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Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling

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In this study, we investigated the effect of reindeer grazing on tundra heath vegetation in northern Norway. Fences, erected 30 yr ago, allowed us to compare winter grazed, lightly summer grazed and heavily summer grazed vegetation at four different sites. At two sites, graminoids dominated the heavily grazed zone completely, while ericoid dwarf shrubs had almost disappeared. In the other two areas, the increase of graminoids was almost significant. At one of the sites where graminoids dominated the heavily grazed area, we also measured plant biomass, primary production and nitrogen cycling. In this site, heavy grazing increased primary production and rate of nitrogen cycling, while moderate grazing decreased primary production. These results were inconsistent with the view that the highest productivity is found at intermediate grazing pressure. These results rather support the hypothesis that intensive grazing can promote a transition of moss-rich heath tundra into productive, graminoid-dominated steppe-like tundra vegetation. Moreover the results suggests that intermittent intensive reindeer grazing can enhance productivity of summer ranges.

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Introduction

Grazing can stimulate the productivity of the vegetation in a wide range of ecosystems, such as East-African savannas (McNaughton 1979, 1985), Canadian saltmarshes (Hik and Jefferies 1990), North American grasslands (Frank and McNaughton 1993) and Asian savannas (Pandey and Singh 1992). Hypothesis has proposed that the highest productivity should be found at intermediate grazing pressure (McNaughton 1979, Hilbert et al. 1981, Hik and Jefferies 1990, Loreau 1995), and this pattern has been found in some studies (McNaughton 1979, 1985, Hik and Jefferies 1990, Frank and McNaughton 1993). However, increasing grazing pressure may decrease primary production, even at moderate levels of grazing (Schlesinger et al. 1990, Pastor and Naiman 1992, Pastor et al. 1993, Milchunas and Lauenroth 1993, Manseau et al. 1996, Milchunas et al. 1998).

Several mechanisms have been proposed to explain how grazing can affect primary productivity, including juvenilisation, reallocation and hormone redistribution of the plant, direct effects of growth promoting substrates in ruminant saliva and nutrient recycling from dung and urine (McNaughton 1979). More recently, several hypotheses focused on the role of increased rate of nitrogen cycling in the promotion of primary productivity by grazing (Loreau 1995, Zimov et al. 1995, de Mazancourt et al. 1998). Increased nutrient cycling by grazing has been found in several ecosystems (Holland and Detling 1990, Ruess and McNaughton 1987, Holland et al. 1992, Frank and McNaughton 1993, Frank and Evans 1997, Frank and Grossman 1998).

To our knowledge, no one has directly showed that grazing increases productivity in the tundra. However

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growth of grasses in the tundra environment is stimulated by nutrient inputs from fertilisers (McKendrick et al. 1978, Shaver and Chapin 1986), animal carcasses and faeces (Batzli et al. 1980, McKendrick et al. 1980) or intensive disturbance by humans or animals (Batzli and Sobaski 1980). In a study from Alaska, Post and Klein (1996) found that productivity was higher on a more intensively grazed meadow than on an adjacent less intensively grazed meadow in one area, but the opposite pattern was found in another area. Caribou decreased the productivity of their summer range in a north-eastern Canadian tundra dominated by lichens and dwarf shrubs (Manseau et al. 1996). Zimov et al. (1995) presented a hypothesis that large herbivores can act as a keystone guild and drive a biome-shift from moss-dominated tundra into a steppe-like, graminoid-dominated community. According to their hypothesis, herbivory favours more productive plant species, improves the litter quality, increases the soil temperature by removing the isolating moss-carpet and consequently increases the net mineralisation rate and the productivity. Thus, the steppe-tundra transition at the end of Pleistocene may have been caused by an extinction of large herbivores by human hunting (Zimov et al. 1995).

The only large native herbivore still common in the Fennoscandian tundra is the semi-domesticated reindeer. In northern Norway, the densities of reindeer have doubled during the last three decades (Bernes 1996), and reindeer strongly influence vegetation patterns (Oksanen and Virtanen 1995). The impact of reindeer on vegetation is especially pronounced along fences separating intensively grazed summer ranges from autumn and winter ranges in northern Norway (Oksanen 1978, Johansen et al. 1995, Evans 1996, Johansen and Karlsen 1996). The impact of reindeer on

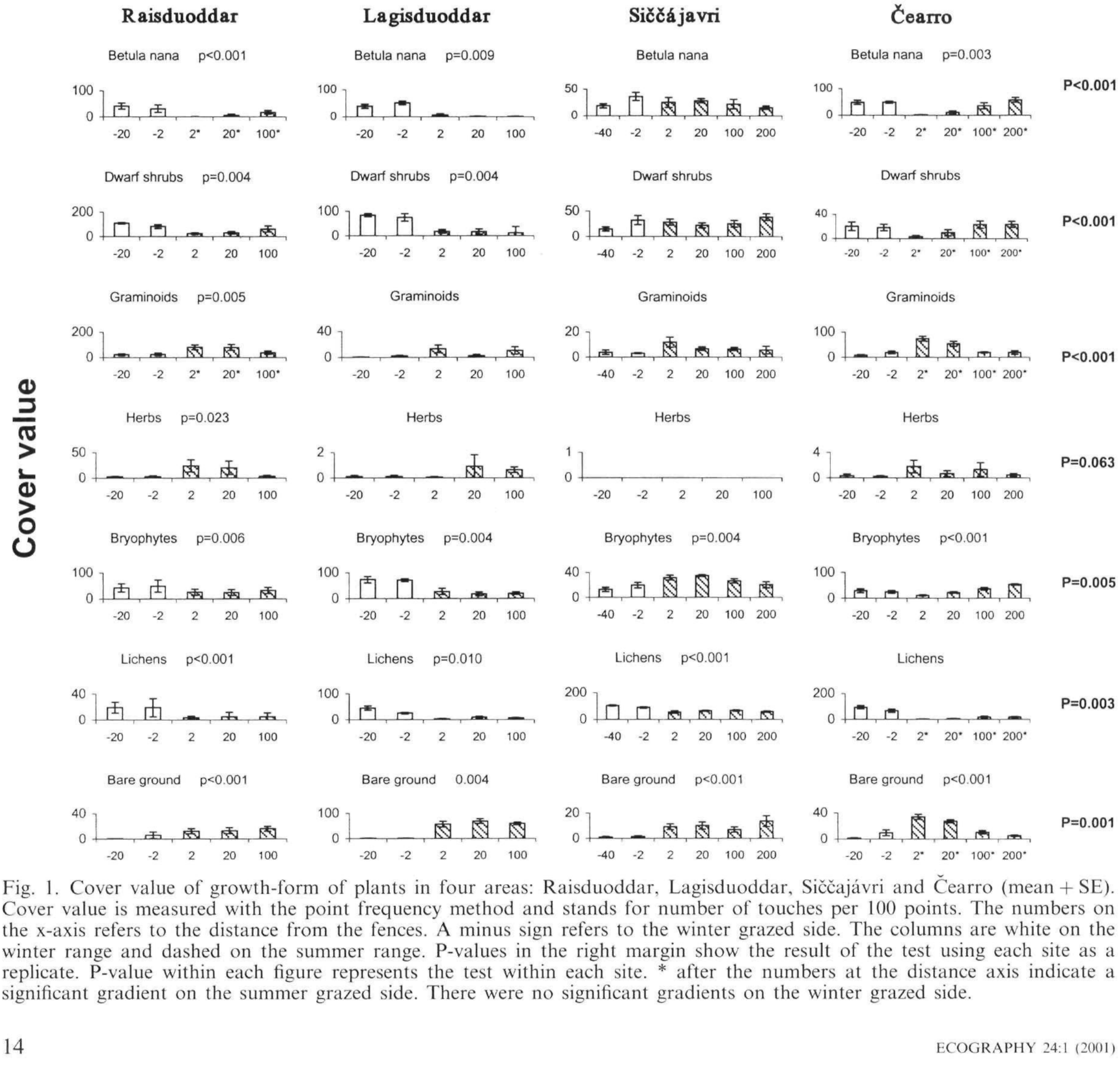

Fig. 1. Cover value of growth-form of plants in four areas: Raisduoddar, Lagisduoddar, Siččajávri and Čearro (mean + SE). Cover value is measured with the point frequency method and stands for number of touches per 100 points. The numbers on the x-axis refers to the distance from the fences. A minus sign refers to the winter grazed side. The columns are white on the winter range and dashed on the summer range. P-values in the right margin show the result of the test using each site as a replicate. P-value within each figure represents the test within each site. * after the numbers at the distance axis indicate a significant gradient on the summer grazed side. There were no significant gradients on the winter grazed side.

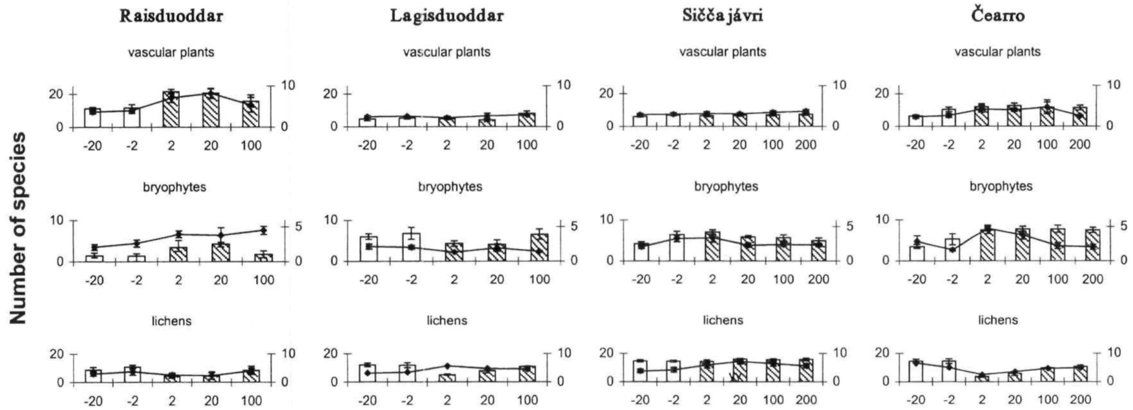

Fig. 2. Number of species 1.25 m^{-2}. Shannon's diversity index (H) of vascular plants, bryophytes and lichens in the four different areas (mean + SE). The numbers on the x-axis refers to the distance from the fences. A minus sign refers to the winter grazed side. The columns indicating number of species are white on the winter range and dashed on the summer range. The line indicates Shannon's diversity index.

the vegetation involves both trampling and grazing. As trampling and grazing cannot normally be quantified separately because of the mobility of the reindeer, we often refer to both as grazing. In this study, we contrasted the vegetation on the two sides of four fences. All four fences were established in the 1960s and thus provide a > 30-yr long grazing manipulation experiment. On the summer-grazed sides of the fences, there are pronounced gradients in grazing-pressure. The zone closest to the fence is intensively trampled and grazed, as reindeer have a tendency to follow fences (Skjenneberg and Slagvold 1968). Within a distance of 100 m, the fence effect disappears (Oksanen 1978). Thus we can compare heavily summer grazed areas near the fences, lightly summer grazed areas further away from the fences and autumn and winter grazed areas on the other side of the fences. (Figs 1 and 2, Table 1)

In this study, we used these natural grazing experiments to examine: 1) whether intense reindeer grazing can change the tundra heath vegetation into a steppe-like, graminoid-dominated community. 2) How reindeer grazing influences primary productivity and nutrient circulation. 3) How reindeer grazing influences species diversity of the vegetation.

Study area

The study was carried out in four different areas in northern Norway. Climatically, they range from continental to suboceanic (Oksanen and Virtanen 1995), and the vegetation varies accordingly. Raisduoddar is located in a suboceanic area in Troms fylke (69°30′N, 27°30′E), between 600 and 700 m a.s.l. The predominating vegetation is heath land of the Arctic Empetrum-Dicranum-Lichen type. Lagisduoddar, Finnmark fylke (70°30′N, 27°30′E) ca 250 m a.s.l., is situated at the border between the suboceanic and the subcontinental sector. The most wide spread vegetation type is the Arctic Empetrum-Dicranum-Lichen type. Čearro is situated in the continental sector (69°40′N, 24°40′E) ca 250 m a.s.l., in Finnmark fylke. The dominating vegetation consists of lichen heaths of the *Betula nana*-Cladina type. Siččajávri is located in a continental area, at the border between Finland and Norway (68°50′N, 23°50′E), at 550 m a.s.l. Heaths of the *Betula nana*-Cladina type dominate the heath vegetation (Oksanen and Virtanen 1995).

In all four sites, fences were established in the 1960s, to reduce the risk that reindeer illegally enter migration areas or winter ranges during the summer. The fences are built of wire between one to two meter high posts, and range several kilometres over the tundra. The fences at Raisduoddar and Lagisduoddar separates summer-ranges from areas grazed in spring- and autumn. In both these areas, those parts of the spring- and autumn range that lie near the fence are only lightly grazed because of deep snow during the spring migration and the motivation of reindeer to move towards winter ranges in autumn. The above view, based on interviews with herdsmen was corroborated with our data. There were few signs, such as hoofpads, droppings or grazing damaged plants in the spring- and autumn-ranges. At Siččajávri, the fence separates the summer ranges for Finnish reindeer from winter ranges for Norwegian reindeer. The winter range near the fence is treated as an emergency reserve and showed no signs of grazing. Even the *Cladina stellaris* carpet was totally undisturbed. The fence at Čearro also separates the summer range from the winter range, but in contrast to Siččajávri, the winter range at Čearro is heavily used.

Table 1. Climatic region, grazing pattern and type of evidence supporting this view for the four different areas. All summer ranges are utilised rather intensively. In all four areas faeces and footprints are common in the summer grazing range. The times of grazing in the summer and winter ranges are based on oral information from local herdsmen and the Norwegian Reindeer Administration.

Area	Climate and vegetation	Summer range	Winter range	Comments
Raisduoddar	Suboceanic Empetrum-Dicranum-lichenes type	Grazed in August	Occasionally grazed in early spring and late autumn.	Almost no faeces and footprints in the winter grazed area. The fence separates winter- and summer ranges used by the same herd.
Lagisduoddar	Suboceanic-subcontinental Empertrum-Dicranum-lichenes type	Mainly grazed in June and August, occasionally in July.	Occasionally grazed in early spring and late autumn	Almost no faeces and footprints in the winter grazed area. The fence separates winter- and summer ranges used by the same herd.
Siččajávri	Continental *Betula nana*-Cladina type	Grazed from June until August	Seldom used winter range.	No faeces or footprints in the winter range and an undisturbed lichen carpet (*Cladina stellaris*). The fence separates winter- and summer ranges used by different herd.
Čearro	Continental *Betula nana*-Cladina type	Grazed from June until August	Grazed in winter	Faeces in the winter range. *Cladina stellaris* carpet severely disturbed. The fence separates winter- and summer ranges used by the same herd.

Method

To examine the effect of grazing on vegetation, transects were laid out randomly perpendicular across the fences, in areas with the vegetation type we wanted to examine. The sampling areas were chosen to be topographically and edaphically uniform, allowing us to assume that the vegetational differences along the transect are caused by grazing and not by environmental variation. As the summer ranges were consistently on the same side at each fence, a degree of pseudoreplication was inevitable. For transects to be independent of each other, we ensured that the distance between subsequent transects exceeded 200 m. With these criteria, we obtained four transects on Raisduoddar, Lagisduoddar and Čearro, and seven transects at Siččajávri. At each site along the fence, large rectangles covering 220 × 25 m were placed unequally over the fence with 20 m on the lightly grazed side and 200 m on the moderately/intensively grazed side. At -20, -2, 2, 20, 100 and 200 m from the fence, a 25 m long transect parallel to the fence with 5 evenly spread 0.5 × 0.5 m plots were established. These plots were the sub-units where we recorded the vegetation. A minus sign in front of the distance refers to the winter range.

We estimated the plant cover in the plots with a modified point intercept method. This index correlates well with plant biomass for single species (Jonasson 1988). We used a transparent plexi-glass table, 50 × 50 cm, with 100 randomly distributed holes. The holes had a diameter of 4 mm. At each hole, a pin with the same diameter was lowered through the vegetation, and we recorded the number of contacts of the pin to each species. For narrow-leafed ericoid dwarf shrubs, only contacts with separate branches were counted. In order to handle species with numerous narrow leaves, we set 10 contacts as the maximum value one species could have at one hole. Bryophytes and lichens were considered to grow in one layer only, and maximum was thus one count per species at each hole. Species found in a plot but not hit by any stick were counted as 0.1.

Standing crop, annual plant production and soil measurements were conducted at one of the sites where graminoids had increased, i.e. the Raisduoddar fence. Biomass and soil-processes were studied at the peak of the vegetation season, in the beginning of August. Twenty-five transects were randomly distributed along the fence. Vegetation was harvested at three distances from the fence at each transect, one distance in the winter range (-10 m from fence), one distance in the heavily summer grazed zone (10 m from the fence) and one distance in the lightly summer grazed zone (100 m). New annual shoots were harvested separately from old plant parts, to enable us to obtain a conservative estimate of above-ground primary production. All plant samples were dried to a constant weight at 60°C.

Six transects were laid out to measure soil processes. The transects were placed along the fence. The distance between the transects was 24 m. Several soil samples were taken from each transect at 12 and − 12 m from the fence. The soil samples were frozen and transported to the laboratory. The samples were kept in a freezer for six months before we started the measurement.

All soil samples were slowly melted and thoroughly mixed to decrease the considerable variation in the natural ^{15}N enrichment, which is typical for tundra soil (Nadelhoffer and Fry 1994, Schulze et al. 1994). Mixing was necessary, because the variation in natural ^{15}N enrichment would disturb the measurement of gross nitrogen mineralization with the isotope dilution method of Hart et al. (1994). Soil was put in a plastic container, capped in gas permeable polyethylene (thickness 10 μm) and preincubated for three days in + 20°C. After that the soil was subsampled for extraction (0.5 M K_2SO_4), gravimetric analysis of moisture and organic matter content and respirometric analysis. Chloroform fumigation (18 h) was used to measure microbial N (Brookes et al. 1985). The remaining soil was put in two plastic containers, one for measuring gross and the other for measuring net mineralization of nitrogen. Dilute solution of $^{15}(NH_4)_2SO_4$ was injected evenly to the gross mineralization samples, and incubated for 3 d at + 20°C. Net mineralization samples were incubated for 4 weeks. Both treatments were capped with the gas permeable polyethylene.

Table 2. Analysis of variance for differences in cover values. The two fixed factors, grazing regime (side of the fence) and area were crossed and distance from fence and transect were nested within grazing regime. Bold F and p-values indicate a significant difference considering grazing regime.

		overall	
		F	p
Betula nana	grazing regime	**49.26**	**<0.001**
	area	1.60	0.201
	area × grazing regime	0.66	0.830
Ericoids	grazing regime	**54.59**	**<0.001**
	area	36.59	<0.001
	area	36.59	<0.001
	area × grazing regime	20.81	<0.001
Graminoids	grazing regime	**25.26**	**<0.001**
	area	17.961	<0.001
	area × grazing regime	4.392	0.008
Herbs	grazing regime	3.591	0.063
	area	5.473	0.002
	area × grazing regime	2.731	0.053
Bryophytes	grazing regime	**8.682**	**0.005**
	area	25.07	<0.001
	area × grazing regime	10.77	<0.001
Lichens	grazing regime	**9.84**	**0.003**
	area	6.70	0.001
	area × grazing regime	16.37	<0.001
Bare ground	grazing regime	**118.13**	**<0.001**
	area	29.61	<0.001
	area × grazing regime	33.52	<0.001

Ammonium was diffused from the extracts into dilute sulphuric acid by an addition of MgO followed by incubation in + 30°C for three days (Crooke and Simpson 1971) and analysed colorimetrically (Bremner 1965). The ^{15}N samples were diffused in the same way, and the dilute sulphur acid was dried in + 45°C. The $^{15}N/^{14}N$ ratio was analysed by mass spectrometry, and the gross mineralization and ^{15}N consumption were calculated using the formula of Kirkham and Bartholomew (1954). Net N mineralization was measured by subtracting the amount of ammonium in the beginning and end of the laboratory incubation.

The extractable organic and microbial nitrogen was quantified by oxidising organic nitrogen to nitrate (Williams et al. 1995) and analysing it by ion chromatography (Dionex DX 100) in both unfumigated and fumigated samples. C mineralization (CO_2 production) by soil organisms was measured in terms of mean basal respiration for 40 h (Nordgren 1988, Nordgren et al. 1988). The respiring microbial biomass C was measured by SIR method of Anderson and Domsch (1978). We also measured the metabolic quotient (respired C per unit microbial biomass C), and the lag time between the addition of glucose and the start of the exponential increase in the respiration rate, as both are indicators of microbial activity (Ohtonen 1994).

The cover of different growth strategies, species number and species diversity were tested with an ANOVA with a two level nested design with two crossed factors. The random-effect factor (transect) was nested within distance from fence that was nested within grazing regime (side of the fence) (Zar 1996). As post-hoc test cannot be done with a significant interaction factor, a two-way ANOVA with a fix factor (distance from fence) nested within grazing regimes were used to analyse the difference between the grazing regime at each fence. The impact of distance from fence was analysed for each side of the fence separately, with a mixed model two-way ANOVA with transect as a random factor and distance from fence as a fixed factor. Standing crops were tested with a two-way ANOVA without replication, with distance from fence as a fixed factor and transect as a random factor. The five quadrates were pooled to get one value for each combination of distance and transect. The data fulfilled the requirement of normality and homogeneity of group variances in most cases. In a few tests, heteroscedasticity between treatments were found, but minor deviations from homoscedasticity will not affect the validity of the analysis (Zar 1996). The nutrient cycling analyses were analysed with Mann-Whitney U-test for two independent samples.

Results

In the overall test, with the four areas as replicate *Betula nana*, ericoids, and lichens decreased in summer grazed

Table 3. Analysis of variance for differences in cover values within each of the four different areas. The two factors, grazing regime and transect were crossed and distances from fence were nested within grazing regime. Bold F and p-values indicate significant differences within a given transect.

		Raisduoddar		Lagisduoddarar		Siččajávri		Čearro	
		F	p	F	p	F	p	F	p
Betula nana	grazing regime	**71.76**	<**0.001**	**37.88**	**0.009**	0.64	0.430	**14.29**	**0.003**
	transect	15.37	0.001	0.74	0.594	0.85	0.544	1.93	0.178
	grazing regime × transect	14.68	0.001	3.50	0.063	0.60	0.726	1.15	0.368
Dwarf shrubs	grazing regime	**14.65**	**0.004**	**64.5**	**0.004**	0.93	0.345	0.68	0.425
	transect	0.13	0.941	0.08	0.966	1.89	0.123	0.45	0.720
	grazing regime × transect	1.02	0.428	2.48	0.127	112.95	<0.001	0.39	0.760
Graminoids	grazing regime	**13.73**	**0.005**	5.62	0.099	3.75	0.064	**14.65**	**0.004**
	transect	3.159	0.079	1.29	0.419	0.78	0.591	0.08	0.966
	grazing regime × transect	1.36	0.316	0.80	0.523	0.29	0.936	2.48	0.127
Herbs	grazing regime	**7.47**	**0.023**	1.10	0.371			2.375	0.149
	transect	4.38	0.037	0.66	0.630			1.02	0.420
	grazing regime × transect	2.97	0.089	1.25	0.349			1.33	0.310
Bryophytes	grazing regime	**12.423**	**0.006**	**65.58**	**0.004**	**10.18**	**0.004**	**39.30**	<**0.001**
	transect	33.01	<0.001	6.72	0.076	0.787	0.589	0.451	0.722
	grazing regime × transect	2.794	0.101	1.45	0.292	0.683	0.665	0.459	0.716
Lichens	grazing regime	**27.04**	**0.001**	**35.3**	**0.010**	**12.92**	**0.001**	0.83	0.380
	transect	5.85	0.017	0.34	0.803	0.56	0.755	0.65	0.599
	grazing regime × transect	1.06	0.412	1.24	0.355	0.941	0.485	0.88	0.476
Bare ground	grazing regime	**23.21**	**0.001**	**66.72**	**0.004**	**15.07**	**0.001**	**29.39**	<**0.001**
	transect	8.446	0.006	1.11	0.466	0.53	0.781	1.52	0.26
	grazing regime × transect	0.772	0.538	2.31	0.145	0.58	0.739	0.61	0.620

Table 4. Analysis of variance for differences in cover value within the summer range of each of the four different areas. The two factors, grazing regime and transect were crossed and distance from fence were nested within grazing regime. Bold F and p-values indicate significant differences within a given transect.

		Raisduoddar		Lagisduoddarar		Siččajávri		Čearro	
		F	p	F	p	F	p	F	p
Betula nana	distance from fence	**5.37**	**0.046**	0.95	0.438	0.59	0.627	**12.06**	**0.002**
	transect	3.27	0.101	0.71	0.580	0.75	0.621	1.84	0.210
Dwarf shrubs	distance from fence	1.28	0.343	0.60	0.580	1.54	0.239	**4.18**	**0.041**
	transect	0.52	0.687	4.56	0.054	1.59	0.207	0.93	0.466
Graminoids	distance from fence	**4.18**	**0.041**	2.73	0.144	0.97	0.427	**16.87**	<**0.000**
	transect	3.12	0.110	0.93	0.466	0.74	0.624	3.053	0.085
Herbs	distance from fence	3.00	0.125	0.93	0.445			0.83	0.510
	transect	6.18	0.029	1.35	0.343			2.41	0.134
Bryophytes	distance from fence	0.70	0.534	1.11	0.390	0.33	0.803	**11.90**	**0.002**
	transect	14.28	0.004	9.06	0.012	1.53	0.224	1.02	0.427
Lichens	distance from fence	0.30	0.749	1.37	0.323	3.14	0.051	**66.66**	<**0.001**
	transect	9.71	0.010	1.35	0.343	0.95	0.486	8.33	0.006
Bare ground	distance from fence	1.825	0.240	0.93	0.445	0.929	0.447	**24.63**	<**0.001**
	transect	23.13	0.001	4.04	0.069	1.209	0.346	0.95	0.458

areas, while graminoids and bare ground increased significantly (Fig. 1, Table 2). Bryophytes responded significantly, even if they increased with summer grazing in some areas and decreased in some areas. Herbs were the only growth forms that did not respond significantly (Fig. 1, Table 2).

When each area was tested separately, to get a more detailed picture of the changes in the vegetation, *Betula nana* decreased significantly with summer grazing in all areas except Siččajávri, and ericoides decreased significantly in two areas (Lagisduoddar and Raisduoddar). Graminoids increased significantly with summer grazing only in Čearro and Raisduoddar, but there was a trend to increase in the other two areas. Bryophytes decreased with summer grazing in the two oceanic areas (Raisduoddar and Lagisduoddar), but increased in the two continental areas (Siččajávri and Čearro). Lichens decreased and bare ground increased significantly with summer grazing in all areas (Fig. 1, Table 3).

None of the plant growth forms differed in abundance between the different distances from the fence on the winter ranges. On the summer grazed side of the fence, no plant growth forms differed in abundance between the different distances from the fence in two areas, Lagisduoddar and Siččajávri (Fig. 1, Table 4). In Raisduoddar and Čearro, there was a clear gradient in grazing pressure with more intense grazing near the fence. *Betula nana* decreased and graminoids increased in heavily summer grazed areas compared to lightly summer grazed areas in both Raisduoddar and Čearro. Dwarf shrubs, bryophytes and lichens all decreased, while bare ground increased with increasing summer grazing pressure at Čearro. None of these growth forms responded significantly in the Lagisduoddar area (Fig. 1, Table 4).

The number of vascular plants, bryophytes and lichens differed between the summer grazing area and the winter grazing area (Fig. 2, Table 5). The diversity of vascular plants, measured as Shannon's diversity index and number of species, showed an trend to increase in all areas even if the difference was only significant in Raisduodddar and in Čearro considering the number of species. Diversity of bryophytes also increased in Raisduoddar and Siččajávri. Lichen diversity increased with summer grazing in Siččajávri and Lagisduoddar but decreased in Raisduoddar and

Table 5. Analysis of variance for differences in numbers of species and in species diversity (Shannon's diversity index). The two fixed factors, grazing regime (side of the fence) and area were crossed and distance from fence and transect were nested within grazing regime. Bold F and p-values indicate a significant difference with reference to grazing regime.

		Vascular plants		Bryophytes		Lichens	
		F	p	F	p	F	p
Number of species	grazing regime	**19.99**	**<0.001**	**5.10**	**0.028**	**22.52**	**<0.001**
	area	33.71	<0.001	4.42	0.007	12.58	<0.001
	area × grazing regime	4.30	<0.001	6.26	0.001	3.40	0.023
Shannon's diversity index	grazing regime	0.147	0.702	0.70	0.407	0.018	0.894
	area	457.32	<0.001	137.43	<0.001	175.51	<0.001
	area × grazing regime	8.61	<0.001	8.67	<0.001	10.08	<0.001

Table 6. Analysis of variance for differences in number of species and species diversity (Shannon's diversity index) within each of the four different areas. The two, factors grazing regime and transect, were crossed and distances from fence were nested within grazing regime. Bold F and p-values indicate significant differences within a given transect.

		Raisduoddar		Lagisduoddarar		Siččajávri		Čearro	
		F	p	F	p	F	p	F	p
number of species vascular plants	grazing regime	**33.70**	**<0.001**	0.48	0.640	4.48	0.125	**6.11**	**0.029**
	transect	6.90	0.010	0.58	0.508	2.14	0.280	1.97	0.173
	transect × grazing regime	2.44	0.131	0.82	0.513	2.74	0.078	0.45	0.720
number of species bryophytes	grazing regime	**7.86**	**0.021**	1.67	0.228	**67.60**	**0.004**	1.54	0.238
	transect	6.41	0.013	0.40	0.760	9.21	0.085	6.67	0.007
	transect × grazing regime	3.41	0.067	0.45	0.724	0.43	0.734	1.54	0.254
number of species lichens	grazing regime	**23.39**	**0.001**	**9.65**	**0.013**	**31.78**	**0.011**	0.31	0.590
	transect	12.17	0.002	2.36	0.139	2.04	0.312	0.56	0.652
	transect × grazing regime	9.46	0.004	0.90	0.480	0.70	0.565	0.29	0.834
Shannon's diversity index vascular plants	grazing regime	**20.54**	**0.001**	0.02	0.880	5.49	0.101	1.83	0.201
	transect	4.47	0.035	1.17	0.372	0.84	0.559	0.239	0.868
	transect × grazing regime	1.03	0.426	1.10	0.399	2.00	0.154	1.19	0.355
Shannon's diversity index bryophytes	grazing regime	4.66	0.059	1.10	0.399	**29.20**	**0.012**	0.90	0.362
	transect	8.85	0.005	13.41	0.005	5.41	0.142	1.30	0.319
	transect × grazing regime	1.49	0.282	2.08	0.173	0.44	0.727	3.70	0.043
Shannon's diversity index lichens	grazing regime	**20.72**	**0.001**	**7.10**	**0.026**	**17.99**	**0.024**	**8.94**	**0.011**
	transect	9.28	0.004	2.95	0.091	1.00	0.524	0.19	0.902
	transect × grazing regime	5.58	0.019	0.73	0.558	0.46	0.714	0.16	0.924

Table 7. Analysis of variance for differences in number of species and species diversity (Shannon's diversity index), within the summer range of each of the four different areas. The two factors grazing regime and transect were crossed and distance from fence were nested within grazing regime. Bold F and p-values indicate significant differences within a given transect.

		Raisduoddar		Lagisduoddarar		Siččajávri		Čearro	
		F	p	F	p	F	p	F	p
number of species	grazing regime	4.01	0.078	4.00	0.079	0.28	0.839	0.76	0.546
vascular plants	transect	8.43	0.014	0.56	0.659	13.68	0.001	2.42	0.133
number of species	grazing regime	1.74	0.253	1.28	0.344	0.10	0.956	**10.76**	**0.002**
bryophytes	transect	6.91	0.023	0.13	0.941	8.38	0.006	25.39	<0.001
number of species	grazing regime	**6.00**	**0.037**	3.31	0.107	**14.50**	**0.001**	1.12	0.390
lichens	transect	16.28	0.003	3.09	0.11	0.79	0.529	0.38	0.768
Shannon's diversity index	grazing regime	3.31	0.107	2.76	0.141	0.84	0.502	0.11	0.95
vascular plants	transect	3.12	0.109	1.40	0.332	5.92	0.016	1.65	0.25
Shannon's diversity index	grazing regime	2.00	0.216	0.51	0.625	**7.20**	**0.009**	3.07	0.083
bryophytes	transect	9.63	0.010	0.52	0.684	3.08	0.083	0.84	0.507
Shannon's diversity index	grazing regime	1.99	0.217	2.06	0.209	**10.48**	**0.003**	1.45	0.29
lichens	transect	4.47	0.057	2.33	0.174	1.09	0.402	0.31	0.82

Čearro (Fig. 2, Table 6). In contrast with the vegetation cover data, there was a gradient in diversity of bryophytes with the highest diversity in the heavily summer grazed area near the fence, both considering species number and diversity indices (Fig. 2, Table 7).

The total plant biomass was highest in the lightly grazed control, lowest in the heavily grazed area while the biomass at the moderately grazed area was somewhere in-between (Fig. 3, Table 8). However, variation in productivity had a totally different pattern, with the highest primary production in the heavily grazed zone, lower in the control and lowest productivity in the moderately grazed part of the summer range (Fig. 4, Table 8). Graminoids and herbs increased dramatically in the heavily grazed zone near the fence, and constituted the major part of the biomass and productivity

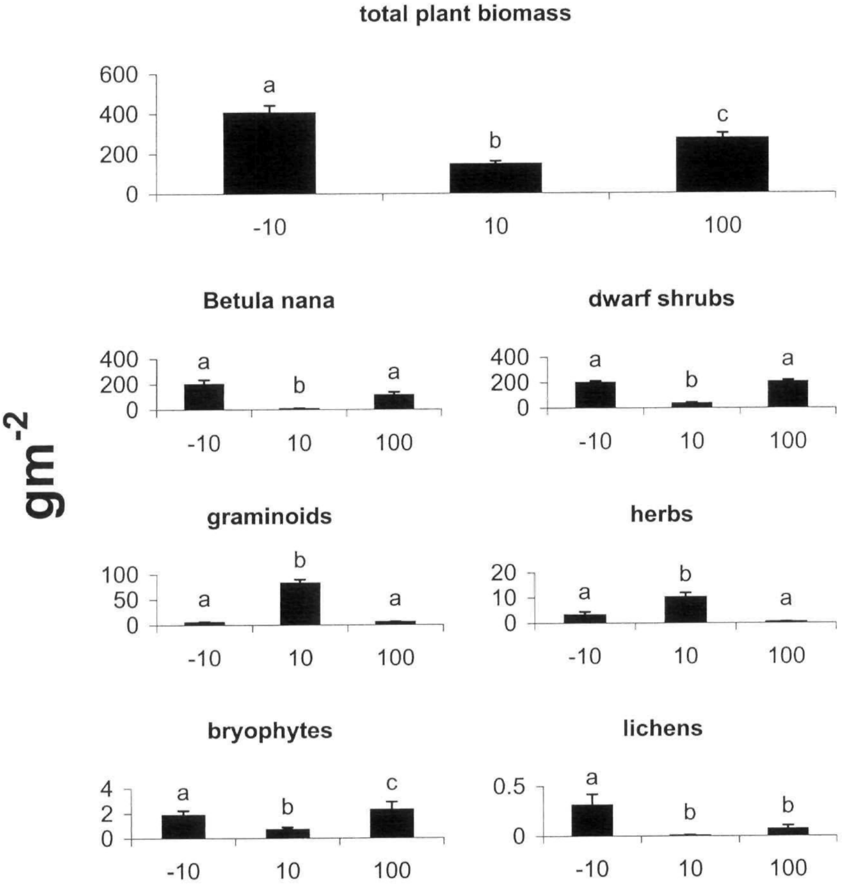

Fig. 3. Total plant biomass and biomass of different plant growth forms, measured as gm^{-2} (mean + SE). Different letter above the bars indicate that the columns are significantly different from each other.

Table 8. Analysis of variance for differences in plant biomass, primary productivity and biomass in the Raisduoddar area. Differences were tested with a two-way ANOVA without replication, with distance from fence as a fix factor and transect as a random factor. Bold F and p-values point out statistical significant.

	F	p
Biomass	**17.876**	**0.000**
Productivity	**5.844**	**0.006**
Betula nana	**11.995**	**0.000**
Dwarf shrubs	**54.657**	**0.000**
Graminoids	**100.89**	**0.000**
Herbs	**15.227**	**0.001**
Bryophytes	**3.645**	**0.034**
Lichens	**5.320**	**0.008**

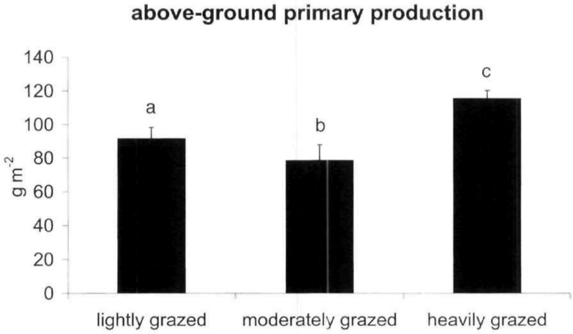

Fig. 4. Plant aboveground primary production measured as g m^{-2} (mean + SE). Different letter above the bars indicate that the columns are significantly different from each other.

here. *Betula nana*, ericoid dwarf shrubs, bryophytes and lichens had almost disappeared. In the moderately grazed area, current year's growth consisted mainly of annual increments of *Betula nana* and ericoid dwarf shrubs. Herbs increased with heavy grazing (Fig. 3, Table 8).

Nutrient cycling was only examined at two grazing intensities, i.e. the lightly grazed area (– 12 m) and the heavily grazed zone (12 m). Nearly all measured variables indicate that reindeer grazing has increased the activity of decomposer microbes. There was a significant difference in initial NH_4, organic N content, and the lag time. C mineralization, gross N mineralization, microbial biomass of C and N, and metabolic quotient appeared to be higher in the grazed area, although the differences were not significant. The NH_4 content decreased during the net mineralization measurement, indicating net immobilization (Table 9).

Discussion

The replacement of dwarf shrubs by graminoids in grazed areas is consistent with previous findings. Intense grazing by sheep in Britain has replaced areas of heather moorland with graminoids, where soil conditions are favourable (Clarke et al. 1995). Tundra heaths in northern Alaska can be replaced by graminoids following mammalian herbivores (McKendrick et al. 1980), fertilisation (McKendrick et al. 1980, Shaver and Chapin 1986, Fox 1992), around animal carcasses and faeces (Batzli et al. 1980, McKendrick et al. 1980) and disturbance (Batzli and Sobaski 1980, Chapin and Shaver 1981). This grass-dominated vegetation has higher tissue-nutrient concentration than ericoid dwarf shrubs, is more digestible, and attracts grazing reindeer (White and Trudell 1980).

Clear transition of the heath vegetation into grassland occurred only along two of the fences, Raisduoddar and Čearro. There was a tendency for graminoids to increase in Lagisduoddar and Siččajávri, but the heavily grazed zones were not dominated by grassland vegetation. In Siččajávri, ericoid dwarf shrubs and bryophytes were not significantly influenced. Apparently, grazing pressure near this fence, where reindeer on the southern Finnish side have no tradition to move to the northern side of the fence, was not high enough to break the dwarf shrub dominance and favour graminoids. At Lagisduoddar, grazing pressure in the heavily grazed zone near the fence was definitely high

Table 9. Mean and SE of below-ground nitrogen and carbon circulation, in the Raisduoddar area. Differences are tested with a paired t-test (Z and p), with six replicates. Bold F and p-values point out statistical significance.

	lightly grazed		heavily grazed				
	mean	SE	mean	SE		Z	p
nhdm1	**2.91**	**1.78**	**18.4**	**2.55**	**mg/dm**	**–2.882**	**0.004**
gross mineralisation	2.06	0.46	3.13	0.63	mg/dm/d	–1.095	0.273
nett minearlisation	–1.16	0.39	–1.75	0.57	mg/dm/d	–1.121	0.262
microbal N	39.5	3.34	50.3	4.80	mg/dm	–1.121	0.262
organic N	**8.10**	**1.03**	**20.2**	**2.99**	**mg/dm**	**–2.402**	**0.016**
rspdm	3.32	0.60	6.50	0.94	mg/dm	–1.601	0.109
microbal C	291.07	39.51	383.24	34.87	mg/dm	–1.281	0.200
metaq	0.0115	0.0015	0.0169	0.0014		–1.601	0.109
lagg	**38.0**	**4.46**	**23.3**	**2.96**		**–2.722**	**0.006**
max	5.57	0.19	4.67	0.44		–1.121	0.262
omckp	0.85	0.051	0.74	0.051	gOM/g	–1.761	0.078

enough for ericoid dwarf shrubs and bryophytes to decrease, as even a high proportion of the ground was bare from all vegetation. We can not explain why graminoids did not increase here in the same way as on Raisduoddar or Čearro. The reason is probable not climate, as Lagisduoddar is intermediate between Raisduoddar and Čearro along an oceanic-continental gradient (Oksanen and Virtanen 1995). At Lagisduoddar, a river with lush vegetation a few hundred meters from the fence attracts the reindeer and enhances grazing pressure near the fence and may create continuously grazing that suppresses the establishment of graminoids. Erecting temporary fences in the heavily grazed zone could test if that is the case.

Even at Raisduoddar and Čearro, graminoids only increased in the heavily grazed zone near the fence. There was a quite sharp border between the grasslands near the fence and the heathlands further away. Strong positive response of graminoids seems to require that dwarf-shrubs and mosses have suffered severely. Moreover, there seems to be a positive feedback between grazing pressure and productivity. When grazing intensity is severe enough to create grassland, the grassland will attract more reindeer, which further enhances summer grazing pressure.

The overall pattern for how grazing influenced diversity did not at all correlate with nutrient richness as Proulx and Mazumder (1998) predicted. Diversity of vascular plants increased in one nutrient rich area (Raisduoddar) and one nutrient poor area (Čearro). Diversity of bryophytes also increased in Raisduoddar but also in the nutrient poor Siččajávri. Lichen diversity increased with summer grazing in one nutrient rich area (Lagisduoddar) and one nutrient poor area (Siččajávri), and decreased in one nutrient rich area (Raisduoddar) and one nutrient poor area (Čearro).

Increased productivity is a common result in grazed grasslands (McNaughton 1979, 1985, Hik and Jefferies 1990, Pandey and Singh 1992, Frank and McNaughton 1993). Generally however, productivity is considered to be highest in intermediately grazed areas (McNaughton 1979, Hilbert et al. 1981, Loreau 1995), and this pattern has been found in some studies in grasslands (McNaughton 1979, 1985, Frank and McNaughton 1993). In this study however, the increase in primary production only occurred in the heavily grazed zone near the fence, while moderate grazing seemed to decrease primary production. Primary production increased when the vegetation has changed from heathland to grassland. The studies mentioned above, investigated productivity within grasslands, whereas our study was in tundra heath. Manseau et al. (1996) found that caribou decreased the carrying capacity of their summer-range in the northeastern Canadian tundra. The grazing pressure in that study should probably be compared with our moderate grazing pressure where productivity decreased, because ericoid dwarf shrubs still were rather common in both cases.

The increase in primary productivity in the heavily grazed zone is associated with an increase in free ammonium, enhanced activity of decomposer microbes and nutrient cycling. This has been found previously both in the African savannah (Ruess and McNaughton 1987, McNaughton et al. 1988) and grasslands in North America (Frank and McNaughton 1993, Frank and Evans 1997, Frank and Grossman 1998). Some theories focus on increases in nutrient cycling as the mechanisms through which grazing increase primary productivity (Loreau 1995, Zimov et al. 1995, de Mazancourt et al. 1998).

Zimov et al. (1995), also emphasised the importance of trampling in transforming unproductive tundra into productive grassland. A bryophyte carpet that tends to keep the soil wet and cold often covers the tundra. Trampling disturbs the bryophyte carpet, makes the soil drier and warmer and thus, may increase the primary productivity. Other processes may also be involved in the increase of primary production in the heavily grazed grassland near the fence. Graminoid litter decomposes quickly (Hobbie 1996), and therefore the domination of graminoids instead of dwarf shrubs can be expected to enhance nutrient cycling. Urine and faeces create an organic nutrient pool where the nutrients are easily decomposable and are quickly recycled to inorganic form (McKendrick et al. 1980). Both these processes most probably contribute considerable to a faster nutrient cycling.

The enhancement of nutrient cycling appears most advantageous for graminoids, because in field manipulations they are noticed to gain most from the addition of nutrients (McKendrick et al. 1980, Shaver and Chapin 1986). Thus, it is unknown how much the change in nutrient content has influenced the species composition, and how much the changes in species composition have in turn influenced the enhanced nutrient cycling. Distributions of plant species are both a cause and a consequence of changes in nutrient cycling (Hobbie 1992), and the effect that plants has on their own fitness, through changes in soil fertility, have largely been neglected (Berendse 1994).

Because reindeer may increase primary production, they enhance the production of their own food resources and may have positive feedback on their own food supply in summer pastures. They also increase the food quality, as graminoids are a more preferred food source than ericoid dwarf shrubs (Batzli et al. 1980). Reindeer may create a transition in vegetation from moss-tundra into more productive grasslands, which could hold a larger population of herbivores. Reindeer at least have the potential to recreate a community, similar to the grass-steppe that dominated in cold areas until the end of Pleistocene. Therefore our results supports the hypothesis of Zimov et al. (1995), that the extinction of large herbivores was the primary reason for the transition of the arctic grasslands into a moss and dwarf-shrub tundra heaths.

The result from this study also suggests that moderate grazing might not be the best way to use the summer ranges. At moderate grazing pressure, the reindeer can be more selective and only eat the most preferred food plants and thus favour less preferred food plants, while the disturbance by trampling is too weak to decrease the occurrence of the less preferred plants. Thus the graminoids and herbs decrease, which may further decrease the nutrient circulation and the primary production (Pastor and Naiman 1992, Pastor et al. 1993). At higher grazing pressure the herbivores tend to be less selective (Westoby et al. 1989) and consume more of the less preferred species, and the importance of trampling increases. Thus, preferred food plants with high grazing tolerance such as graminoids, may be favoured by intensive grazing (Westoby et al. 1989). To create productive summer grazing ranges, the focus should be on keeping the vegetation in the favourable state where the preferred food source (graminoids) dominates the vegetation, and primary production is high. This might be best achieved by periodic intense grazing interspersed with periods of low grazing pressure.

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