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Greater effect of increasing shrub height on winter versus summer soil temperature

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Abstract

Shrub expansion is increasingly observed in arctic and subarctic environments. The development of shrub structure may significantly impact the abiotic environment at the local scale. Our objective was to reconstruct the development of the vertical structure of Betula glandulosa Michx, and to evaluate its effects on winter and summer soil temperature and on snow depth. Stratified sampling of the shrub revealed that shrub biomass distribution followed a similar pattern in stands of contrasting heights. Woody biomass was maximal in the lower stratum and relatively stable in the intermediate strata, while the foliar biomass tracked the vertical development of the shrub structure. Dendrochronological analysis revealed that shrub stands are relatively young; most of the dominant stems started their development after 1990. Shrub height was positively associated with both the dominant stem age and its vertical growth rate. Temperature differences among sites were greater during winter (ca 10°C) than during summer (ca 2°C), while the sum of freezing degree-days varied from 680°C to 2125°C. Shrub height was the most plausible variable explaining snow depth, winter ground level temperature and the sum of freezing degree-days. However, woody biomass in the 30–40 cm strata best explained summer ground level temperature. Our results suggest that the development of a shrub structure will have far-reaching consequences on the abiotic environment of subarctic ecosystems.

1. Introduction

Arctic and subarctic ecosystems have been subjected to rapid and intense climatic change over the last few decades, triggering permafrost degradation, reduction in sea-ice cover and trophic mismatch, to name a few (IPCC 2013). In terrestrial ecosystems, shrub expansion appears to be generalised within the circumpolar area according to numerous studies using either aerial photos or satellite image analyses (Russia: Forbes et al 2010, Blok et al 2011a; Alaska: Sturm et al 2001a, Tape et al 2006; Canada: Hudson and Henry 2009, Lantz et al 2010, Ropars and Boudreau 2012, Tremblay et al 2012, Provencher-Nolet et al 2014, but see Plante et al 2014). Shrub expansion can be associated with the densification or the vertical development of pre-existing shrub stands or with the colonisation of previously shrubless sites (Myers-Smith et al 2011). Long-term vegetation models predict that erect shrubs could replace graminoids, herbs and prostrate shrubs and affect 50% to 70% of all arctic communities by 2050 (Pearson et al 2013).

It is generally accepted that both low temperatures (Parsons et al 1994, Chapin et al 1995, Van Wijk et al 2004, Wu et al 2011, Elmendorf et al 2012) and nutrient availability (Chapin et al 1995, Chapin and Shaver 1996, Zamin and Grogan 2012, Heskel et al 2013) restrict plant growth in arctic and subarctic environments. Shrub species were shown to respond positively to warmer temperatures and increased
nutrient availability (Forbes et al. 2010, Tape et al. 2012, Frost and Epstein 2014) and precipitation (Blok et al. 2011b). Under experimental conditions, increases in foliar, woody and/or root biomass were observed for different shrub species (Parsons et al. 1994, Chapin et al. 1995, Chapin and Shaver 1996, Wu et al. 2011, DeMarco et al. 2014, Paradis et al. 2014).

Sturm et al. (2005) were the first to suggest that shrub expansion was likely associated with a positive feedback loop involving soil temperature, nutrient availability and snowly precipitations. Shrub cover decreases both the redistribution (Liston et al. 2002, Pomeroy et al. 2006) and sublimation of snow by wind (Liston et al. 2002), resulting in greater snow accumulation under shrubs than in the adjacent open tundra (Sturm et al. 2001b, Pomeroy et al. 2006, Myers-Smith and Hik 2013). Since snow has an insulating effect on soil temperature during winter (Hardy et al. 2001, Zhang et al. 2008, Myers-Smith and Hik 2013), winter soil temperatures under shrub cover are warmer than in the open tundra (Sturm et al. 2001b, Myers-Smith and Hik 2013). This phenomenon could increase microbial activity and, therefore, nutrient availability for plant growth during the subsequent growth season (Nadelhoffer et al. 1991, Schimel et al. 2004). Since shrub species are known to efficiently use newly available nutrients for growth (Chapin and Shaver 1996), an increase in nutrient availability resulting from a greater shrub cover could exacerbate shrub development (Sturm et al. 2005). Although one might argue that the shade provided by a denser shrub cover during summer might reduce soil temperature (Blok et al. 2010, Epstein et al. 2013, Myers-Smith and Hik 2013) and microbial activity, it is generally accepted that the warming effect of shrub cover on soil temperature during the winter is greater than its cooling effect during the summer (Lawrence and Swenson 2011, Loranty et al. 2011, Bonfils et al. 2012, Epstein et al. 2013).

The aim of this study was to evaluate the effect of the vertical structure of *Betula glandulosa* Michx on soil temperature and snow cover in order to understand how shrub expansion could influence subarctic terrestrial ecosystems in the near future. To do so, we characterised and reconstructed the development of *B. glandulosa* vertical structure (height, age, biomass, stem length, wood volume) in 22 sites in the Umiujaq region of Nunavik (subarctic Québec) and described the abiotic environment (summer and winter soil temperature, annual freezing and thawing degree-days and snow depth) in each of the stands. We hypothesised that *B. glandulosa* vertical structure influences the abiotic environment mainly during winter through its impact on snow cover. We predicted (i) that snow depth and winter soil temperature would be higher in sites with taller shrubs, (ii) that annual freezing degree-days would be lower in sites with taller shrubs, (iii) that summer soil temperature and thawing degree-days would not be influenced by *B. glandulosa* vertical structure, and (iv) that shrub height would be the most significant variable in explaining winter soil temperature, annual freezing degree-days and snow depth.

2. Methodology

2.1. Study area

The study area is located near the northern community of Umiujaq (56°33′07″N, 76°32′57″O) on the Hudson Bay coast of Nunavik (subarctic Québec), at the forest-tundra ecotone (Payette 1983) and in the discontinuous permafrost zone (Allard and Seguin 1987). According to Ju and Masek (2016), Nunavik is one of the regions that experienced the strongest greening trend in North America over the last three decades. At the regional scale, the landscape is mostly characterised by shrub tundra dominated by *B. glandulosa* (Payette 1976) and other shrub species such as *Alnus viridis* subsp. *crispa* (Aiton) Turrill and *Salix planifolia* Pursh. Black and white spruce (*Picea mariana* [Mill.] BSP and *Picea glauca* [Moench] Voss) are the dominant tree species. Based on data from the Kujujuarapik weather station, located 160 km to the South-West, mean annual temperature for the 1981–2010 period is −4.0 °C (Environment Canada 2013) while incomplete data for the Umiujaq region (1997–2012) suggest that mean annual temperature is −3.0 °C (Nordicana 2014). According to Ménard et al. (1998), mean annual precipitation in Umiujaq is 550 mm, of which 40% falls as snow. Strong winds, blowing from the bay (west and north-west) during winter, can reach >100 km h⁻¹ (Fortier et al. 1994). The region experienced rapid permafrost degradation associated with warming air temperature over the last few decades (Payette et al. 2004, Fortier et al. 2011).

2.2. Study species

*Betula glandulosa* is an erect deciduous shrub species that can grow up to 2.5 m (DeGroot et al. 1997). Its geographical distribution ranges from Greenland to Alaska and all the way south to California (DeGroot et al. 1997). It reproduces either sexually via abundant viable seed production (Hermanutz et al. 1989) or asexually via clonal growth (Weis and Hermanutz 1988, 1993). It can tolerate a wide array of abiotic conditions and can be found on well-drained sites as well as in wetlands. In Eastern Canada, it has been shown to expand rapidly over the last decades in response to climate change (Ropars and Boudreau 2012, Tremblay et al. 2012, Provancher-Nolet et al. 2014).

2.3. Sampling design

A total of 22 stands dominated by *B. glandulosa* were selected for the study. Stands (> 150 m²) were selected to cover the height range of *B. glandulosa* in the region (ca 20 to 140 cm) and were located either in the coastal
area (7), in the Tasiapik Valley (8) or on the plateau between the two (7). In each stand, *B. glandulosa* height was calculated as the average of ten randomly located height measurements. Total shrub cover (all shrub species; nomenclature used: VASCAN; Brouillet *et al.* 2010+) was also estimated using the following cover classes: 0%–1%, 1%–5%, 5%–15%, 15%–25%, 25%–50%, 50%–75%, 75%–90%, 90%–100%. Soil temperature was recorded at ground level every 6 h with iButton Thermochron® data loggers (±0.5 °C, model DS1921G-F5#, Dallas Semiconductor Corporation, Dallas, TX, USA) from September 2013 to August 2014. A long pole (at least 10 cm taller than the shrub stand) was placed in the vicinity of each data logger, making it possible to locate it during winter. In late February 2014, 16 randomly distributed measurements of snow depth were taken in each stand, including one measure near the location of the data logger (ca 25 cm), since most of the poles were still visible above the snow cover (18 sites). For the remaining sites (4), we used GPS coordinates to locate the data loggers. The 15 other measurements were taken within 3 m around the data logger location to make sure snow measurements were taken within the shrub stands. Snow cover was not disturbed during the measurements since it was hard enough to support the weight of a person.

2.4. *Betula glandulosa* vertical structure characterisation

In August 2013, we sampled the vertical biomass of *B. glandulosa* within four 0.5 m² quadrats, randomly located in each stand but at least 4 m apart from the data logger. We sampled *B. glandulosa* leaf and woody biomass within 10 cm vertical strata (starting from the top of the shrub). In the laboratory, we sorted, dried (at 70 °C for 72 h), and weighed leafy and woody biomass with a high precision scale (A&D, Model ER-182A, ±0.0001 g) for each stratified sample. Afterwards, we randomly selected one quadrat per stand and measured the length and diameter of each woody ramification (>1.5 cm long) with an electronic caliper (±0.001 cm). Wood volume (cm³) was then calculated with the following equation:

\[
V = \pi r^2 l
\]

where \(V\) = volume, \(r\) = radius and \(l\) = length of the ramification.

2.5. *Betula glandulosa* vertical structure development

In August 2013, we also collected stems to reconstruct *B. glandulosa* vertical structure development. Five dominant *B. glandulosa* stems per stand were randomly sampled. We sampled the stems at heights (vertical distance from the ground) of 0, 10, 20 cm and so on. Back in the laboratory, samples were dried at room temperature for six weeks, then boiled in water for at least two hours, and sliced with a microtome (ca 20 μm, WLS core-microtome). Slices were coloured with a safranine solution (1% w/v in distilled water) and fixed on permanent microscope slides. Growth rings were counted along two radii for each sample, since dwarf shrubs may form incomplete growth rings. We used the age of the stems (samples collected at height 0 cm) to determine the minimal age of the stands and used the age of the samples collected at the different heights to reconstruct the development (vertical growth rate in cm yr⁻¹) of the vertical structure of the stand. In order to obtain an average growth rate per stand, the growth rate of the 5 stems sampled in each stand was averaged.

2.6. Statistical analyses

All statistical analyses were performed using the software R (version 3.0.3, R Development Core Team, Vienna). Linear regressions were conducted to evaluate if *B. glandulosa* biomass (total, woody and foliar) was a function of stand height and to evaluate the relationship between dependent variables (soil temperature, degree-days and snow cover depth) and shrub structure properties (height, age, biomass). We also used linear regressions to evaluate the relationships between stand height and moss and lichen covers.

We built ecologically relevant statistical models that could explain the following climatic variables: ground-level winter (December–March) and summer (July–August) temperatures, snow depth and annual soil freezing and thawing degree-days. The explanatory variables available to build the linear regression models were all descriptors of the shrub vertical structure and were classified into five categories: height of the stand, minimal age of the stand, woody volume, stem length and biomass. For the latter three categories, data were available for each of the 10 cm-strata. In order to decrease the number of models, we selected only one explanatory variable from each of these categories, based on the Pearson correlation coefficient between these variables and the dependent variables. For example, we built the models to explain snow depth using the woody biomass in the 30–40 cm strata because it was this variable that showed the highest correlation coefficient with snow cover. We did not include interactions between the explanatory variables in the linear models as the degrees of freedom were restricted due to the number of sites.

We used a model selection approach (Alcmodav package, Mazereolle 2014) based on Akaike’s information criterion to determine which model(s) was the most plausible to explain the variable of interest. We tested each model for colinearity using Variance Inflation Factors (VIF; car package, Fox and Weisberg 2011) in order to remove variables from the model when VIF > 10. Because no model had a VIF > 10, we decided to leave all models as initially built even though some variables were correlated due to the nature of the data set. We followed the
recommendations of Burnham and Anderson (2002) who suggest using the multimodel inference if the best model has a wAICc < 0.90 in order to obtain the model-averaged estimate of the parameters, the unconditional standard error and the 95% confidence interval. We concluded that one particular variable had an effect on the dependent variables only if the confidence interval excluded 0.

3. Results

3.1. Betula glandulosa stand characteristics

The height of the B. glandulosa stands varied from 21 to 121 cm. Apart from the dominant B. glandulosa (>50% cover in all sites), other erect shrub species found at the sites included Salix planifolia Pursh. and S. glauca L., although their abundances were lower (<25% of total shrub cover; table 1). Ground layer vegetation was dominated by lichens, mosses and herbaceous species as well as by low shrub species such as Empetrum nigrum subsp. hermaphroditum (hagerup) Böcher, Rhododendron groenlandicum (Oeder) Kron and Judd, R. lapponicum (L.) Wahlenb., Vaccinium uliginosum L., V. vitis-idaea L. and Salix uva-ursi Pursh. Stand height of B. glandulosa had a significant positive effect on moss cover (\( F_{1,20} = 42.00, p < 0.001 \)) but a negative one on lichen cover (\( F_{1,20} = 44.13, p < 0.001 \)).

The abiotic environment varied greatly among the 22 stands. Winter (December–March) and summer (June–August) temperatures at ground level ranged from \(-14.9^\circ\text{C} \) to \( -4.2^\circ\text{C} \) and from \( 11.2^\circ\text{C} \) to \( 13.3^\circ\text{C} \), respectively. Annual freezing degree-days varied from 680 \( ^\circ\text{C} \) to 2125 \( ^\circ\text{C} \) while annual thawing degree-days varied from 1241 \( ^\circ\text{C} \) to 1563 \( ^\circ\text{C} \). Snow depth, measured in February 2014, ranged from 22 to 101 cm.

3.2. Betula glandulosa biomass

Total aboveground biomass of B. glandulosa was significantly related to height (\( F_{1,20} = 71.26, p < 0.001 \); figure 1(a)). This result is however mainly associated with the relationship between woody biomass and height (\( F_{1,20} = 80.47, p < 0.001 \); figure 1(b)) rather than with the one between foliar biomass and height (\( F_{1,20} = 0.00, p = 0.99 \); figure 1(c)).

For all sites, and regardless of the height or age of the B. glandulosa stems, woody biomass was always greatest in the 0–10 cm stratum (figures 2(a)–(c), but see figure S1 for all 22 sites). For B. glandulosa <50 cm, woody biomass decreased sharply above the 0–10 cm stratum (figure 2(a)). For taller shrubs, woody biomass tended to stabilise in the strata above the 0–10 stratum before declining sharply in the 2–3 higher strata (figures 2(b) and (c)). In contrast, foliar biomass appeared to track the development of B. glandulosa vertical structure, moving upwards as the shrubs grew in height (figures 2(a)–(c)). For taller shrubs, leaves were nearly absent from the lower strata.

3.3. Betula glandulosa age and vertical growth

Average stem age for the different sites ranged from 13 to 31 yr. Shrub height (21–121 cm) was positively associated with age (\( F_{1,20} = 30.9, p < 0.001 \); figure 3(a)). The vertical growth rates of individual stems ranged between 1.04 and 8.94 cm yr\(^{-1}\) (figures 3(b)–(d), but see figure S2 for all 22 sites). Once averaged, growth rate per stand varied between 1.80 and 4.67 cm yr\(^{-1}\). Furthermore, average vertical growth rates per stand were positively correlated with shrub height (\( F_{1,20} = 18.37, p < 0.001 \); figure 3(e)), lower shrubs having lower vertical growth rates than taller shrubs.

3.4. Betula glandulosa structure impacts on soil temperature and snow depth

None of the most plausible models that explained variation among sites in winter and summer temperatures at ground level, in annual freezing and thawing degree-days and in snow cover depth had a wAICc >0.90 (table 2). We therefore computed the weighted average of the estimates of the variables included in all models instead of relying solely on the estimates of the best model.

Betula glandulosa height was the sole variable in the most plausible model to explain variations among sites in winter temperature at ground level, in freezing degree-days and in snow depth (table 2). The weighted average of estimates procedure gave slightly different results. For winter temperature, the weighted average of the estimates of all variables revealed that both B. glandulosa height (estimate: 0.06, unconditional SE: 0.02, 95% confidence interval: 0.02, 0.10; figure 4(a)) and age (estimate: 0.023, unconditional SE: 0.12, 95% confidence interval: 0.01, 0.46; figure 4(b)) had a significant positive effect on winter temperature. Similar results were obtained for snow cover depth since B. glandulosa height (est.: 1.94, uncond. SE: 0.94, 95% conf. int.: 0.10, 3.78; figure 4(c)) and age (est.: 0.40, uncond. SE: 0.18, 95% conf. int.: 0.05, 0.75; figure 4(d)) were the only two variables that had a significant effect on this dependent variable. However, the weighted average of the estimates of all variables revealed that B. glandulosa height remained the sole variable with a significant impact on freezing degree-days, (est.: –8.63, uncond. SE: 2.61, 95% conf. int.: –13.75, –3.52, figure 4(e)).

For summer temperature, the model including only the woody biomass H30-40 was the most plausible to explain variations among sites (table 2). This result was supported by the weighted average of the estimates of all variables that revealed that only the woody biomass H30-40 had a significant impact on summer temperature at ground level (est.: -0.01, uncond. SE: 0.00, 95% conf. int.: -0.01, -0.00; figure 4(f)). For thawing degree-days, age was the sole variable in the most plausible model to explain the variation between sites. However, the weighted average of
Table 1. Vegetation cover and characteristics of *Betula glandulosa* in 22 sites sampled during summer 2013, near Umiujaq, Nunavik. Vegetation cover was visually evaluated by cover classes in all shrub stands (>150 m²).

| Sites | Site size (m) | Number of shrub species | *Betula glandulosa* | *Salix* spp. | *Empetrum* spp. | *Rhododendron* spp. | *Vaccinium* spp. | Ground cover (%) | Mean height (cm) | Mean stem age (yr) |
|-------|---------------|--------------------------|---------------------|--------------|-----------------|---------------------|-----------------|------------------|----------------|--------------------|
| 8     | 15 × 20       | 2                        | 50–75               |              |                 |                     | 1–5             | 1–5              | 5–15            | 128 ± 13           |
| 9     | 7 × 20        | 3                        | 75–90               |              |                 | 5–15               |                 | 75–90            | 0–1             | 121 ± 28           |
| 11    | 15 × 20       | 4                        | 75–90               | 1–5          |                 | 5–15               | 0–1             | 75–90            | 0–1             | 110 ± 19           |
| 12    | 15 × 20       | 4                        | 50–75               | 5–15         |                 | 5–15               | 1–5             | 5–15             | 5–15            | 14 ± 15            |
| 14    | 15 × 15       | 2                        | 50–75               |              |                 |                     |                 | 1–5             | 75–90            | 1–5               |
| 16    | 15 × 20       | 4                        | 75–90               | 15–25        |                 |                     | 1–5             | 75–90            | 15–25           | 25 ± 12            |
| 17    | 20 × 20       | 5                        | 50–75               | 0–1          |                 | 5–15               | 0–1             | 0–1             | 5–15            | 21 ± 12            |
| 18    | 15 × 20       | 3                        | 50–75               |              |                 |                     | 1–5             | 15–25            | 5–15            | 43 ± 12            |
| 19    | 10 × 20       | 2                        | 75–90               |              |                 |                     | 5–15             | 5–15             | 5–15            | 81 ± 16            |
| 20    | 10 × 20       | 3                        | 75–90               |              |                 |                     | 0–1             | 5–15             | 5–15            | 73 ± 9             |
| 21    | 15 × 20       | 4                        | 50–75               | 25–50        |                 | 15–25              | 5–15             | 1–5             | 50–75            | 26 ± 6             |
| 22    | 20 × 20       | 5                        | 75–90               | 5–15         | 1–5             | 5–15               | 1–5             | 5–15             | 5–15            | 65 ± 12            |
| 23    | 15 × 15       | 4                        | 75–90               | 1–5          |                 | 0–1                | 0–1             | 75–90            | 5–15             | 43 ± 17            |
| 24    | 15 × 15       | 5                        | 75–90               | 15–25        |                 | 0–1                | 0–1             | 75–90            | 1–5             | 5–15               |
| 26    | 20 × 20       | 4                        | 50–75               | 5–15         |                 | 15–25              |                 | 0–1             | 75–90            | 15–25             |
| 27    | 15 × 20       | 3                        | 50–75               |              |                 | 0–1                | 5–15             | 1–5             | 75–90            | 24 ± 7             |
| 28    | 15 × 15       | 4                        | 75–90               | 15–25        |                 | 0–1                | 5–15             | 75–90            | 15–25           | 26 ± 6             |
| 29    | 15 × 15       | 4                        | 75–90               | 5–15         |                 | 0–1                | 5–15             | 25–50            | 5–15             | 57 ± 14            |
| 30    | 15 × 15       | 4                        | 50–75               | 1–5          |                 | 1–5                | 1–5             | 25–50            | 5–15             | 41 ± 9             |
| 31    | 15 × 20       | 2                        | 50–75               | 1–5          |                 |                     |                 | 25–50            | 5–15             | 48 ± 9             |
| 32    | 15 × 25       | 7                        | 75–90               | 1–5          |                 | 5–15               | 0–1             | 25–50            | 5–15             | 68 ± 18            |
| 33    | 20 × 20       | 2                        | 50–75               |              |                 |                     | 0–1             | 0–1             | 75–90            | 24 ± 6             |
the estimates of all variables revealed that none had a significant effect on thawing degree-days.

4. Discussion

According to Sturm et al (2005), recent observed shrub expansion is likely associated with a positive feedback loop involving warmer soil temperature, increased nutrient availability and increased snow depth under shrub cover. In this study, our objective was to evaluate how shrub vertical structure influences soil temperature and snow cover. We were able to demonstrate that winter temperature at ground level, snow depth and annual freezing degree-days were all significantly influenced by B. glandulosa height, while summer temperature at ground level was influenced solely by the woody biomass in the H30-40 stratum (but the effect size was much lower than for winter ground level temperature). Moreover, none of the variables measured significantly explained the variation in annual thawing degree-days. Thus, our results support the hypothesis that an erect shrub cover has a

Figure 1. Shrub height influence on total (a), woody (b) and foliar (c) biomass. Each point represents the biomass mean of four 0.5 m² quadrats in 22 shrub stands near Umiujaq, Nunavik, harvested during summer 2013. n.s = Not significant.
greater effect on the abiotic environment in winter than in summer (Lawrence and Swenson 2011, Loranty et al 2011, Bonfils et al 2012, Epstein et al 2013).

4.1. *Betula glandulosa* vertical structure development

*Betula glandulosa* was the dominant shrub species in all 22 stands. This result corroborates the observations of previous studies in Northern Québec that showed both the dominance and the recent expansion of this species in lichen-dominated environments (Ropars and Boudreau 2012, Tremblay et al 2012, Provencher-Nolet et al 2014). The positive association between moss abundance and shrub height suggests that shrub canopy development and closure can lead to the replacement of lichens by mosses, a phenomenon that is likely to persist in subsequent years.

The vertical structure of the studied *B. glandulosa* stands was relatively young, ranging from 13 to 31 years. Although we cannot ascertain it, we believe that...
the minimal age of the stand derived from samples taken at the base of the dominant stems is likely a good indicator of the stand age. Such reasoning is based on the fact that the expansion in the region is recent (Provencher-Nolet et al. 2014, Ropars et al. 2015) and because *B. glandulosa* stems can easily live >40 yr. The stem analysis conducted in the different sites allowed us to reconstruct the development of *B. glandulosa* vertical structure. The vertical development appears to be linear for most stems (see slopes on figures 3(b)–(d) and figure S1), a somewhat unexpected result. Such regular increase in height in all studied sites revealed that *B. glandulosa* individuals are able to grow vertically throughout the landscape. Such results, corroborated by personal observations of rapid *B. glandulosa* vertical development at several sites in the region, could have significant implications for the abiotic environment in the Umiujaq region, including an increase of winter soil temperature and an exacerbated rate of permafrost degradation.

Moreover, *B. glandulosa* vertical structure was similar between stands of similar height. Overall, woody biomass was greater in the lower stratum. Woody biomass in this stratum supports most of the

**Figure 3.** Age and vertical growth of *B. glandulosa* (*n* = 5 stems per stand) in each of the 22 shrub stands in Umiujaq, Nunavik. Panel (a) shows the relationship between shrub height and mean minimal age of the stands (calculated from the age of the stems at ground level), Panels (b)–(d) show vertical stem growth for low, medium and tall shrub stands, respectively and Panel (e) illustrates the relationship between mean growth rate and shrub stand height.
Table 2. Candidate models chosen to explain the abiotic properties at Umiujaq, Nunavik. Data in bold represent significant variables that best explained the abiotic properties after multimodel analysis (I.C. excluding 0).

| Models                      | Winter temp. (December, January, February, March) | Summer temp. (July, August) | Snow cover depth | Freezing degree-days | Thawing degree-days |
|-----------------------------|---------------------------------------------------|-----------------------------|-----------------|----------------------|---------------------|
|                             | ΔAICc     | ΔAICcWt | ΔAICc | ΔAICcWt | ΔAICc | ΔAICcWt | ΔAICc | ΔAICcWt | ΔAICc | ΔAICcWt |
| Null                        | 63.39     | 0.00    | 129.95 | 0.00     | 45.48 | 0.00     | 66.22 | 0.00     | 116.74 | 0.00     |
| Betula height               | 0.00      | 0.50    | 1.73   | 0.16     | 0.00  | 0.28     | 0.00  | 0.54     | 2.02   | 0.11     |
| Mean age                    | 4.27      | 0.06    | 2.54   | 0.11     | 0.68  | 0.20     | 5.79  | 0.03     | 0.00   | 0.31     |
| Total volume                | 8.21      | 0.01    | 5.81   | 0.02     | 4.70  | 0.03     | 8.56  | 0.01     | 3.51   | 0.05     |
| Stem length                 | 9.13      | 0.01    | 8.17   | 0.01     | 4.26  | 0.03     | 9.83  | 0.00     | 3.59   | 0.05     |
| Woody biomass H30–H40       | 5.03      | 0.04    | 0.00   | 0.38     | 2.23  | 0.09     | 5.70  | 0.03     | 1.88   | 0.12     |
| Betula height + Total volume| 2.85      | 0.12    | 4.72   | 0.04     | 3.00  | 0.06     | 2.98  | 0.12     | 4.79   | 0.03     |
| Betula height + Stem length | 3.02      | 0.11    | 4.80   | 0.03     | 2.68  | 0.07     | 3.01  | 0.12     | 4.2    | 0.04     |
| Betula height + Woody biomass H30–H40 | 3.02 | 0.11 | 2.37 | 0.12 | 2.91 | 0.07 | 3.02 | 0.12 | 4.79 | 0.03 |
| Mean age + Total volume     | 7.12      | 0.01    | 5.16   | 0.03     | 3.65  | 0.05     | 8.28  | 0.01     | 2.43   | 0.09     |
| Mean age + Stem length      | 6.93      | 0.02    | 5.55   | 0.02     | 2.85  | 0.07     | 8.16  | 0.01     | 2.06   | 0.11     |
| Mean age + Woody biomass H30–H40 | 6.72 | 0.02 | 2.77 | 0.09 | 3.52 | 0.05 | 7.84 | 0.01 | 3.05 | 0.07 |
| Betula height + Mean age + Total volume + Stem length + Woody biomass H30–H40 | 13.75 | 0.00 | 11.62 | 0.00 | 10.44 | 0.00 | 14.25 | 0.00 | 13.34 | 0.00 |
aboveground biomass and provides resistance to gravity and wind (King and Loucks 1978). It is likely the result of a longer period of wood accumulation in the lower strata. In fact, while primary growth leads to axis elongation during the first year of wood formation, secondary growth, which occurs over several years afterwards, leads to stem diameter increase (Raven et al. 2014). Foliar biomass did not follow woody biomass distribution patterns, as it tracks the development of the vertical structure. We found few or no leaves in the lower strata of the taller shrub stands, where photosynthetically active radiation is believed to be limited as the increased foliage density in the upper half of the shrub’s vertical structure absorbs a significant percentage of the incoming solar radiation (Chapin et al. 2005, Blok et al. 2011a), a phenomenon that contributes to a decrease in the albedo of shrubby areas compared to open tundra (Myers-Smith et al. 2011).

### 4.2. Effects of *Betula glandulosa* on the abiotic environment at the stand scale

Our results corroborate studies that have shown greater snow accumulation under shrub cover than in the adjacent open tundra (Sturm et al. 2001b, Pomeroy et al. 2006, Myers-Smith and Hik 2013). We were able

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**Figure 4.** Relationships between abiotic environmental variables and their explanatory variables identified via the selection models analysis. Panels (a) and (b) show respectively the influence of stand height and age on winter ground-level temperature, Panels (c) and (d) show respectively the influence of stand height and age on snow depth, Panel (e) shows the influence of stand height on freezing degree-days and Panel (f) shows the influence of woody biomass in the H30-40 stratum on summer ground-level temperature.
to show that snow depth is positively associated to the height of *B. glandulosa* stands, although shrub height explained only 27.1% of the variation observed in snow depth between sites. The percentage of variance explained is however higher (39.3%) if we removed a single outlier. Moreover, minimal stand age also explained 25% of the variability in snow depth. The relatively low percentage of variation explained by shrub height and minimal stand age suggests that other variables, such as local topography, have a strong influence on snow accumulation (Sturm *et al.* 2001b, Pomeroy *et al.* 2006). Although our experimentation did not allow us to draw any conclusion about snow cover duration, preliminary temperature data suggest that snow accumulates rapidly under shrub cover at the beginning of the winter season, a likely consequence of snow redistribution by wind. The same data also suggest that snow tends to melt rapidly in spring, corroborating the results of studies that have shown that snow albedo was in spring, resulting in warmer air temperature and faster snowmelt (Sturm *et al.* 2001b, Lawrence and Swenson 2011, Loranty *et al.* 2011, Bonfils *et al.* 2012).

Shrub height also had a positive effect on the winter temperature at ground level and a negative effect on the sum of freezing degree-days at the soil–snow interface. While winter temperatures were best explained by shrub height and by minimal stand age, the sum of freezing degree-days was best explained by shrub height only. The range difference in winter ground level temperature (10.7 °C) found among our study sites is comparable to the one observed by Sturm *et al.* (2001b) but is higher than the ca 5 °C difference observed by Lawrence and Swenson (2011) and Myers-Smith and Hik (2013). Other studies have also shown higher ground-level temperature under snow cover (Hardy *et al.* 2001, Sturm *et al.* 2001b, Pomeroy *et al.* 2006, Lawrence and Swenson 2011, Myers-Smith and Hik 2013). Greater snow accumulation was also shown to decrease frost penetration in the soil (Hardy *et al.* 2001) and to increase the depth of the active layer (Loffler *et al.* 2008, Bonfils *et al.* 2012, Epstein *et al.* 2013), triggering permafrost degradation.

Overall, our results show that shrub height is the most significant predictor of the measured winter climatic parameters (temperature, freezing degree-days, snow depth). Although age is also significant for 2 out of 3 variables, we believe that these relationships with age might not stand as well in other arctic or subarctic regions where the development of the vertical structure is hindered by harsher climatic conditions, leading to shorter shrub stands, regardless of the age of the individuals. The inclusion of other variables (biomass, total stem length and wood volume) did not increase the performance of our models. However, these variables might have a greater impact on snow physical properties (Domine *et al.* 2015). For example, reduced snow compaction under shrub cover increases the thermal resistance of snow (Sturm *et al.* 2001b), increasing its insulation capacity.

The effect of shrub vertical structure on average summer temperature was barely significant and calls for caution in extrapolating these results. Variability of ground level temperature in summer was better explained by the woody biomass in the 30–40 cm vertical stratum, a somewhat unexpected result. It is possible that woody biomass in this stratum allows for a greater segregation of the different sites since shorter shrubs had no woody biomass in this stratum (height < 30 cm) while taller ones had an important one. Regardless of this particular result, the variation of ca. 2 °C in average summer temperature between shorter and taller stands was comparable to the one observed between shrub-dominated and shrubless sites in other studies (Blok *et al.* 2010, Myers-Smith and Hik 2013). When compared to the 10.7 °C observed among sites during winter, these results suggest that the impact of the shrub vertical structure is more important in winter than in summer.

One limitation of our study is the difficulty to discriminate the relative effect of shrub height and moss cover on soil temperature due to the fact that both variables are strongly associated. Changes in the abundance of moss species are believed to be an important driver of water and energy balance between soil and atmosphere in tundra ecosystems (McFadden *et al.* 2003, Beringer *et al.* 2005, Blok *et al.* 2011c). In fact, moss species’ low thermal conductivity can have a cooling effect on soil in summer (Gornall *et al.* 2007), a phenomenon likely to favour the persistence of permafrost (Zimov *et al.* 2006). When combined with the shade provided by dense shrub canopy, both phenomena could result in lower summer soil temperature and reduced permafrost degradation (Blok *et al.* 2010). However, our results strongly suggest that the observed effect of shrub vertical structure development, regardless of moss cover, is greater in winter than in summer. While annual freezing degree-days decreased sharply from 2125 °C to 680 °C with increasing stand height, thawing degree-days varied only from 1241 °C to 1563 °C among sites. When considering that an increase of 1 °C or 2 °C in mean annual temperature is sufficient to increase permafrost degradation (Smith 2011), the expansion of shrub cover, and its overall impact on soil thermal regime, is expected to significantly accelerate permafrost degradation.

5. Conclusion

Our study revealed that shrub stand height had a significant impact on snow depth, winter soil temperature and freezing degree-days in the Umiujaq region. Moreover, it highlighted that the vertical structure of *B. glandulosa* stands had developed rapidly over the last three decades. Although our study provided useful
information on the relationship between Betula glandulosa stand structure and snow depth, we did not evaluate how B. glandulosa biomass distribution influenced the quality of the snow. Future studies should then focus on the relationship between woody biomass structure and the characteristics of the snow pack (density, isolation coefficient, etc.).

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References

Allard M and Seguin K M 1987 Le pergélisol au Québec nordique: bilan et perspectives Géophys. Phys. Quaternaire 14 41–52
Beringer J, Chapin F S III, Thompson C C and McGuire A D 2005 Surface energy exchanges along a tundra-forest transition and feedbacks to climate Agric. For. Meteorol. 131 143–61
Blok D, Heijmans M, Schepaem-Strub G, Kononov A V, Maximov T C and Berendse F 2011a The response of Arctic vegetation to the summer climate: relation between shrub cover, NDVI, surface albedo and temperature Environ. Res. Lett. 6 035502
Blok D, Sas-Klaassen U, Schepaem-Strub G, Heijmans M M P D, Raeren P and Berendse F 2011b What are the main climate drivers for shrub growth in Northeastern Siberian tundra? Biogeosciences 8 1169–79
Blok D, Heijmans M M P D, Schepaem-Strub G, van Ruijven J, Parmentier F J W, Maximov T C and Berendse F 2011c The cooling capacity of mosses: controls on water and energy fluxes in a Siberian tundra site Ecosystems 14 1055–65
Bonfils C J W, Phillips T J, Lawrence D M, Cameron-Smith P, Riley W J and Suhin Z M 2012 On the influence of shrub height and expansion on northern high latitude climate Environ. Res. Lett. 7 015103
Brouillet L, Coursof F, Meeh S J, Favreau M, Anion M, Bélisle P and Desmet P 2010 VASCAN, the Database of Vascular Plants of Canada (http://data.canadensys.net/vascan/)
Burns R M and Anderson D 2002 Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (New York: Springer) 488p
Chapin F S and Shaver G R 1996 Physiological and growth responses of arctic plants to a field experiment simulating climatic change Ecology 77 822–40
Chapin F S, Shaver G R, Giblin A E, Nadelhoff K J and Laundre J A 1995 Responses of arctic tundra to experimental and observed changes in climate Ecology 76 694–711
Chapin F S et al 2005 Role of land-surface changes in arctic summer warming Science 310 657–60
DeGroot W J, Thomas P A and Wein R W 1997 Betula nana L. and Betula glandulosa Michx. J. Ecol. 85 241–64
DeMarco J, Mack M C, Bret-Harte M S, Burton M and Shaver G R 2014 Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra Ecosphere 5 72
Domine F, Barrere M, Sarrazin D, Morin S and Arnaud L 2015 Automatic monitoring of the effective thermal conductivity of snow on a low-arctic shrub tundra Cryosphere 9 1265–76
Elmendorf S C et al 2012 Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time Ecol. Lett. 15 164–75
Environment Canada 2013 Historical climate data (http://climatetrends.ec.gc.ca/)
Epstein H E, Myers-Smith I and Walker D A 2013 Recent dynamics of arctic and sub-arctic vegetation Environ. Res. Lett. 8 015040
Forbes B C, Faura M M and Zetterberg P 2010 Russian Arctic warming and ‘greening’ are closely tracked by tundra willows Glob. Change Biol. 16 1542–54
Fortier R, Allard M and Seguin M K 1994 Effect of physical-properties of frozen ground on electrical-resistivity logging Cold Reg. Sci. Technol. 22 361–84
Fortier R, LeBlanc M A and Yu W B 2011 Impacts of permafrost degradation on a road embankment at Umiujaq in Nunavik (Québec), Canada Can. Geotech. J. 48 720–40
Fox J and Weisberg S 2011 An (R) Companion to applied regression, Second Edition (http://socserv.socsci.mcmaster.ca/jfox/Books/Companion)
Frost G V and Epstein H E 2014 Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s Glob. Change Biol. 20 1264–77
Gonnall J, Jonsdottir I, Woodin S and Van der Wal R 2007 Arctic mosses govern below-ground ecosystem and ecosystem processes Oecologia 153 931–41
Hardy J P, Groffman P M, FitzHugh R D, Henry K S, Welman A T, Demers J D, Fahey T J, Driscoll C T, Tierney G L and Nolan S 2001 Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest Biogeochemistry 56 151–74
Hermanutz L A, Innes D J and Weis I M 1989 Clonal structure of arctic dwarf birch (Betula glandulosa) at its northern limit Am. J. Bot. 76 755–61
Heskel M, Greaves H, Kornfeld A, Gough L, Atkin O K, Turnbull M H, Shaver G and Griffin K L 2013 Differential physiological responses to environmental change promote woody shrub expansion Ecol. Evol. 3 1149–62
Hudson J M G and Henry G H R 2009 Increased plant biomass in a high arctic heath community from 1981 to 2008 Ecology 90 2657–63
IPCC 2013 Climate Change 2013: The Physical Science Basis, Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change ed T F Stocker et al (Cambridge: Cambridge University Press) 1359p
Ju J and Masek J G 2016 The vegetation greenness trend in Canada and from the Fondation de la Recherche sur la Civilisation des Peuples et des Cultures de la Province de Québec (Fondation de la Recherche sur la Civilisation des Peuples et des Cultures de la Province de Québec) 1055–65
Lantuit H, Gergel S E and Koks F 2010 Spatial heterogeneity in the shrub tundra ecotone in the Mackenzie Delta region, Northwest Territories: implications for arctic environmental change Ecosystems 13 194–204
Lawrence D M and Swenson S C 2011 Permafrost response to increasing arctic shrub abundance depends on the relative influence of shrubs on solar soil cooling versus large-scale climate warming Environ. Res. Lett. 6 045504
Liston G E, McFadden J P, Sturm M and Pielke R A 2002 Modelled changes in arctic tundra snow, energy and moisture fluxes due to increased shrubs Glob. Change Biol. 8 17–32
Löffler U C M, Cypionka H and Löffler J 2008 Soil microbial activity along an arctic-alpine altitudinal gradient from a seasonal perspective Eur. J. Soil Sci. 59 842–54

Loranty M M, Goetz S J and Beck P S A 2011 Tundra vegetation effects on pan-Arctic albedo Environ. Res. Lett. 6 024014

Mazerolle MJ 2014 Package ‘AICcmodavg’ (http://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf)

McFadden J P, Eugster W and Chapin FS III 2003 A regional study of

Myers-Smith I H

Paradis M, Mercier C and Boudreau S 2014 Response of

Nadelhoffer K J, Giblin A E, Shaver G R and Laundre J A 1991 Effects

Pomeroy J W, Bewley D S, Essery R L H, Hedstrom N R, Link T, Granger R J, Sicari E, Ellis C R and Janowicz J R 2006 Shrub tundra snowmelt Hydrol. Process. 20 923–41

Provencher-Nolet L, Bernier M and Lévesque E 2014 Quantification des changements récents à l’écotone forêt-toundra à partir de l’analyse numérique de photographies aériennes Écoscience 21 419–33

Raven P H, Eichhorn S E and Evert R F 2014 Biologie végétale, De Bock Supérieur 880p

Roper P and Boudreau S 2012 Shrub expansion at the forest-tundra ecotone: spatial heterogeneity linked to local topography Environ. Res. Lett. 7 015901

Roper P, Levesque E and Boudreau S 2013 How do climate and topography influence the greening of the forest-tundra ecotone in northern Quebec? A dendrochronological analysis of Betula glandulosa J. Ecol. 103 679–90

Schimel J P, Bilbrough C and Welker J A 2004 Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities Soil Biol. Biochem. 36 217–27

Smith S 2011 Trends in permafrost conditions and ecology in northern Canada Canadian Biodiversity: Ecosystem Status and Trends 2010, Technical Thematic Report No. 9 Canadian Councils of Resource Ministers 22p

Sturm M, Racine C and Tape K 2001a Increasing shrub abundance in the arctic Nature 411 546–7

Sturm M, McFadden J P, Liston G E, Chapin F S and Holmgren J 2001b Snow-shrub interactions in arctic tundra: a hypothesis with climatic implications J. Clim. 14 336–44

Sturm M, Schimel J, Michaelson G, Welker J M, Oberbauer S F, Liston G E, Fahnestock J and Romanovsky V E 2005 Winter biological processes could help convert arctic tundra to shrubland Bioscience 55 17–26

Tape K, Sturm M and Racine C 2006 The evidence for shrub expansion in Northern Alaska and the pan-arctic Glob. Change Biol. 12 686–702

Tape K D, Hallinger M, Welker J A and Racew R W 2012 Landscape heterogeneity of shrub expansion in Arctic, Alaska Ecosystems 15 711–24

Tremblay B, Levesque E and Boudreau S 2012 Recent expansion of erect shrubs in the low arctic: evidence from Eastern Nunavik Environ. Res. Lett. 7 035501

Van Wijk M T et al 2004 Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change Glob. Change Biol. 10 10–123

Weis I M and Hermanutz L A 1998 The population biology of the arctic dwarf birch, Betula glandulosa: seed rain and the germinable seed bank Can. J. Bot. 66 2055–61

Weis I M and Hermanutz L A 1993 Pollination dynamics of arctic dwarf birch (Betula glandulosa; Betulaceae) and its role in the loss of seed production Am. J. Bot. 80 1021–7

Wu Z T, Dijkstra P, Koch G W, Penuelas J and Hungate B A 2011 Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of ecosystem and plant type responses to global change glob. Change Biol. 17 927–42

Zamin T J and Gregor P 2012 Birch shrub growth in the low Arctic: the relative importance of experimental warming, enhanced nutrient availability, snow depth and caribou exclusion Environ. Res. Lett. 7 034007

Zhang Y, Wang S, Baff A G and Black T A 2008 Impact of snow cover on soil temperature and its simulation in a boreal aspen forest Cold Reg. Sci. Technol. 52 355–70

Zimov S A, Schuur E A G and Chapin F S III 2006 Climate change: permafrost and the global carbon budget Science 312 1612–3