

Louise Ilum Sørensen

GRAZING, DISTURBANCE AND
PLANT SOIL INTERACTIONS IN
NORTHERN GRASSLANDS

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LOUISE ILUM SØRENSEN

**GRAZING, DISTURBANCE AND
PLANT SOIL INTERACTIONS
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Abstract

Plants and soil organisms are closely linked. Plants are the sole source of carbon in the soil and soil organisms are responsible for recycling of nutrients, making them available for plant growth. To understand the function of a system, it is important to understand the interactions between the soil and plants. These interactions have mainly been studied in temperate areas, with few studies in the arctic and subarctic. The aim of this thesis was to investigate the effect of ecological disturbances in sub- and low-arctic grasslands on soil organisms and plant-soil feedback relationships. The effect of removal of vegetation, replanting of a local plant species, and different components of grazing (trampling, defoliation and return of nutrients) on soil decomposer organisms were studied. Whether short term effects of defoliation depended on plant species community was also studied, as well as whether defoliation in the field could create changes in the soil system systems that affect the growth of seedlings. Experiments were conducted under both controlled greenhouse conditions and in field sites.

The results showed that physical disturbance (removal of vegetation and trampling) reduced the abundance and diversity of soil biota. Defoliation increased soil decomposer abundance in the short term. Plant species composition did not affect soil biota and only in a few cases did it changes their responses to defoliation. In the long-term, effects of fertilization and defoliation on the soil biota were context-dependent. However, defoliation did create changes in the soil that reduced the growth of seedlings planted into the soil. Furthermore, plant species community and spatial heterogeneity (revealed by blocking) had important effects on the soil communities.

Keywords: aboveground-belowground interactions, defoliation, disturbances, fertilization, field experiments, grazing, greenhouse experiments, plant community structure, soil communities, spatial heterogeneity, sub-arctic grasslands, trampling

To my parents

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List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Sørensen LI, Kytöviita MM & Mikola J (2009) Persistence of soil fauna in low-arctic meadow after long-term vegetation removal and monoculturing. Manuscript
- II Sørensen LI, Mikola J, Kytöviita MM & Olofsson J (2009) Trampling and spatial heterogeneity explain decomposer abundances in a sub-arctic grassland subjected to simulated reindeer grazing. Manuscript.
- III Sørensen LI, Mikola J & Kytöviita MM (2008) Defoliation effects on plant and soil properties in an experimental low arctic grassland community – the role of plant community structure. *Soil Biology and Biochemistry* 40: 2596–2604.
- IV Sørensen LI, Kytöviita MM, Olofsson J & Mikola J (2008) Soil feedback on plant growth in a sub-arctic grassland as a result of repeated defoliation. *Soil Biology and Biochemistry* 40: 2891–2897.

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1 Introduction

Grasslands, like all terrestrial ecosystems, consist of two sub-systems: an aboveground system (plants) and a belowground system (plant-roots and soil organisms). The most important function of the aboveground system is fixing carbon using solar energy. The belowground system is fuelled by the carbon fixed in the aboveground system and is responsible for decomposition of organic matter and nutrient mineralization, thereby making the nutrients available for the aboveground system. These two sub-systems are strongly dependent upon each other, thus changes in one are likely to cause changes in the other. Therefore, when studying either plants or soil, it is important to take both sub-systems into account.

Grasslands are often disturbed. This disturbance can be anything from a natural disturbance such as herbivore activity that disturbs the plant-soil system by trampling and defoliation, to human-induced disturbances such as land use changes (intensive farming) and complete removal of vegetation (building of houses and roads). When investigating the effects of disturbances on grasslands, it is important not only to include the effects on both aboveground and belowground systems, but also the interactions between them.

1.1 The plant-soil interface

Plants have a controlling effect on soil biota abundance and activity: the activity and biomass of soil organisms are several magnitudes higher in the close vicinity of plant roots (the rhizosphere) than in bulk soil (Griffiths *et al.* 1992, Cheng *et al.* 1996, Hamilton & Frank 2001, Paterson *et al.* 2007, see also review by Griffiths 1994). This increase in soil biota biomass and activity is caused by the carbon in root exudations, secretions and sloughed-off cells, together called rhizodeposition (Paterson *et al.* 1997). Moreover, the activity and biomass of decomposers is higher in the litter-soil interface (detritusphere) than in bulk soil (Rønn *et al.* 1996, Kandeler *et al.* 1999), and plants can also affect soil organisms by changing physical (*e.g.* moisture, temperature, aggregate formation) and chemical (*e.g.* pH) properties of the soil (Ehrenfeld *et al.* 2005).

Plants, on the other hand benefit from the presence of soil biota, as these ultimately govern nutrient release from the dead organic matter entering the soil. Microbes are the primary decomposers breaking down organic matter and mineralizing nutrients. Soil fauna are – due to their microbial-feeding activity –

also playing an important role in the decomposition and mineralization processes; their ability to increase nutrient mobilization (Mikola & Setälä 1998, Bardgett & Chan 1999) and change the microbial community composition and biomass in the rhizosphere (Cole *et al.* 2004) are well known. The positive effects of soil fauna on plant production and nutrient uptake have been shown in several studies where plants have had a greater nutrient uptake and biomass production in the presence of soil fauna (Setälä & Huhta 1991, Bardgett & Chan 1999, Scheu *et al.* 1999). However, the relationship between plant and soil decomposer organisms is not always positive as plants and microbes also compete for nutrients.

The effects of soil decomposer organisms on plants are mostly of an indirect character, but other soil organisms are known to affect plants in a more direct way. Mycorrhizal fungi are known to affect plants in positive way, even though exceptions to this exists (Smith & Read 1997). Other soil organisms can be harmful to the plant, *e.g.* root pathogens, such as some species of fungi and nematodes. These organisms can remove carbon and nutrients from the plant tissue and thereby reduce the growth and survival of the plant (Bever *et al.* 1997). Negative effects of soil on plants have been ascribed to this (Bever 1994, Reinhart *et al.* 2005, Nijjer *et al.* 2007).

Thus several mechanisms exist whereby plant and soil affect one another and sometimes these can create actual feedback effects. Plant soil feedbacks consist of a minimum of two steps: 1) plants changes the soil system (biotic or abiotic) and 2) the changes in the soil can alter plant growth or plant species community. One such potential feedback could occur between the plant and soil decomposers, which are closely linked by a cycle of primary production and decomposition of organic matter. Changes in ex. plant production could create changes in the soil, which could further affect the plants; a feedback effect is thereby created.

1.2 Plant species and community control on soil

The activity, abundance and structure of soil microbial communities have been found to vary between plant species (Bardgett *et al.* 1999, Wardle *et al.* 1999, Van der Krift & Berendse 2001, Johnson *et al.* 2003, Wardle *et al.* 2003, Vale *et al.* 2005, Saj *et al.* 2007, Manning *et al.* 2008). Plant species vary in the amount of carbon they allocate to the soil as rhizodeposition (Van der Krift *et al.* 2001, Warembourg *et al.* 2003), and the difference in the activity and biomass of microbes in the rhizosphere of different plants has been ascribed to this variation

(Warembourg *et al.* 2003). Plant species differs further in quality and quantity of both root and aboveground litter they allocate to the soil, which can also have a controlling effect on soil biota (Wardle 2002). As the abundance and activity of microbes differs between plant species, it can be expected that plant species may also affect the fauna that feeds upon these microbes. This seems to be the case as several experiments have shown that soil fauna communities (abundance/composition) vary between plant species. This has been shown for nematodes (Wardle *et al.* 2003, De Deyn *et al.* 2004, Viketoft *et al.* 2005, Saj *et al.* 2007), and for larger animals, such as microarthropods and earthworms (Coulson *et al.* 2003, Milcu *et al.* 2006).

Thus it can also be expected that soil communities differ with plant species richness and among different plant species combinations. This idea was supported by De Deyn *et al.* (2004), who found in a semi-field experiment that plant species diversity affected the diversity of nematodes. However they also found that plant species composition was more important for nematode diversity than plant species diversity (De Deyn *et al.* 2004). Effects of plant community structure on soil fauna has further been found by Wardle *et al.* (2003), Milcu *et al.* (2006) and Viketoft *et al.* (2009).

Changes in the soil biota and activity due to increase in plant species diversity are likely to feed back to plant growth. This was shown in a recent two-phase experiment, where the soil collected beneath plant communities of different plant species diversity had different effects on the biomass production of new seedlings (Dybzinski *et al.* 2008). Seedlings grown in soil collected beneath plant communities containing 16 plant species produced 70% more biomass than seedlings grown in the soil collected beneath monocultures (Dybzinski *et al.* 2008).

The effects of plant species richness and composition on the stability of plant communities and ecosystem function are well studied, often higher plant diversity/richness increases the stability of the system, although this is not a universal pattern (see review by Ives & Carpenter 2007). For example, Tilman (1996) found that the variability in total aboveground biomass was lower when plant species diversity was high. Furthermore, the higher diversity increased the resistance of the aboveground biomass to drought (Tilman 1996). However diversity experiments such as the carried out by Tilman (1996) have been criticized due to problems with hidden treatments such as the increased probability of including a species with a positive or negative dominant effect when plant species richness is increased (see Huston 1997). The effect of plant

species richness and community composition on the stability of soil communities is less well studied. However, it has been found that the effect of disturbances – such as defoliation – on soil communities, may depend on plant species identity (Guitian & Bardgett 2000, Mikola *et al.* 2001a). Furthermore, a few studies have been published that indicate that the stability of soil microbial communities to disturbance, such as drought, depend on plant species composition, but not plant species richness (Wardle *et al.* 2000, Orwin & Wardle 2005).

1.3 Effects of grazing

Grazing by large mammalian herbivores can influence the structure and productivity of grassland communities (see review by Huntly 1991). Evidence from various grasslands also shows that grazing can affect the abundance, community structure and activity of soil biota. In temperate grasslands, grazing has been found to positively affect microbial activity and biomass (Bardgett *et al.* 1997, 2001), and nematode (Bardgett *et al.* 2001) and collembolan abundances (Dombos 2001), even though negative effects on collembolans are also found in temperate grasslands (Chappel *et al.* 1971, Petersen *et al.* 2004).

Return of nutrients, defoliation and trampling are the major components of grazing that can affect soil organisms. However, very few studies have contrasted these three components of grazing (Kohler *et al.* 2005). Return of nutrients in dung and urine increase nutrient availability for plants by short-cutting the litter decomposition pathway (Frank & Evans 1997, Van der Wal *et al.* 2004), but it can also influence the abundance and activity of decomposers (Griffiths *et al.* 1992). Defoliation (removal of foliar tissue) of plants is known to affect soil organisms by changing the quality and quantity of carbon that enters the soil (Paterson & Sim 2000, Sirotnak & Huntly 2000, Paterson *et al.* 2003, Hamilton *et al.* 2008). In the short term, defoliation can have a positive effect on decomposer organisms, by inducing a pulse of carbon from roots to soil (Hamilton & Frank 2001, Hamilton *et al.* 2008, Henry *et al.* 2008), but this peak of carbon exudation, and consequently the positive effect on microbial growth, seems to cease within a few days after defoliation (Hamilton & Frank 2001, Henry *et al.* 2008). In the long term, defoliation and grazing have been found to decrease the abundance and activity of soil decomposers in low productivity systems (Johnson & Matchett, 2001, Sankaran & Augustine 2004), due to defoliation eventually diminishing carbon supply to the soil (Johnson & Matchett, 2001, Sankaran & Augustine, 2004). There are few studies of the effects of trampling on soil decomposers, but

it seems that trampling can reduce the abundance and diversity of mites, collembolans and soil macrofauna (Wardle *et al.* 2001, Cole *et al.* 2008). These negative effects have been ascribed to soil compaction and reduction of pore space (Drewry *et al.* 2001), and to direct physical damage at least in the case of macrofauna (Wardle *et al.* 2001).

Grazing activity and trampling can further remove the vegetation thereby creating and expanding areas of bare soil, exposing the soil to erosion by rain and wind. As the vegetation is removed, the supply of litter to the soil decreases, which decreases the amount of soil organic matter and the physical stability of the soil (Six *et al.* 2004, Bardgett 2005).

1.4 Cold ecosystems and plant-soil interactions

In Arctic and subarctic systems, plants and microbes are considered to be limited by the availability of nutrients (Jonasson *et al.* 1999). The competition between soil decomposer microbes and plants should therefore be intense and microbes could have a negative impact on plant nutrient availability. Moreover, as soil fauna governs nutrient release and have been found to have a positive effect on plant nutrient uptake, the role of soil biota seems to be increasingly important when nutrient availability is low (Hasse *et al.* 2008). In these cold ecosystems, soil fauna such as enchytraeids, collembolans and nematodes become increasingly important because macrofauna, such as earthworms, are scarce or totally absent (Rusek 1998).

Reindeer (*Rangifer tarandus* L.) are important grazers in Northern Fennoscandia, and their activity is known to affect plant communities and primary production in these northern ecosystems (Olofsson *et al.* 2001). They have also been suggested to have large indirect effects on the ecosystems via changes in soil processes (Van der Wal *et al.* 2004). Studies of grazing effects on soil organisms in the arctic and subarctic areas are scattered, but it has been found that mammal grazing can have both positive (Stark *et al.* 2002) and negative effects on microbial biomass and activity (Stark & Grellmann 2002) and negative effects on nematode abundances (Virtanen *et al.* 2008) in these areas. Of the three effects of grazing animals on soil biota (fertilization, defoliation and trampling), the effects of fertilization have received most attention. Field studies in alpine tundra have shown that nutrient addition can increase mineralization and nitrification (Fisk & Schmidt 1996), and similar positive responses of nematode (Schmidt *et al.* 2000, Ruess *et al.* 2002) and collembolan (Sjursen *et al.* 2005)

abundances have been found in arctic areas. Fewer studies have investigated the effects of trampling and defoliation on soil biota in arctic and subarctic areas, but it has been found that defoliation can decrease microbial respiration (Stark & Kytöviita 2006).

It has been speculated that in cold ecosystems, it is the interaction of the three components of grazing that is responsible for the observed positive effect of grazing on soil microbes. This is because defoliation, trampling and fertilization can each reduce the thickness of the moss layer and increase soil temperature (Van der Wal *et al.* 2001, Olofsson *et al.* 2004), which in turn can increase the activity and biomass of soil microbes (Schmidt *et al.* 2002, Clemmensen *et al.* 2006), as well as the abundance of their nematode grazers (Ruess *et al.* 1999). Conversely, evidence exists of increased soil temperatures decreasing the abundance of collembolans in a subarctic field (Sjursen *et al.* 2005).

In cold areas, soil formation is slow due to low temperatures, so the effects of erosion are likely to be pronounced. Large areas in the European arctic show early or more advanced signs of erosion, and this soil degradation has been ascribed to reindeer grazing (Kashulina *et al.* 1997).

1.5 Aims of the study

Plants and soil decomposers are closely linked. To be able to predict the effect of disturbance on the functioning of the entire ecosystem, it is important to know not only how the organisms react to disturbance, but also how the disturbance affects the interactions between different organisms. Plant-soil interactions have been studied actively the last couple of decades (reviews by Bonkowski 2004, Wardle *et al.* 2004), but few studies are available from the arctic and sub-arctic regions.

This thesis aims to develop a better understanding of how disturbance in sub-arctic and low arctic grasslands affects soil decomposer organisms and plant-soil interactions. The disturbances used include complete removal of vegetation (I) and simulated grazing (consisting of defoliation, nutrient return and trampling) (II). Of the various mechanisms by which grazers can affect soil biota, I chose to investigate the effects of defoliation on soil organisms further as these involve purely indirect effects mediated by the plant and could therefore provide a good example when studying plant-soil interactions. The effect of defoliation on soil biota and plant biomass was further studied in the greenhouse in relation to plant species composition and richness (III). Lastly, the role of defoliation in the feedback to plant growth was studied in the greenhouse by following the growth

of different plant species combinations growing in soil collected from a field experiment involving defoliation (IV).

2 Material and Methods

2.1 The field sites, plants and soil

Two field experiments were set up in Northern Fennoscandia (I, II and part of IV). The disturbance/vegetation removal field experiment I was set up at Kilpisjärvi, Northern Finland in 1999 in two low arctic meadows. The meadows are situated in separate valleys on south-facing slopes of the Saana and Jehkas fjelds, approximately 2.5 km apart, and are both located approximately 600 m above sea level (a.s.l.) In both meadows, the vegetation is dominated by the grass *Deschampsia flexuosa*, and sedges and forbs such as *Solidago virgaurea*, *Trollius europaeus*, *Potentilla crantzii*, and *Bistorta vivipara*. A few species of dwarf shrubs, such as *Betula nana*, *Juniperus communis* and *Vaccinium myrtillus*, also occur in the sites. In these areas, the mean annual temperature is -2.6°C and precipitation 422 mm (1961–1985), measured at Kilpisjärvi meteorological station situated at 483 m a.s.l. (Järvinen & Partanen 2008).

The grazing experiment (II and part of IV) was established in 2002 on a north-facing slope of the valley Kärkevagge in Abisko, Northern Sweden (N $68^{\circ}25'$, E $18^{\circ}19'$). This site is situated 630–720 meters a.s.l. The mountain birch does not grow above 500 m a.s.l. at this site. The vegetation is dominated by graminoids such as *D. cespitosa*, *Carex bigelowii*, *Poa alpina* and *Festuca ovina* and forbs such as *P. crantzii*, *Saussurea alpina*, *Alchemilla glomerulans*, *T. europaeus* and *B. vivipara*. The ground layer is covered by an almost continuous layer of mosses *Pleurozium schreberi* and *Hylocomium splendens*.

The soil and the organisms for the greenhouse studies (III, IV) were collected at the two field sites. For study (III), the soil and the plant seeds were collected next to the Saana field site. Soil and seeds needed in study (IV) were collected from defoliated and non-defoliated treatment plots of the Abisko field experiment (II). The soil used in the greenhouse experiments (III, IV) was transported to the laboratory at Jyväskylä and Oulu Universities, sieved and gently mixed thereby allowing natural and diverse soil communities to persist. To establish plant communities, plant seeds were collected from the same meadow as the soil. To ensure seed germination the seeds were kept cold, before germinating in the greenhouse. The plants used for these experiments were typical of the grasslands where they were collected.

2.2 Experimental designs and treatments

An overview of the experimental treatments and target organisms are given in table 1.

The Kilpisjärvi field experiment (I) was set up in 1999 to examine the effects of vegetation removal on soil communities, and whether a plant monoculture could help the recovery of the soil system after such removal. The experiment consisted of plots of the natural plant community, plots where all vegetation was removed (no vegetation plots) and plots in which all vegetation was first removed and then replanted with *Solidago virgaurea* (monoculture plots). *S. virgaurea* is very common in these meadows and was chosen for the experiment because it was likely that it would survive being transplanted from the surrounding meadow – this proved to be the case – into the monoculture plots. To investigate the effect of the treatments on soil communities, soil samples were collected twice in 2005 (June and August). Using the pots with monocultures of *S. virgaurea* from (III) and pots with no plants from the greenhouse (from experiment III, data from no-plant plots are not published) the effect of *S. virgaurea* monocultures on soil nematodes, protozoa and microbes was also measured in the greenhouse (this is hereafter referred to as additional data).

Experiment (II) was set up to investigate the effects of different components of reindeer grazing on soil decomposer communities (microbes, nematodes, enchytraeids and collembolans). The experiment was composed of three different factors in a full factorial design: *i.e.* defoliation (no defoliation vs. defoliation), fertilization (no fertilization vs. fertilization using NPK-solution), and trampling (no trampling vs. trampling). With this design it was possible to investigate both the main effect of each treatment and the effects of their interactions, thereby giving a fuller picture of how reindeer grazing affects the soil decomposer system. Soil organisms were sampled in this study in June and August 2004.

Table 1. Overview of experimental designs and treatments.

	Experiment I	Experiment II	Experiment III	Experiment IV
Study site/soil collected at	Kilpisjärvi (Saana and Jehkas)	Abisko	Kilpisjärvi (Saana)	Abisko
Type of experiment	Field	Field	Greenhouse	Greenhouse*
Treatment	Vegetation removal Replanting with monoculture	Trampling Fertilization Defoliation	Defoliation Plant community	Defoliation- feedback Plant community
Plant communities	no vegetation plots monocultures of <i>Solidago virgaurea</i> Species rich meadow	Species rich sub-arctic meadow	One, two and four species combinations of: <i>Phleum alpinum</i> <i>Gnaphalium norvegicum</i> <i>S. virgaurea</i> <i>Potentilla crantzii</i> <i>Carex nigra</i>	One, two and four species combinations of: <i>Anthoxanthum odoratum</i> <i>Ranunculus acris</i> <i>Antennaria dioica</i> <i>G. norvegicum</i> <i>P. crantzii</i>
Target organisms	Microbes (PLFA) Nematodes Collembolans	Microbes (PLFA) Nematodes, Enchytraeids, Collembolans, Plant species abundance,	Plant shoot and root Microbes (PLFA) Nematodes Protozoa	Plant root and shoot Shoot N content Also measured (initial values of): N-mineralization, Organic matter quality, Microbes (PLFA), nematodes, plant species abundance

* soil taken from the defoliation and control treatments in experiment (II)

The greenhouse experiment III was designed to test if the effect of defoliation on plant growth and soil organisms (microbes, protozoa and nematodes) is dependent upon plant species richness and composition. The experiment was composed of three factors: defoliation, plant species richness and plant species composition. The defoliation treatment had two levels: plants not defoliated or defoliated twice (3 weeks and 3 days before sampling) to a height of 2 cm. Plant species richness contained three levels (1, 2 and 4 species), and nested within each of these richness levels, three different replicated plant species compositions were

established (chosen by random draw). The experiment was sampled after 23 weeks.

To test if the defoliation treatment in the field would create changes in the soil that could feed back to plant growth in the greenhouse, a two phase study (IV) was performed. The first phase consisted of the defoliation treatment in the Abisko field site (described above for experiment II). For phase two, a greenhouse experiment was established using soil collected from non-defoliated and defoliated field plots. Seedlings were planted in the two soils and the soil feedback was estimated using the difference in plant N uptake and biomass production between the soils after 21 weeks of plant growth. The set-up in the greenhouse further included variation in plant community structure to test if the response to the defoliation-induced feedback depends on plant species richness and composition (plant species richness and composition treatments were established in a similar way as in experiment III).

2.3 Plant and soil analysis

Plant variables measured included abundance of species of vascular plants and mosses in the field (II, IV), plant shoot and root biomass (III, IV) and shoot N content (IV). The abundance of vascular plants and mosses was estimated in the field plots by counting species presence/absence in 20 0.1x0.1 m quadrats (II, IV). In the greenhouse experiments, plant biomass was expressed as dry weight per pot (III, IV), whereas in the field it was expressed as dry weight per m² (IV). Shoots were sorted into species, while roots were washed clean of soil; these materials were then dried and weighed. Plant shoot N was analyzed (IV) using the dynamic flash combustion technique (CE Instruments EA 110 Elemental Analyzer, Wigan, UK).

Soil pH was measured in 1:2.5 (v/v) soil-water suspension (II). Soil organic matter content was measured using loss of ignition (I, II, IV). The soil organic matter quality was described (IV) using a sequential extraction technique, that fractionates the soil organic matter into four fractions *e.g.* non-polar extractives (*e.g.* fatty acids and lipids), water-soluble extractives (*e.g.* sugars and soluble phenols), the acid soluble fraction (*e.g.* cellulose and hemicellulose) and the acid insoluble fraction (*e.g.* cutin, surface waxes, tannins, lignin), according to Ryan *et al.* (1990). Net mineralization rate was measured *in situ* (IV) using undisturbed soil columns placed in PVC tubes (Raison *et al.* 1987). Microbial biomass and community structure was estimated using phospholipid fatty acid (PLFA) analysis

(I, II, III, IV; see detailed description of the method in these papers). Briefly, PLFA's were extracted from the soil, sorted into neutral lipids, glycolipids and phospholipids, and the phospholipids were identified and quantified. The abundance of protozoa (III) was estimated using most probable number method (Rønn *et al.* 1995). Nematodes (I, II, III, IV) and enchytraeids (II) were extracted using wet funnel devices (O'Connor 1962, Sohlenius 1979). Nematodes were counted live and later using preserved samples, identified into genera and allocated to feeding groups according to Yeates *et al.* (1993). Enchytraeids were counted and their length measured live, and the fresh biomass estimated following Abrahamsen (1973).

Collembolans (I, II) were extracted from intact soil cores using a modified high-gradient-extractor (Macfadyen 1961). The animals were then preserved in ethanol and later counted (I, II) and identified (I) according to Fjellberg (1980). Diversity of nematodes and collembolans was calculated using Shannon-Wiener diversity index (H') using the equation (I):

$$H = \sum_{i=1}^s p_i \ln p_i, \quad (1)$$

where p_i is the proportion of the i 'th group compared to the total abundance of all groups.

2.4 Data analysis

The treatment effects were statistically analyzed using analysis of variance (ANOVA and MANOVA) (I, II, III, IV) and t-tests (IV). In case of statistically significant treatment interactions, the main effects of the treatments were analyzed using simple effects (III) (Maxwell & Delaney 1990). To test the belowground effects of the treatments at the community level, principal component analysis (PCA) was performed followed by analyses of the PCA axes scores using ANOVA (I). All data were tested for homogeneity of variances using Levene's test and for normality using Kolmogorov-Smirnov test and model residuals. When necessary, the data were log-, ranked- or square root transformed. When these assumptions could not be met even after transformations, it is reported in the papers. To test the association between plant species composition (19 most common plant species used as predictor variables) and nematode genera composition (15 most common genera of bacterivorous, fungivorous and

omnivorous nematodes used as dependent variables) (II), predictive co-correspondence analysis (CO-CA; ter Braak & Schaffers 2004) was used.

To test if the relative difference in abundance of nematodes, protozoa and microbes between soil from pots with no plants and pots with *S. virgaurea* monoculture (calculated as: (Solidago – no-plant)/no-plant) differed from zero a “one sample t-test” was used (additional data).

The data were analyzed with either SPSS statistical package (version 13 and 16), or in the case of the co-correspondence analysis (II) with the cocorresp package of “R” (version 2.6.1) (Simpson 2008).

3 Results and Discussion

3.1 Vegetation removal and monoculture mitigation of the disturbance

Removal of vegetation in the field plots (I) reduced the amount of organic matter in the soil. Six years after the treatments were implemented, the soil organic matter content of plots with no vegetation was approximately 50% lower than that in the control plots. Such a large reduction is likely to result from the soil profile being mixed when the vegetation was removed. In addition organic soil could have been removed from the plots with the roots. Furthermore, as plants deposit organic matter in the soil as litter and rhizodeposition, the input of organic matter to the soil was also reduced in the plots without vegetation. Not surprisingly, the removal of the vegetation reduced the microbial biomass to 26%, and the abundance of nematodes and collembolans to 18% and 5% respectively of that of the intact meadow soil. Furthermore, the number of species of nematodes and collembolans were reduced to 73% and 46% respectively of that of the intact meadow soil. This is in agreement with a study by Wardle *et al.* (1999), who found that the removal of plants significantly decreased the abundance of soil microbes and animals feeding upon them. However the carbon storage in arctic soil is generally high (McKane *et al.* 1997, Callaghan *et al.* 2004), and even though the organic matter content was reduced, with more than 50% the amount of organic matter in the soil was still relatively high (total carbon content 4.6%). It is nevertheless likely that the carbon left in the soil after six years without inputs from live plants is very recalcitrant and therefore not a good source of carbon for microbes. The vegetation removal treatment severely disturbed the soil and the reduction found in abundance and diversity of collembolans correspond with a study by Maraun *et al.* (2003) where mechanical disturbance of soil, in the form of sieving, reduced the abundance of collembolans with up to 87%, and the number of species from 19 to eight.

Plants have been shown to increase the amount of carbon in the soil and the abundance of soil decomposer organisms (Johnson *et al.* 2003). It was therefore expected that the *S. virgaurea* monocultures would increase the abundance and diversity of the soil decomposer fauna and microbes compared to soil without vegetation. However, six years after establishing the *S. virgaurea* monoculture, characteristics of bacteria, nematodes and collembolans were not different

between removal and monoculture plots. Only the fungal biomass was higher in *S. virgaurea* plots than in plots without vegetation. The presence of an *S. virgaurea* monoculture did not increase soil organic matter content, so it seems likely that the increase in fungal biomass was caused by an increased rhizodeposition. This is further supported by studies which show that rhizodeposition or inputs of recently fixed carbon by plants control microbial activity in the soil (Johnson *et al.* 2003, Paterson *et al.* 2007). Furthermore, *S. virgaurea* increased the amount of arbuscular mycorrhizal (AM) hyphal in the soil and the abundance of root-feeding nematodes, though not statistically significantly. Root-feeding nematodes and AM fungi live in close association with plant roots. Thus it is not surprising that the presence of plants increased the abundance of these two groups of soil organisms.

The changes in biota abundance to the *S. virgaurea* monoculture in the field were also supported by a greenhouse study (additional data). After 23 weeks of plant growth in the greenhouse, abundance of fungi was higher in pots with monocultures of *S. virgaurea* than in pots with no plants ($t = 7.36$; $P = 0.002$; Fig. 1A). The abundance of predatory nematodes was in turn lower in the *S. virgaurea* monoculture pots ($t = 3.01$; $P = 0.039$; Fig. 1B), while other trophic groups of nematodes, numbers of protozoa and bacterial biomass did not differ between the two. As the greenhouse study only lasted 23 weeks the effects of the plant on the fungal biomass is most likely due to root deposition (*e.g.* root exudations, secretion and sloughed-off cells). Surprisingly, neither in the field (I) nor in the greenhouse (additional data) did the increase in fungal biomass in pots with *S. virgaurea* monoculture propagate higher up in the food web. This is in contrast to earlier greenhouse studies where it was shown that an increase in microbial biomass was followed by increase in abundance of microbial grazers (Mikola & Setälä 1998). However these results are similar to the results of Ruess *et al.* (2002), who found, using a field experiment, that the responses of nematode populations to fertilization and addition of carbon did not mirror the response of the microbial biomass.

3.2 Effects of plant species composition

Plant species richness has often been found to increase primary production, although this is not a universal pattern (Tilman *et al.* 2001, Cardinale *et al.* 2007). Furthermore, in those studies that have found an increase in production with increasing plant species richness, a clear increase in production has already occurred when moving from monocultures to four-species systems (Tilman *et al.*

2001, Mikola *et al.* 2002). It was therefore expected that the four-species systems in these studies would have had higher production than systems with less species. However, plant species richness did not have any effects on plant biomass production (III, IV). Aboveground production was instead found to be significantly affected by plant species composition (III, IV), which shows that in this experimental system plant species composition was more important than species richness in determining biomass production. This corresponds well with earlier studies, which have demonstrated that species composition is more important for plant production than is species richness (Tilman *et al.* 1997, Hooper 1998, Mikola *et al.* 2002).

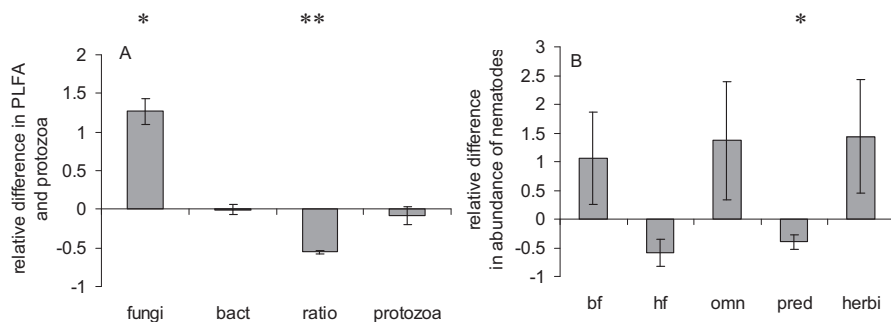


Fig. 1. Relative difference in abundances of soil biota between soil from pots with no plants and soil from pots with *Solidago virgaurea* from the greenhouse (additional data). A) difference in PLFA markers (fungi 18:2 ω 6; total bacterial PLFA marker, ratio of bacterial PLFA to 18:2 ω 6) and numbers of protozoa and B) nematode trophic groups (bf = bacteria feeders, hf = hyphael feeders, omn = omnivores, pred = predators, and herb=herbivores). * indicates significant results of t-test at the 0.05 and ** at the 0.001 level.

Microbial structure (Wardle *et al.* 1999) and abundance of nematodes (Griffiths *et al.* 1992, De Deyn *et al.* 2004) have been shown to depend on plant species composition. It was therefore expected that abundance of soil organisms would differ between different plant species compositions. Furthermore Wardle *et al.* (2003) suggested that the effect of plant species composition on soil communities could be explained by difference in plant production. However, even though plant species composition affected plant production, the effects of plant species composition and richness on belowground communities were limited (III). While

plant species richness affected the abundance of *Aporcelaimellus* nematodes, plant species composition did not affect the abundance of any of the soil organisms studied. However, plant species composition altered the response of fungal biomass to defoliation (III), which suggests that defoliation-induced changes in carbon allocation to the soil (either as root exudates or dead roots) depends on the plant species composition.

In the field (II), it was nevertheless found, using the co-correspondence analysis, that plant species community was a good predictor of the nematode community structure. This agrees well with the study by De Deyn *et al.* (2004), in which nematode community was found to be affected by plant species composition. However, the effects found in the field experiment were not comparable to the greenhouse experiment. The discrepancy in the effects of plant species composition on soil organisms between the greenhouse and field experiments may have several explanations. First, despite using two functional groups of plants (*i.e.* graminoids and herbs) in the greenhouse study (III), different species that affect soil organisms in similar ways may have been selected by chance. Second, as the greenhouse experiment lasted only 23 weeks, any effects of plants on the soil biota were most likely caused by rhizodeposition and dead roots, whereas in the field, the effects on nematodes can also originate from aboveground litter input (II). Third, as most of the variation in both the nematode and plant data was explained by blocking (and therefore spatial variability) in the field (II), the ability to predict nematode community structure using plant community structure could be explained by additional abiotic factors that simultaneously affect both communities.

3.3 Components of grazing affect soil decomposers differently

The activity of browsing reindeer in arctic and subarctic areas is known to affect plant community structure and productivity (Olofsson *et al.* 2002, Olofsson 2006). The results show that of the three components of grazing, only trampling affected the overall abundance of plant species (tested using MANOVA), whereas fertilization and defoliation did not have any overall effects on the plant species abundance (II). However, the abundance of specific plant species was affected by fertilization and defoliation (II, IV).

It was expected that fertilization would increase the abundance of soil biota due to increased nutrient availability (*cf.* Jonasson *et al.* 1999, Clemmensen *et al.* 2008), and that defoliation would decrease their abundance due to reduced inputs

of carbon to the soil (Paterson & Sim 2000, Sironak & Huntly 2000, Paterson *et al.* 2003). In support of this expectation, fertilization did increase bacteria and their nematode feeders. Nevertheless, as this was only the case for the trampled plots, and as defoliation did not have any overall (revealed by MANOVA) or main effects on the abundance of soil decomposer organisms (II, IV) these predictions were only partly supported. Trampling on the other hand had a consistent overall effect on the soil decomposers in the field (II): it reduced the biomass of fungi and enchytraeids, and the abundance of collembolans. Furthermore, the blocking term explained a high proportion of variation in the abundance of the soil decomposers except collembolans (II), meaning that the soil biota was more affected by the spatial heterogeneity than the treatments.

These results indicate that even though the effects of trampling were consistent, the effects of the other components of grazing (defoliation and fertilization) were context dependent (*i.e.*, affected by the other treatments and/or sampling time). The few consistent grazing effects on soil organisms in my study are in agreement with a study by Wardle *et al.* (2001), in which the effect of long term mammalian browsing on soil biota across 30 different locations did not have any consistent effects on the soil micro-food web. Furthermore, in that study, the activity of browsing mammals reduced the abundance of microarthropods and that effect was ascribed to trampling (Wardle *et al.* 2001).

Plant and microbial growth in the arctic and subarctic is considered to be nutrient limited (Jonasson *et al.* 1999). Furthermore, microbes in these systems are known to compete effectively with plants for nutrients (Clemmensen *et al.* 2008). It was therefore predicted that fertilization would increase the microbial biomass and the animals feeding upon it. Fertilization did indeed increase the microbial biomass and the bacterial feeding and omnivorous nematodes, but only in the trampled plots (II). Trampling further decreased the abundance of the moss *Pleurozium schreberi*, and as thinner moss layers have been suggested to lead to better microbial growth conditions *e.g.* increased temperature (Van der Wal & Brooker 2004; Olofsson *et al.* 2004), it seems likely that the soil decomposers could only benefit from the added nutrients when the moss layer had been reduced. The positive effect of fertilization in the fertilized plots could also be caused by the moss layer being less able to acquire the added nutrients. The idea that plants are effective competitors for nutrients in this grassland is suggested by another data set showing that fertilization increased plant biomass production (Olofsson 2009). This is in agreement with other studies from cold systems, where plants are able to take up added nutrients (Stark & Kytoviita 2006,

Eskelinen 2008). However, the fertilization treatment in my studies (II) cannot fully mimic the patchy return of nutrients in urine and dung or the return of labile carbon in dung. Simultaneous return of nutrients and carbon to soil can be important: Schmidt *et al.* (2000) found that nitrogen addition only had an effect on soil microbes if labile carbon was added at the same time. In the Abisko field study (II) this could have happened if defoliation caused an increase in root exudation at the same time as the fertilization was applied. This is partly supported, because the fungal biomass was increased by fertilization but only in those plots that had been defoliated. However this effect might also be a result of defoliation decreasing the ability of the plants to compete for the added nutrients (Bazot *et al.* 2004, Ilmarinen *et al.* 2008).

The most abundant genera of nematodes were not affected by any of the components of grazing (revealed by MANOVA). Instead, plant species community composition appeared to have a more important role in influencing the nematode community (II). Despite this result, and the fact that trampling had an overall effect on plant species abundance (according to MANOVA), the nematode community was not affected by any treatment. Furthermore, the spatial heterogeneity (block effect) did explain a high proportion of the variation in the abundances of nematode genera and many other functional groups of soil organisms at the Abisko field site (II). In addition, soil organic matter content and pH was found to vary between blocks in the Abisko field site (II). One block in particular seemed different from the others: the abundance of most soil decomposer organisms, as well as pH and soil organic matter content was lower in this block than in the others. It is likely that pH and the amount of soil organic matter had a controlling effect on soil biota, given that soil microbial biomass is known to correlate with the content of organic matter in the soil (*e.g.* Bardgett *et al.* 1997), and because pH is a strong controlling factor for the composition of the microbial community (Männistö *et al.* 2007). The soil carbon content is high and is released slowly in arctic and sub-arctic systems. Therefore plant-mediated effects of grazing could take a long time long to influence the abundance of soil organisms. This is supported by Stark *et al.* (2008), who showed that although 18 years of summer and winter reindeer grazing created visible differences between the grazing regimes in vegetation, no differences were found for soil organisms.

3.3.1 Effects of defoliation

The only constant effect of defoliation in these studies was a decrease in root biomass (III, IV). Defoliation reduced the root biomass both in the greenhouse (III) and the field (IV), although in the field this reduction was not statistically significant. In the greenhouse, this resulted in an increase in the ratio of total shoot mass production to root mass production, because shoot mass production was not affected by defoliation (III). These results show how defoliation changes allocation of resources within plants; more resources are allocated to shoot and less to root production (Guitian & Bardgett 2000).

Defoliation has been found to influence soil decomposers such as bacteria and fungi (Guitian & Bardgett 2000, Stark & Grellmann 2002) and their grazers (Hokka *et al.* 2004, Bazot *et al.* 2005, Mikola *et al.* 2005). In the short term, defoliation can increase microbial biomass and activity (Hamilton & Frank 2001, Henry *et al.* 2008), and this effect has been found to propagate to higher trophic levels of the decomposer food-web (Mikola *et al.* 2001b, 2005). It was found that although defoliation decreased fungal biomass, the abundances of fungal-feeding and predatory nematodes were increased by defoliation (III). This implies that defoliation increased fungal production at some point. Similar results were found by Mikola *et al.* (2001b), who suggested that this discrepancy between the response of microbial biomass and their grazers could be explained by a defoliation-induced impulse of resources in the soil, which creates a peak in microbial growth followed by a peak in microbial grazers and their predators.

In the field, it was found that defoliation did not have any overall (MANOVA) or main (ANOVA) effects on the abundance of soil organisms (II, IV). The observed effects of defoliation always depended on trampling, fertilization or sampling time (II). Differences in the results from the greenhouse and field could be caused by differences in temperature and humidity between the field and the greenhouse. Furthermore, the difference in the length of the greenhouse and field experiments could explain the inconsistency of defoliation effects on soil biota. The greenhouse experiment can be considered a short-term experiment, as it was sampled three weeks and three days after defoliation, while in the field defoliation was started in 2001, and the organisms sampled in 2004. In the field, the short-term effects should have disappeared as the positive effects of defoliation on microbial biomass cease within a few days after defoliation (Hamilton & Frank 2001, Henry *et al.* 2008). In the long term, defoliation should decrease the carbon input to the soil and thus have a negative effect on soil decomposers (Sankaran &

Augustine 2004). This idea is supported by the finding that although defoliation did not have any effect on the microbial biomass and abundance of soil fauna (II, IV), it reduced mineralization rate in the field (IV). These results indicate that the soil community investigated with the level of precision that was used here may not serve as a good predictor of net mineralization rate at this field site.

A novel finding of this study was that although defoliation in the field did not affect the abundance of soil decomposers (II, IV), it created changes in the soil that reduced the growth and nitrogen accumulation of seedlings planted into the soil (IV). Defoliation in the field decreased the nitrogen mineralization rate, and the negative effect of defoliation on plant growth in the greenhouse is probably a consequence of this reduction. This fits well with the idea that availability of nitrogen and plant nitrogen uptake is largely determined by the mineralization rate (Pastor *et al.* 1984, Nadelhoffer *et al.* 1985). Bardgett & Wardle (2003) defined three ways whereby herbivores can affect soil processes in ways that create feedback to plants: 1) changes in quantity of resources, 2) changes in resource quality, and 3) changes in the functional composition of the vegetation. The same mechanisms could be responsible for defoliation-induced feedback effects seen in this study. However, in this, defoliation did not have an effect on soil organic matter content (resource quantity) or the soil organic matter quality (resource quality). Furthermore, defoliation decreased the abundance of tall herbs and shrubs (functional composition of the vegetation), and shrubs are known to produce litter that decomposes slowly (Olofsson & Oksanen 2002). The root biomass was reduced in defoliated plots and defoliation did reduce the nitrogen mineralization rate; this could explain the negative feedback effect on seedling growth.

These results demonstrate that defoliation can create long-term changes in the soil that may have a negative effect on the establishment of new plants. However, in natural systems grazing might increase seedling establishment due to competitive release or by creating suitable gaps for establishment of seedlings (Eskelinen & Virtanen 2005).

3.4 Defoliation effects within different plant species compositions

In the greenhouse study, defoliation reduced the root biomass of all plant combinations, except for the *G. norvegicum* monoculture (III). A decrease in root biomass after defoliation is a consequence of reallocation of resources to the regrowth of photosynthetic tissue (Donaghy & Fulkerson 1998), and differences in root response between plant species have been ascribed to differences in adaption to defoliation so that root growth reduction would be a sign of a defoliation-tolerant species (Guitian & Bardgett 2000). This (III) would indicate that *G. norvegicum* is not tolerant to defoliation. This is further supported by the finding that defoliation decreased *G. norvegicum* abundance in the field (IV).

A few studies have reported that the response of soil microbial communities to disturbance depend on plant species composition (Wardle *et al.* 2000, Orwin & Wardle 2005). This is supported by the finding of study (III) since plant species composition determined how some soil organisms responded to defoliation in the greenhouse. However, since only the response of decomposer fungi to defoliation depended on plant species composition, the effect of plant species composition can be considered to be weak. Guitian & Bardgett (2000) the grass *Anthoxanthum odoratum*, which is considered intolerant to grazing, showed no response to defoliation in its root mass to defoliation, However, the microbial biomass and activity under *A. odoratum* had a greater response to defoliation than did grass species considered to be tolerant (Guitian & Bardgett 2000). In study (III) defoliation reduced the root biomass of all plant species compositions except that of *G. norvegicum* monoculture, however, the response of soil biota to defoliation in the pots of *G. norvegicum* monocultures did not differ from that under other plant species combinations (III).

4 Conclusion

These studies increase our knowledge of the mechanisms by which large mammalian herbivores affect soil biota in tundra ecosystems. Earlier studies of ungulate herbivore effects on grassland ecosystems have mainly focused on nutrient return and defoliation processes. However, at the field site of this study, trampling, and not fertilization and defoliation, was found to be the most likely mechanism through which reindeer grazing affected the soil community. Even though the abundance of soil decomposer organisms was not affected by the defoliation treatments in the field, defoliation did affect the nitrogen mineralization rate and altered the soil in a way that negatively affected plant growth (*i.e.*, a negative feedback). This shows that defoliation in the field could create changes in the soil that may have negative effects on seedling establishment. Blocking often explained most of the variation in abundance of soil organisms, indicating that the soil biota is influenced by abiotic parameters such as soil organic matter content and pH, and that even the effect of trampling might be outweighed by spatial heterogeneity of these abiotic factors.

In the short term, in the greenhouse, defoliation was found to have a large impact on soil organisms, indicative of strong aboveground-belowground interactions. Plant species composition and richness was found to have surprisingly few short term effects on the soil biota, and only in few cases did plant species composition affect the response of soil organisms to defoliation. Probably all plant species used in the greenhouse experiments were well adapted to grazing (defoliation). These results suggest that plant species composition may not be very important in determining the effects of defoliation on soil biota.

In the longer term, plant species abundance did affect soil communities, indicating that long term litter inputs could affect soil decomposer communities. However, since a large part of variation of abundance of both plants and soil organisms were explained by blocking effects, it is likely that both plant and soil communities were in part controlled by spatial variability in abiotic factors.

Arctic and sub-arctic grasslands have short growing seasons and low primary production. Soil carbon storage in these grasslands is often high. The results of these studies suggest that the high amount of soil organic matter in these grasslands is probably an important control of the soil biota. In these systems, it takes a long time before changes in plant community structure are reflected in the structure of belowground communities. However, radical disturbances including loss of soil organic matter can create significant effects on soil biota, and

replanting such sites using a plant monoculture is unable to reverse the effects, suggesting that recovery of the soil community is also slow.

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- IV Sørensen LI, Kytöviita MM, Olofsson J & Mikola J (2008) Soil feedback on plant growth in a sub-arctic grassland as a result of repeated defoliation. *Soil Biology and Biochemistry* 40: 2891–2897.

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