OULU 2014
A 645

ACTA
UNIVERSITATIS OULUENSIS

A
SCIENTIAE RERUM
NATURALIUM

Maria Väisänen

ECOSYSTEM-LEVEL CONSEQUENCES OF CLIMATE WARMING IN TUNDRA UNDER DIFFERING GRAZING PRESSURES BY REINDEER

UNIVERSITY OF OULU GRADUATE SCHOOL;
UNIVERSITY OF OULU,
FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY;
UNIVERSITY OF LAPLAND,
ARCTIC CENTRE

ACTA UNIVERSITATIS OULUENSIS
A Scientiae Rerum Naturalium 645

MARIA VÄISÄNEN

ECOSYSTEM-LEVEL CONSEQUENCES OF CLIMATE WARMING IN TUNDRA UNDER DIFFERING GRAZING PRESSURES BY REINDEER

Academic dissertation to be presented with the assent of the Doctoral Training Committee of Technology and Natural Sciences of the University of Oulu for public defence in Kuusamonsali (YB210), Linnanmaa, on 18 December 2014, at 12 noon

UNIVERSITY OF OULU, OULU 2014

Acta Univ. Oul. A 645, 2014

Supervised by
Doctor Sari Stark
Doctor Sofie Sjögersten

Reviewed by
Professor Anders Michelsen
Associate Professor Riikka Rinnan

Opponent
Professor Philip Wookey

ISBN 978-952-62-0699-8 (Paperback)
ISBN 978-952-62-0700-1 (PDF)

ISSN 0355-3191 (Printed)
ISSN 1796-220X (Online)

Cover Design
Raimo Ahonen

JUVENES PRINT
TAMPERE 2014

Väisänen, Maria, Ecosystem-level consequences of climate warming in tundra under differing grazing pressures by reindeer.
University of Oulu Graduate School; University of Oulu, Faculty of Science, Department of Biology; University of Lapland, Arctic Centre
Acta Univ. Oul. A 645, 2014
University of Oulu, P.O. Box 8000, FI-90014 University of Oulu, Finland

Abstract

Grazing by reindeer (*Rangifer tarandus* L.) affects vegetation and soil microbial processes in tundra ecosystems. It is considered that grazing can induce two alternative vegetation states that differ in plant species composition and the rate of nutrient cycling. I hypothesised that these alternative vegetation states differ in ecosystem responses to climate warming. I tested the hypothesis using a factorial warming and fertilisation experiment on long-term lightly grazed (LG) and heavily grazed (HG) tundra.

The reindeer grazing induced vegetation shift from dwarf shrubs to graminoids increased microbial activities for SOM decomposition. The grazer-induced shifts in vegetation and microbial activities in combination with the fertilisation via urine and faeces had important consequences on soil N availability and soil C quality that determined the ecosystem-level consequences of climate warming. Due to higher soil N availability, warming increased plant productivity (GEP) on HG but not on LG tundra, where N limitation prevented the warming-increased plant production. The varying effects of warming on GEP at different grazing intensities determined the effects of warming on ecosystem net C sink, which was unaffected by warming on HG but decreased on LG tundra. Reindeer grazing reduced the soil C quality, as soils under LG stored a higher proportion of carbohydrates vulnerable to microbial decomposition than soils under HG. According to laboratory soil incubations, the grazer-induced reduction in soil C quality mitigated the responses of soil microbial activity to prolonged warming. Warming caused a stronger decrease in concentrations of phenolics, an important means of plant defence against biotic and abiotic stresses, in *Empetrum nigrum* ssp. *hermaphroditum* under HG than LG.

Grazing history by reindeer, with the associated vegetation shift from dwarf shrubs to graminoids, can significantly alter the ecosystem-level consequences of climate warming. Overall, this thesis highlights that the effects of reindeer grazing on soil properties, soil N availability and C quality, are important determinants of the ecosystem responses to climate warming. Therefore, future research on climate warming should take into account herbivores and aim towards a more holistic approach that includes both aboveground and belowground components of the ecosystem.

Keywords: carbon, climate change, decomposition, extracellular enzyme, plant defence, reindeer, tundra

Väisänen, Maria, Ilmaston lämpenemisen ekosysteemitason vaikutukset porolaidunnuspaineeltaan eroavilla tundra-alueilla.
Oulun yliopiston tutkijakoulu; Oulun yliopisto, Luonnontieteellinen tiedekunta, Biologian laitos; Lapin yliopisto, Arktinen keskus
Acta Univ. Oul. A 645, 2014
Oulun yliopisto, PL 8000, 90014 Oulun yliopisto

Tiivistelmä

Tundralla porolaidunnus vaikuttaa kasvillisuuteen ja maaperän mikrobien toimintaan. Porolaidunnus voi aikaansaada kaksi vaihtoehtoista kasvillisuuden tilaa, jotka eroavat toisistaan paitsi kasvilajiston myös ravinnekierron suhteen. Esitin hypoteesin, jonka mukaan ilmaston lämpenemisen vaikutukset eroavat tundratyypeillä, jotka edustavat vaihtoehtoisia kasvillisuustiloja. Testasin hypoteesia faktoriaalisen lämmitys- ja lannoituskokeen avulla tundra-alueilla, joilla poron laidunnuspaine on ollut pitkäaikaisesti joko kevyttä tai voimakasta.

Poron aiheuttama kasvillisuusmuutos varpuvaltaisesta heinävaltaiseksi lisäsi maaperän mikrobien hajotusaktiivisuutta. Poron aiheuttamat erot kasvillisuudessa ja mikrobiaktiivisuuksissa yhdessä virtsan ja papanoiden lannoittavan vaikutuksen kanssa muuttivat maaperän typen saatavuutta sekä hiilen laatua. Erot maaperän ominaisuuksissa puolestaan ohjasivat ilmaston lämpenemisen ekosysteemitason vaikutuksia. Lämmitys kasvatti ekosysteemituotantoa ravinteikkaalla voimakkaasti laidunnetulla tundralla mutta ei kevyesti laidunnetulla tundralla, joka oli typpirajoitteinen. Lämmityksen erilaiset vaikutukset ekosysteemituotantoon eri laidunpaineissa määrittivät lämmityksen vaikutuksen ekosysteemin hiilinieluun, joka pysyi muuttumattomana voimakkaasti laidunnetulla tundralla mutta pieneni kevyesti laidunnetulla tundralla. Porolaidunnus alensi maaperän hiilen laatua, ja kevyesti laidunnetulla tundralla maaperässä oli enemmän mikrobien hajotukselle alttiita hiilihydraatteja kuin voimakkaasti laidunnetulla tundralla. Laboratoriossa suoritetun inkubaatiokokeen perusteella maaperän hiilen alhaisempi laatu lievensi mikrobien hajotusaktiivisuuden vastetta pitkäaikaiseen lämmitykseen. Lämmitys vähensi pohjanvariksenmarjan fenoliyhdisteiden, jotka ovat tärkeä osa kasvien puolustusta bioottisia ja abioottisia stressitekijöitä vastaan, pitoisuuksia enemmän voimakkaasti kuin kevyesti laidunnetulla tundralla.

Poron laidunnushistoria yhdessä kasvillisuusmuutoksen kanssa voi merkittävästi vaikuttaa ilmaston lämpenemisen ekosysteemitason seurauksiin. Tämän väitöstyön tulokset osoittavat, että poron vaikutukset maaperän typpeen ja hiileen määrittävät lämpenemisen vaikutukset ekosysteemissä. Tulevaisuudessa ilmastonmuutostutkimuksen pitäisikin kokonaisvaltaisemmin huomioida sekä herbivorian että ekosysteemin eri osien merkitys.

Asiasanat: hiili, ilmaston muutos, kasvien puolustusyhdisteet, mikrobien hajotus, poro, solunulkoiset entsyymit, tundra

Acknowledgements

Studying the complex interactions between reindeer grazing and climate warming and their effects on ecosystem processes in tundra has been inspiring but also challenging. I would like to sincerely thank my supervisor Sari Stark, firstly for teaching me the importance of a theoretical framework in ecological research and the background of the different theories involved in this thesis – and they were many! Secondly, Sari introduced me to the marvellous world of various soil analyses. This kind of practical work in the laboratory has been really agreeable and concrete. I am thankful for this opportunity and I consider it a privilege, although it took a lot of time. Finally, I would like to thank Sari for giving ideas and solutions for the countless problems in data processing and interpretations, and patiently commenting and correcting the manuscripts.

I would also like to thank my other supervisor Sofie Sjögersten. Sofie taught me how to measure CO_2 fluxes in the field and how to further process the data. Sofie also organised the collaborators for the NMR analysis and environmental modelling – this on short notice. I am grateful for the chance to work at the University of Nottingham for nearly two months. It was nice to meet Sofie's family, especially her son, John, as well as the collaborators at the University of Nottingham. I would like to thank Neil Crout, who conducted the modelling of the CO_2 fluxes, and David Large, Trevor Drage, Miguel Castro-Diaz and Colin Snape, who conducted the NMR analysis. I would also like to thank Darren Hepworth and John Corrie, who helped me with laboratory work, and finally all other people and especially the PhD students at the School of Biosciences. You all made me feel welcome.

During these four years many people have been involved in this thesis project. I am most grateful for Elina Kaarlejärvi and Johan Olofsson and their field assistants, especially Jonas Gustafsson, from the University of Umeå. Elina was responsible for the vegetation analysis during years 2010–2013 and her accuracy in recording the vegetation cover as well as in analysing and interpreting the data was irreplaceable, as were her comments on the manuscripts. Johan's apt and brilliant comments, opinions and ideas on the CO_2 paper as well as on other data were really inspiring and helpful; Johan also provided the NDVI data. I spent summer 2011 in the field with Henni Ylänne from the University of Oulu measuring CO_2 fluxes, and during summer 2013 we, again, did both field work and lab work together. I want to thank Henni for helping with the measurements and for processing the CO_2-flux data from 2011, which formed an essential part of my thesis, and especially for being such a flexible, helpful and hardworking Masters, now PhD, student. It was not always nice to be up in the field under very varying weather conditions, even during the night with devices that usually broke down one by one. Françoise Martz from the Finnish Forest Research Institute, Rovaniemi Research Unit, was responsible for analysing the phenolics of mountain crowberry – a task which turned out to be extremely challenging. Without Françoise's expertise it would not have been possible to publish the article IV in its current form with detailed information on the phenolic compounds. Françoise also taught me the principles, how to process plant samples and analyse plant phenolics, and during the writing process she also showed me that, in addition to the way of an ecologist, there is another way of thinking and interpreting the results – the way of a plant physiologist. I think that this was a good lesson for me and I will try to keep it in mind in the future. Riitta Julkunen-Tiitto helped to analyse and identify plant phenolic compounds. Her expertise on phenolic compounds was valuable.

I owe special thanks to Aarno Niva and Sirkka Aakkonen at the Finnish Forest Research Institute, Rovaniemi Research Unit. Aarno had an irreplaceable role in the practical planning and execution of the field experiment, as he organised the materials for open top chambers and short-term reindeer exclosures as well as helped a lot in the hard work of constructing them. Sirkka contributed significantly to all laboratory analyses involved in this thesis and always helped me with various problems in the lab, she also helped me with the CO_2-flux measurements during summer 2012. Both Aarno and Sirkka contributed to the maintenance of the field experiment, which was a laborious task. I also want to thank Juha Hyvönen from the Finnish Forest Research Institute, Rovaniemi Research Unit, for helping with the statistical design. This thesis project has been fertile and during the years has provided new research ideas and projects that have led to an increasing group of scientists working with the same field experiment. I want to express my gratitude to this wide research network that includes Minna Männistö, Lars Ganzert, Liliane Ruess, Max Häggblom, Ville-Veikko Telkki, Anu Kantola and Alex Nyakumba. They have all been involved in projects, the results of which will hopefully be published in the near future.

From the University of Oulu I would like to thank Satu Huttunen and Minna Vanhatalo for helping me in the beginning and also during my thesis project with practicalities; and the follow-up group members Juha Tuomi, Annamari Markkola and Aino Smolander from the Finnish Forest Research Institute, Vantaa Research Unit, for our annual meetings. I also appreciate the help by Tuulikki Pakonen and Tarja Törmänen in soil analyses. At the Arctic Centre, all colleagues created an inspiring and encouraging working atmosphere, and I am sincerely grateful to all of you. Especially I thank Bruce Forbes, Osmo Rätti, Riitta Aikio, Tuija Katermaa, Arto

Vitikka, Kari Jantunen and Pertti Leinonen as well as Raija Kivilahti and Minna Turunen. I also thank Magne Elvestad from Sappen, Norway, who provided us accommodation facilities during our field trips and valuable information about the field conditions, weather and reindeer migrations.

I thank PhD students Hélène Prouillet-Leplat and Maria Tuomi as well as Hanna Vuorenpää for their peer support. It has been comforting to realize that we have all been dealing with the same problems. I met Hélène and Maria during the thesis project, and I truly hope that we can continue our work and discussions about soil in the future. Finally, I want to thank my family and friends for their support during this project. Tuukka, I want to thank you for sharing with me the ups and downs every day, for encouraging and understanding me and even for helping me in the lab and field work.

This research was conducted in the facilities of the Finnish Forest Research Institute, Rovaniemi Research Station, Arctic Centre, University of Lapland and Department of Biology, University of Oulu. Research was funded by the Academy of Finland (Project number 130507), providing salary and everything for the field and lab work during years 2010–2014; and for finalising the thesis, the Lapland Regional Fund and the Tauno Tönning Foundation.

Rovaniemi, August 2014 Maria Väisänen

Abbreviations

LG	Lightly grazed tundra
HG	Heavily grazed tundra
HGexc	Heavily grazed tundra with short-term reindeer exclosure
CTL	Control
W	Warming
F	Fertilisation
OTC	Open top chamber
NH_4NO_3	Ammonium nitrate
SOM/OM	Soil organic matter/organic matter
C	Carbon
CO_2	Carbon dioxide
NEE	Net ecosystem exchange
GEP	Gross ecosystem production
R_e	Ecosystem respiration
PAR	Photosynthetically active radiation
N	Nitrogen
P	Phosphorus
EEA	Extracellular enzyme activity
AP	Acid-phosphatase
BG	β-glucosidase
LAP	Leucine-aminopeptidase
NAG	*N*-acetylglucosamidase (chitinase)
PO	Phenol oxidase
GC	Gas chromatography
HPLC	High-performance liquid chromatography
CPMAS	Cross-polarisation magic angle spinning
NMR	nuclear magnetic resonance spectroscopy

List of original articles

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

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

II Väisänen M, Sjögersten S, Large D, Drage T & Stark S. Reduced temperature sensitivity of soil C decomposition after long-term reindeer grazing in subarctic tundra. Manuscript.

III Stark S & Väisänen M (2014) Insensitivity of soil microbial activity to temporal variation in soil N in subarctic tundra: Evidence from responses to large migratory grazers. Ecosystems 17: 906-917.

IV Väisänen M, Martz F, Kaarlejärvi E, Julkunen-Tiitto R & Stark S (2013) Phenolic responses of mountain crowberry (*Empetrum nigrum* ssp. *hermaphroditum*) to global climate change are compound specific and depend on grazing by reindeer (*Rangifer tarandus*). Journal of Chemical Ecology 39: 1390-1399.

Contents

1 Introduction

1.1 The role of herbivores in ecosystems

Trophic interactions form one of the fundamental questions of ecology, as the transfer of energy and nutrients between trophic levels drives the functioning of ecosystems. Among the most important trophic interactions is that between plants and herbivores. For several decades scientists have been puzzled by why terrestrial ecosystems are widely covered by vegetation – "Why is the world green?" – despite the existence of herbivores with the capacity to consume plant biomass (Hairston *et al.* 1960). Currently it is acknowledged that aboveground herbivory consumes a relatively small proportion of plant production, because plants commonly defend against herbivores and because predators control herbivore populations. However, herbivores still exert significant effects on energy flow and the cycling of nutrients in most terrestrial ecosystems (Chapin *et al.* 2011).

The effects of herbivores include direct losses of aboveground plant biomass, physical disturbance and excretion of waste products that all form a complex set of interactions between plants and animals (Schulze *et al.* 2005). Herbivores often selectively consume more palatable plant species and therefore provide a competitive advantage to chemically defended unpalatable species (Pastor & Naiman 1992, Augustine & McNaughton 1998). Herbivory may also induce compensatory growth in palatable species, which increases their dominance in the plant communities (Pastor & Naiman 1992, Augustine & McNaughton 1998). Herbivory may enhance the nutrient content of some plant species but in contrast increase the amount of defensive chemicals in other plant groups (Coley *et al.* 1985). Aboveground foliar herbivory may also affect root biomass and the exudation of labile compounds by the roots to the soil (Bardgett *et al.* 1998, Hamilton *et al.* 2008, Hafner *et al.* 2012). Herbivores alter soil processes such as C and N mineralisation, because the effects of herbivory on vegetation influence the quantity and quality of plant litter input to soil, which in turn is a powerful determinant of soil microbial activities (Bardgett a& Wardle 2003). Furthermore, the excretion of urine and faeces directly increases soil N concentrations, and trampling by grazers causes physical disturbance of the soil surface (Bardgett & Wardle 2003). It has also been suggested that the effects of herbivory vary depending on site fertility so that in fertile habitats herbivory increases plant production, forage quality and the rates of soil microbial processes, whereas in infertile habitats the opposite is true (Wardle *et al.* 2004). These grazer-induced interactions through C and N mineralisation create feedback on plant nutrient availability and soil C cycling, which in turn influence plant productivity. A holistic understanding of terrestrial ecosystem functioning should therefore include decomposer microorganisms in addition to plants and herbivores.

Among herbivores, the role of ungulate grazers is probably the most widely recognised. Worldwide, grazing by both domestic and wild ungulates has both ecological and economic significance and is the most widespread means of land use, as half of the Earth's land surface is grazed by ungulates (Olff *et al.* 2002). Many ungulate species execute seasonal long-distance migrations that are among the most spectacular biological phenomena on Earth (Berger 2004). Grazing by ungulates is a major driver of global vegetation dynamics and affects ecosystem productivity, vegetation composition and plant morphological and functional traits (Milchunas & Lauenroth 1993, Diaz *et al.* 2007). In addition to the aboveground vegetation processes, the impacts of ungulate grazing on the belowground soil processes are significant. The effects of ungulates on soil N dynamics have been studied for decades and are relatively well known (Hobbs 1996, Singer & Schoenecker 2003, Augustine & McNaughton 2006, Xu *et al.* 2007), whereas the effects on soil C dynamics are less well known. The ungulate-driven effects on soil C dynamics are important, because globally soils store more than three times as much C as the atmosphere and vegetation (Schmidt *et al.* 2011) and ungulate grazers have the potential to affect global C cycles (Tanentzap & Coomes 2012).

1.2 Effects of reindeer grazing on tundra vegetation and soil

In the circumpolar Arctic, migratory reindeer (*Rangifer tarandus* L.) is a keystone herbivore with significant effects on vegetation and soil processes (Forbes & Kumpula 2009). In unproductive ecosystems, such as tundra, the role of herbivores in controlling vegetation dynamics may be of uttermost importance (Oksanen & Oksanen 2000). Reindeer grazing induces parallel shifts in the vegetation and soil processes (Olofsson *et al.* 2001, Stark & Grellmann 2002, Stark *et al.* 2002, Olofsson *et al.* 2004, van der Wal *et al.* 2004, Stark *et al.* 2012). According to the studies conducted so far, the reindeer-mediated effects on ecosystem processes may be highly site-specific. In contrast with the theory that the direction of the effect of grazing on soil C and nutrient cycling depends on site fertility (Wardle *et al.* 2004), both enhancing and retarding effects of reindeer grazing have been reported for both productive and unproductive habitats, but the sources of this spatial variation are not yet fully understood (Stark 2002, Bardgett 2005, Stark *et al.* 2014).

It has been hypothesised that in some conditions, reindeer grazing causes a shift in vegetation, which in unproductive systems is a transition from lichen to moss dominance and in productive systems is a transition from dwarf shrub to graminoid dominance (van der Wal 2006). According to this theory, the presence or absence of grazing thus creates two alternative steady states of tundra vegetation, and the change between the two states is relatively sudden, predictable and reversible. The theory was based on frequent observations that in nutrient-rich tundra heaths, grazing by reindeer increases the abundance of grasses and herbs relative to dwarf shrubs and enhances plant productivity, litter and soil decomposition rates (Olofsson *et al*. 2001, Olofsson & Oksanen 2002, Stark *et al*. 2002, Olofsson *et al*. 2004). In turn, in nutrient-poor conditions, reindeer grazing reduces the abundance of lichens but often increases the abundance of mosses (Gaare 1997, van der Wal *et al*. 2001, den Herder *et al*. 2003, Boudreau & Payette 2004). At the same time, grazing may increase ecosystem productivity via enhancing soil N cycling, in which fertilisation via urine and faecal deposits and changes in the soil microclimate may constitute major underlying mechanisms (van der Wal 2006). Although it is known that the vegetation shift described by van der Wal (2006) does not always occur (Grellmann 2002, Bråthen *et al*. 2007, Olofsson *et al*. 2010, Tommervik *et al*. 2012), it has been repeatedly shown that in many cases reindeer grazing promotes the abundance of graminoids compared to dwarf shrubs and mosses in tundra vegetation (Manseau *et al*. 1996, Post & Klein 1996, Olofsson *et al*. 2001, Olofsson *et al*. 2004, van der Wal *et al*. 2004, van der Wal & Brooker 2004, Gornall *et al*. 2009, Kitti *et al*. 2009, Zamin & Grogan 2013).

1.3 Potential ecosystem consequences of reindeer-induced shifts in vegetation and soil

Reindeer-induced vegetation shift is considered to increase plant productivity, alter soil abiotic conditions and enhance litter and soil decomposition processes leading to increased soil N availability (*sensu* van der Wal 2006; Fig. 1). However, it is less well known how changes in the vegetation and soil nutrient cycling feedback on aboveground–belowground interactions and ultimately various ecosystem properties and processes (Fig. 1). Because reindeer grazing increases plant production (i.e. C assimilation) but also accelerates microbial decomposition processes (i.e. C release), reindeer may have the potential to affect ecosystem C fluxes and ultimately C balance.

Plants defend against multiple abiotic (e.g. nutrient stress) and biotic stresses (e.g. herbivores and plant pathogens) by producing secondary phenolic compounds in the plant tissues (Ayres *et al.* 1997, Hamilton *et al.* 2001, Vermerris & Nicholson 2006, Hernandez *et al.* 2009, Salminen & Karonen 2011). It has been suggested that N deficiency may induce the biosynthesis of phenolics (Bryant *et al.* 1983), as in nutrient limited conditions, plants may allocate C to the biosynthesis of phenolics instead of plant growth (Herms & Mattson 1992). More recently, it was suggested that the amount of photosynthetically active radiation (PAR) that exceeds plants' photosynthetic capacity causes oxidative stress for plants, which induces synthesising of plant phenolics with high antioxidative properties (Close & McArthur 2002). According to this hypothesis, in cases where low temperature and low soil N availability limit the photosynthetic capacity, the oxidative stress and the need for plant protection by phenolics also increase (Close & McArthur 2002). In tundra, both low temperature and low soil N availability limit plant photosynthesis (Chapin *et al.* 1995), which may cause the oxidative stress in relation to PAR to be high. To date, there have been few investigations on the effects of reindeer grazing on plant defence exist. If soil nutrient availability is an important determinant for plant phenolic concentrations, grazing by reindeer could decrease the need for antioxidative phenolics (Hernandez *et al.* 2009, Khadem & Marles 2010) through increasing soil N availability. In turn, higher risk of biomass losses to reindeer browsing could increase the need for phenolics in herbivore protection (i.e. condensed tannins; Ayres *et al.* 1997). The reindeer-mediated effects on the phenolic concentrations of tundra vegetation may then change forage palatability, pathogen resistance, allelopathic interactions and litter quality.

The chemical quality of belowground soil C is largely determined by the aboveground vegetation composition, because the different plant species and growth forms vary substantially in the decomposability of litter they produce (De Deyn *et al.* 2008). The dominant vegetation composition forms an important determinant for the quality of the accumulated soil C (Hobbie & Gough 2004, Vancampenhout *et al.* 2009). The chemical quality of litter and soil C, in turn, determine the decomposition rates as well as how the decomposition rates respond to changes in temperature sensitivity. According to the kinetic theory, the degradation of highly aromatic organic matter (OM; i.e. high concentrations of phenolic compounds, such as lignin) is slow, but the degradation rates increase with temperature to a greater extent than the degradation rates of labile organic compounds (Bosatta & Ågren 1999, Davidson & Janssens 2006). Increasing temperature sensitivity of decomposition with declining C quality has been repeatedly shown for both soil (Fierer *et al.* 2003, Fierer *et al.* 2006, Conant *et al.* 2008a, Conant *et al.* 2008b, Craine *et al.* 2010a, Craine *et al.*

2010b, Wagai *et al*. 2013, Lefévre *et al*. 2014) and litter (Fierer *et al*. 2005, Conant *et al*. 2008a, Craine *et al*. 2010b).

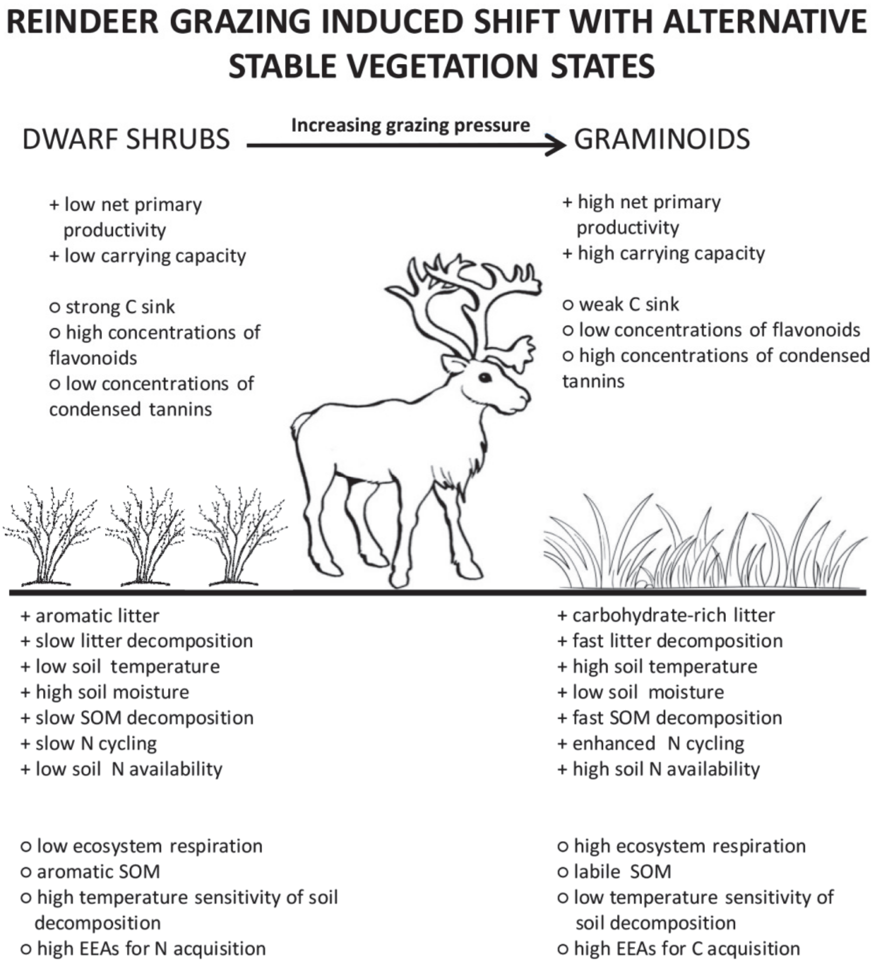

Fig. 1. Shifts in ecosystem processes and properties that parallel a vegetation shift caused by reindeer grazing (after Van der Wal 2006). Shifts that have already been experimentally confirmed are indicated with (+) while potential shifts are indicated with (○).

Although the effects of grazing on vegetation are well documented, it is not known how reindeer-induced vegetation shift might influence the quality of accumulated soil C. As ungrazed tundra are dominated by dwarf shrubs with high aromaticity, whereas grazed tundra are dominated by graminoids with low aromaticity and high proportions of carbohydrates such as cellulose (Hobbie 1996, Cornelissen *et al*. 2007, De Deyn *et al*. 2008), grazing could exert an important influence on soil C quality and ultimately the responses of microbial activity to increasing temperature. Changes in the plant litter quality by reindeer grazing may not be immediately reflected in soil C quality because it takes a long time until plant litter is transformed into accumulated SOM (Stark *et al*. 2008). Most of the ecosystem C pool in tundra ecosystems is stored as soil C (Hartley *et al*. 2012) and tundra soil C stocks are globally important (Davidson & Janssens 2006), thus determining the relationship of grazer-induced vegetation shifts with soil C quality and decomposition processes is very important.

The breakdown of organic compounds in litter and SOM is mediated by hydrolytic and oxidative extracellular enzymes (EEs) produced by soil microbes to catalyse the rate-limiting steps in the degradation of specific organic substrates for microbial assimilation of C and nutrients (Sinsabaugh *et al*. 2008). It is considered that nutrients affect EEAs through the stoichiometry of microbial C:N:P demand. Increased N availability may then specifically enhance enzyme activities related to microbial C acquisition (e.g. β-glucosidase, BG) and microbial P acquisition (e.g. acid-phosphatase, AP), reduce activities related to microbial N acquisition (e.g. leucine-aminopeptidase, LAP; and N-acetylglucosamidase, NAG; Sinsabaugh *et al*. 2008). Some studies suggest, however, that EEAs are also regulated by the availability of substrates that originate from plant and microbial residues, so that each EEA may be increased by high availability of the corresponding substrate (Hernández & Hobbie 2010). So far, how grazing influences the degradation rates of the various organic compounds in SOM has not been investigated. It is also unknown to what extent the impacts of grazing on soil C decomposition are transmitted in relation to timing of grazing due to reindeer migrations. As tundra soils are generally N-poor (Schimel & Bennett 2004), and N constitutes an important component of enzyme structure, it has been hypothesised that N limitation in tundra may limit the capacity of soil microbes to synthesise EEs for C acquisition, such as BG and cellobiohydrolase (Schimel & Weintraub 2003, Wallenstein *et al*. 2009). In tundra ecosystems, the strong grazer-induced increase in soil N availability could thus constitute a prominent mechanism through which reindeer grazing influences soil microbial activity.

1.4 The ongoing climate change in tundra

During the past century, the mean temperatures in the Arctic have increased at nearly twice the rate of the global average, and the projected temperature increase by the year 2100 is predicted to be 2–9 °C (IPCC 2013). Low temperatures and short growing seasons have historically limited the soil C decomposition in tundra and, due to the past accumulation of SOM, tundra soils currently store half of the global soil C pool (Tarnocai *et al.* 2009). The ongoing climate warming is predicted to enhance microbial activities for SOM decomposition and increase mineralisation of both C and N (Hobbie *et al.* 2002, Weintraub & Schimel 2005a). If C stored in these long-term soil pools is released to the atmosphere as CO_2 due to warming, the consequent increase in atmospheric CO_2 concentrations could even outweigh the greenhouse gas emissions from anthropogenic fossil fuel combustion and exert a positive feedback loop on climate change (Cox *et al.* 2000, Davidson & Janssens 2006). Observations that some tundra systems had shifted from net C sinks to net C sources were made in the early 1990s (Oechel *et al.* 1993). Understanding the responses of tundra C cycling to climate warming is thus of uttermost importance.

As plant growth in tundra ecosystems is limited by low temperatures, climate warming is expected to enhance plant productivity. However, it is still unclear to what extent the increases in plant production and C assimilation induced by climate warming can counterbalance the parallel increases in soil decomposition and C release, and whether tundra areas will turn from long-term net C sinks into net C sources (Davidson & Janssens 2006). Along with plant production, climate warming induces changes in plant species composition. Tundra ecosystems have become ‘greener’, which is often associated with increased abundance of shrub biomass and simultaneous decrease in cryptogams (Walker *et al.* 2006). Dwarf birch (*Betula nana*) has especially increased in abundance due to warming (Myers-Smith *et al.* 2011). Climate warming may also enhance litter production (Elmendorf *et al.* 2012). Warming experiments also suggest that climate warming alters plant phenolic concentrations, which could have important effects on plant defence against pathogens as well as forage palatability for herbivores and litter decomposability (Graglia *et al.* 2001, Hansen *et al.* 2006, Nybakken *et al.* 2008).

To date, predictions on the effects of tundra climate warming have emphasised the importance of the ongoing shrub encroachment and the associated impacts on ecosystem processes. Increasing abundance of shrubs may significantly contribute to vegetation productivity (Street *et al.* 2007). Shrub encroachment may also alter decomposition and N mineralisation rates through influencing litter quality

(Cornelissen *et al*. 2007). Shrub encroachment also has complex effects on soil temperatures: wintertime soil temperatures may increase via increased snow accumulation, whereas soil temperatures in the growing season may decrease via increased shading (Myers-Smith *et al*. 2011). However, the responses of vegetation to warming exhibit a strong regional variation (Elmendorf *et al*. 2012). Moreover, it has not yet been investigated how warming affects vegetation and ecosystem processes in intensively grazed tundra, which are dominated by graminoids (van der Wal 2006) and where the increasing abundance of dwarf shrubs due to warming is heavily suppressed by grazing (Post & Pedersen 2008, Olofsson *et al*. 2009). If grazing counteracts the warming-induced increase in dwarf shrubs, grazing by reindeer could mitigate the ecosystem-scale change that would otherwise take place due to climate warming. To date, no clear predictions have been formulated on the consequences of climate warming on vegetation and other ecosystem properties in intensively grazed graminoid-dominated tundra, which theoretically could represent another alternative steady state of tundra vegetation (van der Wal 2006).

2 Aims of the study

In this thesis, I ask the question, “Do the ecosystem-level consequences of climate warming differ between the heavily grazed (HG) and the lightly grazed (LG) tundra, the alternative states of tundra vegetation (*sensu* van der Wal 2006)?” Interactions between reindeer grazing and climate warming were studied using experimental warming and fertilisation treatments employed at two levels of grazing intensity: HG tundra dominated by graminoids and LG tundra dominated by dwarf shrubs. Each study focused on a different ecosystem component, and the main research questions and hypotheses were as follows:

1. *How will climate warming affect ecosystem C balance in lightly and heavily grazed tundra (I)?*

Climate warming is predicted to increase soil C losses via enhanced decomposition (i.e. ecosystem respiration, R_e) but also increase gross ecosystem productivity (GEP). Thus, the effect of climate warming on ecosystem C balance (net ecosystem exchange, NEE) is largely determined by a balance between the effects of warming on GEP and R_e. I firstly predict that (**1.1**) under ambient climate the HG tundra is a weaker sink for C (i.e. NEE less negative) via higher R_e, because grazing enhances litter and soil C decomposition. Secondly, I predict that (**1.2**) warming and fertilisation increase GEP more under HG than LG, as graminoids respond rapidly to environmental change. Because NEE is determined by the balance between GEP and R_e, I expect the responses of NEE to treatments to be weaker under HG than LG. I further predict that (**1.3**) excluding reindeer grazing in the heavily grazed tundra (HGexc) amplifies the effects of warming and fertilisation on GEP and thus the responses of NEE to treatments are weakest under HGexc.

2. *How does grazer-induced vegetation shift influence the chemical quality of soil C and the temperature sensitivity of decomposition (II)?*

The chemical composition of accumulated soil C is mainly determined by the plant species composition (De Deyn *et al.* 2008). Dwarf shrub-dominated vegetation produces lignin-rich (i.e. highly aromatic) and slowly decomposable litter, whereas graminoid-dominated vegetation produces lignin-poor and rapidly decomposable litter (Hobbie 1996, De Deyn *et al.* 2008). Kinetic theory states that decomposition rates of aromatic compounds are slow but respond strongly to increasing temperatures

(Bosatta & Ågren 1999, Fierer *et al.* 2005, Davidson & Janssens 2006). Because LG tundra is dominated by dwarf shrubs whereas HG tundra is dominated by graminoids, I predict that (**2**) in the LG tundra, soil C is more aromatic, and therefore the decomposition is slower overall but increases more with temperature than in the HG tundra.

3. *Does reindeer grazing enhance soil C decomposition through alleviating N-limitation of microbial activity (III)?*

It has been suggested that in tundra ecosystems, low N availability may limit the microbial synthesis of EEs, and in this way, the capacity of microbes for SOM degradation (Schimel & Weintraub 2003, Sistla *et al.* 2012). EEAs also show seasonal variation that parallels variations in soil N availability (Weintraub & Schimel 2005b, 2005c, Wallenstein *et al.* 2009). Soil N availability is higher for HG compared to LG tundra (Olofsson *et al.* 2001, Stark *et al.* 2002, Olofsson *et al.* 2004) and soil microorganisms may synthesise enzymes based on the stoichiometry of microbial C:N demand (Sinsabaugh *et al.* 2008). Thus, I predict that (**3.1**) EEAs related to C acquisition are higher under HG, whereas the EEAs related to N acquisition are higher under LG. I further predict that (**3.2**) the effects of grazing on EEAs are strongest during the specific period of reindeer migration, when the effect of grazing on soil N availability is at its highest.

4. *How does climate warming influence defences in* Empetrum nigrum *ssp.* hermaphroditum *at different levels of grazing intensity (IV)?*

It is generally considered that tundra plants need high levels of defence against biotic stresses (Graglia *et al.* 2001, Nybakken *et al.* 2011) and abiotic stresses (Martz *et al.* 2010). Soil N availability is significantly lower under LG than HG (Olofsson *et al.* 2001, Stark *et al.* 2002, Olofsson *et al.* 2004). Low soil N availability in turn is considered to increase oxidative stress and induce a higher need for synthesising antioxidative phenolics (Close & McArthur 2002). I predict that (**4.1**) concentrations of phenolics are higher under LG than HG and that (**4.2**) due to the alleviation of nutrient limitation, experimental warming decreases phenolic concentrations to a stronger extent under HG than LG.

3 Materials and methods

3.1 Study site

All studies were conducted on a mesic arctic–alpine tundra heath at Raisduoddar Fjell (69° 31′ N, 21° 19′ E) in northern Norway during years 2010–2012 (Fig. 2). Mean temperature and precipitation in 2010 and 2012 were close to the long-term average (–0.5 °C, 500–700 mm), while in 2011 average temperature was 1.5–2.0 °C warmer and precipitation 125% of average. The predominant vegetation in the area is of Arctic Empetrum–Dicranum–Lichen type heath (Oksanen & Virtanen 1995). The study area is bisected by a pasture rotation fence that extends throughout northernmost Norway. The fence was built in the 1960s to reduce the risk of reindeer entering winter ranges during summer. The HG side of the fence is subject to heavy grazing pressure during the reindeer migration in late summer. The LG side of the fence is only briefly used for passage during spring and autumn because the pasture rotation fence prevents any access to the area during summer. In this way, the HG and LG sides of the pasture rotation fence represent two stages of tundra vegetation that differ markedly in their past 50 years of grazing (Fig. 3). This unique experimental set-up enables study of the long-term effects of reindeer grazing-induced vegetation shift on aboveground and belowground processes.

The difference in grazing intensity has induced a shift in dominant vegetation (Olofsson *et al*. 2001, 2004). Under LG, vegetation is dominated by evergreen and deciduous dwarf shrubs (*Empetrum nigrum* ssp. *hermaphroditum*, *Betula nana*, *Vaccinium vitis-idaea*, *V. myrtillus* and *V. uliginosum*). Under HG, vegetation is dominated by graminoids (*Carex* spp., *Deschampsia flexuosa*, *Festuca* spp. and *Juncus trifidus*) with patchy occurrence of mountain crowberry (*E. nigrum* ssp. *hermaphroditum*) and other dwarf shrubs (*V. myrtillus* and *V. vitis-idaea*). Growing season (June–August) soil temperature averaged over 2010–2012 was lower in LG than HG soils (7.5 ± 0.3 and 9.0 ± 0.3 °C, respectively), whereas the surface temperatures were approximately 9.5 °C for both grazing intensities (analysed with EasyLog EL-USB-1, Lascar electronics). Soil ammonium (NH_4^+) concentrations were 19 times higher for HG than LG (888.7 ± 61.7 and 46.8 ± 6.7 mg m^{-2}, respectively) and soil nitrate (NO_3^-) concentrations 4.6 times higher for HG than LG (99.0 ± 31.1 and 21.3 ± 2.7 mg m^{-2}, respectively) in 2010. The soil pH in the area varied within pH 4.8–5.4 and was not affected by grazing.

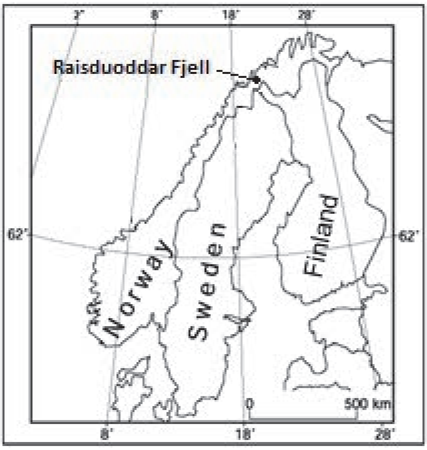

Fig. 2. Study area, Raisduoddar Fjell, located in mesic northern Norway. All studies were conducted in the same area.

Fig. 3. The study site was a tundra heath separated by a pasture rotation fence. The lightly grazed (LG) site is dominated by dwarf shrubs and used briefly for passage, while the heavily grazed (HG) site is dominated by graminoids and intensively browsed, trampled and fertilised by reindeer in August. Photograph by S. Stark.

3.2 Field experiment

To examine the effects of grazing history on ecosystem responses to climate warming, a factorial warming and fertilisation experiment was established in 2010. Eight blocks extending to ca. 300 m distance and traversing the LG and HG side of the fence were selected with similar topography and altitude within blocks. The experimental area covered ca. 1.5 hectares. Each block on both LG and HG tundra had four plots assigned to the following treatments: control (CTL), fertilised (F), warmed (W) and warmed and fertilised (WF; Fig. 4A, B). To study the short-term effects of reindeer grazing, plots on HG tundra were divided into grazed (HG) and ungrazed (HGexc) subplots protected from grazing by short-term exclosures established at the beginning of reindeer migration to the area and removed before winter (Fig. 4C). The experimental design did not include short-term exclosures on LG tundra due to very low grazing pressure.

Warming was achieved using open top chambers (OTCs, ITEX standard) that were set in place at the beginning of the growing season and removed just before reindeer migration. OTCs did not affect growing season (June–August) soil temperature averaged over 2010–2012, but increased the mean daily surface air temperature by 0.9 and 1.8 °C in LG and HG, respectively. Fertilisation was applied as ammonium nitrate (NH_4NO_3, equivalent to 10 g N m^{-2}; Mack *et al.* 2004) early in the growing season (for more details, see paper I). Fertilisation increased NH_4^+ content six-fold for LG, but had no effect for HG. Warming decreased NH_4^+ content by 44.9 %, and combined warming and fertilisation treatment increased NH_4^+ content by 25.8 %. Soil NO_3^- did not respond to any of the treatments.

Fig. 4. The experimental design consisted of factorial treatments of warming with OTCs (A) and fertilisation with NH_4NO_3 (B) and short-term reindeer exclusion at the HG side (C). Photographs by S. Stark.

3.2.1 CO_2 fluxes and vegetation analysis

To examine how responses of ecosystem C fluxes to warming and fertilisation varied under different grazing intensities, NEE (i.e. light measurement) and R_e (i.e. dark measurement, with chamber covered by an opaque white hood) were measured throughout the growing seasons of 2011 and 2012 (Fig. 5A, I). NEE and R_e were used to calculate GEP. The CO_2 concentration (ppm), relative humidity (%) and temperature (°C) were measured using custom-made cylinders with a Vaisala Carbon Dioxide Probe (GMP343) and a Humidity and Temperature Probe (HMP75), and data was logged using a Vaisala Measurement Indicator (MI70, Fig. 5B). To determine how vegetation responded to simulated climate change under different grazing pressures, plant and litter abundances were recorded in mid-August 2010–2012 using a modified point-intercept method (I and IV). Applying fertiliser in a single dose may have caused bias, because high nutrient concentrations may have toxic effects for plants (Phoenix *et al*. 2012).

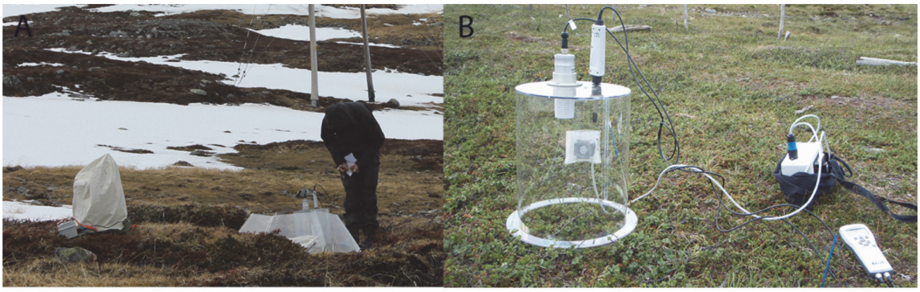

Fig. 5. The CO_2 fluxes were measured in light and dark throughout the growing seasons (A). Measuring was conducted with custom-made cylinders equipped with Vaisala Carbon Dioxide, Humidity and Temperature Probes fitted to the top (B). Photographs by S. Stark.

3.2.2 Microbial extracellular enzyme activities

To investigate seasonal variation in soil N availability and EEAs, and to test the significance of N limitation through experimental fertilisation, soil samples were collected from the vicinity of the CTL plots every two weeks during the 2011 snow-free period from LG and HG sides, and from CTL and F plots in August and

September 2010. The concentrations of total extractable N, NH_4-N and NO_3-N and microbial N were analysed from soil extracts. Microbial respiration was analysed using gas chromatography (GC) and the activities of five different enzymes – AP, BG, LAP, NAG and phenol oxidase (PO) – were analysed spectrophotometrically (Boerner *et al*. 2000) (III).

AP catalyses the release of phosphate by hydrolysing the phosphoric ester bonds of phosphate groups in organic molecules; BG releases glucose from cellulose; LAP catalyses the hydrolytic release of leucine and other amino acids from peptides; NAG hydrolyses N-acetyl glucosamide residues from chitin-derived oligomers; and PO catalyses the oxidative reactions in decomposition of phenolics (Weintraub *et al*. 2007, Sinsabaugh *et al*. 2008). Soil microbes synthesise AP for P acquisition, BG for C acquisition and LAP and NAG for N acquisition (Weintraub *et al*. 2007, Sinsabaugh *et al*. 2008), whereas PO can be synthesised for either C or N acquisition (Sinsabaugh 2010).

3.2.3 Phenolic concentrations of mountain crowberry

To test how the grazer-induced differences in soil N availability interacted with the responses of plant phenolics to climate warming, leaf samples of a dominant evergreen dwarf shrub, mountain crowberry (*E. nigrum* ssp. *hermaphroditum*), were collected during growing seasons 2010 and 2011 from all experimental plots containing crowberry. We selected mountain crowberry for study because phenolics produced by it exert significant ecosystem-level effects, due to their assumed allelopathic effects (Gallet *et al*. 1999). Studies also show that mountain crowberry will increase in abundance in response to climate warming (Wada *et al*. 2002, Buizer *et al*. 2012, Kaarlejärvi *et al*. 2012). From a practical point of view, mountain crowberry was also the only plant species found in the study plots of both LG and HG tundra.

Methanolic extracts were prepared and the concentrations of flavonoids (flavonols, epicatechin and flavanones), phenolic acids (benzoic, chlorogenic and protocatechuic acid derivatives) and stilbenoids (batatasin-III, batatasin derivatives and stilbenes) analysed using high-performance liquid chromatography (HPLC) (IV). The concentrations of condensed tannins were analysed colorimetrically (Porter *et al*. 1986). It is currently considered that each phenolic compound may serve a multitude of functions, but that flavonoids with strong antioxidative properties are important in the protection against oxidative stress (Hernandez *et a*l. 2009, Khadem & Marles 2010), condensed tannins are important in defence against generalist herbivores

(Ayres *et al.* 1997) and stilbenes may have antimicrobial functions (Chong *et al.* 2009), whereas batatasin-III (a stilbenoid) serves as an allelopathic agent (Gallet *et al.* 1999).

3.3 Soil and litter C quality and decomposition temperature sensitivity detected by laboratory incubations

To investigate the consequences of the grazing-induced vegetation shift from dwarf shrubs to graminoids on the quality of plant litter and accumulated SOM, soil samples from LG and HG tundra and litter samples of dominant plant species (*V. myrtillus, V. uliginosum*, *B. nana* and *E. nigrum*. ssp. *hermaphroditum* and a composite moss sample from LG tundra) and graminoid species (*C. bigelowii* from HG tundra) as well as root biomass for HG and LG were collected. Samples were analysed using solid-state ^{13}C cross-polarisation magic angle spinning nuclear magnetic resonance (CPMAS NMR) spectroscopy (II). Compounds in the samples were assigned to the following C classes: aliphatic not O-substituted C, methoxyls, carbohydrates, carbohydrates and aliphatic lignin, aromatic lignin, and carboxyl/carbonyl C. Aromaticity and alkyl-to-O-alkyl ratio were also calculated.

Carbohydrates and methoxyls are labile substrates and easily degradable by many microbial taxa, while aromatic lignin, aliphatic not O-substituted C and carboxyl/carbonyl C are more resistant to microbial degradation and contribute to the formation of SOM (Sjögersten *et al.* 2003). Aromaticity and alkyl-to-O-alkyl ratio depict decomposability of SOM. To further investigate the relationship between litter and soil C quality and decomposition rates and the temperature sensitivity of decomposition, litter and soil samples were incubated at different temperatures for up to 10 months (II). During the incubations, the CO_2 release was analysed using GC, and the CO_2 release was further used to calculate time-integrated CO_2-C loss estimates, and Q_{10}, which depicts the temperature sensitivity of decomposition. After the incubation, soil C quality was again characterised with NMR to determine how the decomposition rates of the different C compounds differed between grazing intensities.

3.4 Statistics

The treatment effects on measured variables were analysed using linear mixed models. In the field experiment grazing intensity (G) was used as a fixed factor together with warming (W) and/or fertilization (F). In the laboratory incubation experiment G, litter type (L) and temperature (T) were used as fixed factors. A random factor, block nested with grazing, and a repeated factor, measurement date (D), were included in the model. In cases of significant interactions, treatment effects were analysed separately for grazing intensities and dates, and *post hoc* tests (Bonferroni and Least Significant Difference) were used. Akaike's information criteria and residual plots were used to assess the model fit, and transformations were made when necessary.

4 Results and discussion

4.1 The consequences of reindeer grazing on ecosystem processes under current climate

The vegetation transition from dwarf shrubs to graminoids induced by reindeer grazing as described by van der Wal (2006), exerted several effects on ecosystem processes, confirming the view of a prominent role of reindeer grazing as driving ecosystem processes in tundra (Forbes & Kumpula 2009). The findings of this thesis show the complexity of the mechanisms by which reindeer influence ecosystem functions through interactions between soil and vegetation. The results did not explicitly support the predictions based on the prevailing theoretical framework on e.g. the regulation of soil microbial activities or plant defence in tundra. These unexpected results highlight the need to understand the ecosystem feedbacks of grazer-induced vegetation shifts and changes in plant defence as well as soil C and N cycling.

Consistent with hypothesis **1.1**, the LG tundra site was a stronger net C sink than the HG tundra site that had been intensively grazed for the past 50 years (I). The difference in NEE between the grazing intensities was explained by higher R_e under HG than LG, whereas there was no difference in response to grazing in GEP (I). Also studies using short-term grazer exclusion have shown a greater C sink strength in ungrazed than grazed tundra sites (Sjögersten *et al.* 2011, Cahoon *et al.* 2012), but have linked these differences to higher GEP in ungrazed sites. However, at the present site the long-term difference in grazing pressure determined ecosystem C balance through higher R_e under HG than LG. This finding demonstrates that the long- and short-term effects of grazing may greatly differ. Higher R_e under HG is likely mediated by increased decomposition. As grazing increases the proportion of graminoids, increases litter abundance (I), and enhances litter (Olofsson & Oksanen 2002) and soil C decomposition (III), these mechanisms in combination with higher soil temperatures explain the higher microbial activity and ultimately higher R_e under HG. Thus, long-term grazing simultaneously altered a number of ecosystem properties with potential to influence R_e. These processes could not be detected after short-term experimental grazer exclusion, as there were no differences between HGexc and HG (I). As the long- and short-term effects of herbivory derive from different mechanisms and processes, the long-term effects of herbivory are both quantitatively and qualitatively different from short-term effects.

The quality of accumulated soil C differed between the grazing intensities. However, there was no difference in aromaticity between LG and HG (II), which contrasted with hypothesis **2** of higher soil aromaticity under dwarf shrub-dominated LG compared to graminoid-dominated HG tundra. Unexpectedly, the proportion of aliphatic not O-substituted C was significantly higher under HG, and the proportion of carbohydrate C was higher under LG. These findings suggest that accumulated SOM under dwarf shrub-dominated vegetation was not more aromatic than under graminoid-dominated vegetation, which contrasts with the view that there is a strong link between aboveground litter and belowground soil C quality (Hobbie & Gough 2004, Vancampenhout *et al.* 2009). This finding may, however, be explained by a number of possible mechanisms. Firstly, the similar aromaticity of soil C at both levels of grazing intensity may be caused by relatively rapid degradation of lignin in litter (Marschner *et al.* 2008). Soils under LG are more dominated by fungi than soils under HG (Männistö *et al.* unpublished). Soil fungi efficiently degrade lignin (Steffen *et al.* 2000), which may be less likely to accumulate to SOM despite its high concentration in the litter.

Secondly, belowground root biomass or aboveground mosses may be more important determinants of soil C quality than aboveground biomass of dwarf shrubs and graminoids. Higher proportions of aliphatic not O-substituted C under HG could be explained by the domination of graminoids, which form a dense root biomass with high concentrations of aliphatic compounds (De Deyn *et al.* 2008, Freschet *et al.* 2013). In turn, higher proportions of carbohydrate C under LG could be explained by high abundance of mosses (I) that contained high concentrations of carbohydrates (II). It is considered that mosses contribute substantially to soil C accumulation in tundra (Vancampenhout *et al.* 2009). Thirdly, it is possible that soil C may be at different stages of decomposition for the HG and LG tundra due to higher rates of decomposition in soils under HG (III). Aliphatic not O-substituted C compounds accumulate to soil as decomposition proceeds (Sjögersten *et al.* 2003) and, therefore, higher alkyl-to-O-alkyl ratio may indicate a more advanced state of decomposition (Kögel-Knabner 1997, Quideau *et al.* 2000). Higher alkyl-to-O-alkyl ratios in the HG area could result from more rapid microbial decomposition, whereas more labile compounds, such as carbohydrates, are accumulated under LG due to lower rates of microbial activity (II and III).

Grazing significantly influenced microbial EEAs and, consistent with hypothesis **3.1**, potential BG (synthesised for microbial C acquisition) and AP (synthesised for microbial P acquisition) activities were higher under HG; whereas potential NAG (synthesised for microbial N acquisition; Sinsabaugh *et al.* 2008) activity was higher under LG. However, in contrast to hypothesis **3.1**, LAP (synthesised for microbial N acquisition; Sinsabaugh *et al.* 2008) activity was higher under HG than LG (III). In contrast to hypothesis **3.2**, the differences in EEAs in response to grazing were not greatest during the reindeer migration, but were insensitive to the drastic seasonal variations in soil N availability due to urine and faecal deposits during this period. These findings did not support the hypothesis that reindeer mediate EEAs through soil N and the stoichiometry of microbial C:N:P demand (Sinsabaugh *et al.* 2008). In C-rich tundra soils, soil microorganisms attack organic substrates in proportion to their availability in SOM (Weintraub & Schimel 2003). Therefore, reindeer grazing may mediate effects on EEAs through affecting substrate availability, which is an important determinant of EEAs (Hernández & Hobbie 2010). As carbohydrate degradation is often regulated by the protection of carbohydrates in the SOM by lignin (Sinsabaugh & Follstad Shah 2011), and vegetation under HG is lignin-poor, higher BG activity under HG could be driven by higher availability of carbohydrates. In addition to plant residues, microbial residues form another important substrate for soil microorganisms (Schmidt *et al.* 2011). Thus, higher NAG activity under LG likely results from greater chitin availability from fungal cell walls as a substrate for soil microorganisms.

Despite the important effects of grazing on vegetation and soil N availability, grazing did not affect the levels of plant defence in the dominant evergreen dwarf shrub, mountain crowberry (IV). This result contrasted with hypothesis **4.1** that the plant's need for protection against photodamage should be higher under nutrient-poor than nutrient-rich conditions (Close & McArthur 2002). However, these findings support earlier studies in tundra showing no consistent relationship between plant phenolic concentrations and site nutrient availability (Jonasson *et al.* 1986, Sundqvist *et al.* 2012). In tundra ecosystems, the temperature limitation of plant photosynthetic capacity – which induces oxidative stress – could be the major determinant for synthesis of plant phenolics (*sensu* Close & McArthur 2002). Therefore, either the direct effects of grazing via browsing and trampling, or the indirect effects of grazing via alleviation of nutrient limitation, may not be the key factors determining plant defence levels in mountain crowberry.

4.2 Strong interactions between reindeer grazing and ecosystem responses to warming

Long-term difference in grazing intensity by reindeer affected both the magnitude and direction of the warming-induced effects on various ecosystem processes. Seen from another perspective, the effect of grazing also differed in warmed compared to the current climatic conditions. Importantly, some differences in response to grazing were even reversed under warmer conditions. This finding shows that the current effects of reindeer grazing on ecosystem processes may not be applicable in a warmer climate.

Consistent with hypothesis **1.2**, warming increased GEP under HGexc and HG and had no effect under LG (I, Table 1). The responses in R_e to warming were consistent at all grazing intensities, which in combination with the varying effects on the GEP had a major effect on NEE: warming under LG decreased the C sink by 38% (NEE less negative), but did not influence NEE under HGexc and HG. This finding shows that the responses of the ecosystem C balance to warming may differ drastically depending on the grazing history. Another important finding was that existing differences in the NEE between the grazing intensities under current conditions were negated by warming; the NEE did not differ between grazing intensities in the warmed plots. Interestingly, under LG combined warming and fertilisation increased GEP, suggesting that GEP was co-limited by low soil N availability and temperature. The lack of similar interactive effects of warming and fertilisation under HGexc and HG indicates that GEP was not limited by nutrients, probably due to the enhanced soil N availability under HG (Olofsson *et al.* 2001). Thus, grazer-induced increase in soil N availability constituted an important mechanism by which grazing affected the responses of GEP – and consequently, ecosystem C sink – to warming. In contrast to hypothesis **1.3**, warming increased GEP similarly for both HGexc and HG (I), highlighting the divergence of short- *vs.* long-term effects of grazer exclusion and suggesting that a brief interval with no grazing at previously heavily grazed tundra sites does not influence ecosystem C balance.

Warming exerted important effects on the abundance of aboveground vegetation and litter, providing insights into the possible mechanisms by which climate warming may influence soil C stocks at different levels of grazing intensity. Although warming increased GEP only under HGexc and HG, it increased aboveground plant biomass similarly for all grazing intensities (I, Table 1). This finding could result from increased resource allocation to root rather than shoot biomass (Olofsson *et al.* 2004, Hafner *et al.* 2012). The roots of graminoids contain high concentrations of decomposition-resistant aliphatic compounds (e.g. suberin), which accumulate in soils (Rasse *et al.* 2005, Freschet *et al.* 2013). Therefore, the combination of warming-induced increase in GEP with the enhanced C allocation to roots could promote the accumulation of stabile soil C stocks under HG, as also indicated by the higher proportion of aliphatic-not-O-substituted C fraction in the SOM (II).

Consistent with earlier findings that grazing drastically suppresses the warming-induced increase in the abundance of evergreen dwarf shrubs (Post & Pedersen 2008, Olofsson *et al.* 2009), warming inside the short-term reindeer exclosures (i.e. HGexc) more than doubled the abundance of evergreen dwarf shrubs and had weaker effects for HG (I). Warming as a sole treatment did not affect the abundance of evergreen dwarf shrubs under LG (I). Warming exerted a similar increase in the abundance of deciduous shrubs at all grazing intensities, but for HGexc and HG the increase may be insignificant at the ecosystem scale due to the generally low abundance of deciduous shrubs compared to graminoids. The response of vegetation to short-term reindeer exclusion highlights that a sudden termination of intensive reindeer grazing on nutrient-rich tundra may induce rapid changes in the aboveground vegetation and biomass (Ravolainen *et al.* 2011). Interestingly, the rapid increase in the abundance of evergreen dwarf shrubs with warming for HGexc may suggest that climate warming could accelerate the recovery of tundra vegetation to the ungrazed vegetation state (*sensu* van der Wal 2006) if grazing pressure rapidly ceased.

Laboratory incubations of litter at the early stage of decomposition showed that graminoid litter had the highest CO_2 release rates and also the strongest response to increasing temperatures. Consistent with the view that evergreen litter decomposes slowly (Hobbie *et al.* 2000), the decomposition of crowberry litter had the lowest decomposition rates of the investigated litter types (II). According to these results, climate warming may enhance the early phases of aboveground litter decomposition and nutrient release under HG graminoid-dominated tundra. Climate warming may thus reinforce the positive effects of grazing on litter turnover caused by the vegetation shift (Olofsson & Oksanen 2002). Laboratory incubations provide insights into the direct effects of temperature on litter decomposition; however, in the long term, the changes in vegetation and associated shift in litter quality will also influence decomposition.

Laboratory incubations of soil showed that the effect of temperature on microbial respiration rates and the temperature sensitivity of decomposition varied in response to grazing intensity, but with complex variation with incubation time that was in contrast with hypothesis **2** (II, Table 1). In the early stages of soil incubation, the CO_2 release showed no difference with grazing intensity and higher temperature sensitivity for HG compared to LG. However, with increasing duration of incubation, both CO_2 release rates and temperature sensitivity increased for LG compared to HG. The short-term microbial responses to temperature in soil incubations may depict the initial responses of microbial activities to temperature, whereas the long-term soil microbial responses to temperature could reflect the responses of soil microbial activities under sustained higher temperatures (Steinweg *et al.* 2008). These results demonstrate for the first time that long-term grazing intensity interacts with soil microbial responses to increasing temperatures. The lower temperature sensitivity of CO_2 release rates under HG suggests that large grazers may dampen the effects of prolonged warming on microbial activity and soil C stocks.

I suggest that differences in soil C quality explain why the temperature sensitivity of microbial activity differed between grazing intensities. The CO_2 release rates in tundra soils correlate positively with the proportion of polysaccharides (Dai *et al.* 2002). Higher proportions of carbohydrates in LG soils could then explain the higher decomposition rates and temperature sensitivity under prolonged warming. In support of this view, the total loss of carbohydrates during the incubation was higher in LG than HG soils (II). Given that carbohydrates in SOM are often stored in ligno-cellulose complexes (Kögel-Knabner 2002, Sinsabaugh & Follstad Shah 2011), they would not be expected to be degraded during the initial stages of incubation but only during prolonged soil incubations. The protection of carbohydrates by lignin most likely also explains why BG activity in fresh soil samples was lower in LG soils (III) despite the overall higher proportion of carbohydrates (II). In contrast, the lower CO_2 release rates as well as lower temperature sensitivity under HG could result from the low availability of decomposable substrates (Hartley *et al.* 2007, Bradford *et a*l. 2008), as evidenced by a high alkyl-to-O-alkyl ratio (II).

Alternatively, microbial temperature acclimation could explain the differing responses of decomposition to temperature at the different grazing intensities. As soil temperatures have been substantially higher for HG than LG (averages +13.5 and +9 °C, respectively; Olofsson *et al.* 2004) for up to 50 years, soils under HG may be dominated by mesophilic compared to cold-adapted soil microbes under LG. Higher CO_2 release rates under LG only during the later phases of incubation may thus reflect a shift from a cold-adapted to a mesophilic microbial community under prolonged warming (Bradford 2013).

The effects of warming on plant phenolics in mountain crowberry varied drastically depending on grazing intensity. In accord with hypothesis **4.2**, warming decreased total soluble phenolics under HG, but had no effect under LG (IV, Table 1). However, a detailed characterisation of phenolics revealed strong variation in the responses of individual phenolic compounds or compound groups. Under LG, some compounds increased while others decreased in response to warming. In contrast, although fewer individual compounds responded to warming under HG, these responses were consistently negative. Compound-specific responses of phenolics to climate warming are consistent with earlier studies in subarctic ecosystems (Graglia *et* *al*. 2001, Hansen *et al*. 2006, Nybakken *et al*. 2008, Martz *et al*. 2009), but these results show for the first time the importance of grazing intensity in determining phenolic responses to warming. Warming caused a general decline in the concentrations of antioxidative phenolics, such as flavonols and benzoic acids (Hernandez *et al*. 2009, Khadem & Marles 2010) at both grazing intensities, in agreement with the concept that increased temperatures decrease the risk of photodamage and, consequently, the need for antioxidative phenolics (Close & McArthur 2002). Dilution of phenolics in increasing plant biomass did not seem to explain the findings, because under LG the warming increased the abundance of mountain crowberry while not affecting the total phenolic concentrations; whereas under HG, warming decreased the concentrations of total phenolics while not affecting the abundance.

Under LG, combined warming and fertilisation decreased flavonols to a greater extent than warming alone (IV, Table 1), suggesting that the grazer-induced increase in soil N availability affected the responses of plant phenolic concentrations to warming. Thus, although temperature may be a more important determinant of plant phenolic concentration than soil N availability (Jonasson *et al*. 1986, Sundqvist *et al*. 2012), the alleviation of temperature limitation by climate warming may decrease plant phenolic concentrations to a greater extent with high compared to low soil nutrient availability. Interestingly, warming under LG increased the concentrations of stilbenes (IV), which often have important antimicrobial functions (Chong *et al*. 2009). Although the mechanism for increasing stilbene concentrations with warming remains unknown, it may be speculated that the risk of fungal pathogen infections may have increased in warmer conditions, and only under LG due to denser crowberry shrubs that could create a more favourable microclimate for pathogens.

Table 1. Summary of the statistically significant responses of ecosystem components to warming under different grazing intensities by the reindeer (light grazing = LG, heavy grazing = HG). The direction of the effect is indicated by ↑ (increase), ↓ (decrease) or ne (no effect). If the warming effect was stronger under different grazing intensities, the difference is indicated by ↑↑ or ↓↓. Whether soil N availability and C quality seemed to mediate the response to warming is also indicated.

Variable	What was the effect of warming under different grazing intensities?	Did grazer-induced effect on soil N availability[1] mediate warming responses?	Did grazer-induced effect on C quality[2] mediate warming responses?
C sink	LG (↓), HG (ne)	yes	
GEP	LG (ne), HG (↑)	yes	
R_e	LG, HG (↑)	no	
Plant biomass	LG, HG (↑)	no	
Plant defence (total phenolics)	LG (ne), HG (↓)	yes	
Antioxidants	LG (↓), HG (↓↓)	yes	
Litter decomposition	LG (↑), HG (↑↑)		yes
Soil C decomposition	LG, HG (↑) at the start LG (↑↑), HG (↑) at the end		yes
Temperature sensitivity	LG (↑), HG (↑↑) at the start LG (↑), HG (↓) at the end		yes

[1] Refers to the higher soil NH_4^+ concentration under HG than LG (III)

[2] Refers to ^{13}C NMR data showing a higher proportion of carbohydrates under LG than HG in the soil, whereas there was a higher proportion of carbohydrates under HG than LG in the litter (II)

4.3 Implications of the grazer-induced interaction in ecosystem responses to warming

In this thesis, I asked the question, “Do the ecosystem-level consequences of climate warming differ between the heavily grazed (HG) and the lightly grazed (LG) tundra, the alternative states of tundra vegetation (*sensu* van der Wal 2006)?” As the results of this thesis show that reindeer grazing simultaneously altered the consequences of warming on several ecosystem components, the answer to this question is “yes”.

However, ecosystem responses to warming under different grazing pressures by reindeer were specific to each measured ecosystem component: some ecosystem responses to warming were stronger on LG tundra, whereas others were stronger on HG tundra. Therefore, at the ecosystem-level it cannot be stated that reindeer grazing would either mitigate or intensify the effects of climate warming.

The fact that ecosystem responses to warming drastically differed between the dwarf shrub-dominated LG tundra and graminoid-dominated HG tundra is an important finding. This is because the current predictions on the effects of climate warming in tundra ecosystems largely focus on the interactive effects between climate warming and increased shrubification, which is expected to also influence soil microbial activities for decomposition via changes in litter quality and quantity as well as soil microclimate (Cornelissen *et al.* 2007, Myers-Smith *et al.* 2011). In HG tundra, however, shrubification is suppressed by the grazers. The results of this thesis showed that warming exerted greatly different consequences on ecosystem C fluxes (GEP and NEE), the levels of plant defence and soil microbial activity in HG compared to LG tundra. Thus, different predictions on the effects of climate warming are needed for HG graminoid-dominated tundra than for the dwarf shrub-dominated LG or ungrazed tundra.

The results show that in cases where reindeer grazing has induced a vegetation shift from dwarf shrubs to graminoids, grazing induces a consistent increase in microbial activities for SOM decomposition that does not depend on seasonal variations in grazing intensity due to reindeer migration (III). The grazer-induced shifts in vegetation and microbial activities combined with the fertilisation effect via urine and faeces had important consequences for soil properties, in which both soil N availability and soil C quality form key factors that eventually determine the ecosystem-level consequences of climate warming (I and II). Due to the positive effect of reindeer grazing on soil N availability, warming increased plant productivity (GEP) on HG but not LG tundra, where nutrient limitation seemed to prevent warming from increasing plant production. The varying effect of warming on GEP at different levels of grazing intensity also determined the effects of warming on ecosystem C sink (I). The characterisation of soil C quality indicated that reindeer grazing reduced the soil C quality, which may act as an important mechanism mitigating soil microbial responses to prolonged warming. The proportion of carbohydrates vulnerable to microbial decomposition was higher under LG than HG (II). Thus, the reindeer-induced vegetation shift from dwarf shrubs to graminoids can significantly alter the consequences of climate warming on ecosystem C cycling via two mechanisms: the indirect effect of grazing on soil N availability (an important determinant of the effect of warming on C sink) and influencing the quality of accumulating soil C (an important determinant of the effect of warming on C source). A warming-induced increase in the concentration of strongly antimicrobial stilbenes under LG but not under HG indicated a potential interaction between reindeer grazing and a biotic stress factor, possibly plant pathogens, but the source of this interaction remains unknown (IV).

This thesis demonstrates that grazing history with the associated vegetation shift may largely regulate the ecosystem responses to climate warming. I suggest that reindeer grazing may influence the ecosystem-level responses to warming via the same mechanisms, through altering soil N availability and C quality, and also on wider geographical scales. The effects of reindeer on the vegetation, soil nutrient cycling and microbial activity are highly site-specific (Grellmann 2002, Stark 2002, van der Wal 2006, Bråthen *et al*. 2007, Olofsson *et al*. 2010, Tommervik *et al*. 2012, Stark *et al*. 2014). Thus, it is plausible that the consequences of climate warming on each ecosystem component are equally variable and even unique to each site. As grazing intensity at decadal and centennial timescales has varied greatly at different locations due to reindeer management practices or historical events influencing reindeer population sizes and migrations routes (Tommervik *et al*. 2010), the different tundra sites have highly variable grazing histories resulting from the combination of natural abiotic and biotic factors, cultural practices and political decisions. However, it may be assumed that grazer-induced effects on soil nutrient cycling and soil C quality are commonly important mechanisms by which the interactions between grazing and climate warming are regulated. Studies on past reindeer grazing patterns at regional and pan-Arctic scales are currently extremely scarce (Räsänen *et al*. 2007, Josefsson *et al*. 2009), leaving a large gap in the ability to assess historical grazing pressures and thus the consequences of climate warming. Furthermore, as climate change and increasing industrial activities are likely to influence the population sizes and migration routes of reindeer and other ungulates (Berger 2004, Forbes & Kumpula 2009, Pape & Löffler 2012), predicting the future grazing intensities at different locations is difficult. At present, the key role of grazing for the ecosystem responses to climate warming is not taken into account in climate change models. Therefore, a holistic approach that integrates the past grazing patterns and the future prospects of grazing intensity of the keystone herbivores is needed to predict the effects of climate warming not only in the Arctic but also worldwide.

5 Conclusions

In a subarctic tundra heath, a vegetation shift from dwarf shrub- to graminoid-dominated tundra due to reindeer grazing was paralleled by changes in soil properties that drive ecosystem processes and affect aboveground–belowground interactions in ecosystems. The results of this thesis showed that the grazing-induced changes in soil properties simultaneously modified several different ecosystem responses to climate warming. However, the interaction between grazing and climate warming was specific to the ecosystem component. Another important finding in this thesis was that the effects of grazing on ecosystem processes were different in a warmer climate compared to the effects under the current climate.

Higher soil N availability in the HG tundra promoted the enhanced plant production (GEP) under warming. The increase in GEP (i.e. gross ecosystem C sink) counteracted the warming-induced increase in ecosystem respiration R_e (i.e. ecosystem C source), and consequently, ecosystem net C sink (NEE) did not change in response to warming in the HG tundra. In contrast, warming in the LG tundra did not increase GEP, because low N availability limited the responses of plant productivity to warming and, therefore, increased R_e led to a significant decrease in ecosystem C sink. Warming also caused a stronger decrease in plant phenolics, an important means of plant defence against biotic and abiotic stresses, for HG compared to LG.

The chemical quality of accumulated soil C differed between LG and HG: the proportion of carbohydrates that are easily degradable for soil microorganisms was higher under LG, whereas the proportion of decomposition-resistant aliphatic not O-substituted C was higher under HG. In laboratory soil incubations, soil microbial activity for C decomposition also increased much more with temperature under LG than HG, which may result from higher availability of easily mineralisable C under LG. These findings suggest that a larger proportion of the soil C under LG may be susceptible to increased microbial decomposition with prolonged warming. Therefore, soils in lightly grazed systems could be more likely to release soil C to the atmosphere under a warmer climate than soils in heavily grazed systems.

This thesis supports the idea of an important role of reindeer in influencing ecosystem processes in tundra, and highlights that the consequences of climate warming at the ecosystem scale can significantly differ for tundra sites with different reindeer-grazing histories. The results show that the indirect effects of reindeer grazing on soil nutrient availability and the chemical quality of accumulated soil C significantly modify ecosystem responses to climate warming. It is plausible that the effects of reindeer grazing on soil nutrients and C quality may be commonly important mechanisms that regulate interactions between climate warming and grazing throughout the circumpolar Arctic. The results of this study show that future research on climate warming should aim towards a more holistic approach that takes into account the role of grazing in both aboveground and belowground components of the ecosystem.

References

Augustine DJ & McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. The Journal of Wildlife Management 62: 1165-1183.

Augustine DJ & McNaughton SJ (2006) Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. Ecosystems 9: 1242-1256.

Ayres MP, Clausen TP, MacLean SF, Redman AM & Reichardt PB (1997) Diversity of structure and antiherbivore activity in condensed tannins. Ecology 78: 1696-1712.

Bardgett RD (2005) The Biology of Soil. Oxford University Press.

Bardgett RD & Wardle DA (2003) Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84: 2258-2268.

Bardgett RD, Wardle DA & Yeates GW (1998) Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. Soil Biology and Biochemistry 30: 1867-1878.

Berger J (2004) The last mile: How to sustain long-distance migration in mammals. Conservation Biology 18: 320-331.

Boerner REJ, Decker KLM & Sutherland E (2000) Prescribed burning effects on soil enzyme activity in a southern Ohio hardwood forest: a landscape-scale analysis. Soil Biology & Biochemistry 32: 899-908.

Bosatta E & Ågren GI (1999) Soil organic matter quality interpreted thermodynamically. Soil Biology and Biochemistry 31: 1889-1891.

Boudreau S & Payette S (2004) Caribou-induced changes in species dominance of lichen woodlands: an analysis of plant remains. American Journal of Botany 91: 422-429.

Bradford MA (2013) Thermal adaptation of decomposer communities in warming soils. Frontiers in Microbiology 4: 1-16.

Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, Mohan JE, Reynolds JF, Treseder KK & Wallenstein MD (2008) Thermal adaptation of soil microbial respiration to elevated temperature. Ecology Letters 11: 1316-1327.

Bryant JP, Chapin FSI & Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40: 357-368.

Bråthen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T & Hausner VH (2007) Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. Ecosystems 10: 773-789.

Buizer B, Weijers S, van Bodegom PM, Alsos IG, Bronken-Eidesen P, van Breda J, de Korte M, van Rijckevorsel J & Rozema J (2012) Range shifts and global warming: ecological responses of *Empetrum nigrum* L. to experimental warming at its northern (high Arctic) and southern (Atlantic) geographical range margin. Environmental Research Letters 7: 025501 (9pp).

Cahoon SM, Sullivan PF, Post E & Welker JM (2012) Large herbivores limit CO_2 uptake and suppress carbon cycle responses to warming in West Greenland. Global Change Biology 18: 469-479.

Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ & Laundre JA (1995) Responses of arctic tundra to experimental and observed changes in climate. Ecology 76: 694-711.

Chapin FS III, Matson PA & Vitousek PM (2011) Principles of Terrestrial Ecosystem Ecology, 2nd edition. New York, Springer.

Chong J, Poutaraud A & Hugueney P (2009) Metabolism and roles of stilbenes in plants. Plant Science 177: 143-155.

Close DC & McArthur C (2002) Rethinking the role of many plant phenolics - protection from photodamage not herbivores? Oikos 99: 166-172.

Coley PD, Bryant JP & Chapin FSI (1985) Resource availability and plant antiherbivore defence. Science 230: 895-899.

Conant RT, Drijber RA, Haddix ML, Parton WJ, Paul EA, Plante AF, Six J & Steinweg JM (2008a) Sensitivity of organic matter decomposition to warming varies with its quality. Global Change Biology 14: 868-877.

Conant RT, Steinweg JM, Haddix ML, Paul EA, Plante AF & Six J (2008b) Experimental warming shows that decomposition temperature sensitivity increases with soil organic matter recalcitrance. Ecology 89: 2384-2391.

Cornelissen JHC, van Bodegom PM, Aerts R, Callaghan T, Van Logtestijn RSP, Alatalo JM, Chapin FS, Gerdol R, Gudmundsson J, Gwynn Jones D, Hartley AE, Hik DS, Hofgaard A, Jónsdóttir IS, Karlsson S, Klein JA, Laundre JA, Magnusson B, Michelsen A, Molau U, Onipchenko VG, Quested HM, Sandvik SM, Schmidt IK, Shaver GR, Solheim B, Soudzilovskaia NA, Stenström A, Tolvanen A, Totland O, Wada N, Welker JM, Zhao X & Team MOL (2007) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecology Letters 10: 619-627.

Cox PM, Betts RA, Jones CD, Spall SA & Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408: 184-187.

Craine J, Spurr R, McLauchlan K & Fierer N (2010a) Landscape-level variation in temperature sensitivity of soil organic carbon decomposition. Soil Biology and Biochemistry 42: 373-375.

Craine JM, Fierer N & McLauchlan KK (2010b) Widespread coupling between the rate and temperature sensitivity of organic matter decay. Nature Geoscience 3: 854-857.

Dai XY, White D & Ping CL (2002) Comparing bioavailability in five Arctic soils by pyrolysis-gas chromatography/mass spectrometry. Journal of Analytical and Applied Pyrolysis 62: 249-258.

Davidson EA & Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440: 165-173.

De Deyn GB, Cornelissen JHC & Bardgett RD (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. Ecology Letters 11: 516-531.

den Herder M, Kytöviita M-M & Niemelä P (2003) Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland. Ecography 26: 3-12.

Diaz S, Lavorel S, McIntyre S, Falczuk V, Casanoves F, Milchunas DG, Skarpe C, Rusch G, Sternberg M, Noy-Meir I, Landsberg J, Zhang W, Clark H & Campbell BD (2007) Plant trait responses to grazing-a global synthesis. Global Change Biology 13: 313-341.

Elmendorf S, Henry GHR, Hollister RD, Björk RG, Bjorkman AD, Callaghan TV, Collier LS, Cooper EJ, Cornelissen JHC, Day TA, Fosaa AM, Gould WA, Grétarsdóttir J, Harte J, Hermanutz L, Hik DS, Hofgaard A, Jarrad F, Jónsdóttir IS, Keuper F, Klanderud K, Klein JA, Koh S, Kudo G, Lang SI, Loewen V, May JL, Mercado J, Michelsen A, Molau U, Myers-Smith IH, Oberbauer SF, Pieper S, Post E, Rixen C, Robinson CH, Schmidt NM, Shaver GR, Stenström A, Tolvanen A, Totland Ø, Troxler T, Wahren C-H, Webber PJ, Welker JM & Wookey PA (2012) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecology Letters 15: 164-175.

Fierer N, Allen AS, Schimel JP & Holden PA (2003) Controls on microbial CO_2 production: a comparison of surface and subsurface horizons. Global Change Biology 9: 1322-1332.

Fierer, N, Craine JM, McLauchlan K & Schimel JP (2005) Litter quality and the temperature sensitivity of decomposition. Ecology 86: 320-326.

Fierer N, Colman BP, Schimel JP & Jackson RB (2006) Predicting the temperature dependence of microbial respiration in soil: A continental-scale analysis. Global Biogeochemical Cycles 20: GB3026.

Forbes BC & Kumpula T (2009) The ecological role and geography of reindeer (Rangifer tarandus) in northern Eurasia. Geography Compass 3: 1356-1380.

Freschet GT, Cornwell WK, Wardle DA, Elumeeva TG, Liu W, Jackson BG, Onipchenko VG, Soudzilovskaia NA, Tao J, Cornelissen HC (2013) Linking litter decomposition of above- and below-ground organs to plant - soil feedbacks worldwide. Journal of Ecology 101: 943-952.

Gaare E (1997) A hypothesis to explain lichen-Rangifer dynamic relationship. Rangifer 17: 3-7.

Gallet C, Nilsson M-C & Zackrisson O (1999) Phenolic metabolites of ecological significance in *Empetrum hermaphroditum* leaves and associated humus. Plant and Soil 210: 1-9.

Gornall, JL, Woodin SJ, Jónsdóttir IS &, van der Wal R (2009) Herbivore impacts to the moss layer determine tundra ecosystem response to grazing and warming. Oecologia 161: 747-758.

Graglia E, Julkunen-Tiitto R, Shaver GR, Schmidt IK, Jonasson S & Michelsen A (2001) Environmental control and intersite variations of phenolics in *Betula nana* in tundra ecosystems. New Phytologist 151: 227-236.

Grellmann D (2002) Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. Oikos 98: 190-204.

Hafner S, Unteregelsbacher S, Seeber E, Becker L, Xu XF, Li X, Guggenberger G, Miehe G & Kuzyakov Y (2012) Effect of grazing on carbon stocks and assimilate partitioning in a Tibetan montane pasture revealed by $^{13}CO_2$ pulse labeling. Global Change Biology 18: 528-538.

Hairston NG, Smith FE & Slobodkin LB (1960) Community structure, population control, and competition. The American Naturalist 94: 421-425.

Hamilton EWI, Frank DA, Hinchey PM & Murray TR (2008) Defoliation induces root exudation and triggers positive rhizospheric feedbacks in a temperate grassland. Soil Biology & Biochemistry 40: 2865-2873.

Hamilton JG, Zangerl AR, DeLucia EH & Berenbaum MR (2001) The carbon - nutrient balance: its rise and fall. Ecology Letters 4: 86-95.

Hansen AH, Jonasson S, Michelsen A & Julkunen-Tiitto R (2006) Long-term experimental warming, shading and nutrient addition affect the concentration of phenolic compunds in arctic-alpine deciduous and evergreen dwarf shrubs. Oecologia 147: 1-11.

Hartley IP, Garnett MH, Sommerkorn M, Hopkins DW, Fletcher BJ, Sloan VL, Phoenix GK & Wookey PA (2012) A potential loss of carbon associated with greater plant growth in the European Arctic. Nature Climate Change 2: 875-879.

Hartley IP, Heinemeyer A & Ineson P (2007) Effects of three years of soil warming and shading on the rate of soil respiration: substrate availability and not thermal acclimation mediates observed response. Global Change Biology 13: 1761-1770.

Herms DA & Mattson WJ (1992) The dilemma of plants: To grow or defend. The Quarterly Review of Biology 67: 283-335.

Hernández DL & Hobbie SE (2010) The effects of substrate composition, quantity, and diversity on microbial activity. Plant and Soil 335: 397-411.

Hernandez I, Alegre L, Van Breusegem F & Munne-Bosch S (2009) How relevant are flavonoids as antioxidants in plants? Trends in Plant Science 14: 125-132.

Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. Ecological Monographs 66: 503-522.

Hobbie SE & Gough L (2004) Litter decomposition in moist acidic and non-acidic tundra with different glacial histories. Oecologia 140: 113-124.

Hobbie SE, Nadelhoffer KJ & 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 SE, Schimel JP, Trumbore SE & Randerson JR (2000) Controls over carbon storage and turnover in high-latitude soils. Global Change Biology 6 (Suppl. 1): 196-210.

Hobbs NT (1996) Modification of ecosystems by ungulates. Journal of Wildlife Management 60: 695-713.

IPCC (2013) Climate Change. The Physical Science Basis. Summary for Policymakers, Technical Summary and Frequently Asked Questions. Working group 1 contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change.

Jonasson S, Bryant JP, Chapin FSI & Andersson M (1986) Plant phenolics and nutrients in relation to variations in climate and rodent grazing. The American Naturalist 128: 394-408.

Josefsson,T, Hörnberg G & Östlund L (2009) Long-term human impact and vegetation changes in a boreal forest reserve: Implications for the use of protected areas as ecological references. Ecosystems 12: 1017-1036.

Kaarlejärvi E, Baxter R, Hofgaard A, Hytteborn H, Khitun O, Molau U, Sjögersten S, Wookey P & Olofsson J (2012) Effects of warming on shrub abundance and chemistry drive ecosystem-level changes in a forest-tundra ecotone. Ecosystems 15: 1219-1233.

Khadem S & Marles RJ (2010) Monocyclic phenolic acids; hydroxy- and polyhydroxybenzoic acids: Occurence and recent bioactivity studies. Molecules 15: 7985-8005.

Kitti H, Forbes BC & Oksanen J (2009) Long- and short-term effects of reindeer grazing on tundra wetland vegetation. Polar Biology 2009: 253-261.

Kögel-Knabner I (1997) ^{13}C and ^{15}N NMR spectroscopy as a tool in soil organic matter studies. Geoderma 80: 243-270.

Kögel-Knabner I (2002) The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biology and Biochemistry 34: 139-162.

Lefévre R, Barré P, Moyano FE, Christensen BT, Bardoux G, Eglin T, Girardin C, Houot S, Kätterer T, Van Oort F & Chenu C (2014) Higher temperature sensitivity for stable than for labile soil organic carbon - Evidence from incubations of long-term bare fallow soils. Global Change Biology 20: 633-640.

Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR & Chapin FS (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. Nature 43: 440-443.

Manseau M, Huot J & Crête M (1996) Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. Journal of Ecology 84: 503-513.

Marschner B, Brodowski S, Dreves A, Gleixner G, Gude A, Grootes PM, Hamer U, Heim A, Jandl G, Ji R, Kaiser K, Kalbitz K, Kramer C, Leinweber P, Rethemeyer J, Schäffer A, Schmidt MWI, Schwark L & Wiesenberg GLB (2008) How relevant is recalcitrance for the stabilization of organic matter in soils? Journal of Plant Nutrition and Soil Science 171: 91-110.

Martz F, Jaakola L, Julkunen-Tiitto R & Stark S (2010) Phenolic composition and antioxidant capacity of bilberry (*Vaccinium myrtillus*) leaves in northern Europe following foliar development and along environmental gradients. Journal of Chemical Ecology 36: 1017-1028.

Martz F, Turunen M, Julkunen-Tiitto R, Lakkala K & Sutinen M-L (2009) Effect of the temperature and the exclusion of UVB radiation on the phenolics and iridoids in *Menyanthes trifoliata* L. leaves in the subarctic. Environmental Pollution 157: 3471-3478.

Milchunas DG & Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soil over a global range of environments. Ecological Monographs 63: 327-366.

Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Levesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Siegwart-Collier L, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Menard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE & Hik DS (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6: 045509 (15pp).

Nybakken L, Klanderud K &Totland O (2008) Simulated environmental change has contrasting effects on defensive compound concentration in three alpine plant species. Arctic, Antarctic and Alpine Research 40: 709-715.

Nybakken L, Sandvik SM & Klanderud K (2011) Experimental warming had little effect on carbon-based secondary compounds, carbon and nitrogen in selected alpine plants and lichens. Environmental and Experimental Botany 72: 368-376.

Oechel WC, Hastings SJ, Vourlitis G, Jenkins M, Riechers G & Grulke N (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. Nature 361: 520-523.

Oksanen L & Oksanen T (2000) The logic and realism of the hypothesis of exploitation of ecosystems. The American Naturalist 155: 703-723.

Oksanen L & Virtanen R (1995) Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. Acta Botanica Fennica 153: 1-80.

Olff H, Ritchie ME & Prins HHT (2002) Global environmental controls of diversity in large herbivores. Nature 415: 901-904.

Olofsson J, Kitti H, Rautiainen P, Stark S & Oksanen L (2001) Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. Ecography 24: 13-24.

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

Olofsson J & Oksanen L (2002) Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. Oikos 96: 507-515.

Olofsson J, Oksanen L, Callaghan T, Hulme PE, Oksanen T & Suominen O (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. Global Change Biology 15: 2681-2693.

Olofsson J, Stark S & Oksanen L (2004) Reindeer influence on ecosystem processes in the tundra. Oikos 105: 386-396.

Pape R & Löffler J (2012) Climate change, land use conflicts, predation and ecological degradation as challenges for reindeer husbandry in northern Europe: What do we really know after half a century of research? AMBIO 41: 421-434.

Pastor J & Naiman RJ (1992) Selective foraging and ecosystem processes in boreal forests. The American Naturalist 139: 690-705.

Phoenix GK, Emmett BA, Britton AJ, Caporn SJM, Dise NB, Helliwell R, Jones L, Leake JR, Leith ID, Sheppard LJ, Sowerby A, Pilkington MG, Rowe EC, Ashmore MR & Power SA (2012) Impacts of atmospheric nitrogen deposition: responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. Global Change Biology 18: 1197-1215.

Porter LJ, Hrstich LN & Bock GC (1986) The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin. Phytochemistry 25: 223-230.

Post E & Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences of the USA 105: 12353-12358.

Post ES & Klein DR (1996) Relationships between graminoid growth form and levels of grazing by caribou (*Rangifer tarandus*) in Alaska. Oecologia 107: 364-372.

Quideau SA, Anderson MA, Graham RC, Chadwick OA & Trumbore SE (2000) Soil organic matter processes: characterization by ^{13}C NMR and ^{14}C measurements. Forest Ecology and Management 138: 19-27.

Rasse DP, Rumpel C & Dignac M-F (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilization. Plant and Soil 269: 341-356.

Ravolainen VT, Bråthen KA, Ims RA, Yoccoz NG, Henden J-A & Killengreen ST (2011) Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. Basic and Applied Ecology 12: 643-653.

Räsänen S, Froyd C & Goslar T (2007) The impact of tourism and reindeer herding on forest vegetation at Saariselkä, Finnish Lapland: a pollen analytical study of a high-resolution peat profile. The Holocene 17: 447-456.

Salminen J-P & Karonen M (2011) Chemical ecology of tannins and other phenolics: we need a change in approach. Functional Ecology 25: 325-338.

Schimel JP & Bennett J (2004) Nitrogen mineralization: Challenges of a changing paradigm. Ecology 85: 591-602.

Schimel JP & Weintraub MN (2003) The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biology and Biochemistry 35: 549-563.

Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kögel-Knabner I, Lehmann J, Manning DA, Nannipieri P, Rasse DP, Weiner S & Trumbore SE (2011) Persistence of soil organic matter as an ecosystem property. Nature 478: 49-56.

Schulze E-D, Beck E & Müller-Hohenstein K (2005) Plant Ecology, 1st edition. Berlin Heidelberg, Springer.

Singer FJ & Schoenecker KA (2003) Do ungulates accelerate or decelarate nitrogen cycling? Forest Ecology and Management 181: 189-204.

Sinsabaugh RL (2010) Phenol oxidase, peroxidase and organic matter dynamics of soil. Soil Biology and Biochemistry 42: 391-404.

Sinsabaugh RL & Follstad Shah JJ (2011) Ecoenzymatic stoichiometry of recalcitrant organic matter decomposition: the growth rate hypothesis in reverse. Biogeochemistry 102: 31-43.

Sinsabaugh RL, Lauber CL, Weintraub MN, Ahmed B, Allison SD, Crenshaw C, Contosta AR, Cusack D, Frey S, Gallo ME, Gartner TB, Hobbie SE, Holland K, Keeler BL, Powers JS, Stursova M, Takacs-Vesbach C, Waldrop MP, Wallenstein MD, Zak DR & Zeglin LH (2008) Stoichiometry of soil enzyme activity at global scale. Ecology Letters 11: 1252-1264.

Sistla SA, Asao S & Schimel JP (2012) Detecting microbial N-limitation in tussock tundra soil: Implications for Arctic soil organic carbon cycling. Soil Biology & Biochemistry 55: 78-84.

Sjögersten S, Turner BL, Mahieu N, Condron LM & Wookey PA (2003) Soil organic matter biochemistry and potential susceptibility to climatic change across the forest-tundra ecotone in the Fennoscandian mountains. Global Change Biology 9: 759-772.

Sjögersten S, van der Wal R, Loonen MJJE & Woodin SJ (2011) Recovery of ecosystem carbon fluxes and storage from herbivory. Biogeochemistry 106: 357-370.

Stark S (2002) Reindeer grazing and soil nutrient cycling in boreal and tundra ecosystems. University of Oulu, Oulu.

Stark S, Eskelinen A & Männistö MK (2012) Regulation of microbial community composition and activity by soil nutrient availability, soil pH, and herbivory in the tundra. Ecosystems 15: 18-33.

Stark S & Grellmann D (2002) Soil microbial responses to herbivory in an arctic tundra heath at two levels of nutrient availability. Ecology 83: 2736-2744.

Stark S, Kytöviita M-M, Männistö MK & Neumann AB (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 MK & Eskelinen A (2014) When do grazers accelerate or decelerate soil carbon and nitrogen cycling in tundra? - A test of theory on grazing effects in fertile and infertile habitats. Oikos, doi: 10.1111/oik.01355.

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

Steffen KT, Hofrichter M & Hatakka A (2000) Mineralization of ^{14}C-labelled synthetic lignin and lignolytic enzyme activities of litter-decomposing basidiomycetous fungi. Applied Microbiolgy and Biotechnology 54: 819-825.

Steinweg JM, Plante AF, Conant RT, Paul EA & Tanaka DL (2008) Patterns of substrate utilization during long-term incubations at different temperatures. Soil Biology & Biochemistry 40: 2722-2728.

Street LE, Shaver GR, Williams M & van Wijk MT (2007) What is the relationship between changes in canopy leaf area and changes in photosynthetic CO2 flux in arctic ecosystems? Journal of Ecology 95: 139-150.

Sundqvist MK, Wardle DA, Olofsson E, Giesler R & Gundale MJ (2012) Chemical composition of plant litter in response to elevation: subarctic vegetation challenges phenolic allocation theories. Functional Ecology 26: 1090-1099.

Tanentzap AJ & Coomes DA (2012) Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? Biological Reviews 87: 72-94.

Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G & Zimov SA (2009) Soil organic carbon pools in the northern circumpolar permafrost region. Global Biogeochemical Cycles 23: GB2023.

Tommervik H, Bjerke JW, Gaare E, Johansen B & Thannheiser D (2012) Rapid recovery of recently overexploited winter grazing pastures for reindeer in northern Norway. Fungal Ecology 5: 3-15.

Tommervik H, Dunfjeld S, Olsson GA & Ostby Nilsen M (2010) Detection of ancient reindeer pens, cultural remains and anthropogenic influenced vegetation in Byrkije (Borgefjell) mountains, Fennoscandia. Landscape and Urban Planning 98: 56-71.

Wada N, Shimono M, Miyamoto M & Kojima S (2002) Warming effects on shoot developmental growth and biomass production in sympatric evergreen alpine dwarf shrubs *Empetrum nigrum* and *Loiseleuria procumbens*. Ecological Research 17: 125-132.

Wagai R, Kishimoto-Mo AW, Yonemura S, Shirato Y, Hiradate S & Yagasaki Y (2013) Linking temperature sensitivity of soil organic matter decomposition to its molecular structure, accessibility, and microbial physiology. Global Change Biology 19: 1117-1125.

Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carroll AB, Epstein HE, Jónsdóttir IS, Klein JA, Magnússon B, Molau U, Oberbauer SF, Rewa SP, Robinson CH, Shaver GR, Suding KN, Thompson CC, Tolvanen A, Totland O, Turner PL, Tweedie CE, Webber PJ & Wookey PA (2006) Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Science USA 103: 1342-1346.

Wallenstein MD, McMahon SK & Schimel JP (2009) Seasonal variation in enzyme activities and temperature sensitivities in Arctic tundra soils. Global Change Biology 15: 1631-1639.

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

van der Wal R, Bardgett RD, Harrison KA & Stien A (2004) Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystem. Ecography 27: 242-252.

van der Wal R, Brooker R, Cooper E & Langvatn R (2001) Differential effects of reindeer on high Arctic lichens. Journal of Vegetation Science 12: 705-710.

van der Wal R & Brooker RW (2004) Mosses mediate grazer impacts on grass abundance in arctic ecosystems. Functional Ecology 18: 77-86.

Vancampenhout K, Wouters K, De Vos B, Buurman P, Swennen R & Deckers J (2009) Differences in chemical composition of soil organic matter in natural ecosystems from different climatic regions - A pyrolysis-GC/MS study. Soil Biology & Biochemistry 41: 568-579.

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH & Wal DH (2004) Ecological linkages between aboveground and belowground biota. Science 304: 1629-1633.

Weintraub MN & Schimel JP (2003) Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. Ecosystems 6: 129-143.

Weintraub MN & Schimel JP (2005a) Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. BioScience 55: 408-415.

Weintraub MN & Schimel JP (2005b) The seasonal dynamics of amino acids and other nutrients in Alaskan Arctic tundra soils. Biogeochemistry 73: 359-380.

Weintraub MN & Schimel JP (2005c) Seasonal protein dynamics in Alaskan arctic tundra soils. Soil Biology and Biochemistry 37: 1469-1475.

Weintraub MN, Scott-Denton LE, Schmidt SK & Monson RK (2007) The effects of tree rhizodeposition on soil exoenzyme activity, dissolved organic carbon, and nutrient availability in subalpine forest ecosystem. Oecologia 154: 327-338.

Vermerris W & Nicholson R (2006) Phenolic Compound Biochemistry, 1st edition. Springer, Dordrecht.

Xu Y, Li L, Wang Q, Chen Q & Cheng W (2007) The pattern between nitrogen mineralization and grazing intensities in an Inner Mongolian typical steppe. Plant and Soil 300: 289-300.

List of original articles

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

II Väisänen M, Sjögersten S, Large D, Drage T & Stark S. Reduced temperature sensitivity of soil C decomposition after long-term reindeer grazing in subarctic tundra. Manuscript.

III Stark S & Väisänen M (2014) Insensitivity of soil microbial activity to temporal variation in soil N in subarctic tundra: Evidence from responses to large migratory grazers. Ecosystems 17: 906-917.

IV Väisänen M, Martz F, Kaarlejärvi E, Julkunen-Tiitto R & Stark S (2013) Phenolic responses of mountain crowberry (*Empetrum nigrum* ssp. *hermaphroditum*) to global climate change are compound specific and depend on grazing by reindeer (*Rangifer tarandus*). Journal of Chemical Ecology 39: 1390-1399.

Reprinted with permission from the publishers Macmillan Publishers Limited (I) and Springer Science + Business Media (III and IV).

Original publications are not included in the electronic version of the dissertation.

ACTA UNIVERSITATIS OULUENSIS

SERIES A SCIENTIAE RERUM NATURALIUM

629. Koskela, Timo (2014) Interaction in asset-based value creation within innovation networks : the case of software industry
630. Stibe, Agnis (2014) Socially influencing systems : persuading people to engage with publicly displayed Twitter-based systems
631. Sutor, Stephan R. (2014) Large-scale high-performance video surveillance
632. Niskanen, Alina (2014) Selection and genetic diversity in the major histocompatibility complex genes of wolves and dogs
633. Tuomikoski, Sari (2014) Utilisation of gasification carbon residues : activation, characterisation and use as an adsorbent
634. Hyysalo, Jarkko (2014) Supporting collaborative development : cognitive challenges and solutions of developing embedded systems
635. Immonen, Ninna (2014) Glaciations and climate in the Cenozoic Arctic : evidence from microtextures of ice-rafted quartz grains
636. Kekkonen, Päivi (2014) Characterization of thermally modified wood by NMR spectroscopy : microstructure and moisture components
637. Pietilä, Heidi (2014) Development of analytical methods for ultra-trace determination of total mercury and methyl mercury in natural water and peat soil samples for environmental monitoring
638. Kortelainen, Tuomas (2014) On iteration-based security flaws in modern hash functions
639. Holma-Suutari, Anniina (2014) Harmful agents (PCDD/Fs, PCBs, and PBDEs) in Finnish reindeer (*Rangifer tarandus tarandus*) and moose (*Alces alces*)
640. Lankila, Tiina (2014) Residential area and health : a study of the Northern Finland Birth Cohort 1966
641. Zhou, Yongfeng (2014) Demographic history and climatic adaptation in ecological divergence between two closely related parapatric pine species
642. Kraus, Klemens (2014) Security management process in distributed, large scale high performance systems
643. Toivainen, Tuomas (2014) Genetic consequences of directional selection in *Arabidopsis lyrata*
644. Sutela, Suvi (2014) Genetically modified silver birch and hybrid aspen – target and non-target effects of introduced traits

Book orders:
Granum: Virtual book store
http://granum.uta.fi/granum/

UNIVERSITY OF OULU P.O. Box 8000 FI-90014 UNIVERSITY OF OULU FINLAND

ACTA UNIVERSITATIS OULUENSIS

ISBN 978-952-62-0699-8 (Paperback)
ISBN 978-952-62-0700-1 (PDF)
ISSN 0355-3191 (Print)
ISSN 1796-220X (Online)

UNIVERSITY of OULU
OULUN YLIOPISTO