

Effects of Simulated Reindeer Grazing, Trampling, and Waste Products on Nitrogen Mineralization and Primary Production

Author: Olofsson, Johan

Source: Arctic, Antarctic, and Alpine Research, 41(3) : 330-338

Published By: Institute of Arctic and Alpine Research (INSTAAR),
University of Colorado

URL: <https://doi.org/10.1657/1938-4246-41.3.330>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Effects of Simulated Reindeer Grazing, Trampling, and Waste Products on Nitrogen Mineralization and Primary Production

Johan Olofsson

*Department of Ecology and
Environmental Science, Umeå
University, S-901 87 Umeå, Sweden
johan.olofsson@emg.umu.se

Abstract

An experiment was conducted in arctic tundra to evaluate the role of reindeer grazing, trampling, and feces and urine deposition in nutrient turnover and primary production. Grazing was simulated by mowing, trampling by the impact of a wooden pole, and waste product deposition by the application of fertilizer. In the first year, aboveground primary production increased with simulated grazing in the fertilized plots and decreased with simulated grazing in the unfertilized plots; this indicates a higher regrowth capacity at higher nutrient levels. However, nitrogen mineralization and primary production were mainly determined by the input or removal of nutrients and, therefore, decreased in plots that were grazed but not fertilized and increased in plots that were fertilized but not grazed. Simulated trampling decreased the depth of the moss layer and increased soil temperatures, but the higher temperatures increased N mineralization only in unmowed plots, and the increased nitrogen availability was not translated into increased primary production. Since aboveground and belowground net primary production in plots with simulated grazing was the same as in plots without simulated animal activity, this study indicates that an entire trophic level can be supported with no apparent effect on primary production.

DOI: 10.1657/1938-4246-41.3.330

Introduction

Herbivores influence the turnover, gains, and losses of nutrients in many ecosystems (Hobbs, 1996; Wardle, 2002; Bardgett and Wardle, 2003). Since nutrients limit plant production in many systems (Hobbs, 1996) and plants have been shown to regrow effectively following defoliation only when there is sufficient nutrient supply (Bazely and Jefferies, 1989; Hik and Jefferies, 1990), the effects of herbivores on nutrient availability can be important for plant growth and thus for the quality and quantity of their own food supply. Herbivores influence nutrient turnover by consuming plants and depositing urine and feces that contain readily available nutrients (Ruess and McNaughton, 1987; Frank et al., 1994; Hobbs, 1996; Frank and Evans, 1997; Frank and Groffman, 1998; Persson et al., 2005). They may, therefore, speed up the nutrient turnover in ecosystems as a result of bypassing plant litter decomposition (Ruess and McNaughton, 1987; Frank and McNaughton, 1993; Pastor et al., 1993; Frank et al., 1994). Herbivores can also influence nutrient turnover by changing the relative abundance of different plant species and thus the quality and quantity of plant litter and soil organic matter (Pastor and Naiman, 1992; Pastor et al., 1993; Richie et al., 1998). Herbivores may have an accelerating effect when they enhance litter quality by preferentially grazing on plants that compensate for tissue loss by rapid regrowth. In order to regrow rapidly, plants need a high nutrient content in their tissues; this is likely to lead to the production of high quality litter that decomposes rapidly (Belovsky and Slade, 2000; Olofsson and Oksanen, 2002). Herbivores may, however, decelerate nutrient cycling by feeding selectively on nutrient-rich plants, thus increasing the proportion of nutrient-poor plants and plants rich in secondary metabolites present in the litter, and hence reducing its quality (Pastor and Naiman, 1992; Richie et al., 1998; Belovsky and Slade, 2000,

Bråthen et al., 2007). Herbivores can also influence nutrient turnover by altering the physical conditions (temperature, salinity, humidity) and carbon availability for the soil microbes and invertebrates involved in the decomposition process (Wilson and Jefferies, 1996; Hamilton and Frank, 2001; van der Wal and Brooker, 2004; Classen et al., 2005; Hamilton et al., 2008).

In the long run, with respect to nutrient availability and primary production, the effects of herbivores on nutrient losses and gains might be more important than their effects on nutrient turnover rates (de Mazancourt et al., 1998; de Mazancourt and Loreau, 2000; Olofsson et al., 2007). Herbivores can influence losses and gains of nutrients at a local scale by feeding and depositing waste products in different habitats (McNaughton, 1983; Senft et al., 1987; Cougenhour, 1991). Herbivores can also influence nutrient losses and gains by affecting processes like volatilization (Schimel et al., 1986; Frank et al., 2004), nitrogen fixation (Bazely and Jefferies, 1989), nutrient leaching (Ruess and McNaughton, 1987; Frank et al., 2000), and plant nutrient uptake efficiency (Ruess and McNaughton, 1987; Buckeridge and Jefferies, 2007).

Reindeer and caribou (*Rangifer tarandus*) have a circumpolar distribution and there is a growing body of evidence demonstrating that they have a significant impact on the vegetation across their entire range (Kashulina et al., 1997; Suominen and Olofsson, 2000; Moen and Danell, 2003; van der Wal, 2006). In all ecosystems where they are present, reindeer reduce the abundance of lichens (van der Wal, 2006) and, in some areas, may even cause a shift in the vegetation from moss or heathland dominated tundra to grass dominated meadow vegetation (Thing, 1984; Zimov et al., 1995; Olofsson et al., 2001, 2004a; Olofsson, 2006; van der Wal and Brooker, 2004; van der Wal et al., 2004; van der Wal, 2006). Although the direct effects of grazing and trampling are well recorded (Suominen and Olofsson, 2000; Moen and Danell, 2003;

TABLE 1

Effects of mowing (M), trampling (T), and waste product addition (F) on plant biomass in spring and autumn, root biomass and moss biomass during 2002–2005, tested using linear mixed effect models. All significant values ($P < 0.05$) are marked in bold.

	d.f.	Plant Biomass Spring		Plant Biomass Autumn		Root Biomass		Moss Biomass	
		<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Fertilized	48	-4.2	<0.001	-7.3	<0.001	0.5	0.601	0.7	0.478
Mowed	48	0.5	0.605	-0.2	0.807	3.9	<0.001	0.5	0.620
Lightly Trampled	48	-0.4	0.694	-1.5	0.144	1.1	0.269	3.2	0.002
Intensively Trampled	48	0.6	0.583	-0.2	0.876	3.0	0.005	4.1	<0.001
Year	168	-0.8	0.422	-1.7	0.093	1.0	0.326	1.9	0.061
F × M	48	1.6	0.112	4.2	<0.001	-3.1	0.003	-1.0	0.313
F × LT	48	1.9	0.063	3.0	0.005	-1.9	0.057	-0.9	0.364
F × IT	48	1.3	0.208	2.5	0.015	-3.8	0.001	-1.4	0.169
M × LT	48	0.1	0.989	0.9	0.399	-1.7	0.097	-1.4	0.175
M × IT	48	0.5	0.605	0.1	0.983	-0.3	0.743	-1.0	0.305
F × Y	168	4.2	<0.001	7.3	<0.001	-0.5	0.601	-0.7	0.475
M × Y	168	-0.5	0.602	0.2	0.813	-3.9	0.001	-0.5	0.618
LT × Y	168	0.4	0.693	1.5	0.139	-1.1	0.265	-3.2	0.001
IT × Y	168	-0.6	0.581	0.2	0.876	-3.0	0.003	-4.1	<0.001
F × M × LT	48	-0.8	0.433	-1.8	0.077	2.9	0.006	0.8	0.430
F × M × IT	48	-0.9	0.372	-1.4	0.176	1.4	0.160	1.4	0.158
F × M × Y	168	-1.6	0.113	-4.2	<0.001	3.1	0.002	1.0	0.309
F × LT × Y	168	-1.9	0.058	-3.0	0.003	1.9	0.053	0.9	0.360
F × IT × Y	168	-1.3	0.203	-2.5	0.013	3.8	<0.001	1.4	0.165
M × LT × Y	168	-0.1	0.989	-0.9	0.396	1.7	0.092	1.4	0.170
M × IT × Y	168	-0.5	0.603	-0.1	0.984	0.3	0.743	1.0	0.301
F × M × LT × Y	168	0.8	0.429	1.8	0.072	-2.9	0.005	-0.8	0.427
F × M × IT × Y	168	0.9	0.368	1.4	0.171	-1.4	0.155	-1.4	0.153

van der Wal, 2006), several recent studies have emphasized the importance of the indirect effects of reindeer activity as a result of changes in nutrient cycling (Olofsson et al., 2001, 2004a; van der Wal and Brooker, 2004; van der Wal et al., 2004; van der Wal, 2006). Plant growth in arctic and boreal regions is often highly constrained by nitrogen availability, since decomposition processes are slow as a consequence of low soil temperatures and poor quality of plant litter and soil organic matter (Chapin and Shaver, 1985; Aerts and Chapin, 2000; Weintraub and Schimel, 2003; Rustad et al., 2001). Any processes that influence nitrogen availability are, therefore, likely to have a great impact on the plant community. Reindeer influence nutrient availability directly via the input of waste products (van der Wal et al., 2004). As a result of trampling, reindeer can also reduce the thickness of the insulating moss layer and thus increase soil temperatures and nitrogen mineralization in the summer (Zimov et al., 1995; Olofsson et al., 2001, 2004a; van der Wal and Brooker, 2004; van der Wal et al., 2004; van der Wal, 2006; Gornall et al., 2007). Fertilization via the deposition of urine and droppings might also decrease the depth of the moss layer by increasing its rate of decomposition (van der Wal et al., 2004). Based on this information, van der Wal et al. (2004) proposed that herbivore activity leads to an increase in production by graminoids in arctic ecosystems via two feedback loops, operating simultaneously. In the first, herbivores reduce the depth of the moss layer, increase the soil temperature and, thus, increase the rate of soil organic matter decomposition. In the second, graminoids benefit directly from the nutrients in urine and feces.

Few studies have separated the effects of grazing, trampling, and waste products, although these are likely to have different effects on nutrient cycling and plant community composition (Olff and Ritchie, 1998). The relative importance of these three factors can be expected to vary since, at least to some extent, reindeer forage, defecate, and traverse different habitats (Nellemann and Thomsen, 1994; Nellemann, 1996; Johnson et al., 2002; Mårell and Edenius, 2006). Here I

present a study in which grazing, trampling, and urination and defecation were simulated by mowing, physical pressure, and fertilizer application, respectively; the experimental design was factorial. I simulated these activities, since it is almost impossible to separate them using real reindeer. The effects of these treatments on species richness are presented in Olofsson and Shams (2007), and the effect of plant soil feedbacks are presented in Sørensen et al. (2008). Here, I present results on the above- and belowground primary production of vascular plants, and on moss biomass, nitrogen mineralization, and soil temperatures. I tested two hypotheses:

- (1) Both trampling and nutrient input increase soil temperature, N mineralization, and primary production by reducing the depth of the moss layer.
- (2) Mowing increases primary production in fertilized plots, in which plants have sufficient resources to regrow following defoliation, but reduces primary production in unfertilized plots, in which resources are scarce.

Materials and Methods

STUDY SITE

This experiment was carried out on a north-facing slope at the mouth of the Kärkevagge valley (68°25'N, 18°19'E) in northern Sweden, between 2002 and 2005. The study sites are alpine meadows located at altitudes between 630 and 720 m above sea level (a.s.l.). The treeline of mountain birch (*Betula pubescens* ssp. *czerepanovii*) occurs at ca. 500 m a.s.l., the mean annual temperature is -1.4°C, and the mean annual precipitation is 848 mm at the closest climatic station (Katterjåkk), located 6 km west of our field site at 517 m a.s.l.

The vegetation is dominated by graminoids and forbs, and an almost continuous layer of moss covers the ground. The dominant graminoids are *Carex bigelowii*, *Festuca ovina*, *Poa alpina*, and

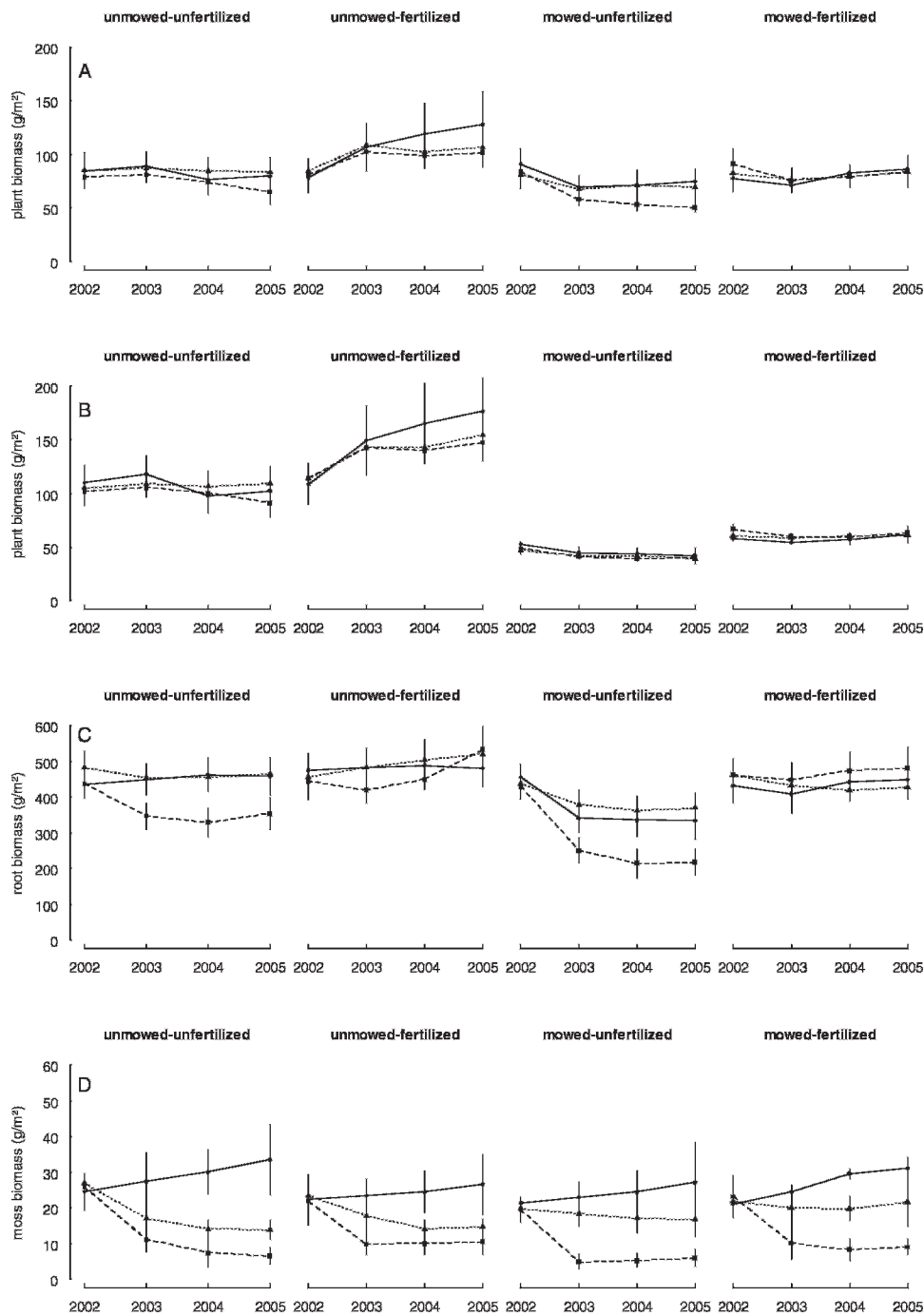


FIGURE 1. Effects of mowing, trampling and fertilization on (A) plant biomass in spring; (B) plant biomass in autumn; (C) root biomass; and (D) moss biomass during 2002–2005 in an alpine meadow in northern Sweden. The solid line represents no trampling, the dotted line light trampling, and the dashed line intense trampling.

Deschampsia cespitosa. The dominant forb species are *Alchemilla glomerulans*, *Potentilla crantzii*, and *Polygonum viviparum*. The moss layer is dominated by *Pleurozium schreberi* and *Hylocomium splendens*. All the dominant graminoids and forbs are consumed by reindeer but *Carex*, *Poa*, *Alchemilla*, and *Polygonum* are grazed preferentially compared to *Festuca* and *Potentilla*. The area is grazed in the summer (June–August) by semi-domesticated reindeer. Although no direct density estimates exist, reindeer density in this meadow is in the middle of the range of that in similar meadows in northern Fennoscandia (Olofsson and Oksanen, 2005).

EXPERIMENTAL DESIGN

In June 2002, we established a randomized block design with five blocks, including factorial combinations of fertilizer application, mowing, and soil disturbance. We investigated two levels of

defoliation (mowed, unmowed), two levels of fertilization (fertilized, unfertilized), and three levels of soil disturbance (undisturbed, lightly disturbed, intensively disturbed), resulting in 12 different treatment combinations. The treatment plots were 1.5 m × 1.5 m and spaced 0.5 m apart in two columns and six rows, resulting in blocks measuring 3.5 m × 11.5 m. Reindeer were excluded from the blocks, but smaller herbivores had free access to the vegetation. This may be important for the results since small mammalian herbivores, especially voles and lemmings, often have a great impact on the vegetation in arctic and alpine ecosystems (Olofsson et al., 2004b).

The mowing treatment involved cutting the vegetation to 2 cm above the moss layer, or to ground level when no mosses were present, in early summer (between 3 and 11 July in 2002 to 2005). The harvested biomass was removed from the plots and dried to a constant weight (60°C, 48 h), and this weight was

TABLE 2

Effects of mowing (M), trampling (T), and fertilization (F) on aboveground primary production, root production, and net nitrogen mineralization, tested with linear mixed effect models. Aboveground primary production was measured annually in all four years (2002–2005). Root production and net N mineralization were measured over three periods (2002–2003, 2003–2004, and 2004–2005). All significant values ($P < 0.05$) are marked in bold.

	d.f.	Aboveground Primary Production		d.f.	Root Production		Net Nitrogen Mineralization	
		<i>t</i>	<i>P</i>		<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Fertilized	48	−5.7	<0.001	48	−0.4	0.704	−1.4	0.161
Mowed	48	0.2	0.858	48	−0.4	0.702	3.2	0.002
Lightly Trampled	48	−2.7	0.010	48	−0.8	0.443	0.4	0.660
Intensively Trampled	48	−2.2	0.030	48	−1.3	0.217	−2.0	0.052
Year	168	−1.9	0.064	108	0.0	0.987	1.9	0.057
F × M	48	2.2	0.032	48	0.0	0.973	−0.6	0.534
F × LT	48	1.7	0.097	48	0.5	0.634	−1.1	0.269
F × IT	48	2.5	0.015	48	−2.4	0.021	0.5	0.639
M × LT	48	1.8	0.074	48	0.3	0.742	−1.0	0.319
M × IT	48	1.3	0.195	48	0.5	0.614	0.0	0.999
F × Y	168	5.7	<0.001	108	0.4	0.703	1.4	0.157
M × Y	168	−0.2	0.856	108	0.4	0.704	−3.2	0.002
LT × Y	168	2.7	0.008	108	0.8	0.441	−0.4	0.658
IT × Y	168	2.2	0.026	108	1.3	0.214	2.0	0.049
F × M × LT	48	−0.7	0.047	48	0.4	0.673	1.5	0.131
F × M × IT	48	−0.8	0.443	48	1.6	0.110	0.1	0.926
F × M × Y	168	−2.2	0.029	108	0.0	0.972	0.6	0.532
F × LT × Y	168	−1.7	0.093	108	−0.5	0.633	1.1	0.265
F × IT × Y	168	−2.5	0.012	108	2.4	0.018	−0.5	0.639
M × LT × Y	168	−1.8	0.070	108	−0.3	0.742	1.0	0.316
M × IT × Y	168	−1.3	0.191	108	−0.5	0.612	0.0	1.000
F × M × LT × Y	168	0.7	0.473	108	−0.4	0.671	−1.5	0.128
F × M × IT × Y	168	0.8	0.440	108	−1.6	0.106	−0.1	0.925

recorded. The biomass removed consisted mainly of vascular plants, and the moss layer was left virtually untouched. Fertilizer was applied once a year (Weibulls Rika, fluid fertilizer, 2 g N m^{−2}, 0.3 g P m^{−2}, and 1.4 g K m^{−2}) at a level chosen to mirror the amount of N removed by the clipping treatment. The fertilizer was dissolved in 10 L of water and distributed evenly over each assigned plot very soon after mowing (between 5 and 12 July in 2002 to 2005). The same amount of water was applied to the unfertilized plots. The fertilizer application was, mainly, to compensate for the mowing treatment, since on average 1.5 g N m^{−2} was removed from the fertilized plots and 1.3 g N m^{−2} from the unfertilized ones. This resulted in a small net addition of N even in fertilized and mowed plots, where these fluxes were intended to be in balance. The fertilizer was distributed across the ground much more evenly than occurs with natural waste products and it is in a form that can be taken up more rapidly by plants and soil microbes. The vegetation and soil were disturbed immediately after any defoliation and fertilization (between 7 and 12 July in 2002 to 2005) by raising a wooden pole (12 kg, diameter 80 mm) 0.4 m above the ground and dropping it on its end. The effects of this treatment varied from hardly noticeable marks to holes several centimeters deep, depending on the vegetation type and soil conditions. The pole was dropped 20 times m^{−2} in the lightly disturbed plots and 100 times m^{−2} in the intensively disturbed plots. The higher intensity is similar to the annual level of trampling in the intensively grazed and trampled areas studied by Olofsson et al. (2004a). The mowing treatment was designed to simulate grazing, the fertilization treatment to simulate the input of waste products, and the soil disturbance treatment to simulate reindeer trampling.

Plant biomass was estimated by harvesting 0.25 m × 0.25 m quadrats in each treatment plot at the beginning of the growing

season (15–25 June) and at the end of the growing season (15–25 August) in all four years (2002–2005). The plants were cut level with the top of the moss layer. Mosses were then harvested in a round (7.3 cm diameter) subplot in the center of the plot from which the vascular plants had been harvested. Harvested material was separated according to species, then dried to constant weight (60°C, 48 h) and the weight recorded. The aboveground primary production (AGNPP) was calculated as the difference in aboveground plant biomass between the end and the beginning of the growing season. The biomass removed by the mowing treatment was added to the difference between autumn and spring biomasses, to estimate primary production in the mown plots. This method can greatly underestimate primary production if the increase in biomass is not monotonic (Sala and Austin, 2000). Biomass increase is, however, known to be fairly monotonic in alpine meadows with short growing seasons, since no typical spring flowers exist and dry periods, which often limit production in temperate grasslands, are rare.

We measured root biomass by collecting root cores, with a diameter of 32 mm, from each of the treatment plots at the beginning of the growing season (15–24 June) and at the end of the growing season (15–25 August) in all four years (2002–2005). Three root cores were collected from each treatment and the average of the three values was used in all statistical analyses. Belowground net primary production (BGNPP) was measured using ingrowth cores (Lauenroth, 2000). Three mesh bags (mesh size 1 mm) with a diameter of 32 mm were filled with sieved soil from a single location, then buried in 10-cm-deep holes immediately after all the treatments had been applied to the plots. This was done in every year and the bags were collected immediately prior to treatment application the following year. BGNPP was estimated by the root biomass present in the

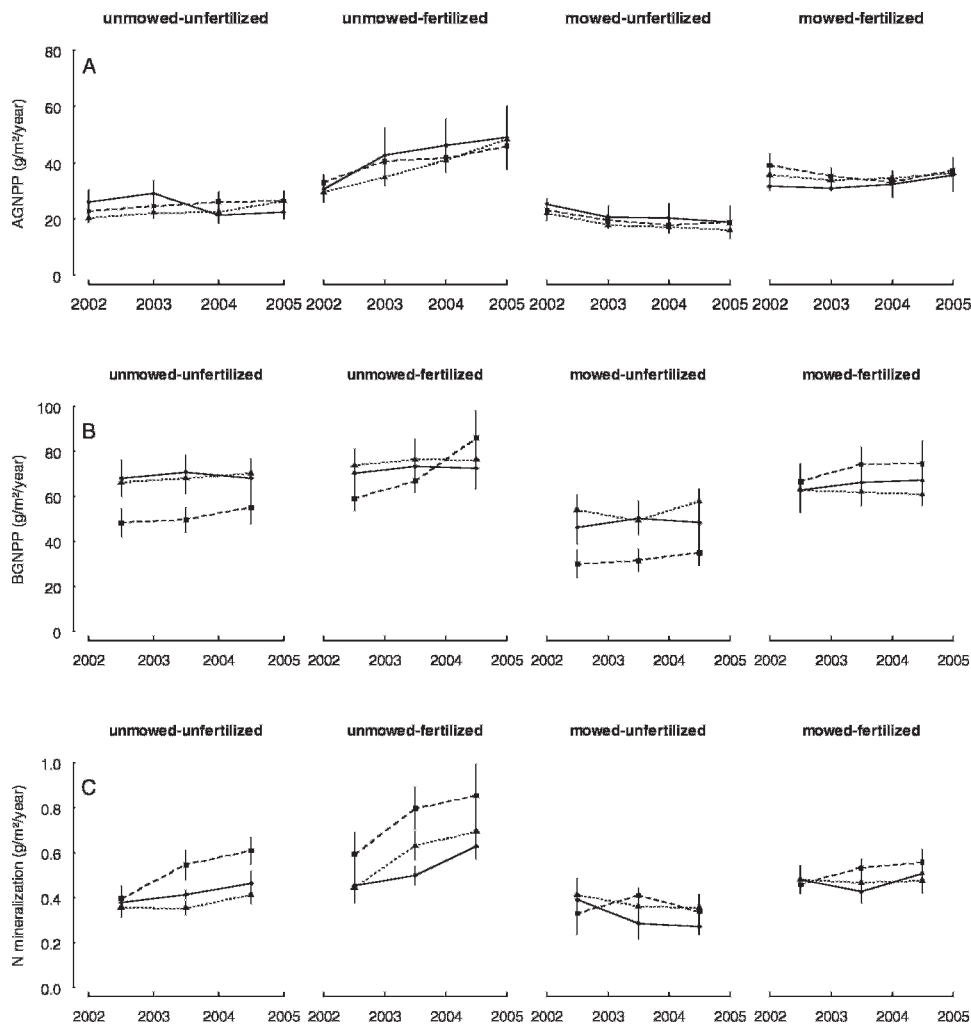


FIGURE 2. Effects of mowing, trampling and fertilization on (A) aboveground net primary production (AGNPP); (B) belowground net primary production (BGNPP); and (C) net nitrogen mineralization. AGNPP was measured annually in all four years (2002–2005) and BGNPP and net N mineralization were measured over the three periods (2002–2003, 2003–2004, and 2004–2005) in an alpine meadow in northern Sweden. The solid line represents no trampling, the dotted line light trampling, and the dashed line intense trampling.

ingrowth cores. As soon as the soil cores and the ingrowth cores had been collected from the field, all samples were processed by sieving (12 meshes cm^{-1}) and floatation (Lauenroth and Whitman, 1971), after which the remaining roots were dried to constant weight (60°C , 48 h) and the weight recorded.

Nitrogen mineralization rate was measured *in situ* using undisturbed soil profiles in PVC tubes with a diameter of 32 mm (Raison et al., 1987). The tubes were inserted into the soil to a depth of 10 cm, closed at the bottom and top with PVC plastic, placed back in their original position and incubated in the field for one year. Incubations commenced immediately after the treatments were applied (mid July) in 2002–2004 and collected immediately prior to treatment application in the following year (early July), 2003–2005. Three incubation tubes were examined for each treatment in each block (180 tubes in total) and the average of the three values was used in all statistical analyses. Available ammonium and nitrate were extracted from sieved soil by shaking 25 g soil in 100 mL 1 M KCl for 1 h. The resulting suspension was filtered through Whatman no. 2 paper and analyzed with a SKALAR continuous flow analyzer (SKALAR, Breda, The Netherlands). Mineralization was defined as the increase in extractable ammonium and nitrate in the PVC tubes and is reported as g N mineralized/g soil/year.

Soil temperature was measured at a depth of 10 cm every hour between 14 July 2003 and 21 August 2004 using Tinytag temperature loggers with external soil probes. Temperatures were not recorded in the lightly trampled plots; this was to reduce to 40 the number of loggers required.

STATISTICAL ANALYSES

The effects of the three experimental treatments (mowing [M], trampling [T], and fertilization [F]) on the response variables (plant biomass, root biomass, moss biomass, APP, net N mineralization, and root production) were analyzed using linear mixed effect models for time series data; the *lme* function within the *nlme* module of the R statistical package (R Development Core Team, 2006) was applied. Mowing, trampling, and fertilization were fixed factors and the random effect was Year (Y), nested within the plots. Relationships between factors were tested using Pearson's correlations.

Results

Vascular plant biomass at the beginning of the growing season increased as a result of fertilization in the absence of mowing ($F \times Y$; Table 1, Fig. 1A), but there were no significant effects of mowing and trampling. Fertilization increased and mowing decreased autumn plant biomass and the differences were already detectable at the end of the first year ($F \times G$, $F \times M \times Y$; Table 1, Fig. 1B). Trampling decreased autumn plant biomass in the fertilized plots, but had no effect in the unfertilized plots ($F \times IT \times Y$, $F \times LT \times Y$; Table 1, Fig. 1B). Mowing and trampling reduced root biomass, but only when there was no fertilization. Mowing and trampling had no effect on root biomass when the plots were fertilized ($F \times IT \times M$; Table 1, Fig. 1C). Intense

TABLE 3

Effects of mowing (M), trampling (T), and fertilization (F) on average soil temperatures from July 2002 until July 2003. The *t*-values from a linear mixed effect model are given in the table. All tests were performed with 28 degrees of freedom and *t*-values greater than 2 are thus regarded as being statistically significant ($P < 0.05$). Significant *t*-values are highlighted in bold. Trampling was the only treatment that had a significant effect on soil temperature. The exact *P*-values for the significant tests are: July 2002, $P = 0.004$; August 2002, $P = 0.008$; June 2003, $P = 0.006$; July 2003, $P = 0.001$.

	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Fertilized	0.5	-0.5	-2.0	1.5	-1.1	-0.9	-0.7	-0.7	-0.9	-0.9	-1.0	0.7	0.6
Mowed	0.7	0.4	0.0	-1.4	0.4	-0.5	-0.3	0.1	0.5	0.1	-0.4	1.0	1.7
Trampled	3.1	2.9	0.9	1.5	0.6	-1.5	-1.4	-1.2	1.3	1.5	1.3	3.0	4.8
F × M	-0.9	0.1	2.0	-1.0	0.7	0.1	-0.3	0.2	0.6	0.9	1.1	-0.5	-1.4
F × T	-1.5	-0.4	-0.2	0.3	0.3	1.3	1.3	1.2	0.6	0.0	0.0	-1.0	-1.3
M × T	-1.3	-1.0	-0.4	0.3	-0.8	0.6	-0.2	0.7	-0.6	-0.9	-0.2	-0.4	-0.8
F × M × T	1.2	0.3	-0.5	0.9	-0.3	-1.0	-0.2	-0.5	-1.1	-0.6	-0.5	0.3	0.3

trampling greatly reduced moss biomass, but there was no significant effect of light trampling, fertilization, or mowing on moss biomass (IT × Y, LT × Y; Table 1, Fig. 1D).

AGNPP was highest in the first year in the plots that were both fertilized and mowed, and lowest in the plots that were not fertilized but were mowed (F × M; Table 2, Fig. 2A). However, AGNPP increased in the plots that were fertilized but not mowed, decreased in plots that were not fertilized but were mowed, and remained constant in the plots that were neither fertilized nor mowed, and those that were both fertilized and mowed (F × M × Y; Table 2, Fig. 2A). Trampling reduced the belowground primary production as early as the first year in the unfertilized plots (F × IT; Table 2, Fig. 2B). BGNPP increased over the next three years in the fertilized plots, but remained low in the unfertilized ones (F × IT × Y; Table 2, Fig. 2B). Trampling increased net nitrogen mineralization (IT × Y; Table 2, Fig. 2C). Mowing reduced net nitrogen mineralization from the first year onwards (M; Table 2, Fig. 2C) and net nitrogen mineralization continued to decrease in the mowed plots, but increased in the unmowed ones (G × Y; Table 2, Fig. 2C).

The intense trampling treatment increased summer soil temperatures (Table 3). This could have been the result of reduced moss cover, since moss biomass and soil temperatures in July were negatively correlated ($t = -2.1$, $df = 38$, $P = 0.042$, $r = -0.32$; Fig 3a). There was no correlation between soil temperature in July and vascular plant biomass ($t = 0.1$, $df = 38$, $P = 0.916$, $r = -0.02$; Fig 3b). As a result of changed soil temperatures or litter quality, moss biomass may influence nitrogen mineralization: moss biomass and net nitrogen mineralization were negatively correlated ($t = -3.5$, $df = 178$, $P < 0.001$, $r = -0.25$; Fig 3c). Nitrogen mineralization was positively correlated with both AGNPP ($t = 6.0$, $df = 178$, $P < 0.001$, $r = 0.41$; Fig 3d) and BGNPP ($t = 2.5$, $df = 178$, $P = 0.015$, $r = 0.18$; Fig 3e).

Discussion

The activities of herbivores may promote plant growth and thus enhance the animals' own food supply in arctic ecosystems (Zimov et al., 1995; Wilson and Jefferies, 1996; Olofsson et al., 2001, 2004a; Person et al., 2003; van der Wal et al., 2004; van der Wal, 2006). These positive effects have typically been found in ecosystems dominated by graminoids or where herbivores have caused a shift in the vegetation from moss or dwarf-shrub-dominated tundra to graminoid-dominated meadows (Zimov et al., 1995; Wilson and Jefferies, 1996; Olofsson et al., 2001, 2004a; Olofsson, 2006; van der Wal et al., 2004; van der Wal, 2006). Van der Wal and Brooker (2004) suggested that herbivores increase the

production of graminoids in arctic ecosystems as a result of two simultaneous positive feedback loops. In the first, herbivore grazing and trampling reduce the depth of the moss layer, thus increasing the soil temperature, and consequently the nutrient supply. In the second loop, graminoids benefit directly from herbivores as a result of the input of additional nutrients from urine and feces. In both cases, rhizomatous graminoids are

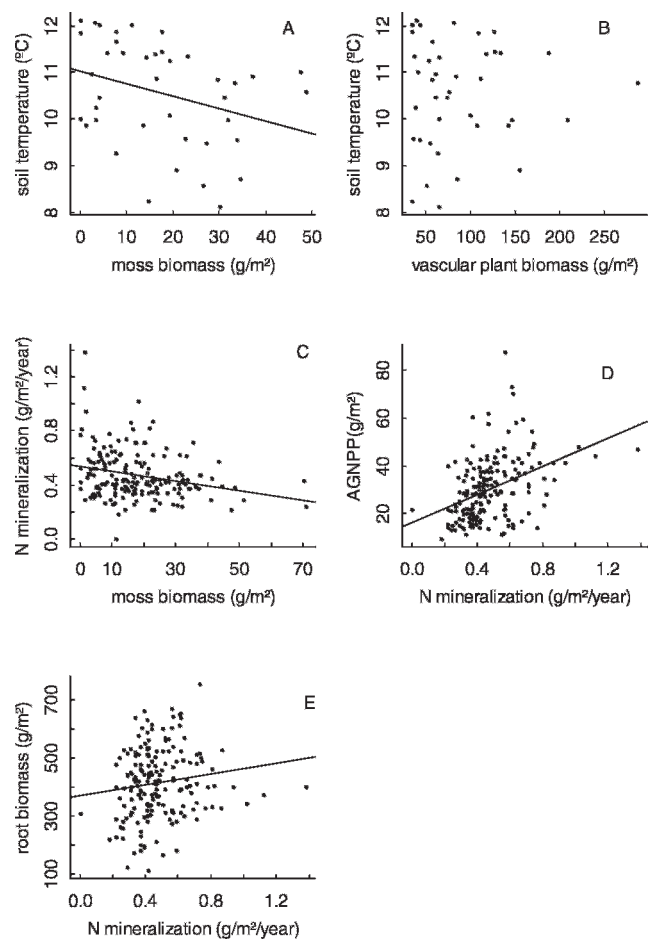


FIGURE 3. Correlations between soil temperatures in July, moss biomass, vascular plant biomass, N mineralization, and aboveground net primary production. The correlations between soil temperatures and moss and vascular plant biomass are based on data from 2004 (the only year this was collected). All other correlations are based on data from all four years. The statistical significance of the correlations was tested using Pearson's product moment correlation, and significant correlations are indicated by a line on the graph.

avored because they respond rapidly to increased temperature and nutrient supplies (Chapin and Shaver, 1985), and they have basal meristems that make them resilient to grazing (McNaughton, 1984). The results of this study only partially support the existence of these two feedback loops. I found that trampling triggered the first feedback loop by reducing the depth of the moss layer, but the hypothesis that fertilization leads to a reduction in the depth of the moss layer and, hence, increased soil temperatures was not supported. Moreover, although trampling enhanced soil temperatures in all plots, N mineralization increased substantially only in the unmowed plots. Therefore, the reduced supply of fresh litter might have limited the positive effect of enhanced temperatures in the mowed plots. Moreover, simulated trampling had only minor effects on plant growth. Although no evidence of overcompensation in primary production due to herbivory was found in this study, there were indications that the positive feedback with respect to plant nutrient supply enables this ecosystem to support an entire trophic level with no apparent effects on primary production.

Although the increased soil temperatures did speed up the nitrogen turnover rate, most of the other positive and negative effects were associated with adding or removing nutrients. Nitrogen mineralization and primary production were both reduced by mowing and the effect was counteracted by fertilizer application. This has important implications for the long-term interpretation of this data since theoretical and empirical work have shown that nutrient losses and gains mediated by herbivores, rather than altered turnover rates, determine plant production in the long term (de Mazancourt et al., 1998; de Mazancourt and Loreau, 2000; Olofsson et al., 2007). However, in this study, N mineralization and primary production decreased rapidly in response to removal of plant tissue. This indicates that, although decomposition processes are slow in arctic ecosystems (Hobbie, 1996), at least some of the nutrients returned to the soil through plant litter are taken up rapidly by plants.

Our results indicate that some reindeer activities are likely to have a positive effect while others are likely to have a negative effect on nutrient availability and primary production. Perhaps the balance between these activities might explain, in part, why reindeer have a positive effect on soil nutrient availability and primary production in some areas (Olofsson et al., 2001, 2004a; Stark et al., 2002) but a negative effect in other areas (Olofsson et al., 2001, 2004a; Grellmann, 2002; Stark and Grellmann, 2002; Bråthen et al., 2007). Reindeer should, therefore, increase primary production in areas where there is high feces deposition, such as preferred resting places close to snow fields, and decrease primary production in sites where their main activity is grazing, but where they do not rest because of insect harassment. Although little data is available on nutrient transportation, Stark and Grellmann (2002) suggested that reindeer may have transported nutrients out of their study area as a result of seasonal migration. However, reindeer can also alter soil nutrient availability and primary production without affecting the size of the nutrient pool. Reindeer increase net nitrogen mineralization and primary production along fences as a result of intensive summer grazing; in these cases the vegetation changes from dwarf shrub heathland to grass-dominated meadows (Olofsson et al., 2001, 2004a; Stark et al., 2002). Even along fences that are almost 40 years old, there is no difference in the size of the total nitrogen pool between the associated grassland and the adjacent heathland (Olofsson et al., 2004a).

One problem with interpreting grazing simulation experiments is that they do not directly mimic real herbivores. The most important difference in this study was that the mowing treatment did not reflect the selectivity of reindeer. This limits the relevance

of this study since it has been suggested that selective grazing of palatable plants is one of the most common mechanisms through which herbivores reduce nutrient turnover (Pastor and Naiman, 1992; Pastor et al., 1993; Ritchie et al., 1998; Sirotinak and Huntly, 2000; Persson et al., 2007). Adding reindeer feces increased the growth of grasses and reduced the thickness of the moss layer in arctic tundra on Svalbard (van der Wal et al., 2004). The greater variability in moss depth indicated that the patchy distribution of reindeer waste products was important for the decay of mosses on Svalbard (van der Wal et al., 2004). In contrast, fertilization did not reduce moss biomass in the study described herein. Evenly distributed fertilizer may be more favorable to mosses than are fecal patches, since toxic levels of nutrients are less likely to be experienced by any single moss shoot. However, differences between the plots that have nothing to do with the treatments, such as soil conditions, plant species pool, and microclimatic conditions may also explain the different results. The defecation, trampling, and grazing simulation treatments were all much more intense than the real impacts of natural grazing in the research area and are probably comparable to grazing intensities in areas where reindeer have been found to cause major vegetation shifts (Olofsson et al., 2001, 2004a). I chose this high level of impact in order to obtain clear effects so that the relative importance of each treatment could be compared in an efficient way and so that the results from this experiment could be compared to studies that have reported reindeer-induced vegetation shifts (Olofsson et al., 2001, 2004a).

The importance of increased nutrient turnover and primary production as a result of a reduced moss layer and increased soil temperatures has been highlighted as an important process in arctic ecosystems (Zimov et al., 1995; van der Wal and Brooker, 2004; van der Wal et al., 2004; Olofsson et al., 2004a). Many herbivores other than reindeer can reduce the cover of the moss layer in arctic ecosystems. Voles and lemmings severely reduce moss cover during peak years (Moen et al., 1993; Virtanen et al., 1997, 2002; Olofsson et al., 2002, 2004b). However, although the effect of mosses on isolation, and its consequent impact on soil temperatures, has been well documented (Gornall et al., 2007), changed albedo of the ground may also be an important factor affecting soil temperatures in grazed areas. Even minimal disturbance can lead to a darkening of the ground surface and so increase heat transmission from above to below the ground (Haag and Bliss, 1974).

The results from this study show that the different activities of reindeer can have both positive and negative effects on soil nutrient availability and primary production, thus providing some explanation of why reindeer sometimes have positive and sometimes have negative impacts on their own food supply.

Acknowledgments

I stayed at the Abisko Scientific Research Station while I conducted this study. This study was supported by grants from the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning and from Stiftelsen Oscar och Lili Lamms Minne. Sari Stark and Rene Van der Wal made valuable comments on a previous version of this paper.

References Cited

- Aerts, R., and Chapin, F. S., 2000: The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, 30: 1–67.
- Bardgett, R. D., and Wardle, D. A., 2003: Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, 84: 2258–2268.

- Bazely, D. R., and Jefferies, R. L., 1989: Lesser snow geese and the nitrogen economy of a grazed salt-marsh. *Journal of Ecology*, 77: 24–34.
- Belovsky, G. E., and Slade, J. B., 2000: Insect herbivores accelerate nutrient cycling and increase plant production. *Proceedings of the National Academy of Science*, 97: 14412–14417.
- Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Fauchald, P., Tveraa, T., and Hausner, V. H., 2007: Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems*, 5: 773–789.
- Buckeridge, K. M., and Jefferies, R. L., 2007: Vegetation loss alters soil nitrogen dynamics in an Arctic salt marsh. *Journal of Ecology*, 95: 283–293.
- Chapin, F. S., III, and Shaver, G. R., 1985: Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, 66: 564–576.
- Classen, A. T., Hart, S. C., Whitman, T. G., Cobb, N. S., and Koch, G. W., 2005: Insect infestations linked to shifts in microclimate: important climate change implications. *Soil Science Society of American Journal*, 69: 2049–2057.
- Cougenhour, M. B., 1991: Spatial components of plant-herbivore interactions in pastoral, ranging, and native ungulate ecosystems. *Journal of Range Management*, 44: 530–542.
- de Mazancourt, C., and Loreau, M., 2000: Effect of herbivory and plant species replacement on primary production. *American Naturalist*, 155: 735–754.
- de Mazancourt, C., Loreau, M., and Abbadié, L., 1998: Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology*, 79: 2242–2252.
- Frank, D. A., and Evans, R. D., 1997: Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology*, 78: 2238–2248.
- Frank, D. A., and Groffman, P. M., 1998: Ungulate vs. landscape control over C and N processes in grasslands of Yellowstone National Park. *Ecology*, 79: 2229–2241.
- 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: 157–161.
- Frank, D. A., Inouye, R. S., Huntly, N., Minshall, G. W., and Anderson, J. E., 1994: The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. *Biogeochemistry*, 10: 163–180.
- Frank, D. A., Groffman, P. M., Evans, R. D., and Tracy, B. F., 2000: Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. *Oecologia*, 123: 116–121.
- Frank, D. A., Evans, R. D., and Tracy, B. E., 2004: The role of ammonia volatilization in controlling the natural N-15 abundance of a grazed grassland. *Biogeochemistry*, 68: 169–178.
- 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.
- Grellmann, D., 2002: Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos*, 98: 190–204.
- Haag, R. W., and Bliss, L. C., 1974: Energy budget changes following surface disturbance to upland tundra. *Journal of Applied Ecology*, 11: 355–374.
- Hamilton, E. W., 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.
- Hamilton, E. W., Frank, D. A., Hinchey, P. M., and Murray, T. R., 2008: Defoliation induces root exudation and triggers positive rhizospheric feedbacks in a temperate grassland. *Soil Biology & Biochemistry*, 40: 2865–2873.
- 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: 180–195.
- Hobbie, S. E., 1996: Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, 66: 503–522.
- Hobbs, N. T., 1996: Modification of ecosystems by ungulates. *Journal of Wildlife Management*, 60: 695–713.
- Johnson, C. J., Parker, K. L., Heard, D. C., and Gillingham, M. P., 2002: Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology*, 71: 225–235.
- Kashulina, G., Reimann, C., Finne, T. E., de Caritat, P., and Niskavaara, H., 1997: The state of the ecosystems in the central Barents region: scale, factors and mechanism of disturbance. *Science of the Total Environment*, 206: 203–225.
- Lauenroth, W. K., 2000: Methods of estimating belowground net primary production. In Sala, O. E., Jackson, R. B., Mooney, H. A., and Howarth, R. W. (eds.), *Methods in Ecosystem Science*. Berlin: Springer, 58–71.
- Lauenroth, W. K., and Whitman, W. C., 1971: A rapid method for washing roots. *Journal of Range Management*, 24: 308–309.
- Mårell, A., and Edenius, L., 2006: Spatial heterogeneity and hierarchical feeding habitat selection by reindeer. *Arctic, Antarctic, and Alpine Research*, 38: 413–420.
- McNaughton, S. J., 1983: Compensatory growth as a response to herbivory. *Oikos*, 40: 329–336.
- McNaughton, S. J., 1984: Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist*, 124: 863–886.
- Moen, J., and Danell, O., 2003: Reindeer in the Swedish mountains: an assessment of grazing impacts. *Ambio*, 32: 397–402.
- Moen, J., Lundberg, P. A., and Oksanen, L., 1993: Lemming grazing on snow-bed vegetation during a population peak, northern Norway. *Arctic and Alpine Research*, 25: 130–135.
- Nellemann, C., 1996: Terrain selection by reindeer in late winter in central Norway. *Arctic*, 49: 339–347.
- Nellemann, C., and Thomsen, M. G., 1994: Terrain ruggedness and caribou forage availability during snowmelt on the arctic coastal plain, Alaska. *Arctic*, 47: 361–367.
- Olf, H., and Ritchie, M. E., 1998: Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, 13: 261–265.
- Olofsson, J., 2006: Short- and long-term effects of changes in reindeer grazing pressure on tundra heath vegetation. *Journal of Ecology*, 94: 431–440.
- Olofsson, J., and Oksanen, L., 2002: Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer, a litterbag experiment. *Oikos*, 96: 507–515.
- Olofsson, J., and Oksanen, L., 2005: Effects of reindeer density on vascular plant diversity on north Scandinavian mountains. *Rangifer*, 25: 5–18.
- Olofsson, J., and Shams, H., 2007: Determinants of species richness in an alpine meadow. *Journal of Ecology*, 95: 916–925.
- Olofsson, J., Kitti, H., Rautiainen, P., Stark, S., and Oksanen, L., 2001: Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, 24: 13–24.
- Olofsson, J., Moen, J., and Oksanen, L., 2002: Effects of herbivory on competition intensity and species diversity in two arctic-alpine tundra communities with different productivity. *Oikos*, 96: 265–272.
- Olofsson, J., Stark, S., and Oksanen, L., 2004a: Herbivore influence on ecosystem processes in the tundra. *Oikos*, 105: 386–396.
- Olofsson, J., Hulme, P. E., Oksanen, L., and Suominen, O., 2004b: Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos*, 106: 324–334.
- Olofsson, J., de Mazancourt, C., and Crawley, M. J., 2007: Contrasting effects of rabbit exclusion on nutrient availability and primary production in grasslands at different time scales. *Oecologia*, 150: 582–589.
- Pastor, J., and Naiman, R. J., 1992: Selective foraging and ecosystem processes in boreal forests. *American Naturalist*, 131: 690–705.
- Pastor, J., Dewey, B., Naiman, R. J., McInnes, P. F., and Cohen, Y., 1993: Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology*, 74: 467–480.

- Person, B. T., Herzog, M. P., Ruess, R. W., Sedinger, J. S., Anthony, R. M., and Babcock, C. A., 2003: Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. *Oecologia*, 135: 583–592.
- Persson, I.-L., Pastor, J., Danell, K., and Bergström, R., 2005: Impact of moose population density on the production and composition of litter in boreal forests. *Oikos*, 108: 297–306.
- Persson, I.-L., Bergström, R., and Danell, K., 2007: Browse biomass production and regrowth capacity after biomass loss in deciduous and coniferous trees in response to moose browsing along a productivity gradient. *Oikos*, 116: 1639–1650.
- R Development Core Team, 2006, *R: a Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing, <<http://www.R-project.org>>.
- Raison, R. J., Cornell, M. J., and Knops, M. H., 1987: Methodology for studying fluxes of soil mineral-N in situ. *Soil Biology and Biochemistry*, 19: 165–177.
- Ritchie, M. E., Tilman, D. J., and Knops, M. H., 1998: Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology*, 79: 165–177.
- Ruess, R. W., and McNaughton, S. J., 1987: Grazing and the dynamics of nutrients and energy regulated microbial processes in the Serengeti grasslands. *Oikos*, 49: 101–110.
- Rustad, L. E., Campbell, J. L., Marion, G. M., Norby, R. J., Mitchell, M. J., Hartley, A. E., Cornelissen, J. H. C., and Gurevitch, J., 2001: A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126: 543–562.
- Sala, O. E., and Austin, A. T., 2000: Methods of estimating aboveground net primary productivity. In Sala, O. E., Jackson, R. B., Mooney, H. A., and Howarth, R. W. (eds.), *Methods in Ecosystem Science*. Berlin: Springer, 31–42.
- Schimel, D. S., Parton, W. J., Adamsen, F. J., Woodmansee, R. G., Senft, R. I., and Stillwell, M. A., 1986: The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. *Biogeochemistry*, 2: 39–52.
- Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., and Swift, D. M., 1987: Large herbivore foraging and ecological hierarchies. *Bioscience*, 37: 789–799.
- Sirotnak, J. M., and Huntly, N. J., 2000: Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology*, 81: 78–87.
- Sørensen, L. I., Kytöviita, M. M., Olofsson, J., and Mikola, J., 2008: Soil feedback on plant growth in a sub-arctic grassland as a result of repeated defoliation. *Soil Biology and Biochemistry*, 40: 2891–2897.
- Stark, S., and Grellmann, D., 2002: Soil microbial responses to herbivory in an arctic tundra heath at two levels of nutrient availability. *Ecology*, 83: 2736–2744.
- Stark, S., Strömmer, R., and Tuomi, J., 2002: Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. *Oikos*, 97: 69–78.
- Suominen, O., and Olofsson, J., 2000: Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: a review. *Annales Zoologici Fennici*, 37: 233–249.
- Thing, H., 1984: Feeding ecology of the West Greenland caribou (*Rangifer tarandus groenlandicus*) in the Sisimiut-Kangerlussuaq region. *Danish Review of Game Biology*, 12: 1–51.
- van der Wal, R., 2006: Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, 114: 177–186.
- Van der Wal, R., and Brooker, R. W., 2004: Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology*, 18: 77–86.
- Van der Wal, R., Bardgett, R. D., Harrison, H. A., and Stien, A., 2004: Vertebrate herbivores and ecosystem control: cascading effects on tundra ecosystems. *Ecography*, 27: 242–252.
- Virtanen, R., Henttonen, H., and Laine, K., 1997: Lemming grazing and structure of a snowbed plant community—A long term experiment at Kilpisjärvi, Finnish Lapland. *Oikos*, 79: 155–166.
- Virtanen, R., Parviainen, J., and Henttonen, H., 2002: Winter grazing by the Norwegian lemming (*Lemmus lemmus*) at Kilpisjärvi (NV Finnish Lapland) during a moderate population peak. *Annales Zoologici Fennici*, 39: 335–341.
- Wardle, D. A., 2002: *Communities and Ecosystems: Linking the Aboveground Components*. Princeton, New Jersey: Princeton University Press.
- Weintraub, M. N., and Schimel, J. P., 2003: Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. *Ecosystems*, 6: 129–143.
- Wilson, D. J., and Jefferies, R. L., 1996: Nitrogen mineralization, plant growth and goose herbivory in an Arctic coastal ecosystem. *Journal of Ecology*, 84: 841–851.
- Zimov, S. A., Chuprynin, V. I., Oreshko, F. S., Chapin, F. S., III, Reynolds, J. F., and Chapin, M. C., 1995: Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. *American Naturalist*, 146: 765–794.

MS accepted January 2009