

Long- and short-term effects of reindeer grazing on tundra wetland vegetation

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Received: 3 June 2008 / Revised: 25 September 2008 / Accepted: 26 September 2008 / Published online: 27 November 2008
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Abstract We studied long-term (50 years) and short-term (4 years) effects of summer grazing of reindeer on subarctic tundra wetland vegetation. The long-term effects of summer grazing were studied by comparing vegetation on Finnish and Norwegian sides of the fence line separating reindeer grazing regimes. The Finnish side was intensively grazed and trampled throughout the year, whereas the Norwegian side was grazed in winter. Experimental fences were erected to examine short-term effects of grazing exclusion. Both in the long- and short-term, summer grazing decreased the height of *Salix lapponum* whereas the short-term effects on willow cover were less clear than the long-term effects. In contrast, *Carex* spp. benefited from grazing. Long-term grazing had little effect on total bryophyte cover. Grazing had negligible effects on the nutrient content of leaves of *S. lapponum* and *Eriophorum angustifolium*. We conclude that tundra wetlands can withstand moderately high grazing pressure sustained over several decades.

Keywords *Rangifer tarandus* · Herbivory · Subarctic · Fennoscandia · *Salix lapponum* · *Eriophorum angustifolium*

Introduction

Herbivores, including reindeer (*Rangifer tarandus*), are an important factor influencing the composition of vegetation at local and landscape scales (Oksanen and Virtanen 1995; Manseau et al. 1996; Olofsson 2006). The combined effects of reindeer grazing, trampling and fecal deposition can modify competitive interactions of plants leading to an almost complete change in the species composition of a community (Manseau et al. 1996; van der Wal et al. 2004). Herbivores are able to generate shifts from one vegetation state to another, thereby changing the productivity of tundra (Zimov et al. 1995; van der Wal 2006). Grazing can also alter plant species' mineral composition (Kielland and Bryant 1998; Grellmann 2001), nutrient mineralization rates (Stark et al. 2000), primary production (Olofsson et al. 2001), and increase soil temperature (Zimov et al. 1995). Grazing may increase or decrease plant species richness, depending on factors such as grazing intensity and nutrient availability (Huntly 1991; Olofsson and Oksanen 2005). Long-term effects may include reduction in the abundance of palatable plants, thus reducing habitat quality (Pastor and Nainam 1992; Milchunas et al. 1995). Some plant species are avoided by herbivores, while others are selected as forage (Staal and Sæbø 1993). Responses of forage species to grazing will vary according to the plant's ability to regenerate after damage, the effects of plant competition, the abiotic conditions, and the type and intensity of herbivory (Crawley 1983; Bryant et al. 1991).

Willows (*Salix* spp.) are one of the dominant components of subarctic wetlands. Many studies have shown that the amount of willows decreases under prolonged grazing pressure by *Rangifer* spp. (Thing 1984; Manseau et al. 1996; Crête et al. 2001; Olofsson et al. 2001; den Herder et al. 2004). In woody species, plant consumption during

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the growing season generally reduces production (Ouellet et al. 1994; Manseau et al. 1996). Long-term data from Fennoscandian tundra suggest that exclusion of grazers leads to increased abundance of woody plants (Moen and Oksanen 1998). It has been shown by den Herder et al. (2004, 2008) that reindeer browsing in summer reduces biomass and diminishes the reproductive success of willow and that prevention of browsing by reindeer for only a few years (4 and 8 years) significantly increases willow growth and reproduction. Apart from the effects of herbivores on woody plants, an increase in biomass has been reported across the circumpolar Arctic because of global warming (Jia et al. 2003). Also shrub abundance has increased in specific regions of Alaska (Chapin et al. 1995; Tape et al. 2006), Fennoscandia (Tømmervik et al. 2004) and Russia (Shvartsman et al. 1999).

The effects of summer grazing on reindeer pastures have received less attention than winter grazing (Suominen and Olofsson 2000), but during the last decade there has been more research on the effect of grazing and trampling on summer pastures (Virtanen 1998; Bråthen and Oksanen 2001; Olofsson et al. 2001). We are not aware of long-term studies about the effects of grazing on wetlands, which are important feeding habitats for reindeer during summer. However, Klein (1968) speculated that summer grazing is seldom permanently destructive to moist subarctic tundra. Within wetlands in the study region, reindeer feed on, e.g., *Salix* spp., *Eriophorum angustifolium* and *Carex* spp. (Staal and Sæbø 1993; Warenberg et al. 1997). Leaves of willow are important forage for reindeer in early summer because they are high in protein at that stage (Nieminen and Heiskari 1989; Staal and Sæbø 1993). According to Warenberg et al. (1997), reindeer feed on *E. angustifolium* and *Carex* spp. year round, but they especially select new shoots and rhizomes.

In this paper we study the effects of reindeer grazing and trampling on wetland habitats in the border zone of Finland and Norway. We studied the effects of long-term (50 years) year-round grazing and trampling, compared to only winter grazing, on wetland habitat. We examined the effects at both the community and species levels and measured the cover of important forage species and genera (*Salix* spp., *Carex* spp. and *Eriophorum angustifolium*) and height of *Salix lapponum*. We also studied the effect of long-term grazing on the chemical composition of nutrients and water-soluble carbohydrates of the leaves of *S. lapponum* and *E. angustifolium*. These taxa have a broad geographical distribution, *E. angustifolium* being circumpolar and *S. lapponum* occurring from Scotland in the west to central Siberia in the east (Hultén and Fries 1986). In a separate experiment we studied the effects of short-term (4 years) exclusion of reindeer in wetlands on the Finnish side of the border where there was grazing year around. We predicted

that reindeer would have a negative impact on the cover of willow. In addition, we expected that a release of grazing pressure would lead to re-growth of *Salix*.

Materials and methods

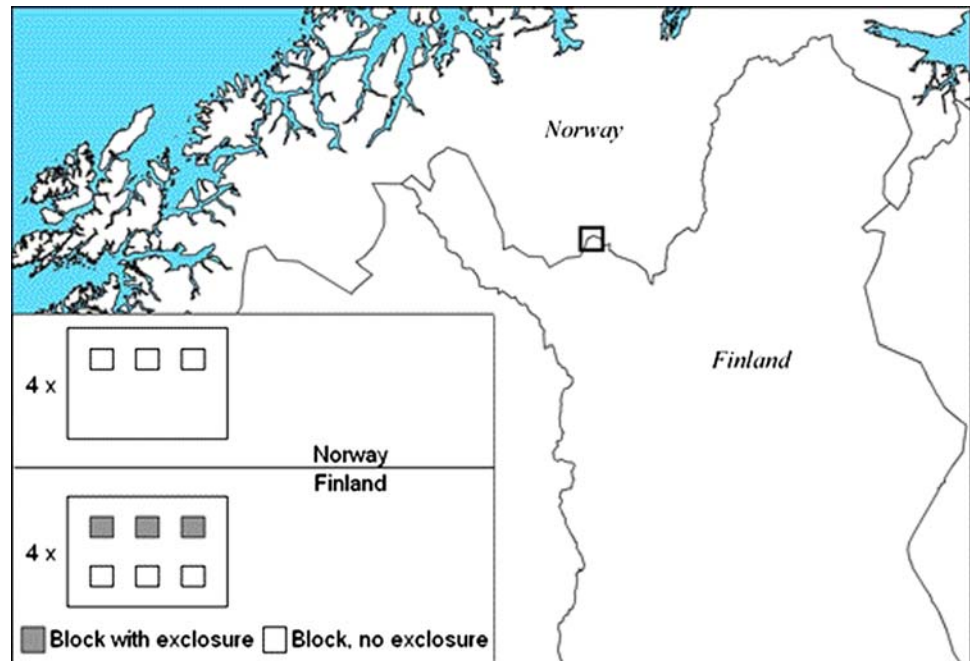
Study area

The study was carried out in Jávrrrešduottar (Fig. 1). It is located in a continental area along the border between Finland and Norway, Enontekiö and Kautokeino commune, at an altitude of 450–510 m a.s.l. The study area was bordered by latitudes 68°47.00'N and 68°50.25'N and longitudes 23°45.25'E and 23°55.25'E. The area is characterized by a mosaic of habitat types in which the prevailing terrain consists of exposed fells and heaths of the *Betula nana-Cladina* type (Virtanen et al. 1999). Heaths are interspersed with smaller, relatively well-circumscribed willow and graminoid-dominated wetlands. These habitats, with soils which remain water saturated virtually throughout the growing season, occupy approximately 10% of the management area. Within a given wetland community devoid of summer grazing, 86–90% of the vascular plant cover is represented by the genera *Salix*, *Carex* and *Eriophorum*. Dominant vascular plant species were *Salix lapponum*, *Carex rotundata*, *C. aquatilis*, *Eriophorum angustifolium*, and *C. canescens*. Dominant bryophyte species were *Straminergon stramineum*, *Warnstorfia exannulata*, *W. sarmentosa* and *Paludella squarrosa*.

The investigation was conducted along the fence between Norway and Finland, which was built in the late 1950s to prevent reindeer from crossing the state border. It separates the winter pastures of Norwegian reindeer from the year-round pastures of Finnish reindeer. On the Norwegian side grazing is not allowed between 5 May and 1 November, and this area is grazed only in winter. On the Finnish side reindeer remain in the area for about 1 month during summer time. They arrive to the area when mosquito harassment increases, typically sometime in mid-June, since high and windy fells in the area provide relief from mosquitoes for the animals. There are approximately 10–12 animals per square kilometer over the whole summer management area (about 150 km²). The grazing pressure and animal density are generally higher in wetland habitats because reindeer feed on them during summer. Herders make use of natural movements of reindeer and keep the reindeer within an area where it is relatively easy to collect them for earmarking. The area is surrounded with fences, which are opened after earmarking so that the animals are free to leave the area.

Information concerning the recent management of the area was provided by reindeer herders through interviews

Fig. 1 Study area and experimental design



and participant observation during the years 2001, 2002, and 2006. The precise study sites in Finland were selected together with herders based on their knowledge of summer pastures during preliminary interviews and field excursions in summer 2001 and late winter 2002.

Sampling

We established four study sites within the summer/winter grazing regime in Finland, and four study sites within the winter grazing regime in Norway in 2002 (Fig. 1). The sites within both regimes were characterized by similar vegetation cover, aspect and slope. For each study site in Finnish side three randomly sampled exclosures of 5×5 m were built in 2002 to prevent reindeer grazing. In the same study site we had three freely grazed sample plots of 5×5 m. Similarly, we had three sample plots of 5×5 m in the regime without summer grazing in Norway. There were thus three treatments: free summer grazing (Finland, no exclosures), blocking of summer grazing since year 2002 (Finland, exclosures), and no summer grazing (Norway). All the plots were randomly located within the study area. Within each plot four 50×50 cm quadrats were randomly chosen out of 25 possible quadrats. All sites were situated within an area of about 30 km^2 .

Measurements of plant cover and height of *S. lapponum* were made in July 2002 in Norwegian sites and Finnish sites inside the exclosures.

Plant samples of *S. lapponum* and *E. angustifolium* for chemical analyses of nutrients N, P, K, Mg, Na, Ca, S, Fe, Cu, Mn, Zn and water-soluble carbohydrates were collected from Norwegian sites and Finnish sites inside the exclo-

tures in July 2002. At each site ten sub samples of current year leaf tissue material were taken. Plant material was transferred to a laboratory facility within 24 h after harvesting and oven dried at 60°C for 24 h. For chemical analysis at the Chemical Analysis Laboratory of the Holt Research Centre (Norway), 5 g of dried material was ground and ashed before solution in aqua regia and filtration. Analyses of elements within the filtrate were performed using a Perkin–Elmer Optima 3300 DV.

Measurements of vascular plant cover and height of *S. lapponum* were made in July 2006 in Norwegian sites and Finnish sites in the plots both outside and inside the exclosures.

The data were collected following the protocol of the International Tundra Experiment, ITEX (Walker 1996). There were 100 ocular points at 5 cm intervals in each within 50×50 cm quadrat. A pin (diameter 3 mm) was dropped from each point and all vascular and non-vascular taxa with which it came into contact were recorded onto sheets that mapped each hit according to vertical and horizontal location with the quadrat. For narrow-leaved ericoid dwarf shrubs, only contacts with separate branches were counted. For other vascular plants each contact was counted. Bryophytes were measured during July 2002 in Norwegian sites and Finnish sites inside the exclosures. Bryophytes were considered to grow in one layer, so the maximum was one count per species at each point. Species found within a plot but not touched by any pin were counted as 0.1. The height of *S. lapponum* was measured in all plots, by measuring the uppermost shoots, with a maximum of five measurements per square. All plots were photographed.

Statistical analysis

We studied separately the effects of long-term grazing and short-term exclusion of reindeer on wetland habitats. Data were analyzed using linear mixed-effects models (Pinheiro and Bates 2000). We had four replicate quadrats in one plot, and this plot was used as a random factor in a mixed-effect model linear model. Since ‘plot’ was used as a random factor we had a nested design. This takes into account the dependence of quadrats within plots and avoids over dispersion. The significance of fixed effects was assessed using ANOVA. All statistical analyses were performed using R statistical software (R Development Core Team 2006). The mixed-effect modeling was done using the R package nlme (Pinheiro et al. 2006).

Results

Long-term grazing

Significant differences between summer grazed (Fig. 2) and non-summer grazed (Fig. 3) sites were found in the cover of *Carex* spp. ($F_{1,22} = 21.69$; $P < 0.001$) (Fig. 4). The cover of *Carex* spp. was greater in summer grazed sites than in non-summer grazed site (Fig. 4). In non-summer grazed sites the average cover of *Salix* spp. was greater than in summer-grazed sites (Fig. 4) but the difference was not quite significant ($F_{1,22} = 3.20$; $P = 0.09$). There was no statistical difference in the abundance of *E. angustifolium* ($F_{1,22} = 0.89$; $P = 0.36$). The average height of *S. lapponum* was significantly ($P < 0.01$) higher in non-summer grazed site compared to summer-grazed site (Fig. 5). The number of vascular plant species was significantly higher ($F_{1,22} = 5.43$; $P = 0.03$) in summer-grazed site than non-summer grazed site (Fig. 6).



Fig. 2 Overview of a plot in summer/winter grazed site in Finland



Fig. 3 Overview of a plot in non-summer grazed site in Norway

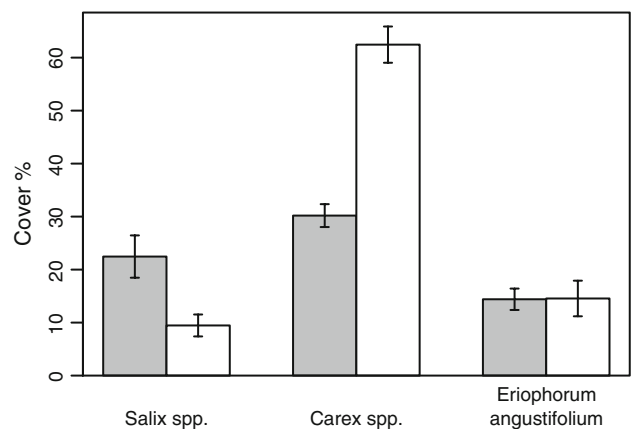


Fig. 4 Cover (mean \pm SE) of vascular plant species in non-summer grazed and summer-grazed sites ($n = 48$). Solid and open histograms refer to non-summer grazed and summer-grazed sites

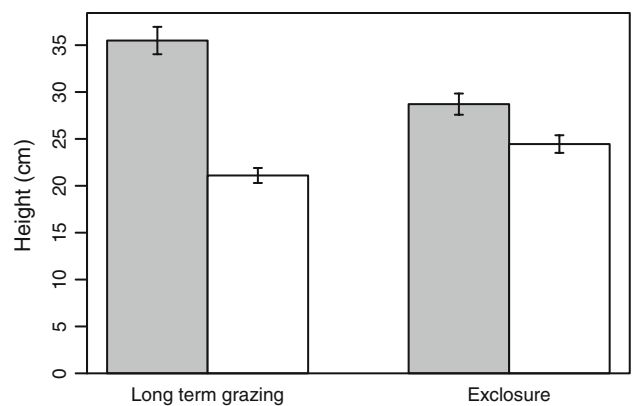


Fig. 5 Height (mean \pm SE) of *Salix lapponum* in non-summer grazed and summer-grazed sites. Solid and open histograms refer to non-summer grazed and summer-grazed sites. Height (mean \pm SE) of *Salix lapponum* in short term exclusion sites treatment ($n = 48$). Solid and open histograms refer to treatment 2002 and treatment 2006

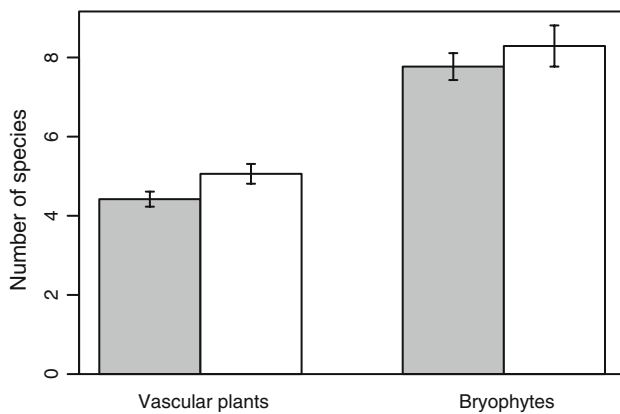


Fig. 6 Number (mean \pm SE) of vascular plant and bryophyte species in non-summer grazed and summer grazed sites ($n = 48$). Solid and open histograms refer to non-summer grazed and summer-grazed sites

The total cover of bryophytes, different bryophyte groups and the number of bryophytes did not differ between summer-grazed sites and non-summer grazed sites (Table 1). At the species level there was greater cover of *Straminergon stramineum* ($P = 0.02$) and *Paludella squarrosa* ($P = 0.04$) in non-summer grazed site compared to summer-grazed site (Table 1).

The concentration of zinc ($P = 0.04$) in the leaves of *E. angustifolium* was significantly higher in summer-grazed sites than in non-summer grazed sites (Table 2). There was also a consistent but not quite significant increase in zinc ($P = 0.11$) in the leaves of *S. lapponum*, and manganese ($P = 0.09$) in the leaves of *E. angustifolium* in summer-grazed sites (Table 2).

Short-term exclusion of reindeer

The 4-year exclusion of reindeer had no effect on the cover of *Salix* spp., *Carex* spp. and *E. angustifolium*. The height of *S. lapponum* had increased inside the enclosure but the difference was not quite significant ($F_{1,13} = 3.74$; $P = 0.08$; Fig. 3). Excluding reindeer had no effect on the number of vascular plant species (Table 3).

Discussion

Effects of long-term grazing

The remarkable differences between vegetation on Finnish and Norwegian side of the fence suggest that long-term summer grazing has changed the vegetation cover of the investigated wetlands. The main difference from non-summer grazed wetlands is the reduced abundance and height of *S. lapponum*, which has been reported by other studies in northern areas (Ouellet et al. 1994; Manseau et al. 1996; Olofsson et al. 2001; Ims et al. 2007). In the study area grazing and trampling are intensive enough to limit regeneration of willows. The mechanisms preventing willow growth at the level of the individual are that reindeer damage or kill shoots by ripping and consuming the leaves and younger twigs, which reduces the number and productivity of the newly formed shoots (den Herder et al. 2008).

In contrast to willows, sedges (*Carex* spp.) had greater cover on the Finnish side with intense summer grazing. This suggests that these sedges (mostly *C. rotundata* and *C. canescens*) may benefit from summer grazing. The sedges may benefit from a reduction in the abundance of willows. These rhizomatous graminoids seem to tolerate grazing, as does *E. angustifolium*, which was not affected by grazing, even though it is a highly palatable species (Warenberg et al. 1997). However, no new *Carex* species were recorded so that through removal of willows space was released for sedge species that were already growing within the sites. Other studies have also demonstrated that graminoids benefit from grazing and trampling (Oksanen 1978; Jefferies et al. 1994; Olofsson et al. 2001; Eskelinen and Oksanen 2006). One reason for the successful reproduction of graminoids is that the situation of the growing point is close to the ground and usually not eaten (Jefferies et al. 1994). Even when damaged, aboveground shoots and leaves regenerate readily in clonal rhizomatous graminoids, drawing on belowground stores of nitrogen and carbohydrates, often within the same growing season (Callaghan et al. 1991). In addition, enhanced nutrient cycling appears to be

Table 1 Cover (mean \pm SE) of bryophytes in non-summer grazed and summer-grazed sites

	No summer grazing	Summer grazing	df	F value	P
Bryophytes	122.0 \pm 5.2	109.4 \pm 5.0	1, 22	1.28	0.27
Bryales	76.0 \pm 6.4	56.1 \pm 4.6	1, 22	1.57	0.22
Marchantiophyta	13.8 \pm 2.7	19.3 \pm 3.4	1, 22	0.12	0.73
<i>Paludella squarrosa</i>	14.7 \pm 2.4	7.2 \pm 2.4	1, 22	4.60	0.04*
<i>Sphagnum</i> spp.	32.3 \pm 3.6	34.0 \pm 4.5	1, 22	0.004	0.95
<i>Warnstorfia</i> spp.	27.7 \pm 5.1	27.0 \pm 3.7	1, 22	0.06	0.81
<i>Straminergon stramineum</i>	28.5 \pm 3.1	13.9 \pm 2.0	1, 22	6.73	0.02*

The statistical analyses are based on a mixed-effect model where the block of quadrats was used as the random effect

Table 2 Amount of dry matter, ash and nutrients (mean \pm SE) in the leaves of *Salix lapponum* and *Eriophorum angustifolium* in non-summer grazed and summer-grazed sites

	No summer grazing	Summer grazing	df	F value	P
<i>Salix lapponum</i>					
Dry matter	93.8 \pm 0.04	93.6 \pm 0.10	1, 6	4.70	0.07
Ash	3.0 \pm 0.05	3.0 \pm 0.20	1, 6	0.09	0.78
N	1.9 \pm 0.02	2.0 \pm 0.10	1, 6	0.34	0.58
P	0.1 \pm 0.005	0.1 \pm 0.01	1, 6	0.24	0.64
Mg	0.2 \pm 0.005	0.3 \pm 0.02	1, 6	0.26	0.63
Ca	0.5 \pm 0.01	0.6 \pm 0.10	1, 6	0.04	0.86
K	0.5 \pm 0.01	0.4 \pm 0.01	1, 6	0.69	0.44
Na	0.04 \pm 0.001	0.04 \pm 0.002	1, 6	2.15	0.19
Cu	3.9 \pm 0.20	3.5 \pm 0.30	1, 6	0.0007	0.98
Fe	68.4 \pm 5.20	89.2 \pm 10.4	1, 6	0.14	0.72
Mn	284.5 \pm 14.50	500.9 \pm 69.0	1, 6	0.65	0.45
Zn	107.8 \pm 7.60	268.2 \pm 31.5	1, 6	3.41	0.11
S	105.8 \pm 2.50	113.5 \pm 5.50	1, 6	1.91	0.22
WSC	8.7 \pm 0.20	8.0 \pm 0.50	1, 6	0.80	0.40
<i>Eriophorum angustifolium</i>					
Dry matter	94.4 \pm 0.03	94.4 \pm 0.10	1, 6	0.50	0.51
Ash	3.2 \pm 0.1	2.9 \pm 0.10	1, 6	0.83	0.40
N	1.4 \pm 0.02	1.3 \pm 0.04	1, 6	0.53	0.50
P	0.1 \pm 0.004	0.1 \pm 0.01	1, 6	2.01	0.21
Mg	0.1 \pm 0.002	0.1 \pm 0.01	1, 6	0.07	0.79
Ca	0.1 \pm 0.003	0.2 \pm 0.01	1, 6	2.55	0.16
K	0.6 \pm 0.03	0.5 \pm 0.04	1, 6	1.73	0.24
Na	0.1 \pm 0.002	0.1 \pm 0.002	1, 6	0.05	0.84
Cu	0.6 \pm 0.10	0.4 \pm 0.16	1, 6	0.43	0.54
Fe	71.0 \pm 6.60	90.5 \pm 20.2	1, 6	0.21	0.66
Mn	35.7 \pm 2.80	80.5 \pm 15.4	1, 6	4.06	0.09
Zn	16.0 \pm 0.80	26.3 \pm 2.95	1, 6	6.39	0.04*
S	107.8 \pm 4.70	82.4 \pm 7.90	1, 6	1.73	0.24
WSC	10.8 \pm 0.2	10.6 \pm 0.47	1, 6	0.84	0.84

The statistical analyses are based on a mixed-effect model where the block of sample plots (four on each grazing regime) was used a random effect

Table 3 Cover (mean \pm SE) of species groups and number of vascular plants after short-term exclusion from reindeer grazing

	Inside enclosure	No enclosure	df	F value	P
Cover of <i>Salix</i> spp.	6.1 \pm 2.0	3.9 \pm 1.0	1, 22	0.002	0.96
Cover of <i>Carex</i> spp.	53.3 \pm 3.6	49.1 \pm 3.9	1, 22	0.57	0.57
Cover of <i>E. angustifolium</i>	17.5 \pm 2.2	12.7 \pm 1.6	1, 22	0.90	0.38
No. of vascular plant species	5.6 \pm 0.3	6.0 \pm 0.4	1, 22	-0.30	0.77

The statistical analyses are based on a mixed-effect model where the block of quadrats was used as the random effect

a prerequisite for a vegetation shift towards graminoids (Stark and Grellman 2002).

The increase of the number of vascular plant species is in agreement with other studies that show that species diversity increases in moderately grazed areas (Oksanen and Virtanen 1995; Väre et al. 1996; Olofsson et al. 2001; Olofsson and Oksanen 2005). Grazing had no effect on the number of bryophyte species. In heaths, grazing increases

the cover of bryophytes (Manseau et al. 1996). The cover of the bryophyte species *Paludella squarrosa* and *Straminergon stramineum* was higher in non-summer grazed sites. We did not measure thickness of the bryophyte layer but it is widely acknowledged that herbivores can reduce thickness of the bryophyte layer in Arctic areas where they trample and graze (Zimov et al. 1995; van der Wal et al. 2001).

There is an ongoing discussion regarding increasing shrub abundance and an overall greening of northern areas, presumably because of climate change (Jia et al. 2003; Tape et al. 2006). An interesting question concerns the relationship between the effects of climate change versus grazing on tundra vegetation. Our results show that reindeer grazing and trampling can decrease the abundance of erect willows over relatively large areas. While herbivory usually decreases the abundance of willows, recent climate warming (ACIA 2005; IPCC 2007) and changes in snow conditions (Sturm et al. 2005) may favor enhanced growth and abundance of *Salix* spp. On the other hand, it is not certain whether high densities of herbivores could offset such gains. From our results, it is clear that reindeer can significantly decrease the regeneration ability and growth of woody plants and thereby limit their abundance within wetland habitats at the local scale, which is confirmed by other studies in Fennoscandia (den Herder et al. 2008).

Effects of short-term exclusion of reindeer

Exclusion of reindeer for 4 years had no effect on overall vegetation cover. Our results contrast with those of comparable studies that are mainly from tundra heath where the exclusion of reindeer significantly affected vegetation cover (Brookshire et al. 2002; den Herder et al. 2004, 2008; Pajunen et al. 2008). In experiments by den Herder et al. (2004) at Kilpisjärvi in nearby Finnish Lapland, the cover and height of rejuvenated willows within reindeer enclosures increased after 4 years (1997–2002) as well as in the 8-year study of Pajunen et al. (2008) from the same area. Our study reveals a stage at which willow cover has begun to increase. Based on the evidence in this and other studies we assume that after a few more years the difference may be significant. Such an increase in willow cover is expected given that willows have responded to the removal of grazing with significant increases in height in other similar studies (Brookshire et al. 2002; den Herder et al. 2004, 2008; Pajunen et al. 2008).

Previous studies have shown that excluding reindeer has a greater effect on unproductive heaths than in more productive habitats (Oksanen et al. 1981; Moen and Oksanen 1998; Olofsson et al. 2002; Pajunen et al. 2008), the so-called ‘exploitation ecosystems hypothesis’ (*sensu* Moen and Oksanen 1998). According to this hypothesis, the exclusion of herbivores from less productive habitat leads to significant changes in vegetation productivity, whereas in productive habitats the changes are modest. However, Houle and Simard (1996) argue that willows are able to compensate quickly, particularly in wet, nutrient-rich habitats. Our own results are more in line with the ‘exploitation ecosystems hypothesis’ because the observed changes were not very strong.

In addition to habitat, the effect of reduced grazing pressure appears to depend on the ability of grazing-intolerant species to regenerate (Olofsson 2006). There is evidence that willows are relatively resilient among northern shrubs and can tolerate herbivory by compensating for tissue loss (Wolff 1978; Bryant et al. 1991; Brookshire et al. 2002). The studies of den Herder et al. (2004, 2008) shows that while reindeer browsing decreases the length of willow shoots, they are able to compensate relatively quickly once grazing has ceased, e.g., inside enclosures.

Are wetlands overgrazed?

Vegetation is one of several different important factors affecting the quality of pastures from the perspective of reindeer herders (Kitti et al. 2006). In our long-term grazing study the vegetation cover changed and willows were replaced with sedges, which also are important forage plants for reindeer (Staal and Sæbø 1993). This indicates that the overall pasture quality as forage resource has remained remarkably consistent over time. This is supported by the fact that grazing had relatively little effect on the nutritional quality of *S. lapponum* and *E. angustifolium*. On either side of the fence, measurable differences in the quality of forage for reindeer were minimal. Our findings contrast with those in eastern Canada where vascular plant species were replaced with less-preferred plants, like ericoids (Manseau et al. 1996). Our findings agree with those of Olofsson et al. (2001) who found that intensive disturbance from trampling and grazing near fences transformed shrub-dominated vegetation to graminoid-dominated cover on mesic sites with organic soil.

Dramatic vegetation changes associated with herbivory are often referred to as ‘overgrazing’ (van der Wal 2006), even when the losses of lichen are apparently due more to summer trampling rather than winter consumption (Oksanen 1978; Forbes 2006). The term overgrazing is value laden and is, in general “much used and abused” in the scientific literature as assessed by impacts on both plants and animals (Mysterud 2006). It is a value judgment whether one habitat is better than another (van der Wal 2006). Since there are different indicators and targets used by different stakeholders for assessing the state of vegetation there are a lot of confusing and misunderstanding with the term overgrazing (Mysterud 2006). Normally, the involved parties more or less subjectively and qualitatively judge whether overgrazing occurs and so this judgment depends strongly on the perspective of the individual as well as the scale of the assessment. We have not applied the indicators of Mysterud (2006) and others, such as animal performance. Yet Helle and Kojola (2006) assert that it is extremely difficult to attribute causation between grazing impacts and animal performance. Lundqvist (2007) reports similar difficulty in

negatively correlating animal condition with both animal density and herd growth. However, at the scale of the habitat, we have looked in detail at the effects of grazing on wetland vegetation cover, composition, height and leaf nutrition. In these respects, we find that subarctic wetlands can withstand moderate to high levels of grazing and trampling pressure sustained over many decades. According to Mysterud (2006), the effects of grazing will be detected first in preferred plants, before any effects of density dependence can be found in animals.

In conclusion, our results indicate that summer grazing is an important factor affecting willow cover and height. Long-term grazing reduces willows and they begin to regenerate when reindeer are excluded. Our findings show that while the length of *Salix* shoots and biomass were lower in Finnish wetland habitats, overall nutrient content of important forage plants and vegetation composition remained almost unchanged in spite of long-term grazing effects. With regard to herbivore driven state changes (van der Wal 2006), our data indicate that subarctic Fennoscandian wetlands characterized by upright willow are structurally and functionally highly resilient. Despite long-term intensive summer grazing, this type of wetland seems to sustain forage value well although the relative abundance of plant groups has changed slightly. Despite the slight reduction in *Salix* cover, the overall character of the Finnish summer-grazed wetlands remains comparable to those grazed only during winter in Norway, even after nearly half a century of contrasting management.

Acknowledgments We wish to thank Satu Huttunen, Risto Virtanen and Birgitta Åhman for valuable comments on previous versions of this manuscript. We thank Karen Inga Kemi, Pilvi Kuure, Tuula Niskanen and Anu Pajunen for help in the field, Anu Eskelinen for bryophyte identification, assistants Vibeke Nordberg and Liv Nessel for laboratory analyses; Jari Hietanen for drawing maps. We also thank reindeer herders Juha Magga, J. Antti Magga, Antti Näkkälä and Samuli Näkkälä for valuable knowledge and transport to the field; Tarmo Lindh Pentti Raittimo, Jarmo Rauhala, and Jouni Unga for building fences. Major funding for this research was provided by the RENMAN project (2001–2004) funded by the European Union's 5th Framework Programme (Contract number QLK5-CT-2000-07459). The ARKTIS graduate school, Arctic Centre, University of Lapland, paid Heidi Kitti's salary during 2006–07. Her fieldwork in 2006 was funded by Saami University College, Kautokeino, Norway.

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