Dynamics at the treeline: differential responses of *Picea mariana* and *Larix laricina* to climate change in eastern subarctic Québec

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Abstract

Treelines are known to be temperature-sensitive ecotones, and therefore could rapidly expand their range limits in response to climate warming. Observations of lack of range expansion, however, indicate that ecological constraints partly control the treeline ecotones. The main objectives of this study were to evaluate *Picea mariana* and *Larix laricina* recruitment and growth at and above the altitudinal treeline of Kangiqsualujjuaq (Nunavik), where warmer temperatures since the 1990s have already triggered shrub expansion. We mapped, harvested, dated and measured tree individuals along two altitudinal gradients from the forested stands below the treeline to hilltops. Since the 1990s, a pulse of *L. laricina* seedling establishment has occurred at and above the treeline. Dendrochronological analysis revealed that *L. laricina* underwent a rapid vertical growth and radial growth that accelerated from the 1990s. No recruitment was observed for *P. mariana* in response to the regional warming, suggesting a regeneration failure of this species. Our results indicated that the *L. laricina* colonization below and above the treeline in recent decades in response to the regional warming should modify the landscape physiognomy of the study area in the near future.

Keywords: treeline, tree recruitment, global warming, *Larix laricina*, *Picea mariana*, dendrochronology, vertical growth, radial growth, plant population and community dynamics

1. Introduction

Treelines are temperature-sensitive ecotones widely considered to be key indicators of climate change (Payette et al 1989, Körner 1998, Callaghan et al 2002, but see Kupfer and Cairns 1996). Trees found at treeline are exposed to harsh summer and winter climatic conditions (Harsch et al 2009), which strongly limit their regeneration and growth (Holtmeier and Broll 2007). It is therefore expected that global warming will affect treeline ecotones (Holtmeier and Broll 2005) by enhancing tree regeneration, survival and growth (Prentice et al 1992, Jeffree and Jeffree 1996, Bakkenes et al 2002). In fact, recent treeline expansion has been reported for several locations around the world: Russia (Devi et al 2008), Alaska (Suarez et al 1999), Scandinavia (Kullman 2001) and Southern Europe (Camarero and Gutiérrez 2004). In Canada,
Luckman and Kavanagh (1998) noticed a slight upslope shift of trees in the Rockies, while Danby and Hik (2007) showed tree expansion only on south facing slopes.

Treeline responses are variable at the global scale. In a recent review, Harsch et al (2009) reported that nearly half of the treelines studied since the beginning of the 20th century had not undergone change, even though extensive warming had occurred at many of these sites. The apparent inertia of some treelines contrasts with reports of shrub expansion at many sites around the circumpolar low Arctic (Myers-Smith et al 2011). This variability in treeline response to climate change suggests that treeline ecotones are also controlled by local ecological constraints, which can mask, in some cases, the impact of warmer temperatures (Kharuk et al 2006). Therefore, the interactions between regional and local factors make it difficult to predict the future response of the forest–tundra ecotone to global warming (Danby 2011).

Apart from treeline shifts, climate warming might trigger other responses, either at the individual or stand level (MacDonald et al 1998). For example, a regional warming could enhance tree growth, as the radial and vertical tree growth of individuals located in extreme environments is strongly regulated by temperature (Lamarche and Stockton 1974, Fritts 1976). Growth increase in response to climate warming has been observed at treeline for Picea mariana (Mill.) BSP. (Gamache and Payette 2004), P. glauca (Moench) Voss (Caccianiga and Payette 2006) and Larix sibirica Ledeb. (Devi et al 2008) among other species. Increased individual growth might lead to a faster and to a greater production of viable seeds (Kullman 2007, Dufour-Tremblay and Boudreau 2011), which could in turn result in stand densification and treeline advance in response to higher recruitment at and above treeline.

Subarctic Québec has long been considered a zone of climatic inertia (Allard et al 1995). In fact, most of the region underwent a cooling trend up to the 1990s (Chouinard et al 2007); a particular climatic context that might explain why few treeline shifts were observed in this region, even though some vertical tree growth changes have been reported (Gamache and Payette 2004). In recent years however, subarctic Québec has warmed (Allard et al 2007, Chouinard et al 2007) and higher temperatures are thought to have led to expansion of shrub species, mainly dwarf birch (Betula glandulosa Michx) (Ropars and Boudreau 2012, Tremblay et al 2012, McManus et al 2012). Moreover, preliminary observations of numerous tree seedlings and saplings above treeline of Kangiqsualujjuaq, on the eastern shore of the Ungava Bay, eastern Nunavik (figure 1). According to Allard et al (1992), the study region overlaps continuous and discontinuous permafrost zones. The landscape in this region is characterized by a mosaic of L. laricina and P. mariana stands in protected areas and of open tundra in the more exposed sites on top of gently rolling hills (about 300 m above sea level—a.s.l.). The plant community zonation is associated with prevailing temperature, humidity and altitude, as described by Payette et al (2001). Along the altitudinal gradient, L. laricina is generally found above P. mariana and is the dominant species at treeline (80 m a.s.l., Tremblay et al 2012) but occasional P. mariana krummholz are found above treeline near the hilltops. Shrub species, which can influence either positively (facilitation) or negatively (competition, allelopathy) tree recruitment (Zackrisson and Nilsson 1992, Oakley et al 2006), are also abundant above location of tree >2 m, Hofgaard et al 2009). We therefore (i) reconstructed recruitment events of L. laricina and P. mariana below and above treeline, (ii) evaluated vertical growth responses to climate warming and (iii) developed radial growth chronologies for each species in order to identify their response to climatic variables. We combined field surveys and dendrochronological analyses to describe the dynamics of these tree species at their altitudinal limit.

2. Methods

2.1. Study area

The study took place near Kangiqsualujjuaq (58°42′39″N–65°59′43″W), an Inuit community located close to the George River on the eastern shore of the Ungava Bay, eastern Nunavik (figure 1). According to Allard et al (1992), the study region overlaps continuous and discontinuous permafrost zones. The landscape in this region is characterized by a mosaic of L. laricina and P. mariana stands in protected areas and of open tundra in the more exposed sites on top of gently rolling hills (about 300 m above sea level—a.s.l.). The plant community zonation is associated with prevailing temperature, humidity and altitude, as described by Payette et al (2001). Along the altitudinal gradient, L. laricina is generally found above P. mariana and is the dominant species at treeline (80 m a.s.l., Tremblay et al 2012) but occasional P. mariana krummholz are found above treeline near the hilltops. Shrub species, which can influence either positively (facilitation) or negatively (competition, allelopathy) tree recruitment (Zackrisson and Nilsson 1992, Oakley et al 2006), are also abundant above location of tree >2 m, Hofgaard et al 2009). We therefore (i) reconstructed recruitment events of L. laricina and P. mariana below and above treeline, (ii) evaluated vertical growth responses to climate warming and (iii) developed radial growth chronologies for each species in order to identify their response to climatic variables. We combined field surveys and dendrochronological analyses to describe the dynamics of these tree species at their altitudinal limit.
treeline (Tremblay et al. 2012). In fact, dwarf birch was shown to have increased substantially over the last few decades (Tremblay et al. 2012).

The nearest climate station with long-term data, located at Kuujjuaj (Environment Canada 2012, figure 1), recorded an extensive warming of 0.17°C yr⁻¹ for the period 1990–2010 (y = 0.1658x − 336, R² = 0.48; F₁,₁₉ = 16.7, P < 0.001; see Tremblay et al. 2012). This warming trend was also observed in several other Inuit communities in subarctic Québec (Allard et al. 2007). Climate data for Kangiqsualujjuaq are only available from 1993 to 2010 but are similar to the ones recorded in Kuujjuaj (Pearson coefficient: 0.98, maximum deviation: ±0.5°C for the overlapping period). Mean annual temperature in Kangiqsualujjuaq over this period was −4.1°C; February and July being the coldest and warmest months (−21.5°C and 10.8°C, respectively).

2.2. Study species

Picea mariana is the dominant tree species throughout most of Northern Québec. It usually forms the subarctic treeline (Payette et al. 2001) except in the north-eastern section of the province, where it is a companion species of Larix laricina. It bears semi-serotinous cones, with seeds being either massively released after fire or more gradually in the absence of fire (Payette and Gagnon 1979). Mineral soil is one of the most suitable seedbeds (Greene et al 2005) along with mosses, especially in alpine ecosystems (Wheeler et al. 2011). According to Payette et al. (1982), sexual reproduction is rather infrequent at treeline, populations maintaining themselves through clonal layering.

Throughout the eastern Québec–Labrador Peninsula, P. mariana coexists with L. laricina, a deciduous conifer species that dominates treeline stands. Its seed production is variable and the usually low seed viability at the treeline is associated with low annual thermal sum (Payette et al. 1982). Germination trials with seeds from Kangiqsualujjuaq harvested in 2010 suggest however that seed viability at the treeline can be >25% (Dufour-Tremblay et al. 2012). Soil moisture availability appears to be more important than seedbed for L. laricina seed germination (Morin and Payette 1984, Brown et al. 1988).

2.3. Reconstruction of treeline expansion

Study sites (2) were selected following the visit of all accessible sites near Kangiqsualujjuaq (about 10). Preliminary observations suggested that tree recruitment above treeline occurred at all sites, regardless of site exposition, although recruitment intensity varied from site to site. To minimize logistical constraints (river crossing, site only accessible at high tide), two easily accessible sites with a south-west aspect were selected to reconstruct P. mariana and L. laricina recruitment events over the last decades.

Tree recruitment above treeline was frequent at the first site but lower at the second one, capturing the variability previously observed. At each site, we randomly located a 80 m wide × 360 m long (2.88 ha) transect extending from below the treeline to the hilltop. The treeline was identified according to tree density and treeline type, as proposed by Harsch and Bader (2011). At site 1 (hereafter referred to as S1), treeline was characterized as abrupt since the tree cover decreased sharply after 20 m along the transect. At site 2 (hereafter referred to as S2), the treeline was diffuse, showing a gradual decrease in tree density over the first 90 m of the transect.

In 2010, we tagged, mapped and measured all living or dead seedlings (<30 cm), saplings (between 30 cm and 2 m) and trees (>2 m) within the two transects. Position of the individuals was recorded with a total station (Leica TC805; Leica Geosystems, Heerbrugg, Switzerland). Tree species, height, basal diameter, mortality and signs of reiteration (sensu Tomlinson 1983) caused by winter damage were noted. Once the mapping exercise completed, we harvested all living individuals for dendrochronological age determination (n = 831). Trees with a basal diameter >5 cm were cored at the lowest possible level (soil level) with a 4.35 mm core borer (Haglof, Långsele, Sweden) fixed to a drill. A full disc was taken at the root collar for smaller individuals. In 2011, sites were re-examined with extra care for seedlings that could have been missed in 2010 and for newly established ones (marked in 2011 with a GS20 GPS unit—±1 m; LeicaGeosystems, Heerbrugg, Switzerland).

In the laboratory, all samples were dried and finely sanded for age determination, according to standard dendrochronological procedures (Cook et al. 1990). Using ArcGIS 9.3 software, we placed individuals positioned with the total station on a map and then superimposed individuals with GPS coordinates. Individuals were then classified by decade (prior to 1951 and the six subsequent decades: 1951–60 to 2001–10). Average limit of establishment (krummholz excluded) was also calculated for the predetermined time periods. To do so, each transect was subdivided into four 20 m-wide altitudinal sub-transects to take into account the treeline spatial heterogeneity. For each of these sub-transects, position of the last individual along the altitudinal gradient was used to calculate the average limit of establishment (average across the four sub-transects) for each decade (see Camarero and Gutiérrez 2004). To facilitate the description of the colonization patterns, transects were divided into four zones: forested zone (below the treeline) and the low-, mid- and high-tundra zones (above the treeline).

2.4. Vertical growth

To evaluate how vertical growth responded to the regional warming trend, we conducted a stem analysis (Gamache and Payette 2004) on all tree individuals with height ranging between 1.0 and 3.5 m (n = 116), found below and above treeline. We sampled main stem cross-sections at 0.25 m intervals. Most individuals were sampled inside transects, while a few were sampled just outside but in the same habitat conditions. Once dried and sanded, each cross section was aged. We then calculated an annual growth rate for each 0.25 m interval by dividing the length of the interval by the age difference between the two cross-sections.
Statistical analyses were performed to evaluate if vertical growth rate varied through time (regardless of the age of the different individuals) and between positions along the altitudinal gradient. These relations were analyzed using a MIXED procedure in the Statistical Analysis System (SAS 9.2, SAS Institute Inc.). All individual growth rates were considered as repeated measurements and sites (S1 and S2) were included as a random effect in the model, to account for potential variability associated with the transect location. Because annual vertical growth rates were extrapolated from the stem analysis data (see above), a more stringent level of significance (0.01) was used. We used a least significant difference test to identify significant differences in vertical growth between the different time periods (prior to 1951, 1951–60, . . . , 2001–10).

2.5. Radial growth and climate

Growth ring analysis of mature individuals was conducted to evaluate the relation between temperature, precipitation and radial growth. We sampled two opposite cores from 50 L. laricina and P. mariana (DBH > 20 cm) at treeline. Cores were taken at the base of the trees with a modified core borer and returned to the laboratory, where they were mounted, sanded and aged. Tree-ring measurement was conducted using a Velmex table measuring system (Velmex Inc. New York, USA).

To detect potential age-related differences in radial growth, three chronologies were built according to age of the individuals (established prior to 1900, between 1901–50 and after 1950). Age validation was made with the COFECHA software (Holmes 1983). An average tree-ring chronology using all individuals was then built since radial growth trend was similar between the different chronologies. Detrending was achieved with a horizontal curve fitted through the raw ring-width series (see Biondi and Qeadan 2008) since there was no important age-related difference between the radial growth chronologies. For the two average chronologies, we calculated an Expressed Population Signal (EPS) to evaluate their quality (Wigley et al 1984) and their average sensitivity to infer their potential for climate–growth analysis (Fritts 1976).

Response functions were used to determine significant correlations among average radial growth chronologies and climatic parameters. Dendrochronological curves were fitted to mean monthly precipitation and temperature with the 3Pbase/PPPHalos program (Guiot and Goeury 1996). Following Guiot and Goeury (1996), we considered growth to be significantly correlated to environmental variables when the coefficient was >1.96 ($P < 0.05$).

3. Results

3.1. Recruitment at and above treeline

Spatio-temporal differences in recruitment intensity were observed between sites (figures 2(a) and (b)). At S1, 519 L. laricina and three P. mariana individuals became established after 1950. Of these, we found 192 individuals in the forested zone below the treeline, 296 in the low-alpine tundra zone and the remaining 31 were established at higher altitudes (table 1, figure 2(a)). Most of the individuals (419/519) became established in the last two decades. The average limit of establishment reached about 185 m in 1961–70 and about 252 m during the decade 2001–10.

Recruitment was not as abundant at S2, where we found only 17 L. laricina and 11 P. mariana individuals established after 1950 (table 1, figure 2(b)). Of these, 140 established in the diffuse treeline zone, resulting in treeline stand densification since 1950 (from 137.5 tree ha$^{-1}$ before 1950 to 331.9 tree ha$^{-1}$ in 2010). Recruitment did not increase in the last two decades with only 31 and 26 individuals established during the 1990s and the 2000s respectively. In fact, the highest number of recruits was found in the 1951–60 decade (55/171). The average limit of establishment at S2 increased from about 134 m in 1950 to about 267 m in 2010.

Overall, few dead individuals were observed at both sites (table 1). We found 18 and 16 dead L. laricina individuals in the treeline zone of S1 and S2 respectively. In the open tundra above treeline, we only found one dead L. laricina individual (in the low-tundra zone at S2). No P. mariana dead individuals were observed at the two sites.

3.2. Vertical growth

Since we recorded only two P. mariana saplings in the sampled transects, the analysis of vertical growth was restricted to L. laricina (63 individuals below treeline, 53 above). The average vertical growth differed through time ($F_{6,1841} = 33.89, P < 0.001$, figure 3). Regardless of their age, individuals underwent a significant and synchronous increase in vertical growth in the 1990s, which continued at a faster rate in the 2000s. Individuals established during the 1991–2000 decade needed only 16 years to reach a 2 m-height, three times less, on average, than the 50 years required by an individual established in the 1950s. The vertical growth of individuals found below or above treeline did not differ significantly ($F_{1,104} = 0.92, P = 0.340$).

3.3. Radial growth

The average growth chronology for L. laricina was built from 47 individuals (97 radii). It covers 204 yr (1806–2009; figures 4(a) and (c)). No age-related trend was detected as the different cohorts showed synchronized growth trends and amplitudes (figure 4(a)). The EPS calculated for the L. laricina tree-ring time series (0.987, figure 4(c)) was above the 0.850 threshold considered as acceptable (Wigley et al 1984). Growth trends were highly synchronized between individuals. Tree-ring widths underwent an abrupt decrease during some periods, likely an indication of larch sawfly outbreak events. For example, the low growth recorded from 1967–70, combined with the frequent occurrence of a light ring in 1966 (another sign of sawfly outbreak according to Girardin et al 2005) strongly supports this hypothesis. In the more recent decades, radial growth slowly
yet steadily increased from 1970 onwards and became more pronounced after 2000. The mean sensitivity of the average chronology was 0.243 and ring widths were significantly and positively correlated with summer temperature (June and July, figure 5). October temperature of the previous year was also a significant predictor of ring width. The model for precipitation was not significant, suggesting a low response of the species to the precipitation regime or that precipitation was not limiting.

*Picea mariana* average growth chronology was built from 40 mature trees (65 radii) sampled below treeline. It spans over 161 years (1849–2009). Individuals established after 1950 had a somewhat higher growth over the last two decades (figure 4(b)). The EPS calculated for the overall tree-ring time series (0.920, figure 4(c)) was also above the 0.850 threshold considered as acceptable (Wigley *et al* 1984). Growth rings of *P. mariana* showed strong inter-annual fluctuations during the first 30 years following their establishment, potentially an artifact of sampling at ground level. After this period, mean individual growth was relatively uniform through time with no particular downward or upward trend. During some periods, tree rings showed low synchrony between
Table 1. Establishment (number of living individuals) and dead individuals of *Larix laricina* by zone and decade within the two sites at Kangiqsualujjuaq, Nunavik. Bold values indicate zones with the highest number of new recruits.

| Site 1 | Prior to | 1951–60 | 1961–70 | 1971–80 | 1981–90 | 1991–2000 | 2001–10 | Total establishment after 1950 | Total % after 1950 | Dead |
|--------|----------|---------|---------|---------|---------|-----------|---------|-----------------------------|-------------------|------|
| Treeline zone | 24 | 14 | 16 | 5 | 14 | 99 | 44 | 192 | 37.0 | 18 |
| Low-tundra zone | 0 | 7 | 6 | 13 | 14 | 112 | 144 | 296 | 57.0 | 0 |
| Mid-tundra zone | 2 | 5 | 3 | 0 | 1 | 14 | 6 | 29 | 5.6 | 0 |
| High-tundra zone | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0.4 | 0 |
| Total | 28 | 26 | 25 | 18 | 31 | 225 | 194 | 519 | 100.0 | 18 |

| Site 2 | Prior to | 1951–60 | 1961–70 | 1971–80 | 1981–90 | 1991–2000 | 2001–10 | Total establishment after 1950 | Total % after 1950 | Dead |
|--------|----------|---------|---------|---------|---------|-----------|---------|-----------------------------|-------------------|------|
| Treeline zone | 99 | 46 | 29 | 10 | 11 | 24 | 20 | 140 | 81.9 | 16 |
| Low-tundra zone | 7 | 6 | 1 | 2 | 1 | 7 | 3 | 20 | 11.7 | 1 |
| Mid-tundra zone | 1 | 2 | 4 | 0 | 0 | 0 | 3 | 9 | 5.3 | 0 |
| High-tundra zone | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 1.2 | 0 |
| Total | 107 | 55 | 34 | 12 | 13 | 31 | 26 | 171 | 100.0 | 17 |

Figure 3. *Larix laricina* vertical growth for individuals (1.0 m < X < 3.5 m) harvested in sites 1 and 2. Each curve represents one individual. Letters indicate significant differences in vertical growth rate by decade. Individuals from the two sites were combined for statistical analyses.

4. Discussion

According to MacDonald *et al* (1998), warmer temperatures at treeline could result either in increased individual tree performance (growth and reproduction), in forested stand densification or in treeline advance. In this study, we were able to demonstrate that the current multi-species treeline dynamics near Kangiqsualujjuaq is driven by the increased growth and reproduction of *L. laricina* individuals, of which abundant recruitment led to both the densification of the

individuals, especially in the last decade (EPS for 2000–9 period: 0.883 for *P. mariana* compared to 0.990 for *L. laricina*). The chronologies built for the three periods reflect this non-synchronized response (figure 4(b)). We found no evidence of insect outbreak events in the *P. mariana* time series. Overall, this species’ mean sensitivity was rather low (0.148). Response function models for temperature and precipitation were not statistically reliable. Consequently, radial growth of *P. mariana* could not be associated with either mean monthly temperature or precipitation.

4.1. Responses of *Larix laricina* at the individual level

At the individual level, *L. laricina* displayed both vertical and radial growth increases over the last decades. The increase in vertical growth rate of all individuals since the 1990s, regardless of their period of establishment, coincides with the warming trend observed in the region. Similar observations were reported for saplings and/or krummholz in the Swedish Scandes (Kullman 2001, 2002), in the Rocky Mountains (Colorado, USA; Weisberg and Baker 1995) and in western

Figure 4. Indexed radial growth of *Larix laricina* (a) and *Picea mariana* (b) established prior to 1900, from 1901 to 1950 and from 1951 onwards. (c) shows the tree-ring chronologies built from all individuals. Curves represent standardized tree-ring widths, bars show the number of individuals used for chronologies.
subarctic Québec (Gamache and Payette 2004). A faster vertical growth rate can reduce the loss of anatomical tissue to ice abrasion above the snowpack and could therefore enhance sapling survival in harsh environments (Weisberg and Baker 1995). It can also lead to early seed production (Payette and Gagnon 1985). Although the increase in vertical growth also coincides with the sudden demographic downfall of the George River Caribou Herd in the 1990s (Boudreau et al 1985), it is unlikely that it results from a grazing pressure response function between Larix laricina radial growth and the average monthly temperature. Bars above the dotted line (1.96) and with an asterisk indicate month’s temperatures that were significantly and positively correlated to ring widths. The letter ‘p’ indicates a month in the previous calendar year. $R^2$ represents the variance explained by the model.

The increase in L. laricina radial growth from 1970 to 2010 precedes the warming trend in the region. Therefore, it cannot be attributed solely to the increase in temperature since the 1990s. It is likely that the growth increase during the first half of this period was associated with recovery following a larch sawfly outbreak at the end of the 1960s. In fact, radial growth in the 1980s was similar to the one recorded in the first half of the 20th century. Unfortunately, no historical record of insect outbreak is available for this region in order to corroborate this hypothesis. Overall, the mean sensitivity of the L. laricina tree-ring chronology was comparable to what was found in other studies (Jardon et al 1994, Girardin et al 2005, Mamet and Kershaw 2011), suggesting that it has a good potential to explore the relationships between radial growth and climate. Response functions suggested that radial growth was positively associated with warmer temperatures in June and July but also with higher temperatures during October, at the end of the previous growing season. The latter result, also observed in previous studies (Girardin et al 2005, Payette 2007, Huang et al 2010), might be linked to increased photosynthetic activity in the fall, which would allow trees to store more energy for the subsequent growing season (Lamarche and Stockton 1974).

Precipitation was not a growth-limiting factor for L. laricina in this study, even though precipitation in spring and fall were previously shown to influence growth of this species in Manitoba, Canada (Girardin et al 2005). Other related variables (e.g. number of dry days) could also be investigated to better evaluate the relationship between radial growth and precipitation. In particularly hot and dry summers, the combined effects of warm temperatures and low precipitation have been shown to be detrimental to radial growth for trees found at treeline (Lloyd and Fastie 2002). In fact, reduced tree-ring widths observed during and after the 2008 growth season could be due to a severe drought during the 2008 growing season, the warmest summer recorded over the last 60 years. This, however, remains to be tested.

4.2. Responses of Larix laricina at the population level

4.2.1. Treeline stand densification. Treeline stand densification, a common response in the forest–tundra ecotone, was recently observed in mountain ranges in Europe and Russia (Camarero and Gutiérrez 2004, Kharuk et al 2006). In our study, treeline stand densification occurred in both sites over the last 60 years. However, the temporal pattern of stand densification differed between the sites. In the forested zone at S1, most of the recruitment occurred over the last two decades while in S2, densification was rather constant from 1950 onwards. A similar L. laricina stand densification was reported near the Rivière-aux-Feuxilles, on the western side of Ungava Bay in subarctic Québec by Morin and Payette (1984), who hypothesized that climate warming since the end of the Little Ice Age had probably resulted in the consolidation of pre-existing stands rather than an advance in treeline.

Evidence of seedling mortality was restricted to the forested zone (34 out of 35 dead seedlings/saplings). No data is available to identify the causes underlying such a pattern, yet increased competition for resources such as light and nutrients (Oakley et al 2006, Batllori et al 2009) and/or a heavier and deeper snowpack (Autio and Colpaert 2005, Sek et al 2005) at treeline are possible candidates.

4.2.2. Tree species limit advance. Spatio-temporal differences in recruitment intensity above treeline were observed between sites, preventing any generalization of treeline advance in the region. However, our results contrast with the scarcity of seedlings found above treeline of the region reported in past studies (Payette et al 1982, Morin and Payette 1984). At S1, recruitment increased substantially over the last two decades in the low-tundra zone with the establishment of several new individuals. Over this time frame, 20 seedlings also became established in the mid-tundra zone. By comparison, only ten and three seedlings became established over the last two decades in the low- and mid-tundra zones at S2. Because both study sites were under the same climatic conditions, lower recruitment above treeline in S2 was probably linked to local constraints inherent to this site. A likely explanation for the observed difference between the two sites is the dense Betula glandulosa cover found above treeline at S2. The important shrub expansion observed in the region between 1964 and 2003 (Tremblay et al 2012) might have hindered seedling establishment (Dufour-Tremblay et al 2012). Shrub densification at treeline
could mask the positive impact of warmer temperatures on tree regeneration by decreasing the availability of suitable seedbeds and increasing competition for resources (Oakley et al 2006, Batllori et al 2009).

Although we do not generalize our data at the regional scale, our results are in accordance with several observations of treeline advance in other regions of the world. In the Swedish Scandes, increased conifer seedlings were observed above treeline, leading to an altitudinal shift of the tree species limit in response to warmer temperatures (Kullman 2002). In the Canadian Rocky Mountains, a treeline advance of 150 m was observed (Roush 2004), while a similar pattern was also noticed, although to a lesser extent, in the Polar Ural Mountains of Russia (Shiyatov et al 2005, 2007). Despite the fact that our results showed an advance of the tree species limit rather than an advance of the treeline (i.e. most of the newly established individuals have not reached tree size yet), seedlings observed in this study appeared to have high survival rates (as inferred by the absence of dead seedlings above treeline) and displayed a regular growth form with few individuals showing reiterates, a sign of terminal leader mortality. The rapid vertical growth rate observed suggests that recently established individuals will reach tree height (about 2 m) within 15 years. Moreover, the production of seeds by these numerous young trees above treeline should further increase recruitment as suggested by Smith et al (2003).

4.3. The inertia of Picea mariana

In contrast to L. laricina increased recruitment, the scarcity of P. mariana seedlings clearly reflects unsuccessful sexual reproduction due to bottlenecks in one or many stages of its regeneration process (Smith et al 2009). According to Walther et al (2005), the phenotypic plasticity associated with the well-known layering capacity of this species could contribute to its low responsiveness to the recent temperature increase. As such, the observed warming trend might be insufficient to trigger an increase in recruitment, as previously suggested by Payette (2007) for P. glauca, another spruce species found in northern Labrador. According to Dufour-Tremblay et al (2012), the lower tolerance of P. mariana seeds to allelopathic compounds released by the three dominant shrub species found in the tundra above treeline (Empetrum nigrum [L.], Vaccinium uliginosum [L.] and B. glandulosa) and the scarcity of suitable seedbeds might also contribute to the phenomenon.

5. Conclusion

Our results showed contrasting responses for the two tree species found at treeline near Kangiqsujujuaq. While Picea mariana recruitment remained low since the 1950s, Larix laricina was successful in colonizing the open tundra above treeline. Increased radial and vertical growth of L. laricina suggests that this altitudinal shift might continue over the next decades. Warmer temperatures were the best factor explaining the expansion of L. laricina. However, local constraints likely played a role in the spatial differences in recruitment intensity. Our results suggest that the landscape of Kangiqsujujuaq could change rapidly in the upcoming years. It also emphasizes the need to consider the biological characteristics of individual species as well as both fine- and coarse-scale environmental parameters when modeling future treeline advance (Danby 2011).

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