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Environmental Research Letters

LETTER

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

Mélissa Paradis[1,2], **Esther Lévesque**[2,3] **and Stéphane Boudreau**[1,2,4]

[1] Département de biologie, Université Laval, 1045 av. de la Médecine, Québec, Qc, G1V 0A6, Canada
[2] Centre d'études nordiques, Université Laval, 2405 rue de la Terrasse, Québec, Qc, G1V 0A6, Canada
[3] Département des Sciences de l'environnement, Université du Québec à Trois-Rivières (UQTR), 3351 boul. des Forges, CP 500, Trois-Rivières, Qc, G9A 5H7, Canada
[4] Author to whom any correspondence should be addressed.

E-mail: stephane.boudreau@bio.ulaval.ca

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Supplementary material for this article is available online

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, McManus *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

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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 snowy 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 Kuujjuarapik 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 northwest) 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, Provencher-Nolet *et al* 2014).

2.3. Sampling design

A total of 22 stands dominated by *B. glandulosa* were selected for the study. Stands (>150 m^2) 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 measures 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 m^2 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 (cm^3) 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 (AICcmodavg package, Mazerolle 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 °C to −4.2 °C and from 11.2 °C to 13.3 °C, respectively. Annual freezing degree-days varied from 680 °C to 2125 °C while annual thawing degree-days varied from 1241 °C to 1563 °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 m^2).

			Shrub cover (%)					Ground cover (%)			*Betula glandulosa*	
Sites	Site size (m)	Number of shrub species	*Betula glandulosa*	*Salix* spp.	Empetrum spp.	*Rhododendron* spp.	*Vaccinium* spp.	Mosses	Lichens	Herbs	Mean height (cm)	Mean stem age (yr)
8	15 × 20	2	50–75				1–5	1–5	75–90	5–15	28 ± 14	12.8
9	7 × 20	3	75–90			5–15		75–90	0–1	25–50	121 ± 28	25.2
11	15 × 20	4	75–90	1–5			0–1	75–90	0–1	5–15	110 ± 19	26.0
12	15 × 20	4	50–75		5–15	5–15	1–5	5–15	75–90	1–5	21 ± 9	13.0
14	15 × 15	2	50–75				5–15	1–5	75–90	1–5	42 ± 17	15.2
16	15 × 20	4	75–90	15–25			1–5	75–90	15–25	5–15	81 ± 25	26.0
17	20 × 20	5	50–75		0–1	5–15	0–1	0–1	75–90	5–15	21 ± 12	15.8
18	15 × 20	3	50–75				1–5	15–25	75–90	1–5	43 ± 12	14.6
19	10 × 20	2	75–90				5–15	50–75	5–15	1–5	81 ± 16	19.2
20	10 × 20	3	75–90			0–1	1–5	5–15	75–90	5–15	73 ± 9	18.2
21	15 × 20	4	50–75		25–50	15–25	5–15	1–5	50–75	5–15	26 ± 6	13.4
22	20 × 20	5	75–90	5–15	1–5		1–5	15–25	50–75	5–15	43 ± 17	16.2
23	15 × 15	4	75–90	1–5		0–1	0–1	75–90	5–15	15–25	65 ± 12	26.8
24	15 × 15	5	75–90	15–25		1–5	0–1	75–90	1–5	5–15	79 ± 19	24.6
26	20 × 20	4	50–75	5–15			15–25	0–1	75–90	15–25	24 ± 7	13.0
27	15 × 20	3	50–75			0–1	5–15	1–5	75–90	5–15	26 ± 6	14.0
28	15 × 15	4	75–90	15–25		0–1	5–15	75–90	15–25	5–15	57 ± 14	16.0
29	15 × 15	4	75–90	5–15		0–1	5–15	25–50	50–75	1–5	41 ± 9	17.0
30	15 × 15	4	50–75	1–5		1–5	1–5	25–50	50–75	1–5	48 ± 9	19.0
31	15 × 20	2	50–75	1–5				25–50	50–75	5–15	68 ± 18	21.2
32	15 × 25	7	75–90	1–5	1–5	5–15	0–1	25–50	25–50	5–15	64 ± 14	31
33	20 × 20	2	50–75				0–1	0–1	75–90	1–5	24 ± 6	14.8

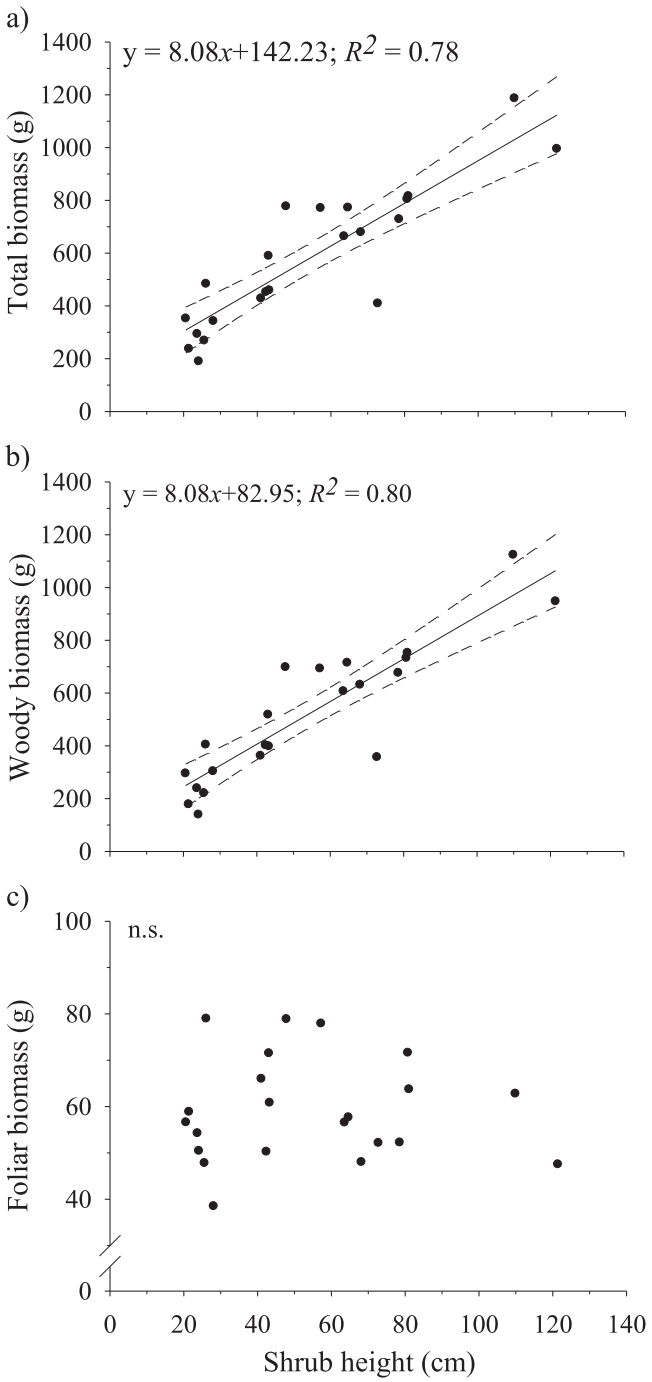

Figure 1. Shrub height influence on total (a), woody (b) and foliar (c) biomass. Each point represents the biomass mean of four 0.5 m^2 quadrats in 22 shrub stands near Umiujaq, Nunavik, harvested during summer 2013. n.s = Not significant.

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

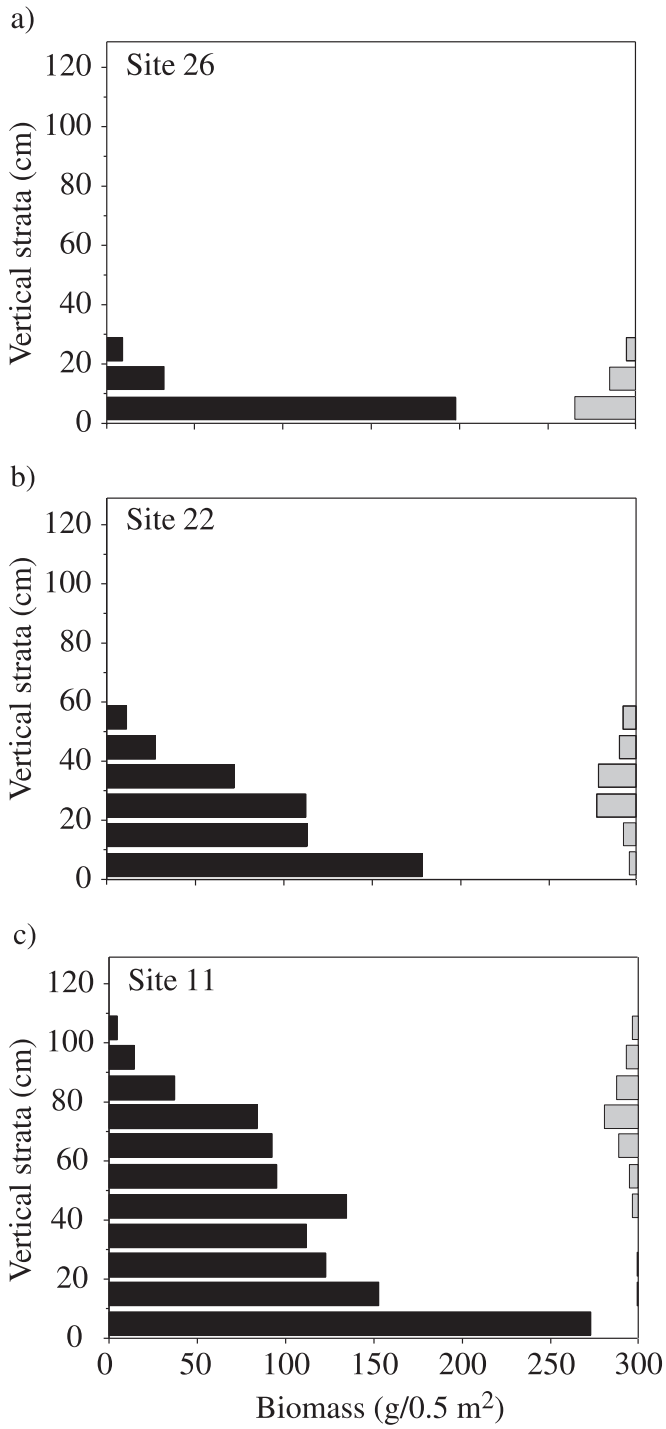

Figure 2. Dwarf birch biomass distribution along 13 vertical 10 cm strata for representative low (a), medium (b) and tall (c) shrub stands near Umiujaq, Nunavik. Black bars represent woody biomass and grey bars represent foliar biomass.

greater effect on the abiotic environment in winter than in summer (Lawrence and Swenson 2011, Lorranty *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

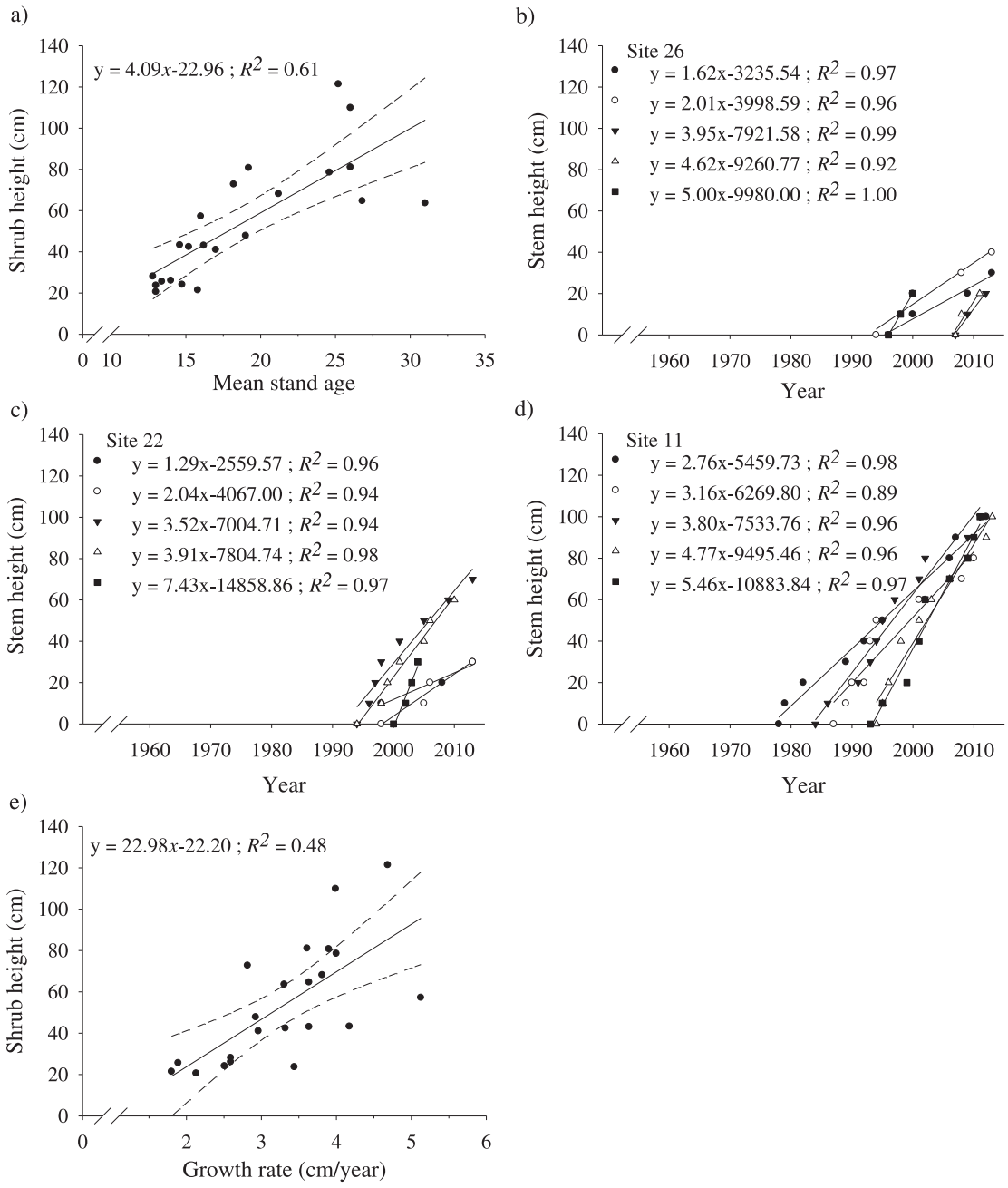

Figure 3. Age and vertical growth of *B. glandulosa* ($n = 5$ stems per stand) in each of the 22 shrub stands in Umiujaq, Nunavik. Panel (a) shows the relationship between shrub height and mean minimal age of the stands (calculated from the age of the stems at ground level), Panels (b)–(d) show vertical stem growth for low, medium and tall shrub stands, respectively and Panel (e) illustrates the relationship between mean growth rate and shrub stand height.

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

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).

	Winter temp. (December, January, February, March)		Summer temp. (July, August)		Snow cover depth		Freezing degree-days		Thawing degree-days	
Models	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

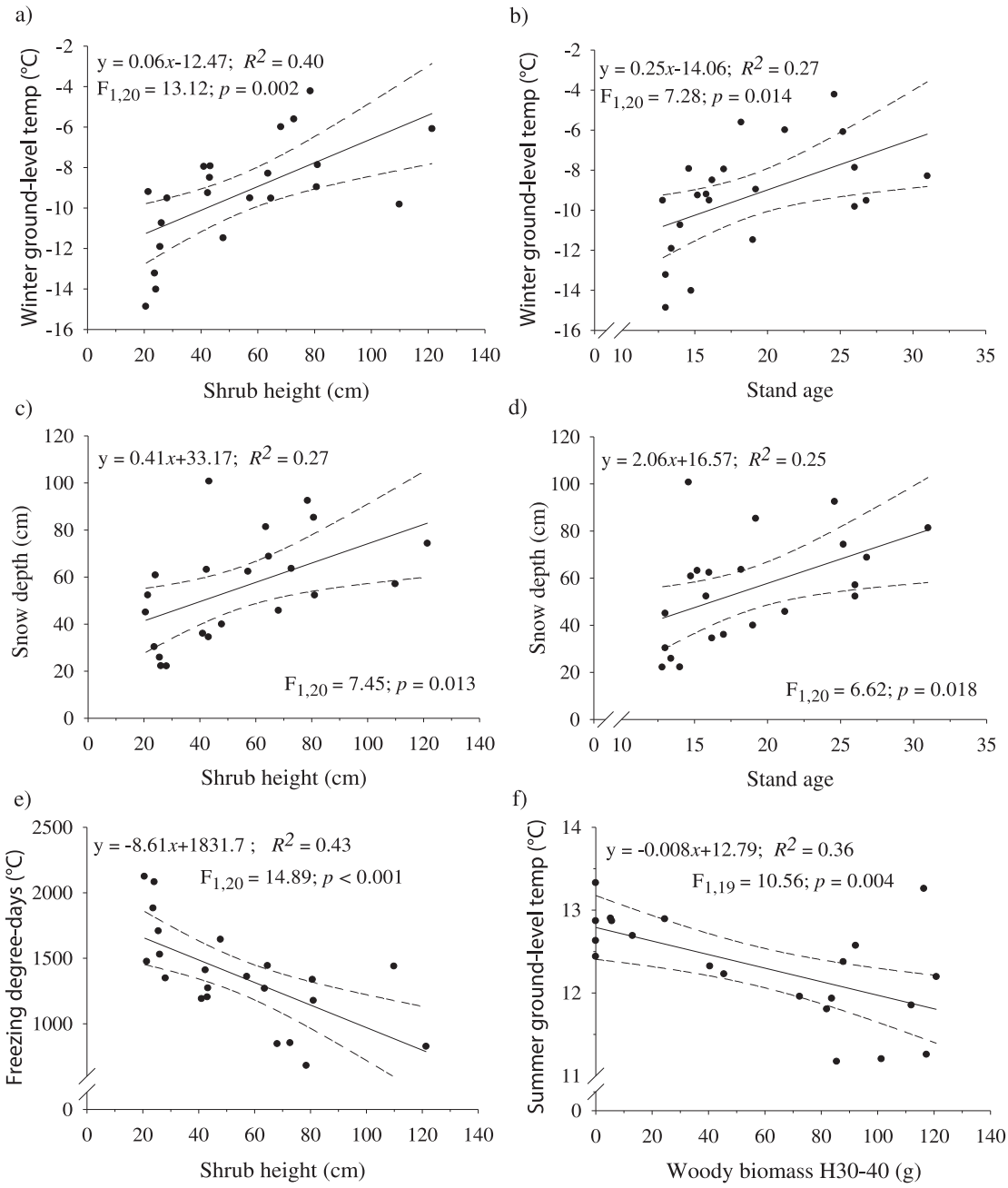

Figure 4. Relationships between abiotic environmental variables and their explanatory variables identified via the selection models analysis. Panels (a) and (b) show respectively the influence of stand height and age on winter ground-level temperature, Panels (c) and (d) show respectively the influence 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.

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

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 influenced by shrub cover during 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 *B. 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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