



Latitudinal response of subarctic tree lines to recent climate change in eastern Canada

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ABSTRACT

Aim The predictions from biogeographical models of poleward expansion of biomes under a warmer $2 \times \text{CO}_2$ scenario might not be warranted, given the non-climatic influences on vegetation dynamics. Milder climatic conditions have occurred in northern Québec, Canada, in the 20th century. The purpose of this study was to document the early signs of a northward expansion of the boreal forest into the subarctic forest-tundra, a vast heterogeneous ecotone. Colonization of upland tundra sites by black spruce (*Picea mariana* (Mill.) BSP.) forming local subarctic tree lines was quantified at the biome scale. Because it was previously shown that the regenerative potential of spruce is reduced with increasing latitude, we predicted that tree line advances and recent establishment of seedlings above tree lines will also decrease northwards.

Location Black spruce regeneration patterns were surveyed across a > 300-km latitudinal transect spanning the forest-tundra of northern Québec, Canada ($55^{\circ}29' - 58^{\circ}27' \text{ N}$).

Methods Elevational transects were positioned at forest-tundra interfaces in two regions from the southern forest-tundra and two regions from the northern forest-tundra, including the arctic tree line. The surroundings of stunted black spruce, forming the species limit in the shrub tundra, were also examined. Position, total height and origin (seed or layer) of all black spruce stems established in the elevational transects were determined. Dendrochronological and topographical data allowed recent subarctic tree line advances to be estimated. Age structures of spruce recently established from seed (< 2.5 m high) were constructed and compared between forest-tundra regions. Five to 20-year heat sum (growing degree-days, > 5 °C) and precipitation fluctuations were computed from regional climatic data, and compared with seedling recruitment patterns.

Results During the 20th century, all tree lines from the southern forest-tundra rose slightly through establishment of seed-origin spruce, while some tree lines in the northern forest-tundra rose through height growth of stunted spruce already established on the tundra hilltops. However, the rate of rise in tree lines did not slow down with latitude. The density of < 2.5-m spruce established by seed declined exponentially with latitude. While the majority of < 2.5-m spruce has established since the late 1970s on the southernmost tundra hilltops, the regeneration pool was mainly composed of old, suppressed individuals in the northern forest-tundra. Spruce age generally decreased with increasing elevation in the southern forest-tundra stands, therefore indicating current colonization of tundra hilltops. Although spruce reproductive success has improved over the twentieth century in the southern forest-tundra, there was hardly any evidence

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that recruitment of seed-origin spruce was controlled by 5- to 20-year regional climatic fluctuations, except for winter precipitation.

Main conclusions Besides the milder 20th century climate, local topographic factors appear to have influenced the rise in tree lines and recent establishment by seed. The effect of black spruce's semi-serotinous cones in trapping seeds and the difficulty of establishment on exposed, drought-prone tundra vegetation are some factors likely to explain the scarcity of significant correlations between tree establishment and climatic variables in the short term. The age data suggest impending reforestation of the southernmost tundra sites, although the development of spruce seedlings into forest might be slowed down by the harsh wind-exposure conditions.

Keywords

Black spruce, ecotone, forest-tundra, krummholz, *Picea mariana*, seedling establishment, subarctic Québec, tree colonization, tree line advance, tree regeneration.

INTRODUCTION

Biogeographical models based on current plant–climate relationships predict poleward or upslope expansion of biomes under a $2 \times \text{CO}_2$ scenario, expected to occur by *c.* 2050 (Emanuel *et al.*, 1985; Prentice *et al.*, 1992; Woodward, 1993; Lenihan & Neilson, 1995). The importance of air temperature in determining vegetation distribution over millennial time-scales has been emphasized in palaeoecological studies (Prentice *et al.*, 1991; MacDonald *et al.*, 1993; Jackson *et al.*, 1997). However, in the short term, tree colonization of open sites is often driven by local factors interacting with climate, including the frequency of disturbance events (Sirois & Payette, 1991; Taylor *et al.*, 1996; Cullen *et al.*, 2001), soil moisture (Weisberg & Baker, 1995), snowpack depth (Taylor, 1995; Rochefort & Peterson, 1996), wind-exposure (Daly & Shankman, 1985) and seedbed suitability (Cowles, 1982; Hobbie & Chapin, 1998). The species' particular life history traits (Cuevas, 2002), species interactions (Hättenschwiler & Körner, 1995), feedback mechanisms between forest structure and climate (Scott *et al.*, 1993) and rarity of sustained short-term warm episodes (Kullman, 1986b; Steijlen & Zackrisson, 1987) have also been invoked to explain limited forest expansion. Discrepancies in vegetation response between regions may be amplified by the spatial heterogeneity of temperature trends, particularly in North America: while the Northwest Territories warmed markedly during the 20th century, the eastern Labrador coast underwent only half of that warming (Houghton *et al.*, 2001).

The subarctic forest-tundra is the ecotonal zone between continuous boreal forest and treeless arctic tundra, where forested lowlands contrast strongly with treeless uplands. South of the latitudinal arctic tree line, i.e. the northernmost limit of arborescent growth, forest–tundra boundaries are formed by subarctic tree lines. Unlike alpine tree lines, such tree lines are not necessarily controlled by the lower

temperatures associated with elevation due to the smooth rolling terrain of the Canadian Precambrian Shield (Payette *et al.*, 2001). Enhanced reproductive success of trees in response to recent climate change has been recorded in the North American forest-tundra, in populations of eastern larch [*Larix laricina* (DuRoi) K. Koch; Morin & Payette, 1984] and white spruce [*Picea glauca* (Moench) Voss; Payette & Filion, 1985; Scott *et al.*, 1987; Szeicz & MacDonald, 1995]. However, colonization of tundra sites by trees has not been surveyed at the entire forest-tundra scale, thus allowing its latitudinal heterogeneity in topography, vegetation structure and climate to act on the forests' response to recent climate change.

Owing to its ubiquity throughout the boreal zone and the fact that it forms most of the North American arctic tree line (Rowe, 1972; Ritchie, 1987), black spruce [*Picea mariana* (Mill.) BSP.] is the main tree species having the potential to change profoundly the modern boreal landscape. Black spruce's widespread distribution is closely linked to the recurrence of fire, by far the main disturbance factor within the boreal zone. The species maintains an aerial seed bank in semi-serotinous cones, until fire heat enables cone opening and seed dissemination (Black & Bliss, 1980; Sirois & Payette, 1989). In the absence of fire, spruce reproduces sporadically, but propagates mainly through vegetative layering of the lower branches (Payette *et al.*, 1985), an efficient adaptation enabling genotypes to be maintained in the long-term (Gamache *et al.*, 2003). In northern Québec, the decrease in the forest cover from the southern to the northern forest-tundra might be linked to a northward decrease in spruce regenerative potential (number of seeds per cone, percentage of filled seeds and germination; Sirois, 2000). Successive failures of the post-fire regeneration process, particularly in the northern forest-tundra, have caused progressive depletion of upland forests into tundra over the late Holocene cooling (last 3000 years; Payette & Gagnon, 1985; Gajewski *et al.*, 1993), giving rise to the forest-tundra ecotone as it appears today. The reduction in

spruce regenerative potential across the forest-tundra is likely to produce a declining population response to climate change with increasing latitude.

In this study, we used dendrochronological, topographical and meteorological data to evaluate recent subarctic tree line advances and colonization of tundra hilltops, as possible responses of black spruce to the 20th century climate warming that has occurred in northern Québec, as revealed by dendroclimatological proxy records (Guiot, 1985, 1987; Jacoby & D'Arrigo, 1989). The sampling of 20 populations distributed over a > 300-km latitudinal transect allowed the evaluation of black spruce regeneration across the forest-tundra ecotone. It is hypothesized that black spruce recruitment response at the tree line follows vegetation zonation across the forest-tundra ecotone, with the northernmost stands showing the greatest inertia to the recent climate change. More specifically, we tested the following predictions: (i) the rate of recent subarctic tree line rise will be reduced northward across the forest-tundra; (ii) the abundance of spruce seedlings colonizing tundra hilltops will decrease with increasing latitude; (iii) the age structure for seed-origin spruce will include proportionally more old, suppressed individuals with increasing latitude; and (iv) spruce recruitment pattern will be controlled by short- or medium-term fluctuations in heat sum and precipitation. To assess the likelihood that spruce newly established on tundra hilltops will develop into forest, we also investigated the roles of establishment substrate and wind-driven winter damage (Hadley & Smith, 1986) as sources of spruce mortality in exposed tree line sites.

STUDY AREA

Airborne surveys using a latitudinal transect extending from 55°29' to 58°27' N along 75°30' W (Fig. 1) allowed the examination of a continental area representative of the north-western part of the Québec–Labrador peninsula (Payette *et al.*, 1989, 2001). The study area is part of the Canadian Precambrian Shield, where granitic and gneissic rocks form a generally uniform, low-elevated plateau (Stockwell *et al.*, 1968). No permanent settlements are found in this pristine forest-tundra ecotone. Well-drained exposed uplands (rocky hills or drumlins) are uniformly distributed along the transect and are interrupted by wetlands and lakes. Most parts of the transect are outside the Tyrrell sea transgression zone and thus free from nutrient-rich marine deposits. The uplands are covered by thin acidic, nutrient-poor ablation till, whereas the valleys are filled mostly with glacial and fluvio-glacial deposits.

The nearest meteorological stations are located along the Hudson Bay coast at Kuujjuaraapik (south) and Inukjuak (north) (Fig. 1). From 55° to 59° N, mean annual temperature falls from -4 to -7 °C, and total annual precipitation from 650 to 450 mm, with 40% falling as snow (Environment Canada, 2003). The annual sum of growing degree-days (GDD > 5 °C) decreases northwards from 600 to 355 (Environment Canada, 2003), reducing the length of the growing season by about 3 weeks in the north.

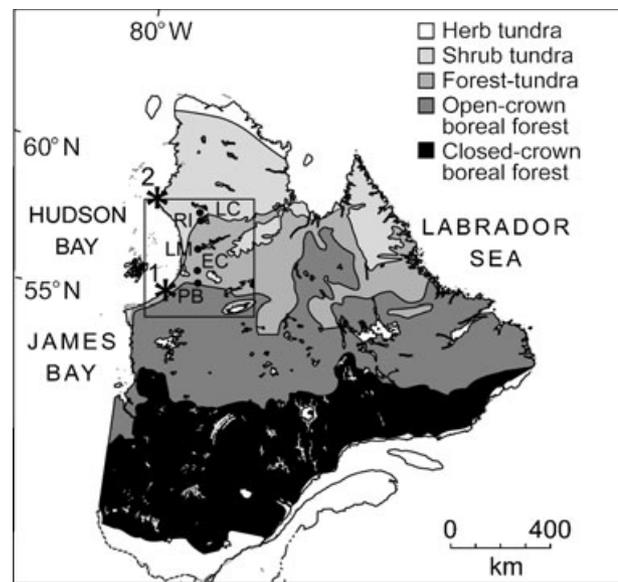


Figure 1 Study area. Vegetation zones northward from the boreal forest are shown (Payette, 1983). Five forest-tundra sites were sampled in the Petite rivière de la Baleine (PB), Rivière à l'Eau Claire (EC), Lac Minto (LM) and Rivière Innuksuac (RI) regions, and 12 isolated black spruce [*Picea mariana* (Mill.) BSP.] clones in the Lac Chavigny (LC) region north of the arctic tree line. Asterisks indicate meteorological stations at Kuujjuaraapik (1) and Inukjuak (2).

The latitudinal climatic gradient is associated with drastic changes in the vegetation cover. North of the open-crown boreal forest (lichen woodland), the study transect crosses the southern and northern parts of the forest-tundra and reaches the southern part of the shrub tundra (Fig. 1). The southern forest-tundra is characterized by an extensive forest cover infrequently broken by tundra gaps on wind-exposed uplands. As the proportion of forest cover drops rapidly northwards, forests become increasingly scattered and confined to wind-protected slopes and depressions (Payette *et al.*, 2001) so that the northern forest-tundra is mainly treeless, with extensive tundra patches. Tundra communities are dominated by lichens (mostly *Cladina* spp. and *Cladonia* spp.), bryophytes and shrubs (mostly Ericaceae and dwarf birch, *Betula glandulosa* Michx.). The arctic tree line forms the limit between the forest-tundra and the treeless shrub tundra.

Black spruce is the dominant tree species throughout the area, with eastern larch as a secondary tree species in the southern part of the transect. Black spruce is a morphologically plastic species that harbours mostly arborescent, spire shapes in the south, and that acclimatizes to increasing harsh winter conditions by adopting progressively stunted growth forms in the north (Lavoie & Payette, 1992). Black spruce extends as scattered krummholz (shrubby growth forms) a few tens of kilometres north of the arctic tree line, into the shrub tundra.

METHODS

Selection of sampling sites

Five regions showing an increasing fragmentation of the forest cover were selected along the transect (Fig. 1). The Petite rivière de la Baleine (PB) and Rivière à l'Eau Claire (EC) regions were chosen to represent southern forest-tundra, and the Lac Minto (LM) and Rivière Innuksuac (RI) regions northern forest-tundra. The latter region coincided with the arctic tree line. The northern end of the latitudinal transect was extended beyond the arctic tree line to include the very last stunted black spruce forming the species limit, in the Lac Chavigny (LC) region. Twelve isolated spruce clones were located, each composed of layered stems of uneven ages. Because the tundra clones were a few kilometres distant from

one another, they could not be sampled as described below. The surroundings of each clone were thus simply examined for the presence of spruce recently established from seed.

Fire drastically influences black spruce recruitment by increasing seed dispersal (Wilton, 1963) and generating even-aged stands (Sirois & Payette, 1989). Thus, the effect of fire had to be excluded to assure a general homogeneity of conditions among the surveyed forest-tundra stands. Fire impact on the stands' recruitment pattern was controlled for by retaining exclusively the areas that escaped previously mapped 20th century fires (Payette *et al.*, 1989). The southernmost region (PB) burned almost completely during this period, so the selected area was limited to a small unburned zone within a large 1920s fire zone.

In the summer of 1999, five nearby sampling sites were selected in each region (Table 1). Each site was defined as one

Table 1 Location parameters of subarctic tree line stands of black spruce [*Picea mariana* (Mill.) BSP.] in northern Québec, Canada

Vegetation zone, region and site	Distance from the arctic tree line (km)*	Latitude (N)	Longitude (W)	Altitude of hilltop (m a.s.l.)†	Altitude of tree line (m a.s.l.)	Mean slope (°)	Aspect
Southern forest-tundra							
Petite rivière de la Baleine							
PBI	-272	55°37'	75°36'	325	324	3	S
PB2	-287	55°29'	75°29'	335	330	4	NE
PB3	-285	55°30'	75°25'	310	307	4	NE
PB4	-282	55°31'	75°33'	325	322	8	S
PB5	-276	55°34'	75°35'	345	342	5	NE
Mean (SE)	-280 (2.6)			328 (5.8)	325 (5.6)	5 (0.9)	
Rivière à l'Eau Claire							
EC1	-204	56°13'	75°30'	290	286	4	W
EC2	-204	56°13'	75°30'	285	282	7	SSW
EC3	-204	56°14'	75°27'	305	304	5	SW
EC4	-206	56°12'	75°26'	305	298	8	SW
EC5	-207	56°12'	75°22'	295	288	13	SW
Mean (SE)	-205 (0.8)			296 (4.0)	292 (4.2)	8 (1.6)	
Northern forest-tundra							
Lac Minto							
LM1	-106	57°06'	75°33'	215	201	7	NW
LM2	-106	57°06'	75°34'	220	211	9	NW
LM3	-105	57°07'	75°33'	279	272	14	SW
LM4	-102	57°08'	75°33'	215	204	7	SE
LM5	-105	57°07'	75°36'	275	271	9	S
Mean (SE)	-105 (0.8)			241 (14.8)	232 (16.3)	9 (1.2)	
Rivière Innuksuac							
RI1	0	58°04'	75°29'	195	190	9	W
RI2	0	58°03'	75°28'	220	209	6	NW
RI3	0	58°03'	75°25'	220	215	3	NW
RI4	0	58°04'	75°30'	230	222	8	W
RI5	0	58°04'	75°33'	225	215	6	NW
Mean (SE)	0 (0)			218 (6.0)	210 (5.5)	6 (1.0)	
Shrub tundra							
Lac Chavigny							
LC1-LC12‡	+32 (2.3)	58°15'–58°27'	75°21'–75°39'	–	–	–	–

*Negative distances represent sites south of the arctic tree line and positive distances, sites north of the arctic tree line.

†Metres above sea level.

‡Each site represents one isolated clone at the species limit.

granitic hill showing a vegetation toposequence typical of the forest-tundra, i.e. tundra on the hilltop and lichen woodland downwards. Thus, each sampling site corresponded to one local subarctic tree line, defined as the uppermost position of ≥ 2.5 m-high single-stemmed or supranival skirted tree growth forms (Lescop-Sinclair & Payette, 1995). Retained sites had to meet the following criteria, checked *in situ*: (i) a $< 15^\circ$ slope allowing upward tree colonization, and (ii) absence of topographical barriers to the advance of trees.

Data collection

A 10-m wide belt transect was randomly positioned on each selected hill, extending downslope from the summit and covering the toposequence to include 10 to 20 spruce trees forming the forest border, below the local tree line. Length of the belt transect varied from 42 to 155 m owing to variations in tundra patch size between sites. Elevation of tree line, mean slope and aspect were recorded for each site using a laser theodolite. Dead stumps still rooted and bearing bark were sometimes present above the tree line, and were recorded as evidence of relatively recent, pre-20th century deforestation of the tundra hilltop. When such stumps were registered, stem cross-sections of nearby trees bearing fire scars were taken for dating purposes.

All living spruce within each belt transect were marked and sampled. Position (x, y, z coordinates), total height and origin (seed or layer) of spruce were determined, stems being identified as layers when strongly curved at the base and having an underground connection with another stem (Payette *et al.*, 1985). Due to the difficulty of delineating the genets (plants belonging to the same genotype) in the northern stands composed mainly of multi-stemmed clones, the tallest rooted stem showing apical dominance within a spatially distinct fragment was sampled.

When present, signs of winter damage (reiterative stems, shrubby growth form, loss of needles and yellowish foliage)

were noted on seed-origin spruce < 2.5 m, which included all the seedlings, saplings and some suppressed spruce (Fig. 2). The type of seedbed of each < 2.5 -m spruce was recorded according to three categories indicative of the position of spruce along the toposequence: exposed mineral soil (tundra mudboils), well-drained lichen mat and moister moss carpet. Exposed mineral soil was located near the hilltop, in an area of severe periglacial activity, while moss carpet was generally located downslope, near the forest border.

For evaluation of the recent tree line advance, all stems > 2.5 m were cross-sectioned at 2.5 m high. For age determination, stems were cross-sectioned at the root collar (root-shoot interface, below ground level) when of seed origin, or at the base of the stem curvature when of layer origin. The age of layered spruce, on which no root collar could be found, corresponded to the approximate year of stem rooting; it was not equivalent to the genet's age, which might be much greater. Stem discs were air-dried, finely sanded and dated by counting annual growth rings under a binocular microscope. The age of stem discs was validated by cross-dating using a chronology of light rings (growth rings with exceptionally few latewood cells; Filion *et al.*, 1986). The ages of the smallest, poorly lignified seedlings were determined by counting the terminal bud scars along the main stem. Some seedlings established on a thick moss carpet showed an adventitious root system on the lower stem complicating dating. Age of these seedlings was evaluated using a combination of terminal bud scar and ring counting (DesRochers & Gagnon, 1997). Some heavily suppressed spruce ($< 2\%$) could not be aged and were excluded from the analyses. Because of inevitable error associated with age determination, spruce ages were grouped into 5-year classes.

The Kuujuaapik weather station was nearer to the southern forest-tundra sites (Fig. 1), but its weather records were incomplete. The Inukjuak weather records were thus preferred to assess the relationship between recruitment pattern of < 2.5 -m seed-origin spruce and regional climate



Figure 2 A subarctic tree line in the Petite rivière de la Baleine (PB) region in northern Québec. The forest border (> 2.5 m) is shown at the back, and spruce < 2.5 m established by seed in the front.

in all subarctic tree line sites. Interannual fluctuations of temperature and precipitation should be similar at the two stations although their absolute values differ, and temperature records from the Inukjuak weather station were shown to be highly representative of the continental conditions prevailing 125 km south-eastwards (Wang *et al.*, 2001).

Statistical analyses

Tree line advance within each elevational transect was evaluated by subtracting the elevation of the oldest position of the tree line (downslope) from the elevation of the present tree line. The oldest position of the tree line was estimated from the position of the spruce in the elevational transect having the oldest stem section at 2.5 m, a method similar to that of Kullman (1986b). The total elevational advance of the tree line was converted to an annually-averaged rate of advance to facilitate comparison between regions.

A regression analysis was performed to test for the effect of latitude on abundance of seed-origin spruce < 2.5 m (for exponential regression, adding a value of 1 to all data to permit the inclusion of 0 values). The temporal patterns of recruitment (age structures) for seed-origin spruce < 2.5 m were compared between sites and regions using Kolmogorov–Smirnov tests with Bonferroni adjustment of the significance level ($\alpha' = 0.05/\text{number of comparisons}$).

Because black spruce's seedlings tend to germinate shortly after snow release (Black & Bliss, 1980), early snow melting resulting from warm spring temperatures may impede the survival of spruce seedlings through greater exposure to late frosts (e.g. Kullman, 1986b; Payette *et al.*, 1996). The growing season was thus subdivided in two parts: the period of discontinuous frost, extending from the end of continuous daily frost to the date of the latest frost, and the frost-free period, extending from the date of the latest frost to the date of the earliest late summer frost (Tuhkanen, 1980). The heat sum > 5 °C (GDD) was computed from the daily average temperature data for both periods of the growing season. Total precipitation recorded over summer (June–August) and winter (November–April) was also summed from daily data. GDD and precipitation were averaged over 5-year periods corresponding to the years included in each age class.

The presence of population depletion trends in the age structures for < 2.5-m seed-origin spruce was verified by applying both negative exponential and power function models, two models shown to describe reliably the age structure of tree populations (Hett & Loucks, 1976). When long-term trends in age were significant, residuals from the regression that best fitted the frequency data were used in the following Pearson's correlations; raw frequency data were used otherwise. The recruitment pattern was correlated with current 5-year heat sum (for both discontinuous frost and frost-free periods) and precipitation (summer and winter). Because, in the absence of fire, semi-serotinous cones require a period of air-drying before seeds can be released, tree establishment could be better correlated with the climate

having occurred at the time of seed formation or maturation, in the preceding years. Thus, recruitment patterns were also correlated with previous 5-year heat sum and precipitation. Temperature and precipitation conditions can also influence post-establishment survival of spruce seedlings. Recruitment patterns could thus be correlated with regional climate over the medium term rather than the short term. To test for this possibility, regional climatic records were averaged forward in time to integrate 10- and 20-year periods (e.g. Szeicz & MacDonald, 1995). For example, the number of trees established in the 1950–54 age class was correlated with heat sum and precipitation averaged for the 1950–59 (10 years) and 1950–69 (20 years) periods. The Bonferroni correction was applied to account for the multiplicity of comparison tests ($\alpha' = 0.05/16 = 0.003$). Multiple linear regressions and best subset regressions (Draper & Smith, 1981) were performed to see if tree establishment could be better predicted from a combination of the studied climatic variables. As these procedures failed to increase sensibly the determination coefficient (R^2) relative to simple Pearson's correlations, they are not presented here.

RESULTS

Milder climatic conditions have been registered at Inukjuak since 1944, as shown by the significant linear trend expressed by most computed climatic variables (Fig. 3). GDD have slightly

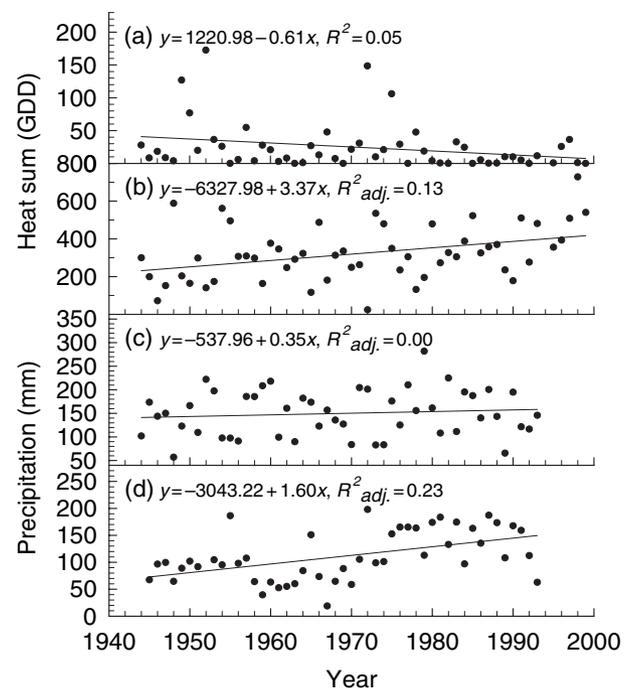


Figure 3 Regional weather records at the Inukjuak station for the 1944–99 period. Growing degree-days (GDD > 5 °C) are divided between the (a) discontinuous frost and (b) frost-free periods of the growing season. Total precipitation over (c) summer (June–August) and (d) winter (November–April) is shown.

declined during the discontinuous frost period of the growing season ($R_{\text{adj}}^2 = 0.05$, $P = 0.049$) and, concomitantly, have risen during the frost-free period of the growing season ($R_{\text{adj}}^2 = 0.13$, $P = 0.005$). The rise in heat sum has resulted at least in part from a generally longer frost-free growing season (linear regression of number of days with mean temperature > 5 °C according to year: $R_{\text{adj}}^2 = 0.20$, $P < 0.001$). Precipitation has also increased in winter ($R_{\text{adj}}^2 = 0.23$, $P < 0.001$), but not in summer ($R_{\text{adj}}^2 = 0.00$, $P = 0.473$). These trends appeared representative of the climatic conditions that have prevailed in the northern Québec area (Environment Canada, 2003).

Dead spruce stumps still rooted and bearing bark were found above present tree limits in nine sites out of 10 in the southern forest-tundra, indicating that hilltops were colonized by trees in the recent past. Fire scars dated 1823 and 1839 were found in nearby surviving trees at PB3 and PB4 sites, respectively. In contrast, dead stumps were absent from the tundra patches in sites of the northern forest-tundra.

Recent rise of tree lines

Over the last decades, elevational tree lines have slightly risen in all regions. Due to the young age of 2.5-m high stem sections in the PB elevational transects (Table 2), tree line movement could be reconstructed only for the last 30–45 years. The mean (\pm SE) elevational difference between the present and oldest positions of the tree line was 1.7 ± 0.5 m, corresponding to a low mean rate of rise of 5 ± 1 cm year⁻¹. In the EC region, 2.5-m high stem sections were older, allowing tree line movement to be reconstructed for the last 61–105 years. The mean elevational difference between the present and previous positions of the tree line was 6.9 ± 2.3 m, corresponding to a mean rate of rise of 10 ± 2 cm year⁻¹. In the LM region, tree line movement was reconstructed for the last 50–92 years, for a mean elevational difference of 5.2 ± 1.8 m and a mean rate of rise of 8 ± 4 cm year⁻¹. In the northernmost RI region, only 5–37 years of tree line movement could be evaluated, leading

Table 2 Range of subarctic tree line rises across the forest-tundra of northern Québec, Canada

Vegetation zone, region and site*	Record period†	Tree line rise (m a.s.l.‡)	Rate of tree line rise (cm year ⁻¹)	Cause of tree line advance
Southern forest-tundra				
Petite rivière de la Baleine				
PB1	1954–99	0.5	1	Tree established by seed in 1942
PB2	1963–99	2.8	8	Tree established by seed in 1938
PB3	1957–99	1.1	3	Tree established by seed in 1937
PB4	1966–99	2.7	8	Tree established by seed in 1949
PB5	1969–99	1.2	4	Tree established by seed in 1937
Mean (SE)		1.7 (0.5)	5 (1)	
Rivière à l'Eau Claire				
EC1	1916–99	4.8	10	Tree established by seed in 1904
EC2	1928–99	3.3	7	Tree established by seed in 1915
EC3	1938–99	2.1	6	Tree established by seed in 1902
EC4	1894–99	10.7	10	Tree established by seed in 1901
EC5	1906–99	13.7	15	Tree established by seed in 1868
Mean (SE)		6.9 (2.3)	10 (2)	
Northern forest-tundra				
Lac Minto				
LM1	1927–99	0.7	1	Growth of layer rooted in c. 1773
LM2	1907–99	4.1	4	Growth of layer rooted in c. 1827
LM3	1949–99	11.3	23	Growth of layer rooted in c. 1765
LM4	1938–99	3.0	5	Growth of layer rooted in c. 1747
LM5	1914–99	6.7	8	Growth of layer rooted in c. 1850
Mean (SE)		5.2 (1.8)	8 (4)	
Rivière Innuksuac§				
RI1	1991–99	0	0	–
RI2	1962–99	0	0	–
RI3	1988–99	0.8	7	Growth of layer rooted in c. 1819
RI4	1994–99	0.04	1	Growth of layer rooted in c. 1840
Mean (SE)		0.2 (0.2)	2 (2)	

*See Fig. 1 and Table 1 for stand locations.

†The first year is the oldest year of stem initiation at 2.5 m high in each elevational transect.

‡Metres above sea level.

§The site RI5 is not included due to tree heights being below the defined threshold of 2.5 m.

to a minor tree line rise of 0.2 ± 0.2 m and a mean rate of rise of 2 ± 2 cm year⁻¹. The slight elevational rises of tree lines of the southern forest-tundra have all occurred through seedling establishment. However, tree lines of the LM region and two tree lines of the RI region have slightly risen through accelerated height growth of spruce shrubs originally < 2.5 m, pre-established on the tundra hilltops. Hence, even if no statistical difference in the mean rates of tree line rise could be detected between the four surveyed regions (ANOVA: $F = 1.86, P > 0.05$), the slight tree line rises in the northern forest-tundra did not result from a genuine regeneration response to climate change as shown by those populations in the southern forest-tundra.

Abundance of < 2.5-m seed-origin spruce according to latitude

All < 2.5-m spruce (100%) in tree line stands of the southern forest-tundra were of seed origin, in sharp contrast with most < 2.5-m spruce (85%) originating from layering in stands of the LM region, in the northern forest-tundra. No < 2.5-m spruce of seed origin was found northwards, in the RI and LC regions.

The density of seed-origin spruce < 2.5 m in the tree line stands varied greatly, ranging from 0 spruce m⁻² (in eight out of 10 sites in the northern forest-tundra) to 1.4 spruce m⁻² in one of the southernmost sites, PB1 (Fig. 4). The latter value represented an extreme; the other nearby sites from the same region included between 0.1 and 0.3 spruce m⁻². The density of < 2.5-m spruce declined exponentially with latitude ($R^2_{adj} = 0.83, P < 0.0001$; Fig. 4).

Age structure for < 2.5-m seed-origin spruce according to latitude

The age structures for < 2.5-m seed-origin spruce differed between some of the five individual stands within each forest-tundra region (Bonferroni-adjusted $P < 0.0125$ for some

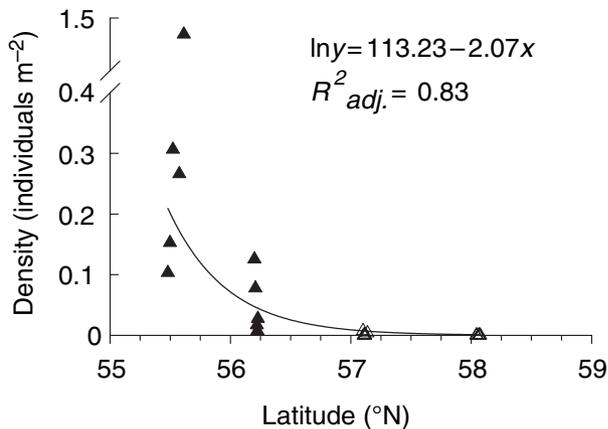


Figure 4 Abundance of seed-origin spruce < 2.5 m according to latitude in subarctic tree line sites across the forest-tundra of northern Québec. Filled triangles represent sites of the southern forest-tundra and open triangles, sites of the northern forest-tundra.

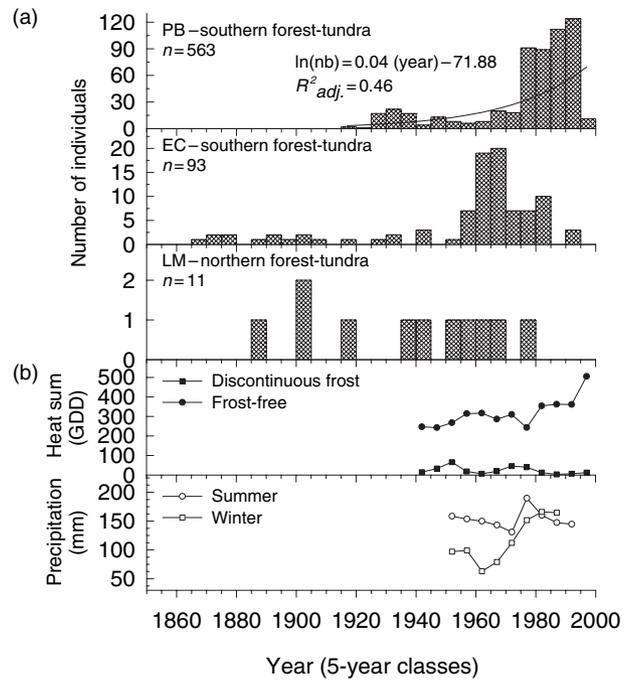


Figure 5 (a) Age structures for < 2.5-m seed-origin black spruce, combined from five subarctic tree line stands in regions of increasing latitude across the forest-tundra of northern Québec. No spruce of seed origin was found north of the Lac Minto (LM) region. Note the y-axes are plotted at different scales. (b) Regional heat sum (GDD > 5 °C) and total precipitation (summer: June–August and winter: November–April) at the Inukjuak weather station from 1944 to 1999, averaged over 5-year periods.

within-region Kolmogorov–Smirnov tests). Yet, age data were pooled by region (Fig. 5a) to obtain an overall picture of the recruitment patterns caused by regional, climatic factors.

Aged spruce of seed origin < 2.5 m surviving today ranged from 2 to 134 years old, and thus were established between 1865 and 1997 (Fig. 5a). The majority (76%) of < 2.5-m spruce from the PB sites were < 25 years old and thus established recently, from the late 1970s to the early 1990s. The population combined from these southernmost stands was the only one showing a significant long-term trend in age, negative exponential modelling providing the best fit ($R^2_{adj} = 0.46, P = 0.002$; Fig. 5a). At these sites, the rarity of seedlings established since 1995 could not be explained by the difficulty of finding small seedlings on the lichen mat because tundra patches were carefully checked. Recruitment of < 2.5-m seed-origin spruce at EC peaked earlier than at PB, i.e. in the 1960s (Fig. 5a). At LM, recruitment of < 2.5-m spruce by seed occurred sporadically, without any recent peak similar to those in the southern forest-tundra. The regeneration pool included suppressed trees over 50 years old that had not achieved yet a height of 2.5 m, respectively 13.5%, 20.4% and 54.5%, in average, from PB to LM. Inter-regional comparisons of the combined age structures indicated that they all differed significantly from those of the two other regions (Bonferroni-adjusted $P < 0.025$, Kolmogorov–Smirnov tests).

Spruce age according to elevation

In all sites of the southern forest-tundra except EC3, spruce age tended to decrease with increasing elevation ($r_s = -0.72$ to -0.27 , $P < 0.01$; Table 3) because of seedlings recently established above present tree limits. In contrast, spruce age was not linked to elevation in sites of the LM region ($r_s = -0.36$ to 0.34 , $P > 0.05$; Table 3), where local tree lines rose through height growth of pre-established shrubs (Table 2). The age of layered stems tended to decrease with elevation in three out of five sites at RI, arctic tree line ($r_s = -0.46$ to -0.28 , $P < 0.05$; Table 3).

Impact of the regional climate on seedling recruitment

The generally poor synchronicity between short-term patterns of recruitment for seed-origin spruce and available weather records is shown in Fig. 5. After the Bonferroni correction, the regional heat sum during the discontinuous frost period was not significantly associated with seedling recruitment for any period of averaging of weather records (previous 5 years, current 5 years and forwarded 10 and 20 years), nor any of the three regions where spruce of seed origin was recorded (PB, EC

and LM) (Table 4). However, in the southernmost PB region late summer frosts seemed to have slightly disfavoured spruce survival in the medium term (20 years; $0.003 < P < 0.05$). Seedling recruitment in all three regions was not significantly associated with heat sum during the frost-free period of the growing season (Table 4), although warm summers were slightly associated with better spruce recruitment over 10- and 20-year periods at PB ($0.003 < P < 0.05$). Total summer precipitation appeared to have no significant effect on the patterns of recruitment of any region, for any short- or medium-term period of averaging (Table 4). Spruce recruitment in the southernmost PB region appeared positively controlled by current winter precipitation ($P = 0.003$; Table 4) and, to a smaller extent, by winter precipitation during the previous 5 years and next 10 years ($0.003 < P < 0.05$; Table 4). In contrast, at LM, recruitment of seedlings was slightly and negatively associated with winter precipitation of the previous 5 years ($0.003 < P < 0.05$; Table 4).

Type of seedbed according to latitude

The proportion of seed-origin spruce < 2.5 m established on exposed mineral soil (tundra mudboils), lichen mat and moss carpet vegetation differed among regions (test of independence: $\chi^2 = 113.03$, d.f. = 4, $P < 0.001$). In the PB and EC regions, similar average proportions of spruce (61.4% and 65.5%, respectively) were established on the lichen mat, by far the most available seedbed along the studied toposequences. However, while more spruce occupied exposed mineral soil than moss carpet at PB, on average (30.9% vs. 7.7%), these proportions were reversed at EC (1.7% vs. 32.8%). The LM region differed strikingly from those of the southern forest-tundra as the 11 seed-origin spruce < 2.5 m registered (100%) were established on moss carpet.

Winter damage on colonizing spruce

The number of seed-origin spruce < 2.5 m showing signs of winter damage differed among regions. Significantly more < 2.5 -m spruce had apparent signs of winter damage in the southernmost PB region (median number = 34) than at EC (median number = 4) (Mann-Whitney rank sum test on values adjusted for the number of < 2.5 -m spruce: $T = 40.0$, $P = 0.008$). In contrast, none of the seed-origin spruce at LM were damaged because of wind-exposure in winter. At PB and EC, only 1.5% and 1.1% (respectively) of the seed-origin spruce < 2.5 m were still bearing only a few needles and, hence, were considered moribund.

DISCUSSION

Recent rise of tree lines

No dead spruce stumps were found above present tree lines in the northern forest-tundra, but they were widespread in the southern forest-tundra. Based on radiocarbon-dated charcoal,

Table 3 Spearman's rank correlations and associated significance levels between age and elevation of black spruce at subarctic tree line sites in northern Québec. Significant correlations ($P < 0.05$) are indicated in bold

Vegetation zone, region and site	r_s	P
Southern forest-tundra		
Petite rivière de la Baleine		
FBI	-0.27	< 0.001
PB2	-0.72	< 0.001
PB3	-0.50	< 0.001
PB4	-0.51	< 0.001
PB5	-0.27	0.002
Rivière à l'Eau Claire		
EC1	-0.67	< 0.001
EC2	-0.59	< 0.001
EC3	0.25	0.19
EC4	-0.36	0.003
EC5	-0.63	< 0.001
Northern forest-tundra		
Lac Minto		
LM1	-0.04	0.80
LM2	-0.21	0.26
LM3	-0.07	0.66
LM4	0.34	0.11
LM5	-0.36	0.09
Rivière Innuksuac		
RI1	0.06	0.66
RI2	-0.28	0.03
RI3	-0.46	0.001
RI4	-0.33	0.02
RI5	-0.22	0.06

Table 4 Pearson's correlations and associated significance values between 5-year age structures for seed-origin black spruce at subarctic tree line stands in northern Québec and regional weather records of the Inukjuak weather station*. Significant correlations† are indicated in bold

Climatic variable	Period of averaging (years)	Southern forest-tundra				Northern forest-tundra	
		Petite rivière de la Baleine‡		Rivière à l'Eau Claire		Lac Minto	
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
GDD§ (discontinuous frost)	Previous 5	0.080	0.815	0.041	0.906	0.476	0.139
	5	-0.176	0.584	-0.138	0.668	0.230	0.472
	10	-0.549	0.080	-0.093	0.786	0.077	0.822
	20	-0.805	0.009	-0.046	0.907	0.288	0.453
GDD (frost-free)	Previous 5	0.110	0.748	-0.088	0.798	-0.210	0.535
	5	-0.228	0.475	-0.219	0.494	-0.542	0.069
	10	0.741	0.009	-0.127	0.710	-0.439	0.177
	20	0.738	0.023	0.066	0.866	-0.474	0.198
Summer precipitation (June–August)	Previous 5	0.265	0.459	0.232	0.518	-0.386	0.270
	5	0.340	0.337	0.063	0.864	0.507	0.134
	10	0.321	0.400	-0.280	0.466	0.105	0.788
	20	0.721	0.068	0.330	0.470	0.070	0.881
Winter precipitation (November–April)	Previous 5	0.794	0.006	-0.486	0.154	-0.659	0.038
	5	0.833	0.003	-0.445	0.197	-0.434	0.210
	10	0.853	0.004	-0.291	0.447	-0.485	0.186
	20	0.695	0.083	0.312	0.495	-0.088	0.851

*Due to the short records of temperature (1940–99) and precipitation (1944–93), spruce established prior to these periods could not be used in the comparisons.

†Significance level (α) Bonferroni adjusted to 0.003.

‡Due to significant long-term trend in age in this population, recruitment residuals from a negative exponential model were used in the correlations.

§Growing degree-days (> 5 °C).

most upland sites across the forest-tundra of northern Québec were deforested over the last 1000 years, mostly during the Little Ice Age (Payette & Gagnon, 1985). The young-aged fire scars at two PB sites suggest that the southernmost upland forests re-established successfully following fires, until their exclusion at the very end of the Little Ice Age. The southernmost outliers of upland tundra at PB might thus mark a southward expansion of the forest-tundra into the boreal forest that took place *c.* 160–175 years ago.

Although there was a slight trend for the mean rate of rise in tree lines to decline with increasing latitude from EC to RI (Table 2), our first hypothesis was not supported statistically. Contrary to our expectations, the mean rate of tree line rise was slightly (although not significantly) reduced in the southernmost PB compared to EC. This could be explained in part by the harsh wind-exposure conditions of the southernmost sites, as suggested by the higher proportion of winter-damaged spruce. Furthermore, tree line spruce trees were younger at PB (Table 2), indicating that the estimated rise in tree lines could be reduced in this region because they have continued to advance under cooler climatic conditions than at EC. Indeed, tree line trees established in 1868–1915 at EC (Table 2), before a period favourable for tree growth (1920–40s), while they

established in 1937–49 at PB (Table 2), before the cooler 1950–70s period (Environment Canada, 2003).

Tree lines have risen during the last decades in practically all sites, but their elevational progression has been of small-scope (see also Paulsen *et al.*, 2000 for the Central Alps). Some white spruce tree lines in north-western Canada showed slow rates of advance similar to the present study (*c.* 1–4 cm year⁻¹; Szeicz & MacDonald, 1995). However, four to 10 times higher rates of rise in tree line were obtained for Norway spruce [*Picea abies* (L.) Karst.] in Sweden, according to dendrochronological and topographical data (Kullman, 1986a). Weaker tree line responses in subarctic Québec could be attributed (i) to less pronounced climate warming in eastern Canada compared with other northern areas (Houghton *et al.*, 2001; see also Briffa *et al.*, 1990 for Fennoscandia), and (ii) to harsher wind-exposure conditions associated with a smoother relief lacking protected slopes.

Colonization of tundra hilltops

A strong contrast exists in the spruce regeneration pattern between the southern and northern forest-tundra. Sexual reproduction has been the primary recruitment mode during

the 20th century in tree line stands of the southern forest-tundra, but not in stands of the northern forest-tundra. Efficient seedling recruitment in the southern forest-tundra allowed tree lines to rise and the PB hilltops to be invaded by seedlings (see also Esper & Schweingruber, 2004 for western Siberia). Not only were seed-origin spruce < 2.5 m far more numerous at PB (Fig. 4), but this was the sole region where an important proportion of these (31%) reached the hill summits and established on exposed mineral soil. In contrast, not only were seed-origin spruce < 2.5 m rare at LM, but their establishment was limited to moss carpet, protected by the proximity of forest border trees. The high variability in the density of seed-origin spruce < 2.5 m among the southern-most PB sites (0.1–1.4 spruce m⁻²) suggests that besides climate, local conditions, most probably slope orientation relative to prevailing winds (Table 1), influence seed dispersal and establishment. In support of our second hypothesis, the abundance of seed-origin spruce < 2.5 m decreased with latitude, following an exponential trend similar to the decrease in the proportion of forest cover across the forest-tundra (Payette *et al.*, 2001).

Our third hypothesis was also verified, as the age structures for < 2.5-m seed-origin spruce included proportionally more old, suppressed individuals from PB to LM. Static age structures reflect both establishment success and subsequent survivorship to the time of sampling. Young population structures were observed at PB, and one could wonder if a proportion of the established seedlings could still die due to harsh wind-exposure conditions or through self-thinning of the populations. In this region, the number of surviving spruce established from 1975 to 1994 was systematically above the value predicted from the best-fitted population depletion curve (Fig. 5a), which might suggest that spruce survival has been better over this period than in the past. In addition, a high mortality rate of seedlings should be detectable by the presence of a large number of dead seedlings on the sites, which was not the case. Although an important proportion of the southern forest-tundra's < 2.5-m spruce were damaged by wind-exposure and had already developed a stunted stature, only a small proportion (*c.* 1%) were showing signs of dieback. Under current climatic conditions, it is thus reasonable to believe that a large part of the regeneration pool should survive, at least as stunted growth forms. The age structures point to the impending reforestation of the PB and, to a smaller extent, of the EC tundra sites.

Contrary to stands of the southern forest-tundra, nearly all < 2.5-m spruce originated from layering in stands of the northern forest-tundra and in the shrub tundra. Similarly, the proportion of trees from vegetative propagation increased with elevation in white spruce in north-western Canada (Szeicz & MacDonald, 1995) and in various forest-tundra tree species in Colorado (Weisberg & Baker, 1995). Black spruce's potential for sexual reproduction is strongly regulated by the regional heat sum, which has proved to be insufficient in the northern forest-tundra to sustain significant production of viable seeds (Sirois, 2000). However, layering appears to be

only indirectly related to climate, depending more on physical factors allowing the contact of living stems with the ground than on warm summers (Laberge *et al.*, 2001). The age of layered spruce stems generally decreased with elevation at RI (Table 3). This trend could reflect the harsher wind-exposed conditions associated with the uppermost sites. Above tree line, severe abrasion of the stems in winter would result in higher stem mortality and faster turnover of the stems.

Indirect impact of the regional climate

The rise of tree lines through seedling establishment in the southern forest-tundra indicates a regeneration response of black spruce to 20th-century climate change. At a shorter timescale, however, the establishment of seed-origin spruce generally was not synchronous with 5-year fluctuations of the regional heat sum and precipitation (Fig. 5 and Table 4). The discrepancies observed here between short-term patterns of recruitment and climate indicate that in the absence of fire, their relationship is not straightforward, leading to the rejection of our fourth hypothesis. The rarity of seedlings established since 1995 at PB, after an early 1990s' peak, suggests that the effect of semi-serotinous cones in trapping the seeds for an unknown number of years before release (up to 25 years; Haavisto, 1975) could be a key factor blurring the link between tree establishment and climate. For white spruce and mountain hemlock [*Tsuga mertensiana* (Bong.) Carr.], two tree line species with non-delayed seed dissemination, tree establishment was actually more directly correlated with temperature fluctuations (Szeicz & MacDonald, 1995; Taylor, 1995; Lloyd & Fastie, 2003). Alternatively, the regional rise in GDD in the latter summers (Fig. 5b) is likely to have been associated with increased drought on the well-drained, exposed lichen mat. This could have exacerbated the difficulty of conifer seedlings establishing on lichen-dominated tundra vegetation, as revealed in previous studies (Cowles, 1982; Morin & Payette, 1984).

Temperature and precipitation conditions in the years following seedling establishment have been shown to determine tree regeneration success in some alpine tree lines (e.g. Kullman, 1986a,b; Szeicz & MacDonald, 1995). In this study, recruitment patterns were only slightly associated with medium-term heat sum during the discontinuous frost period or the frost-free period of the growing season at PB, and were not correlated with medium-term climatic trends at EC and LM. Again, the post-establishment mortality of black spruce in the surveyed tree line populations seems to have been low.

Total winter precipitation appeared to have a much stronger impact than summer precipitation on spruce recruitment patterns in PB tundra sites (Table 4). Black & Bliss (1980) have also emphasized the importance of snowmelt as the major source of water in the soil during the critical germination phase, precipitation over summer having relatively little impact on regeneration success. The slightly negative impact

of snowy winters on the establishment of seedlings at LM, a region characterized by relatively steep slopes compared with other regions (Table 1), could result from delayed snowmelt and shortened growing seasons associated with a greater amount of snow accumulated near the forest border, where seedlings have established.

Anticipated development of the tree line stands

As predicted, the subarctic tree line stands from the northern forest-tundra showed a greater regenerative inertia to recent climate change. It has been observed, from south to north: (i) abundant seedling recruitment and colonization of tundra hilltops at PB; (ii) seedling recruitment less pronounced and more restricted to the protected forest border at EC; (iii) development of krummholz into vertical growth forms at LM (see also Gamache & Payette, 2004), accompanied by episodic seedling recruitment restricted to the forest border; and (iv) no regeneration at RI (arctic tree line) and LC (shrub tundra). The development of a main vertical stem at LM should be the first step towards an increase in the spruce regenerative potential, because its reproductive structures are located on shoots of high branching levels (Bégin & Filion, 1999). Provided that milder climatic conditions (Fig. 3) persist in the region, the LM stands might thus reproduce more abundantly in the decades to come.

Under current wind-exposed conditions, spruce < 2.5 m colonizing the southernmost tundra hilltops will develop into forest only with difficulty, because a large proportion of trees were showing damage caused by wind-exposure. However, the establishment of trees in an open site creates positive feedbacks that promote enhanced growth as well as further establishment. These feedbacks include reduction of wind speeds (Chapin *et al.*, 2000) and increased trapping of snow (which protects stems in winter and increases soil moisture content; Black & Bliss, 1980; Scott *et al.*, 1993). Such facilitation mechanisms could greatly improve growth conditions in the long term, and allow the reforestation of the southern tundra hilltops.

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BIOSKETCHES

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Editor: Philip Stott