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# Impact of reindeer herding on vegetation biomass and soil carbon content: a case study from Sodankylä, Finland

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Factors that strongly affects the dynamics of ground vegetation in northern boreal forests are grazing and trampling by reindeers. *Cladina stellaris*, which is the main species of lichen in northern areas, is also an important food source for reindeer. The population of reindeer is high, and it has a considerable influence on the boreal forest ecosystems. In this study, we describe the reindeer herding effects on above- and below-ground vegetation and on soil carbon (C) content. We compared the changes on both sides of a fence that has excluded reindeer from one area for the last 50 years. As expected, in the grazed area there were significantly smaller amounts of lichens and other vegetation. Total above-ground biomass as well as that of trees was higher in the area where no reindeer grazing occurred. In the ungrazed area, the tree-diameter distribution was strongly skewed towards thinner trees. There was no significant effect of reindeer grazing on the soil C content.

## Introduction

Mammalian herbivors can negatively affect ecosystems (Naiman *et al*. 1986, Owen-Smith 1987, Cantor & Whitham 1989, Collins *et al*. 1998, Stark *et al*. 2010). For example, high density of herbivores tends to reduce plant diversity (Olff & Ritchie 1998). That kind of negative influence has usually resulted from human activities, and reindeer herding is no exception (Helle & Aspi 1983, Oksanen & Virtanen 1995, Väre *et al*. 1995, Suominen & Oloffson 2000, Rees *et al*. 2003, Stark *et al*. 2010).

During summers, in addition to grasses reindeer (*Rangifer tarandus*) eat leaves of *Salix* and *Betula*. In winter, *Cladina* lichens are their main food source (Kojola *et al*. 1995, Heggeberget *et al*. 2002). Reindeer grazing is common in the northern boreal zone and has a long history in Eurasia as reindeer and humans have interacted continuously since the last ice age. Considerable nomadic activity started during the 17th century, and reindeer husbandries developed into a more intensive form during 20th century (Emanuelson 1985, Suominen & Oloffson 2000). The number of managed reindeer has changed over the last century and reached its peak at the beginning of the 1990s (Danell *et al*. 1999, Suominen & Oloffson 2000). The increase in numbers was caused by winter feeding, vaccination and a decrease in

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the number of predators (Kumpula & Nieminen 1992, Väre *et al*. 1996). Since the early 1990s, the number of reindeer slightly decreased due to limited food resources and is currently around 200 000 individuals in Finland (Suominen & Oloffson 2000, Turunen & Vuojala-Magga 2011). Previous studies investigated the influence of reindeer grazing on the above-ground vegetation, tree growth, soil-nutrient cycling, and microbial and microfaunal communities (Jalkanen *et al* 1995, Väre *et al*. 1995, 1996, Fauria *et al*. 2008, Stark *et al*. 2000, 2003, 2007, 2008, 2010).

In the nutrient-poor boreal forests of northern Fennoscandia, the *Cladina* lichen dominates the ground vegetation and constitutes an important food source for reindeer during winter (Ahti 1977, Ahti & Oksanen 1990, Kojola *et al*. 1995, Stark *et al*. 2010). A completely ungrazed *Cladina* carpet would actually be unnatural in the area, but the current heavy grazing pressure is harmful not only to *Cladina* species, but also to other species in an overgrazed area (Kojola *et al*. 1995, Väre *et al*. 1996, Suominen & Olofsson 2000, Heggberget *et al*. 2002, Rees *et al*. 2003, Fauria *et al*. 2008). The main consequence of overgrazing is that *Cladina* lichens are replaced by bryophytes and bare patches of soil (Helle & Aspi 1983, Väre *et al*. 1995, 1996, Rees *et al*. 2003).

In addition, mammalian herbivores have a detrimental effect on forests by damaging the understory. There are several examples of how they affect growth and regeneration of trees (Potvin *et al*. 2003, Casabon & Pothier 2007, Beguin *et al*. 2009, den Herder *et al*. 2007, 2009). Reindeer has been found to limit growth of willows in boreal forests (den Herder *et al*. 2007).

In terrestrial ecosystems, soil represents the major reservoir of organic carbon (IPCC 2007, Rodeghiero *et al*. 2009). According to the global organic soil carbon map, cold boreal regions are the areas with the highest soil organic carbon content (Jones *et al*. 2003). Most of the organic matter that enters the soil originates from plants. In forest ecosystems, the below-ground biomass is more important for the accumulation of soil organic matter than the above-ground litter (Ruess *et al*. 1996, Rasse *et al*. 2005). In natural ecosystems, the release of carbon ($CO_2$, $CH_4$ and BVOCs) from soils results from decomposition and mineralization of soil organic matter (Rodeghiero *et al*. 2009). However, the soil carbon balance can easily be disturbed by fires or human activities (Neary *et al*. 1999, Duguy *et al*. 2006, Janzen 2006, Bond-Lamberty *et al*. 2007). The net accumulation rate of soil carbon depends on the ratio between the gross primary-productivity rate and the decomposition rate that are controlled by several factors, including: soil temperature, moisture and substrate quality (Davidson *et al*. 2006). Temperature, however, seems to be one of the most important factors controlling decomposition of organic matter in the soil (Amundson 2001, Rodeghiero & Cescatti 2005).

Intensive reindeer grazing in northern-boreal forests of Fennoscandia results in the disappearance of the *Cladina* carpet, damage to secondary vegetation mat (bryophyte and vascular plants), and large bare patches of soil becoming increasingly common. This allows the soil to warm up faster and reach higher temperatures than in *Cladina*-covered areas (Suominen & Oloffson 2000, Rees *et al*. 2003). According to several authors this should increase the decomposition rate of soil carbon stock (Kirschbaum 1995, Amundson 2001, Bellamy *et al*. 2005, Rodeghiero & Cescatti 2005). On the other hand, dryness influences bare soils more strongly by exposing the humus layer, which may be harmful to decomposing organisms.

We examined the reindeer herding effect on vegetation, above- and below-ground biomass, and on soil carbon content. We also compared the changes in soil carbon content and vegetation cover between boreal forest grazed by reindeers and an "unnatural" area that has been fenced off and not grazed for more than 50 years.

We hypothesize that reindeer herding affects (1) the vegetation composition, (2) tree growth, and (3) C pool dynamics in soil surface layers.

## Material and methods

### Study area

The study area was situated in Finnish Lapland in Sodankylä (67°21´N, 26°38´E), close to the Arctic Research Centre of the Finish Meteorological Institute, 120 km north of the Arctic Circle. The district of Oraniemi is about 4085 km$^2$ in area, and is among the five largest reindeer herding districts of Finland. The number of reindeer changed during the last 50 years, reaching its maximum of 1.78 animals per $km^2$ in the 1990s. Now it is around 1.58 animals per $km^2$ (8000 animals), which is three times denser than it was in the 1960s (Kumpula *et al*. 2009, Turunen & Vuojala-Magga 2011). The main tree species growing in the area is Scots pine (*Pinus sylvestris*), with tree ages varying from 50 to 130 years. The soils in the area are sandy, with about 0.5 cm layer of humus (conditions are similar on both sides of the fence). Ground vegetation is characteristic of the boreal pine forest. It is dominated by lichens (mostly *Cladina stellaris* and few *Cladonia* sp.) in places where reindeers have no access. In the grazed area, there are also some damaged mosses (*Hylocomium splendens* and *Dicranum* sp.), and vascular plants (*Vaccinium vitis-idaea*, *Empetrum nigrum* and *Calluna vulgaris*). The long-term annual mean temperature is –1.0 °C and the mean precipitation is 499 mm (Finnish Meteorological Institute 1991, Suni *et al*. 2003). The ground is typically covered by snow from October until mid-May, and the uppermost soil layers are frozen during the same period. The fence enclosing the area which has not been grazed was erected about 50 years ago for snow depth measurements, and excluded reindeer since then. The size of the fenced area is $40 \times 50$ $m^2$. In the Oraniemi district, the overall herding pressure 50 years ago was around 2000 animals (0.4 animals per $km^2$) (Turunen & Vuojala-Magga 2011). The site was topographically homogenous and even, but the actual vegetation at that time was not documented.

## Biomass and soil sampling

In order to characterize the soil carbon content and ground vegetation, in August 2011 we established four, 40-m-long transect lines (two lines inside the fence and two lines outside the fence) with each line having soil coring plots every 4 meters. The transect lines were run in parallel at the distances of 2 and 5 m from the reindeer fence. The following tree characteristics were measured in two $10 \times 40$ m plots established inside and outside the fence and enclosing the transect lines: diameter at 1.3 m height, height of a tree, crown height, crown diameter, and stand age. Measured trees in sample plots were then divided into five diameter classes and from every diameter class at least six model trees were selected (modified from Havimo *et al* 2009). Their heights, crown heights, crown diameters (radius of a crown to north, south, east and west direction) and tree age (determined from increment core) were measured. The formulas of Repola (2009) were used for tree-biomass calculations. These formulas are used to calculate the biomass of trees above (e.g. stem, stem bark, branches, and needles) and below ground (roots > 1 cm) based on tree characteristics.

A total of 40 soil-core samples were taken from the transects (20 from ungrazed and 20 from grazed sides of the fence) using a manually-operated sampling device (Westman 1995). The number of analysed samples was based on spatial variability (standard deviation in the C content), that was determined from soil samples taken during the previous year from the same research site. Each core was 5 cm in diameter and about 10 to 25 cm in depth (core depth varied because of the sandy and stony soils). Samples were frozen and transported to a laboratory of the University of Helsinki for further analysis.

Soil profiles of the cores were divided into vegetation, litter containing decomposing organic layer (LF layer), humus layer (humus mixed with mineral soil) (H), and mineral soil layers 0 to 5 cm, 5 to 10 cm and 10+ cm depths. Plants growing on the surface of the core sample were categorized into vascular plants, mosses and lichens. All visible roots were separated from litter and soil. All were oven-dried at 60 °C except soil which was dried at 105 °C for 24 h and their biomass was calculated. After the drying, stones were sieved out from the soil (sieve diameter 2 mm) and the samples were pulverized. The soil C content was measured with an elemental analyser (varioMAX CN, Elementar Analysensysteme GmbH, Germany).

## Data analyses

Normality of the data was verified with Shapiro-Wilk's test, and no transformations were neces-

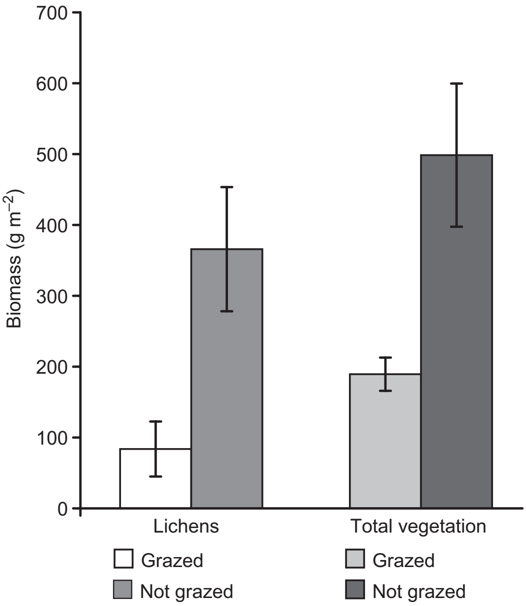


**Fig. 1**. Lichen biomass and total above-ground vegetation biomass (including vascular plants, mosses, and lichens) at the sites grazed and not grazed by reindeer. Error bars show 95% confidence intervals.

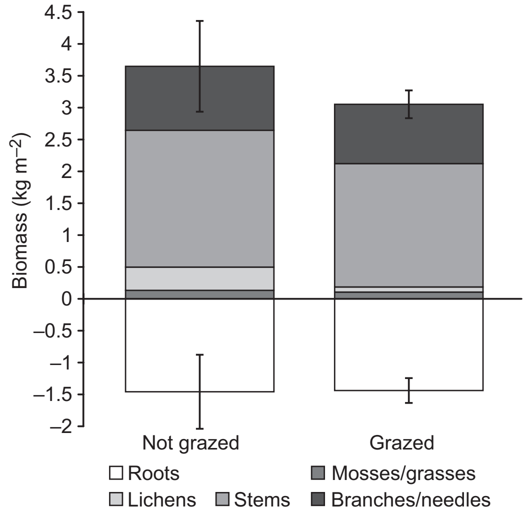


**Fig. 2**. Above- and below-ground (roots) vegetation biomass at the reindeer grazed and ungrazed sites. Error bars show 95% confidence intervals.

sary. The reindeer grazing effect on soil C content was evaluated using a general linear model (GLM) for analysis of variance (ANOVA) with the following fixed factors: biomass of ground vegetation, biomass of trees, treatment (grazed *vs*. ungrazed), and carbon content of the roots. A *t*-test was used for comparisons of means. The statistical analyses were conducted using SAS ver. 9.2 (SAS Institute Inc., Cary, NC, USA).

## Results

The lichen biomass measured from the core samples was significantly higher (*t*-test: $t_{40} = 2.093$, $p = 0.000038$) at the ungrazed site (350 g m$^{-2}$) as compared with that in the area grazing by reindeer (< 90 g m$^{-2}$). Moreover, the total ground vegetation biomass was significantly (*t*-test: $t_{40} = 2.093$, $p = 0.0000049$) affected by reindeer herding. The total ground vegetation biomass was 62% higher in the ungrazed area as compared with that in the grazed area (500 g m$^{-2}$ *vs*. < 200 g m$^{-2}$, respectively) (Fig. 1).

The tree biomass (stem, branches and needles) was significantly higher in the ungrazed area (*t*-test: $t_{151} = 1.989$, $p = 0.0014$). Apart from lichens, the reindeer had the strongest influence on tree-stem biomass (Fig. 2). There was no significant difference between the areas in root biomass (*t*-test: $t_{201} = 12.706$, $p = 0.1073$).

The mean age of the tree stands was around 95–100 years. We also found that in the grazed area there was almost no regeneration and trees were smaller. Grazing significantly affected the diameter and height distribution of the trees (*t*-test: $t_{151} = 2.7765$, $p = 0.0043$). Moreover, in the ungrazed area the tree-diameter distribution was strongly skewed towards thinner trees (Fig. 3). In the ungrazed area, there were many more trees belonging to the first diameter class and about two times more trees belonging to the second diameter class. The two following diameter classes were slightly more frequent in the grazed area, while the number of trees belonging to the 25–30-cm-diameter class was approximately the same in both areas. The mean tree diameters in the grazed and ungrazed areas were 13 and 7 cm, respectively, while the mean tree heights were 11.2 m (max. 15.6 m) and 6.5 m (max. 16.5 m), respectively.

The number of trees per hectare was significantly higher in the ungrazed area as compared with that at the grazed site (2675 trees ha$^{-1}$ and 1100 trees ha$^{-1}$, respectively; *t*-test: $t_{151} = 2.9199$, $p = 0.0006$).

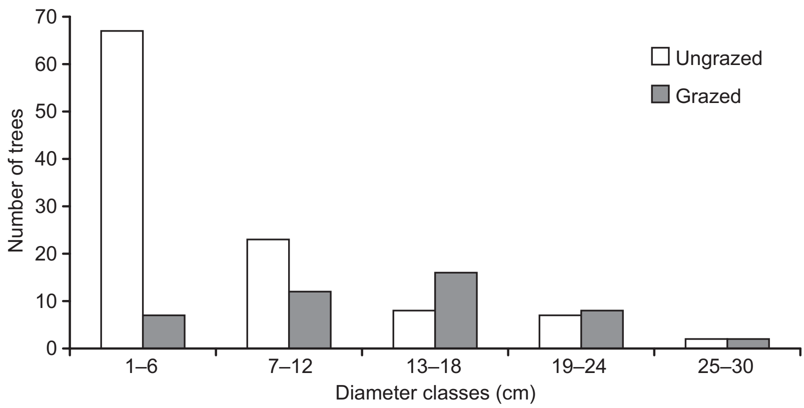


**Fig. 3**. Distribution of trees according to the diameter classes in the areas grazed and not grazed by reindeer.

Grazing had no effect on the soil C content since the difference between grazed and ungrazed area was not significant (*t*-test: $t_{201} = 2.093$, $p = 0.5408$) (Fig. 4). When we analysed the factor effects on the soil C content, we found that it was affected only by root biomass (GLM: $F = 5.47$, $p = 0.0267$) and root C pool (amount of C in the roots per m$^2$ of the soil) (GLM: $F = 6.19$, $p = 0.019$). The type of area (grazed or ungrazed), transect location in the sample plot, ground vegetation biomass, lichen biomass and tree biomass had no effect on soil C content.

The soil C content was the highest in the litter layer and decreased with depth (Fig. 5). The differences between the grazed and ungrazed areas were not statistically significant.

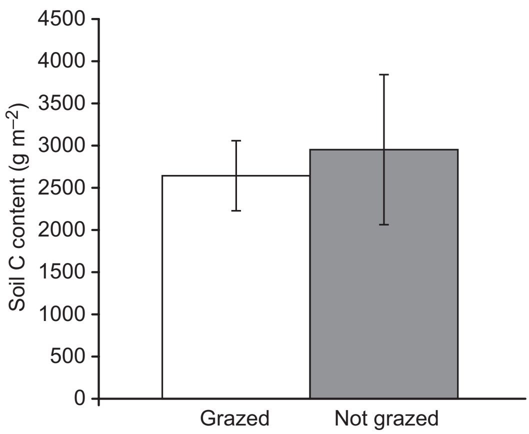


**Fig. 4**. Soil C content at the sites grazed and not grazed by reindeer. 95% significance intervals are shown as error bars.

## Discussion

The influence of reindeer grazing and trampling on the ground vegetation biomass was high as expected. The total ground vegetation biomass was significantly lower in the area grazed by reindeer. Since in our study the initial conditions in both areas were the same, the differences between grazed and ungrazed sites resulted solely from presence or absence of reindeer. This result contradicts the earlier suggestion (Väre *et al*. 1995) that grazing impact might be an artefact resulting from site quality differences in the grazing studies (Helle & Aspi 1983, Ahti & Oksanen 1990). In addition to the effect of reindeer on the total above-ground biomass, we also found that the tree biomass (stems, branches and needles) was higher in the ungrazed area. This result is in accordance with the conclusions of Helle and Aspi (1983) and Jalkanen *et al*. (1995).

No small trees were present in the grazed area, which indicates the lack of natural regeneration. Consequently, negative effects of reindeer herding on tree regeneration, especially after forest harvesting, may be expected to increase with increasing reindeer population being now about three times higher than it was 50 years ago (Kumpula *et al*. 2009, Turunen & Vuojala-Magga 2011).

We found that the loss of vegetation cover did not affect the soil carbon content as the difference between the grazed and ungrazed sites was not statistically significant. The soil carbon content was, however, decreasing with depth at both sites.

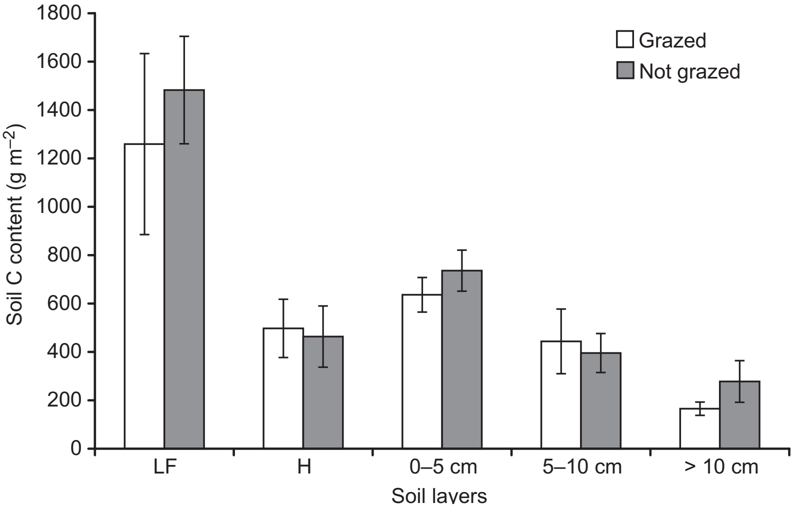


**Fig. 5**. Carbon (C) content in soil layers at the reindeer grazed and ungrazed sites. Error bars show 95% confidence intervals. Mean thickness: LF (grazed) = 2.01 cm, LF (not grazed) = 2.17 cm, H (grazed) = 0.52 cm, H (not grazed) = 0.51 cm).

After the *Cladina* carpet is removed the soil remains exposed before the area is colonized by another species of vascular plants and mosses (Collins *et al*. 1998). This leads to faster warm up of the soil and higher soil temperatures during the vegetation period (Suominen & Oloffson 2000, Rees *et al*. 2003, Susiluoto *et al*. 2008, Rodeghiero *et al*. 2009). Several authors (Kirschbaum 1995, Amundson 2001, Bellamy *et al*. 2005, Rodeghiero & Cescatti 2005) found these to cause faster release of carbon stocks from the soil, however, we could not confirm that in our study. Although mammal herbivores reduce litter production, which in turn leads to a smaller carbon input and smaller carbon accumulation in the surface soil, in our study, we found no difference between grazed and ungrazed sites in this respect. Soil carbon was influenced only by root biomass and root C-content, while grazing mainly affected lichens but not the root biomass. Although there were fewer trees in the ungrazed area, the proportion of trees in the diameter class 13–18 cm that are characterised by dense canopy and high needle biomass was much higher in the areas exposed to reindeer grazing. This diameter class represents trees in their most active growing phase between 40 to 60 years of age.

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## References

Ahti T. 1977. Lichens of the boreal coniferous zone. In: Seward M.R.D. (ed.), *Lichen ecology*, Academic Press Inc., London, pp. 145–181.

Ahti T. & Oksanen J. 1990. Epigiec lichen communities of taiga and tundra regions. *Vegetatio* 86: 39–70.

Amundson R. 2001. The carbon budget in soils. *Annual Review of Earth Planetary Science* 29: 535–562.

Bellamy P.H., Loveland P.J., Bradley R.I., Lark R.M. & Kirk G.J.D. 2005. Carbon losses from all soils across England and Wales 1978–2003. *Nature* 437: 245–248.

Beguin J., Prévost M., Pothier D. & Côté S.D. 2009. Establishment of natural regeneration under severe browsing pressure from white-tailed deere after group seed–tree cutting with scarification on Anticosti Island. *Canadian Journal of Forest Research* 39: 594–605.

Bond-Lamberty P., Beckham S.D., Ahl D.E. & Gower S.T. 2007. Fire as the dominant driver of central Canadian boreal forest carbon balance. *Nature* 450: 89–92.

Cantor L.F. & Whitham T.G. 1989. Importance of belowground herbivory: pocket gophers may limit aspen to rock outcrop refugia. *Ecology* 70: 962–970.

Casabon C. & Pothier D. 2007. Browsing of tree regeneration by white–tailed deer in large clearcuts on Anticosti Island, Quebec. *Forest Ecology and Management* 253: 112–119.

Collins S.L., Knapp A.K., Briggs J.M., Blair J.M. & Steinauer E.M. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280: 745–747.

Danell Ö., Staalland H. & Nieminen M. 1999. Rennäring I Nordvest-Europa. In: Dahle H.K., Danell Ö., Gaare E. & Nieminen M. (eds.), *Reindrift i Nordvest-Europa i 1998 — biologiske muligheter og begrensninger*, Nordisk ministerråd, København, pp. 19–30.

den Herder M., Virtanen R. & Reininen H. 2007. Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. *Basic and Applied Ecology* 9: 324–331.

den Herder M., Kouki J. & Ruusila V. 2009. The effect of timber harvest, forest fire, and herbivores on regeneration of deciduous trees in boreal pine-dominated forest. *Canadian Journal of Forest Research* 39: 712–722.

Duguy B., Rovira P. & Vallejo R. 2006. Land-use history and fire effects on soil fertility in eastern Spain. *European Journal of Soil Science* 58: 83–91.

Emanuelson U. 1985. Human influences on vegetation in theTorneträsk area during the last three centuries. *Ecological Bulletins* 38: 95–111.

Fauria M.M., Helle T., Niva A., Posio H. & 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.

Finland's National Forest Programme 2015. Publications of the Finnish Ministry of Agriculture and Forestry 3b/2008.

Finnish Meteorological Institute. 1991. *Climatological Statistics in Finland 1961–1990. Supplement to the Meteorological Yearbook of Finland*, volume 90, part 1-1990. Finnish Meteorological Institute, Helsinki.

Heggeberget T.M., Gaare E. & Ball J.P. 2002. Reindeer (*Rangifer tarandus*) and climat change: Importance of winter forage. *Rangifer* 22: 13–31.

Helle T. & Aspi J. 1983. Effects of winter grazing by reindeer on vegetation. *Oikos* 40: 337–343.

IPCC 2007. *Climate Change 2007. The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge.

Jalkanen R., Aalto T., Derome K., Niska K. & Ritari A. 1995. Lapin neulaskato. Männyn neulaskatoon 1987 johtaneet tekijät Pohjois-Suomessa. *Metsäntutkimuslaitoksen Tiedonantoja* 544: 1–75.

Janzen H.H. 2006. The soil carbon dilemma: shall we hoard it or use it? *Soil Biology and Biochemistry* 38: 419–424.

Jones R.J.A., Hiederer R., Rusco E., Loveland P.J. & Montanarella L. 2003. Topsoil organic carbon in Europe. In: *Proceedings of the 4th European Congress on Regional Geoscientific Cartography and Information Systems, Bologna, 2003 June 17–20*, pp. 249–251.

Kirschbaum M.U.F. 1995. The temperature dependence of soil organic matter decomposition and the effect of global warming on soil organic carbon storage. *Soil Biology and Biochemistry* 27: 753–760.

Kojola I., Helle T., Niskanen M. & Aikio P. 1995. Effects of lichen biomass on winter diet, body mass and reproduction of semi-domesticated reindeer *Rangifer t. tarandus* in Finlad. *Wildlife Biology* 1: 33–38.

Kumpula J. & Nieminen M. 1992. Pastures, calf production and carcass weights of reindeer calves in the Oraniemi co-operative, Finnish Lapland. *Rangifer* 12: 93–104.

Kumpula J., Tankanen A., Colpaert A., Anttonen M., Törmänen H., Siitari J. & Siitari S. 2009. Porohoitoalueen pohjoisosan talvilaitumet vuosina 2005–2008 — laidunen tilan muutokset 1990-luvun puolivälin jälkeen. *Riista- ja kalatalous — Tutkimuksia* 3: 1–48.

Naiman R.J., Melillo J.M. & Hobbei J.M. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67: 1254–1269.

Neary D.G., Klopatek C.C., DeBano L.F. & Kolliott P.F. 1999. Fire effects on below-ground sustainability: a review and synthesis. *Forest Ecology and Management* 122: 51–71.

Olff H. & Ritchie M.E. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* 13: 261–265.

Oksanen L. & Virtanen R. 1995. Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. Relative importance of climate and grazing. *Acta Botanica Fennica* 153: 1–61.

Owen-Smith N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology* 13: 351–362.

Potvin F., Beaupré P. & Laprise G. 2003. The eradication of balsam fir stands by white-tailed deer on Anticosti Island, Quebec: 150–years process. *Ecoscience* 10: 487–495.

Rasse D.P., Rumpel C. & Dignac M.F. 2005. In soil carbon mostly root carbon? Mechanisms for a specific stabilization. *Plant and Soil* 269: 341–356.

Rees W.G., Williams M. & Vitebsky P. 2003. Mapping land cover in a reindeer herding area of Russian Artic using Landsat TM and ETM+ imagery and indigenous knowledge. *Remote Sensing of Environment* 85: 441–452.

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

Rodeghiero M. & Cescatti A. 2005. Main determinants of forest soil respiration along an elevation/temperature gradient in the Italian Alps. *Global Change Biology* 11: 1024–1041.

Rodeghiero M., Heinemeyer A., Schrumpf M. & Bellamy P. 2009. Determination of soil carbon stocks and changes. In: Kutsch W.L., Bahn M. & Heinemeyer A. (eds.), *Soil carbon dynamics. An integrated methodology*, Cambridge University Press, pp. 49–75.

Ruess R.W., Van Cleve K., Yarie J. & Viereck L.A. 1996. Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forest of the Alaskan interior. *Canadian Journal of Forest Research* 26:1326–1336.

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

Stark S., Tuomi J., Strömmer R. & 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., Julkunen-Tiitto R. & Kumpula J. 2007. Ecological role of reindeer summer browsing in the mountain birch (*Betula pubescens* ssp. *czerepanovii*) forests: effects on plant defense, litter decomposition, and soil nutrient cycling. *Oecologia* 151: 486–498.

Stark S., Kytöviita M.-M., Männistö M. & Neumann A.B. 2008. Microbial and microfaunal communities in Finnish subarctic mountain birch forests used as reindeer ranges. *Applied Soil Ecology* 40: 456–464.

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

Suni T., Berninger F., Vesala T., Markkanen T., Hari P., Mäkelä A., Ilvesniemi H., Hänninen H. Nikinmaa E., Huttula T., Laurila T., Aurela M., Grelle A., Lindroth A., Arneth A., Shibistova O. & Lloyd J. 2003. Air temperature triggers the commencement of evergreen boreal forest photosynthesis in spring. *Global Change Biology* 9: 1410–1426.

Suominen O. & 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. & 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

Turunen M. & Vuojala-Magga T. 2011. *Poron ravinto ja talvinen lisäruokinta muuttuvassa ilmastossa*. Arktisen keskuksen tiedotteita 59, Rovaniemi.

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

Westman C.S. 1995. A simple device for sampling of volumetric forest soil cores. *Silva Fennica* 29: 247–251.