

Four millennia of woodland structure and dynamics at the Arctic treeline of eastern Canada

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Abstract. Paleocological analysis using complementary indicators of vegetation and soil can provide spatially explicit information on ecological processes influencing trajectories of long-term ecosystem change. Here we document the structure and dynamics of an old-growth woodland before and after its inception 1000 years ago. We infer vegetation and soil characteristics from size and age distributions of black spruce (*Picea mariana* (Mill.) B.S.P.), soil properties, plant fossils, and paleosols. Radiocarbon ages of charcoal on the ground and in the soil indicate that the fire return interval was ~300 years between 2750 and 1000 cal. yr BP. No fire evidence was found before and after this period despite the presence of spruce since 4200 cal. yr BP. The size structures of living and dead spruce suggest that the woodland is in equilibrium with present climate in absence of fire. Tree establishment and mortality occurred regularly since the last fire event around 950 cal. yr BP. Both layering and occasional seeding have contributed to stabilize the spatial distribution of spruce over the past 1000 years. Since initial afforestation, soil development has been homogenized by the changing spatial distribution of spruce following each fire. We conclude that the history of the woodland is characterized by vegetation shifts associated with fire and soil disturbances and by millennial-scale maintenance of the woodland's structure despite changing climatic conditions.

Key words: black spruce; boreal forest; climatic change; fire disturbance; forest-tundra; lichen woodland; old-growth forest; paleosol; *Picea mariana*; soil; subarctic; treeline.

INTRODUCTION

Old-growth forests are rare across the temperate and boreal forest biomes (Pickett and White 1985, Oliver and Larson 1996, Lorimer et al. 2001, Franklin et al. 2002, Payette et al. 2008). They may be several hundred or thousand years of age, and are composed of trees regenerating and growing without the direct influence of non-climatic allogenic disturbances (Pickett and White 1985, Oliver and Larson 1996, Payette et al. 2008). Such forest stands are able to maintain themselves through autogenic processes promoting single tree replacements in gaps (Pickett and White 1985). Dominant tree species in old-growth forests are composed of all-aged and all-sized living and dead individuals indicating continuous replacement, with canopy species producing a sufficient number of seedlings and saplings. The age and size (height and diameter) distributions of dominant tree species in old-growth stands correspond to the common reverse J-shaped curves, where a demographic balance exists between canopy tree species and advanced regeneration (e.g., Payette et al. 1990, Kneeshaw and Gauthier 2003, Helms 2004, Lilja et al. 2006). The time elapsed between two consecutive disturbances is gener-

ally longer than the average life span of the dominant species in old-growth forests (Lorimer 1980, Payette et al. 1990, Kneeshaw and Bergeron 1998). However, the life spans of trees vary considerably in old-growth forests located in different regions. For example, a given tree species has a far longer average age at death in warm-temperate forests than in cold-temperate forests (Payette et al. 1990, Lorimer et al. 2001).

In the drier parts of the circum-boreal forest, old-growth stands are rare because of the short fire cycles (Johnson 1992, Payette 1992, Bergeron et al. 2004). Black spruce (*Picea mariana* (Mill.) B.S.P.), one of the dominant tree species in the North American boreal forest, generally takes advantage of fire as it produces semi-serotinous cones that release seeds massively during a fire event and contribute to forest regeneration (Black and Bliss 1980, Viereck and Johnston 1990). In the absence of fire, the species is able to maintain an advanced regeneration population beneath and between canopy trees under steady-state conditions. Near the northern limit of the species in eastern Canada, the fire cycle is slowed greatly because of humid conditions associated with the influence of Hudson Bay (Payette et al. 2008). In this region, woodlands (open forests) are less susceptible to fire, and the lack of extensive forest fuels significantly reduces fire propagation. Although sexual reproduction is low because of the small heat sums during the cool growing season (Sirois 2000, Meunier et al. 2007), regeneration through layering promotes the

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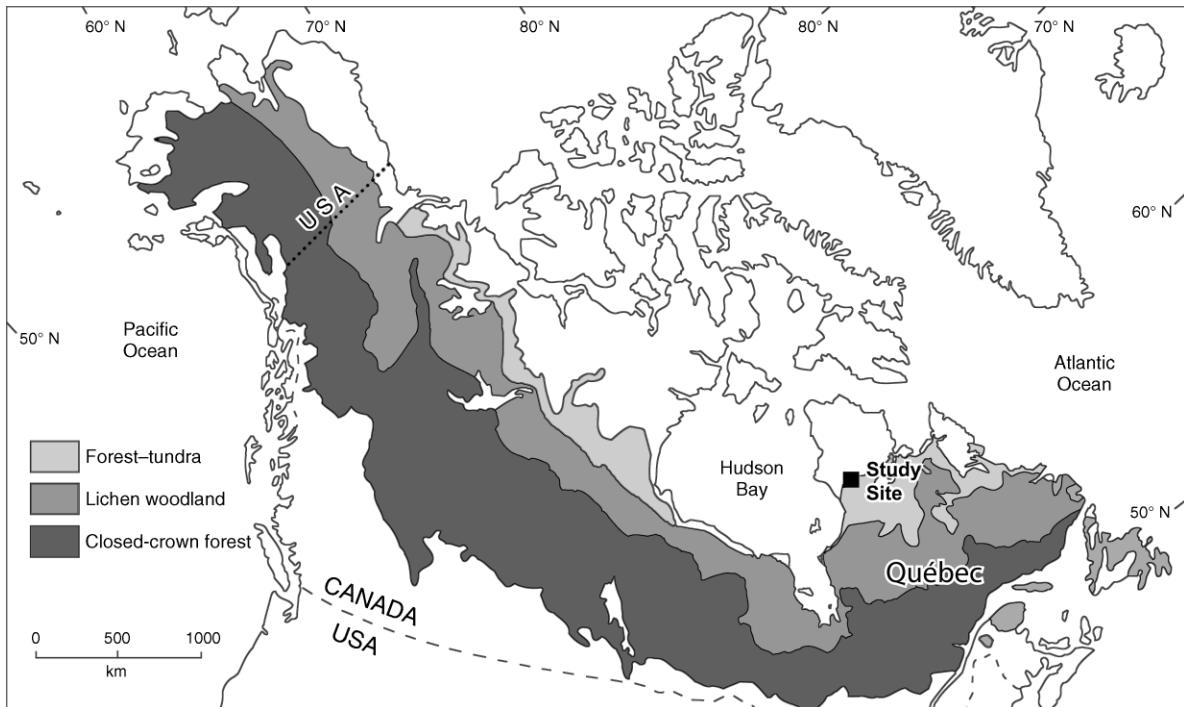


FIG. 1. Location of the study site, Boniface River area, northern Québec, Canada.

maintenance of spruce woodlands. These processes allow forest stands at treeline to survive for centuries and millennia (Payette et al. 2008). Over the last millennia, conversion of forests to tundra or woodlands occurred in several high-latitude regions because of a lack of postfire tree regeneration during periods of climatic deterioration (Cwynar and Spear 1991, Arseneault and Payette 1997, Asselin and Payette 2005, Tinner et al. 2008). However, forests surviving fire during these periods are probably steady-state, old-growth ecosystems that maintain their structure through advanced regeneration (Payette et al. 2008).

The primary objectives of this study were to (1) document the structure of an old-growth woodland at treeline and (2) evaluate the spatial and temporal dynamics of the woodland in relation to past and present fire and climate disturbances, both before and after its postfire inception ~1000 years ago. Vegetation and soil characteristics of the pristine lichen-spruce woodland were analyzed to assess if the stand has been in equilibrium with climatic conditions through time. Whether old-growth ecosystems are in equilibrium with present conditions is an issue of debate in the context of changing climate and species assemblages (Davis 1981, Webb 1986, Prentice et al. 1991, Davis and Shaw 2001). Paleocological analysis provides a long-term perspective necessary to address this issue.

STUDY SITE

The study site is located in the Boniface River area (57°45' N, 76°20' W, northern Québec) at ~30 km from

the Hudson Bay coast and 10 km south of the Arctic treeline (Fig. 1). The Inukjuak (58°28' N, 78°04' W) weather station located on the Hudson Bay coast, 130 km from Boniface River area, is the closest to the study site. The mean annual temperature at Inukjuak is -7°C, the mean temperature of the coldest month (February) -26°C, and that of the warmest month (July) 9°C. The annual precipitation totals 500 mm, 40% of which falls as snow (Environment Canada 2004).

The Boniface River area is located on the granitic and gneissic Precambrian shield of northern Canada composed of low elevated hills of 100–200 m above sea level (a.s.l.). Black spruce, the dominant tree species, established in the region ~6500 cal. yr BP (Bhiry et al. 2007). The vegetation is representative of the northern forest-tundra with spruce-moss forests in moist protected sites, lichen-spruce woodlands on well-drained soils, and lichen-heath-dwarf birch (*Betula glandulosa* Michx.) on wind-exposed treeless hills (Payette et al. 2008).

A preliminary survey using radiocarbon-dated charcoal particles indicates that the study site is occupied by a postfire lichen-spruce woodland that established 1000 years ago. The woodland possesses the principal visual characteristics of old-growth ecosystems, i.e., dominance of living and dead trees of all sizes, and dead trees at all stages of decomposition. The woodland is situated on a 10 degree, well-drained slope exposed to the north-northeast at an altitude of 92–102 m a.s.l. It forms a small island ~2 ha in an area bordered by a narrow spruce-moss forest strip. Outside the forest strip, the landscape is dominated by treeless lichen-heath and snow-patch

communities that replaced woodlands more than 500–1500 cal. yr ago (Payette et al. 2008). The destruction of the regional woodlands by fire over the last centuries caused the fragmentation of forest cover to its present state and the insular character of the study site.

METHODS

An exhaustive sampling of vegetation and soil was done in a plot of 1200 m² (30 × 40 m) representative of the general woodland structure. The plot was positioned to avoid edge effect from the nearby spruce–moss forest strip and to maintain the same slope aspect.

Stand structure

The cover of all living and dead spruce, dwarf birch, and Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron and Judd) was mapped along with the site microtopography using an infrared total station (Leica T1010, 0.05 cm precision; Leica Geosystems, Unterentfelden, Switzerland). The plant composition of the site was recorded systematically at each 25-cm interval along a 40-m line, and the relative frequency of every species was calculated based on the intercept method (Mueller-Dombois and Ellenberg 1974). All other species found at the site but not on the line were also noted.

The basal diameter and height of each spruce stem, either alive or dead, were measured to construct the size structure of the stand. The form and growth anomalies of all spruce stems were also described. The origin (layer or seed) of each individual was determined; a layer generally displays a curved trunk often attached to the mother stem or to another stem located nearby. To preserve this rare ecosystem, no living spruce was cut. A cross section of all dead spruce in the plot was sampled nearest as possible to the base of the stem or at the root collar. All wood sections were dried and finely sanded. The age and the living period of each dead spruce (spruce >1 cm basal diameter) were cross-dated based on a light ring chronology (Filion et al. 1986, Arseneault and Payette 1998). Light rings are tree rings with poorly developed latewood cells and low wood density.

Snow depth

In subarctic environments, snow accumulates preferentially under and around tree vegetation. Podzolization, the major soil-forming process in these environments, is positively influenced by snow because of water infiltration into the soil during snowmelt (Tedrow et al. 1958, Holtmeier and Broll 1992, Payette and Filion 1993, Laberge 1998). Because the field study was done during summer, snow thickness was deduced from damage caused by snow and ice abrasion on trees and shrubs at the snow–air interface. Thus mean snow depths were inferred by measuring mean height of dwarf birch thickets, mean height of spruce stem anomalies, and position above the ground where a change in foliage color was observed (Pereg and Payette 1998).

Soil morphological and chemical analyses

In lichen–spruce woodlands, spruce trees and lichens are distributed in different microsites, which can lead to the formation of different soils. The degree of podzolization is determined by free iron and aluminum percentages (%[Fe+Al]pyro) and (%[Al+1/2Fe]oxalate) in the spodic horizon. The difference between the two parameters is that iron and aluminum extracted by pyrophosphate is directly linked to the podzolization process, whereas iron and aluminum extracted by ammonium oxalate include a certain amount from geomorphic processes and thus is less specific to the podzolization process. Four trenches (1 × 2 m) were excavated under each of the three vegetation covers dominated by lichens, dead spruce, and living spruce. The soils were characterized according to the Canadian Soil Classification System (Soil Classification Working Group 1998). In each trench, the soil horizons were described and sampled (Appendix A). In the laboratory, the color (wet and dry) of each sample was determined with a Munsell color chart (MacBeth 1994). Particle-size analysis was done with the Bouyoucos hydrometer method. The pH of soil samples (in water and CaCl₂) was determined for all samples following the method of McKeague (1978). Nitrogen and organic carbon contents were determined by combustion in a LECO CNS-2000 oven (LECO, St. Joseph, Michigan, USA). Exchangeable cations (Ca, Na, Mg, K) were extracted with ammonium acetate, and iron and aluminum extracted with sodium pyrophosphate, following the protocols of McKeague (1978). The concentrations of these elements were measured with a spectrophotometer (AAAnalyst 200; Perkin Elmer, Waltham, Massachusetts, USA). Percentages of iron and aluminum extracted with sodium dithionite and with ammonium oxalate were also measured with the McKeague (1978) protocols. Total iron percentage was measured after fusion (0.5 g of LiBO₂ mixed with 0.2 g of soil) at 950°C during 20 minutes.

The soil profile (soil pit) and the dominant plant cover at every meter in the plot were described ($n = 1271$ soil samples). Thickness of L, F, H, and Ae horizons was measured in each profile, and the B horizon was sampled in one-half of the profiles examined ($n = 620$). To evaluate soil development in relation to vegetation cover, iron and aluminum were extracted with sodium pyrophosphate in 60 B-horizon samples randomly selected according to the following vegetation cover classes: n spruce = 20 samples, n birch = 10, and n open vegetation = 30.

Charcoal and pollen analyses

Extensive soil coring across the study plot was also executed for the identification and distribution of paleosols. The age of paleosols was based on radiocarbon dating of organic matter extracted from buried organic horizons (Hb). The samples were cleaned of all extraneous materials, including rootlets, before processing for AMS (accelerator mass spectrometry) ¹⁴C dating.

The fire history of the studied site was reconstructed based on charcoal particles at the mineral soil surface and buried in the mineral soil. Large charcoal fragments were collected because a high concentration of pieces ≥ 5 mm indicates the location of trees before the fire event (Ohlson and Tryterud 2000). Charcoal fragments buried in mineral soils were recovered from 25 soil cores (750 cm³/core) systematically sampled along five equidistant lines (five cores per line) (Talon et al. 2005). Samples were immersed in a 5% KOH solution before being sieved with water. Ten charcoal pieces > 2 mm at the mineral soil surface, 15 pieces from the buried organic horizons, and five pieces from the soil cores were cleaned for AMS ¹⁴C dating (Appendix B). All analyses were performed at the ¹⁴C laboratory of the Centre d'Études Nordiques (Université Laval) and the Keck Carbon Cycle AMS Facility (University of California–Irvine). The radiocarbon dates were calibrated with CALIB REV 5.0.1 program (Stuiver and Reimer 1993).

Pollen analysis was performed on the organic horizon of six radiocarbon-dated paleosols according to Faegri and Iversen (1989). *Picea* stomate (resistant guard cells) analysis based on water sieving of organic matter (Hansen 1995) was also performed on the organic horizon of one paleosol devoid of charcoal fragments.

Spatial analysis and statistics

The spatial structure of the woodland was analyzed with Mapinfo (2005), MapStat (Thériault 2006), and Geoda 0.9.5-i beta (Anselin 2004). The surface areas occupied by spruce, birch, and ground vegetation (lichen, herbs, mosses, and other plants) were calculated. The spatial structure (concentrated, random, or dispersed) of the different vegetation covers, dead spruce, and soil samples from which iron and aluminum were extracted was analyzed based on the variance on the mean index (VMI). A grid superimposed on the virtual representation of the plot in MapInfo (2005) allowed the count of points by cells. The probability of obtaining this kind of point distribution by chance was verified with a χ^2 test (H_0 , VMI = 1, the observed spatial distribution is not significantly different from the random distribution; H_1 , VMI > 1 , the observed spatial distribution is more concentrated than the random distribution). Spatial autocorrelation between mortality dates of spruce was determined with the Moran *I*. Distributions of charcoal at the ground surface and under dead spruce and living spruce were compared using bivariate analyses.

The relationships between vegetation cover (spruce, birch, ground) and degree of soil development (%[Fe + Al]pyro) were tested with a nonparametric Kruskal-Wallis test (K-W test). The relationships between organic matter thickness and seven classes of vegetation cover (spruce, dead wood, birch, *Rhododendron*, alpine bilberry [*Vaccinium uliginosum* L.], mosses, and others including black crowberries [*Empetrum nigrum* L. var. *hermaphroditum*] and lichens) were also tested with the

K-W test. The relationships between degree of soil development and inferred snow depth at the sampled points and between spruce height and snow depth were evaluated with linear regression.

RESULTS

Vegetation

The dominant species throughout the study plot is *Empetrum nigrum* (26.5%). The lichen *Cladonia stellaris* (Opiz) Brodo (18.0%) and the moss *Pleurozium schreberi* (BSG.) Mitt. (11.7%) are the second and third most abundant species. Black spruce comes in fourth place (10.5%), and *Rhododendron groenlandicum* (Oeder) Kron & Judd and *Betula glandulosa* are less abundant (5.0% and 2.3%, respectively). The woodland cover is well represented by spruce (17.2%), *Betula glandulosa*–*Rhododendron groenlandicum* (7.6%), and lichen–*Empetrum* (75.2%). The surface covered by spruce (Fig. 2) is approximately the same as it is generally observed (15–25%) in old-growth woodlands of the northern forest–tundra zone of eastern Canada (Payette 1992). The main vegetation covers and dead spruce were all aggregated with VMI > 1 . Most living and dead trees of the stand originated from layering; only five seedlings (< 20 years old) and eight young trees established recently in the open areas of the woodland or near dwarf birch thickets. Several dead spruce were connected to living spruce, although scattered dead spruce stems were also located in open areas. Most charcoal fragments were found in areas without spruce and dwarf birch at present. However, some locations covered by lichens, such as the center of the plot, have neither charcoal nor dead or living spruce, indicating that spruce has not occupied these locations for a long period of time.

Soils

The four soil trenches show that the site is dominated by a sandy loam ($> 70\%$ sand and $\geq 15\%$ silt, respectively) deposit of glacial origin. All the soils are very acidic with pH as low as 2.1 to 3.5 in F (fibrous) and H (humic) horizons, respectively. C:N ratios of organic horizons vary from 30 to 78. Mineral-soil pH is also very low, varying between 3.2 pH in the Ae horizon to 4.4 pH in the C horizon. The soil is extremely nutrient poor with only 3–28% base saturation, and 0.4–12 mol of cation exchange capacity (Appendix A). The organic horizon beneath spruce, dead wood, *Vaccinium uliginosum*, *Rhododendron*, and mosses is significantly thicker than under birch and lichens (K-W test, $P < 0.001$; Fig. 3).

The woodland vegetation currently occupies well-drained, dystric eluviated brunisols and humo-ferric podzols. In the trenches, soils were more developed beneath the living spruce cover (podzols) than under the thin lichen carpet (brunisols) where spruce remains were absent. In the soil pits, no significant differences in percentage of (Fe + Al)pyro were observed between the soils under different types of vegetation cover (K-W test, $P = 0.9581$). These data contrast with those from the

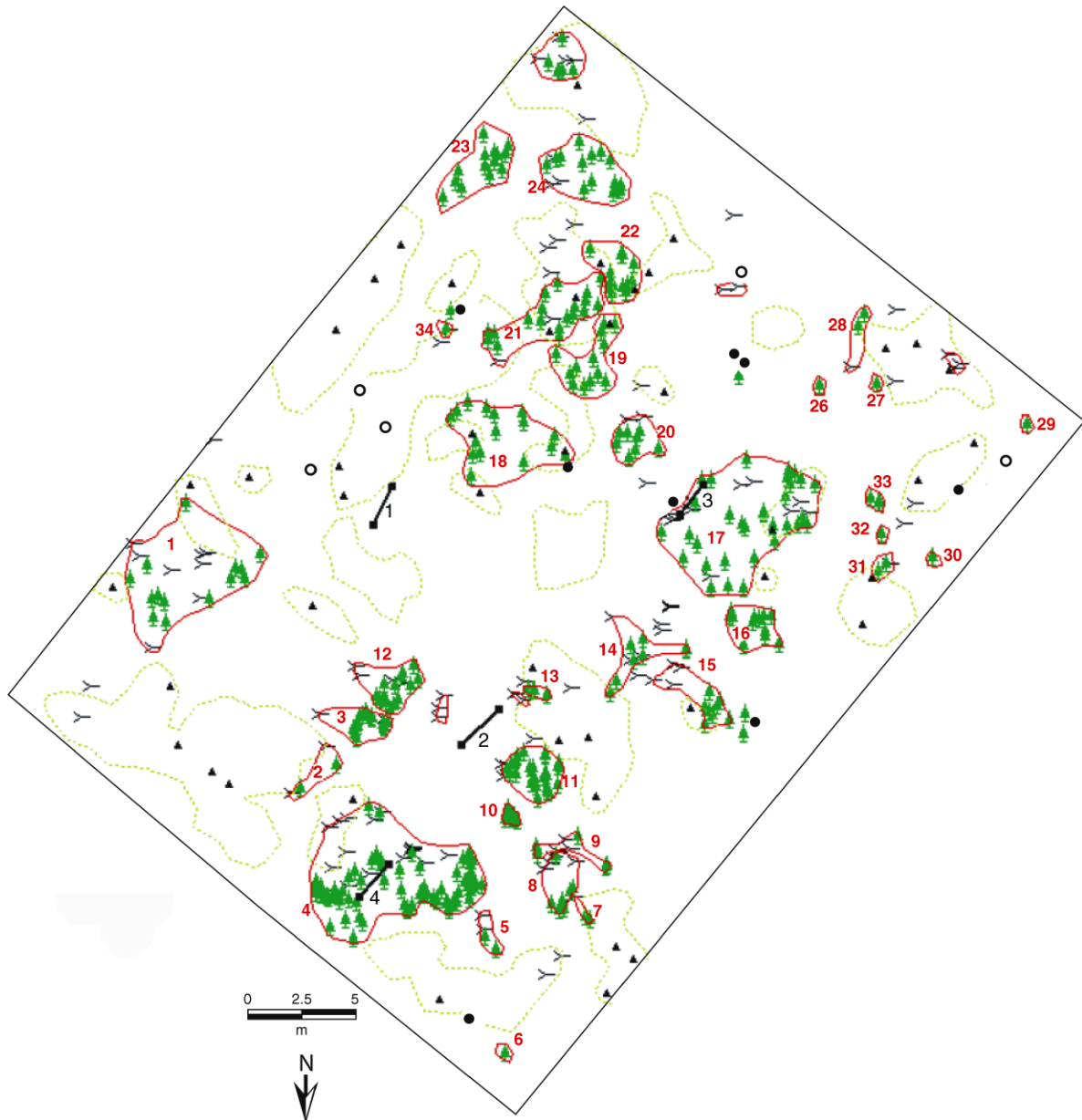


FIG. 2. Main structural features of the study woodland site. Contour and extent of the 34 living spruce clones are delineated in red and identified by a red number. Contour and position of dead clonal spruce are also delineated in red. The green dotted lines correspond to the postulated former limit of spruce clones before the last fire (1000 calibrated yr BP) as deduced from charcoal (≥ 5 mm) surveys at every meter in the plot. Seedlings are identified by open circles, and recently established layers by solid circles. Soil trenches are identified by a short black line and indicated by a black number from 1 to 4 (1, lichen cover; 2, dead spruce cover; 3, living spruce cover without paleosols; 4, living spruce cover with paleosols). Green conifer symbols correspond to living spruce, horizontal Y symbols to dead spruce, and black triangles to charcoal fragments.

trenches, and suggest that most soils developed beneath the spruce and dwarf birch covers are similar to those beneath lichens and heath.

Stand structure

Most living and dead spruce are small individuals with basal diameter < 2 cm (living spruce, 59.4% and dead spruce, 85.6%) and height < 1 m (living spruce,

70.2% and dead spruce, 87.5%). Only 11.6% of the living spruce are > 2.5 m high, the threshold size of most treeline trees in the study area. Spruce morphology varied greatly across the plot, from prostrate to normal spire forms. The growth form and height of living spruce were related to snow depth. The inferred minimum snow depth (33 cm) was recorded in the western and eastern corners of the plot with prostrate spruce. The inferred

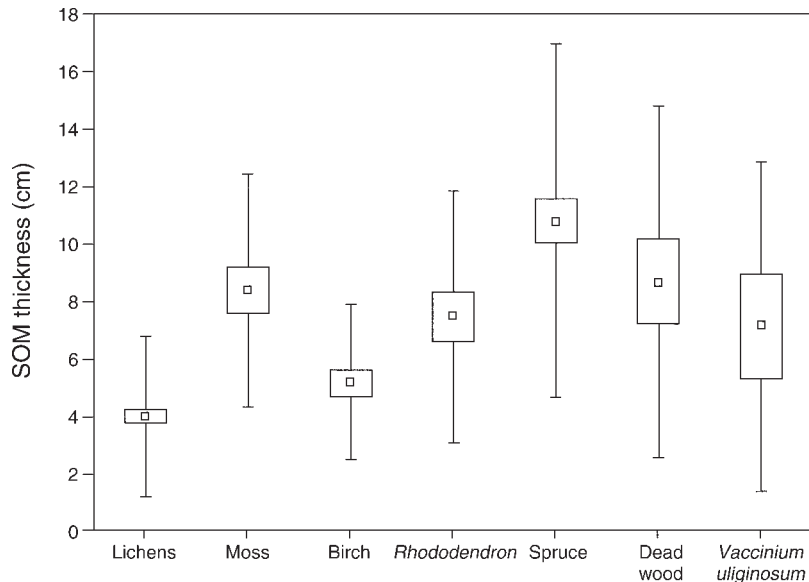


FIG. 3. Thickness of soil organic matter (SOM) in relation to plant cover type. The small squares denote average thickness, rectangles indicate the 95% confidence interval, and the error bars represent \pm SD.

maximum snow thickness (140 cm) was around spruce clones and dwarf birch thickets located at the center and southern corner of the plot. Although weak, the relationship between spruce size and mean snow depth (linear regression, $r^2 = 0.241$, $P < 0.001$) suggests that water supply was greater beneath the spruce cover. However, no significant relationship was found between degree of soil development (podzolization) and mean snow depth (linear regression, $r^2 = 0.014$, $P = 0.386$).

The life span of dead stems >1 m in height varied between 43 and 432 years (Fig. 4). Most adult spruce lived 100–300 years, with an average age at death of 195 years. The age of all dead stems <1 m in height was <50 years (data not included in Fig. 4). One subfossil spruce lying on the ground was almost as old as the oldest black spruce ever recorded, i.e., 504 years old (Payette et al. 1985). A total number of 540 dead spruce layers <1 m high were recorded at the site.

Since initial establishment after fire, black spruce colonized the site continuously (Fig. 5). The minimum establishment date of the oldest subfossil of the woodland was AD 1313. Most living trees of the woodland probably established during the past five hundred years, assuming that the life span of living spruce is similar to that of dead spruce. The size structure of living spruce includes an abundant advanced regeneration and a small number of adult trees. The survivorship curve (semilog distribution) of living spruce illustrates that tree mortality decreases with size (or time) (Fig. 6). The power function model (log–log distribution) also fits the diameter data well ($r^2 = 0.96$), suggesting that the mortality rate is variable (Hett and Loucks 1976). The survivorship model of type III is representative of the

demographic status of living spruce, which indicates a decrease in the mortality risk with an increase in size (or age) of the trees (Harcombe 1987). For the dead spruce population, the good fit of the power function model ($r^2 = 0.76$) confirms that the mortality rate also varied with tree size (or age) as for the living spruce population (Fig. 6).

The age structure of the dead spruce population suggests high mortality of trees during the 1880s (Fig. 5). Spatial autocorrelation in mortality dates was observed in the eastern part of the plot during the 19th century. About one-third of the individuals that died between 1880 and 1894 were in closer proximity to individuals who also died during the same period than to individuals who died at the beginning of this century. However, no spatial autocorrelation was found when all mortality dates were considered globally or for each century. The nonsignificant Moran I ($P = 0.204$) indicates that tree death was not contagious in the study plot. In addition, no spatial autocorrelation was found between the locations of wood charcoal and dead trees ($P = 0.572$), nor between the locations of wood

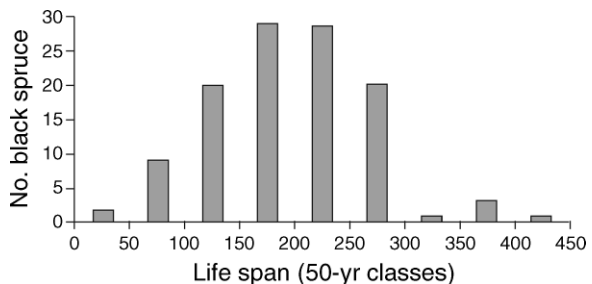


FIG. 4. Life span of dead black spruce >1 m in height.

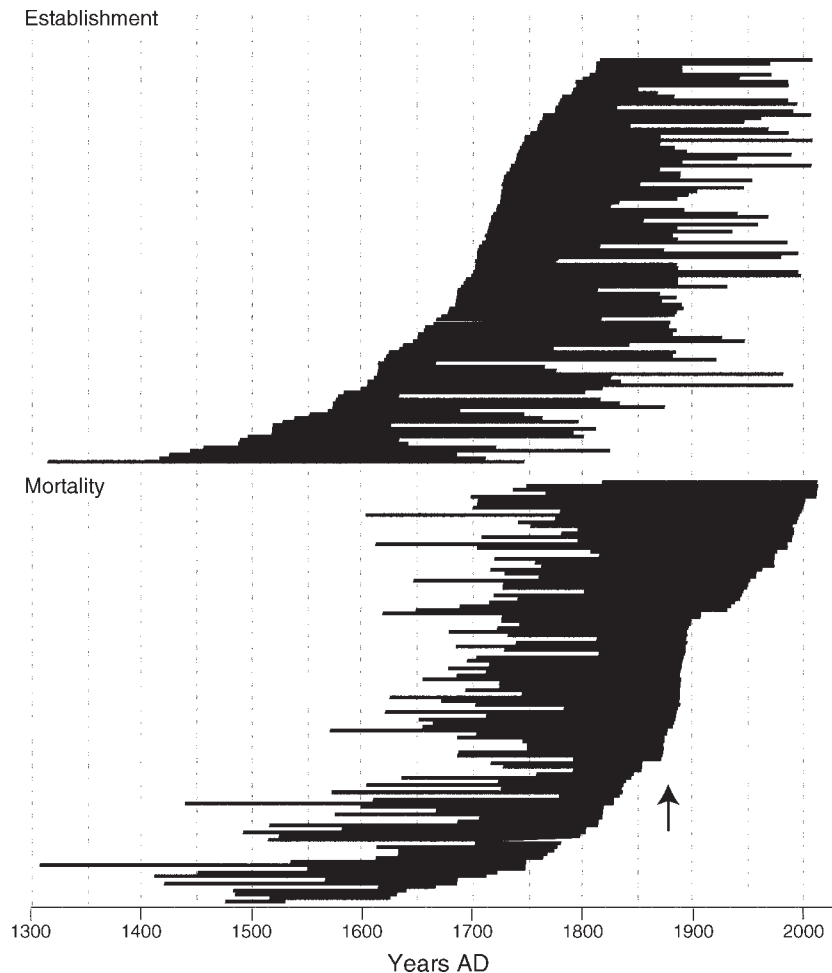


FIG. 5. Establishment and mortality periods of cross-dated black spruce subfossils in the woodland. The outermost rings correspond to the approximate mortality date of each specimen (with an estimated error of ~ 15 years for basal stems with a smooth surface). The arrow shows extensive mortality during the last decades of the 19th century. Note that the same data are presented in each panel.

charcoal and living trees ($P=0.999$). In contrast, a weak positive spatial autocorrelation ($I_{\text{obs}} = 0.0174$; $P \leq 0.001$) was observed between the locations of living and dead trees.

Vegetation and fire histories

Several paleosols were buried during different events, which were likely caused by local landslides as shown by the accumulation of downslope, coarse deposits on undisturbed podzolic soils. These events occurred around 4200, 2730, 2030, and 200 cal. yr BP (Appendix B). The oldest paleosol contained only 1% of spruce pollen, although spruce was probably present at the site or in the surroundings because a stomate was recovered from the organic horizon (Fig. 7). The pollen spectra were dominated by alder (*Alnus viridis* subsp. *crispa* type) at 4200 cal. yr BP, and by birch at ~ 2700 cal. yr BP when the first recorded fire occurred. Arboreal and spruce pollen became dominant at 2000 cal. yr BP, and

particularly at 1000 cal. yr BP with 88% of the pollen sum.

The site burned at least seven times between 2750 and 950 cal. yr BP (Appendix B), but no evidence of charcoal was found before and after those dates (Fig. 8). The youngest three fires were identified from charcoal located at the soil surface, whereas the four oldest fires were recorded by charcoal buried in the mineral soil. Because charcoal is generally produced by dry dead wood, old stem wood lying on the ground and producing charcoal can yield radiocarbon ages older than the real fire dates. For example, it is possible that the charcoal dated 2750 cal. yr BP originated from a wood fragment burned during the 2400 cal. yr BP fire, and the charcoal dated 2150 cal. yr BP from a wood fragment burned during the 1850 cal. yr BP fire. However, the distribution of all the charcoal fragments across the site suggests distinct fire events, and statistical partitioning of the radiocarbon dates suggests a 300-year fire frequency.

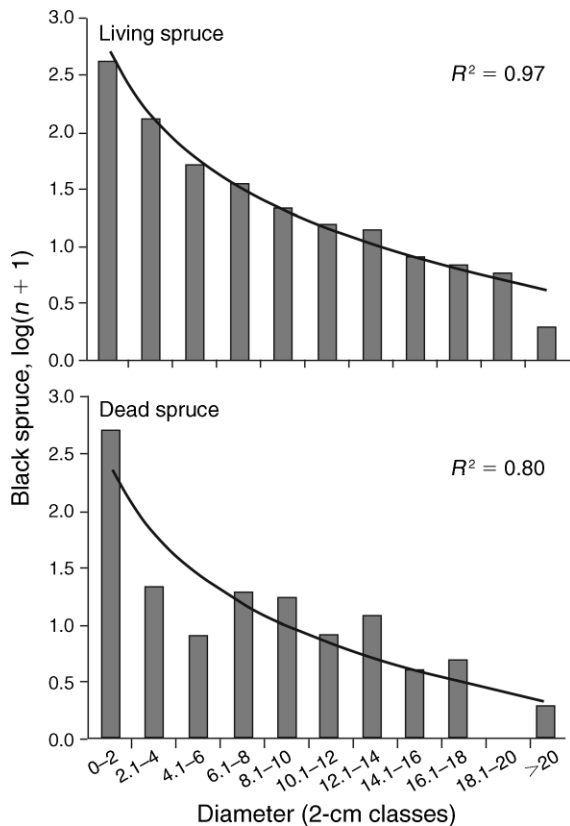


FIG. 6. Diameter distribution by 2-cm classes of living spruce and dead spruce. Negative exponential models were fitted to both diameter distributions.

DISCUSSION

Stand dynamics over the last millennium

The establishment date (AD 1313 or ~ 700 cal. yr BP) of the oldest subfossil spruce and the last fire date (950–1000 cal. yr BP) confirm the ancestral character of the studied woodland. The presence of a 700-year-old subfossil spruce on the ground surface probably corresponds to the limit of wood preservation in this area, which suggests that individuals of the first postfire cohort are all dead and decomposed. The variable living periods of subfossil trees (generally < 400 years) established since 700 cal. yr BP, are evidence that post-fire spruce establishment was followed by continuous regeneration until present time. This regeneration pattern suggests that the woodland is in equilibrium with present climatic conditions and those prevailing since 1000 cal. yr BP.

The reverse J-shaped size structure of trees in the woodland is typical of old-growth forest stands (Oliver and Larson 1996). Although mortality was high among young individuals, layering has provided sufficient advanced regeneration to replace mature and old trees through time. Throughout the last millennium, enough individuals survived from regeneration to the adult stage

to allow the maintenance of the woodland. Whatever the climatic conditions prevailing over the past centuries, steady-state conditions in the woodland were maintained in absence of fire. Fire incidence after 1000 cal. yr BP would have reduced considerably the probability of tree reestablishment because postfire seed regeneration at other sites in this area has been minimal during the past 1000 years (Payette et al. 2008). In the greater Boniface area, the last millennium is atypical of the Holocene in terms of fire-climate-vegetation linkages, as our data suggest that prior to 1000 cal. yr BP, fires were more frequent and climate more amenable to postfire woodland recovery.

The size structure of living spruce in the study woodland differs from that of dead spruce, in that there is a smaller number of dead spruce in the 2–6 cm diameter classes. For stems larger than 6 cm, survival increased with size. The negative exponential survivorship curve indicates that the woodland is currently in equilibrium with present conditions, but the inflection in the mortality histogram of cross-dated stems during the 1880s (Fig. 5) indicates a period of increased mortality. Payette et al. (1985) also observed an increase of spruce mortality during the same decade elsewhere in the region. They hypothesized that spruce trees were gradually defoliated. The limited photosynthetic tissues of these trees did not allow them to take advantage of the favorable growth conditions at the beginning of the 20th century. The same mortality pattern attributable to the same causes has been observed in subalpine white spruce (*Picea glauca* (Moench.) Voss.) populations in northwestern Canada (Szeicz and MacDonald 1995).

The spatial aggregation of one-third of several trees that died during the 1880s supports a pathogen hypothesis. Recent observations suggest that snow molds caused heavy mortality among young and adult spruce when temperatures were around the freezing point during prolonged snowmelt. In 2007, a fungal disease likely caused by three snow mold species (*Lophophacidium hyperboreum* Lagerb., *Phacidium abietis* (Dearn.) J. Reid & Cain, and *Phacidium infestans* P. Karst) (G. Bussi eres, *personal communication*) occurred at our site and in other old-growth woodlands of the Boniface River region. The snow cover in 2007 was thicker than during previous winters, and the snowmelt period lasted longer (until the end of June). This situation coincided with massive death of spruce needles beneath the snowpack line. The hypothesis of the mortal impact of fungal pathogens near the end of the Little Ice Age merits further consideration. In particular, why did such tree mortality not occur during the Little Ice Age or during the 20th century? It is possible that less snow on the ground during the Little Ice Age, as shown in other woodlands of the greater Boniface River area (Payette et al. 1985, Pereg and Payette 1998), limited the growth and expansion of fungal pathogens. Controlled field studies on interactions between snow molds, spruce, and

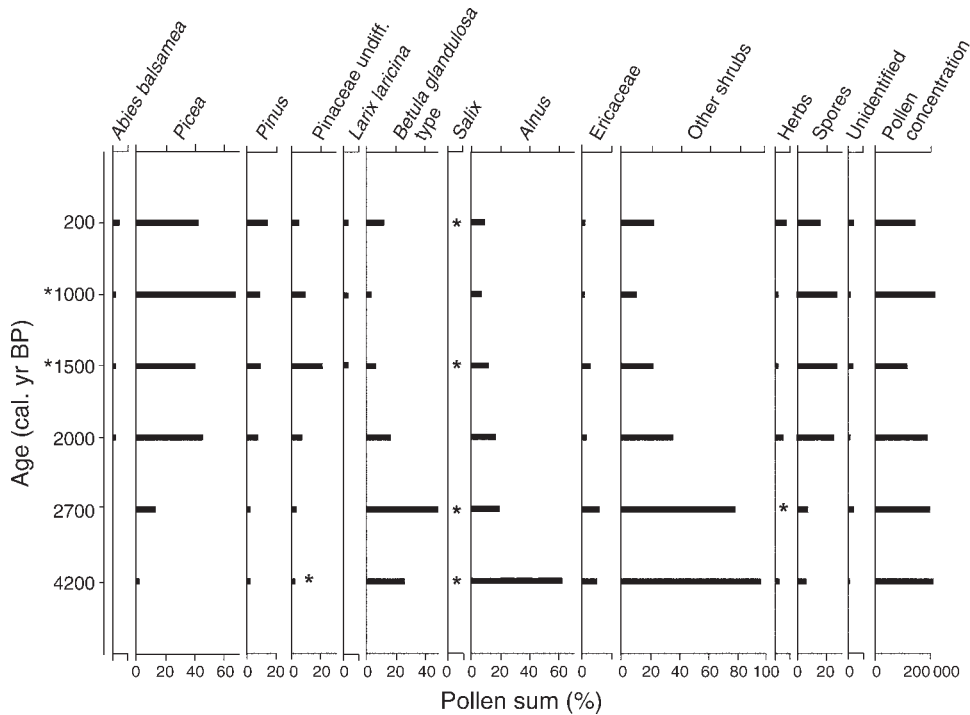


FIG. 7. Pollen assemblages in radiocarbon-dated paleosols. The assemblages are displayed chronologically from the oldest paleosol at 4200 cal. yr BP to the youngest paleosol (200 cal. yr BP). Stars (*) on the age scale indicate radiocarbon-dated charcoal from buried organic horizons, whereas the other dates were from radiocarbon-dated buried organic horizons. Stars in the diagram indicate 0.2% pollen. The scale for *Abies balsamea* and unidentified pollen is 1–5%; pollen concentration is measured in the number of pollen grains per cm³.

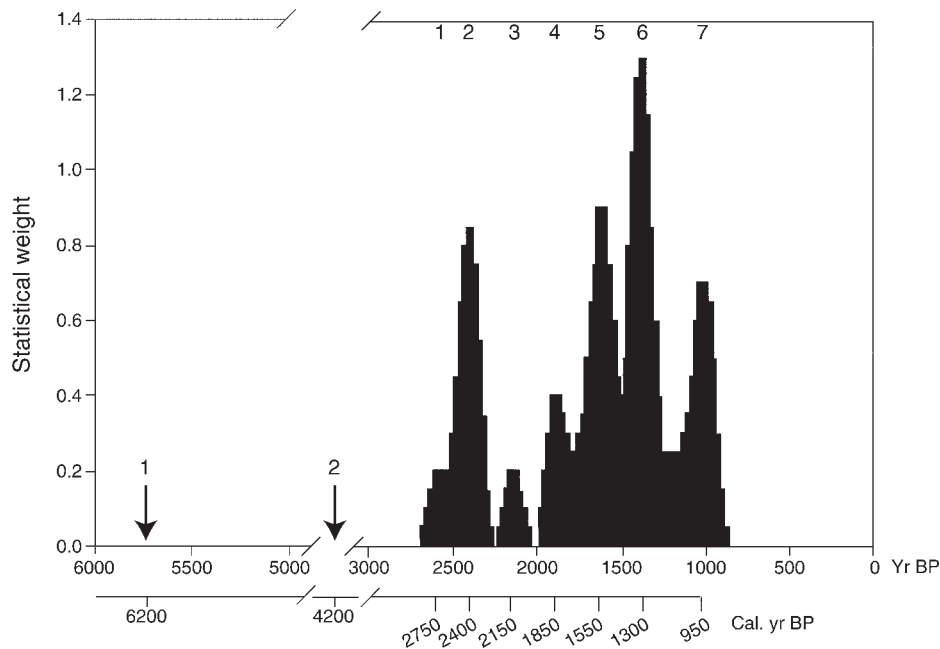


FIG. 8. Fire chronology of the woodland site based on distribution of statistical weight of 30 radiocarbon dates (see Appendix B for ¹⁴C dates and calibrated dates). Statistical weight is computed according to Talon et al. (2005). The timescale is in standard ¹⁴C yr BP and in calibrated yr BP. Arrow 1 corresponds to minimum arrival date of black spruce in the study region, and arrow 2 to minimum arrival date of black spruce in the study site. The calibrated date below each numbered black peak (from 1 to 7) corresponds to a distinct fire event.

snow environment during the snowmelt period would help to test the pathogen hypothesis.

Site dynamics before the last millennium

Several important ecological changes occurred during the history of the site. The dominance of *Alnus* pollen along with the small amount of pollen and a stomata of spruce at 4200 cal. yr BP suggest that the site was at an afforestation stage. The floristic assemblage was similar to that described from lake sediments in the boreal forest and forest tundra east of the Boniface River area (Gajewski et al. 1993) and from dune paleosols along the Hudson Bay coast (Filion 1984a). Pioneer shrub species (e.g., green alder) and scattered trees probably occupied the site between the regional arrival of black spruce at 6200 cal. yr BP and its local occurrence at our study site around 4200 cal. yr BP. This vegetation was replaced by a forest or woodland by 2750 cal. yr BP when the first fire was recorded. Between 2750 and 950 cal. yr BP, fire frequency increased sharply, with a fire event every 300 years. No fire occurred from 950 to 1000 cal. yr BP to present, corresponding to the buildup and growth of the extant old-growth woodland.

The increase in fire frequency at 2700 cal. yr BP occurred within a period (4000–2000 cal. yr BP) when boreal forests reached the maximum extent in the greater Boniface River area (Gajewski et al. 1993). At 3000 cal. yr BP, the forest cover was denser and less fragmented than today (Gajewski et al. 1993). A more continuous forest cover at that time would have favored fire propagation. Drier conditions could have also facilitated fire recurrence (Filion 1984b), but we cannot evaluate this interpretation because no paleoclimate record is available for this time period in the study area.

Soil–vegetation–fire interaction

The absence of spatial autocorrelation between living spruce and charcoal or between dead spruce and charcoal (≥ 5 -mm fragments) indicates that spruce distribution changed after each fire (Fig. 2). Black spruce seeds can germinate freely on exposed mineral soils after fire (Vincent 1965, Black and Bliss 1980, Viereck and Johnston 1990), but the species propagates preferentially by layering in the absence of fire.

Contrary to old-growth temperate forests where gap dynamics is the main ecological process favoring tree regeneration (Lorimer 1980, Payette et al. 1990), several gaps or open areas in the study woodland have not been filled since the last fire event. After tree death, no significant changes were observed in the woodland because of slow spruce regeneration. The prevailing harsh climatic conditions in our study area prevented seedlings from taking advantage of the light-rich gap conditions. Arseneault and Payette (1992) concluded that in the absence of fire, lichen woodlands at treeline maintain their open structure for a long period of time. The long-term maintenance of the open structure is evidenced by the stable position of the main vegetation

covers over the last 1000 years and reflected by the corresponding thickness of the organic horizons. The distribution of living and dead spruce also confirms that no significant changes occurred in their position since the last fire. The predominance of layering as the primary propagation means must have promoted spatial stability of the vegetation cover. However, the distribution of charcoal at the soil surface and in the soil indicates that spruce had apparently occupied almost all the plot surface prior to ca. 1000 cal. yr BP, in particular during the fire period between 2750 and 950 cal. yr BP when postfire seed regeneration was favored.

Podzolization is influenced by spatial stability of the vegetation cover. Soil-forming processes are more active beneath spruce trees, which produce a thick and acidic litter, than under lichens (Holtmeier and Broll 1992, Payette and Filion 1993, Laberge 1998). The soil profile was more developed beneath the spruce cover where macrofossils (wood remains, charcoal, and stomata) confirm its presence over the last thousand years. According to the World Reference Base for Soil Resources (2006), a spodic horizon must contain at least 0.5% $(Al + \frac{1}{2}Fe)_{oxalate}$, and the overlying horizon must contain less than one-half of this value. The spodic horizon developed at our site since 4200 cal. yr BP under a spruce cover contained 0.469% of $(Al + \frac{1}{2}Fe)_{oxalate}$. In Finland, soils developed over the last 4800 years beneath a Norway spruce (*Picea abies*)–Scots pine (*Pinus sylvestris*) cover with similar precipitation conditions (500–600 mm/yr) also contained 0.5% of $(Al + \frac{1}{2}Fe)_{oxalate}$ (Mokma et al. 2004). In contrast, in trench no. 1, soil development was minimal beneath the lichen cover because the soil has not been colonized by spruce for a long period of time. Thus the degree of podzolization reflects a long-lasting interaction between vegetation type and soil substrata. These results are similar to those of Laberge (1998) who observed less developed soils beneath lichens than beneath spruce clones.

On the other hand, pedogenetic values were similar in the soil profiles examined regardless of the types of vegetation cover, i.e., between 0.25% and 0.55% $(Fe + Al)_{pyro}$. Only a small number of samples (8/60) showed $>0.6\%$ $(Fe + Al)_{pyro}$ values. These values are similar to those measured by Payette and Filion (1993) in spodic horizons of sandy, patchy podzolic soils across the northern forest–tundra of eastern Canada. Moreover, the percentage of $(Fe + Al)_{pyro}$ was not correlated with snow depth, which is thicker under spruce and should positively influence the podzolization process (Holtmeier and Broll 1992, Payette and Filion 1993). Several soils beneath a lichen carpet were found as well developed as those under spruce or birch covers. Ugolini et al. (1981) also observed podzols developed under alpine tundra in Alaska. The development of this soil type at our site is probably associated with continuous spruce displacement since 4200 ca. yr BP. If the extant old-growth woodland is maintained in absence of fire and through seed regener-

ation for several centuries, the process of soil homogenization will be reversed and soil differentiation will prevail between the lichen and spruce covers.

CONCLUSIONS

Retrospective studies documenting the millennial-scale dynamics of forest stands have generally focused on wetland sites where macrofossils are abundant and well preserved (e.g., Cwynar and Spear 1991, Filion and Quinty 1993, Bhiry and Filion 1996, Arseneault and Sirois 2004, Tinner et al. 2008). We have studied a well-drained, mineral site to address the long-term dynamics of subarctic tree stands, using vegetation and soil attributes. Results show that, despite the occasional high mortality event of the 19th century, the site has been occupied by an old-growth woodland in the absence of fire over the past 1000 years. The woodland structure and development have been maintained by layering and occasional seeding over the past 1000 years. Tree persistence over the past 4200 years was linked to climatic conditions determining fire frequency, biotic factors influencing fuel availability, seed regeneration and spruce life span, as well as stochastic factors associated with the probability of ignition by lightning. The future of the woodland is uncertain because present climatic conditions would not permit full postfire tree regeneration, as suggested by the very small number of seedlings in most well-drained sites of the study area. The main ecological processes structuring the woodland, i.e., spruce demography (regeneration and mortality), fire frequency, and mortal pathogen incidence, will undoubtedly be affected by future climatic change. The persistence of spruce woodlands at the treeline in the absence of fire should facilitate tree expansion if climatic warming prevails during this century (Gamache 2003, Lloyd 2005, MacDonald et al. 2008).

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APPENDIX A

Description and physical and chemical properties of organic horizons and mineral horizons of the four soil trenches (*Ecological Archives* E091-095-A1).

APPENDIX B

¹⁴C dates and calibrated dates of charcoal samples at the soil surface and buried into the soil, and samples of organic matter from paleosols (*Ecological Archives* E091-095-A2).