



Stability in the patterns of long-term development and growth of the Canadian spruce–moss forest

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ABSTRACT

Aim The spruce–moss forest is the main forest ecosystem of the North American boreal forest. We used stand structure and fire data to examine the long-term development and growth of the spruce–moss ecosystem. We evaluate the stability of the forest with time and the conditions needed for the continuing regeneration, growth and re-establishment of black spruce (*Picea mariana*) trees.

Location The study area occurs in Québec, Canada, and extends from 70°00' to 72°00' W and 47°30' to 56°00' N.

Methods A spatial inventory of spruce–moss forest stands was performed along 34 transects. Nineteen spruce–moss forests were selected. A 500 m² quadrat at each site was used for radiocarbon and tree-ring dating of time since last fire (TSLF). Size structure and tree regeneration in each stand were described based on diameter distribution of the dominant and co-dominant tree species [black spruce and balsam fir (*Abies balsamea*)].

Results The TSLF of the studied forests ranges from 118 to 4870 cal. yr BP. Forests < 325 cal. yr BP are dominated by trees of the first post-fire cohort and are not yet at equilibrium, whereas older forests show a reverse-J diameter distribution typical of mature, old-growth stands. The younger forests display faster height and radial growth-rate patterns than the older forests, due to factors associated with long-term forest development. Each of the stands examined established after severe fires that consumed all the soil organic material.

Main conclusions Spruce–moss forests are able to self-regenerate after fires that consume the organic layer, thus allowing seed regeneration at the soil surface. In the absence of fire the forests can remain in an equilibrium state. Once the forests mature, tree productivity eventually levels off and becomes stable. Further proof of the enduring stability of these forests, in between fire periods, lies in the ages of the stands. Stands with a TSLF of 325–4870 cal. yr BP all exhibited the same stand structure, tree growth rates and species characteristics. In the absence of fire, the spruce–moss forests are able to maintain themselves for thousands of years with no apparent degradation or change in forest type.

Keywords

¹⁴C dating, boreal forest, chronosequence, disturbance, ecosystem stability, fire, lichen woodland, *Picea mariana*, soil organic layer, spruce–moss forest.

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INTRODUCTION

In North America, the boreal forest is divided into three zones along a south–north gradient: the closed-crown forest (spruce–

moss forest), the open forest (lichen woodland), and the forest tundra (Rowe, 1959; Wilton, 1964; Hare & Ritchie, 1972; Rowe & Scotter, 1973; Larsen, 1980; Payette, 1992). Although spruce–moss forests and lichen woodlands can co-exist on

mesic sites in the closed-crown forest zone (Hare, 1959; Hustich, 1965; Gerardin, 1980), it is rare that spruce–moss forests are found in the open forest zone (Payette, 1992). While these two forest types can exist independently from one another, spruce–moss forests can be replaced by lichen woodlands in the closed-crown forest zone (Payette *et al.*, 2000; Jasinski & Payette, 2005).

Several authors have hypothesized that, in the absence of fire, lichen woodlands develop into closed-crown forests (Maikawa & Kershaw, 1976; Kershaw, 1977; Foster, 1985). This succession was noted by Foster (1985) in Labrador, where the climate is particularly wet. In the Northwest Territories, this transformation into spruce–moss forest is rare, and lichen woodlands persist as a result of recurrent fires (Maikawa & Kershaw, 1976; Kershaw, 1977; Johnson, 1981). While the possibility exists of a succession from lichen woodlands to spruce–moss forests, there is no evidence to support this forest transformation in eastern Canada (Payette *et al.*, 2000). Jasinski & Payette (2005) also demonstrated that in the southern boreal forest of Québec, several lichen woodlands do not develop into spruce–moss forests and are thus not a stage in succession. Rather, lichen woodlands are an alternative stable state that persists in the same climatic and edaphic conditions as spruce–moss forests (Jasinski & Payette, 2005). Overall, the spruce–moss forest is the dominant forest ecosystem across boreal North America, particularly in Canada, where it is largely distributed across the Precambrian shelf, east of the Rockies to Newfoundland (Linteau, 1955; Rowe, 1959; Hatcher, 1963; Damman, 1965, 1983; Hustich, 1965; Lafond & Ladouceur, 1968; Cogbill, 1985).

Fire is the principal disturbance that destroys mature spruce–moss forests (Heinselman, 1981; Cogbill, 1985; Bergeron *et al.*, 2004). Severe fires that consume the organic material, exposing the mineral soil, create a favourable environment for black spruce [*Picea mariana* (Mill.) B.S.P.] regeneration (Vincent, 1965; Black & Bliss, 1980). However, little is known concerning the long-term stability of the spruce–moss forest in the absence of fire (Bonan & Shugart, 1989). The conditions favourable for the maintenance of the closed-crown forest are uncertain, and more information is thus required.

Consequently, the first objective of this study was to determine the area of the landscape occupied by spruce–moss forest along a latitudinal gradient in eastern Canada. This information aided in choosing the study sites. The second objective was to characterize the structure of the northern spruce–moss forest on mesic sites. This includes community species composition, depth of the forest-floor organic layer, tree growth rates, fire history and forest cover patterns. These characteristics will allow a better understanding of the spruce–moss forests, and how these forests develop over time. The third objective was to determine what conditions

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Figure 1 Map of Québec with its respective

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1:50,000, obtained from the Québec Department of Natural Resources, allowed for the orthorectification of the aerial photos through the use of ground control points. For the region above 52°00' N, hydrological maps are available only at a scale of 1:250,000. The (x,y) coordinates of the lakes and rivers of the hydrological maps were matched with the same coordinates on the aerial photos, and were used to determine the algorithm to orthorectify the image. Once this process had been performed, the spruce–moss forests were digitized using polygons, with a minimum mapping unit (or pixel size) of 25 m².

The ratio of total spruce–moss forest cover and total land cover was then used to determine the cover of spruce–moss forests along each transect. The total spruce–moss forest cover was determined simply by adding the area occupied by spruce–moss forest along each transect. The total land cover for the first 19 transects is the same total forest cover as determined by Girard *et al.* (2008). Total land cover for transects 20 through 34 was determined by digitizing the lakes of the aerial photo images and subtracting the area covered by water.

Site selection

At least 1 plot per line, for transects 15–28, was initially sought. However, due to the remote conditions of the area, we knew this may not be possible. With the aid of the mapped spruce–moss forests, each line was flown to by helicopter directly from camp. Then the first spruce–moss forest *en route* along that transect that was found to be both large enough for a plot and accessible by helicopter (i.e. within 1 km walk from a bog, lake or beach on which the helicopter could safely land) was chosen as a site. A total of 14 sites were selected this way (Fig. 1). No sites were chosen between transects 2 and 14 as this forest is heavily influenced by anthropogenic disturbances including forestry, mining, agriculture and fire suppression.

An additional five sites near transect 1 were chosen at random within the Parc National des Grands-Jardins and the Réserve faunique des Laurentides, as the histories of these areas are well-known and well-documented. The selected sites, closed spruce–moss stands distributed along forest roads, were identified among a mosaic of burned and logged sites. Five out of 10 identified spruce–moss stands were chosen by random selection. While logging has not occurred since the creation of the Parc National des Grands-Jardins in 1981, forestry activity continues in the Réserve faunique des Laurentides to this day. Also, fire is the most important disturbance in the Parc, whereas it is a rare occurrence in the Réserve. Spruce budworm is prevalent in both areas (Jasinski & Payette, 2005).

Each of the 19 sites was sampled in a spruce–moss forest of unknown age, dominated by black spruce. Balsam fir [*Abies balsamea* (L.) Mill.] occurred often at each site, but its presence was not a predetermined site-selection factor. To ensure comparable data, the 19 sites had similar topography (mid-slope), soil type (well-drained), and substrate (loamy sand) characteristics.

Site characteristics

A randomly placed 500-m² quadrat (50 × 10 m) situated at least 20 m from the bordered edge of the spruce–moss forest was used for sampling purposes. The position of the study quadrat was chosen by a random draw between two preselected contiguous quadrats. Within the quadrat, the diameter at breast height (d.b.h., at 1.3 m) was measured for each tree > 2 cm d.b.h. Tree species and status (live, dead standing, dead fallen) were noted. The 10 most dominant black spruce trees situated within the spruce–moss forest, either within the quadrat or < 10 m from the quadrat edge, were cut at the base for dendrochronological and growth purposes. From these 10 trees sampled, a total of five discs per tree were obtained at equal distances, the precise intervals depending on the height of the tree, in order to perform a stem analysis. In addition, a variable number of the largest balsam fir trees were cut at the base to determine approximate age and possible spruce budworm epidemics. Balsam fir trees, however, were cut at only 11 of the 19 sites sampled.

Tree seedlings and layers < 2 cm d.b.h. were counted in 1-m² subplots, each separated by 1 m along one of the 50-m lines of the quadrat, for a total of 25 subplots. Using the same 50-m line, the vegetation was inventoried using the point–intercept method (Mueller-Dombois & Ellenberg, 1974), where each species frequency was noted based on plant recording at every 50-cm interval, for a total of 101 points. Species present in the site, but not inventoried along the 50-m transect, were also noted.

Soils and fire history

The granular composition (sand, silt, clay) of the mineral soil was measured using a modified Bouyoucos hydrometer method (McKeague, 1978). The CaCl₂-pH of the soil was also determined for each site. This aided in ensuring that each site had similar drainage and soil properties.

In each site, a total of 11 soil profiles were examined at 5-m intervals along the 50-m line of the quadrat. The depth of the organic material layer was then recorded, and measured in the following categories (Canadian Soil Survey Committee, 1978): L (litter), F (fibrose), FH (fibrose-humic), HF (humic-fibrose), H (humic). The position of any charcoal layers within the soil profile, relative to the organic material and mineral soil, were also noted, as this would indicate the severity of the last fire. Individual charcoal fragments were sampled from each profile (when possible) for ¹⁴C dating in order to determine the age of the last fire. When no charcoal layers were found, a thin layer of the organic material in contact with the mineral soil was sampled to obtain an apparent minimum age of the stand.

In order to determine a minimum time since last fire (TSLF) for the 19 sites, a total of 54 ¹⁴C dates were obtained, 49 of which were charcoal and five organic material. It is important to note that for this study, each charcoal sample dated was one single piece of burned wood. ¹⁴C dating by

accelerator mass spectrometry (AMS) techniques permits individual charcoal fragments to be dated separately, thus providing individual fire dates. At least three charcoal dates were obtained at most sites in order to determine the age of the last fire. The radiocarbon dates of soil charcoal approximate the actual dates of fire in sites frequently burned and dominated by small-sized, short-lived tree species, as is generally found to be the case in eastern North America. In the western USA and Canada, the charcoal dates may not approximate actual dates of fire, because of the extended inbuilt age of soil charcoal associated with the greater age of dead wood of large-sized, long-lived species producing charcoal during infrequent fires (Gavin, 2001).

All samples dated were examined under a microscope using a 40× magnification and cleaned to ensure no roots or other contaminants were present. An HCl–KOH pretreatment was conducted at the radiochronology laboratory of the Centre d'études nordiques, Université Laval. Final AMS dating was performed at the Keck Carbon Cycle AMS Facility, University of California, Irvine, CA, USA. All dates presented have been calibrated to 2 sigmas using the Intcal04.14c calibration data set (Reimer *et al.*, 2004) in CALIB 5.0.2html (Stuiver *et al.*, 2005).

The most recent ^{14}C date of charcoal obtained for a site (Table 1) was considered to be the TSLF. For sites 1, 9, 10 and 13, however, the median of the ^{14}C -calibrated age range with the highest probability was younger than the oldest tree sampled. Thus, the oldest date from the end of the calibrated ^{14}C range was considered as a possible age for the sites, and

these dates are consequently considered to be a minimum TSLF. By dating several pieces of charcoal, not only could the actual potential TSLF be obtained, but the dates of other, older fire events could also be determined. The age of the trees sampled for each site was also used to aid in determining the TSLF. As none of the trees sampled had fire scars, the TSLF would thus be greater than the oldest tree sampled.

Site 18 was the only site where the estimated TSLF was obtained by dating the organic matter at contact with the mineral soil. No charcoal fragments were dated because the only charcoal fragment found throughout the site was indeed a piece of charcoal. Thus, for the reason that only an apparent age could be obtained for this site, the TSLF is considered to be a minimum TSLF.

Stand structure and stem growth analysis

Stand structure and stages of stand development were analysed for each site using size structure graphs, where the d.b.h. of the live and dead trees were grouped into 1-cm classes and the number of stems in each class was plotted against its frequency. Diameter size class 1, however, includes all trees < 2 cm d.b.h. This analysis was performed separately for spruce and fir.

Tree discs were dried and finely sanded before dating with a microscope under 16× and 40× magnifications. To ensure the accurate dating of each disc, diagnostic light rings (rings where latewood cells have thin walls, thus appearing light in colour;

Table 1 Summary of time since last fire (TSLF), as well as other past fires, for each of the 19 sites studied in Québec, Canada.

Site	Transect	Latitude	Longitude	Age of oldest*		TSLF (Cal. yr BP)	Min./Max.†	Other fires	
				Fir	Spruce			(Cal. yr BP)	(Cal. yr BP)
1	1	47°37'17.6"	70°57'32.2"	120	122	200	Min.	–	–
2	25	53°40'59.2"	71°02'15.9"	–	194	240	Min.	770	–
3	26	53°55'52.2"	71°02'36.2"	–	215	4870	Max.	–	–
4	26	53°55'57.4"	71°25'17.6"	–	261	1130	Max.	2730	3510
5	23	53°10'49.5"	70°16'32.8"	–	270	470	Min.	1360	1760
6	23	53°10'51.3"	70°50'17.8"	208	257	1950	Max.	2820	3770
7	24	53°26'11.5"	70°26'51.4"	181	199	530	Max.	840	–
8	27	54°10'52.1"	71°33'36.1"	124	192	2420	Max.	3000	–
9	1	47°38'59.0"	71°02'58.9"	118	121	142	Min.	2760	–
10	1	47°42'48.8"	70°59'04.8"	105	120	144	Min.	–	–
11	1	47°44'59.3"	70°48'57.4"	–	78	130	Max.	710	–
12	1	47°36'04.8"	70°59'24.1"	–	123	240	Min.	–	–
13	15	51°07'21.7"	68°52'56.1"	–	104	118	Min.	520	–
14	19	52°11'05.0"	70°41'06.5"	239	252	1770	Max.	2670	3520
15	17	51°41'10.6"	70°37'04.9"	198	245	770	Max.	1120	–
16	18	51°55'59.4"	70°44'24.6"	197	207	240	Min.	700	–
17	17	51°40'55.1"	70°09'44.5"	186	249	480	Min.	–	–
18	28	54°25'45.0"	71°21'15.8"	–	258	2490	Min.	–	–
19	28	54°26'03.1"	70°54'32.8"	224	236	300	Min.	–	–

*Age of the oldest black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) trees sampled in the site, which helped determine the accuracy of the youngest ^{14}C dates obtained as well as the TSLF.

†Whether the TSLF obtained by ^{14}C dates is a minimum (Min.) or a maximum (Max.) estimate.

Filion *et al.*, 1986) were noted and compared with a known light-ring chronology for northern Québec. For those discs taken at the base of each tree sampled, ring widths were measured along two radii using a Velmex micrometer (Velmex Inc., Bloomfield, NY, USA) under a 40× magnification, for a precision of 0.002 mm. Using the ring width data, samples were again cross-dated on a site-by-site basis using the program COFECHA (Holmes, 1983). The homogeneity of samples within the sites were also examined using COFECHA, and radii that were accurately dated but fitted poorly statistically with the average curve of the site (due to growth anomalies such as reaction wood, i.e. < 5% of all tree discs) were disregarded.

Average radial growth was calculated for black spruce and balsam fir by averaging the ring width measurements of each basal disc, and then taking an average (10 basal discs) per site. Average height growth was calculated using the age of each tree disc sampled along the stem, where the height increment was divided by the age increment. If the age of the disc could not be dated precisely (pith not visible due to rot, insect damage, etc.), the disc was not used in the calculated average. Growth analyses were performed only for black spruce.

RESULTS

Spruce–moss forest distribution

Along a south–north gradient, the proportion of spruce–moss forest relative to total land cover in the 1950s follows a skewed bell-shaped distribution, where the majority of the spruce–moss forest occurs roughly between 49° and 51° N (Fig. 2). Just as the

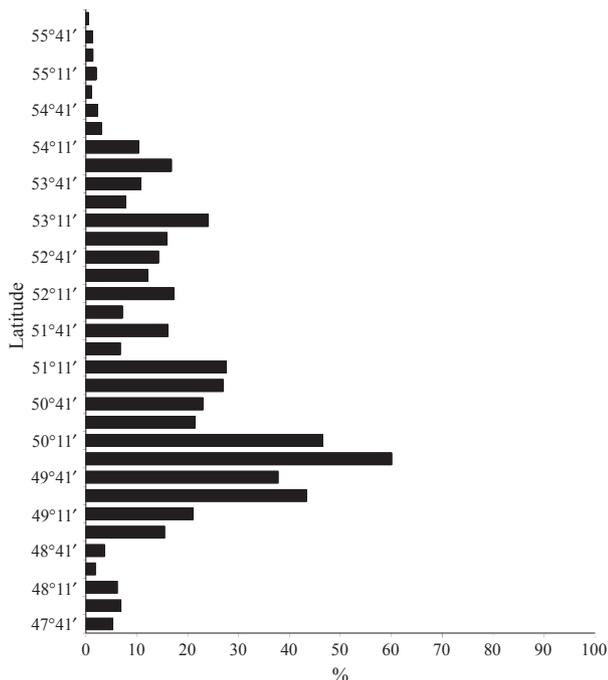


Figure 2 The proportion of spruce–moss forest (relative to total land cover in the 1950s) as a function of latitude.

proportion of spruce–moss forest decreases in the north, the proportion occupied by lichen woodland increases, as shown, for example, by Girard *et al.* (2008). North of 54° N, the spruce–moss forest is restricted to easterly and northerly slopes within a matrix of lichen woodlands. The northern limit of the spruce–moss forest coincides with the southern limit of the forest tundra zone near the Caniapiscou highlands at about 56° N.

Site characteristics

Of the 19 sites sampled, five were on islands where there was no evident slope or aspect; otherwise, the slope for each site was generally between 5° and 10°. Elevation ranged from 360 to 953 m. A total of 62 species of trees, shrubs, herbs and terrestrial mosses, lichens and liverworts were found in the 19 spruce–moss stands studied. Of the tree species, black spruce was the most dominant in all sites, followed by balsam fir.

Soils

The soils were typically podzols or gleyed podzols. Drainage was good to moderate, and the mineral soil texture was sandy loam or loamy sand. The mineral soil was acidic, with a pH ranging from 2.93 to 4.05. Total average depth of organic matter varied among sites, ranging from 16.1 to 44.2 cm (Fig. 3). Site 3, with the highest total average depth, also had the highest total organic matter depth at 79 cm. In general, the F and FH layers were the most prominent organic types among the sites, followed by the more decomposed HF and H layers.

Fire history

As the charcoal layer in nearly all the soil pits examined occurred just below the organic matter, in contact with the mineral soil (Ae horizon), it can be concluded that all of the 19 stands studied established after severe, stand-replacing fires.

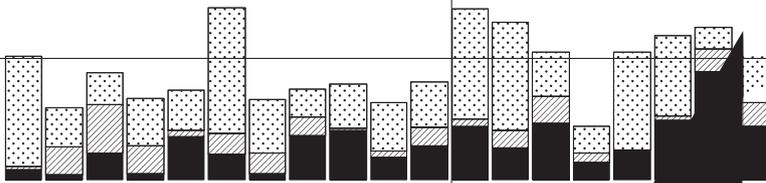
There were very few soil pits where charcoal was found within the organic matter. This was often due to windthrow and soil mixing. Also, because fires do not burn homogeneously, it is possible that there are patches where not all of the organic matter is burned (Miyaniishi & Johnson, 2002).

Time since last fire varied greatly among sites, ranging from 118 to 4870 cal. yr BP (Appendix S1 in Supporting Information). The age of the oldest trees in many of the sites studied is an unreliable detector of TSLF, as the intervals between fires are far longer than the lifespan of spruce and fir (Table 1).

There is a positive linear relationship between TSLF and total average depth of organic matter ($r = 0.76$; $P < 0.01$; Fig. 4). This demonstrates that there is a continuous accumulation of organic material at the surface floor over time.

Stand structure

Concerning live spruce, two different stand structure patterns were found, each corresponding with the age of the stands. In general, for sites with a TSLF < 325 cal. yr BP, such as site 1,



the size-class distribution followed a third-order characteristic of young stands. The number of live spruce trees which is the start of establishment after fire (> 15 cm) d.b.h. is the second highest in the class distribution. With senescence, the second cohort is dominant. This is possible shortly after disturbance. In general, graphs of live spruce have a characteristic diameter distribution (Fig. 5c). This curve is typical of mature, old-growth stands, where the

of small-diameter trees is greater than the abundance of large-diameter trees. The size-class distribution graphs of live fir also show a characteristic reverse-J diameter distribution. With spruce, both young and old stands possess this pattern. In the case of sites with a TSLF < 325 cal. yr BP, fir is slowly becoming more predominant in the stands from the fir trees outside the stand creep in and thus the abundance of small-diameter trees is increasing relative to the abundance of large-diameter trees (Fig. 5b). At sites with a TSLF > 325 cal. yr BP, such as site 3, fir is in equilibrium in the stands, and the same pattern is observed (Fig. 5d). Spruce is always the most abundant tree in the spruce-moss forest, and larger fir trees are often affected by spruce budworm.

Vaccinium angustifolium and *Rhododendron groenlandicum* were the most abundant shrubs, whereas *Pleurozium schreberi* is a characteristic species of the spruce-moss forests), *Ptilium crista-castrensis* and *Sphagnum* species were among the most abundant bryophytes in the spruce-moss forests studied. The presence of these species made up more than 40% of the relative abundance of the vegetation in each site. Several lichen species were also found in the spruce-moss forests studied, but their presence was less evident. *Cladonia stellaris* and *Cladonia rangiferina* were the two most abundant lichens found. *Cladonia rangiferina* occurred under the canopy gaps usually caused by spruce budworm.

The simple linear regressions performed on the percentage relative abundance of *Vaccinium angustifolium*, *Rhododendron groenlandicum*, *Pleurozium schreberi*, *Ptilium crista-castrensis* and *Sphagnum* species demonstrated that there are no significant trends ($P > 0.05$) in relation to TSLF (Fig. 6). Also worth noting is the high variability in abundance regardless of the TSLF, which explains the low r -values (ranging from 0.01 to 0.38).

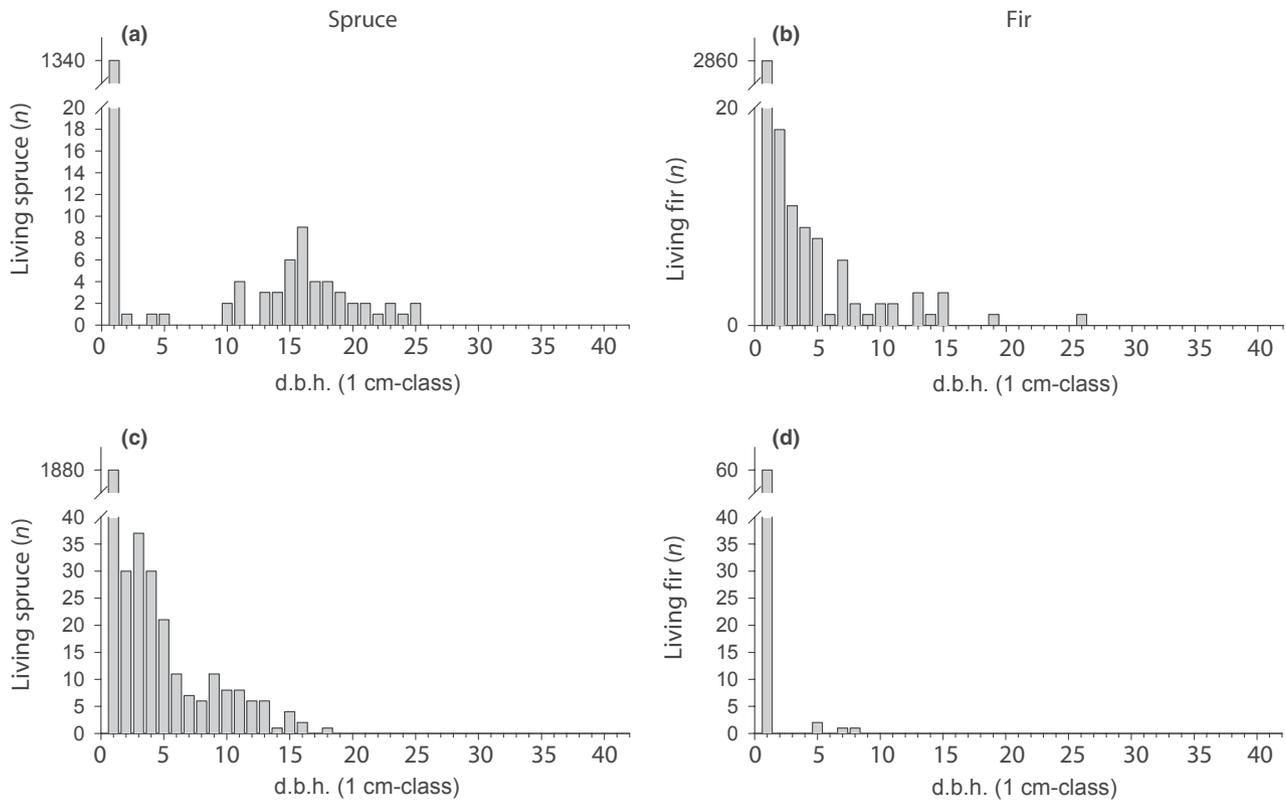


Figure 5 Size-class distribution of (a) live black spruce (*Picea mariana*) in site 1 [time since last fire (TSLF) = 200 cal. yr BP]; (b) live balsam fir (*Abies balsamea*) in site 1 (TSLF = 200 cal. yr BP); (c) live black spruce in site 3 (TSLF = 4870 cal. yr BP); (d) live balsam fir in site 3 (TSLF = 4870 cal. yr BP). Diameter at breast height (d.b.h.) classes are by 1-cm intervals (except d.b.h. class 5 includes d.b.h. values from 5.0 to 5.9 cm); however, d.b.h. class 1 includes all trees with a diameter < 2 cm.

Stem growth analysis

Both the average height and radial growth demonstrated a negative exponential distribution as a function of TSLF (Fig. 7a,d). However, the growth of the trees in the sites with a TSLF < 325 cal. yr BP show a strong negative linear trend over time ($r = 0.87$; $P < 0.01$ for height growth; $r = 0.81$; $P < 0.01$ for radial growth) (Fig. 7b,e). As the stands increase in age, the average growth decreases until a threshold period, which lies between a TSLF of 325 and 500 cal. yr BP (Fig. 7a,d). Beyond a TSLF of 500 cal. yr BP, there is no significant change in height growth ($r = 0.34$; $P > 0.05$) or radial growth ($r = 0.21$; $P > 0.05$) (Fig. 7c,f).

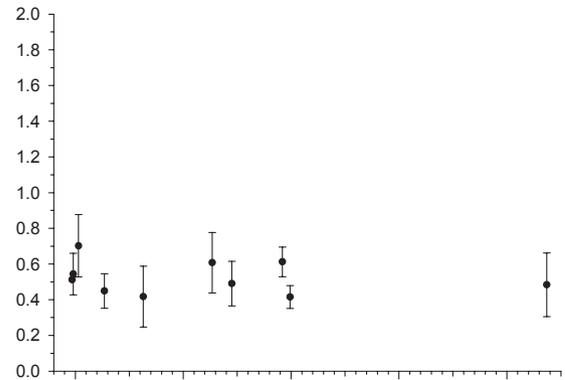
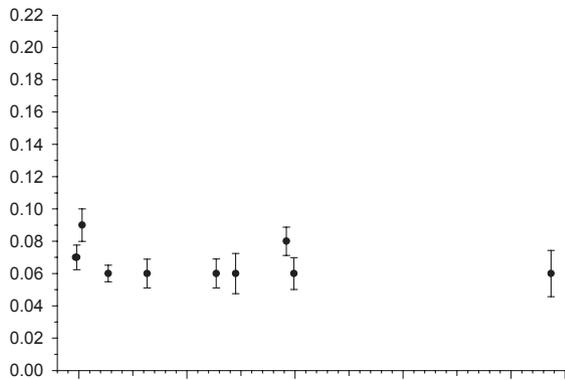
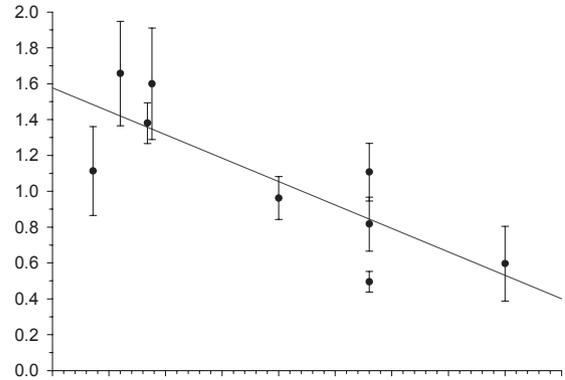
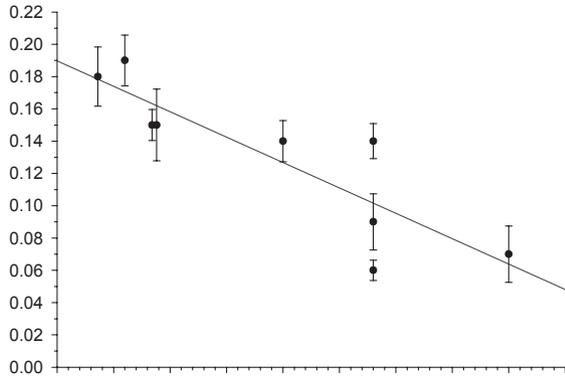
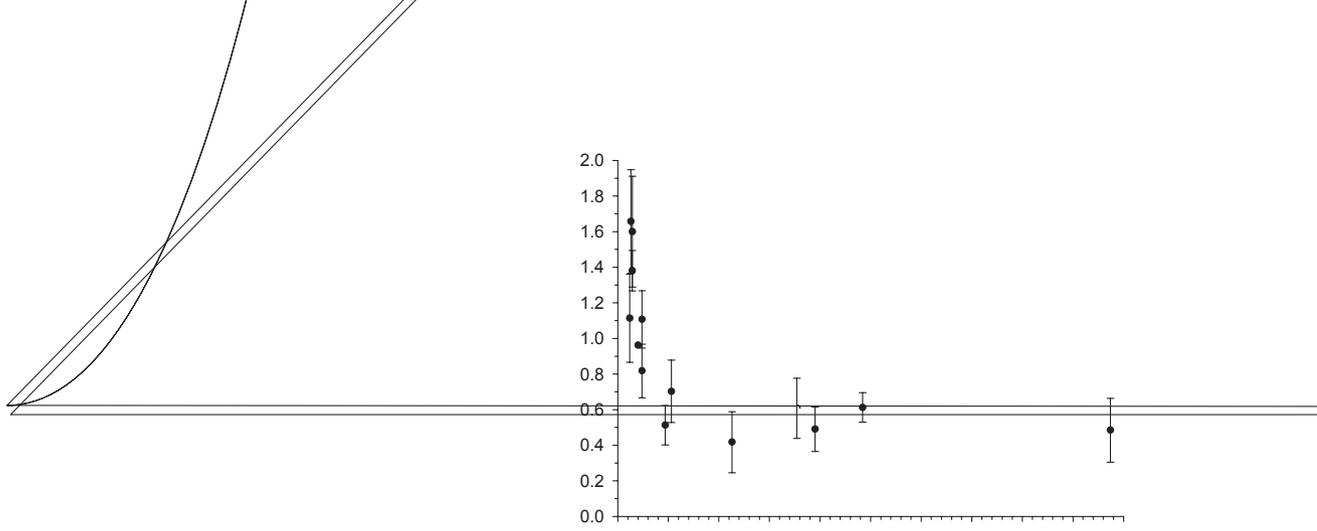
Sites with a TSLF < 325 cal. yr BP represent the growth of trees from the first cohort after disturbance, whereas the trees in the sites with a TSLF > 325 cal. yr BP represent the growth of trees from the subsequent cohorts. The TSLF that divides these two groups reflects the way in which the trees growing on the sites would have regenerated. The first cohort of trees would have developed after fire. The fire would have eliminated surrounding plant competition as well as some, if not most, of the organic matter, releasing nutrients into the soil, and opening the semi-serotinous cones of the black spruce trees. Later, once the forest has matured, the majority of the trees replacing the first cohort would be establishing under very different conditions. Here, black spruce may begin

reproduction not only by seed, but also by layering. The level of competition and the depth of organic matter would be significantly greater than immediately after fire. There are two reasons the cut-off TSLF of 325 cal. yr BP was chosen. The first is that at this point in time there is a shift in the trend in the overall data. The second, more important reason is that a TSLF of 325 cal. yr BP ensured that only the initial post-fire tree cohort was examined, as the second cohort of trees would not have had sufficient time to become the most dominant trees of the stands. This is further justified as the oldest black spruce sampled had minimum ages of just over 250 cal. yr BP (Table 1). Thus grouping the sites into two categories enabled a more accurate interpretation of any influence of TSLF on the average height and radial growth.

DISCUSSION

Characteristics of the spruce–moss forests

Although the majority of the spruce–moss forests that occupy well-drained sites occur within the closed-crown forest zone, several heavily fragmented patches of this forest exist beyond this boundary, into the open forest zone and at the southern edge of the forest tundra zone. These forests are remnant patches of a once more extensive closed-crown forest zone, and



325–4870 cal. yr BP all exhibited the same stand structure and species characteristics. Dominated by black spruce and accompanied by balsam fir, the gap dynamics in these closed-crown forests positively influence the regeneration

required to replace trees that are senescing. Thus, in the absence of fire, the spruce–moss forests are able to maintain themselves for thousands of years with no apparent degradation or change in forest type.

With regard to the understorey vegetation, no differences in species composition or abundance were found with respect to TSLF. It has been suggested that as spruce–moss forests mature, the abundance of *Sphagnum* increases as feather mosses decrease (Taylor *et al.*, 1987; Fenton & Bergeron, 2006; Lecomte *et al.*, 2006; Simard *et al.*, 2007). These studies, however, occur in the Clay Belt of north-eastern Ontario and north-western Québec, an area prone to peat accumulation (so-called paludification) as a result of poorly drained, clay-dominated soils. There, the closed-crown forests are a more extreme hydric variant of the spruce–moss forests, prone to paludification, and are unique to that area. The results of this study differ in that there is no significant change in understorey vegetation, and bryophyte species composition and abundance, in spruce–moss forests that occur in well-drained soils. Furthermore, the spruce–moss forests studied all originated after fires that consumed all the organic material. Fire severity plays an important role in the presence of post-fire vegetation species by killing the regenerative organs of plants on the forest floor (Flinn & Wein, 1977).

It has been argued that spruce–moss forests are an advanced stage of succession of the lichen woodlands (Maikawa & Kershaw, 1976; Kershaw, 1977; Foster, 1985). This is contradictory to the findings of this study. The data here clearly show that spruce–moss forests, on well-drained sites, are not a stage of succession and do not replace lichen woodlands in the absence of fire. Lichen woodlands and spruce–moss forests are two distinct communities. Proof of this lies in the simple fact that the ages of the 19 spruce–moss forest sites examined range from 118 to 4870 cal. yr BP. The only structural difference between young and old spruce–moss forests was that of evenly aged versus unevenly aged. Nor were there any shifts in species composition and abundance associated with stand age. Moreover, all the stands examined occurred on well-drained sites with similar soil texture and pH. All this indicates that the spruce–moss forests should be considered as one alternative stable state. Further evidence comes from the scientific literature, which shows that lichen woodlands are not an early successional stage, but rather an alternative stable state (Jasinski & Payette, 2005). In addition, an exhaustive study by Girard *et al.* (2008) has demonstrated that the lichen woodlands in the closed-crown forest zone may once have been part of the spruce–moss forests. Since the initial fire, these woodlands have remained open forests; that is, they have not undergone a transformation into spruce–moss forest. These lichen woodlands occur under the same set of environmental conditions as the spruce–moss forests of this study. Thus, the transformation of spruce–moss forest to lichen woodland, and the persistence of the lichen woodland over time, demonstrates that these forest types are alternative stable states, and clearly not stages in succession.

Re-establishment of the spruce–moss forests

The re-establishment of spruce–moss forests is largely dependent on the factors that permit an abundance of black spruce

regeneration, such as fire. All of the spruce–moss forests examined in this study established after severe, stand-replacing fires that consumed the organic material. Studies have shown that regeneration (with regard to germination, seedling growth and survival) of coniferous boreal species is inversely related to the amount of unburned organic material (Zasada *et al.*, 1983, 1987; Jayen *et al.*, 2006; Lecomte *et al.*, 2006). Moisture availability is equally important to the germination and survival of black spruce (Foster, 1985) due to its high susceptibility to water stress (Black & Bliss, 1980).

The regeneration of black spruce after severe fires typically results in evenly aged stands, as most of the seedlings generally establish during the first few years after fire (Cogbill, 1985; Morneau & Payette, 1989; Sirois & Payette, 1989). The success of seedling establishment during the first 10–15 years after fire is crucial to the regeneration of the spruce–moss forests (Sirois & Payette, 1991). This is due to a decrease in seed availability and seedbed suitability over time as a result of accumulating organic matter, and an increase in competition from other species that have become established.

Other factors, aside from burn severity, can influence the extent of the post-fire regeneration. Compound perturbations have been shown to yield different ecological consequences (Paine *et al.*, 1998), and in the case of the North American boreal forest, significantly reduce regeneration. In the southern boreal forest of Québec, the impact of both spruce budworm outbreak and fire has led to the transformation of spruce–moss forests into lichen woodlands (Payette *et al.*, 2000; Payette & Delwaide, 2003; Jasinski & Payette, 2005). The interval between fires is another factor that can affect regeneration potential. For example, Le Goff & Sirois (2004) found that black spruce stands subjected to successive fires over short intervals had a drastically reduced quantity of black spruce regeneration.

Post-fire regeneration is thus the key driving force behind future stand development. However, the development of a spruce–moss forest depends on an abundance of successful black spruce germinants. In order for this to occur, the right conditions and disturbances are required. We can assume that the spruce–moss forests examined in this study were subjected to the perturbations required for the continuation of these stands. And since the forests studied were subjected to severe fires, it can be presumed that no other disturbances occurred simultaneously.

Stability of the spruce–moss forests

During the process of verifying the aerial photos in the field, it was observed that many spruce–moss forest stands no longer exist. Large areas of spruce–moss forest, visible on the aerial photos from the 1950s, have since burned. While in many cases not enough time has elapsed since fire to determine the abundance of regeneration, some areas did appear to have become replaced by lichen woodlands. These observations are supported by the recent findings of Girard *et al.* (2008), who found an increase in the area occupied by lichen woodlands,

which were once closed-crown forest, within the same study region.

Worth noting is the abundance of spruce–moss forests found on islands, particularly north of the closed-crown forest zone. As the main source of wildfire in the boreal forest comes from lightning (Heinselman, 1981; Johnson, 1992), the chance of it striking the mainland is much higher than the chance of it striking an island, due to a larger area of intercept. The same can be applied to the size of islands, as larger islands have a higher fire frequency and have been burned more recently than smaller islands (Wardle *et al.*, 1997). The two oldest stands studied here occurred on islands (sites 3 and 18). These two sites also had the highest total average depth of organic matter. Furthermore, it is understood that low-severity fires that do not consume all the soil organic material are prevalent in areas with long fire cycles. This is the result of the thick forest-floor cover that has accumulated throughout the fire-free period (Simon & Schwab, 2005). These forest floors also become denser over time as the lower organic horizons become compacted and humified. The degree to which the forest floor burns depends not only on the conditions of the duff layer, but also on climate and landscape conditions (Miyaniishi & Johnson, 2002). Consequently, it would require a very severe fire under ideal circumstances to consume the entire forest floor that has accumulated in these ancient spruce–moss forests. Given that the regeneration capacity of black spruce decreases along a south–north gradient (Sirois, 2000), the probability that all the required conditions are present for the re-establishment of these spruce–moss forests following fire is not high.

CONCLUSIONS

For this study, the structure of the spruce–moss forests, as well as the conditions required for their continuing regeneration and re-establishment, were determined using a variety of techniques, including aerial photos, ¹⁴C dating (by AMS) and tree-ring dating. The results also allowed for the evaluation of the stability of the northern spruce–moss forest as a function of time and disturbance, including fire. In the absence of fire, the spruce–moss forests of eastern Canada can remain in an equilibrium state, driven by secondary disturbances, for many centuries. The continuing regeneration and re-establishment of the spruce–moss forest, however, is dependent on severe, stand-replacing fires that consume all the organic material. It is equally important that the post-fire regeneration is sufficient to support the establishment of this closed-crown forest. Thus, those factors that influence regeneration drive the state of the forest after major disturbance. The spruce–moss forests are part of an alternative stable state, where compound perturbations and/or fires that do not consume all the organic material cause a shift in states, resulting in the spruce–moss forest being replaced by lichen woodland. Further research is needed to determine why there has been a change in disturbance type over the past few centuries, especially with regard to climate change, which has been controlling the shifting landscape.

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SUPPORTING INFORMATION

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Appendix S1 ¹⁴C dates from the 49 charcoal and five organic material samples for the 19 study sites in Québec, Canada.

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