Mosses mediate grazer impacts on grass abundance in arctic ecosystems

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Summary

1. Large herbivores have significant impacts on the structure and function of temperate and tropical ecosystems. Yet herbivore impacts on arctic systems, particularly the mechanisms by which they influence plant communities, are largely unknown.

2. High arctic vegetation, commonly overlying permafrost soils, is often moss-dominated with sparse vascular plant cover. We investigated the potential influence of large herbivores on arctic plant communities via their impact on the depth of the moss layer, leading to warmer soils and potentially benefiting vascular plants.

3. We found that grazer impacts on moss depth, and subsequently soil temperature, may influence vascular plant abundance and community composition because of the observed positive but growth-form-specific response of vascular plants to soil warming, promoting grasses in particular.

4. We propose that the positive association of grasses and large herbivores in arctic moss-dominated systems results from two simultaneously operating positive feedback loops. First, herbivore grazing and trampling reduces moss layer depth, increasing soil temperatures. Second, grasses benefit directly from grazers as a result of additional nutrients from faeces and urine. Additionally, the tolerance of grasses to grazing may enable grasses to expand despite the losses suffered from herbivory.

Key-words: grass abundance, high-arctic Spitsbergen, indirect grazing effects, moss insulation, nutrient enrichment, Svalbard Reindeer

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Introduction

Large herbivores influence temperate and tropical plant communities largely by their impact on the competitive balance between species, promoting those which are least sensitive to grazing damage (Louda *et al.* 1990; Pacala & Crawley 1992; Augustine & McNaughton 1998). Additionally, indirect, often soil-mediated effects of grazers are also important. First, nutrients returned via faeces or urine are crucial to the plant's ability to regrow rapidly after defoliation (Hik & Jefferies 1990; Hamilton *et al.* 1998). These readily available nutrients may be an important additional driver of plant species change in grazing systems (Frank & Evans 1997; De Mazancourt & Loreau 2000). Second, there is increasing recognition of the importance of indirect effects of grazers on vegetation patterns via modifications of the soil compartment, such as microbial and fungal abundance (Bardgett *et al.* 1998), and nitrogen mineralization and litter decomposition (Frank & Groffman 1998; Stark *et al.* 2000; Olofsson *et al.* 2001).

We might expect the relative importance of indirect grazing effects to be greatest in systems where nutrient availability and uptake strongly limit plant growth, as in soils subject to permafrost conditions. The low temperatures in soils with permafrost may restrict vascular plant growth directly by limiting the rate of tissue respiration (Semikhatova *et al.* 1992) and thus nutrient uptake, or indirectly by slowing the rate of soil decomposition and thus reducing the availability of essential nutrients (Jonasson 1983; Chapin & Shaver 1985b; Rustad *et al.* 2001). Furthermore, frozen soils may present vascular plants with a restricted soil water supply leading to tissue water deficits if air temperatures increase before the soil is thawed (Gold & Bliss 1995).

In such environments, any factors that influence soil temperatures can greatly affect the success of vascular plants. Many plant communities of permafrost regions are moss-dominated, and the often substantial moss layer can insulate the soil and limit the extent to which it thaws during the summer (Bonan 1992; Coulson *et al.* 1993; Matthews *et al.* 1997; Sharratt 1997). The insulating effect of the moss layer on soils with permafrost has been demonstrated in a wide range of habitats. The thick layer of moss and organic material in Alaskan Black Spruce (*Picea mariana*) forests, for instance,

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contributes to the maintenance of permafrost in areas where the ground surface temperature is near 0 °C and the permafrost is discontinuous (Viereck 1970; Luthin & Guymon 1974). In areas with continuous permafrost, the depth of the moss layer influences the thickness of the active layer (the upper layer of the soil that thaws annually). Experimental removal of both moss and organic layer in Alaskan taiga has caused a spectacular increase in the thickness of the active layer, and enhanced soil temperatures in the upper soil layers (Dyrness 1982). Similar insulation effects of the moss layer have been found throughout northern hemisphere environments, including Alaskan tundra vegetation (Miller *et al*. 1980; Hinzman *et al*. 1991), and Norwegian alpine fellfields (Matthews *et al*. 1997). Because of the negative impact of cold soil on vascular plant growth, the presence of a moss layer and its influence on soil conditions may restrict the growth of vascular plant species, and might prevent certain species from entering a community.

In arctic systems, mosses form a considerable part of the diet of many vertebrate herbivores including Lemming (*Lemmus* spp.), Reindeer and Caribou (*Rangifer tarandus*), Muskox (*Ovibos moschatus*), and most arctic breeding geese (Prins 1981; Prop & Vulink 1992; Longton 1997; Van der Wal *et al*. 2000a; Gloutney *et al*. 2001). Not only do arctic herbivores consume substantial amounts of moss tissue, but also the moss mat can suffer trampling damage. Mosses in general are sensitive to physical disturbance such as trampling (Liddle 1997), and this may be especially true in arctic ecosystems where slow growth limits recovery following a disturbance event (Callaghan *et al*. 2001). We would therefore expect widespread and substantial reductions in moss depth in the Arctic, caused by the consumption and trampling of mosses by herbivores.

As predicted by Zimov *et al*. (1995a, 1995b), the important implication of these relationships is that herbivores may, through a reduction in moss depth, control ecosystem function and vascular plant community composition by modifying temperature and moisture in soils subject to permafrost. Specifically, in the absence of herbivores soils are predicted to become colder and wetter due to increased moss depth, followed by a decrease in the abundance of vascular plants. Support for this prediction is limited, and comes only from single-site studies. For instance, increased moss and decreased thaw depth have occurred in long-standing exclosures in wet meadow vegetation at Barrow, Alaska (Miller *et al*. 1980). Similarly, exclusion of geese for 7 years from small plots of moss-dominated meadow vegetation at Ny-Ålesund, Spitsbergen increased moss depth and reduced soil temperature (Van der Wal *et al*. 2001).

We aimed to test the prediction of Zimov *et al*. (1995a, 1995b), and scale up the findings of single-site studies, by investigating the potential influence of herbivore–moss interactions on soil temperature and the abundance of vascular plant species at a larger geographical scale. Understanding how herbivores influence vascular plant abundance in areas subject to permafrost is of particular significance given that soils with permafrost occupy about one-fifth of the Earth's land surface, with greatest representation in the Arctic (Fitzpatrick 1997).

We used a threefold approach to address this problem. First, we determined the response of high-arctic tundra to Reindeer exclusion in a single area to verify grazer-related changes in moss depth and soil nutrient availability. Second, we examined relationships between the composition of plant communities and moss depths and soil temperatures in the field in 14 areas that have, for historical reasons, been subject to varying intensities of Reindeer (*Rangifer tarandus platyrhynchus*) grazing. In these areas, variation in Reindeer density is caused largely by past overhunting and subsequent incomplete population recovery, releasing large areas from grazing for 100–200 years (Wollebæk 1926; Tyler 1987). Third, we considered the relative responsiveness of high-arctic vascular plants to experimentally manipulated changes in soil temperature.

Materials and methods

HERBIVORE EXCLUSION

Moss depth and nitrogen mineralization potential were determined on samples collected on 1 August 2001 in Semmeldalen (area 2 in Fig. 1) inside and outside five Reindeer exclosures (20×30 m). Sets of exclosures and controls were erected, spaced 200–1500 m apart, in late June 1997 in two different, but moss-dominated, tundra habitats. Two sets were erected in *Luzula* heaths and three in grass-rich meadows. In each exclosed or control plot, four subplots were determined at random. The depth of the moss layer, composed predominantly of *Sanionia uncinata*, *Tomentypnum nitens* and *Aulacomnium* spp., was determined in each subplot by cutting out a turf and placing a ruler along each of the four excavated sides. Average moss depth per subplot was used in the analysis. A soil sample was taken under the moss layer of each subplot and was kept cool for several days before analysis. Soil concentrations of mineral N were determined by shaking 10 g fresh soil with 25 ml 1 M KCl for 30 min on an orbital shaker. The resulting suspension was filtered through Whatman no. 1 paper, and concentrations of NH_4^+-N and NO_3^--N in the extracts were determined by auto-analyser procedures (Bran & Luebbe continuous flow AA3, Delavan, USA). Nitrogen mineralization potential was measured as the release of mineral N (NH_4^+-N and NO_3^--N) after incubation of soil samples in the laboratory (10 g) for 14 days at 25 °C (Ross 1990). After incubation, soil samples were extracted with KCl as described above and the concentration of mineral N was determined and corrected for initial concentrations before incubation.

We did not determine the influence of Reindeer on vascular plants by comparing plant abundance inside
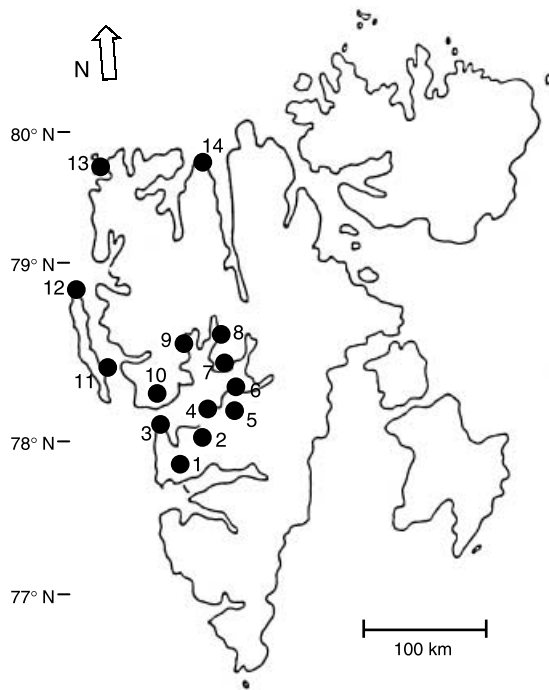
Fig. 1. Locations of the 14 survey sites in Spitsbergen, with the number of recorded plots in brackets. 1 = Camp Millar (60), 2 = Semmeldalen (60), 3 = Kapp Linné (50), 4 = Bjørndalen (60), 5 = Adventdalen (60), 6 = Vindodden (60), 7 = Skansbukta (60), 8 = Dicksonfjorden (60), 9 = Eckmansfjorden (60), 10 = Tryghamna (60), 11 = Prins Karls Forland-South (40), 12 = Prins Karls Forland-North (18), 13 = Danskøya (20), 14 = Gråhuken (20).

and outside fences, because meaningful non-transient changes in vascular plant communities arise only very slowly in high-arctic ecosystems (Wegener & Odasz-Albrightsen 1998). We therefore relied on a field survey comparing areas that have been subject to widely different Reindeer densities for 100–200 years.

FIELD SURVEY

Fourteen sites across the eastern side of central and northern Spitsbergen were visited between 17 July and 24 August 2000 (Fig. 1). Sites were selected on the basis of available information on Reindeer numbers in the archipelago, with the aim of surveying areas with widely differing Reindeer densities. Quadrats were arranged in a grid pattern across each site. A central transect was set out from the bottom of each valley, up the valley sides, until plant cover became very patchy [mean transect length 486 ± 311 m (± SD)]. A line (100–125 m) of six evenly spaced quadrats was placed perpendicular to the central transect at each of 10 equidistant points along the central transect. This produced a grid of 10×6 plots at all sites in the Isfjorden and Van Mijenfjord area (areas 1–10; Fig. 1) except for Kapp Linné, with only 10×5 plots. Four additional sites (11–14) had fewer plots (18–40 per site; Fig. 1) because of time and logistical constraints. For each plot (1×1 m), a visual estimate of total moss, lichen

and liverwort cover, and separate estimates of each species of vascular plant, were taken by agreeing cover estimates between two recorders to minimize variation among plots. At the 10 sites where 50–60 plots were recorded, additional measurements were taken. The depth of the moss layer was determined in the centre of each plot as above. Soil temperature was recorded by allowing a sensor inserted directly beneath the moss layer to equilibrate, while preventing warming from the sun. Similarly, a spot temperature measurement was taken at the moss surface in the shade. Soil moisture content was estimated by inserting a 60 mm capacitance probe (ThetaProbe ML1, Δ-T Devices Ltd, Cambridge, UK) at an angle of 15° directly beneath the moss layer, which measured the soil dielectric constant, a proxy for soil moisture content (Robinson & Dean 1993). Ambient temperature for each of the survey days was calculated from data collected at 10 min intervals at a local (Longyearbyen) weather station.

A mixed soil sample was analysed for soil nitrogen for each of the 14 sites, by pooling equal amounts of soil from 6 to 20 plots per site. Soils were sieved through a 0·2 mm mesh, dried at 50 °C, and analysed for total N content by an automated Dumas combustion procedure (NA1500 Elemental Analyser, Carlo Erba, Milan, Italy).

As there are very few recent estimates of Reindeer density across Spitsbergen, we used pellet group density as a measure of Reindeer occurrence. All Reindeer pellet groups within a 2 m wide band along the full length of the transect were counted. Data were expressed as number of pellet groups per km transect length. Pellets remain visible for many years as their decomposition is very slow. The pellet group counts therefore represent an indication of Reindeer density over the past several years.

GLASSHOUSE EXPERIMENT

Differential response of high arctic vascular plants to soil temperature was studied in a glasshouse in Longyearbyen, Spitsbergen (78° N, 16° E). The temperature in the glasshouse averaged 8·6 °C (SD = 2·2) during the experiment, and was kept close to the outside temperature (6·6 ± 2·2 °C) by covering lower parts of windows with aluminium foil, and keeping windows and doors open at all times.

At the start of the growing season, 13–16 June 2000, 11 target plant species were excavated in intact soil cores (5 cm diameter; each core had one of the target species in its centre but included other plant species) to a depth of approximately 8 cm from an east-facing slope located at the mouth of Bjørndalen, approximately 25 m a.s.l., near Longyearbyen. Target plant species were *Alopecurus borealis*, *Carex rupestris*, *Cerastium regelii*, *Deschampsia alpina*, *Equisetum arvense*, *Luzula arctica*, *Polygonum viviparum*, *Ranunculus sulphureus*, *Salix polaris*, *Saxifraga hieracifolia* and *Stellaria crassipes*. All cores were taken from within

a 100×100 m area. Species were chosen to represent the vascular plant community, accounting for 78% of the total vascular plant cover within the moss-dominated source community. Each soil core was placed in a close-fitting, open-top, 10 cm deep plastic bag from which the vegetation could grow without restriction. The cores were placed in water baths such that only the top 2 cm of the core was above water, the temperature of the water bath setting soil temperature, while the plastic bag prevented the core from soaking. Cores were initially placed in water baths at ambient temperature for 2 days, after which a range of temperatures was set and maintained throughout the season by controlling the relative flow of chilled and warmed water to each of the 12 water baths. Water temperatures were recorded every other day and averaged 4·9, 5·0, 5·4, 6·0, 6·1, 7·3, 8·9, 10·4, 11·7, 11·9, 13·9 and 15·3 °C in the 12 baths over the experimental period of nearly 8 weeks. Each water bath contained six cores of each target species, except for *D. alpina* with only four cores per bath. Cores were kept damp by spraying with cool tap water every day. On 11 August 2000 all soil cores were taken from the water baths and frozen prior to analysis. The mass of live above-ground tissue was recorded after drying at 70 °C for 3 days. The response of plants to simulated soil warming was determined using non-linear regression of final mass against mean water bath temperature and plant growth form (grasses *vs* non-grasses). Data from three pairs of water baths, those at 4·9 and 5·0 °C, 6·0 and 6·1 °C, and 11·7 and 11·9 °C, were combined prior to analysis. The average water bath temperature for each of these pairs was used in the analysis.

DATA ANALYSIS

Data were analysed using SAS version 8·0. Most of the field survey data were analysed using the GLIMMIX macro, which allowed Poisson regression on log-transformed data by the method of residual maximum likelihood (REML), with site and site × dependent variable as random factor. Similarly, exclosure data were analysed using REML, with block (a single set of an exclosure and its control) and plot as random factors. The correct degrees of freedom for each fixed effect in these analyses was computed using the Satterthwaite option (Littell *et al*. 1996). The abundance of grasses in relation to the insulation effect of mosses was analysed using the GENMOD procedure employing a log-link function, assuming a Poisson distribution because the variance was proportional to the mean. Analysis of average grass cover in relation to Reindeer pellet group density was performed with stepwise non-linear regression.

Glasshouse plant mass data were analysed using the GENMOD procedure assuming normal distribution and employing a linear link function. Prior to analysis, mass data for each species were normalized to remove species effects by subtracting the mean per species for each individual data point and dividing this value by the species-specific SD. Regression analysis was then performed in an additive fashion, examining the impact of increasing soil temperature alone, temperature and growth form (grasses *vs* non-grasses), and finally their interactive effect on above-ground live mass.

Results

EFFECTS OF REINDEER EXCLUSION ON MOSS DEPTH AND SOIL NUTRIENT AVAILABILITY

Moss depth was significantly influenced by four years of Reindeer exclusion ($F = 15{\cdot}05$, df = 1,4, $P < 0{\cdot}02$) with 38 ± 6 mm (SE) in grazed controls *vs* 57 ± 10 mm in ungrazed exclosures. NH_4^+-N was significantly less concentrated inside exclosures ($24{\cdot}0 \pm 1{\cdot}4$ µg N g^{-1} dry soil) compared to their grazed controls ($30{\cdot}2 \pm 2{\cdot}2$ µg N g^{-1} dry soil; $F = 7{\cdot}55$, df = 1,4, $P < 0{\cdot}05$). Nitrogen mineralization potential was negatively related to moss depth ($F = 9{\cdot}10$, df = 1,16, $P < 0{\cdot}01$; N mineralization potential (µg N g^{-1} dry soil) = exp[$3{\cdot}601 - 0{\cdot}037 \times$ moss depth (mm)], R_{adj} fixed effect stratum = 0·32) with only positive values (mineralization rather than immobilization) where the moss layer was shallow.

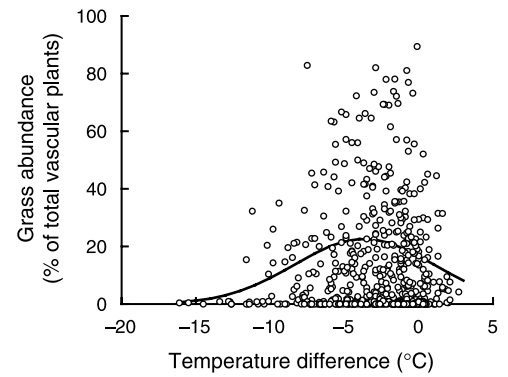### EFFECTS OF MOSS LAYER ON SOIL TEMPERATURE AND ABUNDANCE OF VASCULAR PLANTS

The depth of the moss layer significantly influenced soil temperature ($F = 224{\cdot}07$, df = 1,537, $P < 0{\cdot}0001$) with a 10 cm thick moss mat, on average, causing a 4·4 °C drop in soil temperature. A decline of soil temperature with increasing moss depth was observed at all sites (Fig. 2), but was most evident when ambient temperatures were highest. Indicative were site recordings at Vindodden (Fig. 2), where a drop in average ambient air temperature of nearly 4 °C eliminated the insulation effect of mosses during the colder period. Similar results, showing the insulation effect of the moss layer, were obtained when soil temperature was corrected for ambient air temperature, and expressed as the temperature difference across the moss layer in relation to moss depth ($F = 107{\cdot}31$, df = 1,555, $P < 0{\cdot}0001$; temperature difference = $-1{\cdot}0406 - 0{\cdot}0386 \times$ moss depth). The impact of soil moisture on soil temperature was limited and only marginally significant ($F = 3{\cdot}75$, df = 1,541, $P < 0{\cdot}053$), with a <1 °C drop in temperature over the full range of soil moisture contents measured in the field: very dry (10%) to water-saturated (60%) soils. We conclude that the moss layer acts as an insulating blanket irrespective of soil moisture, and increased moss depth can maintain cold soil temperatures.

Data from the field (Fig. 3) suggest that the abundance of grasses as a proportion of total vascular plant cover was least in plots where the moss layer had greatest insulation effect and kept the soil cool (temperature
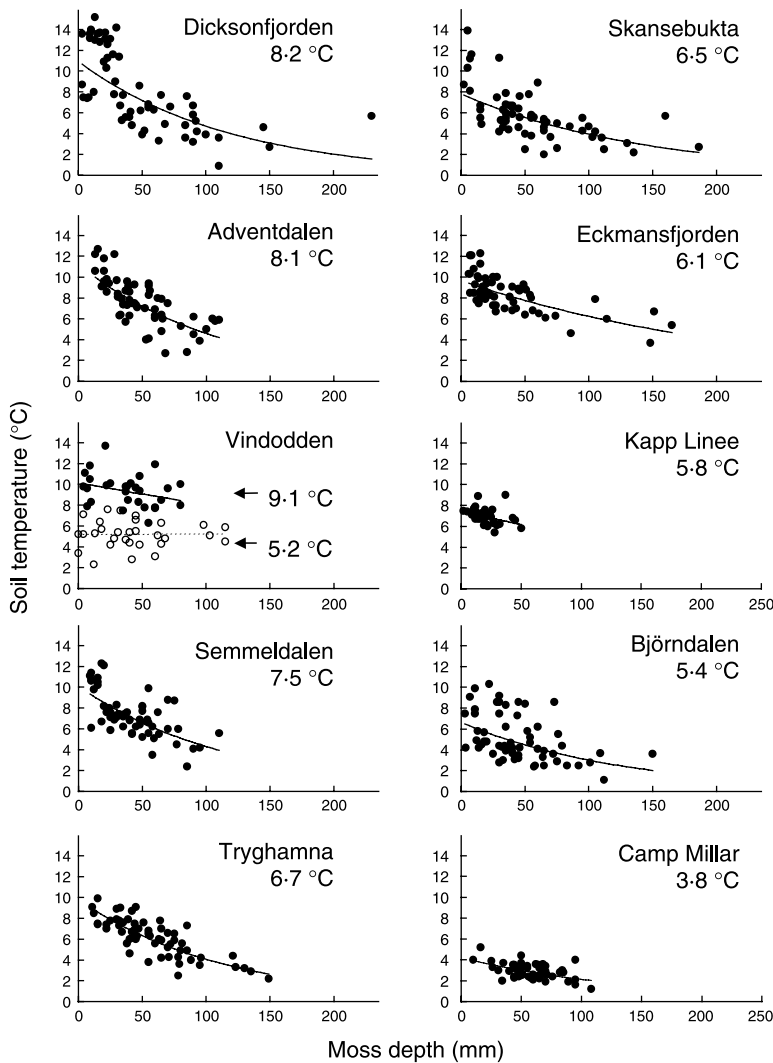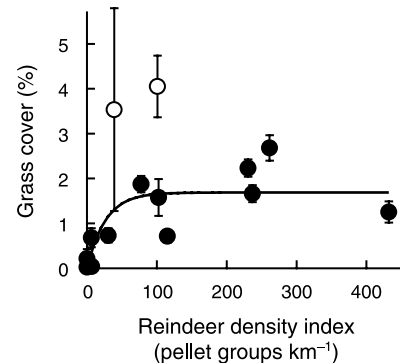
Fig. 2. Effects of depth of moss layer on temperature under moss for 10 different survey sites. Sites are ranked according to average ambient air temperature at the time of surveying (top right corner). For Vindodden, a surge in air temperature strongly influenced the relationship between soil temperature and moss depth, so these data are presented separately for the two observation days with different ambient air temperatures.
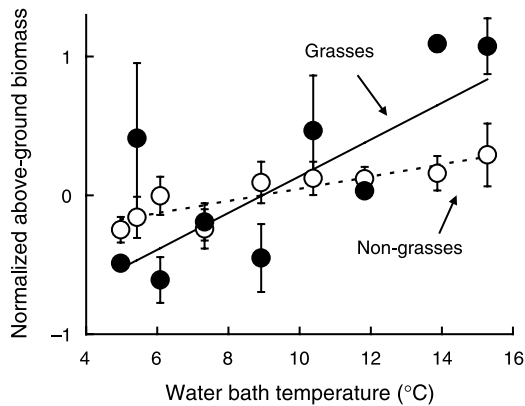

Fig. 3. Percentage of grasses out of total vascular plant cover in relation to insulation effect of mosses, measured as difference between subsoil and moss surface temperature. Fitted equation: $\exp(1{\cdot}7101 + 3{\cdot}9383X - 2{\cdot}8592X^2)$.

Fig. 4. Abundance of grasses (corrected for total plant cover) at sites with contrasting Reindeer densities, estimated as faecal pellet group density. Open circles are sites under bird cliffs where soils were exceptionally nitrogen-rich. Fitted equation: $1{\cdot}69 \times [1 - \exp(-0{\cdot}038X)]$.

ASSOCIATIONS BETWEEN REINDEER DENSITY AND ABUNDANCE OF VASCULAR PLANTS

Total cover of vascular plants was unrelated to Reindeer density across 14 sites throughout Spitsbergen ($F = 0{\cdot}75$, df = 1,12, $P > 0{\cdot}7$). However the abundance of grasses was positively related to Reindeer density (Fig. 4). Where Reindeer were absent or scarce, average grass cover was low; but with greater index of Reindeer presence at a site, grasses were significantly more abundant (non-linear regression: $F = 18{\cdot}47$, df = 1,10, $P < 0{\cdot}005$). Grass cover was positively related to total plant cover ($F = 1{\cdot}66$, df = 1,11, $P < 0{\cdot}01$), and data (Fig. 4) were corrected for this. Grasses reached relatively high densities at the two sites under bird cliffs ($F = 17{\cdot}78$, df = 1,12, $P < 0{\cdot}0025$; Fig. 4). Here soils were enriched by addition of nutrients from fish-eating birds (largely *Alcidae*); extractable mineral N concentration was $2{\cdot}03 \pm 0{\cdot}07\%$ in soils under bird cliffs and only $0{\cdot}54 \pm 0{\cdot}01\%$ in the absence of bird cliffs. Overall regression, including presence or absence of bird cliffs, total plant cover and Reindeer faecal pellet group density, explained 93% of the variation in average grass cover across sites.

difference, $F = 11{\cdot}71$, df = 1,562, $P < 0{\cdot}001$; temperature difference^2, $F = 18{\cdot}97$, df = 1,562, $P < 0{\cdot}0001$). However, in plots where the temperature differential across the moss layer was small, grasses also made up a smaller proportion of the total vascular plant flora. A similar pattern was found when analysing grass abundance as a proportion of total vascular plant cover on the basis of averages per site ($Y = \exp[0{\cdot}78 - 2{\cdot}16X - 0{\cdot}42X^2]$), with the greatest proportion of grasses predicted to occur at a temperature difference of $-2{\cdot}6$ °C (temperature difference, $F = 7{\cdot}22$, df = 1,7, $P < 0{\cdot}05$; temperature difference^2, $F = 8{\cdot}52$, df = 1,7, $P < 0{\cdot}05$). This indicates an optimum moss insulation effect (perhaps related to an optimum moss depth) at which grasses reach greatest relative abundance. Total vascular plant cover did not show any relationship with temperature differential across the moss mat ($F = 2{\cdot}48$, df = 1,565, $P > 0{\cdot}1$).

Fig. 5. Response of grasses and non-grasses to a range of soil temperatures in the glasshouse, expressed as normalized mass of live above-ground tissue.

DIFFERENTIAL RESPONSE OF VASCULAR PLANTS TO CHANGES IN SOIL TEMPERATURE

The glasshouse experiment revealed a generally positive response of above-ground live mass to increasing soil temperature ($F = 23\cdot70$, df = 1,97, $P < 0\cdot0001$). There was a significant interaction between growth form and soil temperature ($F = 7\cdot70$, df = 1,95, $P < 0\cdot0066$) on above-ground live mass. Grasses responded more rapidly to increasing soil temperature, performing less well than non-grasses (relative to overall mean performance) at low temperatures and relatively better at higher temperatures (Fig. 5). From these findings we predict that increased soil temperature in the field can alter the relative composition of the vascular plant community, having a particularly positive effect on grasses.

Discussion

GRASSES AND GRAZERS: AN ADDITIONAL MECHANISM FOR THEIR POSITIVE ASSOCIATION

The common mechanism by which grazers are thought to promote grasses above other functional groups, leading to a positive association of grasses and grazers, stems from the tolerance of grasses to repeated defoliation events. This is largely attributed to the grasses' basal meristems, which lie below average grazing depth (Wright & Illius 1995) and allow rapid regrowth and grass recovery (Crawley 1983). Repeated grazing can lead to the development of grass-dominated 'grazing lawns' (McNaughton 1984) from which herbivores might benefit and increase their food intake rate (McNaughton 1985; Drent & Van der Wal 1999). However, the results of this study suggest an alternative mechanism that may operate in permafrost-dominated environments, whereby the presence of grazers can influence the contribution of grasses to the vascular plant community.

We demonstrated that grasses in high-arctic Spitsbergen are positively associated with the abundance of Reindeer. Grasses were sparsely distributed in areas that had been largely free of Reindeer grazing for periods of 100–200 years as a result of overhunting (Wollebæk 1926; Tyler 1987). Despite current low Reindeer numbers these areas appear to provide good grazing, and the presence of old antlers indicates former use by Reindeer.

Experimental exclusion of Reindeer at one of the study sites demonstrated their strong negative impact on the moss layer, supporting the findings of other small-scale experimental arctic studies at different locations (Miller *et al.* 1980; Van der Wal *et al.* 2001). Intriguingly, potential N mineralization rate was negatively related to the depth of the moss layer, and soil NH_4^+ concentrations were significantly lower inside than outside exclosures, indicating that a reduction in moss depth due to Reindeer may be associated with an increase in soil N availability from which vascular plants could benefit.

The moss layer greatly influenced soil temperature within and across surveyed sites, demonstrating that previous reports on the insulation effect of mosses are not anomalous, but are a feature of cold environments and of relevance to landscape-scale processes. Grasses performed relatively poorly at low soil temperatures, but responded more rapidly than other vascular plants to increased soil temperature, with small increases in soil temperature significantly increasing grass performance. In the field, grasses made up only a small proportion of total vascular plants where moss was deepest and effectively insulated the soil, and reached greater abundance when the moss layer was thinner and had less impact on soil temperature. Grass cover dropped again when moss layer became very thin, and barely had an insulation effect. This indicates either a facilitating impact of mosses on grasses by, for instance, preventing desiccation (Carlsson & Callaghan 1991; Potter 1995), or possibly a coincidence of environmental conditions that retard both moss and grass growth, such as winter exposure on ridges. These data suggest that a reduction in moss depth due to grazing is likely to promote grass growth, but only when the moss layer is initially relatively deep.

It is unlikely that the observed positive association of grasses and Reindeer is solely due to moss-mediated soil temperature effects, but form part of a series of mechanisms by which grazers promote grasses in ecosystems subject to permafrost conditions, including plant tolerance of defoliation and nutrient return via faeces or urine. Grasses can respond rapidly to enhanced nutrient availability, as demonstrated by numerous fertilization studies in both temperate and arctic environments (Chapin & Shaver 1985a, Parsons *et al.* 1995; Jonasson *et al.* 1996; Dormann & Woodin 2002), and the expansion of grasses in many habitats following enhanced atmospheric N deposition (Bobbink *et al.* 1998; Lee 1998; van der Wal *et al.* 2003). Grasses

successfully capture nutrients released from herbivore faeces or urine in a variety of systems (Day & Detling 1990; Haynes & Williams 1993). In Spitsbergen we found that, 3 years after enhanced faecal addition to target plots, there was an associated enhancement of grass growth (van der Wal *et al.* 2004). The survey conducted in the current study provides further evidence of both the ability of grasses to effectively utilize available soil nutrients, and the restriction placed on grass growth in these systems as a result of low soil N availability. We found relatively high densities of grasses under bird cliffs where N concentrations in the soil were raised more than fourfold by guano deposition.

We propose that the proliferation of grasses by herbivores in arctic systems results from two simultaneously operating positive feedback loops (Fig. 6). In the first loop, herbivore grazing and trampling reduces the depth of the moss layer, increasing the soil temperature. Although the direct effects of increased soil temperature on tissue respiration can play a role in enhancing grass growth, it is likely that, given their often rapid response to enhanced nutrient supply (Shaver & Jonasson 1999), grasses in particular will benefit from the indirect effect of increased nutrient availability due to warmer soils, as supported by our data on N mineralization potential. In the second loop, grasses benefit directly from grazers as a result of additional nutrients from faeces and urine. Both feedback loops are self-enforcing and reinforce one another. A greater biomass of palatable species, such as grasses, will attract grazers (Manseau *et al*. 1996; Post & Klein 1996; Van der Wal *et al* 2000b), amplifying their direct and indirect impacts at a site (White 1983) and further promoting grass expansion. Additionally, the tolerance of grasses to grazing may be instrumental in enabling grasses to expand despite the losses suffered from herbivory (Ferraro & Oesterheld 2002). With respect to the distribution of grasses and Reindeer in Spitsbergen we expect that, given the current process of expansion in Reindeer populations and ranges, Reindeer densities in the current low-grazing areas will eventually increase and lead to a concomitant expansion of grasses.

HOW REVERSIBLE ARE CHANGES IN ARCTIC VEGETATION?

Currently we find that grasses are only sparsely distributed in those areas that have been released from Reindeer grazing for 100–200 years. However, overhunting of Reindeer in the 19th century would initially have benefited not only mosses, but also vascular plants including perennial grasses. Reduced grazing of vascular plants would have produced continuous, localized deposition of leaf litter as is commonly found in herbivore exclusion studies (Bazely & Jefferies 1989; Van Wijnen *et al*. 1999; Virtanen 2000), including those on Spitsbergen (Bakker & Loonen 1998; Wegener & Odasz-Albrigtsen 1998). Grass litter is highly reflective (Batzli 1977; Miller *et al*. 1980) and might reduce soil
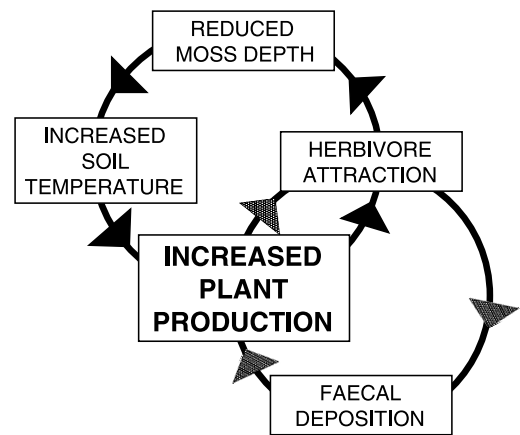

Fig. 6. Conceptual model of the impact of arctic herbivores on the abundance of vascular plants.

temperature by increasing soil surface albedo, further benefiting mosses over grasses as the former are less sensitive to low soil temperature (Van der Wal *et al.* 2001). In support of this hypothesis, a litter addition experiment conducted in Semmeldalen, Spitsbergen revealed that doubling the amount of litter in plots in autumn reduced soil temperatures in the following summer by 0·6 °C ± 0·3 °C, and graminoid biomass by 16% (R.V.D.W., unpublished results). It is possible that increased litter accumulation and subsequent soil cooling were the most rapid effects of reduced grazing pressure and reduced vascular plant off-take following overhunting, and the first in a series of steps leading to a reduction in soil temperature and nutrient availability, and eventually to a reduction of grasses in the vegetation. However, we suggest that a shift from a grass-rich, grazer-dominated system to an ungrazed, moss-dominated system is likely to proceed at a far slower speed than the transformation in the opposite direction, particularly because of the slow rate of moss growth in relation to the rapidity with which grazers disturb the moss layer and grasses respond to increased soil temperature.

The large-scale transition of Beringian ecosystems from productive grass-dominated steppe to unproductive moss-dominated tundra at the end of the Pleistocene has been attributed to the extinction of the Pleistocene mega-herbivores (Zimov *et al*. 1995a, 1995b). Our findings support the prediction of Zimov *et al*. (1995a, 1995b) that herbivores may control the composition of vascular plant communities by modifying the physical condition of soils subject to permafrost through a reduction in moss depth. However, with respect to the exact mechanism involved, different conclusions are drawn. Zimov *et al*. (1995a, 1995b) predicted that due to a reduction in grazing pressure, enhanced moss growth would lead not only to colder but also to wetter soils, short-cutting oxygen and nutrient supplies for vascular plants. Our findings indicate that soil temperature rather than soil moisture is the key mechanism controlled by herbivores and of relevance to the transition between grass-dominated and moss-dominated tundra.

Increased global temperature is predicted to shift moss-dominated arctic vegetation from carbon sink to source as a result of thawing of permafrost and increased soil decomposition (Oechel *et al.* 1993, 2000). The impact of herbivores on the moss layer may play a key role in regulating the rate of carbon release from thawing permafrosted soils and could have consequences for global carbon dynamics. The statement that large herbivores have limited impact on high-arctic vegetation (Wegener & Odasz-Albrigtsen 1998) appears therefore to be premature, and to underestimate their potential importance.

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