Polar Biol (2001) 24: 29–32

ORIGINAL PAPER

René van der Wal · Suzan M. J. van Lieshout
Maarten J. J. E. Loonen

Herbivore impact on moss depth, soil temperature and arctic plant growth

Accepted: 17 April 2000

Abstract We provide evidence for a mechanism by which herbivores may influence plant abundance in arctic ecosystems. These systems are commonly dominated by mosses, the thickness of which influences the amount of heat reaching the soil surface. Herbivores can reduce the thickness of the moss layer by means of trampling and consumption. Exclusion of grazing by barnacle geese and reindeer over a period of 7 years at Ny-Ålesund, Spitsbergen, caused an increase in the thickness of the moss layer, and a reduction in soil temperature of 0.9 °C. Soil temperature was negatively correlated with moss-layer thickness across sites, with highest soil temperatures where moss layers were shallow. We found that moss growth did not respond to experimental manipulation of soil temperature, but the grass *Poa arctica* (arctic meadow-grass) and the dicot *Cardamine nymanii* (polar cress) suffered a 50% reduction in biomass when growing in chilled soils.

Introduction

It is widely accepted that herbivores have a profound impact upon the composition of plant communities (Crawley 1983; Augustine and McNaughton 1998). Studies of the effects of herbivory have tended to concentrate upon temperate and tropical grazed systems, although research has indicated that herbivory may also be an important structuring force within arctic ecosystems (Miller et al. 1980; Manseau et al. 1996; Virtanen et al. 1997a, b). However, the mechanisms by which herbivores influence the abundance of vascular plant species within the Arctic may differ markedly from lower latitudes.

A special feature of the Arctic is the presence of permafrost and the active layer above it, the depth of which restricts plant rooting, and limits nutrient uptake and decomposition processes due to prevailing low soil temperatures (Jonasson 1983; Chapin and Shaver 1985; Atkin and Cummins 1994). Soils with permafrost occupy about one-fifth of the Earth's land surface and probably deserve more attention than they have received (Fitzpatrick 1997). The majority of these ecosystems are moss dominated (Longton 1997). The moss layer insulates the soil and limits the extent to which it thaws during the summer period (Hinzman et al. 1991; Matthews et al. 1997; Sharratt 1997). Therefore, the presence of a dense moss layer may restrict or even prevent the growth of species dependent on an active root system, i.e. vascular plants (Crawford 1989).

We report on both field and greenhouse experiments which provide evidence that herbivores reduce the depth of the moss layer, thereby increasing soil temperatures, which impact on the performance of vascular plant species in arctic regions.

Materials and methods

To test herbivore impact on the depth of the moss layer and, indirectly, on soil temperature, we used four exclosures (1 m^2) erected in 1992 in Ny-Ålesund, Spitsbergen (78°55′N, 11°56′E) spaced > 50 m apart, which fenced out both barnacle geese (*Branta leucopsis*) and Svalbard reindeer (*Rangifer tarandus platyrhynchus*), the only two vertebrate herbivores common to the system. We did not observe enhanced snow accumulation in the fenced areas. All exclosures were placed on moss-dominated tundra vegetation, covering a range of soil moistures (18–51% over the top 5 cm as averaged over the growing season). Soil temperature was measured on 17 August 1999 by inserting thermistors both inside and outside each exclosure directly beneath the moss layer (15 random

---

R. van der Wal (✉) · S. M. J. van Lieshout
Centre for Ecology and Hydrology,
Banchory Research Station, Hill of Brathens,
Glassel, Banchory, AB31 4BY, Scotland
e-mail: rvdw@ceh.ac.uk
Tel.: +44-1330-826337, Fax: +44-1330-823303

M. J. J. E. Loonen
Zoological Laboratory, University of Groningen,
P.O. Box 14,
9750 AA Haren, The Netherlands

measurements per site). To determine moss-layer thickness and root profile of the dominant grass *Poa arctica* (arctic meadow-grass), cores of 23 mm diameter each were taken from both inside and outside exclosures (five randomly selected cores per site). For the root profile, cores were divided into 1-cm-thick sections from the green moslayer downwards. Corresponding soil sections were pooled for each exclosure or control area. Roots of *Poa* were extracted by washing the soil sections over a set of sieves, discarding roots of other species, and the material was then oven-dried at 70 °C for 48 h to determine dry weight.

To test for the impact of soil temperature on plant performance, ten 20×10 cm^2 turves were taken from a wet meadow community into the greenhouse and divided into two. One half was placed on ice to mimic a permafrost situation, whilst the other half was placed on cold water representing warmer soils. A wire cage and plastic sheet prevented direct contact between the turves and either the ice or water. On average, soil temperature in the turves differed by 7 °C between the two treatments. Turves had a 100% moss (*Sanionia uncinata*, *Mnium spicatum*, *Dicranum* sp.) cover, with the grass *P. arctica* and dicot *Cardamine nymanii* (polar cress) growing interspersed within the mosses; turves were kept moist by regular spraying with tap water during the entire experiment. At the start of the experiment (20 June 1999), three cranked wires (Clymo 1970) per turf were placed level with the tops of the moss, to allow measurements of moss growth conducted at the end of the experiment (12 August 1999). Additionally, three small subsamples (13.5 mm diameter) were taken to estimate the biomass of green moss in each turf. Initial (*Poa* only; *Cardamine* had no visible shoots at that stage) and final shoot density (*Poa* and *Cardamine*) were recorded and above-ground plant parts were harvested. Turves were washed over a set of sieves to separate *Poa* root material; all plant material was oven-dried at 70 °C for 48 h to determine dry weight.

Results

Moss height increased significantly in the absence of grazing [paired *t*-test: $t_4 = 4.50$, $P < 0.05$; 33 ± 10 (SE) mm vs. 52 ± 16 mm]. At these sites, where grazing was excluded for 7 years, soil temperature was 0.9 ± 0.15 °C lower than in grazed control areas ($t_4 = 5.85$, $P < 0.01$; 4.8 ± 0.4 °C vs. 5.7 ± 0.3 °C). Moreover, soil temperature correlated negatively with thickness of the moss layer ($r_s = -0.881$, $n = 8$, $P < 0.005$), with the highest soil temperatures at sites where the moss layer was shallow. Within the grazed plots, the majority of *Poa* roots were found at the moss-soil interface. In response to the thicker moss layer of ungrazed sites and corresponding lower temperature, roots of *Poa* seem to shift upwards into the moss layer. Median rooting depth (the depth above which 50% of the root mass was found) of *P. arctica* in ungrazed sites was 9 ± 4 mm less than in grazed sites. This is less than the increase in moss depth following exclusion of grazing (16 ± 7 mm) leading to the presence of a greater proportion of roots in the moss layer.

The impact of manipulated soil temperature on plant performance is summarised in Table 1. Moss growth was found to be independent of soil temperature. However, above-ground biomass of the grass *P. arctica* and the dicot *C. nymanii* growing in cold soils was about 50% of the biomass of plants growing in warmer soils. These differences in above-ground biomass between the treatments in *Poa* were due to a combination of low shoot density and low shoot mass when growing in cold soils. In *Cardamine*, shoot mass was low when growing in cold soils, but shoot density remained unchanged. Our data also suggest a negative effect of low soil temperature on *Poa* root mass ($P = 0.06$), as well as on total plant biomass ($P < 0.05$).

Discussion

We have demonstrated that exclusion of grazing by barnacle geese and reindeer over a period of 7 years caused an increase in the thickness of the moss layer, associated with a reduction in soil temperature of 0.9 °C. Moreover, soil temperature was negatively correlated with moss-layer thickness across sites, with highest soil temperatures when moss layers were shallow.

Although mosses are not commonly grazed in temperate areas, a variety of herbivores in the Arctic include these lower plants in their diet (Prins 1981; Longton 1997). Both Svalbard reindeer (Staaland 1986; Van der Wal et al. 2000) and barnacle geese (Prop and Vulink 1992; Van der Wal and Loonen 1998) were found to consume substantial amounts of mosses. Likewise, mosses are a major food source for the widespread and often numerous lemming (*Lemmus sibericus*) (Virtanen et al. 1997a). Moreover, as mosses in general are sensitive to trampling (Liddle 1997), those growing in fragile systems such as the Arctic are particularly likely to suffer

Table 1 The impact of soil temperature on plant performance on mosses and two vascular plants in a greenhouse experiment. Turves were placed either on ice (cool soils) or cold water (warm soils). Mosses showed no response to the treatment, whereas vascular plants, which are dependent on roots for nutrient and water uptake, showed poorer performance in cooled soils

Species	Source	Cool soils	Warm soils	*t*-value	Significance
Moss sp.	Height increment (mm)	2.4 ± 0.2	2.8 ± 0.4	−1.2	$P = 0.25$
	Live biomass (g/m^2)	200.2 ± 27.7	215.3 ± 21.0	−0.6	$P = 0.57$
Poa arctica	Total live biomass (g/m^2)	4.0 ± 0.8	7.9 ± 1.3	−4.1	$P < 0.01$
	Δ shoot density (no./m^2)	−8.7 ± 2.8	0.1 ± 4.7	5.8*	$P < 0.05$
	Root biomass (g/m^2)	38.1 ± 8.8	51.0 ± 9.4	2.1	$P = 0.06$
Cardamine nymanii	Shoot biomass (g/m^2)	1.7 ± 0.5	3.4 ± 0.7	2.8	$P < 0.05$
	Shoot density (no./m^2)	16.2 ± 5.5	18.0 ± 5.8	0.4	$P = 0.73$

**F* value of a poisson regression on the change in number of shoots over the course of the experiment from grazer-associated trampling effects. We therefore expect reduction of moss growth in the Arctic, due to both herbivore consumption and trampling, to be widespread.

There is little doubt that the moss layer provides thermal insulation of permafrost, as was found in a wide range of habitats such as Alaskan black spruce (*Picea mariana*) forests (Sharratt 1997) and Norwegian alpine fellfields (Matthews et al. 1997). Similarly, in our study we found that soil temperature correlated with moss-layer thickness. Reduction in the extent and thickness of the moss layer by herbivores is thus a likely scenario to raise soil temperature in those systems, which are characterised by the presence of permafrost. Moreover, the length of the growing season for vascular plants is likely to be influenced by herbivores, as the rate at which the active layer thaws over summer is dependent on the depth of the overlying moss layer (Dyrness 1982; Hinzman et al. 1991).

To test for differential response in mosses and vascular plants to low soil temperature, we performed a controlled experiment in which the observed soil temperature differences between grazed and ungrazed areas in the field were amplified to a level which allowed treatment effects to be detected during one growing season. We showed that moss growth was independent of soil temperature, whereas vascular plants had greatly reduced growth in chilled soil. We predict that the lack of herbivores in arctic systems will lead to a proliferation of the moss layer, a lowering of the soil temperature and a restricted growth of vascular plant species, or may even completely prevent certain species from colonising a community. This is in line with findings in coastal tundra at Barrow (Alaska) where decreased thaw depth and increased moss has occurred in long-standing exclosures (Miller et al. 1980). Moreover, soil temperature effects might have been involved in the Beringia herbivore-driven biome shift at the end of the Pleistocene; grass-dominated steppe changed into moss-dominated tundra when herbivore pressure was reduced (Zimov et al. 1995).

Evidence from the field suggests that vascular plants growing in ungrazed systems tend to avoid rooting in cold soil by having a greater proportion of their roots in the decaying moss layer. This is likely to have a profound negative effect on both nutrient (Chapin et al. 1986) and water status (Hinzman et al. 1991) of the plant. Growth of plants rooting in the moss might be particularly constrained during periods of drought, which are common in arctic ecosystems due to low summer precipitation (Chapin et al. 1992). We therefore strongly advocate studies integrating thermal properties, water-retention capacity and nutrient status of mosses to complete our understanding of moss-mediated impact of herbivores upon vascular plant abundance and species diversity in arctic ecosystems.

Acknowledgements We thank Steve Albon and Rob Brooker for critically reviewing earlier versions of the manuscript. The research greatly benefitted from the help at site of Nick Cox and Rob Brooker. Jaap Gomes made it possible for S.M.J.vL. to leave for Spitsbergen.

References

Atkin OK, Cummins WR (1994) The effect of root temperature on the induction of nitrate reductase activities and nitrogen uptake rates in arctic plant species. Plant Soil 159: 187–197

Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J Wildl Manage 62: 1165–1183

Chapin FS, Shaver GR (1985) Arctic. In: Chabot BF, Mooney HA (eds) Physiological ecology of North American plant communities. Chapman & Hall, New York, pp 16–31

Chapin FS, McKendrick JD, Johnson DA (1986) Seasonal changes in carbon fractions in Alaskan tundra plants of differing growth form: implications for herbivores. J Ecol 74: 707–731

Chapin FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J (1992) Arctic plant physiological ecology in an ecosystem context. In: Chapin FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J (eds) Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, New York, pp 441–451

Clymo RS (1970) The growth of *Sphagnum*: methods of measurement. J Ecol 58: 13–49

Crawford RMM (1989) Studies in plant survival. Blackwell, Oxford

Crawley MJ (1983) Herbivory: the dynamics of animal-plant interactions. Blackwell, Oxford

Dyrness CT (1982) Control of depth to permafrost and soil temperature by the forest floor in black spruce/feathermoss communities. Report PNW-396. United States Department of Agriculture, Forest Service, Pacific NW Forest and Range Experiment Station, Portland

Fitzpatrick EA (1997) Arctic soils and permafrost. In: Woodin SJ, Marquiss M (eds) Ecology of Arctic environments. Blackwell, Oxford, pp 1–40

Hinzman LD, Kane DL, Gieck RE, Everett KR (1991) Hydrologic and thermal properties of the active layer in the Alaskan Arctic. Cold Regions Sci Technol 19: 95–110

Jonasson S (1983) Nutrient content and dynamics in north Swedish shrub tundra areas. Holarct Ecol 6: 295–304

Liddle M (1997) Recreation ecology. Chapman & Hall, London

Longton RE (1997) The role of bryophytes and lichens in polar ecosystems. In: Woodin SJ, Marquiss M (eds) Ecology of Arctic environments. Blackwell, Oxford, pp 69–96

Manseau M, Huot J, Crte M (1996) Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. J Ecol 84: 503–513

Matthews JA, Dahl SO, Berrisford MS, Nesje A (1997) Cyclic development and thermokarstic degradation of palsas in the mid-Alpine zone at Leirpullan, Dovrefjell, southern Norway. Permafrost Periglacial Process 8: 107–122

Miller PC, Webber PJ, Oechel WC, Tieszen LL (1980) Biophysical processes and primary production. In: Brown J, Miller PC, Tieszen LL, Bunnell FL (eds) An Arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Stroudsburg, Pa, pp 66–101

Prins HHT (1981) Why are mosses eaten in cold environments only? Oikos 38: 374–380

Prop J, Vulink T (1992) Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. Funct Ecol 6: 180–189

Sharratt BS (1997) Thermal conductivity and water retention of a black spruce forest floor. Soil Sci 162: 576–582

Staaland H (1986) Svalbardreinens ernæring. In: Øritsland NA (ed) Svalbardreinen og dens livsgrunnlag feeding and nutrient of Svalbard Reindeer. Universitetsforlaget AS, Oslo, pp 72–91

Van der Wal R, Loonen MJJE (1998) Goose droppings as food for reindeer. Can J Zool 76: 1117–1122

Van der Wal R, Irvine J, Shepherd N, Albon SD (2000) Faecal avoidance and the risk of infection by nematodes in a natural population of reindeer. Oecologia 124: 19–25

Virtanen RJ, Henttonen H, Laine K (1997a) Lemming grazing and structure of a snowbed plant community – a long-term experiment at Kilpisjärvi, Finnish Lapland. Oikos 79: 155–166

Virtanen RJ, Lundberg PA, Moen J, Oksanen L (1997b) Topographic and altitudinal patterns in plant communities on European arctic islands. Polar Biol 17: 95–113

Zimov SA, Chuprynin VI, Oreshko AP, Chapin FS, Reynolds JF, Chapin MC (1995) Steppe-tundra transition – A herbivore-driven biome shift at the end of the Pleistocene. Am Nat 146: 765–794