Short- and long-term effects of changes in reindeer grazing pressure on tundra heath vegetation

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Summary

1 Previous studies of plant–herbivore interactions have typically focused either on short-term or long-term effects. By directly comparing effects at different temporal scales, I studied whether short-term experiments provide good indications of the long-term effects of herbivory.

2 I reciprocally transplanted turfs of tundra heath vegetation within areas covered by a long-term (40 years) reindeer manipulation experiment, in order to examine the effects of all possible permutations of light, moderate and heavy grazing pre- and post-transplantation.

3 The effects of a short-term (three growing seasons) increase in reindeer grazing pressure gave good qualitative indications of most of the long-term effects of grazing on plant biomass, species richness, moss cover and lichen cover. In contrast, reducing grazing pressure on previously heavily grazed vegetation had no significant effects on any of these variables over the same time-scale.

4 Although few effects on individual species were recorded from the short-term manipulations, all those that were significant were qualitatively similar to the long-term responses of the respective species to herbivory.

5 The grass-dominated vegetation from the heavily grazed area changed little when grazing and trampling pressure were reduced for 3 years. In contrast, the dwarf shrub-dominated vegetation in the lightly grazed area changed rapidly into grasslands when the grazing pressure was enhanced.

6 Re-establishment of dwarf shrubs appears to be both seed and microsite limited, but it appears that dwarf shrubs may be able to re-establish in previously heavily grazed vegetation in the absence of reindeer.

7 Transitions from moss- or dwarf shrub-dominated ecosystems to grass-dominated ecosystems are currently occurring at different locations in boreal, arctic and alpine regions due to atmospheric nitrogen deposition and livestock grazing. This loss of habitat may be reversible, given a relatively long time frame.

Key-words: herbivory, long-term grazing, reindeer, reversible vegetation states, seed banks, seedling establishment, short-term grazing, tundra

Introduction

Previous studies of the effects of herbivores on vegetation have typically focused on their possibly different effects over either long or short temporal scales (but see Milchunas *et al.* 1992; Milchunas & Laurenroth 1995; Milchunas *et al.* 1995). Herbivores influence plants over short temporal scales by removing tissue and sometimes directly killing them, while the indirect effects of herbivory via plant competition and nutrient dynamics operate over longer temporal scales (Mulder 1999). Herbivores can increase forage quality over short temporal scales, even when long-term effects are negative (Pastor & Naiman 1992; Milchunas *et al.* 1995). Current-year defoliation often increases above-ground forage quality as nutrients are translocated from below-ground tissue into new growth (Polley & Detling 1989; Chapin & McNaughton 1989; Milchunas *et al.* 1995), but long-term effects may include reductions

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in the abundance of palatable plants and increases in the abundance of unpalatable plants, thus reducing forage quality (Pastor & Naiman 1992; Milchunas *et al.* 1995). Herbivores initially increase nutrient availability by releasing readily available nutrients for plant growth in their urine and faeces, but in the long term they often decrease nutrient sources by promoting the growth of non-preferred forage species that have a lower litter quality, and by increasing soil nutrient losses as a result of disturbance (Pastor *et al.* 1993; de Mazancourt *et al.* 1998; Sirotnak & Huntly 2000).

In short-term experiments, effects of herbivory have often been studied by excluding herbivores from previously grazed areas, by introducing herbivores or by clipping vegetation in previously ungrazed areas (Huntly 1991; Mulder 1999). Increasing and decreasing grazing pressure affects plant communities via different processes in the short term. The effects of increased grazing pressure depend heavily on the ability of the herbivore to reduce the abundance of the most palatable plants, while the effect of reducing grazing pressure appears to depend on the ability of grazing-intolerant species to invade swards. The direct effect of increasing grazing pressure is likely to be more dramatic than the direct effect of decreasing the grazing pressure, as palatable or sensitive plants are often depleted more quickly than they can re-establish. High densities of reindeer can deplete thick lichen mats in only a few years, but it takes decades for lichen mats to regrow (Tihkomirov 1959; Chernov 1985; Klein 1987; Väre *et al.* 1995; Manseau *et al.* 1996; Cooper & Wookey 2001; Cooper *et al.* 2001; Van der Wal *et al.* 2001; Den Herder *et al.* 2003).

Reindeer can cause a dramatic shift in vegetation from moss- or dwarf shrub-dominated to graminoid-dominated ecosystems (Zimov *et al.* 1995; Olofsson & Oksanen 2002; Van der Wal & Brooker 2004). Grazing and trampling reduce the abundance of dwarf shrubs and mosses, and both temperature and nutrient turnover increase (Olofsson *et al.* 2004), favouring graminoid growth (Brooker & van der Wal 2003). Addition of nutrients from faeces favours grass growth directly by releasing easily available nutrients, but also indirectly by enhancing soil temperatures (Van der Wal *et al.* 2004).

Several kilometres of fencing were established between summer and winter grazing areas in the 1960s in Finnmark, Norway, and this system provides a unique opportunity to study the long-term effects of reindeer grazing. The winter grazing areas close to the fences are little used by reindeer, whereas in summer, areas close to the fences are grazed but those further away are less intensively used. Although treatments will be referred to as light, moderate and heavy grazing, reindeer also affect tundra vegetation by depositing urine and faeces and by trampling.

Earlier studies have shown that long-term heavy grazing in summer by reindeer can cause a shift in the vegetation from dwarf shrubs to graminoids, whereas dwarf shrubs still dominate in moderately grazed areas,

albeit at lower abundance than in lightly grazed areas (Olofsson *et al.* 2001; Olofsson *et al.* 2004). Vegetation shifts can occur in a variety of heathlands, from dry and nutrient-poor to moist and nutrient-rich, throughout Finnmark (Olofsson *et al.* 2001), but all vegetation types within the patchwork landscape do not respond in the same way to grazing. On dry exposed ridges with skeletal soils, for example, graminoids do not seem to increase when dwarf shrubs and mosses are reduced and, as a consequence, in these habitats grazing can lead to areas largely devoid of vegetation (Evans 1996).

I transplanted vegetation across two fences in a factorial design, so that turfs that previously had been lightly, moderately or heavily grazed were transplanted to lightly, moderately or heavily grazed areas in all permutations. Thus, it was possible to compare directly the effects of reducing and enhancing grazing intensity on summer pastures, and to compare short-term responses of transplanted vegetation with the long-term differences between grazing treatments. In addition, seed bank and seed germination trials were conducted in order to further elucidate the mechanisms behind the observed vegetation patterns.

Materials and methods

STUDY AREA AND EXPERIMENTAL DESIGN

The study was carried out at two locations in northern Norway: Lagisduoddar (70°30′ N, 27°30′ E) and Raisduoddar (69°39′ N, 27°30′ E). Lagisduoddar is situated 300 m a.s.l. and 50 m above the timberline in the suboceanic climatic sector, while Raisduoddar is situated 600–700 m a.s.l. and about 100 m above the timberline in the subcontinental climatic sector. Both locations are dissected by fencing built to reduce the risk of reindeer entering the migration areas or winter ranges during the summer and constructed of four or five wires fixed on 1–1.5 m high posts, running for several kilometres over the tundra. The fences have little effect on snow accumulation or wind speed.

In both locations, the highest grazing intensities are found in a zone, about 50 m wide, adjacent to the fence on the side grazed in the summer (hereafter 'the heavily grazed area'). Areas further away from this side of the fence are less intensively used (moderately grazed) and areas close to the fences on the other side are rarely used in winter by reindeer (Olofsson *et al.* 2001), i.e. lightly grazed.

The vegetation is heterogeneous in both locations, and consists of different community types depending on the local typography. The vegetation is sparse and the soil is thin and dry on exposed ridges. Snowbeds or wetlands are found in depressions, depending on the hydrology. The most common vegetation type, found in flat areas with dry soils, low nutrient availability and low grazing pressure, is Arctic Empetrum-Vaccinium heath (Oksanen & Virtanen 1995). The vegetation in the field layer is low but continuous, dominated by

Betula nana (frequency estimates at Lagisduoddar and Raisduoddar are, respectively, 39.6% and 27.8%), *Empetrum hermaphroditum* (26.0%, 60.0%), *Vaccinium myrtillus* (4.8%, 12.8%), *Vaccinium uliginosum* (18.4%, 6.2%), *Vaccinium vitis-idaea* (18.2%, 19.2%), *Dicranum* (17.4%, 21.5%) and *Pleurozium scheberi* (5.4%, 23.6%). The main differences between the two locations are that at Raisduoddar, *E. hermaphroditum* is more dominant and *V. myrtillus* replaces *V. uliginosum*. Nomenclature follows Nilsson (1991).

The effects of herbivory at different grazing intensities were studied by marking out five transects at 100-m intervals, running perpendicular to the reindeer fence, at sites where ungrazed vegetation is dominated by Arctic Empetum-Vaccinium heathland. Flat and homogenous sites, without any pronounced microtopography, were chosen to avoid confounding factors. The thickness of the upper soil layers varies from 5 to 15 cm and areas with skeletal soils were avoided. In late June 2000, four 0.7×0.7 m plots were marked out 10 m from the fence in both the lightly grazed and the heavily grazed areas, and also 100 m from the fence in the moderately grazed area, along each of the five transects at both locations (giving 120 plots in total). The four plots at each point were randomly assigned to non-transplanted control, transplanted back to the origin, and transplanted to the other two grazing treatments (to be replaced by turfs from the other grazing treatments). Transplanting was carried out between 26 and 29 June 2000 in Lagisduoddar and 30 June and 3 July 2000 in Raisduoddar.

Short-term effects of grazing were studied by comparing the changes in vegetation transplanted to the different grazing treatments, while long-term effects of grazing were studied by comparing the vegetation in non-transplanted control plots in the different long-term grazing treatments. I excavated 0.7×0.7 m turfs that included the organic soil layer down to the mineral soil (10 cm depth on average) and transplanted them into holes dug to remove other turfs. I estimated plant biomass non-destructively in both transplanted turfs and control plots with a modified point-intercept method (Jonasson 1988). Measurements were carried out annually from 2000 to 2002, at peak standing crop in early August, using a transparent plexi-glass table, 0.5×0.5 m, with 100 randomly distributed 4-mm holes. A pin of the same diameter was lowered through each hole, and I recorded the number of contacts the pin made for each species in the vegetation beneath it. The biomass of each species was then calculated based on regressions between the number of contacts and the biomass of each species, as described by Olofsson (2001). In addition, the presence of all species within each 0.5×0.5 m plot was recorded.

Changes in plant community composition between 2000 and 2002 were calculated using the Bray-Curtis measure of dissimilarity, B (Bray & Curtis 1957):

$$ B = \frac{\sum |X_{ij} - X_{ik}|}{\sum (X_{ij} + X_{ik})} $$

where X_{ij} is the biomass of species i in sample j and X_{ik} is the biomass of species i in sample k.

The Bray-Curtis measure is strongly influenced by abundant species, so rare species add very little to the value of the coefficient (Krebs 1989).

REINDEER ACTIVITY

Reindeer activity in each grazing treatment was monitored by means of trampling indicators (Bayfield 1971), consisting of nails with a 3 cm long iron wire attached to the top. When the nail is pushed down into the soil the iron wire stands straight up, and bends only when it is trampled. Twenty-five trampling indicators were placed in each of five plots representing each treatment at both locations in July 2000, and the number of indicators trampled was recorded in July 2001.

SEED BANKS AND SEED GERMINATION

In order to survey the seed bank, I collected soil cores (72 mm diameter) to a depth of 5 cm in late August 2004 at each site where turfs were transplanted in the lightly and heavily grazed areas. I did not study seed banks in the moderately grazed area. A 4-m measuring tape was placed on the ground, and soil cores were collected at 20-cm intervals (except where there were too many stones in the ground). The soil samples were kept refrigerated (5 °C) for 3 weeks before glasshouse trials could be started in the middle of September 2004. Twenty-eight cores from each treatment were used for the seed bank experiment (112 in total). I removed the litter and mixed the soil from each core. The soils were spread as a layer (approximately 5 mm thick) in trays $(0.2 \times 0.2$ m), over a 2.5-cm depth of seed-free organic glasshouse soil.

The 112 germination trays were arranged randomly in the glasshouse and the soils were kept constantly moist at about 20 °C. Fourteen additional trays with only glasshouse soil were used to control for the possible presence of seeds in the glasshouse. Emerging seedlings were counted every week for 16 weeks and seedlings were removed upon identification, taking care in separating seedlings from seeds, as were offshoots from stolons and rhizome fragments. As few seedlings emerged during the last 4 weeks of the experiment, most seeds that were initially present had probably germinated during the 16-week period. All seedlings and offshoots were summed by species from each tray, prior to statistical analyses.

Fifty-six cores from each treatment were used to examine their effect on germination. I removed all living plants as well as plant litter from half of the cores and mixed the soil prior to putting it in pots (6 cm diameter). The other cores were placed directly in the pots, leaving the vegetation and surface litter intact. Seeds from *E. hermaphroditum* and *B. nana* were collected at Raisduoddar in early September 2004 and were kept in a freezer (−20 °C) prior to sowing to

increase their germinability. A hundred seeds of one species were sown in each pot (14 replicates for each species × treatment × vegetation removal combination) Seedling emergence was counted in pots where the species were sown and in control (unsown) pots, to correct for emergence from external sources of seed.

STATISTICAL ANALYSES

Results from each of the two locations were analysed separately. The effects of grazing on plant biomass, plant-species richness, moss cover, lichen cover and plant community composition were analysed using a hierarchical ANOVA. The grazing treatments and origin of the transplants were treated as fixed categorical factors and transects as a random block factor. As the experiment has a split-plot design, hierarchical analyses were performed so that each factor was tested with the correct degrees of freedom and error terms. In all cases where significant two-way interactions were found, the data were analysed further using a separate analysis for the grazing treatment from which the transplants originated.

The data from the seed bank and germination trials were analysed using generalized linear models with Poisson errors. In order to account for possible over-dispersion the quasi-routine was used to define different family error structures, thus allowing the variance to increase with the square root of the mean (Crawley 2002). All analyses were performed with the R statistical package (R Development Core Team 2005).

Results

Measurements confirmed that trampling frequency was highest in the heavily grazed treatment, intermediate in the moderately grazed treatment and absent in the lightly grazed treatment. Differences between treatments were significant both at Lagisduoddar and Raisduoddar (Table 1). A Tukey post-hoc HSD test demonstrated that trampling frequencies in all treatments were significantly different from each other in both locations.

There were no statistical differences in plant biomass ($F_{1,30} = 0.5$, $P = 0.503$), moss cover ($F_{1,30} = 0.5$, $P = 0.489$), lichen cover ($F_{1,30} = 1.1$, $P = 0.306$), plant species-richness ($F_{1,30} = 1.5$, $P = 0.235$) or dissimilarity values in plant community composition ($F_{1,30} = 0.7$, $P = 0.406$) between non-transplanted control plots and turfs re-transplanted in their original site for any of the three treatments at either location (Table 2). Thus,

transplantation *per se* did not affect the characteristics of the vegetation and further analyses were performed for the transplanted turfs only. Long-term grazing reduced plant biomass, moss cover and lichen cover at both Raisduoddar and Lagisduoddar but reduced species-richness only in Lagisduoddar (Table 3). Significant origin–transplantation interactions indicated that relative changes in plant biomass ($F_{4,24} = 5.0$, p = 0.004; $F_{4,24} = 5.3$, $P < 0.003$) and species-richness ($F_{4,24} = 0.6$, $P < 0.695$; $F_{4,24} = 4.6$, $P = 0.007$) and dissimilarity in plant community composition between 2000 and 2002 ($F_{4,24} = 16.5$, $P < 0.001$, $F_{4,24} = 14.4$, $P < 0.001$) were affected both by the previous long-term grazing treatment and by the grazing treatment to which the turfs were transplanted. The results of the three previous long-term grazing treatments were therefore analysed separately.

The biomass of lightly grazed vegetation decreased when turfs were transplanted to moderately grazed plots and, even more, in the heavily grazed plots, at both Raisduoddar and Lagisduoddar (Table 2). The total plant biomass of vegetation that had previously been moderately grazed changed when turfs were transplanted to the other grazing treatments at Raisduoddar, but not at Lagisdouddar. The total biomass of previously heavily grazed vegetation did not change significantly when turfs were transplanted to other grazing regimes at either location.

Significant reductions in species richness were recorded when lightly grazed turfs were transplanted to moderately and heavily grazed areas in Lagisduoddar (Table 2). Transplanting had no effect at Raisduoddar, where long-term grazing has no effect on species richness. Transplanting lightly and moderately grazed vegetation to the heavily grazed treatment affects plant community composition but transplanting turfs from heavily grazed vegetation does not (Table 2).

Transplanting turfs with vegetation to other grazing treatments affected the abundance of dwarf shrubs at both locations, as indicated by the significant origin–transplantation interactions (Raisduoddar, $F_{4,24} = 4.6$, $P = 0.002$; Lagisduoddar, $F_{4,24} = 3.4$, $P = 0.024$), but the abundance of graminoids was affected only at Raisduoddar ($F_{4,24} = 6.0$, $P < 0.001$). Forbs were not significantly affected by grazing at either of the two locations. As the interaction terms were significant for dwarf shrubs and graminoids, the effects of transplantation were tested separately for each original grazing treatment. Transplanting turfs from lightly grazed vegetation to moderate and heavy grazing reduced the

Table 1 Reindeer activity measured as percentage of trampling indicators triggered between July 2000 and July 2001. Twenty-five trampling indicators were placed at each of five sites representing three different grazing treatments at each of the two locations

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	Lightly grazed (mean ± SE)	Moderately grazed (mean ± SE)	Heavily grazed (mean ± SE)	$F_{2,8}$	P
Lagisduoddar	0.0 ± 0.0	29.6 ± 2.4	52.0 ± 5.8	43.1	< 0.001
Raisduoddar	0.0 ± 0.0	22.4 ± 2.2	33.6 ± 3.4	38.6	< 0.001

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*Short- and long-
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Table 2 Short-term effects of grazing on plant community properties at the two study locations. Vascular plant biomass was estimated non-destructively with the point-intercept method. Species richness was recorded for vascular plants, mosses and lichens. As the biomass of mosses and lichens cannot be estimated with the point intercept method, basal cover is reported for them instead. Turfs were reciprocally transplanted from previously long-term lightly (LG), moderately (MG) and heavily grazed (HG) areas to each of the three grazing treatments. Plant community composition was investigated using the point-intercept method before the turfs were transplanted in 2000 and in 2002. F-values and levels of significance are presented (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Significant differences between turfs transplanted to different grazing treatments are indicated with different letters

| | | Relative change when transplanted to | | | | | | | | |
| | | Control | | LG | | MG | | HG | | |
	From	Mean	SD	Mean	SD	Mean	SD	Mean	SDx	$F_{2,8}$
Lagisduoddar										
Plant biomass	LG	0.06	0.07	−0.06	−0.08[a]	−0.39	0.20[b]	−0.65	0.08[c]	24.7***
	MG	−0.14	0.31	0.31	0.29[a]	−0.07	0.09[ab]	−0.30	0.52[b]	7.1*
	HG	−0.05	0.11	0.17	0.23	0.10	0.24	0.19	0.11	0.4
Species richness	LG	−0.01	0.08	−0.02	0.11[a]	−0.27	0.10[b]	−0.29	0.21[b]	5.8*
	MG	−0.10	0.19	0.27	0.10[a]	−0.08	0.17[b]	−0.34	0.23[c]	9.8***
	HG	0.03	0.13	0.01	0.19	−0.10	0.27	−0.02	0.18	0.8
Dissimilarity	LG	0.16	0.02	0.19	0.03[ab]	0.37	0.18[b]	0.59	0.12[c]	12.7**
	MG	0.25	0.22	0.31	0.06[a]	0.29	0.07[a]	0.60	0.26[b]	27.1***
	HG	0.14	0.04	0.33	0.05[a]	0.30	0.06[a]	0.22	0.01[b]	25.3***
Moss cover	LG	0.11	0.13	0.05	0.32[a]	0.00	0.06[a]	−0.55	0.41[b]	7.7*
	MG	−0.01	0.24	0.90	1.66	−0.51	0.60	−0.75	0.42	8.5*
	HG	−0.01	0.01	8.2	14.4	0.04	0.40	0.76	0.53	1.5
Lichen cover	LG	0.03	0.26	0.11	0.16[a]	−0.51	0.29[b]	−0.53	0.44[b]	8.5*
	MG	0.02	0.03	−0.21	0.42	−0.02	0.64	−0.36	0.50	2.1
	HG	−0.07	0.15	−0.10	0.22	0.33	1.04	−0.10	0.22	1.0
Raisduoddar										
Plant biomass	LG	0.01	0.05	−0.07	0.12[a]	−0.38	0.24[b]	−0.74	0.08[c]	22.6***
	MG	0.01	0.08	0.37	0.39[a]	−0.02	0.11[ab]	−0.22	0.16[b]	7.4*
	HG	0.00	0.06	0.14	0.17	0.09	0.13	0.07	0.14	0.4
Species richness	LG	0.04	0.06	−0.06	0.08	−0.15	0.15	−0.19	0.24	1.3
	MG	0.05	0.09	0.02	0.14	−0.02	0.13	0.00	0.28	0.1
	HG	−0.02	0.06	−0.08	0.18	−0.11	0.09	0.02	0.18	0.9
Dissimilarity	LG	0.09	0.03	0.17	0.05[a]	0.28	0.09[a]	0.49	0.09[b]	26.2***
	MG	0.10	0.03	0.34	0.33[b]	0.14	0.08[a]	0.34	0.03[b]	11.5**
	HG	0.09	0.03	0.19	0.03	0.18	0.08	0.15	0.03	0.4
Moss cover	LG	0.05	0.06	0.08	0.21[a]	−0.38	0.14[b]	−0.42	0.21[b]	10.2**
	MG	0.03	0.28	0.77	1.02[a]	−0.07	0.15[ab]	−0.56	0.32[b]	6.6*
	HG	−0.19	0.25	0.44	1.24	0.40	0.82	0.42	0.74	0.0
Lichen cover	LG	0.11	0.51	−0.08	0.21	−0.27	0.39	−0.25	0.57	0.6
	MG	−0.10	0.15	0.70	1.29	−0.05	0.48	−0.17	0.74	1.4
	HG	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.51	0.3

Table 3 Long-term effects of grazing on plant community properties at the two study locations. Vascular plant biomass was estimated non-destructively in 2002 with the point-intercept method. Species richness was recorded for vascular plants, mosses and lichens. As the biomass of mosses and lichens cannot be estimated with the point intercept method, percentage cover is reported instead. Significant differences between treatments are indicated with different letters

| | Lightly grazed | | Moderately grazed | | Heavily grazed | | | |
	Mean	SE	Mean	SE	Mean	SE	$F_{2,8}$	P
Lagisduoddar								
Biomass g/m^2	91.7	14.2[a]	42.6	9.3[ab]	26.9	6.9[b]	12.3	0.004
Species richness	17.4	1.9[a]	12.3	1.4[ab]	11.4	1.2[b]	5.0	0.039
Moss cover (%)	40.5	8.4[a]	20.4	8.7[ab]	8.1	2.6[b]	4.9	0.041
Lichen cover (%)	18.0	6.1[a]	3.4	2.5[b]	0.5	0.4[b]	6.3	0.022
Raisduoddar								
Biomass g/m^2	91.1	6.3[b]	68.3	2.8[a]	72.8	4.3[a]	6.4	0.021
Species richness	15.7	0.7	16.4	1.1	14.4	1.0	1.2	0.364
Moss cover	72.0	6.3[a]	25.7	8.9[b]	15.4	7.7[b]	16.4	0.001
Lichen cover	20.2	5.6[a]	4.9	2.2[b]	0.2	0.2[b]	10.6	0.006

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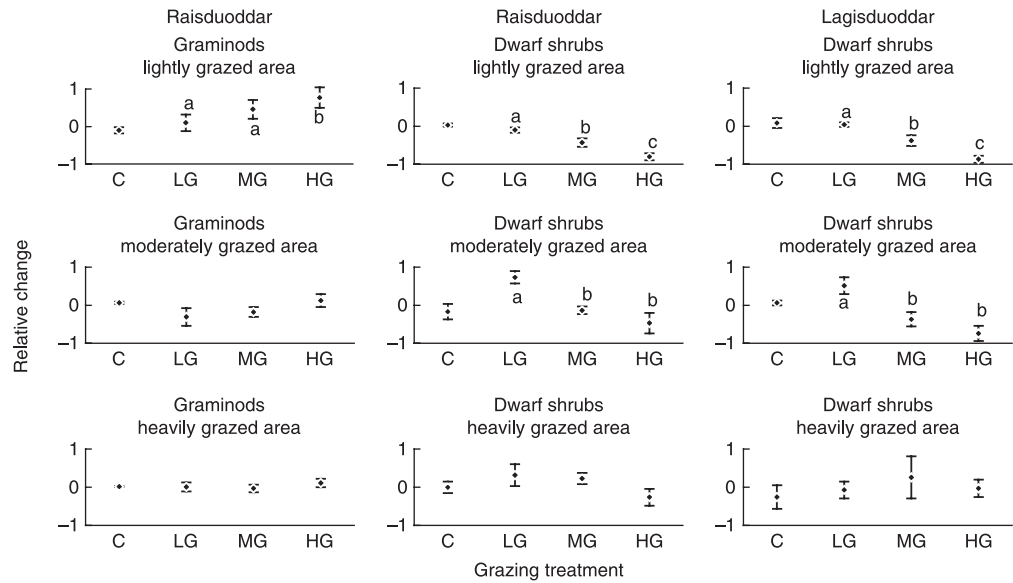*Journal of Ecology*
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Fig. 1 Relative changes in abundance between 2000 and 2002 (mean ± 1 SEM) of dwarf shrubs and graminoids at the two locations, Raisduoddar and Lagisduoddar. Different letters indicate that means of the different transplanted turfs were significantly different based on Tukey HSD post-hoc test. No untransplanted control (C) plots were significantly different from the turfs transplanted back to the treatment they came from. The untransplanted controls were thus not included in further statistical modelling.

abundance of dwarf shrubs at both locations (Fig. 1, Raisduoddar, $F_{4,24} = 7.1$, $P = 0.016$; Lagisduoddar, $F_{2,8} = 44.3$, $P < 0.001$). Transplanting previously moderately grazed turfs to the lightly grazed treatment increased the abundance of dwarf shrubs (Fig. 1, Raisduoddar, $F_{2,8} = 6.8$, $P = 0.019$; Lagisduoddar, $F_{2,8} = 10.1$, $P = 0.006$) but transplantation to heavily grazed areas had no significant effect. Transplanting previously heavily grazed turfs to moderately and lightly grazed treatments had no significant effect on the abundance of dwarf shrubs (Raisduoddar, $F_{2,8} = 1.6$, $P = 0.221$; Lagisduoddar $F_{2,8} = 0.2$, $P = 0.843$). Transplanting lightly grazed turfs to the moderate and heavy grazing treatments significantly increased the abundance of graminoids in Raisduoddar (Fig. 1, $F_{2,8} = 7.1$, $P = 0.017$), but there were no significant effects on the abundance of graminoids when moderately and heavily grazed turfs ($F_{2,8} = 3.0$, $P = 0.109$; $F_{2,8} = 1.0$, $P = 0.421$) were transplanted to lightly grazed areas.

Transplanting previously lightly grazed turfs to the moderately and heavily grazed treatment decreased moss cover (Table 2). Moss cover also decreased when previously moderately grazed vegetation was transplanted to the heavily grazed areas but increased following transplantation to lightly grazed areas (Table 2). Transplantation to moderately or lightly grazed treatments did not influence the moss cover of previously heavily grazed vegetation. Lichen cover was significantly reduced only when previously lightly grazed vegetation at Lagisduoddar was transplanted to other grazing regimes (Table 2).

Nine and seven species, respectively, differed in abundance between long-term heavily and lightly grazed treatments at Lagisduoddar and Raisduoddar,

but only three of these were significantly affected in short-term transplantation experiments (Table 4). However, in all cases, species that were significantly influenced by short-term treatments were also qualitatively influenced in the same way by long-term treatments. Interestingly, the grass, *Deschampsia flexuosa*, and the sedge, *Carex vaginata*, decreased in abundance when heavily grazed turfs were transplanted to the lightly grazed areas.

Seeds of *Empetrum hermaphroditum* were more abundant in the seed bank from the lightly grazed treatment than the heavily grazed treatment in both Lagisduoddar (d.f. = 26, $z = 5.7$, $P < 0.001$) and Raisduoddar (d.f. = 26, $z = 6.8$, $P < 0.001$). Herbs (Raisduoddar, d.f. = 26, $z = 9.2$, $P < 0.001$; Lagisduoddar, d.f. = 26, $z = 4.9$, $P < 0.001$) and graminoids (Raisduoddar, d.f. = 26, $z = 38.7$, $P < 0.001$; Lagisduoddar, d.f. = 26, $z = 38.4$, $P < 0.001$) were more abundant in the seedbank from the heavily grazed treatment. In contrast, *Betula nana* was more abundant in the seedbank from the lightly grazed treatment in Lagisuoddar (d.f. = 26, $z = 6.1$, $P < 0.001$) and seeds of this species were not found in Raisduoddar (Fig. 3).

In the germination trials, the establishment of *E. hermaphroditum* (Raisduoddar, d.f. = 52, $z = 9.9$, $P < 0.001$; Lagisduoddar, d.f. = 52, $z = 8.2$, $P < 0.001$) and *B. nana* (Raisduoddar, d.f. = 52, $z = 6.4$, $P < 0.001$; Lagisduoddar, d.f. = 52, $z = 6.6$, $P < 0.001$) seedlings was enhanced when the competing vegetation was removed. Less than 1% of the seeds germinated in intact vegetation. However, a significant interaction between grazing treatment and vegetation removal for *B. nana* in Raisduoddar (d.f. = 52, z = −2.7, $P = 0.008$) indicates that seedlings established better in the

Table 4 Short- and long-term effects of grazing on the abundance of plants at the species level recorded as number of hits at 100 points. The abundance of plants in the long-term heavily grazed (HG) treatment and the long-term lightly grazed (LG) treatment is shown, together with relative changes in abundance between 2000 and 2002 of these species in vegetation transplanted between the different grazing treatments. *F*-values and levels of significance are presented (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$)

|						Relative change in abundance after short-term transplantations									
	Abundance after long-term grazing					from LG to					from HG to				
	LG		HG			LG		HG			LG		HG		
	Mean	SE	Mean	SE	$F_{2,8}$	Mean	SE	Mean	SE	$F_{2,8}$	Mean	SE	Mean	SE	$F_{2,8}$
Lagisduoddar															
Agrostis mertensii	0.5	1.0	7.2	2.0	9.4*	0.35	0.22	0.95	1.57	0.7	0.57	0.29	1.07	0.17	11.2*
Betula nana	39.6	10.1	0	0	12.7**	0.60	0.36	0.33	0.40	1.3	1.00	0.00	1.00	0.00	1.0
Carex vaginata	0.6	0.9	14.8	11.4	7.7*	1.00	0.00	1.00	0.00	1.0	1.07	0.17	1.50	0.19	14.0**
Deschampsia flexuosa	12.2	5.2	38.3	20.3	11.0**	0.79	0.29	1.42	1.17	1.3	0.99	0.11	1.61	0.53	6.7*
Empetrum hermaphroditum	26.0	38.3	0	0	8.3*	0.99	0.17	0.41	0.34	11.6*	1.00	0.00	1.00	0.00	1.0
Loiseleuria procumbens	0.1	0.1	4.0	1.4	40.1*	1.00	0.00	1.00	0.00	1.0	1.00	0.00	0.98	0.14	0.2
Poa alpina	0.0	0.0	2.9	4.0	9.6*	1.00	0.00	1.00	0.00	1.0	1.17	0.23	1.00	0.00	2.7
Vaccinium vitis idaea	18.2	8.7	0	0	11.5**	0.79	0.47	0.44	0.32	1.9	1.00	0.00	1.00	0.00	1.0
Barbilophozia sp.	0.6	1.8	7.8	3.8	15.9**	1.12	0.58	1.15	0.34	0.1	1.00	0.00	1.00	0.00	1.0
Raisduoddar															
Carex bigelowii	2.8	2.3	49.8	25.8	16.4**	1.18	0.29	0.75	0.35	4.5	0.83	0.39	1.00	0.00	0.1
Carex brunnescens	0.9	2.0	34.5	24.2	9.6*	1.00	0.00	1.00	0.00	1.0	1.22	0.53	1.05	0.23	0.5
Carex lachenalii	0.0	0.0	1.1	0.9	7.6*	0.90	0.22	1.00	0.00	1.0	1.00	0.00	1.40	0.89	1.0
Empetrum hermaphroditum	60.0	32.9	7.9	8.0	11.8**	0.93	0.18	0.35	0.41	8.5*	0.85	0.32	1.10	0.22	1.9
Festuca ovina	1.6	3.0	59.6	46.7	9.1*	0.92	0.18	0.88	0.27	0.1	0.70	0.22	1.17	0.41	3.8
Luzula spicata	0.0	0.0	0.7	0.3	22.5***	1.00	0.00	1.00	0.00	1.0	1.00	0.00	0.80	0.27	2.7
Dicranum scoparium	21.5	5.4	1.9	1.7	59.4***	1.31	0.57	0.51	0.08	9.6*	1.24	0.93	1.13	1.10	0.1
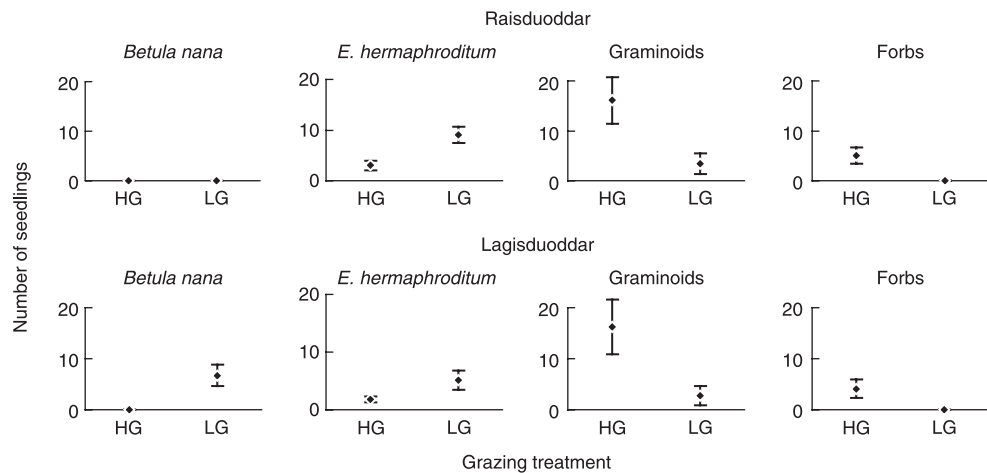
Fig. 2 Number of seedlings (mean ± 1 SEM) of the dwarf shrub species *Betula nana* and *Empetrum hermaphroditum* and two herbaceous groups, graminoids and forbs, emerging from seed banks in lightly and heavily grazed areas at two locations, Raisduoddar and Lagisduoddar.

previously heavily grazed soil in the absence of competition (Fig. 3).

Discussion

This study shows that responses of plant communities to increasing and decreasing grazing intensity are asymmetric (Fig. 4). Long-term intensive grazing has transformed the dwarf-shrub and moss-dominated heathlands into grass and sedge meadows with higher soil temperatures, higher nutrient turnover and higher primary production (Olofsson *et al.* 2001, 2004).

Reciprocal transplantation of turfs indicated that the transitions between these vegetation states are reversible, but the rates at which the transitions occur differ between the two directions. The abundance of dwarf shrubs, mosses and lichens was substantially reduced and the abundance of graminoids increased within 3 years when lightly grazed vegetation was transplanted to heavily grazed areas, but when heavily grazed turfs were transplanted to lightly grazed areas, the total abundance of graminoids and dwarf-shrubs did not change significantly over this time-scale and mosses increased in only one of the two locations. Decreases in
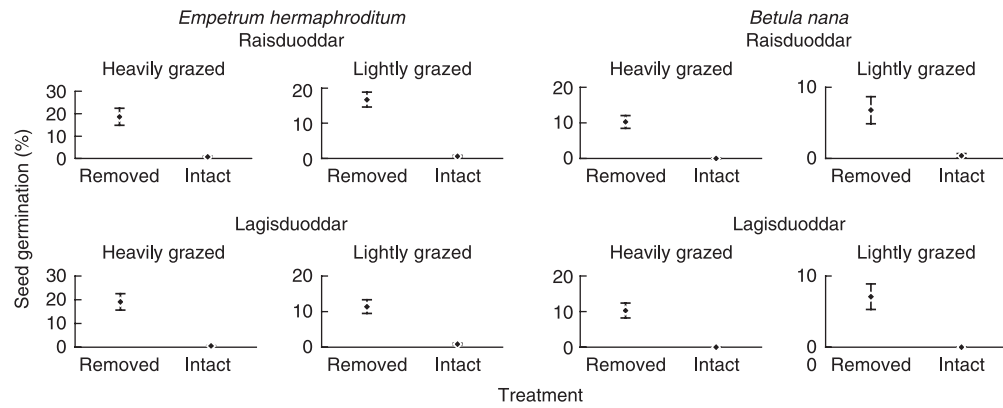
Fig. 3 Seed germination as a percentage (mean ± 1 SEM) of *Empetrum hermaphroditum* and *Betula nana* in lightly and heavily grazed treatments, with (intact) and without (removed) competing plants at two locations, Raisduoddar and Lagisduoddar. See text for experimental details.
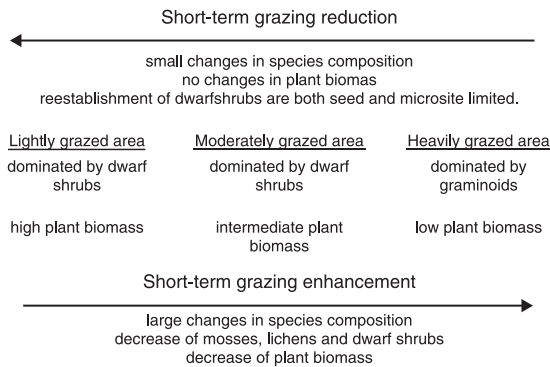

Fig. 4 Summary chart of the main results illustrating the asymmetry in the responses of functional groups to an altered grazing regime.

three common graminoids, *A. mertensii*, *C. vaginata* and *D. flexuosa*, after 3 years of reduced grazing and good germination of dwarf shrub seeds in soils from heavily grazed treatments, however, suggests that there is still potential for reversibility.

The dominant dwarf shrubs, *B. nana* and *E. hermaphroditum*, did not increase in turfs transplanted from the heavily grazed treatments to the lightly grazed treatments. A slow growth rate alone cannot explain this lack of recovery, as dwarf shrubs recovered rapidly in the moderately grazed area. One explanation could be that graminoids out-compete dwarf shrubs, as soil temperature and nutrient availability are higher in the heavily grazed treatments. Both higher nutrient availability (Strengbom *et al*. 2002; Van der Wal *et al*. 2004) and enhanced soil temperature (Brooker & Van der Wal 2003; Van der Wal & Brooker 2004) favour the competitiveness of graminoids over dwarf shrubs and mosses. Alternatively, seed banks may have been almost totally depleted of dwarf shrub seeds after 40 years of heavy grazing.

As tundra plants produce large numbers of seeds when weather conditions are suitable (Molau & Larson 2000) and seeds of *B. nana* disperse over long distances (Molau & Larson 2000; Welling & Laine 2002), *B. nana* seeds would be expected to reach graminoid-dominated areas, at least in some years. Seedling

emergence rates are, however, low in established swards in tundra plant communities (Welling & Laine 2002). In this study, less than 1% of the dwarf shrub seeds germinated in intact swards, whereas between 10 and 20% germinated when swards were removed. Although soil mixing and glasshouse conditions might confound the interpretation of these results, the results indicate that recovery of dwarf shrubs is both seed and microsite limited.

Short-term manipulation experiments appear poor indicators of long-term ecosystem change. This is not surprising as the effects of herbivory on forage quality (Milchunas *et al*. 1995) and nutrient cycling (Pastor *et al*. 1993; de Mazancourt *et al*. 1998; Sirotnak & Huntly 2000) differ at different temporal scales. However, short-term grazing enhancement proved to be an effective indicator of long-term effects, although the same was not true of short-term grazing reduction. This is particularly interesting as most short-term studies involve grazing reduction (i.e. exclosures), which is easier to reproduce under field conditions than grazing enhancement. Another interesting aspect is that the results of these short-term studies provide a fairly good indicator of long-term responses at the individual species level, but they are poor indicators of long-term responses of ecosystem traits such as species richness and the amount of plant biomass.

As only two fences were used in this study, pseudoreplication is an issue as grazing is confounded with area. However, the graminoid-dwarf shrub transition is not a gradual cline, but is represented as a sharp boundary at the fence (Olofsson *et al*. 2001; Olofsson *et al*. 2004). Thus, it is highly unlikely that the vegetation transition is caused by an environmental gradient other than grazing, especially as it occurs across the boundary of different fences (Olofsson *et al*. 2001). The different transects were also spaced hundreds of metres from each other and the reciprocal transplantation of turfs was a manipulative experiment showing that grazing, and not additional confounding factors, caused the observed patterns.

Grazing by large herbivores and nitrogen deposition are causing a transition from dwarf shrub- and

moss-dominated vegetation to grass-dominated vegetation in a number of tundra, mountain and boreal ecosystems (Thing 1984; Alonso *et al.* 2001; Strengbom *et al.* 2002; Van der Wal *et al.* 2003; Van der Wal & Brooker 2004; Van der Wal *et al.* 2004; Croll *et al.* 2005). My results indicate that the reindeer-induced transition from dwarf shrub- to graminoid-dominated ecosystems (Olofsson *et al.* 2001, 2004) is reversible, but that the recovery of dwarf shrubs is a slower process than the increase of graminoids. This is in agreement with studies from boreal ecosystems, where dwarf-shrubs replace graminoids after only a few years of fertilization (Strengbom *et al.* 2002), whereas it takes decades for the dwarf shrubs to recover after fertilization has ended (Strengbom *et al.* 2001). Further evidence for the reversibility of the dwarf shrub-graminoid transition can be found from islands in the Aleutian archipelago (Croll *et al.* 2005) where grasses dominate the vegetation in areas fertilized by sea birds. Islands where foxes were introduced a century ago, and the number of sea birds has therefore been reduced, have been transformed back into dwarf shrub-dominated ecosystems. The transition from dwarf shrub- to graminoid-dominated ecosystems probably increases the quality of summer pasture for reindeer (Olofsson *et al.* 2004). However, this vegetation shift has been regarded as habitat degradation in many other ecosystems, as the graminoid dominated vegetation stage is regarded as unnatural or less valuable (Alonso *et al.* 2001; Strengbom *et al.* 2001, 2002; Van der Wal *et al.* 2003).

Acknowledgements

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