

**REINDEER GRAZING AND SOIL
NUTRIENT CYCLING IN
BOREAL AND TUNDRA
ECOSYSTEMS**

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AND TUNDRA ECOSYSTEMS**

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Abstract

In northernmost Fennoscandia, grazing by reindeer (*Rangifer tarandus* L.) has a substantial impact on the vegetation of boreal forests and arctic-alpine tundra heaths, which are reflected in below-ground processes, such as nutrient mineralization and soil organic matter decomposition. In the present thesis, the effects of reindeer grazing on soil nutrient cycling were studied by comparing grazed situation with an ungrazed control area in ten boreal forests and six arctic-alpine tundra heaths.

In boreal forests, reindeer grazing reduced microbial respiration in both the oligotrophic and mesotrophic study areas, indicating a deficiency of labile substrates for the soil microbes due to reindeer grazing. Simultaneously, there was heterogeneity in the impact on nitrogen mineralization rates as at some sites, mineralization was enhanced by grazing. The fertilization effect of urine and faeces can therefore be strong enough a factor to outweigh a reduction in quality of soil organic matter. In the oligotrophic forests, low soil moisture content in the grazed areas could sometimes limit the mineralization rates even when the potential for mineralization was enhanced by grazing.

In the tundra ecosystems, there was spatial variation in the impact of grazing on microbial respiration and nitrogen mineralization. Low grazing intensity occurring outside the growing season had a retarding impact on nutrient cycling in both unfertilized, nutrient-poor and fertilized, nutrient-rich conditions. In contrast, a relatively high grazing intensity enhanced the mineralization rates in two nutrient-poor and two nutrient-rich tundra heaths. When three different grazing intensities were compared in one oceanic, nutrient-rich and one continental, nutrient-poor tundra heath, the strongest positive effect of grazing on soil nutrient cycling occurred in the heavily grazed areas. The data do not support the assumption that soil nutrient availability regulates whether herbivores enhance or retard nutrient cycling in the soil. Instead, the net effect of grazing is determined by the balance between the underlying mechanisms that may work at opposite directions. The most important of these mechanisms are the grazer-mediated impact on the decomposability of the dominant vegetation and fertilization by urine and faeces.

The duration, intensity and seasonal timing of the grazing seem to be important factors that regulate whether reindeer grazing enhances or retards soil nutrient cycling in each specific area. Due to the high spatial and temporal variation in the effects of grazing observed in this study, it is not possible to generalize the overall impact of grazing. Further study is required in order to determine the exact conditions under which grazing enhances or it retards soil nutrient cycling.

Keywords: nitrogen, herbivory, microbial biomass, microbial respiration, litter decomposition, carbon, mineralization

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List of original publications

- I Stark S, Wardle DA, Ohtonen R, Helle T & Yeates GW (2000) The effect of reindeer grazing on decomposition, mineralization and soil biota in a dry oligotrophic Scots pine forest. *Oikos* 90: 301-310.
- II Stark S, Tuomi J, Strömmer R & Helle T (2002) Non-parallel changes in microbial carbon and nitrogen dynamics due to reindeer grazing in northern boreal forest soils. *Ecography*, in press.
- III Stark S, Strömmer R & Tuomi J (2002) Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. *Oikos*, in press.
- IV Stark S & Grellmann D (2002) Soil microbial responses to herbivory in an arctic tundra heath at two levels of nutrient availability. *Ecology*, in press.
- V Olofsson J, Stark S & Oksanen L (2002) Herbivore influence on ecosystem processes in tundra plant communities. Manuscript.

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Abstract

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1 Introduction

1.1 Interactions between herbivory and soil microbial processes

By modifying the structure of the above-ground ecosystem, herbivory exerts many direct and indirect effects on soil microbial processes such as organic matter decomposition and nutrient mineralization. Consequently, herbivores have feedback effects on plant nutrient availability and productivity (McNaughton 1985, Chapin 1991, Hobbie 1992, Pastor *et al.* 1993, Augustine & McNaughton 1998). Although mammalian herbivores frequently influence the rate of soil nutrient cycling, the direction of the change varies between ecosystems. Herbivores have different or even opposite effects on soil nutrient cycling rates in different systems, and, consequently, either increase or decrease ecosystem productivity (Chapin 1991, Hobbie 1992, Milchunas & Lauenroth 1993, Augustine & McNaughton 1998). Understanding the factors that determine whether herbivory has a net positive or negative effect on soil nutrient cycling is therefore of major importance in elucidating the role of herbivory in ecosystems.

Herbivores influence the below-ground processes in several different ways. Herbivores strongly affect the amount and chemical composition of the organic matter in the soil by changing the species composition of the plant community. Herbivores often selectively consume more palatable and decomposable plant species, thus increasing the proportion of less decomposable species in the plant community. This reduces the quality of the organic matter and has a retarding effect on soil nutrient cycling (Pastor & Naiman 1992, Pastor *et al.* 1993, Grime *et al.* 1996, Pastor & Cohen 1997, Ritchie *et al.* 1998). On the other hand, herbivores may also increase the quality of decomposing material by increasing the nutrient content of plants through induced compensatory growth, which has a promoting effect on the soil nutrient cycling (McNaughton 1985, Frank & Groffman 1998). The shift in plant species composition caused by herbivores may therefore have either positive or negative effects on the nutrient turnover rates, depending on whether the plant community changes towards less or more decomposable plant species (Chapin 1991, Augustine & McNaughton 1998).

The herbivore-driven changes in the plant community structure also often have a considerable influence on the soil microclimate (Georgiadis *et al.* 1989, Insam *et al.*

1996, Zimov *et al.* 1995). Because microbial processes are strongly dependent on the soil moisture and temperature regimes, the impact of grazing on the soil microclimate may act as an indirect mechanism in its effects on microbial processes in the soil. If the soil microbes become limited by soil moisture as a result of the herbivore-driven impact on the soil microclimate, N mineralization rates may be retarded by herbivory even when the potential for N mineralization is increased by herbivores (Georgiadis *et al.* 1989). On the other hand, in tundra ecosystems where the soil microbial processes are mainly limited by low temperatures, large mammalian herbivores may increase the soil temperature and, through this, substantially enhance soil nutrient cycling rates (Zimov *et al.* 1995).

Furthermore, herbivores affect the soil microbial processes by inducing certain physiological responses in plants. By inducing an increase in the amount of defensive chemicals in plants, herbivores indirectly retard the litter decomposition rates (Bryant *et al.* 1991). Herbivores often influence the root dynamics and the amount of organic substances exuded by plant roots, and this has a major impact on microbial C dynamics (Holland *et al.* 1992, Bargdett *et al.* 1998, Ruess *et al.* 1998). Herbivores directly improve organic matter quality via their urine and faecal N input, which increases the nutrient concentrations in the soil and enhances the mineralization rates (McKendrick *et al.* 1980, Ruess & McNaughton 1987, Sirotnak & Huntly 2000). Direct fertilization by mammalian waste products occurs in all ecosystems, but it may be overshadowed by the indirect mechanisms that reduce the quality of decomposing material. The net effect of herbivory may therefore vary from positive to negative depending on the magnitude of the mechanisms involved (Augustine & McNaughton 1998).

According to a hypothesis proposed by Chapin (1991), ecosystem nutrient availability is a key factor that determines when herbivores enhance or retard soil nutrient cycling. Under nutrient-rich conditions, herbivores often induce compensatory growth in plants, which increases nutrient uptake by plants and favours fast-growing and easily decomposing plants, such as graminoids (McNaughton 1985, Chapin 1991). Under nutrient-poor conditions, however, the low nutrient availability in the soil does not permit compensatory growth, and slowly decomposable plant species - that are also not preferred by herbivores - gain the competitive advantage in the system (Bryant *et al.* 1983, Coley *et al.* 1985, Chapin 1991). As a result, herbivory may enhance soil nutrient cycling in fertile soils and retard it in infertile soils (Chapin 1991, Hobbie 1992).

The grazing intensity also has implications for the net effect of herbivory on soil nutrient cycling. When the proportion of the vegetation that is consumed by herbivores is high, the effect of direct fertilization through urine and faeces can be high enough to overshadow the indirect retarding impact of the selective feeding of more decomposable plant species (Cargill & Jefferies 1984, Sirotnak & Huntly 2000). Due to variations in the grazing intensity, the balance between mechanisms that enhance and retard soil nutrient cycling is thus liable to vary in space and time (Sirotnak & Huntly 2000, Wardle *et al.* 2001).

1.2 Grazing mammals in northernmost Fennoscandia

Reindeer (*Rangifer tarandus* L.) has been present in northern Fennoscandia throughout the post-glacial period (Oksanen *et al.* 1995). The reindeer was domesticated during the 16th century, and their population densities have been constantly high during the last few decades (Kojola & Helle 1993). As a result, grazing has had a considerable influence on the vegetation of boreal forests (Ahti 1977, Helle & Aspi 1983, Väre *et al.* 1995, 1996, Suominen 1999, Suominen & Olofsson 2001) and arctic-alpine tundra heaths (Oksanen 1978, Oksanen & Virtanen 1995, Oksanen *et al.* 1995, Olofsson *et al.* 2001, Suominen & Olofsson 2001). In northernmost Fennoscandia, the differences in climate between the Atlantic coast and inland create a natural gradient in vegetation, plant productivity and nutrient availability in the soil (Ahti *et al.* 1968, Haapasaari 1988, Oksanen & Virtanen 1995). Reindeer utilise this gradient by annually migrating between different areas. The continental, nutrient-poor areas are used as winter pastures because lichens, which are the main food resources for the reindeer during the winter, are dominant in the vegetation in such areas (Danell *et al.* 1994). Reindeer grazing considerably reduces the biomass of lichens, and favours dwarf shrubs containing high levels of defensive chemicals in the vegetation (Oksanen & Virtanen 1995, Olofsson *et al.* 2001). The oceanic, more nutrient-rich areas are used as summer pastures, because the vegetation is dominated by herbs, grasses and deciduous trees, which constitute their main food sources during the summer (Danell *et al.* 1994). In these areas, reindeer grazing has been found to increase herbs and graminoids in relation to dwarf shrubs (Oksanen & Virtanen 1995, Olofsson *et al.* 2001). In northern Finland, reindeer stay within the same area throughout the year, because access to the oceanic areas is prevented by man-made borders. This causes additional disturbance to the forest vegetation, because the lichen cover is strongly affected by trampling during the summer (Suominen & Olofsson 2001).

In addition to reindeer, small rodents such as vole (*Clethrionomus rufocanus* L.) and lemming (*Lemmus lemmus* L.) also have a significant influence on the vegetation in tundra ecosystems (Moen *et al.* 1993, Virtanen *et al.* 1997, Moen & Oksanen 1998, Grellmann 2002). The impact of small herbivores is especially evident during the population peaks (Moen *et al.* 1993), but herbivory at even relatively low intensities may have significant impacts on the plant biomass and plant species composition (Grellmann 2002).

1.3 Boreal forests

In the oligotrophic Scots pine forests in northern Finland, the reduction in the thickness of the lichen cover due to reindeer grazing can be expected to have considerable impacts on the quality and quantity of soil organic matter. Moreover, in the absence of a thick lichen cover, fluctuations in soil moisture and temperature are considerably higher than those under an undisturbed lichen cover (Kershaw 1985). During the winter – when most of the organic matter decomposition takes place (Moore 1984) – soil temperatures in grazed areas have been found to be lower relative to corresponding ungrazed areas (Ritari & Mikola 1995, Sutinen *et al.* 1998, Broll 2000). During the summer, the soil moisture

content can be very low in grazed areas, and this probably has important consequences for the microbial activity in the soil (Väre *et al.* 1996).

In boreal ecosystems, studies on moose herbivory have shown that herbivory has a retarding effect on soil nutrient cycling, because moose feed selectively on plants that produce high quality litter, thus favouring species with low-quality litter (Pastor & Naiman 1992, Pastor *et al.* 1993, Pastor & Cohen 1997). In pine forests, however, the tree species composition is not affected by herbivores, and the potential changes in the decomposability of plant litter are only in the ground vegetation. Moreover, herbivores usually prefer plant species that also produce easily decomposable litter (Pastor & Naiman 1992, Grime *et al.* 1996). However, lichens – the main food resource for the reindeer during the winter - produce very slowly decomposable litter (Moore 1984, Parinkina *et al.* 1998) and constitute an exception to this rule. Therefore, the effect of reindeer grazing on soil nutrient cycling cannot be predicted on the basis of other studies conducted in boreal systems.

In this thesis, the effect of reindeer grazing on soil microbial processes was studied in five oligotrophic, lichen-dominated and five mesotrophic, dwarf shrub-dominated boreal forests in northern Finland (I, II). The relative importance of changes in organic matter quality and the soil microclimate for the effects of grazing was studied using reciprocal transplant experiments. It was hypothesised that, if the mechanism through which reindeer grazing modifies the functioning of the ecosystem, is to change the quality of the soil organic matter, then grazing would have the same effect on soil C and N mineralization in both mesotrophic forests and oligotrophic ones. Alternatively, if changes in the soil microclimate mediate the effects of grazing, then no or much weaker effects would be expected in the mesotrophic forests, where soil moisture is less susceptible to change as a result of grazing.

1.4 Arctic-alpine tundra heaths

Mammalian herbivores often have profound impacts on tundra plant communities (Chapin 1980, McKendrick *et al.* 1980, Zimov *et al.* 1995, Post & Klein 1996, Kryazhimskii & Danilov 2000, Grellmann 2002). Because dwarf shrubs are favoured by reindeer grazing in nutrient-poor conditions, and graminoids in nutrient-rich conditions (Oksanen & Virtanen 1995), reindeer-driven changes in the decomposability of the plant species seem to support the hypothesis proposed by Chapin (1991) that ecosystem nutrient availability determines whether herbivores improve or reduce the quality of organic matter, and therefore enhance or retard soil nutrient cycling. In this thesis, the hypothesis was tested in two studies. Firstly, a natural productivity gradient in northernmost Fennoscandia was used to compare the impact of reindeer grazing on C and N mineralization rates between oceanic, nutrient-rich and continental, nutrient-poor arctic-alpine tundra heaths (III). Secondly, soil microbial responses to reindeer and rodent grazing were studied in fertilized and unfertilized tundra heath in northern Norway (IV). Following the hypothesis of Chapin (1991), it was predicted that grazing would have an enhancing impact on C and N mineralization in nutrient-rich situations, and a retarding impact in nutrient-poor situations.

Finally, the role of grazing intensity in the net effect on soil nutrient cycling was studied by comparing three different grazing intensities in an oceanic and a continental tundra heath in northernmost Norway (V).

2 Material and methods

2.1 Study areas and experimental designs

The research was conducted by comparing a fenced, ungrazed control area with the grazed area in ten boreal forests (I, II) and six arctic-alpine tundra heaths (III-V). The boreal study sites consisted of five oligotrophic forests, Kätksuvanto (68°07'N, 23°25'E), Kaamanen (69°20'N, 27°10'E), Naruska (66°68'N, 29°08'E), Kevo (69°46'N, 26°57'E) and Raja-Jooseppi I (68°25' N, 28°30' E), and five mesotrophic forests, Kelloselkä (66°51'N, 29°02'E), Rajajooseppi II (68°25' N, 28°30' E), Pallasjärvi (68°00'N, 24°05'E), Värriö (67°48'N, 29°40'E) and Angeli (69°05'N, 25°45'E). The study sites were either situated along the border between Finland and Russia or between Finland and Norway, where the Norwegian or Russian side of the border fence was used as the ungrazed control, or reindeer exclosures established for research purposes were used. In the tundra vegetation, two subcontinental arctic-alpine tundra heaths in northern Finland, Jesnalvaara (69°46'N, 26°57'E; III) and Nuorttitunturi (67°48'N, 29°40'E; III), two suboceanic tundra heaths in northernmost Norway (Lagisduoddar, 70°30'N, 27°30'E; III, Raisduoddar, 69°30'N, 27°30'E; III, V), and one subcontinental tundra heath in northernmost Norway, Cearro (location 69°40' N, 24°40' E; V), were investigated. The sites were established above the forest line in the low oroarctic zone (Ahti *et al.* 1968, Haapasaari 1988, Oksanen & Virtanen 1995). A reindeer exclosure was used in Jesnalvaara and the eastern border fence in Nuorttitunturi as ungrazed control areas. Raisduoddar, Lagisduoddar and Cearro, on the other hand, are cut by a fence that was built during the 1960's to prevent reindeer entering the winter ranges during the summer. The winter range side of the fence was referred to as the ungrazed control, because reindeer mainly use it only for passage in spring and autumn. In all study sites, sampling plots were established on both the grazed and ungrazed sides of the reindeer fences, the distance between the replicates on the same side of the fence being twice the distance from the fence. The sampling strategy was to collect one bulk sample from each sampling plot and to use subsamples for a number of analyses.

The role of soil microclimate in the effects of grazing was experimentally studied in four oligotrophic pine forests (I, II). At Kätksuvanto, three subplots were established in

each plot inside the enclosure; in the first the lichens were left intact, in the second the lichens were trimmed to the same height as the lichens growing outside the enclosure, and in the third the lichens were removed down to the level of the litter layer (I). Two subplots were set up on the plots outside the enclosure: one with intact lichens and the other with all the lichens removed. The rate of decomposition of *Vaccinium myrtillus* L. leaf litter was measured in these plots. At Kätkäsvanto, Raja-Jooseppi I, Naruska and Kevo, reciprocal transplant incubations were conducted (II). 16 sampling plots on both the grazed and ungrazed sides of the fence were established, and composite soil samples consisting of 3 soil cores were taken from each plot. Net N mineralization was measured by the buried bag method (Eno 1960). On half of the plots the subsamples were buried in the same place where they had been taken. On the other plots the subsamples were buried in corresponding plots on the other side of the fence, i.e. from the ungrazed to the grazed side or vice versa. The samples were incubated *in situ* for one year.

The impact of reindeer and rodent grazing was studied in a tundra heath in Joatka (69°45' N, 23°58' E; IV), northern Norway. The area was a well-drained, relatively nutrient-deficient tundra heath, with vegetation dominated by dwarf shrubs. In 1991 and 1997, four randomly chosen treatment areas (size 2,500 m²) had been fertilized with NPK fertilizer, and four areas of the same size established as control areas (Grellmann 2001). Plant productivity and the proportion of graminoids were considerably increased by fertilization (Grellmann 2001). In 1991, enclosures of two types were built in each area; four enclosures to exclude reindeer and four to exclude both rodents and reindeer. The enclosures were 0.8 x 1.2 m in size, and they were made of galvanized net (mesh size 1.2 x 1.2 cm). As the enclosure treatments were performed in both the unfertilized and fertilized areas, the design provided a possibility to compare the effects of herbivory at two levels of nutrient availability. For studying the impact of different treatments on below-ground processes, composite soil samples were taken from inside both types of herbivore enclosure and from the grazed area.

2.2 Soil properties and N and P pools

Homogenized samples were analysed for bulk density, gravimetric moisture (105°C, 12 h) and organic matter content (400°C, 4 h; I - V). Soil N and P pools were determined by extracting subsamples with 0.5M K₂SO₄ and analyzed for inorganic N and P by colorimetric methods (Bremner 1965, Crooke & Simpson 1971; I, II), or by automated flow injection (QuikChem 8000, Lachat Instruments, Inc.; III, IV, FIA Instruments; V). Total dissolved N and P were analysed in the extracts by oxidising all extractable N and P into NO₃ and PO₄ (Williams *et al.* 1995), and assayed as inorganic N and P (I - V). Microbial N and P were extracted from the soils using 0.5 M K₂SO₄ after chloroform fumigation (18 hours) (Brookes *et al.* 1985), and analysed as total dissolved N and P (I - V). Total C and N concentrations in the soil (III - V) and plant (IV, V) samples were measured on an automated analyzer (EA 1110, CHNS-O, CE Instruments).

2.3 N and C mineralization and litter decomposition

The impact of grazing on N mineralization rates was measured by means of *in situ* soil incubations by the buried bag method (Eno 1960; I, II, V), or by laboratory incubations (III). The gross N mineralization rate was measured in the laboratory by the isotope dilution method (Hart *et al.* 1994b; I - III), and the rates of gross N mineralization and immobilization calculated using the equation of Kirkham & Bartholomew (1954). The organic matter decomposition rates were assessed by measuring microbial respiration using a respirometer (Nordgren 1988, Nordgren *et al.* 1988; I - V). Substrate-induced respiration (SIR) was analysed as the index of microbial biomass C (Anderson & Domsch 1978, Ohtonen 1994), and the metabolic efficiency of the soil microbes (qCO_2) was calculated as the ratio of microbial respiration to SIR (I, III, IV, V) or microbial C (II). The effect of grazing on microbial respiration rates was measured in different layers of the soil profile, in lichens, litter, humus and mineral soil in Kätkäsvanto (I).

Decomposition of *V. myrtillus* litter (Kätkäsvanto; I, Raisduoddar and Cearro; V) and *D. flexuosa* litter (Raisduoddar and Cearro; V) was measured by leaving litter bags to decompose *in situ* for one year. Oven-dry weight (80°C, 24 h) was determined, and the N concentration measured by the micro-Kjeldahl method (I) or on an automated analyzer (EA 1110, CHNS-O, CE Instruments; V). N loss from the litter was calculated by subtracting the value for N concentration \times litter mass at sampling from that at the time of the litter bag placement.

3 Results and discussion

3.1 The effects of grazing on soil C and N mineralization in boreal forests

The microbial respiration rates and metabolic activity in the humus layer of the forest soils were significantly lower in the grazed than in the ungrazed areas in both the oligotrophic and mesotrophic forests (I, II). Soil moisture was significantly lower in the grazed than in the ungrazed areas in the oligotrophic forests, but not in the mesotrophic forests. The reduction in soil microbial activity therefore occurred irrespective of the effects of grazing on soil moisture. A decrease in the microbial respiration rates indicates that, in forest ecosystems, reindeer grazing creates a deficiency of labile C for the soil microbes (Nordgren 1988, Ohtonen 1994, Cheng *et al.* 1998). In contrast to the consistent negative effect on C release from the soil organic matter, there was variation in the impacts of grazing on microbially mediated N transformations; the effect of grazing on the N mineralization rates was site-specific, varying from no change to positive and negative effects (II). The impact of grazing in terms of how much C the soil microbes released from decomposing organic matter therefore did not correlate with the impact on the nutrient mineralization rates. A simultaneous reduction in microbial respiration rates and an increase in N mineralization rates emphasize the importance of urine and faeces in the effects of herbivory (Ruess & McNaughton 1987, Frank & Groffman 1998, Sirotnak & Huntly 2000). This may be a strong enough mechanism to outweigh a reduction in overall soil microbial activity and, through this, uncouple soil N dynamics from soil C quality.

In Kätkäsvanto, which is an oligotrophic forest, microbial respiration was also measured in the individual layers down the soil profile. Although microbial respiration and C in the humus layer were decreased by grazing, in the lichen and litter layers they were increased by grazing (I). At the same time, net N mineralization in the humus layer was enhanced by grazing, while there was no difference in the gross N mineralization rates. The enhanced net N mineralization is therefore due to a lack of available C relative to N in the decomposing material (Holland & Detling 1990, Ohtonen *et al.* 1992, Hart *et al.* 1994a). This can be a result of a simultaneous increase in soil N through an input of

urine and faeces and a decrease in C input in the plant litter. Owing to the growth form of *Cladina* lichens, the litter production in grazed lichen-dominated forests differs considerably from the ungrazed state. The bases of the lichen podetia begin to die and form litter for soil decomposers after about 10 years of undisturbed growth. Due to grazing, however, lichens are unlikely to ever reach this stage and hence there will be no dead bases in the lichens (Ahti 1977, Helle & Aspi 1983, Kumpula *et al.* 1997). Owing to the decrease in the production of lichen litter, the soil organic matter may generally be older in the grazed areas, and recalcitrant organic compounds probably accumulate in the soil (Berg & Staaf 1981).

Considering the high degradation of the lichen cover due to reindeer grazing in the oligotrophic forests (Ahti 1977, Helle & Aspi 1983, Väre *et al.* 1995), but relatively small impact on the ground vegetation in the mesotrophic forests (Suominen 1999), the similarity between the effect of reindeer grazing on microbial C transformations in the heavily grazed lichen-dominated forests and in the less affected dwarf-shrub dominated forests is surprising. Changes in plant root dynamics and root exudation often play an important role in the effects of herbivory (Ruess *et al.* 1998, Bargdett *et al.* 1998) and, as grazing by reindeer/caribou has been shown to cause root damage (Väre *et al.* 1996, Morneau & Payette 2000), they may considerably contribute to the decrease in labile C availability. Therefore, the physical disturbance caused by herbivores can play a significant role in the system even when they do not consume the plants, and thus have no major influence on plant species composition. The higher soil bulk density observed in the grazed areas may also reduce the microbial activity (Jordan *et al.* 1999, Ponder & Tadros 2001).

However, the reindeer-mediated impact on soil microbial processes seems to be regulated by both the quality of decomposing matter and the soil microclimate. In Kätkäsvanto, the decomposition of *V. myrtillus* leaves was retarded in the grazed area, as well as in the subplots from which lichens had been artificially removed in the ungrazed area (I). However, the reciprocal transplant experiments showed no relationship between the reindeer-mediated impact on net N mineralization and the soil microclimate (II). These experiments, however, do not give any information about the separate roles of soil moisture and temperature. In Kätkäsvanto, net N mineralization was significantly enhanced by grazing in the summer of 1997, whereas no effect was detected in the summer of 1998, probably due to the very low moisture content in the grazed area (II). The reindeer-mediated impact on soil moisture therefore creates a source of temporal variation in the effects of grazing even in areas where the potential for N mineralization is enhanced. However, due to the spatial variation in the impact on N mineralization potential and the temporal variation in soil moisture, estimating the role of the soil microclimate in the effects of reindeer grazing requires a long-term study.

3.2 Does soil nutrient availability determine the effect of herbivory on soil nutrient cycling in tundra ecosystems?

Microbial respiration rates were enhanced by grazing in the suboceanic, nutrient-rich study areas, Raisduoddar and Lagisduoddar, where graminoids were also increased by

grazing (Olofsson *et al.* 2001), i.e. the vegetation had shifted towards more decomposable species (Hobbie 1996; III). In the subcontinental, lichen-rich tundra heaths, Jesnal and Nuorttitunturi, grazing had no effects on soil respiration rates, indicating that poor C quality was constraining the microbial decomposition activity (III). The impacts of grazing on microbial C dynamics thus varied between the suboceanic and subcontinental tundra heaths, and supported the hypothesis of Chapin (1991). However, the gross N mineralization rates were higher in soils from all the study sites in the grazed areas, indicating that reindeer grazing leads to increased rates of nutrient cycling in both nutrient-poor and nutrient-rich tundra heaths. Because the organic matter decomposition rate was not affected by grazing in the subcontinental tundra heaths, the increased soil N concentrations and N mineralization rates were most probably due to fertilization by urine and faeces, which may enhance the N mineralization rates even though the quality of soil C is not improved by grazing.

Contrary to the hypothesis of Chapin (1991), herbivory by reindeer and small rodents retarded the microbial respiration rates and had a negative impact on soil N pools in both the unfertilized and fertilized areas in Joatka (IV). The amount of microbial C was also lower in the grazed areas than in the herbivore exclosures, indicating that herbivores limit the amount of energy available for the soil microbes. Furthermore, grazing had a negative impact on the amount of microbial N in the fertilized areas but not in the unfertilized ones. Thus, there was a surplus of N in the fertilized areas that could be immobilized into the microbial biomass only when access of herbivores was prevented, indicating that mammalian grazers affect the resource coupling between the plant and microbial trophic levels. The decrease in microbial respiration rates coincides with a decrease in the abundance of graminoids in relation to dwarf shrubs, due to grazing (Grellmann 2002). Graminoids – a favoured food resource for herbivores – gain the competitive advantage in relation to evergreen and deciduous dwarf shrubs because of their fast capacity for regrowth after the loss of biomass (Chapin *et al.* 1986). However, this is possible only when soil nutrient availability is high enough to permit compensatory growth (Oksanen 1990). However, although plant productivity and N concentrations in the plant tissues were considerably increased by fertilization, grazing caused a shift in the plant community structure to less decomposable species (cf. Coley *et al.* 1985, Bryant *et al.* 1991) in both the unfertilized and fertilized areas.

One of the reasons for the retardation of nutrient cycling in Joatka may be that grazing mainly occurred outside the growing season, i.e. during the seasonal migrations of reindeer; and by overwintering voles and lemmings (IV). Fertilization by urine and faeces therefore did not occur when the plants were taking up nutrients. Therefore, when mammalian waste products do not act as an underlying mechanism affecting soil nutrient cycling, herbivores seem to retard soil nutrient cycling even when soil nutrient availability is high. Another mechanism accounting for the retardation of soil nutrient cycling may be an output of N from the system, because reindeer used the area during migration (Grellmann 2001). The grazing pressure in the area was also comparatively low during the study period. The area is located at some distance from the main route of the reindeer, with only a few hundred reindeer passing through the area, and the highest rodent densities were also an order of magnitude lower than those documented during peak years (Turchin *et al.* 2000, Grellmann 2001). During vole population peaks, the direct effects of urine and faecal deposition may have a stronger impact than the negative,

indirect effects acting through herbivore-mediated changes in the plant species composition (Sirotnak & Huntly 2000).

In conclusion, the effect of grazing on soil nutrient cycling and organic matter decomposition rates was not related to the soil nutrient availability, and did not support the hypothesis that soil nutrient availability determines whether herbivores enhance or retard soil nutrient cycling (Chapin 1991). In contrast, the intensity and seasonal timing of herbivory, and the balance between nutrient input and output, seemed to play an important role.

3.3 The impact of high intensity grazing on tundra ecosystems

In Raisduoddar, a suboceanic site, and in Cearro, a continental site, grazing significantly enhanced the litter decomposition and the contents and concentrations of inorganic, microbial and soil total N (V). At the same time, a shift in the vegetation from domination of dwarf shrubs into graminoids had occurred, which was strongest in the heavily grazed area. Interestingly, grazing enhanced above-ground plant productivity in the suboceanic tundra heath and the below-ground productivity in the continental tundra heath. The dominance of graminoids in relation to dwarf shrubs as a result of grazing has a positive influence on soil nutrient cycling because it improves the decomposability of plant litter (Olofsson & Oksanen 2002). Fertilization by urine and faeces can be expected to strengthen this impact. However, a substantial difference in the soil temperature between the heavily and lightly grazed areas was observed. In Raisduoddar, the time length when the soil temperature was above +9 °C – considered to be a critical limit for soil microbial activity in tundra ecosystems (Nadelhoffer *et al.* 1991) - was almost two times longer in the heavily compared to the lightly grazed area. Therefore, three mechanisms, 1) a shift in the vegetation towards more decomposable plant species, 2) fertilization by urine and faeces, and 3) an increase in the soil temperature, all contributed to the positive impact of herbivory on the decomposition and mineralization processes, and the relative importance of each of these mechanisms is therefore difficult to evaluate.

Graminoids gain from heavy grazing because of both their high tolerance for disturbance (Chapin *et al.* 1986), and their strong capacity to exploit increased soil nutrient availability (McKendrick *et al.* 1980). Because the domination of graminoids further enhances the soil nutrient cycling, their establishment in the vegetation creates a feed-back effect in which the distribution of plant species are both cause and effect in soil nutrient cycling (Hobbie 1992, Olofsson *et al.* 2001). The impact of grazing on the soil nutrient cycling, plant productivity and the proportion of graminoids in the vegetation was significantly affected by the grazing intensity, supporting an assumption that grazing intensity is an important factor that determines the impact on soil nutrient cycling in tundra ecosystems (Olofsson *et al.* 2001, IV, V).

In the keystone herbivore –hypothesis, Zimov *et al.* (1995) proposed that the extinction of large mammals was the primary reason for a shift in the vegetation from steppe-like, productive grassland into low-productivity dwarf shrub tundra in the late Pleistocene, because the presence of large mammals improved the soil microclimate by

reducing the soil moisture through favouring graminoids in the vegetation. The results provide possible evidence for the hypothesis (V). In the natural population density of reindeer, which is limited by lichens during the winter, the grazing intensity would probably not be high enough to break the dominance of dwarf shrubs and cause a shift into graminoids (Olofsson 2001), but the domestication of reindeer and feeding during the winter have considerably increased the grazing pressure on the summer grazing areas (Olofsson 2001, Kumpula *et al.* 2002).

In Cearro, soil C pool had increased after the start of the heavy grazing during the 1960's (V), which is consistent with the observation that herbivores have a potential to increase the ecosystem pool of soil organic C (Molvar *et al.* 1993, Franzluebbers *et al.* 2000, Kryazhinskii & Danilov 2000). This may have implications for the C balance in the tundra ecosystems (Kryazhinskii & Danilov 2000). The production of decomposing material was increased due to the presence of large amounts of fine root biomass in the grazed area but, surprisingly, the microbial respiration rate in 2001 was lower in the heavily grazed than in the lightly grazed area. This is contradictory with the assumption that plant C in the grazed areas is more easily decomposable (Hobbie 1996, Olofsson & Oksanen 2002). When soil nutrient availability is increased, a parallel increase in the soil organic matter content and a decrease in microbial respiration are common phenomena that are caused by a decrease in the availability of soil C resulting from increasing formation of stabilized organic matter (Nohrstedt *et al.* 1989, Berg *et al.* 1995). It can therefore be hypothesised that the impact of herbivory on the fraction of organic matter that undergoes humification may be one of the mechanisms causing the accumulation of soil C.

3.4 Sources and implications for the spatial variation in the effects of grazing

The high spatial variation in the outcome of reindeer grazing can be explained by the relative balance between different underlying mechanisms, which can work at opposite directions. In the tundra ecosystems, there were three different outcomes of grazing (Table 1). In Joatka, the mechanisms that have negative impacts on the soil microbial processes were stronger than the positive ones: the shift in the plant community structure into less decomposable plant species outweighed the fertilizing effect of urine and faeces, resulting in the retardation of soil nutrient cycling (IV). In Jesnal and Nuorttitunturi, the fertilization effect of urine and faeces enhanced the soil N mineralization rates in the case where the decomposability of soil C was not affected by grazing (III). In Raisduoddar, Lagisduoddar and Cearro, a shift into more decomposable plant species had occurred due to grazing, and this had a positive influence on soil nutrient cycling rates (Olofsson *et al.* 2001, Olofsson & Oksanen 2002, III, V). Fertilization by urine and faeces only strengthened this impact. In Raisduoddar and Cearro, improved soil nutrient availability increased plant productivity (Olofsson *et al.* 2001). In Lagisduoddar, however, a continuously high grazing pressure suppressed the establishment of graminoids, plant productivity being limited by severe

grazing rather than by soil N availability. In contrast, microbial N increased five-fold as a result of grazing, which is in accordance with the view that, in arctic ecosystems, a decline in the sink strength of nutrients results in a considerable increase in microbial N immobilization (Jonasson *et al.* 1999). Thus, soil nutrient availability was improved by grazing, but was targeted to different components of the biota.

Table 1. Summary of the different outcomes of grazing on the rates of soil organic matter decomposition and soil N cycling in tundra and boreal ecosystems (original paper references denoted by Roman numerals).

Tundra Ecosystems	Study sites
Grazing causes a shift into less decomposable plant species. Fertilization by urine and faeces is not a strong enough factor to outweigh the reduced soil C quality, resulting in the retardation of soil N cycling.	Joatka (IV)
Grazing causes no shift in the decomposability of plant species. Fertilization by urine and faeces enhances soil N cycling even though soil C quality is not affected by grazing.	Jesnal (III) Nuorttitunturi (III)
Grazing causes a shift in the vegetation into more decomposable plant species, which improves soil C quality. Fertilization by urine and faeces strengthens the positive impact, resulting in strong enhancement of soil N cycling.	Raisduoddar (III, V) Lagisduoddar (III) Cearro (V)
Boreal Ecosystems	
Grazing reduces microbial respiration rates through a reduction in the quantity and quality of soil C. The rate of soil N cycling is either not affected or retarded by grazing.	Kevo, Naruska, Pallasjärvi Pikkulehto, Raja-Jooseppi I and II, Värriö, Angeli (II)
Grazing reduces microbial respiration rates through a reduction in the quantity and quality of soil C. Fertilization by urine and faeces is a strong enough factor to outweigh the reduced soil C quality, resulting in enhancement of soil N cycling.	Kätkäsuvanto (I, II) Kaamanen (II)

In contrast to tundra ecosystems, the microbial respiration rates were consistently retarded by grazing in all the studied forests, but there was spatial variation in the effects of grazing on N mineralization, the causes of which are most probably the same as in the tundra ecosystems (Table 1). The differences in the herbivore-driven impact on soil C cycling between the forest and tundra ecosystems indicates that the question of whether soil microbes are limited by C or by nutrients may regulate the impacts of herbivores on soil microbial level. In ecosystems where the soil C pool is small - as in oligotrophic boreal forests with a thin organic layer or in well-drained arctic-alpine tundra heaths - grazing seems to decrease the amount of energy available for the soil microbes. However, if considerable reservoirs are formed through organic matter accumulation, and the soil microbes are limited by nutrient rather than C availability (Jonasson *et al.* 1996), then it may act as a buffer against microbial C deficiency caused by the grazer-mediated decrease in plant biomass. The amount of available energy also regulates the strength of the microbial sink for nutrients (Michelsen *et al.* 1999). As C availability is not a limiting factor, the increased soil N concentration due to grazing often results in increased microbial N immobilization in arctic-alpine ecosystems (III, V), but not in boreal forests (I, II).

The heterogeneity in the impact of grazing on nutrient cycling may have important ecological implications. If grazing has sufficiently strong effects on soil microbial processes, and these effects are simultaneously highly site-specific then, by reinforcing the patterns of nutrient availability, grazing may increase spatial variation in the vegetation and plant productivity at the landscape level (McNaughton 1985). The site-specific variation in the effects of reindeer grazing underlines the need for large-scale, long-term studies on patterns in the interactions between herbivory and soil microbial processes. The challenge of this research would be to determine the conditions under which grazing enhances, slows down, or has no effect on nutrient cycling.

4 Conclusions

By influencing the vegetation of northern boreal forests and arctic-alpine tundra heaths in northernmost Fennoscandia, reindeer grazing indirectly affects nutrient mineralization and organic matter decomposition rates. There is high spatial variation in the direction of this impact. In oligotrophic and mesotrophic boreal forest soils, reindeer grazing reduces microbial respiration, which indicates that grazing decreases availability of labile C substrates for the soil microbes. Changes in the ground vegetation and a decrease in the root exudation of forest trees most probably account for this reduction. However, the N mineralization rate is simultaneously enhanced by grazing in some cases, most probably due to fertilization effect of urine and faeces that can be strong enough a factor to outweigh a reduction in quality of soil organic matter. In tundra ecosystems, reindeer grazing may either enhance or reduce microbial respiration, depending on the herbivore-driven shift in the vegetation or the relative limitation of C or nutrients for the soil microbes. Furthermore, there is spatial variation in whether grazing enhances or retards the soil N mineralization rates in tundra ecosystems.

In a tundra ecosystem, a low grazing intensity occurring outside the growing season had a retarding impact on nutrient cycling in both unfertilized, nutrient-poor and fertilized, nutrient-rich conditions. In contrast, relatively high grazing intensity enhanced the soil N mineralization rates in two nutrient-poor and two nutrient-rich tundra heaths. When three different grazing intensities were compared in an oceanic, nutrient-rich and one continental, nutrient-poor tundra heath, the strongest positive effect of grazing on soil nutrient cycling was observed in the heavily grazed areas. The data could provide some evidence for the keystone herbivore hypothesis, stating that large mammalian herbivores are able to cause a shift in the tundra vegetation that can maintain higher plant productivity and a more favourable soil microclimate for microbial activity and plant productivity. The data do not support the hypothesis that soil nutrient availability determines whether herbivores enhance or retard soil nutrient cycling. In contrast, through affecting the balance between different underlying mechanisms in the effects of grazing, the duration, intensity and seasonal timing of grazing seem to have an important role in determining whether grazing has a positive or a negative impact on soil nutrient cycling in each specific case.

5 References

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