Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment

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Heavy grazing and trampling by reindeer increase nutrient cycling and primary production in areas where grasslands have replaced shrub and moss tundra. One way in which herbivores can affect nutrient cycling is through changing the litter decomposition processes. We studied the effect of herbivory on litter decomposition rate by reciprocal transplantation of litter between lightly grazed and heavily grazed areas, using the litterbag technique. We used litter from two of the most common species on the lightly grazed side, Betula nana and Empetrum nigrum, and two of the most common species on the heavily grazed side, Carex bigelowii and Deschampsia flexuosa. We found that herbivory improved litter quality by favouring species with easily decomposed litter. However, herbivory also improved litter quality by increasing the nitrogen content and lowering the C/N ratio of each species. Decomposition rates even correlated with the abundance of the plant category in question. Shrub litter decomposed faster in the lightly grazed area where shrubs were common, and graminoid litter decomposed faster in the heavily grazed area where graminoids were common. These results indicate that the decomposer micro-organisms are adapted to the most common litter types. This study shows that detailed information about the effect of herbivory on litter quality is important to understand differences between the short-term and long-term effects of herbivory on nutrient cycling and primary production.

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There are contrasting views about how herbivores influence the productivity of ecosystems. One group of hypotheses predicts that herbivores have an accelerating effect on nutrient cycling (McNaughton 1985, Holland et al. 1992, Zimov et al. 1995, Ritchie et al. 1998, Sirotnak and Huntly 2000). Increased tissue loss in grazed areas should favour grazing-tolerant species with a high regrowth rate. To be able to have a high growth rate the plants have a high nutrient uptake and a high nutrient content in plant tissue. The higher nutrient content in plant tissue results in fast decomposing litter, high nutrient mineralization and high nutrient availability. An alternative hypothesis predicts that herbivores have a decelerating effect on nutrient cycling (Bryant et al. 1991, Pastor and Naiman 1992). Herbivores feed selectively on plants with a high nutrient content and thus increase the dominance of plant species with low nutrient content. This results in low litter quality, low decomposition rate and low nutrient availability.

Both hypotheses have support from empirical studies. Grazing-enhanced nutrient cycling and primary production have been reported from African savannas grazed by native ungulate herbivores (McNaughton 1979, 1985, Seagle et al. 1992), cattle grazed grasslands in India (Singh et al. 1991, Pandey and Singh 1992), geese grazed sub-arctic salt marsh (Cargill and Jefferies 1984, Bazely and Jefferies 1985, 1989, Hik and Jefferies 1990) and bison and elk grazed grasslands in North America (Frank and McNaughton 1993, Frank and

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Evans 1997). However, herbivory depressed nutrient cycling and primary production in boreal forests in North America (McInnes et al. 1992, Pastor and Naiman 1992, Pastor et al. 1993) and in North American Oak Savanna (Ritchie et al. 1998).

Grazing influences the cycling of nutrients mainly in two ways: through transforming plants into urine and faecal material and by influencing litter decomposition (Hobbs 1996, Bardgett et al. 1998). The direct consumption of plants by herbivores normally enhances nutrient cycling, as the nutrient release from faeces tends to be faster than the nutrient release from litter (Ruess and McNaughton 1987, Ruess et al. 1989, Hobbs 1996). However, the direct effect of herbivores on nutrient cycling is not always positive as the release of nutrients from faeces produced when grazers are facing nutrient shortage is slower than the release from plants and plant litter (Floate 1970, Pastor et al. 1993), because much of the nutrients in the plant material are taken up by the herbivore during digestion (Pastor et al. 1993). The nutrient pathway through urine and faeces is important in systems where a large proportion of the vegetation is consumed by herbivores, as in sub-arctic salt marshes grazed by lesser snow geese, where about 80% of the above-ground production was consumed (Cargill and Jefferies 1984). In most ecosystems, the largest part of the plant material reaches the soil as litter, rather than being consumed by herbivores (McNaughton et al. 1989, Cebrian 1999) and it is therefore essential to have a grasp of the effect of herbivory on the litter quality if we wish to understand the effect of herbivory on nutrient cycling.

In many ecosystems, the indirect effect of herbivores on litter quality and quantity is more important for the primary production and nutrient dynamics than the direct effect through urine and faeces (McInnes et al. 1992, Pastor et al. 1993, Turner et al. 1993, Kielland and Bryant 1998, Sirotnak and Huntly 2000). Herbivory might influence the litter quality by changing the species composition (Bryant et al. 1991, Huntly 1991, Pastor and Naiman 1992, Kielland and Bryant 1998) as litter from different species differ in decomposition rate (Grime et al. 1996). However, herbivory might also alter the decomposition rate by changing the litter quality within a species (Hobbie 1992, Findlay et al. 1996, Kielland et al. 1997) or by changing the abiotic condition relevant for litter decomposition, such as soil temperature or soil water content (Knapp and Seastedt 1986, Zimov et al. 1995, Kielland and Bryant 1998).

In an earlier study, heavy reindeer grazing has been reported to increase plant primary production and enhance nutrient cycling in the Fennoscandian tundra (Olofsson et al. 2001). In this study, we tested whether changes in litter decomposition rate might cause these changes in nutrient cycling and primary production. We performed a reciprocal transplantation of litter between lightly grazed and heavily grazed areas, using the litterbag technique. We used litter from two of the dominant species on the lightly grazed area and two of the dominant species on the heavily grazed area. In combination with earlier published data on primary production of the different species (Olofsson et al. 2001), the data thus obtained allowed evaluation of the relative importance of the changes in litter quality for nutrient cycling and primary productivity.

Study area and methods

Research was conducted in the mountain area of Raisduoddar, Troms Fylke, northernmost Norway (69°30'N, 27°30'E), at a suboceanic tundra site (Oksanen and Virtanen 1995), at altitudes between 600 and 700 m a.s.l. The predominating vegetation consists of tundra heath of the Arctic Empetrum-Dicranum-Lichen type (Oksanen and Virtanen 1995). The study was conducted along a reindeer fence, established in the 1960s, to reduce the risk that reindeer illegally enter migration areas or winter ranges during the summer. The fence was built of wire attached to two-metre-high posts, and stretches in a north-south direction with the summer range on the west side of the fence and the spring and autumn range on the east side. This part of the summer range is heavily grazed in August. The spring and autumn range is almost ungrazed, except for the vicinity of the gate, which has been avoided in this study. Few signs of reindeer, such as hoof-pads and faeces, are found in the spring and autumn range. The few reindeer in the spring and autumn range graze in this area right before they enter, or right after they leave the summer range. Thus, there is no crucial time difference between the grazing in the summer range and the spring and autumn range. The spring and autumn range is referred to as the lightly grazed side and the summer range is referred to as the heavily grazed side. At the heavily grazed side, the original dwarf shrub heath has been replaced by graminoid-dominated vegetation (Olofsson et al. 2001).

Primary production of different plant species was estimated by harvesting annual increments of all plant species inside 25 squares of 0.25 m² in each grazing treatment and by drying samples to a constant weight. The data on primary production have been previously published on the collective plant community level (Olofsson et al. 2001). Here the data have been analysed by the plant categories used in the litter decomposition experiment. Leaves of *Carex bigelowii*, *Deschampsia flexuosa*, *Betula nana* and *Empetrum nigrum* were collected 10 m from the fence at ten different sites with 100 m in between, at the heavily grazed side and the lightly grazed side of the fence, on 26 and 27 August. At this time of the year, the autumn processes (hardening and withdrawal of chlorophyll) had started, but the leaves were still attached to the plants. We collected the leaves when they were still attached to the plants to ensure that the litter was coming from the grazing treatment intended. On tundra, litter can be carried over long distances by strong autumn winds. A consequence of this method of collecting leaves is that our litter samples probably had higher N contents and higher decomposition rates than litter fallen to the ground, as the plants had not yet withdrawn all nutrients. This is especially true for the leaves from the evergreen *Empetrum nigrum* where we used leaves that had hardened but not withered. However, as the main objective of this study was to compare decomposition rates of litter between the different grazing treatments, we prioritised certainty of the litter source. Although the way we collected the litter clearly influenced the absolute decomposition rates, it should not alter the relative decomposition rate of litter from different species or different grazing treatments. The plant material was dried to constant weight (48 h, 60°C). In total, 160 litterbags were made of polyester net $(15 \times 15 \text{ cm})$ with 1.0 mm mesh size, 20 litterbags of each litter type, and about 1 g of dried plant material was placed in each bag. Before placing the litter in the litterbags, samples were taken for chemical analysis of initial litter quality.

On 10 July 1999, litterbags containing plant material from the heavily grazed populations and the lightly grazed populations of each species (eight bags) were laid out at ten different sites (100 m in between, 10 m from the fence) for decomposition on the heavily grazed side and the lightly grazed side, respectively. After one year of exposure on the tundra, the litterbags were collected and parts of plants, which had been growing into the bags, were sorted out. The remaining litter was dried to constant weight and weighed with an accuracy of 0.1 mg. The C and N contents were analysed on oven-dried milled material using a Elemental analyser, Perkin Elmer mod. 2400 CHN Norwalk, Connecticut, USA, in six litterbags of each combination of species, litter origin and decomposition condition and six samples of initial plant material (i.e. total number of samples was 96). The initial and final C and N contents, weight loss and C and N loss were tested with a three-way analysis of variance, with origin of litter, decomposition location and species as fix factors. The data fulfilled the assumptions of normality and homoscedasticity.

Results

The over-all primary production of vascular plants was higher in the heavily grazed area than in the lightly grazed area (t = 2.30, d.f. = 48, p = 0.026; Fig. 1), but different plant categories responded differently. Grasses (t = 5.23, d.f. = 48, p < 0.001) and sedges (t = 6.66, d.f. = 48, p < 0.001) had higher primary production in the heavily grazed area than in the lightly grazed area. Evergreen (t = 4.89, d.f. = 48, p < 0.001) and deciduous (t = 6.17, d.f. = 48, p < 0.001) shrubs had higher primary production in the lightly grazed area than in the heavily grazed area. The production of forbs did not differ significantly between the two grazing treatments (t = 1.32, d.f. = 48, p = 0.192).

The identity of the plant species from which the litter originated had the largest impact on decomposition rates, and influenced significantly both the relative weight loss, the relative C loss and the relative N loss from the litterbags (Fig. 2, Table 1). The relative weight loss and the C loss were higher in litter from *Carex bigelowii and Deschampsia flexuosa* than in litter from *Betula nana* or *Empetrum nigrum*, both on the lightly grazed and on the heavily grazed side (Fig. 2, Table 1). The N loss from the litterbags was higher for litter from *C. bigelowii*, *D. flexuosa* and *B. nana* than for litter from *E. nigrum* (Fig. 2, Table 1).

The decomposition rate of the litter within each species was clearly influenced by grazing. Litter from plants growing on the heavily grazed side had higher weight loss than litter from plants growing on the lightly grazed side (Fig. 2, Table 1), for all species except *E. nigrum*, where there was no significant rela-



primary production

Fig. 1. Above-ground primary production (mean + SE) on the heavily and lightly grazed sides of the fence.

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10 0 Carex bigelowii Deschampsia Betula nana flexuosa Empetrum nigrum

tionship between previous grazing regime and decomposition rate of the plant material. Even though the influence of previous grazing regime of the plant that the litter originated from was not significant for C and N (Fig. 1, Table 1), the trend was the same for all three measurements of decomposition rate.

The decomposition rate was also influenced by the location where the decomposition took place (Fig. 2, Table 1). Even if the effect of decomposition site for the decomposition rate was only significant for the total N loss, the site \times species interaction was significant for relative weight loss, C loss and N loss (Table 1). *C. bigelowii* and *D. flexuosa* had higher decomposition rate on the heavily grazed site, while *B. nana* and *E. nigrum* decomposed faster on the lightly grazed side (Fig. 2, Table 1).

The initial C and N concentrations differed between the different species and between the different previous grazing regimes (Tables 2, 3). The N concentration was highest in litter from *B. nana* (Table 2). The C concentration was higher in litter from *B. nana* and *E. nigrum* than in litter from *C. bigelowii* and *D. flexuosa* (Table 2). The initial C concentration was lower and the initial N concentration was higher in the litter from plants growing in the heavily grazed side than in the litter from plants growing in the lightly grazed side (Tables 2, 3). from lightly grazed side on lightly grazed side

from heavily grazed side on lightly grazed side

□ from lightly grazed side on heavily grazed side

from heavily grazed side on heavily grazed side Fig. 2. a. Relative weight loss, b. relative nitrogen loss and c. relative carbon loss in litterbags that have decomposed for one year either in a lightly grazed area or in a heavily grazed area. The litterbags are filled either with litter collected from plants on the lightly grazed side or with litter collected from plants on the heavily grazed side.

Differences in C and N concentrations between litter from the four different plant species after one year of decomposition on the tundra followed the initial C and N concentrations (Tables 2, 3). There were no statistically significant differences between the final C concentration in the decomposed litter between litterbags located in the heavily or lightly grazed area. However, the final N concentration was dependent both on the species \times site and the species \times litter quality interactions (Tables 2, 3). Final N concentration was higher in litter originating from previously grazed plants for D. flexuosa and E. nigrum, but lower in plant material coming from heavily grazed plants for B. nana. The final N concentration was higher in litter of D. flexuosa decomposing on the heavily grazed side while the final N concentration was lower in litter from B. nana and E. nigrum decomposing on the heavily grazed side (Tables 2, 3).

Discussion

Reindeer grazing is influencing the litter decomposition processes in tundra areas. As expected, litter from different species decomposes at different rates, and litter originating from heavily grazed plants decomposed faster than litter originating from lightly grazed plants. Even if there was no significant effect of the location of the litterbag for the decomposition rate, the decomposition conditions still differed between the lightly grazed and heavily grazed site, as there was a significant interaction term between the species and the location of the litterbag. Both litter N content and decomposition rate were higher than expected for the species used in this study. This is a consequence of that we, in order to ensure the origin of the litter, collected the plant material before the plants had withdrawn all nutrients and dropped the leaves.

The two graminoids, C. bigelowii and D. flexuosa, decomposed faster than the deciduous shrub, B. nana, and the evergreen dwarf shrub, E. nigrum. As the species within each of the three growth-form categories (graminoids, evergreen shrubs and deciduous shrubs), have similar litter decomposition rates, these categories are probably useful for generalising effects of species composition on decomposition (Chapin et al. 1995). That graminoid litter decomposed faster than litter from deciduous shrubs and evergreen dwarf shrubs corresponds to the result of Hobbie (1996), who found the same pattern in a study from the Alaskan tundra. However, the slow decomposition of the B. nana litter appears surprising, as deciduous plants usually decompose faster than evergreen plants (Pastor et al. 1993, Chapin et al. 1995) and as the B. nana litter had the highest initial nitrogen content and the lowest C/N ratio of the plant species studied here. Both high nitrogen content and a low C/N ratio are characteristics that are associated with a fast decomposition rate (Hobbie 1992). However, the high lignin content and the low content of soluble carbohydrates might explain the low decomposition rate of *B. nana* (Hobbie 1996).

As previously presented by Olofsson et al. (2001), 40 years of grazing had led to a pronounced dominance of graminoids, while deciduous and evergreen shrubs dominated the lightly grazed area. Grazing thus increased the abundance of rapidly growing and rapidly decomposing plants and decreased the abundance of slowly decomposing plants. This result is in contrast to the results of Pastor et al. (1993), that herbivores should reduce the litter quality as they feed selectively on the most nutritious plants, which also decompose faster. It is logical to expect a correlation between herbivore preference and decomposition rate as the plant tissue in both situations is decomposed by microorganisms, either in the stomach of the herbivore or in the soil (Pastor et al. 1993) and herbivore preference and decomposition rate is correlated (Grime et al. 1996). In tundra areas, graminoids are indeed more preferred food for reindeer than B. nana or evergreen dwarf shrubs (Aleksandrova et al. 1964, Skjenneberg and Slagvold 1968). However, graminoids also have a high re-growth capacity (McNaughton 1984). A high capacity for re-growth after herbivory can be seen as an alternative strategy to low palatability for tolerance of high grazing pressure (Herms and Mattson 1992).

Table 1. Results from three-way analyses of variance on the weight loss, nitrogen loss and carbon loss of litter. Statistically significant differences are marked with bold font.

Source	DF	MS	F	р	
Weight loss					
Species	3	0.622	0.622	< 0.001	
Litter quality	1	0.03	0.034	0.003	
Site	1	0.0007	0.0007	0.669	
Species \times Litter quality	3	0.004	0.004	0.319	
Species × Site	3	0.028	0.028	< 0.001	
Site × Litter quality	1	0.011	0.014	0.080	
Species \times Site \times Litter quality	3	0.001	0.001	0.790	
Error	134	0.004			
Loss N					
Species	3	8.7×10^{-5}	48.0	< 0.001	
Litter quality	1	4.8×10^{-6}	2.6	0.109	
Site	1	4.4×10^{-5}	24.2	< 0.001	
Species \times Litter quality	3	2.5×10^{-6}	1.4	0.248	
Species × Site	3	5.8×10^{-5}	32.1	< 0.001	
Site × Litter quality	1	1.8×10^{-6}	1.0	0.320	
Species \times Site \times Litter quality	3	1.0×10^{-6}	0.6	0.640	
Error	80	1.8×10^{-6}			
Loss C					
Species	3	3.8×10^{-2}	48.4	< 0.001	
Litter quality	1	2.3×10^{-3}	2.9	0.093	
Site	1	8.4×10^{-5}	0.1	0.745	
Species \times Litter quality	3	7.0×10^{-4}	0.9	0.456	
Species × Site	3	4.5×10^{-3}	9.4	< 0.001	
Site × Litter quality	1	1.7×10^{-3}	2.2	0.142	
Species × Site × Litter quality	3	1.1×10^{-3}	1.4	0.238	
Êrror	80	7.9×10^{-4}			

	litter collected from	litter decomposed on	Carex bigelowii	Deschampsia flexuosa	Betula nana	Empetrum nigrum
initial C%						
	lightly grazed	lightly grazed	46.1 ± 0.20	45.6 ± 0.13	51.8 ± 0.17	54.3 ± 0.13
	heavily grazed	lightly grazed	45.2 ± 0.36	45.6 ± 0.18	51.5 ± 0.13	53.7 ± 0.16
	lightly grazed	heavily grazed	45.9 ± 0.10	45.6 ± 0.19	51.7 ± 0.16	54.5 ± 0.14
1	heavily grazed	heavily grazed	45.1 ± 0.14	45.5 ± 0.22	51.4 ± 0.16	53.7 ± 0.12
initial N%			1 54 . 0 02	1.66 + 0.02	a a 1 + a a a	1 50 1 0 02
	lightly grazed	lightly grazed	1.74 ± 0.03	1.66 ± 0.02	2.81 ± 0.02	1.78 ± 0.02
	heavily grazed	lightly grazed	2.42 ± 0.04	1.78 ± 0.02	2.95 ± 0.04	1.89 ± 0.04
	lightly grazed	heavily grazed	1.80 ± 0.05	1.72 ± 0.03	2.76 ± 0.02	1.77 ± 0.02
final $C^{0/2}$	neavily grazed	neavily grazed	2.43 ± 0.04	1.81 ± 0.02	2.90 ± 0.02	1.91 ± 0.04
IIIIai C70	lightly grazed	lightly grazed	47.2 ± 0.10	47.8 ± 0.28	51.2 ± 0.30	55.8 ± 0.10
	heavily grazed	lightly grazed	47.2 ± 0.10 47.7 ± 0.20	47.8 ± 0.28 48.3 ± 0.18	51.2 ± 0.30 52.0 ± 0.28	55.8 ± 0.19 55.7 ± 0.32
	lightly grazed	heavily grazed	46.3 ± 0.83	47.8 ± 0.16	52.0 ± 0.20 51.4 ± 0.20	56.0 ± 0.12
	heavily grazed	heavily grazed	40.5 ± 0.05 47 5 ± 0.22	47.0 ± 0.20 47.1 ± 0.71	51.4 ± 0.20 51.2 ± 0.26	56.0 ± 0.12 56.0 ± 0.29
final N%	neavily grazed	neuvity grazed	47.5 1 0.22	47.1 + 0.71	51.2 - 0.20	50.0 - 0.25
1111111 1 1 / 0	lightly grazed	lightly grazed	1.67 ± 0.10	1.57 ± 0.09	2.94 ± 0.11	1.95 ± 0.06
	heavily grazed	lightly grazed	1.99 ± 0.15	1.96 ± 0.07	2.80 ± 0.07	2.16 ± 0.11
	lightly grazed	heavily grazed	1.66 + 0.13	1.87 + 0.17	2.86 + 0.08	1.81 + 0.05
	heavily grazed	heavily grazed	1.66 ± 0.17	2.11 ± 0.08	2.65 ± 0.05	2.02 ± 0.12

Table 2. Mean \pm SE nitrogen and carbon content in reciprocally transplanted litter before and after one year of decomposition.

Somehow, intense grazing by reindeer appears to favour plants with high regrowth capacity, whereas welldefended plants decrease. There are at least three likely explanations for this. First, reindeer consume such a large part of the plant biomass in the area that they have to eat even the less preferred plants. Second, palatable and less palatable plants grow so intermingled that the cost of discriminatory foraging exceeds the gains. Third, the importance of unselective disturbance, such as trampling, is high.

The decomposition rate on the lightly grazed side was higher for all four species for specimens originally growing on the heavily grazed side than for specimens originally growing on the lightly grazed side. However, there was no difference in decomposition rate between heavily grazed and lightly grazed B. nana and E. nigrum decomposing on the heavily grazed side. As characteristics which often enhance the quality of litter, such as high N content, high content of non-structural carbohydrates, low C/N ratio, low fibre content, low phenolic content and low lignin content often are found in previously grazed plants (Danell and Huss-Danell 1985, Oksanen et al. 1987, Jefferies et al. 1994, Klemola et al. 2000), the positive impact of grazing on the quality of litter might be a general feature of many ecosystems. Kielland et al. (1997) found that browsing increased the litter quality of the three deciduous shrub and tree species Alnus tenuifoilia, Populus balsamifera and Salix alaxensis. However, some plant species are known to induce defence substances after herbivore damage (Karban and Myers 1989, Wold and Marquis 1997), substances that might also decrease the decomposition rate of the litter (Hobbie 1992, Findlay et al. 1996).

The decomposition of litter from the two shrub species was higher in the lightly grazed area, and the litter from the two different graminoid species was decomposing faster on the heavily grazed area. As each litter type decomposed faster in its origin site, this interaction suggests that decomposers in an ecosystem are adapted to the most prevalent types of litter. Hunt et al. (1988) have previously recorded higher decomposition of litter in its site of origin. We would have expected that litter from all species should decompose faster in the heavily grazed area than in the lightly grazed area, as grazing increased nutrient availability and microbial activity in this area (Olofsson et al. 2001). Moreover, grazing and trampling have been found to increase the decomposition rate of litter from a common source by changing the microclimate, nutrient availability or microbial activity (Shariff et al. 1994, Kielland et al. 1997, Kielland and Bryant 1998).

The steppe-tundra transition hypothesis of Zimov et al. (1995) proposes that increased hunting pressure, reducing the density and diversity of herbivores, accounted for the vegetation shift from a cold grassland to a moss dominated tundra in Beringia at the end of the Pleistocene. As the predominance of grazing-tolerant graminoids reduces soil moisture more and isolates the soil less than moss-dominated vegetation, grazing and trampling should increase nutrient cycling and primary production by increasing soil temperature and by improving drainage. Thus, the vegetation in arctic areas should have two alternative equilibria, a productive grassland with abundant large herbivores and lowproductive moss tundra with few herbivores. The vegetation shift occurring today in areas heavily grazed by reindeer in northern Norway might be a local recreation of the Pleistocene grassland. However, this study reports that the mechanism behind the increased N cycling is not a change in soil temperature or moisture, but improved litter quality, due to changes in plant community composition and plant chemistry.

In the boreal forest, different indirect effects of herbivory have opposite impacts on litter decomposition rate (Kielland et al. 1997). Moose browsing improves litter decomposition conditions and litter quality directly by increasing nutrient availability through urine and faeces and by increasing the quality of the browsed plants (Kielland et al. 1997, Kielland and Bryant 1998), which should enhance nutrient cycling and primary production in the short term. In the long term, however, moose browsing decreased litter decomposition rate, nutrient cycling and primary production, as moose feed selectively on plants producing high-quality litter, thus favouring species with low-quality litter (McInnes et al. 1992, Pastor and Naiman 1992, Pastor et al. 1993). Increased abundance of slower decaying species seems to occur in all studies where grazing decreases primary production (Ritchie et al. 1998, Sirotnak and Huntly 2000). In grasslands, where grazing often enhance nutrient cycling (Coppock et al. 1983, McInnes et al. 1992, Pastor et al. 1993, Turner et al. 1993, Frank

and Evans 1997, Frank and Grossman 1998, Tracy and Frank 1998), the importance of changes in species composition might be minor compared to tundra areas or boreal forests as species from the same functional group of plants, graminoids, dominate the vegetation regardless of grazing pressure, and species from the same functional group often have similar litter quality (Hobbie 1996). Instead, the changes in quality in grazed plants might be important as herbivory might increase the content of soluble carbohydrates and nitrogen in grasses (Chapin and Shaver 1981, McNaughton 1984). However, changes in physical and biotic decomposition conditions (Shariff et al. 1994) and the application of urine and faeces (Ruess and McNaughton 1987, Hobbs 1996) might also be important for nutrient cycling and primary production in grasslands.

This study shows that herbivory influences litter decomposition rate in several ways. Herbivory altered the plant species composition, changed the plant chemistry and thus the litter quality and altered the conditions for decomposition. As herbivores avoid well-defended plants and prefer rapidly decomposing plants (Grime et

Table 3. Results from tree-way analyses of variance on initial and final nitrogen and carbon content of the litter. Statistically significant differences are marked with bold font.

Source	DF	MS	F	р	
Initial C					
Species	3	444.51	2341	< 0.001	
Site	1	0.04	0.2	0.641	
Litter quality	1	5.61	29.5	< 0.001	
Species × Site	3	0.07	0.4	0.778	
Species × Litter quality	3	0.87	4.6	0.005	
Site × Litter quality	1	0.02	0.1	0.744	
Species \times Site \times Litter quality	3	0.04	0.2	0.871	
Error	80	0.19			
Initial N					
Species	3	6.084	1012.4	< 0.001	
Site	1	0.001	0.2	0.627	
Litter quality	1	1.609	267.8	< 0.001	
Species × Site	3	0.013	2.1	0.107	
$S_{pecies} \times Litter quality$	3	0.450	74.9	< 0.001	
Site × Litter quality	1	0.001	0.1	0.723	
Species \times Site \times Litter quality	3	0.002	0.3	0.831	
Error	80	0.006			
Final N%					
Species	3	5.61	80.4	< 0.001	
Site	1	0.06	0.9	0.345	
Litter quality	1	0.00	5.8	0.019	
Species × Site	3	0.21	2.9	0.038	
Species × Litter quality	3	0.26	3.7	0.014	
Site × Litter quality	1	0.11	1.6	0.211	
Species \times Site \times Litter quality	3	0.03	0.4	0.731	
Error	80	0.07	011	01701	
Final C0/					
Filial C70	2	286.2	510 5	< 0.001	
Site	1	200.5	20	< 0.001	
Litter quality	1	2.2	2.9	0.092	
Species × Site	1	1.4	1.0	0.101	
Species × Litter quality	3	1.2	1.2	0.320	
Site \times Litter quality	5	1.2	1.7	0.105	
Species \times Site \times Litter quality	3	14	1.2	0.279	
Frror	80	0.7	1.7	0.177	
	80	0.7			

al. 1996), selective herbivory often decreases nutrient cycling (Pastor et al. 1993). However, while low and moderate densities of herbivores favour well-defended plants, dense populations, which damage even the welldefended plants, either by grazing or trampling, might favour rapidly re-growing and rapidly decomposing plants, thus enhancing nutrient cycling (Westoby et al. 1989). Thus, the effect of herbivory on nutrient cycling and primary production might reflect differences in the dynamics of the herbivores. The negative impacts on nutrient cycling have been recorded in systems where predation might have a regulatory role keeping herbivory pressure at a moderate level, whereas the positive impacts of herbivory on nutrient cycling have been recorded in systems where herbivores appear to be resource limited. As the critical information on the role of predators is largely missing, the idea presented above might be regarded as an untested conjecture. However, it seems obvious that dynamics of herbivores can influence their impact on the vegetation.

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References

- Aleksandrova, V. D., Andreev, V. N., Vahtina, V. T. et al. 1964. Kormovaja harakteristika rostenij Krajnego Severa. – Rastitel'nost Krajnego Servera i ee osvoenie 5: 1–484.
- Bardgett, R. D., Wardle, D. A. and Yeates, G. W. 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. – Soil Biol. Biochem. 30: 1867–1878.
- Bazely, D. R. and Jefferies, R. L. 1985. Goose facees: a source of nitrogen for plant growth in a grazed salt marsh. – J. Appl. Ecol. 22: 693–703.
- Bazely, D. R. and Jefferies, R. L. 1989. Lesser snow geese and the nitrogen economy of a grazed salt marsh. – J. Ecol. 77: 24–34.
- Bryant, J. P., Provenza, F. D., Pastor, J. et al. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. – Annu. Rev. Ecol. Sys. 22: 431–446.
- Cargill, M. S. and Jefferies, R. L. 1984. The effects of grazing by lesser snow geese on the vegetation of a subarctic salt marsh. – J. Appl. Ecol. 21: 669–686.
- Cebrian, J. 1999. Patterns in the fate of production in plant communities. Am. Nat. 154: 449–468.
- Chapin III, F. S. and Shaver, G. R. 1981. Changes in soil properties and vegetation following disturbance of Alaskan arctic tundra. J. Appl. Ecol. 18: 605–617.
- Chapin III, F. S., Shaver, G. R., Giblin, K. G. et al. 1995. Responses of arctic tundra to experimental and observed changes in climate. – Ecology 76: 694–711.
- Coppock, D. L., Detling, J. K., Ellis, J. E. and Dyer, M. I. 1983. Plant-herbivore interactions in a North American mixed-grass prarie: effects of black-tailed prarie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. – Oecologia 56: 1–9.
- namics and plant species diversity. Oecologia 56: 1–9. Danell, K. and Huss-Danell, K. 1985. Feeding by insects and hares on birches earlier affected by moose browsing. – Oikos 44: 75–81.

- Findlay, S., Carreiro, M., Krischik, V. and Jones, C. G. 1996. Effects of damage to living plants on leaf litter quality. – Ecol. Appl. 6: 269–275.
- Floate, M. J. S. 1970. Decomposition of organic materials from hill soils and pastures. II. Comparative studies on the mineralization of carbon, nitrogen, and phosphorus from plant materials and sheep faeces. – Soil Biol. Biochem. 2: 173–185.
- 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. 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 Grossman, P. M. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone national park. – Ecology 79: 2229–2241.
- Grime, J. P., Cornelissen, J. H. C., Thompson, K. et al. 1996. Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. – Oikos 77: 489–494.
- Herms, D. A. and Mattson, W. J. 1992. The dilemma of plants: to grow or defend. Q. Rev. Biol. 67: 283–335.
- Hik, D. S. and Jefferies, R. L. 1990. Increases in the net above-ground primary production of a salt-marsh forage grass: a test of the predictions of the herbivore-optimization model. – J. Ecol. 78: 180–195.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. – Trends Ecol. Evol. 7: 336–339.
- Hobbie, S. E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. – Ecol. Monogr. 66: 503–522.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. – J. Wildl. Manage. 60: 695–713.
- Holland, E. A., Parton, W. J., Detling, J. K. and Coppock, D. L. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. – Am. Nat. 140: 685–706.
- Hunt, H. W., Ingham, E. R., Coleman, D. C. et al. 1988. Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. – Ecology 69: 1009–1016.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. – Annu. Rev. Ecol. Syst. 22: 477–503.
- Jefferies, R. L., Klein, D. R. and Shaver, G. R. 1994. Vertebrate herbivores and northern plant communities: reciprocal influences and responses. – Oikos 71: 193–206.
- Karban, R. and Myers, J. H. 1989. Induced plant-responses to herbivory. – Annu. Rev. Ecol. Syst. 20: 331–348.
- Kielland, K. and Bryant, J. P. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. – Oikos 82: 377–383.
- Kielland, K., Bryant, J. B. and Ruess, R. W. 1997. Moose herbivory and carbon turnover of early successional stands in interior Alaska. – Oikos 80: 25–30.
- Klemola, T., Norrdahl, K. and Korpimäki, E. 2000. Do delayed effects of overgrazing explain population cycles in voles? – Oikos 90: 509–516.
- Knapp, A. K. and Seastedt, T. R. 1986. Detritus limits productivity in tallgrass prarie. – Bioscience 36: 662–668.
- McInnes, P. F., Naiman, R. J., Pastor, J. and Cohen, Y. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. – Ecology 73: 2059–2075.
- McNaughton, S. J. 1979. Grazing as an optimization progress: grass-ungulate relationships in the Serengeti. – Am. Nat. 113: 691–703.
- McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form and coevolution. – Am. Nat. 124: 863–886.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. – Ecol. Monogr. 55: 259–294.

- McNaughton, S. J., Osterheld, M., Frank, D. A. and Williams, K. J. 1989. Ecosystem level patterns of primary productivity and herbivory in terrestrial habitats. – Nature 341: 142–144.
- Oksanen, L. and Virtanen, R. 1995. Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. – Acta Bot. Fenn. 153: 1–80.
- Oksanen, L., Oksanen, T., Lukkari, A. and Sirén, S. 1987. The role of phenol-based inducible defense in the interaction between tundra populations of the vole *Clethrionomus rufocanus* and the dwarf shrub *Vaccinium myrtillus*. – Oikos 50: 371–380.
- Olofsson, J., Kitti, H., Rautiainen, P. et al. 2001. Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. – Ecography 24: 13–24.
 Pandey, C. B. and Singh, J. S. 1992. Rainfall and grazing
- Pandey, C. B. and Singh, J. S. 1992. Rainfall and grazing effects on net primary productivity in a tropical savanna, India. – Ecology 73: 2007–2021.
- Pastor, J. and Naiman, R. J. 1992. Selective foraging and ecosystem processes in boreal forests. – Am. Nat. 139: 690–705.
- Pastor, J., Dewey, B., Naiman, R. J. et al. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. – Ecology 74: 467–480.
- Ritchie, M. E., Tilman, D. and Knops, J. 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 nutrient and energy regulated microbial processes in the Serengeti grasslands. – Oikos 49: 101–110.
- Ruess, R. W., Hik, D. S. and Jefferies, R. L. 1989. The role of lesser snow geese as nitrogen processors in a sub-arctic marsh. – Oecologia 79: 23–29.

- Seagle, S. W., McNaughton, S. J. and Ruess, R. W. 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grasslands. – Ecology 73: 1105–1123.
- Shariff, A. R., Biondini, M. E. and Grygiel, C. E. 1994. Grazing intensity effects on litter decomposition and soil nitrogen mineralization. – J. Range Manage. 47: 444– 449.
- Singh, R. S., Raghubanshi, A. S. and Singh, J. S. 1991. Nitrogen mineralization in dry tropical savanna: effects of burning and grazing. – Soil Biol. Biochem. 23: 269– 273.
- 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.
- Skjenneberg, S. and Šlagvold, L. 1968. Reindriften og dens naturgrunnlag. – Universitetsforlaget, Oslo.
- Tracy, B. F. and Frank, D. A. 1998. Herbivore influence on soil microbial biomass and nitrogen mineralization in a northern grassland ecosystem: Yellowstone National Park. – Oecologia 114: 556–562.
- Turner, C. L., Seastedt, T. R. and Dyer, M. I. 1993. Maximation of aboveground grassland production: the role of defoliation frequency, intensity and history. – Ecol. Appl. 3: 175–186.
- Westoby, M., Walker, B. and Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. – J. Range Manage. 42: 266–274.
- Wold, E. N. and Marquis, R. J. 1997. Induced defence in white oak: effects on herbivores and consequences for the plant. – Ecology 78: 1356–1369.Zimov, S. A., Chuprynin, V. I., Oreshko, A. P. et al. 1995.
- Zimov, S. A., Chuprynin, V. I., Oreshko, A. P. et al. 1995. Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. – Am. Nat. 146: 765–794.