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Effects of Simulated Grazing in Ungrazed Wet Sedge Tundra in the High Arctic

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Abstract

Wet sedge tundra communities in the High Arctic are valuable sources of forage for several resident and migratory herbivores; however, the effects of grazing on these systems have been rarely studied. We simulated grazing in two wet sedge meadows at a site on Ellesmere Island that has not been affected by grazing. Over two summers, we clipped plots at four different frequencies and removed litter to assess effects on aboveground net primary production, availability of soil nitrogen, shoot concentrations of carbon and nitrogen, and soil temperature and moisture regimes. Available soil nitrate and ammonium were highest in plots with intermediate clipping frequencies. Shoot nitrogen concentrations were also greater at intermediate clipping frequencies in two of the four species studied. Aboveground net primary production decreased after clipping, regardless of frequency. Litter removal resulted in slightly increased soil moisture, but had no effect on aboveground net primary production. Soil temperature was not affected by any of our treatments. These results suggest that nitrogen cycling is stimulated by intermediate frequencies of simulated grazing, but clipping decreased aboveground net primary production in ungrazed high arctic wet sedge tundra.

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Introduction

The arctic climate has warmed noticeably over the past 30 years (ACIA, 2005; Hill and Henry, 2010) and the effects have been measured in a number of systems (ACIA, 2005; Hinzman et al., 2005; Aerts et al., 2006). In terrestrial ecosystems, significant increases in biomass have been measured in high arctic dwarf shrub heath (Hudson and Henry, 2009) and wet sedge tundra (Hill and Henry, 2010). Recent studies in the Arctic indicate that herbivory may negate the effects of warming on forage communities (Post and Pedersen, 2008) and the uptake of nitrogen (N) by plants (Rinnan et al., 2009). However, predictions about large mammal populations in the Arctic are difficult to make (Post and Pedersen, 2008). If populations of large herbivores increase due to ameliorated conditions, they will require additional forage and may move into previously unused areas. Therefore, it is important to better understand how ecosystem processes in previously ungrazed plant communities in the Arctic will be affected by increased herbivory.

The response of aboveground net primary production (NPP) to grazing varies across different plant communities. Moderate levels of grazing can increase aboveground NPP in communities dominated by terrestrial graminoids (Hik and Jefferies, 1990). Evidence of increased aboveground NPP in response to grazing has been documented in salt marshes (Cargill and Jefferies, 1984; Hik and Jefferies, 1990), savannas of the Serengeti (McNaughton, 1979), and western North American grasslands (Frank and McNaughton, 1993). In the High Arctic, Henry and Svoboda (1994) and Elliott (2009) found that sites grazed by muskoxen had higher aboveground NPP than sites that were not grazed.

Grazing alters the availability of nitrogen in the soil, which affects other ecosystem processes. The frequency and intensity of grazing and changes in the nutrient availability control the relative growth rate of plants by determining how fast plants recuperate

from defoliation (Ferraro and Oesterheld, 2002). Nutrient addition through animal excrement can increase the availability of soil ammonium (NH_4^+) and nitrate (NO_3^-) (Bazely and Jefferies, 1985; Henry and Svoboda, 1994; Henry, 1998) and influences inter-specific plant relationships because species vary in their responses to fertilization (Mulder, 1999). Aboveground plant production also responds to this addition of nutrients; for example, aboveground NPP increased with the addition of goose feces in subarctic salt marsh systems grazed by lesser snow geese (*Chen caerulescens caerulescens*) (Hik et al., 1991).

Concentrations of nutrients in plant tissues change in response to defoliation. Grazing can affect the demography of shoots and leaves, increasing the proportion of young age classes (Tolvanen and Henry, 2000; Tolvanen et al., 2001, 2002), which grow more vigorously and have higher N concentrations compared to ungrazed plants (Ruess, 1984). Defoliated plants may also compensate for nutrient loss by increasing their nutrient uptake (McNaughton, 1979; Jaramillo and Detling, 1988; Oesterheld and McNaughton, 1988). The nutrients are then allocated preferentially to the regrowth of plant shoots (Green and Detling, 2000). If defoliation causes N concentrations to increase in plant shoots, decomposition and nutrient cycling accelerate because of the higher initial N concentrations (Taylor et al., 1989). Younger leaves may have lower carbon (C) concentrations because of less cellulose in their cell walls (Whaley et al., 1952). Furthermore, the concentration of defensive compounds in leaves may decrease with increasing soil nutrient availability (Dormann, 2003), resulting in an increase in litter quality and more rapid decomposition.

Soil moisture is affected by both trampling by herbivores and experimental defoliation. Rainfall infiltration in heavily grazed areas is reduced by trampling because soil bulk density increases (Warren et al., 1986). Experimental defoliation can also affect soil moisture levels because transpiring leaves are lost and the ground

surface is exposed to more solar radiation (Day and Detling, 1994; Wan et al., 2002).

Restricting the access of grazers to forage causes the accumulation of plant litter, which alters light reception, soil temperatures, soil moisture, and nutrient dynamics (Facelli and Pickett, 1991). Litter abundance can change interactions between plant species (Foster and Gross, 1998). In dry and mesic arctic tundra systems, grazing reduces the cover of mosses and litter, resulting in warmer soil surfaces as they are exposed to increased levels of solar radiation (Ruess et al., 1997; van der Wal and Brooker, 2004). In wet sedge tundra, the reduction in litter may increase moss growth because of the increased exposure to sunlight (Henry, 1998). Moss and litter also maintain water within their structure and reduce evaporation from the soil (Gornall et al., 2007); however, the annual ratio of evapotranspiration to precipitation in the Arctic is usually low (Oberbauer and Dawson, 1992).

High Arctic lowlands with favorable soil moisture levels and microclimates support wet sedge meadows, which are the most productive plant communities in this region (Henry et al., 1990). The relatively high NPP of these plant communities is due to the physiological and morphological adaptations of the dominant graminoid species to the wet and cool soils (Henry et al., 1990). High Arctic wet sedge tundra communities are important sources of forage for resident herbivores such as muskoxen (*Ovibos moschatus*), Peary caribou (*Rangifer tarandus pearyi*), and migratory birds such as the greater snow goose (*Chen caerulescens atlanticus*) (Henry et al., 1990; Henry, 1998).

In the High Arctic, the cold dry climate limits decomposition, which results in the immobilization of nutrients in plant litter (Brathen and Odasz-Albrigtsen, 2000). Decomposition and mineralization rates in wet sedge tundra are further reduced because of low oxygen concentrations and rates of diffusion (Jonasson and Shaver, 1999). In addition to low decomposition rates, litter accumulation in ungrazed high arctic sedge meadows is higher than in grazed meadows because of the absence of large herbivores (Henry et al., 1990; Henry, 1998; Elliott, 2009).

Ecological studies conducted in high latitude systems have examined the response of plants, plant communities, and ecosystems to grazing. In the High Arctic, Henry (1998) noted that wet sedge tundra grazed by muskoxen had increased cover of moss and the sedge *Carex aquatilis* ssp. *stans* and less litter and attached dead plant material compared to ungrazed sites. In addition, Henry and Svoboda (1994) and Elliott (2009) found that sites grazed by muskoxen had greater amounts of aboveground NPP than ungrazed sites. In an experimental defoliation study at a site with high densities of muskoxen, Raillard and Svoboda (1999) reported that shoot growth of *Carex aquatilis* ssp. *stans* remained constant, but N concentrations increased. Most studies of grazing in high arctic forage communities have been conducted at sites that supported resident and migratory herbivores. The focus of our study was to examine the effects of experimental defoliation and litter removal on ecosystem function in ungrazed wet sedge tundra.

We predicted that experimentally clipping ungrazed high arctic wet sedge tundra would: (a) increase aboveground NPP; (b) have little effect on availability of soil N (NO_3^- and NH_4^+); (c) increase N and have little effect on C concentrations in shoots of the dominant vascular species; and (d) have no effect on soil moisture and soil temperatures. We also expected that the removal of accumulated litter would increase aboveground NPP and soil temperatures, but have no effect on soil moisture. To test these predictions, we established a defoliation experiment with combinations of clipping frequencies and litter removal treatments in ungrazed high arctic sedge meadows at a site on eastern Ellesmere Island.

Methods

SITE DESCRIPTION

The study was conducted at a coastal lowland adjacent to Alexandra Fiord (AF) (78°53'N, 75°46'W) on the central east coast of Ellesmere Island, Nunavut, Canada. The Alexandra Fiord lowland is ca. 8 km² and is a polar oasis that has a warmer climate, higher species diversity, greater plant cover, and higher primary productivity than the surrounding area (Freedman et al., 1994). Wet sedge plant communities occur on gleysolic cryosol soils on flat sites with impeded drainage (Henry et al., 1990; Muc et al., 1994a). The plant communities are dominated by *Eriophorum angustifolium* ssp. *triste*, *Carex aquatilis* ssp. *stans*, *C. membranacea*, *Dryas integrifolia*, and *Salix arctica* (Henry et al., 1990; Muc et al., 1994b; Henry, 1998). More detailed descriptions of AF are outlined in Svoboda and Freedman (1994).

The lowland is used very sporadically by muskoxen and caribou and migratory snow geese (Henry et al., 1986; Trefry et al., 2010). The nearest population of muskoxen is approximately 15–20 km to the north on the Bache Peninsula (Henry et al., 1986; Freedman et al., 1994). These large mammalian grazers are rare along the north coast of the Johan Peninsula and populations have likely never been large in the AF lowland region (G. H. R. Henry, unpublished observations). The geographical isolation and relatively small size of the Alexandra Fiord lowland makes it unsuitable to sustain significant populations of muskoxen or caribou (Henry et al., 1986; Muc et al., 1989). The accumulation of litter is considerably higher in the ungrazed meadows of AF compared to grazed polar oases because of this lack of large herbivores (Muc et al., 1994b; Henry, 1998; Elliott, 2009).

CLIPPING EXPERIMENTS

Clipping experiments were established at AF in 2007 in visually homogeneous areas of two wet sedge meadows representative of dominant wet tundra in the AF lowland (Muc et al., 1989; Henry et al., 1990). In these experiments (Grid 1 and Grid 2), there were six replicates per treatment applied to 50 cm × 50 cm plots separated by 1.5 m. Plots were randomly assigned to one of five treatments that were maintained throughout the 2007 and 2008 growing seasons. This was a two factor experiment with combinations of litter removal and clipping levels as the treatments. Litter removal treatments were conducted by carefully removing the unattached dead plant material within each plot. Clipping treatments were applied to each plot by cutting and collecting all live and dead plant material over 1.5 cm in height. We were careful not to remove attached and unattached dead plant material below that height so that we could have clipped treatments with no litter removal. This height was chosen because muskoxen leave the lower sections of grazed sedge shoots intact (Raillard, 1992; Raillard and Svoboda, 1999).

The treatments included: (a) control—no clipping, no litter removal; (b) LR—no clipping with litter removal; (c) 1×—one clipping/season, no litter removal; (d) 2×—two clippings/season, no litter removal; and (e) 3×—three clippings/season, no litter removal. Treatments were applied to the same plots in 2007 and 2008, but clipping dates varied between the two years because it was necessary to complete all clipping treatments in 2008 before the harvest of aboveground plant material. Harvests were conducted at the peak of live aboveground biomass (peak season), which typically occurs the last week of July to the first week of August in high arctic plant communities (Henry et al., 1990). Litter was removed from selected treatments in mid-June in 2007 and 2008.

Plant material removed from each of the clipping treatments was placed into paper bags, sorted to species and into live and dead material, and dried in the field lab at ca. 30 °C. In addition, all vascular vegetation was harvested from 20 cm × 50 cm quadrats during peak season in 2008 by placing quadrats in the center of each 50 cm × 50 cm plot. All aboveground plant material was then cut at the ground, sorted to species and into live and dead material, dried, and sent to the Tundra Ecology Lab at the University of British Columbia where the samples were dried again for 24 to 30 hours at 60 °C before weighing. The weights of plant material from the current year's growth including reproductive tissues were used to calculate aboveground NPP and all values were converted to g m⁻² prior to analysis. To quantify aboveground NPP for each plot, we summed the weights of the plant material that was clipped during the year of the harvest and the aboveground vegetation harvested at peak season. Aboveground NPP was calculated as the difference between peak season green biomass and the average of overwinter green material harvested from 10 quadrats (20 cm × 50 cm) just after snowmelt from both sites. The net production of dwarf shrubs was estimated using the adjustments from Henry et al. (1990).

SOIL NO₃⁻ AND NH₄⁺ AVAILABILITY

Plant Root SimulatorsTM (PRS) (ion exchange membranes) were used to measure soil NO₃⁻ and NH₄⁺ availability in each plot during the 2008 growing season. Four cation and four anion probes were separately inserted vertically to a depth of ca. 10 cm in each plot on 20 June and removed on 16 August. The PRS probes were washed with deionized water and scrubbed with a coarse brush to remove soil residue immediately after removal from each plot. The probes were combined for each plot and they were sent to Western Ag Innovations in Saskatoon, Canada, for ion extraction and analysis (Western Ag Innovations, 2008).

SHOOT NITROGEN AND CARBON CONCENTRATIONS

Shoot N and C concentrations were measured on subsamples taken from plant material that was harvested in the second year to measure aboveground NPP. Subsamples from the control, 1×, 2×, and 3× clipping frequencies were obtained from samples of *C. membranacea* (Grid 1) and *C. aquatilis stans* (Grid 2). In addition, subsamples of *E. triste* (Grid 1) and *S. arctica* (Grid 2) were taken from the control and 3× treatment. For *S. arctica*, both new leaf and shoot growth were sampled. Different species were chosen for each grid because there was insufficient aboveground biomass for a single species from both experimental sites. Nitrogen and carbon concentrations in ground tissue samples were measured by dry combustion with a Carlo-Erba NA-1500 NCS analyzer at the Analytical Chemistry Laboratory of the BC Ministry of Forests and Range in Victoria, British Columbia.

SOIL TEMPERATURE

In both study years, thermistors were placed in the soil to a depth of 10 cm in eight plots in each of the clipping grids on 20 June and removed on 1 August. The thermistors were connected to data loggers which were programmed to read temperatures every 10 minutes. The number of thermistors was limited by their availability at the research site. The temperature data were gathered from three control, two LR, and two 3× treatments. In 2007, all temperature data was lost in Grid 2 because of equipment

failure. In 2008, two thermistor cables in Grid 1 were damaged by wildlife preventing the collection of data from two plots.

SOIL MOISTURE

Soil moisture was measured with a time domain reflectometry (TDR) probe (Hydrosense, Campbell Scientific Corp., Edmonton, Canada). Soil moisture was not measured in 2007; however, measurements were done in both grids during the 2008 growing season on 24 July, 2 August, and 16 August. Average soil water contents for the summer were then calculated from these three measurement days. The TDR probe was inserted vertically to a depth of 12 cm for each measurement.

DATA ANALYSIS

All statistical analyses were completed using SAS (version 9.1) (SAS Institute Inc., 2009). The assumptions of normality and constant variance of the residuals were met in all analysis of variance (ANOVA) tests. Analysis of variance was used to test if litter removal affected aboveground NPP and soil moisture levels compared to control plots. In cases when there were data for both Grids, variables were first tested to see if there was an effect of grid × treatment. If no interaction was found, the data for the two grids were pooled for analysis.

Linear regression was used to analyze the effects of increased clipping frequencies on aboveground NPP and soil water contents. The response of C, N, and C:N in the shoots of four plant species to increased clipping frequencies was measured with linear and quadratic regression analysis. In addition, the availability of soil NO₃⁻ and NH₄⁺ was analyzed with linear and quadratic regression models. For these analyses, we first fit a linear regression using PROC GLM in SAS. We then used the quadratic equation: $y = b_0 + b_1x + b_2x^2$, where the y-variable was the variable of interest. We decided that relations were curvilinear if the scatter plot revealed a unimodal curve, the quadratic term (b_2) was significantly different from zero ($P < 0.05$), the overall model was significant ($P < 0.05$), and the variation explained by the model (R^2) was greater than that of the linear model.

Results

ABOVEGROUND NPP

Aboveground NPP decreased with increased clipping frequency ($P < 0.01$; Fig. 1a). Aboveground NPP (Mean ± S.E.) was similar in the control ($41.01 ± 4.14$ g m⁻²) and litter removal treatments ($34.09 ± 2.59$ g m⁻²) ($P = 0.16$, ANOVA; Table 1). Data from both experimental sites were pooled as there was no site × treatment interaction.

SOIL NO₃⁻ AND NH₄⁺ AVAILABILITY

The availability of NO₃⁻ and NH₄⁺ in the soil in relation to clipping frequency was best described by a quadratic equation (Fig. 1). The linear relation for NO₃⁻ availability in the soil was not significant ($R^2 < 0.01$, $P = 0.81$), whereas the quadratic was significant and explained more variation in the data ($R^2 = 0.29$; $P = 0.03$). The availability of NO₃⁻ was greatest in plots clipped 2× in the growing season. A quadratic equation also better explained the relation of clipping frequency to the availability of NH₄⁺ in the soil ($R^2 = 0.29$; $P = 0.04$) compared to the linear relation ($R^2 < 0.01$; $P = 0.99$). The availability of NH₄⁺ increased in plots clipped

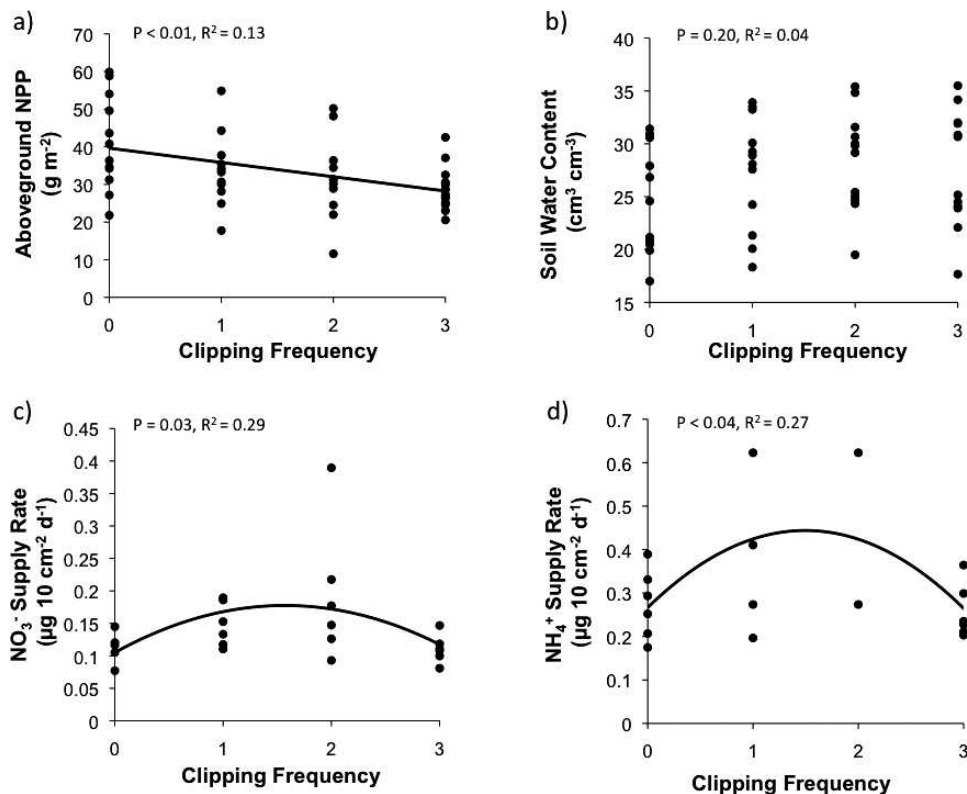


FIGURE 1. The relation between clipping frequency and (a) aboveground net primary production (NPP); (b) soil moisture; (c) soil nitrate (NO_3^-) availability; and (d) soil ammonium (NH_4^+) availability measured in two experimental grids at Alexandra Fiord in 2008. Linear regression models were used to fit (a) and (b), whereas quadratic equations were used for (c) and (d). Individual data points correspond to values obtained for each plot. Significance values of $P < 0.05$ are represented by solid regression lines, while dashed lines represent values of $P < 0.1$.

once or twice in the season relative to controls ($0\times$) and plots clipped three times each season. Data from both meadows were pooled for analysis as there was no site \times treatment interaction.

SHOOT NITROGEN AND CARBON CONCENTRATIONS

Concentrations of N in the shoots of four plant species from AF responded differently to clipping. Table 2 shows that increased clipping frequencies resulted in higher shoot N concentrations in *E. triste* ($P < 0.01$), but N decreased in *S. arctica* shoots ($P = 0.04$). Quadratic regressions showed that at intermediate clipping frequencies concentrations of N in shoots of *C. membranacea* were significantly higher ($P < 0.01$) and marginally higher in the shoots of *C. aquatilis stans* ($P = 0.06$).

Decreases in the C concentrations in two of the four plant species at AF occurred in response to clipping (Table 2). Carbon concentrations declined in the shoots of *S. arctica* ($P < 0.01$), but remained similar regardless of clipping frequency in *E. triste* ($P = 0.36$). Carbon concentrations in the shoots of *C. membranacea* decreased with increased clipping frequencies ($P < 0.01$); the quadratic term was not significant for this relation. In contrast, quadratic regression analysis showed that there were lower concentrations of C in the shoots of *C. aquatilis stans* at intermediate clipping frequencies ($P < 0.01$).

TABLE 1

Results of ANOVA for effects of litter removal on aboveground net primary production (NPP) and soil moisture. Significant P -values shown in bold.

Variable	DF	MS	F value	P-value
Aboveground NPP	1,1	287.51	2.28	0.15
Soil Moisture	1,1	29.26	3.18	0.09

The C:N decreased in shoots of *E. triste* ($P < 0.01$) as clipping frequencies increased (Table 2). Quadratic regressions indicated that the C:N in *C. membranacea* ($P < 0.01$) and *C. aquatilis stans* ($P = 0.01$) were lower at intermediate clipping frequencies. Clipping frequency had no effect on C:N in the new shoots of *S. arctica* ($P = 0.15$).

SOIL TEMPERATURE

Due to equipment failure in the field, we did not have enough data to compare soil temperature data with ANOVA models. By comparing mean \pm SE values, it appears that soil temperatures were similar for control and litter removal treatments in Grid 1 and Grid 2 in 2008 (Table 3). Soil temperatures between control plots and $3\times$ clipping plots did not differ in 2008 in either Grid 1 or Grid 2, and the values for these two treatments were also similar in Grid 1 in 2007. No data were available for the control plots of Grid 2 in 2007; however, soil temperatures in control plots of Grid 1 appeared to be warmer by about 3°C in 2007 than in 2008.

SOIL MOISTURE

Soil moisture responded to litter removal treatments, but not to increased clipping frequencies. Plots with litter removed had slightly higher soil moisture contents ($27.40 \pm 0.66 \text{ cm}^3 \text{ cm}^{-3}$) compared to control plots ($25.19 \pm 0.60 \text{ cm}^3 \text{ cm}^{-3}$) ($P = 0.09$, ANOVA; Table 1). With data from both sites combined, soil moisture did not respond to changes in clipping frequency ($P = 0.20$; Fig. 1b).

Discussion

As temperatures in the Arctic rise due to global warming it is likely that populations of resident and migratory herbivores will increase due to increased forage growth (e.g. Hudson and Henry,

TABLE 2

Results of linear and quadratic regression models for nutrient concentrations (% dry weight) in four plant species in response to different clipping frequencies at Alexandra Fiord in 2008. Significant *P*-values ($P < 0.05$) are shown in bold.

Nutrient	Species	Clipping Frequencies	Regression		R ²	<i>P</i> -value Model
			Model	<i>b</i> ₁ ; <i>P</i> -Value		
N	<i>C. membranacea</i>	0, 1×, 2×, 3×	Linear	0.12; <0.01	0.31	<0.01
N	<i>C. membranacea</i>	0, 1×, 2×, 3×	Quadratic	0.52; <0.01	-0.13; <0.01	<0.01
N	<i>C. stans</i>	0, 1×, 2×, 3×	Linear	2.24; <0.01		0.12
N	<i>C. stans</i>	0, 1×, 2×, 3×	Quadratic	2.16; <0.01	-0.08; 0.07	0.06
N	<i>E. triste</i>	0, 3×	Linear	0.07; <0.01		<0.01
N	<i>S. arctica</i>	0, 3×	Linear	-0.09; 0.04		0.37
C	<i>C. membranacea</i>	0, 1×, 2×, 3×	Linear	-0.25; <0.01		0.45
C	<i>C. membranacea</i>	0, 1×, 2×, 3×	Quadratic	-0.44; 0.05	0.06; 0.36	0.47
C	<i>C. stans</i>	0, 1×, 2×, 3×	Linear	-0.43; <0.01		0.50
C	<i>C. stans</i>	0, 1×, 2×, 3×	Quadratic	-1.03; <0.01	0.20; 0.05	0.58
C	<i>E. triste</i>	0, 3×	Linear	-0.05; 0.36		0.09
C	<i>S. arctica</i>	0, 3×	Linear	-1.12; <0.01		0.68
C:N	<i>C. membranacea</i>	0, 1×, 2×, 3×	Linear	-1.84; <0.01		0.40
C:N	<i>C. membranacea</i>	0, 1×, 2×, 3×	Quadratic	-7.10; <0.01	1.75; 0.01	0.69
C:N	<i>C. stans</i>	0, 1×, 2×, 3×	Linear	-0.79; 0.03		0.20
C:N	<i>C. stans</i>	0, 1×, 2×, 3×	Quadratic	-3.04; <0.01	0.75; 0.05	0.34
C:N	<i>E. triste</i>	0, 3×	Linear	-1.62; <0.01		0.56
C:N	<i>S. arctica</i>	0, 3×	Linear	1.28; 0.15		0.19

2009; Hill and Henry, 2010) and better survivorship, especially of young animals (ACIA, 2005). With the possibility of greater numbers of herbivores and increased grazing pressure, it is important to understand the effects of grazing in ungrazed areas such as the sedge meadows at Alexandra Fiord, Ellesmere Island.

In our study, aboveground NPP decreased significantly with increased clipping frequency. Smith (1996) also found that aboveground NPP in *E. triste* decreased with more intense clipping on Banks Island, in an area used by muskoxen. However, Raillard and Svoboda (1999) found that *C. aquatilis stans* showed no decline in growth in response to clipping at Sverdrup Pass, Ellesmere Island, regardless of clipping frequency. Raillard and Svoboda (1999) conducted their study by erecting enclosures in wet sedge meadows that were heavily grazed by muskoxen; therefore, the grazing history of the sites must be considered when making comparisons between these studies (e.g. Elliott, 2009). For example, nutrients from muskox excrement in the surrounding grazed areas were likely carried by flowing surface and subsurface water into experimental plots in the study by Raillard and Svoboda (1999).

Plant phenological stage can influence responses to clipping. In our study, the single clipping treatment (1×) was conducted

TABLE 3

Average temperatures (°C) at 10 cm below soil surface in clipping treatment plots. Temperatures recorded between 21 June and 31 July in both 2007 and 2008.

Year	Grid	Treatment	Number of plots	°C mean ± SE
2007	1	Control	2	7.7 ± 0.9
2007	1	Litter removed	3	5.6 ± 0.5
2007	1	3× clipping	2	7.4 ± 1.3
2007	2	Litter removed	2	6.4 ± 1.0
2007	2	3× clipping	2	5.0 ± 0.9
2008	1	Control	1	4.1 ± 1.0
2008	1	Litter removed	3	4.8 ± 0.6
2008	1	3× clipping	2	5.1 ± 1.0
2008	2	Control	3	4.5 ± 0.9
2008	2	Litter removed	3	4.6 ± 0.8
2008	2	3× clipping	2	4.7 ± 1.5

during the middle of the growing season in early July in both seasons, and aboveground NPP was lower in this treatment compared to control plots. Results from other arctic defoliation studies varied depending on the time of vegetation removal. Archer and Tieszen (1983) found that defoliating *E. vaginatum* plants early in the growing season resulted in less aboveground shoot growth when compared to plants that were either defoliated later in the season or not at all. However, long-term results from Archer and Tieszen (1983) indicated that increasing the number of defoliation events per year decreased production in *E. vaginatum* more than applying early clipping treatments. In their study, photosynthetic inputs were likely reduced in plants that were clipped more frequently (Archer and Tieszen, 1983). In contrast, Raillard and Svoboda (1999) found that aboveground NPP in *C. aquatilis stans* was similar in all treatments regardless of the timing and frequency of defoliation events in a high arctic wet sedge meadow that was relatively heavily grazed by muskoxen. In salt marsh plant communities subjected to grazing by lesser snow geese (*C. caerulescens caerulescens*), Hik et al. (1991) found that aboveground NPP was lower in *Puccinellia phryganodes* swards grazed later in the growing season compared to those grazed earlier. It was suggested that *P. phryganodes* needed a period free of grazing at the end of the summer to acquire nutrients and carbohydrate reserves for the winter and upcoming growing season (Hik et al., 1991). The plants in our experiment responded similarly to those in the study by Hik et al. (1991), suggesting that they may not have had enough time in the short growing season to recover the lost aboveground tissue.

Defoliation affects the aboveground to belowground distribution of plant material. In defoliation studies conducted in growth chambers on two grass species from the Pampas of Argentina, the relative growth rate of belowground plant material decreased (Oosterheld, 1992). In addition, grazing decreased belowground production in mid-grass and tall-grass prairies in the United States (Johnson and Matchett, 2001; Derner et al., 2006). In contrast, belowground plant material was greater in grazed high arctic wet sedge meadows compared to ungrazed meadows (Elliott, 2009). Shoot to root ratios in High Arctic wet sedge tundra are low compared to the graminoid ecosystems mentioned above partly because of restricted belowground

nutrient availabilities (Bliss et al., 1973; Wielgolaski et al., 1981). Therefore, plants in high arctic sedge meadows may allocate more growth to roots so that they can obtain more nutrients and store carbohydrates for rapid growth in the spring. Although we did not measure belowground biomass in our study, it is possible belowground plant growth may have been reduced by defoliation in these meadows.

Soil NH_4^+ and NO_3^- availabilities were higher in plots subjected to intermediate levels of clipping, contrasting with the prediction that soil N would remain constant regardless of clipping frequency. Hamilton and Frank (2001) found that defoliation of *Poa pratensis* in growth chambers increased available N in the soil because plant roots exuded more C, leading to higher rates of microbial activity. The nutritional status of plants controls root exudation (Dakora and Phillips, 2002), and plants subjected to intermediate clipping frequencies may have higher concentrations of nutrients such as N (Leriche et al., 2003). Therefore, root exudation may have been highest in our plots that were subjected to intermediate frequencies of defoliation, which increased microbial activity and N availability.

Nitrogen was not added to our plots, and the lack of N input may help to explain the decrease in aboveground NPP as clipping frequencies increased. In experimental defoliation studies, nutrients are not usually returned to the soil in the form of animal excrement or chemical fertilizers. In contrast to our results, Raillard and Svoboda (1999) found compensatory regrowth in clipping experiments in a heavily grazed wet sedge tundra site at Sverdrup Pass, Ellesmere Island. Greater availability of soil NH_4^+ helps to explain the larger amounts of aboveground NPP and belowground biomass at Sverdrup Pass compared to the ungrazed meadows at Alexandra Fiord (Elliott, 2009). The importance of increased available N was also noted by Hik et al. (1991) in northern coastal salt marshes where fertilized *P. phryganodes* plants that were clipped had higher aboveground NPP compared to those plants that were clipped but not fertilized. Aboveground NPP was significantly higher in fertilized compared to unfertilized plots in the coastal salt marshes, suggesting that primary productivity is limited by inorganic N in those systems (Cargill and Jefferies, 1984; Bazely and Jefferies, 1985). These results suggest that greater levels of available soil N in the grazed and fertilized sites aided the regrowth of vegetation because plants did not have to rely only on the slow mineralization of N in plant litter (Ruess and McNaughton, 1987; Henry, 1998; Knapp et al., 1999).

Higher clipping frequencies resulted in increased concentrations of N in shoots of *E. triste* compared to samples from the control plots, supporting our initial predictions. In arctic Alaska, N concentrations in the leaves of *E. vaginatum* and *C. aquatilis* in clipped plots were higher than in plants that were not defoliated and concentrations rose as clipping frequencies increased (Chapin, 1980). In addition, clipping increased shoot N in graminoid plants in arctic wet tundra (Ouellet et al., 1994; Ruess et al., 1997; Raillard and Svoboda, 1999), mixed prairies (Green and Detling, 2000), and tall-grass prairies (Turner et al., 1993). Defoliation also increased shoot N concentrations in *Kyllinga nervosa*, a sedge from the Serengeti plains (Ruess et al., 1983). Graminoids use belowground nutrient reserves to support the regrowth of shoots in response to grazing (Bryant et al., 1983). It is possible that roots enhanced N uptake and allocated it preferentially to shoots following defoliation (Green and Detling, 2000). High concentrations of N in leaves support increased photosynthetic rates which could lead to compensatory growth (Welker et al., 2004).

Concentrations of N were significantly higher in the shoots of *C. membranacea* and marginally higher *C. aquatilis stans* at intermediate clipping frequencies. Nitrogen yield to grazers in the

Serengeti was highest under moderate levels of simulated grazing (Leriche et al., 2003), supporting our results and indicating that the nutrient status of plants may increase at intermediate clipping frequencies. In contrast, concentrations of N in shoots of the deciduous dwarf shrub *S. arctica* decreased with clipping. Chapin (1980) found that deciduous shrubs allocate maximum nutrients to their shoots early in the summer. In our experiment it was possible that N-rich plant material in *S. arctica* was removed in the first clipping event in the 3× treatment and levels of this nutrient did not recover by the time the plots were harvested.

Carbon concentrations in *C. membranacea* and *S. arctica* declined as clipping frequencies increased, supporting the predictions of our study. Ouellet et al. (1994) measured C as total non-structural carbohydrates, a surrogate for C concentrations, in sedges and *S. lanata* in meadows on Southampton Island in the Canadian Arctic. They found that total non-structural carbohydrates decreased in plants that were clipped more frequently. In our study, plants that were clipped more frequently had younger leaves. The newer cells in these younger leaves may have had lower proportions of cellulose in their walls (Whaley et al., 1952).

We predicted that soil temperatures would increase in plots that were clipped; however, this did not happen in our study. The removal of aboveground plant material by defoliation opens the plant canopy, increasing the amount of solar radiation that reaches and subsequently heats the soil surface (Frank and McNaughton, 1993; Semmartin and Oosterheld, 1996; Bremer et al., 1998). Soil warming may accelerate nutrient mineralization and decomposition rates (Nadelhoffer et al., 1992), but increases in mineralization rates are not always significant (Sorensen et al., 2008). In our study, soil temperatures were similar in control and 3× treatments in both Grids in 2007 and 2008. Soil temperatures also remained similar in control and litter removal plots in both Grids; they did not increase when litter was removed as we predicted. The statistical power required to detect differences in this variable was limited by equipment failures that reduced sample sizes.

It was predicted that litter removal would increase aboveground NPP in our study mainly through an increase in soil temperature. Large standing crops of litter relative to living plant biomass may shade the surface, reducing soil temperatures (Bazely and Jefferies, 1986; Knapp and Seastedt, 1986; Henry, 1998). However, the combined data from both grids indicated that aboveground NPP did not change when litter was removed from plots, and we found that there was no difference in soil temperatures between litter removal and control plots. Therefore, litter removal treatments may not have increased soil temperatures sufficiently to stimulate plant growth or decomposition/mineralization rates. In general, clipping (or litter removal) experiments cannot completely simulate grazing; for instance, decomposition rates can increase in grazed plant communities because there is more contact of dead plant material with soil microbes from trampling (Willms et al., 2002; Zacheis et al., 2002).

In contrast to our predictions, soil moisture was slightly greater in plots with litter removed. Litter removal may have increased the amount of incoming solar radiation that reached the soil surface; however, our data did not indicate any differences in soil temperatures. The increased energy available at the soil surface may have been used in evaporation (Oke, 1978), drawing additional soil moisture into the plot. At the larger ecosystem scale, the increased evaporation could draw more moisture to the soil surface as there is no longer sensible heat exchange at the litter layer.

Plant production, nutrient cycling, and soil conditions in ungrazed sedge meadows will change if these communities are subjected to grazing by increased numbers of high arctic herbivores because of climate warming. Overall, our study isolated

the effects of defoliation and litter removal on several biotic and abiotic variables in high arctic wet sedge tundra which had not been previously grazed. Our results indicate that intermediate levels of grazing, which would include addition of nutrients through animal excrement, could be sustained in these unique systems.

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References Cited

- ACIA, 2005: *Impacts of a Warming Arctic: Arctic Climate Impact Assessment*. Cambridge: Cambridge University Press.
- Aerts, R., Cornelissen, J. H. C., and Dorrepaal, E., 2006: Plant performance in a warmer world: general responses of plants from cold, northern biomes and the importance of winter and spring events. *Plant Ecology*, 182: 65–77.
- Archer, S., and Tieszen, L. L., 1983: Effects of simulated grazing on foliage and root production and biomass allocation in an arctic tundra sedge (*Eriophorum vaginatum*). *Oecologia*, 58(1): 92–102.
- Bazely, D. R., and Jefferies, R. L., 1985: Goose feces—A source of nitrogen for plant-growth in a grazed salt-marsh. *Journal of Applied Ecology*, 22(3): 693–703.
- Bazely, D. R., and Jefferies, R. L., 1986: Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. *Journal of Ecology*, 74(3): 693–706.
- Bliss, L. C., Courtin, G. M., Pattie, D. L., Riewe, R. R., Whitfield, D. W. A., and Widden, P., 1973: Arctic tundra ecosystems. *Annual Review of Ecology and Systematics*, 4: 359–399.
- Brathen, K. A., and Odasz-Albrigtsen, A. M., 2000: Tolerance of the arctic graminoid *Luzula arctica* ssp. *confusa* to simulated grazing in two nitrogen environments. *Canadian Journal of Botany*, 78(8): 1108–1113.
- Bremer, D. J., Ham, J. M., Owensby, C. E., and Knapp, A. K., 1998: Responses of soil respiration to clipping and grazing in a tallgrass prairie. *Journal of Environmental Quality*, 27(6): 1539–1548.
- Bryant, J. P., Chapin, F. S., and Klein, D. R., 1983: Carbon nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*, 40(3): 357–368.
- Cargill, S. M., and Jefferies, R. L., 1984: The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt-marsh. *Journal of Applied Ecology*, 21(2): 669–686.
- Chapin, F. S., 1980: Nutrient allocation and responses to defoliation in tundra plants. *Arctic and Alpine Research*, 12(4): 553–563.
- Dakora, F., and Phillips, D., 2002: Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant and Soil*, 245: 35–47.
- Day, T. A., and Detling, J. K., 1994: Water relations of *Agropyron smithii* and *Bouteloua gracilis* and community evapotranspiration following long-term grazing by prairie dogs. *American Midland Naturalist*, 132: 381–392.
- Derner, J., Boutton, T., and Briske, D., 2006: Grazing and ecosystem carbon storage in the North American Great Plains. *Plant Soil*, 280: 77–90.
- Dormann, C. F., 2003: Consequences of manipulations in carbon and nitrogen supply for concentration of anti-herbivore defence compounds in *Salix polaris*. *Ecoscience*, 10(3): 312–318.
- Elliott, T. L., 2009: A comparison of grazed and ungrazed sedge meadows in the Canadian High Arctic. MSc thesis. University of British Columbia, Vancouver, 95 pp.
- Facelli, J. M., and Pickett, S. T. A., 1991: Plant litter—Light interception and effects on an old-field plant community. *Ecology*, 72(3): 1024–1031.
- Ferraro, D., and Oosterheld, M., 2002: Effect of defoliation on grass growth. A quantitative review. *Oikos*, 98: 125–133.
- Foster, B. L., and Gross, K. L., 1998: Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology*, 79(8): 2593–2602.
- Frank, D. A., and McNaughton, S. J., 1993: Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia*, 96(2): 157–161.
- Freedman, B., Svoboda, J., and Henry, G. H. R., 1994: Alexandra Fiord—An ecological oasis in the polar desert. In Svoboda, J., and Freedman, B. (eds.), *Ecology of a Polar Oasis: Alexandra Fiord, Ellesmere Island, Canada*. Toronto: Captus Press Inc., 1–9.
- Gornall, J. L., Jonsdottir, I. S., Woodin, S. J., and van der Wal, R., 2007: Arctic mosses govern below-ground environment and ecosystem processes. *Oecologia*, 153: 931–941.
- Green, R. A., and Detling, J. K., 2000: Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. *Oikos*, 91(2): 280–284.
- Hamilton, E. W., III, and Frank, D. A., 2001: Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology*, 82: 2397–2402.
- Henry, G. H. R., 1998: Environmental influences on the structure of sedge meadows in the Canadian High Arctic. *Plant Ecology*, 134(1): 119–129.
- Henry, G. H. R., and Svoboda, J., 1994: Comparisons of grazed and non-grazed high arctic sedge meadows. In Svoboda, J., and Freedman, B. (eds.), *Ecology of a Polar Oasis: Alexandra Fiord, Ellesmere Island, Canada*. Toronto: Captus Press Inc., 193–194.
- Henry, G. H. R., Freedman, B., and Svoboda, J., 1986: Survey of vegetated areas and musk-ox populations in east-central Ellesmere Island. *Arctic*, 39(1): 78–81.
- Henry, G. H. R., Svoboda, J., and Freedman, B., 1990: Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. *Canadian Journal of Botany*, 68(12): 2660–2667.
- Hik, D. S., and Jefferies, R. L., 1990: Increases in the net aboveground primary production of a salt-marsh forage grass—A test of the predictions of the herbivore-optimization model. *Journal of Ecology*, 78(1): 180–195.
- Hik, D. S., Sadul, H. A., and Jefferies, R. L., 1991: Effects of the timing of multiple grazings by geese on net aboveground primary production of swards of *Puccinellia phryganodes*. *Journal of Ecology*, 79(3): 715–730.
- Hill, G., and Henry, G. H. R., 2010: Responses of high arctic wet sedge tundra to climate warming since 1980. *Global Change Biology*, 17: 276–287, doi: 10.1111/j.1365-2486.2010.02244.x.
- Hinzman, L. D., Bettez, N. D., Bolton, W. R., Chapin, F. S., Dyrurgerov, M. B., Fastie, C. L., Griffith, B., Hollister, R. D., Hope, A., Huntington, H. P., Jensen, A. M., Jia, G. J., Jorgenson, T., Kane, D. L., Klein, D. R., Kofinas, G., Lynch, A. H., Lloyd, A. H., McGuire, A. D., Nelson, F. E., Oechel, W. C., Osterkamp, T. E., Racine, C. H., Romanovsky, V. E., Stone, R. S., Stow, D. A., Sturm, M., Tweedie, C. E., Vourlitis, G. L., Walker, M. D., Walker, D. A., Webber, P. J., Welker, J. M.,

- Winker, K., and Yoshikawa, K., 2005: Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change*, 72(3): 251–298.
- Hudson, J. M. G., and Henry, G. H. R., 2009: Increased plant biomass in a high arctic heath community from 1981–2008. *Ecology*, 90: 2657–2663.
- Jaramillo, V. J., and Detling, J. K., 1988: Grazing history, defoliation, and competition—Effects on shortgrass production and nitrogen accumulation. *Ecology*, 69(5): 1599–1608.
- Johnson, L. C., and Matchett, J. R., 2001: Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology*, 82: 3377–3389.
- Jonasson, S., and Shaver, G. R., 1999: Within-stand nutrient cycling in arctic and boreal wetlands. *Ecology*, 80(7): 2139–2150.
- Knapp, A. K., and Seastedt, T. R., 1986: Detritus accumulation limits productivity of tallgrass prairie. *Bioscience*, 36(10): 662–668.
- Knapp, A. K., Blair, J. M., Briggs, J. M., Collins, S. L., Hartnett, D. C., Johnson, L. C., and Towne, E. G., 1999: The keystone role of bison in North American tallgrass prairie—Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *Bioscience*, 49(1): 39–50.
- Leriche, H., LeRoux, X., Desnoyers, F., Benest, D., Simioni, G., and Abbadie, L., 2003: Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. *Ecological Applications*, 13: 1346–1354.
- McNaughton, S., 1979: Grazing as an optimization process: grass ungulate relationships in the Serengeti. *American Naturalist*, 113(5): 691–703.
- Muc, M., Freedman, B., and Svoboda, J., 1989: Vascular plant communities of a polar oasis at Alexandra Fiord (79° N), Ellesmere Island, Canada. *Canadian Journal of Botany*, 67(4): 1126–1136.
- Muc, M., Svoboda, J., and Freedman, B., 1994a: Soils of an extensively vegetated polar desert oasis. In Svoboda, J., and Freedman, B. (eds.), *Ecology of a Polar Oasis: Alexandra Fiord, Ellesmere Island, Canada*. Toronto: Captus Press Inc., 41–50.
- Muc, M., Svoboda, J., and Freedman, B., 1994b: Aboveground standing crop in plant communities of a polar desert oasis, Alexandra Fiord, Ellesmere Island. In Svoboda, J., and Freedman, B. (eds.), *Ecology of a Polar Oasis: Alexandra Fiord, Ellesmere Island, Canada*. Toronto: Captus Press Inc., 65–74.
- Mulder, C. P. H., 1999: Vertebrate herbivores and plants in the Arctic and subarctic: effects on individuals, populations, communities and ecosystems. *Perspectives in Plant Ecology, Evolution, and Systematics*, 2: 29–55.
- Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., and Linkins, A. E., 1992: Microbial processes and plant nutrient availability in arctic soils. In Chapin, F. S., Jefferies, R. L., Reynolds, J. R., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective*. San Diego: Academic Press, Inc., 281–300.
- Oberbauer, S. F., and Dawson, T. E., 1992: Water relations of arctic vascular plants. In Chapin, F. S., Jefferies, R. L., Reynolds, J. R., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective*. San Diego: Academic Press, Inc., 259–280.
- Oosterheld, M., 1992: Effect of defoliation intensity on aboveground and belowground relative growth-rate. *Oecologia*, 92: 313–316.
- Oosterheld, M., and McNaughton, S. J., 1988: Intraspecific variation in the response of *Themeda triandra* to defoliation—The effect of time of recovery and growth-rates on compensatory growth. *Oecologia*, 77(2): 181–186.
- Oke, T. R., 1978: *Boundary Layer Climates*. London: Methuen and Co Ltd.
- Ouellet, J. P., Boutin, S., and Heard, D. C., 1994: Responses to simulated grazing and browsing of vegetation available to caribou in the Arctic. *Canadian Journal of Zoology*, 72(8): 1426–1435.
- Post, E., and Pedersen, C., 2008: Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences*, 105(34): 12353–12358.
- Raillard, M., 1992: Influence of muskox grazing on plant communities of Sverdrup Pass (79 N), Ellesmere Island, N.W.T. Canada. PhD thesis. University of Toronto, Toronto, Ontario, Canada., 262 pp.
- Raillard, M., and Svoboda, J., 1999: Exact growth and increased nitrogen compensation by the arctic sedge *Carex aquatilis* var. *stans* after simulated grazing. *Arctic, Antarctic, and Alpine Research*, 31: 21–26.
- Rinnan, R., Stark, S., and Tolvanen, A., 2009: Responses of vegetation and soil microbial communities to warming and simulated herbivory in a subarctic heath. *Journal of Ecology*, 97: 788–800.
- Ruess, R. W., 1984: Nutrient movement and grazing—Experimental effects of clipping and nitrogen-source on nutrient-uptake in *Kyllinga nervosa*. *Oikos*, 43: 183–188.
- Ruess, R. W., and McNaughton, S. J., 1987: Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. *Oikos*, 49(1): 101–110.
- Ruess, R. W., McNaughton, S. J., and Coughenour, M. B., 1983: The effects of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an east-African sedge. *Oecologia*, 59(2–3): 235–261.
- Ruess, R., Uliassi, D., Mulder, C., and Person, B., 1997: Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: implications for geese-ecosystem dynamics in western Alaska. *Ecoscience*, 4: 170–178.
- SAS Institute Inc., 2009: SAS Online Doc 9.1.3 (<http://support.sas.com/>).
- Semmartin, M., and Oosterheld, M., 1996: Effect of grazing pattern on primary productivity. *Oikos*, 75(3): 431–436.
- Smith, D. L., 1996: Muskoxen/sedge meadow interactions, north-central Banks Island, Northwest Territories, Canada. PhD thesis. University of Saskatchewan, Saskatoon, Saskatchewan, Canada, 214 pp.
- Sorensen, P. L., Michelsen, A., and Jonasson, S., 2008: Nitrogen uptake during one year in subarctic plant functional groups and in microbes after long-term warming and fertilization. *Ecosystems*, 11: 1223–1233.
- Svoboda, J., and Freedman, B. (eds.), 1994: *Ecology of a Polar Oasis: Alexandra Fiord, Ellesmere Island, Canada*. Toronto: Captus Press Inc.
- Taylor, B. R., Parkinson, D., and Parsons, W. F. J., 1989: Nitrogen and lignin content as predictors of litter decay-rates—A microcosm test. *Ecology*, 70(1): 97–104.
- Tolvanen, A., and Henry, G. H. R., 2000: Population structure of three dominant sedges under muskox herbivory in the High Arctic. *Arctic, Antarctic, and Alpine Research*, 32: 449–455.
- Tolvanen, A., Schroderus, J., and Henry, G. H. R., 2001: Demography of three dominant sedges under contrasting grazing regimes in the High Arctic. *Journal of Vegetation Science*, 12(5): 659–670.
- Tolvanen, A., Schroderus, J., and Henry, G. H. R., 2002: Age- and stage-based bud demography of *Salix arctica* under contrasting muskox grazing pressure in the High Arctic. *Evolutionary Ecology*, 15(4–6): 443–462.
- Trefry, S. A., Freedman, B., Hudson, J. M. G., and Henry, G. H. R., 2010: Breeding bird surveys at Alexandra Fiord, Ellesmere Island, Nunavut (1980–2008). *Arctic*, 63(3): 308–314.
- Turner, C., Seastedt, T. R., and Dyer, M. I., 1993: Maximization of aboveground grassland production—The role of defoliation frequency, intensity, and history. *Ecological Applications*, 3(1): 175–186.
- van der Wal, R., and Brooker, R., 2004: Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology*, 18: 77–86.
- Wan, S., Luo, Y., and Wallace, L. L., 2002: Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. *Global Change Biology*, 8(8): 754–768.

- Warren, S., Thurow, T., Blackburn, W., and Garza, N., 1986: The influence of livestock trampling under intensive rotation grazing on soil hydrologic characteristics. *Journal of Range Management*, 39: 491–495.
- Welker, J. M., Fahnestock, J. T., Povirk, K. L., Bilbrough, C. J., and Piper, R. E., 2004: Alpine grassland CO₂ exchange and nitrogen cycling: grazing history effects, Medicine Bow Range, Wyoming, USA. *Arctic, Antarctic, and Alpine Research*, 36(1): 11–20.
- Western Ag Innovations, 2008: About PRS-TM-probes. Western Ag Innovation Inc. (<http://www.westernag.ca/innov>).
- Whaley, W. G., Mericle, L. W., and Heimsch, C., 1952: The wall of the meristematic cell. *American Journal of Botany*, 39(1): 20–26.
- Wielgolaski, F. E., Bliss, L. C., Svoboda, J., and Doyle, G., 1981: Primary production of tundra. In Bliss, L. C., Heal, O. W., and Moore, J. J. (eds.), *Tundra Ecosystems—A Comparative Analysis*. Cambridge: Cambridge University Press, 187–226.
- Willms, W. D., Dormaar, J. F., Adams, B. W., and Douwes, H. E., 2002: Response of the mixed prairie to protection from grazing. *Journal of Range Management*, 55(3): 210–216.
- Zacheis, A., Ruess, R., and Hupp, J., 2002: Nitrogen dynamics in an Alaskan salt marsh following spring use by geese. *Oecologia*, 130: 600–608.

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