Scientific paper

Changes in soil and vegetation properties under different land uses in Northern Scandinavia

Manfred Bölter[1][*], Rolf Möller[1] and Stephan Peth[2]

[1]*Institute for Polar Ecology, University of Kiel,*
Wischhofstr. 1-3, Bldg. 12, 24148 Kiel, Germany
[2]*Institute for Plant Nutrition and Soil Science, University of Kiel,*
Olshausenstr. 40, 24098 Kiel, Germany
[*]*Corresponding author. E-mail: mboelter@ipoe.uni-kiel.de*

Abstract: We studied changes in vegetation, soil microbiology and soil properties during a 3 years study in a Fennoscandia tundra. The test sites were located at the border between Norway and Finland, a region which is divided by a fence to different areas of land use by reindeer herding. The Norwegian site acts as winter pasture only, the Finnish site is under use all the year. Due to shifts of the fence some years ago, an area of recover was found. Reindeer grazing and trampling changed not only vegetation cover, mainly from lichen heaths in Norway to grass and shrub land at the Finnish side. This had also consequences on soil properties, the microbial community and soil respiration. Differences in these items, however, are not directly to changes in vegetation cover; more dangerous are trampled and probably highly grazed spots which show barren soils. Main effect to soil respiration is temperature, which shows significant higher levels at the Finnish side, which leads to higher evaporation, thus lower moisture and thereof reduced microbial activity.

key words: soil respiration, reindeer, grazing, trampling, lichen heath, tundra, Fennoscandia

1. Introduction

Land management in northern landscapes has not gained much interest in the past. But climate change and herewith connected northward shifts of boundaries for tillage and intensifications of herding reindeer provide new aspects in northern Scandinavia and Russia. Reindeer husbandry is a traditional land use in this area, but has gained considerable changes during the last century. Fencing, extra fodder during winter, meet production and slaughtering by external rules from the European Market mark changes in nature and social conditions (Müller-Wille, 1987). The effects are visible in the vulnerable social systems and become evident by competition with other land uses, mainly forestry, tourisms and energy production (Forbes *et al*., 2004, 2006; Müller-Wille *et al*., 2006).

Changes in herding by increasing animals per square meter and fencing herding

districts (Palsikuntas) occur in an area with sensitive soils in pine forest and tundra environments with weak stability of the organic horizon (Van der Wal *et al.*, 2001; Uhlig *et al.*, 2004). Soils in these areas are mainly nutrient-poor shallow podzols, which show only thin layers of organic matter (Schultz, 2000; Zech and Hintermaier-Erhard, 2002). This pattern can be related to low rates of primary production and the dominance of acidic litter from pine forests or lichen heaths. Hence, the soils are highly susceptible to compaction and erosion, lichen heaths are brittle and highly sensitive to grazing and trampling (Manseau *et al.*, 1996, 1999; Bölter and Möller, 2006; Peth and Horn, 2006; Uhlig and Zink, 2006) in areas with intensive herding.

A three years study was initiated by a group of herders and scientists of different disciplines and funded by a European Community research program (RENMAN, *cf.* Forbes *et al.*, 2004, 2006). The aim of this study was an evaluation of the state of the soils in a forest environment next to the village Vuotso, and tundra environment in the vicinity of the village Näkkälä, both located in northern Finland. The objective was to formulate management plans for reindeer herding in these two Paliskuntas (herding districts). This contribution focuses on the latter area, which offered the chance to compare the different ways of management at the border to Norway, where the Finnish herders use their areas all year around, the Norwegians use their area only during winter; both are separated by a fence. Thus, vegetation and soils have undergone changes and show a clear differentiation (Käyhkö and Pellikka, 1994; Kumpula, 2006). This was used as a chance to compare the effects of different herding strategies by methods of soil science and soil biology.

This paper describes data on changes in soil properties and microbial activity related to changing vegetation cover affected by grazing and trampling. Changes in vegetation cover affect significantly soil organic matter due to erosion but also by changes by lichen heaths to coverage with shrubs and other rooting plants, which have further consequences on soils temperature, both are main drivers for microbial activity, hence nutrient cycling and further soil biological properties.

2. Material and methods

2.1. Location

The study was carried out in Northern Scandinavia at the border between Finland and Norway named Roavveoaivi (Raavvoai'vi). It is located north of the Sámi village Näkkälä in the Jauristunturit region, Enontekiö (Hetta) and Finnmark Commune (details of this location are presented by Forbes *et al.*, 2004, 2006). The landscape is a fjell at an altitude of about 350 m a.s.l. A reindeer fence separates the fjell, a treeless tundra area, into a northern region (Norway), which is used as winter pasture only, and a southern region (Finland), which is used by reindeer all the year around. Part of this area has become special attention, where the fence was moved south and the vegetation could recover for about 12 years (Fig. 1). Hence, in this area we find three different areas of land use: winter pastures (Norway), and year around pastures (Finland), as well as a transition region under recovery since 1990, when the fence was shifted south.

The primary vegetation, as visible in the Norwegian area, is formed by a lichen heath, mostly by *Cetraria* sp., *Cladonia* sp., and *Cladina* sp. The Finnish side is only
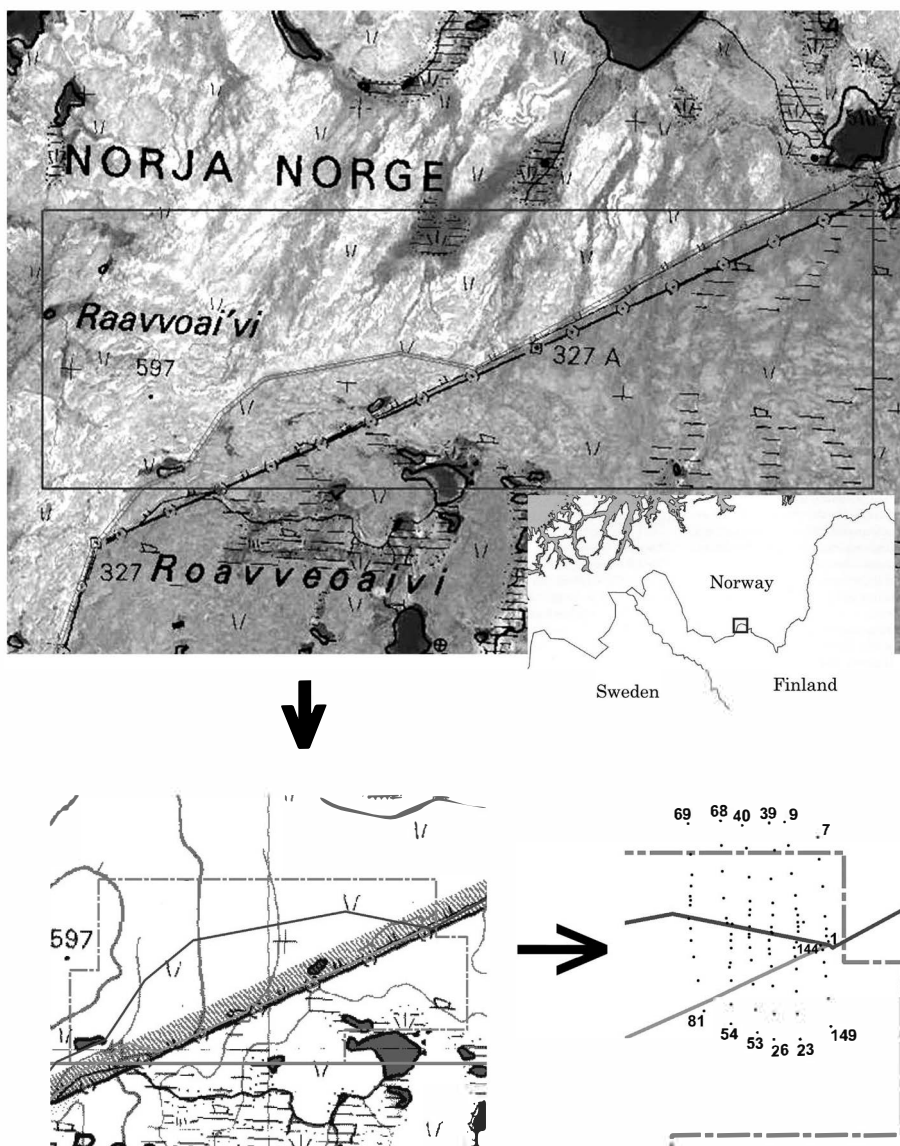
Fig. 1. Map of the investigation area Roavveoaivi (Raavvoai'vi) at the border between Norway and Finland (square in the insert map).   An area of $3 \times 1\,km$ was set (above) in which the fence separates the Norwegian and Finnish grazing grounds.   The fence is indicated by a broken line, nearly diagonal through the rectangle.   The top figure is a Satellite photo (Kumpula, 2006) under laid with mapping informations, it shows the lighter grounds in Norway due to the dense cover with lichens (area of winter pastures), the area of vegetation recovery (light greyish), and the Finnish area (dark grey).   The figure below (left) shows the area of the three grazing types and (right) the positions of the sampling points (1–149) at six transects.

sparsely covered by lichens, here shrubs, *Empetrum* sp., *Salix* sp., *Betula nana* and other herbs and grasses dominate the ground (Kitti and Forbes, 2006). Further, some areas are barren grounds, probably due to trampling, they are suspected to erosion.

2.2. Field methods

The field campaigns for measurements of environmental parameters (temperature, humidity, precipitation) and samplings were carried out in summers 2002 and 2003. The above described three different regions were sampled by six transects from north to south crossing the three regions of land use. Sampling was performed by a metal soil corer (diameter and hight 4 cm). Samples were stored cool and air-dry until processing in the laboratory. In total, 149 sampling points were considered and surface samples (0–5 cm) were analysed for soil properties (Peth and Horn, 2006); digital photographs covering about 1 square meter were analysed for vegetation cover (lichen, shrubs and herbs, and barren soils); 82 samples were analysed for microbiological properties. The edges of the rectangular are given by the plots 69 (68.827°N, 23.802°E), 7 (68.827°N, 23.808°E), 81 (68.824°N, 23.803°E), and 149 (68.824°N, 23.809°E) (Fig. 1).

Temperature measurements were performed by probes in 3 soils, each of them located in a heavy, low, and medium grazed area, *i.e.*, in one of the three test fields. Data loggers recorded temperature at different layers every 10 min. The sensors were placed in the vegetation layer, and at soil depths of 2 cm (organic layer), 5, 10, and 15 cm. Thus, the region of main microbial activity was covered. Temperatures used for the models of this paper were obtained between July 8 and August 28, 2002.

2.3. Laboratory methods

Bulk density and soil organic matter measured by loss on ignition (LOI, 540°C) were analysed to describe the soils and calculating data from mass to area. The analyses of the microbial community were performed by epifluorescence microscopy (bacterial number and biomass and thereof derived parameters like mean cell volumes, cell surfaces) (Bölter *et al*., 2002). Soil respiration data were obtained by incubating sub-samples (10–25 g, depending on bulk density) at different temperatures by infra-red measure of CO_2 in an open chamber device (Bölter *et al*., 2003a). Soils were rewetted to 50% water-holding capacity. Data were interpreted by means of non-parametric statistics, *i.e.*, the use of descriptors like medians, minima and maxima.

3.   Results

The overall data on soil organic matter do not show a clear indication to separate the three areas (Fig. 2). The median values for all samples from Norway ($n=42$) is 48.3% (range: 14.3–89.1), the samples from Finland ($n=21$) is 50.4% (5.1–78.5), and for the transition area ($n=23$) is 45.5% (12.9–80.9). These data of organic matter content show close relations to vegetation cover. Lowest values are found in barren soils at the Finnish site, sites with herb vegetation do not show generally lower values than the lichen heath.

The organic matter can be suspected to influence the microbial community. Hence, relationships between LOI and bacterial number and biomass can be evaluated.
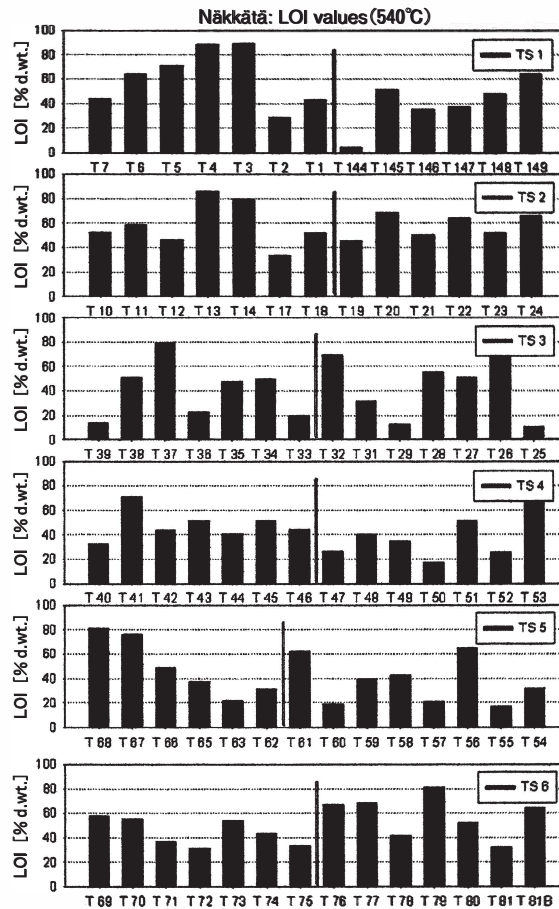
Fig. 2.   Contents of organic matter in soils (LOI) samples of transects 1–6.   The vertical
lines indicate the place of the actual border between Norway and Finland.

However, this relationship is not evident for all locations as the quality of organic matter
may influence the community size.   Differences in the bacterial communities due to
sizes of bacteria are not observed, a nearly straight relationship exist between bacterial
number and biomass (Fig. 3), indicating a fairly homogeneous population structure.

Soil respiration shows great variability related to soil organic matter and organism's
abundance.   The view on the respiration data per mass unit of each plot shows a pattern
comparable to LOI.   No clear evidence seems to be apparent separating the three areas.
Thus, the data of these areas are combined to three groups according to the sampling
areas.   These groups show evidence to be useful descriptors for differences between the
sites (Fig. 4).   In a similar way, it is possible to differentiate between these three re-
gional aspects (Table 1).   Thus, the main points for separating the stages of soil pro-
perties became evident.

The next step in this study is to look for the temperature profiles in soils with respect
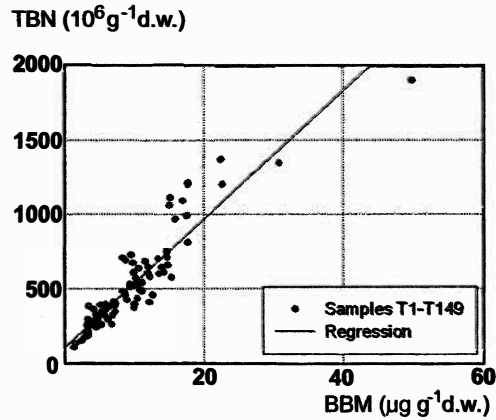
TBN ($10^6 g^{-1}$d.w.)

Fig. 3. Relationship between bacterial number (TBN) and bacterial biomass (BBM) in samples of the transects.
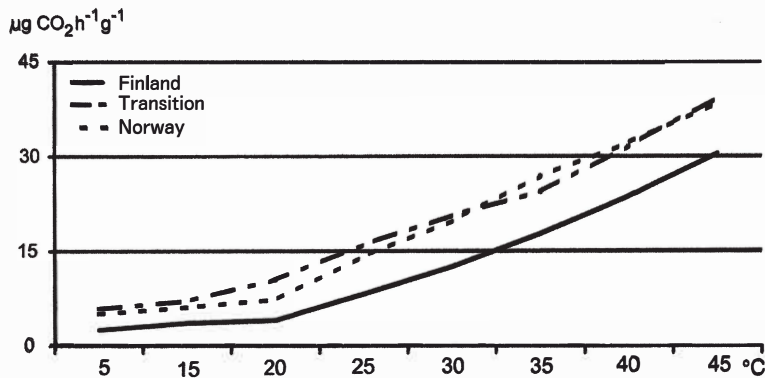
μg $CO_2 h^{-1} g^{-1}$

Fig. 4. Soil respiration data (median values for sample groups) of sampling regions Finland, Transition zone and Norway for incubation temperatures 5–45°C.

to the three sampling areas (Norway, Finland, transition) and combining them with the data obtained for microbial activity, *i.e.*, CO_2-evolution.   The profiles of soil temperature are calculated to time spans for which active temperatures are present (temperature ranges 5°C), as shown in Fig. 5.   These time spans can be used to calculate potential soil respiration for depths zonations.   For this approach, only the upper soil horizon (0–5 cm) is used, since soil respiration data are only available for this layer.   Further, these data are calculated for data on soil respiration per square meter taking into account the local bulk density (*cf.* Bölter *et al.*, 2003a).   It becomes evident, that the most abundant temperatures in these soils are between 5 and 15°C (Fig. 5).

The data on potential soil respiration per area for individual temperatures (Table 1b) are given per hour.   They are multiplied with the related temperature spans for the upper soil horizon (Fig. 5) and thus yield the following data of CO_2-evolution for the time of temperature measurement (July 8–August 28):

*Table 1.   Properties of soil samples, soil respiration and plant cover of the regions
Norway, Transition and Finland.*

a) Soil properties (dB: bulk density, LOI: loss on ignition at 540°C, TBN: total number of bacteria, BBM: bacterial biomass, MCV: mean bacterial cell volume, TBS: total bacterial surface)

		dB	LOI	TBN	BBM	MCV	TBS
		$g\ cm^{-3}$	% d.wt.	$n\ 10^{12}\ m^{-2}$	$g\ w.wt.\ m^{-2}$	μm^3	$cm^2\ g^{-1}$
Norway	median	1.23	47.60	24.70	0.51	0.017	0.052
	min	1.00	14.30	4.59	0.06	0.012	0.046
	max	1.50	89.10	98.56	2.59	0.030	0.061
Transition	median	1.22	42.60	18.08	0.43	0.021	0.055
	min	1.11	5.10	8.66	0.15	0.009	0.043
	max	1.34	80.90	56.59	1.07	0.028	0.060
Finland	median	1.26	51.20	23.04	0.41	0.017	0.052
	min	0.94	10.90	6.64	0.08	0.012	0.046
	max	1.45	78.50	73.90	1.22	0.023	0.056

b) Soil respiration at different temperature steps

		$g\ CO_2\ m^{-2}\ h^{-1}$			
		5 °C	15 °C	25 °C	35 °C
Norway	median	0.026	0.039	0.099	0.155
	min	0.003	0.009	0.022	0.031
	max	0.203	0.215	0.256	0.286
Transition	median	0.027	0.051	0.094	0.154
	min	0.006	0.011	0.043	0.023
	max	0.155	0.181	0.284	0.297
Finland	median	0.036	0.021	0.064	0.128
	min	0.013	0.008	0.022	0.016
	max	0.221	0.279	0.357	0.273

c) Plant cover of herbs and lichens and barren soil

		%		
		Herbs	Lichens	Barren
Norway	median	7.5	91.6	0.0
	mean	15.8	82.5	1.7
	min	0.0	0.0	0.0
	max	95.3	100.0	57.2
Transition	median	11.8	81.7	0.0
	mean	12.1	70.1	17.8
	min	0.0	5.3	0.0
	max	30.6	100.0	89.5
Finland	median	13.3	69.0	0.0
	mean	20.8	64.5	14.7
	min	0.0	4.3	0.0
	max	59.0	100.0	94.3

Finland (heavy grazed): $19.4\ g\ CO_2\ m^{-2}$
Intermediate (medium grazed): $37.0\ g\ CO_2\ m^{-2}$
Norway (low grazing): $33.3\ g\ CO_2\ m^{-2}$

These data give a rough estimate on total potential CO_2-evolution in these regions. Although these data need more specification by respecting moisture and contents of available organic matter, they show an important feature of soil microbial activity under these different management systems.
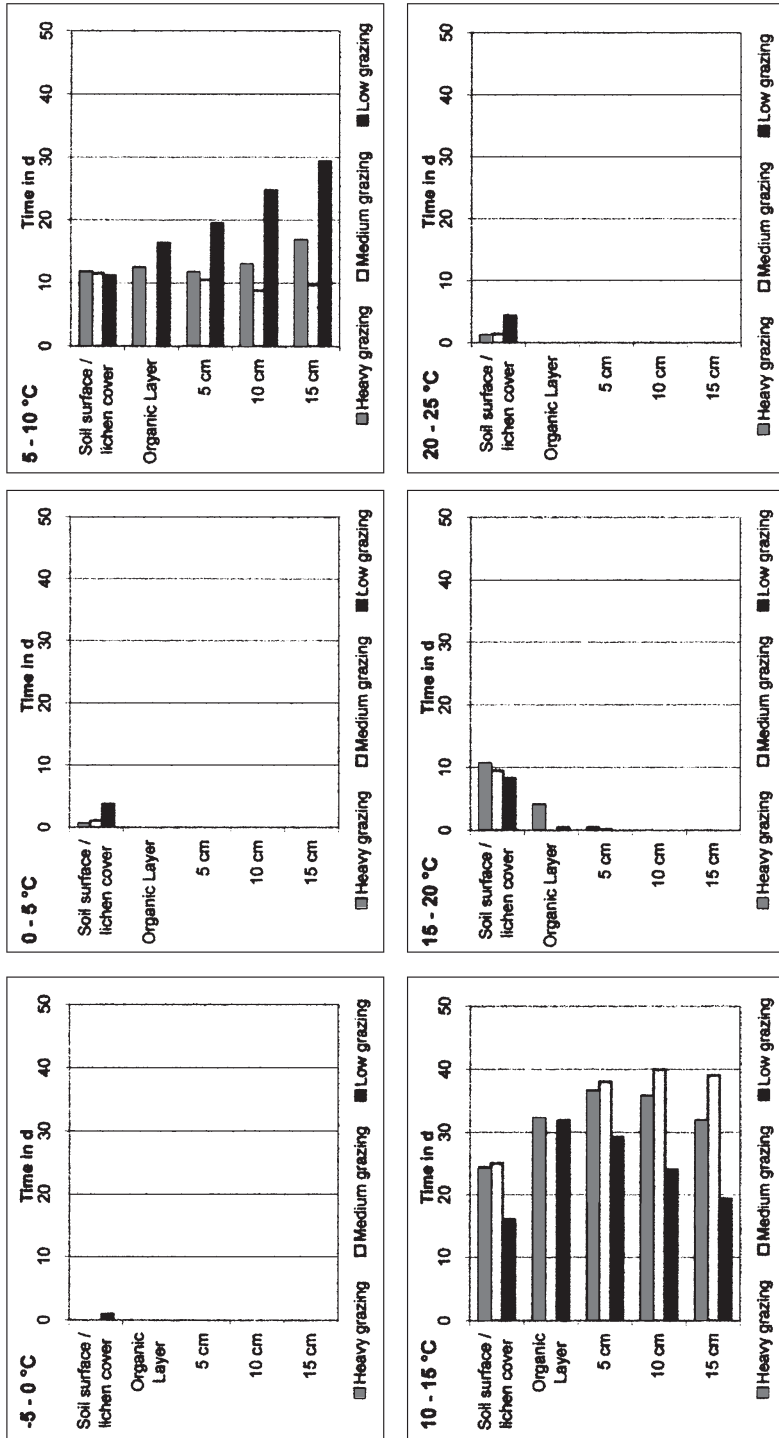
Fig. 5. Time spans of active temperature (5°C-steps) in the profiles of the three soil regions.

4. Discussion

Habitat fragmentation and concomitant loss of natural environments in the Arctic are results of several often interrelated factors. As such, commercial logging, overgrazing, foreign species introduction, natural resource extraction, pollution, and other anthropological effects contribute to reductions and significant changes in habitats of Arctic regions. These factors combine with long term changes in features such as climate warming and precipitation, condition of permafrost, and thus show impacts on vegetation and soils, and may have wide impacts on regional ecosystem health (Bölter, 1996; Stonehouse, 1999).

The cumulative ecological impacts now taking place in the Arctic are cause for much concern. Habitat loss has far-reaching ramifications. Anthropological effects need special attention, such as road building, forestry, hydroelectric power, and increasing summer and winter tourism (Müller-Wille, 1987; Forbes *et al*., 2004, 2006). Weather and snow conditions, *e.g*., the number of warm days during winter $T > 0°C$, and summer conditions show strong effects on local reindeer production (Kumpula and Colpaert, 2003). Both, the increasing atmospheric nitrogen deposition and the increased grazing pressure lead to changes in northern plant communities (Van der Wal *et al*., 2003). The change of plant communities, especially the shift from lichen dominated communities to higher plant communities, can also be mediated by climate change effects. This is due to the different growth rates of the plants and their ability to be more successful competitors (Cornelissen *et al*., 2001).

The differences in vegetation between grazed and non-grazed sites along the fence in our study area are of concern for several ecological reasons. The loss of a dense lichen cover cannot longer prevent from erosion of a thin layer of organic material. Further, soils are strongly affected by changes in temperature and moisture (Peth and Horn, 2006; Uhlig and Zink, 2006). During spring and autumn freeze-thaw cycles pose further stress on the soil organisms, which may result in higher respiration rates (Larsen *et al*., 2002).

Moisture and temperature are the dominant factors, which set the frames of these ecosystems (Kennedy, 1993; Bölter *et al*., 2003b); soil water content is lower in the northern landscapes because the soils have only low clay and silt contents and thus lower field capacity. This also leads to higher transports of organic and inorganic matter by water flows after spring melt and precipitation events. Hence, the recovery of areas devoid of a dense lichen cover by higher plants can be significantly hampered by erosion and sparse seed germination. Although the satellite photographs show a clear separation between the three sites in our study region (*cf*. Tabel 1; Käyhkö and Pellikka, 1994; Kumpula, 2006), a recovery in vegetation and soil activity has taken place. The intermediate region even exhibits high potential CO_2-evolution (Table 1), comparable to those estimated for the Norwegian region. The lower values in Norway must be attributed to less time of elevated temperature due to the isolating plant cover. Relatively high amounts of organic matter in all three sites indicate that a change in vegetation has occurred but that this did not significantly influence the content of total organic matter (Table 1).

It is known that reindeer grazing increases the proportion of graminoids in tundra

heaths (Oksanen and Virtanen, 1995; Manseau *et al.*, 1996; Post and Klein, 1996; Olofsson *et al.*, 2001). But grazing affects not only the herbs and grasses on the ground (grasses etc.) but also the woody plants, such as shrubs and even trees in their growth and reproduction (Den Herder and Niemelä, 2003). Further, grazing affects not only above-ground but also below-ground processes, *i.e.*, nutrient mineralization and organic matter decomposition. In forest soils grazing reduces microbial respiration but mineralization increased, in tundra soils a strong spatial variation of respiration and mineralization was monitored depending on local aspects (Stark, 2002). In Finland, grazing by mammalian herbivores has shown a decelerating effect on soil nutrient cycling and reduced soil respiration on both fertilized and unfertilized areas (Stark and Grellmann, 2002). Thus, our results which show a decrease in soil respiration and potential mineralization underline this finding. Such feedback mechanisms between grazing and plant nutrient availability as well as plant relations to productivity are also known from other grazed ecosystems (McNaughton, 1979; Chapin, 1991; Insam *et al.*, 1996). For Finland, effects of grazing on vegetation and soil biota were shown by Stark *et al.* (2000). Both, positive and negative effects of grazing on soil biota could be monitored.

An important aspect is the change of the near-bottom microclimate when the plant cover is removed. Owen (1980) hypothesized a mutual relation between grazers and graminoids, which benefit from grazers. This can be of special importance for impoverished environments, which has been used as a support for a co-evolution theory. However, this is in contradiction to the point, which has been made above, and thus may not be valid for regions like vulnerable tundra systems.

On the other hand, well approved differentiation of this theory becomes necessary when considering lichen dominated tundra systems: Väre *et al.* (1996) showed significant changes in vegetation due to grazing effects. The lichen *Cladina stellaris* was decreasing, while *C. arbuscular* and *C. rangifera* as well as the moss *Dicranum* sp. showed benefits from grazing, shrubs also decreased. Further, grazing in nutrient-rich Finnish tundra heaths was found to promote herbs and graminoids more than shrubs, on nutrient-poor inland tundras, shrubs were in favour (Stark *et al.*, 2002). Stark (2002) found that in nutrient rich tundra ecosystem grazing causes shifts in the vegetation, abundance of herbs and grasses increase in relation to dwarf shrubs. In nutrient poor lichen heaths shrubs were favoured grazing fodder.

The increase in soil respiration in the transition area can be well affected by a mixture of microbial activity and root respiration. Rooting will change soil conditions by its chemical and physical properties. It could be shown by Chiariello and Gulmon (1991) that flowering plants increase flowering under grazing and Chapin (1980) supposed that tundra graminoids increase root production in order to have better access to nutrients. Such changes by grazing also affects the community structure of vascular plants, *e.g.*, seedlings of pine, due to reduced lichen extracts which are known to prevent the growth of mycorrhiza (Brown and Mikola, 1974).

Such effects on above-ground community patterns are followed by the below-ground community. Although comparable studies are only available from forests and grasslands, it was shown that forest soils have decreasing fungi occurrence inclusive mycorrhiza and related feeding organisms, while bacterial communities increase (Bååth, 1980; Pietikäinen and Fritze, 1995; Bååth *et al.*, 1995). In our study, the greatest effect

on bacterial numbers could be shown for the transition area (Table 1). Bacterial biomass, however, had its lowest level in the Finnish area. Fungi as well as soil algae were observed only sporadically and did not seem to be evident for the microbial communities in these soils, probably due to the very conditions during the summers 2002 and 2003.

Our data on soil respiration remain at fairly low levels (max $0.15\,\mathrm{g}\ CO_2\,m^{-2}\,h^{-1}$; Table 1) when compared to studies in birch forests, *e.g.*, Rustad *et al.* (2001) found 0.8 mg $CO_2\,m^{-2}\,h^{-1}$, and Maljanen *et al.* (2003) describe 1–10 g CO_2-C $m^{-2}\,d^{-1}$ (~0.2–2 g $CO_2\,m^{-2}\,h^{-1}$). Thus, our data compare more to those from mineral soils in southern Finland, which range between 0.07 and 0.6 g $CO_2\,m^{-2}\,h^{-1}$ (Lohila *et al.*, 2003). Heikkinen *et al.* (2002) show a CO_2-production at dry places (strings) on wet environments in spring between 40 and 434 mg $CO_2\,m^{-2}\,h^{-1}$, measured in N-Finland (near Kaamanen). The low soil respiration data found in our study may also be affected by long drought during the summer 2003, and thus probably low levels of primary production followed by low levels of freshly produced organic matter.

However, especially in environments like tundras where most plant biomass is located below-ground, root respiration can have considerable share in this activity measurement. Root respiration is calculated to be responsible for 90% of total soil respiration (Dugas *et al.*, 1999), 15–70% (Norman *et al.*, 1992), 50% (Hanson *et al.*, 1993), and 40% (Kucera and Kirkham, 1971). This is a very broad range and shows the great vagueness in calculating ratios between soil microbial carbon and related C-loss.

Acknowledgments

References

Bååth, E. (1980): Soil fungal biomass after clear-cutting of a pine forest in central Sweden. Soil Biol. Biochem., **12**, 495–500.

Bååth, E., Frostegard, Å., Pennanen, T. and Fritze, H. (1995): Microbial community structure and pH response in relation to soil organic matter quality in wood-ashed fertilized, clear-cut or birned coniderous forest soils. Soil Biol. Biochem., **27**, 229–240.

Bölter, M. (1996): Consequences of global warming on soil processes in Arctic regions. Polarforschung, **66**, 1–10.

Bölter, M. and Möller, R. (2006): Changing microbial ecology with changes in grazing and its management. Reindeer Management in Northernmost Europe: Linking Practical and Scientific Knowledge in Social-Ecological Systems, ed. by B.C. Forbes *et al.* Berlin, Springer, 265–295 (Ecol. Stud. **184**).

Bölter, M., Bloem, J., Meiners, K. and Möller, R. (2002): Enumeration and biovolume determination of microbial cells—a methodological review and recommendations for applications in ecological research. Biol. Fertil. Soils, **36**, 249–259.

Bölter, M., Möller-Lupp, W., Takata, K., Yabuki, H. and Möller, R. (2003a): Potential CO_2-production in aerobic conditions from a Siberian tundra environment. Polar Biosci., **16**, 70–85.

Bölter, M., Möller, R. and Müller-Lupp, W. (2003b): CO_2-release from permafrost soils in relation to

temperature changes. Social and Environmental Impacts in the North: Proceedings of the NATO Advanced Research Workshop, Apatity, Russia, from 8 to 12 May 2002, ed. by R.O. Rasmussen and N.E. Koroleva. Amsterdam, Kluwer, 7–24 (NATO Science Series IV: Earth and Environmental Sciences, Vol. 31).

Brown. R.T. and Mikola, P. (1974): The influence of fruticose soil lichens upon the mycorrhizae and seedling growth of forest trees. Acta Forest. Fenn., **141**, 1–22.

Chapin, F.S., III (1980): Nutrient allocation and responses to defoliation in tundra plants. Arct. Alp. Res., **12**, 553–563.

Chapin, F.S., III (1991): Effects of stresses on nutrient availability. Response of Plants to Multiple Stresses, ed. by H.A. Mooney *et al*. San Diego, Academic Press, 67–76.

Chiariello, N.R. and Gulmon, S.L. (1991): Stress effects on plant reproduction. Response of Plants to Multiple Stresses, ed. by H.A. Mooney *et al*. San Diego, Academic Press, 161–188.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, M., Michelsen, A., Graglia, E. and 17 other authors (2001): Global change and arctic ecosystems: is liche decline a function of increases in valcular plant biomass? J. Ecol., **89**, 984–994.

Den Herder, M. and Niemelä, P. (2003): Effects of reindeer on the re-establishment of *Betula pubescens* subsp. *czerepanovii* and *Salix phylicifolia* in a subarctic meadow. Rangifer, **23**, 3–12.

Dugas, W.A., Heuer, M.L. and Mayeux, H.S. (1999): Carbon dioxide fluxes over bermudagras, native prairie, and sorghum. Agric. For. Meteorol., **93**, 121–139.

Forbes, B.C. *et al*., ed. (2004): RENMAN—Final Report. The challenges of modernity for reindeer management: Integration and sustainable development in Europe's Subarctic and Boreal regions. Arctic Centre Reports **41**, 100 p.

Forbes, B.C., Bölter, M., Müller-Wille, L., Hukkinen, J., Müller, F., Gunslay, N. and Konstantinov, Y., ed. (2006): Reindeer Management in Northernmost Europe: Linking Practical and Scientific Knowledge in Social-Ecological Systems. Berlin, Springer, 397 p. (Ecol. Stud. **184**).

Hanson, P.J., Wullschleger, S.D., Bohlman, S.A. and Todd, D.E. (1993): Seasonal and topographic patterns of forest floor CO_2 effects from an upland oak forest. Tree Physiol., **13**, 1–15.

Heikkinen, J.E.P., Maljanen, M., Aurela, M., Hargreaves, K.J. and Martikainen, P.J. (2002): Carbon dioxide and methane dynamics in a sub-Arctic peatland in northern Finland. Polar Res., **21**, 49–62.

Insam, H., Rangger, A., Henrich, M. and Hitzl, W. (1996): The effect of grazing on soil microbial biomass and community structure on alpine pastures. Phyton, **36**, 205–216.

Käyhkö, J. and Pellikka, P. (1994): Remote sensing of the impact of reindeer grazing on vegetation in northern Fennoscandia using SPOT XS data. Polar Res., **13**, 115–124.

Kennedy, A.D. (1993): Water as limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis. Arct. Alp. Res., **25**, 308–315.

Kitti, H. and Forbes, B.C. (2006): Vegetation: Structure, cover and biomass of subarctic tundra wetlands used as summer pastures. Reindeer Management in Northernmost Europe: Linking Practical and Scientific Knowledge in Social-Ecological Systems, ed. by B.C. Forbes *et al*. Berlin, Springer, 187–198 (Ecol. Stud. **184**).

Kucera, C.L. and Kirkham, D.R. (1971): Soil respiration studies in tallgrass prairie in Missouri. Ecology, **52**, 912–915.

Kumpula, J. and Colpaert, A. (2003): Effects of weather and snow conditions on production and survival of semi-domesticated reindeer (*R. t. tarandus*). Polar Res., **22**, 225–233.

Kumpula, T. (2006): Very high resolution remote sensing data in reindeer pasture inventory in northern Fennoscandia. Reindeer Management in Northernmost Europe: Linking Practical and Scientific Knowledge in Social-Ecological Systems, ed. by B.C. Forbes *et al*. Berlin, Springer, 167–185 (Ecol. Stud. **184**).

Larsen, K.S., Jonasson, S. and Michelson, A. (2002): Repeated freeze-thaw cycles and their effects on biological processes in two arctic ecosystem types. Appl. Soil Ecol., **21**, 187–195.

Lohila, A., Aurela, M., Regina, K. and Laurila, T. (2003): Soil and total ecosystem respiration in agricultural fields: effect of soil and crop type. Plant Soil, **251**, 303–317.

Maljanen, M., Liikanen, A., Silvola, J. and Martikainen, P.J. (2003): Nitrous oxide emissions from boreal organic soil under different land-use. Soil Biol. Biochem., **35**, 689–700.

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

Manseau, M., Huot, J. and Bergman, C. (1999): Ecosystem processes characterizing and influencing grazing systems, productivity and sustainability: the caribou herds of the Quebec/Labrador Peninsula. An International Workshop on the Human Role in Reindeer/Caribou Systems—Coping with Threats to Environmental Security in Northern Landscapes. February 10–14, 1999, The Arctic Centre, Rovaniemi, Finland (Abstract).

McNaughton, S.J. (1979): Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am. Nat., **113**, 691–703.

Müller-Wille, L. (1987): Indigenous peoples, land-use conflicts, and economic development in circumpolar lands. Arct. Alp. Res., **19**, 351–356.

Müller-Wille, L., Hukkinen, J., Müller, F., Bölter, M. and Forbes, B.C. (2006): Synthesis: Environmental and socio-political conditions for modern reindeer management in Europe's North. Reindeer Management in Northernmost Europe: Linking Practical and Scientific Knowledge in Social-Ecological Systems, ed. by B.C. Forbes *et al*. Berlin, Springer, 366–379 (Ecol. Stud. **184**).

Norman, J.M., Garica, R. and Verma, S.B. (1992): Soil surface CO_2 fluxes and the carbon budget of a grassland. J. Geophys. Res., **97**, 18845–18853.

Oksanen, L. and Virtanen, R. (1995): Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. Acta Bot. Fenn., **153**, 1–80.

Olofsson, J., Kitti, H., Rautiainen, P., Stark, S. and Oksanen, L. (2001): Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. Ecography **24**, 13–24.

Owen, D.F. (1980): How plant may benefit from the animals that eat them. Oiko, **35**, 230–235.

Peth, S. and Horn, R. (2006): Consequences of grazing for soil physical and mechanical properties in forest and tundra environments. Reindeer Management in Northernmost Europe: Linking Practical and Scientific Knowledge in Social-Ecological Systems, ed. by B.C. Forbes *et al*. Berlin, Springer, 217–243 (Ecol. Stud. **184**).

Pietikäinen, J. and Fritze, H. (1995): Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration and nitrification. Soil Biol. Biochem., **27**, 101–109.

Post, E.S. and Klein, D.R. (1996): Relationships between graminoid growth form and levels of grazing by caribou (Rangifer tarandus) in Alaska. Oecologia, **107**, 364–372.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C. and Gurevitch, G. (2001) A meta-analysis of the response of soil respiration and net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia, **126**, 532–562.

Schulz, J. (2000): Handbuch der Ökozonen. Stuttgart, Verlag Eugen Ulmer, 577 p.

Stark, S. (2002): Reindeer grazing and soil nutrient cycling in boreal and tundra ecosystems. PhD Thesis, Dept Biol, Univ. Oulu, Oulu University Press, 31 p.

Stark, S. and Grellmann, D. (2002): Soil microbial responses to herbivory in an arctic tundra heath at two levels of nutrient availability. Ecology, **83**, 2736–2744.

Stark, S., Wardle, D.A., Ohtonen, R., Helle, T. and Yeates, G.W. (2000): The effect of reindeer grazing on decomposition, mineralization and soil biota in a dry oligotrophic Scots pine forest. Oikos, **90**, 301–310.

Stark, S., Strömmer, R. and Tuomi, J. (2002): Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. Oikos, **97**, 69–76.

Stonehouse, B. (1999): Biological processes in cold soils. Polar Rec., **35**, 5–10.

Uhlig, C. and Zink, A. (2006): Changes in organic-horizon soil properties due to reindeer haerding and changing management. Reindeer Management in Northernmost Europe: Linking Practical and Scientific Knowledge in Social-Ecological Systems, ed. by B.C. Forbes *et al*. Berlin, Springer, 245–264 (Ecol. Stud. **184**).

Uhlig, C., Sveistrup, T. and Schjeldrup, I. (2004): Impacts of reindeer grazing on soil properties on Finnmarksvidda, Northern Norway. Rangifer, Spec. Issue, **15**, 83–91.

Van der Wal, R., van Lieshout, S.M.J. and Loonen, M.J.J.E. (2001): Herbivore impact on moss depth, soil

temperature and arctic plant growth. Polar Biol., **24**, 29–32.

Van der Wal, R., Pearce, I., Brooker, R., Scott, D., Welch, D. and Woodin, S. (2003): Interplay between nitrogen deposition and razing causes habitat degradation. Ecol. Lett., **6**, 141–146.

Väre, H., Ohtonen, R. and Mikkola, K. (1996): The effect and extent of heavy grazing by reindeer in oligotrophic pine heaths in northeastern Fennoscandia. Ecography, **19**, 245–253.

Zech, W. and Hintermaier-Erhard, G. (2002): Böden der Welt. Heidelberg, Spektrum Akademischer Verlag, 120 p.