

## CONTRASTED DYNAMICS OF NORTHERN LABRADOR TREE LINES CAUSED BY CLIMATE CHANGE AND MIGRATIONAL LAG

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**Abstract.** The northern Québec–Labrador tree lines are the most climatically stressed tree ecosystems of eastern North America. In particular, white spruce (*Picea glauca*) tree line populations distributed between 56° N and 58° N and 61° W and 66° W show contrasted responses to recent changes in climate according to their geographic position relative to the Labrador Sea. Along the coast, the northernmost latitudinal and altitudinal tree lines responded positively to warming over the last 50 years with invading spruce several tens of meters above the current tree line. In contrast, white spruce tree lines across the wind-exposed Labrador plateau are located much higher in altitude and have receded a few tens of meters beginning around AD 1740–1750 and have not yet recovered. Whereas no field evidence of recent fire and insect damage was found, all inland tree line stands were progressively damaged likely due to mechanical defoliation of wind-exposed trees. Massive tree death in the 19th century caused a reduction in the number of seed-bearing trees, and declining tree lines were not replenished by seedlings. Recent warming reported for northern latitudes has not been strong enough to change the regressive tree line trajectory in interior Labrador. However, white spruce expansion above coastal tree line in the northernmost forest site in Labrador is in line with current climatic trends. It is hypothesized that the species is still advancing toward its potential tree line higher in altitude due to delayed postglacial migration. The slow advance of white spruce in northernmost coastal Labrador is likely caused by the rugged topography of the Tornqat-Kaumajet-Kiglapait mountains.

**Key words:** boreal forest; climate change; dendroecology, Labrador; migrational lag; northern Québec; *Picea glauca*; postglacial tree migration; spruce beetle; subarctic; tree line; white spruce.

### INTRODUCTION

Northern tree lines are ecosystems sensitive to changes in climatic conditions, and are used as proxies of biotic changes at different temporal scales (Lamb 1985, Cwynar and Spear 1991, Kullman 1998, 2001, 2002, Crawford 2000, Skre et al. 2002, Walther 2003, Gamache and Payette 2004). Most recent changes in the dynamics of northern tree lines are attributed to increased warmth since the end of the Little Ice Age, in the late 19th century. Tree lines responded positively to increased warmth with upward and northward tree species invasion into the tundra (Kullman 1998, 2001, 2002, Esper and Schweingruber 2004) in Sweden and Siberia, respectively. In North America, northern tree lines are primarily under the control of climate that varied across the continent during the Holocene and the still ongoing process of postglacial tree migration (Ritchie 1987). However, tree line movements across the northern hemisphere can be caused by several factors not necessarily associated with changing climatic conditions. This is the case particularly in northern

Europe where tree line positions are often controlled by herbivores (Cairns and Moen 2004).

Depending on tree species, site history, site conditions, and position relative to major landforms and water bodies, tree lines respond differentially to climate forcing (Payette et al. 2001, Rupp et al. 2001). Most tree lines have moved readily upward and northward during the last 100 years of climatic warming. Seedling establishment at tree line and beyond in the tundra occurred from the late 19th century to the mid-20th century in northern Canada (Morin and Payette 1984, Lamb 1985, Payette and Filion 1985, Szeicz and MacDonald 1995, MacDonald et al. 1998b), Alaska (Cooper 1986, Suarez et al. 1999, Lloyd and Fastie 2003, Wilmking et al. 2004), Fennoscandia (Hustich 1958, Kullman 1979, 1998, 2002), and Russia (Esper and Schweingruber 2004). In contrast, only two sites with declining high-altitude forest and tree line stands were reported so far in Sweden (Kullman 1987) and eastern Siberia (MacDonald et al. 1998a), respectively, because of death of seed-bearing trees and consecutive failure of seedling establishment over the last centuries.

The present study was undertaken after a reconnaissance of white spruce (*Picea glauca* (Moench) Voss) tree lines in northern Labrador and adjacent Québec showing a contrasted pattern of tree population dynamics in coastal and inland sites. The widespread

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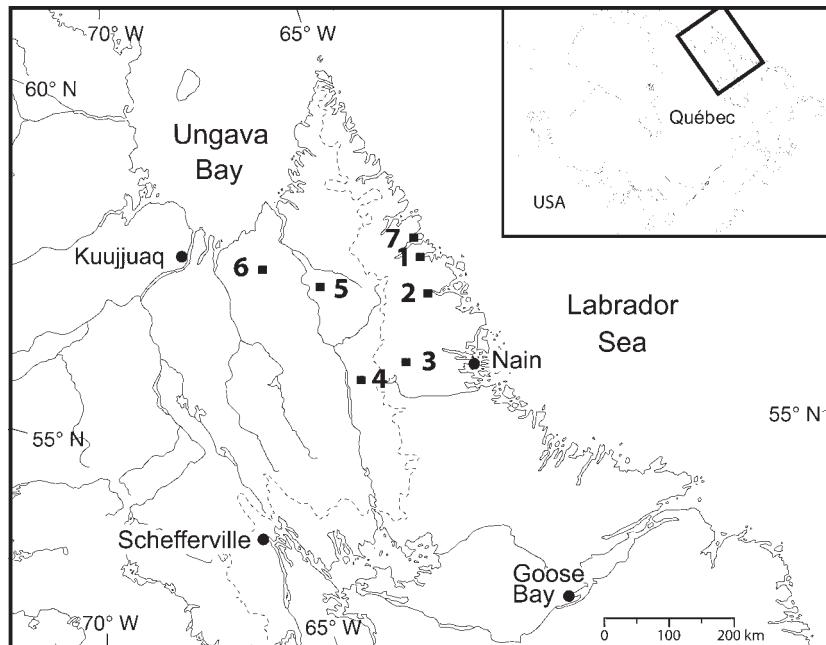


FIG. 1. Map of the Labrador study area and site locations: 1, Napaktok Bay sites; 2, Okak Bay site; 3, Éli-Vincent site; 4, Hutte-Sauvage site; 5, Pyramid sites; 6, Qairajutait site; 7, Hebron fjord. Weather stations are located at Kuujuaq, Schefferville, and Goose Bay.

occurrence of dead trees in most inland tree line sites, along with the absence of recent fire conflagrations and epidemics, strongly contrasts with the growth of healthy trees at and above tree line in fjords of the northern Labrador coast. The main objective of this study was to evaluate and to explain the contrasted dynamics of coastal and inland white spruce tree lines in northern Labrador and adjacent Québec with, in retrospect, the recent changes in climate associated with the Little Ice Age and the 20th century warmth (Houghton et al. 2001, Parmesan and Yohe 2003).

#### STUDY AREA

Tree line sites on both sides of the water divide between north-eastern Québec and Labrador were surveyed from 56° N to 58° N and 61° W to 66° W (Fig. 1). The study area is underlain by granitic and gneissic rocks of Precambrian age displayed in the form of a tilted erosional plateau. The inland plateau on both sides of the water divide lies between 300 and 800 m above sea level (a.s.l.) while the coastal land is strongly dissected by fjords and long bays surrounded by small mountain ranges with peak summits at an elevation of 1600–1800 m, particularly in the Torngat, Kaumajet, and Kiglapait Mountains. The main vegetation zones are the forest tundra in the south and the shrub and herb tundra in the north and along the coast (Hare 1959, Payette 1983). White spruce is the dominant tree species along the Labrador coast, whereas black spruce (*Picea mariana* (Mill.) B.S.P.) and eastern larch (*Larix laricina* (DuRoi) K. Koch) are widespread inland. Extensive

white spruce stands are located in lowlands surrounding the main river courses (e.g., Kogaluk and Fraser rivers) and large embayments (from Nain to Napaktok Bay). White spruce stands predominate at several tree line sites across the interior plateau, particularly on the upper slopes of the main valleys of Tunulic, George, Ford, Siimitalik, and Falcoz rivers. In several instances, the representative toposequence is composed of white spruce stands located on the upper slope and mixed black spruce and eastern larch stands distributed down slope. The northernmost forests are located in the Koroc River valleys and are dominated by black spruce and eastern larch. Based on present knowledge, the absence of white spruce in this valley is a noteworthy biogeographical trait of the regional biota.

#### METHODS

In this study, tree line trees are defined as symmetrical spruce stems  $\geq 2.5$  m high. Two coastal tree line sites were sampled, i.e., the Napaktok and the Okak sites. The Napaktok site (57°55' N, 62°38' W) harbors the northernmost (latitudinal) boreal forest in eastern North America, along the Labrador coast. The site was sampled from the current position of the uppermost forest limit (175 m a.s.l.) to the upland tundra (>300 m a.s.l.). A belt transect positioned at random was used to sample white spruce individuals from the forest limit to the last individual located upslope in the tundra. The belt transect was composed of 54 quadrats (10 × 20 m each) and sampling was done systematically at every two quadrats with the first quadrat selected at random. Thus

27 quadrats (distance of 20 m from each other) were used for the analysis over a distance of 1.08 km from the forest limit to the uppermost tundra. The forest limit is an old-growth forest similar in structure to a nearby forest (Elliott-Fisk 1983), and composed of all-sized living and dead trees suggesting the long-term maintenance of the tree habit. In each quadrat selected, all spruce individuals were recorded (diameter, height, growth form) and sampled for age determination at the root collar. Wood sections were air-dried and polished for age count and measurement of ring width. The soil surface along the belt transect (10 800 m<sup>2</sup>) was examined for the presence of wood remains. Several trees from a lowland white spruce forest about 20–30 m a.s.l. along Napaktok Bay also were sampled for tree-ring growth patterns and dating of tree mortality associated with a recent infestation of the spruce beetle (*Dendroctonus rufipennis* Kirby). The Okak Bay site (57°22' N, 62° 52' W) is an altitudinal tree line (about 300 m a.s.l.) near Umiakovik Lake, 60 km south of Napaktok Bay. The same sampling design was used for the description and sampling of all spruce individuals from the forest limit to the upland tundra, except that all the quadrats (10 × 20 m) were contiguous for a total distance of 540 m. Another site north of Napaktok Bay, the Hebron Fjord site (58°12' N, 62°38' W), was also considered in this study to assess the position of the tree line along the Labrador coast. The northernmost known position of white spruce based on voucher specimens is from this site.

Five sites of subarctic tree lines in interior Québec–Labrador plateau were retained for the reconstruction of tree line woodland development associated with recent changes in climatic conditions. The sampling design of three sites (Hutte-Sauvage site, 56°21' N, 64°34' W; Éli-Vincent site, 56°17' N, 63°33' W; and Qairajutait site, 57°51' N, 65°53' W) was similar to that of the Okak site with a belt transect about 500 m long composed of contiguous quadrats (10 × 20 m). The other two sites, the Pyramid sites (57°27' N, 65°12' W), were analyzed separately as they are parts of a representative toposequence distributed across the highlands. The toposequence is composed of a wind-exposed, hilltop stand (Pyramid 1 at 380 m a.s.l.) harboring dead trees, and a nearby woodland stand located in a large depression about 15 m below (Pyramid 2 at 365 m a.s.l.). At both sites, a large quadrat (40 × 75 m) was used to record and to sample all tree species individuals (trees, saplings, and seedlings) as in the previous studied sites. The two Pyramid stands originated from a fire evidenced by charcoal fragments beneath the current vegetation layer. The charcoal fragments were radiocarbon-dated (accelerator mass spectrometry [AMS] dating at Beta Analytic Radiocarbon Dating Laboratory), and the measured radiocarbon age was calibrated using CALIB 4.4 html (program available online).<sup>2</sup>

Dating and cross-dating of living and dead wood sections were done using diagnostic light rings, i.e., growth rings with exceptionally few latewood cells (Filion et al. 1986). Cross-dating also was checked using the program COFECHA (Holmes 1983). Dating accuracy of dead stems varies according to degree of preservation of the wood, either in an upright position or leaning on the ground for a given period of time. Weathering of the outermost rings occurs most often and rapidly in trees dead for more than one hundred years and leaning on the ground. Tree ring widths were measured with a Velmex micrometer (precision of 0.002 mm) under a binocular microscope at 40×. Tree-ring width chronologies of all the studied stands were built. Also, all the tree-ring series were used to detrend spruce growth according to age. The series were then standardized with a horizontal line fit corresponding to mean tree-ring width to produce dimensionless chronologies. The standardization procedure was used to highlight high-frequency variability of spruce growth. The tree-ring chronologies of the Pyramid sites are shown in this paper. The chronologies were used for comparisons of growth variations associated with patterns of spruce establishment and mortality through time at Pyramid 1 and Pyramid 2.

The CALROB program from the PPPHALOS Package (Guiot 1991) was used for calculating response functions of white spruce growth to climatic parameters at all the study stands. Data from the Kuujuaq, Schefferville, and Goose Bay weather stations (Environment Canada 2003) were used for the calculation of response functions, in particular mean monthly temperatures and total monthly precipitation during the current growth year and the past year from September ( $N - 1$ ) to December ( $N - 1$ ). Weather data were transformed in principal components to remove autocorrelation between climatic variables. The bootstrap method (Efron 1979, Guiot 1991) was used for the response functions based on the repetitive calculation (200 simulations) of multiple regressions on the same set of climatic variables. Calibration years were those selected at random, whereas verification years corresponded to the remaining years. At the end of the procedure, mean values and standard deviations were calculated for correlation coefficients between actual values and values simulated from climatic data, on both calibration and verification data sets. In the same way mean values and standard deviations of each partial regression coefficients were calculated. The squared mean correlation coefficient ( $R^2$ ) of the calibration dataset assesses the variance explained by the model. The ratio of the mean correlation coefficient  $r$  of the verification data set on its standard deviation (mrv/SD) was used to assess the global significance of the relationship between climatic parameters and tree ring growth. The significance of each bootstrapped regression coefficient (climatic parameters) is provided by the

<sup>2</sup> (www.calib.org)

ratio between the mean value calculated from the results of the 200 simulations and their standard deviation.

## RESULTS

### *Coastal tree line sites*

The Napaktok and the Okak sites along the Labrador coast show similar trends of spruce expansion from the forest limit-tree line boundary to the upland tundra (Fig. 2). According to the current position of the tree line (composed of all-sized and all-aged white spruce stems—up to 250–300 years old—and contemporaneous to the tree line position several hundred years ago as shown by dead symmetrical tree stems on the ground), spruce (as seedlings and saplings) expanded from 175 to about 300 m a.s.l. at Napaktok, and from 300 to 355 m a.s.l. at Okak. Spruce expansion occurred during the last 50–60 years at both sites, beginning during the 1940s. At Napaktok, the tree line (symmetrical trees >2.5 m) rose a little more than 15 m (at 190 m a.s.l.) over the last 50 years. No tree remains were found on the soil surface of the tundra, suggesting that the current white spruce establishment is a recent biogeographical event.

On the other hand, a relatively large part of the lowland forest along Napaktok Bay experienced massive tree mortality between 1989 and 1991 (Fig. 3) likely caused by the spruce beetle. Tree mortality caused by the insect extended toward the tree line, i.e., a few tens of meters below the forest limit. Although at a lesser degree porcupine (*Erethizon dorsatum* L.) feeding caused the death of white spruce trees in the lowland forest. Several trees of this forest also were harvested by Inuit for domestic use.

### *Inland tree line sites*

In contrast to coastal tree lines, no spruce invasion in the tundra was noticed at the inland tree line sites, i.e., Hutte-Sauvage, Éli-Vincent, and Qairajutait sites. At the three inland sites where belt transects were used for recording and sampling, the position of the tree line along the slope regressed about 10–15 m during the last two centuries because of death of white spruce trees. The Hutte-Sauvage tree line recession is shown here as representative of the three sites (Fig. 4). Cross-dating of small dead trees, either standing or leaning on the ground above the current tree line, shows that spruce growing in the 16th and the 17th centuries died during the 19th century and the 20th century.

This pattern of tree line retreat is most exemplified by white spruce behavior at the two Pyramid sites. Both Pyramid stands developed after a fire dated 1410 cal. yr BP (conventional radiocarbon age of  $1540 \pm 40$  BP, Beta-191513). Pyramid 2 stand in the valley is an old-growth woodland composed of all-sized and all-aged trees with abundant medium to large-sized dead trees in standing position or leaning on the ground. The oldest spruces are about 400 years old, and tree establishment occurred sporadically over the last centuries with a marked episode during the 1940s and the 1950s (Fig. 5).

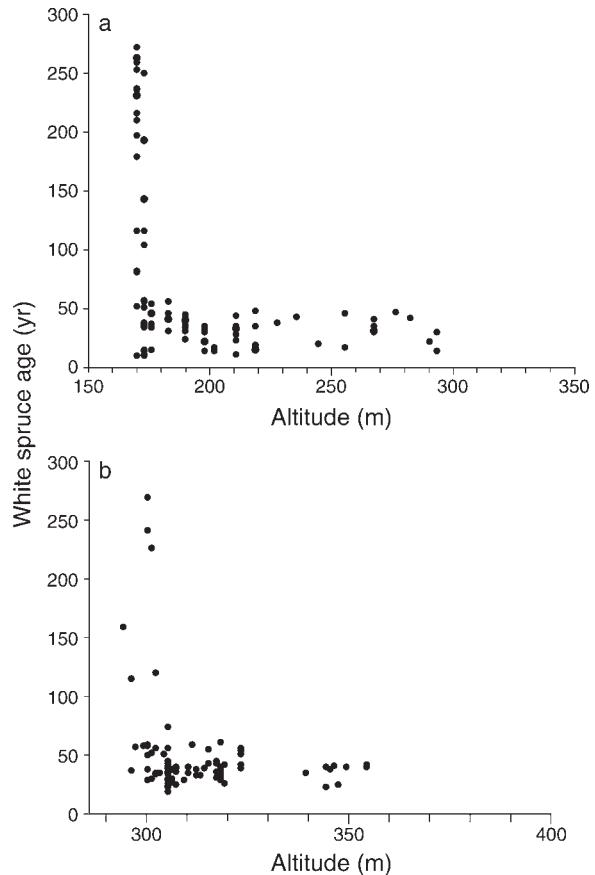


FIG. 2. White spruce expansion above tree line at (a) Napaktok Bay and (b) Okak Bay. The tree line corresponds to the position of all-aged trees at about 175 m a.s.l. in Napaktok Bay and 300 m a.s.l. at Okak Bay.

The overall age structure is roughly exponential (J-shaped distribution) indicative of a rather stable population in size structure. The tallest and largest trees are about 10 m high and 40 cm in diameter above ground. Height-diameter relationship is highly significant ( $R^2 = 0.84$ ;  $P = 0.001$ ), particularly in trees less than 4 m high. Age-diameter relationship is also highly significant ( $R^2 = 0.80$ ;  $P = 0.001$ ), whereas age-height relationship is less so ( $R^2 = 0.664$ ;  $P = 0.01$ ). Spruce less than 70–80 years old are subdominant canopy trees showing contrasted growth performance at the local scale. Although height-diameter relationship is greater ( $R^2 = 0.88$ ;  $P = 0.001$ ), age-diameter and age-height relationships among these trees are far less strong (with lower  $R^2$  values of 0.41 and 0.38, respectively) than for the whole population. Spruce mortality occurred more or less regularly over the last 300 years, but more particularly between 1820 and 1920 and 1960–1980.

The wind-exposed Pyramid 1 stand is a sub-fossil woodland composed of dead single- and multi-stemmed (clonal) white spruce trees (Fig. 6). A small number of living branches (or layers) still attached to dead white spruce tree trunks is present at the site. Also two healthy

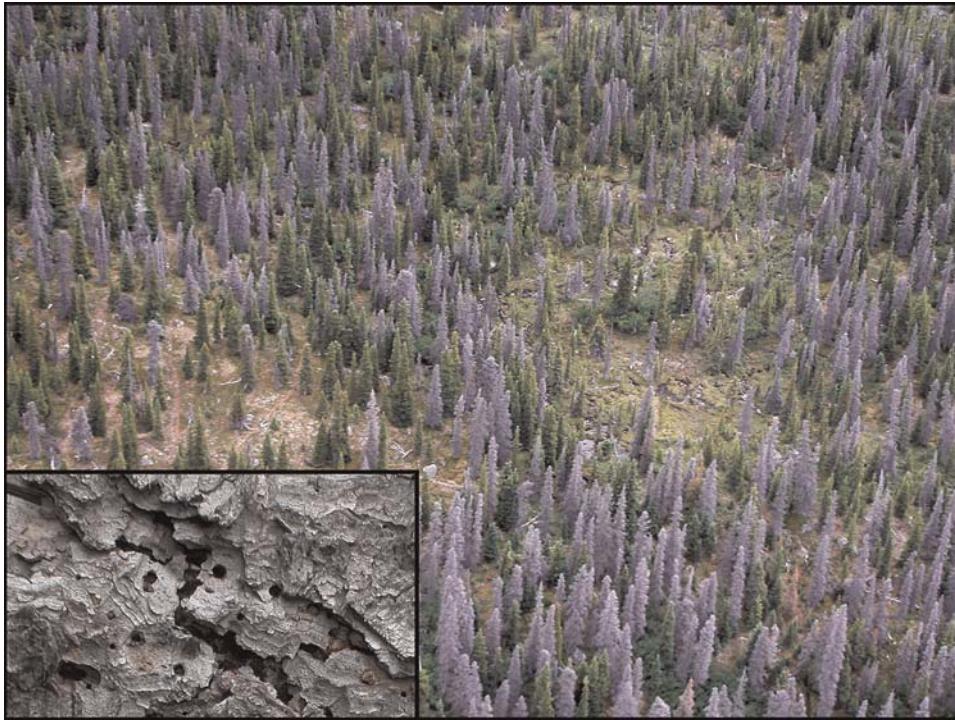


FIG. 3. White spruce trees probably killed by the spruce beetle (*Dendroctonus rufipennis*) in a lowland forest of Napaktok Bay. The inset shows holes in the bark of a white spruce tree made by the insect.

black spruce shrubs about 1–1.5 m high and two dead stems of eastern larch were also recorded in the quadrat. The overall size structure of the sub-fossil woodland indicates that trees as tall as 6 m high and as large as 29 cm basal diameter were growing on the hill in the recent past. Tree-ring cross-dating of most dead stems ( $n = 71$ ) provided years of tree establishment and mortality (Fig. 7). Before the tree population collapsed, the woodland was an old-growth stand with all-sized and all-aged trees including several white spruces more than 300 years old, and even 450 years old in one particular case. The age structure of the sub-fossil woodland shows that spruce establishment stopped after 1740–1760, and only a small

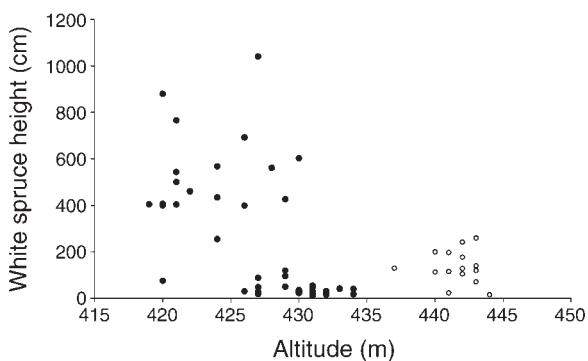


FIG. 4. Recession of the tree line at Hutte-Sauvage site. Solid circles correspond to living white spruce trees, and open circles to dead trees.

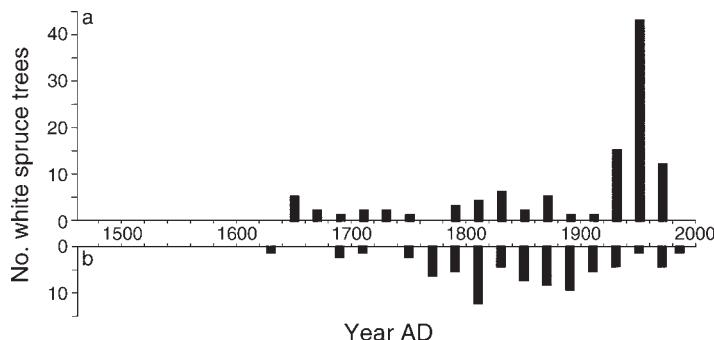
number of basal branches are still living. Stem mortality has been a continuous demographic process throughout the last 250 years, beginning around 1760. Most spruce trees died during two main periods, i.e., between 1820 and 1920, and 1960 and 1980. Stem mortality was not associated with age as dead stems were all-aged, i.e., from less than 60 years old to more than 400 years old (Fig. 7).

The main patterns of tree-ring growth in the two Pyramid sites (Fig. 8) are similar for the period prior to 1855 ( $r = 0.80$ ), whereas they diverged dramatically after 1855 ( $r = 0.46$ ). The collapse of Pyramid 1 woodland likely began after AD 1740–1750 and climaxed during the 19th century. Most trees died before ca. 1880 when renewed rapid growth started in Pyramid 2 woodland. The long-term trends of ring growth are a vivid illustration of the overall trends of recruitment and mortality recorded at both stands. In particular, the temporal patterns of spruce mortality of the two stands are similar (Kolmogorov-Smirnov test,  $D_{0.1} = 0.32$ ).

#### Response functions

The response functions of white spruce (based on the indexed tree-ring chronologies of all the studied stands) to climatic parameters show tree growth to be most often positively influenced by temperatures of the current growth season (June to August) and the preceding fall (Table 1). Mean temperature of October of the preceding year appears to be the main factor

FIG. 5. Age structure (20-year classes) of the Pyramid 2 woodland: (a) date of establishment of living white spruce; (b) date of mortality of dead white spruce stems (with an estimated error of about 10–15 years for basal stem remains with a smooth surface).



influencing positively tree ring growth in most sites (and November at the Napaktok lowland forest). Tree growth at all sites, except at the Napaktok site, was positively correlated with summer temperatures, particularly in July. Mean temperatures of April and May negatively affect ring growth in lowland Napaktok site. Mean annual temperatures at the Kuujjuaq, Schefferville, and Goose Bay weather stations (Fig. 9) showed similar trends over the last 50 years. Overall the main trends depicted by the 3-yr running means are decreasing mean annual temperature from the 1950s to the early 1990s, and a sharp increase since 1993–1994. Marked temperature decreases occurred between the 1960s and the 1980s with a through in the early 1990s. One major point of the response function data is that monthly precipitations of the current growth season and the

preceding fall among the three weather stations had no significant effect on spruce growth at all studied tree line stands.

DISCUSSION

Coastal tree lines in northern Labrador are advancing, whereas inland tree lines on the adjacent high plateaus are receding. At the outset, this contrasting pattern of tree line movements is singular given the fact that it is observed within a short distance from one another. But the Labrador area includes a large and diversified land in terms of climatic, geological, and geomorphological conditions where the northernmost trees of the boreal forest converge. When looking at the site conditions prevailing at both coastal and inland tree lines two sets of forcing factors may explain the different



FIG. 6. General view of the Pyramid 1 sub-fossil woodland. Several well-preserved vertical stems of white spruce are lying on the ground with scattered living basal branches still attached to the stems. Pyramid 2 woodland is in the background.

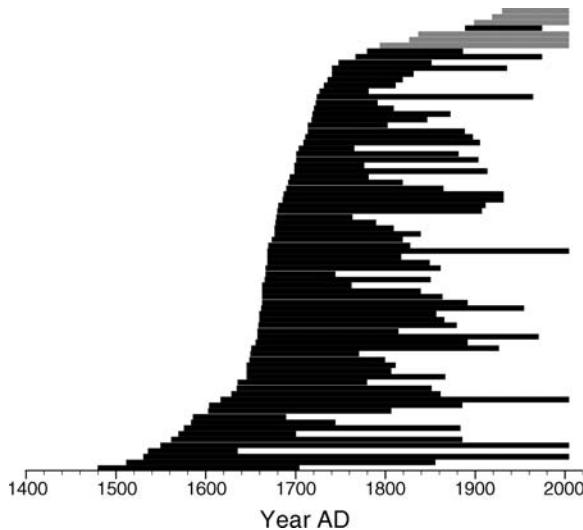


FIG. 7. Live periods of cross-dated white spruce remains in the Pyramid 1 sub-fossil woodland. The outermost rings correspond to the time of death of each specimen (with an estimated error of about 10–15 years for basal stem remains with a smooth surface). Gray lines correspond to basal branches, and black lines to basal stems (<30 cm height from the ground).

dynamics, i.e., climate change and postglacial tree migration.

#### *Impact of climate change on tree line dynamics*

Coastal tree lines at Napaktok and Okak show a similar pattern of spruce invasion into the upland tundra over the last 50–60 years, in the mid-20th century. This trend also was recorded in the Pyramid 2 woodland, where spruce regeneration was abundant between dominant canopy trees, but not at the inland tree line sites. The age structure of Pyramid 2 stand is similar to that of the old-growth Napaktok white spruce stand studied by Elliott-Fisk (1983) with a recruitment peak in the 1940–1950s. Although seedling establishment is episodic, these stands show an exponential age structure indicative of stable populations in the long term. Tree recruitment at tree lines in central northern Québec (Morin and Payette 1984) and tree invasion into the treeless tundra of Siberia (Shiyatov 1992, Esper and Schweingruber 2004) also occurred in the 1940s and 1950s, and correspond to the 20th century warming. Dates obtained from ring counts are minimum dates of establishment because aging at the root collar was not always possible, which suggests that establishment peaks at all sites likely occurred between the 1930s and the 1950s.

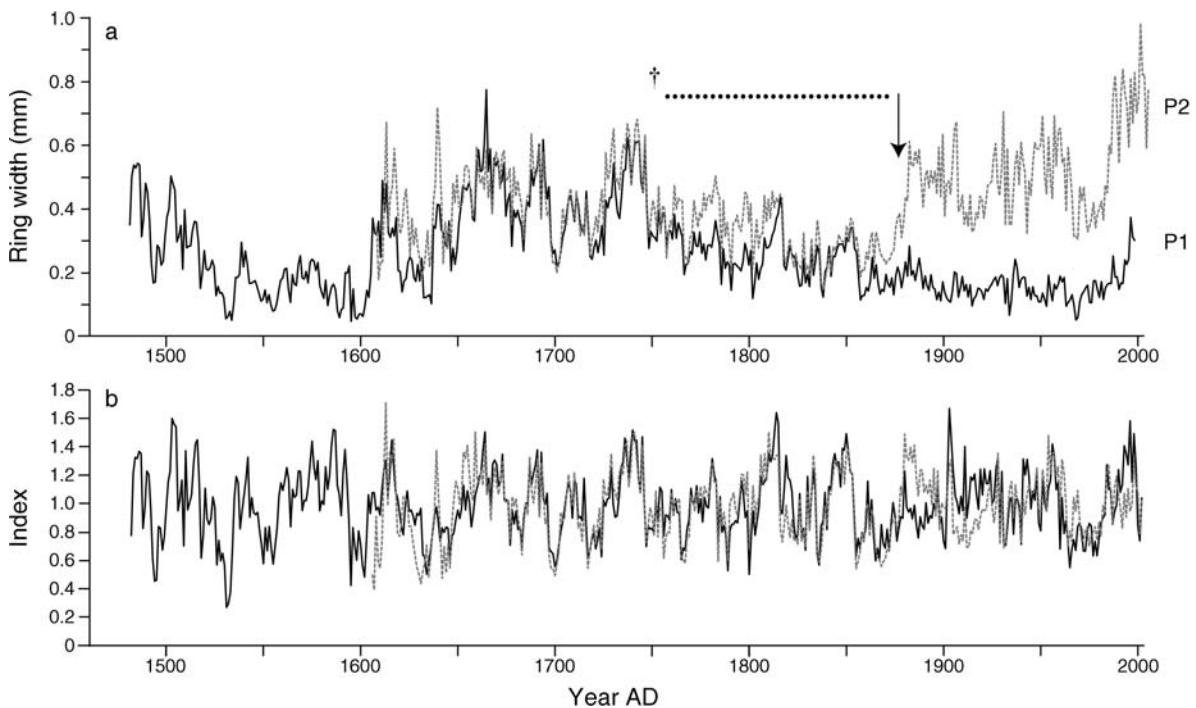


FIG. 8. Tree-ring chronologies from white spruce from Pyramid 1 (P1, solid line) and Pyramid 2 (P2, dotted line) sites: (a) tree-ring width series, (b) indexed series. The dagger corresponds to the period of extended stem mortality at both sites, particularly between AD 1740 and 1880. Radial growth resumed sharply after 1880 at Pyramid 2, whereas only slow radial growth of surviving basal branches was maintained at Pyramid 1. The arrow indicates the time when stem growth significantly diverged between the two sites, likely at the end of the Little Ice Age and start of the present warming stage. The ring-width series gives a better account of the long-term growth trends in both stands than the indexed series. P1 chronology is based on 30 trees and 46 rays, and P2 chronology is based on 59 trees and 66 rays.

TABLE 1. Ratio of the mean correlation coefficient and standard deviation of the verification data set of mean monthly temperatures during the current growth year and the past year (from September to December).

Sites	<i>N</i>	Sep ( <i>N</i> - 1)	Oct ( <i>N</i> - 1)	Nov ( <i>N</i> - 1)	Dec ( <i>N</i> - 1)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Weather station
L8	17 (20)	0.959	<b>2.756</b>	-0.286	-0.585	-0.342	0.026	0.745	0.738	-1.56	0.879	<b>1.715</b>	1.365	Kuujuuaq
L2	59 (66)	1.076	<b>2.791</b>	-0.32	-1.214	-1.147	-0.846	-0.061	1.634	-1.306	<b>2.052</b>	<b>1.948</b>	<b>2.634</b>	Kuujuuaq
L7	12 (19)	0.886	<b>2.962</b>	0.044	-1.099	-1.158	<b>-1.691</b>	0.645	0.26	-0.945	1.604	<b>2.234</b>	1.277	Kuujuuaq
L6	12 (14)	0.854	<b>1.937</b>	-0.572	0.004	-1.23	-0.982	1.001	1.089	-1.573	1.594	1.129	<b>1.672</b>	Kuujuuaq
L4	15 (20)	0.921	<b>2.746</b>	-0.984	-0.978	0.481	-0.901	0.104	-0.352	-1.459	0.519	1.163	0.503	Kuujuuaq
L3	11 (22)	0.272	0.857	<b>2.626</b>	-0.316	1.418	0.12	-0.419	<b>-1.847</b>	<b>-1.854</b>	0.474	<b>3.476</b>	0.224	Goose Bay
L5	12 (14)	0.354	<b>2.253</b>	<b>2.520</b>	-0.336	-0.267	-0.946	0.265	0.605	-0.695	<b>1.868</b>	<b>3.010</b>	0.187	Schefferville

Notes: Ratios in boldface type show significant response functions. Key to site abbreviations: L8, Qairajutait site; L2, Pyramid 2 site; L7, Hutte-Sauvage site; L6, Eli-Vincent site; L4, Napaktok tree line site; L3, Napaktok lowland site; L5, Okak Bay site. When the ratio ranges from 1.65 to 1.95, 1.96 to 2.57, 2.58 to 3.29, and >3.29, the significance of the response function and of its corresponding regression coefficient attains 90%, 95%, 99%, and 99.9% of probability, respectively. *N* is the number of trees sampled (number of rays measured).

In the Labrador area and the adjacent North Atlantic region, warming was apparently caused by natural climatic forcing associated with reduced sea ice cover, weakening of the North Atlantic Oscillation (Bengtsson et al. 2004), and changes in the thermohaline circulation (Sutton and Hodson 2005). Instrumental records also indicate that between 1935 and 1955 temperatures in the Arctic were approximately 1.5°C higher than they were at the end of the 19th century (Chapman and Walsh 1993). Stem mortality at the Pyramid sites between 1960 and 1980 is noteworthy, and may be caused by reduced temperatures over the North Atlantic region as reported by Sutton and Hodson (2005). In particular, the decreasing temperature trend depicted during this period may have been caused by salinity anomalies in the North Atlantic region, as for example during the 1970s (Mysak et al. 1990, Sutton and Hodson 2005). Winter temper-

atures averaged for coastal Labrador stations were very cold in 1972–1974 (see Fig. 9). Salinity-anomaly-type variations may have played a role in the interdecadal variations of the climate along the Labrador coast, in which runoff from the Mackenzie and other rivers provides a source of low-salinity waters into the North Atlantic (Mysak et al. 1990, Mysak and Power 1991).

The collapse of high-altitude tree lines appears to be a major ecological event on the Labrador plateau. Although the magnitude of tree line recession was relatively small, i.e., about 15 m, it is translated to a large area of declining woodlands given the fact that the altitudinal slice occupied by declining tree line woodlands, i.e., between 360 and 460 m a.s.l., corresponds to a surface of several hundreds of square kilometers. White spruce trees started to decline in the mid 18th century, and stem mortality climaxed during the 19th

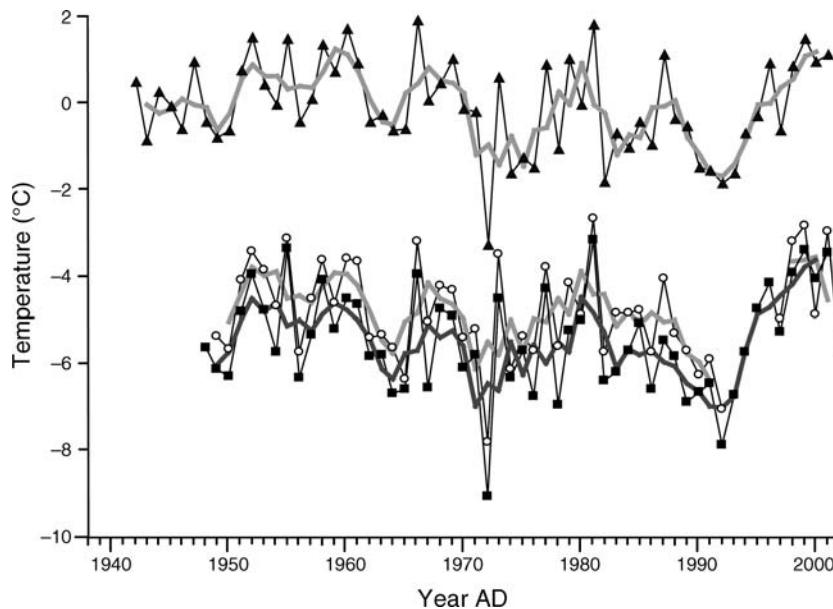


FIG. 9. Mean annual temperatures at Kuujjuuaq (squares), Schefferville (open circles), and Goose Bay (triangles). Gray lines correspond to three-year running means.

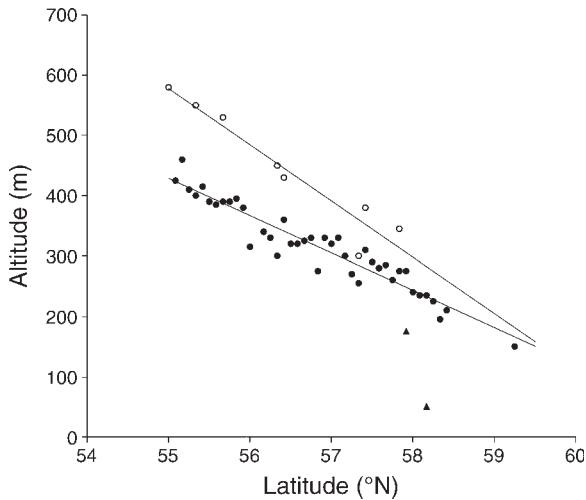


FIG. 10. Maximum altitudes of white spruce tree lines (open circles) according to latitude from the southern limit of the forest tundra (the position of the three uppermost circles, from Lamb [1985]) to the arctic tree line (triangle at 190 m a.s.l. in Napaktok Bay) and the species limit (triangle at 58°12' N near Hebron) in the arctic tundra. Also shown are maximum altitudes of black spruce stands (solid circles) according to latitude in central northern Québec (modified from Payette et al. [2001]).

century, likely during a 100-year period from 1820 to 1920. Because the same pattern of tree mortality occurred in the Pyramid sites and at the other tree line sites without any evidence of insect attacks and fire, it is probable that the lengthy tree mortality process (at least over 100 years) was triggered by sustained cold and windy winter conditions particularly during the 19th century. Trees probably died by attrition with the progressive loss of foliage and death of vegetative buds. The age of all dead trees varied largely, which also suggests that death was not associated with stem senescence. The death of several white spruces probably affected the woodland canopy causing greater mortality due to wind exposure, thinner snow cover, and wind-drifted conditions. Similar 19th century widespread mortality of upland trees has been reported for Scots pine (*Pinus sylvestris* L.) in Sweden (Kullman 1987) and Dahurian larch (*Larix dahurica* Turcz.) in Siberia (MacDonald et al. 1998a). According to Kullman (1987), a virgin high-altitude pine forest in Sweden declined during the Little Ice Age (AD 1300–1850). The long-term failure of recruitment and death of trees were postulated to have been caused by weather-induced loss of foliage and root dysfunction. Also, upland woodlands dominated by Dahurian larch in eastern Siberia declined during the 19th century, whereas tree recruitment occurred in the lowlands during the 20th century (MacDonald et al. 1998a) as in the inland Labrador woodlands. Evidence from this study, Sweden and Siberia indicates that increased mortality occurred in the 19th century at tree line stands. In contrast, massive tree recruitment in these areas and elsewhere at other

tree line stands climaxed during the 20th century (Hustich 1958, Kullman 1979, Morin and Payette 1984, Payette and Filion 1985, MacDonald et al. 1998b, Suarez et al. 1999, Gervais and MacDonald 2000, Lloyd and Fastie 2003, Esper and Schweingruber 2004). Tree growth at tree line in northern Labrador and adjacent northeastern Québec is positively correlated to temperatures both during the current growth period and the preceding fall period. However, the lack of significant control of precipitation on white spruce tree growth in Labrador strongly contrasts with reduced growth reported in several forest and tree line sites in Alaska apparently caused by temperature-induced drought during the past 50 years (Jacoby and D'Arrigo 1995, Barber et al. 2000, Wilmking et al. 2004). It is possible that monthly precipitation may not be shown to affect tree growth although they may be stressed by higher temperatures in the future.

Likely a new facet of northern ecology in Labrador forests is the severe infestation of spruce beetle in the lowland forest of Napaktok Bay in the late 20th century, reported here for the first time. Most recent outbreaks of the spruce beetle were recorded in western Canada and United States where the species affected large tracks of forests, particularly in the Yukon and Alaska (Holsten et al. 1985). The causes of the infestation are unknown, and more work is needed to investigate the impact of the insect on the northernmost, and most isolated forest of eastern North America.

#### *Postglacial migration of white spruce*

The opposing trends in tree line dynamics also suggest the possible influence of factors associated with the biogeographical history of white spruce along the Labrador coast (Lamb 1984, 1985, Ritchie and MacDonald 1986, Ritchie 1987). The respective coordinates (latitude and altitude) of tree line trees in the northeastern Québec–Labrador region may help to sort out the past and recent behavior of white spruce. The altitudinal position of white spruce tree lines according to latitude in the study area drops more rapidly than that of black spruce in interior northern Québec (Fig. 10). When excluding the position of the Napaktok tree line and the northernmost white spruce tree located at Hebron (corresponding to the northern limit of the species), the relationship between altitude and latitude of white spruce tree lines in Labrador ( $R^2 = 0.91$ ,  $P < 0.001$ ) is similar to that of black spruce tree lines ( $R^2 = 0.91$ ; Payette et al. 2001). Also the northernmost limit of white spruce can potentially reach around 59°30' N, i.e., at the same position than black spruce inland (Fig. 10). According to this extrapolated limit, the northernmost white spruce individual located at Hebron (58°12' N, 62°38' W) about 50 m a.s.l. (extrapolated elevation based on the voucher specimen of N. Polunin collected in 1936, reported by Rousseau 1974) is well within the range limit of the species along the coast. The position of the studied tree line in Napaktok Bay at about 190 m

a.s.l. is outside the range of all the other tree lines, and there are at least two other forest stands of white spruce in Napaktok Bay, constrained in the lowlands of Pistolet Bay, where the tree lines are just a few tens of meters a.s.l. Although there are probably local tree lines above the current position of the studied tree line in Napaktok they remain below 200–210 m a.s.l. The plotting of the altitudinal limit of seedling establishment (about 300 m a.s.l.) in the Napaktok transect in Fig. 2 would increase significantly the relationship between altitude and latitude of white spruce trees in the area (i.e.,  $r = 0.93$ ). This suggests that the species is still in the process of colonization of suitable lowland sites, although spruce woodland established in northern Labrador, in particular the Okak area, around 4500 years BP and declined after 2500 years BP (according to pollen data from Short and Nichols 1977, Lamb 1984, 1985). Pollen diagrams in the George River area, i.e., near the two Pyramid sites (Short and Nichols 1977) and Hutte-Sauvage site (McAndrews and Samson 1977) also suggest woodland development at 4500 years BP and decline after 2500 years BP. No pollen data are available for the northernmost forest at Napaktok Bay but present distribution of the forest suggests a late arrival of the species. The dissected nature of the Labrador coast and the mountainous relief probably have caused a pronounced time lag to white spruce migration and forest expansion throughout the postglacial, in particular in the northernmost parts of the coast where the Torngat-Kaumajet-Kiglapait mountains are forming a major physical barrier to plant migration. It is possible that the ridge-and-valley landscape of Labrador has reduced any farther movement north. Indeed, topography exerts a strong influence on vegetation distribution at northern latitude (Rupp et al. 2001).

#### CONCLUSION

White spruce growth at tree line in northeastern Québec–Labrador is controlled by temperatures during the current growing season (June to August) and the preceding fall season (October–November), whereas precipitation is not a limiting factor contrary to the situation prevailing in western Canada and Alaska where white spruce growth declined during the second half of the 20th century because of dryness. Outside the realm of response functions of white spruce growth to standard climatic parameters, other climatic factors linked to winter conditions were instrumental in determining long-term growth and survival of tree line trees. Important changes occurred in white spruce tree line stands over the last 250 years. Inland tree lines retreated a few tens of meters since the mid-18th century, whereas tree lines and seedling establishment in alpine tundra near the Labrador coast increased during the 20th century. Natural climatic forcing associated with reduced ice cover, weakening of the North Atlantic Oscillation, and changes in the thermohaline circulation were apparently the driving factors

behind white spruce expansion along the coast. This expansion not recorded inland on the high plateaus was an opportunistic response of white spruce to fill potential forest sites likely because of the slow migration of the species due to the physical barriers formed by the rugged coastal highlands and mountains.

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