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To cite this article: Catherine Dumais *et al* 2014 *Environ. Res. Lett.* **9** 094001

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Are low altitude alpine tundra ecosystems under threat? A case study from the Parc National de la Gaspésie, Québec

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Received 6 May 2014, revised 1 August 2014

Accepted for publication 4 August 2014

Published 9 September 2014

Abstract

According to the 2007 IPCC report, the alpine tundra ecosystems found on low mountains of the northern hemisphere are amongst the most threatened by climate change. A treeline advance or a significant erect shrub expansion could result in increased competition for the arctic-alpine species usually found on mountaintops and eventually lead to their local extinction. The objectives of our study were to identify recent changes in the cover and growth of erect woody vegetation in the alpine tundra of Mont de la Passe, in the Parc National de la Gaspésie (Québec, Canada). The comparison of two orthorectified aerial photos revealed no significant shift of the treeline between 1975 and 2004. During the same period however, shrub species cover increased from 20.2% to 30.4% in the lower alpine zone. Dendrochronological analyses conducted on *Betula glandulosa* Michx. sampled at three different positions along an altitudinal gradient (low, intermediate and high alpine zone) revealed that the climatic determinants of *B. glandulosa* radial growth become more complex with increasing altitude. In the lower alpine zone, *B. glandulosa* radial growth is only significantly associated positively to July temperature. In the intermediate alpine zone, radial growth is associated positively to July temperature but negatively to March temperature. In the high alpine zone, radial growth is positively associated to January, July and August temperature but negatively to March temperature. The positive association between summer temperatures and radial growth suggests that *B. glandulosa* could potentially benefit from warmer temperatures, a phenomenon that could lead to an increase in its cover over the next few decades. Although alpine tundra vegetation is not threatened in the short-term in the Parc National de la Gaspésie, erect shrub cover, especially *B. glandulosa*, could likely increase in the near future, threatening the local arctic-alpine flora.

Keywords: alpine tundra, climate change, dendrochronology, *Betula glandulosa*, shrub expansion, treeline

1. Introduction

The alpine tundra is a highly fragmented biome due to its geographical distribution restricted to mountaintops (Nagy

and Grabherr 2009). These tundra 'islands' cover *ca.* 3% of the land surface of the Earth but harbor *ca.* 4% of the higher plant species (Korner and Spehn 2002). Those species, well adapted to harsh climatic conditions, contribute significantly to regional plant diversity. Because species found in the alpine tundra are highly sensitive to the development of an erect woody vegetation cover (Korner and Spehn 2002), this biome is believed to be amongst the most threatened with regards to climate change (Grabherr *et al* 1995, Theurillat and



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Guisan, 2001, Chapin *et al* 2005, Walther *et al* 2005) as warmer temperatures might trigger treeline advance of shrub expansion. Treeline advance or erect shrub cover densification would result in the shrinkage of the area occupied by the alpine tundra ecosystems, a phenomenon which might eventually lead to the local extinction of species confined to mountaintops. Of particular concern are the isolated, southern occurrences of alpine tundra within the matrix of boreal and temperate biomes (IPCC 2007).

One of the major functional responses of high latitude or alpine terrestrial ecosystems to climate warming is the expansion of erect shrub species (see Myers-Smith *et al* 2011). Recent NDVI studies revealed a greater increase in photosynthetic activity in regions where tall shrub species are the dominant functional group (Raynolds *et al* 2006, McManus *et al* 2012), a result corroborated by the comparison of aerial photographs and satellite images (Alaska: Sturm *et al* 2001, Tape *et al* 2006; subarctic Québec: Ropars and Boudreau 2012, Tremblay *et al* 2012). Dendrochronological studies suggest that the growth of deciduous shrub species is positively correlated with warmer temperatures (Bär *et al* 2006, Forbes *et al* 2010, Hallinger *et al* 2010, Blok *et al* 2011, Boudreau and Villeneuve-Simard 2012), increased summer precipitation (Blok *et al* 2011) or changes in snow cover (Hallinger *et al* 2010). Other studies have shown that erect shrub species respond positively to experimental warming (Chapin *et al* 1995, Chapin and Shaver 1996, Hobbie and Chapin 1998, Bret-Harte *et al* 2001, 2002, Van Wijk *et al* 2003, Jonsdottir *et al* 2005, Wahren *et al* 2005, Walker *et al* 2006), although to a lesser extent than to nutrient addition (Nams *et al* 1993, Chapin *et al* 1995, Bret-Harte *et al* 2001, 2002, Van Wijk *et al* 2004, Zamin and Grogan 2012). The expansion of erect woody vegetation will undoubtedly alter the dynamics of alpine tundra ecosystems as it will impact both the abiotic and the biotic environments (Myers-Smith *et al* 2011). Such changes in the vertical structure of plant communities will alter surface energy exchange and soil temperatures (Liston *et al* 2002, Pomeroy *et al* 2006, Marsh *et al* 2010), nutrient cycling (Schimel *et al* 2004, Cornelissen *et al* 2007, Buckeridge and Grogan 2008, Baptist *et al* 2009, Buckeridge *et al* 2010) and biodiversity and ecosystem services (Cornelissen *et al* 2001, Wilson and Nilsson 2009, Pajunen *et al* 2011).

The objectives of this study were to identify changes in the cover and growth of erect woody vegetation in the alpine tundra of Mont de la Passe (Parc National de la Gaspésie, Québec, Canada) in response to the modest warming trend observed in the region (0.5 °C between 1960 and 2003, Yagouti *et al* 2006). The specific objectives were (i) to evaluate if there has been an upward movement of the treeline and/or an expansion of the erect shrub species over the last 30 years; (ii) to build *Betula glandulosa* Michx. growth ring chronologies, and (iii) to identify which climatic parameters influence *B. glandulosa* growth along the altitudinal gradient of Mont de la Passe, if any. To do so, we compared aerial photographs of Mont de la Passe taken in 1975 and 2004 and we sampled *B. glandulosa* individuals at different locations

along an altitudinal gradient in the alpine tundra for dendrochronological analyses.

2. Methods

2.1. Study area

The Parc National de la Gaspésie (PNG), founded in 1937, is located in the center of the Gaspésie peninsula in southeastern Québec (figure 1(a)). It includes part of the Chics-Chocs and the McGerrigle mountain ranges with several mountains peaking over an altitude of 1000 m. Mont Jacques Cartier (1268 m) is the highest mountain in the region, followed by Mont de la Passe (1242 m). The study was conducted on the latter since it is a strict conservation area, i.e. no tourists are allowed on the mountain.

Mont de la Passe presents a steep altitudinal gradient, which influences the composition and structure of plant communities (figures 1(b), (c)). At low altitude, tall balsam fir (*Abies balsamea* ((L) Mill)) and white spruce (*Picea glauca* ((Moench) Voss)) stands are found, as well as paper birch (*Betula papyrifera* (Marsh)) individuals. As the altitude rises, tall forests are replaced by a white spruce krummholz belt, which surrounds the mountain. Alpine tundra, dominated by several shrub species such as *B. glandulosa*, *Vaccinium uliginosum* L. and *Ledum groenlandicum* Oeder, is found above the krummholz belt. The higher portion of the mountain harbors many arctic-alpine species (*Diapensia lapponica* L. and *Kalmia procumbens* L. for example).

The annual mean temperature recorded at the nearest weather station (Ste-Anne-des-Monts; 49°08'N, 66°28'W, ca. 44 km to the North-West, 15.5 m a.s.l.) is 3.2 ± 0.9 °C for the 1981–2004 period, with the highest and lowest mean monthly temperatures recorded in July (20.8 °C) and February (−16.0 °C), respectively (Environment Canada 2014). Over this period, annual precipitation averaged 864 mm, of which ca. 28% fell as snow. Temperature recorded during the growing season (June–August) at the Ste-Anne-des-Monts weather station and on Mont Jacques-Cartier for the years 1993–1998 and 2001 revealed a significant correlation between the two data sets with temperature on Mont Jacques-Cartier being 2.6 to 4.6 °C cooler (table 1). According to the analysis of Yagouti *et al* (2006) based on several weather stations, the region has experienced a generalized warming of 0.5 °C since the early 1970s. A more detailed examination of the Ste-Anne-des-Monts temperature data from 1963 to 1998, used for the function response analysis (see below), revealed significant temperature increase in April (0.37 °C decade^{−1}) and September (0.40 °C decade^{−1}) and marginally significant ones in May (0.38 °C decade^{−1}) and October (0.24 °C decade^{−1}). For total precipitation, a significant increase was observed for November (11.3 mm decade^{−1}). Marginally significant increases (February, 5.1 mm decade^{−1}) and decreases (August, 8.6 mm decade^{−1}) in precipitation were also observed.

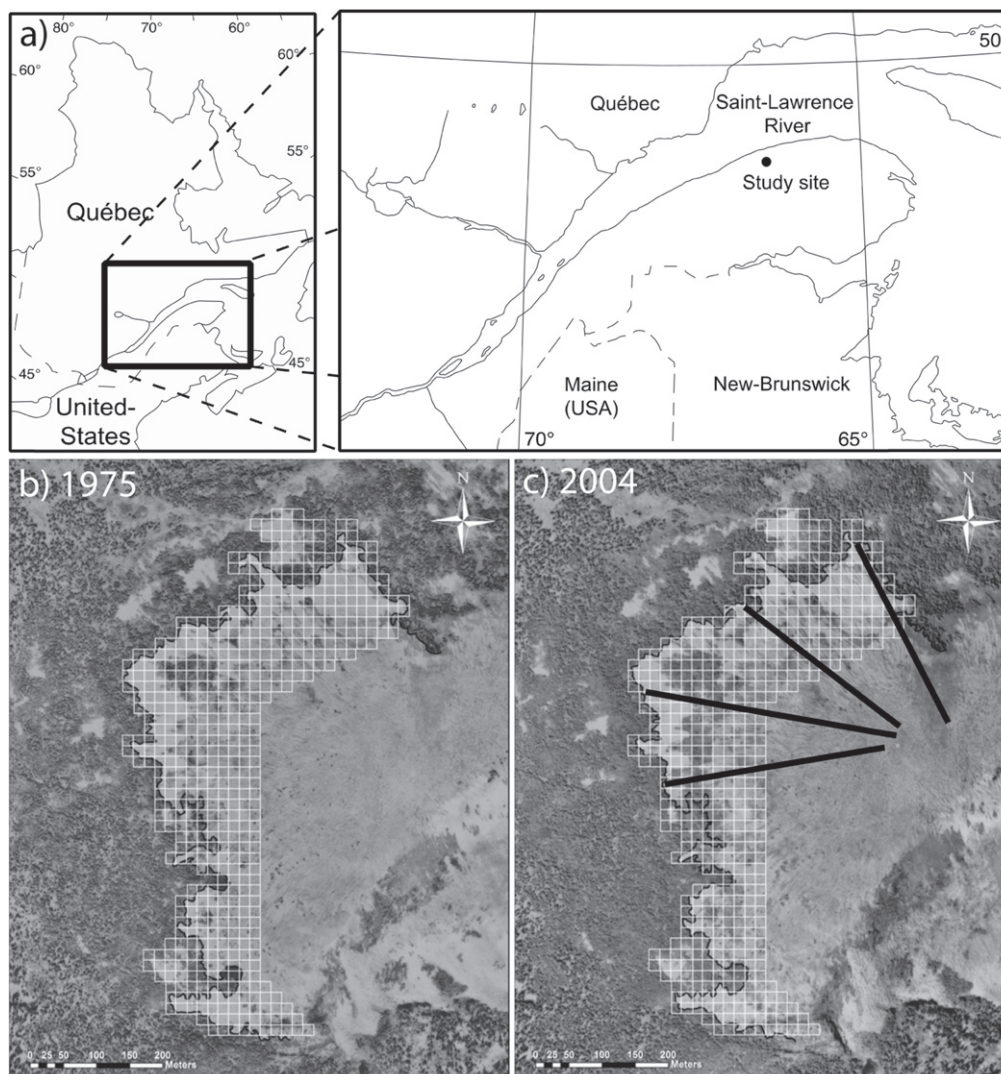


Figure 1. Study site location (a) and (b) 1975 and (c) 2004 aerial photographs used in the analysis. White grid: cells used for the evaluation of shrub cover; thin black lines: treeline position in 1975 and 2004; thick black lines: location of the transects for the vegetation surveys.

Table 1. Concordance between temperatures recorded at the Ste-Anne-des Monts weather station and on Mont Jacques-Cartier in the Parc National de la Gaspésie.

Year	Start date	End date	Days (n)	Pearson		$\Delta T \pm \text{sd}$ (°C)
				corr. coeff.	P-value	
1993	26/06	31/08	56	0.44	<0.01	3.95 ± 3.70
1994	26/06	31/08	67	0.60	<0.01	3.64 ± 3.09
1995	24/06	31/08	69	0.62	<0.01	2.89 ± 3.50
1996	26/06	31/08	67	0.66	<0.01	2.64 ± 3.90
1997	25/06	31/08	68	0.52	<0.01	4.08 ± 3.50
1998	24/06	31/08	69	0.59	<0.01	4.60 ± 3.20
2001	26/06	31/08	67	0.66	<0.01	3.83 ± 2.73

2.2. Treeline advance

Changes in treeline position or in erect shrub cover in the low alpine zone (see below for zone delimitation) were evaluated through the comparison of two 1:15 000 aerial photographs

taken on 14 September 1975 and on 8 September 2004 (figures 1(b), (c)). Both aerial photographs were projected in the MTM 5 NAD 83 map projection using ERMAPPER V7.1 in order to remove topographic distortions. These manipulations resulted in 0.15 m-resolution ortho-photos. The spatial offset between the photos averages 3.3 m.

To determine if the Mont de la Passe treeline advanced between 1975 and 2004, we delineated the treeline on both aerial photos (1975 and 2004) using the Edit toolbox in ArcGIS 10.0 (ESRI). Trees are easily recognizable by their distinctive color and texture. The distance between the two treelines was then measured using *Near function*. This function calculated the nearest distance between the two polylines for 2868 points (one at every meter) along the 2.87 km treeline. The criteria used to identify significant zones of treeline advance or retreat was 10 consecutive measures greater than the spatial offset between the two pictures (>3.3 m for treeline advance; <-3.3 m for treeline retreat).

2.3. Shrub expansion

Changes in erect shrub cover were also evaluated through the comparison of the two aerial photos by two independent observers. Erect shrub species are recognizable by their darker shade and roundish aspect. Shrub cover identification was therefore based on both the pixel color and the texture of the ortho-photo. Because erect shrubs are mostly found in the low alpine subzone of Mont de la Passe (see below for zone delimitation), the analysis was restricted to this subzone. In the laboratory, a grid consisting of 569 cells ($16\text{ m} \times 16\text{ m}$, 256 m^2) was overlaid on both ortho-photos (figures 1(b), (c)). Shrub cover was estimated within each cell and assigned to one of the following shrub cover classes: (1) 0%, (2) 1–25%, (3) 26–50%, (4) 51–75%, and (5) 76–100%. Total shrub cover was calculated by averaging the median value of the cover class assigned to each cell. Shrub cover change was then calculated as the difference in shrub cover between 2004 and 1975.

2.4. Vegetation survey

In summer 2008, the alpine zone was subdivided into three subzones (low, intermediate and high) according to the overall composition and structure of the plant communities. Four transects were established from the *P. glauca* krummholz line to the summit (SW, W, NW and NNW). No transects were established on the eastern section of the mountain because of the extreme slope steepness.

To describe shrub communities in each of the alpine subzones, vegetation surveys were carried out in adjacent 100 m^2 quadrats along each of the four transects (figure 1(c)). In each quadrat, linear surveys were conducted along 15 randomly located 1 m-long segments, following the method described in Mueller-Dombois and Ellenberg (1974). The 1 m long segments were subdivided into ten and the cover of each species was assigned to one of the following cover classes: 0; <1%; 1–10% 11–20%,..., 91–100% in each of the 10 cm long sub-segments. For each quadrat, the cover of the different species was calculated by summing the cover class median value for each of the sub-segments in a quadrat, including the sub-segments in which the species was not found. Species cover per subzone was then calculated by averaging the results of the different quadrats of a particular subzone.

2.5. *B. glandulosa* radial growth analysis

To evaluate the radial growth of *B. glandulosa* in each of the alpine subzones, wood samples were harvested from randomly selected healthy individuals at the end of the 2008 growing season. A total of 40 samples were harvested near the transects in each subzone, for a total of 120 samples (10 samples $\times$ 4 transects $\times$ 3 subzones). Samples were either taken at the root collar (junction between roots and stems) or at the base of the larger stem of one individual. A total of 40 samples were harvested in each subzone, for a total of 120 samples (10 samples $\times$ 4 transects $\times$ 3 subzones). Samples were cleaned and left to dry at room temperature for a

minimum of six weeks before being processed for dendrochronological analyses. For radial growth determination, thin sections (*ca.* $20\text{ }\mu\text{m}$) of *B. glandulosa* were prepared using a sledge microtome. Samples were boiled for 2 h before being sliced. Subsequently, thin sections were stained with safranin (1% solution for 120 s), rinsed once in distilled water and twice in ethanol (50% and 95%, respectively) and permanently mounted on microscope slides using Cytoseal 60, a low-viscosity mounting medium. Samples were scanned at high resolution (1200 dpi).

Age determination was carried-out under a dissecting microscope and in Adobe Photoshop V.7.0 while ring width was measured using LignoVision V.1.36, a software used for dendrochronological analyses. A single radius was measured for each sample since some slices were incomplete. Growth measurements were verified with COFECHA, a statistical crossdating program (Holmes 1983). A cubic smoothing spline function (λ ranging from 11 to 32 yr) was first applied to all raw chronologies to remove mid- to low frequency trends associated with the age of the individuals (ARSTAN software). A growth ring chronology was then produced for each of the three alpine subzones. The signal-to-noise ratio (SNR) was used to evaluate the average sensitivity of the chronologies and to infer their potential for climate-growth analysis (Fritts 1976) while the expressed population signal (EPS) was used as an indicator of the reliability of the chronologies (Wigley *et al* 1984).

In order to evaluate the importance of temperature and precipitation on *B. glandulosa*'s radial growth, response function analyses (RFA) were conducted with the *bootRes* package (Zang 2012) in the R software (v.3.0.2, R Development Core Team 2009). The *dcc* function calculates bootstrapped response function coefficients in a similar way as the Dendroclim2002 software (Biondi and Waikul 2004). It calculates multivariate estimates from a principal component regression model in which tree-ring values are predicted from monthly climate variables. The significance of response function coefficients is tested using the 95% percentile range method (Dixon 2001) from 1000 random bootstrapped samples. This analysis allows one to identify which month (or any particular period) has a significant impact on the radial growth of the species of interest. We used the available mean monthly temperatures (1963–1998, excluding 1968, 1977 and 1981) and total monthly precipitation (1963–1998, excluding 1965–1968, 1971 and 1980) data from the Ste-Anne-des-Monts climatic station. Years when temperature or precipitation data were missing or incomplete were excluded.

3. Results

3.1. Treeline advance

The distance between the treeline position in 1975 and 2004 was calculated from 2868 points. It averages -0.4 m but ranges between -11.1 m and 18.2 m . Overall, no major trend in treeline position was observed since most of the measured distances (72.0%) were within the spatial offset between the

two ortho-photos (± 3.3 m; figure 2(a)). Based on the criterion described in the methods section, we identified 16 segments (average length: 19.2 ± 7.0 m) for which treeline retreated by 4.7 ± 0.8 m between 1975 and 2004 (figure 2(a)). We also identified 8 segments (average length: 26.4 ± 26.7 m) for which the treeline advanced by 5.6 ± 2.2 m during the same period.

3.2. Shrub expansion

Shrub cover in the low alpine subzone was evaluated on both aerial photographs by two independent observers (figure 2(b)). Shrub cover was estimated between 19.3% and 21.1% in 1975 and between 29.7% and 31.1% in 2004. Over the 29-year period, shrub cover increase ranged between 8.6% (obs. #1) and 11.8% (obs. #2). Both observers assigned fewer cells to the low cover classes (0%, 1–25%) and more cells to the high cover classes (50–75%, 76–100%) in 2004 than in 1975 (figure 2(c)).

3.3. Vegetation survey

In the low alpine subzone, vegetation survey revealed a total shrub cover of 30.7% in 2008. The shrub community was dominated by *B. glandulosa* (10.1%) and *V. uliginosum* (7.4%). Crawling shrub species, such as *Vaccinium vitis-idaea* L. (7.1%) and *Empetrum nigrum* L. (5.1%) were also abundant. Other species that were observed in this subzone were *L. groenlandicum*, *Betula minor* (Tuckerman) Fernald, *Arctous alpina* L. Niedenzu, *Sibbaldiopsis tridentata* (Sol.) Rydb.

Shrub cover in the intermediate alpine subzone was lower (22.8%), but the shrub community was still dominated by *B. glandulosa* (8.4%) and *V. uliginosum* (8.0%) while *V. vitis-idaea* and *E. nigrum* cover declined sharply. Other shrub species found in this zone were *B. minor*, *L. groenlandicum*, *A. alpina*, *S. tridentata*, *D. lapponica*, *K. procumbens* and *Salix uva-ursi* Pursh.

In the high alpine subzone, shrub cover was even lower (15.0%) but still dominated by *V. uliginosum* (6.8%) and *B. glandulosa* (4.4%), all individuals of the latter being <50 cm tall. Only *Rhododendron lapponicum* (L.) Walhenb. was restricted to this subzone. However, four of the previously observed species had their highest abundance in this subzone (*S. uva-ursi*, *D. lapponica*, *S. tridentata* and *K. procumbens*).

3.4. *Betula glandulosa* radial growth

Tree-ring chronologies were developed for the low, intermediate and high alpine subzones based on 30, 29 and 32 individuals, respectively (figure 3). The SNR ranged from 10.4 to 13.9 while the EPS for each chronology was well above the 0.85 threshold needed to be considered valid (Wigley *et al* 1984).

Response functions between radial growth and climatic variables (mean monthly temperature and total precipitation) suggested that the climatic determinants of *B. glandulosa* radial growth vary between the different subzones, being more complex at higher altitude (figure 4). Indeed, while the

radial growth of individuals harvested in the low alpine subzone was only positively associated with July mean temperature, the growth of individuals harvested in the intermediate alpine subzone was additionally negatively influenced by March mean temperature. Moreover, response functions suggest that in addition to the previously described relationships with March and July temperatures, radial growth of individuals harvested in the high alpine zone was also positively associated with temperatures in January and August. Based on RFA, radial growth does not appear to be associated with monthly precipitation.

4. Discussion

In this study, we demonstrated that shrub species have expanded from 1975 to 2004 in the lower portion of the alpine zone of Mont de la Passe in the Parc National de la Gaspésie, (Québec, Canada). Shrub expansion is believed to be mainly associated with infilling of already established patches rather than colonization of new areas. Treeline did not show a significant position shift over the same period. We also identified that the climatic drivers of *B. glandulosa* radial growth become more complex along an altitudinal gradient extending from the lower (near the treeline) to the higher alpine (at the summit) subzone.

4.1. Treeline inertia

At the global scale, treeline response to climate change is heterogeneous. In a review published in 2009, Harsch *et al* (2009) reported that nearly half of the treelines studied since the beginning of the 20th century had not undergone significant shifts, even though extensive warming had occurred at many of the studied sites. In this regard, the absence of a major treeline shift at Mont de la Passe was expected, given the relatively modest warming observed in the region (Yagouti *et al* 2006). The apparent low responsiveness of the treeline could be associated with the stunted growth form of the white spruce individuals found at the treeline. Some tree species only produce significant amounts of viable seeds when they display an erect growth form (Bégin and Filion 1999). The lack of suitable germination sites could also be responsible for the absence of recruitment above the treeline. Mont de la Passe is characterized by large boulder fields that are indeed not suitable for seedling establishment. Moreover, the presence of shrub species with allelopathic properties, as it was observed near Kangiqsualujjuaq in Nunavik (subarctic Québec), could limit white spruce seedling establishment (Dufour-Tremblay *et al* 2012). In fact, very few spruce seedlings were observed above the treeline at Mont de la Passe (S. Boudreau; pers. obs.).

4.2. Shrub expansion

Shrub expansion is arguably the most frequent response of terrestrial tundra ecosystems to climate change throughout the circumpolar region (Sturm *et al* 2001, Tape *et al* 2006, Beck

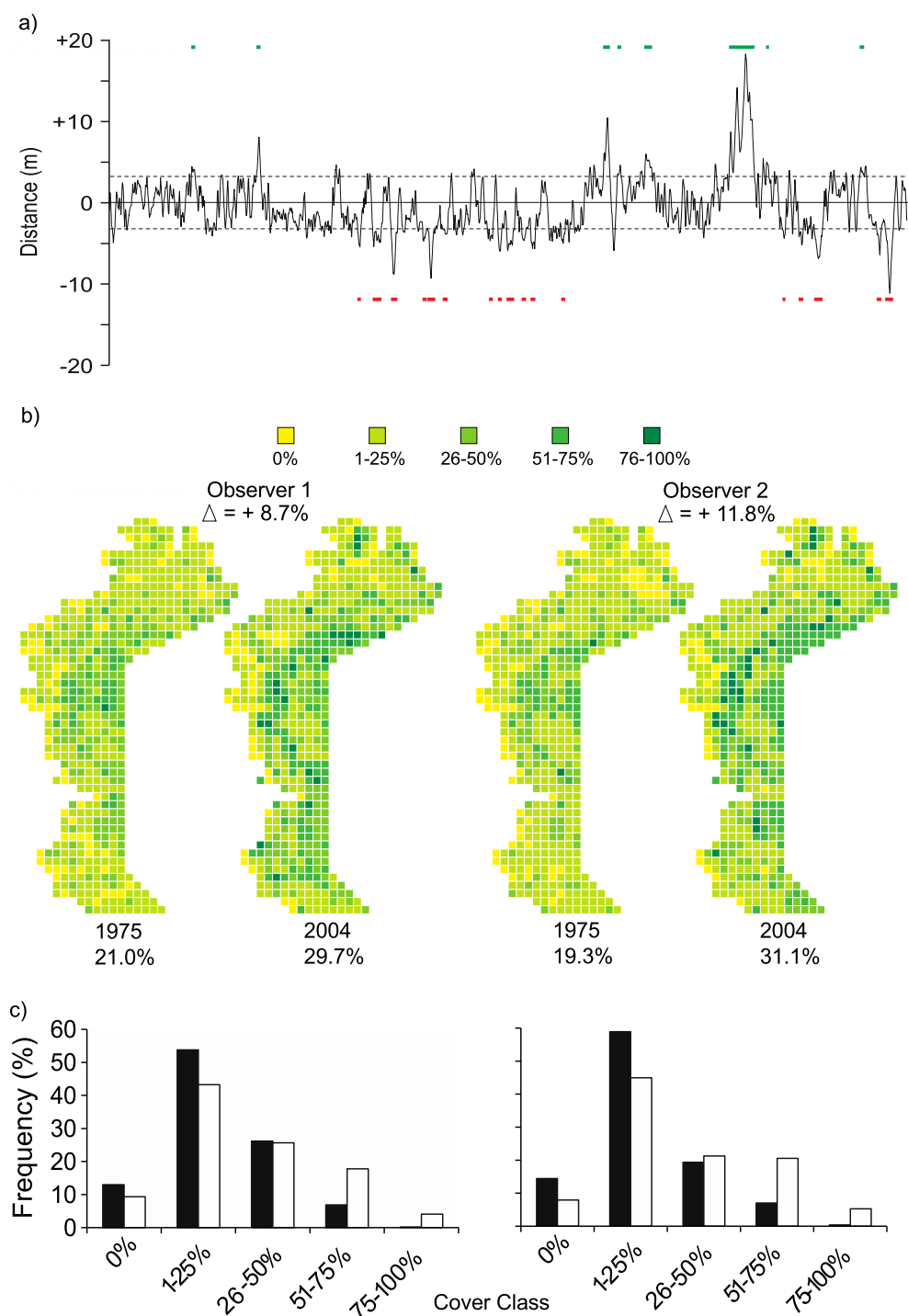


Figure 2. Results of the aerial photograph analyses to detect an advance of the treeline or a densification of the shrub cover. (a) Distances between treeline positions in 1975 and 2004. Dashed line: spatial offset between the two pictures; green and red lines: segments ≥ 10 m long for which the distances between the treeline position in 1975 and 2004 was greater than the spatial offset between the two pictures; (b) assigned shrub cover in each of the cells on the 1975 and 2004 photographs by the two observers; (c) frequency distribution of cell cover classes in 1975 (black bars) and 2004 (white bars) for each observer.

and Goetz 2011, Ropars and Boudreau 2012, Tremblay *et al* 2012, but see Plante *et al* 2014). It was also observed in many high-latitude mountain and other alpine ecosystems in different regions of the world (Alaska: Dial *et al* 2007, Yukon: Myers-Smith 2011; subarctic Sweden: Hallinger *et al* 2010; European Alps: Dullinger *et al* 2003, Anthelme *et al* 2007, Cannone *et al* 2007). Our results are broadly

consistent with these studies. We found an increase of *ca.* 10% in the shrub cover in the lower subzone of the alpine tundra at Mont de la Passe. Although we did not specifically record seedling abundance during the vegetation survey, shrub seedling occurrence was low overall, suggesting that the observed expansion occurs mainly through infilling of already established shrub patches. The colonization of new

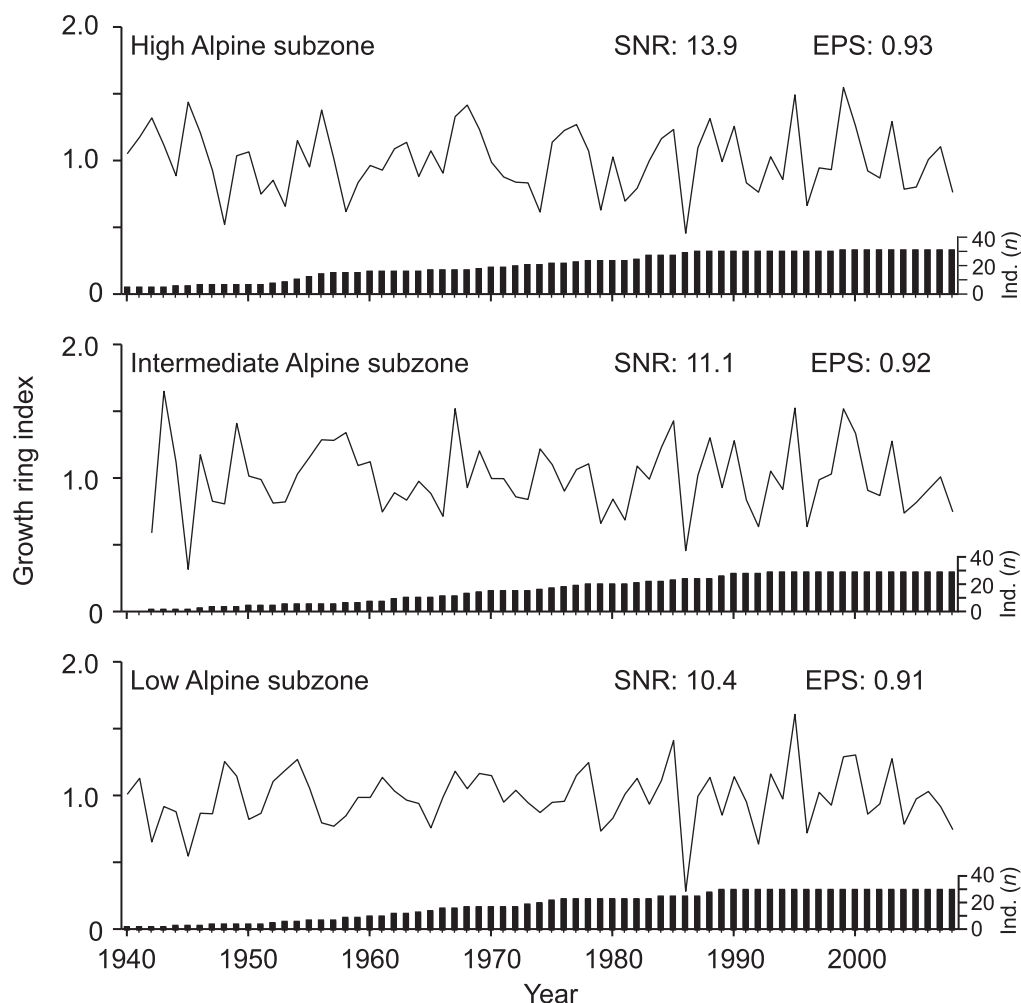


Figure 3. *Betula glandulosa* growth chronologies and associated statistics (SNR: signal to noise ratio, EPS: expressed population signal) for each of the alpine subzones. Histograms show the number of individuals used to construct each chronology.

sites on Mont de la Passe (and on surrounding mountains) could be limited by the relative scarcity of suitable germination sites as the mountaintop harbors large boulder fields. In fact, it is possible that the boulder fields could slow down shrub expansion on Mont de la Passe in future, protecting the arctic-alpine flora.

Differences between shrub cover inferred from our 2004 aerial photograph analysis (29.7% and 31.1%) and those measured in the field in 2008 (30.7%) are negligible, suggesting that the aerial photograph analysis is reliable. Although our vegetation surveys do not allow us to identify precisely the species responsible for this expansion, our personal observations strongly suggest that the expansion is mainly associated with *B. glandulosa* and to a lesser extent to *V. uliginosum* and *L. groenlandicum*. We were unfortunately not able to conduct the aerial photograph analysis for the intermediate and the higher subzones of the mountains due to the difficulty in differentiating shrub cover in those subzones. It would however be of great interest since a significant shrub expansion in those subzones could lead to the local extinction of the arctic-alpine species restricted to those subzones.

4.3. Climatic drivers of *Betula glandulosa* radial growth

Over the last few years, shrub species have been used frequently for dendrochronological analyses. Shrub species growth has been associated positively (Bär *et al* 2008, Liang and Eckstein 2009, Forbes *et al* 2010, Hallinger *et al* 2010, Hantemirov *et al* 2011, Boudreau and Villeneuve-Simard 2012, Franklin 2013) or negatively (Liang *et al* 2012) to summer temperatures, or positively (Liang and Eckstein 2009, Hallinger *et al* 2010, Liang *et al* 2012, Franklin 2013) or negatively (Schmidt *et al* 2010) to snow cover and precipitation. In this study, we found that the climatic drivers of *B. glandulosa* radial growth varied as a function of altitude. In the lower alpine subzone, *B. glandulosa* radial growth was only significantly associated with July temperature while it was also associated negatively to March temperature in the intermediate zone. We believe that this difference between the two adjacent subzones is linked to the differential snow accumulation during winter. Greater snow accumulation near the treeline would prevent shrubs of the lower subzone from becoming physiologically active following warm temperatures in March and therefore, prevent damages associated with late

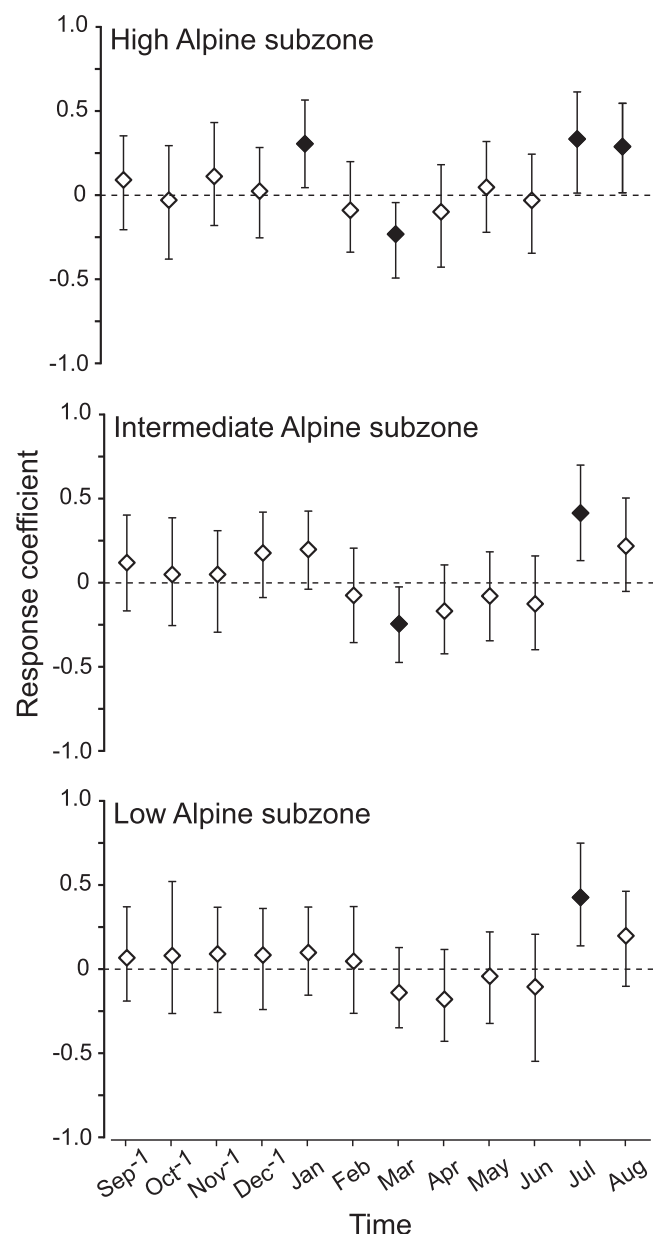


Figure 4. Response functions between *Betula glandulosa* radial growth and mean monthly temperatures. Dark diamonds indicate significant correlations.

frosts in April or May. Climatic drivers of *B. glandulosa* radial growth are even more complex in the higher alpine subzone (hilltop) since it was also positively associated with January and August temperature. The positive effect of January temperature is likely associated with reduced frost damage. On hilltops where there is almost no snow accumulation, it is likely that cold temperatures in January result in greater frost damage or winter desiccation. Because conditions are harsher on the mountaintop, it is also likely that shrub individuals found there will benefit from warmer temperatures in August that would extend the growing season. In fact, August temperatures were nearly significant for *B. glandulosa* radial growth in the other two subzones.

5. Conclusions

This research shows a substantial increase in shrub cover for the lower alpine zone of Mont de la Passe between 1975 and 2004. During this period, the treeline did not show any significant shift in its position. The increase in shrub cover could continue over the next decades since the radial growth of *B. glandulosa*, one of the most abundant species, is positively associated with warmer temperatures during the growing season (July and August). We also demonstrated that the climatic drivers of *B. glandulosa* radial growth become more complex with increasing altitude, with January and March temperatures being more important for the growth of the individuals found near the hilltop.

Acknowledgments

This research project was funded by the Fonds Québécois de la Recherche sur la Nature et les Technologies Québec (FQRNT) via the New researchers start-up program (S Boudreau). The authors would like to thank Vanessa Duclos, Nicolas Fontaine, Marianne Ricard, Florence Pagé-Larivière and Marie-Pascale Villeneuve-Simard for their assistance in the field and the Parc National de la Gaspésie for its logistical support.

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