2019

Winter Snow Depth in Arctic Alaska Results in Complex Changes in Caribou Forage Quality

Jessica C. Richert
South Dakota State University

WINTER SNOW DEPTH IN ARCTIC ALASKA RESULTS IN COMPLEX CHANGES

IN CARIBOU FORAGE QUALITY

BY

JESSICA C. RICHERT

A thesis submitted in partial fulfillment of the requirements for the

Master of Science

Major in Biological Sciences

South Dakota State University

2019

THESIS ACCEPTANCE PAGE

Jessica C. Richert

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

A. Joshua Leffler
Advisor Date

Michele R. Dudash
Department Head Date

Dean, Graduate School Date

ACKNOWLEDGMENTS

I owe my sincere appreciation to a great number of people who have supported my graduate education and research. I would especially like to thank my graduate advisor, Dr. A. Joshua Leffler, for his experience, support, patience, and knowledge of all things related to R. I would also like to extend my gratitude to the other members of my committee, Dr. Jonathan Jenks and Dr. Jeffrey Welker, for their extensive knowledge, guidance, and feedback over the last few years. A special thank you goes to my fellow graduate students, Kaj Lynöe and Heidi Becker, as well as our field technicians, Monica Ague, Jeremy Buttler, Brooke Davis, and Makyla Hammer, for aiding me in collecting thousands of field samples in the middle of rain, snow, and the occasional mosquito; I could not have done it without their help. I would also like to thank Dr. Don Spalinger, Dr. Kathy Kelsey, Dr. Stine Højlund-Pedersen, and John Ferguson at University of Alaska Anchorage as well as Dr. Derek Brake and Jason Griffin in the Animal Science Department at South Dakota State University for their assistance with various lab analysis procedures and additional data collection. Finally, I would like to thank South Dakota State University, the Department of Natural Resource Management, the wonderful administrative assistants who were always happy to lend an ear and a cup of coffee, and my fellow graduate students who provided a wealth of knowledge and experience in the classroom and the field. Thank you to you all.

Funding was provided through NSF awards ARC1604249 and ARC1602440.

TABLE OF CONTENTS

ABSTRACT

WINTER SNOW DEPTH IN ARCTIC ALASKA RESULTS IN COMPLEX CHANGES IN CARIBOU FORAGE QUALITY

JESSICA C. RICHERT

2019

Caribou (*Rangifer tarandus*) rely on the short growing season for much of their annual nutrition, making them susceptible to even small changes in forage quantity and quality. Body condition in the summer and fall is linked to winter survival rates and fecundity in cows, critical factors in the robustness of caribou populations. Due to a warmer, wetter climate, snowfall is predicted to increase over Alaska's North Slope in the next several decades. Deeper snow results in higher soil temperatures, allowing microbial mineralization of nitrogen to continue throughout the winter and increasing the availability of nitrogen for plants in spring and summer; however, deeper snow can also delay the onset of spring and initial plant growth. These biophysical changes may impact the quantity, quality, and seasonality of caribou forage. I used a 20+ year snow manipulation to evaluate how a set of winter climate change scenarios may affect tussock tundra vegetation community composition and forage quality in northern Alaska. I sampled leaf tissue of six plant species (*Salix pulchra, Betula nana, Rhododendron tomentosum, Vaccinium vitis-idaea, Carex bigelowii,* and *Eriophorum vaginatum*) weekly between leaf-out and senescence in two consecutive years in areas of ambient, reduced, and added snow. Leaf tissue was analyzed for %N, dry matter digestibility, and digestible protein to quantify temporal changes in nutrition as well as differences between species and among functional groups (deciduous shrubs, evergreen dwarf shrubs, and

graminoids). Deeper snow increased leaf %N and digestible protein in the two deciduous shrubs and graminoids, but not the evergreen shrubs. Dry matter digestibility varied between species with small differences associated with divergent winter snow depths. Deeper snow also increased the duration of higher-protein forage by as much as 25 days in *S. pulchra* and 6-9 days in *B. nana* and *C. bigelowii*. Consequently, predicted increases in winter snow over the North Slope by the end of the century may enhance both summer and autumn forage quality and availability for caribou. Through multiplier effects of increased nutrition on body condition, survivorship, and fecundity, better forage conditions may improve the health and welfare of caribou in northern Alaska.

CHAPTER 1: INTRODUCTION

Caribou and reindeer (*Rangifer tarandus*) populations in the circumpolar Arctic face many challenges (Osborne et al. 2018). Forage availability, forage quality, predation, insect harassment, increasing human development, and extreme weather events have all been implicated as possible reasons for the declines of caribou and reindeer populations around the world in recent decades (Mörschel and Klein 1997, Vors and Boyce 2009, Festa-Bianchet et al. 2011, Fauchald et al. 2017). Though caribou and reindeer 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 global populations is cause for concern and suggests a widespread driver like climate change may be partially responsible.

Changes in the Arctic's weather patterns and overall climate present additional challenges to caribou and reindeer populations. Over the past 60 years, the mean annual temperature has risen almost twice as fast in the Arctic as the rest of the world (ACIA 2004), with temperatures already rising by almost 2°C since the early 1900s (Osborne et al. 2018). Temperatures are predicted to continue rising by another 2-9°C by the end of the century (IPCC 2013). This increase in air temperature may worsen already existing stressors in caribou and reindeer as well as introduce new ones (Mallory and Boyce 2017). Caribou begin exhibiting signs of heat stress at temperatures above 22°C (Thompson and Barboza 2014), decreasing forage intake and reducing activity (Mörschel and Klein 1997). Insect harassment from mosquitoes and flies also increases with temperature (Mörschel and Klein 1997, Bali et al. 2013) with severe harassment affecting forage intake and large-scale movement patterns observed in air temperatures over

13.5°C (White et al. 1975). Higher temperatures also increase the frequency and risk of extreme weather events like rain on snow and icing of pastures (Rennert et al. 2009), which can lead to starvation and mortality as animals are cut off from important winter forage (Hansen et al. 2014, Mallory and Boyce 2017), though significant die-offs during such extreme events may also be due in part to density-dependent factors, that is the density of caribou or reindeer exceeds the necessary forage resources to support the herd (Tyler 2010, Hansen et al. 2019).

Warmer weather during the growing season may also decrease forage quality and contribute to phenological mismatches between migratory caribou and their food sources at a nutritionally critical part of year (Walsh et al. 1997, Fauchald et al. 2017). Warming reduces leaf-level nitrogen (N) concentrations and increases anti-herbivory compounds such as digestibility-reducing tannins (Jonasson et al. 1986, Turunen et al. 2009, Zamin et al. 2017a) while simultaneously promoting growth of deciduous shrubs like *Alnus* and *Betula spp*. These shrubs are naturally higher in anti-herbivory compounds than graminoids, potentially decreasing forage quality even as forage availability increases (Fauchald et al. 2017). Warmer temperatures may also shift the growing season earlier into the spring, potentially decoupling annual caribou physiological stages from both the timing and seasonality of critical nutrients on the landscape. While spring forage quality and availability may not be as important to capital breeders like caribou that rely more on winter body reserves for calf production and survival (Veiberg et al. 2017), phenological mismatches in the summer and fall have the potential to severely impact both individuals and populations due to the influence of even small changes in forage intake and weight

gain on growth rates and fecundity (White 1983, Cebrian et al. 2008, Proffitt et al. 2016, Gustine et al. 2017).

Effects of higher temperatures on caribou may not always be negative, however. Warmer air temperatures cause warmer springs, earlier snowmelt, and consequently, longer growing seasons (Linderholm 2006). Plant communities are already responding to these 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 (Sturm et al. 2001b, Wahren et al. 2005, Tape et al. 2006, Hobbie et al. 2017, Carlson et al. 2018), although important winter forage like lichens is also declining (Wahren et al. 2005, Hobbie et al. 2017). Asynchronous green-up of forage due to differences in snow melt-off dates between areas of shallow and deep snow in response to warmer springs may also benefit caribou by creating spatial heterogeneity of high-quality forage across the landscape and extending the length of time that such forage is available (Searle et al. 2015, Veiberg et al. 2017).

Winter precipitation patterns over the Arctic are also expected to shift along with higher air temperatures. Projections for the central Arctic region of Alaska call for an increase in winter precipitation of 13-48% by mid-century and an increase of 36-77% by the end of the century, mostly in the form of snow (Martin et al. 2009), though predictions for the entire Arctic are variable (Callaghan et al. 2011). As snow is a defining feature of Arctic ecosystems for up to nine months of the year, changes in snow cover and duration may have a greater effect on northern plant communities than a warmer growing season (Rieley et al. 1995, Jones et al. 1998, Wahren et al. 2005, Fu et al. 2014). Snow cover plays a vital role in insulating the ground from harsh winter

conditions, with even moderate increases in snow depth raising the soil surface temperature by as much as 15°C (Walker et al. 1999, Schimel et al. 2004, Pattison and Welker 2014). Higher soil temperatures allow microbial mineralization of soil nitrogen to continue throughout the winter and increases active layer thaw depths in the summer (Johansson et al. 2013) while also increasing available nitrogen pools in the soil that plants can utilize (Schimel et al. 2004, Welker et al. 2005).

Changes in winter precipitation also alter the timing of snow melt and subsequent green-up, potentially shortening or lengthening the growing season in areas. Even though the Alaskan Arctic is predicted to have more winter precipitation, the overall duration of snow cover is expected to decrease (Callaghan et al. 2011). The timing of melt-off is critical to the onset of new growth in plants as photosynthesis begins and soils thaw enough for nutrient uptake (Walsh et al. 1997, Borner et al. 2008). Deep snow accumulations may delay green-up by as much as 3-4 weeks, reducing an already short growing season and potentially reducing both productivity and overall biomass (Wipf and Rixen 2010), though this may be mitigated in some cases by a corresponding increase in photosynthesis from higher leaf N concentrations (Leffler and Welker 2013, Bosiö et al. 2014).

Moderate increases in snow depth also favor deciduous shrub growth (Wahren et al. 2005, Tape et al. 2006, Berner et al. 2018). Taller shrubs trap snow around themselves, creating deeper drifts in winter and forming a positive feedback loop wherein climate-induced increases in snowfall increases shrub growth which in turn further increases local snow depth (Sturm et al. 2001a, 2005, Jespersen et al. 2018). This loop eventually shifts vegetation communities from graminoid and ericaceous shrub-

dominated to those dominated by deciduous *Alnus, Betula,* and *Salix* species (Tape et al. 2006, 2012).

The highest nutritional demands on caribou and reindeer occur during the summer and autumn when animals are recovering from winter deprivations, cows are lactating, and calves are growing rapidly (Denryter et al. 2017, Gustine et al. 2017, Veiberg et al. 2017). Plants with higher leaf-level N concentrations, like deciduous shrubs, provide more protein to caribou and are preferentially selected during foraging (White and Trudell 1980, Denryter et al. 2017), especially early in the season when leaf N concentration is maximal (Klein 1990).

Both deciduous shrub biomass and leaf-level N increase with snow depth (Walker et al. 1999, Welker et al. 2005, Borner et al. 2008, Leffler and Welker 2013), potentially mitigating any dilution of nitrogen due to increased growth and providing caribou with an abundance of high-protein forage (Turunen et al. 2009, Zamin et al. 2017a). In addition, higher soil nitrogen can decrease the carbon-based secondary compounds, including condensed tannins and other phenolics, commonly found in arctic shrubs (De Long et al. 2016). Tannins and other phenolic compounds reduce the digestibility and available protein of plants either through binding directly to proteins in forage or by interfering with digestive enzymes in an animal's stomach (Robbins et al. 1987b, 1987a, Lambers et al. 2008). Fertilization treatments have decreased total phenolic content at multiple arctic and alpine sites (Bryant et al. 1983, Coley et al. 1985, Graglia et al. 2001, De Long et al. 2016), though effects of snow and fertilization on the actual protein-precipitating capacity of plants is less known.

This study builds on decades of research from the same site, providing a continued examination of long-term trends in leaf-level nutrients after 25 years of snow manipulation as well as short-term temporal changes during the growing season. While multiple studies have examined the effects of warming, snow, and higher CO_2 on vegetation composition and leaf-level nutrients, few have specifically examined how such responses relate to caribou nutrition. This study seeks to fill in that gap and determine what effects changes in winter snow depth associated with projected climate change have on the availability and quality of forage for caribou on Alaska's North Slope.

CHAPTER 2: WINTER SNOW DEPTH IN ARCTIC ALASKA RESULTS IN COMPLEX CHANGES IN CARIBOU FORAGE QUALITY

Introduction

Due to Arctic amplification, northern latitudes are warming nearly twice as fast as the rest of the world (Martin et al. 2009), and temperatures are projected to continue rising throughout this century (IPCC 2013). Precipitation patterns are also shifting over much of the Arctic, with significant increases in winter precipitation expected over the next few decades (though model projections are variable), particularly in the form of increased snow fall (Callaghan et al. 2011). In particular, Alaska's North Slope, home to the Central Arctic Herd of caribou (*Rangifer tarandus granti*), is predicted to see a 35-70% increase in winter precipitation over portions of the herd's home range by the end of the century (Scenarios Network for Alaska and Arctic Planning 2011).

Snow cover is a defining feature of Arctic ecosystems for up to nine months of the year and changes in extent, depth, and duration may have a greater effect on northern plant communities than warming growing season temperatures (Wahren et al. 2005, Fu et al. 2014). Snow cover plays a vital role in insulating the soil from harsh winter conditions. Deeper snow results in higher soil temperatures in winter (Walker et al. 1999, Schimel et al. 2004) because snow decouples the soil from the frigid arctic air. These less cold soils lead to a deeper active layer depth in summer (Johansson et al. 2013, Pattison and Welker 2014) and facilitate microbial mineralization of organic nitrogen throughout the entire winter, increasing the soil nitrogen available for plants in the early spring (Bilbrough et al. 2000, Schimel et al. 2003, 2004, Sturm et al. 2005, Welker et al. 2005) and thus, higher leaf N all summer long.

Secondary compounds are a critical attribute of tundra plants as related to herbivory and digestibility. These compounds, including tannins and other similar phenolic anti-herbivory compounds that reduce digestible protein of plants may change in response to environmental conditions (Peñuelas et al. 1997, Nybakken et al. 2013). For instance, tannin content of leaves may decrease with higher soil nutrients in Arctic and alpine sites (Bryant et al. 1983, Coley et al. 1985, Graglia et al. 2001, Schimel et al. 2004, De Long et al. 2016). There are few experimental studies that quantify whether warmer summers or changes in winter snow affect secondary compounds in tundra plants, however, an attribute that may be critical to determine as we seek to understand how climate changes will affect forage nutrition for caribou in Alaska and globally.

One of the most important facets of understanding how tundra systems will adapt as weather and climate changes is woven into the individualistic nature of plant species and functional group responses to change (Chapin III and Shaver 1985). This foundation of tundra ecology is still apparent today, as given uniform changes in environmental conditions, not all species and not all traits (i.e. flowering, leaf out, leaf-level nutrition, leaf physiology, etc) behave in a uniform manner (Arft et al. 1999). Recent changes across the Arctic are a mixture of responses with potential community and ecosystem consequences such as a strong growth response of some shrub species to warmer summers and/or deeper snow (Elmendorf et al. 2011, Tape et al. 2012). This perspective is especially important as related to caribou forage as individualistic changes in abundance in combination with changes in both magnitude and duration of higher-quality forage in spring or autumn may have large consequences for the carrying capacity of the

landscape for caribou as well as the ability to support early season or prolonged nutrition during critical physiological stages of this keystone ungulate.

The primary question that this study addresses, then, is: how do various winter climate scenarios (deeper or shallower snow) affect the availability and quality of forage in tussock tundra for caribou? To address forage availability, I asked: does snow depth affect vegetation community composition and biomass? To address forage quality, I asked: does snow depth affect nutritional factors like digestibility and protein content in common tussock tundra plan species. Based on previous snow manipulation, warming, and fertilization experiments that demonstrates the effect of snow on vegetation community composition and nitrogen content, I hypothesized that: (1) enhanced growth due to warmer soil temperatures and enhanced microbial activity under deep snow would benefit deciduous shrubs over other functional groups due to deeper roots and higher phenological plasticity, leading to higher biomass; and (2) due to increased availability of nitrogen in warmer winter soils and a decrease in phenolic content in plants with experimental fertilization, measures of caribou forage quality like leaf N, digestibility, and digestible protein would be highest in areas of deeper snow, with the greatest impact on deciduous shrubs.

Materials and Methods

Study Site

This research was conducted from 2017 to 2018 in moist-acidic tussock tundra near Toolik Field Station (68°38’ N 149°38W) in the foothills of the Brooks Range, Alaska, USA. The mean annual temperature 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). Mean precipitation is 250-350 mm, with 40-45% falling as snow (Schimel et al. 2004). In winter, snow depths reach 30-80 cm on average, but can drift 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 non-tussock forming graminoids intermixed throughout the inter-tussock areas (Whalen 2002). A wooden snow fence (3 x 60 m) was erected on the moist-acidic tussock tundra site in 1994 to artificially increase snow depth, with snow drifts reaching a maximum depth of 3m directly behind the snow fence and declining to ambient snow depths (0.5-1 m) 50-60 m from the fence (Jones et al. 1998, Walker et al. 1999, Welker et al. 2000).

Field Sampling

To test whether winter snow depth affects summer forage quality, I collected samples of six common plant species present in moist-acidic tussock tundra. These species represented three functional groups: deciduous shrubs, evergreen dwarf shrubs, and sedges. Samples of two species from each functional group were collected on a weekly basis from 19 June-7 August 2017 and 22 June-25 August 2018. 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 sedges *Carex bigelowii* and *Eriophorum vaginatum*. Sampling methods mimicked caribou browsing, with leaves of deciduous shrubs stripped by hand and evergreen dwarf shrubs and sedges clipped at ground level. Five leaf tissue samples of each species were collected in each of three snow depth zones: + snow (1-2 m snow), - snow (0.5 m snow), and ambient (0.5-1 m snow; control), for a total of 90 samples a week over a 10-12 week period throughout the growing season. After collection, all samples were dried in a forced-air oven at 70°C for 72 hours. These samples were analyzed for C and N content and dry matter digestibility. An additional five samples of *S. pulchra* and *B. nana* were collected every other week 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 in forages due to anti-herbivory compounds (Robbins et al. 1987a).

To test whether snow depth affects forage availability by altering plant community composition and abundance, I sampled biomass at three locations within each snow depth zone at peak growing season biomass of both years (13 July and 29 July, respectively) for a total of six plots per snow zone. Biomass for *S. pulchra* and *B. nana* was harvested in 1 m^2 quadrats, while biomass of all other species was harvested in three 20 cm^2 quadrats nested within the larger 1 m^2 plot. All samples were sorted to species, then dried in a forced-air oven at 70°C for 72 hours before being weighed to obtain the total biomass per species. Species were combined into functional groups for analysis.

In addition to forage and biomass samples, I measured snow depth during the winter of 2018-2019 and active layer depth during the summer of 2018. I measured snow depth along 12 transects perpendicular to the snow fence. Snow depths were recorded at

2-5 m intervals from the snow fence to 80 m north of the fence using 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. I also recorded active layer depth on a weekly basis during the 2018 growing season by inserting a probe to the freeze boundary at 5 m intervals along a 50 m transect in each snow zone. Due to late snowmelt, the + snow treatment zone was separated into two active layer depth transects, one along the shallower end of the snow drift and one along the deeper end. Measurements for these two transects began at their respective melt-off dates.

Laboratory Analyses

I quantified forage quality by measuring neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), dry matter digestibility (DMD), percent nitrogen (N), crude protein (CP), and digestible protein (DP) in each sample (ca. 1600). Protein precipitation capacity was determined on the additional 2018 deciduous shrub samples (ca. 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 analysis (determination of NDF, ADF, and ADL- See Appendix 2) was conducted on all samples using the ANKOM Technology method (ANKOM Technology 2003a, b, 2011) 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). NDF residues were then extracted with an acid detergent solution to yield ADF (a measure of the least

digestible plant components like cellulose and lignin). The ADF residue was digested with 72% sulfuric acid to determine ADL, then ashed in a muffle furnace at 500°C for 5 hours to determine the total proportion of non-digestible lignin-cutin and inorganic matter. Percent N was analyzed via combustion at 1800°C in tin capsules using an elemental analyzer (ECS 4010, Costech Analytical Technologies Inc., Valencia, California, USA).

I assessed the protein-precipitating capacity of tannins in the deciduous shrubs, *S. pulchra* and *B. nana*, using bovine serum albumin (BSA) according to the methods developed by 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, Swedesboro, New Jersey, USA). Extracts were then serially diluted with a standard solution of BSA and an acetate buffer solution 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 I read the absorbance at 595 nm on a UV-Vis microplate spectrometer (Synergy HT Multi-Mode Microplate Reader, BioTek Instruments Inc., Winooski, Vermont, USA).

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

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

$$DP = -3.97 + 0.9283*CP - 11.82*PPC \qquad \text{eq. (2)}$$

where LIG is the lignin/cutin fraction calculated from sequential fiber analysis (See Appendix 2).

Statistical Analyses

Snow depth at the snow fence was calculated using a second order polynomial local area regression to interpolate between transect readings. Mean snow depth of each snow zone was then extracted from the area sampled. To examine the effect of snow depth on forage availability I ran a one-way ANOVA using the statistical computing language R (R Core Team 2018) on the biomass of each functional group and used lsmeans to determine where specific differences among the snow zones occurred. In this analysis differences among snow zones were considered significant at $p < 0.05$.

I examined the effect of snow depth on forage quality of each species using the nlme package (Pinheiro et al. 2018) to perform a linear mixed-effects analysis of the relationship of leaf-level N (Table 1) and dry matter digestibility (Table 2) of each species as well as the protein-precipitating capacity of the deciduous shrubs (Table 3) to the snow treatment zones. The base model included day of year 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 percent nitrogen content, percent dry matter digestibility, and protein-precipitating capacity (expressed as mg BSA precipitated/mg dry matter (DM)). This base model was compared to additional models that include additive and multiplicative interactions between snow depth treatments and day of year as well as a quadratic day of year term to account for rapid changes in the response variable during leaf expansion and senescence and slower changes during mid-summer. All proportionate data were arcsine square-root

transformed prior to analysis, and I selected the top model for each independent variable using AIC (Burnham and Anderson 2002). The top model was used to calculate predicted means and 95% confidence intervals for each variable over the sample period.

For all species except the deciduous shrubs, digestible protein was calculated directly from eq. 2 with the assumption that PPC=0. Since digestible protein is directly related to leaf N (through the crude protein variable in eq. (2)), the top N model was used with the calculated digestible protein values to obtain the predicted means and confidence intervals over the sampling period. For the 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 crude protein and PPC estimates and standard errors of the estimates. I then randomly sampled from a normal distribution for each daily estimate of crude protein and PPC and calculated digestible protein using eq. (2). This procedure was repeated 1000 times for each day, producing a daily estimate and 95% confidence interval of digestible protein for both shrubs throughout the sampling period that accounts for the error of both crude protein and PPC trends.

Results

Snow and Active Layer Depth

My designated snow treatment zones matched snow depth collected in March 2019 (Fig. 1). Snow depth in the Ambient zone was 39 $\pm$ 11 cm, while snow depth in the - snow and + snow zones was 20 $\pm$ 3.4 cm and 147 $\pm$ 18 cm respectively.

Active layer depths increased rapidly throughout the growing season until DOY 217-220, when they approached maximum depth (See Appendix 1). Depths at the

beginning of the growing season (DOY 173) were only 8 ± 1 cm in the shallow end of the + snow treatment, 17 ± 6 cm in the - snow treatment, and 14 ± 5 cm in ambient conditions. Half of the + snow treatment zone was still covered by a snow drift that was 38 ± 11 cm deep. By the end of the growing season (DOY 237), active layer depths in all zones were 45-60 cm, with the snow-covered area of the + snow treatment increasing from an initial depth of 10 ± 1 cm at DOY 180 to 61 ± 10 cm at DOY 237. The ambient zone depth increased to similar levels at 60 ± 9 cm, and the - snow treatment and shallow end of the + snow treatment reached depths of 51 ± 10 cm and 49 ± 7 cm respectively.

Forage Availability

Overall biomass was not significantly different among the three snow zones, with 828.60 ± 106.31 g/m^2 in the ambient plots, 748.24 ± 35.26 g/m^2 in the – snow treatment plots, and 764.62 ± 106.30 g/m^2 in the + snow treatment plots. Broken down by functional group though, the - snow and + snow treatments differed from ambient conditions in a few key ways. Both treatments had a higher biomass of deciduous shrubs than ambient (Fig. 2), with a statistically significant ($F_{2,15}$ = 5.027, $p < 0.05$) higher biomass of deciduous shrubs occurring in the - snow treatment at 165.36 ± 14.38 g/m^2 (compared to 135.82 ± 14.79 g/m^2 in the + snow treatment). The - snow treatment also had the highest biomass of evergreen dwarf shrubs (138.56 ± 43.17 g/m^2), while the + snow treatment had the lowest (59.45 ± 13.38 g/m^2). Both the - snow and + snow treatments had significantly ($F_{2,15}$ = 11.8, $p < 0.001$) lower lichen biomass (2.43 ± 1.80 and 8.51 ± 4.10 g/m^2 respectively) compared to ambient (50.68 ± 12.47 g/m^2). For all treatments, total biomass of lichens and forbs was small compared to other functional groups, while all snow zones had similarly high biomass of both moss and graminoids. In

almost all functional groups, however, there was considerable spatial variation with each snow zone, resulting in high variation between individual plots.

Nitrogen Content

Snow depth affected N content of all sampled species except *V. vitis-idaea*, with all top models including either an additive or multiplicative interaction with snow and the quadratic day of year term (Table 1). Increased snow depth had the strongest effect on the deciduous shrub and graminoid functional groups. For both, N content was significantly greater in the + snow treatment, while there was little to no difference between the - snow treatment and ambient conditions (Fig. 3). This difference in N content among the snow zones remained relatively constant throughout the growing season. For *S. pulchra*, deep snow resulted in 11.4% greater N at the beginning of the growing season (DOY 173) compared to the ambient plots. The difference among the treatments remained relatively constant even as overall N levels declined during the season, leading to plants in the + snow plots having 90.0% higher leaf N when leaf senescence began (DOY 237). *B. nana* followed a similar pattern, although with a lesser increase in N content of 8.35% in + snow plots compared to ambient areas at the beginning of the growing season and 25.3% by the end.

Both sedges, *C. bigelowii* and *E. vaginatum*, demonstrated different patterns of N content throughout the growing season (Fig. 3). *C. bigelowii* followed much the same pattern as the shrubs, with highest N levels at the beginning of season and in the + snow treatment, declining steadily over time. While the - snow treatment and ambient plots maintained similar N levels through most of the growing season, N content of plants in ambient conditions declined sharply with the onset of senescence, resulting in 107%

higher N levels in the + snow treatment by the end of the growing season. *E. vaginatum* did not follow the same temporal pattern of N content as *C. bigelowii* or the deciduous shrubs. Instead, N content was low (~2%) over the course of the entire growing season. Plants in the + snow zone still had higher leaf N, especially near the end of the season, with a 30.4% increase over ambient.

For the evergreen dwarf shrubs, N content remained low throughout the entire growing season, with few samples ever rising above 2%. For *V. vitis-idaea*, snow depth did not have an effect on leaf N, while for *R. tomentosum* N was highest in the - snow treatment over the first few weeks of the growing season before falling below + snow levels by mid-season and rising again in the last weeks of August when N content in the + snow treatment began to decrease.

Dry Matter Digestibility

Snow depth affected dry matter digestibility less than N content for all species, with only a slight increase in digestibility of *B. nana* in the + snow treatment (Fig. 4). 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 digestibility in both the ambient and – snow plots increased slightly to match that of the + snow plots.

Few clear patterns emerged in dry matter digestibility of other sample species despite often including a snow term in the top models (Table 2). There was no effect of snow depth on the evergreen dwarf shrub, *V. vitis-idaea,* and the sedge, *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 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 sedge, *E. vaginatum,* showed curvilinear trends through time as well as a slight effect of snow depth. Plants in all three snow zones exhibited similar digestibility at the beginning of the season (~45-50% in *R. tomentosum* and ~60-70% in *E. vaginatum*) only to diverge in the latter half (Fig. 4).

Protein-precipitating Capacity and Digestible Protein

Since digestible protein is directly correlated with the amount of nitrogen in a forage while also accounting for the protein loss due to anti-herbivory compounds in certain plants, digestible protein shows the same temporal patterns as the N content of each species (Fig 6). In the deciduous shrubs, however, anti-herbivory compounds like tannins bind to proteins in the plant and lower the total digestible protein an animal can obtain from them, decreasing overall forage quality (Robbins et al. 1987a). For *B. nana*, the top model for protein-precipitating capacity included snow depth (Table 3), with estimated PPC highest in the + snow treatment in the middle of the growing season at 0.276 $\pm$ 0.014 mg BSA precipitated/mg DM (Fig. 5). 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 to a high of 0.357 ± 0.015 mg BSA precipitated/mg DM by DOY 217 before declining to 0.334 ± 0.023 mg BSA precipitated/mg DM by senescence (Fig. 5).

Caribou need a minimum of 7-8 g DP/100g DM in their diet to maintain body condition (red line in Fig. 6) (Thompson and Barboza 2017). Even with the additional protein-precipitating capacity of anti-herbivory in the deciduous shrubs, digestible protein levels of both *S. pulchra* and *B. nana* remained above maintenance levels well into the growing season, especially in the + snow treatment (Fig. 6), with values as high as 20-25 g/100g DM. 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 ca. 2 g/100g DM throughout the sample period. Digestible protein in *C. bigelowii* mirrored the same pattern as the deciduous shrubs, beginning the season at 15-20 g/100g DM and declining steadily with time until falling below maintenance levels near senescence. *E. vaginatum*, while not high in digestible protein, remained above the maintenance threshold for most of the growing season in all snow zones, and plants in the + snow treatment stayed just over the minimum protein requirement during the entire sampling period.

Discussion

My results demonstrate that increased snow depth affects both the availability and quality of forage species important to caribou on Alaska's North Slope. Deep snow areas had higher biomass of preferred functional groups over ambient snow areas as well as a decrease in the proportion of unpalatable evergreen dwarf shrubs. Deep snow also increased leaf-level N and digestible protein in both deciduous shrubs and graminoids,

despite increasing the protein-precipitating capacity of anti-herbivory compounds in *B. nana*. While changes to forage digestibility due to snow were mixed, overall digestibility in preferred forages was high over the entire growing season. Increases in snow depth, then, may enhance both forage quantity and quality for caribou.

Effects of Snow Depth on Forage Availability

The most obvious changes in biomass among the three snow zones occurred in the deciduous shrub, evergreen dwarf shrub, and lichen functional groups, though only significantly so for deciduous shrubs and lichens. The deep snow area had the lowest evergreen shrub biomass, which is consistent with previous snow manipulation and fertilization studies (Chapin III et al. 1995, Demarco et al. 2014, Zamin et al. 2014). Many studies have also found a concomitant increase in biomass (Wipf and Rixen 2010) and/or percent cover (Wahren et al. 2005, Johansson et al. 2013, Leffler et al. 2016) of deciduous shrubs in areas with deeper snow, yet my results show the opposite, with the highest biomass of deciduous shrubs found in the reduced snow area, although both the reduced snow and deeper snow areas have higher shrub biomass than ambient conditions.

One plausible explanation for the discrepancy is that small-scale vegetation communities within the boundaries of the snow fence vary considerably, making differences due to snow depth difficult to quantify without a larger sample size than the six 1-m^2 plots used in this study. Another possible explanation is that several previous studies included additional treatments such as summer warming or additional N through fertilization combined with winter snow depth and the deciduous shrub response was greatest when deep winter snow interacted with these other treatments (Demarco et al. 2014, Leffler et al. 2016). Additionally, the snow depth in the deeper snow area may now

be too deep, with the snow fence amplifying natural increases in snow fall in the two decades since the fence was erected. Some studies have found decreased shrub cover in areas with deep snow (> 2 m) as opposed to areas with more moderate snow cover (1-2 m) (Wahren et al. 2005, Borner et al. 2008, Johansson et al. 2013) suggesting there is a maximum snow load a shrub-dominated community can tolerate. The number of growing degree days needed for onset of green-up at northern latitudes has a positive correlation with the amount of winter precipitation (Fu et al. 2014). With an already short growing season, snow depths that regularly delay green-up by more than two weeks may reduce productivity and eventually deplete energy reserves in plants, inducing mortality and reducing the abundance of certain species like deciduous shrubs and *Eriophorum spp.* (Walker et al. 1999, Borner et al. 2008, Wipf and Rixen 2010). In either case, the availability of important summer forage species like *S. pulchra* should increase with moderately more snow. The same cannot be said for important winter forages, including lichens and evergreen dwarf shrubs (Boertje 1984, Ophof et al. 2013), both of which decrease with more snow in this and other studies.

Effects of Snow Depth on Forage Quality

Additional snow increased leaf N in both the deciduous shrubs and sedges (Fig. 3), as has been found in previous studies across multiple arctic and alpine sites (Walker et al. 1999, Van der Wal et al. 2000, Welker et al. 2005, Leffler and Welker 2013). Increased snow depth had the greatest impact on N content in *S. pulchra*, but *B. nana* and the sedge *C. bigelowii* exhibited similar increases. This partially supports my hypothesis of snow having the greatest impact on the quality of deciduous shrubs due to deeper roots that can take advantage of higher soil nitrogen 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). The impact of deep snow on N content of *C. bigelowii* is curious, though, as leaf N in *E. vaginatum*, another sedge, does not respond similarly to deeper snow, remaining low overall throughout the study period.

There are a few possible explanations for the difference seen in N content over the growing season between the two sedges. First, *E. vaginatum* replaces its roots annually (Chapin III 1986, Sullivan and Welker 2005) and it may not be able 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 (pers. obs.). 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. 3), with changes in N reflecting a 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). I observed high N concentrations earlier in the growing season in the low snow area, which was snow free earliest in the

season. Leaves of *R. tomentosum* in the deep snow area exhibited similar N concentrations several weeks later, following later snow melt of the deeper snow drift. Hence, deeper snow shifted leaf production and subsequent peak leaf N in this species later in the growing season.

Interestingly, leaf N was higher for most species in the deeper snow area despite having the shallowest active layer depth over half the + snow zone (See Appendix 1). This suggests that higher nitrogen uptake by plants may rely more on snow insulating the soil enough for enhanced microbial activity during the winter than on the release of new nutrients as soils thaw deeper during the growing season (Schimel et al. 2004). While active layer depth is generally correlated with snow depth (Johansson et al. 2013), other factors such as soil moisture content, albedo and insulating properties of the vegetation types covering the soil surface cannot be discounted (Loranty et al. 2011).

Snow depth did not have as great an impact on leaf dry matter digestibility as leaf N, results similar to previous studies examining the effects of various environmental factors like shading, air temperature, and precipitation on forage quality (Lenart et al. 2002). Individual species within each functional group responded differently from one another, ranging from phenological shifts to no significant effects, and overall changes in dry matter digestibility trends, whether through time or with snow depth, usually spanned only a few percentage points. Even small changes in digestibility, however, can 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.

The protein-precipitating capacity of the deciduous shrubs did not respond to the winter climate change scenarios the way I initially expected. PPC of *S. pulchra* was unaffected by snow depth; however, PPC increased with snow depth in *B. nana*, albeit only slightly. Previous studies in tussock tundra in the Toolik Lake area found that concentrations of phenolics in *B. nana* increased with N fertilization treatments (Graglia et al. 2001), while other studies found a more generalized increase 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, one might expect to see lower PPC as plants use available nitrogen to shunt carbon tied up in secondary compounds into new growth rather than defense (Chapin III 1989). The results presented here show just the opposite, however.

Protein-precipitating capacity of *B. nana* was highest in the deeper snow area and lowest in the reduced snow area, 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 area, as values of PPC in leaf tissue of plants in deeper snow followed roughly the same pattern as those in the ambient snow area, just offset by two weeks. One explanation for the seemingly opposite results of studies in tussock tundra surrounding Toolik Lake arises from different assays used to quantify various secondary compounds. Most studies measure total phenolic content as opposed to protein-precipitating capacity (Graglia et al. 2001, Zamin et al. 2017a), 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. *B. nana* in this experiment exhibit a similar lower PPC in deeper snow areas at about the same time as prior studies; however, I observed considerable variation when analyzing trends over the entire growing season. 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 III 1989, Haukioja et al. 1998).

Despite the dampening effect of PPC on digestible protein content in the deciduous shrubs, deeper snow increased the amount of digestible protein in certain forage species (primarily through enhancing overall N content) while also increasing the length of time that digestible protein content is above the minimum maintenance levels required by caribou during the summer. The largest impact is on the value of deciduous shrubs and sedges as a protein source. For example, deep snow resulted in ~25 additional days of digestible protein 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 in ambient snow conditions and mimics the increased duration of protein observed along latitudinal gradients (Barboza et al. 2018). The duration of time that digestible protein in *B. nana* and *C. bigelowii* remained above maintenance levels was also extended, albeit more modestly at 6 and 9 days respectively. In addition, while the digestible protein content of *E. vaginatum* was lower overall than other species for most of the growing season, levels in the deeper snow area 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.

Limitations

There are a few limitations with this study that must be addressed. First, this study took place at a single snow fence located in moist acidic tussock tundra. There are strong regional variations in responses of tundra to warming and fertilization experiments (Wipf and Rixen 2010, Elmendorf et al. 2011), suggesting that complex interactions among climate, geology, and hydrology also determine how specific vegetation communities respond to change. However, my largest observed responses to deeper snow (i.e. higher N in *S. pulchra* and *B. nana*) are broadly consistent with several studies in different locations (Walsh et al. 1997, Schimel et al. 2004, Welker et al. 2005, Leffler and Welker 2013, Semenchuk et al. 2015). It should also be noted that the deepest snow drifts created by the snow fence in this experiment are deeper than even the most extreme predictions of increased winter precipitation in the region (Scenarios Network for Alaska and Arctic Planning 2011). More moderate increases in snow, though, may actually result in greater long-term changes to plant communities than exceptionally deep snow associated with snow fence studies (Borner et al. 2008, Wipf and Rixen 2010). For assessing forage quality, I also make a few assumptions. Since I only analyzed protein-precipitating capacity for the deciduous shrubs, I assumed the PPC for all other species was 0 when calculating digestible protein. While graminoids are low in phenolic compounds that bind protein, 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 digestible protein values are

already well below the maintenance threshold, so their value as summer forage remains unchanged. Although the results of this study may not apply to tundra ecosystems as a whole, it still provides one of the few examples of how long-term changes in snow depth affect certain tundra plants and what that means for both the quantity and quality of forage for large arctic herbivores now and in the future.

Conclusions

Because tundra ecosystems are so nutrient-limited (Bryant et al. 1983), small changes in both availability and quality of forage containing essential nutrients like protein can have outsize impacts at both the individual and population levels (White 1983). Larger quantities of high-quality plants increase forage intake by caribou, which increases the rate and amount of weight gained during the short growing season (White and Trudell 1980). Only a few kilograms of weight gain can increase the chance of conception by as much as 60% (White 1983, Proffitt et al. 2016). As capital breeders, caribou rely on body stores of fat and protein to support pregnancy and early lactation during the winter and early spring (Barboza et al. 2018). An increase in summer forage quality reduces the time needed to recover body reserves from both winter deprivations and the nutritional demand of lactation while increasing calf weight gain and growth rates (White et al. 1975, Veiberg et al. 2017). A small positive change in future forage nutrition from the increased snow predicted by climate models and observed over the past 20+ years, may potentially mitigate declines in forage quality due to higher temperatures (Jonasson et al. 1986, Turunen et al. 2009, Fauchald et al. 2017, Zamin et al. 2017a) and lead to higher survival, recruitment, and population growth rates of caribou in N Alaska.

Tables

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

Model	logLik	AIC_c	ΔAIC_c	*df*	weight
S. pulchra					
SNOW*DOY*DOY^2	869.63	-1707.23	0.00	15	0.87
SNOW + DOY*DOY^2	861.12	-1703.49	3.74	9	0.13
DOY*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
B. nana					
SNOW + DOY*DOY^2	840.98	-1663.23	0.00	9	0.87
SNOW*DOY*DOY^2	845.71	-1659.41	3.82	15	0.13
DOY*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
L. palustre					
SNOW*DOY*DOY^2	980.25	-1928.56	0.00	15	0.99
SNOW + DOY*DOY^2	968.63	-1918.55	10.01	9	0.01
DOY*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
V.vitis-idaea					
DOY	968.84	-1927.45	0.00	5	0.46
SNOW + DOY*DOY^2	972.45	-1926.21	1.24	9	0.25
DOY + DOY^2	968.90	-1925.47	1.98	6	0.17
DOY*DOY^2	969.30	-1924.17	3.28	7	0.09
SNOW*DOY*DOY^2	977.24	-1922.58	4.87	15	0.04
C. bigelowii					
SNOW*DOY*DOY^2	861.93	-1691.93	0.00	15	1.00
SNOW + DOY*DOY^2	843.04	-1667.37	24.56	9	0.00
DOY*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
E. vaginatum					
SNOW* DOY*DOY^2	861.04	-1690.19	0.00	15	0.65
SNOW + DOY*DOY^2	853.83	-1688.97	1.23	9	0.35
DOY*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

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

Model	logLik	AIC_c	ΔAIC_c	*df*	weight
S. 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
B. 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
L. palustre					
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
V.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
C. 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
E. 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

Table 3. Model selection results for protein-precipitating capacity of *S. pulchra* and *B. nana*

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

Figures

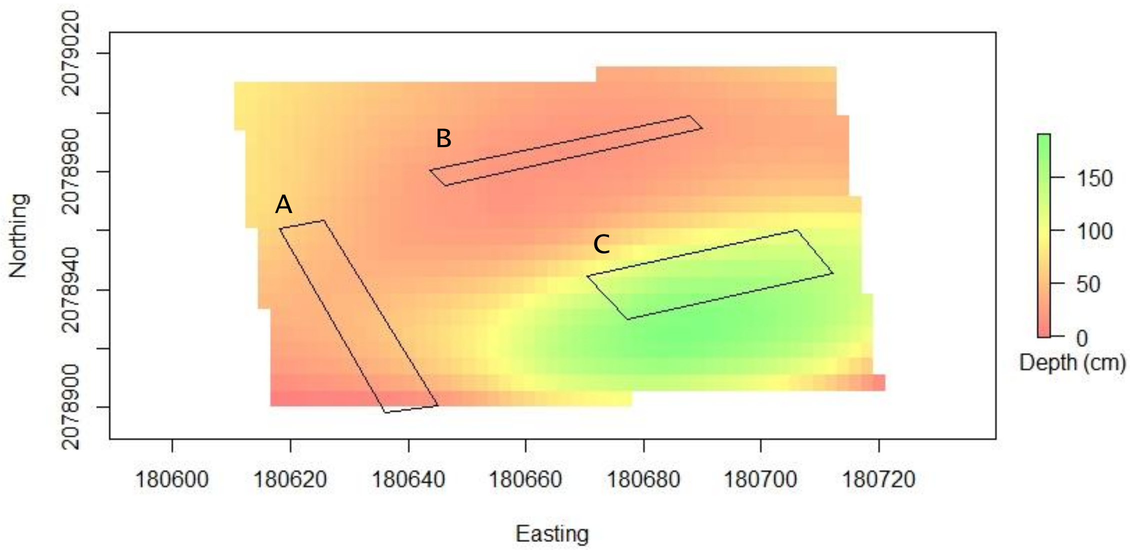


Figure 1. Snow depth (cm) of sampling area behind the snow fence (located along southeast corner) in March 2019. Polygons indicate the areas sampled. **A** represents the ambient snow treatment zone; **B** represents the – snow treatment zone; **C** represents the + snow treatment zone.

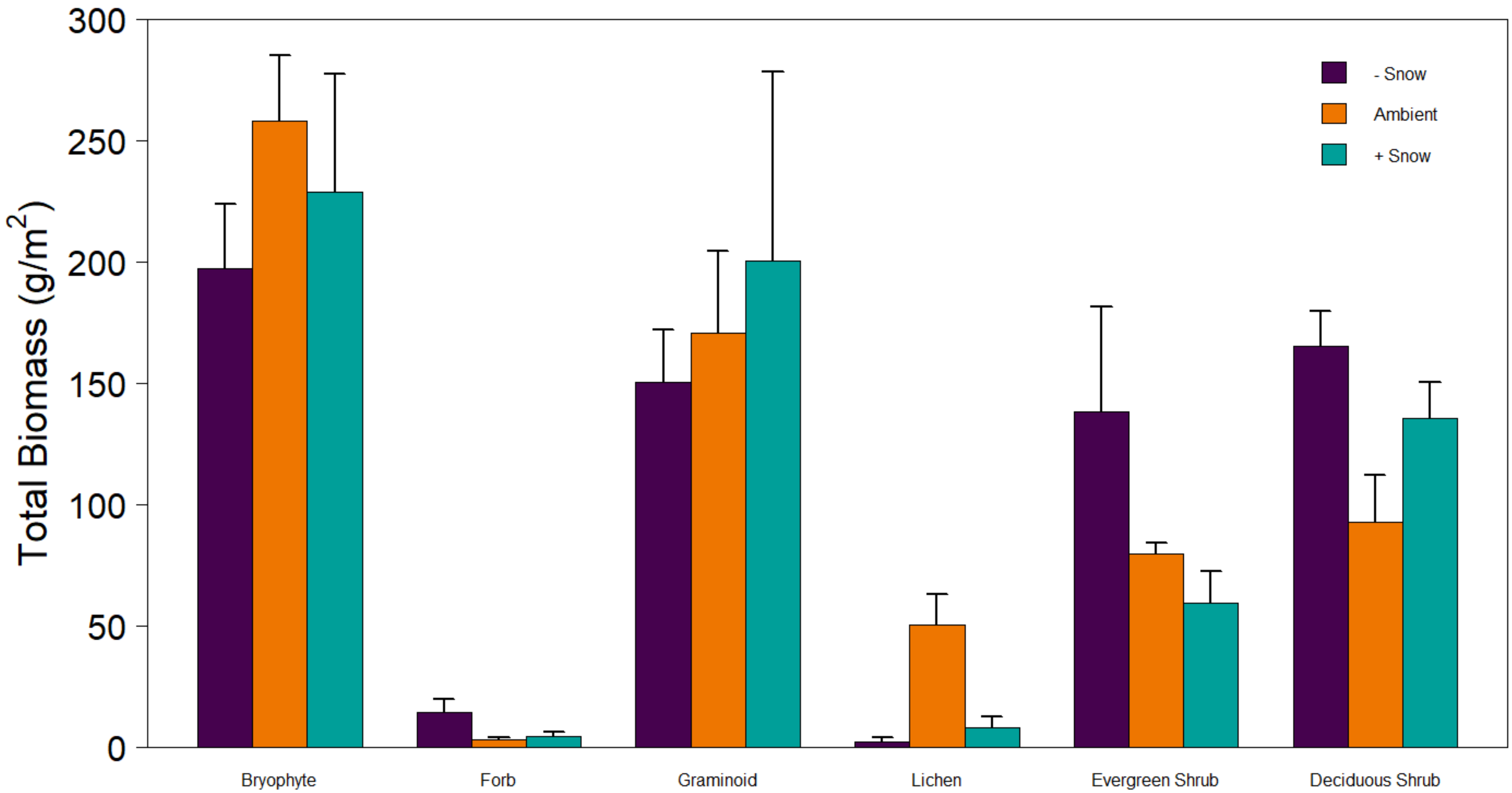


Figure 2. Total biomass (g/m^2) for each functional group by snow treatment

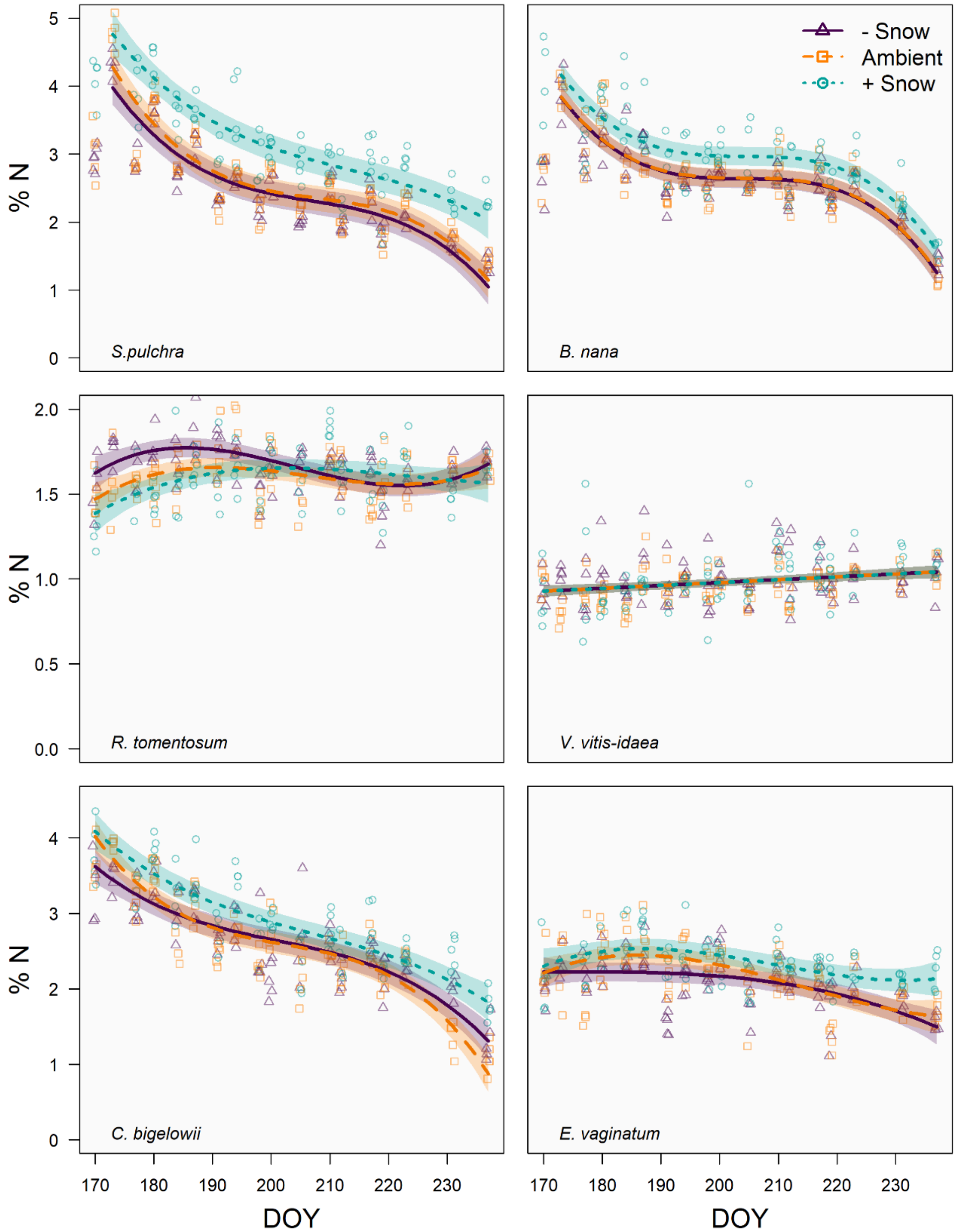


Figure 3. Leaf tissue N concentration by species throughout the growing season. Points indicate individual measurements, while trend lines are the predicted median + 95% confidence intervals in shaded polygons. Pre-leaf emergence values for S. pulchra and B. nana are not included in the model. Note that y-axis range differs among functional groups.

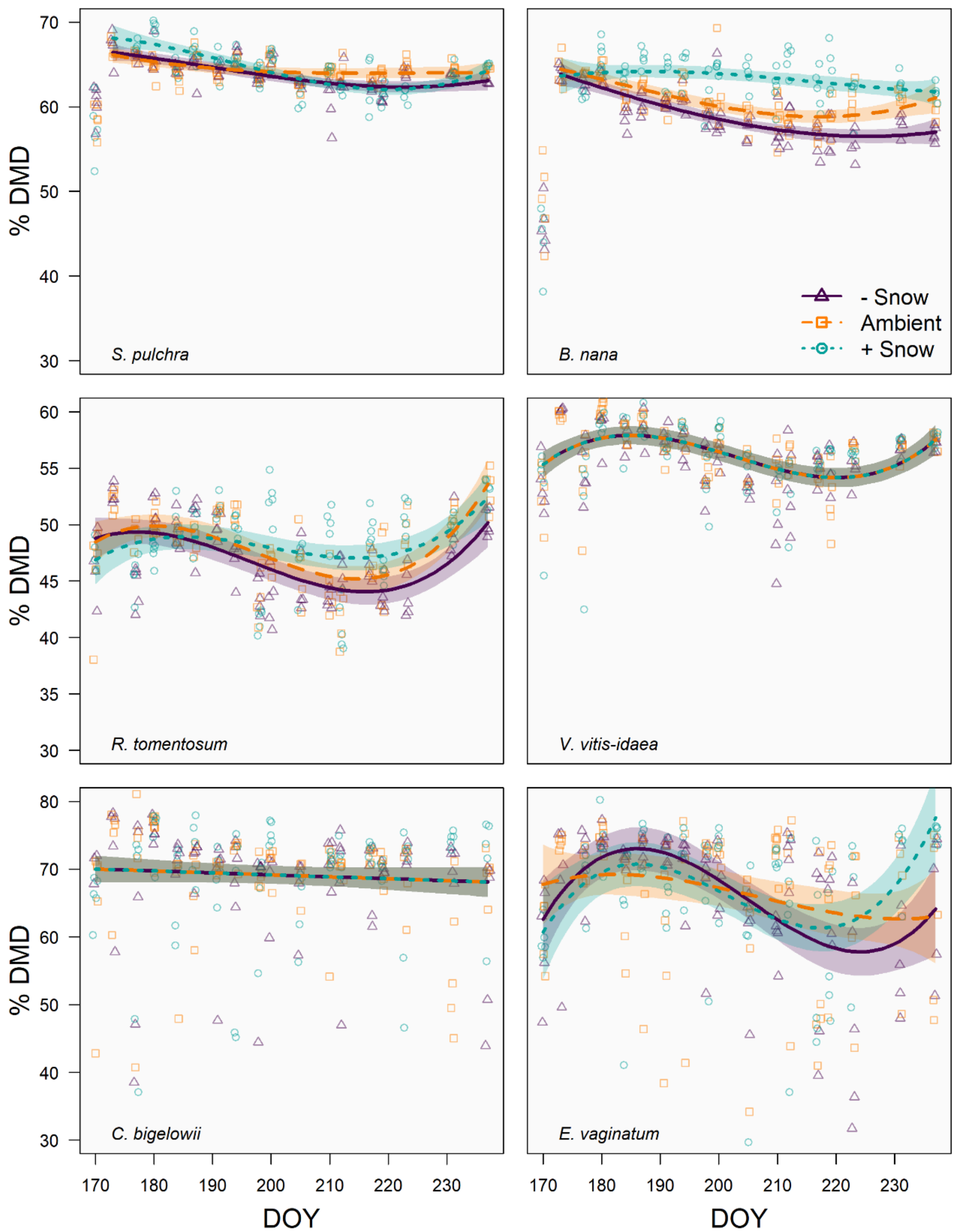


Figure 4. Leaf tissue dry matter digestibility by species throughout the growing season. Points indicate individual measurements while trend lines are the predicted median + 95% confidence intervals in shaded polygons. Pre-leaf emergence values for *S. pulchra* and *B. nana* are not included in the model. Note that y-axis range differs among functional groups.

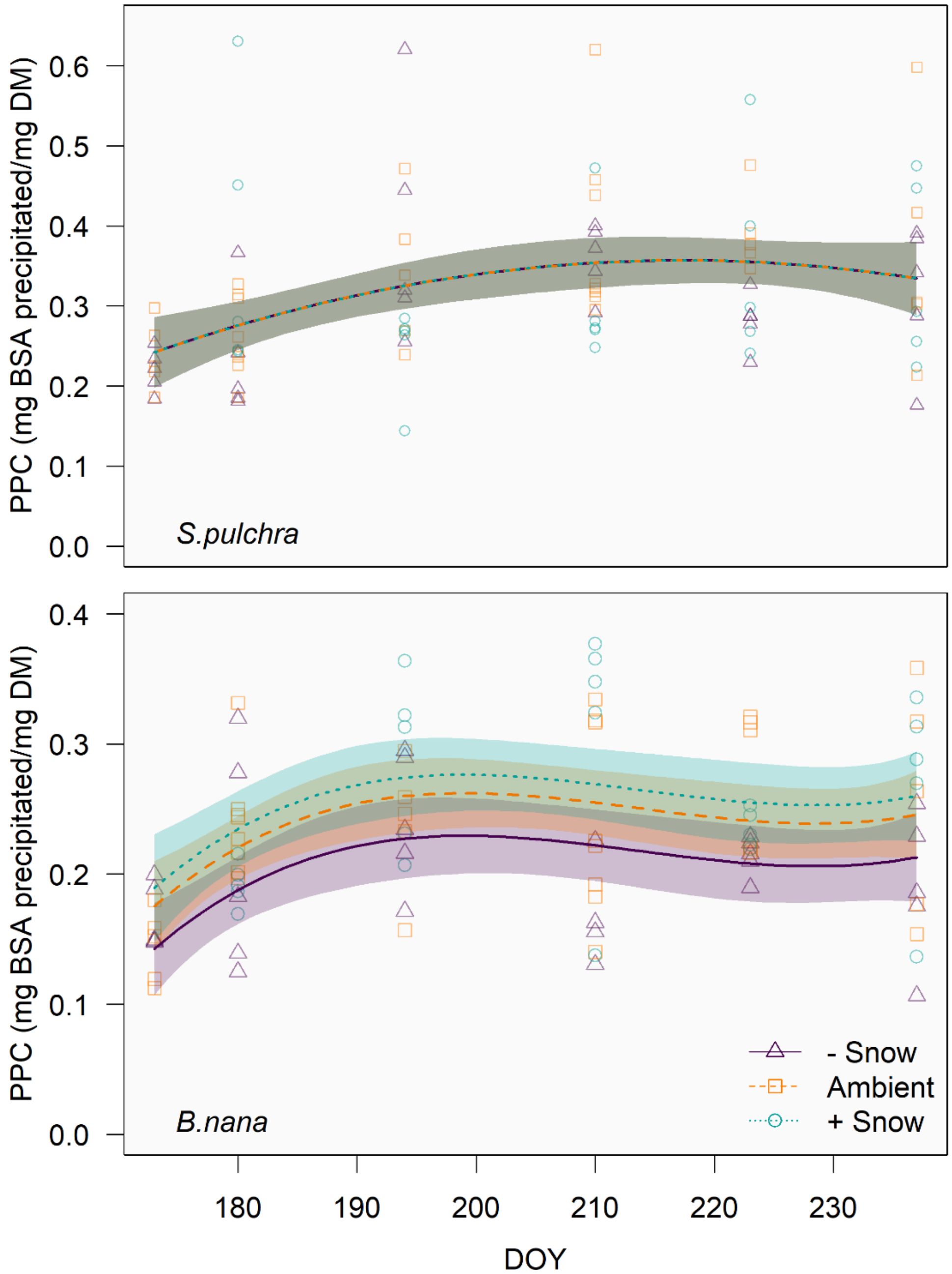


Figure 5. Protein-precipitating capacity by species through the growing season. Points indicate individual measurements, while trend lines are the predicted median ± 95% confidence intervals in shaded polygons. Pre-leaf emergence values were not included in the model.

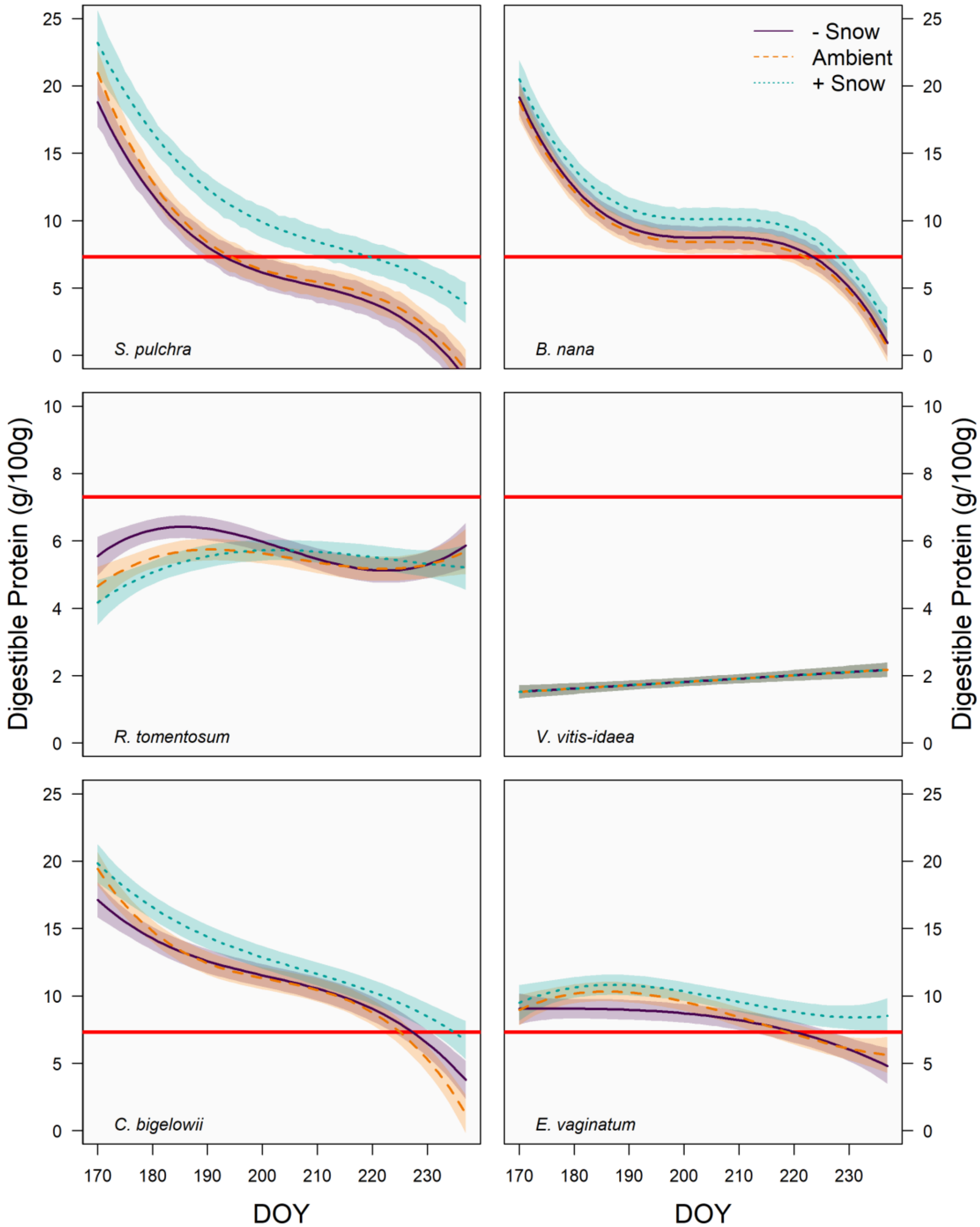


Figure 6. Leaf tissue digestible protein. Trend lines are the predicted median ± 95% confidence intervals in shaded polygons. The maintenance level protein required by caribou (7-8 g/100g DM) is highlighted in red. Note that y-axis range differs among functional groups.

CHAPTER 3: CONCLUSIONS

Results of this research indicate that projected increases in winter precipitation over Alaska's North Slope may indirectly increase the quality of caribou forage. Deeper snow insulates the soil and allows microbial mineralization to continue throughout the winter, increasing soil nitrogen available for plant uptake in early spring. Snow depth may not have as large an impact on dry matter digestibility as leaf-level nutrients, but even the small increases seen in this study may influence forage intake, with subsequent multiplier effects on survival and fecundity. Direct changes in N availability and indirect changes in vegetation community structure, though, may have a stronger influence on overall caribou nutrition in the Arctic than species-specific changes in forage digestibility.

Caribou and reindeer populations around the Arctic face many challenges: extreme weather, predation, insect harassment, the encroachment of human development (Morschel and Klein 1997, Vors and Boyce 2009, Festa-Bianchet et al. 2011), but climate change presents a new challenge, bringing increased temperatures, shifting precipitation patterns, and altering forage availability and quality (Callaghan et al. 2011, Fauchald et al. 2017, Mallory and Boyce 2018). 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. 2017b), 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. 2001b, 2005,

Tape et al. 2006). Arctic herbivores may adjust to the increase in available forage and potentially curb the trend towards shrubification (Gough et al. 2007, Zamin and Grogan 2013, Kaarlejärvi 2014, Kaarlejärvi et al. 2017), though perhaps only in the short term 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 be positive or negative for caribou. This question of the net effect, as a balance of positive feedback and feedforward, has been of interest for several decades now in the Arctic (Welker et al. 1997).

One of the major discussions as of late has been the seasonality of caribou forage as a critical component of meeting animal metabolic needs during the autumn rut and pre-winter preparation and its importance to subsequent winter survival and herd fecundity (Gustine et al. 2017, Veiberg et al. 2017, Barboza et al. 2018). My data support the prediction that one of the major consequences of deeper snow in winter is that caribou available protein (CAP), delivered primarily by *Salix*, will be greatly extended through the short growing season by as much as three weeks. This higher level of CAP during a hyper-critical season may be especially important to sustaining the health and welfare of caribou in northern Alaska.

LITERATURE CITED

ACIA, 2004. Impacts of a Warming Arctic: Arctic Climate Impact Assessment. ACIA Overview report. Cambridge University Press. 140 pp.

Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G. H. R. Henry, M. H. Jones, R. D. Hollister, I. S. Jónsdóttir, K. Laine, E. Lévesque, G. M. Marion, U. Molau, P. MØlgaard, U. Nordenhäll, V. Raszhivin, C. H. Robinson, G. Starr, A. Stenström, M. Stenström, Totland, P. L. Turner, L. J. Walker, P. J. Webber, J. M. Welker, and P. A. Wookey. 1999. Responses of Tundra plants to experimental warming: Meta-analysis of the International Tundra Experiment. Ecological Monographs 69:491–511.

Bali, A., V. A. Alexeev, R. G. White, D. E. Russell, A. D. McGuire, and G. P. Kofinas. 2013. Long-term patterns of abiotic drivers of mosquito activity within summer ranges of Northern Alaska caribou herds (1979-2009). Rangifer 33:173–176.

Barboza, P. S., L. L. Van Someren, D. D. Gustine, and M. S. Bret-Harte. 2018. The nitrogen window for arctic herbivores: Plant phenology and protein gain of migratory caribou (Rangifer tarandus). Ecosphere 9:1–17.

Berner, L. T., P. Jantz, K. D. Tape, and S. J. Goetz. 2018. Tundra plant above-ground biomass and shrub dominance mapped across the North Slope of Alaska. Environmental Research Letters 13.

Bilbrough, C. J., J. M. Welker, and W. D. Bowman. 2000. Early spring nitrogen uptake by snow-covered plants: a comparison of arctic and alpine plant function under the

snowpack. Arctic, Antarctic, and Alpine Research 32:404–411.

Boertje, R. D. 1984. Seasonal diets of the Denali caribou herd, Alaska. Arctic 37:161–185.

Borner, A. P., K. Kielland, and M. D. Walker. 2008. Effects of simulated climate change on plant phenology and nitrogen mineralization in Alaskan Arctic tundra. Arctic, Antarctic, and Alpine Research 40:27–38.

Bosiö, J., C. Stiegler, M. Johansson, H. N. Mbufong, and T. R. Christensen. 2014. Increased photosynthesis compensates for shorter growing season in subarctic tundra—8 years of snow accumulation manipulations. Climatic Change 127:321–334.

Bret-Harte, M. S., G. R. Shaver, J. P. Zoerner, J. F. Johnstone, J. L. Wagner, A. S. Chavez, R. F. Gunkelman IV, S. C. Lippert, and J. A. Laundre. 2001. Developmental plasticity allows betula nana to dominate tundra subjected to an altered environment. Ecology 82:18–32.

Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357–368.

Callaghan, T. V., M. Johansson, R. D. Brown, P. Y. Groisman, N. Labba, V. Radionov, R. G. Barry, O. N. Bulygina, R. L. H. Essery, D. M. Frolov, V. N. Golubev, T. C. Grenfell, M. N. Petrushina, V. N. Razuvaev, D. A. Robinson, P. Romanov, D. Shindell, A. B. Shmakin, S. A. Sokratov, S. Warren, and D. Yang. 2011. The changing face of arctic snow cover: A synthesis of observed and projected changes. Ambio 40:17–31.

Carlson, L. G., K. H. Beard, and P. B. Adler. 2018. Direct effects of warming increase woody plant abundance in a subarctic wetland. Ecology and Evolution 8:2868–2879.

Cebrian, M. R., K. Kielland, and G. Finstad. 2008. Forage quality and reindeer productivity: multiplier effects amplified by climate change. Arctic, Antarctic, and Alpine Research 40:48–54.

Chan-McLeod, A. C. A., R. G. White, and D. F. Holleman. 1994. Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. Canadian Journal of Zoology 72:938–947.

Chapin III, F. S. 1986. Seasonal changes in carbon fractions in Alaskan tundra plants of differing growth form: Implications for herbivory. Journal of Ecology 74:707–731.

Chapin III, F. S. 1989. The cost of tundra plant structures: Evaluation of concepts and currencies. The american Midland Naturalist 133:1–19.

Chapin III, F. S., and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology 66:564–576.

Chapin III, F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses of Arctic tundra to experimental and observed changes in climate. Ecology 76:694–711.

Coley, P. D., J. P. Bryant, and F. S. Chapin III. 1985. Resource availability and plant antiherbivore defense. Science 230:895–899.

Demarco, J., M. C. MacK, M. S. Bret-Harte, M. Burton, and G. R. Shaver. 2014. Long-term experimental warming and nutrient additions increase productivity in tall

deciduous shrub tundra. Ecosphere.

Denryter, K. A., R. C. Cook, J. G. Cook, and K. L. Parker. 2017. Straight from the caribou's (Rangifer tarandus) mouth: detailed observations of tame caribou reveal new insights into summer – autumn diets. Canadian Journal of Zoology.

Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Bjork, A. D. Bjorkman, T. V Callaghan, L. S. Collier, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, A. M. Fosaa, W. A. Gould, J. Gretarsdottir, J. Harte, L. Hermanutz, D. S. Hik, A. Hofgaard, F. Jarrad, I. S. Jonsdottir, F. Keuper, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, S. I. Lang, V. Loewen, J. L. May, J. Mercado, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, S. Pieper, E. Post, C. Rixen, C. H. Robinson, N. M. Schmidt, G. R. Shaver, A. Stenstrom, A. Tolvanen, O. Totland, T. Troxler, C.-H. Wahren, P. J. Webber, J. M. Welker, and P. A. Wookey. 2011. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecology Letters.

Fauchald, P., T. Park, H. Tømmervik, R. Myneni, and V. H. Hausner. 2017. Arctic greening from warming promotes declines in caribou populations. Science Advances 3.

Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Cote, and A. Gunn. 2011. Conservation of caribou (Rangifer tarandus) in Canada: An uncertain future. Canadian Journal of Zoology 89:419–434.

Fu, Y. H., S. Piao, H. Zhao, S. J. Jeong, X. Wang, Y. Vitasse, P. Ciais, and I. A. Janssens. 2014. Unexpected role of winter precipitation in determining heat requirement for

spring vegetation green-up at northern middle and high latitudes. Global Change Biology 20:3743–3755.

Gough, L., E. A. Ramsey, and D. R. Johnson. 2007. Plant-herbivore interactions in Alaskan Arctic tundra change with soil nutrient availability. Oikos 116:407–418.

Graglia, E., R. Julkunen-Tiitto, G. Shaver, I. K. Schmidt, S. Jonasson, and A. Michelsen. 2001. Changes in birch phenolic compounds in long term manipulations of temperature, nutrients and light in Alaska and N. Sweden. New Phytologist 151:227–236.

Gunn, A. 2003. Voles, lemmings and caribou - population cycles revisited? Rangifer:105–112.

Gustine, D., P. Barboza, L. Adams, B. Griffith, R. Cameron, and K. Whitten. 2017. Advancing the match-mismatch framework for large herbivores in the Arctic: Evaluating the evidence for a trophic mismatch in caribou. PLoS ONE 12:e0171807.

Hansen, B. B., M. Gamelon, S. D. Albon, A. M. Lee, A. Stien, R. J. Irvine, B. E. Sæther, L. E. Loe, E. Ropstad, V. Veiberg, and V. Grøtan. 2019. More frequent extreme climate events stabilize reindeer population dynamics. Nature Communications 10:1–8.

Hansen, B. B., K. Isaksen, R. E. Benestad, J. Kohler, Å. Pedersen, L. E. Loe, S. J. Coulson, J. O. Larsen, and Ø. Varpe. 2014. Warmer and wetter winters: Characteristics and implications of an extreme weather event in the High Arctic. Environmental Research Letters 9.

Haukioja, E., V. Ossipov, J. Koricheva, T. Honkanen, S. Larsson, and K. Lempa. 1998. Biosynthetic origin of carbon-based secondary compounds: Cause of variable responses of woody plants to fertilization? Chemoecology 8:133–139.

Hobbie, J. E., G. R. Shaver, E. B. Rastetter, J. E. Cherry, S. J. Goetz, K. C. Guay, W. A. Gould, and G. W. Kling. 2017. Ecosystem responses to climate change at a Low Arctic and a High Arctic long-term research site. Ambio 46:S160–S173.

Jefferies, R. L., D. R. Klein, and G. R. Shaver. 1994. Vertebrate herbivores and northern plant communities: Reciprocal influences and responses. Oikos 71:193–206.

Jespersen, R. G., A. J. Leffler, S. F. Oberbauer, and J. M. Welker. 2018. Arctic plant ecophysiology and water source utilization in response to altered snow: isotopic (δ18O and δ2H) evidence for meltwater subsidies to deciduous shrubs. Oecologia 187:1009–1023.

Johansson, M., T. V. Callaghan, J. Bosiö, H. J. Åkerman, M. Jackowicz-Korczynski, and T. R. Christensen. 2013. Rapid responses of permafrost and vegetation to experimentally increased snow cover in sub-arctic Sweden. Environmental Research Letters 8.

Jonasson, S., J. P. Bryant, F. S. Chapin III, and M. Andersson. 1986. Plant phenols and nutrients in relation to variations in climate and rodent grazing. The American Naturalist 128:394–408.

Jones, M. H., J. T. Fahnestock, D. A. Walker, M. D. Walker, and J. M. Welker. 1998. Carbon dioxide fluxes in moist and dry arctic tundra during the snow-free season: Responses to increases in summer temperature and winter snow accumulation.

Arctic and Alpine Research 30:373–380.

Kaarlejärvi, E. 2014. The role of herbivores in mediating responses of tundra ecosystems to climate change. Umea Universitet.

Kaarlejärvi, E., A. Eskelinen, and J. Olofsson. 2017. Herbivores rescue diversity in warming tundra by modulating trait-dependent species losses and gains. Nature Communications 8.

Klein, D. R. 1990. Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology. Rangifer:123–130.

Lambers, H., F. S. Chapin III, and T. L. Pons. 2008. Ecological Biochemistry: Allelopathy and Defense against Herbivores. Pages 445–489 Plant Physiological Ecology. 2nd edition. Springer Science, New York.

Lavola, A., and R. Julkunen-Tiito. 1994. The effect of elevated carbon dioxide and fertilization on primary and secondary metabolites in birch, Betula pendula (Roth). Oecologia 99:315–321.

Leffler, A. J., E. S. Klein, S. F. Oberbauer, and J. M. Welker. 2016. Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra. Oecologia 181:287–297.

Leffler, A. J., and J. M. Welker. 2013. Long-term increases in snow pack elevate leaf N and photosynthesis in Salix arctica: responses to a snow fence experiment in the High Arctic of NW Greenland. Environmental Research Letters 8:25023.

Lenart, E. A., R. T. Bowyer, J. Ver Hoef, and R. W. Ruess. 2002. Climate change and

caribou: effects of summer weather on forage. Canadian Journal of Zoology 80:664–678.

Linderholm, H. W. 2006. Growing season changes in the last century. Agricultural and Forest Meteorology 137:1–14.

Loe, L. E., B. B. Hansen, A. Stien, S. D. Albon, R. Bischof, A. Carlsson, R. J. Irvine, M. Meland, I. M. Rivrud, E. Ropstad, V. Veiberg, and A. Mysterud. 2016. Behavioral buffering of extreme weather events in a high-Arctic herbivore. Ecosphere 7:1–13.

De Long, J. R., M. K. Sundqvist, M. J. Gundale, R. Giesler, and D. A. Wardle. 2016. Effects of elevation and nitrogen and phosphorus fertilization on plant defence compounds in subarctic tundra heath vegetation. Functional Ecology 30:314–325.

Loranty, M. M., S. J. Goetz, and P. S. A. Beck. 2011. Tundra vegetation effects on pan-Arctic albedo. Environmental Research Letters 6.

Mallory, C. D., and M. S. Boyce. 2017. Observed and predicted effects of climate change on Arctic caribou and reindeer. Environmental Reviews.

Mallory, C. D., and M. S. Boyce. 2018. Observed and predicted effects of climate change on Arctic caribou and reindeer. Environmental Reviews 26:13–25.

Martin, P. D., J. L. Jenkins, F. J. Adams, M. T. Jorgenson, A. C. Matz, D. C. Prayer, P. E. Reynolds, A. C. Tidwell, and J. R. Zelenak. 2009. Wildlife Response to Environmental Arctic Change: Predicting Future Habitats of Arctic Alaska. Report of the Wildlife Response to Environmental Arctic Change (WildREACH): Predicting Future Habitats of Arctic Alaska Workshop, 17-18 November 2008.

Fairbanks, Alaska.

McKane, R. B., L. C. Johnson, G. R. Shaver, K. J. Nadelhoffer, E. B. Rastetter, B. Fry, A. E. Giblin, K. Kielland, B. L. Kwlatkowski, J. A. Laundre, and G. Murray. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415:68–71.

Morschel, F. M., and D. R. Klein. 1997. Effects of weather and parasitic insects on behavior and group dynamics of caribou of the Delta Herd, Alaska. Canadian Journal of Zoology 75:1659–1670.

Murray, C., and P. C. Miller. 1982. Phenological observations of major plant growth forms and species in montane and Eriophorum vaginatum tussock tundra in central AK. Pages 109–116 Holarctic Ecology. San Diego, California.

Nybakken, L., K. Klanderud, and Ø. Totland. 2013. Simulated environmental change has contrasting effects on defensive compound concentration in three alpine plant species. Arctic, Antarctic, and Alpine Research 40:709–715.

Ophof, A. A., K. W. Oldeboer, and J. Kumpula. 2013. Intake and chemical composition of winter and spring forage plants consumed by semi-domesticated reindeer (Rangifer tarandus tarandus) in Northern Finland. Animal Feed Science and Technology 185:190–195.

Osborne, E., J. Richter-Menge, M. Jeffries, and Eds. 2018. Arctic Report Card 2018:114.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

Pattison, R. R., and J. M. Welker. 2014. Differential ecophysiological response of decidous shrubs and a graminoid to long-term experimental snow reductions and additions in moist acidic tundra, Northern Alaska. Oecologia 174:339–350.

Peñuelas, J., M. Estiarte, and J. Llusià. 1997. Carbon-based secondary compounds at elevated CO2.

Proffitt, K. M., M. Hebblewhite, W. Peters, N. Hupp, and J. Shamhart. 2016. Linking landscape-scale differences in forage to ungulate nutritional ecology. Ecological Applications 26:2156–2174.

Rennert, K. J., G. Roe, J. Putkonen, and C. M. Bitz. 2009. Soil thermal and ecological impacts of rain on snow events in the circumpolar arctic. Journal of Climate 22:2302–2315.

Rieley, G., J. M. Welker, T. V. Callaghan, and G. Eglinton. 1995. Epicuticular waxes of two arctic species: Compositional differences in relation to winter snow cover. Phytochemistry 38:45–52.

Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. L. Baker, and W. W. Mautz. 1987a. Role of tannins in defending plants against ruminants: Reduction in protein availability. Ecology 68:98–107.

Robbins, C. T., S. Mole, A. E. Hagerman, and T. A. Hanley. 1987b. Role of tannins in defending plants against ruminants: Reduction in dry matter digestion? Ecology 68:1606–1615.

Scenarios Network for Alaska and Arctic Planning. 2011. A Climate Change Analysis An

Assessment of Climate Change Variables in the National Petroleum Reserve in Alaska.

Schimel, J. P., C. J. Bilbrough, and J. M. Welker. 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. Soil Biology and Biochemistry 36:217–227.

Schimel, J. P., C. Bilbrough, and J. M. Welker. 2003. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. Soil Biology and Biochemistry 36:1–11.

Searle, K. R., M. B. Rice, C. R. Anderson, C. Bishop, and N. T. Hobbs. 2015. Asynchronous vegetation phenology enhances winter body condition of a large mobile herbivore. Oecologia.

Semenchuk, P. R., B. Elberling, C. Amtorp, J. Winkler, S. Rumpf, A. Michelsen, and E. J. Cooper. 2015. Deeper snow alters soil nutrient availability and leaf nutrient status in high Arctic tundra. Biogeochemistry 124.

Sturm, M., J. P. McFadden, G. E. Liston, F. S. Chapin III, C. H. Racine, and J. Holmgren. 2001a. Snow-shrub interactions in arctic tundra: a hypothesis with climatic implications. Journal of Climate 14:336–344.

Sturm, M., C. Racine, and K. Tape. 2001b. Increasing shrub abundance in the Arctic. Nature 411:546–547.

Sturm, M., J. Schimel, G. Michaelson, J. M. Welker, S. F. Oberbauer, G. E. Liston, J. Fahnestock, and V. E. Romanovsky. 2005. Winter biological processes could help

convert arctic tundra to shrubland. BioScience 55:17–26.

Sullivan, P. F., M. Sommerkorn, H. M. Rueth, K. J. Nadelhoffer, G. R. Shaver, and J. M. Welker. 2007. Climate and species affect fine root production with long-term fertilization in acidic tussock tundra near Toolik Lake, Alaska. Oecologia 153:643–652.

Sullivan, P. F., and J. M. Welker. 2005. Warming chambers stimulate early season growth of an arctic sedge: Results of a minirhizotron field study. Oecologia 142:616–626.

Tape, K. D., M. Hallinger, J. M. Welker, and R. W. Ruess. 2012. Landscape heterogeneity of shrub expansion in Arctic Alaska. Ecosystems 15:711–724.

Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12:686–702.

Thompson, D. C., and K. H. McCourt. 1981. Seasonal diets of the Porcupine Caribou Herd. The american Midland Naturalist 150:70–76.

Thompson, D. P., and P. S. Barboza. 2014. Nutritional implications of increased shrub cover for caribou (Rangifer tarandus) in the Arctic. Canadian Journal of Zoology 92:339–351.

Thompson, D. P., and P. S. Barboza. 2017. Seasonal energy and protein requirements for Siberian reindeer (Rangifer tarandus). Journal of Mammalogy 98:1558–1567.

Turunen, M., P. Soppela, H. Kinnunen, M. L. Sutinen, and F. Martz. 2009. Does climate change influence the availability and quality of reindeer forage plants? Polar

Biology 32:813–832.

Tyler, N. J. C. 2010. Climate, snow, ice, crashes, and declines in populations of reindeer and caribou (Rangifer tarandus L.). Ecological Monographs 80:197–219.

Veiberg, V., L. E. Loe, S. D. Albon, R. J. Irvine, T. Tveraa, E. Ropstad, and A. Stien. 2017. Maternal winter body mass and not spring phenology determine annual calf production in an Arctic herbivore. Oikos 126.

Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15:2626–2633.

Wahren, C. H. A., M. D. Walker, and M. S. Bret-Harte. 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. Global Change Biology 11:537–552.

Van der Wal, R., N. Madan, S. van Lieshout, C. Dormann, R. Langvatn, and S. D. Albon. 2000. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. Oecologia 123:108–115.

Walker, M. D., D. A. Walker, J. M. Welker, A. M. Arft, T. Bardsley, P. D. Brooks, J. T. Fahnestock, M. H. Jones, M. Losleben, A. N. Parsons, T. R. Seastedt, and P. L. Turner. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Processes 13:2315–2330.

Walsh, N. E., T. R. McCabe, J. M. Welker, and A. N. Parsons. 1997. Experimental manipulations of snow-depth: effects on nutrient content of caribou forage. Global

Change Biology 3:158–164.

Welker, J. M., J. T. Fahnestock, and M. H. Jones. 2000. Annual CO2 flux in dry and moist arctic tundra: field responses to increases in summer temperatures and winter snow depth. Climatic Change 44:139–2000.

Welker, J. M., J. T. Fahnestock, P. F. Sullivan, and R. A. Chimner. 2005. Leaf mineral nutrition of Arctic plants in response to warming and deeper snow in northern Alaska. Oikos 109:167–177.

Welker, J. M., U. Molau, A. N. Parson, C. H. Robinson, and P. A. Wookey. 1997. Responses of Dryas octopetala to ITEX environmental manipulations: a synthesis with circumpolar comparisons. Global Change Biology 3:61–73.

White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377–384.

White, R. G., B. R. Thomson, T. Skogland, S. J. Person, D. E. Russell, D. F. Holleman, and J. R. Luick. 1975. Ecology of caribou at Prudhoe Bay, Alaska.

White, R. G., and J. Trudell. 1980. Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. Arctic and Alpine Research 12:511–529.

Wipf, S., and C. Rixen. 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. Polar Research 29:95–109.

Zamin, T. J., M. S. Bret-Harte, and P. Grogan. 2014. Evergreen shrubs dominate responses to experimental summer warming and fertilization in Canadian mesic low

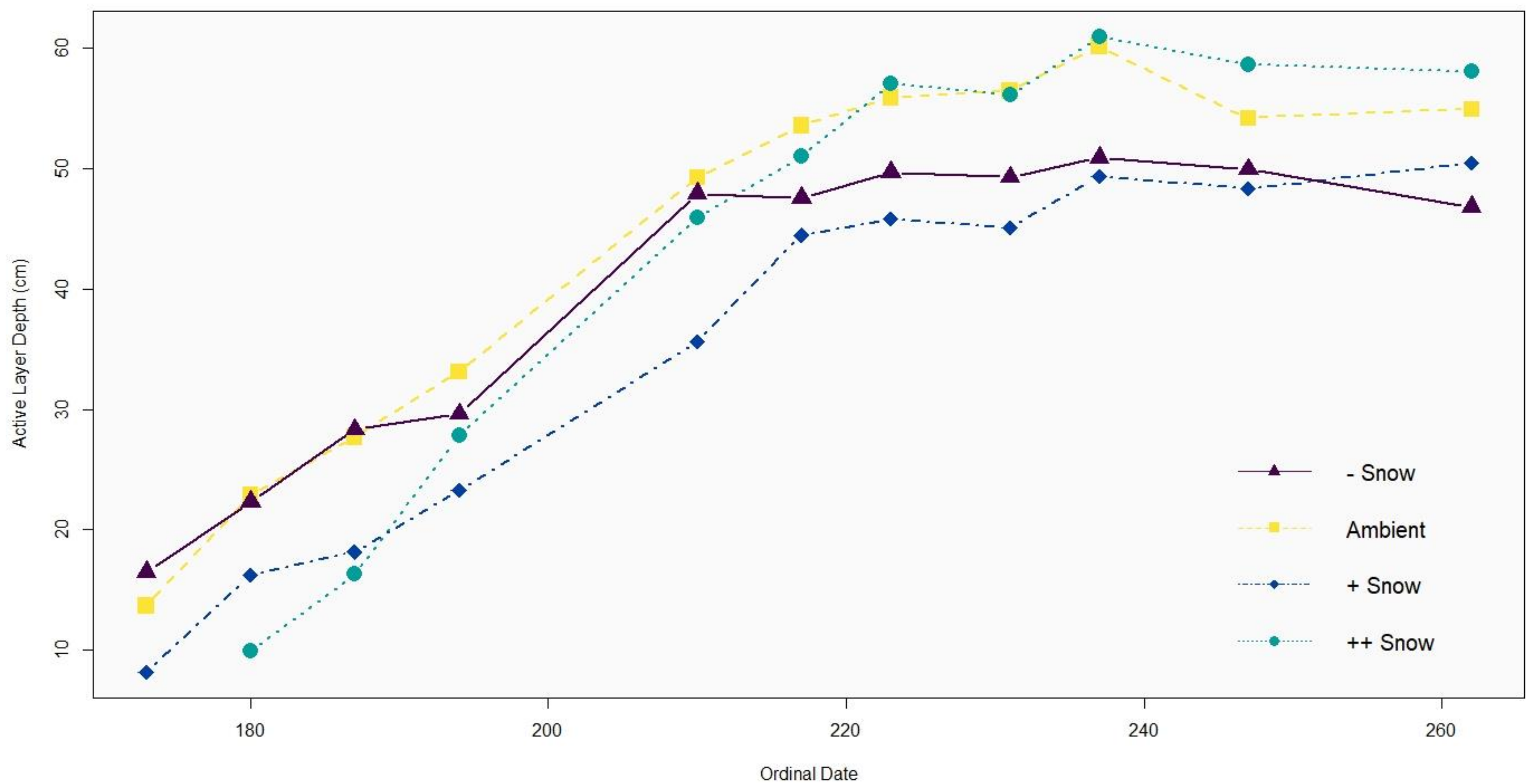
arctic tundra. Journal of Ecology 102:749–766.

Zamin, T. J., S. D. Côté, J. P. Tremblay, and P. Grogan. 2017a. Experimental warming alters migratory caribou forage quality: Ecological Applications 27.

Zamin, T. J., S. D. Côté, J. P. Tremblay, and P. Grogan. 2017b. Experimental warming alters migratory caribou forage quality: Ecological Applications 27:2061–2073.

Zamin, T. J., and P. Grogan. 2013. Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra. Journal of Ecology 101:671–683.

APPENDIX 1



Appendix 1-1. Active layer depth throughout the 2018 growing season for each snow zone. Due to late snow melt in the + snow treatment zone, measurements were taken in both the shallow (+ snow) and deep (++ snow) drift areas.

APPENDIX 2: Sequential fiber analysis components by species and snow zone

S. pulchra		NDF (g/g DM)						ADF (g/g DM)						Cellulose (g/g DM)						Lignin (g/g DM)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.231	0.029	0.252	0.021	0.286	0.053	0.193	0.024	0.217	0.020	0.245	0.047	0.099	0.014	0.106	0.013	0.137	0.025	0.092	0.013	0.107	0.018	0.105	0.022
	177	0.164	0.005	0.160	0.006	0.144	0.007	0.120	0.005	0.118	0.003	0.110	0.005	0.061	0.003	0.060	0.002	0.058	0.001	0.056	0.004	0.055	0.005	0.049	0.005
	184	0.195	0.004	0.214	0.011	0.190	0.016	0.137	0.004	0.143	0.007	0.135	0.011	0.075	0.001	0.076	0.003	0.072	0.008	0.060	0.004	0.065	0.007	0.061	0.006
	191	0.208	0.016	0.211	0.006	0.186	0.019	0.135	0.006	0.143	0.005	0.124	0.013	0.074	0.006	0.079	0.004	0.066	0.007	0.058	0.004	0.063	0.004	0.056	0.012
	198	0.220	0.006	0.221	0.010	0.224	0.023	0.142	0.003	0.136	0.004	0.139	0.013	0.076	0.002	0.073	0.002	0.076	0.008	0.065	0.003	0.061	0.005	0.061	0.008
	205	0.230	0.004	0.228	0.006	0.251	0.015	0.144	0.002	0.144	0.003	0.150	0.008	0.076	0.005	0.073	0.006	0.073	0.016	0.067	0.005	0.070	0.006	0.075	0.012
	212	0.233	0.016	0.219	0.011	0.256	0.012	0.140	0.006	0.138	0.007	0.152	0.003	0.073	0.003	0.075	0.002	0.079	0.005	0.062	0.009	0.056	0.007	0.066	0.003
	219	0.261	0.007	0.235	0.015	0.261	0.014	0.160	0.008	0.142	0.007	0.155	0.011	0.080	0.002	0.079	0.003	0.077	0.006	0.073	0.009	0.059	0.005	0.073	0.007
2018	173	0.143	0.017	0.153	0.012			0.109	0.017	0.117	0.010			0.056	0.002	0.063	0.003			0.049	0.016	0.048	0.007		
	180	0.165	0.020	0.172	0.010	0.123	0.004	0.125	0.016	0.135	0.008	0.096	0.004	0.064	0.004	0.067	0.005	0.058	0.001	0.055	0.012	0.064	0.011	0.032	0.004
	187	0.192	0.019	0.165	0.009	0.155	0.018	0.134	0.014	0.120	0.008	0.118	0.014	0.072	0.002	0.024	0.097	0.064	0.004	0.059	0.013	0.049	0.005	0.050	0.010
	194	0.183	0.016	0.185	0.013	0.173	0.021	0.125	0.011	0.128	0.010	0.128	0.014	0.073	0.006	0.070	0.007	0.068	0.010	0.049	0.006	0.055	0.004	0.054	0.005
	200	0.195	0.013	0.192	0.009	0.185	0.010	0.133	0.010	0.132	0.008	0.125	0.006	0.074	0.005	0.077	0.005	0.073	0.005	0.053	0.007	0.049	0.005	0.048	0.003
	210	0.252	0.023	0.223	0.008	0.217	0.009	0.171	0.022	0.141	0.007	0.141	0.006	0.083	0.006	0.082	0.004	0.080	0.005	0.083	0.022	0.056	0.002	0.056	0.002
	217	0.244	0.003	0.245	0.009	0.247	0.036	0.153	0.005	0.153	0.005	0.154	0.021	0.080	0.005	0.084	0.004	0.081	0.005	0.067	0.003	0.062	0.002	0.065	0.018
	223	0.220	0.005	0.207	0.007	0.254	0.007	0.143	0.002	0.131	0.006	0.160	0.005	0.079	0.004	0.074	0.002	0.081	0.007	0.058	0.003	0.052	0.004	0.073	0.006
	231	0.219	0.002	0.213	0.006	0.223	0.010	0.141	0.002	0.133	0.002	0.139	0.005	0.076	0.003	0.073	0.003	0.076	0.004	0.059	0.001	0.054	0.004	0.056	0.005
	237	0.240	0.004	0.223	0.006	0.207	0.006	0.151	0.002	0.140	0.002	0.126	0.002	0.081	0.001	0.077	0.003	0.067	0.001	0.063	0.003	0.054	0.003	0.054	0.002

S. pulchra		Ash (g/g DM)						Cell Solubles (% of DM)						Cell Wall (% of DM)						Lig/Cut (% of NDF)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.003	0.001	0.003	0.001	0.003	0.001	76.859	2.910	74.776	2.093	71.408	5.251	23.141	2.910	25.224	2.093	28.592	5.251	39.798	3.091	42.460	5.377	36.707	2.060
	177	0.003	0.001	0.003	0.001	0.002	0.002	83.569	0.513	84.020	0.635	85.594	0.746	16.431	0.513	15.980	0.635	14.406	0.746	33.971	2.238	34.117	1.632	34.173	2.031
	184	0.003	0.000	0.002	0.000	0.002	0.000	80.496	0.422	78.558	1.108	81.007	1.560	19.504	0.422	21.442	1.108	18.993	1.560	30.505	1.477	30.188	1.699	32.277	2.864
	191	0.003	0.001	0.001	0.001	0.002	0.001	79.210	1.573	78.901	0.640	81.403	1.893	20.790	1.573	21.099	0.640	18.597	1.893	28.064	2.012	29.725	1.457	30.141	3.571
	198	0.002	0.001	0.001	0.000	0.001	0.000	77.989	0.621	77.931	1.043	77.636	2.267	22.011	0.621	22.069	1.043	22.364	2.267	29.325	1.575	27.753	1.515	27.389	2.955
	205	0.002	0.001	0.002	0.000	0.001	0.000	76.970	0.442	77.209	0.567	74.922	1.523	23.030	0.442	22.791	0.567	25.078	1.523	29.105	2.455	30.595	2.267	30.038	5.039
	212	0.005	0.002	0.007	0.002	0.007	0.003	76.679	1.619	78.075	1.062	74.376	1.174	23.321	1.619	21.925	1.062	25.624	1.174	26.675	2.390	25.422	2.753	25.745	1.274
	219	0.007	0.002	0.005	0.002	0.004	0.003	73.946	0.701	76.470	1.461	73.937	1.368	26.054	0.701	23.530	1.461	26.063	1.368	27.941	2.916	24.917	0.718	28.102	1.291
2018	173	0.004	0.001	0.006	0.001			85.689	1.744	84.698	1.245			14.311	1.744	15.302	1.245			33.626	6.443	31.160	1.941		
	180	0.006	0.001	0.004	0.001	0.006	0.001	83.468	2.018	82.754	0.973	87.744	0.403	16.532	2.018	17.246	0.973	12.256	0.403	33.004	3.954	37.231	4.322	25.915	2.616
	187	0.003	0.001	0.047	0.095	0.004	0.001	80.834	1.867	83.546	0.911	84.516	1.840	19.166	1.867	16.454	0.911	15.484	1.840	30.521	3.446	29.986	1.487	31.744	3.083
	194	0.003	0.001	0.004	0.001	0.006	0.001	81.720	1.627	81.490	1.344	82.710	2.067	18.280	1.627	18.510	1.344	17.290	2.067	26.768	1.696	29.482	0.722	31.399	3.618
	200	0.006	0.001	0.006	0.002	0.004	0.001	80.550	1.295	80.783	0.871	81.464	0.957	19.450	1.295	19.217	0.871	18.536	0.957	26.958	2.119	25.600	2.054	25.682	0.985
	210	0.005	0.001	0.003	0.001	0.005	0.002	74.754	2.253	77.682	0.810	78.263	0.860	25.246	2.253	22.318	0.810	21.737	0.860	32.470	5.607	24.893	0.467	25.661	0.641
	217	0.005	0.002	0.007	0.001	0.007	0.002	75.625	0.344	75.465	0.893	75.337	3.617	24.375	0.344	24.535	0.893	24.663	3.617	27.643	1.364	25.406	0.313	25.959	3.452
	223	0.005	0.001	0.005	0.001	0.006	0.000	78.037	0.454	79.296	0.711	74.638	0.670	21.963	0.454	20.704	0.711	25.362	0.670	26.355	1.292	25.161	1.465	28.560	1.804
	231	0.006	0.002	0.005	0.001	0.007	0.003	78.098	0.238	78.702	0.555	77.676	0.998	21.902	0.238	21.298	0.555	22.324	0.998	27.156	0.782	25.489	1.410	25.228	2.187
	237	0.006	0.002	0.008	0.001	0.005	0.001	76.020	0.380	77.735	0.573	79.329	0.645	23.980	0.380	22.265	0.573	20.671	0.645	26.261	1.290	24.447	0.971	26.197	1.212

S. pulchra		NDF digestibility (%)						NDS digestibility (%)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	3.581	0.663	3.498	0.818	5.050	0.925	56.899	2.418	55.169	1.739	52.370	4.363
	177	3.290	0.348	3.168	0.170	2.851	0.221	62.476	0.427	62.851	0.528	64.158	0.620
	184	4.553	0.258	5.071	0.221	4.128	0.687	59.922	0.351	58.312	0.921	60.347	1.296
	191	5.447	0.816	5.101	0.276	4.415	0.534	58.853	1.307	58.597	0.532	60.676	1.573
	198	5.429	0.473	5.834	0.421	6.065	1.136	57.839	0.516	57.791	0.867	57.545	1.884
	205	5.754	0.666	5.314	0.526	6.099	1.323	56.992	0.367	57.191	0.471	55.290	1.266
	212	6.464	0.453	6.457	0.732	7.423	0.630	56.750	1.345	57.910	0.883	54.836	0.976
	219	6.857	0.840	7.056	0.327	6.768	0.160	54.479	0.583	56.577	1.214	54.472	1.137
2018	173	2.918	0.481	3.457	0.119			64.237	1.449	63.414	1.035		
	180	3.426	0.184	2.996	0.417	3.526	0.320	62.392	1.677	61.799	0.809	65.945	0.335
	187	4.458	0.281	3.925	0.117	3.398	0.174	60.203	1.552	62.457	0.757	63.263	1.529
	194	5.054	0.571	4.527	0.419	3.956	0.978	60.940	1.352	60.748	1.117	61.762	1.718
	200	5.322	0.346	5.605	0.507	5.376	0.344	59.967	1.076	60.161	0.724	60.726	0.795
	210	5.434	0.872	6.723	0.313	6.313	0.400	55.151	1.873	57.584	0.673	58.067	0.714
	217	6.478	0.414	7.204	0.343	7.007	0.367	55.875	0.286	55.742	0.742	55.635	3.006
	223	6.183	0.343	6.148	0.314	6.464	0.374	57.879	0.378	58.925	0.591	55.054	0.557
	231	5.945	0.270	6.231	0.260	6.634	0.727	57.930	0.198	58.431	0.461	57.579	0.829
	237	6.781	0.401	6.828	0.319	5.866	0.436	56.202	0.316	57.627	0.476	58.953	0.536

B. nana		NDF (g/g DM)						ADF (g/g DM)						Cellulose (g/g DM)						Lignin (g/g DM)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.414	0.030	0.365	0.051	0.433	0.051	0.335	0.038	0.306	0.055	0.359	0.044	0.127	0.010	0.105	0.008	0.139	0.017	0.203	0.029	0.195	0.055	0.213	0.030
	177	0.199	0.009	0.183	0.006	0.213	0.011	0.122	0.004	0.121	0.004	0.143	0.010	0.047	0.002	0.048	0.002	0.058	0.003	0.074	0.008	0.052	0.040	0.082	0.010
	184	0.274	0.018	0.237	0.010	0.203	0.010	0.170	0.010	0.153	0.005	0.128	0.008	0.073	0.004	0.068	0.003	0.062	0.003	0.094	0.008	0.082	0.004	0.065	0.006
	191	0.249	0.003	0.250	0.014	0.205	0.024	0.149	0.006	0.158	0.011	0.121	0.016	0.063	0.004	0.068	0.006	0.056	0.002	0.083	0.006	0.087	0.008	0.064	0.013
	198	0.286	0.011	0.260	0.011	0.251	0.026	0.157	0.008	0.151	0.004	0.148	0.029	0.063	0.003	0.065	0.001	0.064	0.011	0.093	0.006	0.085	0.003	0.082	0.020
	205	0.293	0.024	0.275	0.025	0.206	0.019	0.173	0.007	0.167	0.010	0.123	0.011	0.068	0.001	0.069	0.004	0.059	0.002	0.104	0.006	0.095	0.009	0.062	0.012
	212	0.290	0.026	0.280	0.015	0.193	0.025	0.169	0.016	0.174	0.006	0.112	0.013	0.068	0.003	0.069	0.002	0.056	0.003	0.097	0.013	0.100	0.005	0.050	0.009
	219	0.301	0.025	0.274	0.015	0.216	0.027	0.174	0.019	0.165	0.016	0.122	0.017	0.062	0.005	0.066	0.001	0.058	0.006	0.107	0.016	0.094	0.017	0.057	0.016
2018	173	0.186	0.012	0.180	0.023			0.131	0.010	0.135	0.018			0.059	0.004	0.061	0.003			0.067	0.007	0.070	0.015		
	180	0.197	0.017	0.184	0.011	0.160	0.019	0.134	0.007	0.132	0.009	0.117	0.013	0.059	0.005	0.061	0.002	0.058	0.004	0.070	0.005	0.068	0.008	0.052	0.011
	187	0.244	0.021	0.213	0.017	0.167	0.014	0.160	0.012	0.146	0.014	0.117	0.009	0.068	0.007	0.063	0.003	0.059	0.003	0.087	0.009	0.079	0.013	0.055	0.008
	194	0.250	0.021	0.219	0.015	0.189	0.025	0.147	0.013	0.138	0.015	0.125	0.019	0.064	0.005	0.064	0.008	0.061	0.006	0.079	0.009	0.070	0.008	0.060	0.013
	200	0.263	0.040	0.220	0.062	0.199	0.012	0.172	0.024	0.151	0.044	0.128	0.007	0.071	0.002	0.065	0.017	0.066	0.004	0.094	0.024	0.081	0.027	0.057	0.003
	210	0.299	0.028	0.278	0.035	0.242	0.026	0.183	0.021	0.165	0.021	0.147	0.020	0.074	0.005	0.075	0.007	0.072	0.006	0.105	0.017	0.088	0.016	0.070	0.015
	217	0.308	0.026	0.289	0.011	0.240	0.029	0.193	0.015	0.191	0.010	0.145	0.020	0.075	0.004	0.077	0.004	0.067	0.006	0.112	0.012	0.109	0.007	0.071	0.015
	223	0.308	0.017	0.249	0.028	0.249	0.028	0.191	0.020	0.153	0.017	0.147	0.025	0.066	0.003	0.066	0.009	0.065	0.009	0.118	0.014	0.081	0.011	0.076	0.018
	231	0.278	0.010	0.237	0.015	0.235	0.012	0.174	0.011	0.150	0.007	0.139	0.008	0.067	0.002	0.067	0.003	0.066	0.003	0.101	0.012	0.078	0.003	0.067	0.008
	237	0.295	0.012	0.260	0.014	0.241	0.011	0.185	0.010	0.170	0.009	0.149	0.006	0.068	0.002	0.072	0.001	0.068	0.004	0.109	0.006	0.092	0.008	0.074	0.007

B. nana		Ash (g/g DM)						Cell Solubles (% of DM)						Cell Wall (% of DM)						Lig/Cut (% of NDF)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.005	0.002	0.005	0.001	0.007	0.002	58.578	3.038	63.535	5.060	56.675	5.126	41.422	3.038	36.465	5.060	43.325	5.126	48.871	4.282	52.781	7.746	49.167	3.192
	177	0.000	0.006	0.021	0.041	0.004	0.001	80.053	0.874	81.704	0.578	78.705	1.144	19.947	0.874	18.296	0.578	21.295	1.144	36.972	2.701	28.669	21.770	38.327	2.945
	184	0.003	0.000	0.002	0.001	0.002	0.000	72.634	1.837	76.263	0.965	79.715	0.950	27.366	1.837	23.737	0.965	20.285	0.950	34.412	2.003	34.714	1.183	31.877	2.257
	191	0.002	0.001	0.003	0.002	0.001	0.001	75.093	0.320	75.007	1.379	79.493	2.352	24.907	0.320	24.993	1.379	20.507	2.352	33.523	2.318	34.919	1.347	30.802	2.907
	198	0.002	0.001	0.002	0.001	0.002	0.001	71.427	1.058	74.038	1.060	74.947	2.583	28.573	1.058	25.962	1.060	25.053	2.583	32.526	1.437	32.689	0.602	32.398	5.141
	205	0.002	0.001	0.003	0.003	0.002	0.000	70.659	2.412	72.517	2.493	79.353	1.903	29.341	2.412	27.483	2.493	20.647	1.903	35.396	1.208	34.634	1.518	30.027	2.756
	212	0.005	0.002	0.005	0.002	0.005	0.003	70.996	2.589	72.041	1.509	80.715	2.527	29.004	2.589	27.959	1.509	19.285	2.527	33.286	1.790	35.948	0.835	26.083	2.159
	219	0.004	0.001	0.005	0.003	0.006	0.005	69.892	2.518	72.554	1.482	78.386	2.651	30.108	2.518	27.446	1.482	21.614	2.651	35.469	3.128	34.102	4.422	26.144	4.758
2018	173	0.004	0.002	0.005	0.001			81.399	1.159	81.993	2.320			18.601	1.159	18.007	2.320			36.211	1.805	38.306	3.776		
	180	0.005	0.003	0.003	0.000	0.006	0.002	80.316	1.657	81.616	1.066	84.002	1.894	19.684	1.657	18.384	1.066	15.998	1.894	35.755	3.069	36.774	2.943	32.370	3.876
	187	0.004	0.003	0.003	0.002	0.003	0.002	75.561	2.051	78.659	1.722	83.292	1.363	24.439	2.051	21.341	1.722	16.708	1.363	35.606	2.432	37.126	3.946	32.949	3.268
	194	0.004	0.002	0.004	0.001	0.004	0.001	74.970	2.069	78.098	1.508	81.092	2.492	25.030	2.069	21.902	1.508	18.908	2.492	31.493	1.607	31.702	1.801	31.573	2.877
	200	0.006	0.002	0.005	0.002	0.005	0.002	73.716	3.960	77.957	6.207	80.104	1.212	26.284	3.960	22.043	6.207	19.896	1.212	35.318	5.237	36.012	3.346	28.694	1.499
	210	0.004	0.000	0.004	0.001	0.005	0.001	70.077	2.800	72.174	3.531	75.830	2.568	29.923	2.800	27.826	3.531	24.170	2.568	35.069	3.712	30.965	2.340	28.876	3.147
	217	0.006	0.001	0.005	0.002	0.007	0.002	69.204	2.614	71.087	1.111	75.969	2.878	30.796	2.614	28.913	1.111	24.031	2.878	36.384	1.401	37.596	1.307	29.383	2.896
	223	0.006	0.003	0.006	0.001	0.006	0.003	69.187	1.685	75.064	2.800	75.098	2.779	30.813	1.685	24.936	2.800	24.902	2.779	38.242	2.596	32.510	2.037	30.123	3.571
	231	0.006	0.003	0.004	0.002	0.006	0.002	72.175	1.003	76.317	1.471	76.522	1.230	27.825	1.003	23.683	1.471	23.478	1.230	36.345	2.919	32.909	1.598	28.436	2.583
	237	0.008	0.003	0.007	0.001	0.007	0.002	70.478	1.202	74.022	1.358	75.850	1.114	29.522	1.202	25.978	1.358	24.150	1.114	36.880	1.085	35.378	1.212	30.538	1.604

B. nana		NDF digestibility (%)						NDS digestibility (%)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	4.252	0.677	3.151	0.653	4.382	0.742	41.708	2.524	45.827	4.205	40.127	4.260
	177	3.489	0.373	7.818	10.743	3.497	0.322	59.554	0.727	60.926	0.480	58.434	0.951
	184	5.370	0.614	4.583	0.297	4.460	0.427	53.389	1.526	56.405	0.802	59.273	0.790
	191	5.092	0.516	4.776	0.241	4.701	0.278	55.432	0.266	55.360	1.146	59.089	1.955
	198	6.088	0.354	5.490	0.311	5.403	0.928	52.386	0.879	54.555	0.881	55.311	2.147
	205	5.509	0.711	5.336	0.671	4.908	0.236	51.747	2.004	53.292	2.072	58.973	1.582
	212	5.956	0.363	5.109	0.417	5.497	0.792	52.027	2.151	52.896	1.254	60.104	2.100
	219	5.627	0.666	5.491	0.886	6.136	0.781	51.110	2.092	53.322	1.231	58.169	2.203
2018	173	3.356	0.244	2.939	0.193			60.672	0.963	61.166	1.928		
	180	3.673	0.763	3.248	0.416	3.428	0.392	59.772	1.377	60.852	0.886	62.836	1.574
	187	4.550	0.635	3.729	0.680	3.510	0.510	55.821	1.705	58.395	1.431	62.246	1.133
	194	5.581	0.439	4.834	0.205	4.184	0.324	55.330	1.719	57.929	1.253	60.417	2.071
	200	4.896	0.449	3.932	0.890	5.053	0.563	54.288	3.290	57.812	5.158	59.597	1.007
	210	5.699	0.748	6.473	0.611	6.050	0.396	51.264	2.327	53.006	2.934	56.045	2.134
	217	5.507	0.429	4.898	0.207	5.871	0.390	50.539	2.173	52.103	0.924	56.160	2.392
	223	5.074	0.366	5.323	0.679	5.896	0.468	50.524	1.400	55.408	2.327	55.437	2.309
	231	5.005	0.501	4.979	0.613	6.032	0.654	53.008	0.833	56.449	1.222	56.620	1.022
	237	5.167	0.268	4.861	0.166	5.625	0.300	51.598	0.999	54.542	1.128	56.061	0.926

R. tomentosum		NDF (g/g DM)						ADF (g/g DM)						Cellulose (g/g DM)						Lignin (g/g DM)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.443	0.029	0.441	0.041	0.431	0.016	0.315	0.022	0.334	0.050	0.319	0.020	0.142	0.014	0.143	0.010	0.146	0.011	0.169	0.026	0.186	0.048	0.168	0.011
	177	0.463	0.019	0.405	0.013	0.452	0.021	0.312	0.019	0.267	0.011	0.297	0.020	0.119	0.008	0.109	0.005	0.112	0.007	0.188	0.018	0.154	0.009	0.180	0.014
	184	0.391	0.024	0.405	0.016	0.380	0.025	0.275	0.014	0.285	0.008	0.270	0.022	0.113	0.007	0.123	0.009	0.111	0.011	0.157	0.010	0.158	0.005	0.154	0.013
	191	0.381	0.014	0.365	0.007	0.364	0.012	0.273	0.012	0.264	0.006	0.263	0.009	0.112	0.009	0.113	0.004	0.114	0.009	0.157	0.008	0.148	0.005	0.145	0.009
	198	0.459	0.024	0.471	0.034	0.498	0.010	0.328	0.011	0.336	0.029	0.366	0.013	0.122	0.003	0.141	0.014	0.150	0.003	0.202	0.011	0.191	0.017	0.211	0.013
	205	0.438	0.030	0.425	0.041	0.420	0.028	0.318	0.019	0.310	0.028	0.310	0.020	0.120	0.012	0.121	0.008	0.120	0.005	0.195	0.029	0.185	0.024	0.186	0.021
	212	0.438	0.020	0.493	0.033	0.493	0.024	0.315	0.012	0.354	0.022	0.366	0.022	0.129	0.012	0.140	0.012	0.138	0.007	0.180	0.008	0.211	0.015	0.223	0.022
	219	0.476	0.027	0.453	0.039	0.447	0.007	0.345	0.017	0.331	0.034	0.327	0.007	0.144	0.014	0.147	0.013	0.139	0.007	0.195	0.006	0.173	0.028	0.179	0.010
2018	173	0.365	0.012	0.366	0.012			0.253	0.006	0.258	0.014			0.117	0.008	0.114	0.009			0.128	0.007	0.136	0.008		
	180	0.370	0.016	0.396	0.015	0.432	0.013	0.276	0.008	0.292	0.012	0.320	0.009	0.123	0.006	0.136	0.009	0.149	0.005	0.145	0.010	0.147	0.008	0.163	0.007
	187	0.376	0.034	0.410	0.021	0.400	0.022	0.282	0.026	0.294	0.010	0.286	0.020	0.123	0.012	0.129	0.007	0.127	0.010	0.154	0.019	0.158	0.005	0.152	0.013
	194	0.418	0.023	0.369	0.009	0.391	0.020	0.308	0.022	0.277	0.011	0.288	0.013	0.122	0.014	0.122	0.005	0.130	0.010	0.181	0.014	0.149	0.006	0.151	0.004
	200	0.467	0.034	0.437	0.020	0.359	0.030	0.354	0.025	0.328	0.010	0.263	0.019	0.141	0.015	0.149	0.007	0.119	0.009	0.204	0.015	0.170	0.005	0.136	0.010
	210	0.469	0.013	0.464	0.028	0.382	0.018	0.350	0.007	0.347	0.021	0.294	0.020	0.143	0.010	0.149	0.010	0.128	0.006	0.200	0.009	0.192	0.017	0.159	0.016
	217	0.442	0.016	0.433	0.014	0.379	0.023	0.324	0.011	0.319	0.009	0.291	0.015	0.137	0.010	0.135	0.005	0.121	0.009	0.178	0.011	0.175	0.009	0.162	0.007
	223	0.469	0.023	0.393	0.029	0.378	0.022	0.347	0.020	0.293	0.020	0.279	0.011	0.145	0.005	0.121	0.008	0.124	0.009	0.193	0.019	0.163	0.012	0.147	0.010
	231	0.394	0.027	0.372	0.012	0.386	0.021	0.292	0.022	0.275	0.009	0.285	0.014	0.120	0.008	0.117	0.009	0.121	0.014	0.162	0.014	0.150	0.007	0.157	0.008
	237	0.381	0.015	0.336	0.026	0.330	0.017	0.271	0.012	0.247	0.017	0.247	0.012	0.107	0.007	0.102	0.009	0.099	0.006	0.154	0.009	0.137	0.011	0.141	0.007

R. tomentosum		Ash (g/g DM)						Cell Solubles (% of DM)						Cell Wall (% of DM)						Lig/Cut (% of NDF)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.004	0.001	0.005	0.001	0.004	0.001	55.710	2.931	55.925	4.059	56.872	1.585	44.290	2.931	44.075	4.059	43.128	1.585	37.987	3.949	41.820	6.595	38.974	1.267
	177	0.005	0.001	0.004	0.001	0.005	0.001	53.716	1.909	59.453	1.320	54.796	2.128	46.284	1.909	40.547	1.320	45.204	2.128	40.690	3.107	38.002	1.251	39.754	1.724
	184	0.005	0.000	0.005	0.001	0.005	0.001	60.934	2.372	59.526	1.640	62.015	2.459	39.066	2.372	40.474	1.640	37.985	2.459	40.205	1.851	39.054	2.099	40.584	1.735
	191	0.005	0.003	0.003	0.002	0.004	0.000	61.908	1.369	63.479	0.745	63.633	1.207	38.092	1.369	36.521	0.745	36.367	1.207	41.232	0.974	40.648	1.173	39.907	2.112
	198	0.004	0.001	0.004	0.001	0.005	0.001	54.148	2.398	52.853	3.406	50.238	0.959	45.852	2.398	47.147	3.406	49.762	0.959	44.167	1.555	40.446	2.105	42.488	2.336
	205	0.003	0.001	0.004	0.001	0.004	0.001	56.202	2.977	57.460	4.055	58.031	2.751	43.798	2.977	42.540	4.055	41.969	2.751	44.257	4.095	43.358	1.606	44.153	2.275
	212	0.005	0.002	0.003	0.002	0.005	0.001	56.239	2.049	50.650	3.322	50.703	2.377	43.761	2.049	49.350	3.322	49.297	2.377	41.210	1.404	42.755	2.176	45.173	2.872
	219	0.006	0.001	0.011	0.004	0.009	0.002	52.355	2.720	54.735	3.931	55.273	0.735	47.645	2.720	45.265	3.931	44.727	0.735	41.016	1.672	38.086	3.817	40.050	1.913
2018	173	0.007	0.001	0.008	0.001			63.476	1.234	63.407	1.178			36.524	1.234	36.593	1.178			35.179	2.190	37.025	1.821		
	180	0.009	0.003	0.008	0.002	0.009	0.002	62.976	1.588	60.414	1.458	56.762	1.300	37.024	1.588	39.586	1.458	43.238	1.300	39.137	1.428	37.217	1.741	37.579	0.941
	187	0.005	0.002	0.007	0.001	0.006	0.002	62.422	3.446	58.973	2.056	59.954	2.164	37.578	3.446	41.027	2.056	40.046	2.164	40.982	2.314	38.514	0.948	37.941	1.505
	194	0.005	0.001	0.006	0.000	0.007	0.002	58.171	2.290	63.090	0.919	60.870	2.011	41.829	2.290	36.910	0.919	39.130	2.011	43.174	2.637	40.264	0.870	38.765	2.226
	200	0.009	0.001	0.008	0.002	0.008	0.001	53.332	3.435	56.320	1.956	64.060	3.042	46.668	3.435	43.680	1.956	35.940	3.042	43.738	1.642	39.031	1.345	37.920	0.910
	210	0.007	0.000	0.006	0.002	0.007	0.001	53.071	1.261	53.617	2.809	61.806	1.798	46.929	1.261	46.383	2.809	38.194	1.798	42.654	2.131	41.314	2.749	41.654	2.694
	217	0.008	0.004	0.009	0.003	0.008	0.001	55.835	1.577	56.745	1.414	62.103	2.285	44.165	1.577	43.255	1.414	37.897	2.285	40.401	2.387	40.527	1.309	42.867	0.905
	223	0.009	0.002	0.009	0.001	0.009	0.001	53.144	2.324	60.703	2.860	62.208	2.216	46.856	2.324	39.297	2.860	37.792	2.216	41.190	2.310	41.564	0.754	38.925	2.314
	231	0.009	0.004	0.008	0.003	0.007	0.002	60.579	2.707	62.769	1.160	61.355	2.096	39.421	2.707	37.231	1.160	38.645	2.096	41.044	0.827	40.209	1.680	40.720	2.814
	237	0.010	0.004	0.008	0.002	0.007	0.003	61.860	1.532	66.446	2.575	66.963	1.722	38.140	1.532	33.554	2.575	33.037	1.722	40.255	1.437	40.681	1.003	42.732	1.754

R. tomentosum		NDF digestibility (%)						NDS digestibility (%)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	7.429	1.192	6.266	1.284	6.866	0.275	39.325	2.436	39.504	3.373	40.291	1.317
	177	6.860	0.837	6.747	0.341	6.955	0.489	37.668	1.587	42.436	1.097	38.565	1.769
	184	5.906	0.694	6.460	0.894	5.633	0.534	43.666	1.971	42.496	1.363	44.564	2.044
	191	5.476	0.199	5.398	0.325	5.570	0.564	44.476	1.138	45.781	0.619	45.909	1.003
	198	5.791	0.578	7.047	0.829	6.789	0.703	38.027	1.993	36.951	2.831	34.777	0.797
	205	5.526	0.801	5.545	0.350	5.292	0.388	39.734	2.474	40.779	3.370	41.254	2.286
	212	6.314	0.596	6.661	0.909	5.955	0.628	39.765	1.703	35.121	2.761	35.164	1.976
	219	6.952	0.870	7.536	1.007	6.801	0.571	36.537	2.261	38.514	3.267	38.962	0.611
2018	173	6.931	0.751	6.375	0.533			45.778	1.026	45.721	0.979		
	180	5.853	0.323	6.841	0.621	7.334	0.357	45.363	1.319	43.234	1.212	40.199	1.080
	187	5.474	0.599	6.682	0.599	6.678	0.348	44.903	2.863	42.037	1.709	42.852	1.798
	194	5.542	0.706	5.543	0.151	6.334	0.879	41.370	1.903	45.458	0.763	43.613	1.671
	200	6.013	0.728	6.956	0.683	6.011	0.681	37.349	2.855	39.832	1.625	46.264	2.528
	210	6.356	0.700	6.681	0.884	5.405	0.541	37.132	1.048	37.586	2.334	44.390	1.494
	217	6.628	0.813	6.426	0.383	5.073	0.492	39.429	1.310	40.185	1.175	44.637	1.899
	223	6.756	0.481	5.570	0.466	6.065	0.786	37.193	1.931	43.475	2.376	44.725	1.841
	231	5.708	0.229	5.619	0.461	5.742	0.915	43.371	2.249	45.191	0.964	44.016	1.742
	237	5.737	0.393	4.949	0.439	4.457	0.502	44.435	1.273	48.247	2.140	48.676	1.431

V. vitis-idaea		NDF (g/g DM)						ADF (g/g DM)						Cellulose (g/g DM)						Lignin (g/g DM)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.383	0.024	0.395	0.026	0.365	0.034	0.246	0.018	0.260	0.035	0.272	0.041	0.126	0.009	0.135	0.016	0.140	0.006	0.116	0.015	0.119	0.020	0.127	0.041
	177	0.389	0.029	0.381	0.059	0.403	0.056	0.233	0.024	0.239	0.033	0.262	0.045	0.124	0.010	0.124	0.013	0.133	0.008	0.104	0.016	0.111	0.023	0.125	0.042
	184	0.336	0.019	0.334	0.008	0.391	0.189	0.222	0.010	0.212	0.004	0.205	0.008	0.131	0.007	0.123	0.006	0.117	0.006	0.079	0.022	0.085	0.006	0.085	0.007
	191	0.322	0.016	0.333	0.015	0.332	0.007	0.215	0.016	0.226	0.010	0.226	0.006	0.121	0.012	0.127	0.005	0.126	0.004	0.091	0.005	0.097	0.008	0.097	0.005
	198	0.359	0.024	0.361	0.015	0.366	0.026	0.243	0.025	0.248	0.014	0.252	0.030	0.128	0.008	0.134	0.007	0.132	0.011	0.112	0.018	0.110	0.007	0.117	0.019
	205	0.371	0.012	0.335	0.019	0.346	0.019	0.261	0.014	0.232	0.012	0.243	0.016	0.137	0.012	0.115	0.018	0.128	0.008	0.120	0.004	0.113	0.015	0.113	0.011
	212	0.366	0.039	0.344	0.018	0.360	0.035	0.260	0.033	0.235	0.010	0.256	0.035	0.135	0.009	0.130	0.005	0.125	0.019	0.119	0.026	0.102	0.007	0.126	0.025
	219	0.360	0.026	0.383	0.030	0.342	0.015	0.256	0.021	0.274	0.032	0.239	0.013	0.141	0.010	0.136	0.011	0.133	0.009	0.106	0.011	0.131	0.022	0.100	0.005
2018	173	0.295	0.007	0.290	0.005			0.201	0.007	0.205	0.009			0.123	0.008	0.119	0.007			0.072	0.008	0.080	0.003		
	180	0.317	0.030	0.285	0.011	0.306	0.012	0.227	0.017	0.203	0.009	0.220	0.006	0.136	0.011	0.118	0.007	0.130	0.003	0.085	0.009	0.077	0.005	0.084	0.004
	187	0.304	0.009	0.296	0.011	0.304	0.026	0.217	0.010	0.204	0.009	0.211	0.018	0.123	0.001	0.115	0.006	0.122	0.015	0.089	0.012	0.082	0.003	0.084	0.006
	194	0.332	0.027	0.267	0.106	0.297	0.016	0.237	0.017	0.226	0.013	0.216	0.010	0.134	0.013	0.127	0.011	0.119	0.020	0.097	0.008	0.092	0.006	0.091	0.011
	200	0.336	0.011	0.335	0.021	0.306	0.020	0.246	0.008	0.236	0.013	0.217	0.010	0.137	0.010	0.135	0.007	0.122	0.011	0.103	0.009	0.095	0.008	0.087	0.003
	210	0.405	0.047	0.353	0.025	0.364	0.021	0.301	0.043	0.259	0.017	0.271	0.021	0.157	0.013	0.143	0.011	0.149	0.012	0.138	0.034	0.110	0.017	0.115	0.011
	217	0.350	0.009	0.361	0.010	0.351	0.019	0.252	0.009	0.260	0.007	0.258	0.010	0.138	0.002	0.144	0.010	0.146	0.008	0.107	0.010	0.109	0.009	0.105	0.003
	223	0.340	0.024	0.329	0.012	0.335	0.006	0.253	0.018	0.237	0.007	0.244	0.006	0.134	0.009	0.133	0.006	0.134	0.006	0.111	0.010	0.098	0.005	0.101	0.003
	231	0.326	0.009	0.324	0.013	0.312	0.019	0.235	0.006	0.235	0.008	0.229	0.012	0.129	0.008	0.130	0.005	0.122	0.008	0.098	0.007	0.099	0.006	0.100	0.004
	237	0.310	0.014	0.307	0.011	0.303	0.017	0.224	0.009	0.224	0.009	0.221	0.011	0.116	0.010	0.120	0.007	0.117	0.011	0.101	0.003	0.096	0.005	0.097	0.004

V. vitis-idaea		Ash (g/g DM)						Cell Solubles (% of DM)						Cell Wall (% of DM)						Lig/Cut (% of NDF)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.004	0.001	0.005	0.001	0.004	0.001	61.713	2.425	60.550	2.631	63.459	3.415	38.287	2.425	39.450	2.631	36.541	3.415	30.286	2.433	30.256	4.659	34.360	7.298
	177	0.005	0.001	0.004	0.001	0.004	0.001	61.112	2.857	61.856	5.865	59.681	5.576	38.888	2.857	38.144	5.865	40.319	5.576	26.683	3.305	28.940	2.602	30.469	5.679
	184	0.012	0.018	0.004	0.001	0.003	0.000	66.361	1.871	66.596	0.833	60.934	18.888	33.639	1.871	33.404	0.833	39.066	18.888	23.442	5.985	25.447	1.261	24.577	7.474
	191	0.003	0.001	0.003	0.001	0.003	0.001	67.750	1.618	66.674	1.491	66.804	0.679	32.250	1.618	33.326	1.491	33.196	0.679	28.206	0.312	29.079	1.756	29.102	1.645
	198	0.003	0.001	0.004	0.004	0.003	0.000	64.137	2.380	63.850	1.533	63.418	2.593	35.863	2.380	36.150	1.533	36.582	2.593	31.057	3.233	30.429	1.195	31.900	3.605
	205	0.004	0.001	0.004	0.002	0.002	0.000	62.861	1.220	66.510	1.930	65.356	1.921	37.139	1.220	33.490	1.930	34.644	1.921	32.254	0.848	33.744	4.877	32.502	1.967
	212	0.006	0.004	0.003	0.001	0.005	0.003	63.419	3.935	65.573	1.768	64.000	3.524	36.581	3.935	34.427	1.768	36.000	3.524	32.248	3.933	29.611	1.582	34.870	4.790
	219	0.008	0.002	0.008	0.003	0.007	0.002	63.964	2.555	61.683	2.993	65.820	1.482	36.036	2.555	38.317	2.993	34.180	1.482	29.499	1.065	33.908	3.478	29.195	0.659
2018	173	0.006	0.000	0.005	0.001			70.477	0.736	70.956	0.534			29.523	0.736	29.044	0.534			24.510	2.607	27.667	1.039		
	180	0.007	0.001	0.008	0.003	0.006	0.001	68.291	2.959	71.533	1.068	69.377	1.230	31.709	2.959	28.467	1.068	30.623	1.230	26.674	1.068	27.116	1.725	27.364	1.167
	187	0.005	0.001	0.006	0.001	0.005	0.002	69.565	0.919	70.437	1.138	69.619	2.554	30.435	0.919	29.563	1.138	30.381	2.554	29.309	3.259	27.772	0.937	27.554	1.341
	194	0.005	0.001	0.006	0.001	0.007	0.001	66.828	2.699	73.311	10.629	70.321	1.598	33.172	2.699	26.689	10.629	29.679	1.598	29.405	2.641	47.073	39.349	30.819	5.425
	200	0.006	0.002	0.006	0.002	0.008	0.002	66.392	1.068	66.519	2.128	69.379	1.961	33.608	1.068	33.481	2.128	30.621	1.961	30.725	2.377	28.278	1.311	28.626	2.560
	210	0.005	0.001	0.006	0.001	0.006	0.001	59.499	4.731	64.722	2.471	63.563	2.088	40.501	4.731	35.278	2.471	36.437	2.088	33.746	4.562	31.118	3.458	31.537	1.437
	217	0.007	0.001	0.007	0.001	0.008	0.002	64.973	0.897	63.914	1.012	64.863	1.878	35.027	0.897	36.086	1.012	35.137	1.878	30.592	2.130	30.289	2.639	29.831	1.368
	223	0.008	0.003	0.007	0.001	0.009	0.002	66.006	2.422	67.054	1.172	66.489	0.606	33.994	2.422	32.946	1.172	33.511	0.606	32.495	1.852	29.640	1.638	30.265	1.261
	231	0.008	0.003	0.006	0.002	0.007	0.003	67.363	0.912	67.591	1.292	68.841	1.892	32.637	0.912	32.409	1.292	31.159	1.892	30.052	2.446	30.660	1.500	32.027	0.980
	237	0.007	0.002	0.008	0.001	0.008	0.001	69.025	1.374	69.313	1.105	69.654	1.675	30.975	1.374	30.687	1.105	30.346	1.675	32.547	1.421	31.348	2.042	31.984	2.117

V. vitis-idaea		NDF digestibility (%)						NDS digestibility (%)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	9.021	0.624	9.476	2.154	7.301	1.608	44.313	2.015	43.347	2.187	45.764	2.838
	177	10.846	1.539	9.562	1.570	9.454	1.561	43.814	2.374	44.432	4.874	42.625	4.634
	184	11.098	3.333	9.789	0.346	14.379	13.987	48.176	1.555	48.371	0.692	43.667	15.696
	191	8.342	0.385	8.302	0.645	8.268	0.672	49.331	1.345	48.436	1.239	48.544	0.564
	198	8.177	0.838	8.468	0.559	8.056	1.086	46.328	1.978	46.090	1.274	45.731	2.155
	205	8.012	0.466	6.893	1.516	7.398	0.673	45.268	1.014	48.300	1.604	47.341	1.596
	212	7.874	0.678	8.381	0.796	6.980	1.317	45.731	3.270	47.521	1.469	46.214	2.929
	219	8.782	0.351	7.677	0.759	8.458	0.412	46.184	2.123	44.289	2.487	47.726	1.231
2018	173	9.073	1.102	7.707	0.417			51.596	0.612	51.994	0.443		
	180	8.793	0.838	7.763	0.769	8.242	0.608	49.779	2.459	52.474	0.887	50.682	1.022
	187	7.536	0.898	7.810	0.552	8.124	1.054	50.838	0.763	51.563	0.945	50.884	2.123
	194	8.207	1.360	6.150	3.453	7.032	1.765	48.564	2.243	53.951	8.833	51.467	1.328
	200	7.796	0.851	8.641	0.685	7.855	1.307	48.202	0.888	48.307	1.768	50.684	1.630
	210	8.152	0.845	8.057	1.192	8.112	0.457	42.474	3.931	46.814	2.054	45.851	1.735
	217	8.152	0.583	8.552	1.038	8.480	0.973	47.022	0.745	46.142	0.841	46.931	1.561
	223	7.262	0.727	8.014	0.727	7.915	0.550	47.881	2.013	48.752	0.974	48.282	0.504
	231	7.813	0.924	7.520	0.576	6.803	0.703	49.009	0.758	49.198	1.073	50.237	1.572
	237	6.611	0.656	6.921	0.764	6.669	1.022	50.389	1.141	50.629	0.918	50.913	1.392

C. bigelowii		NDF (g/g DM)						ADF (g/g DM)						Cellulose (g/g DM)						Lignin (g/g DM)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.599	0.030	0.647	0.046	0.635	0.008	0.257	0.016	0.300	0.057	0.291	0.017	0.230	0.009	0.241	0.020	0.243	0.008	0.007	0.047	0.057	0.051	0.046	0.012
	177	0.631	0.014	0.614	0.010	0.657	0.014	0.256	0.011	0.243	0.011	0.265	0.010	0.175	0.078	0.188	0.079	0.184	0.090	0.079	0.077	0.048	0.072	0.080	0.081
	184	0.682	0.019	0.704	0.033	0.701	0.019	0.277	0.003	0.302	0.027	0.284	0.011	0.247	0.005	0.246	0.043	0.238	0.025	0.028	0.005	0.054	0.043	0.044	0.021
	191	0.611	0.031	0.644	0.013	0.653	0.025	0.247	0.015	0.280	0.013	0.281	0.023	0.198	0.050	0.246	0.010	0.245	0.016	0.047	0.045	0.032	0.003	0.035	0.011
	198	0.655	0.016	0.655	0.026	0.663	0.026	0.271	0.019	0.290	0.026	0.274	0.020	0.217	0.037	0.253	0.020	0.227	0.010	0.053	0.049	0.035	0.007	0.045	0.024
	205	0.642	0.015	0.648	0.044	0.664	0.019	0.268	0.011	0.288	0.044	0.285	0.029	0.223	0.027	0.251	0.036	0.234	0.047	0.042	0.020	0.037	0.010	0.051	0.020
	212	0.601	0.008	0.635	0.021	0.628	0.015	0.236	0.010	0.266	0.023	0.250	0.018	0.187	0.051	0.231	0.024	0.217	0.020	0.046	0.048	0.032	0.003	0.028	0.007
	219	0.614	0.015	0.614	0.019	0.631	0.013	0.262	0.017	0.264	0.012	0.271	0.010	0.226	0.019	0.229	0.006	0.235	0.009	0.032	0.003	0.032	0.007	0.031	0.004
2018	173	0.607	0.018	0.586	0.015			0.262	0.011	0.240	0.009			0.232	0.030	0.214	0.020			0.025	0.028	0.022	0.024		
	180	0.638	0.018	0.620	0.009	0.617	0.016	0.262	0.019	0.255	0.008	0.256	0.006	0.242	0.014	0.235	0.009	0.233	0.010	0.016	0.005	0.015	0.008	0.017	0.011
	187	0.674	0.013	0.662	0.008	0.646	0.018	0.288	0.006	0.286	0.018	0.268	0.014	0.255	0.010	0.243	0.032	0.240	0.014	0.029	0.009	0.040	0.021	0.024	0.013
	194	0.638	0.008	0.640	0.012	0.644	0.006	0.273	0.012	0.278	0.010	0.271	0.006	0.237	0.007	0.250	0.011	0.197	0.064	0.032	0.012	0.025	0.005	0.069	0.061
	200	0.664	0.009	0.647	0.015	0.653	0.015	0.322	0.012	0.289	0.015	0.285	0.016	0.277	0.024	0.255	0.020	0.262	0.012	0.040	0.018	0.030	0.007	0.017	0.005
	210	0.673	0.036	0.639	0.032	0.639	0.014	0.286	0.021	0.279	0.015	0.277	0.012	0.252	0.019	0.235	0.020	0.244	0.012	0.029	0.009	0.040	0.028	0.028	0.002
	217	0.615	0.021	0.630	0.009	0.624	0.018	0.275	0.009	0.274	0.007	0.263	0.012	0.232	0.020	0.242	0.005	0.233	0.010	0.038	0.018	0.026	0.003	0.024	0.004
	223	0.595	0.022	0.580	0.020	0.575	0.023	0.272	0.016	0.268	0.016	0.258	0.016	0.241	0.013	0.229	0.028	0.200	0.059	0.025	0.004	0.034	0.017	0.051	0.049
	231	0.585	0.018	0.630	0.022	0.559	0.015	0.268	0.014	0.312	0.019	0.243	0.013	0.233	0.018	0.219	0.052	0.220	0.015	0.028	0.007	0.087	0.045	0.018	0.003
	237	0.616	0.021	0.630	0.052	0.558	0.008	0.296	0.025	0.324	0.042	0.256	0.012	0.218	0.074	0.284	0.034	0.218	0.029	0.072	0.056	0.034	0.011	0.030	0.029

C. bigelowii

Year	DOY	Ash (g/g DM) - Snow Mean	SD	Ambient Mean	SD	+ Snow Mean	SD	Cell Solubles (% of DM) - Snow Mean	SD	Ambient Mean	SD	+ Snow Mean	SD
2017	170	0.020	0.037	0.003	0.001	0.002	0.000	40.100	2.983	35.305	4.604	36.550	0.824
	177	0.002	0.001	0.006	0.008	0.002	0.000	36.881	1.420	38.638	0.972	34.314	1.444
	184	0.002	0.001	0.002	0.000	0.002	0.000	31.750	1.946	29.640	3.315	29.874	1.922
	191	0.002	0.003	0.003	0.003	0.001	0.001	38.870	3.055	35.621	1.289	34.698	2.500
	198	0.001	0.001	0.001	0.000	0.002	0.002	34.491	1.612	34.464	2.563	33.704	2.567
	205	0.002	0.001	0.001	0.000	0.001	0.001	35.828	1.539	35.212	4.417	33.576	1.868
	212	0.004	0.002	0.004	0.002	0.005	0.003	39.935	0.761	36.545	2.098	37.243	1.546
	219	0.004	0.001	0.004	0.002	0.004	0.001	38.623	1.454	38.647	1.922	36.941	1.281
2018	173	0.005	0.001	0.004	0.001			39.302	1.848	41.420	1.513		
	180	0.005	0.002	0.005	0.002	0.006	0.001	36.161	1.774	37.999	0.868	38.343	1.635
	187	0.004	0.001	0.004	0.002	0.004	0.001	32.570	1.291	33.767	0.822	35.375	1.824
	194	0.004	0.001	0.004	0.001	0.005	0.001	36.157	0.763	36.001	1.164	35.606	0.601
	200	0.005	0.002	0.004	0.001	0.006	0.002	33.602	0.926	35.302	1.522	34.727	1.460
	210	0.004	0.001	0.005	0.001	0.004	0.001	32.696	3.561	36.086	3.184	36.087	1.449
	217	0.005	0.001	0.006	0.002	0.005	0.002	38.513	2.077	36.974	0.928	37.632	1.805
	223	0.006	0.001	0.005	0.002	0.007	0.002	40.545	2.243	41.979	1.972	42.532	2.263
	231	0.007	0.002	0.006	0.002	0.005	0.001	41.547	1.775	37.026	2.181	44.116	1.463
	237	0.005	0.002	0.006	0.003	0.007	0.002	38.358	2.101	36.954	5.155	44.241	0.823

Year	DOY	Cell Wall (% of DM) - Snow Mean	SD	Ambient Mean	SD	+ Snow Mean	SD	Lig/Cut (% of NDF) - Snow Mean	SD	Ambient Mean	SD	+ Snow Mean	SD
2017	170	59.900	2.983	64.695	4.604	63.450	0.824	0.985	7.973	8.428	6.755	7.196	1.795
	177	63.119	1.420	61.362	0.972	65.686	1.444	12.469	12.195	7.852	11.907	12.255	12.614
	184	68.250	1.946	70.360	3.315	70.126	1.922	4.037	0.708	7.549	5.755	6.178	2.864
	191	61.130	3.055	64.379	1.289	65.302	2.500	7.815	7.526	4.898	0.315	5.283	1.503
	198	65.509	1.612	65.536	2.563	66.296	2.567	8.050	7.308	5.378	0.876	6.755	3.382
	205	64.172	1.539	64.788	4.417	66.424	1.868	6.578	2.972	5.609	1.139	7.715	3.128
	212	60.065	0.761	63.455	2.098	62.757	1.546	7.521	7.766	4.968	0.477	4.438	1.099
	219	61.377	1.454	61.353	1.922	63.059	1.281	5.276	0.468	5.147	1.061	4.997	0.599
2018	173	60.698	1.848	58.580	1.513			4.155	4.697	3.748	3.874		
	180	63.839	1.774	62.001	0.868	61.657	1.635	2.464	0.714	2.394	1.240	2.790	1.720
	187	67.430	1.291	66.233	0.822	64.625	1.824	4.265	1.372	6.021	3.214	3.737	2.029
	194	63.843	0.763	63.999	1.164	64.394	0.601	4.997	1.979	3.876	0.872	10.684	9.446
	200	66.398	0.926	64.698	1.522	65.273	1.460	6.029	2.848	4.624	1.283	2.663	0.684
	210	67.304	3.561	63.914	3.184	63.913	1.449	4.348	1.264	6.117	4.187	4.414	0.475
	217	61.487	2.077	63.026	0.928	62.368	1.805	6.193	2.884	4.166	0.457	3.904	0.610
	223	59.455	2.243	58.021	1.972	57.468	2.263	4.186	0.589	5.929	3.040	8.917	8.855
	231	58.453	1.775	62.974	2.181	55.884	1.463	4.801	1.180	13.973	7.213	3.187	0.541
	237	61.642	2.101	63.046	5.155	55.759	0.823	11.793	9.483	5.389	1.358	5.388	5.174

C. bigelowii		NDF digestibility (%)						NDS digestibility (%)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	55.234	20.697	41.675	8.954	42.437	3.208	26.353	2.479	22.368	3.826	23.403	0.684
	177	37.000	17.122	43.586	16.326	39.120	17.709	23.678	1.180	25.138	0.808	21.545	1.200
	184	52.520	1.746	47.104	10.116	49.224	5.421	19.414	1.618	17.661	2.755	17.855	1.597
	191	41.359	11.469	47.643	0.461	47.513	2.213	25.331	2.539	22.631	1.071	21.864	2.078
	198	43.562	11.125	47.444	0.843	45.386	5.444	21.692	1.340	21.669	2.130	21.038	2.134
	205	44.290	5.177	46.390	2.080	43.740	6.865	22.803	1.278	22.292	3.671	20.931	1.552
	212	41.102	11.199	46.824	1.803	47.455	2.290	26.216	0.633	23.399	1.743	23.979	1.284
	219	44.676	1.764	44.902	1.409	46.484	1.735	25.126	1.208	25.145	1.597	23.728	1.065
2018	173	47.245	8.979	46.052	6.362			25.690	1.536	27.450	1.257		
	180	52.725	1.217	51.436	2.662	50.264	3.317	23.080	1.474	24.607	0.721	24.893	1.358
	187	51.465	3.819	47.009	6.663	50.532	4.234	20.096	1.073	21.091	0.683	22.426	1.516
	194	47.210	4.426	49.639	2.260	39.211	14.708	23.076	0.634	22.947	0.967	22.618	0.499
	200	47.029	6.157	48.592	3.740	53.440	1.470	20.953	0.769	22.366	1.265	21.888	1.214
	210	51.061	2.606	45.256	7.314	48.374	2.096	20.200	2.959	23.017	2.646	23.018	1.204
	217	43.186	5.319	48.211	0.378	48.286	1.700	25.034	1.726	23.755	0.771	24.302	1.500
	223	45.425	1.152	41.351	5.859	37.698	12.346	26.723	1.864	27.915	1.639	28.374	1.881
	231	43.517	2.920	32.436	11.286	44.697	1.792	27.555	1.475	23.798	1.813	29.690	1.216
	237	35.799	13.014	45.588	2.730	41.121	8.030	24.905	1.746	23.739	4.284	29.794	0.684

E. vaginatum		NDF (g/g DM)						ADF (g/g DM)						Cellulose (g/g DM)						Lignin (g/g DM)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.692	0.025	0.690	0.026	0.721	0.017	0.368	0.032	0.348	0.038	0.381	0.021	0.296	0.006	0.285	0.021	0.310	0.017	0.068	0.034	0.061	0.021	0.069	0.010
	177	0.663	0.012	0.679	0.022	0.682	0.007	0.298	0.018	0.307	0.012	0.310	0.006	0.264	0.018	0.271	0.009	0.271	0.014	0.031	0.017	0.033	0.008	0.036	0.015
	184	0.712	0.029	0.713	0.018	0.725	0.024	0.306	0.014	0.307	0.012	0.311	0.005	0.275	0.010	0.254	0.020	0.247	0.052	0.029	0.004	0.052	0.025	0.062	0.053
	191	0.676	0.021	0.683	0.021	0.645	0.020	0.305	0.014	0.300	0.024	0.263	0.013	0.278	0.012	0.222	0.073	0.217	0.014	0.025	0.005	0.078	0.064	0.043	0.016
	198	0.684	0.014	0.672	0.011	0.687	0.015	0.284	0.007	0.276	0.007	0.294	0.011	0.238	0.029	0.249	0.010	0.246	0.037	0.045	0.032	0.026	0.005	0.046	0.035
	205	0.720	0.033	0.711	0.013	0.700	0.008	0.313	0.018	0.304	0.013	0.314	0.006	0.243	0.024	0.218	0.082	0.217	0.097	0.069	0.034	0.085	0.075	0.096	0.094
	212	0.663	0.014	0.650	0.012	0.682	0.030	0.276	0.011	0.268	0.010	0.300	0.020	0.246	0.014	0.215	0.061	0.223	0.082	0.027	0.010	0.049	0.056	0.073	0.073
	219	0.699	0.015	0.705	0.014	0.671	0.009	0.344	0.031	0.349	0.016	0.296	0.007	0.290	0.044	0.294	0.027	0.213	0.042	0.049	0.018	0.051	0.038	0.079	0.038
2018	173	0.668	0.011	0.671	0.010			0.285	0.005	0.296	0.006			0.236	0.039	0.271	0.006			0.043	0.039	0.022	0.003		
	180	0.673	0.010	0.688	0.008	0.647	0.022	0.296	0.011	0.288	0.013	0.288	0.021	0.271	0.007	0.264	0.010	0.261	0.014	0.020	0.004	0.020	0.005	0.021	0.012
	187	0.686	0.021	0.673	0.017	0.665	0.006	0.302	0.018	0.294	0.014	0.286	0.007	0.273	0.014	0.241	0.047	0.260	0.009	0.025	0.005	0.049	0.045	0.023	0.010
	194	0.685	0.010	0.662	0.020	0.649	0.006	0.306	0.002	0.291	0.013	0.293	0.016	0.269	0.015	0.236	0.057	0.261	0.016	0.032	0.016	0.049	0.062	0.028	0.015
	200	0.701	0.034	0.682	0.011	0.677	0.007	0.306	0.020	0.304	0.009	0.303	0.011	0.262	0.006	0.273	0.011	0.271	0.023	0.039	0.015	0.026	0.004	0.028	0.018
	210	0.758	0.017	0.720	0.018	0.680	0.026	0.370	0.014	0.323	0.017	0.307	0.005	0.298	0.022	0.293	0.013	0.274	0.007	0.068	0.013	0.025	0.008	0.029	0.004
	217	0.724	0.020	0.701	0.017	0.668	0.019	0.338	0.006	0.305	0.011	0.297	0.011	0.252	0.065	0.190	0.055	0.200	0.051	0.080	0.065	0.108	0.049	0.091	0.054
	223	0.690	0.013	0.631	0.018	0.616	0.027	0.327	0.016	0.292	0.011	0.281	0.017	0.187	0.100	0.224	0.056	0.226	0.055	0.135	0.087	0.063	0.052	0.050	0.044
	231	0.660	0.022	0.622	0.022	0.594	0.019	0.300	0.009	0.282	0.009	0.273	0.006	0.220	0.036	0.228	0.040	0.238	0.027	0.075	0.039	0.050	0.041	0.025	0.017
	237	0.636	0.011	0.600	0.028	0.549	0.019	0.296	0.005	0.277	0.012	0.251	0.015	0.239	0.034	0.207	0.050	0.231	0.013	0.050	0.038	0.065	0.050	0.015	0.003

E. vaginatum		Ash (g/g DM)						Cell Solubles (% of DM)						Cell Wall (% of DM)						Lig/Cut (% of NDF)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	0.004	0.002	0.002	0.001	0.003	0.002	30.768	2.521	30.967	2.584	27.895	1.684	69.232	2.521	69.033	2.584	72.105	1.684	9.730	4.524	8.826	2.720	9.532	1.360
	177	0.003	0.000	0.003	0.001	0.004	0.001	33.739	1.181	32.073	2.202	31.795	0.693	66.261	1.181	67.927	2.202	68.205	0.693	4.620	2.570	4.884	1.080	5.222	2.204
	184	0.002	0.000	0.002	0.000	0.002	0.000	28.759	2.923	28.663	1.816	27.468	2.444	71.241	2.923	71.337	1.816	72.532	2.444	4.110	0.363	7.172	3.308	8.415	7.039
	191	0.002	0.001	0.001	0.001	0.003	0.001	32.386	2.111	31.673	2.070	35.489	2.024	67.614	2.111	68.327	2.070	64.511	2.024	3.671	0.672	11.431	9.469	6.733	2.486
	198	0.001	0.001	0.002	0.001	0.002	0.001	31.557	1.356	32.830	1.093	31.272	1.451	68.443	1.356	67.170	1.093	68.728	1.451	6.446	4.500	3.926	0.827	6.622	4.980
	205	0.002	0.001	0.001	0.000	0.002	0.001	28.039	3.343	28.930	1.313	29.973	0.758	71.961	3.343	71.070	1.313	70.027	0.758	9.410	4.239	12.073	10.841	13.663	13.393
	212	0.003	0.001	0.004	0.001	0.004	0.002	33.710	1.395	35.050	1.187	31.781	3.032	66.290	1.395	64.950	1.187	68.219	3.032	4.016	1.580	7.597	8.939	10.972	11.442
	219	0.004	0.001	0.005	0.001	0.004	0.001	30.147	1.513	29.476	1.426	32.856	0.877	69.853	1.513	70.524	1.426	67.144	0.877	7.047	2.665	7.120	5.209	11.785	5.784
2018	173	0.005	0.001	0.004	0.001			33.238	1.135	32.855	0.961			66.762	1.135	67.145	0.961			6.392	5.632	3.204	0.354		
	180	0.005	0.002	0.003	0.001	0.006	0.002	32.675	0.959	31.234	0.812	35.262	2.214	67.325	0.959	68.766	0.812	64.738	2.214	2.970	0.665	2.924	0.652	3.190	1.752
	187	0.004	0.001	0.004	0.001	0.003	0.001	31.419	2.124	32.679	1.673	33.523	0.606	68.581	2.124	67.321	1.673	66.477	0.606	3.624	0.646	7.273	6.636	3.463	1.451
	194	0.004	0.001	0.005	0.001	0.005	0.002	31.464	1.017	33.794	2.029	35.118	0.640	68.536	1.017	66.206	2.029	64.882	0.640	4.692	2.344	7.392	9.244	4.255	2.202
	200	0.005	0.002	0.005	0.003	0.004	0.001	29.949	3.439	31.829	1.094	32.323	0.714	70.051	3.439	68.171	1.094	67.677	0.714	5.476	1.913	3.840	0.565	4.176	2.592
	210	0.005	0.001	0.004	0.001	0.004	0.001	24.155	1.714	28.001	1.845	32.037	2.638	75.845	1.714	71.999	1.845	67.963	2.638	8.924	1.765	3.514	1.065	4.237	0.562
	217	0.006	0.001	0.008	0.002	0.007	0.002	27.605	2.032	29.944	1.669	33.204	1.920	72.395	2.032	70.056	1.669	66.796	1.920	11.105	9.139	15.417	7.023	13.451	7.858
	223	0.005	0.002	0.005	0.001	0.005	0.001	31.039	1.255	36.875	1.775	38.412	2.672	68.961	1.255	63.125	1.775	61.588	2.672	19.757	12.911	10.076	8.483	8.346	7.762
	231	0.005	0.001	0.003	0.001	0.010	0.012	34.043	2.160	37.838	2.216	40.573	1.851	65.957	2.160	62.162	2.216	59.427	1.851	11.295	5.660	8.057	6.388	4.121	2.724
	237	0.006	0.002	0.004	0.002	0.005	0.002	36.395	1.102	39.976	2.844	45.092	1.897	63.605	1.102	60.024	2.844	54.908	1.897	7.870	5.791	10.763	8.194	2.710	0.576

E. vaginatum		NDF digestibility (%)						NDS digestibility (%)					
Year	**DOY**	**- Snow**		**Ambient**		**+ Snow**		**- Snow**		**Ambient**		**+ Snow**	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2017	170	41.705	7.185	42.935	4.107	43.384	3.227	18.598	2.095	18.763	2.147	16.211	1.399
	177	49.940	5.701	50.313	1.818	49.926	4.548	21.067	0.982	19.683	1.829	19.452	0.576
	184	54.620	1.644	47.961	6.057	47.261	11.715	16.929	2.429	16.849	1.509	15.856	2.031
	191	52.895	1.812	40.225	14.375	44.159	4.986	19.943	1.754	19.350	1.720	22.521	1.682
	198	47.845	7.896	51.979	2.324	47.820	8.845	19.254	1.127	20.312	0.909	19.017	1.205
	205	43.833	6.356	41.248	14.743	39.013	15.761	16.331	2.778	17.071	1.091	17.937	0.630
	212	51.158	3.682	45.087	14.226	42.164	16.135	21.043	1.159	22.156	0.986	19.440	2.519
	219	47.203	5.710	48.063	9.326	37.515	10.213	18.083	1.258	17.525	1.185	20.333	0.729
2018	173	47.155	9.746	53.645	0.961			20.650	0.943	20.333	0.799		
	180	54.378	1.931	55.647	1.358	51.783	2.644	20.183	0.797	18.985	0.675	22.333	1.840
	187	53.742	0.303	46.192	11.603	52.594	3.684	19.139	1.765	20.186	1.390	20.888	0.504
	194	51.412	5.052	46.243	14.144	49.605	4.482	19.177	0.845	21.113	1.686	22.213	0.532
	200	50.493	1.886	52.921	0.801	52.022	5.730	17.918	2.858	19.480	0.909	19.890	0.594
	210	46.956	4.091	56.747	2.279	51.850	2.741	13.103	1.425	16.299	1.533	19.653	2.192
	217	43.211	15.781	33.844	12.954	35.248	12.570	15.970	1.688	17.913	1.387	20.623	1.596
	223	29.833	16.172	39.040	12.470	40.947	12.881	18.824	1.043	23.673	1.475	24.951	2.221
	231	37.430	9.345	41.074	10.297	45.748	4.757	21.319	1.795	24.474	1.842	26.747	1.539
	237	42.129	9.617	35.721	11.570	44.853	1.454	23.274	0.916	26.250	2.364	30.501	1.576