the creation of the park. Black spruce dominates the PGJ; spruce–lichen woodlands grow adjacent to spruce–moss stands, forming a mosaic of closed-crown and open forests. Lichen woodlands occupy about 10% (~ 28 km²) of the PGJ, and they are mostly found on well-drained sites of the Malbaie River watershed, at an altitude of 700 to 800 m (Fig. 1). They grow on dry, acidic Podzolic soils, which developed on glacial deposits, namely fluvio-glacial sands and gravel in flat sites and valleys, and till on the slopes. Jack pine and tamarack (*Larix laricina* (DuRoi) K. Koch) are found in low density in some lichen woodlands.

Methods

Large-scale survey

The first part of the fieldwork focused on mapping the spruce decline throughout the study area to determine the ecological conditions associated with the decline. This survey gave an overview of the decline and was used for selection of sampling sites. Potential sites were first identified with aerial photographs and maps of recent disturbances (fire and logging). These disturbances, which generated the present even-aged stands, were dated with fire and logging scars and records of logging activities in the PGJ. Potential sites had to be reasonably accessible and homogenous in terms of stand origin, topography, soil deposits, drainage, and vegetation composition. Sites were selected to obtain the greatest diversity in terms of decline severity, stand age, drainage, soil deposits, topography, and associated vegetation.

At each site, the vegetation cover, soils, and topographic conditions were noted. Because *Bryoria* was closely associated with the dead parts of trees, decline severity was evaluated according to the abundance of *Bryoria* on spruce trees. A simplified version of a method developed by Stevenson (Stevenson and Enns 1993) was used to assess the epiphytic lichen cover on each tree. The cover of *Bryoria* was determined on all aspects of the trees according to pre-established classes: 0–4, 5–24, 25–49, 50–74, 75–99, and 100%, the reference (100%) being the area occupied by the crown of the tree added to the area occupied by the pendular portions of the epiphytic lichens (Stevenson and Enns 1993). The 100% class indicated that the tree was dead.

The cover of *Bryoria* was evaluated using 10 parallel 20×1 m transects; the first transect was located at random, and the others were systematically placed at 5-m intervals. The origin (layers versus seed origin) of every standing tree (live and dead) in the transects was noted. In the lichen woodland, layers are easily distinguished from trees originating from seed by the marked curve at the stem base, which is usually still attached to the mother tree or

pointing towards a cut stump. Tree height was also measured (<1 , 1–3, 3–6, 6–9, >9 m), and given the large quantity of small layers in several sites, only individuals taller than 0.5 m were included in the sample. The lichen cover class of each tree was then noted according to the method previously described. To classify the different sites according to the severity of decline, we developed a decline index (DI) that quantifies lichen abundance in the stands, according to the following equation:

$$[1] \quad DI = (5n_{5-24} + 25n_{25-49} + 50n_{50-74} + 75n_{75-99} + 100n_{100}) / \sum n$$

where n_{5-24} is the number of trees >3 m in the 5–24% cover class, etc., and $\sum n$ is the sum of trees >3 m. The proportion of trees in each cover class is multiplied by the lowest limit of that class to give more weight to high cover classes. Only trees taller than 3 m were included so that the DI would represent health conditions of dominant trees. The DI is dimensionless, proportional to the cover of *Bryoria* on trees, and can theoretically assume values from 0 to 100.

Site selection and soil analysis

To select sampling sites, survey data were used to identify ecological conditions associated with severe decline. Stand age was closely associated with decline severity in lichen woodlands, with young stands (<60 years) typically having a low percent cover of *Bryoria* ($DI < 20$) and older stands (>80 years) showing a high percentage of lichen cover ($DI > 40$). Accordingly, stands of different age (with origins centered around 1960, 1940, 1920, and 1900) were selected for tree-ring analysis. A stand logged in 1963 (site 18; see Table 1 for description of sites) was chosen at random among the three stands that were logged in the 1960s (sites 5, 11, and 18). Site 10 was excluded from the draw because not all the trees were cut in the same year, resulting in an uneven-aged stand. Only one fire occurred in the 1940s, so site 16 (1940 fire) was automatically chosen. Similarly, only one fire of known age (dated with fire scars, as opposed to minimum age given by oldest living tree) was available for both the 1920s (site 27, burned in 1921) and 1900s (site 4, burned in 1897). We deliberately selected site 27 among the three sites located in the 1921 fire (sites 1, 15, and 27), because it was the only one that contained jack pine trees, which had to be sampled as a non-host species of the spruce budworm. In addition, site 1 was located in a shallow depression in which periodic frost events occur during the growing season affecting black spruce growth (S. Payette, unpublished data), while site 15 was close to the 1940 fire border, raising doubts on the homogeneity of stand origin. According to survey data, black spruce trees had a lower DI when mixed with balsam fir, the principal host of the spruce budworm. A mixed balsam fir – black spruce stand (site 24, logged ca. 1950) located close to but outside of the lichen woodland area was thus selected. Of the two mixed stands surveyed, site 24 was preferred because black spruce and balsam fir had a similar height structure (Fig. 2), as the result of clear-cutting. Site 26 was rejected because it was composed primarily of small (<3 m) balsam fir trees and tall (>9 m) black spruce trees, a structure that would not allow an unbiased comparison of the impact of spruce budworm on both species. Although most stands showing high lichen cover (high DI) were well-drained lichen woodlands (drainage class 2 or 3), some wetter sites also showed high DI. Therefore, we selected an open black spruce stand growing at the edge of a peatland (site 28, drainage class 5) to compare the tree-ring patterns of stands with contrasting drainage classes. All sites but one were surveyed in June and July 1997 and sampled in September and October of the same year; site 28 was surveyed and sampled in September 1998.

At each site, the soils were described and sampled for texture and pH (CaCl_2 0.01 M). Exchangeable bases (K, Na, Ca, and Mg)

and acidity (H + Al) were determined with an unbuffered saline solution (Amacher et al. 1990). Effective cation exchange capacity (ECEC) was measured as the sum of exchangeable cations. Base saturation was calculated by dividing exchangeable bases by the ECEC.

Tree-ring analysis

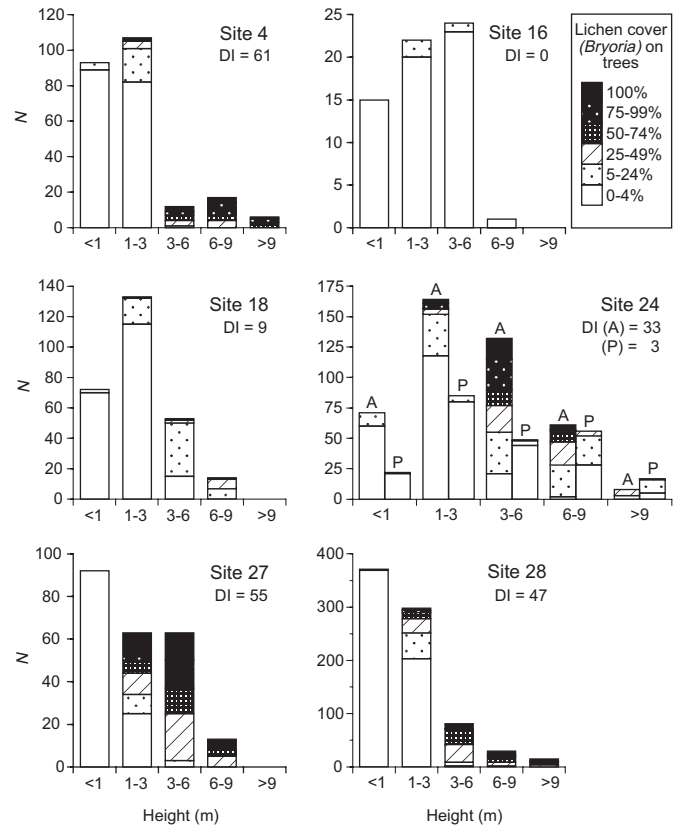
Live trees

A tree-ring chronology was constructed for each tree species in each site, for a total of eight series: six for black spruce; one for balsam fir, the primary host of the spruce budworm; and one for jack pine, a species generally not considered as a host of this insect. In each site, 25 trees >3 m in height were sampled systematically (5-m intervals) along a transect placed at random. Complete cross sections of black spruce and balsam fir trees were sampled 30 cm above the ground to identify incomplete and missing rings; jack pine trees were cored at 30 cm (for each tree, one core was taken at the west, east, and south). Additional old-aged pines were also sampled throughout the PGJ to extend the regional jack pine chronology (Payette et al. 2000). Sanded cross sections and cores were cross-dated to locate incomplete and missing rings. Cross dating of black spruce and balsam fir was done using frost-ring master chronologies (Simard 2000). Frost rings are frequent in black spruce and balsam fir in the PGJ, and they are characterized by one or several layers of cells deformed by growing-season frost (Glerum and Farrar 1966). Frost rings are considered to be more reliable as climatic pointer years than rings widths, as ring widths can be influenced by both climate and insect defoliation. Ring widths of all tree species were measured on three radii (west, south, and east) with a Velmex micrometre (precision of 0.002 mm) under 40× magnification. Individual series were standardized conservatively (straight line of negative slope, negative exponential, or second-degree function, depending on the shape of the curve) to keep low-frequency variations associated with insect defoliation. Dating and homogeneity of the series were checked with COFECHA (Holmes 1983). Mean series were smoothed with a digital low-pass (9 year) filter (Swetnam et al. 1985) to retain long-term variations like those induced by spruce budworm defoliations, which typically last from 5 to 10 years (Blais 1968). The maximum growth reduction for 1 year was calculated in host chronologies (Swetnam et al. 1985). It corresponds to the largest growth reduction for a single year during a budworm outbreak, and it is calculated as the difference between the chronology's mean index (~1.0) and the minimum index value during the outbreak. Maximum growth reduction was plotted against the DI for the six sampled stands. A power function was used for the regression of maximum growth reductions on the DI because it provided the best fit. Also, when fitted to our data set, this model has an intercept of zero and tends toward (100, 100). Regression was done on the logarithmically transformed data to linearize the relationship between both variables.

Dead trees

Fifty standing dead balsam fir trees >3 m (site 24) and 50 standing dead black spruce trees >3 m (site 27) were sampled, following the same method used for live trees, to determine the date and frequency of death. Site 27 was selected for this analysis because it showed the highest mortality among the four lichen woodlands selected for tree-ring analysis (sites 4, 16, 18, and 27). All trees were cross-dated with the frost-ring chronologies. Skeleton plots of each tree were constructed, including narrow, incomplete, and missing rings. The initiation of morbidity corresponded to the years preceding tree death where rings were incomplete or very narrow (Jardon et al. 1994a; Filion et al. 1998). Mortality corresponded to the year of formation of the outermost ring. All dead trees still retained

Fig. 2. Lichen cover according to tree height classes in the six sampled stands. The decline index (DI) in site 24 is given for each conifer species (A, *Abies balsamea*; P, *Picea mariana*).



bark indicating that no rings were lost by weathering or decomposition.

Results

Survey

Twenty-eight sites were surveyed, representing the majority of stand types in the PGJ and showing DIs ranging from 0 to 78 (Fig. 1, Table 1). Most surveyed stands are well-drained black spruce – lichen woodlands (drainage classes 2 and 3), but wetter sites, including a peatland (drainage class 5), are also described (Table 1). The majority of sites are located at similar altitudes (700–800 m) on <5° slope. Among the 28 sites surveyed, five of the sites selected for tree-ring analysis (see Methods) have well-drained soils on loamy till and fluvial sands (Table 2). Although all these soils meet the chemical criteria for a Podzolic B horizon (Canadian Soil Survey Committee 1978), only three sites (sites 16, 18, and 24) have a B horizon thick enough (10 cm) to be classified as Humo-Ferric Podzols; sites 4 and 27 are eluviated Dystric Brunisols. The soils have a thin solum (10–20 cm) and an organic layer 1–6 cm thick, but they are somewhat better developed in the fir–spruce stand (site 24) (solum = 36 cm; FH horizon = 17 cm). The soils are very acidic (pH = 2.6 to 3.8 in FH; 3.9 to 5.1 in Bf) and nutrient poor, as shown by the low cation exchange capacity (<40 cmol(+)·kg⁻¹ in FH, <5 cmol(+)·kg⁻¹ in Bf) and base saturation (<50%) values (Table 3). The epiphytic lichen flora was surveyed in five sites, but seems to be similar in

Table 1. Characteristics of surveyed stands.

Site	Type ^a	Origin and year ^b	Altitude (m)	Deposits ^c	Slope (°)	Drainage class ^d	Frost ^e	Dominant species ^f	No. of stems ^g	Layers ^h (%)	Dead ⁱ DI ⁱ	Dead ^j (%)
1	LW	Fire, 1921	720	FG	0	3	+	<i>Cladina</i> spp.	282	93	29	4
2	LW	Fire, <1890	710	FG	0	2		<i>C. stellaris</i>	526	97	61	6
3	LW	Fire, 1847	710	FG	5	2–3		<i>C. stellaris</i>	348	94	47	4
4*	LW	Fire, 1897	730	FG	4	2		<i>Cladina</i> spp.	234	91	61	7
5	LW	TC, 1963	730	Till	0	2		<i>C. stellaris</i>	300	97	21	3
6	LW	Fire, <1886	760	FG	0	3	++	<i>Cladina</i> spp.	176	94	9	3
7	LW	Fire, <1899	750	Till	2	2		<i>C. stellaris</i>	362	97	65	8
8	LW–M	Fire, <1880	760	FG	0	2–3		<i>C. stellaris</i>	558	93	60	6
9	LW	Fire, <1893	740	Till	17	2–3		<i>Cladina</i> spp.	344	96	40	7
10	LW–M	PC, 1964	730	Till	0	3–4		<i>Cladina</i> spp.	508	99	41	6
11	LW–M	TC, 1964	770	Till	0	3–4		<i>Cladina</i> spp.	291	100	10	2
12	LW–M	Fire, <1882	770	Till	0	3	+	<i>Cladina</i> spp.	517	96	29	5
13	LW	Fire, <1885	730	Till	0	2–3		<i>C. stellaris</i>	283	96	44	7
14	LW	Fire, <1897	770	Till	0	3	+	<i>Cladina</i> spp.	284	96	24	4
15	LW	Fire, 1921	710	FG	0	2–3		<i>Cladina</i> spp.	287	92	37	4
16*	LW	Fire, 1940	710	Till	0	2		<i>Cladina</i> spp.	62	5	0	3
17	LW–M	Fire, <1819	730	Till	0	2–3		<i>C. stellaris</i>	350	96	57	11
18*	LW	TC, 1963	710	FG	3	2		<i>Cladina</i> spp.	274	99	9	3
19	LW	Fire, <1884	710	FG	5	2–3		<i>C. stellaris</i>	394	98	50	4
20	SM	Fire, <1884	740	Till	7	4		<i>Pleurozium</i>	520	99	40	6
21	LW	Fire, <1885	730	FG	0	3	++	<i>Cladina</i> spp.	101	75	2	0
22	LW	Fire, <1897	715	Till	0	2		<i>C. stellaris</i>	360	98	54	9
23	SM–L	Fire, <1897	705	FG	3	3–4		<i>Pleurozium</i>	495	100	55	4
24*	BF–BS	TC, ca. 1950	800	Till	12	3		<i>Pleurozium</i>	Ab, 434 Pm, 233	— 100	33 3	12 13
25	LW	Fire, <1885	710	FG	0	2–3		<i>C. stellaris</i>	493	99	78	11
26	BF–BS	Fire, <1897	840	Till	15	3–4		<i>Pleurozium</i>	Ab, 413 Pm, 93	100 —	16 30	2 11
27*	LW	Fire, 1921	710	FG	0	2		<i>Cladina</i> spp.	Pm, 231 Pb, 25	68 —	55 2	12 0
28*	SS	Fire, <1871	750	Till	0	5		<i>Sphagnum</i> spp.	783	99	47	7

Note: Stands with asterisks were sampled for tree-ring analysis.

^aVegetation type are as follows: LW, lichen woodland; LW–M, lichen woodland with mosses; SM, spruce–moss forest; SM–L, spruce–moss forest with lichen; BF–BS, balsam fir – black spruce forest; SS, spruce–*Sphagnum*.

^bTC, total cutting; PC, partial cutting. When date of stand establishment is unknown because of lack of scars, a minimum age is given (e.g., <1890) based on the age of the oldest trees determined with increment cores.

^cFG, fluvioglacial deposits.

^dDrainage class according to the Canadian system of soil classification (Canadian Soil Survey Committee 1978). Those classes are approximate, as soil was sampled with a probe, with the exception of sites 4, 16, 18, 24, 27, and 28, where a pedon was dug.

^eInfluence of frost occurring throughout the growing season (S. Payette, unpublished data) and affecting black spruce trees growing in shallow topographic depressions. ++, important; +, present.

^fDominant species of the ground cover. *C. stellaris*, *Cladina stellaris*; *Pleurozium*, *Pleurozium schreberi*.

^gTotal number of black spruce (if not stated otherwise) stems surveyed in ten 20-m² quadrats. Ab, *Abies balsamea*; Pm, *Picea mariana*; Pb, *Pinus banksiana*.

^hPercentage of layers, including living and dead stems.

ⁱDecline index, following eq. 1.

^jPercentage of standing dead stems, including layers and trees originating from seed.

the other sites. Two species of *Bryoria* (*Bryoria nadvornikiana* and *Bryoria furcellata*) make up the bulk (>90%) of epiphytic lichens growing on black spruce. Secondary species included at least two species of *Usnea* (*Usnea subfloridana* and *Usnea filipendula*), as well as *Evernia mesomorpha*, *Hypogymnia physodes*, and *Cetraria pinastri*. In the fir–spruce stand (site 24), only one species of *Bryoria* (*B. nadvornikiana*) was identified.

Several old stands were given a minimal stand age (from increment cores taken from the oldest trees) because of the

absence of fire scars (Table 1). Other indications of old stand age are the continuous lichen cover of *Cladina stellaris*, which dominates lichen woodlands older than 100 years (Morneau and Payette 1989), and the low proportion of trees originating from seed, suggesting a forest of at least two generations.

Survey data suggest that the severity of decline is influenced by stand age and species composition but not by soil drainage. Young stands (site 16, burned in 1940, and sites 5, 11, and 18, clear-cut in the 1960s) are less damaged than old

Table 2. Physical characteristics of well-drained soils.

	Site				
	4	16	18	24	27
Deposits	FG ^a	FG	FG	Till	FG
Drainage class ^b	2	2	2	3	2
Thickness (cm)					
FH	2	6	1	17	5
Ae	3	4	2	6	7
B	4	10	19	13	9
Solum	9	20	22	36	21
C horizon texture					
Sand (%)	74	97	87	73	99
Silt (%)	24	2	8	20	0
Clay (%)	2	1	5	7	1

^aFG, fluvioglacial deposits.

^bDrainage class according to the Canadian system of soil classification (Canadian Soil Survey Committee 1978).

stands (except for stands affected by recurrent frost events) (Table 1). In addition, only trees >3 m are affected (>50% lichen cover), whereas small layers (<3 m) are not (Fig. 2). Also, jack pine is not affected by the decline (DI = 2), compared with black spruce (DI = 55) growing at the same site (site 27, Table 1). In a mixed, closed-crown fir–spruce stand (site 24), balsam fir shows severe decline (DI = 33), whereas black spruce is unaffected (DI = 3) (Fig. 2, Table 1). The inverse response observed in the other fir–spruce stand (site 26, Table 1) is probably the result of the height difference between the two species. In contrast to site 24, where fir and spruce have the same height structure (Fig. 2), site 26 is composed of young balsam fir (<3 m), and the dominant trees (>9 m) are black spruce (Simard 2000). Soil drainage does not seem to influence decline severity. Two sites (site 22 and 23) located at the extremes of a drainage gradient have similar DI values (Table 1). Moreover, an old-age stand growing in a peatland with a high water table (site 28, drainage class 5) shows a high DI (47), a value common to well-drained, old-age lichen woodlands (e.g., sites 3 and 4).

Growth curves

From the 28 sites surveyed, six were selected for tree-ring analysis to isolate the effects of ecological factors that likely influenced decline severity, namely stand age, drainage, and species composition. Tree-ring chronologies of black spruce were constructed from well-drained lichen woodlands of different ages (centered around 1960, 1940, 1920, and 1900) and from an old-age stand growing in a peatland (site 28, drainage class 5). A regional jack pine chronology was also constructed, along with chronologies of balsam fir and black spruce from a closed-crown stand.

In the lichen woodlands (sites 4, 27, 16, and 18, established in 1897, 1921, 1940, and 1963, respectively), the ground cover is dominated by *Cladina* with some *Pleurozium schreberi*, and the shrub stratum is composed of *Betula glandulosa*, *Ledum groenlandicum*, *Kalmia angustifolia*, and *Vaccinium* spp.; jack pine and tamarack are the only other tree species. In contrast, the ground cover in the peatland stand is composed of *Sphagnum* and other mosses, with tamarack interspersed among the spruce trees.

Table 3. Chemical characteristics of well-drained soils.

Site and horizon	pH	ECEC ^a (cmol(+)-kg ⁻¹)	BS ^b (%)
4			
F	2.7	25.8	18
H	2.9	7.6	9
Bf ₁	4.0	0.4	43
16			
F	2.6	36.3	39
H	2.7	17.4	26
Bf ₁	3.9	4.4	12
18			
FH	3.0	14.0	23
Bf	4.2	0.5	21
24			
F	2.7	27.8	50
H	2.6	43.2	56
Bhf ₁	4.0	5.3	11
27			
F	2.8	12.6	17
Fh	3.8	3.2	10
Bf	5.1	0.5	30

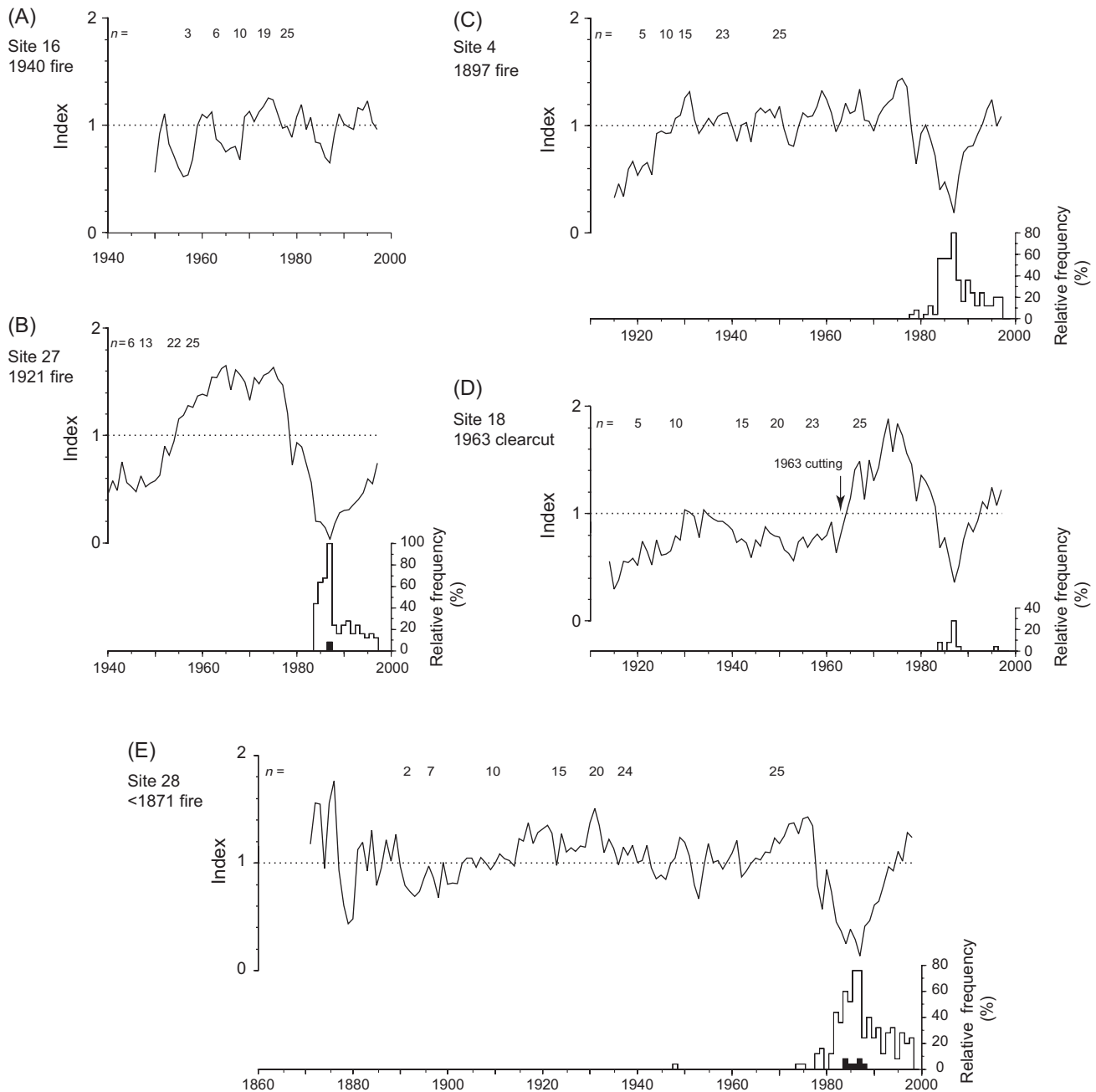
^aECEC, effective cation exchange capacity.

^bBS, base saturation.

Regardless of age or drainage class, these stands show a synchronous, sharp growth reduction in the late 1970s, but of varying intensity (Fig. 3). The growth reduction occurred in two steps (1978 and 1982), with the lowest index value in 1987. Furthermore, a high frequency of incomplete rings (beginning around 1982) and missing rings (1984–1988) is associated with the growth decreases. The youngest stand (site 16) shows the least growth reduction with no missing rings (Fig. 3A). Even though some stands are more than 100 years old, no growth reduction of this amplitude occurred before 1980, although a slight depression is observed in the 1950s (Figs. 3C and 3E). The jack pine chronology does not show a comparable growth depression during that same period, neither does it include incomplete rings (Fig. 4A). The contrast between the growth pattern of black spruce and jack pine is highlighted in the filtered chronologies (Fig. 4B). Dead spruce trees were sampled in the lichen woodland with the highest mortality (site 27). All the dead trees sampled in this site ($n = 50$) died recently, after a period of low growth that was synchronous to the growth reduction depicted in living spruce trees (1979–1985) (Fig. 5). Mortality was highest during the first years of low growth (1984–1990), but no spruce trees died before 1984 (Fig. 5B).

Chronologies of balsam fir and black spruce were made from a closed-crown fir–spruce stand (site 24), where the ground cover is dominated by mosses, and white birch is scattered among the conifers. After a period of growth suppression, the balsam fir chronology shows a growth release following logging, then two successive drastic growth reductions (1977–1979 and 1984–1987) (Fig. 6A). A high proportion of incomplete and missing rings again characterizes the depressions and reaches a maximum in 1986 (96% incomplete, 56% missing); incomplete rings prior to 1950 are as-

Fig. 3. Standardized chronologies of black spruce in well-drained lichen woodlands (A–D) and in a peatland (E). Sites 16 (A), 27 (B), 4 (C), and 28 (E) were burned in 1940, 1921, 1897, and before 1871, respectively, and site 18 (D) was established after clear-cutting in 1963. Bars represent relative frequency of incomplete (open) and missing (solid) rings. n is the cumulative number of trees used in the chronologies.



sociated with the growth suppression period. Black spruce shows the same growth pattern (Fig. 6B), but at a lesser degree (Fig. 6C). The growth pattern of dead fir is similar to that of live fir (Fig. 7). The first growth depression (1977–1979) in the balsam fir chronology (Fig. 6A) corresponds to the initiation of stem morbidity, whereas the second depression (1984–87) corresponds to a peak in fir mortality (Fig. 7B).

To verify if the DI was a good estimator of tree vigor, the DIs of the sampled stands were plotted against a descriptor of the growth reductions, i.e., the maximum growth reduction for 1 year (Swetnam et al. 1985). There is a highly sig-

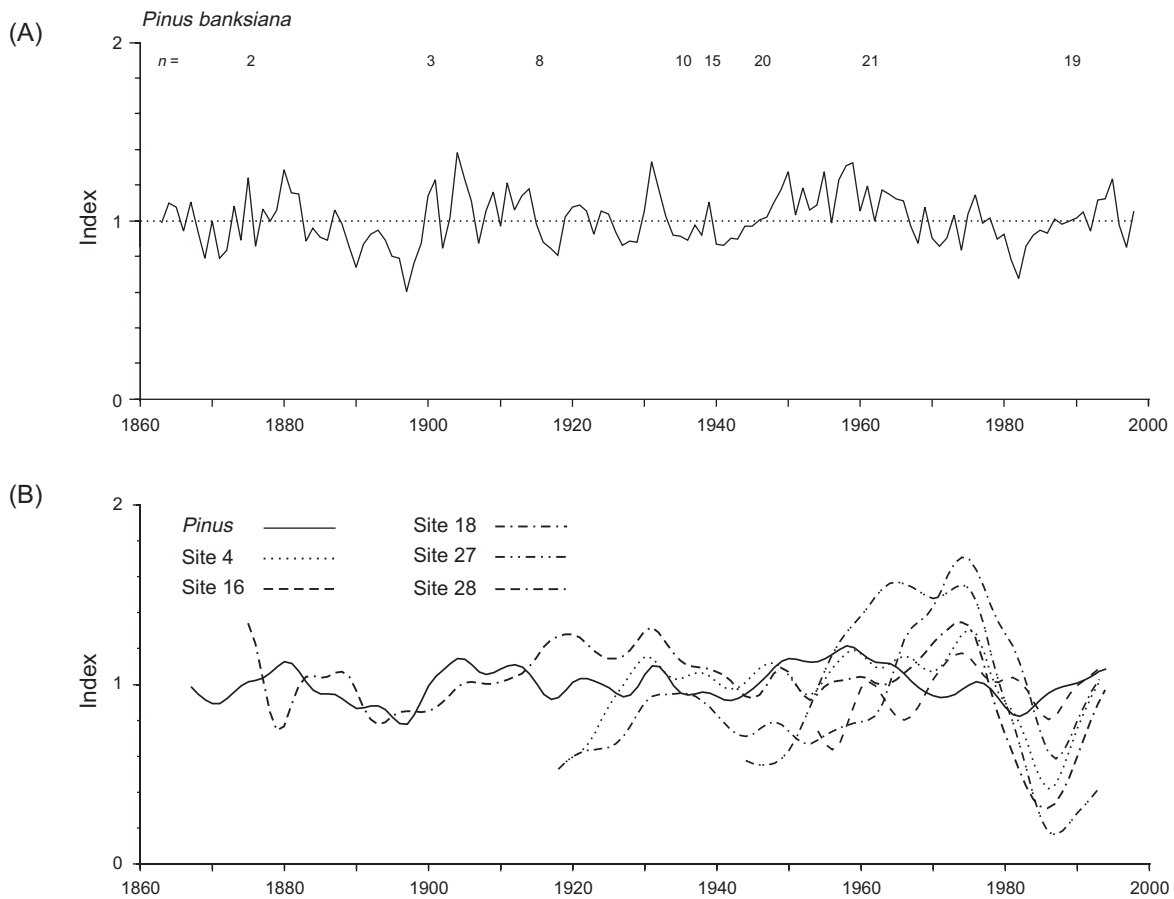
nificant relationship between both variables ($t = 7.493$, $df = 5$, $p = 0.0007$), and the DI accounts for 90% of total variation in maximum growth reduction in 1 year (Fig. 8).

Discussion

Impact of the spruce budworm

Tree-ring data clearly indicate that the lichen–spruce woodland of the PGJ was severely affected by an infestation of the spruce budworm in the late 1970s and mid-1980s. In all the studied stands, tree growth shows an abrupt and syn-

Fig. 4. (A) Standardized chronology of jack pine in the Parc des Grands-Jardins. n is the cumulative number of trees used in the chronology. (B) Filtered chronologies (9-year low-pass filter) of jack pine (solid line) and black spruce (broken lines).



chronous reduction between 1978 and 1987, in spite of the great differences in stand age and drainage (Figs. 3, 4B, and 6). This period of growth depression is also characterized by a high frequency of incomplete and missing rings. The growth patterns are typical of massive defoliation caused by insect infestations (O'Neil 1963; Swetnam et al. 1985; Swetnam and Lynch 1989, 1993; Jardon et al. 1994a, 1994b; Krause and Morin 1995, 1999; Filion et al. 1998). The growth reductions affect black spruce and balsam fir, which are host species of the spruce budworm, whereas jack pine, a non-host species, does not show a similar growth depression (Fig. 4). In addition, the budworm infestation produced a mass mortality (MacLean 1980) of both black spruce (Fig. 5) and balsam fir (Fig. 7), following a period of morbidity initiated during the outbreak.

The presence of the budworm in the PGJ is also confirmed by defoliation aerial surveys (Gouvernement du Québec, ministère des Ressources naturelles, Direction de la conservation des forêts) and by insect surveys in the field (Forest Insect and Disease Survey National Database, Canadian Forest Service). The outbreak started in western Québec around 1967 and affected the RFL from 1974 through 1985. The spruce budworm infested the PGJ in 1976–1977, then, after a short pause, in 1981–1985. Blais (1985) reported a remission of the infestation at high altitudes (>700 m), which is clearly expressed in most PGJ chronologies as a bimodal depression in radial growth (Figs. 3 and 6)

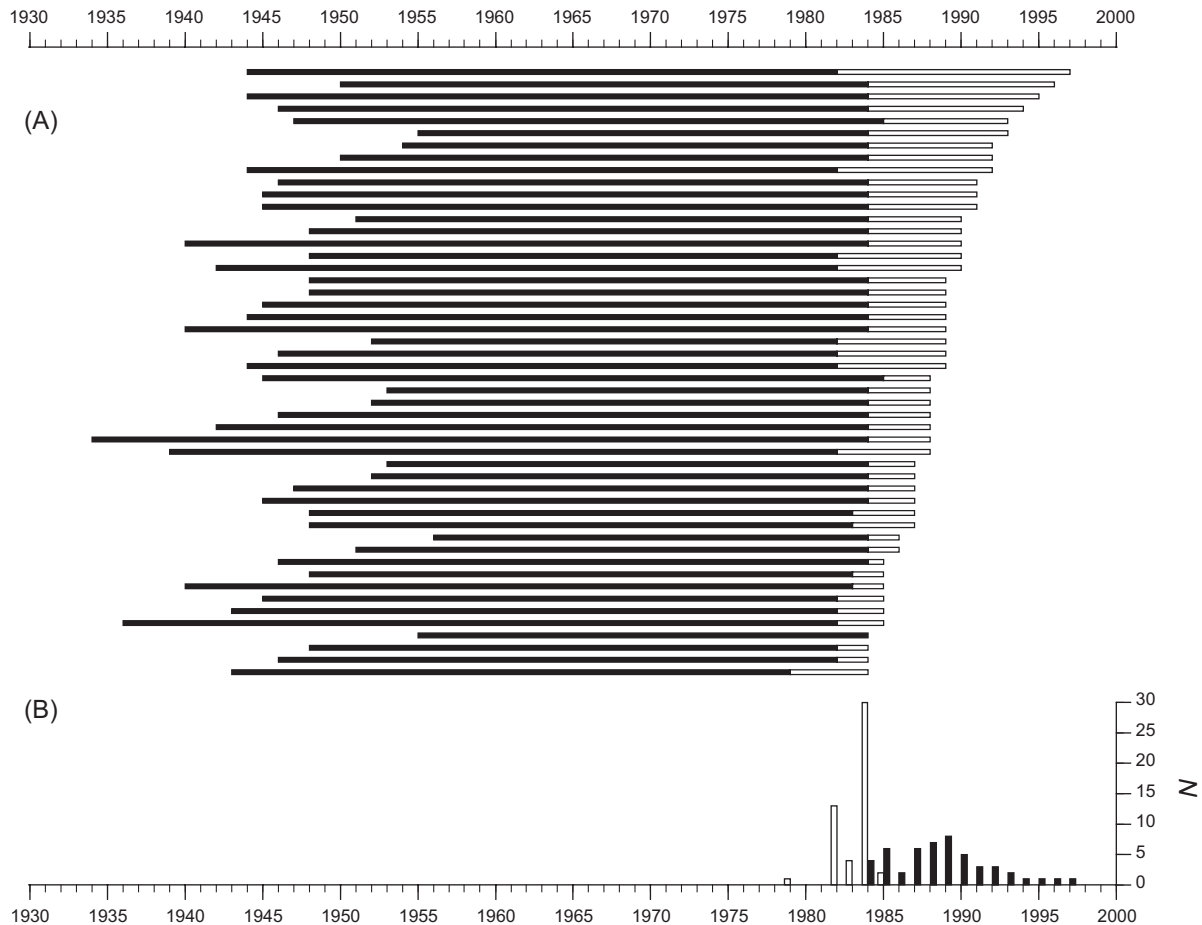
and a double peak of incomplete rings (Figs. 3E and 6A). A second growth reduction in 1952–1953 in some chronologies (Figs. 3C and 3E) likely corresponds to the spruce budworm outbreak recorded in the RFL between 1946 and 1957 (Blais 1964, 1965; Lussier 1997).

The different intensity of radial-growth depressions between sites and host species reflects the severity of defoliation, as those reductions are proportional to the intensity and duration of spruce budworm defoliation (Piene and Little 1990). Young stands, regardless of origin (fire, site 16, or clearcut, site 18) were thus less affected by the infestation than the older (sites 4, 28) post-fire stands (Fig. 8). Old stands are known to be more susceptible to spruce budworm attack (Mott 1963). Also, balsam fir is more vulnerable (sensu Mott 1963) than black spruce to the budworm (MacLean 1980), which is expressed in the fir–spruce stand (site 24) as greater growth reductions and a higher frequency of incomplete and missing rings in balsam fir than in black spruce (Figs. 6 and 8).

Towards an etiology of black spruce decline

During the spruce budworm outbreak, several summers (1977, 1978, and 1982) were characterized by low precipitations in the PGJ (Saint-Urbain weather station, Gouvernement du Québec, ministère de l'Environnement, Direction du milieu atmosphérique), which brings up the issue of the possible role of drought in the spruce decline. Insect out-

Fig. 5. (A) Life-span of 50 dead black spruce trees in site 27, showing the period of normal growth (solid bars) and the period of morbidity (open bars) preceding death. Morbidity corresponds to the years prior to death where rings are incomplete or very narrow. (B) Frequency of morbidity initiation (open columns) and death (solid columns).



breaks often occur during droughts (Mattson and Haack 1987), and some authors have hypothesized that a series of dry and warm years can trigger outbreaks of the spruce budworm (Greenbank 1956; Martinat 1987). However, the causality between these two events still has to be demonstrated. Both hydric stress (Zahner 1968) and insect defoliation reduce radial growth of woody plants; therefore, when an insect outbreak occurs during a drought period their respective effects are confounded in host chronologies. The extent to which drought has affected black spruce decline is unknown. However, it probably played a lesser role than spruce budworm defoliation, as many droughts occurred before and after the infestation (Saint-Urbain weather station, Gouvernement du Québec, ministère de l'Environnement, Direction du milieu atmosphérique), with no associated radial-growth decreases in black spruce. Also, soil physicochemical properties were fairly similar among the lichen woodland sites, as they all have thin, coarse-textured, acidic, nutrient-poor soils with good drainage. Therefore, soil physicochemical properties do not by themselves readily explain the differences in the intensity of growth reduction among sites. However, both drought and soil conditions may have exacerbated the impact of spruce budworm. Therefore, we hypothesize that if drought and soil conditions had detri-

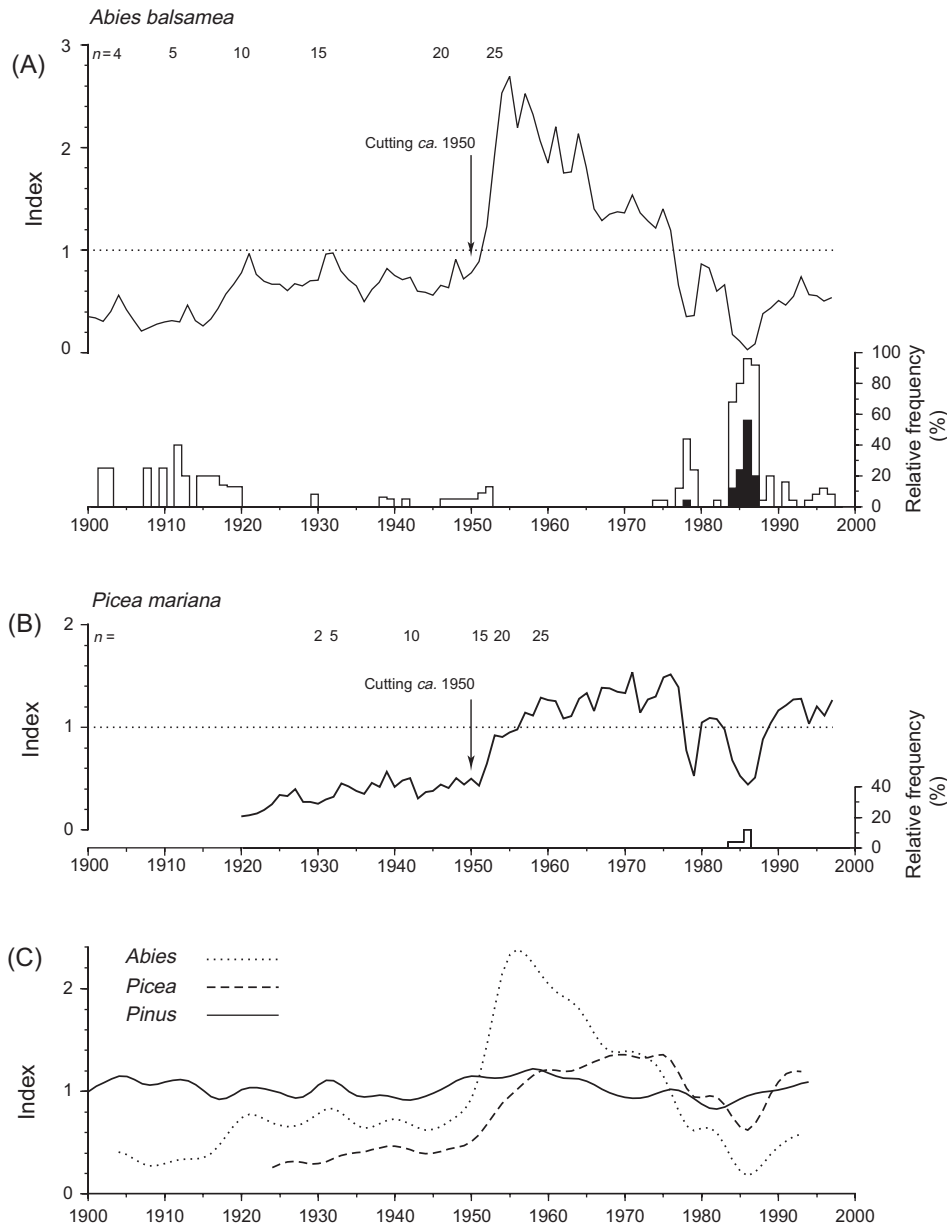
mental effects on black spruce, they were of secondary importance, and that spruce budworm defoliation was the predominant factor that triggered black spruce decline.

The role of the epiphytic lichen *Bryoria* in the spruce decline is still unknown. There is a strong relationship between the intensity of radial-growth reductions caused by the spruce budworm and the abundance of *Bryoria* (Fig. 9), indicating that there might be a link between spruce budworm defoliation and the presence of *Bryoria*. One hypothesis would be that *Bryoria* could be only growing on the parts of trees that were defoliated during spruce budworm infestations, thus acting as a marker of the defoliation.

Future of damaged stands

Although several lichen woodlands were heavily affected by the spruce budworm, tree-ring data show that they are now recovering, as mortality has stopped and radial growth of surviving trees has returned to pre-outbreak levels (index = 1). Even the most damaged stands (e.g., site 27), where many mature trees were killed, have several small, healthy layers (Fig. 2) that will eventually replenish the stands. However, standing dead trees and damaged surviving trees, both covered with *Bryoria*, still abound in many lichen woodlands, giving the false impression that the decline is

Fig. 6. Balsam fir (A) and black spruce (B) standardized chronologies in the mixed stand (site 24), which was clear cut ca. 1950. Bars represent relative frequency of incomplete (open) and missing (solid) rings. *n* is the cumulative number of trees used in the chronologies. (C) Filtered chronologies (9-year low-pass filter) of balsam fir (dotted line), black spruce (broken line), and jack pine (solid line).



still occurring. The persistence of the visual impact of the infestation is likely associated with the dominance of black spruce. In the fir–spruce forests, the opening created by the death of mature trees is rapidly filled by fir seedlings, which experience fast growth release (MacLean 1984). In contrast, the lichen woodland is a low-diversity ecosystem driven by autosuccession (sensu Mueller-Dombois 1993), i.e., a single self-replacing tree species (here, black spruce). Therefore, after a spruce budworm outbreak, there is no early successional species to take over, and only the slow growth of black spruce layers will lead to the reconstruction of healthy lichen woodland stands. The destruction of a cohort of individuals does not imply the disappearance of the species; therefore the black spruce decline may be seen as a nat-

ural phenomenon in the cyclic development of black spruce stands, similar to other natural forest declines (Mueller-Dombois 1987, 1992, 1993).

On the contrary, the long-term maintenance of lichen woodlands in the PGJ could be compromised if fire occurs in stands damaged by the spruce budworm. Black spruce stands severely damaged by the budworm infestation seem to have a low seed bank (S. Payette, A. Delwaide, and M. Simard, in preparation), which would impair post-fire regeneration. The occurrence of fire in such stands would thus result in the opening of the forest or in further clearing of the lichen woodlands. Such shifts from closed-crown spruce–moss forests to lichen woodlands have been documented, and it has been proposed that the combined impact of spruce

Fig. 7. (A) Life-span of 50 dead balsam fir trees in site 24, showing the period of normal growth (solid bars) and the period of morbidity (open bars) preceding death. Morbidity corresponds to the years prior to death where rings are incomplete or very narrow. (B) Frequency of morbidity initiation (open columns) and death (solid columns). Some trees had their last rings isolated from the rest of the series by an undetermined number of missing rings. Because these rings could not be cross-dated, they are represented by the “+” sign at the end of the series in Fig. 7A, and they were not included in the mortality data in Fig. 7B.

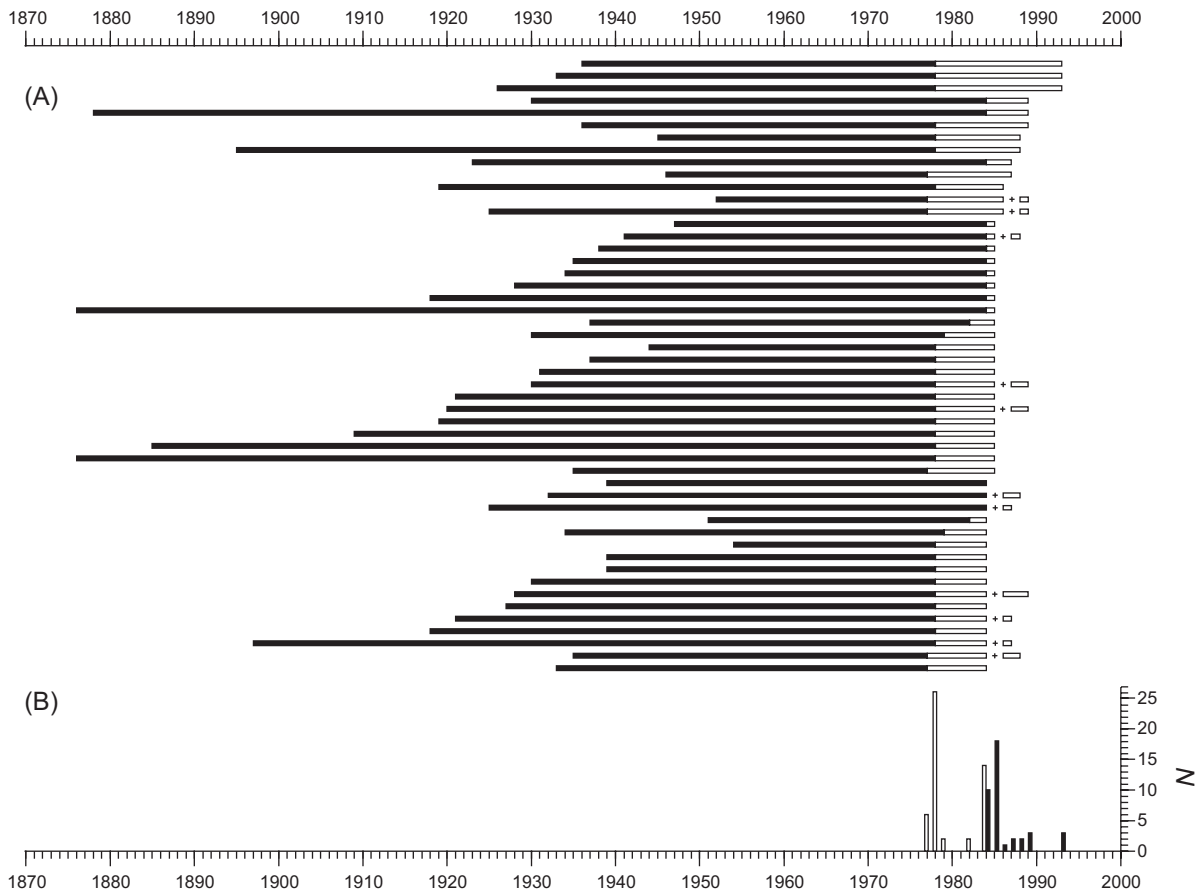
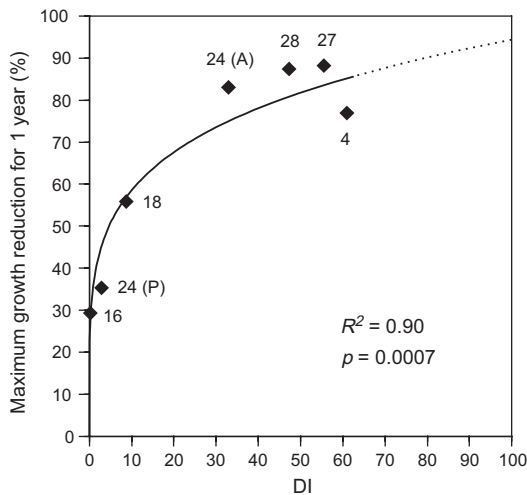


Fig. 8. Relationship between the decline index (DI) and maximum growth reduction for 1 year during the spruce budworm outbreak. Analysis of variance was done on logarithmically transformed data. The regression equation between the DI (x) and the maximum growth reduction for 1 year (y) is $y = 36.224x^{0.208}$. Each symbol represents a site. In site 24, conifer species (A, *Abies balsamea*; P, *Picea mariana*) are identified.



budworm infestation and fire accounts for the presence of low-latitude lichen woodlands (Payette et al. 2000).

Conclusion

Although little is known about the occurrence of spruce budworm infestations in black spruce – lichen woodlands (Payette et al. 2000), this study has shown the major impact of the last outbreak of this defoliator on several lichen woodlands at their southernmost range limit. Spruce budworm defoliation caused temporary growth reductions and mortality in black spruce stands, which are now covered with *Bryoria*. Epiphytic lichen cover (and therefore decline index) is related to the intensity of past defoliation, not to the present health status of the trees. Consequently, even black spruce stands that have survived defoliation and show radial-growth recovery presently bear high loads of *Bryoria* and were given a high decline index. Therefore, the phenomenon that we described as “black spruce decline” may not conform to Manion’s (1991) definition of “decline disease”, i.e., a disease of complex abiotic and biotic origins, with at least three factors involved (one each from the categories of predisposing, inciting, and contributing), leading to a gradual reduction in health and growth. Nevertheless, the black

spruce decline shares with many other past and current forest declines the common characteristic of having an etiology that is not completely understood (Sinclair and Hudler 1988; Houston 1992).

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