Applied Soil Ecology 76 (2014) 14–25

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Response to reindeer grazing removal depends on soil characteristics in low Arctic meadows

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ARTICLE INFO

Article history:
Received 11 July 2013
Received in revised form 4 December 2013
Accepted 5 December 2013

Keywords:
Deschampsia flexuosa
PLFA
Soil fauna
Below-ground above-ground
Community
Soil enzymatic activity

ABSTRACT

In Arctic tundra, grazing is expected to exert a positive influence on microbial activity thus enhancing nutrient cycling and promoting the presence of high productive graminoids. We investigated the changes occurring in two low Arctic meadow sites after 10 years exclusion from grazing. We compared plant, soil fauna and microbial community composition, extracellular enzymes activities, and soil nutrients in ungrazed and adjacent grazed area in two low Arctic meadows. The two closely located experimental sites were both dominated by the common grass *Deschampsia flexuosa* which covered more than 50% of the meadows. Plant community was affected significantly by site and grazing, but the effect of grazing was stronger in the site that was more nutrient rich. Grazing decreased litter abundance in both sites, but did not influence the amount of total plant biomass. Grazing had a negative effect on some species of Collembola (e.g. *Isotomiella minor*) and Enchytraeidae were reduced by 40% by grazing. Also the site itself contributed in shaping the microarthropod community. Microbial community structure was not affected by grazing. In the nutrient rich site grazing also significantly decreased some extracellular enzyme activities. Our results showed that grazing had a strong effect on plant and microarthropod community structure, but the effects were very dependent on local characteristics.

1. Introduction

One of the tasks of ecological studies is to investigate how climate, biotic factors, among those grazing, and abiotic factors, such as topography interact in determining plant and soil community assembly rules and processes. It has been suggested that in the Arctic biotic disturbance exerted by reindeer grazing is a strong determinant of the vegetation structure (Olofsson et al., 2004; van der Wal, 2006). In the whole of northern Fennoscandia reindeer herding is one the most important economic and cultural activities. The number of animals has been rising steadily from the middle of the past century thanks to the supplement of extra forage in the winter and modern veterinary practice, reaching densities that are far above the natural carrying capacity of the pasture (Kojola and Helle, 1993; Suominen and Olofsson, 2000). The disruption of the natural migratory routes between summer pastures, located in Norway by the coast, and winter pasture situated in Finland (Aarseth, 1989) increased even more the pressure exerted by large herds of reindeer continuously present on the territory (Kojola and Helle, 1993). van der Wal (2006) suggested that the presence of a large number of animals does not necessarily translate in detrimental effects into the ecosystem. Instead, grazing can promote a positive loop where the ecosystem is pushed toward stages of increasing productivity, transforming a moss dominated tundra into a graminoid dominated steppe. In the framework proposed by van der Wal (2006) Arctic tundra occurs in three different vegetation stages (lichen, mosses and grasses dominated) and herbivores are the main drivers of the transition among these three stages, where a higher grazing density corresponds to the more productive grass and sedges dominated stage. The work by Zimov et al. (1995) on the steppe-tundra transition between Pleistocene and Holocene supports this framework showing that herbivores already in the past have been capable of promoting such a large stage transition at the ecosystem level.

Grazing modulates ecosystem properties by several mechanisms. Firstly, it has a direct effect on plants by removing foliage, which has cascading effects on root dynamics and production of exudates (Bardgett et al., 1998; Morneau and Payette, 2000), and plant resource allocation patterns (Strauss and Agrawal, 1999). Grazing can increase or decrease the production of phenolic secondary compounds (Bryant et al., 1983), resulting in altered quantity and quality of the litter input to the soil. Furthermore, grazing by large ungulates exerts mechanical disturbance to the soil due to trampling, which can have detrimental effects on roots

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http://dx.doi.org/10.1016/j.apsoil.2013.12.003

(Alessa and Earnhart, 2000) and soil fauna (Sørensen et al., 2009). Grazing may affect microbial decomposer community directly and indirectly through its action on plant and soil. Bacteria can respond positively to the increased root exudation following a grazing event (Bardgett et al., 1998; Hamilton and Frank, 2001). However, in low productivity systems, defoliation exerts the opposite effect in the long term and decreases the activity and abundance of soil decomposers (Holt, 1997; Johnson and Matchett, 2001; Sankaran and Augustine, 2004). Soil fertility increase promoted by grazing can also affect directly the bacterial community structure, and high N availability may select for copiotrophic bacterial groups over oligotrophic ones (Ramirez et al., 2010). The reduction in the moss layer due to trampling can lead to higher soil temperatures in the summer, which can positively affect microbial activity (van der Wal and Brooker, 2004; Sørensen et al., 2009). However, the effects of grazing on nutrient cycling and microbial activity and biomass in Arctic are quite controversial: positive and negative responses are observed (negative: Stark and Grellmann, 2002; Bråthen et al., 2007; Stark et al., 2012; positive: Stark et al., 2002; Olofsson and Oksanen, 2002; Olofsson et al., 2004). Whether grazers have a negative or a positive effect on ecosystem processes is often dependent on ecosystem productivity and soil nutrient level, which direct the effect of herbivory on litter decomposability through vegetation changes (Wardle et al., 2004). According to this view, grazing in nutrient-rich environments generally promotes abundance of rapidly decomposable plant species, high rates of soil nutrient cycling and higher abundance of soil bacteria, while grazing in nutrient-poor environments indirectly promotes abundance of slowly decomposable plant species, slow rates of soil nutrient cycling and higher abundance of soil fungi. Grazing in nutrient rich systems can in fact retard the vegetation succession resulting in plant community characterized by plant species producing easily decomposable litter, which in turn enhances and promotes nutrient cycling, establishing a positive loop between grazing, plant and soil (Bardgett, 2005).

Soil disturbance and dung deposition by herbivores can increase small scale spatial variation (Adler et al., 2001; Frank et al., 2003). However, the question that remains open is the importance of grazing relative to landscape factors in determining plant and microbial communities where small scale spatial heterogeneity may outweigh the importance of grazing (Sørensen et al., 2009). Spatial heterogeneity in resources is widely accepted to shape species coexistence and the maintenance of community diversity and productivity (Ettema and Wardle, 2002). Spatial variation at the local scale results in a mosaic of vegetation, and generally it is believed that heterotrophic communities follow the same pattern, although this may not always be the case (Ettema and Wardle, 2002).

We investigated how two low Arctic meadows responded to 10 years of reindeer grazing exclusion. We compared plant, soil fauna and microbial community composition, activities of extracellular enzymes, and soil nutrient concentrations in the grazed and ungrazed areas in both meadows.

Based on the theories by Wardle et al. (2004) and van der Wal (2006), we predicted that (i) grazer exclusion should reduce soil nutrient availability, abundance of soil bacteria and soil microbial activity and change plant and soil community composition; (ii) grazer exclusion should have consistent effects in sites with the same vegetation type, independently from the scale of investigation.

2. Material and methods

2.1. Study area and sampling design

The study was carried out in two Arctic meadow sites located in the Kilpisjärvi area, Northern Scandinavia. The soil in the Kilpisjärvi area is classified as a Leptosol (Jones et al., 2010). The meadows are situated around 600 masl. in Saana fell (69°03′N, 20°50′E) and Jehkas fell (69°05′N, 20°47′E) and both are exposed to the south. The meadows are characterized by the predominance of the grass *Deschampsia flexuosa*, but other graminoids such as *Deschampsia cespitosa*, *Carex* sp., *Festuca ovina*, herbs such as *Solidago virgaurea*, *Potentilla crantzii*, *Bistorta vivipara, Trollius europaeus*, small woody plants (*Betula nana, Empetrum nigrum, Vaccinium* spp.) and mosses are common. *D. flexuosa* and *S. virgaurea* are among the preferred forage plants by reindeer (Bråthen and Oksanen, 2001; Gaare and Skogland, 1975). The length of the growing season is *c.* 90 days, and the mean annual temperature and precipitation measured at Kilpisjärvi meteorological station, which is situated at 483 masl., are −1.9 °C (1979–2009) and 489 mm year^{-1} (1979–2009), respectively (data from Finnish Meteorological Institute). The average soil temperature between years 2000 and 2007 at 3–5 cm depth during the warmest months, July and August was +10.5 °C (Kytöviita, unpublished data).

Both sites (Saana and Jehkas) are part of the reindeer grazing area and grazing history can be dated back for at least two centuries. The official estimate of the number of reindeer during 2008–2009 is 4.2 individuals (adults and calves) per km^2 in the study district (Unknown, 2010). In both study sites, two exclosures prevented a portion (about 10 × 30 m) of the meadow from reindeer grazing since 10 years at the time of sampling. We had a specific spatial structure in our sampling scheme spanning three levels (Fig. 1): the site, the block within site and the samples within blocks. Variation between sites accounted for spatial variation on the large scale (>10 m). Variation among blocks accounted for spatial variation at the medium scale (between 5 and 10 m). Variation among samples accounted for spatial variation at the smallest scale (between 1 and 5 m). This design was chosen because a previous study on the same system showed that effects by reindeer grazing were outweighed by spatial heterogeneity at the block level (Sørensen et al., 2009). The sites were at 3 km distance from each other. In both sites, the meadow was divided in three adjacent blocks so that each block (about 10 × 10 m) included the area inside and outside the exclosure. For soil analyses for each block, eight samples were taken (four inside and four outside the fence), so that for each site there were 24 samples, 12 inside the exclosure and 12 outside the exclosure (Fig. 1). For vegetation analyses, for each block, plant coverage % was recorded 10 times (five times inside and five times outside the fence), so that for each site we recorded it 30 times (Fig. 1). For the plant biomass 16 samples were collected in each site: eight in the grazed area and eight in the ungrazed area (Fig. 1). Within block, the samples were taken randomly. No samples were collected near the fence to avoid margin effect. Replicate samples were collected at least 1 m distance from each other. In the study three components of the ecosystem were analysed: vegetation (plant biomass and coverage), soil parameters (organic matter content, pH, nutrients and enzymatic activity), and soil fauna (specifically microarthropods, Enchytraeidae and Nematoda). The plant community observations were conducted in both grazing treatments and sites in August 2010. The soil samples were collected from both grazing treatments and sites on July the 15th 2009. Vegetation sample corresponded to plant coverage estimation in 50 × 50 cm frames and plant biomass in 25 × 25 cm plots (details below). Each soil sample consisted of six soil cores (6 cm length, 3 cm diameter) taken within 1 m distance from each other and pooled. The soil samples were sieved through a 4 mm sieve. Part of the soil was immediately frozen at −20° C and used for phospholipids fatty acids (PLFAs), soil nutrient content and pH measurements; part of it was stored at +4° C and used for enzymatic activity measurements. At the same time, separate soil samples for fauna extraction were collected (details below).