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Authors: Lemay, Evelyne, Côté, Steeve D., and Tremblay, Jean-Pierre

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How will snow retention and shading from Arctic shrub expansion affect caribou food resources?

Evelyne Lemay[a], Steeve D. Côté[a] and Jean-Pierre Tremblay[a,b]

[a]Département de Biologie, Centre d'études Nordiques and Caribou Ungava, Université Laval, Québec, QC, Canada; [b]Centre d'étude de la forêt, Université Laval, Québec, QC, Canada

ABSTRACT
Increased snow cover and attenuation of light due to shrub expansion can lead to changes in the quantity and nutritional quality of food resources for migratory caribou (*Rangifer tarandus*). To determine how vegetation is affected by snow accumulation and shade, we conducted an experiment that simulated the light and snow conditions created by increased shrub cover at Deception Bay (Nunavik, Canada), within the summer range of the Rivière-aux-Feuilles caribou herd. We estimated the foliar biomass of two major components of the caribou diet (*Betula glandulosa* and *Carex* spp.). We also harvested foliar tissue to conduct chemical composition analyses (nitrogen, fibre, total phenolics). Experimental light attenuation was found to increase the nitrogen concentrations in *B. glandulosa* and *Carex* spp. throughout the growing season. Phenolic concentration in *B. glandulosa* decreased in early summer but was otherwise consistent in response to light attenuation and increased snow cover. Increased snow cover combined with ambient light had a positive effect on the foliar biomass of *B. glandulosa*. Increased snow cover and shade caused by shrub densification may therefore increase forage quantity and quality for caribou. We suggest investigating the effects of shrub expansion on other components of the caribou diet, such as lichens and forbs.

RÉSUMÉ
La rétention de la neige au sol ainsi que l'atténuation de lumière causées par la densification du couvert arbustif peuvent entraîner des changements dans la quantité et la qualité des ressources alimentaires du caribou migrateur (*Rangifer tarandus*). Afin de déterminer comment l'augmentation du couvert de neige et l'atténuation de la lumière affectent l'abondance et la qualité de la végétation, nous avons installé un dispositif expérimental simulant les conditions induites par la densification des arbustes dans la région de Baie Déception, Nunavik, qui se situe à l'intérieur de l'aire d'estivage du troupeau de caribous Rivière-aux-Feuilles. Nous avons estimé la biomasse foliaire de deux composantes majeures du régime alimentaire du caribou migrateur (*Betula glandulosa* et *Carex* spp.) en utilisant la méthode du point d'interception et nous avons récolté des échantillons de leurs tissus foliaires afin de réaliser des analyses de leur composition chimique (azote, fibres et phénols totaux). Le traitement d'ombrage a augmenté significativement la concentration d'azote dans les feuilles de *Carex* spp. et de *B. glandulosa* tout au long de la saison de croissance. Le traitement d'ombrage et celui d'augmentation du couvert de neige ont diminué la concentration en phénols totaux de *B. glandulosa* en début de saison seulement. La combinaison d'un couvert de neige plus profond et de la pleine lumière a augmenté la quantité de biomasse foliaire produite par *B. glandulosa*. L'augmentation du couvert de neige et l'atténuation de lumière causées par la densification du couvert arbustif pourraient donc augmenter la qualité et la quantité de ressources alimentaires pour le caribou. Toutefois, puisque la densification des arbustes risque d'avoir des impacts nutritionnels sur d'autres groupes d'espèces végétales, nous suggérons d'élargir la recherche à d'autres composantes du régime alimentaire du caribou migrateur, telles que les lichens et les herbacées.

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Introduction

Over the past several decades, arctic regions have been transformed by climate change. Warmer air temperatures have led to higher plant productivity in tundra ecosystems, mainly reflected by the densification of shrub layers (Hallinger et al. 2010; Fraser et al. 2014; Weijers et al. 2018). This phenomenon, known as shrubification, can impact the ecosystem in several ways. Shrubs can influence various abiotic factors, including the light intensity that the vegetation underneath the shrub cover receives, as well as the accumulation and

CONTACT Jean-Pierre Tremblay e.lemay12@hotmail.com Département de Biologie, Centre d'études Nordiques and Caribou Ungava, Université Laval, Québec, QC, Canada; Centre d'étude de la forêt, Université Laval, Québec, QC, Canada

distribution of snow cover (Sturm et al. 2001; McKinney and Goodell 2010; Myers-Smith et al. 2011). Indirectly, shrubification can affect soil moisture, soil temperature, and the freeze-thaw cycles of the top-soil layer (Pomeroy et al. 2006; Blok et al. 2010; Marsh et al. 2010). Although the biophysical effects of the growing presence of shrubs in herbaceous tundra are relatively well known (Lawrence and Swenson 2011; Myers-Smith and Hik 2013; Domine et al. 2016), there is little information on the nutritional impact that these changes have on herbivores.

The body condition and reproductive success of herbivores are known to be largely influenced by the quantity and quality of their forage (Sinclair et al. 1982; Parker et al. 2005; Herfindal et al. 2006). Forage quality is often determined based on nitrogen content because nitrogen is one of the most essential nutrients for herbivores (Albon and Langvatn 1992; Cook et al. 1996; Barboza et al. 2018). Nitrogen is required for many vital functions, such as growth, reproduction and lactation (White 1993; Parker et al. 2005). Some forage constituents, such as phenolics and fibre, however, can limit the amount of nitrogen that is available to herbivores due to properties that decrease forage digestibility (Allen 1996; Palo and Robbins 1991; McSweeney et al. 2001). Therefore, high nutritional forage quality is associated with high levels of nitrogen and low levels of phenolics and fibres (Allen 1996; Bryant et al. 1983; Hjältén J and Palo T 1992; Danell et al. 1994). In addition to the nutritional quality of forage, plant biomass is another key driver of herbivore success, as it partly regulates the foraging behaviour of herbivores and therefore their body condition (Canon et al. 1987; Langvatn et al. 1996).

Changes in vegetation related to shrubification are likely to alter the food supply and foraging behaviour of arctic herbivores, such as the migratory caribou (*Rangifer tarandus*; Turunen et al. 2009). The denser vertical structure of vegetation retains more snow, which increases snow cover depth (Sturm et al. 2001, 2005), the temperature of the soil active layer (Sturm et al. 2005; Paradis et al. 2016), and consequently, soil microbial activity (Nobrega and Grogan 2007; Buckeridge and Grogan 2008). Increased microbial activity due to snow isolation results in greater nitrogen immobilization in the fall (Brooks et al. 2011) and greater nitrogen flow in the spring (Weintraub and Schimel 2003, 2005; Schimel et al. 2004), thus increasing the nitrogen concentration in plant leaves (Torp et al. 2010b; Semenchuk et al. 2015). The concentration of phenolics in forage also increases with deeper snow cover through the insulating effect of snow and the related fertilisation effects (Torp et al. 2010a), resulting in a detrimental and antinutritional effect for herbivores. However, the response of these plants can also be influenced by other factors, such as plant phenology and habitat type (Torp et al. 2010a). Finally, deeper snow cover can increase foliar biomass in several plant species (Addis and Bret-Harte 2019).

In addition to altering snow distribution, shrubs intercept solar radiation and reduce the light received by the vegetation underneath during the growing season, thus affecting soil parameters and plant metabolism. Since UV-B radiation is known to enhance the production of total phenolics (Turunen et al. 2009), light attenuation, and therefore UV-B attenuation, should decrease total phenolic concentrations in plants. Indeed, shading generally decreases phenolic content and increases nitrogen concentrations (Graglia et al. 2001), especially in woody plants (Hansen et al. 2006), thus increasing forage quality for herbivores. Plants under a natural or artificial canopy also appear to produce less fibre than plants under full sunlight (Belsky 1992; Kephart and Buxton 1993). On the other hand, shrub cover is associated with decreased soil temperatures (Myers-Smith and Hik 2013), which can increase water viscosity and decrease root conductivity (Murai-Hatano et al. 2008). This can in turn lead to a slower flow of nutrients through plant roots and a negative impact on the nutritional quality of plant leaves. In contrast to the positive effect of snow on plant biomass, the light attenuation created by shrubs can decrease the amount of biomass produced by understory plants (Lenart et al. 2002; Pajunen et al. 2011).

The nutritional quality and quantity of vegetation are also known to be associated with vegetation phenology (Johnson et al. 2018). For instance, plant nitrogen levels are at their highest early in the growing season and decrease as the season progresses (Doiron et al. 2014; Semenchuk et al. 2015; Barboza et al. 2018). A different pattern occurs with foliar biomass, which increases rapidly early in the season and remains relatively stable until the beginning of senescence (Manseau and Gauthier 1993; Doiron et al. 2014). Given the potential interactive effects of shading, increased snow depth, and plant phenology over time, it is difficult to predict vegetation response to shrubification and the subsequent consequences for caribou.

Previous work has hypothesized that declines in forage availability and quality are partly responsible for declines in several caribou populations in Arctic North America (Crête and Huot 1993). Indeed, during the plant growing season, caribou select high-quality food sources that are rich in nitrogen and low in secondary compounds and fibre (Bryant et al. 1983; White 1983; Klein 1990), including dwarf shrubs (*Salix* spp., *Betula glandulosa, Vaccinium* spp.), graminoids, and forbs (Crête et al. 1990). Moreover, because the dry matter intake of caribou at the peak of summer is more than double the amount consumed in winter (White 1983; Boertje 1990), caribou also depend on the quantity of food that is available in summer.

We conducted an experiment to test the effect of increased snow depth and light attenuation on food resources for caribou throughout the summer. We focused on the summer resources that are most consumed by migratory caribou, such as shrubs and graminoids, which account for nearly half of their diet (Bergerud et al. 2007). Due to their widespread availability at the study site, we chose to use dwarf birch (*Betula glandulosa*) to represent shrubs and sedges (*Carex* spp.) to represent graminoids. The species that contributes the most to the shrubification of subarctic regions is *B. glandulosa* (Ropars and Boudreau 2012). Its quality can be influenced by the effects of its own snow retention, and to a lesser extent, by shading imposed by taller individuals, which blocks low-angle sunlight at high latitudes. For plants under the shrub canopy, we hypothesized that light attenuation would increase nutritional quality and decrease forage biomass, while increased snow depth would increase nutritional quality and forage biomass.

Material and methods

Study area

Deception Bay (62°08′41″ N, 74°41′52″ W) in Nunavik, Québec, Canada, is within the summer range of the Rivière-aux-Feuilles migratory caribou herd (Taillon et al. 2012). The region is characterized by an arctic herbaceous tundra with dwarf shrubs (Ministère des Forêts, de la Faune et des Parcs 2018) and dominated by Poaceae (mainly *Poa arctica, Calamagrostis lapponica* and *Anthoxanthum monticola* subsp. *alpinum*), Cyperaceae (*Carex bigelowii, Carex vaginata, Carex rupestris* and *Eriophorum angustifolium* subsp. *angustifolium*), erect shrubs (mainly *Betula glandulosa* and *Salix* spp.), evergreen shrubs (mainly *Vaccinium vitis-idaea* and *Empetrum nigrum*) and bryophytes (Walker et al. 2005). The mean summer temperature (June to August 2015–2018) was 5.3°C and precipitation ranged from 130 to 175 mm. Measurements were recorded in Salluit, the closest village (ca. 40 km) near Deception Bay (Environment and Climate Change Canada 2019). This area is underlaid by continuous permafrost (Ministère des Forêts, de la Faune et des Parcs du Québec 2017). The soil in this region is acidic (pH < 5.5) and has a thin or absent organic layer (Walker et al. 2005). The shrubification of the study site was not at an advanced stage, likely due to significant caribou browsing and harsh abiotic conditions (Plante et al. 2014). Shrub stratification is therefore not yet developed.

Experimental design

We implemented an experimental design that simulated the light and snow conditions induced by increased shrub cover (Figure 1). To account for the inherent spatial variability, we used a split-plot design composed of nine blocks that were placed along an 8-km transect. Each block was in a location that was free from topographic structures that may influence the wind or snow

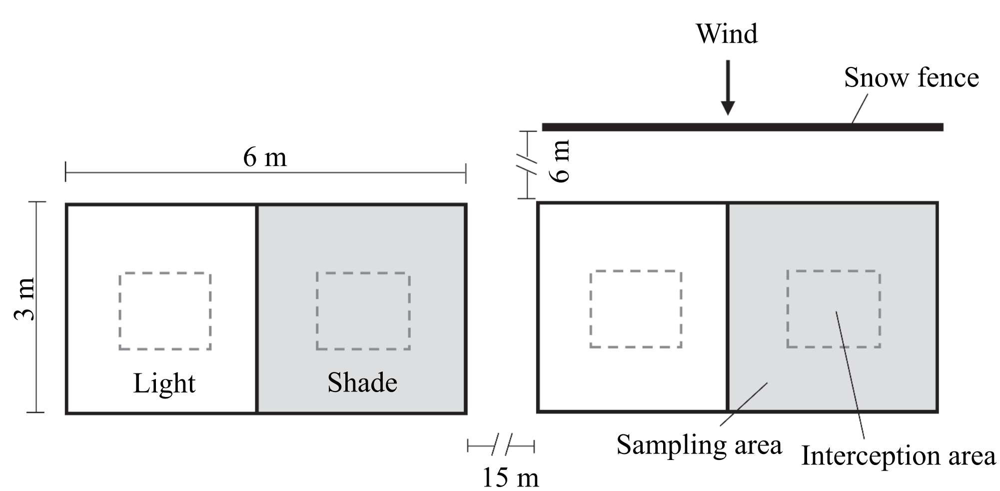

Figure 1. Representation of one of the nine blocks in the experiment testing the effect of light attenuation and increased snow cover on the quantity and quality of caribou summer forage. The plot on the right is under increased snow cover (50–75 cm) created by a 1-m high snow fence while the plot on the left is under ambient snow cover (5–20 cm). The dark grey subplot is exposed to 60% shaded light while the white subplot is exposed to ambient light. We estimated biomass in the interception area and sampled vegetation for chemical analyses in the sampling area.

distribution. These locations were covered in homogenous vegetation that consisted mainly of shrubs and graminoids, both of which are consumed by migratory caribou in summer (Bergerud et al. 2007). Each block was composed of paired main plots, in which one of two snow depth treatments was applied: unfenced, representing the ambient unmanipulated snow cover of the study area (snow depth = 5–20 cm) or fenced, in which the snow cover is experimentally increased using snow fences (snow depth = 50–75 cm). Snow fences (9 m long and 1 m high) were installed perpendicular to the prevailing south-easterly winter winds, at 6 m from the plot, to allow snow to accumulate evenly throughout the length of the plot (Cooper et al. 2011). The snow fences reduce wind speed, which allows for wind-transported snow to be deposited on the lee side of the fence and for snow to accumulate in the fenced main plot (Semenchuk et al. 2015). Each main plot (unfenced and fenced) was then divided to form two adjacent subplots to which we assigned one of the two levels of light intensity: light (ambient light) or shade. We applied the shade treatment by installing shading tarps (SunBlocker®, Farmtek, Connecticut, United States) at the end of May and removing them at the end of August. The shading tarp reduced sunlight by 60%, which is similar to the reduction in global radiation found under a shrub canopy (Jonasson et al. 1999). The shading setup was designed using the Sketch Up 3D software package (version Pro 7.1, Trimble, California, United States) to optimize shading within the plot, despite the different orientations of the sun over the course of the day and during the summer, at the latitude of the study area. To verify the uniform effect of the snow fences in each plot, we estimated snow depth using snow rulers and camera traps during the winter before the start of the experiment. The experimental setup was installed in 2015, but we collected data in the summer 2018. Most of the experimental setup was left in place all year except for the shading tarps, which were removed at the end of each year and reinstalled the following year to prevent damage caused by snow.

Forage quality and NIRS calibration

We collected leaf samples in the sampling area (approx. 8 m^2) of each subplot (n = 36; Figure 1). Samples were collected over four different time periods (16–18 July, 4–6 August 2011–13 August and 19–22 August 2018) for *B. glandulosa* and over three periods (16–18 July, 4–6 August and 19–22 August 2018) for *Carex* spp., for a total of 144 *B. glandulosa* samples and 108 *Carex* spp. samples. The late snow melt in 2018 delayed the bud burst and the beginning of the growing season, explaining the first sampling date in July. There was not enough foliage available to support a fourth sampling period for *Carex* spp. For *B. glandulosa*, we harvested leaves from different plants by moving around within the sampling area, stripping a few branches at a time to imitate a caribou bite. For *Carex* spp., we harvested a few leaves from different plants in a similar way by moving within the sampling area and carefully pulling at the base of the leaves without uprooting the plants. For both species, we took special care not to collect samples that might have been naturally shaded by other plants to avoid any confounding effects. Each sample weighed approximately 20 g and was placed in a labelled paper bag. Samples were air-dried using a fan for 48 hours following the day of harvest. The samples were re-dried in the laboratory at 50°C for 48 hours and milled to 0.5 mm (Ultra Centrifugal Mill ZM200 ©Retsch, Haan, Germany) after the field campaign. To estimate forage quality, we used a combined approach of laboratory analyses and near-infrared reflectance spectrophotometry (NIRS) (Champagne et al. 2018). NIRS is a spectroscopic method based on the absorption of near-infrared rays by organic matter and is widely used in agriculture to optimize forage analyses (Corson et al. 1999; Decruyenaere et al. 2009). All samples were first scanned with a NIRS DS2500 near-infrared spectrophotometer (FOSS Analytics, Hillerød, Danemark) at intervals of 0.5 nm to acquire a near-infrared spectrum of 780 to 2498 nm that is unique to each sample. To select the samples to be analyzed in the laboratory, we used WinISI calibration software (version 4.8.0, FOSS Analytics, Hillerød, Danemark). The *select* function in this software identifies redundant and deviant samples of NIR spectra based on Principal Component Analysis (PCA) scores (Næs and Martens 1988). These identified spectra were set aside and a random subset across the remaining spectra was selected for laboratory analyses. Deviant spectra were then added to this subset to be analyzed in the laboratory since their values cannot be predicted by WinISI software. We then performed laboratory analyses to determine nitrogen content (N), acid detergent fibre (ADF: cellulose and lignin) and total phenolic content. We estimated the nitrogen content ($n_{B.\ glandulosa}$ = 80, $n_{Carex\ spp.}$= 51) with a Trumac CNS determinator (Leco, St-Joseph, Michigan, United States) and the leaf fibre content using acid-detergent fibre analyses ($n_{B.\ glandulosa}$ = 80, $n_{Carex\ spp.}$ = 108; ANKOM Fiber Analyser 200, ANKOM Technology). For *B. glandulosa*, we estimated the total phenolic content (n = 80) using the Folin-Ciocalteu method (Singleton and Rossi 1965), following the protocol described in Dudonné et al. (2015). The obtained chemical values of each sample were paired to their respective spectrum through the

WinISI software package in order to establish empirical calibrations for plant constituents (N, ADF and phenolics) of each forage type (*B. glandulosa* and *Carex* spp.). These calibrations were developed using modified partial least-squares regressions with cross-validation (Shenk and Westerhaus 1991) in WinISI. Using this method, the chemical content of samples that had not been analyzed in the laboratory could be predicted directly from their respective spectra. We selected the model with the lowest standard error when cross-validated with candidate models produced with a variety of mathematical treatments applied to the spectra, including degree of derivatization, smoothing, and scatter correction (DeGabriel et al. 2008). All calibrations were validated using an independent set of 20 *B. glandulosa* samples and 12 *Carex* spp samples. This combined approach allowed us to minimize the cost of laboratory analyses and the amount of plant matter required while providing reliable estimates of forage quality variables.

Forage biomass

We estimated the biomass of *B. glandulosa* leaves and vegetation under the canopy (*Carex* spp.) in each subplot over five time periods (4–7 July 2016–18 July, 4–6 August 2011–13 August and 19–22 August 2018). We used the point intercept method with 25 systematic points within a 75 × 75 cm frame (Jonasson 1988; Brathen and Hagberg 2004). To ensure that the number of intercepted hits represents an unbiased estimate of biomass, we applied the point intercept method in 0.56-m^2 plots outside the experimental setup. We then harvested all the *B. glandulosa* and *Carex* spp. leaves within those plots. Samples were air-dried with a fan for 48 hours following the day of harvest. The samples were then re-dried in the laboratory at 50°C for 48 hours and weighed. To establish an equation to estimate the leaf biomass in experimental point-intercept plots, we correlated the sample weights with the number of intercepts for both species (*B. glandulosa* leaves: $y = 1.19x + 1.38$, $R^2 = 0.76$, n = 55 plots; *Carex* spp.: $y = 1.74x + 6.32$, $R^2 = 0.49$, n = 30 plots, where y = leaf biomass and x = number of intercepts).

Statistical analyses

We examined the effects of the snow and shade treatments throughout the growing season on nitrogen content, total phenolic content (*B. glandulosa* only), ADF content, and leaf biomass for *B. glandulosa* and *Carex* spp. We used a linear mixed model (package nlme, Pinheiro et al. 2016) with snow treatment, shade treatment, and sampling period as fixed effects, and with the random intercepts being a subplot nested in the main plot of each block (Figure 1). We also modelled the heterogeneous structure of variance across sampling periods to visually check for autocorrelation between repeated measures (package stats, R Core Team 2019). No temporal autocorrelation was found in the model residuals and all statistical assumptions were fulfilled. We analyzed the pairwise differences of significant effects ($\alpha < 0.05$) using protected least square means (package lsmeans, Lenth 2016). All statistical analyses were performed in R version 3.5.3 (R Core Team 2019).

Results

Nitrogen concentration in *B. glandulosa* was influenced by the interaction between sampling period and light intensity (Table 1; $F_{3,96} = 9.9$, $p < 0.01$). Early in the growing season (17 July), the nitrogen concentration was higher in leaves growing in the shade than in leaves under ambient light conditions (Figure 2a). The differences in leaf nitrogen concentrations between shade and ambient light conditions decreased progressively over time but remained significant until the end of the growing season (Figure 2a). Nitrogen concentration in *Carex* spp. was also influenced by the interaction between sampling period and light intensity (Table 1; $F_{2,64} = 12.4$, $p < 0.01$). The difference in nitrogen content between shaded plots and ambient light was not significant early in the growing season, but the difference increased progressively over time and became significant by mid-season (Figure 2b). Nitrogen concentration was not influenced by snow depth for either *B. glandulosa* ($F_{1,8} = 0.7$, $p = 0.42$; Table 1) or *Carex* spp. ($F_{1,8} = 2.6$, $p = 0.14$; Table 1).

Total phenolic concentration in *B. glandulosa* was also influenced by the interaction between the sampling period and light intensity ($F_{3,96} = 10.1$, $p < 0.01$; Table 1). Phenolic concentrations in shaded leaves were lower than for leaves in ambient light early in the growing season (17 July), but the difference was not significant after this period (Figure 3a). In addition, total phenolic concentration was influenced by the interaction between the sampling period and snow depth ($F_{3,96} = 5.1$, $p < 0.01$; Table 1); deeper snow decreased the phenolic concentration in *B. glandulosa* leaves early in the season (17 July) compared to ambient snow depth, but the effect of snow depth on phenolic concentration dissipated over the growing season (Figure 3b).

ADF concentration in *B. glandulosa* was not influenced by light intensity ($F_{1,16} = 0.06$, $p = 0.81$; Table 1) or snow depth ($F_{1,8} = 0.36$, $p = 0.57$; Table 1), but ADF concentrations decreased over the growing season

Table 1. Summary of the ANOVA used to test the effects of light attenuation and snow accumulation on chemical components of *B. glandulosa* and *Carex* spp. in the summer 2018 at Deception Bay, Nunavik (Québec, Canada). ANOVAs include subplots (light treatment) nested in main plots (snow treatment) nested in blocks as a random intercept. The degrees of freedom (df) of the numerator (num) and denominator (den) and the effect of snow treatment (S), light treatment (L), and sampling period (P) on each chemical component are shown. Degrees of freedom for foliar biomass are in parentheses, as there were five sampling periods for this variable.

			Source of variation						
Species	Response variable		Snow (S)	Light (L)	Sampling period (P)	S × L	S × P	L × P	S × L × P
Betula glandulosa	df	num–den	1–8	1–16	3–96	1–16	3–96	3–96	3–96
			(1–8)	(1–16)	(4–128)	(1–16)	(4–128)	(4–128)	(4–128)
	Nitrogen	F ratio	0.72	51.87	162.55	1.94	1.35	9.90	1.13
		P value	0.42	<0.01	<0.01	0.18	0.26	<0.01	0.34
	Total phenolics	F ratio	1.34	11.15	34.07	0.29	5.14	10.06	0.40
		P value	0.28	<0.01	<0.01	0.60	<0.01	<0.01	0.76
	ADF	F ratio	0.36	0.06	44.41	0.14	0.63	0.56	1.15
		P value	0.57	0.81	<0.01	0.72	0.60	0.64	0.33
	Foliar biomass	F ratio	3.14	0.50	33.23	4.55	1.99	0.79	0.91
		P value	0.11	0.49	<0.01	0.04	0.10	0.54	0.46
Carex spp.	df	num–den	1–8	1–16	2–64	1–16	2–64	2–64	2–64
			(1–8)	(1–16)	(4–128)	(1–16)	(4–128)	(4–128)	(4–128)
	Nitrogen	F ratio	2.63	162.40	158.08	0.45	0.34	12.36	0.225
		P value	0.14	<0.01	<0.01	0.51	0.71	<0.01	0.80
	ADF	F ratio	0.01	15.56	7.69	8.44	1.43	1.06	1.32
		P value	0.92	<0.01	<0.01	0.01	0.25	0.35	0.27
	Foliar biomass	F ratio	3.65	0.17	25.83	1.91	1.40	0.36	0.53
		P value	0.09	0.69	<0.01	0.18	0.24	0.83	0.71

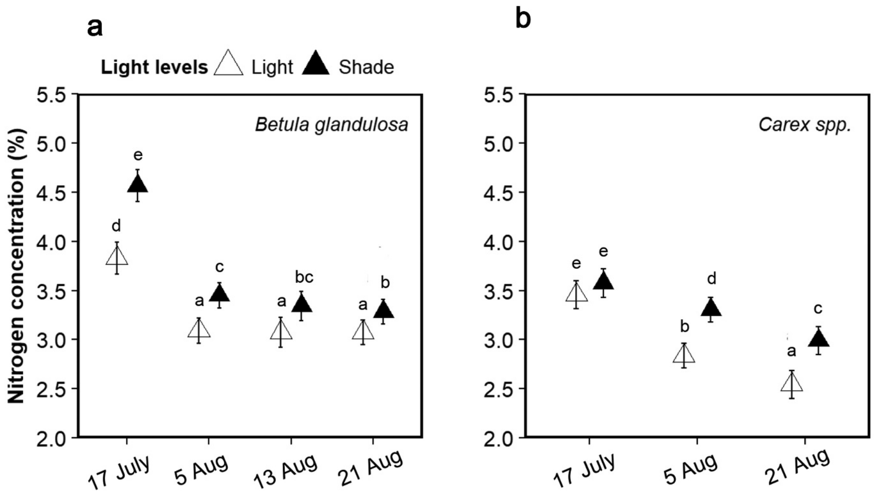

Figure 2. Leaf nitrogen concentration (%) and 95% confidence intervals throughout summer 2018 for (a) *Betula glandulosa* and (b) *Carex* spp. for shaded (n = 18) and ambient light (n = 18) plots in the arctic tundra at Deception Bay, Nunavik, Canada. The analysis was performed using a linear mixed model with blocks (n = 9) and all interactions involving blocks as random factors. Predictions that share a common letter are not significantly different (Protected lsmeans, α = 0.05).

($F_{3,96}$ = 44.4, p < 0.01; Table 1). Fibre concentration was at its highest at the first sampling period, then rapidly dropped, and finally remained relatively stable afterwards (Figure 4a). The concentration of ADF in *Carex* spp. showed a slight but statistically significant variability over time (Figure 4b) and across treatment combinations (Figure 5).

The foliar biomass of *B. glandulosa* was influenced by the interaction between snow depth and light intensity ($F_{1,16}$ = 4.55, p = 0.04, Table 1); in ambient light, *B. glandulosa* produced more biomass under deep snow cover than under ambient snow cover (Figure 6). As expected, foliar biomass increased throughout the growing season both for *B. glandulosa* ($F_{1,16}$ = 33.23, p < 0.01, Table 1) and *Carex* spp. ($F_{1,16}$ = 25.83, p < 0.01, Table 1). Otherwise, we found no statistical differences between experimental treatments for *Carex* spp. (Table 1).

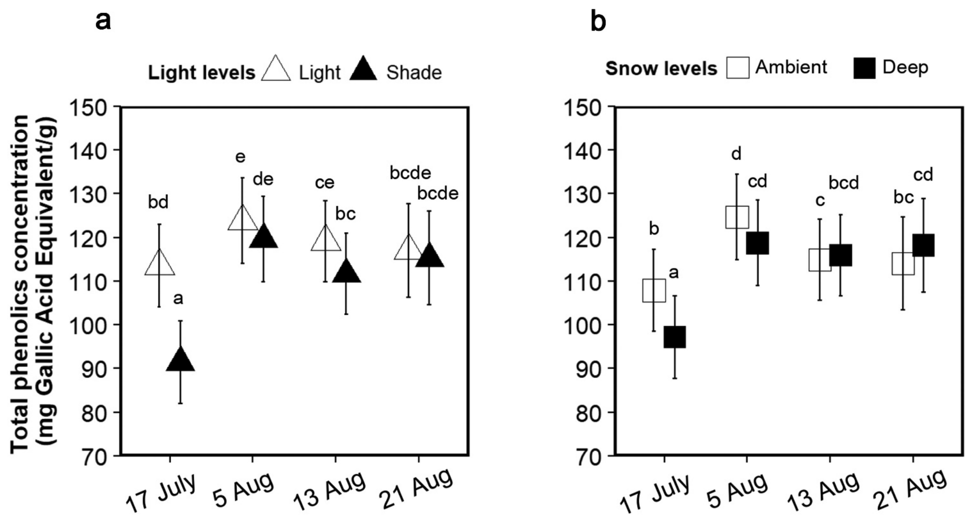

Figure 3. Total phenolic concentration (mg Gallic Acid Equivalent/g) and 95% confidence intervals throughout summer 2018 for *Betula glandulosa* for (a) shaded (n = 18) and ambient light (n = 18) plots and for (b) deep snow (n = 18) and ambient snow depth plots (n = 18) in the arctic tundra at Deception Bay, Nunavik, Canada. The analysis was performed using a linear mixed model with blocks (n = 9) and all interactions involving blocks as random factors. Predictions that share a common letter are not significantly different (Protected lsmeans, α = 0.05).

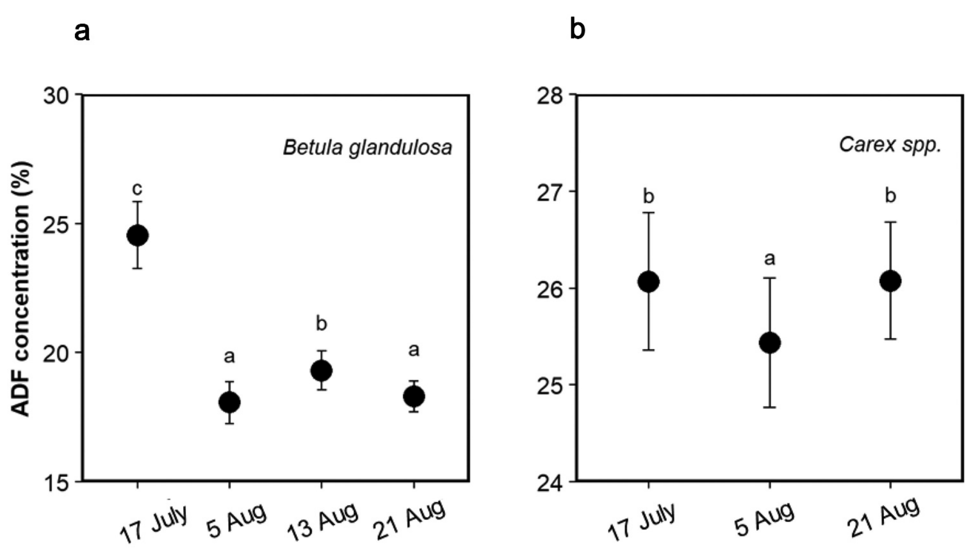

Figure 4. Acid detergent fibre (ADF) concentration (%) and 95% confidence intervals throughout summer 2018 for (a) *Betula glandulosa* and (b) *Carex* spp. for all experimental plots (n = 36) in the arctic tundra at Deception Bay, Nunavik, Canada. The analysis was performed using a linear mixed model with blocks (n = 9) and all interactions involving blocks as random factors. Predictions that share a common letter are not significantly different (Protected lsmeans, α = 0.05).

Discussion

We experimentally tested the effects of increased snow depth and light attenuation, two of the most significant impacts of shrub densification in arctic environments, on forage quality and quantity for caribou during the summer. We observed the greatest differences in nutrient quality early in the season, which coincides with the period of highest nutritional requirements for caribou (Taillon et al. 2013). Our results therefore suggest that the light attenuation created by shrub expansion might provide higher quality forage.

Leaves in shaded conditions have higher nitrogen concentrations than leaves under ambient light conditions, both for *Carex* spp. and *B. glandulosa*, which is consistent with other studies (Graglia et al. 2001; Hansen et al. 2006). Our results indicate that *Carex* spp. under shrub cover would be of higher nutritional quality than those exposed to ambient light. These results can be explained by a nitrogen dilution effect, where plants

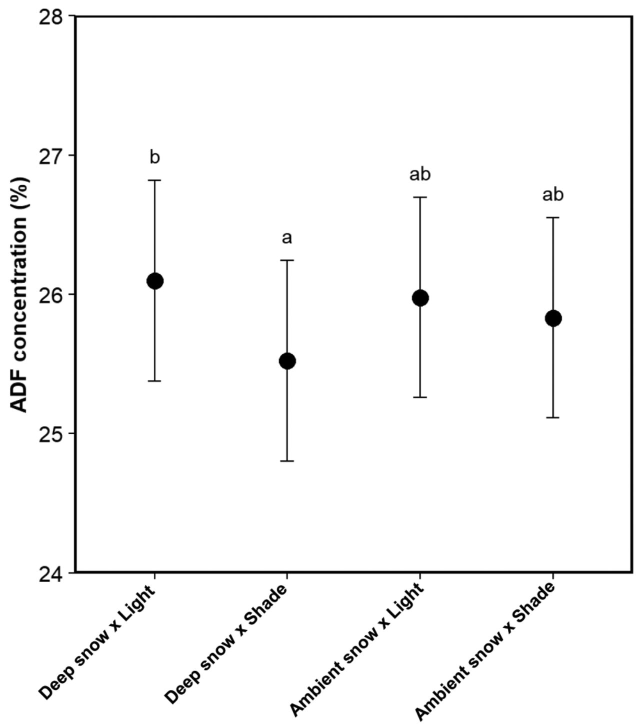

Figure 5. Acid detergent fibre (ADF) concentration (%) and 95% confidence intervals for *Carex* spp. for each experimental plot (n = 36) in the arctic tundra at Deception Bay, Nunavik, Canada. The analysis was performed using a linear mixed model with blocks (n = 9) and all interactions involving blocks as random factors. Predictions that share a common letter are not significantly different (Protected lsmeans, α = 0.05).

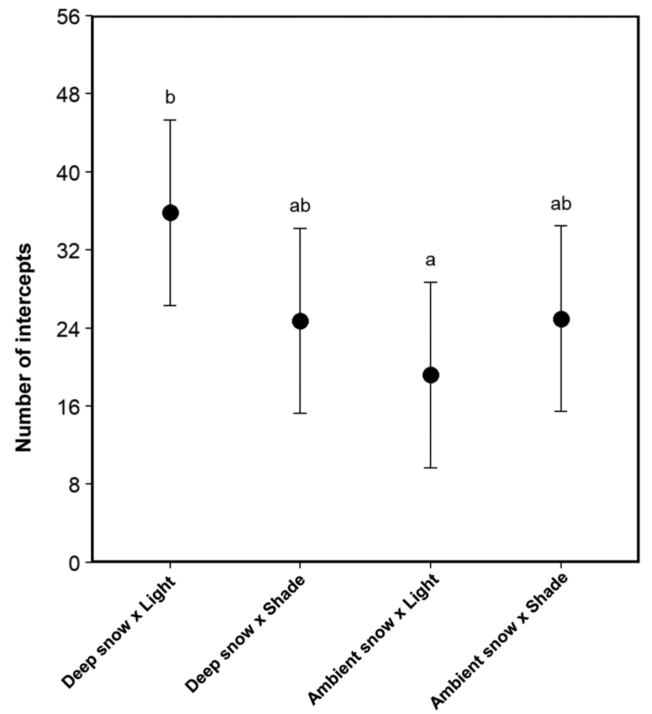

Figure 6. Number of leaf intercepts (proxy of foliar biomass) and 95% confidence intervals for *B. glandulosa* for each experimental subplot (n = 36) in the arctic tundra at Deception Bay, Nunavik, Canada. The analysis was performed using a linear mixed model with blocks (n = 9) and all interactions involving blocks as random factors. Predictions that share a common letter are not significantly different (Protected lsmeans, α = 0.05).

exposed to full sunlight could produce more nitrogen-free photoprotective compounds such as carotenoids (Demmig-Adams and Adams 1992) and anthocyanins (Hatier and Gould 2008). An alternative explanation is that the shading treatment might have reduced soil evapotranspiration. This may have allowed plants to benefit from a greater flow of water and nutrients such as nitrogen, ultimately increasing nitrogen concentrations in the leaves (Walters and Reich 1997). In contrast to results from other studies (Van der Wal et al. 2000; Walsh et al. 1997; Welker et al. 2005), increased snow depth did not alter the nitrogen content in the leaves of plants in our experiment.

The physical condition and reproductive capacity of caribou have been shown to be closely linked to the nitrogen content in their diet (McEwan and Whitehead 1970; Parker et al. 2005; Barboza and Parker 2006). For *B. glandulosa*, the differences in nitrogen content in response to variations in light levels decreased throughout the season, while they increased for *Carex* spp. This could be because *Carex* spp. have the ability to draw resources from their rhizomes, a concentrated source of nitrogen, under stressful conditions (Brooker et al. 1999). For *B. glandulosa*, the difference between the quality of shaded leaves and leaves under ambient light was at its greatest in early July. This timing coincides with the period of peak lactation for caribou (Taillon et al. 2013), an energetically costly period for females (Boertje 1990), and is also when caribou most often select *B. glandulosa* over other forage species (Crête et al. 1990). These behaviours emphasize the positive effect that higher forage quality (induced by shade) can have in the early summer. Finally, we did not observe snow depth to have any effect on nitrogen concentrations in leaves, which contrasts with the hypothesis from Sturm et al. (2005) related to the potential fertilization effect of deeper snow cover. However, in our study, the effect of snow depth may not have been significant due to the short duration of our experiment in the low-productivity environment that is characteristic of the arctic tundra. In this context, snow-induced changes in soil and therefore in foliar content might take a few more years to occur.

Our results showed that *B. glandulosa* leaves in shade or in deep snow cover contained lower phenolic concentrations than leaves in ambient light or ambient snow cover in early season, which corresponds to the peak of caribou foraging (Crête et al. 1990; Bergerud et al. 2007). The lower phenolic concentrations could be induced by the delayed growth of shaded or snow-covered plants, resulting in a delay in the production of secondary metabolites such as phenolics. At the beginning of the season, plants invest more resources in growth than in defence and production of secondary metabolites (Feeny 1970; Mattson 1980; Bryant et al. 1983). There is evidence that caribou may select *B. glandulosa* early in the growing season (Bergerud 1972; Crête et al. 1990; Bergerud et al. 2007) because of the low phenolic content. Moreover, it has been previously shown that caribou optimize their foraging behaviour by selecting plants with a high ratio of nutrients to secondary metabolites (Kuropat and Bryant 1980). Lower phenolic production in shrubs could increase the food quality for caribou in the context of shrubification, at least in shrubs growing under the canopy of larger shrubs or those exposed to less sunlight.

The ADF concentration for *B. glandulosa* leaves was highest at the beginning of the season, which is consistent with the results from Klein (1990), but contrasted with the gradual increase in ADF that is generally expected over the growing season (Reeves 1987; Manseau and Gauthier 1993). This inconsistency could be due to bud scales contaminating the samples, because several leaves were still in the bud during the first sampling session. Indeed, since the leaves were harvested by stripping the branches to imitate caribou, it is possible that some leaves in an earlier stage of development or even in the form of buds were harvested with the samples. The higher lignin content of *B. glandulosa* buds compared to leaves (Polák et al. 2006) may have affected the ADF concentration of the samples, although we did not find any examples of this type of contamination in the literature. No precise data were collected regarding the developmental stages of the leaves contained in each sample, although we visually assessed that most of the leaves collected in the field were fully open. Regardless of these circumstances, the values reported in our results still reflect the caribou forage because they generally consume the leaves of shrubs by stripping the shoots from the base to the tip, likely consuming some bud scales in the process (Béland et al., unpublished data). The high-fibre content at the beginning of the season could therefore slightly decrease shrub digestibility (Reeves 1987). Nevertheless, ADF content in *B. glandulosa* is low compared to that of other plant groups such as evergreens (Klein 1990) and is similar to that of *Carex* spp. For *Carex* spp., the date influenced ADF concentration but the changes over time were small and thus likely had little impact on the nutritional quality of the leaves for caribou.

The foliar biomass in *B. glandulosa* increased when exposed to ambient light and deep snow, suggesting that shrubs produce more leaves under these conditions. This increase, in combination with shrubification itself, is therefore likely to have a positive nutritional impact on caribou if overgrown shrubs or those located north (i.e., away from the sun) of neighbouring plants within the patch constitute a significant proportion of the shrub population. However, since the increase in *B. glandulosa* biomass can negatively influence the cover of other shrub species (such as *Salix planifolia*; Ropars et al. 2015) that are also consumed by caribou (Bergerud et al. 2007), it is possible that this increase in biomass may reduce the availability of other caribou forage. Both *B. glandulosa* and *Carex* spp. followed the usual pattern of increasing foliar biomass throughout the growing season (Beamish et al. 2016), no matter the experimental treatment. However, regardless of the snow treatment, the shading treatment did not impact biomass, which is not what we expected to observe. We expected that a 60% reduction in solar radiation would negatively affect the amount of biomass produced. This unexpected result could be explained by the fact that in arctic environments, nutrients are more limiting than light (Shaver et al. 1986). Considering the limited availability of nutrients, the light level required to achieve maximum growth is probably less than 60% of natural solar radiation. This explanation is consistent with the results from Jonasson et al. (1999).

Since we use experimental simulations in a natural environment, there are inherent limitations to our study. For logistical reasons, in our experimental setup, the shading treatment had to be applied to all vegetation in the plots, including shrubs. However, shrubification in the natural environment would result in shrubs receiving full light being in the highest layer of vegetation, while vegetation under the canopy (forbs, sedges, graminoids, etc.) would be shaded by shrubs. Nevertheless, given the vertical growth structure of shrubs (Paradis et al. 2016), some younger or smaller individuals or those positioned north in a shrub patch are likely to be shaded by taller shrubs that partially block the sun, especially at high latitudes, where they are at low angles relative to the horizon. For the purpose of our experiment, we considered the shrubs located in the shaded plots to be representative of those smaller shrubs that would be shaded in the natural environment. The shrubs in ambient light plots were considered to be representative of the larger shrubs that would receive full light in the natural environment. An evaluation of the availability and use of shrubs growing in shaded conditions is required to fully understand the implications of our results. Another limitation was our inability to simulate the soil enrichment that results from the additional litter produced by shrubs during shrub expansion. As reported by

Buckeridge et al. (2010), litter accumulation enhances nitrogen cycling as well as nitrogen pools in the soil, which may impact the nitrogen concentration in leaves. In addition, the total nitrogen measurements from our study did not allow us to assess changes in nitrogen compounds at a finer scale. For instance, if the excess nitrogen in the shaded leaves is inorganic rather than organic, the nutritional value of the leaves would be lower because they would be more difficult to digest (Mattson 1980). Finally, because caribou do not consume as much *B. glandulosa* in western Canada compared to eastern Canada, likely due increased phenols (Bryant et al. 2014), this could limit the scope of our results concerning this species.

Although our results show an overall positive effect on caribou summer forage, some inherent aspects of shrubification could be detrimental for caribou. Chagnon and Boudreau (2019) have shown that shrubs may outcompete lichens, the primary winter forage for caribou (Danell et al. 1994), through competition for light and soil nutrients. Increased shrub cover may also lead to decreased food availability in shaded areas due to physical constraints, even though the shaded leaves would be of higher quality. Moreover, increased snow cover created by shrub snow retention could increase energy costs associated with caribou movement (Fancy and White 1987). Shrubification will likely increase the abundance of other ungulates such as moose (Tape et al. 2016) in the long term, increasing competition for food resources.

Few studies have examined the effect of shrubification on the nutritional value of caribou forage. Our results suggest that caribou may benefit from the positive effects of shading and deeper snow cover on the quantity and quality of two common components of their diet, *B. glandulosa* and *Carex* spp. However, since shrub expansion may also impact other plant groups that are consumed by caribou, we suggest widening the investigation of the nutritional impact of shrub expansion to lichens and forbs using a combination of experimental and observational approaches.

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