Influences of Reindeer Grazing on Above- and Below-Ground Biomass and Soil Carbon Dynamics

Authors: Köster, Kajar, Berninger, Frank, Köster, Egle, and Pumpanen, Jukka

Influences of reindeer grazing on above- and below-ground biomass and soil carbon dynamics

Kajar Köster[1,2,3]

Frank Berninger[1]

Egle Köster[1] and

Jukka Pumpanen[1]

[1]Department of Forest Sciences, P.O. Box 27, FI-00014 University of Helsinki, Finland
[2]Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 1, EE-51014 Tartu, Estonia
[3]Corresponding author: Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, Kreutzwaldi 5, EE-51014 Tartu, Estonia, kajar.koster@emu.ee

Abstract

Reindeer (*Rangifer tarandus* L.) are the most important large mammalian herbivores in Lapland, strongly affecting the dynamics of vegetation by grazing and trampling, and this is likely in turn to have consequences for the soil processes. We have investigated the changes occurring in above- and belowground biomasses, and soil C dynamics (CO_2 efflux, soil C content, soil microbial biomass) among areas grazed and not grazed by reindeer. Our study areas are located in the northern boreal subarctic coniferous forest (undisturbed Scots pine [*Pinus sylvestris* L.] forests that are naturally lichen-dominated). Our study showed that grazing by reindeer decreased the biomass and cover of lichens in the area significantly. Also the tree regeneration was affected by grazing, as we had much less tree regeneration in the grazed areas. In subarctic mature pine forest, grazing did not affect the soil temperature or the soil moisture. We found no statistically significant effect of grazing on the soil CO_2 efflux, soil C stock, and the soil microbial C biomass. Soil microbial N biomass was significantly lower in the grazed areas compared to the non-grazed areas. Our results indicate that in the northern boreal subarctic coniferous forests, grazing by reindeer can be considered as "C neutral."

Introduction

Reindeer (*Rangifer tarandus* L.) herding is one of the oldest land use forms in northern boreal zone, and in northern Finland it is based on the use of natural pastures. The number of reindeer in northern Finland has changed over the last century and reached its peak at the beginning of the 1990s (Suominen and Olofsson, 2000; Väre et al., 1996). Today, there are around 1.5 animals per square km in Finland (Susiluoto et al., 2008; Jaakkola et al., 2013), and they graze freely all or most of the year (Kivinen and Kumpula, 2014). Thus, reindeer are the most important large mammalian herbivores in Lapland (Oksanen et al., 1995) that can strongly influence the plant diversity (Väre et al., 1996, 1995). At the same time, changes caused by reindeer in vegetation have indirect effects on physical features of the soil, for example, soil microclimate, root biomass, and also on soil C dynamics (Suominen and Olofsson, 2000; Väisänen et al., 2014; Väre et al., 1996) and soil organic matter (SOM) decomposition (Stark et al., 2010). Arctic and boreal ecosystems cover around 40% of the Earth surface, thus they are a crucial part of the climate system and C cycle, containing about 60% of the C bound in global forest biomes (Tarnocai et al., 2009). Climate warming in Arctic may lead to enhanced decomposition processes in soil, and this, in combination with long-term grazing that may affect a number of ecosystem properties, can lead to accelerated CO_2 release from the soils (Väisänen et al., 2014).

The role of reindeer grazing in ground vegetation dynamics and in soil carbon (C) dynamics has been earlier investigated mostly in tundra heaths (Olofsson, 2006; Olofsson et al., 2004; Stark et al., 2002; van der Wal, 2006). Only a few studies concerning the influence of reindeer grazing on boreal subarctic coniferous forests can be found (Olofsson et al., 2010; Stark et al., 2010, 2003, 2000). Reindeer grazing may have multiple effects on the stand vegetation and regeneration dynamics—they trample vegetation (Suominen and Olofsson, 2000; Väre et al., 1996) and graze plants selectively (Hobbie, 1992; Stark et al., 2002). In his previous study, van der Wal (2006) pointed out that vegetation diversity and composition in

tundra is strongly dependent on the reindeer density, and thus also from grazing pressure—areas with low reindeer density are lichen dominated, whereas areas with higher reindeer density are moss or grass dominated. Thus, reindeer grazing has a strong reducing effect on the biomass of lichens (Akujärvi et al., 2014; Köster et al., 2013; Olofsson et al., 2009, 2010; Stark et al., 2000; Suominen and Olofsson, 2000; Susiluoto et al., 2008). At the same time, the biomass of *Vaccinium* sp. dwarf shrubs and mosses may be unaffected by grazing (Stark et al., 2000), or even benefit from grazing (Susiluoto et al., 2008; Van der Wal, 2006), although they are also important forage plants for reindeer. The effect of reindeer grazing on tree regeneration has been found to be negative, meaning there is less regeneration in grazed areas (Köster et al., 2013; Oksanen et al., 1995; Suominen and Olofsson, 2000). The subarctic mature and old Scots pine (*Pinus sylvestris* L.) forests (over 80 years old) are highly preferred by reindeer (Kumpula et al., 2007), especially during the winter because of the higher availability of their main food source, lichens, on these areas (Kivinen and Kumpula, 2014; Kumpula et al., 2013). The lower amount of tree regeneration in grazed areas is also affecting negatively the amount of tree root biomass and microbial activity in the soil (Väre et al., 1996).

The effect of reindeer grazing on soil moisture and temperature regimes in the lichen-dominated Arctic ecosystems has been found to be considerable (Fauria et al., 2008; Olofsson et al., 2010; Suominen and Olofsson, 2000; Väre et al., 1996). Removing the lichen carpet and damaging the secondary vegetation mat (pryophyte and vascular plants) make patches of bare soil become common (Suominen and Olofsson, 2000; Väre et al., 1996), and these factors in combination with trampling alow for soil to warm up faster, reach higher temperatures, and the soil moisture content to be reduced (Väre et al., 1996). All this may affect the CO_2 efflux from the soil because temperature and moisture are important factors regulating the microbial processes in soil (Karhu et al., 2014). Thus, large herbivores could strongly influence decomposition, nutrient mineralization, and C dynamics in northern ecosystems (Cahoon et al., 2012; Hobbie et al., 2002; Olofsson et al., 2009).

Earlier studies have mostly reported a decrease in soil microbial biomass in areas grazed by reindeer (Stark et al., 2003, 2000; Väre et al., 1996). Only, Stark et al. (2008) reported no differences in the microbial biomass between grazed and non-grazed areas. The effect of grazing on microbial N biomass has also been found to be variable (Stark et al., 2010, 2003). It is generally accepted that microbial biomass and activity are positively related to SOM content, which may be an early and sensitive indicator to distinguish changes in soil, caused by management or disturbances (Li et al., 2004). Controversial results have been achieved from comparing the SOM decomposition rates and soil CO_2 efflux values between grazed and non-grazed areas. It has been stated, that reindeer grazing results in higher SOM decomposition (Olofsson et al., 2004), which should lead to higher CO_2 effluxes in grazed areas. But there are also studies that have shown lower soil CO_2 effluxes and litter decomposition in grazed areas (Ohtonen and Väre, 1998; Stark et al., 2003), or found no differences between the grazed and non-grazed areas (Stark et al., 2002).

The objectives of this study were to investigate the effects of reindeer grazing in the northern boreal forests on (1) ground vegetation biomass in general, (2) ground vegetation structure and species composition, and (3) tree regeneration. We also wanted to examine if and how reindeer grazing is affecting the soil C dynamics (CO_2 efflux from the soil, C storage in soil, microbial biomass in the soil), and whether there are changes in soil temperature between the grazed and non-grazed areas, which could affect the SOM decomposition and belowground C stocks.

We expected that reindeer grazing reduces the ground vegetation coverage and biomass, and also the number of tree regeneration. We predicted that due to the reduction of ground vegetation coverage, the soil temperatures would be higher in the grazed areas. We also hypothesized that soil CO_2 efflux and microbial biomass will be higher in the non-grazed areas due to higher above- and belowground biomasses in these areas, and due to the fact that the soil in non-grazed areas is not compressed by trampling.

Materials and Methods

STUDY SITES

The measurements were conducted in the northern boreal subarctic coniferous forests, in Värriö Strict Nature Reserve (67°46′N, 29°35′E), in Finnish Lapland. The sites are situated north of the Arctic Circle, near to the northern timberline, at an average of 300 m altitude. The main tree species in the area is Scots pine, and the ground vegetation consists of *Vaccinium myrtillus, Vaccinium*

vitis-ideae, Empetrum nigrum, and *Cladina* sp. The study area is located at the zone of the last intact forest landscapes in Fennoscandia (Potapov et al., 2008), where large areas of relatively undisturbed subarctic Scots pine forests can still be found (Kivinen and Kumpula, 2014). The climate in the area is subcontinental. The soil has no underlying permafrost: the snow covers the ground for 200–225 days per year, and the length of the growing season is 105–120 days. The average temperature during the growing season (from June to August) is around 12 °C. Long-term mean annual precipitation in the area is 592 mm, average annual air temperature is –1 °C (Susiluoto et al., 2008; Köster et al., 2014), and average soil temperature (measured in organic layer of the soil) is 3 °C (Köster et al., 2014). The soil in the area is classified as haplic podsol (FAO, 1990) with sand tills, where the bulk of the mineral soil is composed of sand, with average pH of 4.4 (Köster et al., 2014).

In order to observe the effects of reindeer grazing on the vegetation structure, soil C content, and soil CO_2 fluxes, we selected the sites to be used in the experiment from pristine forest areas from the Värriö strict nature reserve. Such pristine forest areas, which have not been exposed to forest harvesting or other human influence, exist only in strict nature reserves. We established the experiment as a split plot experiment with five plots (sample plots in Nuortti 1 and Nuortti 2 areas) that were divided into grazed and non-grazed parts (Table 1). The grazed area directly adjacent to the fence was not used in the sample plot because it was disturbed, but the plot's border was about 10 m from the fence. The plots were situated along the borderline between Finland and Russia, where the non-grazed area was excluded from the reindeer grazing already in 1918 (Stark et al., 2002, 2003), to prevent the Finnish reindeer from going to the Russian side. There are not many reindeer on the Russian side of the area (Stark et al., 2002).

STAND CHARACTERISTICS AND GROUND VEGETATION MEASUREMENTS

To characterize the stands, we established circular sample plots with an area of 400 m². All trees (starting with height 0.1 m) inside the sample plots were measured. The stem diameter at 1.3 m height, tree height, crown height, and crown diameter were measured. The diameter for trees lower than 1.3 m was measured close to the ground. For tree biomass calculations, the formulas of Repola (2009) were used. On every sample plot, four 0.5 × 0.5 m ground vegetation squares were established for species composition and coverage measurements. Ground vegetation biomass was determined from four sample squares (0.2 × 0.2 m) located systematically inside the circular sample plots (close to the ground

TABLE 1

Description of the study sites. The column "Composition" denotes the tree species composition (%) in canopy, where Pi = Scots pine, Sp = spruce, and Bi = birch

	Composition (%)	Trees/ha (trees higher than 1.3 m)	Regeneration/ha (trees lower than 1.3 m)	Average soil temperature in growing season	Soil water content (% in June/% in August)	Soil pH	Overall C storage in soil (g m^{-2})	Overall N content in soil (g m^{-2})	Average soil CO_2 efflux (mg CO_2 m^{-2} s^{-1})
Nuortti 1 grazed ($n = 2$)	60Pi 36Sp 4Bi	790	500	11.2	19.2/11.6	4.7	2388.4	57.7	0.142
Nuortti 1 ungrazed ($n = 2$)	45Pi 44Sp 11Bi	775	1400	10.9	18.9/10.2	4.6	2231.3	66.7	0.122
Nuortti 2 grazed ($n = 3$)	98Pi 1Sp 1Bi	583	3490	11.4	18,1/10.4	4.3	1420	33.9	0.112
Nuortti 2 ungrazed ($n = 3$)	95Pi 4Bi 1Sp	598	7100	11.5	18.9/10.8	4.4	1296.2	32.1	0.094

vegetation squares). For biomass calculations, ground vegetation was classified into three functional groups—mosses, lichens, and vascular plant (including dwarf shrubs)—and oven dried at 60 °C.

SOIL CO_2 EFFLUX AND SOIL C CONTENT

In order to determine the CO_2 efflux from soil to atmosphere, manual chamber measurements were performed on six collars at each sample plot from June until September (five times per collar) at measuring intervals of two weeks. For CO_2 efflux measurements, a portable chamber was used (0.24 m height and 0.22 m in diameter), made of Plexiglas and covered with aluminum foil to keep the interior dark. The CO_2 concentration was recorded during a 5 minute chamber deployment time with a diffusion-type CO_2 probe (GMP343), and air humidity and temperature were measured with a relative humidity and temperature sensor (HM70, Vaisala Oyj, Vantaa, Finland). In addition, soil temperature during the growing season (from June until September) was measured continuously on all sample plots at 3 hour intervals with iButton temperature sensors (Maxim Integrated, San Jose, California, U.S.A.), installed permanently into the humus layer, under the moss and organic layer. At each site, the moisture content of the soil (water content in the soil in percentages) was measured in June and August with a soil moisture sensor (Trime-Pico 64, IMKO GmbH, Germany).

Background information about air temperature, precipitation, soil water content changes, and soil temperature was continuously measured at the Station for Measuring Ecosystem Atmospheric Relations (SMEAR-I) located 8 km from our sample plots.

We took five soil cores (150 mm in length and 50 mm in diameter) from every sample plot and stored them at 4 °C. In the laboratory, the soil cores were divided according to the morphological soil horizons, to litter and organic layer (O-horizon) and humus layer (A-horizon). The layers in mineral soil were divided to eluvial (E-horizon) and illuvial (B-horizon), and sieved. All visible roots were separated (bigger roots by sieving the soil through a 2-mm sieve and smaller roots by picking) for root biomass calculations. The roots were identified as tree and understory (mainly dwarf shrubs and grasses) roots and rhizomes based on morphology and color. The soil C content was measured with an elemental analyzer (varioMAX CN elemental analyzer, Elementar Analysensysteme GmbH, Germany) after drying the samples in an oven at 105 °C for 24 hours.

SOIL MICROBIAL BIOMASS

Soil microbial biomass was measured from five soil samples per sample plot. Soil from the lower humus layer was collected from a rectangular area of 0.25 m^2 to a plastic bag, homogenized, and mixed thoroughly. To determine the soil microbial C biomass (C_{mic}) and soil microbial N biomass (N_{mic}) we have used a chloroform fumigation direct extraction method described by Brookes et al. (1985) and Beck et al. (1997). From the soil samples, two sets of subsamples were prepared (5 g of soil in each), one non-fumigated sample set and the other for a fumigation experiment. Distilled water (1 mL) was added to all tubes and then the tubes were placed in two separate vacuum desiccators. An amount of 20 mL of chloroform was added to one desiccator, and the samples were fumigated for 24 hours at 28 °C with ethanol-free chloroform vapor. Samples in the other vacuum desiccator were left untreated. Then the fumigated and non-fumigated control samples were placed to cups with 30 mL of 0.5M K_2SO_4 and shaken for 1 hour (200 rpm). The extract was filtered (vacuum filtering) through 0.45 μm membrane filter (Pall Corporation, Michigan, U.S.A.), and the solution was stored at –21 °C until C_{mic} and N_{mic} analyses. For analyzing the amount of C_{mic} and N_{mic} the amount of C (μg g^{-1}) and N (μg g^{-1}) of samples were measured with Multi N-C TN/TC analyzer (Analytik Jena AG, Jena, Germany).

STATISTICS

Data were checked for normality with the Shapiro-Wilk test and logarithm transformation was calculated for the recorded CO_2 fluxes. To test the effects of different factors (grazed or non-grazed, location of sample plot, collar location, seasonal variation in CO_2 efflux measurements, root biomass, etc.) on soil CO_2 efflux, soil C content, and soil microbial biomass, a generalized linear model procedure for mixed models (PROC MIXED) was used. Sample plot and measurements were treated as random factor, while grazed or non-grazed areas were treated as fixed factor and, in the case of the location of the CO_2 efflux measurements, measuring point (collar) was treated as repeated fixed factor. To perform random effect analysis of variances (to estimate the different components of variance and observe variations), nested procedure (PROC NESTED) was used. A Tukey's HSD (honest significant difference) test was used for comparison of means. We used linear regressions for testing the relationships of C_{mic}, N_{mic}, C_{mic}, to N_{mic} ratio, root biomass, and soil CO_2 efflux with soil C stock, and soil microbial biomass with root biomass in soil. We estimated the resolution of our sampling setup (ability to detect a certain difference from the mean) with the following equation for CO_2 efflux:
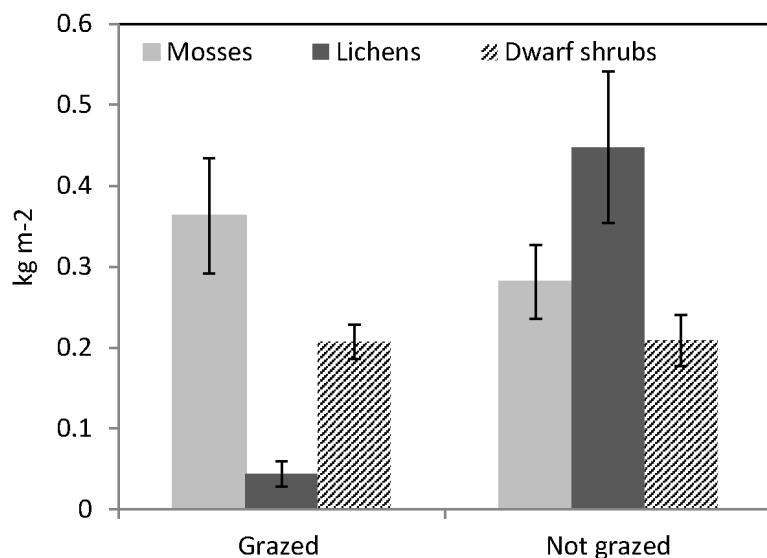
$$\Delta CO_2 = \frac{1.96\sigma}{\sqrt{n}} \qquad (1)$$

where ΔCO_2 is the difference observed from the mean value of the CO_2 effluxes in a specific measurement area with 95% confidence interval, 1.96 is the approximate value of the 95th percentile point of the normal distribution, σ is standard deviation, and n is the number of measurement collars. Similarly, the same formula was also used to estimate the difference in soil C, but then the n was the number of soil samples. All calculations and statistical analyses used the plot as the experimental unit and a significance level of $p = 0.05$. All the statistical analyses were performed with SAS version 9.3 (SAS Institute Inc., Cary, North Carolina, U.S.A.).

Results

VEGETATION STRUCTURE

The total ground vegetation biomass (mosses, lichens, and dwarf shrubs) was significantly higher ($p = 0.007$) in the non-grazed area compared to the grazed area (0.938 kg m^{-2} [SE ± 0.07] vs. 0.614 kg m^{-2} [SE ± 0.09] respectively). When comparing distinct ground vegetation classes, the main impact of reindeer grazing on the ground vegetation structure was the reduction of the lichen biomass (*Cladina* sp. and *Cladonia* sp.) (Fig. 1). The lichen biomass was significantly higher ($p < 0.05$) on the non-grazed site (0.448 kg m^{-2} [SE ± 0.09]), compared to the grazed site (0.044 kg m^{-2} [SE ± 0.02]). The biomass of grasses and dwarf shrubs was similar in both areas, and the biomass of mosses was slightly higher in the grazed areas, but the difference was not statistically significant ($p > 0.05$). The variation in the ground vegetation biomass was mostly the result of sites (grazed or non-grazed) (56%), while random error resulted in 44% of the variation.

FIGURE 1. The average ground vegetation (mosses, lichens, dwarf shrubs) biomass (kg m^{-2}) at the sites grazed and not grazed by reindeer. Error bars represent SE.
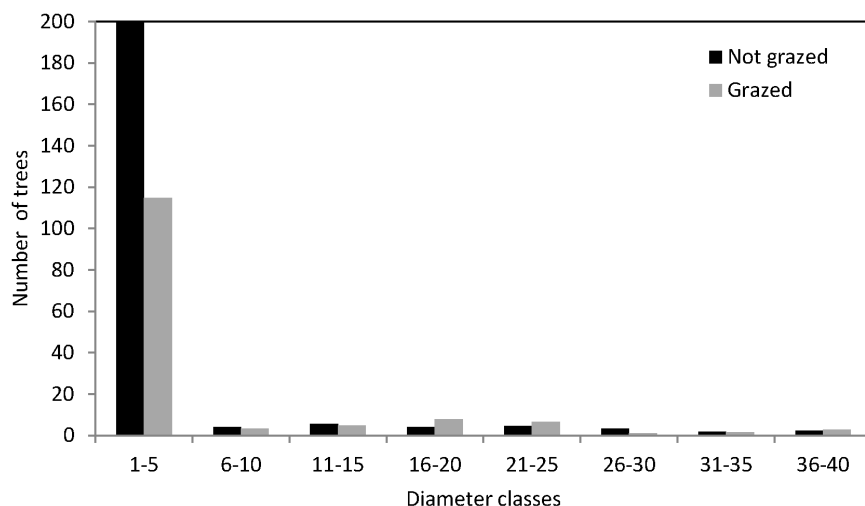
The mean stand age in study area was around 150 years. There was no difference between the areas according to the number of trees taller than 1.3 m per hectare (Table 1). The difference between the areas was mostly coming from the amount of regeneration (the number of trees shorter than 1.3 m), as there was essentially less regeneration in the grazed areas (Table 1). The number of regeneration per hectare was significantly ($p < 0.05$) higher in the non-grazed areas (3291 trees ha^{-1}) compared to the grazed areas (1788 trees ha^{-1}). Grazing was also found to affect the tree diameter distribution among the areas; it was strongly skewed toward thinner trees in the non-grazed areas (Fig. 2). There were almost twice as many trees belonging to the first diameter class in the non-grazed areas compared to the grazed areas (Fig. 2).

Although there was a difference in the total number of trees between the compared areas, the total tree biomass varied not significantly (Fig. 3). The total tree biomass was found to be slightly smaller in the non-grazed areas compared to the grazed areas, but there was no statistical difference ($p > 0.05$) between the areas.

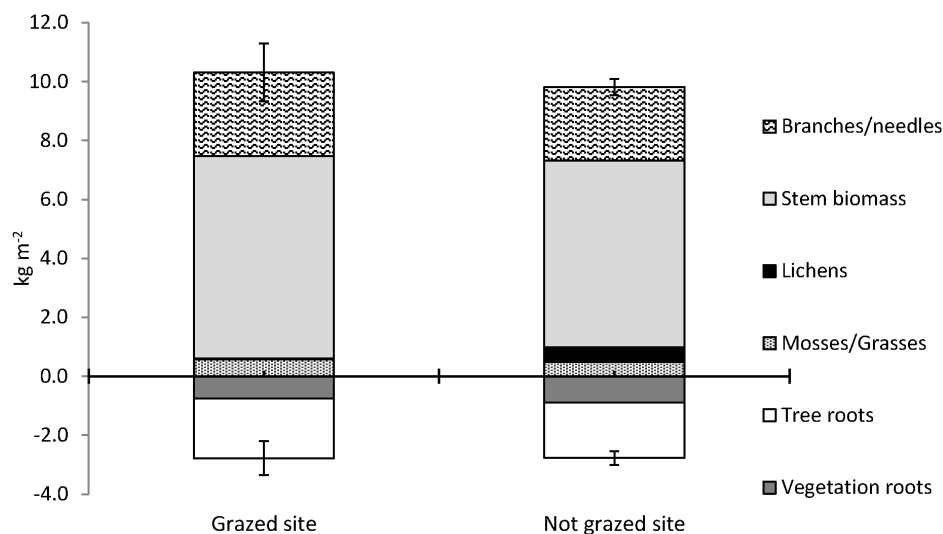There was also no significant difference in the total root biomass between the grazed and non-grazed areas (Fig. 3).

ENVIRONMENTAL FACTORS

The average soil temperatures during the measurement period (from June until September) were similar in all areas, ranging from 10.9 to 11.5 °C (Table 1). The minimum temperatures within the growing season were measured in September, when the temperature dropped down to 2 °C in all study areas. The maximum temperatures were measured at the beginning of July almost at midday (at 13:00), and they ranged from 19 to 22 °C between the areas. There were no differences in daily average temperatures between grazed and non-grazed areas. There was also no difference between grazed and non-grazed area when the water content in the soil was analyzed. The average soil moisture content was higher at the beginning of the summer (in June) compared to the measurements taken at the end of the summer (in August) (Table1). In both areas, the water content in the soil

FIGURE 2. Distribution of trees according to diameter classes (diameter in cm) in grazed and non-grazed areas.

FIGURE 3. Above- and below-ground biomass (kg m^{-2}) in grazed and non-grazed areas. Error bars show SE of total above- and below-ground biomass.

remained 18.1%–19.2% in June and 10.2%–11.6% in August (Table 1). There was also no difference in soil pH between grazed and non-grazed areas (Table 1).

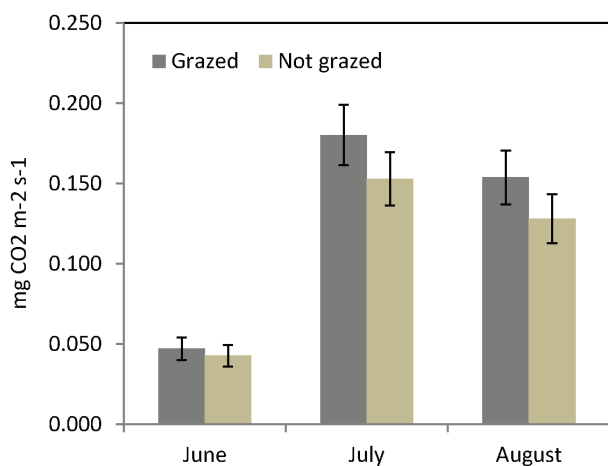### SOIL CO$_2$ EFFLUX, SOIL C STOCK, AND MICROBIAL BIOMASS

There were no significant differences in the soil CO$_2$ efflux between the grazed and non-grazed areas ($p = 0.2478$). This means that, although the soil CO$_2$ efflux was mostly lower in the non-grazed area, reindeer herding had no significant influence on the soil CO$_2$ efflux (Fig. 4). When we analyzed the effects of different factors (grazed or non-grazed area, root biomass, soil C content, etc.) on soil CO$_2$ efflux, we found that almost none of the analyzed factors affected the soil CO$_2$ effluxes. The only factor significantly affecting the soil CO$_2$ efflux was the time when the measurements were made. The CO$_2$ effluxes were lowest in June (0.043 mg CO$_2$ m^{-2} s^{-1} [SE ± 0.007] in the non-grazed areas and 0.047 mg CO$_2$ m^{-2} s^{-1} [SE ± 0.007] in the grazed areas) (Fig. 4). In July and August the CO$_2$ effluxes were more than two times higher compared to June (0.180 mg CO$_2$ m^{-2} s^{-1} [SE ± 0.019] and

0.154 mg CO$_2$ m^{-2} s^{-1} [SE ± 0.017] in the grazed areas, and 0.153 mg CO$_2$ m^{-2} s^{-1} [SE ± 0.017] and 0.128 mg CO$_2$ m^{-2} s^{-1} [SE ± 0.015] in the non-grazed areas, respectively) (Fig. 4). In the case of soil CO$_2$ effluxes, most of the variation (77%) resulted from random error, while sample plot and site (grazed or non-grazed) explained only 21% and 2%, respectively. Our sampling scheme was able to detect 19% differences in soil CO$_2$ effluxes between the areas with 95% confidence interval.
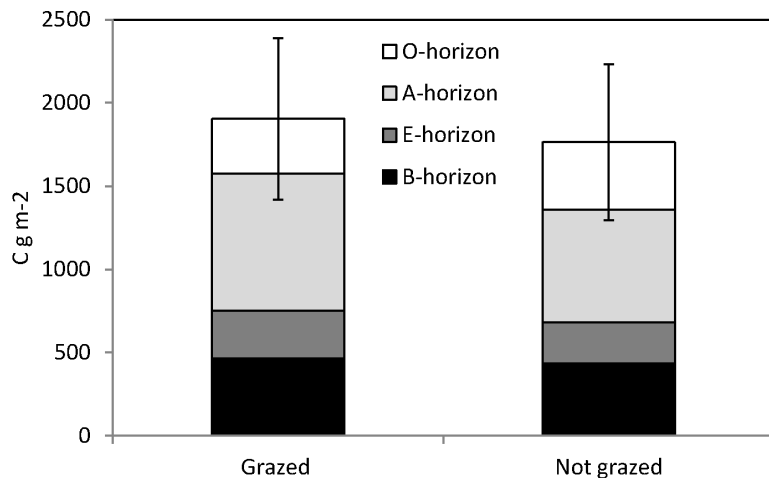
Surprisingly, root biomass did not affect the average soil CO$_2$ efflux from the soil ($p < 0.05$). When we divided the soil CO$_2$ for monthly values (Fig. 4), the CO$_2$ efflux was significantly affected by the root biomass in August ($p < 0.05$), but not in June or in July ($p > 0.05$).

Grazing also had no effect on soil C stock since the difference between grazed and non-grazed site was not significant ($p > 0.05$) (Fig. 5). The variation in the soil C content resulted mostly from random error (76%), while the site (grazed or non-grazed) and sample plot had small influences (22% and 2%, respectively). Our sampling scheme was able to detect 14% differences in soil C content between the areas with 95% confidence interval. The total C storage in the grazed areas was 1904 g m^{-2} (SE ± 484) and in the non-grazed areas 1763 g m^{-2} (SE ± 467), and it was positively correlated with root biomass ($r = 0.59$, $p < 0.05$), meaning that in the areas with the higher C storage, the amount of root biomass was also higher.
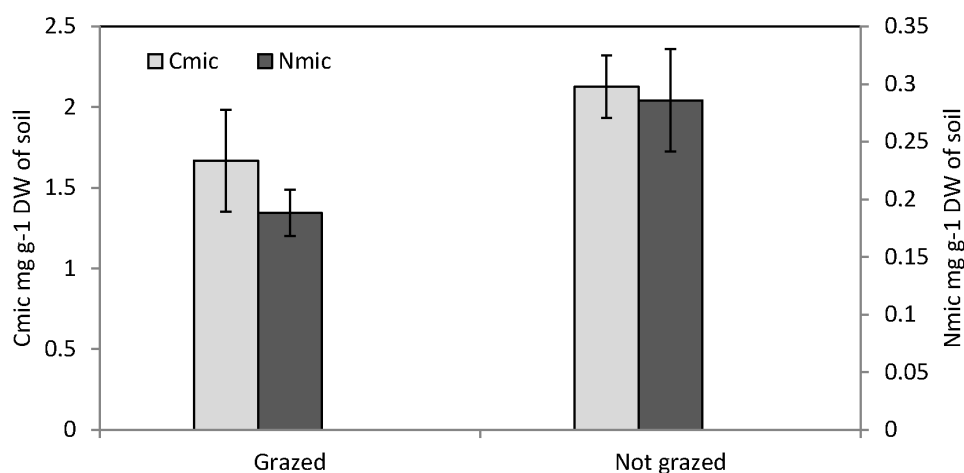
The microbial biomass C (C_{mic}) measured from the humus horizon was lower in the grazed areas compared to the non-grazed areas (1.67 mg C_{mic} g^{-1} DW [SE ± 0.19] of soil in the grazed areas and 2.12 mg C_{mic} g^{-1} DW [SE ± 0.28] of soil in the non-grazed areas) (Fig. 6), but the difference was not statistically significant. However, the microbial biomass N (N_{mic}) was significantly lower ($p > 0.05$) in the grazed areas compared to the non-grazed areas (0.19 mg N_{mic} g^{-1} DW [SE ± 0.02] of soil in the grazed areas compared to 0.29 mg N_{mic} g^{-1} DW [SE ± 0.04] of soil in the non-grazed areas) (Fig. 6). The C_{mic} to N_{mic} ratio was significantly ($p < 0.05$) lower in the non-grazed areas compared to the grazed ones. The average C_{mic} to N_{mic} ratio in the grazed areas was 7.9 and in the non-grazed areas 5.5. We found no correlation between the soil C and soil microbial values: C_{mic} ($r = 0.04$, $p > 0.05$), N_{mic} ($r = 0.01$, $p > 0.05$), and C_{mic} to N_{mic} ratio ($r = 0.01$, $p > 0.05$).

FIGURE 4. Soil CO$_2$ effluxes (mg CO$_2$ m^{-2} s^{-1}) in reindeer grazed and non-grazed areas. Error bars represent SE.

KAJAR KÖSTER ET AL. / 499

FIGURE 5. Soil carbon storage (g m^{-2}) in litter and organic layer (O-horizon), in humus layer (A-horizon), in mineral eluvial (E-horizon) and illuvial (B-horizon) layers, at the sites grazed and not grazed by reindeer. The sampling depth was ~15 cm. Error bars represent SE of total carbon storage on sites.

FIGURE 6. Average microbial biomass C (C$_{mic}$ mg g^{-1} DW of soil) and average microbial biomass N (N$_{mic}$ mg g^{-1} DW of soil) in areas grazed and not grazed by reindeer. Error bars show SE.

Discussion

Reindeer grazing had contrasting effects on vegetation biomass, soil C stocks, and soil CO$_2$ effluxes. We found that grazing had a significant effect on the abundance and biomass of lichens, while changes in other biomass components were small or there was no effect. The lichen biomass in northern Fennoscandia can be as high as 0.5 kg m^{-2} (Wielgolaski and Kjelvik, 1975). In our study areas, grazing by reindeer removed on average about 95% of the lichen biomass, which is a rather high value. Similar decreases in lichen biomass by grazing have been observed by Akujärvi et al. (2014) and Susiluoto et al. (2008), and more than 75% of the lichen biomass loss has been reported also by Köster et al. (2013) and Olofsson et al. (2010). We found no effect of reindeer grazing on the total C storage in soil and on soil pH, which is in accordance with findings from Stark et al. (2000, 2008) and Köster et al. (2013). The similar soil C stocks and pH at the grazed and nongrazed sites in our study could be explained by changes that are taking place in the vegetation structure and probably these changes counteract each other. We may predict that with grazing the biomass of lichens and dwarf shrubs is reduced and due to that also the amount of litter in the grazed area is smaller and this would affect decomposition rates in grazed areas—the decomposition rates would be smaller in grazed areas. But this is probably the case in

open tundra heats. In forested areas the main litter input comes from the trees and in our case there was no difference in aboveground biomass between the areas. On the other hand, reindeer droppings (feces and urine) may contribute to the increasing availability of N compounds, provide highly decomposable resources, and stimulate soil microbial biomass and activity as stated by Turunen et al. (2013), and this should have an effect on soil C content. Lichens itself are not an important functional group if we are talking about the C exchange, thus their decrease due to reindeer grazing does not affect the C stocks in the soil, but the other factors resulting from grazing may have an effect on soil C stocks. But similarly to our study, Stark et al (2000 and 2010) found no effect of grazing on the soil organic C on most of their sample plots in boreal forests. Previous studies refer to the increase of the proportion of graminoids at the expense of evergreen and deciduous shrubs in tundra areas as a consequence of reindeer grazing, and this in turn may enhance the litter and soil C decomposition (Olofsson et al., 2004; van der Wal, 2006). In forested areas, where light is the limiting factor for the growth of graminoids (Strengbom et al., 2004), the amount of graminoids was really small, and there was no difference in their occurrence between the grazed and nongrazed areas. In our study area, also the biomass of dwarf shrubs (*Vaccinium* sp.) was not significantly affected by grazing. Although *Vaccinium uliginosum* and *Vaccinium myrtillus* are important for-

age plants for the reindeer during the summertime (Susiluoto et al., 2008), they tolerate and recover well from trampling and grazing (Kellomäki and Saastamoinen, 1975). In fact, in our study, dwarf shrubs and mosses seemed to benefit from grazing, most likely due to decreased competition from lichens—when reindeer were eating the lichens the dwarf shrubs and mosses were overtaking the areas quickly. Similar results have also been found by Klein (1987).

In our reindeer grazed areas, the dwarf shrubs and mosses were taking over quickly the exposed soil patches after the lichens were eaten, and no bare ground was exposed. One can speculate that soils were warming faster in the spring (during the snow melt period) in the grazed areas (Fauria et al., 2008), but as we have no data available from late spring (when the snow was melting) particular conclusions are improper to make. We installed the temperature sensors at the end of May (the beginning of growing season, just after snow melt). Earlier studies have shown that taller and tenser vegetation (vegetation is more abundant or protrudes above the snowpack) may result in earlier snow melt (and with that also higher soil temperatures) as the vegetation above the snow increases the absorption of solar radiation in winter (Cohen et al., 2013). In our case, the trees and their stems may increase the absorption of solar radiation, but the large difference in the number of trees was in first diameter class (trees with diameter from 1–5 cm), and these trees are mostly under the snow. We found no evidences of earlier snow melting between the areas.

Earlier studies have shown that reindeer grazing may affect the soil temperature during the snow-free period because the insulating lichen cover is decreased. For example, Olofsson et al. (2010) and Fauria et al. (2008) have observed lower soil temperatures beneath the thick lichen mats in the summer compared to areas exposed to reindeer grazing and having less lichen. We found no differences in soil temperature and soil moisture content between the grazed and non-grazed areas. This is probably because the bare patches of soil were rare at our sites unlike in the study of Väre et al. (1996), who observed that probably due to herbivores the proportion of bare ground was significantly higher in grazed areas compared to non-grazed areas.

Although the vegetation structure was changed due to the grazing in our study areas, we found that it had no effect on soil CO_2 effluxes. The reason why no differences in soil CO_2 effluxes were observed between the areas might be because soil temperature, soil moisture, and root biomass did not differ between the grazed and non-grazed areas. This distinguishes our study from other studies investigating the effects of reindeer grazing on soil C balance and soil CO_2 efflux (Ohtonen and Väre, 1998; Stark et al., 2003; Väre et al., 1996). According to Stark et al. (2003), soil respiration and microbial activity were significantly lower in the grazed areas compared to the non-grazed ones in northern boreal forests, which they explained by decreased microbial activity and pine root biomass in the soil organic layer as a result of reindeer grazing. On the other hand, Stark et al. (2002) found that grazing did not change soil respiration in subcontinental tundra heats. Root and rhizosphere respiration compose at least half of the total soil CO_2 efflux in boreal Scots pine forests (Högberg et al., 2010). As mosses and lichens do not have living biomass below ground, they are not as an important functional group for soil CO_2 effluxes as vascular plants with active root system. Therefore, trees and dwarf shrubs, and their contribution to the root and rhizosphere respiration could result in differences in soil CO_2 effluxes between grazed and non-grazed sites. Since root biomasses in our study were similar in the grazed and nongrazed sites, we did not observe differences in soil CO_2 effluxes either. There was, however, a clear seasonal cycle in soil biological activity that was reflected in soil CO_2 ef-

fluxes. The monthly CO_2 effluxes were significantly lower in June compared to the other months because in the beginning of June the soil temperatures were still low (close to 0 °C) and some soil layers were probably still frozen. The highest values were measured in July and August, which is typical for boreal forests (Köster et al., 2011; Ullah et al., 2009).

Another important source of soil CO_2 efflux is the microbial respiration. There was no difference in the soil microbial C biomass (C_{mic}) pool between the grazed and non-grazed areas, but the microbial N biomass (N_{mic}) was lower in the grazed areas. Similar results were also found by Stark et al. (2008, 2010) and Ohtonen and Väre (1998). Other studies have mostly shown a decrease in microbial biomass due to the reindeer grazing (Stark et al., 2003; Väre et al., 1996). Microbial biomass has been found to be correlated with root biomass (Wardle, 1992), but in our study there was no difference in root biomass between the grazed and non-grazed areas. This may partly explain why we did not observe differences in C_{mic} between the grazed and non-grazed areas. However, we found a difference in N_{mic}, which resulted in significantly different in C_{mic} to N_{mic} ratio between the grazed and non-grazed areas, being much higher in grazed areas.

The year 2013 was extremely dry in the region when compared to the long-term annual precipitation rate (592 mm) (Korhonen and Haavanlammi, 2012; Susiluoto et al., 2008). More than 100 mm lower precipitation than the average has resulted in lower soil moisture contents at all sample plots. Although the low soil moisture content affects soil CO_2 efflux and microbial biomass, it influenced these values in both studied areas at the same time and with the same intensity. We can assume that the values for soil CO_2 efflux and microbial biomass were lower in this year compared to average years, but as our aim was to see the differences between the grazed and non-grazed areas, this should not affect the end result as both areas were exposed to the same weather conditions.

Some of the study plots of Stark et al. (2002, 2003) and Susiluoto (2008) are close to our study areas (at approximately 2 km distance from our study areas). Still, as their sites are located at open subcontinental tundra heaths while ours are located in subcontinental boreal pine forests, the results cannot be considered imitative and are not completely comparable. For example, while a major proportion of soil CO_2 effluxes is originating from recent photosynthates by trees allocated to the root system, at open tundra heaths there are no trees and consequently the amount of C available for root and rhizosphere respiration is smaller leading to lower soil CO_2 effluxes (Bahn et al., 2008). Earlier studies have found that in lichen-dominated forests with a very thin humus layer, reindeer grazing causes C limitation for the soil microbes and reduces the soil respiration (Stark et al., 2002, 2000; Väre et al., 1996).

The sites selected for our study were homogeneous in terms of their soil type and tree structure. Still, the variation in both soil CO_2 effluxes and soil C stocks was remarkably large. In the case of soil CO_2 effluxes and soil C content, most of the variation resulted from random error, while sample plot and site (grazed or non-grazed) explained only a small part of the variation. One could argue that the soil C stocks and soil CO_2 effluxes, but also vegetation biomasses, are strongly site dependent, and therefore the differences not resulting from reindeer grazing but other site factors would mask the effects of reindeer grazing. This was, however, not the case in our study, where our intention was to select sites as similar as possible in terms of site history, age, soil type, climate, and elevation. This is the reason we decided to focus our study in the few pristine forests that remained in Lapland in the Värriö Strict Nature Reserve. If the sites selected had been managed forests or forest that had been exposed to selected cuttings in the past, the ef-

fects of other factors than reindeer grazing could have masked the effect of reindeer grazing, which was not our intention.

Overall, our study showed that grazing decreased significantly the biomass and cover of lichens in the northern boreal subarctic coniferous forests. Also, the tree regeneration was affected by grazing as we had much less tree regeneration in the grazed areas compared to the non-grazed areas. In subarctic mature pine forest, grazing did not affect the soil temperature or the soil moisture. We found no significant effect of grazing on the soil CO_2 efflux, soil C stock, and the soil microbial C biomass. Soil microbial N biomass was significantly lower in the grazed areas compared to the non-grazed areas. We may say that in the northern boreal subarctic coniferous forests grazing by reindeer could be considered as "C neutral," as forests might be less sensitive to abiotic and biotic changes compared to tundra.

References Cited

Akujärvi, A., Hallikainen, V., Hyppönen, M., Mattila, E., Mikkola, K., and Rautio, P., 2014: Effects of reindeer grazing and forestry on ground lichens in Finnish Lapland. *Silva Fennica*, 48(3): 1153.

Bahn, M., Rodeghiero, M., Anderson-Dunn, M., Dore, S., Gimeno, C., Drösler, M., Williams, M., Ammann, C., Berninger, F., Flechard, C., Jones, S., Balzarolo, M., Kumar, S., Newesely, C., Priwitzer, T., Raschi, A., Siegwolf, R., Susiluoto, S., Tenhunen, J., Wohlfahrt, G., and Cernusca, A., 2008: Soil respiration in European grasslands in relation to climate and assimilate supply. *Ecosystems,* 11: 1352–1367.

Beck, T., Joergensen, R. G., Kandeler, E., Makeschin, F., Nuss, E., Oberholzer, H. R., and Scheu, S., 1997: An inter-laboratory comparison of ten different ways of measuring soil microbial biomass C. *Soil Biology and Biochemistry,* 29: 1023–1032.

Brookes, P. C., Landman, A., Pruden, G., and Jenkinson, D. S., 1985: Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology and Biochemistry*, 17: 837–842.

Cahoon, S. M. P., Sullivan, P. F., Post, E., and Welker, J. M., 2012: Large herbivores limit CO_2 uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology,* 18: 469–479.

Cohen, J., Pulliainen, J., Ménard, C. B., Johansen, B., Oksanen, L., Luojus, K., and Ikonen, J., 2013: Effect of reindeer grazing on snowmelt, albedo and energy balance based on satellite data analyses. *Remote Sensing of Environment,* 135: 107–117.

FAO, 1990: Soil map of the world, revised legend. Rome, Italy: FAO, World Soil Resources Report no. 60.

Fauria, M. M., Helle, T., Niva, A., Posio, H., and Timonen, M., 2008: Removal of the lichen mat by reindeer enhances tree growth in a northern Scots pine forest. *Canadian Journal of Forest Research*, 38: 2981–2993.

Hobbie, S., Nadelhoffer, K., and Högberg, P., 2002: A synthesis: The role of nutrients as constraints on carbon balances in boreal and Arctic regions. *Plant and Soil,* 242: 163–170.

Hobbie, S. E., 1992: Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution,* 7: 336–339.

Högberg, M. N., Briones, M. J. I., Keel, S. G., Metcalfe, D. B., Campbell, C., Midwood, A. J., Thornton, B., Hurry, V., Linder, S., Näsholm, T., and Högberg, P., 2010: Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytologist,* 187: 485–493.

Jaakkola, L. M., Heiskanen, M. M., Lensu, A. M., and Kuitunen, M. T., 2013: Consequences of forest landscape changes for the availability of winter pastures to reindeer (*Rangifer tarandus tarandus*) from 1953 to 2003 in Kuusamo, northeast Finland. *Boreal Environment Research*, 18: 459–472.

Karhu, K., Auffret, M. D., Dungait, J. A. J., Hopkins, D. W., Prosser, J. I., Singh, B. K., Subke, J.-A., Wookey, P. A., Agren, G. I., Sebastia, M.-T., Gouriveau, F., Bergkvist, G., Meir, P., Nottingham, A. T., Salinas, N., and Hartley, I. P., 2014: Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature,* 513: 81–84.

Kellomäki, S., and Saastamoinen V. L., 1975: Trampling tolerance of forest vegetation. *Acta Forestalia Fennica,* 147: 1–22.

Kivinen, S., and Kumpula, T., 2014: Detecting land cover disturbances in the Lappi reindeer herding district using multi-source remote sensing and GIS data. *International Journal of Applied Earth Observation and Geoinformation,* 27(A): 13–19.

Klein, D. R., 1987: Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. *Journal of Range Management*, 40: 336–338.

Korhonen, J., and Haavanlammi, E., 2012: *Hydrological Yearbook 2006–2010*. Helsinki: Suomen ympäristö, 234 pp.

Köster, K., Püttsepp, Ü., and Pumpanen, J., 2011: Comparison of soil CO_2 flux between uncleared and cleared windthrow areas in Estonia and Latvia. *Forest Ecology and Management*, 262: 65–70.

Köster, E., Köster, K., Aurela, M., Laurila, T., Berninger, F., Lohila, A., and Pumpanen, J., 2013: Impact of reindeer herding on vegetation biomass and soil carbon content: a case study from Sodankylä, Finland. *Boreal Environment Research,* 18: 35–42.

Köster, K., Berninger F., Lindén, A., Köster, E., and Pumpanen, J., 2014: Recovery in fungal biomass is related to decrease in soil organic matter turnover time in a boreal fire chronosequence. *Geoderma*, 235–236: 74–82.

Kumpula, J., Colpaert, A., and Anttonen, M., 2007: Does forest harvesting and linear infrastructure change the usability value of pastureland for semi-domesticated reindeer (*Rangifer tarandus tarandus*)? *Annales Zoologici Fennici*, 44: 161–178.

Kumpula, J., Kurkilahti, M., Helle, T., and Colpaert, A., 2013: Both reindeer management and several other land use factors explain the reduction in ground lichens (*Cladonia* spp.) in pastures grazed by semi-domesticated reindeer in Finland. *Regional Environmental Change*, 14: 541–559.

Li, Q., Lee Allen, H., and Wollum Ii, A. G., 2004: Microbial biomass and bacterial functional diversity in forest soils: effects of organic matter removal, compaction, and vegetation control. *Soil Biology and Biochemistry,* 36: 571–579.

Ohtonen, R., and Väre, H., 1998: Vegetation composition determines microbial activities in a Boreal Forest Soil. *Microbial Ecology,* 36: 328–335.

Oksanen, L., Moen, J., and Helle, T., 1995: Timberline patterns in northernmost Fennoscandia: relative importance of climate and grazing. *Acta Botanica Fennica*, 153: 93–105.

Olofsson, J., 2006: Short- and long-term effects of changes in reindeer grazing pressure on tundra heath vegetation. *Journal of Ecology,* 94: 431–440.

Olofsson, J., Stark, S., and Oksanen, L., 2004: Reindeer influence on ecosystem processes in the tundra. *Oikos*, 105: 386–396.

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., and Suominen, O., 2009: Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, 15: 2681–2693.

Olofsson, J., Moen, J., and Östlund, L., 2010: Effects of reindeer on boreal forest floor vegetation: Does grazing cause vegetation state transitions? *Basic and Applied Ecology,* 11: 550–557.

Potapov, P., Yaroshenko, A., Turubanova, S., Dubinin, M., Laestadius, L., Thies, C., Aksenov, D., Egorov, A., Yesipova, Y., Glushkov, I., Karpachevskiy, M., Kostikova, A., Manisha, A., Tsybikova, E., and Zhuravleva, I., 2008: Mapping the world's intact forest landscapes by remote sensing. *Ecology and Society,* 13(2): 51.

Repola, J., 2009: Biomass equations for Scots pine and Norway spruce in Finland. *Silva Fennica*, 43: 625–647.

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

Stark, S., Strömmer, R., and Tuomi, J., 2002: Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. *Oikos,* 97: 69–78.

Stark, S., Tuomi, J., Strömmer, R., and Helle, T., 2003: Non-parallel changes in soil microbial carbon and nitrogen dynamics due to reindeer grazing in northern boreal forests. *Ecography*, 26: 51–59.

Stark, S., Kytöviita, M. M., Männistö, M. K., and Neumann, A. B., 2008: Soil microbial and microfaunal communities and organic matter quality in reindeer winter and summer ranges in Finnish subarctic mountain birch forests. *Applied Soil Ecology*, 40: 456–464.

Stark, S., Männistö, M. K., and Smolander, A., 2010: Multiple effects of reindeer grazing on the soil processes in nutrient-poor northern boreal forests. *Soil Biology and Biochemistry,* 42: 2068–2077.

Strengbom, J., Näsholm, T., and Ericson, L., 2004: Light, not nitrogen, limits growth of the grass *Deschampsia flexuosa* in boreal forests. *Canadian Journal of Botany,* 82: 430–435.

Suominen, O., and Olofsson, J., 2000: Impacts of semi-domesticated reindeer on structure of tundra and forest communities in fennoscandia: a review. *Annales Zoologici Fennici,* 37: 233–249.

Susiluoto, S., Rasilo, T., Pumpanen, J., and Berninger, F., 2008: Effects of grazing on the vegetation structure and carbon dioxide exchange of a fennoscandian fell ecosystem. *Arctic, Antarctic, and Alpine Research*, 40: 422–431.

Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., and Zimov, S., 2009: Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, 23: GB2023.

Turunen, M., Oksanen, P., Vuojala-Magga, T., Markkula, I., Sutinen, M. L., and Hyvönen, J., 2013: Impacts of winter feeding of reindeer on vegetation and soil in the sub-arctic: insights from a feeding experiment. *Polar Research,* 32: 18610, http://dx.doi.org/10.3402/polar.v32i0.18610.

Ullah, S., Frasier, R., Pelletier, L., and Moore, T. R., 2009: Greenhouse gas fluxes from boreal forest soils during the snow-free period in Quebec, Canada. *Canadian Journal of Forest Research,* 39: 666–680.

van der Wal, R., 2006: Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, 114: 177–186.

Väisänen, M., Ylänne, H., Kaarlejärvi, E., Sjögersten, S., Olofsson, J., Crout, N., and Stark, S., 2014: Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Climate Change*, 4: 384–388.

Väre, H., Ohtonen, R., and Oksanen, J., 1995: Effects of reindeer grazing on understorey vegetation in dry *Pinus sylvestris* forests. *Journal of Vegetation Science,* 6: 523–530.

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

Wardle, D. A., 1992: A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. *Biological Reviews,* 67: 321–358.

Wielgolaski, F. E., and Kjelvik, S., 1975: Production of plants (vascular plants and cryptogams) in alpine tundra, Hardangervidda. *In* Bliss, L. C., and Wielgolaski, F. E. (eds.), *Primary Production and Production Processes, Tundra Biome*, Edmonton, Canada: Tundra Biome Steering Committee, 75–86.