

Forage Quality and Reindeer Productivity: Multiplier Effects Amplified by Climate Change

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Abstract

We investigated the effects of experimental manipulations of snowmelt on the flowering phenology and forage chemistry (digestibility and nitrogen concentration) of tussock cottongrass (*Eriophorum vaginatum*) on the Seward Peninsula, Alaska. Early snowmelt accelerated reproductive phenology by 11 days, and resulted in higher floral digestibility both early and late during inflorescence development. Nitrogen concentrations of inflorescences in late snowmelt plots were initially the highest among treatments, but decreased nearly 40% during inflorescence development. Thus, changes in climate that lead to changes in snow cover can alter both the timing of flowering and chemistry of *Eriophorum* and, consequently, its value as reindeer and caribou forage. We then used published relationships between forage chemistry and body weight gain of reindeer (White, 1983) to model the possible effects of altered forage chemistry on food intake and growth in reindeer. Model output shows that reindeer foraging on *Eriophorum* inflorescences may increase digestible dry matter intake twofold by selectively foraging on early-emergent inflorescences. The multiplicative effects of forage quality and food intake result in a near doubling in the rate of weight gain during this critical early spring period. Such increases in body weight gain have potentially great consequences for reindeer at both individual and population levels.

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Introduction

Climate-driven changes in seasonal patterns of vegetation phenology and growth have important ramifications for arctic herbivores, such as reindeer, caribou, and muskoxen. These and other large herbivores depend on seasonally available forage that makes them sensitive to the timing of availability of forage plants (Pettorelli et al., 2005). An increasing number of studies indicate that changes in climatic regimes are occurring in the Arctic. Most of the Arctic has warmed in recent decades (Serreze et al., 2000; Folland et al., 2001), and since the 1960s the melt date in northern Alaska has advanced by approximately eight days (Stone et al., 2002). Early snowmelt has subsequently contributed to the lengthening of the active growing season (Myneni et al., 1997), affecting the timing of emergence of forage plants in spring.

This study focused on the flowering phenology of *Eriophorum vaginatum* (tussock cottongrass) in relation to simulated changes in climate manifested by changes in the timing of snowmelt. *Eriophorum vaginatum* is a common arctic sedge (Britton, 1966; Walker et al., 1982) and an important forage plant for reindeer and caribou in early spring (Kelsall, 1968; Wein, 1973; Thompson and McCourt, 1981). *Eriophorum* emerges early during snowmelt and represents up to 77% of caribou diet during calving (Thompson and McCourt, 1981). Whereas several studies have been conducted on its vegetative growth (Archer and Tieszen, 1980; Chapin and Shaver, 1996; Shaver and Laundré, 1997; Walsh et al., 1997), the interaction between reproductive phenology and chemistry, and the subsequent value of *Eriophorum* inflorescences as forage to reindeer and caribou has yet to be determined. Russell et al. (1993) found that tussock meadows, the habitat where *Eriophorum* is most commonly found, were favored by caribou

from the Porcupine Herd during pre-calving and calving periods. Moreover, selective use of habitats containing more *Eriophorum* inflorescences greatly increased intake rates of caribou from the Western Arctic Herd (Kuopat, 1984), because *Eriophorum* inflorescences were more digestible than alternative forages available at this time. However, annual variation in flowering of *Eriophorum* appears to exhibit greater inter-annual variation than that conferred spatially by region or microsite (Shaver et al., 1986).

We investigated the effects of experimental advance and delay of snowmelt on the flowering phenology and nutrient characteristics of *Eriophorum vaginatum* and the possible effects that such variation in flowering phenology and chemistry might have on growth and reproduction in reindeer (*Rangifer tarandus*) on the Seward Peninsula, Alaska. The availability of nutritious forage is particularly critical to female reindeer and caribou during calving. Reindeer with access to high-quality forage produce more milk (Chan-McLeod et al., 1994) and recover faster from winter loss of body condition (Adamczewski et al., 1987; Chan-McLeod et al., 1994). Changes in forage availability that increase energy intake of reindeer and caribou during calving increase milk production and body condition. Reindeer in the Seward Peninsula calve in late April (Chetkiewicz, 1993), coincident with snowmelt and emergence of high-quality forage for lactating females and their growing calves.

The purpose of this study was to examine the interaction between reproductive phenology and inflorescence chemistry of *Eriophorum* in relation to timing of snowmelt. We predicted that advancing the onset of snowmelt would advance and accelerate *Eriophorum* floral phenology and would result in increased quality

TABLE 1

The reproductive phenology protocol established by the Reindeer Research Program, University of Alaska Fairbanks, as adapted from Finstad and Kielland (unpublished).

| Growth stage | Description |
|--------------|--|
| 0 | Dormant, no new floral buds or floral buds closed |
| 1 | Floral buds forming or swelling |
| 2 | Inflorescences opening |
| 3 | Full inflorescence/anthesis |
| 4 | Post inflorescence, fruit or pod developing (females), pollen has been shed (males) |
| 5 | Mature fruit/seed set (females), inflorescences senesced (males) |
| 6 | Fruits, seeds dispersed (females), inflorescences senesced (males); fruits (females), inflorescences (males) may have fallen off plant |

(digestibility and nitrogen concentration) of the inflorescences. We then examined the scenario of early emergence of *Eriophorum* inflorescences in relation to energy intake, mass gain, and productivity of female reindeer based on plant chemistry–animal productivity relationships proposed by White (1983). From our empirical measurements and predictions of White's (1983) "multiplier model," we assessed the potential consequences of climate-induced effects on reindeer at the individual and population level.

Material and Methods

The research was conducted during 2001 and 2002 on McCarthy's Marsh near the confluence of the Fish River and the Pargon River (64°59'37"N, 163°06'16"W) on the Seward Peninsula, Alaska, approximately 48 km north of the village of White Mountain. Classified as Ecological Site #42B (Swanson et al., 1985), the site is composed predominantly of low-lying tussock tundra with patches of taiga within small riparian corridors.

In 2001, we established three replicate experimental blocks in tussock tundra. Each block contained three 5 × 25 m² plots separated by 5-m buffer strips. Within each block, plots were randomly assigned the following treatments: control, early snowmelt, and late snowmelt. Early snowmelt was achieved by placing black Typar® mesh fabric on top of the snow in early May for two weeks or until snowmelt, whichever came first. Late snowmelt plots were established using 20-m-long, 1.2-m-tall snow fences erected perpendicular to the prevailing northeast winds. Snow within 5 m of the snow fence constituted the delayed snowmelt plots (designated late snowmelt).

Snow depth measurements were taken both at the snow fence and from a Natural Resource Conservation Service (NRCS) snow telemetry (SNOTEL) station at the site. Air temperature measurements were also downloaded from the NRCS SNOTEL weather station (<http://www.ambcs.org>).

All plots were monitored for *E. vaginatum* reproductive development from 15 May 2002 until seed set in late June 2002. Phenological stages were recorded according to protocol established by Finstad and Kielland (unpublished; Table 1). Ten inflorescences were randomly collected from each plot at every reproductive phenological stage starting from stage 2. Stages 0 and 1 occurred under the snow and consequently were not recorded. Sampling commenced upon protrusion of floral buds above the snow cover. The inflorescences, including the peduncle, were plucked manually from the lowest point above-ground and oven-dried at 60°C until constant weight. The 10 inflorescences from each treatment plot were pooled and constituted one analytical sample due to weight requirements for nitrogen (0.01 g) and in vitro dry matter digestibility (IVDMD; 0.25 g) chemical analyses. In the laboratory, the samples were ground in a Wiley mill using

a size 20 mesh. In vitro dry matter disappearance (IVDMD) of *E. vaginatum* inflorescences was determined using a modified Van Soest method (Tilley and Terry, 1969; Handl and Rittenhouse, 1975; Van Soest, 1976, 1994).

Rumen extract was obtained from captive reindeer fed a diet of *E. vaginatum* for four days prior to the digestibility trials. Dried samples (0.25 g) were placed in sterile Ankom® rumen filter bags, weighed, then added to the buffered rumen content and allowed to digest for four days in a Daisy® incubator (ANKOM Technology 2052 O'Neil Road, Macedon, NY 14502, U.S.A.; Vogel et al., 1999). The filter bags were subsequently removed from the rumen extract, treated with pepsin, dried, and weighed.

Nitrogen concentration of *E. vaginatum* inflorescences was measured using a LECO 200 CNS elemental analyzer. Subsamples of approximately 0.01 g were weighed into aluminum foil cups and then combusted at 800°C to convert elemental nitrogen into N₂. We then used the IVDMD data along with dry matter intake rate (117 g kg^{-0.75} d⁻¹; where kg^{0.75} = metabolic body weight) for reindeer (White, 1983) to derive digestible dry matter intake (DDMI) of *E. vaginatum* inflorescences as affected by the date of snowmelt. We computed potential mass change of reindeer based on predicted values of DDMI (White, 1983) of reindeer foraging on *E. vaginatum* inflorescences under simulated climate change scenarios given the equation:

$$\text{Body Mass (BM) change (g d}^{-1}\text{)} = -507 + 10.5 \times (\text{DDMI}) \quad (1)$$

Linear regression equations were developed from relationships between forage quality, dry matter intake, and rate of body weight gain based on White (1983) as follows:

$$\% \Delta \text{DMI} = 1.93 \times (\% \Delta \text{DMD}), \quad (2)$$

$$\% \Delta \text{BM} = -10.47 + 10.51 \times (\% \Delta \text{DMI}), \quad (3)$$

where DMI, DMD, and BM refer to dry matter intake, dry matter disappearance (digestibility), and body mass, respectively, and Δ denotes change in the parameter as a function of experimental treatment. These equations allowed us to estimate proportional changes in potential DMD, DMI, and body weight change of reindeer foraging on *E. vaginatum* inflorescences of different chemical characteristics.

STATISTICAL ANALYSIS

Data did not deviate markedly from assumptions of normality. Statistical analyses included an ANCOVA on nitrogen and IVDMD data using treatment and stage as class variables and date as covariate. A two-factor ANOVA was used to analyze inflorescence biomass and timing of flowering using treatment and stage as class variables. Type IV Sum of Square Error was used in

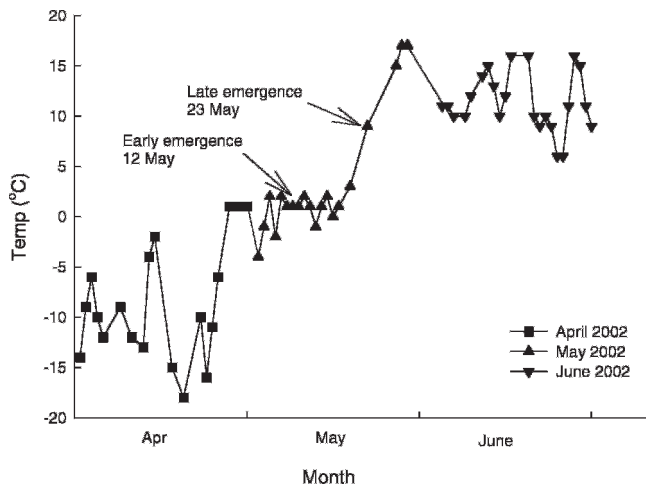


FIGURE 1. Daily mean air temperature at Pargon Creek for the period of 1 April–30 June 2002. Temperatures during emergence of cottongrass inflorescences in early and late snowmelt plots are indicated. Data from NRCS SNOTEL station at the research site (<http://www.ambc.org>).

the analyses due to empty cells (Neter et al., 1996; SAS Institute, 2001) due to missing data for stage 3 late snowmelt plots.

Results

AIR TEMPERATURES

Although late winter-spring 2002 was normal with average temperatures and snow conditions at our sites, air temperatures during the latter part of May (Fig. 1) were quite high, which accelerated snowmelt. However, after approximately 2 weeks the temperature increase leveled off and exhibited normal daily range.

TIMING OF FLOWERING

Snowmelt manipulations changed the timing of flowering of *E. vaginatum* (ANOVA, $p < 0.0001$, $\alpha = 0.05$, $df = 4$; Fig. 2). On average, inflorescences in the control plots initially emerged from

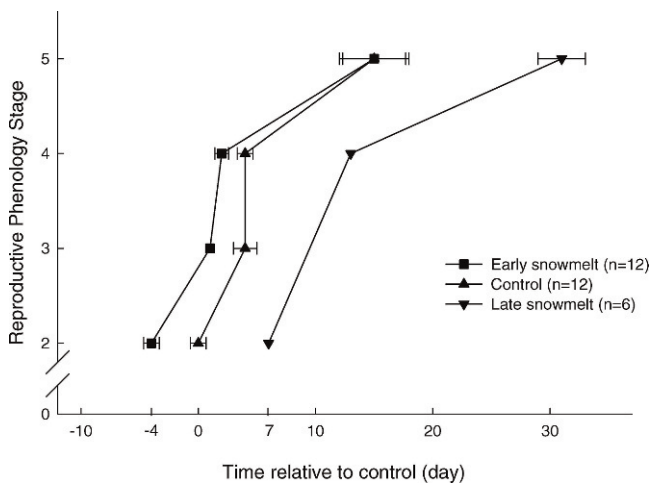


FIGURE 2. Reproductive phenology of *E. vaginatum* under early and late snowmelt relative to control plots on the Seward Peninsula, Alaska. Data are means and standard errors.

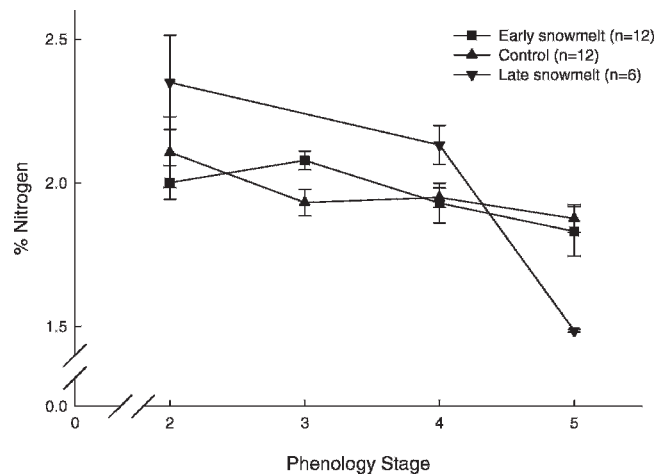


FIGURE 3. Relationship between reproductive phenology and nitrogen concentration in *E. vaginatum* inflorescences under early and late snowmelt relative to control plots on the Seward Peninsula, Alaska. Data are means with standard errors.

under the snow during stage 2 on 17 May 2002. The early snowmelt treatment advanced the emergence of stage 2 *E. vaginatum* inflorescences by 4 days relative to control. Stage 2 inflorescences from the snow fence plots emerged 7 days after those from the control plots. The dates when the inflorescences transitioned into each phenology stage were different among treatments at all stages (ANOVA, $p < 0.0001$, $\alpha = 0.05$, $df = 18$). Development from stage 2 to stage 4 took 6 days in the early snowmelt plots compared to 8 days in the late snowmelt plots. However, inflorescences in the snow fence plots moved from stage 4 to stage 5 in 17 days, 6 days longer than those in the early snowmelt plots. No differences were observed in the overall rate of phenological development among treatments (Figure 2).

FORAGE CHEMISTRY

Snowmelt manipulations had significant effects on both nitrogen concentrations and digestibility of *Eriophorum* inflorescences (ANCOVA, $p = 0.0016$, $\alpha = 0.05$, $df = 4$). Inflorescences at the earliest recorded phenological stage (stage 2) from the early-snowmelt plots had 15% lower nitrogen concentration (2.00%) than those from the late-snowmelt plots (2.35%). However, by stage 5, inflorescences from the early-snowmelt plots had 19% higher nitrogen concentration than those from the late-snowmelt plots (Fig. 3). Nitrogen concentration of inflorescences from the late snowmelt plots declined 37% from stage 2 to stage 5 compared to an 8% decline in the early snowmelt plots for the same interval. There was a significant interaction between treatment and phenology stage (ANOVA, $p = 0.0037$, $\alpha = 0.05$, $df = 10$).

Snowmelt manipulations also had a significant effect on IVDMD (ANCOVA, $p = 0.0270$, $\alpha = 0.05$, $df = 4$; Fig. 4). At stage 2, early snowmelt inflorescences were 4% more digestible than late snowmelt inflorescences. But by stage 5, early snowmelt inflorescences were 8% more digestible than late snowmelt inflorescences. Digestibility of early snowmelt inflorescences declined 9% from stage 2 to stage 5 compared to a 13% decline in inflorescences from the late snowmelt plots for the same interval.

No significant differences were detected in floral mass among treatments at stages 2, 3, and 4 (Fig. 5). By stage 5, however,

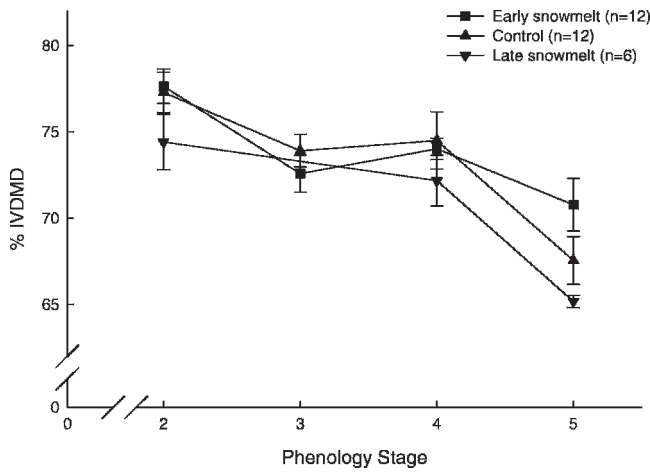


FIGURE 4. Relationship between reproductive phenology and in vitro dry matter digestibility of *E. vaginatum* under early and late snowmelt relative to control plots on the Seward Peninsula, Alaska. Data are means and standard errors.

inflorescences from the late snowmelt plots had increased by 79% in mass from stage 2, while inflorescences from the early snowmelt plots had gained only 35% more mass over the same interval.

MODELING

Increases in digestibility by one unit may result in a twofold increase in dry matter intake (DMI) for female reindeer within the range of values obtained here (*sensu* White, 1983). Thus, the small increase in digestibility (4%) of early-emergent *Eriophorum* inflorescences translated into an 8% increase in potential DMI by reindeer under these conditions. This increase in DMI, in turn, was predicted to confer a 78% increase in daily weight gain for reindeer foraging on early-emergent *Eriophorum* inflorescences (Fig. 6). Consequently, increases in forage digestibility result in a large proportional change (nearly twentyfold) in body weight in relation to change in this plant parameter. Thus, small changes in forage quality can be greatly amplified through animal behavior and physiology, with significant consequences for both reproduction and survival.

Discussion

TIMING OF FLOWERING

Snowmelt manipulations changed the timing of emergence by *Eriophorum* inflorescences from under the snow. However, the inflorescences from all treatment plots emerged from under the snow at the same phenological stage irrespective of treatment. With the snow cover removed and the tussocks exposed to the sun, advancing snowmelt resulted in earlier flowering of *E. vaginatum*, while delaying snowmelt delayed flowering. Similar findings of temporal adjustment in floral development coincident with manipulations of early or late snowmelt have been documented in other studies of *E. vaginatum* (Borner, 2006) and other arctic and alpine species (Starr et al., 2000; Galen and Stranton, 1995; Inouye et al., 2003; Price and Waser, 1998). Late snowmelt may also delay vegetative phenology in *E. vaginatum* (Walsh et al., 1997). By contrast, increases in air temperature *per se* do not appear to affect the date at which *E. vaginatum* inflorescence buds open, as greenhouse field experiments have shown (Chapin and Shaver, 1996).

Whereas the timing of flowering was advanced in parallel with snowmelt, the rate of phenological development, however, did not differ between treatments, despite the marked differences in air temperatures, indicating that there is an apparent fixed time required for floral development. Pollen production was complete within one week of inflorescence emergence regardless of treatment. Moreover, inflorescences from all treatments exhibited rapid development from bud emergence (stage 2) to full inflorescence (stage 4), but then slower development from stage 4 to seed set (stage 5). The rapid development from stage 2 to stage 4 supports the idea that the pattern of flowering is a reflection of the short growing season characterizing arctic ecosystems. Development from stage 4 to stage 5 took two weeks on average, allowing the fruit to develop and disperse in time for the surrounding ground to be snow-free.

FORAGE CHEMISTRY

Higher digestibility of inflorescences from the early-snowmelt plot than inflorescences from the late-snowmelt plots suggests that fiber formation in inflorescences from the late snowmelt plots occurred under the snow. Inflorescences from the late snowmelt plots were under snow cover 11 days longer than those from the early snowmelt plots, potentially allowing them to lengthen the peduncles while under the snow. The insulative properties of snow along with the ability of *Eriophorum* to photosynthesize under the thawing spring snow (Starr and Oberbauer, 2003) may have influenced growth of the peduncles. Peduncles from the late-emerging inflorescences may have been larger than those from the early-emerging inflorescences, increasing structural carbon that could lower digestibility in the late-emerging inflorescences. However, because the peduncles were not measured, this assertion remains to be quantified. Nevertheless, the difference in IVDMD between early-emerging inflorescences and late-emerging inflorescences indicates that delaying snowmelt decreased the digestibility of *E. vaginatum* inflorescences through mechanisms that are not clear.

Since *Eriophorum* inflorescences are initiated during the prior autumn (with no subsequent development under the snow until the following spring), nitrogen concentration at stage 2 is largely determined by what is stored in the floral bud and what may have already been translocated from below-ground stores. It is unlikely that root uptake contributed to significant changes in nitrogen

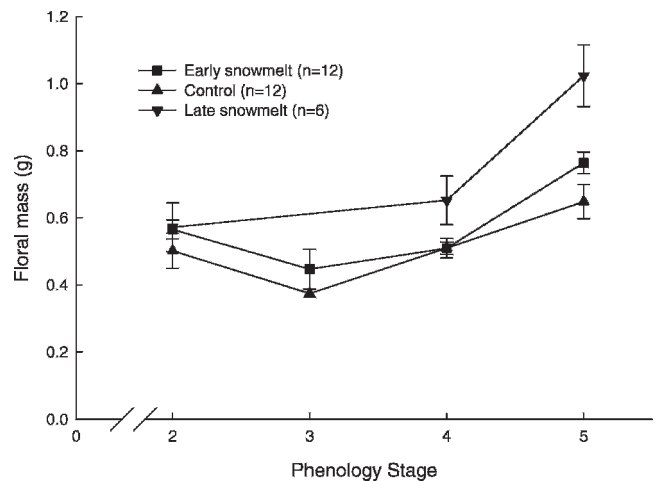


FIGURE 5. Relationship between reproductive phenology and mass of *E. vaginatum* inflorescences under early and late snowmelt relative to control plots on the Seward Peninsula, Alaska. Data are means with standard errors.

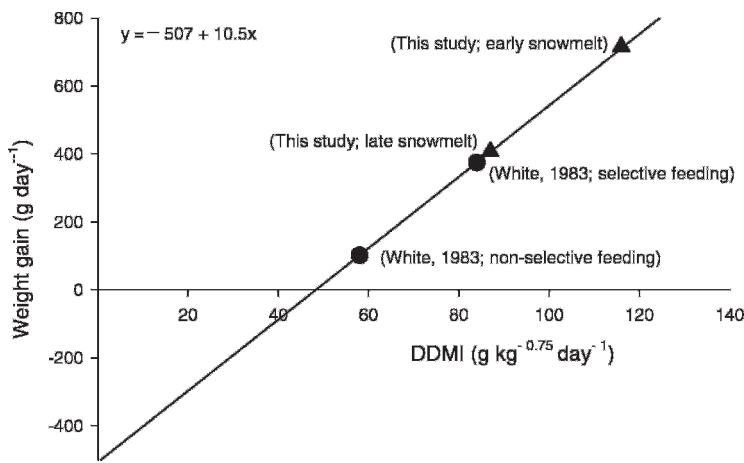


FIGURE 6. Relationship between digestible dry matter intake (DDMI) and potential mass gain for reindeer based on White (1983) (filled circles) and the present study (filled triangles).

concentration of inflorescences from the early-snowmelt plots (Bilbrough et al., 2000) because the soil was still frozen even though the tops of the tussocks were snow-free. We hypothesize that the higher N concentration of inflorescences from late-emergent plots were in part due to shifts in carbon pools (ratio of structural to nonstructural carbon) and overall lower total carbon pools due to respiration under the snow. The rapid decline in nitrogen concentration in inflorescences in the late snowmelt plots between stages 4 and 5 was probably due to dilution of nitrogen by the increased amount of structural tissue accumulated at that stage. Because we included the peduncle as part of the sampling unit, floral biomass measurements included more structural tissue accumulated toward the latter part of the growing season. Despite having similar biomass from stage 2 to stage 4, inflorescences from the late snowmelt plots had the highest biomass at stage 5, possibly due to larger peduncles. Though the peduncles were not weighed separately from the inflorescences, visual inspection of the samples at stage 5 suggested that inflorescences from the late snowmelt plots tended to have longer peduncles than those from the other treatment plots. The interaction between nitrogen concentration and phenological stage indicates that nitrogen concentration declined at a faster rate in inflorescences from the late snowmelt plots than those in the early snowmelt plots. The increase in floral biomass may explain the rapid decline in nitrogen concentration possibly because of what appears to be the enlargement of peduncles in inflorescences from the late snowmelt plots, especially during the last phenological stage.

MODEL

The functional (multiplier) effects between forage digestibility, forage intake, and growth in reindeer demonstrate how climate-induced changes in timing of flowering can have significant ecological effects on reindeer productivity and demography because of the strong relationship between increased body weight and reproductive success in both female reindeer and caribou (Reimers et al., 1983; Cameron et al., 1993; Adams and Dale, 1998; Prichard et al., 1999; Finstad and Prichard, 2000). Because reindeer calves are generally born prior to green-up, females require body stores to transfer energy and protein to their calves (Reimers et al., 1983; Crête and Hout, 1993). *Eriophorum* inflorescences represent the highest quality forage available during snowmelt that allows reindeer to replenish stores quicker and gain weight earlier. In recent studies of both reindeer (Prichard et al., 1999; Finstad and Prichard, 2000) and caribou (Adams and Dale, 1998), females that produced calves as 2-year-olds averaged

approximately 5 kg heavier in the prior fall than those that did not calve. Therefore, the improved potential weight gain from foraging on early-emergent inflorescences may have significant population consequences. We used digestible dry matter intake (DDMI; $\text{g kg}^{-0.75} \text{d}^{-1}$) in order to calculate potential weight gain of reindeer (*sensu* White, 1983) foraging on early versus late-emergent *Eriophorum* inflorescences. The difference in DDMI between early and late emergent inflorescences was relatively small, but estimated DDMI from foraging on inflorescences was at least twice that of maintenance requirements (Fig. 6). An average female reindeer (calves 30 kg, yearlings 60 kg, adults 80 kg; Prichard et al., 1999) feeding on early-emergent *Eriophorum* inflorescences would gain more (Fig. 5—this study; early snowmelt) than a similar female foraging on what is otherwise available in late winter (Fig. 6—White 1983; non-selective feeding). Our empirical findings with captive animals show that they may gain approximately 500 g d^{-1} under optimal conditions (Finstad et al., 2007), which is close to our model results. These caveats notwithstanding, it is clear that reindeer female calves, yearlings, and adults feeding on early-emergent *Eriophorum* inflorescences would allow for greater weight gain, which in turn influences reproductive rates and overall production of the population (Prichard et al., 1999; Finstad and Prichard, 2000).

The local emergence of *Eriophorum* inflorescences may be more critical for reindeer productivity than for caribou. Caribou will use the landscape more broadly by shifting pre-calving and calving areas to habitats with a greater abundance of *Eriophorum* inflorescences (Kuopat, 1984; Russell et al., 1993). Reindeer, on the other hand, are very sedentary and demonstrate higher site fidelity than caribou (Finstad et al., 2006). Thus, they are more nutritionally dependent upon grazing conditions in a relatively small calving area.

Earlier snowmelt and flowering of *Eriophorum* brought about by climate change may result in earlier availability of higher quality forage for reindeer recovering from winter losses of fat and protein and for females during lactation. High energy intake increases protein deposition in the adult female and increases fat deposition in non-breeding adult female *Rangifer* (Cameron et al., 1993; Crête and Hout, 1993; Chan-McLeod et al., 1994). However, another benefit of a high energy diet for lactating females is the increased production of milk (Chan-McLeod et al., 1994). Reindeer calves, therefore, also stand to gain from early availability of *Eriophorum* inflorescences. With greater milk production from the mother, calf growth increases (Loudon and Kay, 1984; White and Luick, 1984), which in turn confers higher calf survival (Guinness et al., 1978; Skogland, 1985). After weaning, intake of high energy forage increases calf growth

(Verme and Ozoga, 1980), which greatly affects the probability of reproduction in females at two years of age (Adams and Dale, 1998). These cascading ecological effects demonstrate the potential mechanistic linkages between climate-driven factors that act on reindeer populations (Weladij and Holand 2003). The scenarios shown here illustrate that shifts in timing of phenological development of a primary forage species can result in small changes in forage quality which confer proportional changes in *Rangifer* energy intake that ultimately have significant consequences for growth and productivity at the individual and population levels. The effects of early availability of high-quality forage on reindeer may be more pronounced if the current trend toward earlier green-up in the Arctic continues.

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