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Higher Temperatures Have Contrasting Effects on Different Components of Forage Quality for Caribou in Northern Alaska

Heidi Becker
South Dakota State University

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HIGHER TEMPERATURES HAVE CONTRASTING EFFECTS ON DIFFERENT COMPONENTS OF FORAGE QUALITY FOR CARIBOU IN NORTHERN ALASKA

BY

HEIDI A. BECKER

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THESIS ACCEPTANCE PAGE

Heidi A. Becker

This thesis is approved as a creditable and independent investigation by a candidate for the master's degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

A.Joshua Leffler
Advisor Date

Michele R. Dudash
Department Head Date

Nicole Lounsbery, PhD
Director, Graduate School Date

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CONTENTS

ABSTRACT

HIGHER TEMPERATURES HAVE CONTRASTING EFFECTS ON DIFFERENT COMPONENTS OF FORAGE QUALITY FOR CARIBOU IN NORTHERN ALASKA

HEIDI A. BECKER

2020

Rising temperatures in the Arctic may affect vegetation, which in turn can affect herbivores, such as caribou, that rely on these plants for forage. Several plant traits contribute to forage quality, including digestibility, nitrogen content, and anti-herbivory secondary compounds, but the effect of temperature on these traits individually and combined is unclear. I conducted a three-component study on the effect of higher temperatures on the forage quality of graminoids, deciduous shrubs, and evergreen dwarf shrubs on the North Slope of Alaska. The components included: 1) short and long-term experimental warming, 2) natural temperature variation between south and north-facing slopes, and 3) natural temperature variation along a latitudinal gradient. Metrics measured were dry matter digestibility (DMD), leaf nitrogen concentration (N), and protein-precipitating capacity (PPC) of plant secondary compounds. Leaf N and PPC were integrated to calculate digestible protein (DP) available to caribou.

In the warming experiment, DMD in June was higher while DP was lower under short-term warming compared to other treatments in *Betula nana* and *Salix pulchra* (deciduous shrubs). Conversely, *Eriophorum vaginatum* (graminoid) experienced lower DMD but higher leaf N in June under short-term warming. These contrasting metric responses suggest that higher temperatures may mitigate overall effects on forage quality early in the growing season. There was no difference in *E. vaginatum* DMD or N in either long-term warming plots compared to ambient plots, suggesting long-term acclimation to higher temperatures. In deciduous shrubs, DP was higher in July under long-term warming compared to other treatments, and on south-facing slopes compared to north-facing slopes in July 2019, indicating that many summers of warming may improve deciduous shrub forage quality in late summer. However, different responses in the slope aspect study between 2018 and 2019 may reflect differences in winter snow rather than summer temperature. In the latitudinal temperature gradient study, leaf N varied greatly among species, and no patterns were detected. Overall, responses differed among species and between summer months. Deciduous shrubs, which are preferred by caribou, are becoming increasingly abundant and may experience improved forage quality in late summer under long-term warming, which will further benefit caribou.

INTRODUCTION

The Arctic is impacted by climate change more significantly than the rest of the world. Temperature in the Arctic is predicted to increase faster than the rest of the world (IPCC 2014), wherein Alaska is warming two times faster than the global rate (Markon et al. 2018). Furthermore, the northernmost areas of Alaska are experiencing the greatest warming, which includes the North Slope at 1.9°C between 1981 and 2012 (Bieniek et al. 2014). In contrast, precipitation changes across decades in Alaska are more variable, and trends are less clear (Bieniek et al. 2014). In fact, changes in precipitation are small, as the North Slope experienced decreased precipitation at a rate of only 1.02 mm per decade between 1925 and 2019. (NOAA 2020). Due to the large magnitude and rate, warming may have greater impacts on Alaskan ecosystems than elsewhere.

Climate change may pose consequences for Arctic herbivores, which include widely distributed herds of caribou and reindeer (*Rangifer tarandus*) across the Arctic (Mallory and Boyce 2018). Population size of the main caribou herds is variable among years (Danell et al. 2006), and population growth of some herds were associated with existing climate patterns, such as the Arctic Oscillation and the Pacific Decadal Oscillation in Alaska (Joly et al. 2011). However, climate change may further affect *Rangifer* herds through factors such as increased insect harassment (Weladji et al. 2003), predation risk (Bastille-Rousseau et al. 2018), and increasing rain-on-snow events during winter (Albon et al. 2017). The size of many caribou populations in North America have declined (Fauchald et al. 2017), but not all have a decreasing trend. For instance, the Central Arctic Herd in northern Alaska reached a maximum in 2010, then decreased until 2016 and has increased most recently (Curl 2020).

Variation in caribou populations may be affected by individuals’ nutritional status. Caribou are capital breeders, depending primarily on stored body mass to reproduce (Danell 2006). For example, nitrogen (N) for fetus growth and milk production at calving comes primarily from the mother’s body protein (Taillon et al. 2013). Dietary N also contributes to milk production, but Taillon et al. (2013) suggest its main function is to replenish females’ body reserves. Body protein, which is linked to caribou body mass (Gerhart et al. 1996), declined in female reindeer and caribou during winter (Perry S. Barboza and Katherine L. Parker 2008), and late winter body mass is linked to adult and calf survival, fecundity, recruitment, and ultimately population growth (Albon et al. 2017). In fact, Svalbard reindeer that weighed less than 50 kg in April experienced a 54% decline in the pregnancy rate of ovulating females (Albon et al. 2017). Therefore, body mass is a crucial factor affecting caribou population dynamics.

Climate change may alter the caribou diet by impacting plant abundance and community composition. Plant biomass has increased in the North American Arctic (Fauchald et al. 2017), but not all species or functional groups are increasing equally. Experimental warming studies have shown that an increase in total aboveground biomass is complex, with clear increases in deciduous shrubs and graminoids, but a decrease in evergreen shrubs, mosses, lichens, and forbs (DeMarco et al. 2014). Warming decreased species diversity (Chapin et al. 1995, Marilyn et al. 2006) and promoted deciduous shrub dominance (DeMarco et al. 2014), but Leffler et al. (2016) found that summer warming alone did not change community composition. Other studies showed no overall change in biomass (Dormann and Woodin 2002) or slight decreases (Chapin et al. 1995). However, deciduous shrubs are predicted to dominate the low Arctic tundra (Mekonnen et al.

2018), driven by concurrent increases in nutrient availability from warming (Chapin et al. 1995). Future shrub growth may be limited by factors affecting establishment, such as the ability of the existing plant community above the shrubline to inhibit shrub germination (Angers-Blondin et al. 2018), moisture limitations associated with increasing temperatures (Ackerman et al. 2018, Saucier et al. 2019), and caribou and reindeer browsing (Pajunen 2009, Saucier et al. 2019).

Although deciduous shrubs are preferred (high ratio of plant use to availability) by caribou (Denryter et al. 2017) and reindeer (White and Trudell 1980), increasing shrub abundance may adversely affect caribou nutrition. Shrub leaves contain tannins that reduce protein digestion (Robbins et al. 1987a), and a diet that consists of forage with abundant secondary compounds but low in species diversity could reduce intake of protein and energy (Thompson and Barboza 2014). For example, when reindeer diet was restricted to willow leaves, rumen turnover time increased, supposedly leading to decreased intake (White and Trudell 1980), which can possibly lead to lower body fat in late summer (Thompson and Barboza 2014). Deer may include mixtures of different forages in their diet to reduce deleterious effects of tannins (Hodgman et al. 1996), a strategy also suggested to be used by reindeer (Turunen et al. 2009), but reduced plant diversity could limit the ability of caribou to mitigate the negative effects of tannins.

Summer forage quality is critical for caribou to gain fat (Danell et al. 2006). *Rangifer* body mass is positively related to food intake (Thompson and Barboza 2014) and digestible dry matter (Cebrian et al. 2008), energy, and N of forage plants (Thompson and Barboza 2017) during the growing season. Although plant traits such as N and digestibility positively contribute to caribou body condition, some plants contain anti-herbivory secondary compounds, such as tannins, therefore reducing forage quality. Consequently, these plant traits contribute to overall forage quality either positively or negatively, and they relate to one another. For example, N was positively related to digestibility in the summer (Klein 1990), but N and the protein-precipitating capacity of tannins were negatively related (McArt et al. 2009). Forage quality traits also affect caribou preferences for individual plants. For example, caribou select for highly digestible forage (White and Trudell 1980) rather than against secondary compounds (Thompson and Barboza 2014). Because of the intertwined effect of these traits, examining their net effects is critical for understanding any role that climate change may play in forage quality for caribou.

Higher temperatures may alter forage quality by changing plant N concentrations. A literature review of climate change experiments found that the effect of warmer temperatures on plant N content was variable among species and experiments (Turunen et al. 2009). These contrasting responses may dampen overall plant nutrient changes at the community level. For example, experimental warming caused increased N pools in some species but decreased N pools in other species (Chapin and Shaver 1996), redistributing N among species (Hobbie and Chapin III 1998) or from non-vascular to vascular plants, resulting in no overall difference in plant N pools (Chapin et al. 1995). However, declines in N within species appear to be a common response to warming, as leaf N concentration decreased in deciduous shrubs (Graglia et al. 2001, Hansen et al. 2006, Leffler et al. 2016, Zamin et al. 2017), evergreen shrubs (Michelsen et al. 1996, Jonasson et al. 1999, Hansen et al. 2006) and sedges (Jónsdóttir et al. 2005, Nybakken et al. 2011). However, these declines may be minimal, as some of the studies report declines in N of only about

10% (Jónsdóttir et al. 2005, Hansen et al. 2006, Zamin et al. 2017). Conversely, other studies have found no differences in N responses to warming (Chapin and Shaver 1996, Tolvanen and Henry 2001, Doiron et al. 2014). Declines in plant N may be due to a dilution of N with higher biomass (Jonasson et al. 1999, Jónsdóttir et al. 2005), but a meta-analysis of climate change experiments in the Arctic found no significant changes in leaf N concentration or support for a dilution effect due to warming, except slightly for evergreen shrubs (Dormann and Woodin 2002). Nonetheless, studies have found that warmer temperatures increased plant biomass (Weih and Karlsson 2001, Dormann and Woodin 2002, Jónsdóttir et al. 2005). Specifically, a 2.5°C increase in temperature caused a nearly 2-fold increase in vascular plant aboveground biomass at one study site in Sweden (Jonasson et al. 1999).

In addition to increasing plant biomass, warmer temperatures increase soil nutrients. Warmer temperatures increase N mineralization (Aerts et al. 2006) and availability in the soil (Chapin et al. 1995), which then increase deciduous and evergreen shrub N (Jonasson et al. 1999). Deeper snow can increase soil temperatures and N mineralization during winter (Schimel et al. 2004). This higher N availability can lead to higher plant N levels, as deeper snow increased summer leaf N concentration of some species in moist acidic tundra (Richert 2019), and deeper winter snow plus higher summer temperature produced greater increases in leaf N than either treatment alone (Welker et al. 2005). However, increases in maximum snow water equivalent are predicted to be modest in northern Alaska, between 0 and 15%, by 2049-2060 (Callaghan et al. 2011), so investigating the effects of higher summer temperature on soil nutrients may be more predictable in the context of climate change.

However, enhanced soil fertility may lag behind increases in plant biomass. For example, total soil N, C, and P did not respond to either experimental warming or nutrient addition over the course of a 5-year study in Sweden (Jonasson et al. 1999), and even after 18 years of warming, soil inorganic N concentration was similar or lower than control plots (DeMarco et al. 2014). This time lag creates a temporal separation of the impacts of climate change, such that plant growth response is a short-term effect, and greater nutrient availability will be a long-term effect (Chapin et al. 1995). In the long term, plants may benefit from favorable conditions of both warmer temperatures promoting growth and more available soil nutrients promoting higher forage quality. In fact, experimental warming plus added nutrients synergistically produced greater increases in aboveground biomass than the single variable treatments, and the combined treatment increased N pools in shoots (DeMarco et al. 2014). However, Chapin et al. (1995) found a decrease in both biomass and N concentration in *Eriophorum vaginatum* in the combined temperature and nutrient enhancements compared to nutrient enhancement only.

In contrast to the general trend of lower plant N, warming effects on secondary compounds, such as tannins that act as anti-herbivory defense (Coley 1986) are inconclusive. One issue is that researchers report quantitative results from various compounds, such as total phenolics (Zamin et al. 2017), all carbon-based secondary compounds (Nybakken et al. 2008, Nybakken et al. 2011), and condensed and hydrolysable tannins (Graglia et al. 2001). Concentrations of secondary compounds under warming differed by species (Hansen et al. 2006). For example, condensed tannins increased in *Vaccinium vitis-idaea*, did not respond in *Salix herbacea* x *polaris* (Hansen et al. 2006), and carbon-based secondary compound concentration decreased in the alpine forb *Tofieldia pusilla* in Norway (Nybakken et al. 2011). These compounds can behave differently from one another, making generalizable trends in response to warming difficult to detect. For example, concentrations of low molecular weight phenolics decreased under experimental warming in *Salix herbacea* x *polaris*, while condensed tannins did not change (Hansen et al. 2006). Experimental warming plus added nutrients more strongly reduced total concentration of carbon-based secondary compounds in *Salix reticulata* than the single variable treatments (Nybakken et al. 2008), suggesting that increased soil nutrients resulting from long-term warming could reduce secondary compounds. However, the ability of tannins to limit digestion by precipitating plant proteins is more relevant to herbivores rather than simply the quantity of tannins in a plant (Martin and Martin 1982). Therefore, methods that determine protein-precipitating capacity (PPC) of tannins are preferred for evaluating their relevance for herbivores (Martin and Martin 1982) and how it may change with warming.

Warming effects on digestibility are unclear, as little research has been conducted on this forage quality component of arctic plants, but some existing studies show variable responses to warming. For example, Lenart et al. (2002) found an increase in digestibility of graminoids (mainly *Carex bigelowii*) at senescence under warming in one of the two study years, but Zamin et al. (2017) found no significant differences in acid detergent fiber and lignin in the graminoid *Eriophorum vaginatum* or the deciduous shrub *Betula glandulosa* under warming. Apart from temperature affects, digestibility was also variable among species in response to different winter snow depths (Richert 2019) and under ambient conditions throughout the growing season (Côté 1998).

Overall, summer warming impacts on N, secondary compounds, and digestibility are unclear. Even species within functional groups responded differently to temperature (Chapin et al. 1995), perhaps due to species differences in rate of growth and nutrient uptake (Tolvanen and Henry 2001). Therefore, investigating individual species, rather than functional group alone, will be more beneficial to evaluate the influence of warming on forage quality traits (Dormann and Woodin 2002).

With the great variation in individual forage quality components, identifying impacts on caribou nutrition is difficult without examining the net effects of all three metrics, on which little research has been done in the context of elevated summer temperatures. Studying the changes in the forage properties of plants is critical to understanding how they might affect caribou. In this study, I examined how elevated temperatures during summer influence these plant traits collectively and how these changes may translate into forage quality specifically for caribou. Using multiple methods to test temperature effects on vegetation, an approach supported by Elmendorf et al. (2015), I investigated forage quality responses to temperature using experimental warming and natural temperature variation. In the warming experiment, I examined forage quality responses to short-term and long-term warming. Although short-term (3-year) effects were not representative of long-term (9-year) effects on plant biomass (Chapin et al. 1995), examining short-term effects of warmer temperature on plants may provide insight on the direct role of temperature in forage quality and whether it continues to be a significant driver through the long term. In the natural temperature variation components of my research, I examined plant responses to temperature differences on a small scale between warmer south-facing slopes and cooler north-facing slopes, and on a large scale along a latitudinal temperature gradient, with generally warmer southern latitudes and cooler northern latitudes. These natural variations in temperature served as proxies for long-term differences in temperature as the plants had been growing under the respective temperature regimes over their lifetime.

I hypothesized that 1) forage quality will decrease with short-term increases in temperature primarily due to a dilution effect in leaf N with increasing biomass, which will also lead to a concurrent increase in fiber and a decrease in digestibility, but 2) forage quality will increase under long-term warming due to increased N availability resulting from increased soil N mineralization. However, responses will be variable due to uncontrolled environmental factors such as geography, soil moisture, and nutrient deposition. I evaluated warming effects on species preferred by caribou as well as those less preferred. Investigating responses of both groups of species will provide insight on how different components of the caribou range might change, which can help us predict how caribou might adapt by shifting their own diets accordingly.

MATERIALS AND METHODS

Study Site

I conducted my study on the North Slope of Alaska, an arctic tundra region extending from the Brooks Range in the south to the Arctic Ocean in the north (Bieniek et al. 2012). The mean annual temperature and precipitation was -10.0°C and 278 mm, respectively (NOAA 2020). Three zones describe the climate of the North Slope from south to north: Arctic Foothills, Arctic Inland, and Arctic Coastal (Zhang et al. 1996). These regions experience below-freezing temperatures for nine months of the year, with temperatures annually averaging -8.6°C in the Arctic Foothills and -12.4°C in the Arctic Inland and Arctic Coast; average number of days of the thaw season are 122, 129, and 106, respectively (Zhang et al. 1996). The large-scale latitudinal gradient study took place along the segment of the Dalton Highway which runs through these three climate zones (Figure 1).

I conducted the warming experiment and landscape study at Toolik Field Station near Toolik Lake on the North Slope of Alaska. Toolik Lake (68°63'N, 149°60'W; 740 m elevation) falls within the Arctic Foothills climate zone of the North Slope (Zhang et al. 1996) and experiences a mean air temperature of about 11°C in July and -21°C in January and a mean annual precipitation of 309 mm (Environmental Data Center Team 2020a). The experiment occurred in a moist acidic tussock tundra area, which included the species *Eriophorum vaginatum*, *Carex spp*., *Betula nana*, *Salix pulchra*, *Vaccinium vitis-idaea* and *Rhododendron tomentosum*.

Experimental Design

Experimental Warming

Hexagon fiberglass open-top chambers (OTCs) following the International Tundra Experiment (ITEX) design (Molau and Mølgaard 1996) were used for the warming experiment. OTCs were 40 cm tall (Walker et al. 1999), and consisted of both small (1.0 m) and large (1.5 m) sizes (Marion et al. 1997). Ten OTCs were placed at Toolik Field Station on 30 June 2018, to serve as short-term warming plots. They were selectively placed to include adequate amounts of each of the three target species sampled. Nearby, ten OTCs were selected from those that have been in place nearly every summer between mid-June and late August since 1994 (Walker et al. 1999, Wahren et al. 2005, Welker et al. 2005) to serve as long-term warming plots (ca. 25 summers of warming). Within the same plant community, eight control plots with no OTCs were delineated from the area between the short-term and long-term OTCs. Within each OTC and control plot, tissue samples from one sedge, *Eriophorum vaginatum*, and two deciduous shrubs, *Betula nana* and *Salix pulchra*, were harvested by taking green *E. vaginatum* tillers and stripping leaves from the shrubs. I collected leaves into two coin envelopes of each species from each OTC and control plot in 2018 and 2019 – one for analysis of fiber digestibility and leaf N content, and the other for protein-precipitating capacity (PPC) analysis of plant secondary compounds. Plants were sampled in 2018 on 29 June-1 July (hereafter termed the June sampling period) and 29-30 July (hereafter termed the July sampling period). Plants were also sampled in 2019 on 21 June and 22 July, and OTCs were installed two weeks prior to sampling in June. Samples from the short-term warming plots in June 2018 were excluded from analysis due to insufficient initial warming time between OTC installation date and sampling date. Temperature data loggers (Thermochron, model DS1921G, Maxim Integrated, San Jose, CA, USA) were installed in the soil approximately 10 cm deep, and on the ground surface (on top of moss layer) in three OTCs and three control plots during summer in 2018 and 2019. All loggers recorded temperature hourly. Soil moisture was measured on 24 June and 22 July 2019 within OTCs and control plots to a depth of 11.9 cm with a portable soil moisture meter (model 6440FS, FieldScout TDR 100, Spectrum Technologies, Inc., Aurora, IL, USA).

South vs. North-facing Slopes

Two hills with north and south-facing slopes (site 1 and site 2) were selected at Toolik Field Station to examine differences in forage quality on naturally warmer south-facing slopes compared to cooler north-facing slopes. Slope degree and aspect were measured with a clinometer for each south and north-facing slope at each site to calculate insolation. Tissue samples were harvested from six species belonging to three functional groups at each site: deciduous shrubs (*Betula nana* and *Salix pulchra*), evergreen dwarf shrubs (*Vaccinium vitis-idaea* and *Rhododendron tomentosum*), and graminoids (*Eriophorum vaginatum* and *Carex spp*.). I collected green *E. vaginatum* tillers, green leaves from the deciduous shrubs, and leaves including the upper portion of the stem to which leaves were attached from the evergreen dwarf shrubs. I collected leaves into two coin envelopes of each species from each slope in 2018 and 2019 – one for analysis of fiber digestibility and leaf N content, and the other for PPC analysis. In 2019, each slope was divided longitudinally into five zones, so I collected leaves into two coin envelopes of each species from each zone. Plants were sampled on 9 August 2018, and on 22-24 June and 23-24 July 2019. Temperature loggers as described above were placed on the ground surface (on top of moss layer, if present) of each slope during summer in 2018 and 2019, and additional temperature loggers were installed approximately 10 cm deep in the soil during summer in 2019. All loggers recorded temperature hourly. Soil moisture was measured on 24 June and 23 July 2019 on each slope to a depth of 11.9 cm with a portable moisture meter.

Latitudinal Temperature Gradient

Aboveground vegetation biomass was harvested from nine locations accessible from the Dalton highway (Figure 1). These points, established by an earlier study, extended 200 km from near Toolik Lake in the south to near the Arctic coast at Prudhoe Bay in the north (Barboza et al. 2018). Each point consisted of three 1 m^2 main plots, and within each main plot there were three 0.2 m^2 subplots; plots and subplots were designated by PVC quadrat frames. Deciduous shrubs were harvested from the main plots, and all other vegetation was harvested from the subplots. Biomass was clipped to 3 cm deep within the moss layer, collected in paper bags, and sorted by species or functional group. Species used for analyses included deciduous shrubs (*B. nana* and *S. pulchra*), evergreen dwarf shrubs (*V. vitis-idaea* and *R. tomentosum*), and graminoids (*E. vaginatum* and *Carex spp*., pooled together due to difficult identification). Harvesting took place in mid-June and mid-July of 2017 and 2018. Environmental data were collected at each point and consisted of soil moisture to a depth of 11.9 cm using a portable soil moisture meter; air (1 m above ground), surface (on top of moss layer), and soil temperature (10 cm deep) measured by temperature data loggers installed at the nine sample points along the Dalton highway.

Laboratory Analyses

Plant Fiber Analysis

I determined different fractions of dry matter digestibility (DMD) of forage using sequential steps according to the methods outlined by ANKOM Technology (2018a, b). Leaves of deciduous shrubs and graminoids, and leaves with the upper portion of the stem to which leaves were attached of the evergreen dwarf shrubs were analyzed. Plant material was oven-dried at 60-70°C for 3 days and ground to pass a 1 mm mesh using a cutting-type mill (3375E15 Wiley Mill Model 4 [used in 2018] and 3383L10 Wiley Mini Cutting Mill [used in 2019], Thomas Scientific, Swedesboro, NJ, USA). Ground material was placed into 25 micron porosity filter bags. The bags were placed in an automated fiber digester (model 200, ANKOM Technology, Macedon, NY, USA) and digested with neutral detergent solution (water; sodium lauryl sulfate; EDTA disodium, dihydrate; sodium borate, decahydrate; sodium phosphate, dibasic, anhydrous; triethylene glycol [neutral detergent dry concentrate with triethylene glycol, ANKOM Technology, Macedon, NY, USA]) with sodium sulfite (sodium sulfite A.C.S., ANKOM Technology, Macedon, NY, USA) and alpha-amylase enzyme (amylase, sodium chloride, sorbitol, water [alpha amylase, ANKOM Technology, Macedon, NY, USA]) yielding neutral detergent fiber (NDF), then digested with acid detergent solution (water, sulfuric acid concentrate, cetyltrimethylammonium bromide [acid detergent liquid concentrate diluted with water, ANKOM Technology, Macedon, NY, USA]) yielding acid detergent fiber (ADF). The bags were then soaked in 72% sulfuric acid yielding acid detergent lignin and cutin (ADL), and lastly the bags were ashed in a muffle furnace at 450-500°C for at least three hours, yielding mineral content. From these components, DMD was calculated as the sum of digestible NDF and digestible neutral detergent solubles (NDS)(Hanley et al. 1992, Spalinger et al. 2010), using the following equation which combines equations from Robbins et al. (1987b) for mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*), and Spalinger et al. (2010) for moose (*Alces alces*):

$$DMD = (92.31e^{-0.0451*(LC)}*NDF) + (0.831*NDS - 6.97), \qquad \text{eq. (1)}$$

where LC is the percent lignin and cutin of NDF. Due to the large number of samples collected and processing time, DMD was not calculated for plants across the latitudinal temperature gradient. In 2019, the ADF solution was mistakenly over diluted. However, the mean %ADF from the diluted solution was compared to the mean %ADF from the correct concentration and differences were negligible.

Plant Nitrogen Analysis

I measured N concentration on the same tissue used for fiber analysis. The initially ground material was placed into 2 mL micro-centrifuge tubes with four 2.3 mm chrome steel beads and ground to a fine powder in a ball mill (model 607, Mini-Beadbeater-16, Biospec Products, Inc., Bartlesville, OK, USA) for two minutes. Afterwards, tubes were placed in an oven at 100°C for at least 24 hours, then stored in a desiccator. Weighing with a microbalance, 3.0 – 3.5 mg of sample was placed into 5 x 9 mm tin capsules. Standards of alfalfa and atropine also were placed into capsules and weighed. Weighed capsules were placed into 96-well plates, and tissue percent N was determined by combustion using a CHNSO elemental analyzer (model ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA, USA). Calibration curves had a fit of $R^2 \geq 0.999$.

Protein-Precipitating Capacity Analysis

Following the methods used by (McArt et al. 2006), I used a bovine serum albumin (BSA) binding assay to determine the protein-precipitating capacity (PPC) of secondary compounds in *B. nana* and *S. pulchra*. Plant material was stored on dry ice the field, frozen upon return from the field, then freeze-dried and ground to pass a 1 mm mesh. I used an accelerated solvent extractor (ASE-200, Dionex Corporation, Sunnyvale, CA, USA) to extract secondary compounds with aqueous methanol. The resulting solution was pipetted into a microplate and increasingly diluted with methanol. BSA protein was added, followed by Coomassie Brilliant Blue protein dye (Thermo Fisher Scientific Inc., Waltham, MA, USA) reagent to indicate the presence of protein. The dyed solutions' absorbance was measured with a UV-Vis microplate spectrophotometer (Synergy HT Multi-Mode Microplate Reader, BioTek Instruments Inc., Winooski, VT, USA). The amount of BSA precipitated was calculated from these readings using a standard curve and regressed with amount of forage dry matter. Incorporating the results from PPC and N analysis, I calculated digestible protein (DP) with the following equation from Robbins et al. (1987a) for mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*):

$$DP = -3.87 + 0.9283*CP - 11.82*PPC, \qquad \text{eq. (2)}$$

where CP is crude protein, calculated as 6.25 x percent nitrogen.

Graminoids contain relatively low amounts of secondary compounds (Jung et al. 1979, Robbins et al. 1987a, Zamin et al. 2017, Barboza et al. 2018), so PPC in *E. vaginatum* and *Carex* was not measured. In contrast, evergreen dwarf shrubs have relatively high levels of secondary compounds (Jung et al. 1979, Zamin et al. 2017); however, these species are low quality forages with low digestibility and N concentration (Johnstone et al. 2002), and they did not contribute largely to summer diets of caribou (Russell et al. 1993) and reindeer (White and Trudell 1980) in northern Alaska.

Therefore, PPC of these species is irrelevant to caribou nutrition during summer and was not measured. PPC was not measured in the deciduous shrubs in 2018 of the landscape study, because that year functioned as a pilot study. In graminoids and evergreen dwarf shrubs, DP was calculated as a function of N in equation 2, by setting the PPC term equal to 0; therefore, DP exhibited the same patterns as N in these species. PPC was not measured in the deciduous shrubs in the latitudinal gradient study due to workload and time restraints; therefore, DP could not be accurately calculated in this case.

Statistical Analysis

In all three study components, responses of DMD, N, and PPC to independent variables were arcsine square-root transformed to satisfy the normality assumption of parametric statistics, then analyzed by creating linear mixed-effects models in the nlme package in the computer program R (R Core Team 2020). In the warming experiment, fixed effects were treatment (short-term warming, long-term warming, or control) and sample date (June or July), and random effects were intercept, and plot nested within year. In the 2018 slope aspect study, the fixed effect was slope aspect (south or north-facing slope), and the random effects were intercept and hill site. In the 2019 slope aspect study, the fixed effects were slope aspect and sample date, and random effects were intercept, and sample zone nested within hill site. In the latitudinal temperature gradient, fixed effects were latitude (continuous variable) and sample date, and random effects were intercept, and plot nested within year. Models of individual fixed effects, additive fixed effects, and multiplicative fixed effects were compared, and top models were selected using Akaike's Information Criteria (AIC) in the bbmle package. The AICcmodavg package in R was used to predict values and standard error (95%

confidence intervals were then calculated from standard error) for arcsine square-root transformed values of DMD, N, and PPC generated from the linear mixed-effects models, which values and confidence intervals were then back-transformed.

To calculate DP for the deciduous shrubs, I predicted values and standard error for PPC and CP from untransformed data generated from linear mixed-effects models (CP model used the same fixed and random effects as the N model) using the AICcmodavg package in R, generated random deviates from these values, which I input into equation 2 and ran 5,000 iterations. Then I calculated quantiles to predict the median and 95% confidence intervals of DP. To calculate DP for the graminoids and evergreen dwarf shrubs, I used predicted values and standard error (95% confidence intervals were then calculated from standard error) for arcsine-square root transformed CP values generated from a linear mixed-effects model (CP model used the same fixed and random effects as the N model), which values and confidence intervals were then back-transformed. Due to instances of negative DP values in the latitude temperature gradient study, I replaced these negative values with 0 prior to arcsine square-root transforming and inputting into the DP equation.

Growing degree days (GDDs) were calculated for the warming experiment and south vs. north-facing slopes by taking 2018 and 2019 pooled median daily temperatures and calculating the cumulative sum over all recorded days for soil and surface. Significant differences in total GDDs were determined by creating linear mixed-effects models. In the warming experiment, the fixed effect was treatment, and random effects were intercept and individual data logger nested within year. In the slope aspect study, the fixed effect was slope aspect, and random effects were intercept and individual data logger nested within year. Models of individual fixed effects, additive fixed effects, and multiplicative fixed effects were compared, and top models were selected using AIC. Daily mean temperatures of the warming experiment and slope aspect study were determined by calculating the daily median temperature of each data logger, then averaging the medians for each day. In the latitude gradient study, temperature was analyzed by calculating the daily median temperature of each data logger and creating linear mixed-effects models, where the fixed effects were latitude and sample date, and random effects were intercept year. Models of individual fixed effects, additive fixed effects, and multiplicative fixed effects were compared, and top models were selected using AIC.

Insolation in the slope aspect study was calculated as watts per square meter (converted to megajoules) received on south and north-facing slopes at site 1 and site 2 from days 180 to 218 for the year 2020 using the insol package in R. Inputs included latitude, longitude, and altitude of Toolik Field Station (latitude = 68.6, longitude = -149.6, altitude = 740 m); slope degree and aspect at each hill site (site 1 – north-facing slope: 4°, south-facing slope: 4°; site 2 – north-facing slope: 6°, south-facing slope: 1°); and azimuth (assumed 0° for north-facing slopes and 180° for south-facing slopes).

Gravimetric water content (GWC) was calculated using the following non-linear regression model determined by measuring volumetric water content (VWC) and GWC on local gravel and organic soils at Toolik Field Station:

$$GWC=VWC*2.857^{-03} + VWC^{2}*-6.392^{-07} + VWC^{3}*5.299^{-11} - 3.632$$

GWC values were analyzed by creating linear mixed-effects models. In the warming experiment, fixed effects were treatment (short-term warming, long-term warming, or control) and sample date (June or July), and random effects were intercept and plot. In the slope aspect study, the fixed effect was slope aspect (south or north-facing slope), and the random effects were intercept, and sample zone nested within hill site. In the latitudinal temperature gradient, fixed effects were latitude (continuous variable) and sample date, and random effects were intercept, and plot nested within year. Models of individual fixed effects, additive fixed effects, and multiplicative fixed effects were compared, and top models were selected using AIC. The sample point at latitude 69.2 was missing soil temperatures in June and July.

RESULTS

Climatic Conditions

The summer of 2018 at Toolik Field Station was cooler and drier than the summer of 2019. Average June air temperature (measured 3 m above ground) was 4.8°C in 2018 and 8.2°C in 2019; average July temperature was 10.3°C in 2018 and 12.3°C in 2019; and average August temperature was 4.2°C in 2018 and 4.4°C in 2019 (Environmental Data Center Team 2020a). Total June precipitation was 37 mm in 2018 and 83 mm in 2019; total July precipitation was 106 mm in 2018 and 59 mm in 2019; and total August precipitation was 117 mm in 2018 and 179 mm in 2019, resulting in total summer precipitation (June – August) of 259 mm in 2018 and 321 mm in 2019 (Environmental Data Center Team 2020a). The maximum recorded snow depth at Toolik Field Station was greater in the winter prior to summer 2018 than in the winter prior to summer 2019 (46.0 cm and 28.2 cm, respectively) (Environmental Data Center Team 2020a). Plant phenology at Toolik Field Station was later in 2018 than in 2019, as the start of green-up was on day 158.4 ± 8.9 days in 2018, but on 140.1 ± 7.2 days in 2019 (Environmental Data Center Team 2020b). Peak NDVI occurred during days 205-222 in 2018, and slightly earlier in 2019 during days 189-203 (Environmental Data Center Team 2020b).

Experimental Warming

Experimental warming of study plots with passive open-top chambers (OTCs) significantly increased surface temperature relative to ambient temperature. The top model for total growing degree days (GDDs) on the ground surface included the experimental treatment (Table 1). OTC plots accumulated ca. 60 more growing degree days than control plots on the surface between early July and mid-August (days of year

183-225, Figure 2, Table 2). The OTCs were an average of 1.0°C warmer than the control plots on the surface, and 1.5°C warmer during the hours near solar noon (12:00 – 16:00, Table 3). There was no significant difference in total GDDs between the warming and control plots in the soil (Table 1). Also, there were no significant differences in soil GWC among treatments (Table 4, Figure 3).

Dry matter digestibility (DMD) was slightly higher in the warmed plots than control plots and was higher in late June compared to late July in *B. nana*, but DMD responses were more complex in *S. pulchra* and *E. vaginatum* (Figure 4). The top model for *B. nana* DMD included month and treatment (Table 5). Compared to the control plots, *B. nana* DMD was 1.5% higher in the short-term warming plots and 2.1% higher in the long-term warming plots, indicating DMD was similar between short and long-term warming plots. Additionally, DMD was 5.2% higher in June than in July. The top model for *S. pulchra* was an interaction between month and treatment, where in June, DMD was 2.2% higher in the long-term warming plots than in the control plots, and DMD was similar between short and long-term warming plots. The top model for *E. vaginatum* also included an interaction between month and treatment, where in June, DMD was lower in the short-term warming plots by 7.0% compared to the control plots, and by 5.6% compared to the long-term warming plots.

Leaf N concentration responded in the opposite direction of DMD under short-term warming in *B. nana* and *E. vaginatum*, and leaf N was higher in late June compared to late July in *S. pulchra* (Figure 5). Leaf N was similar between the long-term warming plots and control plots in *B. nana* and *E. vaginatum*. The top model for leaf N in *B. nana* included an interaction between month and treatment (Table 6), where leaf N was 12.6%

lower in the short-term warming plots in June than in the other treatments in June, and it was 8.1% lower in the short-term vs. the long-term warming plots in July. The top model for *E. vaginatum* also included an interaction between month and treatment, where leaf N was 9.3% higher in the short-term warming plots in June than in the other treatments in June. The top model for *S. pulchra* only included month, where leaf N was 30.1% higher in June than in July, and there were no differences among treatments.

PPC was lower in the warming plots than in the control plots in *B. nana*, and PPC was lower in June than in July in *S. pulchra* (Figure 6). The top model for *B. nana* PPC included treatment (Table 7), where PPC was 14.3% lower in the short and long-term warming plots than in the control plots, and especially so following long-term warming (17.2% lower than control). There was no difference between sample dates in *B. nana*. The top model for *S. pulchra* PPC included month, where PPC was 21.9% lower in June than in July, and there were no differences among treatments.

Digestible protein (DP) in the deciduous shrubs was lower in the short-term warming plots than in other treatments in June, but in July it was higher in the long-term warming plots than in other treatments; DP was also higher in June than in July in the shrubs (Figure 7). In June, DP was lower in the short-term warming plots than in the control and long-term warming plots by 17.6% in *B. nana* and by 15.8% in *S. pulchra*. In July, DP was higher in the long-term warming plots than in the control (*B. nana*: 12.4%, *S. pulchra*: 33.6%) and short-term warming plots (*B. nana*: 21.5%, *S. pulchra*: 17.4%). Overall, DP was higher in June than in July by 30.3% in *B. nana* and by 93.0% in *S. pulchra*. Since PPC was not measured in graminoids, DP in *E. vaginatum* was simply a linear function of crude protein and therefore exhibited the same response to warming as did leaf N.

South vs. North-facing Slopes

The south-facing slopes received more solar radiation than the north-facing slopes between late June and early August (days of year 180-218, Figure 8). The ratio of solar energy received on the south-facing slope to the north-facing slope was 1.05 at both site 1 and site 2 (Table 8). Despite this modeled energy difference, no temperature difference was detected between the slopes. The top model for total GDDs only included the intercept both on the surface and in the soil (Table 9), meaning there was no significant difference of total GDDs between north and south-facing slopes either on the surface or in the soil during days 180-218. The mean temperature difference between aspects was only 0.5°C on the surface, but the difference was larger (1.0°C) during daytime between hours 12:00 and 16:00 (Table 10), although not significant. Soil temperature was 1.5°C warmer on the south vs. north-facing slope overall and between hours 12:00 and 16:00, although not significant. However, variance was large, explaining why the difference in GDDs was non-significant. For example, mean and standard deviation for daily surface temperatures was 12.0 ± 0.5°C on the south-facing slope and 11.5 ± 1.0°C on the north-facing slope (Table 10), which translated into the large standard deviation of total surface GDDs (464.9 ± 26.1 and 455.6 ± 34.9, respectively, Table 11, Figure 9). The top model for soil GWC included slope (Table 12), and soil GWC was 8.9% higher on the north-facing slope than the south-facing slope (Figure 10).

DMD responses to slope aspect varied in 2018 and 2019, and DMD was higher in June than in July in many species in 2019. In 2018, the top model for DMD included slope for *B. nana*, *S. pulchra, E. vaginatum* and *V. vitis-idaea* (Table 13); where DMD was higher on the south-facing slope by 4.5% in *B. nana*, 1.6% in *E. vaginatum*, and 3.1% in *V. vitis-idaea*, but DMD was lower on the south-facing slope by 2.4% in *S. pulchra* (Figure 11). There was no difference in DMD between slopes in *Carex* and *R. tomentosum* in 2018 (Table 13). In 2019, the top model for DMD included an interaction between month and slope for *B. nana* and *R. tomentosum* (Table 14), where DMD was lower on the south vs. north-facing slope in June by 2.1% in *B. nana* and by 2.5% in *R. tomentosum* (Figure 12). In these same two species, DMD was also higher on the south vs. north-facing slope in July by 2.4% and 3.8%, respectively, which appeared to reduce the typical seasonal decline of DMD. The top model for *Carex* DMD in 2019 included additive month and slope, where DMD was 2.0% higher on the south vs. the north-facing slope, and DMD was also 2.0% higher in June than in July. The top model for DMD included month for *S. pulchra*, *E. vaginatum*, and *V. vitis-idaea* in 2019, where DMD was higher in June than in July by 1.9%, 2.3%, and 7.9%, respectively, and there was no difference in DMD between slopes in these species.

Leaf N was lower on the south vs. the north-facing slope in all but one species in 2018 (Figure 13). The top model for leaf N included slope in all species except *V. vitis-idaea* in 2018 (Table 15), where leaf N was lower on the south vs. the north-facing slope by 15.4% in *B. nana*, 9.8% in *S. pulchra*, 5.1% in *E. vaginatum*, 25.9% in *Carex*, and 8.8% in *R. tomentosum*. This response of reduced leaf N was the opposite response of DMD in *B. nana* and *E. vaginatum*, which perhaps buffered the overall difference in forage quality on south vs. north-facing slopes. Taken together, the responses of DMD and leaf N resulted in lower forage quality in *S. pulchra, Carex*, and *R. tomentosum*. The top model for *V. vitis-idaea* leaf N in 2018 only included the intercept, meaning there was no difference between slopes. However, due to higher DMD, *V. vitis-idaea* appeared to have higher overall forage quality on the south-facing slope.

Leaf N responses to slope aspect were mixed in 2019, and leaf N was higher in June than in July in most species (Figure 14). The top model for leaf N included additive terms of month and slope in *B. nana*, *S. pulchra*, and *R. tomentosum* (Table 16). Leaf N was lower on the south vs. north-facing slope by 6.0% in *B. nana* and 4.9% in *R. tomentosum*, but leaf N was higher on the south vs. north-facing slope by 5.0% in *S. pulchra*. Additionally, leaf N was higher in June than in July by 16.3% in *B. nana*, 22.7% in *S. pulchra*, and 4.0% in *R. tomentosum*. In *R. tomentosum*, leaf N response was the same response as DMD in June, but it was the opposite in July, indicating overall lower forage quality in June and a mitigating effect in July on the south-facing slope. The top model for *Carex* leaf N in 2019 included an interaction between month and slope, where leaf N was 8.7% lower on the south vs. north-facing slope in June. This leaf N response was the opposite of DMD, but only in June, indicating a dampening effect of overall forage quality in June and higher forage quality in July on the south-facing slope. The top model for leaf N included month in *E. vaginatum* and *V. vitis-idaea* in 2019, where leaf N was 21.5% higher in June than in July in *E. vaginatum*, but leaf N was 6.3% lower in June than in July in *V. vitis-idaea*; there was no difference in leaf N between slope aspects in these species.

PPC was lower on the south vs. north-facing slope in *B. nana*, and in July in *S. pulchra* (PPC was only measured in plants in 2019; Figure 15). The top model for *B. nana* included slope (Table 17), where PPC was 26.1% lower on the south vs. north-facing slope, and there was no difference between sample dates. The top model for *S. pulchra* included an interaction between month and slope aspect, where PPC was 27.8% lower on the south vs. north-facing slope in July, indicating a reduction in the typical seasonal increase of PPC. PPC was not measured in either the graminoids or in the evergreen dwarf shrubs.

In 2019, DP was higher on the south vs. north-facing slope in *S. pulchra* during respective sample dates, and in *B. nana* in July, but DP was lower on the south vs. north-facing slope in June in *B. nana* (Figure 16). In *B. nana*, DP was 10.3% lower on the south vs. north-facing slope in June, but 9.8% higher in July. Also, DP was overall higher in June than in July by 27.9%. This response of DP followed the same pattern as DMD in *B. nana*, resulting in overall lower forage quality in June but higher forage quality in July, buffering the typical seasonal decline of forage quality on south-facing slopes. In *S. pulchra*, DP was 11.3% higher on the south vs. north-facing slope in June and 98.4% higher in July. Also, DP was overall higher in June than in July by 101.9%. Since the difference in DP was greater in July than in June on the south vs. north-facing slope, the seasonal decline of DP appeared to have been reduced. Taken together, the responses of forage quality metrics in *S. pulchra* indicated higher overall forage quality on the south vs. north-facing slope in both June and July, with a dampening of seasonal decline. DP could not be accurately calculated for deciduous shrubs in 2018 since PPC was not measured in shrubs that year. Also, PPC was not measured in the graminoids or evergreen dwarf shrubs in either 2018 or 2019; therefore, DP was calculated as a linear function of crude protein and exhibited the same response to slope aspect as did N in respective years (2018: Figure 17, 2019: Figure 16).

Latitudinal Temperature Gradient

The top model for both soil and surface temperature included an interaction between month and latitude (Tables 18 & 19). Soil and surface temperatures were variable across latitude, but they tended to be lower at higher latitudes in late June and were relatively constant across latitude in late July (Figures 18 & 19). The top model for soil GWC across latitude included an interaction between month and latitude (Table 20). GWC generally increased northward in both June and July, but it varied between months at mid-latitudes (Figure 20).

Leaf N varied greatly by latitude and month among species (Figure 21). The top model for *S. pulchra* included an interaction between month and latitude (Table 21), where leaf N decreased with increasing latitude in June, but leaf N was relatively constant across latitude in July. This decrease resulted in 95.0% higher leaf N at the lowest vs. highest latitude in June. Also, at the lowest latitude, leaf N was 74.6% higher in June than in July in *S. pulchra*. The top model for *V. vitis-idaea* included an interaction between month and latitude, but the pattern was the reverse of *S. pulchra*: leaf N was relatively constant across latitude in June, and leaf N decreased with increasing latitude in July. Leaf N was 33.8% higher at the lowest vs. highest latitude in July in *V. vitis-idaea*. The top model for graminoids included an interaction between month and latitude, where leaf N decreased with increasing latitude in June, but increased with increasing latitude in July. Leaf N was 42.6% higher at the lowest vs. highest latitude in June but was 11.6% lower at the lowest vs. highest latitude in July. Leaf N was approximately equal in June and July at the lowest latitude (1.9%), but leaf N was 38.1% lower in June than in July at the highest latitude in the graminoids. The top model for *B. nana* included month, where leaf N was an average of 67.4% higher in June than in July, but there were no differences in leaf N across latitude. The top model for *R. tomentosum* also included month, where leaf N was an average of 8.5% lower in June than in July, but there were no differences in leaf N across latitude.

DMD and PPC were not calculated in samples across the latitudinal gradient due to the large workload and processing time of samples. Because PPC was not measured, DP could not be accurately calculated in the deciduous shrubs; however, DP was calculated for graminoids and evergreen dwarf shrubs as a linear function of crude protein, resulting in the same response pattern as leaf N (Figure 22).

DISCUSSION

The three study components demonstrated that forage quality responses to experimental and natural variation in temperature is highly variable with unique responses among forage quality components and species. Short-term experimental warming caused contrasting responses of DMD and DP in the three species studied in June. Long-term experimental warming in July had no effect on *E. vaginatum* forage quality while improving forage quality in deciduous shrubs, and the same results were found on south-facing slopes in July 2019, suggesting that deciduous shrubs may experience higher late-summer forage quality after long-term climate warming. However, different responses were found in the slope aspect study between 2018 and 2019, potentially due to winter snow conditions rather than summer temperature. Also, several species had different patterns of leaf N across latitude depending on the month, while some did not differ across latitude, suggesting that forage quality was driven by differences in phenology and species-specific responses to environmental factors other than temperature.

My hypotheses were partially supported by the results: 1) instead of a consistent decline in forage quality primarily driven by declines in leaf N under short-term warming, leaf N responded differently in all three species in the warming experiment, and negative responses were often mitigated by positive responses of other metrics; 2) as hypothesized, forage quality increased in the long term, but only in the deciduous shrubs in July where leaf N increased and PPC decreased in *B. nana*, and DP increased in *S. pulchra*. The deciduous shrubs also had higher forage quality on the south-facing slope in July 2019, in which the south-facing slope served as a proxy for long-term warming, but responses were different in 2018. 3) Only *V. vitis-idaea* had higher forage quality at lower latitudes, and species responses were highly variable across the latitudinal temperature gradient.

Effects of Experimental Warming on Forage Quality

Forage quality responses to experimental warming varied within and among species at different times of the growing season, suggesting that responses are species-specific. For example, *B. nana* and *E. vaginatum* were more sensitive to warming than *S. pulchra*, but these two species responded to warming in opposite directions of each other in leaf N concentration and DMD. Previous work in interior Alaska also demonstrated varying effects of warming between species, as DMD of graminoids (including *Carex bigellowi*) increased at senescence under experimental warming in one of the study years, but DMD of prostrate willows (including *S. arctica* and *S. reticulata*) was not significantly different under warming than control plots (Lenart et al. 2002). This observation of species-specific responses is also evident in changes in biomass, in which an earlier experiment demonstrated different changes in mass per shoot among species (including *B. nana* and *E. vaginatum*) in response to warming, nutrient addition, and shading (Chapin and Shaver 1985). Forage quality exhibits inherent natural variability, as N, PPC, and DP differed among species, years, time of season, and sites in south-central Alaska (McArt et al. 2009), so changes in the environment may yield correspondingly variable responses among species.

These species-specific responses in forage quality may be driven by differences in resource allocation, possibly explained by species' unique life histories, resource limitations, competitive dynamics, and specialization of resource use within the community (Chapin and Shaver 1985). In fact, it is expected that species within a community respond differently to environmental change because each species is theoretically distributed on the landscape according to its unique resource limitations (Chapin and Shaver 1985). When plant growth is limited by a specific resource, processes related to acquisition of that resource are upregulated (Chapin et al. 1987), so the different responses of the metrics may reflect compensation for limiting resources. For example, in northern Sweden, the boreal understory plants *V. vitis-idaea* and *V. myrtillus* increased carbon allocation to leaves in response to N fertilization, suggesting that plant N was no longer limiting, so plants acquired more C to alleviate their light limitation (Hasselquist et al. 2016). Also, adding N and increasing temperature caused varying responses among different secondary compound groups even within species, consistent with the resource allocation theory (Nybakken et al. 2008). Therefore, warming in my study may have altered the balance of resources within plants, such as C and N, and caused each species to compensate for a limiting resource, resulting in a different balance of N, C (which influences DMD), and secondary compounds unique to each species.

Under short-term warming, DMD and either leaf N or DP responded in opposite directions, potentially dampening opposing effects. For example, this dampening effect was most prominent in *E. vaginatum*, where DMD decreased but leaf N increased under short-term warming compared to other treatments in June. To a lesser extent than *E. vaginatum,* the deciduous shrubs *B. nana* and *S. pulchra* also exhibited dampening effects, but in reverse, as DMD increased but DP decreased under short-term warming in June. The lower DP in *B. nana* could be due to a dilution of leaf N with larger leaves in response to warming, although I did not measure leaf area. In fact, higher air temperature increased leaf area while decreasing leaf N content in *Betula pubescens* seedlings in Sweden (Weih and Karlsson 2001). Therefore, the benefit of increased DP in *E. vaginatum* may be reduced by the decrease in DMD, and vice-versa in the deciduous shrubs, in the short-term warming plots in June, potentially resulting in a neutral net effect on caribou nutrition in early summer.

Some explanations for increased leaf N in *E. vaginatum* could be increased N uptake or lower biomass. *E. vaginatum* could have rapidly increased N uptake to compensate for higher temperatures, as a rapid response was demonstrated by Chapin (1977), who found that *E. vaginatum* physiologically compensated for temperature by increasing the rate of phosphate absorption when grown at a lower temperature, and its affinity for phosphate increased within a few minutes. Alternatively, the increase in leaf N concentration under warmer temperatures could have been attributed to lower leaf mass, as two growing seasons of warming decreased blade and sheath mass of *E. vaginatum* (Chapin and Shaver 1985).

Generally, the largest effects of short-term warming occurred in June, indicating a stronger response when plants normally have higher forage quality in early summer, and a diminished response when N allocation shifts in late summer. In the spring, *B. nana* and *S. pulchra* transferred N from stems and roots into their leaves, and *E. vaginatum* transferred N from rhizomes into leaves, as well as roots (Chapin et al. 1980). Forage quality was generally higher in June than in July, consistent with other findings of seasonal decreases in DMD (Côté 1998) and leaf N (Tolvanen and Henry 2001, Lenart et al. 2002), and increases in PPC (McArt et al. 2009), so the effects of warming may be greatest on young leaves in early summer when forage quality is high. In fact, deciduous shrubs in south-central Alaska had 70% higher leaf DP in the early growing season than late in the growing season (McArt et al. 2009). *B. nana* leaves expanded earlier in warming plots than in control plots (Chapin and Shaver 1996), so leaves may have accumulated biomass earlier in the short-term warming plots, possibly leading to diluted leaf N. Another deciduous shrub, *Betula glandulosa*, also exhibited a reduction in leaf N in the early season under warming in Canada (Zamin et al. 2017). Chapin et al. (1980) found that leaf N declined in *S. pulchra* later in the season likely due to a transfer of leaf N back to belowground structures. This late-season transfer perhaps reduced the effect of treatments on forage quality of the deciduous shrubs in late July. Similarly, in the graminoid *Carex bigelowii*, warming did not change the N allocation pattern from aboveground tissue to belowground rhizomes in August (Jónsdóttir et al. 2005), perhaps explaining *E. vaginatum's* lack of response to warming in late July.

While short-term warming caused dampening effects on forage quality, long-term warming caused no differences in *E. vaginatum* overall forage quality or *B. nana* leaf N compared to the control, suggesting acclimation of these traits after many growing seasons of higher temperatures. Despite the large changes under short-term warming in June, DMD and leaf N in *E. vaginatum* exhibited smaller differences under long-term warming compared to control plots, suggesting acclimation of these traits by returning to levels under ambient temperature over time. Leaf N in *B. nana* was also similar between long-term warming plots and control plots in June and July, suggesting acclimation of leaf N. Chapin and Shaver (1996) found an increase in biomass of *E. vaginatum* after nine years of warming, so the short-term response of increased leaf N in *E. vaginatum* may have been diluted as biomass increases over years of summer warming, lowering the leaf N concentration to similar levels as in ambient plots.

In contrast to potential acclimation of leaf N and DMD in *E. vaginatum* and leaf N in *B. nana* over time, long-term warming increased DP in July in the deciduous shrubs compared to other treatments, suggesting that deciduous shrubs have higher forage quality in the late growing season after many years of higher summer temperatures. Further, because DP in June was similar between long-term warming plots and ambient plots, the increase in July DP indicates that long-term warming dampened the natural seasonal decline of forage quality in deciduous shrubs. The increased DP in July in *B. nana* was likely due to a decrease in PPC, which was lowest in the long-term warming plots and similar between June and July, enabling more protein available to caribou in July. Although there was no treatment effect on PPC in *S. pulchra*, July PPC levels were lowest in the long-term warming plots compared to other treatments, suggesting that PPC also decreased under long-term warming in July in *S. pulchra* and contributed to the increase in DP.

This decrease in PPC may be due to enhanced soil nutrients after long-term warming. Although I did not measure soil nutrients in my treatment plots, another study conducted near my study site found that their plots contained greater soil nutrient availability after nine years of warming (Chapin and Shaver 1996). PPC may have declined in response to these enhanced nutrients in the long-term warming plots, because plants invest more resources into growth as opposed to secondary compounds linked to defense against herbivory under a more N-rich environment (Chapin et al. 1987).

In conclusion, tundra plant responses to warming were complex, but warming affected species and forage quality metrics differently in ways that potentially dampened net effects on early season nutritional quality in some species in the short term, and improved late season forage quality in deciduous shrubs in the long term. Using the threshold for minimum protein requirement for reindeer to maintain body mass (I used the lowest value of 7% DP), calculated by Thompson and Barboza (2017), I found that despite changes in forage quality, warming did not alter the natural pattern of DP relative to this threshold in any species (Figure 12). However, even minute changes in forage quality can affect reindeer body condition, as a 4% increase in digestibility of early season *E. vaginatum* flowers was projected to increase reindeer daily weight gain by 78% (Cebrian et al. 2008). Thus, the modest increase of DP in deciduous shrubs, which are favored forages, may benefit caribou by retaining more available protein during the natural decline of forage quality and providing caribou a longer period to gain weight prior to winter.

Forage Quality on South and North-facing Slopes

In 2019, overall forage quality between south and north-facing slopes differed in opposite ways between *B. nana* and *S. pulchra* in June, but both deciduous shrubs had higher forage quality in July on the south-facing slope, suggesting improved late-season forage quality in deciduous shrubs after long-term warming. Since I used south-facing slopes as proxies for long-term warming, this finding is consistent with that from the warming experiment. *B. nana* DMD and DP were lower in June but higher in July on the south-facing slope, and *S. pulchra* forage quality was higher on the south-facing slope in both June and July. The higher DP on the south-facing slope in July may have been primarily driven by decreases in PPC in both species. For example, *B. nana* DP was higher in July despite lower leaf N on the south-facing slope. Although *S. pulchra* had higher leaf N and DP in both June and July, PPC was lower on the south-facing slope only in July, resulting in considerably higher DP on the south-facing slope than the north-facing slope in July (ca. 95%) than in June (ca. 11%).

Aside from the common response of improved late-season forage quality in the deciduous shrubs during 2019, species generally responded differently from each other to slope aspect, suggesting that differences in forage quality may be influenced by environmental factors other than temperature alone. These species-specific responses may be attributed to the drier soil on the south-facing slope, which may have affected soil nutrient levels. Soil moisture was negatively linked to soil and air temperatures, and inorganic soil N was positively linked to soil moisture in a Greenland tundra (Higgens et al. 2020), so the drier south-facing slopes in my study could have contained less soil N than the north-facing slopes. However, there was no difference in soil pore-water nitrate, ammonium, and phosphate between slope aspects on lawn and hummock microhabitats within Scandinavian peatlands, although there was higher dissolved organic carbon in soil pore-water on south-facing slopes than north-facing slopes (Robroek et al. 2014). Further, Yuan et al. (2019) found no effect of slope aspect on soil characteristics in China, but rather soil moisture was influenced by slope angle and position on the slope, and total soil N and organic C were affected by position on the slope; the authors suggested that these factors may dampen the effect of radiation on south and north-facing slopes. Therefore, the variable, but low, slope angles of the hills in my study (1°-6°) may have contributed to variable soil characteristics that diminished the effect of slope aspect.

Alternatively, winter conditions may affect soil N and, consequently, plant forage quality, through different patterns of snow drifting on hillsides of different aspect. The predominant wind direction at Toolik Lake originates from the south-southeast, so wind carries snow from south-facing slopes and deposits it on north-facing slopes (Dery et al. 2004). Deeper snow compared to ambient snow levels increased winter soil temperatures and both winter and summer N mineralization in moist tussock tundra (Schimel et al. 2004). This increase in available N may explain why plant leaf N in summer increased in plots receiving deeper winter snow in deciduous shrubs and graminoids in tussock tundra (Richert 2019).

Because my study site received more winter snow in 2018 than in 2019, and leaf N was consistently lower on the south-facing slope in August 2018, leaf N may be more strongly influenced by snow depth during the previous winter than summer temperature or radiation budget. In 2019, leaf N differences between slope aspects were more variable among species, when the area received less snow in winter than the previous year, presumably leading to less extreme differences in snow depth between north and south-facing slopes. Even though snow drifting may not have been as extreme as in 2018, north-facing slopes likely still received deeper winter snow than south-facing slopes in 2019. Thus, the lower PPC on south-facing slopes in the deciduous shrubs is consistent with Richert (2019), who found higher PPC in *B. nana* in deep snow plots compared to lower-than-ambient snow plots, although there was no difference in *S. pulchra* PPC.

Similar to results from the warming experiment, there were some contrasting differences between DMD and leaf N within species on south-facing slopes compared to north-facing slopes, suggesting that warmer south-facing slopes may dampen overall differences in forage quality between slope aspects in some species. However, unlike the warming experiment, these instances were not consistent, as they occurred in different months. For example, DMD was higher and leaf N was lower on the south-facing slopes in *B. nana* and *E. vaginatum* in August 2018 and in *Carex* in June 2019, and vice versa in *R. tomentosum* in July 2019.

In conclusion, forage quality on south and north-facing slopes varied among species and months, but patterns in leaf N and PPC, considered with the different winter conditions between my study years, reveal that forage quality may be driven more strongly by winter snow rather than summer temperature. Despite these variable responses, one pattern revealed that deciduous shrubs had higher forage quality on the south-facing slope in July. Therefore, caribou may select different species depending on whether it is early or late in the season and the plants' position on the landscape. In fact, heavier body weight in red deer in Norway was related to a greater diversity of slope aspects and altitudes as opposed to only access to a greater area of north-facing slopes and high altitudes (Mysterud et al. 2001). Therefore, the heterogeneity of the landscape may provide a wide selection of forages which allow caribou to mitigate differences of forage quality in individual species.

Forage Quality Across a Latitudinal Temperature Gradient

Leaf N varied by species and month across latitude, but patterns of leaf N in June are perhaps better explained by differences in phenology rather than temperature. The thaw date is later (Gustine et al. 2017) and plant green-up is ca. 10-15 days later on the coastal plains in the north than on the foothills in the south (J. Sexton, unpublished data), so leaves were likely younger to the north. However, leaf N in the graminoids and *S.*

pulchra decreased northward in June, perhaps because more dead leaves comprised the samples as fewer new leaves had emerged.

The variation in forage quality among species in late June and later phenology at northern latitudes when caribou are present indicates that caribou do not follow peak forage quality. *Rangifer* on the Arctic plains at Prudhoe Bay, Alaska, forage on vegetation as it emerges from the declining water table during the summer (Skogland 1980). However, graminoids, which have higher biomass than deciduous shrubs and a forb within the Central Arctic Herd's summer range on the North Slope (Barboza et al. 2018), had lower leaf N at higher latitudes in late June. Therefore, although caribou may follow the emergent vegetation in spring, they seemingly do not follow the peak in forage quality, which occurred later in the summer in the graminoids. There is no significant greening trend, measured by maximum annual summer NDVI, across much of the tundra (Berner et al. 2020). Similarly, I found no consistent trends in forage quality across latitude, so climate warming may not cause consistent widespread increases in biomass or forage quality.

Leaf N responses in July were also inconsistent among species across latitude. For example, with increasing latitude, leaf N increased in graminoids, decreased in *V. vitis-idaea*, and did not change in *B. nana*, *S. pulchra*, or *R. tomentosum*. Since there was no trend in surface temperature across latitude in July, these variable responses suggest that species may have been responding differently to other factors that vary across a large area, such as precipitation, thaw depth, length of the growing season, and geology. For instance, I found that soil moisture tended to increase with increasing latitude, but it differed by month at mid-latitudes.

One explanation for *B. nana*’s consistency in leaf N concentration across latitude is compensation in other leaf traits. For example, *B. nana* had greater leaf area and less foliar C concentration at warmer and drier locations across an east-west landscape temperature gradient in a Greenland tundra in mid-July, but no patterns in leaf N concentration (Higgens et al. 2020), suggesting that leaves simultaneously experienced diluted N content but also lower C:N ratios in warmer areas, resulting in no net differences in leaf N. Higgens et al. (2020) also found that there were no patterns in leaf area or foliar C or N concentrations in *S. glauca* across the gradient, similar to my finding of little difference in *S. pulchra* leaf N across latitude in July.

In conclusion, leaf N varied widely among species, over the growing season, and across the landscape, perhaps more strongly driven by differences in phenology and environmental factors other than temperature. The variation in forage quality among species may allow caribou to buffer seasonal changes in forage quality by providing high quality species at different times during the growing season and at different locations within their summer range.

Limitations

Several limitations of my study must be considered when evaluating results. In the warming experiment, samples were collected soon after OTCs were installed in June 2018, giving plants only a short time to respond to warming, so the short-term warming plot samples from June were excluded from analysis in 2018, eliminating my ability to capture year-to-year variability in June. Although OTCs increased air temperatures above ambient temperatures, they warmed air temperature more during midday than at night. In addition to increasing maximum annual temperatures, minimum annual temperatures are also increasing on the North Slope at a similar rate (0.2°C and 0.3°C per decade, respectively, between 1925 and 2019) (NOAA 2020). Therefore, my warming experiment may have elicited weaker plant responses than under more realistic climate warming conditions of both higher maximum and minimum temperatures.

Although modeling demonstrated a small difference in solar radiation between north and south-facing slopes, I did not detect a significant difference in surface or soil temperature between the slope aspects. This lack of observed temperature difference may be explained by the shallow angle of the hillside, large variance in soil GDDs among temperature data loggers, or lower soil moisture on the south-facing slope. Another study on slope aspect also modeled greater solar radiation on south vs. north-facing slopes but only detected temperature differences at one of their three study sites, which the authors suggest that this lack of temperature difference was due to evaporative cooling or shading from greater biomass on the south-facing slope (Robroek et al. 2014). Another limitation to this study component was the difference in study design between the two years. The study in 2018 served as a pilot study where I only conducted one sampling in August, and samples were not collected for PPC analysis. Therefore, in 2018 I was unable to investigate a difference in forage quality between early and late summer, and the lack of PPC samples prevented me from determining DP in the deciduous shrubs that year.

Some limitations to the latitudinal temperature gradient study included small sample sizes and missing forage quality metric analyses. Results may have misrepresented species due to low and unequal sample sizes. Species diversity decreased moving northward, leaving fewer evergreen dwarf shrubs and *B. nana* to be collected at higher latitudes. Also, since phenology of leaf emergence was later in the north than in the south, live leaves were more limited in the north during the June sampling. During sampling, all aboveground biomass was harvested from sample subplots, which led to a large amount of plant material to process. Consequently, the large workload prevented me from analyzing DMD and PPC from the latitude gradient, restricting the comparability of overall forage quality with the other study components. Although the latitudinal temperature gradient study was intended to represent long-term warming, my results indicated that responses in June were most likely caused by differences in phenology rather than temperature, so only responses in July potentially represented plant forage quality along a temperature gradient. Nonetheless, this component further supported the significance of the impact of seasonal variation in forage quality and how it varies among species across the landscape.

Conclusions

While results from the warming experiment may most strongly represent the direct effects of temperature on forage quality in the short and long term, the natural temperature variation studies were limited in explaining long-term plant responses to temperature alone. Temperature effects were complicated by other potentially stronger environmental factors, such as patterns in snow drifting during winter and differences in plant phenology across the landscape. In fact, increased summer temperature combined with deeper winter snow resulted in a greater increase in leaf N compared to control plots than temperature or snow depth alone in moist tussock tundra (Welker et al. 2005), and temperature may be rather an indirect factor influencing plant nutrients (Chapin et al. 1995). In this study I found great variability of responses among species, supporting these studies that temperature may be more important as an indirect driver of forage quality by influencing other environmental factors to which plants more strongly respond.

My results revealed species-specific responses to higher temperatures, and in some cases the dampening of opposing effects of different forage quality metrics within species, indicating that climate change may induce a diversity of forage quality effects in plants that buffer overall change. Therefore, this variability may buffer overall forage quality change from warming and prevent drastic fluctuations that could be detrimental to caribou nutrition. The growing season is short in the Arctic, so caribou are limited in time to obtain adequate protein to recover lost body stores from winter and rebuild protein reserves to survive the following winter. This timeframe is limited even further by the rapid decline of forage quality over the growing season, so dampening effects to changes in forage quality will be important to provide caribou adequate nutrients in the summer amidst ongoing climate change.

Caribou already face the challenge of naturally fluctuating forage quality, so they are equipped to adapt to additional nutritional variation over the landscape under climate warming. Caribou strongly select among species (Denryter et al. 2017), and reindeer select forage based on availability and the forage quality metrics used in my study (White and Trudell 1980). Caribou and reindeer have been known to adjust their diet. For example, reindeer living on the island of Svalbard consumed kelp to supplement their diet in response to ground-ice (Hansen et al. 2019). Therefore, caribou exhibit plastic behavior, so they have the potential to adapt to small changes, perhaps by simply consuming different amounts of species at different times throughout the growing season.

Nonetheless, some patterns of responses emerged that may have implications for caribou. In the warming experiment, I found contrasting forage quality responses to short-term warming in June of the three species I measured. This contrast was due to a decrease in DP and an increase in DMD in the deciduous shrubs, but vice versa in *E. vaginatum*. Reindeer selection was positively related to total non-structural carbohydrates and N:fiber in plants (Skogland 1984), but sufficient amounts of digestible N are available for a shorter period than energy for caribou in summer on the North Slope of Alaska, meaning caribou are more constrained by N than energy (Barboza et al. 2018). Female caribou lost body N during milk production, and lactation increased minimum N intake requirements by 110% (Perry S. Barboza and Katherine L. Parker 2008), so high DP is important for lactating females during the summer. The diet of the Porcupine Caribou Herd, which calves in northwestern Canada into northeastern Alaska, consisted of graminoids, moss, and lichens prior to and during calving, then switched to primarily deciduous shrubs and forbs through July, with an increased contribution of lichens in late July (Russell et al. 1993). Therefore, under short-term warming, a diet consisting largely of deciduous shrubs may fail to provide enough protein for lactating females in late June, and caribou may include more *E. vaginatum* in their diet, which increased in DP. However, reindeer forage to maximize digestibility, and they select against fiber concentration (Skogland 1984), so they may have to make a trade-off between the higher DP but lower DMD in *E. vaginatum* in late July.

However, this negative change in deciduous shrubs may subside after long-term warming. Not only will long-term warming have no effect on deciduous shrub DP in late June, but it may improve in late July, potentially providing caribou a longer period to forage on deciduous shrubs and the opportunity to build more body protein stores shortly before winter. Caribou gain body protein mass and body fat from summer to fall (Couturier et al. 2008), so increased DP could enhance these body gains. Siberian reindeer had lower intake of dry matter, digestible energy, and digestible protein in fall compared to summer (Thompson and Barboza 2017), but greater concentrations of DP may allow caribou to maintain intake of DP even with lower biomass intake. Also, higher DP may allow female caribou to regain more body reserves amidst the high demands of pregnancy and milk production, as their lower body condition was demonstrated by the lower body fat and protein of lactating females compared to non-lactating females from the Central Arctic Herd in the fall (Gerhart et al. 1996). The North Slope of Alaska has experienced increased cover of tall shrubs (> 0.5 m) from 2000 to 2010 (Duchesne et al. 2018), and the annual net primary production of shrubs has been predicted to increase in the low Arctic from 2010 to 2100 under a climate change model (Mekonnen et al. 2018), so climate warming over time may benefit caribou by improving the quantity and quality of favorable forage during late summer.

TABLES

Table 1. Model selection results for growing degree days of the warming experiment

Model	logLik	AIC	ΔAIC	df	weight
Surface					
treatment	-53.1	116.3	0	5	0.9982
intercept	-60.4	128.9	12.6	4	0.0018
Soil					
intercept	-64.9	137.9	0	4	0.69
treatment	-64.7	139.5	1.6	5	0.31

Table 2. Total surface and soil growing degree days of open-topped chambers (OTC) vs. control (CT) plots from days 183 to 225 (mean ± standard deviation)

	Surface	Soil
OTC	457.9 ± 13.5	148.5 ± 58.2
CT	398.3 ± 31.9	168.8 ± 58.6

Table 3. Daily (24-hr) and daytime (12:00 – 16:00) temperatures (^{o}C) of open-topped chambers (OTC) vs. control (CT) plots (mean ± standard deviation). Differences are relative to control plots.

	Surface	Soil
OTC		
24-hr	10.5 ± 0.5	3.5 ± 1.5
12:00 - 16:00	17.0 ± 5.5	3.5 ± 2.0
CT		
24-hr	9.5 ± 0.5	4.0 ± 1.5
12:00 - 16:00	15.5 ± 5.5	4.5 ± 2.0
Difference		
24-hr	1.0	-0.5
12:00 - 16:00	1.5	-1.0

Table 4. Model selection results for gravimetric water content of soils in the warming experiment in 2019

Model	**logLik**	**AIC**	**dLogLik**	**ΔAIC**	**df**	**weight**
intercept	23.1	-40.3	0	0	3	0.31
month*treatment	27.9	-39.7	4.7	0.6	8	0.23
treatment	24.7	-39.4	1.6	0.9	5	0.2
month	23.5	-39	0.4	1.3	4	0.16
month+treatment	25.1	-38.1	1.9	2.2	6	0.1

Table 5. Model selection results for dry matter digestibility of each species in the warming experiment

Model	**logLik**	**AIC**	**ΔAIC**	**df**	**weight**
B. nana					
month+treatment	247.2	-480.4	0	7	0.584
month*treatment	248.6	-479.3	1.1	9	0.34
month	243.1	-476.3	4.1	5	0.076
treatment	221.3	-430.6	49.7	6	<0.001
intercept	219.3	-430.5	49.8	4	<0.001
S. pulchra					
month*treatment	284.8	-551.6	0	9	0.534
month+treatment	282.6	-551.3	0.3	7	0.45
month	277.3	-544.6	7	5	0.016
treatment	269.8	-527.7	24	6	<0.001
intercept	265.7	-523.3	28.3	4	<0.001
E. vaginatum					
month*treatment	171.5	-324.9	0	9	0.446
intercept	165.6	-323.1	1.8	4	0.183
treatment	167.5	-322.9	2	6	0.164
month	166.2	-322.3	2.6	5	0.122
month+treatment	167.8	-321.6	3.3	7	0.085

Table 6. Model selection results for leaf percent nitrogen of each species in the warming experiment

Model	logLik	AIC	ΔAIC	df	weight
B. nana					
month*treatment	342.8	-667.6	0	9	0.6988
month+treatment	340	-665.9	1.7	7	0.2954
month	334	-658	9.6	5	0.0058
treatment	310.2	-608.4	59.2	6	<0.001
intercept	301.6	-595.3	72.4	4	<0.001
S. pulchra					
month	321.9	-633.8	0	5	0.53
month*treatment	325.3	-632.6	1.2	9	0.28
month+treatment	322.9	-631.8	2	7	0.19
intercept	274.3	-540.6	93.2	4	<0.001
treatment	276.2	-540.4	93.4	6	<0.001
E. vaginatum					
month*treatment	351.1	-684.2	0	9	0.49
month	346.8	-683.6	0.6	5	0.37
month+treatment	347.8	-681.7	2.5	7	0.14
intercept	312.4	-616.8	67.5	4	<0.001
treatment	312.7	-613.4	70.9	6	<0.001

Table 7. Model selection results for protein-precipitating capacity of each species in the warming experiment

Model	logLik	AIC	ΔAIC	df	weight
B. nana					
treatment	96.6	-181.1	0	6	0.41
intercept	94.2	-180.5	0.7	4	0.296
month+treatment	96.6	-179.2	2	7	0.155
month	94.3	-178.5	2.6	5	0.112
month*treatment	96.8	-175.6	5.5	9	0.026
S. pulchra					
month	68.8	-127.5	0	5	0.5121
month+treatment	70.4	-126.8	0.7	7	0.3573
month*treatment	71.4	-124.7	2.8	9	0.1263
treatment	64.4	-116.8	10.8	6	0.0023
intercept	62.2	-116.4	11.1	4	0.002

Table 8. Solar radiation (megajoules) received on south vs. north-facing slopes at hill sites 1 and 2 from days 180 to 218. Ratio is relative to south-facing slopes.

	South	North	Ratio
Site 1	1095.87	1040.47	1.05
Site 2	1076.57	1024.55	1.05

Table 9. Model selection results for growing degree days of south vs. north-facing slopes

Model	logLik	AIC	ΔAIC	df	weight
Surface					
intercept	-75.6	159.2	0	4	0.67
slope	-75.3	160.6	1.4	5	0.33
Soil					
intercept	-63.3	134.7	0	4	0.56
slope	-62.6	135.2	0.5	5	0.44

Table 10. Daily (24-hr) and daytime (12:00 – 16:00) temperatures (^{o}C) of south vs. north-facing slopes (mean ± standard deviation). Differences are relative to south-facing slopes.

	Surface	Soil
South		
24-hr	12.0 ± 0.5	5.0 ± 2.5
12:00 - 16:00	21.5 ± 7.5	5.5 ± 2.5
North		
24-hr	11.5 ± 1.0	3.5 ± 1.0
12:00 - 16:00	20.5 ± 7.0	4.0 ± 1.5
Difference		
24-hr	0.5	1.5
12:00 - 16:00	1.0	1.5

Table 11. Mean total surface and soil growing degree days of south vs. north-facing slopes from days 180 to 218 (mean ± standard deviation)

	Surface	Soil
South	464.9 ± 26.1	200.4 ± 98.1
North	455.6 ± 34.9	145.8 ± 45.7

Table 12. Model selection results for gravimetric water content of soils of south vs. north-facing slopes in 2019

Model	**logLik**	**AIC**	**dLogLik**	**ΔAIC**	**df**	**weight**
slope	41	-72	1.2	0	5	0.319
intercept	39.8	-71.6	0	0.4	4	0.264
month+slope	41.5	-70.9	1.7	1.1	6	0.188
month	40.3	-70.5	0.5	1.5	5	0.154
month*slope	41.5	-69.1	1.7	2.9	7	0.074

Table 13. Model selection results for dry matter digestibility of each species on the south vs. north-facing slopes on August 9, 2018

Model	**logLik**	**AIC**	**ΔAIC**	**df**	**weight**
B. nana					
slope	48.7	-89.5	0	4	0.89
intercept	45.7	-85.3	4.2	3	0.11
S. pulchra					
slope	63	-118	0	4	0.978
intercept	58.2	-110.5	7.6	3	0.022
E. vaginatum					
slope	59.8	-111.6	0	4	0.89
intercept	56.7	-107.3	4.2	3	0.11
V. vitis-idaea					
slope	59.4	-110.9	0	4	0.955
intercept	55.4	-104.7	6.1	3	0.045
R. tomentosum					
intercept	49.3	-92.5	0	3	0.56
slope	50	-92.1	0.5	4	0.44
Carex spp.					
intercept	47.6	-89.3	0	3	0.72
slope	47.7	-87.3	1.9	4	0.28

Table 14. Model selection results for dry matter digestibility of each species on the south vs. north-facing slopes in 2019

Model	logLik	AIC	ΔAIC	df	weight
B. nana					
month*slope	105.9	-197.7	0	7	0.81
month	102.1	-194.1	3.6	5	0.14
month+slope	102.1	-192.2	5.6	6	0.05
intercept	94.3	-180.6	17.1	4	<0.001
slope	94.3	-178.6	19.1	5	<0.001
S. pulchra					
month	120.3	-230.5	0	5	0.4897
month+slope	120.7	-229.4	1.1	6	0.2877
month*slope	121.4	-228.9	1.6	7	0.2149
intercept	114.7	-221.4	9.1	4	0.0051
slope	115	-220	10.5	5	0.0026
E. vaginatum					
month	102.7	-195.4	0	5	0.6268
month+slope	102.8	-193.6	1.8	6	0.2572
month*slope	103	-191.9	3.5	7	0.1103
intercept	96.6	-185.3	10.1	4	0.004
slope	96.7	-183.5	11.9	5	0.0016
V. vitis-idaea					
month	124.7	-239.4	0	5	0.54
month+slope	124.9	-237.7	1.6	6	0.24
month*slope	125.8	-237.6	1.8	7	0.22
intercept	93.5	-179	60.3	4	<0.001
slope	93.5	-177.1	62.3	5	<0.001
R. tomentosum					
month*slope	101.1	-188.3	0	7	0.709
month	97.9	-185.9	2.4	5	0.211
month+slope	98	-183.9	4.3	6	0.081
intercept	84.8	-161.6	26.7	4	<0.001
slope	84.8	-159.6	28.7	5	<0.001
Carex spp.					
month+slope	91.5	-171	0	6	0.388
month*slope	92.5	-170.9	0	7	0.38
slope	89.2	-168.3	2.6	5	0.104
month	89.1	-168.2	2.8	5	0.097
intercept	86.9	-165.9	5.1	4	0.03

Table 15. Model selection results for leaf percent nitrogen of each species on south vs. north-facing slopes on August 9, 2018

Model	**logLik**	**AIC**	**ΔAIC**	**df**	**weight**
B. nana					
slope	68.1	-128.2	0	4	0.9911
intercept	62.4	-118.8	9.4	3	0.0089
S. pulchra					
slope	71.2	-134.4	0	4	0.88
intercept	68.3	-130.5	3.9	3	0.12
E. vaginatum					
slope	78.3	-148.6	0	4	0.59
intercept	76.9	-147.9	0.7	3	0.41
V. vitis-idaea					
intercept	80.6	-155.3	0	3	0.7
slope	80.8	-153.6	1.7	4	0.3
R. tomentosum					
slope	81.8	-155.6	0	4	0.959
intercept	77.7	-149.3	6.3	3	0.041
Carex spp.					
slope	71.6	-135.1	0	4	1
intercept	58.6	-111.2	23.9	3	<0.001

Table 16. Model selection results for leaf percent nitrogen of each species on south vs. north-facing slopes in 2019

Model	logLik	AIC	ΔAIC	df	weight
B. nana					
month+slope	133.7	-255.5	0	6	0.51
month*slope	134.2	-254.4	1.1	7	0.3
month	131.7	-253.5	2	5	0.19
slope	124.4	-238.7	16.8	5	<0.001
intercept	123.2	-238.4	17.1	4	<0.001
S. pulchra					
month+slope	132.4	-252.7	0	6	0.42
month	131.3	-252.7	0	5	0.41
month*slope	132.5	-250.9	1.8	7	0.17
intercept	119.2	-230.3	22.4	4	<0.001
slope	119.7	-229.4	23.3	5	<0.001
E. vaginatum					
month	141.9	-273.9	0	5	0.53
month+slope	142.5	-273	0.9	6	0.34
month*slope	142.5	-271.1	2.8	7	0.13
intercept	124.5	-240.9	32.9	4	<0.001
slope	124.6	-239.3	34.6	5	<0.001
V. vitis-idaea					
month	147.4	-284.8	0	5	0.364
intercept	146.1	-284.2	0.7	4	0.26
month+slope	147.7	-283.3	1.5	6	0.171
slope	146.3	-282.6	2.3	5	0.117
month*slope	148	-282	2.8	7	0.088
R. tomentosum					
month+slope	155	-298	0	6	0.379
slope	153.6	-297.2	0.9	5	0.248
month*slope	155.4	-296.8	1.2	7	0.21
month	152.6	-295.3	2.8	5	0.096
intercept	151.3	-294.5	3.5	4	0.067
Carex spp.					
month*slope	140.8	-267.5	0	7	0.76
month	137	-264	3.5	5	0.13
month+slope	137.9	-263.8	3.7	6	0.12
intercept	114.2	-220.4	47.2	4	<0.001
slope	114.4	-218.7	48.8	5	<0.001

Table 17. Model selection results for protein-precipitating capacity of each species on south vs. north-facing slopes in 2019

Model	logLik	AIC	ΔAIC	df	weight
B. nana					
slope	36.7	-63.4	0	5	0.471
month*slope	38.3	-62.5	0.9	7	0.295
month+slope	36.7	-61.5	2	6	0.176
intercept	33.3	-58.6	4.8	4	0.042
month	33.3	-56.6	6.8	5	0.016
S. pulchra					
month*slope	40.1	-66.2	0	7	0.7895
month+slope	37.7	-63.5	2.7	6	0.1998
month	33.3	-56.7	9.6	5	0.0066
slope	32.8	-55.6	10.7	5	0.0038
intercept	29.4	-50.8	15.4	4	<0.001

Table 18. Model selection results for median surface temperature across latitude in 2017 and 2018

Model	logLik	AIC	dLogLik	ΔAIC	df	weight
lat*month	-1739	3490	167.2	0	6	1
lat+month	-1748.1	3506.2	158.1	16.1	5	<0.001
month	-1764	3535.9	142.3	45.9	4	<0.001
lat	-1892.4	3792.9	13.8	302.8	4	<0.001
intercept	-1906.2	3818.4	0	328.4	3	<0.001

Table 19. Model selection results for median soil temperature across latitude in 2017 and 2018

Model	logLik	AIC	dLogLik	ΔAIC	df	weight
lat*month	-1103.8	2219.6	120.2	0	6	1
lat+month	-1126.8	2263.5	97.2	43.9	5	<0.001
month	-1130.1	2268.2	93.8	48.6	4	<0.001
lat	-1218.5	2445	5.5	225.4	4	<0.001
intercept	-1224	2453.9	0	234.3	3	<0.001

Table 20. Model selection results for gravimetric water content of soils across latitude in 2017 and 2018

Model	**logLik**	**AIC**	**dLogLik**	**ΔAIC**	**df**	**weight**
lat*month	136.5	-259	71.7	0	7	0.9971
lat+month	129.7	-247.3	64.8	11.7	6	0.0029
lat	109	-208	44.2	51	5	<0.001
month	85.4	-160.9	20.6	98.1	5	<0.001
intercept	64.8	-121.6	0	137.4	4	<0.001

Table 21. Model selection results for leaf percent nitrogen across the latitudinal gradient

Model	**logLik**	**AIC**	**ΔAIC**	**df**	**weight**
B. nana					
month	105.2	-200.4	0	5	0.52
latitude*month	106.6	-199.3	1.1	7	0.29
latitude+month	105.2	-198.4	2	6	0.19
intercept	85.9	-163.7	36.7	4	<0.001
latitude	86.4	-162.7	37.7	5	<0.001
S. pulchra					
latitude*month	44.5	-75	0	7	0.783
month	40.3	-70.7	4.4	5	0.088
latitude+month	41	-70	5	6	0.064
latitude	39.7	-69.4	5.7	5	0.046
intercept	37.8	-67.5	7.5	4	0.018
Graminoid					
latitude*month	242.7	-471.4	0	7	0.9919
month	235.5	-461	10.4	5	0.0055
latitude+month	235.8	-459.5	11.9	6	0.0026
intercept	223.2	-438.4	33	4	<0.001
latitude	223.8	-437.7	33.7	5	<0.001
V. vitis-idaea					
latitude*month	159.3	-304.7	0	7	0.344
latitude	157.3	-304.6	0.1	5	0.321
latitude+month	158.1	-304.2	0.5	6	0.273
month	155	-299.9	4.8	5	0.032
intercept	153.9	-299.9	4.8	4	0.031
R. tomentosum					
month	148.4	-286.7	0	5	0.304
intercept	147.3	-286.5	0.2	4	0.278
latitude+month	148.8	-285.6	1.1	6	0.176
latitude	147.7	-285.3	1.4	5	0.149
latitude*month	149.2	-284.4	2.4	7	0.093

FIGURES

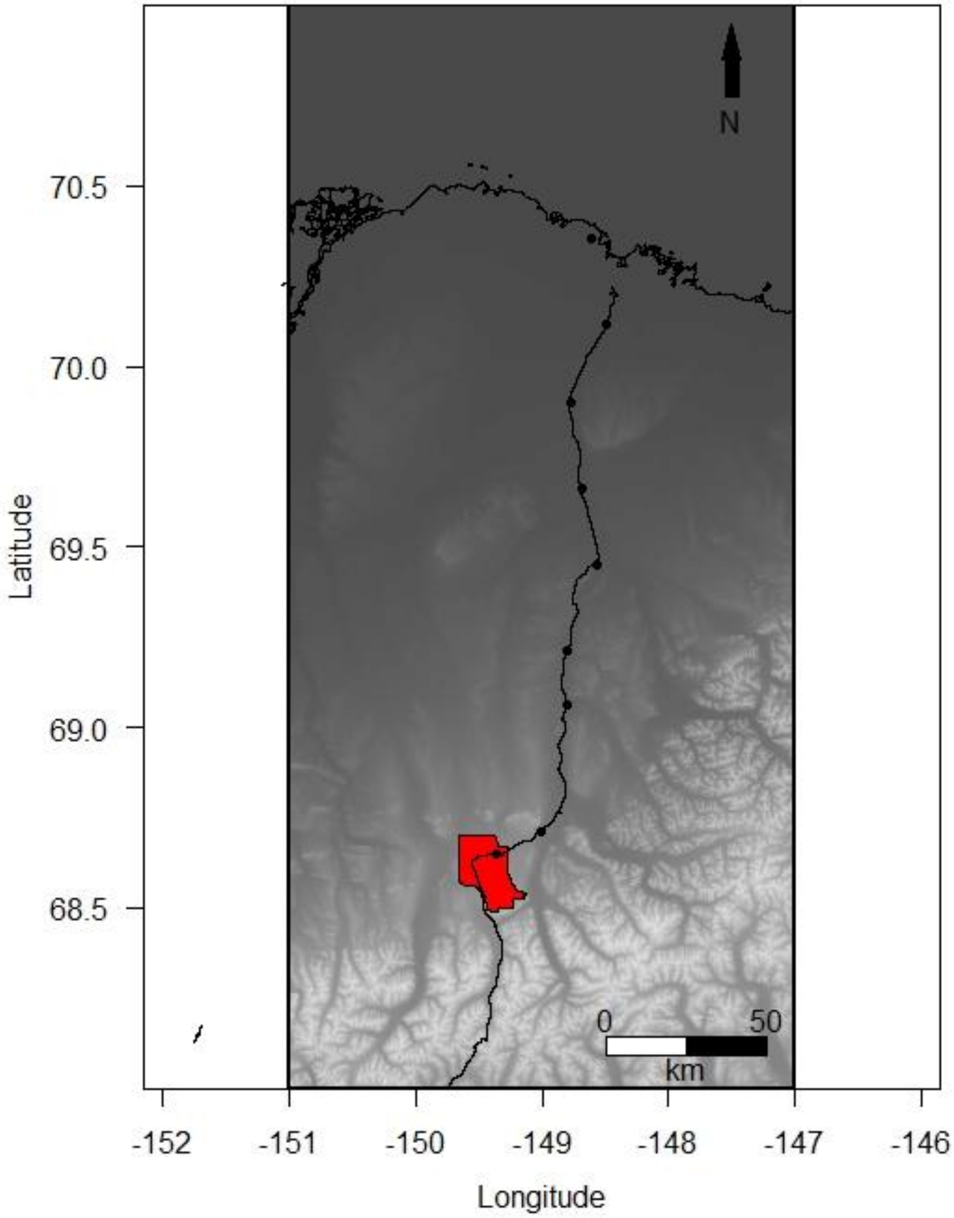

Figure 1. Points sampled in 2017 and 2018 along the Dalton Highway on the North Slope of Alaska. Red polygon is Toolik Field Station’s Research Natural Area boundary.

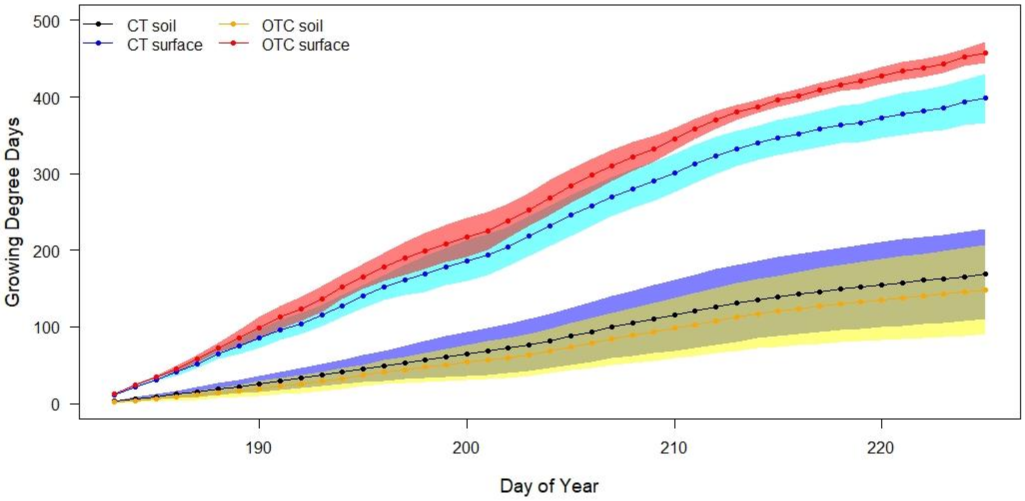

Figure 2. Surface and soil growing degree days of open-topped chambers (OTC) vs. control (CT) plots from days 183 to 225. Points are the cumulative sum of median temperatures for each day, and polygons are mean ± standard deviation.

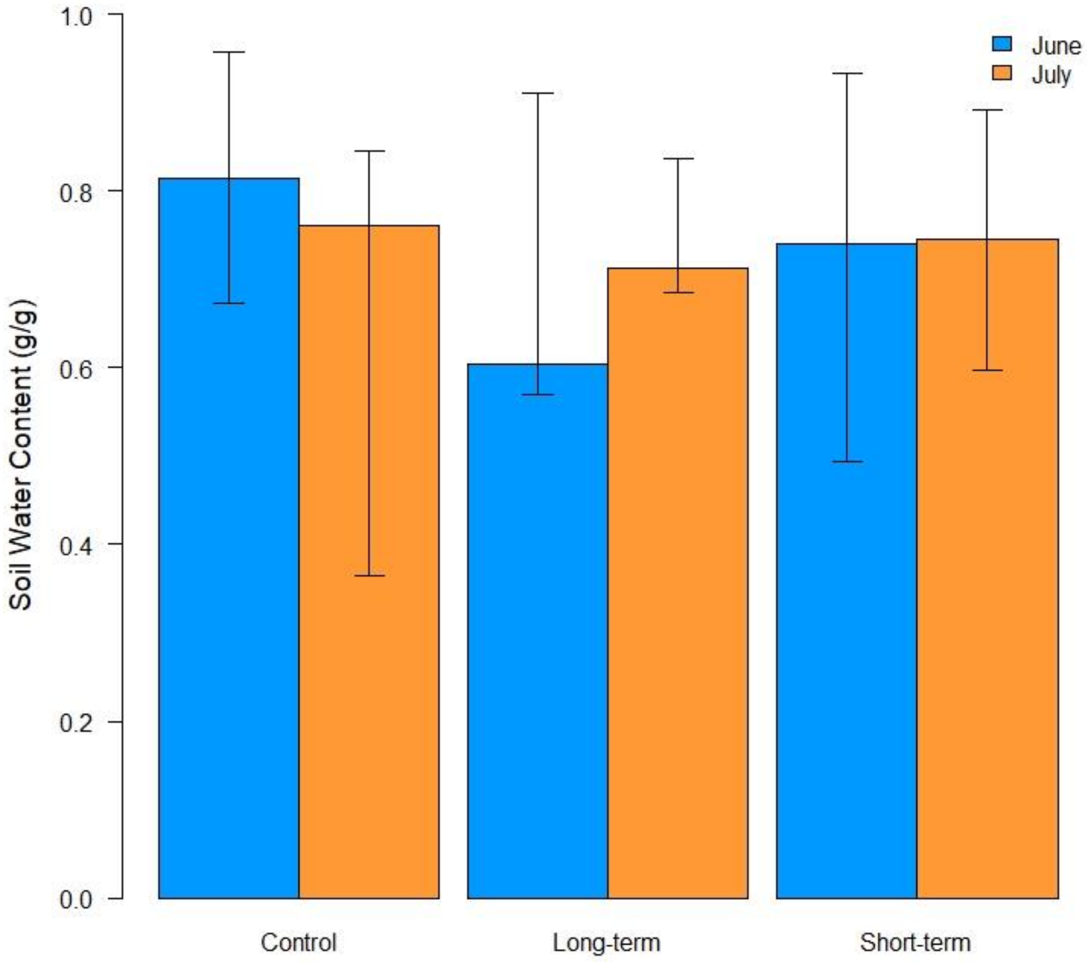

Figure 3. Gravimetric water content of soils among treatments in the warming experiment in June and July 2019. Colored bars are means, and error bars are standard deviation.

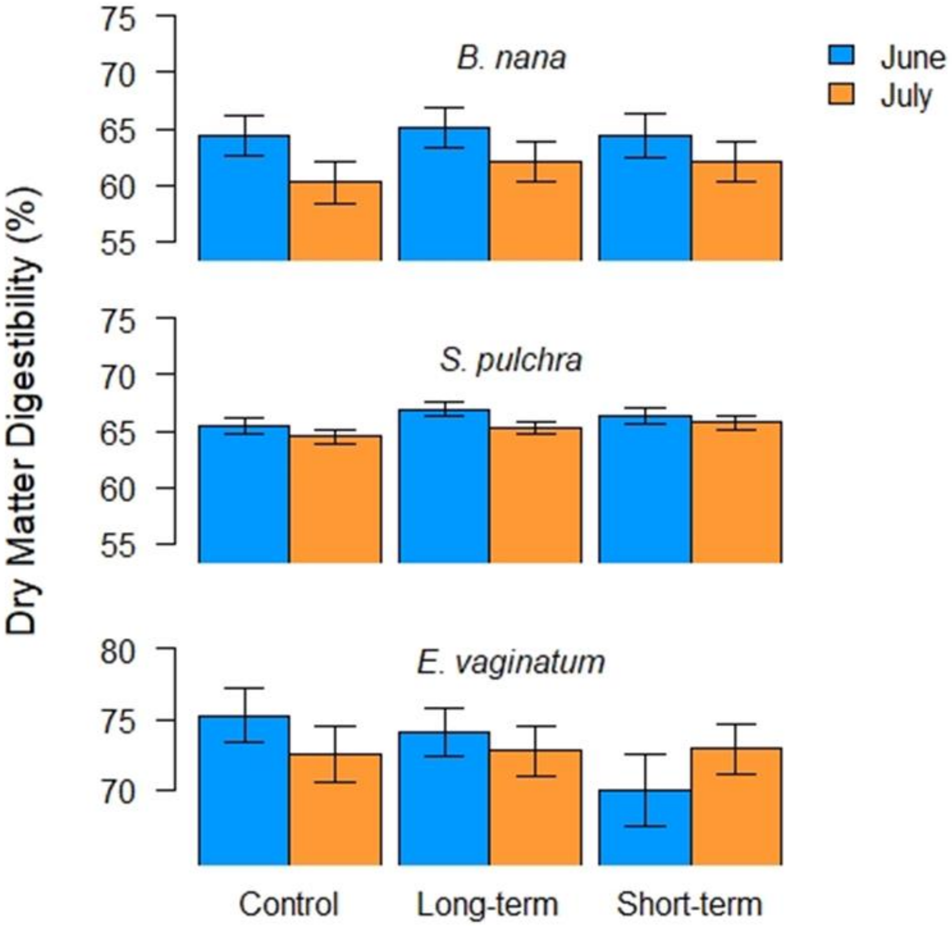

Figure 4. Dry matter digestibility response to treatments of the warming experiment in June and July. Colored bars are predicted values, and error bars are 95% confidence intervals. Note that y-axis is different for *E. vaginatum*.

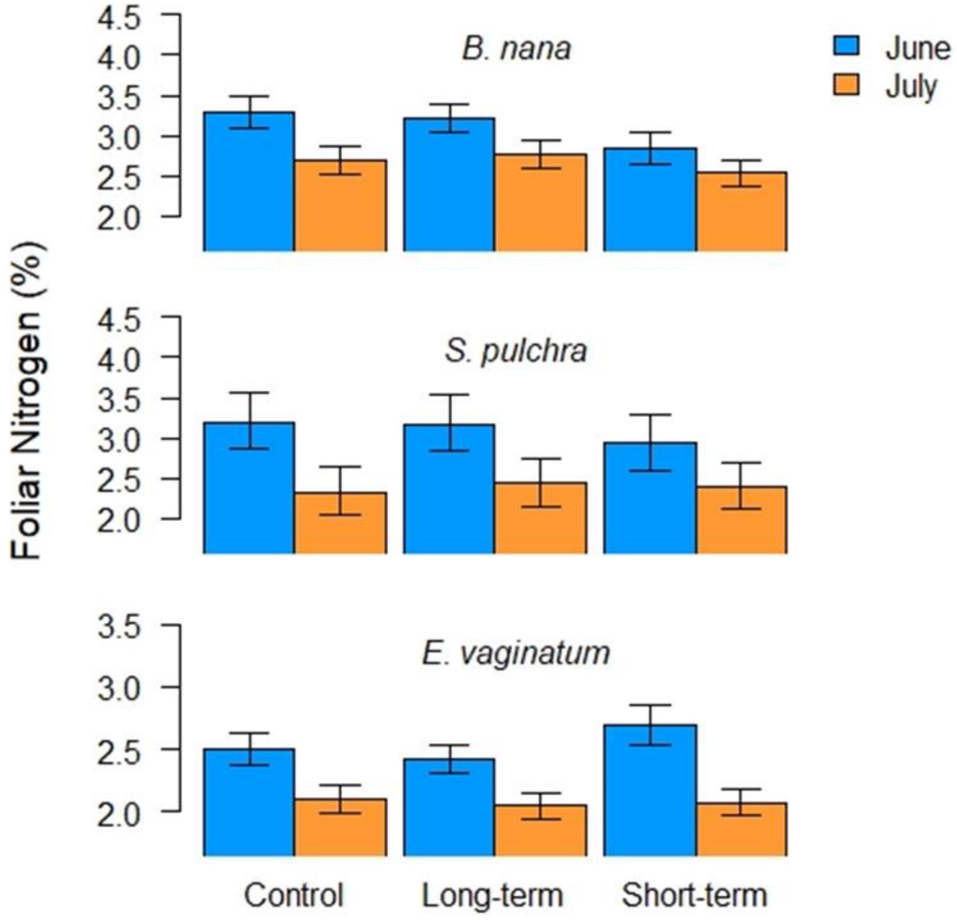

Figure 5. Nitrogen response to treatments of the warming experiment in June and July. Colored bars are predicted values, and error bars are 95% confidence intervals. Note that y-axis is different for *E. vaginatum*.

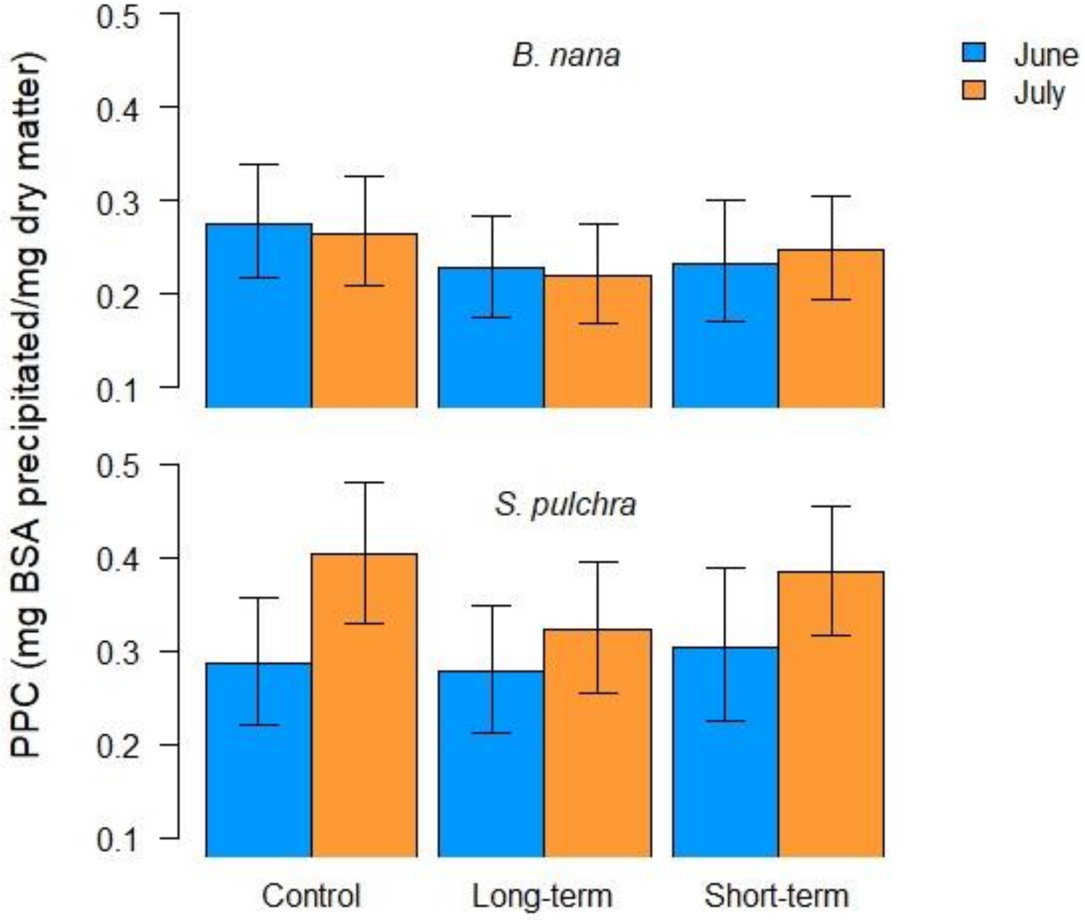

Figure 6. Protein-precipitating capacity response to treatments of the warming experiment. Colored bars are predicted values, and error bars are 95% confidence intervals.

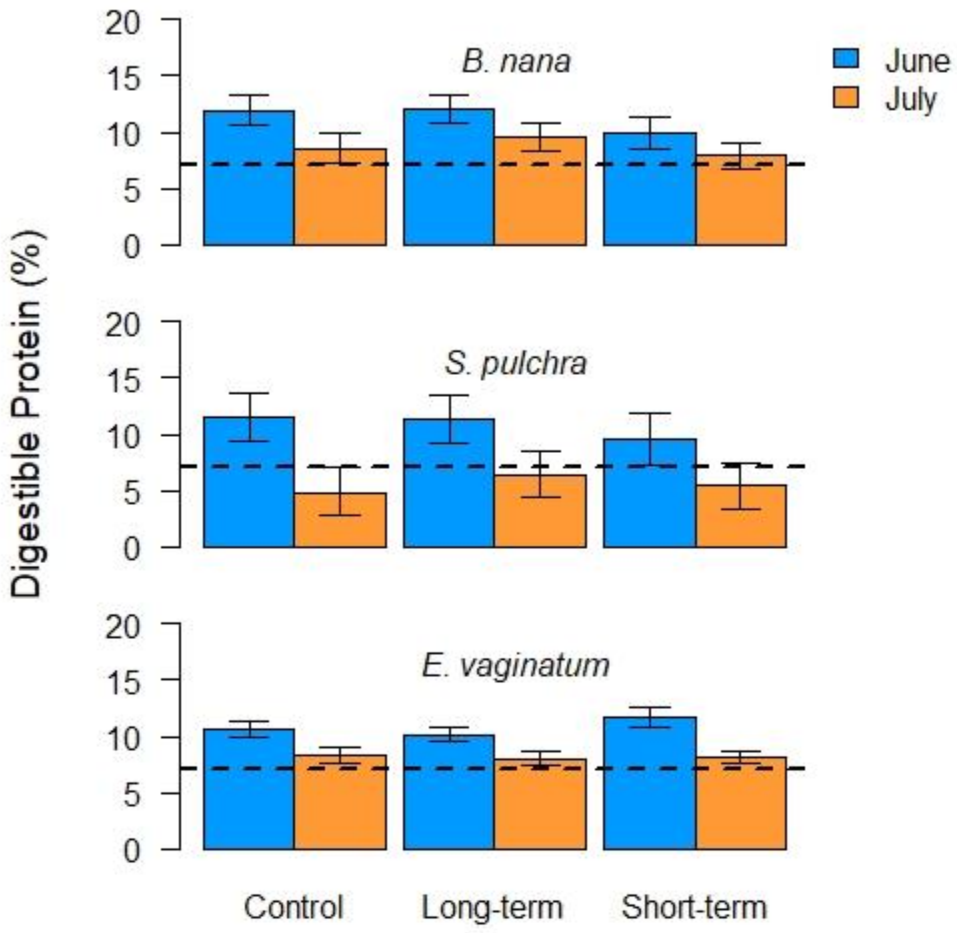

Figure 7. Digestible protein response to treatments of the warming experiment in June and July. Colored bars are predicted medians, and error bars are 95% confidence intervals. The dotted line represents the minimum digestible protein level required for reindeer to maintain body mass (lowest estimate of 7% DP)(Thompson and Barboza 2017).

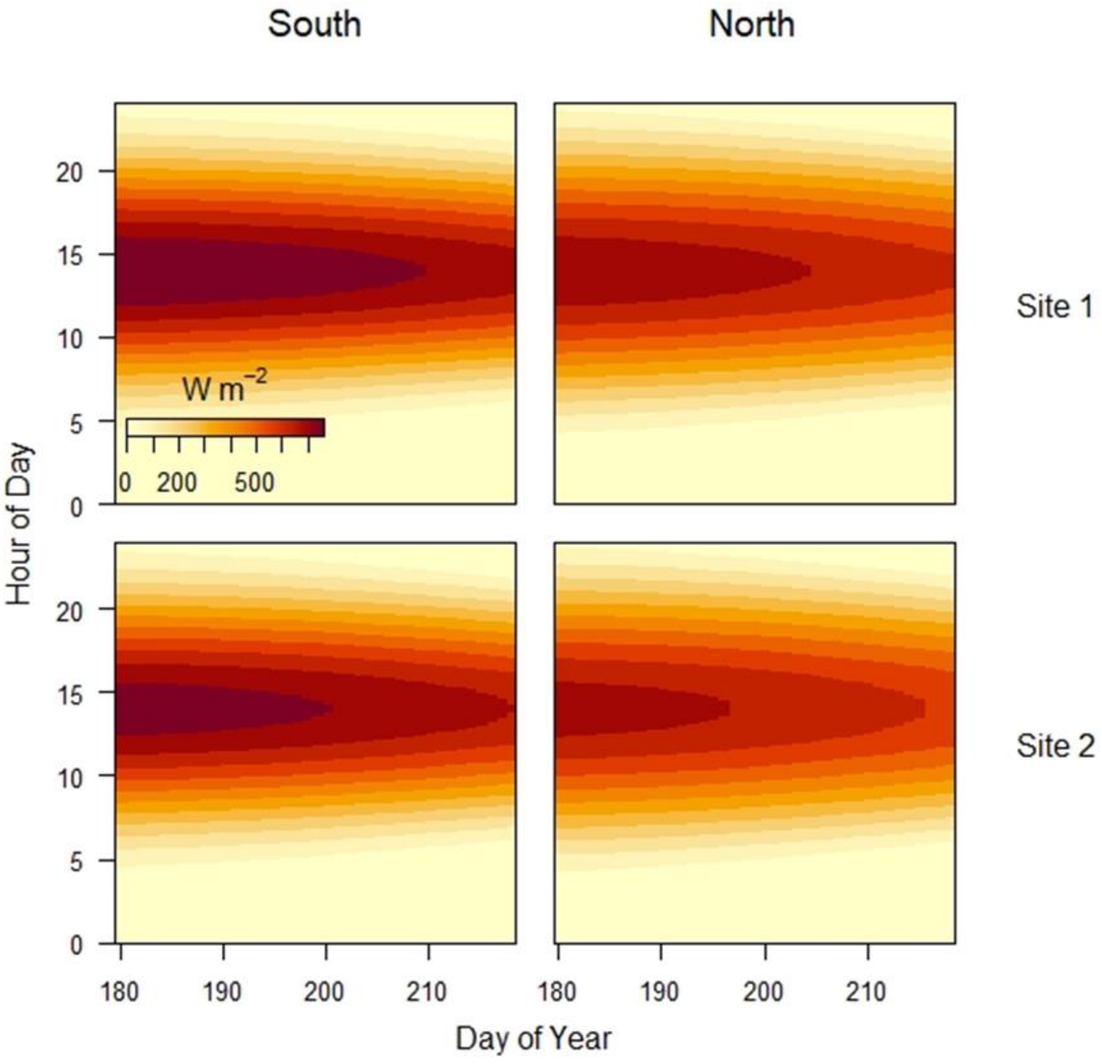

Figure 8. Solar radiation (W m^{-2}) received on south vs. north-facing slopes at hill sites 1 and 2 from days 180 to 218.

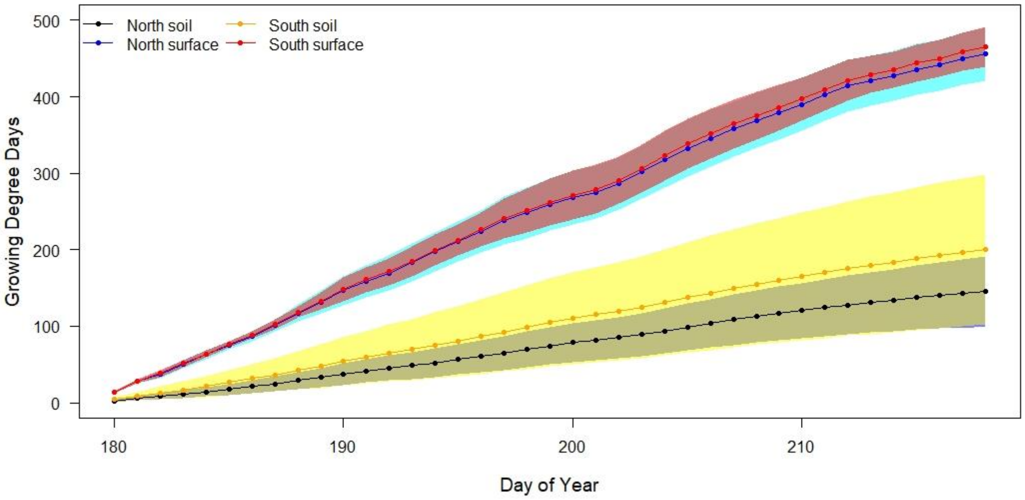

Figure 9. Surface and soil growing degree days of north vs. south-facing slopes from days 180 to 218. Points are the cumulative sum of median temperatures for each day, and polygons are mean ± standard deviation.

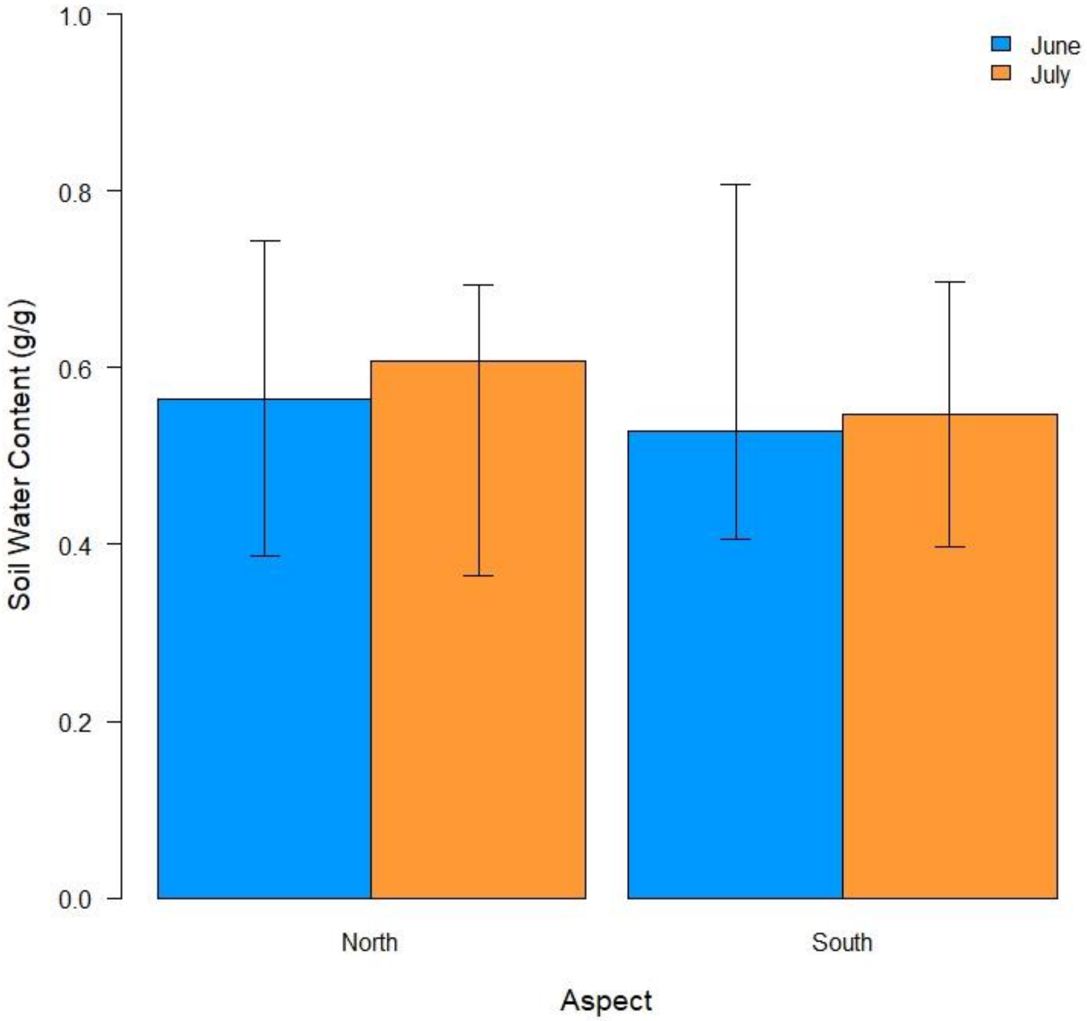

Figure 10. Gravimetric water content of soils between north vs. south-facing slopes in June and July 2019. Colored bars are means, and error bars are standard deviation.

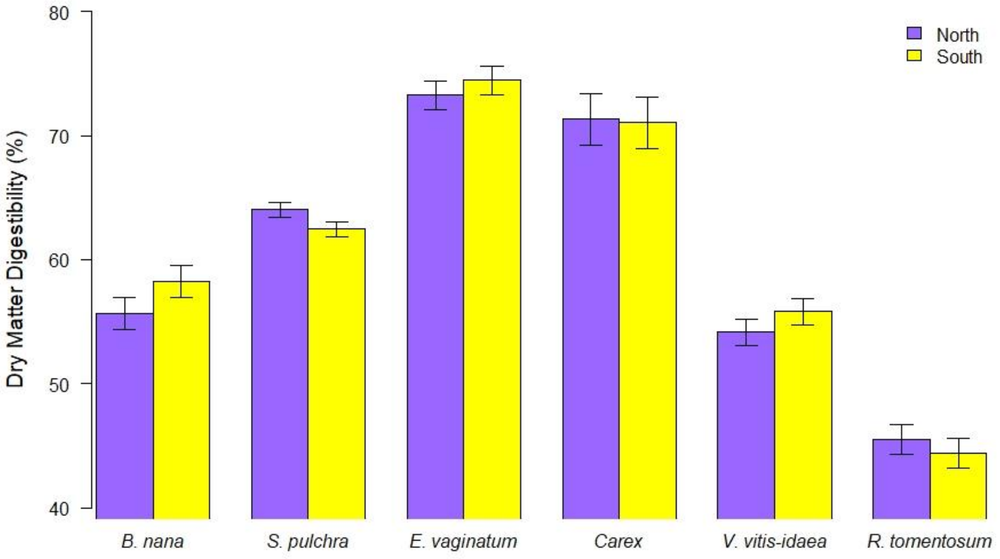

Figure 11. Dry matter digestibility response on north vs. south-facing slopes in August 2018. Colored bars are predicted values, and error bars are 95% confidence intervals.

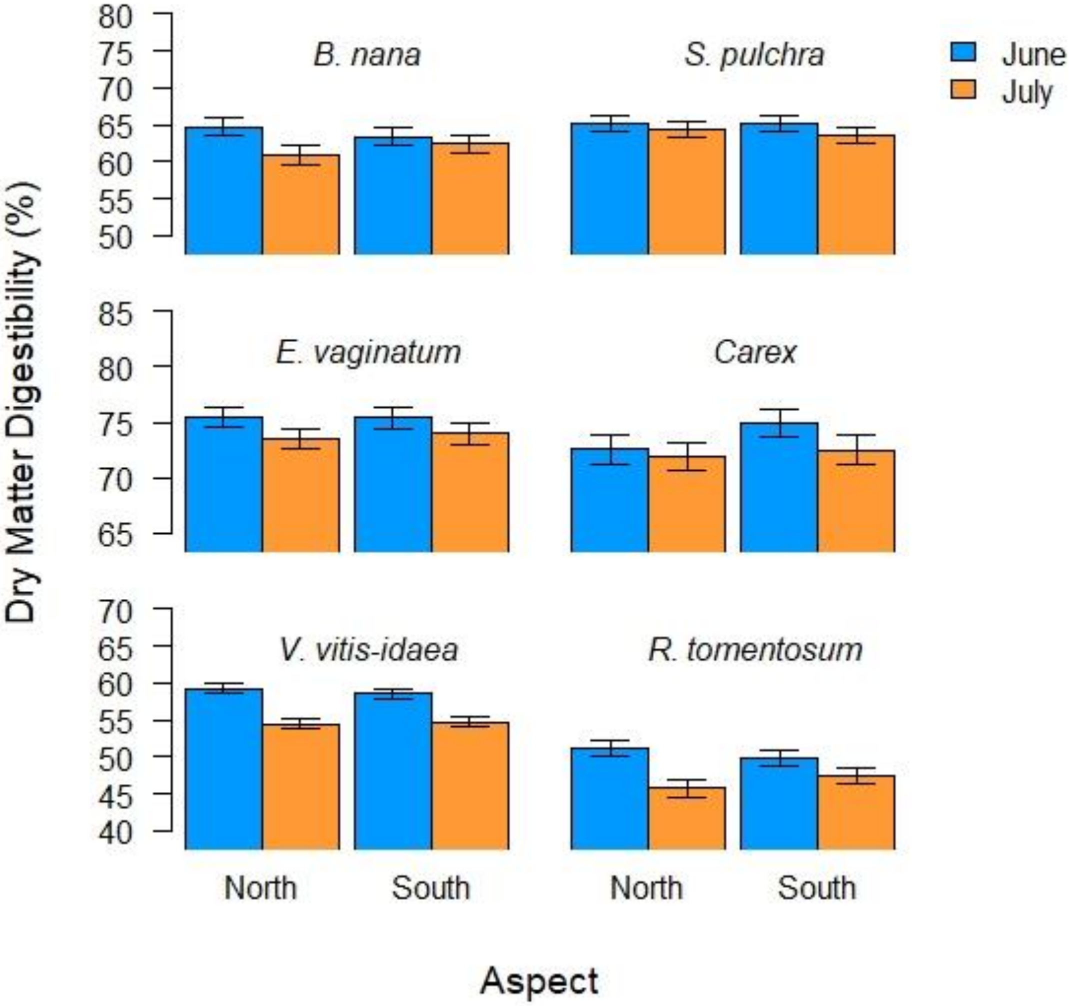

Figure 12. Dry matter digestibility response on north vs. south-facing slopes in June and July 2019. Colored bars are predicted values, and error bars are 95% confidence intervals. Note that y-axis differs among functional groups.

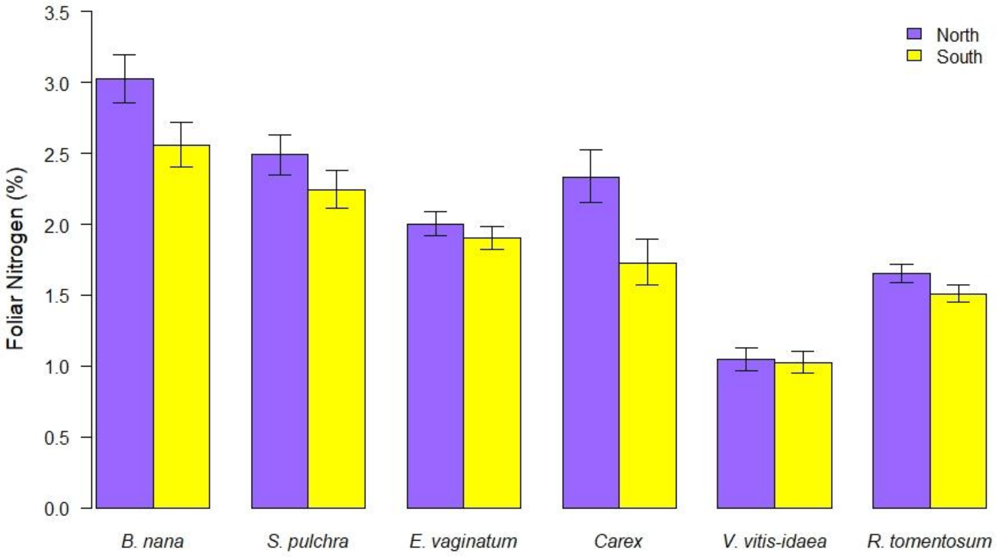

Figure 13. Foliar nitrogen response on north vs. south-facing slopes in August 2018. Colored bars are predicted values, and error bars are 95% confidence intervals.

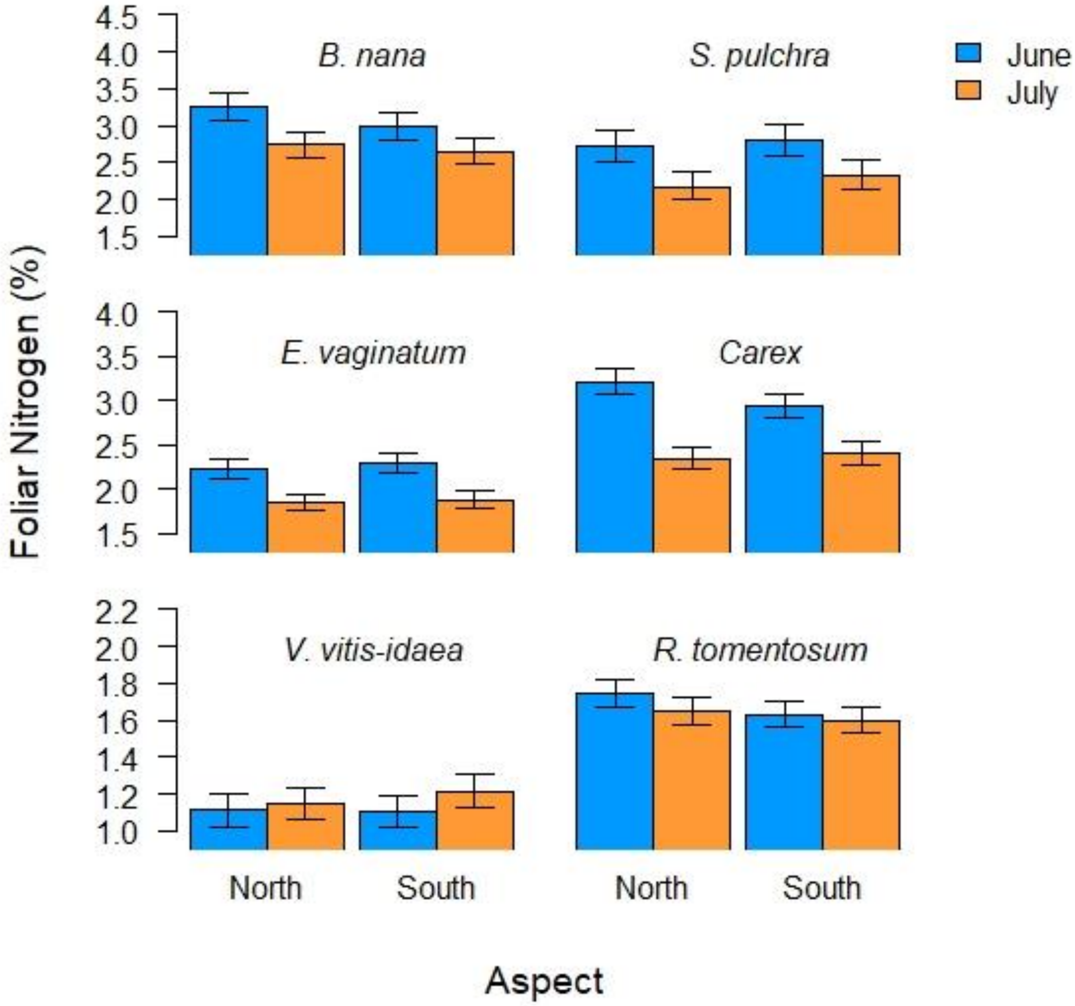

Figure 14. Foliar nitrogen response on north vs. south-facing slopes in June and July 2019. Colored bars are predicted values, and error bars are 95% confidence intervals. Note that y-axis differs among functional groups.

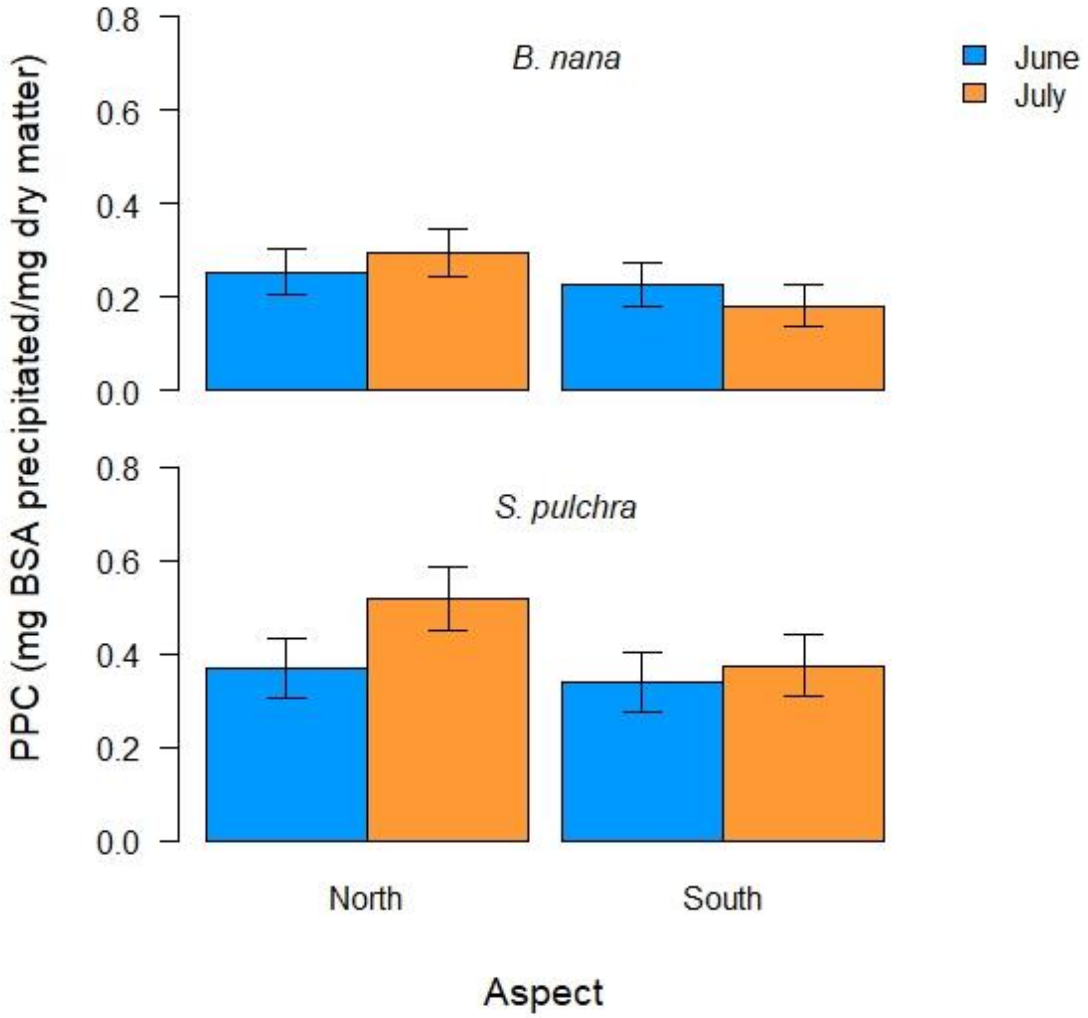

Figure 15. Protein-precipitating capacity response on north vs. south-facing slopes in June and July 2019. Colored bars are predicted values, and error bars are 95% confidence intervals.

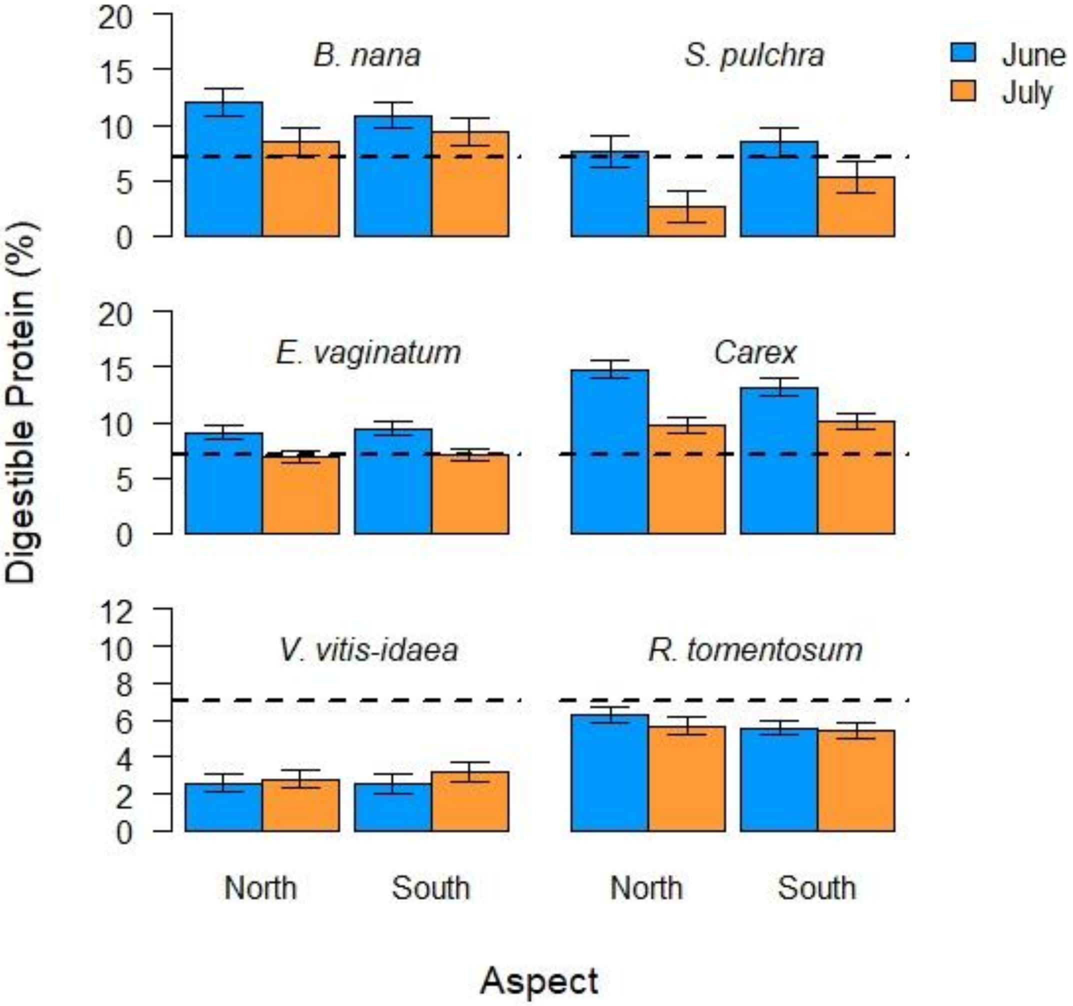

Figure 16. Digestible protein response on north vs. south-facing slopes in June and July 2019. Colored bars are predicted medians, and error bars are 95% confidence intervals. Note that y-axis is different for the evergreen dwarf shrubs. The dotted line represents the minimum digestible protein level required for reindeer to maintain body mass (lowest estimate of 7% DP).

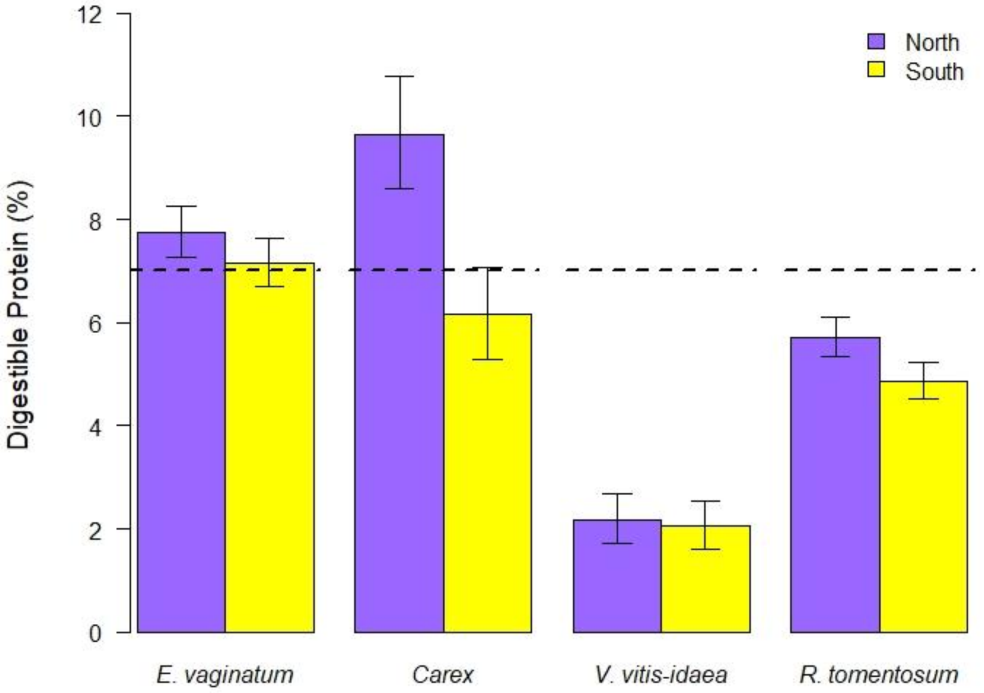

Figure 17. Digestible protein response on north vs. south-facing slopes in August 2018. Colored bars are predicted medians, and error bars are 95% confidence intervals. The dotted line represents the minimum digestible protein level required for reindeer to maintain body mass (lowest estimate of 7% DP)(Thompson and Barboza 2017).

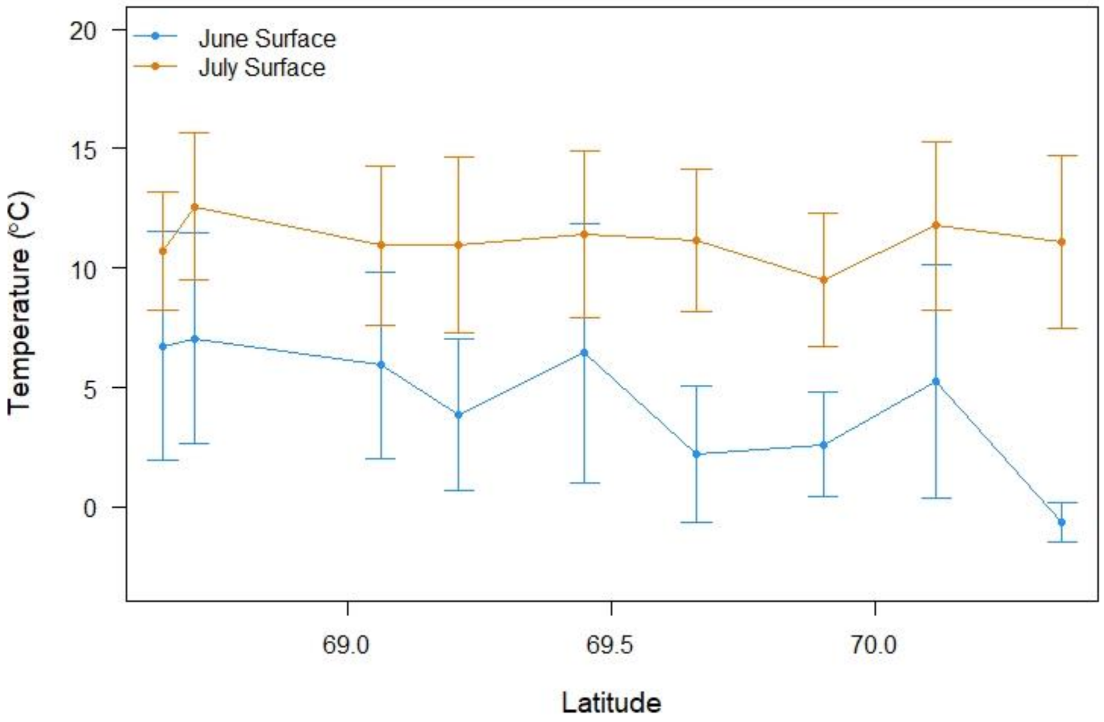

Figure 18. Daily surface temperature across latitude in June and July in 2017 and 2018. Points are means of median daily temperatures, and error bars are standard deviation.

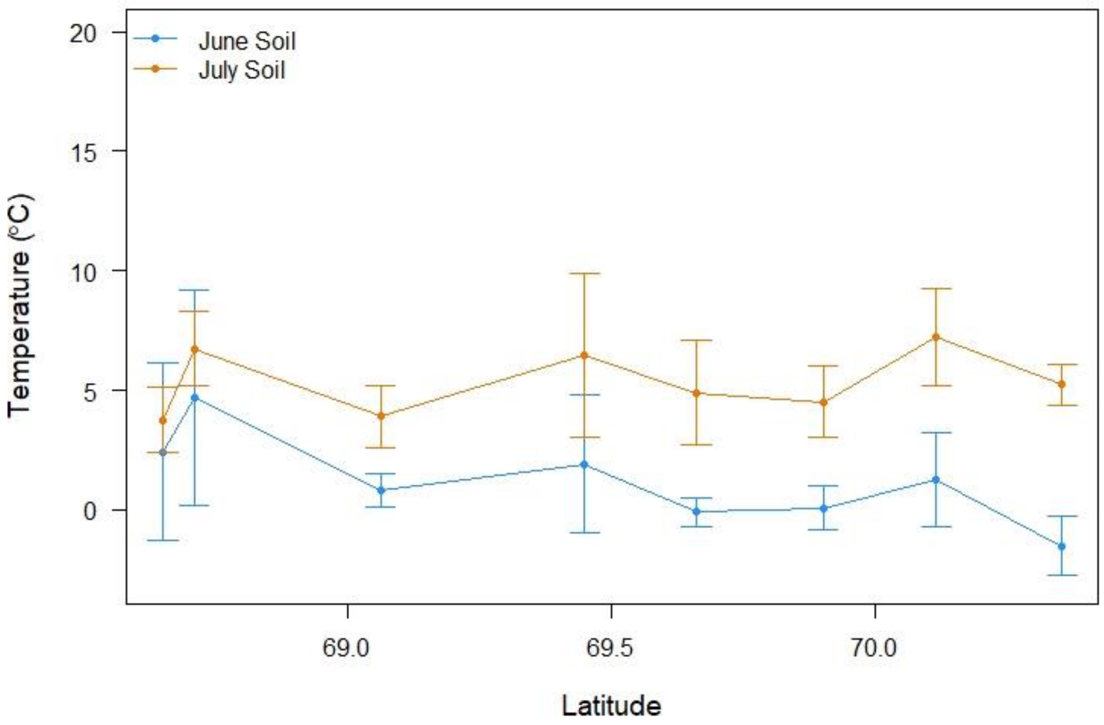

Figure 19. Daily soil temperature across latitude in June and July in 2017 and 2018. Points are means of median daily temperatures, and error bars are standard deviation.

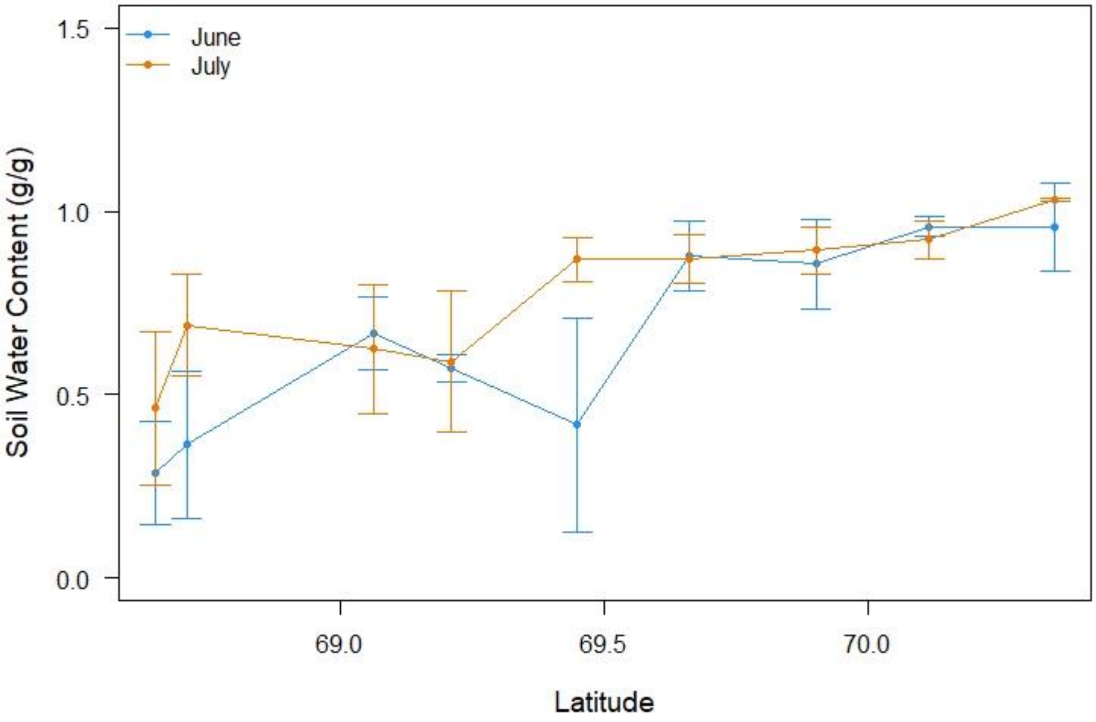

Figure 20. Gravimetric water content of soils across latitude in June and July in 2017 and 2018. Points are means, and error bars are standard deviation.

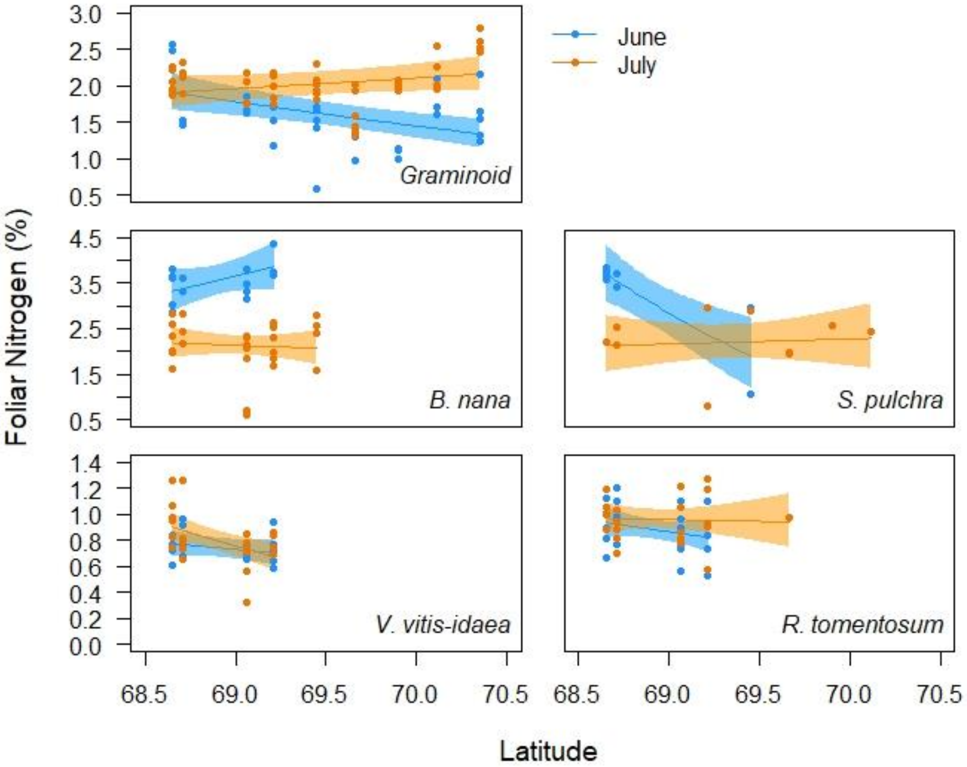

Figure 21. Foliar nitrogen response across latitude in June and July. Points are observed values, trend lines are predicted values, and polygons are 95% confidence intervals. Note that y-axis differs among functional groups.

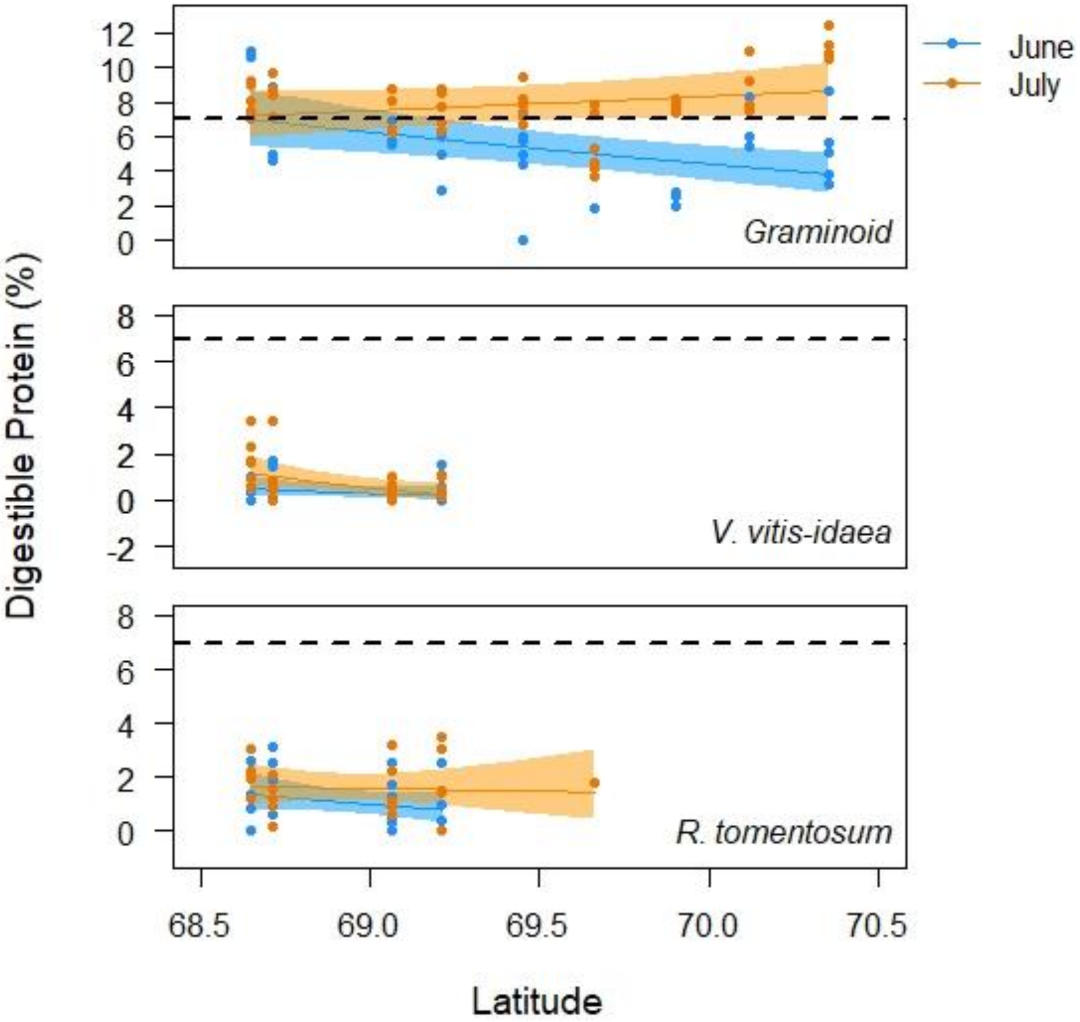

Figure 22. Digestible protein response across latitude in June and July. Points are observed values, trend lines are predicted values, and polygons are 95% confidence intervals. Note that y-axis differs among species. The dotted line represents the minimum digestible protein level required for reindeer to maintain body mass (lowest estimate of 7% DP)(Thompson and Barboza 2017).

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