Height growth response of tree line black spruce to recent climate warming across the forest-tundra of eastern Canada

ISABELLE GAMACHE and SERGE PAYETTE

NSERC Northern Research Chair, Département de biologie and Centre d'études nordiques, Université Laval, Québec, QC, Canada G1K 7P4

Summary

1 The northward expansion of the boreal forest vegetation zone is generally predicted under a warmer doubled CO_2, but the delay associated with vegetation development processes often has been overlooked. In the subarctic forest-tundra of northern Québec, reforestation of tundra uplands appears currently limited by the poor reproductive capacity of shrubby black spruce (*Picea mariana*), and the development of erect stems through accelerated height growth should be the first registered response to 20th century climate warming. The subarctic forest-tundra is characterized by small- and large-scale heterogeneity in topography, vegetation structure and climate. This spatial heterogeneity, added to the complexity of tree growth–climate relationships, can cause various growth responses of subarctic tree line black spruce to 20th century climate change.

2 Twenty spruce populations at subarctic tree lines and seven isolated clones at the species limit were sampled along a > 300-km latitudinal transect from the southern forest-tundra to the shrub tundra. Height growth patterns of black spruce at tree line and above tree line were examined (i) over their life span, using dendrochronological dating of stem cross-sections, and (ii) for the recent decades, using leader shoot elongation measurements. Indexed elongation chronologies were compared with regional climate data.

3 Height growth of tree line trees generally decreased with increasing latitude. However, tree line trees in the northern forest-tundra have experienced an acceleration of height growth since the 1970s, with their growth comparable to that of trees in the southern forest-tundra. Height growth response of spruce trees appeared increasingly delayed from the northern forest-tundra to the species limit. Above the subarctic tree line, wind-exposed conditions obscured the decrease in height growth with latitude observed for tree line trees.

4 Leader shoot elongation of spruce trees established on tundra hilltops appeared more controlled by summer heat sums than those at tree line all over the forest-tundra, except at the arctic tree line. Winter precipitation also was linked to leader shoot elongation in some forest-tundra sites. The increasing snow cover associated with recent warming appeared to have reduced the shoot elongation of spruce at forest margins showing the steepest slopes, hence subjected to snow overloading.

5 In the northern forest-tundra sites, the recent increase in height growth and positive trend in leader shoot elongation, consistent with a 1990s' increase in heat sums, point to the development of spruce krummholz into erect growth forms. In the southern forest-tundra, reforestation of tundra hilltops and northward expansion of the boreal forest predicted under doubled CO_2 conditions could be delayed, as suggested by suppressed height growth of spruce above tree line.

Key-words: boreal forest, climate change, dendrochronology, forest-tundra, krummholz, *Picea mariana*, shoot elongation, snow cover, stem analysis, wind-exposure

Journal of Ecology (2004) **92**, 835–845

Correspondence: Isabelle Gamache (fax +1 418 656 2043; e-mail Isabelle.Gamache@bio.ulaval.ca).

Introduction

At high latitudes, global climate warming (Houghton *et al*. 2001) has often led to enhanced growth of trees in the 20th century relative to the previous Little Ice Age period (Lavoie & Payette 1994; Hessl & Baker 1997; Suarez *et al*. 1999; Lloyd & Fastie 2002). While summer temperature has been traditionally identified as the climatic variable determining tree growth (Norton 1984; Jacoby *et al*. 1985; Graumlich & Brubaker 1986; Briffa *et al*. 1995), several studies have emphasized the complexity of the relationship between growth and climate. Intraspecific competition for water and soil nutrients in dense forest stands (Black & Bliss 1980; Lloyd 1998) and disturbance events (Cullen *et al*. 2001) can disrupt tree growth–climate relationships. Abrupt climatic events, like summer frosts, can be more influential for tree growth than averaged climatic parameters (Dorming 1982; Payette *et al*. 1996). Moreover, beyond a certain threshold, rising summer temperatures can induce drought stress and reduce tree growth sensitivity to temperature (Barber *et al*. 2000; Lloyd & Fastie 2002).

Winter conditions have often been overlooked, although they can strongly influence tree growth in subarctic and subalpine environments. Increasing winter precipitation is associated with recent climate warming in northern areas (Houghton *et al*. 2001), and this can lead to delayed snowmelt and shortened growing seasons, therefore altering the response of tree growth to rising temperatures (Kirdyanov *et al*. 2003). In wind-protected forests, excess snowfall can reduce tree growth by mechanical damage caused by snow pressure and breakage of stems (Kajimoto *et al*. 2002). However, in wind-exposed tree line sites, the synergistic effect of reduced snow cover and low winter temperatures can cause severe growth reduction due to desiccation of needles and defoliation of stems (Payette *et al*. 1996). Clearly, in wind-exposed sites, winter conditions have to improve for trees to be able to respond positively to warmer temperatures in summer.

To what extent recent climate warming has been favourable for tree growth is an important issue for the future development of the subarctic forest-tundra in eastern Canada, a climate-sensitive ecotonal zone dominated by black spruce (*Picea mariana* [Mill.] BSP.), which occurs between continuous boreal forest and treeless arctic tundra. The subarctic forest-tundra is fragmented in forested lowlands and treeless uplands. Forest–tundra boundaries are outlined by subarctic tree lines which, unlike alpine tree lines, are not necessarily controlled by elevation due to the smooth relief of the Canadian Precambrian Shield (Payette *et al*. 2001). Black spruce is a morphologically plastic tree species adopting progressively stunted growth forms in response to increasing harsh winter conditions (Lavoie & Payette 1992). Decrease of forest cover from the southern to the northern forest-tundra is linked to spruce krummholz (shrubby growth forms) having low reproductive capacity (Sirois 2000) because it lacks the high

branching level stems that bear the reproductive structures (Bégin & Filion 1999). Previous studies (Lescop-Sinclair & Payette 1995; Gamache & Payette, in press) have proposed that an acceleration of spruce height growth would promote the change from krummholz to arborescent trees with better reproductive potential. This would allow the reforestation of tundra uplands and the northward expansion of the boreal forest predicted under a doubled CO_2 scenario (Emanuel *et al*. 1985; Lenihan & Neilson 1995). However, latitudinal heterogeneity in topography, vegetation structure and regional climate makes it unlikely that height growth of spruce stands can respond uniformly to climate warming all over the forest-tundra.

This study aims to evaluate the intensity and timing of the height growth response of black spruce to 20th century climate warming across the forest-tundra of northern Québec, Canada. In this area, heterogeneity of conditions for tree growth is expressed at both regional and local scales, the former through the northward decrease in air temperature, and the latter through the differences in wind-exposure associated with position relative to local subarctic tree lines. We sampled 20 spruce populations along a > 300-km latitudinal transect spanning the forest-tundra. Height growth was examined as the height growth of vertical stems over their entire life span, and as annual shoot elongation of the apical part of vertical stems in the recent decades. Regional weather records for 1944–99 allowed identification of the most influential climatic factors. We hypothesized that height growth of trees further north along the latitudinal gradient and of more exposed trees within each region will be slower, more dependent on climatic conditions and will have responded more to recent climate warming.

Methods

STUDY AREA

A continental area representative of the north-western part of the Québec–Labrador peninsula, surveyed in previous studies (Payette *et al*. 1989, 2001), was examined through airborne surveys along a latitudinal transect extending from 55°29′ to 58°27′ N at 75°30′ W (Fig. 1). The study area is a pristine forest-tundra ecotone with no permanent settlements. It is part of the Canadian Precambrian Shield, where granitic and gneissic rocks form a generally uniform, low-elevated plateau (Stockwell *et al*. 1968). Well-drained exposed uplands (rocky hills or drumlins) are uniformly distributed along the transect and are interrupted by wetlands and lakes.

The nearest weather stations are located along the Hudson Bay coast at Kuujjuaraapik (south) and Inukjuak (north) (Fig. 1). From 55° to 59° N, mean annual temperature varies from −4 °C to −7 °C, and total annual precipitation from 650 to 450 mm, with 40% as snow (Environment Canada 2003). Climatic conditions
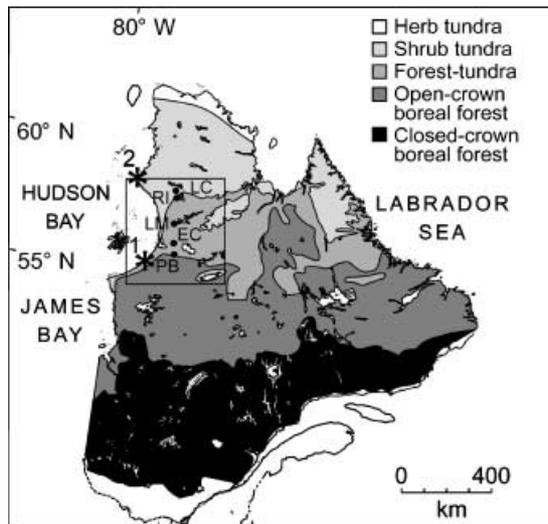
Fig. 1 Study area, showing vegetation zones northward from the boreal forest (Payette 1983). Five forest-tundra sites were sampled in the Petite rivière de la Baleine (PB), Rivière à l'Eau Claire (EC), Lac Minto (LM) and Rivière Innuksuac (RI) regions, and seven isolated black spruce clones in the Lac Chavigny (LC) region north of the arctic tree line. Asterisks indicate weather stations at Kuujjuaraapik (1) and Inukjuak (2).

become harsher for tree growth as the annual sum of growing degree-days (> 5 °C) decreases northwards from 600 to 355 (Environment Canada 2003). As a result, the growing season extends from early June to early September in the south and from mid-June to late August in the north.

The latitudinal climatic gradient is associated with drastic changes in the vegetation cover from open-crown boreal forest (lichen woodland) to shrub tundra (Fig. 1). The southern parts of the forest-tundra are characterized by extensive forest cover, infrequently broken by tundra gaps on wind-exposed uplands. The proportion of forest cover drops rapidly and forests become increasingly scattered and confined to wind-protected slopes and depressions (Payette *et al.* 2001) so that the northern forest-tundra is predominantly treeless, with extensive tundra patches.

SELECTION OF SAMPLING SITES

Five regions showing 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 represent southern forest-tundra, and the Lac Minto (LM) and Rivière Innuksuac (RI) regions northern forest-tundra. RI is located at the arctic tree line but the species limit occurs in the Lac Chavigny (LC) region, a few tens of kilometres further north, where our transect includes northernmost stunted black spruce individuals.

In the summer of 1999, five nearby sampling sites were selected in each forest-tundra region, and seven isolated spruce clones were located at the species limit (Table 1). Each site was a granitic hill with a typical

vegetation toposequence, i.e. tundra vegetation on the hilltop and lichen woodland downslope, and therefore contained a local subarctic tree line. Sites were selected to be relatively homogeneous in terms of mean slope (< 15°) and mean thickness of snow cover on the hilltop, as estimated from mean height of dwarf birch (Arseneault & Payette 1992).

DATA COLLECTION

A 10 m-wide belt transect was randomly positioned on each selected hill, extending downslope from the summit to below the local tree line, defined as the uppermost position of ≥ 2.5-m single-stemmed or supranival skirted tree growth forms (Lescop-Sinclair & Payette 1995). (Transect length 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.

The main vertical stem of all living spruce > 1 m tall within each belt transect was sampled. Spruce < 1 m were excluded to minimize growth differences related to age. The northern forest-tundra stands were mainly composed of multi-stemmed clones, regenerated by layering of the lower branches, and the tallest vertical stem was sampled. Stems were cross-sectioned at the root collar (root–shoot interface, below ground level) or at the base of the stem curvature when no root collar could be found, and at successive 0.5-m intervals along the stem.

HEIGHT GROWTH OF STEMS

Stem discs were air-dried, finely sanded and dated by counting annual growth rings under a binocular microscope. Dating of stem discs was validated using a chronology of light rings (growth rings with exceptionally few latewood cells; Filion *et al.* 1986). Mean height growth curves were constructed separately for black spruce growing at tree line (> 2.5 m high) and above tree line (< 2.5 m high).

The height reached by the fully exposed (< 2.5-m) and less exposed (> 2.5-m) spruce stems in each forest-tundra region was presented as a function of (i) age of trees, to evaluate stem development irrespective of climatic conditions, and (ii) year of stem initiation, to account for changes in climatic conditions during stem development. A 95% confidence interval (95% CI) of the mean age or year was computed at each 0.5-m height interval for all growth curves. Mean height growth curves with overlapping 95% CI were considered to have reached corresponding heights at the same time.

LEADER SHOOT ELONGATION IN RELATION TO CLIMATE

The apical part (*c.* 1 m) of the sampled stems was brought to the laboratory. Annual shoot elongation was obtained by measuring the distance between successive terminal

Table 1 Location parameters of subarctic tree line stands of black spruce in northern Québec, Canada

Vegetation zone Region 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	n
Southern forest-tundra								
Petite rivière de la Baleine								
PB1	−272	55°37′	75°36′	325	324	3	S	20
PB2	−287	55°29′	75°29′	335	330	4	NE	33
PB3	−285	55°30′	75°25′	310	307	4	NE	18
PB4	−282	55°31′	75°33′	325	322	8	S	15
PB5	−276	55°34′	75°35′	345	342	5	NE	48
Mean (SE)	−280 (2.6)			328 (5.8)	325 (5.6)	5 (0.9)		27 (6.1)
Rivière à l'Eau Claire								
EC1	−204	56°13′	75°30′	290	286	4	W	21
EC2	−204	56°13′	75°30′	285	282	7	SSW	23
EC3	−204	56°14′	75°27′	305	304	5	SW	18
EC4	−206	56°12′	75°26′	305	298	8	SW	28
EC5	−207	56°12′	75°22′	295	288	13	SW	32
Mean (SE)	−205 (0.8)			296 (4.0)	292 (4.2)	8 (1.6)		24 (2.5)
Northern forest-tundra								
Lac Minto								
LM1	−106	57°06′	75°33′	215	201	7	NW	21
LM2	−106	57°06′	75°34′	220	211	9	NW	29
LM3	−105	57°07′	75°33′	279	272	14	SW	44
LM4	−102	57°08′	75°33′	215	204	7	SE	19
LM5	−105	57°07′	75°36′	275	271	9	S	23
Mean (SE)	−105 (0.8)			241 (14.8)	232 (16.3)	9 (1.2)		27 (4.5)
Rivière Innuksuac								
RI1	0	58°04′	75°29′	195	190	9	W	39
RI2	0	58°03′	75°28′	220	209	6	NW	12
RI3	0	58°03′	75°25′	220	215	3	NW	34
RI4	0	58°04′	75°30′	230	222	8	W	19
RI5	0	58°04′	75°33′	225	215	6	NW	35
Mean (SE)	0 (0)			218 (6.0)	210 (5.5)	6 (1.0)		28 (5.2)
Shrub tundra								
Lac Chavigny								
LC1–LC7‡	+35 (3.3)	58°15–58°27′	75°21′–75°39′	–	–	–	–	7

*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.

bud scars (internode) downwards from the sampling year (1999) until secondary growth of stems (thick bark) hampered counting of bud scars. The starting year of each series of elongation measurements was validated by counting the number of growth rings on the basal cross-section of the oldest internode measured. Stems (< 5%) showing abrupt, traumatic growth decreases (> 50% growth reduction for > 5 consecutive years) were discarded.

At each site, elongation measurements were averaged for the period common to stems from all individual sites (1990–98). The latitudinal trend in absolute values of recent height growth was assessed for stems growing at tree line and above tree line. Regression analysis of elongation according to latitude was not performed due to unequal variances between sites. ANOVAS on ranks (Kruskal–Wallis [K–W] tests; Sokal & Rohlf 1995) with the Dunn's procedure of pairwise multiple comparisons were performed on mean annual elonga-

tion between regions. Subsequently, individual elongation series were standardized to give equal weight to slow and faster growing trees, without altering the series' low-frequency trends, as these could indicate a response to recent climate warming. Horizontal curve standardization (Fritts 1976) was based on annual growth divided by mean annual growth of each series, to obtain a dimensionless elongation index. Elongation indices were averaged by year to construct elongation chronologies of > 2.5-m and < 2.5-m black spruce in each region. Elongation chronologies were compared among the differently exposed stems and regions using Pearson's product–moment correlations. The Bonferroni correction was applied to account for the multiplicity of comparison tests ($\alpha' = 0.05/8 = 0.006$).

Although the Kuujjuaraapik weather station was nearer to the southern forest-tundra stands (Fig. 1), its weather records were incomplete. Interannual fluctuations of temperature and precipitation should, however, 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). Climatic data from the Inukjuak weather station were therefore used to evaluate the relationship between spruce annual leader shoot elongation and regional climate for all sites.

By promoting earlier starting of growth, warm temperatures in spring can increase the probability of freezing injury to needles and buds due to late frosts, and therefore reduce spruce growth (Kullman 1986; Payette *et al.* 1996). The growing season was thus subdivided into the period of discontinuous frost (from the end of continuous daily frost to the date of the latest frost) and the frost-free period (from latest frost to the earliest late summer frost). The sum of growing degree-days (GDD, > 5 °C) was computed from the daily average temperature data for both periods. Cold winters also could affect subsequent growth by causing desiccation and mechanical loss of needles (Payette *et al.* 1996). The sum of degree-days (DD) < 0 °C (heat deficit) for November–April was therefore calculated. Finally, total precipitation recorded during summer (June–August) and winter (November–April) was summed from daily data. Growth of conifers at tree line sometimes correlates better with previous than current summer temperature (James *et al.* 1994; Takahashi 2003). The correspondence between > 2.5-m and < 2.5-m elongation chronologies and climatic variables was therefore assessed for all regions and for both current and previous years' data, using Pearson's correlations with Bonferroni adjustment of the significance level ($\alpha' = 0.05/10 = 0.005$). Multiple linear regressions and best subset regressions (Draper & Smith 1981) were performed to see if spruce elongation could be better predicted from a combination of climatic variables, but did not increase the determination coefficient (r^2) significantly relative to simple Pearson's correlations, and are not presented here.

Results

HEIGHT GROWTH ACCORDING TO AGE OF TREES

Mean height growth with age of black spruce at tree line and above tree line in regions of increasing latitude is shown in Fig. 2. The younger mean ages sometimes observed at higher stem levels are artefacts caused by the reduction in the number of sampled cross-sections with increasing height. The slope of the mean growth curves represents height growth rate at different periods during stems' life span.
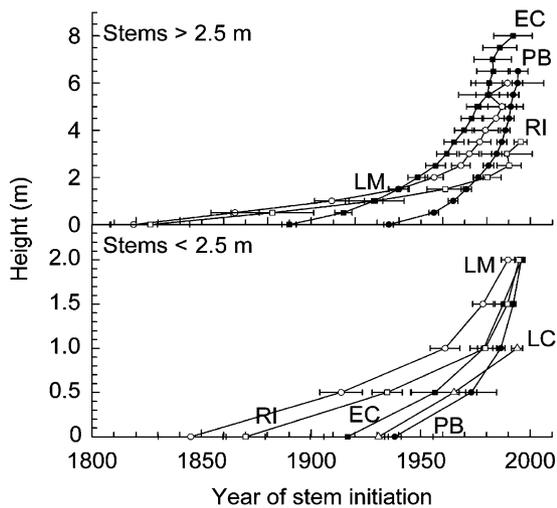
In the southern forest-tundra, height growth of the > 2.5-m stems initially increased with age (Fig. 2), but slowed down slightly at *c.* 100 years old at EC. Overall, height growth of tree line spruce in the southern forest-tundra was steady compared to that at LM, where
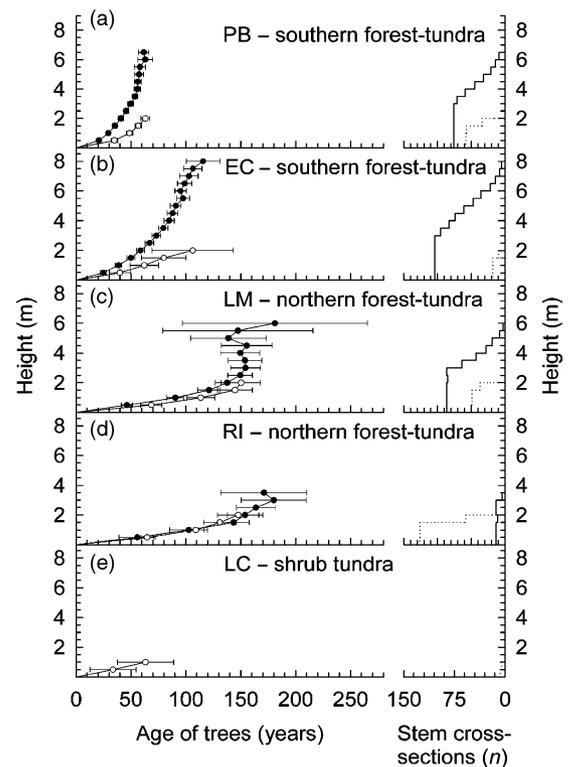
Fig. 2 Mean height growth according to age of black spruce trees at tree line (> 2.5 m, black dots) and above tree line (< 2.5 m, white dots), from the southern forest-tundra to the shrub tundra in northern Québec (region abbreviations as in Fig. 1). Confidence intervals (95%) of the mean age of trees are shown at each 0.5-m height interval. The number of stem cross-sections at each 0.5-m height interval is indicated by thin solid (> 2.5-m stems) and dotted (< 2.5-m stems) lines.

stems grew at an initially very reduced rate, taking 138–161 years (95% CI) to reach a height of 2.5 m. Height growth of these LM stems has increased afterwards, although the age at which trees reached subsequent height levels was highly variable. Height growth of arborescent stems at RI (arctic tree line) has not changed markedly with age, although it increased slightly once stems reached 1.5 m, at 129–158 years old. From PB (south) to RI (north), height growth of > 2.5-m spruce stems decreased northwards, with stems reaching the same heights at progressively older ages (Fig. 2). However, 95% CI of mean age of trees overlapped at 5.5–6 m for the EC and LM regions and at all heights for the two northern forest-tundra regions (LM and RI), so that height growth did not differ significantly.

Height growth of < 2.5-m stems did not decrease with increasing latitude as consistently as for the arborescent stems. Based on the examination of 95% CI (Fig. 2), height growth of wind-exposed stems from PB was comparable to that of stems from EC and from the species limit (LC) within their common height range (i.e. below 1 m). Above 1 m, height growth of exposed stems from the two southern forest-tundra regions diverged, with EC comparable to the two northern forest-tundra regions.

Fig. 3 Mean height growth curves as a function of year of stem initiation for > 2.5-m black spruce at tree line and < 2.5-m black spruce above tree line, from the southern forest-tundra to the shrub tundra in northern Québec (region abbreviations as in Fig. 1). PB, black dots; EC, black squares; LM, white dots; RI, white squares and LC, white triangles. Note the *y*-axes are plotted at different scales. Confidence intervals (95%) of the mean year are shown at each 0.5-m height interval.

The contrast in height growth between > 2.5-m and < 2.5-m stems decreased northwards (Fig. 2). Confidence intervals of the mean age of trees of the differently exposed stems overlapped above 1.5 m in height at LM, and at all heights at RI, indicating that there was little growth difference due to exposure in the northern forest-tundra.

HEIGHT GROWTH ACCORDING TO YEAR

Figure 3 shows mean height growth curves of > 2.5-m and < 2.5-m spruce from the 19th century to present. In the southern forest-tundra (PB and EC), stems > 2.5 m showed no evidence of abrupt changes in height growth. In the northern forest-tundra, tree line stems were suppressed until 1964–72 at LM and until 1985–96 at RI (95% CI of the mean year at 2.5 m), but then LM stems grew at a rate comparable to EC (1971–97) and PB (1979–93). These changes in height growth rate were confirmed by the heterogeneity of the linear regression slopes before and after stems reached a height of 2.5 m (tests of homogeneity of slopes: $P < 0.05$).

Stems < 2.5 m showed a constant height growth rate during most of their life span, with slight recent increases in 1971–76 (PB), 1945–68 (EC), 1954–68 (LM) and 1976–83 (RI) (Fig. 3) occurring when stems reached a height of 0.5 m in the southern forest-tundra, and 1 m in the north (tests of homogeneity of linear regression slopes: $P < 0.05$). RI stems grew as fast as those in southern forest-tundra regions in 1984–93 (overlapping 95% CI of the mean year at 1.5 m and above). In contrast, isolated clones at the species limit (LC) showed a slow height growth rate throughout their life span.
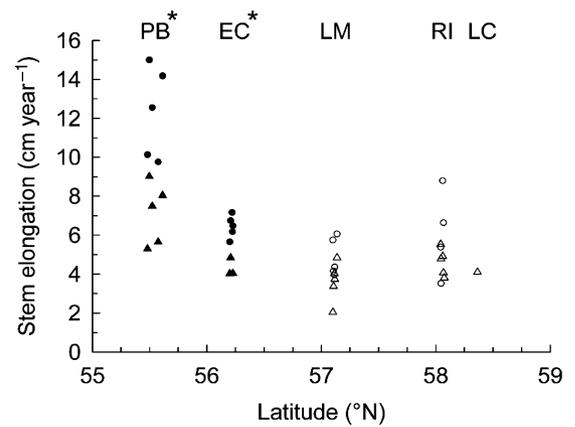
Fig. 4 Annual elongation (1990–98) of the main stem of black spruce at tree line (> 2.5 m; dots) and above tree line (< 2.5 m; triangles) according to latitude across the forest-tundra and the shrub tundra of northern Québec. Values are means of individual sites. Filled symbols represent sites of the southern forest-tundra and open symbols, sites of the northern forest-tundra and the shrub tundra. Regions (abbreviated as in Fig. 1) where mean elongation of > 2.5-m and < 2.5-m stems differs are indicated by asterisks.

LATITUDINAL TREND IN MEAN LEADER SHOOT ELONGATION

Absolute values of annual leader shoot elongation between 1990 and 1998 were compared between trees at and above tree line within each region (Fig. 4). Variability in annual shoot elongation was generally greater in PB than in the other regions. Mean annual elongation in 1990–98 differed among regions for > 2.5-m trees (K–W test: $H = 12.65$, $P = 0.005$) and < 2.5-m trees (K–W test: $H = 11.88$, $P = 0.018$). For both stem groups, the only regions that differed significantly following the multiple comparison procedure were PB and LM (Dunn's tests: $P < 0.05$). Annual elongation of the main stem differed significantly (*t*-tests) between stems at and above tree line in southern sites (PB: $t = 4.13$, $P = 0.003$; EC: $t = 5.45$, $P = 0.002$), but not in the north (LM: $t = 1.99$, $P = 0.082$; RI: $t = 1.41$, $P = 0.200$) (Fig. 4).
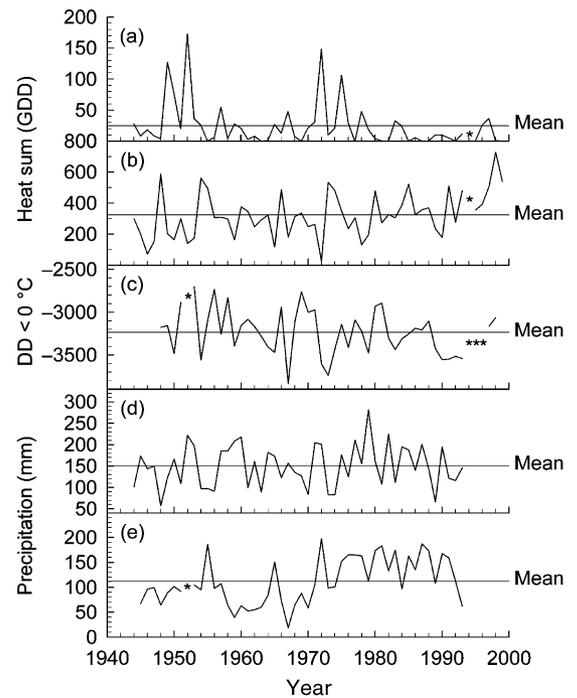
LEADER SHOOT ELONGATION CHRONOLOGIES

Figure 5 shows mean leader shoot elongation indices for black spruce growing at and above tree line. Inter-annual variations and longer-term trends in leader shoot elongation were common to most chronologies (Table 2), suggesting that, beyond the differences among sites in absolute values of shoot elongation (Fig. 4), stem growth has responded to common forcing factors. Mean chronologies at LM go back to the 1950–60s, but chronologies were shorter for > 2.5-m trees at other regions due to faster growth and thus fewer number of years being included in the 1-m sample in the southern forest-tundra, and a higher frequency of traumatic shoots further north.
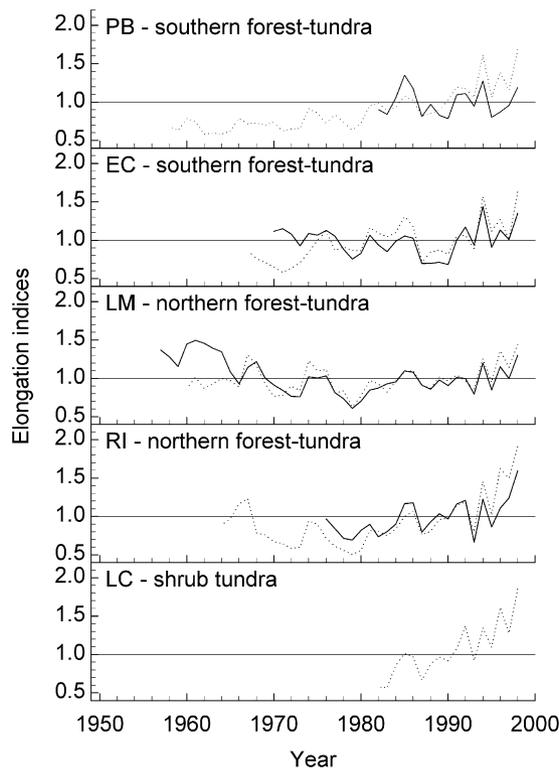
Fig. 5 Mean chronologies of leader shoot elongation of black spruce at tree line (> 2.5 m, solid lines) and above tree line (< 2.5 m, dotted lines) across the forest-tundra and the shrub tundra of northern Québec. Region abbreviations as in Fig. 1. Chronologies are cut at the point where the number of series falls below five.

Fig. 6 Regional weather records at the Inukjuak station for the 1944–99 period. Sum of growing degree-days (> 5 °C) during the (a) discontinuous frost and (b) frost-free periods of the growing season; (c) sum of degree-days < 0 °C during winter (November–April; 1948–98); total (d) summer (June–August) and (e) winter (November–April) precipitation (1944–93). *Missing data.

In PB, spruce stems above tree line showed reduced elongation until growth release in the early 1980s (Fig. 5). Before the 1970s, stems at LM and < 2.5-m stems at RI showed decreasing shoot elongation. The 1970s to mid-1980s was a period of reduced shoot elongation all over the forest-tundra. There has been a positive trend in mean leader shoot elongation since the early 1990s, particularly in the northernmost (RI and LC) regions (Fig. 5).

LEADER SHOOT ELONGATION IN RELATION TO CLIMATE

Comparison with the climatic record (Fig. 6) suggests that annual elongation of spruce stems above tree line is more strongly controlled by climate than that of > 2.5-m stems (significant correlations in Table 3). High heat sums during the frost-free period of both the previous and current growing seasons were significantly favourable to leader shoot elongation of > 2.5-m stems only at

Table 2 Pearson's correlation coefficients among indexed elongation chronologies of black spruce in regions of increasing latitude across the forest-tundra and the shrub tundra of northern Québec. Values in bold are significant at adjusted $P < 0.006$. Region names in row headings are abbreviated in column headings

	Stems > 2.5 m				Stems < 2.5 m				
	PB	EC	LM	RI	PB	EC	LM	RI	LC
Stems > 2.5 m									
Petite rivière de la Baleine	1.000								
Rivière à l'Eau Claire	**0.726**	1.000							
Lac Minto	**0.649**	**0.606**	1.000						
Rivière Innuksuac	0.633	**0.645**	**0.868**	1.000					
Stems < 2.5 m									
Petite rivière de la Baleine	0.519	**0.526**	0.049	**0.783**	1.000				
Rivière à l'Eau Claire	**0.698**	0.544	0.560	0.705	**0.846**	1.000			
Lac Minto	0.463	**0.571**	0.495	**0.842**	0.618	0.612	1.000		
Rivière Innuksuac	0.381	**0.508**	**0.680**	**0.874**	**0.813**	0.717	**0.812**	1.000	
Lac Chavigny	0.404	**0.730**	**0.759**	**0.825**	**0.869**	0.668	**0.870**	**0.944**	1.000

Table 3 Pearson's correlations and associated significance values between indexed elongation chronologies of black spruce, located at tree line (> 2.5 m) or above tree line (< 2.5 m) in the forest-tundra or in the shrub tundra of northern Québec, and regional weather records of the Inukjuak weather station. Significant correlations* are indicated in bold

		Southern forest-tundra				Northern forest-tundra				Shrub tundra	
		PB		EC		LM		RI		LC	
Climatic variable	Year	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Stems > 2.5 m											
GDD†	Previous	0.482	0.059	0.097	0.625	−0.125	0.434	0.099	0.661	–	–
(discontinuous frost)	Current	−0.277	0.300	0.181	0.358	−0.141	0.380	−0.169	0.453	–	–
GDD	Previous	0.545	0.029	0.480	0.010	0.250	0.114	**0.648**	**0.001**	–	–
(frost-free)	Current	0.580	0.019	0.274	0.158	0.094	0.561	**0.575**	**0.005**	–	–
DD < 0 °C‡	Previous	0.315	0.273	0.038	0.854	−0.076	0.648	0.188	0.428	–	–
(November–April)	Current	−0.307	0.286	−0.219	0.281	−0.135	0.412	−0.115	0.630	–	–
Summer precipitation	Previous	0.328	0.274	−0.176	0.399	−0.103	0.539	0.005	0.985	–	–
(June–August)	Current	0.031	0.924	−0.171	0.423	−0.115	0.498	−0.446	0.063	–	–
Winter precipitation	Previous	−0.321	0.284	−0.441	0.027	**−0.652**	**< 0.001**	−0.221	0.364	–	–
(November–April)	Current	−0.106	0.744	−0.220	0.302	**−0.556**	**< 0.001**	0.073	0.773	–	–
Stems < 2.5 m											
GDD	Previous	−0.166	0.307	−0.085	0.651	−0.021	0.902	−0.191	0.280	0.431	0.095
(discontinuous frost)	Current	−0.182	0.261	−0.244	0.185	0.047	0.781	−0.138	0.436	0.014	0.958
GDD	Previous	**0.455**	**0.003**	**0.521**	**0.003**	**0.610**	**< 0.001**	**0.503**	**0.002**	0.541	0.030
(frost-free)	Current	**0.590**	**< 0.001**	**0.489**	**0.005**	0.333	0.041	**0.484**	**0.004**	0.544	0.029
DD < 0 °C	Previous	0.261	0.113	0.112	0.564	0.181	0.290	0.149	0.417	0.297	0.302
(November–April)	Current	0.018	0.915	−0.056	0.775	0.134	0.436	0.026	0.888	−0.245	0.399
Summer precipitation	Previous	−0.104	0.542	0.116	0.558	0.181	0.290	−0.224	0.225	−0.079	0.797
(June–August)	Current	−0.157	0.362	−0.011	0.958	−0.316	0.069	−0.284	0.128	−0.410	0.186
Winter precipitation	Previous	0.256	0.127	0.176	0.370	−0.251	0.146	−0.163	0.380	−0.329	0.273
(November–April)	Current	0.342	0.041	0.266	0.181	−0.152	0.392	−0.277	0.139	−0.322	0.307

*Significance level (α′) Bonferroni-adjusted to 0.005.
†Sum of growing degree-days (> 5 °C).
‡Sum of degree-days < 0 °C.

RI, but of < 2.5-m stems at all regions except LC (and LM for the current season). GDD during the frost-free period of the previous growing season almost always had a stronger impact on leader shoot elongation than those of the current growing season (Table 3). At tree line, winter precipitation was significantly correlated with stem elongation at LM. The three other climatic variables included in the comparisons, i.e. GDD during the discontinuous frost period of the growing season, DD < 0 °C and summer precipitation, were not significantly correlated with any elongation chronology (Table 3).

Discussion

LATITUDINAL TREND IN HEIGHT GROWTH

In northern Québec, the dichotomy between the southern and northern forest-tundra, which has been previously revealed in fire cycle (Payette *et al*. 1989), vegetation structure (Payette *et al*. 2001) and tree reproductive patterns (Sirois 2000; Gamache & Payette, in press), also applies generally to tree height growth patterns. Tree line spruce in the southern forest-tundra showed normal height development with age compared to suppression for nearly 150 years in the northern forest-tundra (Fig. 2). Height growth of > 2.5-m trees has also been higher in the southern forest-tundra during most of their life span, with height growth at the LM subarctic tree line becoming comparable only in the 1970–90s (Fig. 2). Furthermore, mean annual leader shoot elongation during the last decade (1990–98; Fig. 4) differed significantly between the southernmost stems (PB) and those of LM. The southern and northern forest-tundra also differed in the contrast in height growth between stems at and above tree line, with mean height growth (Fig. 2) and absolute values of stem elongation (Fig. 4) lower for wind-exposed stems only in the south. The range between maximum and minimum elevations decreases with latitude across the forest-tundra of northern Québec (Payette *et al*. 2001) and the reduced contrast appears to reduce the differences due to wind-exposure.

WIND-EXPOSURE AS A SUPPRESSION FACTOR OF GROWTH

Wind-exposure clearly acts as a homogenizing factor obscuring the latitudinal trends in height growth

shown by > 2.5-m tree line trees. Wind speeds are significantly greater among scattered trees (typical of sites beyond tree line) than forest trees (Chapin *et al.* 2000) and the resulting air cooling (e.g. James *et al.* 1994) appears to have smoothed the latitudinal gradient of temperature on hilltops relative to that inside forest margins. Within their common height range (0–1 m), height growth of wind-exposed trees from the southern forest-tundra was actually comparable to that of isolated clones from the species limit. Also, disparity in leader shoot elongation (1990–98; Fig. 4) was reduced between the < 2.5-m trees from PB and LM relative to > 2.5-m trees. The ecological implications of these results are of great importance in the context of possible reforestation of tundra hilltops. The numerous spruce seedlings that have established beyond the tree line on the southernmost tundra hilltops, as a result of recent warming (Gamache & Payette, in press), will be subjected to severe wind-exposed conditions similar to those occurring in the northern forest-tundra, and their development into vertical growth forms is likely to be delayed. However, positive feedbacks (due for instance to reduction of wind speed [Chapin *et al.* 2000] and increased trapping of snow [Scott *et al.* 1993]) may gradually promote height growth if tree establishment is maintained.

HEIGHT GROWTH RESPONSE TO CLIMATE WARMING

Based on the acceleration in mean height growth (Fig. 3), tree line trees in LM showed the greatest response to 20th century climate warming. In the same region, development of spruce shrubs into vertical growth forms was shown to have caused recent rises in tree lines in the forest-tundra of northern Québec (Gamache & Payette, in press). The LM region, located near the middle of the forest-tundra (Fig. 1), is probably a key transition zone, where tree line spruce had conserved enough photosynthetic biomass during the Little Ice Age for height growth to be able to respond markedly to the recent climatic amelioration. Southwards, tree line trees are already arborescent, and climate warming appears currently to have more effect on their reproductive patterns (Gamache & Payette, in press), while northwards, climate has not improved enough to allow changes in growth forms. At the arctic tree line (RI), only the beginning of a response in tree height growth could be observed (mid-1980s to mid-1990s, Fig. 3), while at the species limit, the positive trend in mean leader shoot elongation registered since the early 1990s (Fig. 5) was not yet observable in mean height growth (Fig. 3). Thus, height growth response of spruce to recent climate warming was increasingly delayed from the LM region to the species limit. Height growth of < 2.5-m wind-exposed trees has slightly speeded up at *c*. 0.5–1 m in all forest-tundra regions (Fig. 3), possibly indicating that stems have passed through the most intense winter-abrasion zone, immediately above the snow–air

interface (Pereg & Payette 1998), allowing their apical parts to respond more positively to climate warming.

CLIMATIC CONTROL OF LEADER SHOOT ELONGATION

The reduced shoot elongation of spruce stems observed all over the forest-tundra before the mid-1980s (Fig. 5) is likely to have resulted from the regional cooling trend of the 1960–80s (Environment Canada 2003). The same period was associated with reduced seed regeneration and radial growth in white spruce (*Picea glauca* [Moench] Voss) populations along the eastern coast of Hudson Bay (Payette & Filion 1985).

The hypothesis that leader shoot elongation depends more on climatic conditions in the northernmost forest-tundra regions was not confirmed, with differences observed instead between trees at and above subarctic tree line (Table 3). The shoot elongation of tree line trees was significantly controlled by GDD (frost-free; Table 3) only at RI, in accordance with the recent homogenization of height growth rates in the more southerly regions (> 2.5 m; Fig. 3) where, presumably, a warmer microclimate has made shoot elongation less dependent on climatic fluctuations. Leader shoot elongation of spruce above tree line, in contrast, appeared significantly controlled by GDD (frost-free) all over the forest-tundra (Table 3). The less significant correlation between shoot elongation and GDD (frost-free) at the species limit is probably attributable to the small number of individual elongation series (*n* = 7) included in the mean. Furthermore, GDD (frost-free) almost always had more impact on leader shoot elongation in the following than in the current year (Table 3). Black spruce shoot elongation may rely on the photosynthetic reserves already stored in buds and adjacent stems (James *et al.* 1994; Takahashi 2003), whose constitution would be more or less strongly determined by GDD during the frost-free period of the growing season.

After GDD (frost-free), total winter precipitation was the most influential climatic variable for leader shoot elongation. Winter precipitation was negatively correlated with leader shoot elongation of tree line stems in LM, where the snow from the summit slides more easily down the steeper slopes (Table 1), and forest margins are therefore likely to accumulate more snow. The negative impact of snowy winters on tree stems at the forest margin could be due to delayed snowmelt and shortened growing seasons, or to snow overloading damage, supported by the characteristic deformed growth forms (Kajimoto *et al.* 2002) seen at LM.

This study represents the first survey of recent growth trends at subarctic tree line sites spanning the entire forest-tundra of northern Québec, comparing regions, identifying changes associated with 20th century climate warming and identifying key climatic variables. In the northern forest-tundra, the recent increase in mean height growth (Fig. 3) and positive trend in leader shoot elongation (Fig. 4), consistent

with a 1990s' increase in heat sums (Fig. 6), point to development of spruce krummholz into erect growth forms. In the southern forest-tundra, however, height growth of spruce is strongly suppressed above tree line (Fig. 2), and reforestation of tundra hilltops and northward expansion of the boreal forest could be delayed even if CO_2 levels double. Future studies trying to refine rising CO_2 scenarios should bear in mind that in the fragmented landscape of the subarctic forest-tundra, differences as small as the position of trees at or just a few metres above tree line can produce differences in climate response as large as those occurring between stands more than a hundred kilometres apart.

Acknowledgements

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