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Abstract. Caribou (*Rangifer tarandus*) rely on the short Arctic growing season to restore body condition, support the demands of lactation, and prepare for the long arctic winter, making them susceptible to even small changes in forage availability or quality. Body condition in the summer and autumn is linked to winter survival rates and fecundity in cows, critical factors in the productivity of caribou populations. Climate change predictions of warmer and wetter northern winters suggest increased snowfall over Alaska's North Slope, which has recently been verified between 1995 and 2017. However, a comprehensive analysis of how deeper snow will affect caribou forage quality is absent across Alaska. In this study, we quantify how snow depth alters the quality and seasonality of caribou forage using a long-term (24 yr) International Tundra Experiment snow depth manipulation to evaluate how winter climate change scenarios may affect tussock tundra systems in northern Alaska. Deeper snow in prior winters leads to increases in growing season leaf N and digestible protein (DP) in deciduous shrubs (*Salix* spp. and *Betula* spp.) and graminoids (*Carex* spp. and *Eriophorum* spp.), but not evergreen dwarf shrubs (*Rhododendron* spp. and *Vaccinium* spp.). Dry matter digestibility varied among species with small differences (<5%) associated with snow depth. Most striking was the discovery that deeper snow in the prior winter increased the duration of DP levels above the minimum threshold for protein gain in caribou by as much as 25 d in *Salix pulchra* and 6–9 d in *Betula nana* and *Carex bigelowii* in late summer and early autumn. Consequently, deeper winter snow may provide an extended window of opportunity for foraging and the accumulation of lean body mass and fat reserves which promote winter survival and successful calving the following spring and potentially improve the productivity of caribou in northern Alaska.

Key words: digestibility; leaf N; *Rangifer tarandus*; secondary compounds; snow depth.

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INTRODUCTION

Caribou and reindeer populations in the circumpolar Arctic face many challenges. Forage availability, forage quality, predation, insect harassment, increasing human development, and extreme weather events have all been suggested as possible reasons for the declines of caribou and reindeer populations around the world in recent decades (Mörschel and Klein 1997, Festa-Bianchet et al. 2011, Fauchald et al. 2017, Johnson et al. 2019). Though barren-ground caribou are highly susceptible to abiotic stochastic effects (Jefferies et al. 1994, Tyler 2010, Hansen et al. 2014) and

populations are prone to decadal fluctuations in size (Gunn 2003), the near-synchronous decline of populations in North America is cause for concern and suggests a widespread driver such as climate change may be partially responsible (Fauchald et al. 2017).

Changes in the Arctic's weather patterns and overall climate present additional challenges to caribou and reindeer populations (Loe et al. 2020). Due to Arctic amplification, northern latitudes are warming nearly twice as fast as the rest of the world (Coumou et al. 2018), and temperatures are projected to continue rising throughout this century (IPCC 2013). Warmer weather during the growing season may decrease leaf-level nitrogen (N) and increase concentrations of anti-herbivory compounds in spring and summer forage (Jonasson et al. 1986, Turunen et al. 2009, Zamin et al. 2017). Warmer temperatures may also result in phenological mismatch (Post and Forchhammer 2008, Beard et al. 2019). Though caribou exhibit significant physiological and behavioral resilience to phenological mismatches (Mallory et al. 2020), shift of the growing season earlier into the spring could decouple annual caribou physiological stages like parturition and lactation from both the timing and seasonality of critical nutrients on the landscape (Walsh et al. 1997, Fauchald et al. 2017). Mismatches in the summer and fall may have the potential to severely impact both individuals and populations due to the influence of small changes in forage intake and weight gain during this critical period on growth rates and fecundity (White 1983, Cebrian et al. 2008, Proffitt et al. 2016, Gustine et al. 2017).

Higher temperatures may not necessarily lead to negative consequences for caribou. Warmer air temperatures cause earlier snowmelt, earlier spring green-up, and consequently, longer growing seasons (Linderholm 2006, Elmendorf et al. 2012a, b, Loe et al. 2020). Plant communities are already responding to these temperature changes. Preferred summer forages like deciduous shrubs and graminoids (White et al. 1975, Thompson and McCourt 1981, Denryter et al. 2017) are thriving at the expense of less palatable evergreen shrubs and nonvascular plants as warming continues across much of the Arctic (Sturm et al. 2001, Wahren et al. 2005, Tape et al. 2006, 2012, Hobbie et al. 2017, Carlson et al.

2018). While the acceleration of green-up has become a foundation for understanding warming's direct impact on forage during the spring and summer (Prevéy et al. 2017, 2019, Bjorkman et al. 2018), the consequences of changes to winter weather and its subsequent effect on forage phenology, quality, and quantity are exceedingly important in a holistic perspective of the annual cycle of caribou forage (Walsh et al. 1997, Sturm et al. 2005, Gustine et al. 2017).

Winter precipitation in Arctic Alaska is expected to increase with higher temperatures which has been reported over the last 15 yr for the foothills of N Alaska (Stuefer et al. 2020). Changes in snow extent, depth, and duration may have a greater effect on forage quality than warmer growing season temperatures (Walsh et al. 1997, Wahren et al. 2005, Fu et al. 2014). Snow cover insulates the soil, effectively decoupling soil temperature from the extreme winter air temperatures (Walker et al. 1999, Schimel et al. 2004). These warmer soils increase active layer depths in summer (Johansson et al. 2013, Pattison and Welker 2014) as well as facilitate microbial mineralization of organic nitrogen throughout the winter. The continuous microbial activity increases soil nitrogen available for plants in the early spring (Bilbrough et al. 2000, Schimel et al. 2004, Sturm et al. 2005, Welker et al. 2005), resulting in higher leaf N in forage plants during summer (Leffler and Welker 2013, Leffler et al. 2016). Asynchronous green-up of forage due to differences in snow melt-off dates between areas of shallow and deep snow may benefit caribou by creating spatial heterogeneity of high-quality forage across the landscape and extending the length of time that such forage is available over the growing season (Searle et al. 2015, Veiberg et al. 2017).

The objectives of this study were to (1) quantify the effects of increased and decreased winter snow accumulation on the growing season nutritional phenology of arctic plants accessible by caribou and (2) integrate our results within a framework of previously published studies of tundra plant phenology and nutritional changes associated with climate change that are producing a New Arctic. Due to increased availability of nitrogen in warmer winter soils (Schimel et al. 2004, Leffler and Welker 2013, Leffler et al. 2016) and a decrease in phenolic content in plants with

experimental nitrogen addition (Graglia et al. 2001, De Long et al. 2016), we hypothesize that forage quality metrics including leaf N, digestibility, and digestible protein will be highest in areas of deeper snow because deep snow acts as an insulating layer, raising soil temperatures, and promoting N mineralization during winter (Schimel et al. 2004, Leffler and Welker 2013). Moreover, we predict the greatest impact will be on the forage quality of deciduous shrubs, which appear to benefit the most from warmer Arctic temperatures (Sturm et al. 2005). We capitalized on a 24-yr International Tundra Experiment (ITEX) at the Toolik Lake Field Station in Northern Alaska where snow depth and temperatures have been manipulated to examine long-term changes in leaf-level nutrients as well as short-term temporal changes during the growing season (Jones et al. 1998, Welker et al. 2000, 2005, Schimel et al. 2004, Leffler et al. 2016, Jespersen et al. 2018). While multiple studies have examined the effects of warming, snow, and higher atmospheric CO_2 on vegetation composition and leaf-level nutrients (Chapin and Shaver 1985, Parsons et al. 1994, Walsh et al. 1997, Welker et al. 1997, Sharp et al. 2013), few have examined how such responses relate specifically to caribou nutrition.

MATERIALS AND METHODS

Study site

Research took place in moist-acidic tussock tundra near Toolik Field Station (68°38′ N 149°38′ W) in the foothills of the Brooks Range, Alaska, USA. The mean annual temperature at Toolik Field Station is −8°C, with mean summer temperatures of 10–12°C and winter temperatures averaging −20°C (Hobbie and Kling 2014, Environmental Data Center Team 2019). Annual precipitation is ~250–350 mm, with 40–45% occurring as snow (Schimel et al. 2004). In winter, snow depths reach 30–80 cm on average, but snow can accumulate much deeper in response to winds and topography. The ground freezes to the depth of permafrost during winter, with maximum active layer depths in the summer averaging 30–50 cm (Jones et al. 1998, Hobbie and Kling 2014). The site is located within the home range of the Central Arctic Herd of caribou (*Rangifer tarandus granti*) on Alaska's North Slope and is dominated by the tussock-forming sedge,

Eriophorum vaginatum, with deciduous shrubs, evergreen dwarf shrubs, mosses, lichens, and other nontussock-forming graminoids throughout the intertussock areas.

As part of ITEX, a wooden snow fence (3 m high × 60 m long) was erected at the site in 1994 to experimentally alter snow depth and address questions linking winter conditions to spring and summer ecosystem function (Jones et al. 1998, Walker et al. 1999, Welker et al. 2000, Sullivan and Welker 2005). Snowdrifts reach a maximum depth of ~2–3 m directly behind the fence, tapering to 1–2 m ~40 m from the fence, and to 25–50 cm ~70 m from the fence (Blanc-Betes et al. 2016, Jespersen et al. 2018). The ambient snow zone is located out of the snow fence's footprint to the west of the experimental zone and typically has ~50 cm of snow (Pattison and Welker 2014). Snowdrifts at the fence and within the vicinity typically melt-off between the last week of May and the third week of June, depending on snow depth and ambient air temperatures. While spatial replication of the snow fence is lacking, this site represents one of the longest-term climate change forcing experiments in the arctic and its plant community is representative of the majority of Alaska's North Slope (Buchhorn et al. 2016).

Field sampling

To test whether long-term differences in winter snow depth affect summer forage quality, we collected samples of six common plant species in moist-acidic tussock tundra during the growing season of 2017 and 2018. These species represented three functional groups: deciduous shrubs, evergreen dwarf shrubs, and graminoids. Samples of two species from each functional group were collected on a weekly basis from 19 June to 7 August 2017 and 22 June to 25 August 2018. This time frame encompasses nearly the entire growing season from leaf emergence to leaf senescence with later leaf collection in the second year to ensure senesced leaf tissue is represented in the data. The species collected were the deciduous shrubs *Salix pulchra* and *Betula nana*, the evergreen dwarf shrubs *Rhododendron tomentosum* (formerly *Ledum palustre*) and *Vaccinium vitis-idaea*, and the graminoids *Carex bigelowii* and *E. vaginatum*. Three snow depth zones were established: +snow (1–2 m snow), −snow (0.5 m snow), and ambient (0.5–1.0 m snow;

control) and separated into five plots within each zone (~10 × 5 m, but variable in size depending on the species being collected). Leaf tissue samples of each of the six species were collected from multiple individuals in each of the plots in each snow zone, beginning at leaf emergence in each snow zone and continuing at weekly intervals until the onset of senescence in all zones. Sampling methods mimicked caribou browsing, with leaves of deciduous shrubs stripped by hand and evergreen dwarf shrubs and graminoids clipped at ground level. After collection, all samples were dried in a forced-air oven at 70°C for 72 h. These samples were analyzed for N content and dry matter digestibility. An additional five samples (one per plot) of *S. pulchra* and *B. nana* were collected every other week in each snow zone during the 2018 growing season and immediately frozen for later chemical analysis of protein-precipitating capacity (PPC), a measure of the reduction in protein digestibility by herbivores due to naturally occurring anti-herbivory compounds, like phenolics or condensed tannins, within some plants (Robbins et al. 1987).

As an additional verification of the effectiveness of the snow fence, we measured snow depth during the winter of 2018–2019. Snow depths were measured along 12 transects perpendicular to the snow fence. We recorded snow depths at 2–5 m intervals beginning at the snow fence and ending 80 m north of the fence. We used a combination of a MagnaProbe (Snow-Hydro, Fairbanks, Alaska, USA) in snow to 1 m depth and an avalanche probe in areas of deeper snow. Snow depth was interpolated between sample points using a second-order polynomial local area regression at a distance of 1 m. Mean snow depth in each snow zone was extracted from this modeled snow surface using polygons delimiting the sample area (Appendix S1: Fig. S1). Due to the unequal distribution of snowdrifts on the landscape, the snow depth zones were not all equal in size. Snow depth in the ambient snow zone was 39 ± 11 cm (mean ± standard deviation), while snow depth in the −snow and +snow zones was 20 ± 3.4 cm and 147 ± 18 cm, respectively.

Laboratory analyses

We quantified forage quality by measuring neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), percentage of dry matter digestibility (DMD), percentage of nitrogen (N), percentage of crude protein (CP), and digestible protein (DP) in each sample (~1600). Protein precipitation capacity was determined on the additional 2018 deciduous shrub samples (~200 samples) collected for this purpose. Prior to chemical analysis, all samples were ground to 1 mm particle size using a Wiley mill (Thomas Scientific, Swedesboro, New Jersey, USA).

Sequential fiber analyses (determination of NDF, ADF, and ADL) were conducted on all samples using the ANKOM Technology method (ANKOM Technology 2016, 2017*a*, *b*) and an ANKOM fiber analyzer (model 200; ANKOM Technology, Macedon, New York, USA). Forages were first extracted in a neutral detergent solution with agitation at 100°C to obtain the easily digested, or solubilized, fraction (neutral detergent solubles, NDS) and insoluble fraction (NDF), measured in g/g dry matter (DM). Neutral detergent fiber residues were then extracted with an acid detergent solution to yield ADF (a measure of the least digestible plant components like cellulose and lignin), measured in g/g DM. The ADF residue was digested with 72% sulfuric acid to determine ADL and then ashed in a muffle furnace at 500°C for 5 h to determine the total proportion of nondigestible lignin-cutin and inorganic matter, measured in g/g DM. Leaf tissue N was analyzed on samples ground to a fine powder in a mechanical beadbeater via combustion at 1800°C in tin capsules using an elemental analyzer (ECS 4010; Costech Analytical Technologies, Valencia, California, USA) and expressed as a percentage.

We assessed the PPC of tannins (mg BSA [bovine serum albumin] precipitated/mg DM) in the deciduous shrubs, *S. pulchra* and *B. nana*, using BSA (McArt et al. 2006). Samples were freeze-dried and ground to 1 mm particle size before the tannins were extracted in aqueous methanol using an accelerated solvent extractor (Dionex ASE-200, ASE-350; Thomas Scientific). Extracts were then serially diluted with a standard solution of BSA and an acetate buffer before the precipitate, and 50 μL of solution was filtered into an optically clear microplate. Bradford Protein Reagent (Fisher Scientific, Pittsburgh, Pennsylvania, USA) was added, and the resulting

solution was incubated at room temperature for six minutes before the absorbance at 595 nm was read using a UV-Vis microplate spectrometer (Synergy HT Multi-Mode Microplate Reader; BioTek Instruments, Winooski, Vermont, USA).

DMD and DP of each sample were calculated using the following digestibility equations for cervids (Robbins et al. 1987, Spalinger et al. 2010):

$$\%DMD = (92.31e^{-0.0451(LIG)} \times NDF)$$
$$+ (0.831 \times NDS - 6.97) \quad (1)$$

$$DP(g/100\,g\,DM) = -3.87 + 0.9283$$
$$\times CP - 11.82 \times PPC \quad (2)$$

where LIG is the lignin/cutin fraction calculated during sequential fiber analysis. We estimated crude protein content in plants by assuming that the typical protein in a plant is approximately 16% nitrogen (CP = N × 6.25).

Statistical analyses

We examined the effect of snow depth on forage quality of each species using linear mixed-effects models in the R statistical computing framework (R Development Core Team 2017). Analyses were run using the nlme package (Pinheiro et al. 2018) to examine the dependence of leaf N (Table 1) and DMD (Table 2) of each plant species as well as the PPC of the deciduous shrubs (Table 3) on snow treatment zones. The base model included day of year (DOY) as an independent variable, with plot and year as random effects to account for repeated sampling throughout the growing season and sampling in different years. Dependent variables were N content, DMD, and PPC. This base model was compared to additional models that included additive and multiplicative interactions between snow zone and DOY as well as a quadratic DOY term to account for rapid changes in the response variable during leaf expansion and senescence and slower changes during mid-summer (Leffler et al. 2019). All proportional data were arcsine square-root transformed prior to analysis, and we selected the top model for each independent variable using Akaike's information criterion. The top model was used to calculate predicted means and 95% confidence intervals for each variable over the sample period (see parameter estimates in Appendix S1: Tables S1–S3).

For all species except the deciduous shrubs, DP was calculated directly from Eq. 2 with the assumption that PPC = 0. Since DP is directly related to leaf N (i.e., Eq. 2), the top N model was used with the calculated DP values to obtain the predicted means and confidence intervals over the sampling period. For the deciduous shrubs, *S. pulchra* and *B. nana*, the top N and PPC models for both species (including snow zone where significant) were used to obtain daily CP and PPC estimates and standard errors of the estimates. We then randomly sampled from a normal distribution for each daily estimate of CP and PPC and calculated DP using Eq. 2. This procedure was repeated 1000 times for each day, producing a daily estimate and 95% confidence interval of DP for both shrubs throughout the sampling period that accounts for the error of both CP and PPC trends. Since caribou require a minimum of 7–8 g/100 g DM of digestible protein in their diet to maintain body condition (Thompson and Barboza 2017), we measured our results against that threshold to calculate approximately how long the six plant species in each snow zone remained a viable source of protein for caribou during the growing season.

RESULTS

Nitrogen content

Snow depth affected N content of all sampled species except *V. vitis-idaea*. All top models included either an additive or multiplicative interaction with snow zone and the quadratic DOY term (Table 1 and Appendix S1: Table S1). Increased snow depth had the strongest effect on the deciduous shrub and graminoid functional groups. For both functional groups, N content was significantly greater in the +snow zone, while there was little to no difference between the −snow zone and ambient conditions (Fig. 1). This difference in N content among the snow zones remained relatively constant throughout the growing season. For *S. pulchra*, +snow resulted in 11.4% greater N at the beginning of the growing season (DOY 173) compared to the ambient zone (i.e., 4.8% N vs. 4.3% N). The difference among the three snow zones remained even as N levels declined during the season and led to plants in the +snow zone having 73.3–89.6% higher leaf N when leaf senescence began

Table 1. Model selection results for nitrogen content (N) of each species.

Model	logLik	AIC_c	ΔAIC_c	df	Weight
Deciduous shrubs					
Salix pulchra					
$SNOW \times DOY \times DOY^2$	869.63	−1707.23	0.00	15	0.87
$SNOW + DOY \times DOY^2$	861.12	−1703.49	3.74	9	0.13
$DOY \times DOY^2$	742.27	−1470.08	237.14	7	0.00
$DOY + DOY^2$	727.04	−1441.75	265.48	6	0.00
DOY	725.91	−1441.58	265.65	5	0.00
Betula nana					
$SNOW + DOY \times DOY^2$	840.98	−1663.23	0.00	9	0.87
$SNOW \times DOY \times DOY^2$	845.71	−1659.41	3.82	15	0.13
$DOY \times DOY^2$	808.27	−1602.09	61.14	7	0.00
$DOY + DOY^2$	756.96	−1501.58	161.66	6	0.00
DOY	751.51	−1492.77	170.46	5	0.00
Evergreen shrubs					
Rhododendron tomentosum					
$SNOW \times DOY \times DOY^2$	980.25	−1928.56	0.00	15	0.99
$SNOW + DOY \times DOY^2$	968.63	−1918.55	10.01	9	0.01
$DOY \times DOY^2$	962.00	−1909.55	19.01	7	0.00
$DOY + DOY^2$	654.51	−1896.69	31.87	6	0.00
DOY	950.75	−1891.26	37.30	5	0.00
Vaccinium vitis-idaea					
DOY	968.84	−1927.45	0.00	5	0.46
$SNOW + DOY \times DOY^2$	972.45	−1926.21	1.24	9	0.25
$DOY + DOY^2$	968.90	−1925.47	1.98	6	0.17
$DOY \times DOY^2$	969.30	−1924.17	3.28	7	0.09
$SNOW \times DOY \times DOY^2$	977.24	−1922.58	4.87	15	0.04
Graminoids					
Carex bigelowii					
$SNOW \times DOY \times DOY^2$	861.93	−1691.93	0.00	15	1.00
$SNOW + DOY \times DOY^2$	843.04	−1667.37	24.56	9	0.00
$DOY \times DOY^2$	815.11	−1615.79	76.14	7	0.00
$DOY + DOY^2$	795.53	−1578.74	113.19	6	0.00
DOY	793.40	−1576.57	115.36	5	0.00
Eriophorum vaginatum					
$SNOW \times DOY \times DOY^2$	861.04	−1690.19	0.00	15	0.65
$SNOW + DOY \times DOY^2$	853.83	−1688.97	1.23	9	0.35
$DOY \times DOY^2$	832.92	−1651.42	38.77	7	0.00
$DOY + DOY^2$	831.19	−1650.07	40.13	6	0.00
DOY	820.93	−1631.64	58.55	5	0.00

Notes: AIC_c, Akaike's information criterion, corrected for sample sizes. The dependent variable (N) was investigated in relation to the independent variables: snow depth (SNOW), day of year (DOY), and a quadratic day of year term (DOY^2).

(DOY 237; i.e., 1.06% N in −snow and 1.16% N in ambient vs. 2.01% N in +snow). *B. nana* followed a similar pattern, although with a lesser increase in N content of 8.35% in the +snow zone compared to the ambient zone at the beginning of the growing season and 25.3% difference during senescence.

Despite representing the same functional group, the two graminoids demonstrated different patterns of N concentrations throughout the growing season (Fig. 1). N concentrations in *C. bigelowii* followed the same pattern as the deciduous shrubs, with the highest N levels during the early growing season (i.e., green leaves partially emerged) and in the +snow zone and declining steadily over the course of the season. N content of individuals from the −snow and ambient zones declined at a similar rate through most of the growing season. Plants in both snow zones declined sharply

Table 2. Model selection for dry matter digestibility (DMD) of each species.

Model	logLik	AIC_c	ΔAIC_c	df	Weight
Deciduous shrubs					
Salix pulchra					
SNOW × DOY × DOY^2	710.34	−1388.64	0.00	15	1.00
SNOW + DOY × DOY^2	686.75	−1354.76	33.89	9	0.00
DOY × DOY^2	682.45	−1350.45	38.20	7	0.00
DOY + DOY^2	679.38	−1346.42	42.23	6	0.00
DOY	664.83	−1319.42	69.22	5	0.00
Betula nana					
SNOW × DOY × DOY^2	624.33	−1216.64	0.00	15	1.00
SNOW + DOY × DOY^2	607.62	−1196.49	20.15	9	0.00
DOY + DOY^2	535.26	−1058.17	158.47	6	0.00
DOY × DOY^2	535.51	−1056.56	160.08	7	0.00
DOY	530.52	−1050.8	165.84	5	0.00
Evergreen shrubs					
Rhododendron tomentosum					
SNOW × DOY × DOY^2	581.01	−1130.12	0.00	15	0.90
SNOW + DOY × DOY^2	572.15	−1125.6	4.52	9	0.09
DOY × DOY^2	566.10	−1117.76	12.36	7	0.00
DOY + DOY^2	543.41	−1074.49	55.63	6	0.00
DOY	526.78	−1043.34	86.79	5	0.00
Vaccinium vitis-idaea					
DOY × DOY^2	594.41	−1174.4	0.00	7	0.62
SNOW + DOY × DOY^2	595.81	−1172.92	1.48	9	0.30
SNOW × DOY × DOY^2	601.14	−1170.37	4.03	15	0.08
DOY	569.53	−1128.83	45.56	5	0.00
DOY + DOY^2	569.74	−1127.17	47.23	6	0.00
Graminoids					
Carex bigelowii					
DOY	291.43	−572.63	0.00	5	0.43
DOY + DOY^2	292.36	−572.4	0.23	6	0.39
DOY × DOY^2	292.52	−570.59	2.04	7	0.16
SNOW + DOY × DOY^2	295.56	−566.41	6.22	9	0.02
SNOW × DOY × DOY^2	297.52	−563.12	9.51	15	0.00
Eriophorum vaginatum					
SNOW × DOY × DOY^2	253.19	−474.5	0.00	15	0.50
DOY × DOY^2	244.35	−474.27	0.23	7	0.44
SNOW + DOY × DOY^2	244.51	−470.34	4.16	9	0.06
DOY	232.26	−454.3	20.21	5	0.00
DOY + DOY^2	232.27	−452.21	22.29	6	0.00

Notes: AIC_c, Akaike's information criterion, corrected for sample sizes. The dependent variable (DMD) was investigated in relation to the independent variables of snow depth (SNOW), day of year (DOY), and a quadratic day of year term (DOY^2).

with the onset of senescence which resulted in 107% higher N levels in the +snow treatment by the end of the growing season (i.e., 0.88% N in ambient vs. 1.82% N in + snow). In contrast, leaf N content in *E. vaginatum* was low (~2% N) over the course of the entire growing season. Plants in the +snow zone still had higher leaf N, though, especially near the end of the season, with a 30.4% increase over ambient levels.

For the evergreen dwarf shrubs, N content remained low throughout the entire growing season, with few samples above 2% N at any point. For *V. vitis-idaea*, snow depth did not have a significant effect on leaf N. For *R. tomentosum*, N was highest in the −snow treatment over the first few weeks of the growing season but fell below +snow levels by mid-season and rose again near senescence when N content in the +snow treatment began to decrease.

Table 3. Model selection results for protein-precipitating capacity (PPC) of the deciduous shrubs *Salix pulchra* and *Betula nana*.

Model	logLik	AIC_c	ΔAIC_c	df	Weight
S. pulchra					
$DOY + DOY^2$	83.39	−156.07	0.00	5	0.56
$DOY \times DOY^2$	83.60	−154.20	1.87	6	0.22
DOY	80.94	−153.41	2.66	4	0.15
$SNOW + DOY \times DOY^2$	84.46	−151.16	4.92	8	0.05
$SNOW \times DOY \times DOY^2$	91.72	−149.91	6.16	14	0.03
B. nana					
$SNOW + DOY \times DOY^2$	127.56	−237.34	0.00	8	0.81
$DOY \times DOY^2$	123.20	−233.40	3.94	6	0.11
$DOY + DOY^2$	121.17	−231.63	5.71	5	0.05
$SNOW \times DOY \times DOY^2$	131.91	−230.22	7.11	14	0.02
DOY	117.39	−226.31	11.02	4	0.00

Notes: AIC_c, Akaike's information criterion, corrected for sample sizes. The dependent variable (PPC) was investigated in relation to the independent variables of snow depth (SNOW), day of year (DOY), and a quadratic day of year term (DOY^2).

Dry matter digestibility

Snow depth affected DMD less than N content for all species, with only a slight increase in digestibility of *B. nana* in the +snow zone (Fig. 2). Even then, the increase was modest, with the highest digestibility occurring mid-season with an increase of 6.82% over ambient. By senescence, the gap among the three snow zones closed as DMD in both the ambient and −snow zone increased slightly to match that of the +snow zone.

Few clear patterns emerged in DMD of other sample species despite often including a snow term in the top models (Table 2 and Appendix S1: Table S2). There was no effect of snow depth on the evergreen dwarf shrub, *V. vitis-idaea*, and the graminoid, *C. bigelowii*, although both species showed different temporal patterns. Digestibility of *C. bigelowii* (~70%) changed little throughout time, while digestibility of *V. vitis-idaea* showed a curvilinear trend over the growing season, with a lower overall digestibility of ~50–60%. For the deciduous shrub, *S. pulchra*, the +snow treatment showed higher digestibility at the beginning of the growing season. By mid-season, digestibility in the +snow treatment fell to the same level as the −snow treatment, both of which were below ambient levels. All three snow zones, however, differed by only a few percentage points throughout the entire growing season. Both the dwarf shrub, *R. tomentosum*, and the graminoid, *E. vaginatum*, showed curvilinear

trends through time as well as a slight effect of snow depth. Individual samples from all three snow zones exhibited similar digestibility at the beginning of the growing season (~45–50% in *R. tomentosum* and ~60–70% in *E. vaginatum*), only diverging from one another in the latter half of the season (Fig. 2).

Protein-precipitating capacity and digestible protein

Digestible protein (Fig. 3) is directly correlated with digestible N and therefore parallels the trends seen in Fig. 1. For *B. nana*, the top model for predicting PPC included snow depth (Table 3 and Appendix S1: Table S3), with estimated PPC highest in the +snow treatment in the middle of the growing season at 0.276 ± 0.014 mg BSA precipitated/mg DM (Fig. 4). Both the +snow and ambient zones were similar however, and temporal variation was high, resulting in substantial overlap of confidence intervals between the two zones. For *S. pulchra*, there was no effect of snow on PPC, but PPC did increase throughout the growing season from an estimated low of 0.226 ± 0.027 mg BSA precipitated/mg DM at the beginning of summer to a high of 0.357 ± 0.015 mg BSA precipitated/mg DM by DOY 217 before declining slightly to 0.334 ± 0.023 mg BSA precipitated/mg DM by senescence (Fig. 4).

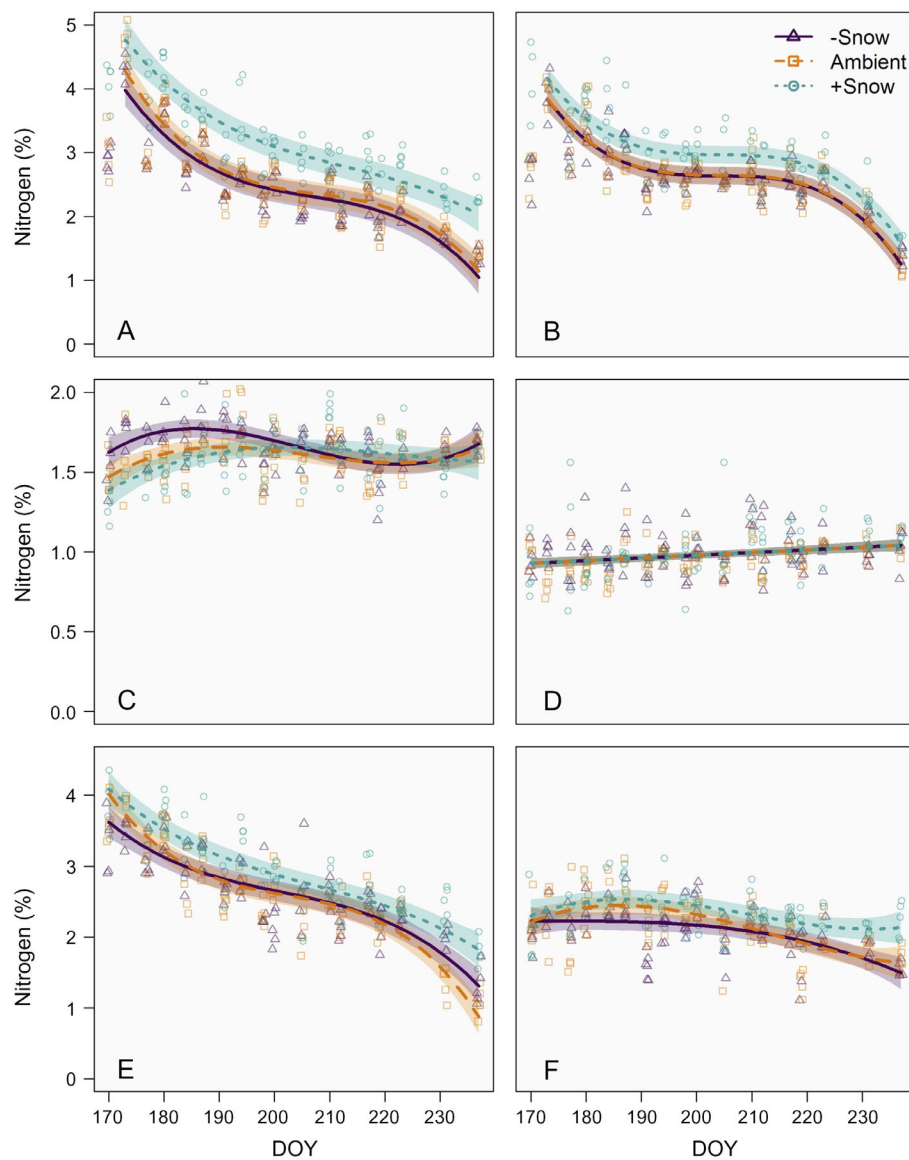Even with the additional PPC of anti-herbivory compounds in the deciduous shrubs,

Fig. 1. Leaf tissue N concentration (%) by species throughout the growing season, denoted by day of year (DOY), starting at leaf emergence (DOY 170) and ending at leaf senescence (DOY 245). Points indicate individual measurements, while trend lines are the predicted median ± 95% confidence intervals in shaded polygons calculated from the top model. Note that the *y*-axis range differs among functional groups: deciduous shrubs, *Salix pulchra* (A) and *Betula nana* (B); evergreen dwarf shrubs, *Rhododendron tomentosum* (C) and *Vaccinium vitis-idaea* (D); and graminoids, *Carex bigelowii* (E) and *Eriophorum vaginatum* (F). Preleaf emergence values for the deciduous shrubs are not included in the model.

DP levels of both *S. pulchra* and *B. nana* remained above maintenance levels well into the growing season, especially in the +snow treatment (Fig. 3), with values as high as 20–25 g/100 g DM at leaf emergence. The evergreen dwarf shrubs remained a poor source of protein through the entire season, never rising above the maintenance threshold, and in the case of *V. vitis-idaea*, remaining at ~2 g/100 g DM throughout the sample period. DP in *C. bigelowii* mirrored
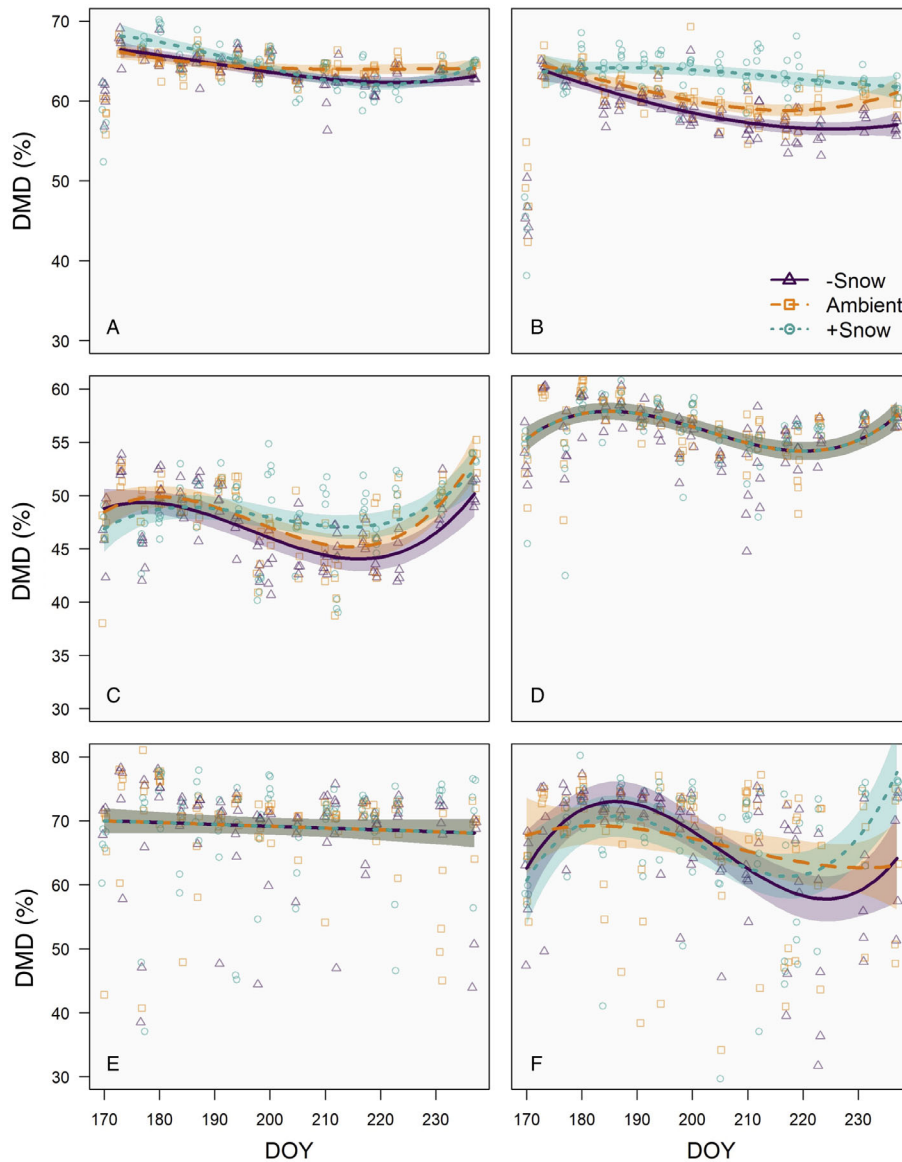
Fig. 2. Leaf tissue dry matter digestibility (%) by species throughout the growing season, denoted by day of year (DOY), starting at leaf emergence (DOY 170) and ending at leaf senescence (DOY 245). Points indicate individual measurements while trend lines are the predicted median ± 95% confidence intervals in shaded polygons calculated from the top model. Note that the *y*-axis range differs among functional groups: deciduous shrubs, *Salix pulchra* (A) and *Betula nana* (B); evergreen dwarf shrubs, *Rhododendron tomentosum* (C) and *Vaccinium vitis-idaea* (D); and graminoids, *Carex bigelowii* (E) and *Eriophorum vaginatum* (F). Preleaf emergence values for the deciduous shrubs are not included in the model.

the same pattern as the deciduous shrubs, beginning the season at 15–20 g/100 g DM and declining steadily with time until falling below maintenance levels near senescence. *E. vaginatum*, while not high in DP, remained above the maintenance threshold for most of the growing season in all snow zones, and plants in the +snow treatment remained over the minimum protein requirement during the entire sampling period.
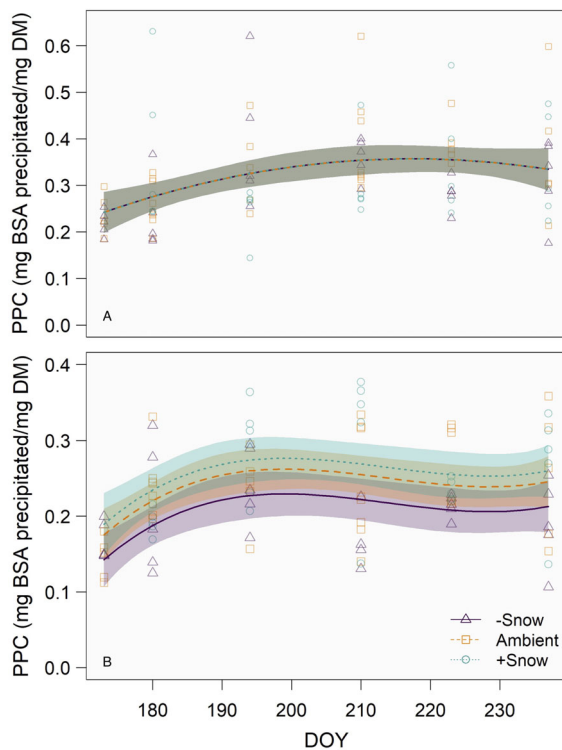
Fig. 3. Protein-precipitating capacity (PPC in mg/BSA precipitated/mg dry matter) of the deciduous shrubs by species throughout the growing season, denoted by day of year (DOY), starting at leaf emergence (DOY 170) and ending at leaf senescence (DOY 245). Points indicate individual measurements while trend lines are the predicted median ± 95% confidence intervals in shaded polygons calculated from the top model. Both panels show deciduous shrubs, *Salix pulchra* (A) and *Betula nana* (B). Preleaf emergence values are not included in the model.

DISCUSSION

Our results demonstrate that increased snow depth affects the quality of forage species important to caribou in northern Alaska at this study site. Deep snow increased leaf-level N and DP in both deciduous shrubs and graminoids despite increasing the PPC of anti-herbivory compounds in *B. nana*. While changes to forage digestibility due to snow were mixed, overall digestibility in caribou preferred forages was high during the growing season. Increases in snow depth, then, may enhance forage quality

for caribou, especially during late summer and early autumn when caribou are foraging in preparation for the approaching winter and their subsequent spring migration back to the calving grounds. While snowdrifts created by large snow fences such as the one in this experiment may be deeper than predictions of increased winter precipitation in the region, they are consistent with topographically controlled snowdrifts (snow beds) and the increasing snow trends in the foothills of northern Alaska (Stuefer et al. 2020). Moderate increases in snow, while directly affecting the forage nutrition of existing plant species, may result in even greater long-term changes to plant communities (Sturm et al. 2005, Borner et al. 2008, Wipf and Rixen 2010, Tape et al. 2012), with concomitant impacts on caribou nutrition.

Nitrogen content

Additional snow increased leaf N in both the deciduous shrubs and graminoids (Fig. 1) at this site, as has been found in previous studies across multiple arctic and alpine sites (Walsh et al. 1997, Van der Wal et al. 2000, Schimel et al. 2004, Welker et al. 2005, Leffler and Welker 2013). Increased snow depth had the greatest impact on leaf-level N content in *S. pulchra*, but N in *B. nana* and the graminoid, *C. bigelowii*, also increased slightly with deep snow. This strong shrub response partially supports our hypothesis of snow having the greatest impact on the quality of deciduous shrubs. This may be due to deeper roots that can take advantage of higher soil N as well as greater phenological plasticity in the face of environmental changes (Bret-Harte et al. 2001, Sullivan et al. 2007, Wipf and Rixen 2010). Overall, observations of higher leaf N in response to deeper snow have been a consistent observation from this ITEX experiment (Welker et al. 2005), although this may be due in part to phenological delays in areas with deep snow. The impact of deep snow on N content of *C. bigelowii* is curious, though, as leaf N in *E. vaginatum*, another sedge, remained low throughout the study period regardless of snow depth.

There are a few possible explanations for the difference seen in N content over the growing season between the two graminoids. First, *E. vaginatum* replaces its roots annually (Chapin III 1986, Sullivan and Welker 2005) and it may not be able
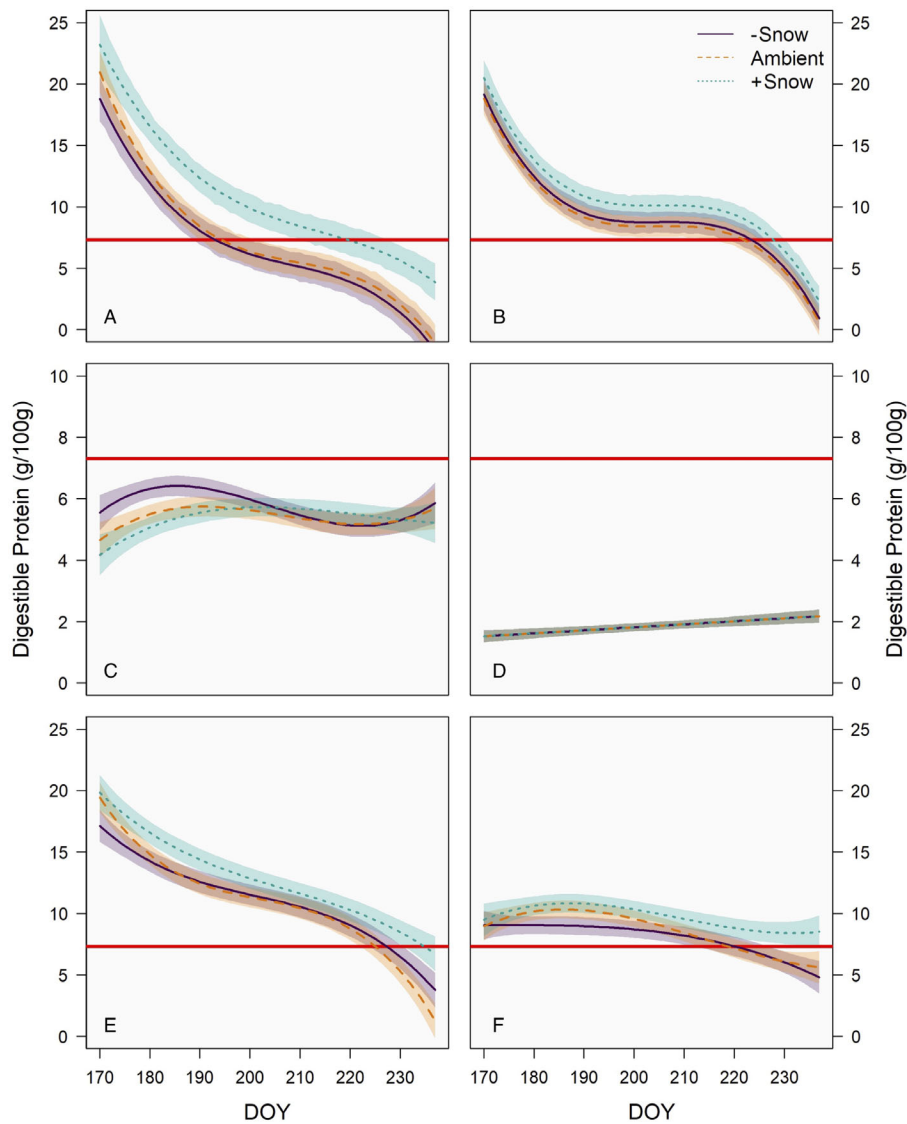
Fig. 4. Leaf tissue digestible protein (in g/100 g) by species throughout the growing season, denoted by day of year (DOY), starting at leaf emergence (DOY 170) and ending at leaf senescence (DOY 245). Trend lines are the predicted median ± 95% confidence intervals in shaded polygons calculated from the top model. The maintenance level protein required by caribou (7–8 g/100 g DM) is highlighted in red. Note that the *y*-axis range differs among functional groups: deciduous shrubs, *Salix pulchra* (A) and *Betula nana* (B); evergreen dwarf shrubs, *Rhododendron tomentosum* (C) and *Vaccinium vitis-idaea* (D); and graminoids, *Carex bigelowii* (E) and *Eriophorum vaginatum* (F).

to take advantage of the transient increase in nutrients in the soil as early in the growing season as *C. bigelowii*, though that does not fully explain the low N levels in *E. vaginatum* throughout the entire growing season. Furthermore, *E. vaginatum* and *C. bigelowii* preferentially uptake different forms of nitrogen, with *E. vaginatum* using primarily ammonium and *C. bigelowii* using

primarily nitrate (McKane et al. 2002). Deep snow increases availability of both forms of nitrogen in the soil, especially in intertussock areas (Schimel et al. 2004, Semenchuk et al. 2015) where *C. bigelowii* tends to be located (J. C. Richert, *personal observation*). Because nitrate levels are so low in arctic soils, there is more competition among plants for ammonium (McKane et al. 2002). Even as snow

increases both forms of nitrogen, then, *C. bigelowii* may be better positioned to take advantage of the timing, location, and form of soil nitrogen than *E. vaginatum*.

Snow depth also influenced N concentrations in *R. tomentosum* (Fig. 1), with changes in N reflecting a possible phenological shift rather than a change in mean. As an evergreen, *R. tomentosum* normally produces new vegetative growth from mid-late July under ambient conditions (Murray and Miller 1982). We observed high N concentrations earlier in the growing season in the −snow zone, which was snow-free earliest in the season. N concentration of *R. tomentosum* leaves in the +snow zone was similar to those in the reduced snow zone several weeks later, following later snow melt of the deeper snowdrift. Hence, deeper snow shifted leaf production and subsequent peak leaf N in this species later in the growing season.

Dry matter digestibility

Snow depth did not have as great an impact on leaf DMD compared to leaf N, a result similar to previous studies examining the effects of other environmental factors such as shading, air temperature, and precipitation on forage quality (Lenart et al. 2002). Overall changes in DMD, whether through time or with snow depth, spanned only a few percentage points (Fig. 2). Individual species within each functional group also responded differently from one another, ranging from phenological shifts to no significant effects. Even small changes in digestibility can, however, significantly impact dry matter intake of caribou (White 1983) and subsequent deposition of both body fat and protein (Chan-McLeod et al. 1994). As maternal winter body mass and body fat correlate strongly with animal survival and calf production (Parker et al. 2009, Proffitt et al. 2016, Veiberg et al. 2017), changes in summer forage digestibility and energy intake can propagate from the individual to the population level.

Protein-precipitating capacity

While not a direct measure of the quantity of protein-precipitating compounds with anti-herbivory properties within a plant, lower PPC values in vegetation samples generally indicate that less protein is being bound by phenolics and condensed tannins, resulting in more protein available to herbivores. The PPC of the deciduous shrubs in our experiment did not respond to the winter climate change scenarios the way we initially expected. Protein-precipitating capacity of *S. pulchra* was unaffected by snow depth; however, PPC of *B. nana* increased with snow depth, albeit only slightly. Previous studies in tussock tundra in the Toolik Lake area found that concentrations of phenolics in *B. nana* decreased with N fertilization treatments (Graglia et al. 2001), while other studies demonstrated a more generalized decrease in carbon-based secondary compounds (including phenolics and tannins) with N fertilization (Lavola and Julkunen-Tiito 1994, De Long et al. 2016). With the increase in available soil nutrients with deep snow cover, we might expect to see lower PPC as plants use available N to produce essential amino acids and new growth rather than flavonoids that result in defensive tannins (Chapin 1989).

Our results showed that PPC of *B. nana* was highest in the deeper snow zone and lowest in the reduced snow zone, although there was substantial variation among sample dates. The seasonal variation may be due in part to a phenological shift with later melt-off of the deeper snow zone, as values of PPC in leaf tissue of plants in deeper snow followed roughly the same pattern as those in the ambient snow zone, offset by approximately two weeks. One explanation for the seemingly opposing results of studies in tussock tundra near Toolik Field Station arises from different assays used to quantify various secondary compounds. The majority of studies measure total phenolic content as opposed to PPC (Graglia et al. 2001, Zamin et al. 2017), though some have measured both (De Long et al. 2016) and found a similar decrease in PPC when N is added as a fertilizer to tundra. These fertilization responses may be sensitive to timing however, as most measurements of both phenolic content and PPC were taken near the end of July. We observed similarly low PPC in the deeper snow zone for *B. nana* in late July, consistent with higher N in the fertilization experiments (Graglia et al. 2001, De Long et al. 2016), but also found considerable variation throughout the entire growing season (Fig. 4). Responses of both phenolic content and PPC to fertilization may also be specific to certain

secondary compounds that use different biosynthetic pathways that may or may not compete with the synthesis of proteins necessary for plant growth (Chapin 1989, Haukioja et al. 1998).

Since we only analyzed PPC for the deciduous shrubs, we assumed the PPC for all other species was 0 when calculating DP. Graminoids are low in phenolic compounds that bind protein (Jonasson et al. 1986) but evergreen dwarf shrubs have high concentrations of secondary compounds that make them relatively unpalatable (Bryant et al. 1983). While the PPC of the evergreen shrubs remains unaccounted for in this study, the calculated DP values are already well below the threshold for protein gain, so their value as summer forage is minimal even without accounting for PPC.

Digestible protein

Deeper snow increased the amount of DP in certain forage species (primarily through enhancing overall N content) while also increasing the length of time that DP content remained above the minimum maintenance levels required by caribou during the summer. The largest impact was on the value of deciduous shrubs and graminoids as a protein source. For example, deep snow resulted in ~25 additional days of DP above the maintenance threshold in *S. pulchra* compared to low snow and ambient conditions. This doubles the length of time that caribou can gain sufficient protein to recover body condition and sustain weight gain under ambient snow conditions and matches the increased duration of protein in forages observed along latitudinal gradients across the North Slope of Alaska (Barboza et al. 2018). The duration of time that DP in *B. nana* and *C. bigelowii* remained above maintenance levels was also extended, albeit more modestly at 6 and 9 d, respectively. In addition, while the DP content of *E. vaginatum* was lower overall than other species for most of the growing season, levels in the deeper snow zone did not fall below the maintenance threshold during the sampling period, suggesting that *E. vaginatum* may remain a useful protein source throughout much of the year (Klein 1990, Ophof et al. 2013) with deeper snow. Finally, since caribou are highly selective foragers (White and Trudell 1980, Boertje 1984, Denryter et al. 2017), we anticipate they will select for these more DP-rich forages in the future.

A conceptual model of a New Arctic forage cycle

The timing of the caribou forage cycle is shifting, especially at the beginning and end of the snow-free period (Fig. 5). One possible scenario (Fig. 5B) is driven by warming and the advancement of spring growth (Elmendorf et al. 2012*a*, Kerby and Post 2013). Under these conditions, high-quality forage may be available earlier along with advancement of peak biomass. Under this earlier spring scenario, a shorter winter may alleviate some of the stressful conditions and possibly improve caribou health. However, the forage quality and availability associated with changes in winter are slightly more complex (Fig. 5C). Deeper snow in winter may delay spring growth and green-up (Starr et al. 2000, Wipf and Rixen 2010, Bosiö et al. 2014, Legault and Cusa 2015). However, once the landscape is snow-free, higher-quality forage becomes available in the middle of the summer and into autumn, expanding the nutritional window immediately ahead of winter (Fig. 5C). Both scenarios potentially lead to higher-quality forage for caribou, but at different times of the growing season. In the former scenario, the abundance of high-quality spring forage is enhanced during calving and early lactation (Barboza et al. 2018) while in the latter scenario the extended autumn forage nutrition may lead to more favorable nutritional landscapes for caribou and support the health of individual animals, better body conditions going into winter, lower winter mortality, and a higher likelihood of calving in the subsequent spring (White 1983, Cebrian et al. 2008, Veiberg et al. 2017).

Conclusions

The seasonality of caribou forage is a critical factor influencing animal metabolic needs during the autumn and subsequent winter survival and herd fecundity (Gustine et al. 2017, Veiberg et al. 2017, Barboza et al. 2018). Our data support the prediction that one of the major consequences of deeper snow in winter is that protein available to caribou, delivered primarily by *S. pulchra*, will be extended through the short growing season by as much as three weeks
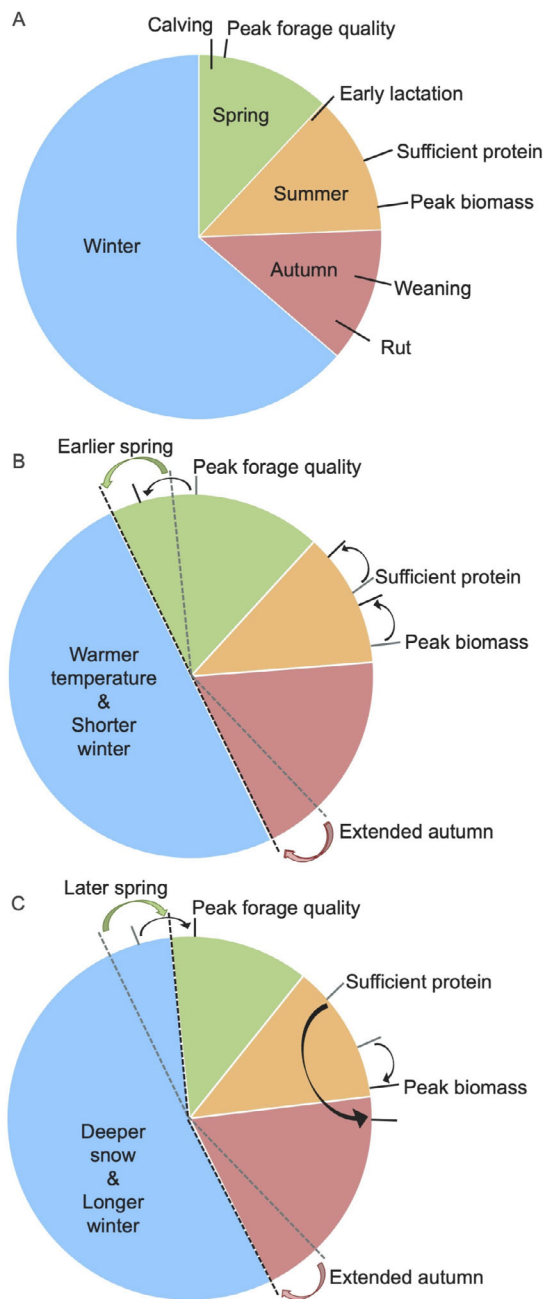
Fig. 5. The annual caribou forage cycle under current (A) and future (B, C) conditions. Earlier springs due to warmer temperatures shift peak forage quality and biomass earlier into the growing season (B), but deeper snow mitigates these shifts somewhat and increases the duration of forage with sufficient protein content into an extended autumn (C). This creates a matrix of low- and high-quality forage across the landscape.

(Fig. 3). Higher available protein during autumn migration may be especially important to sustaining the productivity of caribou in northern Alaska. While the plant community used in this experiment is representative of moist-acidic tussock tundra in much of Northern Alaska and we report here on a climate change forcing of 25 yr, we do urge caution in extending these results broadly since our sampling was limited to a single study site.

Caribou and reindeer populations around the Arctic face many challenges: extreme weather, predation, insect harassment, the encroachment of human development (Mörschel and Klein 1997, Festa-Bianchet et al. 2011), but climate change presents new challenges: increased temperatures, altered precipitation patterns, and changes in forage availability and quality (Callaghan et al. 2011, Fauchald et al. 2017, Mallory and Boyce 2018, Loe et al. 2020). While warmer growing season temperatures are associated with declines in forage quality due to increased vegetative growth and nutrient dilution (Turunen et al. 2009, Fauchald et al. 2017, Zamin et al. 2017; but see Gustine et al. 2017), increases in winter snow may mitigate the magnitude of such declines. Additionally, the availability of preferred forages like deciduous shrubs is expected to continue increasing as the Arctic becomes shrubbier, though certain species, like *B. nana* (which is less preferred than *Salix* spp.), may spread more rapidly (Bret-Harte et al. 2001, Sturm et al. 2001, 2005, Tape et al. 2006). Arctic herbivores may adjust to the increase in available forage and potentially dampen the trend toward shrubification (Gough et al. 2007, Zamin and Grogan 2013, Kaarlejärvi et al. 2017). Herbivore mediation of shrubification may be minimal, however, due to the strong influence of abiotic stochasticity on both plant and animal populations in such extreme environments (Jefferies et al. 1994, Loe et al. 2016). Warmer temperatures and increased shrub cover may also decrease important winter forages such as lichens and evergreen dwarf shrubs (Wahren et al. 2005, Hobbie et al. 2017), so it is difficult to say whether the net effect of changes in temperature and precipitation in the Arctic will benefit or inhibit caribou nutrition, individual health, and population productivity.

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Data Availability

Data are available from the Arctic Data Center: https://doi.org/10.18739/A2MS3K28M

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3617/full