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ARTICLE
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Short-term effects of summer warming on caribou forage quality are mitigated by long-term warming

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Abstract

Rapid Arctic climate change is leading to woody plant-dominated ecosystems with potential consequences for caribou foraging and nutritional ecology. While warming has been clearly linked to shrub expansion, the influence of higher temperatures on variables linked to the leaf-level quality of caribou forage is equivocal. Moreover, warming results in a complex set of ecosystem changes that operate on different timescales such as not only rapidly accelerating phenology, but also slowly increasing thaw depth and plant access to soil resources. Here, we compare changes in leaf nitrogen (N) concentration, digestibility, and protein-precipitating capacity (PPC) in short-term (i.e., <1–2 summers) and long-term (approximately 25 years) experimental warming plots with ambient temperature plots for three species commonly included in caribou summer diets: *Salix pulchra* (diamond-leaf willow), *Betula nana* (dwarf birch), and *Eriophorum vaginatum* (cottongrass). Short-term warming modestly decreased leaf N concentration in *B. nana*. Long-term and short-term warming slightly increased the digestibility of *S. pulchra*, but only short-term warming increased digestibility in *B. nana*. Greater dry matter digestibility in both shrubs occurred through reductions in the lignin and cutin quantity in plant cells. Long-term warming had no impact on PPC and equivocal impact on digestible protein of *B. nana*. Overall, we found short-term warming to be more impactful on forage quality than long-term warming at Toolik Lake, Alaska. Apart from a long-term warming reduction of approximately 13% in acid detergent lignin in *S. pulchra* and *B. nana*, other differences were only observed in the short-term warming plots. Hence, our results indicate acclimation of plants to long-term warming or possible negative feedback in the system to reduce warming effects. We suggest that warming summers may have a lesser effect on caribou forage than changes in winter precipitation or the influence of climate change on the abundance of critical species in the caribou diet.

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KEYWORDS
digestibility, leaf N concentration, long-term warming, *Rangifer tarandus*, secondary compounds, short-term warming, temperature

INTRODUCTION

The Arctic is warming more rapidly than lower latitudes with observed and further predicted consequences for ecosystems of the far north (Hinzman et al., 2013; Landrum & Holland, 2020; Serreze et al., 2009). Anthropogenic climate change has already resulted in an approximately 2°C increase in the Arctic mean annual temperature (Post et al., 2019) causing advancement of springtime phenology (Box et al., 2019; Zhao et al., 2015) and shrub expansion and increased height at the expense of mosses, lichens, and forbs (Berner et al., 2018; DeMarco et al., 2014; Macias-Fauria et al., 2012; Myers-Smith et al., 2011; Pattison et al., 2015; Tape et al., 2006). Warming by the latter part of the 21st century may exceed 8°C with continued northward expansion and infilling of woody vegetation (Bjorkman et al., 2018; Elmendorf et al., 2012; Hinzman et al., 2013; Vavrus et al., 2012).

The size of caribou herds is highly variable (Danell, 2006), but recent coordinated declines in population size throughout North America suggest climatic changes leading to greater woody shrub abundance (Fauchald et al., 2017) or shrub growth beyond approximately 1.5-m browse height (Forbs et al., 2010) may be partly responsible. During the summer, the caribou diet contains substantial shrub biomass (Denryter et al., 2017; Klein, 1990; White & Trudell, 1980) including *Betula* spp. (birch) and *Salix* spp. (willow). In the early summer, these shrubs are high in leaf nitrogen (N) concentration (>3%) and high in dry matter digestibility (DMD) (>60%) and help animals recover protein deficits incurred during winter, reproduction, and lactation (Couturier et al., 2009; Crête & Huot, 1993; Richert et al., 2021; Taillon et al., 2013). Shrubs, however, are also high in secondary compounds such as tannins and phenols that bind proteins, reduce digestibility, and act as anti-herbivory defenses (Coley et al., 1985; Robbins, Hanley, et al., 1987; Thompson & Barboza, 2014; Turunen et al., 2009). Moreover, *Salix* spp. is typically lower in secondary compound concentration than *Betula* spp. (Christie et al., 2015; Graglia et al., 2001; Richert et al., 2021). Consequently, caribou benefit from a mixed diet of shrubs, graminoids, and forbs to limit exposure to these anti-herbivory compounds (Turunen et al., 2009).

Although shrub biomass is clearly increasing, the impact of warming on the forage quality of shrubs is less well understood. Shrub leaf N concentration generally increases with warmer soils from deeper snow during winter (Leffler et al., 2016; Leffler & Welker, 2013; Richert et al., 2021; Sullivan & Welker, 2007; Welker et al., 2005). Warm summers may decrease leaf N concentration by accelerating the synthesis of structural carbohydrates that dilute N and other key nutrients in leaves. Moreover, structural carbohydrates can also reduce the digestion of all dry matter components including those that contain N, reducing available N for animals and eventually N addition to soils (Chapin et al., 1995; Turunen et al., 2009; Zamin et al., 2017). Experiments involving fertilizer addition in the Arctic suggest that leaf N concentration is susceptible to rates of decomposition and mineralization, which alter N availability in soils (DeMarco et al., 2014; Shaver & Chapin III, 1980); these processes are also sensitive to temperature (Fierer et al., 2005; Pold et al., 2021; Salazar et al., 2021).

Similarly, the digestibility of leaf tissue often declines during the growing season (Barboza et al., 2018; Richert et al., 2021) and warming may accelerate the shift from high digestibility in the spring to lower digestibility later in the summer (Zamin et al., 2017). Digestibility is frequently described as three components of plant cells: neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL), all of which reduce digestibility. Highly digestible forage is low in NDF, a measure of cell wall fraction of forage; and ADF, which is less digestible cellulose, lignin, cutin, and mineral matter (Van Soest, 1994). High NDF can limit animal intake, while high ADF will limit digestion. Highly digestible forage is also low in ADL, which are compounds that physically block rumen microbes from breaking down otherwise digestible material (Moore & Hans-Joachim, 2001). Previous studies, however, document few changes in plant fiber and lignin content with warming (Dumont et al., 2015; Zamin et al., 2017) although warming may increase lignification (Wilson et al., 1991).

Tissue concentrations of plant secondary compounds such as tannins and phenolics used as anti-herbivore defense are highly variable. Their abundance has been linked to carbohydrate and N status of plants, and differs among identified compounds and plant species, and through space and time of production (Coley et al., 1985; Dormann, 2003; Gebauer et al., 1998; Haukioja et al., 1998). Additionally, these compounds can be induced by herbivory; hence, their abundance is potentially a feedback with animal consumption and difficult

to study in situ if prior exposure to herbivory is unclear (Agrawal, 1998; Kaplan et al., 2008). The influence of warming on these compounds appears inconsistent (Bidart-Bouzat & Imeh-Nathaniel, 2008). For example, elevated temperature had no effect on *Betula nana* secondary compounds in Abisko, Sweden, but tannin concentration increased in this species at Toolik Lake, Alaska (Graglia et al., 2001). Separately, warming reduced total phenolics in *B. pendula* and *Salix myrsinifolia* in Finland (Kuokkanen et al., 2001; Veteli et al., 2002) but did not alter total phenolics or condensed tannins in *S. polaris* on Svalbard, Norway (Dormann, 2003).

Forage quality responses to warming involve multiple processes that operate on different time scales. Nearly all plant growth is influenced by cumulative heat (i.e., growing degree days) that critically influences the maturation and phenology of key seasonal activities such as budburst and flowering (Collins et al., 2021; May et al., 2020; Prevéy et al., 2022). The cumulative heat effect of warming should drive immediate- to short-term responses in forage quality. For example, we anticipate that a warmed plant will have lower leaf N concentration and lower digestibility if sampled on the same day as an ambient temperature plant because the warmed plant matures more rapidly (Dumont et al., 2015) and because leaf N concentration and digestibility decline during the growing season (Barboza et al., 2018; Richert et al., 2021). Additionally, warming can influence processes that operate on longer timescales such as those mediated by soil resources (Geml et al., 2016; Schaeffer et al., 2013; Semenova et al., 2015). For example, warmer soils in winter through additional snow insulation previously increased N availability and leaf N concentration in multiple high-latitude settings (Leffler et al., 2016; Leffler & Welker, 2013; Richert et al., 2021; Schimel et al., 2004; Sullivan & Welker, 2007; Welker et al., 2005). Moreover, the cumulative effect of multiple years of warming is greater biomass, suggesting total canopy N may increase even though leaf N concentration declines or is not affected (DeMarco et al., 2014). The most important yet often overlooked concept is that separate short-term and long-term consequences of climate change are not mutually exclusive (Mack et al., 2004) and potentially alter forage quality in opposite directions.

Here, we use a combination of recently established (less than 2 years) and older (approximately 25 years) experimental plots to investigate the immediate- and long-term consequences of Arctic warming for variables contributing to caribou forage quality. Among climate change studies, this is one of the longest experiments to investigate the consequences of warming. Long-term experiments yielding insights on persistent consequences of a warmer world are necessary to inform decision-making for the conservation and management of plant and animal resources. We hypothesize that short-term warming will result in nearly immediate changes in forage quality parameters closely linked to growth and maturation such as leaf tissue N concentration and digestibility, but that fewer forage quality-related parameters will be affected in long-term warming plots because of processes that mitigate the impact of warming such as a deeper active layer or more rapid decomposition.

METHODS

We conducted this experiment at Toolik Lake Field Station (68°63′ N, 149°60′ W; 740-m elevation) on the North Slope of Alaska. Toolik Lake is within the Arctic Foothills and experiences a mean air temperature of approximately 11°C in July and −21°C in January; the mean annual precipitation is approximately 310 mm (Environmental Data Center Team, 2020a). The experiment occurred in moist acidic tussock tundra with dominant species including the deciduous shrubs *B. nana* (dwarf birch) and *Salix pulchra* (diamond-leaf willow), the evergreen dwarf shrubs *Vaccinium vitis-idaea* (lingonberry) and *Rhododendron tomentosum* (formerly *Ledum palustre*, Labrador tea), and sedges including *Eriophorum vaginatum* (cottongrass) and several species in the genus *Carex*. The species targeted for sampling in this experiment were *B. nana*, *S. pulchra*, and *E. vaginatum*.

Hexagon fiberglass open-top chambers (OTCs) following the International Tundra Experiment design were used for the warming experiment. Chambers were 40 cm tall, either 1.0 or 1.5 m in basal diameter (Marion et al., 1997; Walker et al., 1999), and randomly arranged. Ten OTCs that have been in place between mid-June and late August nearly every summer since 1994 (Wahren et al., 2005; Walker et al., 1999; Welker et al., 2005) served as long-term warming plots (approximately 25 summers of warming). Nearby, 10 additional OTCs were placed to serve as short-term warming plots. New locations for the OTCs were selected based on species composition to ensure adequate amounts of each of the three target species for this experiment. Within the same plant community, eight control plots with no OTCs were delineated from the area between the short-term and long-term OTCs. Chambers were placed on 27–30 June in 2018 and 7 June in 2019. Differences in the timing of placement of OTCs between years were due to differences in the date the site became accessible due to snow depth and snowmelt timing in 2018 and 2019. Chambers were removed in mid-August both years. In past experiments at this study site, OTCs warmed air temperature and soil 5 cm deep by approximately 1–1.5°C with the most pronounced air temperature increases near solar noon (Leffler et al., 2016;

Walker et al., 1999). Here, 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 the moss layer) in three OTCs and three control plots during summer 2019. All loggers recorded temperature hourly.

Samples from the three target species (*B. nana*, *S. pulchra*, and *E. vaginatum*) were collected twice each summer in 2018 and 2019. Within each OTC and control plot, tissue samples were harvested by taking green *E. vaginatum* tillers and stripping leaves from the shrubs to most accurately simulate the material consumed by caribou. We collected two samples from each species (samples may or may not have come from the same individual depending on the abundance of each species in a plot), one for analysis of fiber digestibility and leaf N concentration, and the other for protein-precipitating capacity (PPC) analysis of plant secondary compounds. Samples collected for PPC analysis were stored on dry ice in the field and rapidly transferred to a −20°C freezer at the field station to minimize compound degradation prior to analysis. Plants were sampled in 2018 on 29 June–1 July and 29–30 July; and in 2019 on 21 June and 22 July.

Leaves of deciduous shrubs, graminoids, and evergreen dwarf shrubs, including the upper portion of the stem to which leaves were attached to the dwarf shrubs, were analyzed for leaf N concentration. 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 (Wiley Mill Model 4 [used in 2018] and Wiley Mini Cutting Mill [used in 2019], Thomas Scientific, Swedesboro, NJ, USA). The initially ground material was placed into 2-ml microcentrifuge 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 2 min. Afterward, the tubes were placed in an oven at 100°C for at least 24 h, then stored in a desiccator. Weighing with a microbalance, 3.0–3.5 mg of sample was placed into 5 × 9 mm tin capsules and tissue N (% by weight) was determined by combustion using a CHNSO Elemental Analyzer (model ECS 4010; Costech Analytical Technologies, Inc., Valencia, CA, USA) at the University of Alaska Anchorage.

We measured the DMD of the same forage samples using the sequential method outlined by ANKOM Technology (2018a, 2018b). The ground material was placed into 25-μm porosity filter bags. The bags were placed in an automated fiber digester (model 200, ANKOM Technology, Macedon, NY, USA) and digested with a neutral detergent solution (neutral detergent dry concentrate with triethylene glycol, ANKOM Technology, Macedon, NY, USA) with sodium sulfite and an alpha-amylase enzyme solution (alpha-amylase; ANKOM Technology, Macedon, NY, USA) yielding NDF. The material was then digested with acid detergent solution (acid detergent liquid concentrate diluted with water, ANKOM Technology, Macedon, NY, USA) yielding ADF. The bags were then soaked in 72% sulfuric acid yielding ADL and cutin, and lastly ashed in a muffle furnace at 525°C for at least 3 h, yielding mineral content. From these components, DMD (% by weight) was calculated as the sum of digestible NDF and digestible neutral detergent solubles (NDS; Hanley et al., 1992, Spalinger et al., 2010), using equations from Robbins, Mole, et al. (1987) for mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*), and Spalinger et al. (2010) for moose (*Alces alces*):

$$\mathrm{DMD} = \left(92.31\mathrm{e}^{-0.0451\times(\mathrm{LC})} \times \mathrm{NDF}\right) + (0.831 \times \mathrm{NDS} - 6.97), \quad (1)$$

where LC is the percent lignin and cutin of NDF. In 2019, the acid detergent solution used to process a random portion of the samples was mistakenly over-diluted. However, the mean %ADF of samples and standards processed with the over-diluted solution was comparable to the mean %ADF of samples and standards processed with the correct acid detergent solution concentration.

We used a bovine serum albumin (BSA) binding assay (McArt et al., 2006) to determine the PPC of secondary compounds in *B. nana* and *S. pulchra*. Plant material was freeze-dried and ground to pass a 1-mm mesh. We used an accelerated solvent extractor (ASE-200; Dionex Corporation, Sunnyvale, CA, USA) to extract secondary compounds in aqueous methanol. The resulting extract was increasingly diluted with methanol, and BSA protein was added with Coomassie Brilliant Blue protein dye (Thermo Fisher Scientific Inc., Waltham, MA, USA) to indicate the presence of protein. The absorbance was measured with a UV–visible microplate spectrophotometer (Synergy HT Multi-Mode Microplate Reader, BioTek Instruments Inc., Winooski, VT, USA) at 595 nm. The quantity of BSA precipitated was calculated from these readings using a standard curve adjusted for the quantity of forage dry matter used in extraction. To combine the results from the analysis of leaf N concentration and PPC into a single metric of protein available to consumers, we calculated digestible protein (DP; % by weight), which is the remaining protein that can be incorporated into animal tissue after accounting for binding by secondary compounds using a general equation developed for cervids (Robbins, Hanley, et al., 1987):

$$\mathrm{DP} = -3.87 + 0.9283 \times \mathrm{CP} - 11.82 \times \mathrm{PPC}, \quad (2)$$

where CP (% by weight) is crude protein, calculated as 6.25 × percent nitrogen. The PPC of *E. vaginatum* was not measured in this study because graminoids typically

contain relatively low amounts of secondary compounds that bind proteins (Barboza et al., 2018; Jung et al., 1979; Robbins, Hanley, et al., 1987; Zamin et al., 2017).

We analyzed for significant differences between treatments and controls using a linear mixed-model framework implemented in the nlme package within the R statistical computing framework (R Core Team, 2021). Since all measured variables are proportions, we used the arcsine square root transformation prior to analysis. Fixed effects were time of sample and treatment (control, short-term warming, and long-term warming) with the control coded as the reference level. We treated time of sample as continuous with distinct sample periods enumerated as 0–3 indicating the number of months of warming experienced in this study. We included an interaction between time of sample and treatment and anticipated a significant interaction effect since the short-term plots would be reacting to a sudden change in temperature, while the long-term warming plots would be experiencing similar summer conditions as in the past 25 years. The study plot was declared as a random effect, and we analyzed each response with a first-order autocorrelation structure to account for repeated sampling of the same OTCs. The mixed-model fit was followed with a two-way ANOVA test of significance for fixed effects. Means were separated among treatments using Tukey's adjusted marginal means when the interaction between time and treatment was significant. We rejected the null hypothesis of ANOVA when $p < 0.05$, but separated means within a treatment at $p < 0.10$.

RESULTS

The summer of 2018 at Toolik Field Station was cooler and drier than the summer of 2019 (Environmental Data Center Team, 2020a). The mean air temperature (3 m above surface) was 4.8, 10.3, and 4.2°C in June, July, and August 2018, respectively. In 2019, the mean temperature in the same months was 8.2, 12.3, and 4.4°C. In 2018, June precipitation was 37 mm, July precipitation was 106 mm, and August precipitation was 117 mm. In 2019, precipitation in the same months was 83, 59, and 179 mm. During the winter prior to summer 2018, maximum snow depth was 46 cm, but in the winter prior to summer 2019, maximum snow depth was only 28 cm. Consequently, snowmelt and plant phenology at Toolik were delayed in 2018 compared with 2019. In situ measurement of green-up date was 7 June (day of year = 158.4 ± 8.9) in 2018, but 20 May (day of year = 140.1 ± 7.2) in 2019 (Environmental Data Center Team, 2020b). Additionally, peak NDVI (i.e., maximum greenness) occurred 24 July to 10 August (day of year 205–222) in 2018, but 8 July to 22 July (day of year 189–203) in 2019 (Environmental Data Center Team, 2020b), suggesting a seasonal phenology difference of approximately 2 weeks between the 2 years of this study.

Open-top chambers warmed experimental plots in this study by approximately 1°C during July 2019 (Figure 1). Here, we measured soil surface temperature and soil temperature at 10-cm depth. The mean July soil surface temperature was 8.7°C in the ambient plots and 9.7°C in the warmed plots. During midday (11:00 AM–5:00 PM) when the warming effect of OTCs is most extreme, the surface temperature difference between treatments was only slightly greater (13.9°C warmed and 12.8°C ambient). The mean soil temperature at 10-cm depth was not greater in the warmed plots (3.1°C warmed and 3.8°C ambient).

We observed significant time of sample × warming treatment interaction effects for leaf N concentration in *S. pulchra*, *B. nana*, and *E. vaginatum* (Table 1). Post hoc multiple comparisons to separate means among warming treatments, however, only yielded significant differences for *B. nana* (Figure 2). In this species, leaf N concentration was lower in the short-term warming treatment (2.76%) compared with both the control and long-term plots (2.99% in both), representing a 7.7% reduction in leaf N concentration for *B. nana* in response to short-term warming.

We observed a significant time of sample × warming treatment interaction effect for DMD in *S. pulchra* (Table 1). Post hoc multiple comparisons to separate

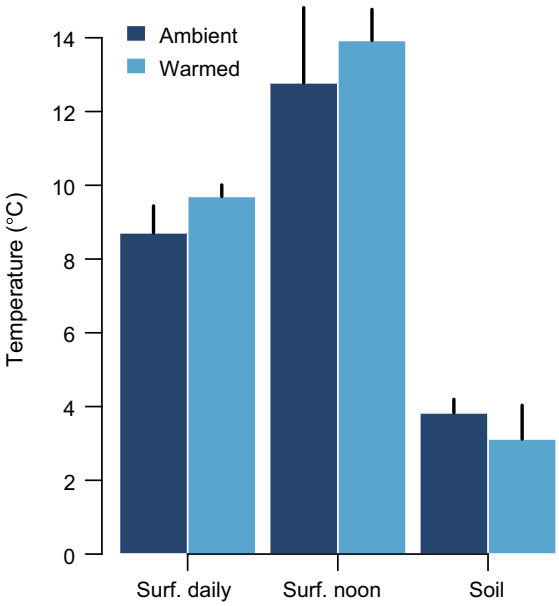


FIGURE 1 Temperature during July 2019 in ambient and warmed by open-top chamber plots. Values are the daily surface or soil (10-cm depth) means among three plots in each treatment or the mean surface temperature 3 h before and after solar noon. Error bars are 1 SD among plots.

TABLE 1 Test of fixed effects from mixed-model analysis of forage quality data. Values shown are df[a], *F*, and *p* values for each test with $p < \sim 0.05$ in boldface.

			F/*p*						
Species	**Effect**	**df**	**N**	**DMD**	**NDF**	**ADF**	**ADL**	**PPC**	**DP**
Salix pulchra	Treatment	2	0.29 0.752	9.4 **<0.001**	3.21 0.058	5.01 **0.015**	10.01 **0.001**	1.983 0.159	1.433 0.258
	Time	1	186.23 **<0.001**	1.3 0.266	1.93 0.169	0.97 0.328	0.149 0.701	0.2584 0.613	341.3 **<0.001**
	Treatment × time	2	5.58 **0.006**	5.0 **0.009**	4.09 **0.021**	7.33 **0.001**	4.788 **0.011**	0.1490 0.862	5.173 **0.008**
Betula nana	Treatment	2	4.221 0.27	3.26 0.055	0.916 0.413	1.954 0.163	5.841 **0.008**	1.874 0.174	3.348 **0.052**
	Time	1	61.222 **<0.001**	24.48 **<0.001**	9.824 **0.002**	30.68 **<0.001**	23.54 **<0.001**	3.591 0.062	84.83 **<0.001**
	Treatment × time	2	3.527 **0.034**	0.74 0.478	0.114 0.893	1.407 0.251	2.505 0.088	1.209 0.304	3.076 **0.052**
Eriophorum vaginatum	Treatment	2	0.493 0.617	1.13 0.339	5.64 **0.010**	1.64 0.215	1.677 0.207	...	...
	Time	1	1.695 0.197	4.02 **0.048**	392.4 **<0.001**	61.27 **<0.001**	0.9774 0.326	...	...
	Treatment × time	2	5.593 **0.005**	0.11 0.895	0.27 0.763	4.59 **0.013**	0.1396 0.870	...	...

[a]Denominator degrees of freedom are 25 for "Treatment" and between 66 and 81 for "Time" and "Time × treatment."

means among warming treatments suggest slightly higher DMD in both the short-term and long-term warming plots compared with the control (Figure 2). Digestibility in the control treatment was 64.8% compared with 66.3% in the warming plots. This difference represents a 2.3% increase in digestibility in *S. pulchra* in response to warming.

For the components of digestibility, we observed either significant time of sample × warming treatment interaction effects or significant warming treatment main effects for each species. Although NDF varied among warming treatments for each species (Table 1), post hoc mean separation only yielded differences among warming treatments in *S. pulchra* and *E. vaginatum* (Figure 3). For *S. pulchra*, short-term warming resulted in lower NDF than control (17.2% vs. 18.4%), but long-term warming differed from neither short-term warming nor control. For *S. pulchra*, warming resulted in a 6.5% reduction in NDF. In *E. vaginatum*, however, warming resulted in higher NDF (65.6% vs. 63.9%), an increase of 2.3%. Acid detergent fiber varied among warming treatments for *S. pulchra* and *E. vaginatum* (Table 1), but means only separated in our post hoc test for *S. pulchra*. In *S. pulchra*, the pattern of mean separation for ADF was the same as for NDF (Figure 3); ADF was lower in short-term warming (12.0%) than in either control (12.9%) or long-term warming (12.3%), an approximately 4.5% reduction in ADF for both warming treatments. For ADL, we observed a significant time of sample × warming treatment interaction effect for *S. pulchra* and a significant warming treatment effect for *B. nana* (Table 1). In both species, means were separated such that short-term warming and long-term warming were lower in ADL than control. *Salix pulchra* leaves in warmed plots had 5.3% ADL, while leaves in control plots had 6.1% ADL. This is a 13% decline due to warming. *Betula nana* leaves in warmed plots had 6.7% ADL, while leaves in control plots had 7.7% ADL, also a 13% reduction.

We observed no significant time of sample × warming treatment interaction or warming treatment main effects for PPC, but the time of sample × warming treatment interaction was significant for DP in *S. pulchra* and *B. nana* (Table 1). For DP in *S. pulchra*, however, post hoc mean separation did not reveal any significant differences among treatments (Figure 4). For *B. nana*, short-term warming resulted in lower DP (9.1%) than control (10.3%) and long-term warming (10.8%). This decline in *B. nana* DP in response to short-term warming was 14.2% lower than the control.

DISCUSSION

Long- and short-term experimental warming had modest and inconsistent effects on variables related to forage

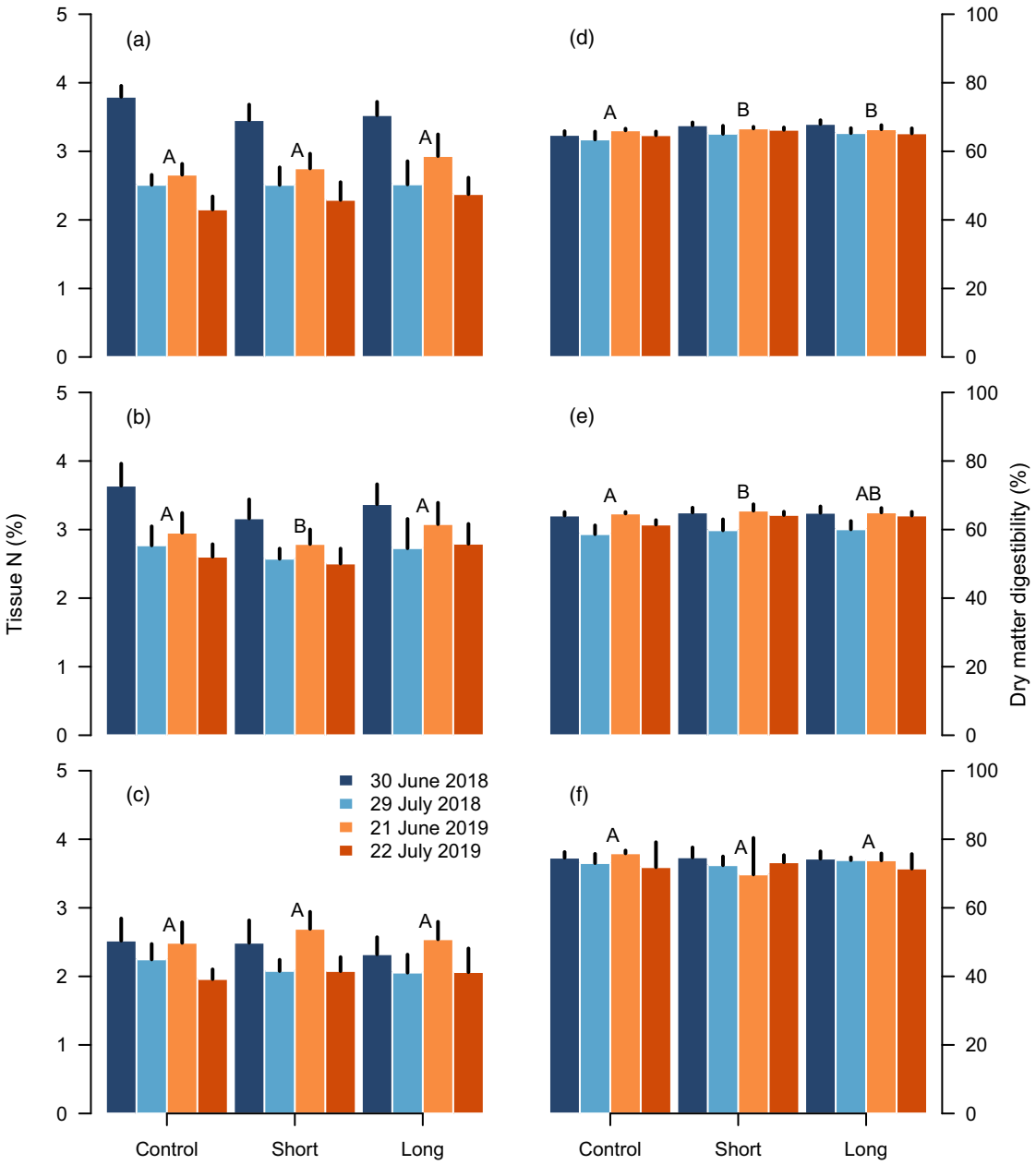


FIGURE 2 Leaf tissue N concentration (a–c) and dry matter digestibility (d–f) on four sample dates in 2018 and 2019 for *Salix pulchra* (a and d), *Betula nana* (b and e), and *Eriophorum vaginatum* (c and f). Values (percent dry weight) are means and 1 SD. Capital letters indicate differences among control, short-term warming, and long-term warming.

quality in *S. pulchra*, *B. nana*, and *E. vaginatum*. Consistent with our hypothesis, we found a greater number of significant differences in forage quality between ambient temperature and short-term warming than we did between ambient temperature and long-term warming. Short-term warming influenced leaf N concentration, dry matter digestibility, and digestibility components for at least one species, while long-term warming only influenced dry matter digestibility and ADL of the two shrub species. These results suggest that immediate warming impacts are mitigated by consistently warmer summers except for a small increase in digestibility. We also observed all but one of our significant effects to be interactions between time and treatment, suggesting that long-term and short-term effects changed at different rates during this experiment, likely indicating continued modification of the short-term response, while the long-term response was more stable.

Leaf N concentration declined by nearly 8% (an absolute change of 0.23% N) in *B. nana*, but only in response to short-term warming. Previous measurements on the same long-term warming plots yielded no significant difference

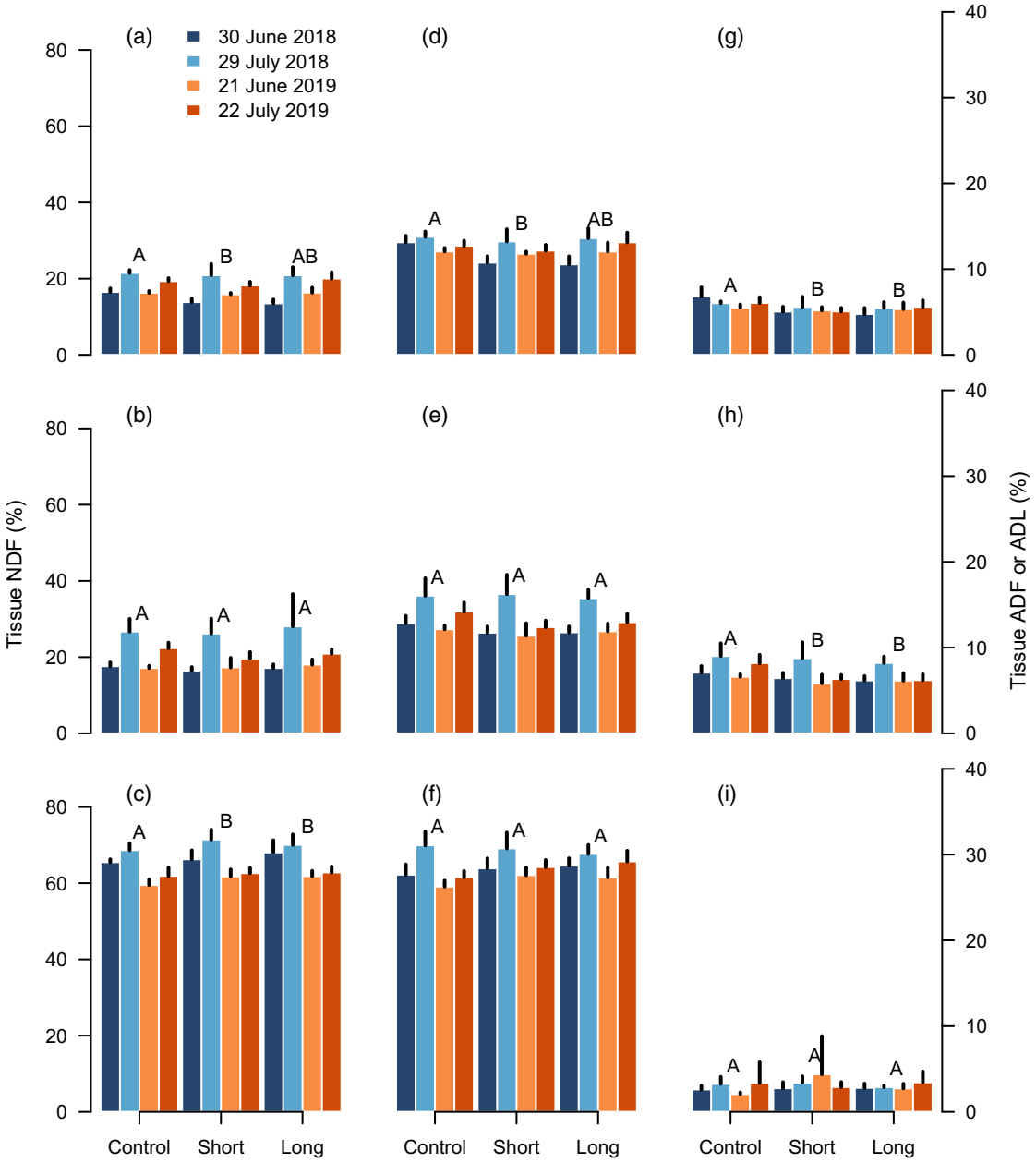


FIGURE 3 Leaf tissue neutral detergent fiber (NDF, a–c), acid detergent fiber (ADF; d–f), and acid detergent lignin (ADL; g–i) on four sample dates in 2018 and 2019 for *Salix pulchra* (a, d, and g), *Betula nana* (b, e, and h), and *Eriophorum vaginatum* (c, f, and i). Values (percent dry weight) are means and 1 SD. Capital letters indicate differences among control, short-term warming, and long-term warming.

in leaf N concentration between treatment and control for *B. nana* and *S. pulchra* (Leffler et al., 2016; Welker et al., 2005). The significant short-term warming impact, but lack of long-term consequences, implies that lower N concentration may be due to differences in phenology such that leaf expansion was more rapid in the short-term warming plots leading to more rapid dilution of leaf nutrients with structural carbohydrates (Chapin III & Shaver, 1996). In a separate study, leaf N concentration in the closely related species *B. glandulosa* also declined in response to warming in the early-growing season, but not later in the summer (Zamin et al., 2017). Meta-analyses report a modest increase (Bai et al., 2013) or no change (Dumont et al., 2015) in leaf N in response to warming. The similarity between control plots and long-term warming suggests some level of acclimation to warming perhaps through more rapid mineralization leading to additional soil N resources or increasing thaw depth leading to a greater volume of soil available for plants to exploit. Moreover, leaf tissue stoichiometry of shrubs and graminoids appears somewhat resistant to warming (Pold et al., 2021).

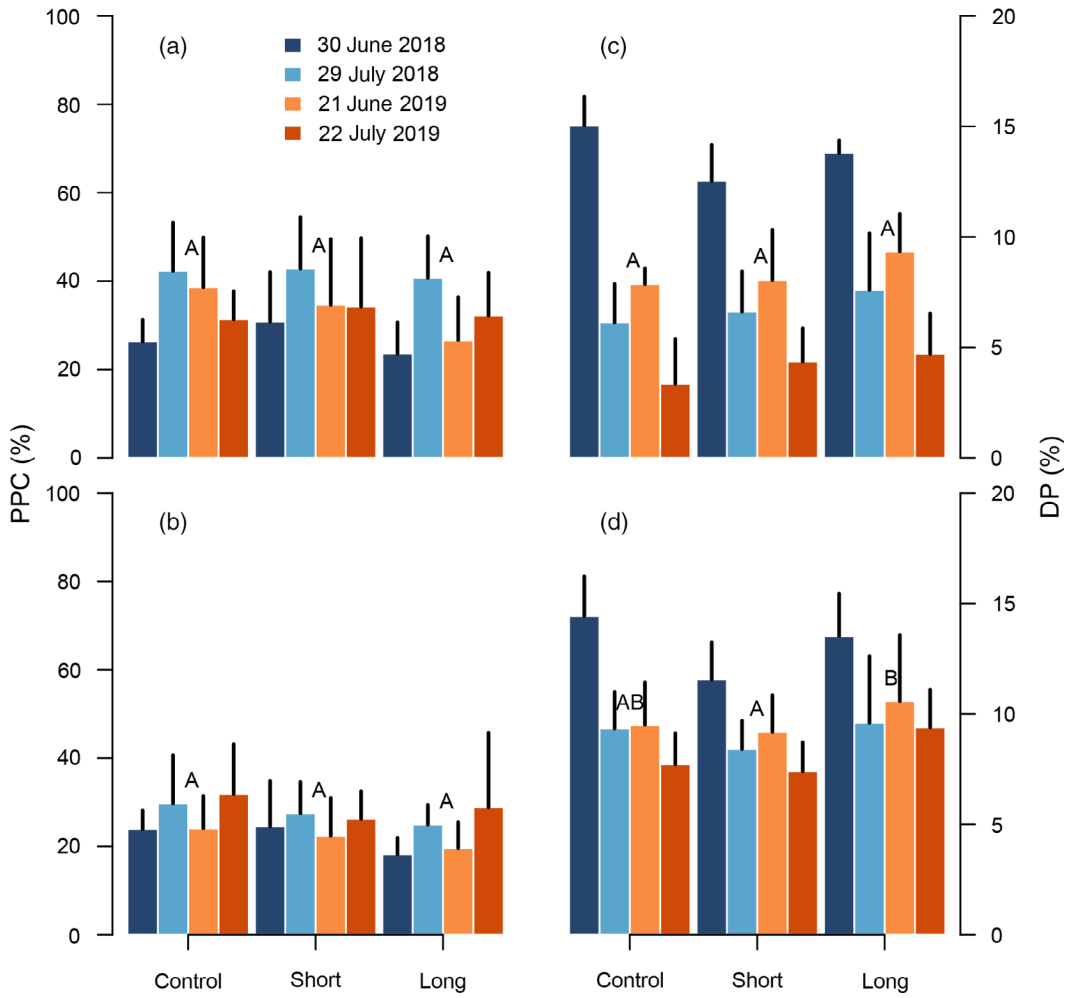


FIGURE 4 Protein-precipitating capacity (PPC; a and b) and digestible protein (DP; c and d) on four sample dates in 2018 and 2019 for *Salix pulchra* (a and c) and *Betula nana* (b and d). Values (percent dry weight) are means and 1 SD. Capital letters indicate differences among control, short-term warming, and long-term warming.

The impact of warming on dry matter digestibility and the fiber components of digestibility was minimal even when it was significant. Moreover, changes in NDF and ADF were not consistent among species; for example, in response to warming NDF declined in *S. pulchra* but increased in *E. vaginatum*. Lower NDF generally indicates higher quality forage because NDF and digestible energy are negatively correlated (Van Soest, 1994). We also observed a 4.5% reduction in ADF in *S. pulchra* in warmer conditions. Since lower ADF also indicates higher digestibility (Van Soest, 1994), changes in NDF and ADF in *S. pulchra* in response to warming are responsible for the 2.3% increase in dry matter digestibility in this species. A previous study found no change in dry matter digestibility under experimental warming during summer in *S. arctica* and *S. reticulata*, both prostrate tundra willows, and in *Carex bigelowii*, another sedge, except at the time of senescence (Lenart et al., 2002). Here, we did not collect data at senescence, so we cannot preclude significant differences in the late season, but elsewhere, warming had no effect on NDF or ADF in *B. glandulosa* or *E. vaginatum* (Zamin et al., 2017).

The least digestible component of forage, ADL, changed most substantially with warming in *S. pulchra* and *B. nana*. In both species, ADL declined by 13% averaged between short-term and long-term warming. The ADL fraction of forage includes the lignin, cutin, and mineral matter. Lignin is a structural component of plant cell walls, and cutin is bound with waxes to reduce diffusion on epidermal surfaces; both interfere with fiber digestibility by rumen microbes (Moore & Hans-Joachim, 2001). Warming had an immediate and persistent impact on ADL in both shrubs, but lower ADL resulted in only a 2.3% increase in dry matter digestibility in *S. pulchra* since ADL makes up a relatively small fraction of total biomass. Others report no significant difference in ADL between warmed and control plots for *B. glandulosa* or *E. vaginatum* although ADL in

B. glandulosa decreased in response to warming (Zamin et al., 2017). Climate change experiments on ADL are scarce, but a meta-analysis suggested a nonsignificant mean reduction of <10% under warmer conditions although the impact of warming was greater than that of drought or elevated CO_2 (Dumont et al., 2015). Lower ADL in the shrubs is likely not related to advanced phenology since later stages of growth typically have similar or higher ADL than early stages of growth (Martiniello et al., 1997; Masoero et al., 2006).

Warming did not affect PPC of plant secondary compounds. Secondary compounds such as tannins and phenolics reduce the quantity of protein that animals can obtain from digestible forage (Coley et al., 1985; Feeny, 1976), but the production of secondary compounds in response to environmental variation is not well understood. In fact, secondary compound response to warming is inconsistent across studies and species. For example, warming resulted in higher concentrations of condensed tannins but lower concentrations of hydrolyzable tannins in *B. nana* at Toolik Lake, but no effect of warming was observed in the same species and several other species in Abisko, Sweden (Graglia et al., 2001; Hansen et al., 2006). Moreover, warming increased total phenolics in *E. vaginatum* but not in *B. glandulosa* (Zamin et al., 2017), indicating that different species exposed to the same climate forcing can have independent responses in secondary compounds. Winter snowpack depth modestly increased PPC of *B. nana* at Toolik Lake, possibly linking PPC to warmer soils in winter, but *S. pulchra* was unaffected by snow depth in the same experiment (Richert et al., 2021). Because fertilization can reduce tannin and phenolic concentration (De Long et al., 2016; Lavola & Julkunen-Tiitto, 1994), we expected the reverse to be true and anticipated that warmer conditions would increase PPC in both shrub species since warming reduced leaf N concentration at this study site, although the reduction was not statistically significant (Leffler et al., 2016). Since we observed no influence of warming on PPC, lower DP in the short-term warming treatment for *B. nana* is likely due only to lower leaf N concentration.

Quantifying the effect of environmental conditions on plant secondary compounds or PPC is challenging because many of these compounds can be induced by herbivory making them highly variable in space and time (Mithöfer & Boland, 2012). Additionally, all researchers do not examine the same compounds (i.e., condensed and hydrolyzable tannins, total phenolics, or PPC) in response to environmental perturbation making comparison among studies difficult since each compound can come from a different metabolic pathway and may compete with protein synthesis (Haukioja et al., 1998). Moreover, higher tannin or phenolic concentration does not necessarily increase PPC during digestion since some ungulate species produce tannin-binding salivary proteins to disrupt the anti-herbivory action of these compounds (Hagerman & Robbins, 1993). The PPC observed here and elsewhere, however, is high enough to limit available nitrogen such that small increases in PPC may make these common forage species not useful for building animal proteins by mid-summer (Richert et al., 2021).

The response of *S. pulchra*, *B. nana*, and *E. vaginatum* to warming was modest, especially considering that the long-term warming treatment began in 1994. The modest effects of warming may be due to the limited influence of OTCs on temperature. Although increasing temperature by approximately 1°C at this site previously increased shrub dominance and enhanced carbon uptake (Leffler et al., 2016; Wahren et al., 2005), the magnitude of warming in our experiment is smaller than in other studies (i.e., Hansen et al., 2006; Zamin et al., 2017) and smaller than the temperature difference observed in this study between 2018 and 2019. Additionally, the North Slope of Alaska warmed 1.9°C between 1981 and 2014 (Bieniek et al., 2014) exposing all plots to a temperature change similar to that provided by OTCs. Moreover, the warming experienced on the North Slope over this period was most pronounced in the summer and autumn (Bieniek et al., 2014), which partially coincided with our OTC use in this experiment.

In most cases where we observed significant differences among treatments, it was the short-term warming treatment rather than the long-term warming treatment that differed from the control. We anticipated that short-term changes would be most closely associated with advanced phenology, while long-term changes would result from persistent impacts such as altered soil N, greater shrub biomass, or increased thaw depth. The limited long-term impacts of warming, however, may suggest negative feedback in the system. One possible feedback is between warming and shrub cover because shrubs shade the soil even as they decrease canopy albedo (Loranty et al., 2014) and shading reduces subcanopy temperature (Blok et al., 2010; Loranty et al., 2018) leading to cooler soils. Additionally, high shrub biomass results in greater water use and occasional water deficit, potentially limiting plant response to warmer conditions (Finger Higgens et al., 2021; Gamm et al., 2017). Ultimately, the most impactful change in response to warming might be at the whole-plant or ecosystem level rather than altering leaf-level chemistry. Shrubs have expanded and grown taller throughout the Arctic (Berner et al., 2018; DeMarco et al., 2014; Macias-Fauria et al., 2012; Myers-Smith et al., 2011; Pattison et al., 2015; Tape et al., 2006), and the long-term plots

used in this experiment have become increasingly shrub-dominated (Leffler et al., 2016; Wahren et al., 2005). Shrub tundra retains more snow in winter than shrub-free tundra and warms winter soils; warmer soils during winter increase thaw depth, microbial activity, and nutrient cycling, a positive rather than negative feedback that further promotes shrub expansion (Leffler et al., 2016; Leffler & Welker, 2013; Schimel et al., 2004; Sturm et al., 2001). This ecosystem-level response points to important biophysical linkages between winter and summer conditions (Kelsey et al., 2021; Richert et al., 2021).

Although the influence of warming we observed here is modest, small changes can have important implications for herbivores such as caribou. Recent work on *S. pulchra* in deeper snow drifts suggests that an approximately 11% greater leaf N concentration at the start of the growing season can lead to a 90% greater leaf N concentration at senescence and extend the window of high-quality forage for caribou by over 3 weeks (Richert et al., 2021). Conversely, a 10% decline in leaf N concentration in the early-growing season in response to warming (Zamin et al., 2017) may negatively affect cows and calves because of high nutrient demand at the end of winter and during lactation (Crête & Huot, 1993; Taillon et al., 2013). Finally, a larger-scale analysis of caribou in eastern Canada suggested body fat in the autumn was influenced by vegetation quality in the early summer (Couturier et al., 2009).

Our results and those of prior studies suggest that warmer summers have only modest influences on forage quality at the leaf level (Dumont et al., 2015) for these and closely related species that are important components of the caribou diet. Short-term warming reduces leaf N concentration and increases digestibility in some species, but these changes are partially mitigated by long-term warming. However, we cannot discount that greater climate variability in the future might make short-term changes in forage quality more impactful by preventing the Arctic from arriving at a future equilibrium in an increasingly woody plant-dominated landscape. Moreover, while caribou and reindeer face many challenges for the future, warmer summers negatively impacting forage quality may be of lesser impact than changes in winter temperature, snow cover, and snow properties (Pedersen et al., 2021), or altered plant communities with greater or reduced abundance of critical forage species.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Leffler et al., 2021) are available from the NSF Arctic Data Center: https://doi.org/10.18739/A2ST7DZ2Q.

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