Plant-soil-herbivore interactions in a high Arctic wetland Feedbacks to the carbon cycle

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Abstract

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Over a time period of three years three *in-situ* field studies were conducted. In paper one and two of this thesis treatments were applied that simulate plausible responses of the muskoxen population with climate change. In paper I muskoxen was excluded from part of the Zackenberg mire, thus representing a decrease in the population. In paper II the grazing pressure was increased, by clipping of plots twice each summer. In paper IV the main in-situ drivers of the spatial variability of CH_4 flux was studied. Further, a laboratory study (paper III) was conducted to make an in-depth study on the C allocation pattern in the area and the consequences of clipping.

To our surprise, the results from paper I and II showed that the ecosystem responded in similar ways to changes in grazing pressure despite the contrasting treatments. Both increased and decreased grazing resulted in a decrease in the density of vascular plants, in particular of *Eriophorum scheuchzeri (Erioph),* and in a substantial decrease in CO_2 and CH_4 fluxes. The third year into the exclusion experiment in paper I the mean Net Ecosystem Exchange (NEE) of CO_2 had decrease with 47%, while the CH_4 emission had decreased with 44%. In the clipping experiment in paper II NEE decreased already in year one of the experiment and had after three years decreased with on average 35%. A change in CH_4 emission was apparent in year two and over the last two years CH_4 emission decreased with on average 26%. In the laboratory study, several factors indicated that clipping altered the C allocation pattern and resulted in more C allocation to above ground vegetation and more root exudation. The results from paper IV showed that there is a strong dependence of the spatial variability in CH_4 flux on productivity and C input to vegetation and pore water. The main driver of this carbon input is the vegetation composition, with high number of *Erioph* tillers leading to high input. Consequently, since both decreased and increased grazing pressure resulted in a decrease in *Erioph* density both these treatments ultimately resulted in lower productivity and decreased CH_4 fluxes.

In conclusion, the results from this thesis clearly show that herbivores are of great importance for the C balance of this wet arctic ecosystem, the driving forces behind this effect being interactions between plants, soil and herbivores. The results from this thesis further points to the importance of considering the impact of herbivory when the past, present or future C balance in the arctic is discussed.

Key words: Arctic wetlands, carbon balance, herbivory, increased grazing pressure, methane fluxes, muskox exclusion, substrate avalibility, vegetation composition and density

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Feedbacks to the carbon cycle

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I FALK, J. M., SCHMIDT, N. M., CHRISTENSEN, T. R. & STRÖM, L. 2014. Large herbivore grazing alters vegetation structure and greenhouse gas balance in a high arctic mire. *Manuscript submitted for publication in Ecosystems*.

II FALK, J. M., SCHMIDT, N. M. & STRÖM, L. 2014. Effects of simulated increased grazing on carbon allocation patterns in a high arctic mire. *Biogeochemistry,* 119**,** 229-244.

III FALK, J. M., JACKOWICZ-KORCZYNSKI, M., MASTEPANOV, M. & STRÖM, L. 2014. ^{14}C-allocation pattern and carbon balance of a high arctic mire – effect of simulated grazing. *Manuscript.*

IV STRÖM, L., FALK, J.M., SKOV, K., CHRISTENSEN, T.R., JACKOWICZ-KORCZYNSKI, M. & SCHMIDT, N.M. 2014 Controls of spatial and temporal variability in CH_4 flux in a high arctic fen over three years. *Manuscript submitted for publication in Biogeochemistry*

Contribution

Paper I, II, III. The author was responsible for data analysis, led the writing of the manuscripts and carried out most of the field and laboratory work.

Paper IV. The author was involved in the data analysis, writing of the manuscript and carried out most of the field work.

Abstract

Arctic ecosystems hold massive amounts of the global carbon in their soils and are of great importance for the global terrestrial exchange of greenhouse gases to the atmosphere. The arctic region has in general been acting as a C sink for the past 10000 years, however with climate change the C balance in some areas is shifting towards becoming a C source. Herbivory are an important part of many ecosystems and have been found to have an important impact on the C balance. This seemingly important aspect of the C balance in arctic ecosystems are however very rarely considered. In this project, the interactions between plants, soil and herbivores have been studied in a high arctic mire in Zackenberg, northeast Greenland. The aim of the project was to study the impact of the large herbivores muskoxen on the vegetation composition and density, CO_2 and CH_4 fluxes and substrate availably for CH_4 production.

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To our surprise, the results from paper I and II showed that the ecosystem responded in similar ways to changes in grazing pressure despite the contrasting treatments. Both increased and decreased grazing resulted in a decrease in the density of vascular plants, in particular of *Eriophorum scheuchzeri*, and in a substantial decrease in CO_2 and CH_4 fluxes. The third year into the exclusion experiment in paper I the mean Net Ecosystem Exchange (NEE) of CO_2 had decrease with 47%, while the CH_4 emission had decreased with 44%. In the clipping experiment in paper II NEE decreased already in year one of the experiment and had after three years decreased with on average 35%. A change in CH_4 emission was apparent in year two and over the last two years CH_4 emission decreased with on average 26%. In the laboratory study, several factors indicated that clipping altered the C allocation pattern and resulted in more C allocation to above ground vegetation and more root exudation. The results from paper IV showed that there is a strong dependence of the spatial variability in CH_4 flux on productivity and C input to vegetation and pore water.

The main driver of this carbon input is the vegetation composition, with high number of *Eriophorum* tillers leading to high input. Consequently, since both decreased and increased grazing pressure resulted in a decrease in *Eriophorum* density both these treatments ultimately resulted in lower productivity and decreased CH_4 fluxes.

In conclusion, the results from this thesis clearly show that herbivores are of great importance for the C balance of this wet arctic ecosystem, the driving forces behind this effect being interactions between plants, soil and herbivores. The results from this thesis further points to the importance of considering the impact of herbivory when the past, present or future C balance in the arctic is discussed.

Keyword: Arctic wetlands, carbon balance, herbivory, increased grazing pressure, methane fluxes, muskoxen exclusion, substrate availability, vegetation composition and density.

Resumé

Omkring halvdelen af den globale kulstof mængde som findes i jorden, er lagret i de arktiske jorde. Arktiske jorde har været anset for at være vigtige kulstof reservoirs de sidste 10.000 år, hvor der bliver optaget mere kulstof end der frigives. Dette skyldes blandt andet den langsomme omsætning af organiske materiale på grund af de kolde forhold, men også de store mængder kulstof som ligger gemt i permafrosten. Men med klimaændringer er der tegn på at denne balance er ved at ændre sig og flere har observeret at arktiske økosystemer nu frigiver mere kulstof end de optager. En stor del de arktiske økosystemer er påvirket græssende dyr, som også har stor betydning for kulstof balancen. Deres påvirkning er dog sjældent inkluderet i diskussionen omkring kulstof balancen i en natur som står overfor store klimaændringer.

Dette PhD projekt, omhandler netop den interaktion der er mellem planter, jord og moskusokser i et højarktisk vådområde, i Zackenberg Nordøstgrønland. Det er svært at sige hvad der vil ske med moskusokse populationen med klimaændringer, hvor to modsatrettede senarier er sandsynlige. Ved klimaændringer i Nordøstgrønland følger øget snemængder og flere tø-episoder i den ellers kolde vinter; øget snemængde og de islag som dannes ved tø-episoder vil påvirke populationen negativt, da de ikke vil være i stand til finde føde om vinteren. Klimaændringer vil dog også føre til højere temperaturer som vil øge biomasse produktionen, hvilket vil give dem bedre leve vilkår om sommeren, hvilket vil kunne øge populationen af moskusokserne. Konsekvensen for kulstof balancen i de to scenarier, blev gennem tre år studeret i Zackenberg, hvor både vegetationssammensætningen, CO_2 udvekslingen og metan frigivelsen blev moniteret i sommer perioden. Til vores store overraskelse så vi at begge scenarier reagerede på samme vis. I det ene projekt blev moskusokserne ekskluderet ved hjælp af store ”udhegninger”, og her så vi efter tre år at antallet af kærplanter havde faldet drastisk, hvilket førte til et fald på 47% af det samlede CO_2 optag og et fald på 44% af metan frigivelsen. I det andet scenarie studie, øgede vi græsnings trykket ved at klippe plots to gange om sommeren, som allerede var udsat for moskusokse græsning. Her så vi allerede første år at CO_2 optaget faldt drastisk, gennem de tre års målinger faldt CO_2 optaget med 35%. Efter et år havde metan udslippet også faldet, for de sidste to år var metan udslippet faldet med 26%. I et tredje projekt fandt vi en tydelig sammenhæng mellem, hvor produktive planterne var, hvor meget CO_2 som blev optaget og den mængde metan som blev frigivet. Og herved kan færre kærplanter ved både øget græsning og ingen græsning forklare både et fald i CO_2 optag men også udslippet af metan.

I et mindre laboratorie forsøg så vi på hvordan kulstoffet blev fordelt i små tørv-plante prøver fra Zackenberg. Her var der flere indikationer af at kulstoffet bliver fordelt anderledes når disse prøver blev udsat for klipning; hvor mere kulstof blev fordelt til vegetationen over jorden.

Vores resultater har vist at moskusokserne har stor betydning for kulstof balancen i et vådt højarktisk økosystem og deres tilstedeværelse er vigtig at holde for øje når man diskuterer fortidens, nutidens men ikke mindst fremtidens kulstof balance.

Contents

Introduction

The Arctic region is very sensitive towards changes in climate, as it can easily affect the vegetation, snow, ice and permafrost regimes, which will affect the ecosystem and the carbon (C) balance. Changes in the arctic climate is of global importance as they hold massive quantities of C in their soils (Ping *et al.*, 2008, Post *et al.*, 1982, Tarnocai *et al.*, 2009). The Arctic region (60˚N - 90˚N) has since the 1960s and 1970s in average become 1-2˚ C warmer (ACIA, 2005) and temperatures continues to rise (IPCC, 2013). During the last decades numerous researchers have studied the C balance of the arctic. The main studied question has been: Is the arctic tundra acting as C sink or a source? For many decades it was believed that the arctic in average was acting as a C sink and had been doing that for the past 10000 years (ACIA, 2005, Hicks Pries *et al.*, 2012). New research is however pointing towards that the arctic tundra has changed to currently acting as a weak C sink (McGuire *et al.*, 2012) or even a C source (Belshe *et al.*, 2013) on annual basis. Despite of the indications that the C balance of the arctic regions is changing from being a positive to becoming a negative feedback on the climate the C uptake during growing seasons have increased since the 1990s (Belshe *et al.*, 2013, McGuire *et al.*, 2012), which mainly has been attributed higher temperatures, longer growing season and higher productivity.

Although, the northern permafrost region only covers about 16% of the earth, they are estimated to hold around 50% of today's total below-ground organic C (McGuire *et al.*, 2009, Ping *et al.*, 2008, Post *et al.*, 1982, Tarnocai *et al.*, 2009), and arctic wetlands are holding a large portion of that. The large C stocks found in arctic wetlands are caused by slow decomposition under anoxic and cold conditions (Tarnocai *et al.*, 2009), which leads to a large build-up of organic matter (peat formation) (Callaghan *et al.*, 2004, Callaghan *et al.*, 2005, Ström *et al.*, 2005a). The anaerobic conditions and anaerobic decomposition are the reason for CH_4 production and emission from these areas. Global wetlands are the largest natural single source of CH_4 to the atmosphere (IPCC, 2013) and the arctic region has been found to account for a substantial part of the global atmospheric CH_4 emission (McGuire *et al.*, 2009). CH_4 is a strong greenhouse gas, as its heat retention in the atmosphere is high compared to CO_2, the Global Warming Potential in a 100 year perspective is 34-times that of CO_2 (with climate carbon feedbacks) (IPCC, 2013).

1.1 The C balance

The C balance is often expressed as the differences between C input (photosynthesis) and the C output (respiration) and in wet habitats CH_4 emission should be considered. The CO_2 balance is expressed as net ecosystem exchange (NEE), respiration from both soil and vegetation as ecosystem respiration (R_{eco}), while photosynthesis; the gross primary production (GPP) is the difference between NEE and R_{eco}.

Photosynthesis

The green biomass of plants assimilates CO_2 from the atmosphere, and forms organic carbohydrates. Through photosynthesis, energy is fixed from photosynthetic active radiation (PAR (400-700nm)) and can be used for either growth, maintenance or reproduction (Oke, 1996). Approximately half of GPP is used for the plants own growth and maintenance (Schlesinger, 1997) and is at some point respired back to the atmosphere. The net primary production (NPP) refers to the C that remains within the primary producers (plants) after plant respiration ($NPP=GPP-R_{plant}$).

$$CO_2 + H_2O + \text{Energy} \rightarrow CH_2O + O_2$$

The photosynthesis rate is general dependent on the solar radiation, the atmospheric CO_2 concentrations, humidity, air- and soil temperature and vegetation species and density (Elberling *et al.*, 2008a, Oke, 1996) and in permafrost areas the active layer depth (Schuur *et al.*, 2008).

Respiration

Respiration is the process where energy is released from the C-compounds fixed in photosynthesis so that it can be used in plant processes. It can be divided into heterotrophic and autotrophic respiration, where the heterotrophic is respiration by the microbial organism (decomposition) and the autotrophic is plant respiration.

$$CH_2O + O_2 \rightarrow\ CO_2 +\ H_2O + Energy$$

Respiration is depended on several factors: temperature, soil moisture, the quantity and quality of the organic matter and the soils oxygen level. In an arctic environment active layer thickness and snow cover/depth is very important for the respiration. A strong correlation between higher temperature and respiration has been found (e.g., Elberling *et al.*, 2008a, Groendahl, 2006, Oechel & Hastings, 1993) however, the heterotrophic respiration is active below zero degrees and has been measured down to -18˚C (Elberling *et al.*, 2008a). The autotrophic respiration varies depending on the plant community (Elberling *et al.*, 2008b, Ström *et al.*, 2005a).

CH_4 production

In wet ecosystems where O2 content is low the decomposition of organic matter in water saturated sediments of the soil will mainly be through anaerobic metabolism. The microorganism that produces methane are collectively referred to as methanogens and belong to the genera archaea which are distinct from bacteria. In anaerobic decomposition CH_4 is produced as a by-product in the decomposition process (Whalen, 2005). Substrate availability of organic acid are of major importance for CH_4 formation. Primarily acetic acid which is the only organic substrate used by methanogens in a process called acetoclastic methanogenesis (Christensen *et al.*, 2003a, Ström *et al.*, 2003). Substrates are generated from two main sources: 1) from fermentative microbes producing organic acid (e.g., acetic and formic acid) from residuals (Killham, 1994) and 2) from root exudation (Ström *et al.*, 2003). When CH_4 has been produced, oxidation is likely to occur, when the gas travels through more aerobic conditions to the surface. 20 to 90 % of the CH_4 that is produced in the anaerobic zone is estimated to get oxidized (Frenzel & Karofeld, 2000). The balance between methanogenesis and methane oxidation determines the methane emission. CH_4 can be transported from the soil to the atmosphere in three different ways: diffusion, ebullition or through the aerenchyma in plants, where vascular plants acts as gas conduits. Vascular plants are very important for the transportation of methane (Frenzel & Karofeld, 2000, Ström *et al.*, 2005a, Whalen, 2005), by removal of vascular plants the methane emission is found to decrease with 50 to 85 % (Whalen, 2005).

CH_4 emission is strongly correlated to temperature, vegetation cover, plant production and water table depth (Callaghan *et al.*, 2004, Christensen *et al.*, 2003a, Joabsson & Christensen, 2001, Ström & Christensen, 2007, Ström *et al.*, 2005a, Ström *et al.*, 2012, Whalen, 2005). Different vascular species affect CH_4 emission differently through: formation of substrate (i.e., root exudation), rhizospheric oxidation and emission (transportation through the aerenchyma) (Ström & Christensen, 2007, Ström *et al.*, 2005a, Ström *et al.*, 2012). The formation of the substrate acetate has been found to be very high in the root vicinity of the vascular plant *Eriophorum scheuchzeri* in an arctic mire compared to other plants (Ström *et al.*, 2005a, Ström *et al.*, 2012). Furthermore, higher photosynthetic rates may result in higher C assimilation to below-ground and higher NEP may increase root biomass, which most likely will increase the input of labile C to the ground, enhance the formation of acetate and hereby CH_4 production (Christensen *et al.*, 2003a, Joabsson & Christensen, 2001, Joabsson *et al.*, 1999, Ström & Christensen, 2007). In permafrost areas the thickness of the active layer will be an additional factor for CH_4 production and emission (Friborg *et al.*, 2000). The arctic CH_4 emission varies a lot throughout the year. Low temperature and frozen soils in winter limits the production and the transportation of CH_4 and during summer the thickness of the active layer is an additional factor for CH_4 production and emission (Friborg *et al.*, 2000). Autumn measurements from a high arctic fen in northeast Greenland have however shown surprisingly large CH_4 emissions during a soil freeze-in (Mastepanov *et al.*, 2008). Even though a lot of studies have been made on methanogenesis there are still many uncertainties within this processes.

Many studies have been made on the arctic C balance, manly focusing on the feedbacks of climate change. However, what is often forgotten in these studies and discussions is feedbacks between climate change and external factors such as herbivory, which can change rapidly in magnitude (e.g., changes in population sizes) with climate change.

1.2 Herbivores impact on the arctic C balance

It has been suggested that mammalians impact on the ecosystem can have an essential impact on the vegetation composition (Owen-Smith, 1987, Zimov *et al.*, 1995) which may alter the C balance. Owen-Smith (1987) presented the keystone-herbivore hypothesis where large herbivores are found to be the reason for an open vegetation landscape. With a decline in herbivory, landscapes can undergo succession from being an open vegetation landscape to becoming woodland or shrubland (Owen-Smith, 1987). It is believed that mega fauna in the Pleistocene kept the tundra-steppe biome dominated be grasses, as their trampling kept mosses down, their grazing kept the litter layer down and their manure fertilized the soil (Zimov *et al.*, 1995).

Plant-soil-herbivore interactions are complex and involves both direct and indirect impacts and may influence a number of processes such as C sequestration, greenhouse gas production, assimilation and emission, vegetation composition and density, decomposition rate, nutrient and C allocation and the physical parameters of the soil (temperature and moisture) (e.g., Sjögersten *et al.*, 2008, Tanentzap & Coomes, 2012). A simple illustrating of how herbivores influences the ecosystem and C balance are shown in figure 1.

Consumption of the above-ground biomass by herbivores changes the below-ground C pool, as less C will be transported to below-ground through the living plants and less litter will be added to the ecosystem (Sjögersten *et al.*, 2011, Tanentzap & Coomes, 2012, Van der Wal *et al.*, 2007). Additional, the C allocation pattern have been found to change with grazing, as vegetation will use C and nutrient reserves to rebuild the plant and grow new plants shoots instead of storing C below-ground (Beaulieu *et al.*, 1996, Chapin, 1980, Green & Detling, 2000, Mulder, 1999). Changes in allocation pattern and an reduction in release of C to the rhizosphere following defoliation (Butenschoen *et al.*, 2008), can influence the microbial community and thereby the organic matter and the C fluxes.

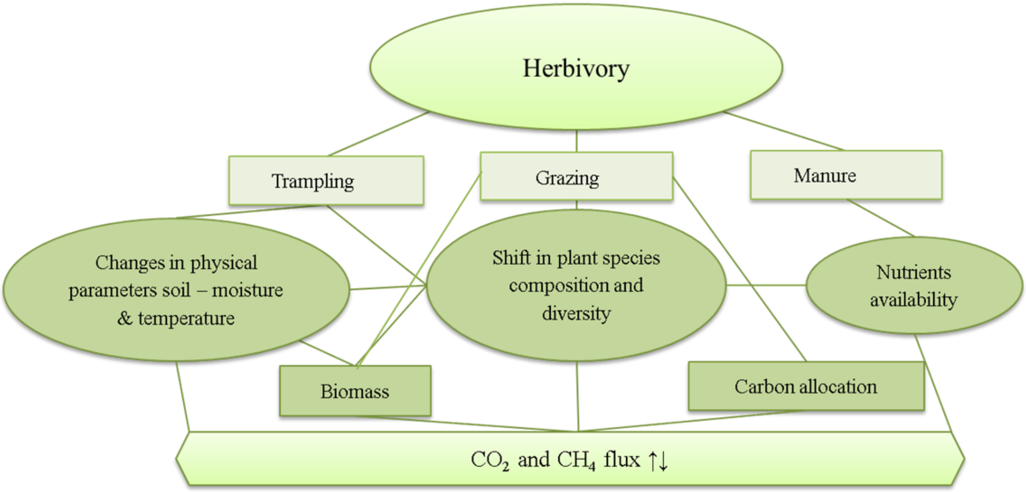


Figure 1. An illustration of how herbivory general effects the ecosystem and C balance.

Grazing in the arctic have been found to change vegetation composition - towards being more herb and graminoid dominated (Cahoon *et al.*, 2012, Olofsson *et al.*, 2009, Ouellet *et al.*, 1994, Post & Pedersen, 2008, Sjögersten *et al.*, 2008, Stark *et al.*, 2002, Susiluoto *et al.*, 2008, Van der Wal, 2006). Graminoids are well adapted to grazing and known to be capable of rapid regrowth (Henry, 1998) and are therefore often found in habitats with herbivores. Mosses are known to be very sensitive towards trampling (Liddle, 1997) and are often found to increase when grazing pressure decreases (Olofsson *et al.*, 2001, Thing, 1984, Van der Wal & Brooker, 2004, Van der Wal *et al.*, 2001, Zimov *et al.*, 1995). Additionally, the density of shrubs are often lower, as they are slow growing and therefore more sensitive towards grazing and trampling (Post & Klein, 1996). Soil physical properties may also be affected by herbivores. Soil temperature can increase due to removal of litter and standing biomass (Olofsson et al. 2004; Van der Wal and Brooker 2004) leaving the ground more exposed to solar radiation, which may enhance evaporation and lead to lower soil moisture (Elliott and Henry 2011). Increased soil temperature can also affect many of the processes involved in greenhouse gas production and emission (see section 1.1) as well as the active layer thickness. With thawing permafrost leading to release of previously stored C. Walter et al. (2006) for instance showed that Pleistocene C with an age of 35,260–42,900 years was released as CH_4 due to permafrost thaw in Siberia (Walter *et al.*, 2006).

Many of the impacts described above influence the C balance directly or indirectly and herbivory has been found to have an important impact on the artic C balance (Cahoon *et al.*, 2012, Sjögersten *et al.*, 2008, Speed *et al.*, 2010, Van der Wal *et al.*, 2007, Welker *et* *al.*, 2004). The presence or absence of herbivores have been found to determine whether an ecosystems C balance is acting as a C sink or a source (Sjögersten *et al.*, 2011, Welker *et al.*, 2004). The general impact of grazing in the artic appears to be somewhat ambiguous and depends on the habitat and grazing pressure. Most studies report no effect or a decrease in net primary production (NPP) with grazing (e.g., Bagchi & Ritchie, 2010, Beaulieu *et al.*, 1996, Cahoon *et al.*, 2012, Sjögersten *et al.*, 2011, Van der Wal *et al.*, 2007), while fewer have found an increase in NPP (Cargill & Jefferies, 1984, Olofsson *et al.*, 2001, Olofsson *et al.*, 2004, Van der Wal *et al.*, 2004). Increases in NPP in nutrient poor habitats have especially been found as nutrients are added to the ecosystem by the herbivores excreta (Stark & Grellmann, 2002, Van der Wal *et al.*, 2004). Wet arctic habitats are very productive and are an important source of forage for many herbivore species (Forchhammer *et al.*, 2008, Henry *et al.*, 1990, Henry, 1998, Kristensen *et al.*, 2011), which may be why these ecosystems have been found to be sensitive towards changes in grazing pressure (Sjögersten *et al.*, 2008, Speed *et al.*, 2010). Despite that arctic wetlands are a large atmospheric CH_4 source, only few studies have looked at how CH_4 emission may potentially be affected by herbivores. In two studies conducted in the arctic and sub-alpine region no changes in the CH_4 emission was however found (Sjögersten *et al.*, 2011, Sjögersten *et al.*, 2012).

The high arctic environment can be seen as a simple ecosystem as it has few species both regarding animals and vegetation, which makes it somewhat easier to study a single impact such as large herbivores. It is also of particular importance since these ecosystem are of great global importance for the global C balance.

1.3 Aim and objectives

The aim of the PhD project was to study the Plant-Soil-Herbivore interactions in the Arctic, in order to broaden the knowledge of the C balance in high arctic mires. Three grazing experiments with somewhat different approaches were conducted during 2010 to 2013. Two of the experiments were *in-situ* field experiments conducted in the same high arctic mire in the growing seasons of 2010-2013 (Paper I and II). The purpose of paper I was to study the effect of excluding the large native herbivores muskoxen while the purpose of paper II was to see the effects of increased grazing pressure (by clipping plots which were already exposed to natural grazing). In paper III the allocation patterns from the same mire were studied in the laboratory on material (monoliths) collected from the arctic mire. Here half of the monoliths were clipped to simulate grazing. This experiment lasted only for one “growing season”. In paper IV are the main driving factors of CH_4 fluxes in the Zackenberg mire studied.

The objectives were to study:

- How does grazing effect greenhouse gas fluxes of CO_2 and CH_4 in a high arctic mire (Paper I, II, III, IV)?
    - Excluding large herbivore in an arctic mire (Paper I)
    - Increasing the grazing pressure in an arctic mire (Paper II)
    - Studying the in-depth effect of grazing (clipping) in a laboratory ^{14}C experiment (Paper III)
    - Analysing the special variation of CH_4 fluxes including areas where large herbivores were excluded (Paper IV)
- How is C allocated to different vegetation fractions, peat layer, pore-water and emitted as CO_2 and CH_4 in an high arctic mire? How is grazing affecting the allocation patterns (Paper III)?
- Does grazing affect the composition and density of vegetation on a short time scale (Paper I, II, III)?
- Are the substrate availability for methane production (organic acids, mainly acetate) in pore-water affected by grazing (Paper II, III)?

Methodology

2.1 The study site

The Zackenberg Research Station is situated in the National Park of NE Greenland (74°30’N 20°30W) (Figure 2), the studies took place in a mire not far from the station. The climate in the Zackenberg valley are defined as high arctic (Meltofte & Rasch, 2008), with an annual mean air temperature around -9˚C. The warmest month (July) has a mean monthly air temperature (MMAT) of 5.8˚C, while the coldest month (February) has a MMAT of -22.4˚C. The mean annual precipitation was 260 ml in the period 1996-2005, with only 10% falling as rain during summer (Hansen *et al.*, 2008). The valley is underlain by continues permafrost, and depending on the ecosystem the active layer is varying from 45 to 80 cm (Christiansen *et al.*, 2008). Five main plant communities are identified in the valley: *Cassiope* heath, *Dryas* heath, Grassland, mire and *Salix* snow-bed (Bay, 1998). In the mire (our study site), the vegetation is dominated by a few vascular plant species, e.g., the grass *Arctagrostis latifolia* and the sedges *Carex sp, Dupontia fisheri ssp. psilosantha*, *Eriophorum scheuchzeri* and *Equisetum sp*. (Paper I & II). Underneath these plants a dense moss cover is found, dominated by *Tomenthypnun*, *Scorpidium*, *Aulacomnium* and *Drepanoclaudus* (Ström *et al.*, 2012). The area has relatively high pH-values around 6.5-6.9 (Paper I & II) and the peat layer depth was measured to be between 7-20 cm at the site (Paper I & II).

During the last 15 years a significant annual warming of 2.25 ˚C has been recorded in Zackenberg (Hansen *et al.*, 2008). Climate change is predicted to continue especially in the Arctic region. By the year 2080 the average temperature is predicted to have increased with 4-5˚ C (ACIA, 2005). The projected precipitation for the Arctic in 2071 - 2090 is expected to increase with approximately 12% compared to the period 1981-2000. This increase will mainly occur during winter (ACIA, 2005). With increasing temperatures the region is expected to experience a further greening and a transformation in plant composition towards a higher density of shrubs (Hill & Henry, 2011, Hudson & Henry, 2009, Myers-Smith *et al.*, 2011, Tagesson *et al.*, 2010, Walker *et al.*, 2006).

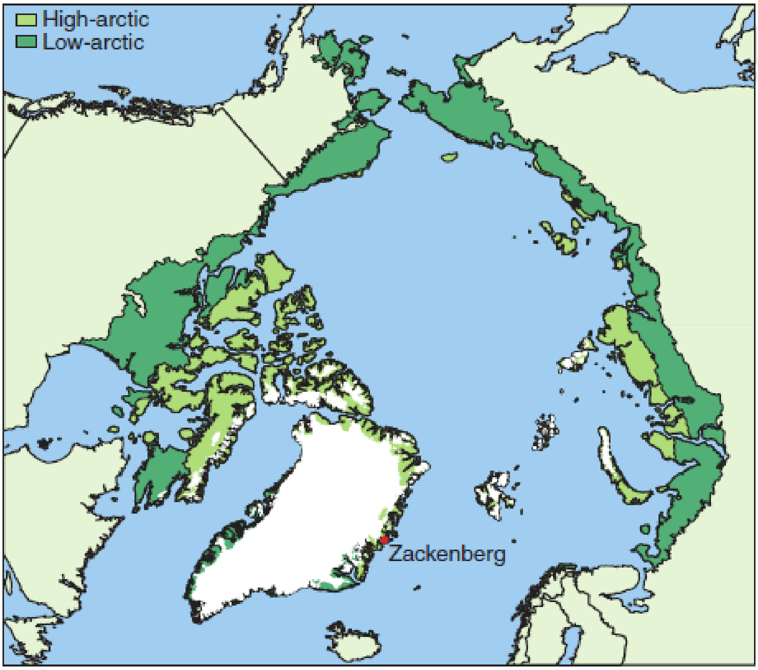


Figure 2. A map with the Zackenberg position and the low- and high-arctic zones: source (Meltofte & Rasch, 2008).

Muskoxen *Ovibos moschatus* (picture 1) are a natural part of the ecosystem and are found in very high numbers in the Zackenberg valley (Schmidt unpublished results), they are the only large herbivore in NE Greenland. Muskoxen are present year-round, and feed in grasslands and mires during summer (Kristensen *et al.*, 2011, Thing *et al.*, 1987), and in areas with thin snow-cover where the vegetation is easily assessable in winter (Berg *et al.*, 2008). Areas, such as the mire, with high density of plant biomass and forage makes the muskoxen gather in larger herds (Forchhammer *et al.*, 2008). Around 80% of their graminoid-dominated summer forage is obtained in the mire areas (Kristensen *et al.*, 2011). In a changing climate, the future of the large herbivores muskoxen in NE Greenland is unknown. Predictions suggesting that a temperature rise increases the growth of biomass (forage) (Hill & Henry, 2011), which will increase the herbivore population (Hudson & Henry, 2009), are commonly accepted. The number of muskoxen in Zackenberg, has increased substantially during the last decade (Forchhammer *et al.*, 2008). However with predictions about increasing numbers of thawing days during winter (Stendel *et al.*, 2008), which can lead to ice-crust formation, and increased snow-cover (Stendel *et al.*, 2008), a decline in the muskox population is very likely since hard and deep snow cover increases the mortality of muskoxen during the winter (Forchhammer *et al.*, 2002). The muskox population is significantly affected by the previous winter conditions, increased snow-cover has a negative effect on the population, and it can explain 65 % of the inter-annual variation that are observed in Zackenberg (Forchhammer *et al.,* 2008). Deep snow-cover during winter will also lead to less and later biomass production the following growing season (Tamstorf *et al.*, 2007). The population of muskoxen is significantly depended on the length of the growing season; long growing season will increase the number of muskoxen the following year (Forchhammer *et al.*, 2008).

Picture 1 Muskoxen *Ovibos moschatus*. Photo taken by Julie M. Falk in 2012.

2.2 In-situ field studies

As previously mentioned two main *in-situ* field approaches were carried out to study the effect large herbivores have on the ecosystem and its carbon balance. Paper IV are likewise based on data from parts of these field studies. In 2011-2013 data from all control plots from Paper I and II were used and 2013 also data from an automated chamber system and from the treated plots in paper I (see description below). Details about the automated chamber system can be seen in Materpanov et al., (2007, 2013).

Approach 1 (Paper I):

In July 2010, exclosures were permanently installed in the Zackenberg mire, to prevent muskoxen in grazing and trampling inside the exclosures. The full experimental set-up consists of five replicate blocks, each including the following: 1) an un-manipulated 10*10 m control area (C), where muskoxen move and graze freely, 2) an exclosure (Ex) (10*10m) where a one meter high fence is inhibiting muskoxen in the area (picture 2a) and 3) a snow control area (SC) (picture 2b) which acts as a control for a potential snow fence effect. The blocks are located on a slight downhill slope that is water-saturated in the beginning of the growing season. Block 1 and 2 are positioned farthest uphill in a drier part of the mire, while block 3, 4 and 5 are placed further downstream in a wetter and more flat part of the mire. In all areas the peat is underlain with silt. Inside each treatment C, EX and SC between 2-4 measuring plots were permanently installed (n=41). The measuring period and measured parameters can be seen in Table 1. For a further description of the setup see Paper I.

Picture 2 Approach 1, 2a) Exclosure 4, 21 september 2012 and 2b) Snow control 3, 3 August 2011. Photo taken by Julie M. Falk.

Approach 2 (Paper II):

In 2008, five blocks were established in a homogenous lowland part of the mire. The five replicate blocks consisted of three measuring plots placed closely together, to minimize the variation in active and peat-layer depth, water-table depth and soil temperature. Each block consisted of: 1) a plot which had all vascular plants removed in 2008 and leaving only mosses, new shoots were thereafter removed each summer, 2) a plot that as of 2010, had the vegetation cut approximately 3-4 cm above the surface twice each summer to thus mimick increased muskox grazing and 3) a plot which served as an un-manipulated control, though still exposed to ambient muskox grazing and trampling. The set-up is visualised in picture 3. For further description of the setup see Paper II. The measuring period and measured parameters can be seen in table 1.

Picture 3 Approach 2. Measuring plot to the left: increased grazing simulation plots where vegetation is cut. The middle plot: all vascular plants were removed. Plot to the right: control plot. Photo taken 28 July 2012 by Julie M Falk.

Table 1. List of measuring periods, gas analyser and measurements

Experiment	Time period	Gas analyzer	Measurements
Paper I	30. June - 8 August 2011	FTIR	CO_2 and CH_4 fluxes
(Exclosures)	6. July - 7. Sep. 2012	FTIR	Vegetation analysis 2011,2013
	2. July - 17. August 2013	FTIR	Vegetation harvest 2013
			Physical parameters*
Paper II	21. June - 7. August 2010	EGM, LGR	CO_2 and CH_4 fluxes
(Grazing simulation)	23. June - 5. August 2011	FTIR	Organic acid
	1. July - 18. October	FTIR	Vegetation analysis 2011
			Physical parameters*
Paper III	1. Feb -14. April 2012	FTIR	CO_2 and CH_4 fluxes
(Laboratory)			C allocation ^{14}C
			Vegetation harvest
Paper IV	1. July - 10. August 2011	FTIR	CO_2 and CH_4 fluxes
(Spacial variation)	1. July - 10. August 2012	FTIR	Organic acid
	1. July - 10. August 2013	EGM, LGR , FTIR	Vegetation analysis 2011,1013
			Physical parameters*

*Physical parameters: Active layer depth, Water table depth and Soil temperature

2.2.1 Greenhouse gas measurements

The fluxes of CO_2 and CH_4 were measured using a closed chamber technique (Christensen *et al.*, 2000, Ström & Christensen, 2007). For each plot measurement we performed a light and a dark measurement to determine NEE and ecosystem respiration (R_{eco}). The transparent Plexiglas chamber used were 41L, equipped with a fan to mix the air and a metal frame with a rubber list to ensure an airtight seal against an aluminium frame permanently installed in the ground (see frames in picture 3). In 2010, gas concentrations of CO_2 and CH_4 were measured using a LGR Fast Methane Analyser (DLT200, Los Gatos Research) and an infrared CO_2 gas analyser (EGM-4, PP-systems, Hitchin, Hertfordshire, UK), for further details see Paper II. In 2011 and the following years CO_2 and CH_4 were measured using a portable Fourier Transform Infrared (FTIR) spectrometer (Gasmet Dx 40-30, Gasmet Technologies Oy). For further description see Paper I, II and III.

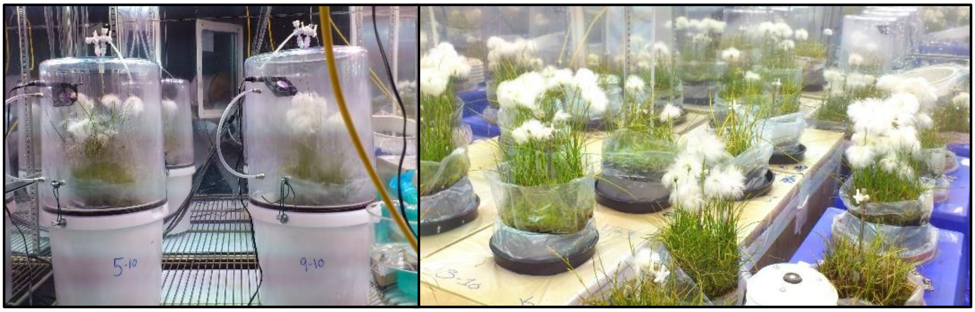
CO_2 and CH_4 fluxes were calculated from changes in gas concentration in the chamber as a function of time using linear fitting, following procedures by Crill et al. (1988). Data were, corrected for the ambient air temperature and air pressure. The release of CO_2 and CH_4 are denoted by positive values, while an uptake is denoted by negative values. Gas fluxes are expressed as mg m^{-2} h^{-1} of CH_4 or CO_2. The mean of light and dark measurements were calculated and used in the CH_4 flux analysis, as a strong significant correlation ($R>0.947$, $p<0.0001$) between the two CH_4 fluxes for individual plots were found. Gross Primary Production (GPP) was calculated by subtracting R_{eco} from NEE. For further description see Paper I, II and III.

2.2.2 Organic acid measurements

In Paper II and IV the pore-water were analysed for organic acid (OA), as easily available substrates for methanogens are found to be closely linked to the magnitude of CH_4 emission (Christensen *et al.*, 2003a, Ström & Christensen, 2007, Ström *et al.*, 2005a, Ström *et al.*, 2012). Pore-water were collected shortly after the gas flux measurements. Pore-water was drawn from stainless steel tubes, which were permanently installed inside the measuring plots, placed at different peat depths. The tubes were equipped with a three-way valve that enabled sampling without air penetrating to below-ground. With an equal amount of water from the different depths, the samples was immediately filtered through a low protein binding non-pyrogenic sterile pre-rinsed filter (Acrodisc PF 0.8/0.2 µm diameter 32 mm) and frozen shortly after. For further sampling details see Paper II and IV. The pore-water was subsequently analysed for OAs by using a liquid chromatography-ionspray tandem mass spectrometry system. The system consisted of a Dionex ICS-2500 liquid chromatography (LC) system and an Applied Biosystems 2000 Q-trap triple quadrupole mass spectrometer (MS). The LC-MS method and instrumental set-up is described in detail in Ström et al. (2012).

2.3 Laboratory study (Paper III)

Knowledge of the C allocation pattern are important if we want to fully understand the magnitude and mechanisms behind C emission and C uptake. In 2012 an in-depth laboratory study were made on monoliths from the high arctic mire in Zackenberg. The general allocation patterns of C to vegetation above- and below-ground, peat, pore-water and emitted as CO_2 and CH_4, were studied using ^{14}C pulse labelling technique. In order to get a better understanding of the effect of grazing on the ecosystem half of the monoliths were cut to simulate grazing. Eight monoliths were collected and brought back to Lund, Sweden for in-depth study of the C allocation pattern in a controlled laboratory environment.



Picture 4. The monoliths from the Zackenberg mire inside the climate chamber. The picture to the left are the two monoliths which were sealed to enable mearurement of the emitted $^{14}CO_2$ and $^{14}CH_4$. The picture to the right are the monoliths before half of them were clipped to simulate grazing.

^{14}C has a long life half time and low toxicity (Warembourg & Paul, 1973), which makes it good for determining C allocation and respiration patterns. The monoliths were placed in a climate chamber (picture 4) where air temperature, moisture and the light level could be regulated. After an initial period simulating spring conditions, the monoliths were kept at conditions similar to the summer months in Zackenberg. After a month, the spring increase of CO_2 and CH_4 flux from the monoliths had stabilized and they were labelled with 46MBq $^{14}CO_2$. By adding 10% H_2SO_4 to sodium bicarbonate ($NaH^{14}CO_3$, Specific Activity: 40-60mCi (1.48-2.22GBq)/mmol, Perkin Elmer) $^{14}CO_2$ were generated. To determine the efficiency of the $^{14}CO_2$ uptake, 90 min following labelling, air samples were taken repeatedly, shaken with NaOH and subsequently counted for radioactivity by the standard scintillation technique. Hionic-Flour™ (CIAB) was used as scintillation cocktail and counting was done on a Packard Tri-Carb 21000TR liquid scintillation analyser (USA). Two of the monoliths were kept in sealed chambers (picture 4 (left)) after labelling to measure the continuously emitted $^{14}CO_2$ and $^{14}CH_4$ for 30 days following labelling. For further details on the labelling and measured emitted $^{14}CO_2$ and $^{14}CH_4$ see Paper III. CO_2

and CH_4 fluxes were measured according to the procedure described in section 2.2.1 using the FTIR (Gasmet) approximately every second day (see Paper III). Pore-water samples were collected in connection to the flux measurements and were analysed for radioactivity (see Paper III). 30 days after labelling the monoliths were harvested and sorted into the dominating vascular plant species, mosses (fresh and old), stems, roots, litter and peat (without roots that could be visually sorted from the peat). The different fractions were dried at 60°C and weighted and analysed for radioactivity (See Paper III).

Results and Discussion

3.1 Herbivores impact on vegetation cover

Vegetation cover in the north is dynamic and changing with climate change and herbivory. Evidence of a "greening" occurring in the tundra have been found in several studies, which is likely due to increased biomass and changes in the plant community composition (Epstein *et al.*, 2013). It is safe to assume that these changes in vegetation cover will influence the feedbacks mechanism to the climate by changing the energy balance, carbon balance and plant-herbivore interactions.

The vegetation density of the dominating plant species in paper I and II were non-destructively analysed inside the plots where the fluxes of greenhouse gases were measured. The third year into the exclusion experiment the vegetation density had changed significantly in ungrazed plots. The density of total vascular plants had decreased with 30% and the density of *Eriophorum* tillers had decrease with 51% (paper I). These findings with a decrease in graminoid, are consistent with several other artic herbivory studies (e.g., Henry, 1998, Olofsson *et al.*, 2001, Post & Pedersen, 2008, Van der Wal *et al.*, 2001). The magnitude is however larger in our experiment, indicating that the responses to changed herbivory in the Zackenberg mire are large and rapid. The explanation for the decrease in vegetation density can mainly be explained by two factors. 1) Three years into the exclusion experiment the dry-weight of the moss-layer had increased significantly (55%) as had the amount of litter (230%) in ungrazed plots (see figure 3 and picture 5 (right)). Mosses are sensitive towards trampling (Liddle, 1997) and have been found to increase with a reduction in herbivory in several studies (e.g., Olofsson *et al.*, 2001, Van der Wal & Brooker, 2004). A thick moss-layer is an effective heat insulator (Van der Wal & Brooker, 2004, Van der Wal *et al.*, 2001, Zimov *et al.*, 1995) and together with the shading of the standing litter the soil temperatures can decrease, which were measured the third year in ungrazed plots (paper I). The active layer depth were likewise measured to be 9% lower the third year, which may be explained by the decrease in soil temperature. Lower temperature may reduce vegetation growth. The thicker moss-layer are also forcing the vascular plants to adapt to the new conditions using more C on growing longer leaves to reach the light at the expense of forming many shoots (personal observation). The mean height of all the vascular plants and *Eriophorum* tillers had significantly increased with 27% the third year (paper I), which verifies the need for longer leaves. 2) The second plausible explanation for the decreased vegetation density in ungrazed plots may be found in the flowering/seed setting pattern. Many of the flowering shoots are grazed during germination in spring, already the first year into the experiment we observed (picture 5 (left)) a higher number of flowering seeds in ungrazed plots. This is likely due to different C allocation patterns of plants when they are grazed. Grazed plants will allocate C to regrowth and shoots formation (vegetative reproduction) and therefor they won't be able to reproduce flowers within the same growing season (Hendrickson & Olson, 2006).

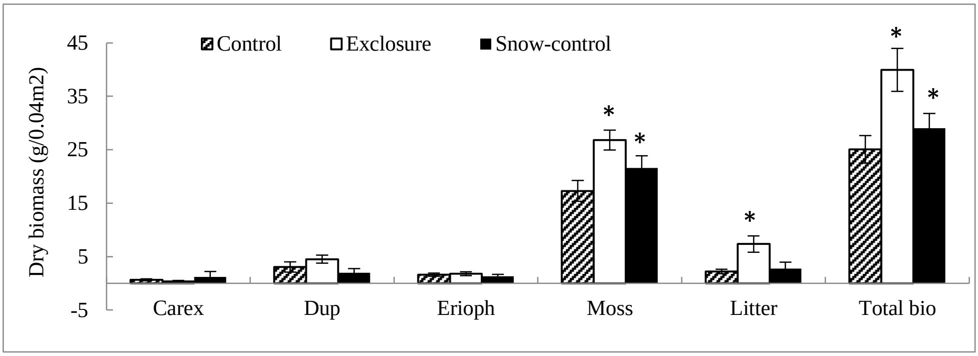


Figure 3. Mean dried biomass (g) from exclosure experiment (paper I). Harvested samples were in 2013 divided into vascular plants: *Carex sp* (Carex), *Dupontia psilosantha* (Dup) and *Eriophorum scheuchzeri* (Erioph) and fresh mosses (Moss), old biomass (Litter) and the total weight of the dried biomass (Total biomass). The significance for the differences (nonparametric test) between control and treatments are indicated with asterisk above the bars * p ≤ 0.05 (paper I)

Picture 5. Photo of exclousre 4, picture to the left August 2011 and to the right July 2013

In the clipping experiment the vegetation analysis were unfortunately only conducted at the second growing seasons in the clipping experiment. Despite the short responds time a tendency of less total number of vascular plant (20%) (p = 0.07) and *Eriophorum* tillers (42%) (p = 0.09) were found in plots with increased grazing pressure (paper II). It might be speculated that the higher grazing pressure causes a too high stress and that the short artic summer may be too short for recovery, as found in other studies (Elliott & Henry, 2011).

The dominating plant species *Eriophorum* and *Dupontia* are known to be well adapted to grazing (Henry, 1998). Consequently, the vegetation composition in the Zackenberg mire indicates an ecosystem well adapted to grazing. The ecosystem seems to be very sensitive towards small changes despite whether the changes are due to an increase or a decrease in grazing pressure. The vascular plants seems to react in the same way irrespectively of the two opposite treatments ungrazed and increased grazing pressure. In both treatments a reduction in density of vascular plants and especial the number of *Eriophorum* tillers are found. The thickness of mosses which can have large effect on the soil physical conditions are, however, responding very differently in the two experiments.

In the laboratory experiment no significant differences were found in the vegetation density between control and clipped monoliths, which may be explained by the short experiment period.

3.2 Herbivores impact on the C balance in the artic mire

3.2.1 CO_2 balance

The magnitude of NEE is positively correlated to living plant biomass (e.g., Sjögersten *et al.*, 2008, Ström & Christensen, 2007), as the photosynthetically active biomass to a great extent is controlling the CO_2 uptake. This connection is verified as a reduction of 113% in NEE is found when all vascular plants are removed (paper II) and a by the strong correlation between NEE and number of *Eriophorum* tillers ($R = -0.786$) found in paper VI.

With a substantial reduction in the density of vascular plants with exclusion of large herbivores (paper I) and increased grazing pressure (paper II) a reduction in NEE and GPP may be expected. The third year into the exclosure experiment a significant decrease in NEE and GPP were found in both ungrazed and snow control plots compared to control plots (figure 4 and table 2). This can to some extend be explained by the decrease in vascular plants the same year (section 3.1 and paper I). The decrease in soil temperature and active layer depth (paper I and section 3.1) found in ungrazed plots the same year may also explain some of the decrease found in NEE, as the photosynthetic rate and respiration is influenced by soil temperature and active layer depth (section 1.1). A much faster responds time were found in the simulation of increased grazing pressure (figure 4), as NEE decreased significantly immediately after clipping, which persisted through the growing season and the following years as clipping continued (paper II). In table 2 the percent with which the treatments differs from control plots (normally grazed) can be seen. The explanation to the immediate response to increased grazing pressure may be found in the removal of biomass by clipping the plots 3-4 cm above surface twice per season, which results in a quick drop in CO_2 uptake just after clipping (paper II).

Table 2. The percent that the treatments in paper I and II differs from the grazed controlled plots. In paper I the percent represent the last last year 2013, while it in paper II is the mean percent over the three measuring years for CO_2 and the last two for CH_4

	Treatment	NEE	R_{eco}	GPP	CH4
Paper I	Exclusion- non-grazed	47% ↓	0%	21% ↓	44% ↓
	Snow control	34% ↓	25% ↓	28% ↓	-
Paper II	Cut- increased grazing	35% ↓	0%	21% ↓	26% ↓
	No vegetation	113% ↓	62% ↓	89% ↓	82% ↓

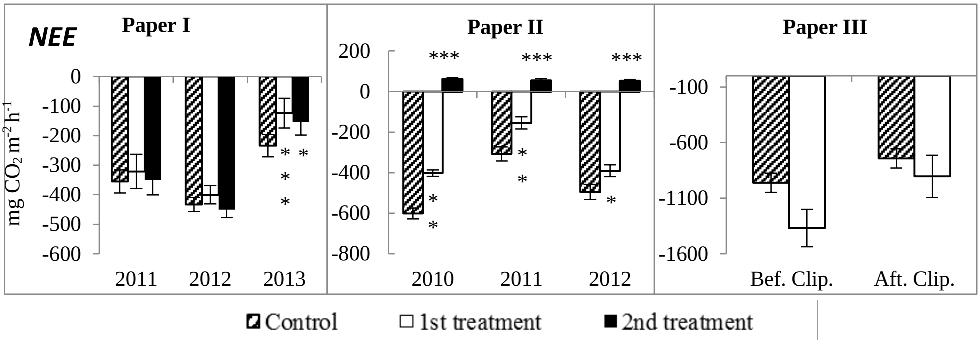


Figure 4. The mean Net Ecosystem Exchange (NEE) in mg CO_2 $m^{-2}h^{-1}$ from each measuring period from paper I, II & III. In paper III are the two measuring periods before (Bef. Clip) and after (Aft. Clip) half of the monoliths were clipped. Control plots in all experiments are illustrated with stripped bars, while first treatment: Exclosure (paper I) and Clipped plots (paper II and III) are illustrated with open bars. Second treatment: Snow-control (paper I) and No vegetation (paper II) (closed black bars). Significant differences between control and treatments are indicated with asterisks above bars, *** $p \leq 0.001$, **$p \leq 0.01$ and * $p \leq 0.05$.

In the laboratory experiment we found no significant change in NEE between control and clipped monoliths (figure 4). However, when looking at GPP a tendency of clipped monoliths having higher GPP before and after clipping compared to control monolith was found, p=0.081, p=0.094, for before and after respectively. Half of the monoliths had been clipped the year before the laboratory experiment, which may explain some of the differences seen before clipping. Higher GPP in clipped monoliths is in line with paper I, where grazed plots had significantly higher NEE and GPP, we can however not elucidate whether the change is due to vegetation change since no thorough vegetation analysis was made before the start of the experiment in paper III. The fluxes of NEE and GPP are much higher in the monoliths measured in the laboratory compared to what was measured in the field as seen in figure 4, which likely are due to the higher temperatures in the laboratory compared to the field (paper III).

Few have studied how the CO_2 balance is influenced by herbivores in the arctic. The majority of the existing studies have found a decrease in NEE with grazing (Cahoon *et al.*, 2012, Elliott & Henry, 2011, Sjögersten *et al.*, 2011, Sjögersten *et al.*, 2008, Vaisanen *et al.*, 2014, Van der Wal *et al.*, 2007). Alteration in vegetation composition and density are the main explanation for changes in NEE with herbivory (Cahoon *et al.*, 2012, Sjögersten *et al.*, 2011, Sjögersten *et al.*, 2008, Van der Wal *et al.*, 2007) which is in line with our findings. In paper IV we found a correlation between NEE and number of *Eriophorum* tillers in both control and ungrazed plots, which is clearly stating the connection and showing how fewer tillers in ungrazed plots leads to lower NEE values (paper IV). Ecosystems vegetation cover seems to react differently to herbivory depending on the habitat and the herbivores. This seems to be the main driver for changes in NEE. The exclusion experiment by Sjörgersten et al. (2001) from a similar wet habitat on Svalbard found in contrast to our exclusion experiment an increase in NEE as they had an increase in vascular plants with herbivore exclusion. This habitat was influenced by geese which have another impact on the ecosystem than muskoxen as they destroy the below-ground biomass with grubbing in the soil. Another study working with muskox exclusion from west Greenland have also in contrast to our results found an increase in NEE with exclusion as they after 8 years found an increase in shrubs (Cahoon *et al.*, 2012). The habitats in this study were however drier which may explain the different response. The study was however also conducted over a longer time period and the development in response to excluded grazing in Zackenberg needs to be followed under coming years to elucidate future succession in the ecosystem.

Several studies have found a decrease in ecosystem respiration of CO_2 with herbivory (Cahoon *et al.*, 2012, Sjögersten *et al.*, 2011, Stark & Grellmann, 2002, Van der Wal *et al.*, 2007), as the C allocation to below-ground and root growth is decreased with grazing (section 1.2, paper III). In our *in-situ* field studies we have however found no changes in R_{eco} with herbivory (Table 2), which may be due to that CO_2 respiration to a higher degree is controlled by the water table depth in a wet habitat as ours (section 1.1). With removal of all vascular plants in paper II, we found a substantial decrease in R_{eco} (table 2), which is pointing towards the important of the autotrophic respiration (paper II).

3.2.2 CH_4 balance

The spatial variability in CH_4 fluxes are large and have been found to rage from 9.1 mg CH_4 m^{-2} h^{-1} in continuous fen to -0.03 in heath areas in the Zackenberg valley (Tagesson *et al.*, 2013). The fluxes can vary greatly (measurements paper I, II and IV) within the same ecosystem type on plots only a few meters apart. Despite that many of the controlling factors for CH_4 fluxes have been identified (section 1.1), there are still many uncertainties. One of the main drivers for CH_4 fluxes in the Zackenberg mire during three growing seasons were found to be GPP. The year when all the potential drivers (fluxes of CO_2, soil and air temperature, water table and active layer depth, PAR, pore-water concentration of total organic acids and acetate acid and the vascular plant composition and density) were measured the main drivers was found to be in order of strength NEE, GPP and acetic acid and they were all highly correlated to the number of *Eriophorum* tillers (paper IV). To conclude from paper IV were the spatial variability in CH_4 flux strongly depended on productivity and C input to vegetation and pore water. The main driver of this C input is the vegetation composition, with high number of *Eriophorum* tillers leading to high C input. The importance of vascular plants for C input and hereby CH_4 fluxes were also found in paper II, where removal of all vascular plants lead to a substantial decrease in GPP and CH_4 emission (table 2). Tendencies of CH_4 fluxes being correlated to the amount of ^{14}C allocated to roots/stems and the biomass (paper III) may likewise indicate that productivity and C uptake is important drivers for CH_4 fluxes. The density of *Eriophorum* have decreased with a higher percentage compared to total vascular plants in both experiments (paper I and II) which could indicate that *Eriophorum* are more sensitive towards changes in grazing pressure. As the density of *Eriophorum* have been found to be important for C uptake, will a decrease in special these vascular plants have an impact on the CH_4 emission.

The strong correlation between C assimilation (GPP, NEP, NEE) and CH_4 emission (section 1.1) are verified in paper II, III and IV. With a decrease in NEE and GPP (paper I and II) in the two grazing experiments exclusion and increased grazing pressure a decrease in CH_4 are somewhat expected in the treatments. Three years of muskox exclusion resulted in a significant decrease of 44% in CH_4 fluxes. Despite of the opposite treatment with increased grazing pressure the same responds were found in paper II, with a decrease of 26% (figure 5) due to suppressed vegetation growth. No significant changes were found in the short time laboratory experiment. However some indications of increased GPP and CH_4 emission from clipped monoliths were found, which will be elaborated further in the sections below. No other arctic study (to our knowledge) have found any changes in CH_4

fluxes with herbivory or exclusion of herbivory (Sjögersten *et al.*, 2011). The study by Sjörgersten et al., (2011) had however much lower fluxes in comparison to our studies.

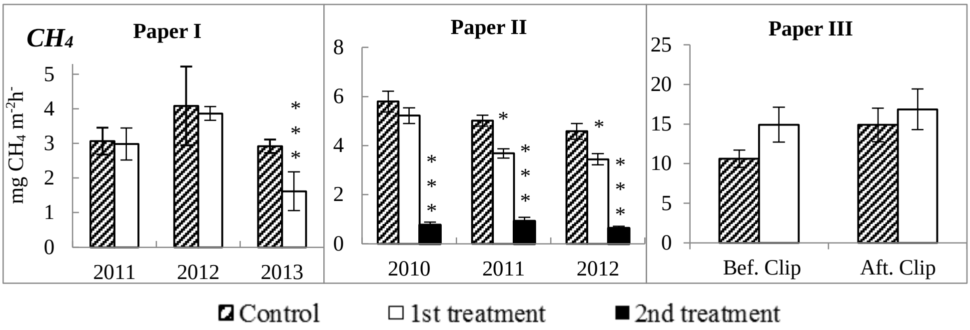


Figure 5. The mean CH_4 fluxes mg CH_4 $m^{-2}h^{-1}$ from each measuring period from paper I, II & III. In paper III the two measuring periods before (Bef. Clip) and after (Aft. Clip) half of the monoliths were clipped are shown. Control plots in all experiments are illustrated with stripped bars, while first treatment: Exclosure (paper I) and Clipped plots (paper II and III) are illustrated with open bars. Second treatment: Snow-control (paper I) and No vegetation (paper II) (closed black bars). Significant differences between control and treatments are indicated with asterisks above bars, *** $p \leq 0.001$, **$p \leq 0.01$ and * $p \leq 0.05$.

Substrate availability

Substrate availability have been found to be of great importance for the magnitude of CH_4 fluxes (section 1.1 and paper IV). To fully understand the changes we see in CH_4 fluxes due to herbivory the concentration of organic acids were measured in pore-water in paper II. In paper III the ^{14}C-allocated to pore-water and in the peat fraction were also studied, which indicates the substrate availability.

Substrate availability are well correlated to vegetation density, and the vascular plant *Eriophorum scheuchzeri* have in several studies been found to be particularly connected to high substrate availability (section 1.1). In paper IV a clear connection were found between the density of *Eriophorum* and the total concentration of organic acids and in particular acetic acid. In the field acetic acid were found to be the dominating organic acid (paper II and IV), which is in line with other artic mire studies (Ström & Christensen, 2007, Ström *et al.*, 2012). The first two years into the clipping experiment no differences were found in total organic acids or acetic acid between control and clipped plots. The third year into the experiment the acetic acid concentration in clipped plots was however significantly lower

(27%) compared to control plots (figure 6). The mean concentration was very similar to what was found in plots with no vegetation (paper II). This may indicate that the C allocation pattern have changed so that the majority of assimilated C is allocated to regrowth instead of below ground. For further discussion on C allocation patterns see section below and paper III.

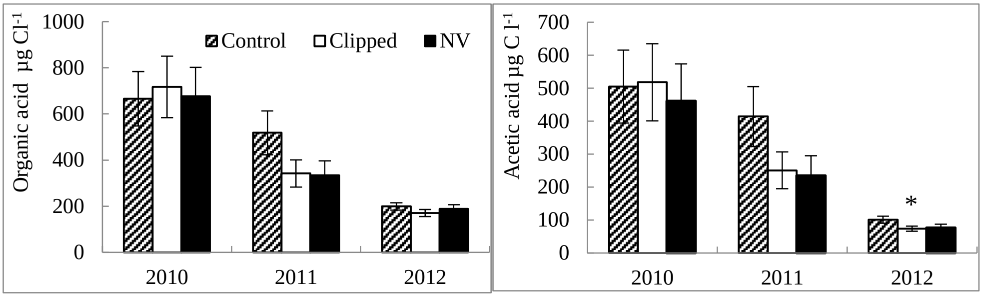


Figure 6. The concentration of total organic acids (left) and acetic acid (right) (µg C l^{-1}) from the clipping experiment (paper II)

In short time laboratory studies root exudation have been found to increase following defoliation (Butenschoen *et al.*, 2008, Hamilton *et al.*, 2008, Paterson *et al.*, 2005). An increase in root exudation following grazing is explained by larger C flow to roots as a higher demand for C nutrient trade-off for regrowth is needed (Holland *et al.*, 1996, Paterson, 2003). In our laboratory study we found a tendency ($p = 0.077$) of the peat fraction in clipped monoliths having more ^{14}C 30 days after labelling. This could indicate an increase in root exudation as ^{14}C found in the peat are assumed to be C allocated to root exudates, fine roots and microorganism (paper III). However, no differences was found in ^{14}C in pore-water to verify this, even though some indications of a more unstable ^{14}C flow to the pore-water was found as the standard error increased substantially following clipping and 10 days onwards (paper III). It might be suggested that a large amount of acetic acid adheres to peat and hair (or small) root surfaces and that ^{14}C in peat therefore is a more representative estimate of root exudation/allocation to roots than pore-water concentrations. It is also safe to conclude that ^{14}C can't have been incorporated into peat over such a short time period. In a single pilot study of a pore-water sample from a clipped and control monolith, acetic and lactic acid were found to account for 23-37% of the radioactivity signal in the samples, supporting that a large portion of ^{14}C found in pore-water originate from root exudation. An increase in root exudation with grazing doesn't support the finding of a decrease in acetic acid and CH_4 in the clipping field study the third year (paper II). It is however important to note the short time respond in the laboratory study and that the number of especially *Eriophorum* tillers had decreased with increased grazing pressure which is most likely affecting the substrate availability to a higher degree, as seen in paper IV. It should also be noted that no replicates renders a conclusion from the pilot study impossible.

3.2.3 C-allocation pattern

To understand the changes seen in C balance with herbivory in a high arctic mire, it is important to understand the general C allocation pattern of those particular ecosystem. As no studies (to our knowledge) have looked at the allocation pattern of a high arctic mire a small in-depth study were made on monoliths from the Zackenberg mire (section 2.3). 30 days after ^{14}C labelling, the recaptured ^{14}C in the biomass and peat fraction had on average been distributed with 62% allocated to above-ground biomass, while 38% was found below-ground. This correspond well to what has been found in a subarctic mire (Christensen *et al.*, 2003b). The C allocation pattern varies with ecosystems and depends in general on the stage of the plant development and on the nutrient availability (Kuzyakov & Domanski, 2000, Warembourg & Estelrich, 2000). In nutrient poor ecosystem there will be a higher demand for C allocation to below-ground, as the release of organic compounds such as organic acids in soil often are used for nutrient trade-off (Kuzyakov & Domanski, 2000, Ström *et al.*, 2005b). Two of the monoliths in our laboratory experiment (one control and one clipped) were hermetically sealed for a more detailed carbon allocation study. 30 days after ^{14}C labelling more than 70% of the injected ^{14}C were recaptured, excluding the first two days of $^{14}CO_2$ and $^{14}CH_4$ emission following labelling as a leak was found in one of the monoliths. The C distribution can be seen in table 3. The monolith that had been properly sealed emitted 2.8 MBq as $^{14}CO_2$ the first two days, which correspond to an increase of 44% of the total $^{14}CO_2$ emitted during the full experimental period, which increased the recovery to 75%. The high $^{14}CO_2$ respiration emitted the first days seems to come from above-ground biomass as the mean maximum translocation time of assimilated CO_2 to the pore-water was 5-7 days. The turnover time from assimilated $^{14}CO_2$ to $^{14}CH_4$ were 10-15 days, pointing towards a time lag from C uptake through photosynthesis via root exudation, fermentation to heterotrophic respiration and CH_4 production and emission of the corresponding number of days. In the closed ^{14}C budget (excluding the first two days) around 57% of ^{14}C was allocated above-ground to vascular plants and green moss (table 3, paper III). In the properly sealed monolith were 19% of the recaptured ^{14}C emitted as $^{14}CO_2$ and $^{14}CH_4$ which were within the same magnitude as Christensen et al., (2003b).

Table 3. The ^{14}C % distribution of recaptured ^{14}C, 30 days after ^{14}C pulse labelling. Given that the recaptured ^{14}C correspond to 100%. Data are from the two enclosed monoliths (n=1). The distrubtion doesn't include the first two days of emitted $^{14}CO_2$ and $^{14}CH_4$, due to leakage (paper III)

	Control %	Clipped %
Above-ground		
Green leaves + mosses	42.6	48.3
Withered leaves + mosses	12.9	10.8
Below-ground		
Roots + stems	20.7	11.7
Peat	11.6	17.4
Emitted $^{14}CO_2$	11.3	10.5
Emitted $^{14}CH_4$	0.6	0.8
Estimated ^{14}C emitted in pore-water	0.3	0.3
Sum	100	100

Herbivory

No significant differences was found with herbivory, which to a certain degree can be explained by the few replicates and the large variability between the monoliths that was evident already from the beginning of the experiment. Further discussions around spatial variability can be found in paper IV. In the laboratory experiment the closed ^{14}C budget and several other factors point towards a changed C allocation pattern following grazing. Subsequently we found an increased root exudation, more C allocated to above-ground to support regrowth and higher CH_4 and GPP fluxes (paper III). Supporting the results in the ^{14}C-study most variables point to the same interactions between plants-soil and herbivory as seen in all the other studies presented in this thesis. Consequently the results from this thesis combined all point towards the importance of considering herbivory when discussing C balance in the arctic.

3.2.4 Total C balance

As mentioned in the beginning any discussions about the C balance in wet habitats should include both CO_2 and CH_4 fluxes. In this section the impact of herbivory on the C balance in the Zackenberg mire will be discussed. In our field studies grazed, ungrazed and increased grazing plots were found to be CO_2 sinks during the growing/measuring period during all years that were included in this thesis (figure 4). In the plots where all vascular plants were removed the ecosystem however shifted from being a CO_2 sink to a CO_2 source. The assimilation and the net ecosystem exchange of CO_2 where found to be significantly smaller with exclusion and increased grazing compared to normal grazed plots, which have a negative impact on the level of greenhouse gases in the atmosphere as less CO_2 will be assimilated by vegetation and potential stored below-ground. The emission of the strong greenhouse gas CH_4 (section 1.1) is however also decreasing substantially with changes in herbivory, which potentially could compensate for the decrease in CO_2 uptake.

In paper I a back of the envelope calculation was made of the mean hourly Global Warming Potential (100 years, CH_4=34 (CO_2 equivalents), IPCC 2013) on the CO_2 and CH_4 fluxes combined. The calculations were only made for the third year where a significant change between grazed and ungrazed was found. The CO_2 equivalents were -182 and -81 (mg CO_2 equivalents m^{-2} h^{-1}) for grazed and ungrazed areas, respectively. This simple calculation showed that the sink function of CO_2 would remain, however, being less than half if the herbivores disappeared from the mire, in comparison to present day values. If the same calculations were to be made for the increased grazing experiment the last year of the clipping experiment the CO_2 equivalents were -340, -274 and 74 (mg CO_2 equivalents m^{-2} h^{-1}) for control, increased grazing and no vegetation plots. Which indicates that plots with no vascular plants are acting as a C source to the atmosphere while plots with increased grazing still acted as a C sink. The sink function had however decreased substantially when grazing pressure increased. Further studies are however needed to fully understand the C-balance of these ecosystems and the intricate interactions between herbivores and ecosystem development in these regions.

The ^{14}C laboratory, although no significant effects of grazing was found, supports the findings in paper I. The results indicated higher GPP, NEE, root exudation and CH^4 flux from clipped monoliths and a relationship between GPP and CH^4 flux. If we allow ourselves to speculate around the two monoliths with a closed C budget, despite the fact that we have no replication, we see further indications along the same line. Here we see a ^{14}C shoot to root ratio of 2 in unclipped control and of 4:1 in clipped indicating that 2 times more CO_2 is assimilated into aboveground biomass when plants are clipped.

3.3 The future C balance with changing herbivore density

The future of the muskoxen population in Zackenberg is unknown, as the population can either increase or decrease with climate change (section 2.1). There is no doubt that the climate is changing in the high arctic. The question is whether the ecosystem and its residents, despite their plasticity, are able to adapt to the new conditions within the short time scale. In our two *in-situ* field studies both scenarios were tested and to our surprise we found that both treatments had similar effects on the C balance as the density of vascular plants more or less reacted in the same way, leading to a substantial decrease in the C uptake. From our experiments we see that changes in muskox population in Zackenberg would rapidly alter the vegetation density and composition in the mire, ultimately affecting the carbon balance.

Herbivory have in the arctic been found to constrain the biomass of deciduous shrubs (Post & Klein, 1996), after three years of muskox exclusion we found no evidence of shrubs becoming more dominant in ungrazed areas. Shrub dominated ecosystems are a stronger C sinks compared to graminoid dominated (Cahoon *et al.*, 2012). Shrub expansion have been found to have a time delay of at least 5 years in areas with both herbivore exclusion and temperatures raise (Post & Pedersen, 2008) which may explain that no such development is seen in our experiment. Additionally, no general indications of shrub expansion in Zackenberg has been observed despite the increasing temperatures (Schmidt *et al.*, 2012). This is likely due to the slow responses of the high arctic vegetation (Elmendorf *et al.*, 2012). The high density of muskoxen in the area could however also be partly responsible for the absence of shrub expansion (Myers-Smith *et al.*, 2011).

To be able to predict how herbivores will influence the future C balance studies with combined herbivory and warning are needed. Such experiments have in other areas shown that herbivores inhibit the increase in deciduous dwarf shrub vegetation cover (Post & Pedersen, 2008, Rinnan *et al.*, 2009) and reduces the extra biomass production that occurred due to warming within the range of 11-46% (Post & Pedersen, 2008).

It is indeed difficult to predict what will happen with the future carbon balance in arctic mires, but it is crucial to consider the impact large herbivores have on the ecosystem and on its C balance.

Conclusion

- Three years of muskox exclusion lead to a decrease in NEE of 47%, while an increase in grazing pressure immediately lead to a decrease of 35% (mean of the three measuring years). The decreased C uptake could in both cases be attributed to a decrease in the density of vascular plants

- The significant decrease in NEE and density of vascular plants lead to a decrease in the CH_4 emission. The third year into the exclusion experiment the CH_4 emission had decreased with 44% and by 26% mean for the last two years of the clipping experiment.

- There is a strong dependence of the spatial variability in CH_4 flux on productivity and C input to vegetation and pore water. The main driver of this C input is the vegetation composition, with high number of *Eriophorum* tillers leading to high input. Consequently, the impact of herbivores on the C balance seems to be mainly driven by how the vegetation composition and density responds to herbivory.

- The density of the vascular plant *Eriophorum scheuchzeri* decrease more than other vascular species with both increased and decreased herbivory, indicating the sensitivity of this species towards changes in herbivory. Changes in the density of *Eriophorum* are of special importance due to its effect on CH_4 production and emission.

- Future scenarios of both increased and decreased grazing pressure might have similar results on the C balance of the ecosystem. If the muskox population increases due to climate change, the density of vascular plants are likely to decrease as the grazing pressure becomes too high for them to regrow during short arctic summer. On the other hand, if the muskox population decreases as snow-cover and ice-crust formation increases with climate change this will most likely be followed by a decrease in vascular plant coverage.

- The response of the Zackenberg mire ecosystem to changes in grazing pressure is both rapid and dramatic. Consequently, herbivory have been found to be a controlling factor for the vegetation cover and the C balance in a high arctic mire and their impact should be considered when discussing the past, present or future C balance in the arctic.

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References

Acia (2005) *Arctic Climate Impact Assessment* New York, Cambridge University Press.

Bagchi S, Ritchie ME (2010) Introduced grazers can restrict potential soil carbon sequestration through impacts on plant community composition. *Ecology Letters,* **13**, 959-968.

Bay C (1998) Vegetation mapping of Zackenberg valley. *Northeast Greenland, Danish Polar Center & Botanical Museum, University of Copenhagen, Copenhagen*.

Beaulieu J, Gauthier G, Rochefort L (1996) The Growth Response of Graminoid Plants to Goose Grazing in a High Arctic Environment. *Journal of Ecology,* **84**, 905-914.

Belshe EF, Schuur EaG, Bolker BM (2013) Tundra ecosystems observed to be CO2 sources due to differential amplification of the carbon cycle. *Ecology Letters,* **16**, 1307-1315.

Berg TB, Schmidt NM, Høye TT, Aastrup PJ, Hendrichsen DK, Forchhammer MC, Klein DR (2008) *High-Arctic Plant-Herbivore Interactions under Climate Influence*.

Butenschoen O, Marhan S, Scheu S (2008) Response of soil microorganisms and endogeic earthworms to cutting of grassland plants in a laboratory experiment. *Applied Soil Ecology,* **38**, 152-160.

Cahoon SMP, Sullivan PF, Post E, Welker JM (2012) Large herbivores limit CO2 uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology,* **18**, 469-479.

Callaghan T, Chernov Y, Chapin T *et al.* (2004) Effects of Changes in Climate on Landscape and Regional Processes, and Feedbacks to the Climate System. *Ambio,* **33**, 459-468.

Callaghan TV, Björn LO, Chapin Iii FS *et al.* (2005) *Arctic Tundra and Polar Desert Ecosystems,* Cambridge, Cambridge University Press.

Cargill SM, Jefferies RL (1984) The Effects of Grazing by Lesser Snow Geese on the Vegetation of a Sub- Arctic Salt Marsh. *Journal of Applied Ecology,* **21**, 669-686.

Chapin FS (1980) Nutrient Allocation and Responses to Defoliation in Tundra Plants. *Arctic and Alpine Research,* **12**, 553-563.

Christensen TR, Ekberg A, Ström L, Mastepanov M (2003a) Factors controlling large scale variations in methane emissions from wetlands. *Geophysical Research Letters,* **30**, 67-61 - 67-64.

Christensen TR, Friborg T, Sommerkorn M *et al.* (2000) Trace gas exchange in a high-Arctic valley: 1. Variationsin CO2 and CH4 Flux between tundra vegetation types. *Global Biogeochem. Cycles,* **14**, 701-713.

Christensen TR, Panikov N, Mastepanov M *et al.* (2003b) Biotic controls on CO2 and CH4 exchange in wetlands – a closed environment study. *Biogeochemistry,* **64**, 337-354.

Christiansen HH, Sigsgaard C, Humlum O, Rasch M, Hansen BU (2008) Permafrost and Periglacial Geomorphology at Zackenberg. In: *Advances in Ecological Research.* pp Page.

Elberling B, Nordstrom C, Grondahl L *et al.* (2008a) High-arctic soil CO2 and CH4 production controlled by temperature, water, freezing and snow. *Advances in Ecological Research*, 441-472.

Elberling B, Tamstorf MP, Michelsen A *et al.* (2008b) Soil and Plant Community-Characteristics and Dynamics at Zackenberg. In: *Advances in Ecological Research.* pp Page.

Elliott TL, Henry GHR (2011) Effects of Simulated Grazing in Ungrazed Wet Sedge Tundra in the High Arctic. *Arctic, Antarctic, and Alpine Research*, 198.

Elmendorf SC, Henry GHR, Hollister RD *et al.* (2012) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters,* **15**, 164-175.

Epstein HE, Myers-Smith I, Walker DA (2013) Recent dynamics of arctic and sub-arctic vegetation. *Environmental Research Letters,* **8**, 015040.

Forchhammer MC, Post E, Stenseth NC, Boertmann DM (2002) Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. *Population Ecology,* **44**, 113-120.

Forchhammer MC, Schmidt NM, Hoye TT, Berg TB, Hendrichsen DK, Post E (2008) Population dynamical responses to climate change. *Advances in Ecological Research,* **40**, 391-420.

Frenzel P, Karofeld E (2000) CH4 emission from a hollow-ridge complex in a raised bog: The role of CH4 production and oxidation. *Biogeochemistry,* **51**, 91-112.

Friborg T, Christensen TR, Hansen BU, Nordstroem C, Soegaard H (2000) Trace gas exchange in a high-Arctic valley: 2. Landscape CH4 fluxes measured and modeled using eddy correlation data. *Global Biogeochemical Cycles,* **14**, 715-723.

Green RA, Detling JK (2000) Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. *Oikos,* **91**, 280-284.

Groendahl L (2006) Carbon dioxide exchange in the High Arctic – examples from terrestrial ecosystems. Unpublished Ph.D. Institute of Geography, University of Copenhagen, Copenhagen, 214 pp.

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

Hansen BU, Sigsgaard C, Rasmussen L *et al.* (2008) Present-Day Climate at Zackenberg. In: *Advances in Ecological Research.* pp Page. San Diego, Elsevier Academic Press Inc.

Hendrickson J, Olson B (2006) Understanding Plant Response to Grazing. In: *Targeted Grazing: A natural approach to vegetation management and landscape enhancement.* (eds R D, Rj D, Associates I, Logan, Ut) pp Page, http://www.webpages.uidaho.edu/rx-grazing/handbook/Chapter_4_Targeted_Grazing.pdf, American Sheep Industry, Agricultural Research Service.

Henry GHR, Svoboda J, Freedman B (1990) Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. *Canadian Journal of Botany,* **68**, 2660-2667.

Henry GR (1998) Environmental influences on the structure of sedge meadows in the Canadian High Arctic. *Plant Ecology*, **134**, 119-129.

Hicks Pries C, Schuur EG, Crummer KG (2012) Holocene Carbon Stocks and Carbon Accumulation Rates Altered in Soils Undergoing Permafrost Thaw. *Ecosystems,* **15**, 162-173.

Hill GB, Henry GHR (2011) Responses of High Arctic wet sedge tundra to climate warming since 1980. *Global Change Biology*, **17**, 276-287.

Holland JN, Cheng W, Crossley DaJ (1996) Herbivore-induced changes in plant carbon allocation: Assessment of below-ground C fluxes using carbon-14. *Oecologia (Berlin),* **107**, 87-94.

Hudson JMG, Henry GHR (2009) Increased Plant Biomass in a High Arctic Heath Community from 1981 to 2008. *Ecology*, 2657.

Ipcc (2013) Working group I contribution to the IPCC fifth Assessment, Report (AR5), Climate Change 2013: The Physical Science Basis. pp Page, WMO, UNEP.

Joabsson A, Christensen TR (2001) Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. *Global Change Biology,* **7**, 919-932.

Joabsson A, Christensen TR, Wallen B (1999) Vascular plant controls on methane emissions from northern peatforming wetlands. *Trends in Ecology and Evolution,* **14**, 385-388.

Killham K (1994) *Soil ecology,* Cambridge University Press.

Kristensen DK, Kristensen E, Forchhammer MC, Michelsen A, Schmidt NM (2011) Arctic herbivore diet can be inferred from stable carbon and nitrogen isotopes in C3 plants, faeces, and wool. *Canadian Journal of Zoology,* **89**, 892-899.

Kuzyakov Y, Domanski G (2000) Carbon input by plants into the soil. Review. *Journal of Plant Nutrition and Soil Science*, **163**, 421-431.

Liddle M (1997) *Recreation ecology: the ecological impact of outdoor recreation and ecotourism,* Chapman & Hall Ltd.

Mastepanov M, Sigsgaard C, Dlugokencky EJ, Houweling S, Ström L, Tamstorf MP, Christensen TR (2008) Large tundra methane burst during onset of freezing. *Nature,* **456**, 628-630.

Mcguire AD, Anderson LG, Christensen TR *et al.* (2009) Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs,* **79**, 523-555.

Mcguire AD, Christensen TR, Hayes D *et al.* (2012) An assessment of the carbon balance of arctic tundra: comparisons among observations, process models, and atmospheric inversions. *Biogeosciences Discuss.,* **9**, 4543-4594.

Meltofte H, Rasch M (2008) The Study Area at Zackenberg. In: *Advances in Ecological Research.* pp Page. San Diego, Elsevier Academic Press Inc.

Mulder CPH (1999) Vertebrate herbivores and plants in the Arctic and subarctic: effects on individuals, populations, communities and ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics,* **2**, 29-55.

Myers-Smith IH, Hik DS, Forbes BC *et al.* (2011) Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters,* **6**.

Oechel WC, Hastings SJ (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature,* **361**, 520-524.

Oke TR (1996) *Boundary Layer Climates,* London, Routledge.

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, 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.

Ouellet J-P, Boutin S, Heard DC (1994) Responses to simulated grazing and browsing of vegetation available to caribou in the Arctic. *Canadian Journal of Zoology,* **72**, 1426-1435.

Owen-Smith N (1987) Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology,* 351-362.

Paterson E (2003) Importance of rhizodeposition in the coupling of plant and microbial productivity. *European Journal of Soil Science,* **54**, 741-750.

Paterson E, Thornton B, Midwood Andrew J, Sim A (2005) Defoliation alters the relative contributions of recent and non-recent assimilate to root exudation from Festuca rubra. *Plant, Cell & Environment,* **28**, 1525-1533.

Ping CL, Michaelson GJ, Jorgenson MT, Kimble JM, Epstein H, Romanovsky VE, Walker DA (2008) High stocks of soil organic carbon in the North American Arctic region. *Nature geoscience,* **1**, 615-619.

Post E, Klein D (1996) Relationships between graminoid growth form and levels of grazing by caribou (Rangifer tarandus) in Alaska. *Oecologia,* **107**, 364-372.

Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America,* **105**, 12353-12358.

Post WM, Emanuel WR, Zinke PJ, Stangenberger AG (1982) Soil carbon pools and world life zones *Nature (London),* **298**, 156-159.

Rinnan R, Stark S, Tolvanen A (2009) Responses of vegetation and soil microbial communities to warming and simulated herbivory in a subarctic heath. *Journal of Ecology,* **97**, 788-800.

Schlesinger WH (1997) *Biogeochemistry: An Analysis of Global Change; 2nd Edition,* London, UK, Academic press, Harcourt Brace & CO. Publishers.

Schmidt NM, Kristensen DK, Michelsen A, Bay C (2012) High Arctic plant community responses to a decade of ambient warming. *Biodiversity,* **13**, 191-199.

Schuur EaG, Bockheim J, Canadell JG *et al.* (2008) Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle. *BioScience,* **58**, 701-714.

Sjögersten S, Van Der Wal R, Loonen MJE, Woodin SJ (2011) Recovery of ecosystem carbon fluxes and storage from herbivory. *Biogeochemistry,* **106**, 357-370.

Sjögersten S, Van Der Wal R, Woodin SJ (2008) Habitat type determines herbivory controls over CO2 fluxes in a warmer arctic. *Ecology (Washington D C),* **89**, 2103-2116.

Sjögersten S, Yanez-Serrano A, Llurba R, Ribas A, Sebastià MT (2012) Temperature and moisture controls of C fluxes in grazed subalpine grasslands. *Arctic, Antarctic, and Alpine Research,* **44**, 230-246.

Speed JDM, Woodin SJ, Tommervik H, Van Der Wal R (2010) Extrapolating herbivore-induced carbon loss across an arctic landscape. *Polar Biology,* **33**, 789-797.

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

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

Stendel M, Christensen JH, Petersen D (2008) Arctic Climate and Climate Change with a Focus on Greenland. In: *Advances in Ecological Research.* (eds Hans Meltofte TRCBEMCF, Morten R) pp Page., Academic Press.

Ström L, Christensen TR (2007) Below ground carbon turnover and greenhouse gas exchanges in a sub-arctic wetland. *Soil Biology & Biochemistry*, **39**, 1689-1698.

Ström L, Ekberg A, Mastepanov M, Christensen TR (2003) The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. *Global Change Biology*, **9**, 1185-1192.

Ström L, Mastepanov M, Christensen TR (2005a) Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. *Biogeochemistry (Dordrecht)*, **75**, 65-82.

Ström L, Owen AG, Godbold DL, Jones DL (2005b) Organic acid behaviour in a calcareous soil implications for rhizosphere nutrient cycling. *Soil Biology and Biochemistry*, **37**, 2046-2054.

Ström L, Tagesson T, Mastepanov M, Christensen TR (2012) Presence of Eriophorum scheuchzeri enhances substrate availability and methane emission in an Arctic wetland. *Soil Biology and Biochemistry*, **45**, 61-70.

Susiluoto S, Rasilo T, Pumpanen J, Berninger F (2008) Effects of Grazing on the Vegetation Structure and Carbon Dioxide Exchange of a Fennoscandian Fell Ecosystem. *Arctic, Antarctic, and Alpine Research*, 422.

Tagesson T, Mastepanov M, Mölder M *et al.* (2013) Modelling of growing season methane fluxes in a high-Arctic wet tundra ecosystem 1997-2010 using in situ and high-resolution satellite data. *Tellus B*, **65**.

Tagesson T, Mastepanov M, Tamstorf MP *et al.* (2010) Satellites reveal an increase in gross primary production in a greenlandic high arctic fen 1992–2008. *Biogeosciences Discussions*, **7**, 1101-1129.

Tamstorf MP, Illeris L, Hansen BU, Wisz M (2007) Spectral measures and mixed models as valuable tools for investigating controls on land surface phenology in high arctic Greenland. *BMC Ecology*, **7**, 9.

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 S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochem. Cycles*, **23**, GB2023.

Thing H (1984) Feeding ecology of the West Greenland caribou (Rangifer tarandus groenlandicus) in the Sisimiut-Kangerlussuaq region [vegetation, food selection, forage quality, rumen samples, chemical analysis, migration]. *Danish Review of Game Biology (Denmark)*.

Thing H, Klein DR, Jingfors K, Holt S (1987) Ecology of muskoxen in Jameson Land, northeast Greenland. *Ecography*, **10**, 95-103.

Vaisanen M, Ylanne H, Kaarlejarvi E, Sjogersten S, Olofsson J, Crout N, Stark S (2014) Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Clim. Change*, **advance online publication**.

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 Ecosystems. *Ecography,* 242.

Van Der Wal R, Brooker RW (2004) Mosses Mediate Grazer Impacts on Grass Abundance in Arctic Ecosystems. *Functional Ecology,* 77.

Van Der Wal R, Sjögersten S, Woodin SJ *et al.* (2007) Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. *Global Change Biology,* **13**, 539-545.

Van Der Wal R, Van Lieshout SMJ, Loonen MJJE (2001) Herbivore impact on moss depth, soil temperature and arctic plant growth. *Polar Biology,* **24**, 29-32.

Walker MD, Wahren CH, Hollister RD *et al.* (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America,* **103**, 1342-1346.

Walter KM, Zimov SA, Chanton JP, Verbyla D, Chapin FS (2006) Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming. *Nature,* **443**, 71-75.

Warembourg FR, Estelrich HD (2000) Towards a better understanding of carbon flow in the rhizosphere: a time-dependent approach using carbon-14. *Biology and Fertility of Soils,* **30**, 528-534.

Warembourg FR, Paul EA (1973) The use of C14O2 canopy techniques for measuring carbon transfer through the plant-soil system. *Plant and Soil,* **38**, 331-345.

Welker J, Fahnestock J, Povirk K, Bilbrough C, Piper R (2004) Alpine Grassland CO2 Exchange and Nitrogen Cycling: Grazing History Effects, Medicine Bow Range, Wyoming, U.S.A. *Arctic, Antarctic, and Alpine Research,* **36**, 11-20.

Whalen SC (2005) Biogeochemistry of Methane Exchange between Natural Wetlands and the Atmosphere. *Environmental Engineering Science,* **22**, 73-94.

Zimov SA, Chuprynin VI, Oreshko AP, Iii FSC, Reynolds JF, Chapin MC (1995) Steppe-Tundra Transition: A Herbivore-Driven Biome Shift at the End of the Pleistocene. *The American Naturalist,* **146**, 765-794.

Paper I

Large herbivore grazing alters vegetation structure and greenhouse gas balance in a high arctic mire

Short headline: Large herbivores alters artic mire ecosystems

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Abstract

Herbivory is an important part of many ecosystems and its presence affects the ecosystems carbon balance both directly and indirectly. Little is known about herbivory and its impact on the carbon balance in high arctic mire ecosystems. We hypothesized that trampling and grazing by large herbivores influence the vegetation density and composition and hereby also the carbon balance.

In 2010, an *in-situ* field experiment in northeast Greenland was initiated, exclosures were established to exclude muskoxen *(Ovibos moschatus*) that is a natural part of these ecosystems. During the growing season, since 2011, CO_2 fluxes and water table depth, active layer depth and soil temperature have been measured and in wet blocks were CH_4 fluxes additionally measured. Studies on the vegetation cover were performed in 2011 and 2013.

The third year after the start of the experiment, a significant decrease in total number of vascular tillers (33-44%) and of *Eriophorum scheuchzeri* tillers (51-53%) were found in ungrazed plots, as the moss-layer and litter amount had increased substantially. This resulted in a significant decrease in net ecosystem uptake of CO_2 (47%) and in CH_4 emission (44%) in ungrazed plots the third year.

The future of the muskox population in a changing arctic environment are unknown, this experiment is pointing towards the potentially large effect that herbivory has on the carbon balance of natural ecosystems in the Arctic. It also points towards the possible importance of grazing mammals and their population dynamics for understanding natural ecosystem greenhouse gas exchanges in the past.

Key-words: Arctic, Carbon dioxide flux, Exclosures, Eriophorum, Methane flux, Muskox, Plant–herbivore interactions, Vegetation composition

Introduction

Half of the Earths land surface is influenced by large herbivores (livestock or native) (Olff et al., 2002), and their presence may have great influence on the ecosystem (e.g., Mulder, 1999; Tanentzap and Coomes, 2012). The high latitude terrestrial ecosystems are currently estimated to hold approximately 50% of the total belowground organic carbon pool (Tarnocai et al., 2009), and the present and future carbon balance of these ecosystems are thus of great global importance. The plant-soil-herbivore interactions are complex, and involves both direct and indirect impacts, which may influence a variety of ecosystems processes, such as carbon sequestration, greenhouse gas production and emission, vegetation species composition, soil physical parameters (i.e., soil moisture and soil temperature), decomposition rate and nutrient availability (e.g., Sjögersten et al., 2008; Tanentzap and Coomes, 2012). In the Arctic, herbivory has been shown to impact the carbon cycle (e.g., Welker et al., 2004; Van der Wal et al., 2007; Sjögersten et al., 2008; Speed et al., 2010; Sjögersten et al., 2011; Cahoon et al., 2012; Falk et al., 2014). Indeed, the presence or absence of herbivores may determine whether the system is a net carbon source or sink (Welker et al., 2004; Sjögersten et al., 2011). Nonetheless, the general impact of grazing on the carbon balance, appears somewhat ambiguous. Although most studies have shown no effect or a decrease in net primary production (NPP) (e.g., Beaulieu et al., 1996; Van der Wal et al., 2007; Bagchi and Ritchie, 2010; Sjögersten et al., 2011; Cahoon et al., 2012), other studies have documented a grazing-induced increase in NPP (Cargill and Jefferies, 1984;

Olofsson et al., 2001; Olofsson et al., 2004b). These contrasting results may be related to ecosystem type and grazing pressure. In Arctic nutrient poor regions, increased herbivory has led to an increase in NPP (Olofsson et al., 2004b; Van der Wal et al., 2004) as nutrient addition by animal excreta may increase the labile nutrient availability (Stark et al., 2002; Van der Wal et al., 2004). Grazing most often also change nutrient and carbon allocation patterns within plants, as vegetation uses carbon and nutrients reserves to regrow new plant shoots instead of building below-ground reserves (Chapin, 1980; Beaulieu et al., 1996; Mulder, 1999; Green and Detling, 2000; ACIA, 2004; Falk et al., 2014).

In 1987 Owen-Smith presented the keystone-herbivore idea, which hypothesise that large herbivores are causing the open landscape vegetation (Owen-Smith, 1987). With a decline in herbivory, landscapes may undergo succession from being an open landscape to becoming woodland or shrubland. The same theory has been used to explain the large vegetation changes at the end of the Pleistocene, where a decline in megafauna changed the semiarid grass steppe to a moss-dominated wet tundra (Zimov et al., 1995). Presumably, as herbivore trampling kept mosses and shrubs down, their grazing kept the litter layer to a minimum and their manure fertilized the soil (Zimov et al., 1995). Supporting this theory, grazing in the arctic has been shown to result in a shift in vegetation composition, towards a more herb and graminoid dominated ecosystem (e.g., Olofsson et al., 2001; Post and Pedersen, 2008; Sjögersten et al., 2008; Kitti et al., 2009; Cahoon et al., 2012; Vaisanen et al., 2014).

Compared to other arctic habitats, mires are highly productive and they are an important source of forage for many herbivore species (Henry et al., 1990; Henry, 1998; Forchhammer et al., 2008; Kristensen et al., 2011). Consequently, mires may be more affected by herbivory than mesic habitats (Sjögersten et al., 2008; Speed et al., 2010). Arctic wetlands hold massive amounts of carbon, as the decomposition rate of organic matter is slow under cold and anoxic conditions (Tarnocai et al., 2009). Natural and agricultural wetlands together contribute with more than 40% of the annual atmospheric emissions of CH_4 and are considered the largest single contributor of this gas to the troposphere (Cicerone and Oremland, 1988; Mikaloff Fletcher et al., 2004). Despite the likely impact herbivory might have on the carbon balance in arctic wetlands and on the controlling aspects for CH_4 production and emission, only very few studies have focused on herbivory and CH_4 fluxes in the arctic or sub-alpine regions (Sjögersten et al., 2011; Sjögersten et al., 2012; Falk et al., 2014). We recently showed that simulated increased grazing pressure in a high arctic mire resulted in decreased CH_4 emissions by more than 25% (Falk et al., 2014). This, however, contrasts the findings of others studies (Sjögersten et al., 2011; Sjögersten et al., 2012) who showed no effect of herbivory on CH_4 emissions. Many of the factors that influence both CO_2 and CH_4 fluxes are either directly or indirectly influenced by herbivory. These include soil temperature and water table depth (Torn and Chapin, 1993; Waddington et al., 1996) and vegetation composition and density (Ström et al., 2003; Ström and Christensen, 2007; Ström et al., 2012). Some vascular plant species, such as *Eriophorum scheuchzeri*, may have a huge impact on the magnitude of CO_2 and CH_4 fluxes (Ström et al., 2003; Ström and Christensen, 2007; Ström et al., 2012). Hence, to understand the effect of herbivores on the total carbon balance in the artic, it is crucial to understand the potential impact they have on both CO_2 and CH_4 fluxes.

Here we focus on how the vegetation composition and carbon balance change when muskoxen are excluded from parts of an arctic mire. We hypothesise that exclusion of muskoxen will 1) change the composition and density of the vegetation, with an increase in vascular plants (see Falk et al., 2014), which in turn 2) will lead to an increase in net ecosystem exchange (NEE), gross primary production (GPP) and CH_4 emission. In order to test our hypotheses, we utilised an herbivore exclosure experiment initiated in a mire in Zackenberg, high arctic Greenland, in 2010. Over a three year period (2011-2013) we measured CO_2 and CH_4 fluxes and several ecosystem properties (soil temperature, active layer and water table depth) inside and outside the exclosures. In 2011 and 2013 a vegetation analyses were furthermore conducted.

Materials and methods

Site description

The field study took place in a large mire in the Zackenberg valley, situated in the National Park of NE Greenland (74°30’N 20°30W). The area is high arctic, with an annual mean air temperature around -9˚C. The warmest month (July) has a mean monthly air temperature (MMAT) of 5.8˚C, while the coldest month (February) has a MMAT of -22.4˚C. The mean annual precipitation was 260 ml in the period 1996-2005, with only 10% falling as rain during summer (Hansen et al., 2008). During the last 15 years the annual temperature has increased by 2.25 ˚C in northeast Greenland, Zackenberg (Hansen et al., 2008). The valley is underlain by continuous permafrost, and the active layer thickness varies from 45 to 80 cm depending on the type of ecosystem (Christiansen et al., 2008). The five dominating plant communities in the valley are *Cassiope* heath, *Dryas* heath, Grassland, Mire and *Salix* snow-bed (Bay, 1998). At the study site, the vegetation is dominated by a few vascular plant species, e.g., the grass *Arctagrostis latifolia* and the sedges *Carex sp, Dupontia fisheri ssp. psilosantha, Eriophorum scheuchzeri* and *Equisetum sp* (see Table 1). Underneath these plants a dense moss cover is found, dominated by *Tomenthypnun, Scorpidium, Aulacomnium* and *Drepanoclaudus* (Ström et al., 2012). The area has relatively high pH-values around 6.5 (Falk and Ström unpublished results) and the peat layer depth was measured to be between 7-18 cm at the site (Falk and Ström unpublished results).

The muskox *Ovibos moschatus* is a natural part of the ecosystem and is the only large herbivore in NE Greenland, and is found at Zackenberg in very high numbers (Schmidt unpublished results). Muskoxen are present year-round, and feed in grasslands and mires during summer (Thing et al., 1987; Kristensen et al., 2011), and in areas with thin snow-cover where the vegetation is easily assessable in winter (Berg et al., 2008). Around 80% of their graminoid-dominated summer forage is obtained in the mire areas (Kristensen et al., 2011). It has been projected that muskoxen can consume up to 20% of the available vegetation (Jefferies et al., 1994), while other studies have shown that they general consumes 1-2% of the sedges per year (Bliss, 1986). In a changing climate, the future of muskoxen in NE Greenland is unknown. The population of muskoxen is depended on the biomass production and the length of the growing season; a long growing season will increase the number of muskoxen the following year (Forchhammer et al., 2008). However, with predictions about increasing numbers of thawing days during winter (Stendel et al., 2008), which can lead to ice crust formation and increased snow-cover (Stendel et al., 2008), a decline in the muskox population is very likely. As hard and deep snow cover increases the mortality of muskoxen during the winter, since they are not able to reach the vegetation (Forchhammer et al., 2002).

Experimental setup

In July 2010, permanent muskox exclosures were established in the mire in Zackenberg. The experiment consists of five replicate blocks, each including the following: 1) an un-manipulated 10*10 m control area (C), where muskoxen move and graze freely. The C areas are discretely marked in each corner by a 15-20 cm high iron rod. 2) a 10*10 m exclosure area (Ex) where a one meter high standard sheep fence inhibit muskoxen in grazing and trampling inside the area. 3) a 10*10 m snow control area (SC) which acts as a control for a potential snow fence effect. SC areas are only fenced towards NNW (the dominant wind direction in winter (Hansen et al., 2008)) and muskoxen can move and graze freely inside these areas. The blocks are located on a slight downhill slope that is water-saturated in the beginning of the growing season, while it often dries out later in the season (depending on the quantities of snow in winter). Block 1 and 2 are positioned farthest uphill in a drier part of the mire, while block 3, 4 and 5 are placed further downstream in a wetter and more flat part of the mire. In all areas the peat is underlain with silt. Despite the similar water table depth, the conditions in block 5 are quite different from block 3 and 4, since the peat layer is lower and in addition mixed with silt.

In 2010 two measurement plots (39.5*39.5 cm) were permanently installed inside each treatment (n=30). In 2011 two new control areas were established, one in block 3 and one in block 4, due to differences in vegetation composition between the initial C, EX and SC areas in these blocks, which were clearly visible early in the season. The theoretical reason for these area additions was our previous findings (Ström et al., 2003; Ström et al., 2012), which showed that the vascular plant species composition is of great importance for CH_4 fluxes. We were hence concerned that the difference between the initial C, EX and SC plots would mask the effects of grazing and consequently, making it impossible to verify the aims of this study. A total of 11 new plots were installed in the new control areas and inside EX 3 and EX 4 (total set-up measurement plot n=41). For the CH_4 analysis (n=14), only C and EX from block 3 and 4 were included, the treatment areas had comparable environmental conditions, vegetation composition and significant CH_4 fluxes in the beginning of 2011. Thus, block 1 and 2 were excluded due to dryer conditions and lack of significant CH_4 fluxes and block 5 due to the mixture of silt into the peat layer and a very different vegetation composition between the treatment areas within this block (C strongly dominated by *Carex)*. Each plot consisted of an aluminium frame that is fitted 15 cm into the ground. In these plots CH_4 and CO_2 fluxes and ecosystem parameters were measured approximately once per week over the main part of the growing seasons. Block 3 and 4 were, however, measured more frequently (approximately twice per week) for a more detailed study of CH_4 fluxes. Maximum two blocks per day were measured. The measurements took place between 10 am and 5 pm and were performed under both sunny and cloudy conditions. No measurements were made under windy conditions (when wind speed exceeded around 10 m s^{-1}) due to loss of measurement quality.

In 2011 CO_2 flux measurements took place between 30 June to 8 August (June n=0-1, July n=4-5, August n=1), in 2012 between 6 July to 7 September (July n=3-4, August n=3-4, September n=1) and in 2013 between 2 July to 17 August (July n=4, August n=2). CH_4 measurements in 2011 took place between 5 July and 8 August

(July n= 8, August n=2), in 2012 between 7 July to 6 October (July n=6, August n=6, September n=5, October n=2) and in 2013 between 1 July to 17 August (July n=7, August n=4).

Vegetation analysis

In 2011 and 2013 the density and species composition of vascular plants was non-destructively estimated inside the measuring plots by counting the number of tillers of the dominant plant species. In 2013 the analysis were performed on all our measuring plots (n=41), while it in 2011 only were performed on block 3, 4 and 5 (n=26).

In mid-August 2013 biomass samples (20*20 cm) was harvested in proximity to each of the measuring areas in C, EX and SC. The quadrat was randomly placed in the areas and all biomass was harvested a couple of cm below surface, i.e. below the fresh moss layer. The samples were sorted into vascular plant species and fresh mosses. The number of tillers of *Carex*, *Dupontia* and *Eriophorum* and green leaves was counted and their mean height was estimated. The different fractions were weighed, dried at 60˚C for 48 h and re-weighed to obtain the dry weight of above-ground biomass.

Flux measurements

The carbon exchange between ecosystems and atmosphere were measured using a closed chamber technique (Livingston and Hutchinson, 1995). Measurements were performed with a transparent Plexiglas chamber (41 L), equipped with a metal frame with a rubber list, to ensure an airtight seal against the ground fitted aluminium frame. The Plexiglas chamber reduced PAR by <10% (Christensen et al., 2003). For each measurement, a light and a dark measurement was made to establish NEE and the ecosystem respiration (R_{eco}) respectively. For dark measurements the chamber was covered by a non-transparent plastic hood. Prior to the measurements, which lasted between 3 to 7 minutes depending on flux magnitude, the chamber was carefully placed on the aluminium frame to avoid disturbance. Air pressure inside the chamber was equalized by a small hole in the chamber, which was closed with a rubber stopper as soon as the measurement began.

Gas concentrations of CO_2 and CH_4 were simultaneously recorded once per second by a portable Fourier Transform Infrared (FTIR) spectrometer (Gasmet Dx 40-30, Gasmet Technologies Oy). The air from the chamber was pumped at a rate of 3.4 L min^{-1} to the analytical box before it was non-destructively returned to the chamber. The FTIR was calibrated with a zero gas every second week. Stable cell temperature of the FTIR between 20 and 32˚C are required for high quality measurements, this could be retained by the internal heating system during summer. During the cold conditions in September and October 2012 the instrument was warmed with heating cables. CO_2 and CH_4 fluxes were calculated from changes in gas concentration in the chamber as a function of time using linear fitting following procedures by Crill et al. (1988), where data were, corrected for the ambient air temperature and air pressure. Replicate block measurements were all performed under stable and similar weather conditions (within one day), and we did no further corrections for environmental conditions. Release of gas from the ecosystem to the atmosphere is denoted by positive values and uptake by negative. Gas fluxes are expressed as mg m^{-2} h^{-1} of CH_4 or CO_2. Due to a strong significant correlation (R=0.947, p<0.0001) between light and dark CH_4 fluxes for individual plots, the mean of these two measurements were calculated and used in the CH_4 flux analysis. Gross Primary Production (GPP) was calculated as the difference between NEE and R_{eco}.

Ecosystem variables

In addition to the flux measurements several ecosystem variables were measured within or in close proximity to each plot replicate. We determined the water table depth (WtD, cm below moss surface), the active layer thickness (AL, cm below moss surface), photosynthetically active radiation (PAR, µmol $m^{-2}s^{-1}$) and soil temperature (T_s,10 cm below moss surface). The WtD was not measured inside the individual plots but just outside in order to minimize disturbance in the individual plots. WtD was measured using a water permeable tube (2.5 cm in diameter) that was permanently installed in ground fitted with a float (made of cork). AL was measured manually with a metal stick. PAR was measured both inside the chamber 25 cm from the surface (each minute) and at one meters height (hourly), using a Minikin QTi data-logger (EMS Brno). T_s was measured manually by inserting a 150 mm digital temperature probe (Viking, Eskilstuna, Sweden) into the ground.

Data analysis

Vegetation composition

Data from the vegetation analysis were transformed to number of tillers per m^2 and tested for normality. The density of tillers was normal distributed for all vegetation species except for *Carex* and *Equisetum*. Data were despite not all being normally distributed treated equally and an independent t-test, where homogeneity of variance is assumed, was performed on all species. The analyses were performed on the whole dataset (n=26, n=41 for 2011 and 2013, respectively) as well as on the plots used in the CH_4 analysis (n=14). For the statically analysis the most dominating vegetation species *Arctagrostis, Carex, Dupontia, Eriophorum* and *Equisetum* and the total number of these vegetation species are included. The harvested biomass samples were not normally distributed, and therefore a nonparametric test with related samples were performed on these samples, where the block structure was considered in the model. Note the different area size between harvested samples (0.04 m^2) and vegetation analysis (1 m^2).

Carbon fluxes

For the CO_2 analysis the whole dataset was used (n=41 plots). Effects of the herbivore exclusion on the carbon flux measures were examined using general mixed linear models with treatment as fixed factor. Block and plot were regarded as random factors, and plot nested within block. We included a Gaussian autoregressive component within plots in the models due to the expected temporal dependence in fluxes. The analysis was conducted using the PROC MIXED procedure (SAS Institute Inc. 2000). Model reduction was based on likelihood ratio tests and successive removal of non-significant variables ($p>0.05$). As post-hoc test we used Tukey HSD tests ($p<0.05$).

Results

Vegetation analysis

The vegetation analysis in m^2 from 2011 and 2013 showed a large spatial variation in vegetation species composition within the area (Table 1). In 2011, no significant difference was found in the density of any vascular plant species or total tillers between any of the treatments. The density of *Eriophorum* tillers in EX compared to C had however a tendency of being lower already in 2011. In 2013 the densities of *Eriophorum* and total tillers were significantly lower in EX compared to C (decreased by 51% and 33%, respectively). Additionally a tendency of lower *Arctagrostis* in EX was observed in 2013. In contrast no significant differences were found between C and SC for any of the vascular plant species in 2013, although a strong tendency of *Eriophorum* density being lower in SC compared to C was observed (Table 1). In 2011 and 2013 the dominating species *Arctagrostis*, *Carex*, *Dupontia*, *Eriophorum* and *Equisetum* on average accounted for 99% of the total vascular plant species in the measuring plots. In 2011 the mean percentile distribution for the species was 6, 14, 43, 37 and 16 while it in 2013 was 3, 7, 55, 35, and 0.7 for *Arctagrostis*, *Carex*, *Dupontia*, *Eriophorum* and *Equisetum*, respectively.

Harvested biomass samples

Biomass dry weight: There were significant differences ($p<0.03$) in several of the dry weight fractions of the harvested biomass between C and both EX and SC (Fig. 1). Significant differences were all following the same pattern with higher biomass in EX and SC areas compared to C. In EX treatments the total dry weights of biomass were 59% higher, the litter (old vascular plant) 230% higher and mosses 55% higher than in C. In SC treatments the total dry biomass were 15% higher and mosses 25% higher than in C. For the biomass fractions *Carex* and *Dupontia*, no significant differences were found ($p>0.180$) for EX-C and SC-C. In EX a trend of less *Eriophorum* dry weight compared to C ($p=0.083$) were found, this was not seen in SC ($p=0.655$) (Fig. 1).

Density of tillers: The density of total vascular plant tillers as well as the *Eriophorum* tillers in the harvested biomass samples inside EX treatments were significantly lower than in C (the density decreased by 44% and 53%, respectively). The density of *Dupontia* and *Carex* tillers were, however not significantly different between the two treatments. Furthermore no differences between C and SC in total tillers or any of the species were found (Table 2).

Green leaves: The density of green leaves and green *Eriophorum* leaves were significantly lower in EX compared to C, it decreased by 54% and 55%, respectively. No significant chances were found in green *Dupontia* or *Carex* leaves between EX and C. Moreover no significant differences were found of any of the species or total green leaves between C and SC (Table 2).

Height of tillers: The *Dupontia* and *Eriophorum* tillers were significantly longer inside EX compared to C, the length increased by 29% and 27%, respectively. Additionally, the mean height of all the vascular plants in EX were significantly longer compared with C (the length increased by 27%). In contrast, no significant differences were found between the height of any of the vascular plant species between C and SC (Table 2).

CO_2

NEE: The third year after the initiation of the exclosure experiment C areas had significantly higher net CO_2 uptake (NEE) than both EX ($p<0.001$) and SC ($p=0.028$) areas (Fig. 2, Table 3). The difference was highest between C and EX areas with 47% lower NEE in EX, while it was 34% lower in SC areas compared to C. During the first two measurement years (2011 and 2012) no significant differences in NEE between C and EX or between C and SC were found (Table 3).

R_{eco}: The first two measurement years (2011 and 2012), no significant differences in R_{eco} between C and EX or C and SC were found. No difference was likewise observed between C and EX the third year (2013), however a significant difference was found between C and SC, the mean R_{eco} decrease compared to C being 25% (Table 3).

GPP: The first measuring year 2011 no significant differences in GPP were seen between C and any of the treatment areas. However, already the second year GPP was significantly lower in EX compared to C (mean -8%), while no differences was observed between C and SC. The third year GPP was significantly lower in EX and SC compared to C, mean decrease were 21% and 28% for EX and SC, respectively (Table 3).

CH_4 analysis

CH_4 flux: During the first two measurement years (2011 and 2012), no significant differences in CH_4 fluxes between C and EX were observed. However, the third year the CH_4 fluxes were significantly lower (44%) inside EX (Fig. 3). Further, there was a large variation in the mean CH_4 flux (mg CH_4 $m^{-2}h^{-1}$) the three years, in 2011 it ranged between; 1.6 to 4.4 and 1.9 to 3.6 for C and EX. In 2012 it ranged between 2.6 to 7.0 and 3.4 to 4.3, while it in 2013 ranged between 1.9 to 4.6 and 0.6 to 2.3 for C and EX, respectively. Please observe that SC is not included in the analysis, due to reasons described above.

Vegetation analysis: The vegetation analysis made on the plots used in the CH_4 analysis showed no significant differences for the density of any of the dominating vascular plant species or total tillers in 2011 (Table 4). In 2013, however, a significantly lower density of *Eriophorum* tillers (55%) and total tillers (33%) were found. There were however no significant differences in *Arctagrostis*, *Dupontia* or *Equisetum* between EX and C. In 2011 and 2013 the dominating species *Arctagrostis*, *Dupontia*, *Eriophorum* and *Equisetum* were on average counting for 99% of the total vascular plants in the plots. In 2011 the mean percentile distribution for the vegetation species was 3, 53, 40 and 3 while it in 2013 was 3, 63, 33 and 0.7 for *Arctagrostis*, *Dupontia*, *Eriophorum* and *Equisetum*, respectively (Table 4).

Ecosystem parameters

WtD: The first two measuring years no significant differences in WtD were observed between C and EX or C and SC. In 2013 WtD was, however, significantly higher in both EX and SC compared to C, the mean difference was higher in EX (19%) compared to SC (9%) (Table 3).

AL: In 2011 and 2012 no significant differences in AL were observed between C and EX or C and SC. In 2013 AL was, however, significantly lower (9%) in EX compared to C, while no difference was observed in SC (Table 3).

Ts: The first year after the initiation of the exclosure experiment Ts was significantly lower in EX (4%). The following year 2012 Ts was significantly higher in EX (13%), while it in 2013 again became significantly lower (12%). In contrary Ts was not significantly different in SC compared to C for any of the three measuring years (Table 3).

Discussion

Vegetation composition

Rhizomatous graminoids species such as *Carex aquatilis stans, Eriophorum angustifolium, Eriophorum scheuchzeri, Dupontia fisheri* and *Alopecurus alpinus* are known to be well adapted to grazing (Henry, 1998). This rhizomatous graminoid species pool is consistent with the dominating vascular plant species we found in the Zackenberg valley, e.g., *Eriophorum scheuchzeri, Dupontia fisheri ssp. psilosantha, Arctagrostis latifolia, Carex sp. and Equisetum sp.* The species composition thus supports an ecosystem that is heavily influenced by grazing and that is likely to respond when the grazing pressure changes.

Our results showed that only three years exclusion of muskoxen have had marked effects on vegetation composition, structure and density. In general we found an increase in standing biomass and a decrease in the density of vascular plant tillers in ungrazed plots. Harvesting of biomass samples in 2013 showed that the moss-layer, litter-layer and the total dry weight of biomass were significantly higher in ungrazed compared to grazed areas. An increase in the amount of litter inside the exclosures was expected (Henry et al., 1990; Henry, 1998; Van der Wal and Brooker, 2004) as the biomass is no longer removed by herbivore consumption. The decomposition rate in the arctic is very low (Tarnocai et al., 2009) and the accumulation of litter can be quite pronounced, which can explain the large increase in litter in ungrazed areas. Mosses grow slowly and are very sensitive towards disturbance such as trampling (Liddle, 1997), which may explain the increase in mosses when muskoxen were excluded (Fig. 1). Some arctic wetland studies have found stable or higher moss-cover in response to grazing (Henry, 1998; Kitti et al., 2009; Sjögersten et al., 2011). However, in line with our results, the majority of other arctic studies have found an increasing moss-layer with exclusion or reduction in herbivore numbers (Thing, 1984; Zimov et al., 1995; Olofsson et al., 2001; Van der Wal et al., 2001; Van der Wal and Brooker, 2004; Van der Wal et al., 2007).

The thickness of the moss-layer is influencing soil conditions. A thick moss-layer can lower the soil temperature, as it is an effective heat insulator with its low thermal conductance (Zimov et al., 1995; Van der Wal et al., 2001; Van der Wal and Brooker, 2004). Shading by the standing litter (Henry, 1998) will together with the higher reflection of dry litter (Lorenzen and Jensen, 1988) contribute to further cooling of the soil. Soil moisture can also be influenced by the moss dominance, as transpiration from mosses are very low compared to vascular plants and soil moisture may therefore increase with increasing moss dominance (Zimov et al., 1995). Large herbivore movement in the area can also affect soil moisture as the soil bulk density increases with trampling (Warren et al., 1986). A moss-dominated vegetation may furthermore lower the availability of nitrogen as mosses have a low nitrogen concentration compared to other litter types (Zimov et al., 1995). However, in a pilot study, we found no effects of exclusion of grazing on ammonium and nitrate in pore water or in nitrogen content of *Eriophorum* tillers (Falk and Ström, unpublished results). These results, however, does not include nitrogen in all vascular species and mosses, further studies are thus needed to verify these aspects as well as to establish the future development in this respect. Both in 2011 and in 2013 we found significantly lower Ts inside exclosures, while it in 2012 was significantly higher (Table 3). The temperature decrease in our study (0.4˚C in 2011 and 0.6˚C in 2013) is in the same order of magnitude as found in other studies (Van der Wal et al., 2001; Van der Wal and Brooker, 2004). The most likely explanation for the change in Ts is the increasing isolating moss-layer. However, our results show an increase in Ts in 2012, one explanation could be that Ts in 2011 and 2013 primarily was measured in dry soils, water table depth quickly dropped below 10 cm those summers, while Ts in 2012 mainly was measured in a water saturated soil throughout the measuring season. In support of the effect of water table depth on Ts we in 2013 found a significant increase in water table depth in ungrazed areas, most likely due to the expansion of the moss-layer that drives the surface upwards. In 2013 the lower Ts in ungrazed areas also seemed to significantly affect the active layer depth, which was 9% lower in ungrazed areas.

With an increasing amount of litter and more developed moss-layers, the graminoids need to adapt to the new environmental conditions. The length of *Dupontia* and *Eriophorum* tillers in the harvested biomass samples was significantly longer in the ungrazed areas compared to grazed areas (Table 2), most likely due to shading by the moss-layer and litter. The consequence of the need for resource allocation to long leaves subsequently seems to feedback to the number of tillers produced. After three years of muskox exclusion the density of total tillers was lower in exclosures

(33% in flux plots (1 m^2) and 43% in harvested samples (0.04 m^2)) and the density of *Eriophorum* tillers was half (Table 1 and 2). Another plausible explanation is that, in a heavily grazed habitat the flowering shoots are likely to be grazed during germination in spring. They will consequently not be able to set new flowers (seeds) that year, but will instead allocate carbon to more shoots/tillers growth. Supporting this, it was from visual observation already the first year into the experiment noticeable that there were more flowering *Eriophorum* in the exclosures (see photo from 2011 and 2013 Fig. 4). These findings are consistent with several arctic studies in both heath and mires, where an exclusion or reduction in herbivore numbers has resulted in a decrease in graminoids (Thing, 1984; Zimov et al., 1995; Henry, 1998; Olofsson et al., 2001; Van der Wal et al., 2001; Van der Wal and Brooker, 2004; Post and Pedersen, 2008; Kitti et al., 2009). The magnitude of our increase was somewhat larger than found in other long-term studies (Olofsson et al., 2004b; Kitti et al., 2009; Vaisanen et al., 2014) and clearly shows that the response to excluded grazing in the Zackenberg mire is dramatic both in terms of species development and speed.

CO_2 fluxes

Strong relationships between NEE and the living plant biomass are found in several studies (e.g., Ström and Christensen, 2007; Sjögersten et al., 2008), as a reduction of the photosynthetically active biomass will lead to less carbon uptake. In our study GPP was already in 2012 significantly lower (-8%) in ungrazed areas and in 2013 the reduction had increased to -21% (Table 3). These findings are most likely directly coupled to the decrease in density of tillers (Table 2 and 3) as vascular plants have much greater photosynthetic activity compared to mosses (Otieno et al., 2009; Ward et al., 2009). Very few studies have looked at how herbivory in the artic is influencing the carbon balance. In contrast to our findings the majority of the studies have found that NEE decreases with grazing pressure (Van der Wal et al., 2007; Sjögersten et al., 2008; Sjögersten et al., 2011; Cahoon et al., 2012; Falk et al., 2014; Vaisanen et al., 2014). The difference between our findings and others can presumably be explained by differences in ecosystem type, grazing pressure, time scale and/or grazer community studied. The studies by Sjögersten et al. (2008, 2011) and Van der Wal et al. (2007) concerned areas where grazing by large herbivores had been excluded or the number had decreased for a longer time period and the experiments were, additionally, conducted in drier habitats. Other studies have shown a shrub expansion with herbivore exclusion and temperature increase, which has a time delayed of approximately 5 years (Olofsson et al., 2004a; Post and Pedersen, 2008). This may indicate that over time shrubs may become more dominant in our exclosure experiments and potentially alter the carbon balance again, since shrub dominated ecosystems normally are a stronger C sink compared to a graminoid ecosystem. These seemingly contradictory findings indicate that there is a clear difference in the response of the ecosystem to removal of grazing or a change in grazing pressure as well as a possibility of further changes over time in the Zackenberg mire as the succession in the ecosystem progresses.

Several arctic herbivory studies have found a decrease in ecosystem respiration in response to herbivory (Stark and Grellmann, 2002; Van der Wal et al., 2007; Sjögersten et al., 2011; Cahoon et al., 2012), while Vaisanen et al (2014) found that respiration was higher in the heavily grazed areas. In our study, however, we found no significant changes in ecosystem respiration in ungrazed compared to grazed areas. This can probably be attributed to CO_2 respiration being controlled to a higher degree by the water table depth in wet arctic mires. Furthermore, mosses may assimilate as much as 51-98% of the CO_2 that is respired from tundra soils (Sommerkorn et al., 1999), and with a thicker moss-layer more CO_2 can potentially be assimilated before emitted to the atmosphere.

The magnitude of the mean CO_2 fluxes (Fig. 2 and Table 3) varies greatly over the three measuring years. However, since the study was only conducted over three years it is hard to make any substantial conclusions as to what is causing the variation in flux magnitude. It can however be speculated that the inter-annual differences largely is due to variations in soil temperature and water table depth (Table 3). The year 2013 was a very dry and cold year compared to the two previous years. These conditions will likely lead to a reduction in growth and productivity as seen with much less tillers in 2013 compared to 2011 (Table 1) and result in lower NEE. The dry conditions are however promoting R_{eco} since aerobic decomposition rates increase (Oberbauer et al., 1992), which explains the generally higher R_{eco} values in 2013 (Table 3). The different length of the measuring seasons is also affecting the mean values. In 2012 the measuring period continued into autumn and the mean value reflects both summer and autumn fluxes. The mean values for the growing season in 2012 would have been somewhat different, with even higher CO_2 uptake (NEE). Despite the inter-annual variations both grazed and ungrazed areas are acting as CO_2 sinks during growing season, where more CO_2 is taken up than emitted. However, in 2013, ungrazed areas acts as a much lower sink as the mean CO_2 uptake is almost half of what it was in grazed areas.

CH_4 emission

Very few studies have looked at how CH_4 emissions are influenced by herbivores in the artic (Sjögersten et al., 2011; Falk et al., 2014). The lower CH_4 emission in our ungrazed areas contrasts the two only other studies (to our knowledge) made on herbivory and CH_4 fluxes in a wet high arctic habitat. In a study on Svalbard Sjögersten et al., (2011) reported no changes in the CH_4 fluxes between grazed and un-grazed plots, where geese had been excluded for 4 years. Their CH_4 fluxes were, however, very low (-0.046 to 0.025 mg CH_4 m^{-2} h^{-1}) in comparison to this study (0.6 to 7 mg CH_4 m^{-2} h^{-1}) and consequently, responses on CH_4 fluxes may not be expected to be in the same order of magnitude as in the Zackenberg productive mire. In our recent study of simulated increased grazing pressure in the same mire, lower CH_4 emission was found in clipped plots (Falk et al., 2014), and this, as for NEE, indicates that there is a clear difference in the response of the ecosystem to removal of grazing or a change in grazing pressure. Our recent study (Falk et al., 2014) further showed a close linkage between CH_4 flux, productivity and vegetation composition, with higher CH_4 fluxes in productive plots. A strong correlation between CH_4 emissions and net ecosystem production (NEP) or GPP has also been found in several other studies (e.g., Waddington et al., 1996; Christensen et al., 2000; Joabsson and Christensen, 2001; Ström and Christensen, 2007). The relationship is often explained by the effect of productivity and photosynthesis on methanogenesis, where a higher carbon uptake will result in more supply of methanogenic substrates to the root zone and subsequently to higher CH_4 emissions (Joabsson et al., 1999). In our study we found that the mean CH_4 flux were 44% lower in ungrazed areas the third year into the exclosures experiment (Fig. 3). This can most likely be attributed to the substantial decrease in GPP (Table 3).

We have previously shown that there is a clear linkage between CH_4 flux, the number of *Eriophorum* tillers and the amount of labile substrate for CH_4 production in the Zackenberg mire (Ström et al., 2012; Falk et al., 2014), with higher *Eriophorum* coverage leading to higher substrate availability and CH_4 flux. Studies from other ecosystems (or performed in laboratory) confirm the importance of *Eriophorum* species for methane emissions (e.g., Greenup et al., 2000; Joabsson and Christensen, 2001; Ström et al., 2003; Ström and Christensen, 2007) and substrate availability (acetic acid) in pore water (Ström et al., 2003; Ström et al., 2005; Ström and Christensen, 2007). In correspondence with these studies, the ungrazed areas had a significantly lower density of *Eriophorum* and total tillers in 2013 (Table 4), which in turn can explain the lower CH_4 emission. Furthermore, vascular plants are known to mediate methane transport directly from anoxic peat depth to the atmosphere and thus decreasing methane oxidation in oxic upper peat layers (Bellisario et al., 1999; Frenzel and Karofeld, 2000; Greenup et al., 2000; Whalen, 2005). This effect may be of additional importance to the relationship between vascular plant density and higher CH_4 flux in grazed areas. The depth down to the water table was in 2013 deeper in ungrazed areas (Table 3). This could also partly explain the decrease in CH_4 emission, as more CH_4 could be oxidized. However, a correlation between CH_4 flux and WtD in the control plots did not offer substantial support to this suggestion ($R=0.179$, $p=0.380$) (Ström and Falk, unpublished results).

The impact of snow-fences

In early spring 2012 we measured the snow depth in all treatments, and found no significant effects of the fences (Schmidt, unpublished results). Nonetheless, we found some examples of significant differences between the snow control and the grazed areas. As these differences are not due to differences in snow accumulation, an alternative explanation could be found in the foraging behaviour of muskoxen around the fences, which may affect the vegetation composition in these areas. The dry weight of mosses were significantly higher in snow control compared to grazed areas, although the differences were much lower than in ungrazed vs. grazed areas (Fig. 1). The differences in mosses influence the total weight of biomass that has increased significantly in snow control areas. The density of *Eriophorum* tillers in

2013 additionally had a tendency of being lower in snow control areas compared to grazed (p=0.085). The lower density of *Eriophorum* tillers, is the most likely reason for the lower NEE that is also seen in snow control areas (a decrease of 34%). We therefore speculate that the higher biomass of mosses indicates that muskoxen are grazing and trampling less in these areas. This can however not be verified, but a thorough future monitoring of the snow control areas would provide the needed evidence for these speculations.

Possible herbivore influence on the carbon balance in a changing climate

With predictions about a warming of the Arctic (AMAP, 2011), the region is expected to experience a greening and a transformation in plant composition towards a higher density of shrubs (Walker et al., 2006; Hudson and Henry, 2009; Tagesson et al., 2010; Hill and Henry, 2011; Myers-Smith et al., 2011). With the increasing temperatures in Zackenberg there has however been no indications of shrub expansion (Schmidt et al., 2012), which is likely due to the slow responses of high arctic vegetation (Elmendorf et al., 2012), but the high density of muskoxen in the area could also be partly responsible (Myers-Smith et al., 2011). In our study, after three years of muskox exclusion, we found no evidence of shrubs becoming more dominant in ungrazed areas. Nonetheless, it is not unlikely that this may change in future with continued successional development of the ungrazed areas.

Combined warming and grazing experiments in the Arctic have shown that grazing can have a large effect on the carbon uptake, which is higher than the effects of increased temperature. Grazing is often found to mitigate the increase in biomass production and the change toward more shrubs (Klein et al., 2007; Post and Pedersen, 2008; Sjögersten et al., 2008; Olofsson et al., 2009; Rinnan et al., 2009; Cahoon et al., 2012; Vaisanen et al., 2014). This delicate interplay between large herbivores and shrubs (Post and Pedersen, 2008) makes them an important component in the functioning of this high arctic mire.

Our study shows that a change in the abundance of muskoxen at Zackenberg may rapidly alter the mire vegetation, ultimately affecting the carbon balance. Although, both grazed and ungrazed areas currently are acting as CO_2 sinks, the sink function decreases substantially in ungrazed plots. However, the CH_4 emissions have likewise decreased substantially, which influences the total greenhouse gas balance. To give an estimate of the effect grazing exclusion have on the total greenhouse gas balance in terms of heat retention in the atmosphere we made a back of the envelope calculation of the mean hourly Global Warming Potential (100 years, CH_4=34 (CO_2 equivalents), (IPCC, 2013)) on the CO_2 and CH_4 fluxes combined. For the 2013 flux the CO_2 equivalents were -182 and -81 (mg CO_2 equivalents m^{-2} h^{-1}) for grazed and ungrazed areas, respectively. This simple calculation showed that the sink function of CO_2 would be less than half if the herbivores disappeared from the mire, in comparison to present day values. Further studies are however needed to fully understand the C-balance of these ecosystems and the intricate interactions between herbivores and ecosystem development in these regions. It is indeed difficult to predict what will happen with the future carbon balance in arctic mires, but it is crucial to consider the impact large herbivores have on the ecosystem and on its carbon balance.

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References

ACIA. 2004. Impacts of a warming arctic - Arctic Climate Impact Assessment. New York: Cambridge University.

AMAP. 2011. Snow, water, ice and permafrost in the Arctic (SWIPA). Oslo: Arctic Monitoring and Assessment Programme (AMAP).

Bagchi S, Ritchie ME. 2010. Introduced grazers can restrict potential soil carbon sequestration through impacts on plant community composition. Ecology Letters 13: 959-968.

Bay C. 1998. Vegetation mapping of Zackenberg valley. Northeast Greenland, Danish Polar Center & Botanical Museum, University of Copenhagen, Copenhagen.

Beaulieu J, Gauthier G, Rochefort L. 1996. The Growth Response of Graminoid Plants to Goose Grazing in a High Arctic Environment. Journal of Ecology 84: 905-914.

Bellisario LM, Bubier JL, Moore TR, Chanton JP. 1999. Controles on CH4 emissions from a nothern peatland. Global Biogeochem. Cycles 13: 81-91.

Berg TB, Schmidt NM, Høye TT, Aastrup PJ, Hendrichsen DK, Forchhammer MC, Klein DR. 2008. High-Arctic Plant-Herbivore Interactions under Climate Influence. 275-298p.

Bliss LC. 1986. Arctic Ecosystems: Their Structure, Function and Herbivore Carrying Capacity. Gudmundsson O editor. Grazing Research at Northern Latitudes: Springer US, p5-25.

Cahoon SMP, Sullivan PF, Post E, Welker JM. 2012. Large herbivores limit CO2 uptake and suppress carbon cycle responses to warming in West Greenland. Global Change Biology 18: 469-479.

Cargill SM, Jefferies RL. 1984. The Effects of Grazing by Lesser Snow Geese on the Vegetation of a Sub- Arctic Salt Marsh. Journal of Applied Ecology 21: 669-686.

Chapin FS. 1980. Nutrient Allocation and Responses to Defoliation in Tundra Plants. Arctic and Alpine Research 12: 553-563.

Christensen TR, Ekberg A, Ström L, Mastepanov M. 2003. Factors controlling large scale variations in methane emissions from wetlands. Geophysical Research Letters 30: 67-61 - 67-64.

Christensen TR, Friborg T, Sommerkorn M, Kaplan J, Illeris L, Soegaard H, Nordstroem C, Jonasson S. 2000. Trace gas exchange in a high-Arctic valley: 1. Variationsin CO2 and CH4 Flux between tundra vegetation types. Global Biogeochem. Cycles 14: 701-713.

Christiansen HH, Sigsgaard C, Humlum O, Rasch M, Hansen BU. 2008. Permafrost and Periglacial Geomorphology at Zackenberg. Advances in Ecological Research, p151-174.

Cicerone RJ, Oremland RS. 1988. Biogeochemical aspects of atmospheric methane. Global Biogeochemical Cycles 2: 299-327.

Crill PM, Bartlett KB, Harriss RC, Gorham E, Verry ES, Sebacher DI, Madzar L, Sanner W. 1988. Methane flux from Minnesota Peatlands. Global Biogeochemical Cycles 2: 371-384.

Elmendorf SC, 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.

Falk JM, Schmidt NM, Ström L. 2014. Effects of simulated increased grazing on carbon allocation patterns in a high arctic mire. Biogeochemistry 119: 229-244.

Forchhammer MC, Post E, Stenseth NC, Boertmann DM. 2002. Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. Population Ecology 44: 113-120.

Forchhammer MC, Schmidt NM, Hoye TT, Berg TB, Hendrichsen DK, Post E. 2008. Population dynamical responses to climate change. Advances in Ecological Research 40: 391-420.

Frenzel P, Karofeld E. 2000. CH4 emission from a hollow-ridge complex in a raised bog: The role of CH4 production and oxidation. Biogeochemistry 51: 91-112.

Green RA, Detling JK. 2000. Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. Oikos 91: 280-284.

Greenup AL, Bradford MA, McNamara NP, Ineson P, Lee JA. 2000. The role of Eriophorum vaginatum in CH4 flux from an ombrotrophic peatland. Plant and Soil 227: 265-272.

Hansen BU, Sigsgaard C, Rasmussen L, Cappelen J, Hinkler J, Mernild SH, Petersen D, Tamstorf MP, Rasch M, Hasholt B. 2008. Present-Day Climate at Zackenberg. Advances in Ecological Research. San Diego: Elsevier Academic Press Inc, p111-149.

Henry GHR, Svoboda J, Freedman B. 1990. Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. Canadian Journal of Botany 68: 2660-2667.

Henry GR. 1998. Environmental influences on the structure of sedge meadows in the Canadian High Arctic. Plant Ecology 134: 119-129.

Hill GB, Henry GHR. 2011. Responses of High Arctic wet sedge tundra to climate warming since 1980. Global Change Biology 17: 276-287.

Hudson JMG, Henry GHR. 2009. Increased Plant Biomass in a High Arctic Heath Community from 1981 to 2008. Ecology: 2657.

IPCC. 2013. Working group I contribution to the IPCC fifth Assessment, Report (AR5), Climate Change 2013: The Physical Science Basis. WMO, UNEP.

Jefferies RL, Klein DR, Shaver GR. 1994. Vertebrate Herbivores and Northern Plant Communities: Reciprocal Influences and Responses. Oikos 71: 193-206.

Joabsson A, Christensen TR. 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. Global Change Biology 7: 919-932.

Joabsson A, Christensen TR, Wallen B. 1999. Vascular plant controls on methane emissions from northern peatforming wetlands. Trends in Ecology and Evolution 14: 385-388.

Kitti H, Forbes B, Oksanen J. 2009. Long- and short-term effects of reindeer grazing on tundra wetland vegetation. Polar Biology 32: 253-261.

Klein JA, Harte J, Zhao X-Q. 2007. Experimental Warming, Not Grazing, Decreases Rangeland Quality on the Tibetan Plateau. Ecological Applications: 541.

Kristensen DK, Kristensen E, Forchhammer MC, Michelsen A, Schmidt NM. 2011. Arctic herbivore diet can be inferred from stable carbon and nitrogen isotopes in C3 plants, faeces, and wool. Canadian Journal of Zoology 89: 892-899.

Liddle M. 1997. Recreation ecology: the ecological impact of outdoor recreation and ecotourism: Chapman & Hall Ltd.

Livingston G, Hutchinson G. 1995. Enclosure-based measurement of trace gas exchange: applications and sources of error. Biogenic trace gases: measuring emissions from soil and water. Oxford UK: Blackwell Sciences, p14-51.

Lorenzen B, Jensen A. 1988. Reflectance of blue, green, red and near infrared radiation from wetland vegetation used in a model discriminating live and dead above ground biomass. New Phytologist 108: 345-355.

Mikaloff Fletcher SE, Tans PP, Bruhwiler LM, Miller JB, Heimann M. 2004. CH4 sources estimated from atmospheric observations of CH4 and its 13C/12C isotopic ratios: 2. Inverse modeling of CH4 fluxes from geographical regions. Global Biogeochemical Cycles 18: GB4005.

Mulder CPH. 1999. Vertebrate herbivores and plants in the Arctic and subarctic: effects on individuals, populations, communities and ecosystems. Perspectives in Plant Ecology, Evolution and Systematics 2: 29-55.

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

Oberbauer SF, Gillespie CT, Cheng W, Gebauer R, Serra AS, Tenhunen JD. 1992. Environmental effects on CO2 efflux from riparian tundra in the northern foothills of the Brooks Range, Alaska, USA. Oecologia 92: 568-577.

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

Olofsson J, E. Hulme P, Oksanen L, Suominen O. 2004a. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. Oikos 106: 324-334.

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, 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. 2004b. Reindeer influence on ecosystem processes in the tundra. Oikos 105: 386-396.

Otieno DO, Wartinger M, Nishiwaki A, Hussain MZ, Muhr J, Borken W, Lischeid G. 2009. Responses of CO2 Exchange and Primary Production of the Ecosystem Components to Environmental Changes in a Mountain Peatland. Ecosystems 12: 590-603.

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

Post E, Pedersen C. 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences of the United States of America 105: 12353-12358.

Rinnan R, Stark S, Tolvanen A. 2009. Responses of vegetation and soil microbial communities to warming and simulated herbivory in a subarctic heath. Journal of Ecology 97: 788-800.

Schmidt NM, Kristensen DK, Michelsen A, Bay C. 2012. High Arctic plant community responses to a decade of ambient warming. Biodiversity 13: 191-199.

Sjögersten S, Van der Wal R, Loonen MJE, Woodin SJ. 2011. Recovery of ecosystem carbon fluxes and storage from herbivory. Biogeochemistry 106: 357-370.

Sjögersten S, Van der Wal R, Woodin SJ. 2008. Habitat type determines herbivory controls over CO2 fluxes in a warmer arctic. Ecology (Washington D C) 89: 2103-2116.

Sjögersten S, Yanez-Serrano A, Llurba R, Ribas A, Sebastià MT. 2012. Temperature and moisture controls of C fluxes in grazed subalpine grasslands. Arctic, Antarctic, and Alpine Research 44: 230-246.

Sommerkorn M, Bölter M, Kappen L. 1999. Carbon dioxide fluxes of soils and mosses in wet tundra of Taimyr Peninsula, Siberia: controlling factors and contribution to net system fluxes. Polar Research 18: 253-260.

Speed JDM, Woodin SJ, Tommervik H, van der Wal R. 2010. Extrapolating herbivore-induced carbon loss across an arctic landscape. Polar Biology 33: 789-797.

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

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

Stendel M, Christensen JH, Petersen D. 2008. Arctic Climate and Climate Change with a Focus on Greenland. Hans Meltofte TRCBEMCF, Morten R editors. Advances in Ecological Research: Academic Press, p13-43.

Ström L, Christensen TR. 2007. Below ground carbon turnover and greenhouse gas exchanges in a sub-arctic wetland. Soil Biology & Biochemistry 39: 1689-1698.

Ström L, Ekberg A, Mastepanov M, Christensen TR. 2003. The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Global Change Biology 9: 1185-1192.

Ström L, Mastepanov M, Christensen TR. 2005. Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. Biogeochemistry (Dordrecht) 75: 65-82.

Ström L, Tagesson T, Mastepanov M, Christensen TR. 2012. Presence of Eriophorum scheuchzeri enhances substrate availability and methane emission in an Arctic wetland. Soil Biology and Biochemistry 45: 61-70.

Tagesson T, Mastepanov M, Tamstorf MP, Eklundh L, Schubert P, Ekberg A, Sigsgaard C, Christensen TR, Ström L. 2010. Satellites reveal an increase in gross primary production in a greenlandic high arctic fen 1992–2008. Biogeosciences Discussions 7: 1101-1129.

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 S. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. Global Biogeochem. Cycles 23: GB2023.

Thing H. 1984. Feeding ecology of the West Greenland caribou (Rangifer tarandus groenlandicus) in the Sisimiut-Kangerlussuaq region [vegetation, food selection, forage quality, rumen samples, chemical analysis, migration]. Danish Review of Game Biology (Denmark).

Thing H, Klein DR, Jingfors K, Holt S. 1987. Ecology of muskoxen in Jameson Land, northeast Greenland. Ecography 10: 95-103.

Torn MS, Chapin FS. 1993. Environmental and biotic controls over methane flux from Arctic tundra. Chemosphere 26: 357-368.

Vaisanen M, Ylanne H, Kaarlejarvi E, Sjogersten S, Olofsson J, Crout N, Stark S. 2014. Consequences of warming on tundra carbon balance determined by reindeer grazing history. Nature Clim. Change advance online publication.

Van der Wal R, Bardgett RD, Harrison KA, Stien A. 2004. Vertebrate Herbivores and Ecosystem Control: Cascading Effects of Faeces on Tundra Ecosystems. Ecography: 242.

Van der Wal R, Brooker RW. 2004. Mosses Mediate Grazer Impacts on Grass Abundance in Arctic Ecosystems. Functional Ecology: 77.

Van der Wal R, Sjögersten S, Woodin SJ, Cooper EJ, Jonsdottir IS, Kuijper D, Fox TAD, Huiskes AD. 2007. Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. Global Change Biology 13: 539-545.

Van der Wal R, Van Lieshout SMJ, Loonen MJJE. 2001. Herbivore impact on moss depth, soil temperature and arctic plant growth. Polar Biology 24: 29-32.

Waddington JM, Roulet NT, Swanson RV. 1996. Water table control of CH4 emission enhancement by vascular plants in boreal peatlands. Journal of Geophysical Research: Atmospheres 101: 22775-22785.

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 Ø, 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 Sciences of the United States of America 103: 1342-1346.

Ward SE, Bardgett RD, McNamara NP, Ostle NJ. 2009. Plant functional group identity influences short-term peatland ecosystem carbon flux: evidence from a plant removal experiment. Functional Ecology 23: 454-462.

Warren SD, Thurow TL, Blackburn WH, Garza NE. 1986. The Influence of Livestock Trampling under Intensive Rotation Grazing on Soil Hydrologic Characteristics. Journal of Range Management 39: 491-495.

Welker J, Fahnestock J, Povirk K, Bilbrough C, Piper R. 2004. Alpine Grassland CO2 Exchange and Nitrogen Cycling: Grazing History Effects, Medicine Bow Range, Wyoming, U.S.A. Arctic, Antarctic, and Alpine Research 36: 11-20.

Whalen SC. 2005. Biogeochemistry of Methane Exchange between Natural Wetlands and the Atmosphere. Environmental Engineering Science 22: 73-94.

Zimov SA, Chuprynin VI, Oreshko AP, Iii FSC, Reynolds JF, Chapin MC. 1995. Steppe-Tundra Transition: A Herbivore-Driven Biome Shift at the End of the Pleistocene. The American Naturalist 146: 765-794.

Figures and Tables

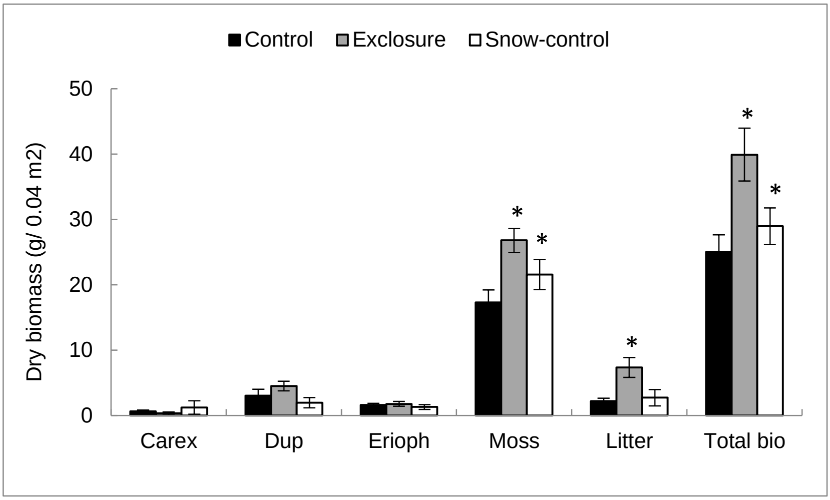

Figure 1. Mean dried biomass (g) ± SE for the harvested samples (0.04 m^2) in 2013 for controls (black squares), and the two treatments: exclosure (gray squares) and snow-control (closed squares). Samples were divided into vascular plants: *Carex sp* (Carex), *Dupontia psilosantha* (Dup) and *Eriophorum scheuchzeri* (Erioph) and fresh mosses (Moss), old biomass (Litter) and the total weight of the dried biomass (Total bio). In August 2013, one sample were collected in each block and treatment (C n=7, EX n=5, SC n=5). The significance for the differences (nonparametric test) between control and treatments are indicated with asterisk above the bars * $p \leq 0.05$

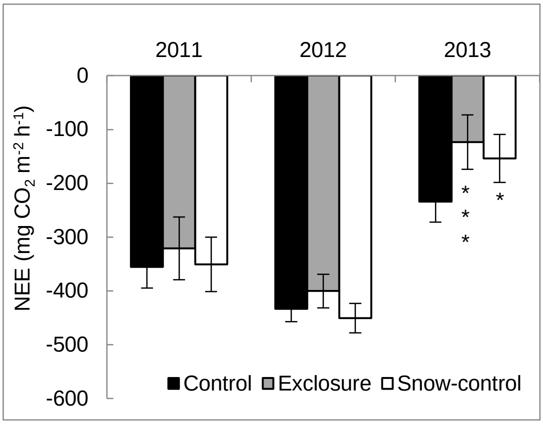

Figure 2. Mean Net Ecosystem Exchange (NEE) mg CO_2 m^{-2} h^{-1} ± SE, for 2011, 2012 and 2013 for controls (stripped squares), and the two treatments: exclosure (open squares) and snow-control (closed squares). Data is based on all blocks and all treatments; control n=15, exclosure n=16 and snow-control n=8. The significance for the differences (general mixed linear models) between control and treatments are indicated with asterisk above the bars, *** $p \leq 0.001$, * $p \leq 0.05$

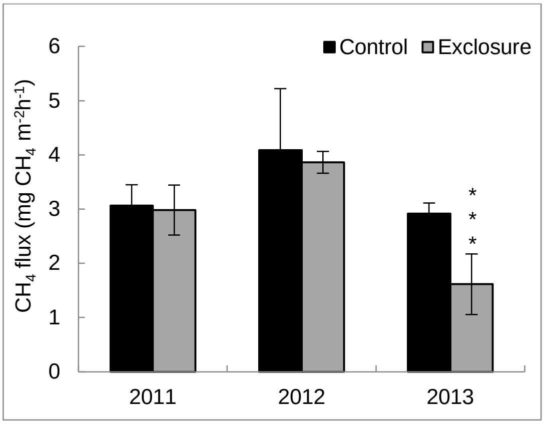

Figure 3. Mean CH_4 flux mg CH_4 m^{-2} h^{-1} ± SE, for 2011, 2012 and 2013 for controls (stripped squares) and exclosure (open squares). Data is based on plots from block three and four, control n=7, exclosure n=7. The significance for the differences (general mixed linear models) between control and exclosure are indicated with asterisk above the bars, *** $p \leq 0.001$

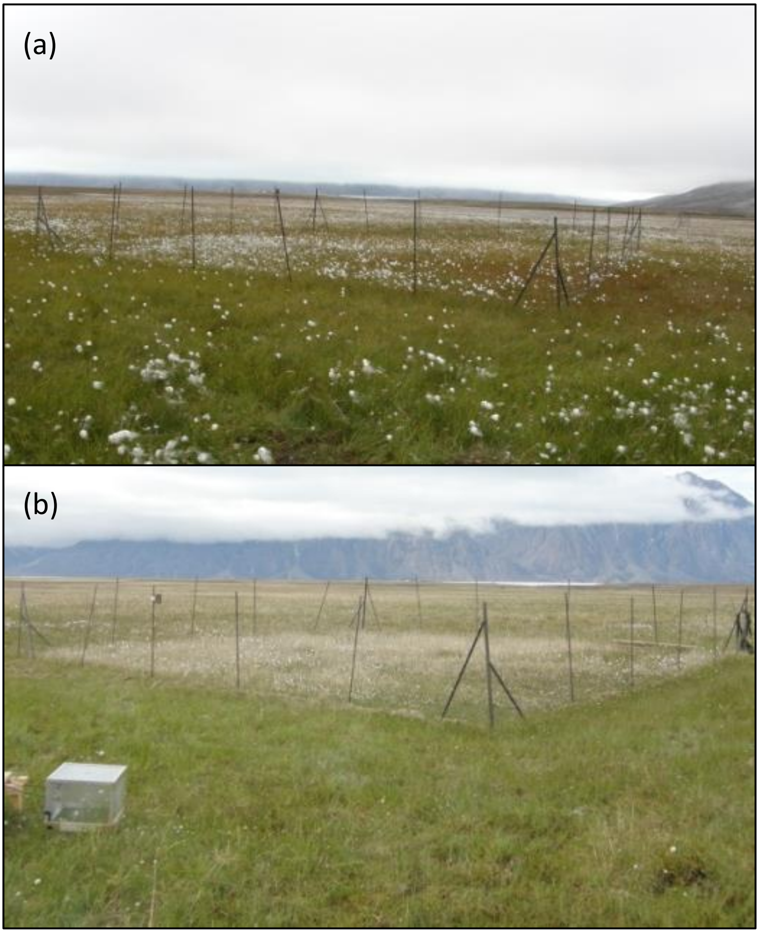

Figure 4. Photo of block four, in front is the control treatment, while the exclosure is seen in the back, a=4 August 2011, b=2 July 2013.

Year		Arctagrostis			Carex			Dupontia			Eriophorum			Equisetum			Sum		
		C	EX	SC	C	EX	SC	C	EX	SC	C	EX	SC	C	EX	SC	C	EX	SC
2011	Mean	498	266	315	383	20	2057	2556	3263	1702	2700	1784	1869	904	734	1210	6136	5333	5944
	Max	1588	1288	1369	3313	200	6163	4131	5125	5063	5219	3544	2981	5319	3375	4850	8869	7456	9225
	Min	0	0	0	0	0	0	0	750	0	31.3	188	669	0	0	0	2969	2700	1225
	SE (±)	142	139	231	275	20	1025	401	383	978	452	352	486	505	372	745	555	500	1376
	p		0.267	0.491		0.213	0.223		0.228	0.466		0.144	0.261		0.309	0.238		0.309	0.876
2013	Mean	153	58	69	84	60	394	1663	1378	1463	1280	**627**	946	24	16	14	3181	**2122**	2872
	Max	881	188	394	700	488	1881	2813	2019	3013	2306	1094	1813	244	213	94	4163	2844	4075
	Min	0	0	0	0	0	0	0	106	0	544	188	419	0	0	0	2369	1438	1381
	SE (±)	54	19	38	47	42	216	173	155	385	120	64	152	15	15	19	137	113	361
	p		0.11	0.288		0.717	0.242		0.238	0.653		0.000	0.085		0.708	0.625		0.000	0.282

Table 1. The mean, maximum, minimum and standard error (SE) (±) for the number of vascular plants tillers per m^{-2}, for control (C) and the two treatments exclosure (EX) and snow-control (SC). The vegetation analyses were carried out in 2011 and 2013. In 2011 the analysis was made on block 3, 4 and 5 (C n=13, EX n=10, SC n=6) while it in 2013 was on all the plots (C n=17, EX n=14, SC n=10). Significant

		Number of tillers				Number of green leaves				Height of tillers			
		Dup.	Carex	Erioph.	Total	Dup.	Carex	Erioph.	Total	Dup.	Carex	Erioph.	Mean
C	Mean	69±22	6±1	79±23	154±15	108±37	15±5	110±31	234±25	10±2.7	9±0.9	11±0.4	11±0.5
	Max	115	12	168	180	201	27	228	291	15	11	12	12
	Min	0	4	48	98	0	0	57	142	0	6	10	10
EX	Mean	47±16	4±2	**37±7**	**87±13**	53±18	6±4	**50±11**	**108±13**	**14±3.6**	5±3.4	**15±0.9**	**15±0.9**
	Max	88	10	57	109	101	23	86	143	19	16	17	18
	Min	0	0	21	40	0	0	22	68	0	0	12	13
	p (C vs EX)	0.18	0.18	0.025	0.025	0.18	0.317	0.025	0.025	0.046	0.655	0.025	0.025
SC	Mean	49±20	24±23	48±9	121±21	66±33	51±47	64±13	181±48	8±2.2	4±2.7	10±0.6	10±0.5
	Max	102	114	76	183	184	240	108	305	13	11	11	12
	Min	0	0	20	56	0	0	32	70	0	0	8	9
	p (C vs SC)	0.317	0.317	0.655	0.655	0.317	1	0.655	0.655	0.317	0.317	0.655	0.317

Table 2. The mean (± SE), maximum and minimum number and the height (cm) of the dominant vascular plant species and the sum, from harvested biomass samples (0.04 m^{-2} m) for control (C) and the two treatments: exclosure (EX) and snow-control (SC). The dominating species were in 2013 *Dupontia psilosantha* (Dup), *Carex stans* (Carex) and *Eriophorum scheuchzeri* (Erioph.). In August 2013, one sample

Year	Treatment		NEE	R_{eco}	GPP	WtD	AL	Ts
2011	C	Mean	-355 ± 21	340 ± 16	-699 ± 29	6.8 ± 0.7	56.5 ± 1.1	7.9 ± 0.2
		Max	61.2	665	-124	22.0	76.0	13.4
		Min	-833	18	-1447	-4.0	4.0	4.9
	EX	Mean	-321 ± 23	321 ± 12	-638 ± 27	6.0 ± 0.7	56.8 ± 1.0	**7.5 ± 0.2**
		Max	104	570	-101	23.0	76.0	12.7
		Min	-856	49	-1328	-4.0	35.0	5.0
		p	0.843	0.966	0.814	0.975	0.556	0.029
	SC	Mean	-350 ± 15	309 ± 10	-659 ± 20	5.7 ± 0.5	59.5 ± 0.9	8.3 ± 0.9
		Max	30.4	582	-147	16.0	77.0	12.5
		Min	-695	42	-1200	-6.0	38.0	5.3
		p	0.274	0.951	0.394	0.487	0.829	0.980
2012	C	Mean	-433 ± 41	303 ± 16	-739 ± 51	2.3 ± 0.3	59.2 ± 1.5	6.1 ± 0.3
		Max	1698	818	-3	10.0	81.0	15.9
		Min	-1495	40	-1878	-4.0	17.0	0.3
	EX	Mean	-400 ± 41	264 ± 12	**-678 ± 54**	2.3 ± 0.4	59.7 ± 1.5	**6.9 ± 0.4**
		Max	273	582	-8	10.0	82.0	22.9
		Min	1540	30	-2181	-7.0	26.0	0.3
		p	0.809	0.317	0.044	0.602	0.343	0.045
	SC	Mean	-450 ± 52	275 ± 16	-726 ± 63	2.3 ± 0.5	59.2 ± 2.2	7.0 ± 0.5
		Max	104	591	-21	10.0	82.0	18.3
		Min	-1280	38	-1617	-4.0	24.0	0.3
		p	0.735	0.994	0.648	0.668	0.954	0.281
2013	C	Mean	-234 ± 24	385 ± 16	-620 ± 34	14.1 ± 0.8	49.1 ± 1.3	5.2 ± 0.2
		Max	169	749	-168	30.0	68.0	10.6
		Min	749	117	-1262	0.0	29.0	2.2
	EX	Mean	**-124 ± 25**	363 ± 17	**-487 ± 33**	**16.8 ± 0.8**	**44.8 ± 1.3**	**4.6 ± 0.2**
		Max	337	821	-55	26.0	71.0	9.0
		Min	-639	127	-1140	3.0	20.0	1.8
		p	<0.0001	0.808	0.0001	<0.0001	0.0005	<0.0001
	SC	Mean	**-154 ± 27**	**290 ± 21**	**-444 ± 40**	**15.4 ± 1.0**	49.0 ± 1.8	5.4 ± 0.2
		Max	137	585	-62	28.0	70.0	9.4
		Min	773	23	-1337	1.0	29.0	2.5
		p	0.028	0.013	0.001	0.0003	0.919	0.822

Table 3. The mean (± SE), maximum and minimum values of net ecosystem exchange (NEE), respiration (R_{eco}) and photosynthesis (GPP) (mg CO_2 m^{-2} h^{-1}), water table depth (WtD) and active layer depth (AL) (cm from the peat layer) and soil temperature (Ts) (10 cm below surface) in 2011, 2012 and 2013 for control (C), and the two treatments exclosure (EX) and snow-control (SC). Data is based on all blocks and all treatments; control (n=15), exclosure (n=16) and snow-control (n=8). Significant differences (nonparametric test) between control vs exclosure and control vs snow-control are shown in bold types

Year		Arctagrostis		Dupontia		Eriophorum		Equisetum		Sum	
		C	EX	C	EX	C	EX	C	EX	C	EX
2011	Mean	340 ± 220	96 ± 76	3450 ± 148	3546 ± 162	3123 ± 526	2175 ± 386	166 ± 91	266 ± 192	6913 ± 664	5818 ± 379
	Max	1588	550	4131	4038	5219	3544	594	1419	8869	7456
	Min	0	0	2994	2763	1375	900	0	19	4756	4775
	p		0.316		0.666		0.172		0.648		0.184
2013	Mean	185 ± 122	13 ± 10	1993 ± 159	1746 ± 83	1371 ± 196	**623 ± 47**	38 ± 34	2 ± 2	3548 ± 220	**2381 ± 109**
	Max	881	69	2813	2019	2306	825	244	13	4163	2844
	Min	0	0	1450	1375	756	444	0	0	2763	2044
	p		0.208		0.194		0.008		0.33		0.001

Table 4. The mean, maximum, minimum and standard error (SE) (±) for the number of vascular plants tillers per m^{-2}, for control (C) and exclosures (EX) for plots used in the CH_4 analysis. The vegetation analysis was carried out in 2011 and 2013 (C n=7, EX n=7). Significant differences (nonparametric test) between control vs exclosure and control vs snow-control are shown in bold

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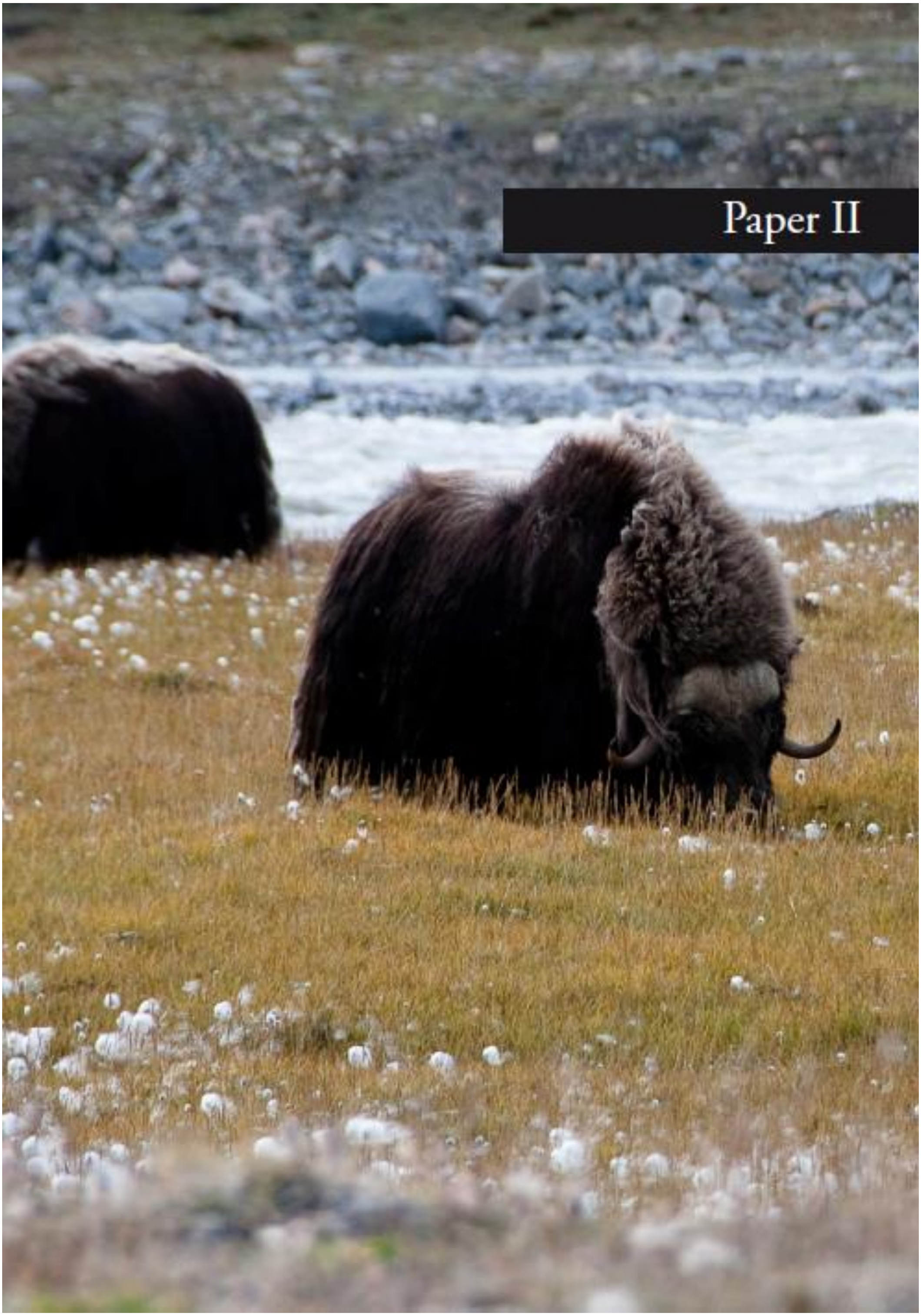

Paper II

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Effects of simulated increased grazing on carbon allocation patterns in a high arctic mire

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Abstract Herbivory is an important part of most ecosystems, and grazing alone can have a considerable impact on the ecosystems carbon balance with both direct and indirect effects. Removal of above-ground biomass by consumption of herbivores will change the below-ground carbon stock; the reduction of litter that goes into the ground will influence the total ecosystem carbon content. Little is however known about how plant-herbivory interactions effect the carbon balance, in particular methane emissions, of high arctic mires. We hypothesized that increased grazing pressure will change carbon allocation patterns resulting in decreased net ecosystem uptake of carbon and subsequently in lower methane emissions. An in-situ field experiment was conducted over 3 years in a high arctic mire at Zackenberg in NE Greenland. The experiment consisted of three treatments, with five replicates of each (1) control, (2) vascular plants were removed (NV), (3) clipped twice each growing season in order to simulate increased muskox grazing. Immediately after the initiation of the experiment net ecosystem uptake of CO_2 decreased in clipped plots (mean total decrease for the three following years was 35 %). One year into the experiment a significantly lower CH_4 emission was observed in these plots, the total mean reduction for the following 2 years was 26 %. Three years into the experiment significantly lower substrate (acetic acid) availability for CH_4 production was observed (27 % reduction). NV plots had a mean decrease in CO_2 uptake of 113 %, a 62 % decrease in ecosystem respiration and an 84 % decrease in CH_4 emission (mean of all 3 years). Our study shows that increased grazing pressure in a high arctic mire can lead to significant changes in the carbon balance, with lower CO_2 uptake leading to lower production of substrate for CH_4 formation and in lower CH_4 emission.

Keywords Arctic · Carbon · Grazing · Methane · Mire · Muskox · Organic acid

Introduction

Half of the Earth's land surface is influenced by large mammalian herbivores, livestock or native herbivores (Olff et al. 2002), which makes it important to consider the influence they have on the ecosystem. Removal of

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above-ground biomass by consumption of herbivores will change the below-ground carbon stock and the reduction of litter that goes into the ground will influence the total ecosystem carbon content (Mulder 1999; Sjögersten et al. 2011; Tanentzap and Coomes 2012; Van der Wal et al. 2007). In the Arctic, herbivory has been shown to have an important impact on the carbon cycle (e.g., Cahoon et al. 2012; Mulder 1999; Olofsson et al. 2004; Sjögersten et al. 2008, 2011; Speed et al. 2010; Van der Wal et al. 2007; Welker et al. 2004). The arctic ecosystems are an important global carbon sink and despite that the northern permafrost region only covers about 16 % of the earth, it stores approximately 50 % of the global below-ground organic carbon (McGuire et al. 2009; Ping et al. 2008; Post et al. 1982; Tarnocai et al. 2009). Arctic wetlands in particular are holding large amounts of carbon, as the decomposition rate of organic matter is slow under cold and anoxic conditions (Tarnocai et al. 2009). Anoxic decomposition and methanogenesis and thereby CH_4 production prevails under wet conditions. Artic wetland ecosystems produce approximately 40 % of the natural global emissions of CH_4 (Cicerone and Oremland 1988; Mikaloff Fletcher et al. 2004).

Plant-soil-herbivore interactions are complex, and involve both direct and indirect impacts, and may influence a variety of ecosystems processes, such as carbon sequestration, greenhouse gas production and emission, vegetation species composition, soil physical parameters (i.e., soil moisture and soil temperature), decomposition rate and nutrient availability (e.g., Sjögersten et al. 2008; Tanentzap and Coomes 2012). Depending on the ecosystem and grazing pressure, herbivory may either lead to an increase in net primary production (NPP) (Cargill and Jefferies 1984; Olofsson et al. 2001, 2004) or a decrease in NPP (e.g., Bagchi and Ritchie 2010; Beaulieu et al. 1996; Cahoon et al. 2012; Ouellet et al. 1994; Sjögersten et al. 2011; Susiluoto et al. 2008; Van der Wal et al. 2007). In nutrient poor high arctic areas a number of studies have shown an increase in NPP as a result of increased herbivory (Olofsson et al. 2004; Van der Wal et al. 2004) as nutrient addition by animal excrement can increase the labile nutrient level (Stark et al. 2002; Van der Wal et al. 2004). Most studies on the impacts of grazing have however reported no effect or a decrease in aboveground NPP (Milchunas and Lauenroth 1993). In some cases grazing can change the carbon balance from being a carbon sink when not influenced by herbivores to becoming a carbon source when grazed (Sjögersten et al. 2011; Welker et al. 2004).

Additionally, studies of grazing in the high arctic have demonstrated that herbivory can result in a shift in vegetation composition—towards being more herb and graminoid dominated (Cahoon et al. 2012; Olofsson et al. 2009; Ouellet et al. 1994; Post and Pedersen 2008; Sjögersten et al. 2008; Stark et al. 2002; Susiluoto et al. 2008; Van der Wal 2006). Grazing has also been shown to change nutrient allocation patterns, as vegetation uses carbon and nutrients reserves for regrowth of new plant shoots instead of building reserves below-ground (Beaulieu et al. 1996; Chapin 1980; Green and Detling 2000; Mulder 1999). Compared to other habitats in the arctic, the mires is highly productive (Arndal et al. 2009) and they are generally more exposed to grazing, as these habitats are preferred by many herbivores. Consequently, they may have a higher carbon loss, than mesic habitats (Sjögersten et al. 2008; Speed et al. 2010).

Despite the potentially large impact of herbivory on the carbon cycle of arctic wetlands and on many of the controlling aspects for CH_4 production and emission, only few studies have focused on the effects of herbivory on CH_4 fluxes in the arctic and sub-alpine regions (Sjögersten et al. 2011, 2012, respectively). These studies showed no effect of herbivory on CH_4 emissions (Sjögersten et al. 2011, 2012). The arctic study was however, focusing on barnacle geese (Sjögersten et al. 2011) and the sub-alpine study were performed in a much drier habitat (Sjögersten et al. 2012), so comparability of the studies is limited.

Many factors are known to influence the CH_4 flux; these include soil temperature, water table depth (Torn and Chapin 1993; Waddington et al. 1996), substrate availability and quality (organic acids) (Christensen et al. 2003; Joabsson et al. 1999; Ström et al. 2003), and the presence of certain vascular plant species e.g. *Eriophorum scheuchzeri* (Ström and Christensen 2007; Ström et al. 2003, 2012). During plant growth, low molecular weight organic acids are released to the rhizosphere, and of these, acetic acid is a substrate of particular importance for methanogenesis. The organic acids are generated from two main sources: (1) from fermentative microbes producing organic acid (OA) (e.g., acetic and formic acid) from plant residues (Charlatchka and Cambier 2000; Gounou et al. 2010; Killham 1994), and (2) from root exudation (Kuzyakov and Domanski 2000; Ström et al. 2003). Despite that organic acids generally accounts for less than 10 % of the dissolved organic matter (DOC), they are essential for the carbon biogeochemistry and nutrient cycle in the soil, as they are bioavailable (Fischer et al. 2007). Hence, to understand the potential effects of herbivory on CH_4 emission it is vital to increase our knowledge of the effects grazing have on below-ground substrate availability.

This study focuses on how increased grazing pressure effects the carbon balance, in particular CH_4 emissions, in a high arctic mire. We hypothesis that increased grazing will: (1) play an essential role in the carbon cycle and will decrease net ecosystem exchange (NEE) and gross primary production (GPP); (2) decrease substrate availability for CH_4 production as fixed carbon will be allocated primarily to above-ground regrowth and to a lesser extent to the root system; (3) lower below-ground C-allocation will lead to decreased CH_4 fluxes in plots where increased grazing is simulated; and (4) change the vegetation composition/density. In order to test our hypotheses, an experiment in a high arctic mire, that already is exposed to muskox grazing (Kristensen et al. 2011), was conducted where increased muskox grazing were simulated by clipping the vegetation. Over a 3 year period we measured CO_2 fluxes, CH_4 fluxes, the OA concentration in pore-water and the ecosystem properties (water table depth, active layer depth and soil temperature). Additionally, we examined the changes in the vegetation composition induced by increased grazing pressure. Though large herbivores, such as muskoxen, may affect the ecosystem both by grazing, trampling and adding nutrients to the ecosystem (e.g., Tanentzap and Coomes 2012), the present study only considers the effect caused by removal of additional vegetation following clipping.

Materials and methods

Site description

The study took place in the arctic valley Zackenberg in NE Greenland (74°30′N 20°30′W). The area is situated in the high arctic, with an annual mean temperature around −9 °C, the warmest month (July) has a mean monthly air temperature (MMAT) of 5.8 °C, and in the coldest month (February) MMAT is −22.4 °C. The mean annual precipitation was 261 mm in the period 1996–2005, with only 10 % falling as rain during summer (Hansen et al. 2008). The area is in a zone with continuous permafrost, and the active layer thickness (i.e. the upper layer of the soil that thaws every summer) varies from 45 to 80 cm depending on the type of area (Christiansen et al. 2008). There are five dominating plant communities classified in the valley: Mire, Grassland, Salix snow-bed, Cassiope heath and Dryas heath (Elberling et al. 2008). The measuring site is located in the freshwater lowland mire *Rylekæret*. The mires cover approximately 4 % of the valley (Arndal et al. 2009). This ecosystem is normally water-saturated throughout the growing season, years with little snow can, however, lead to a drying during the growing season. pH is relatively high with values around 6.9 ± 0.2 (Ström et al. 2012). The dominating vascular plant species are the three sedges *Carex stans*, *Dupontia psilosantha* and *Eriophorum scheuchzeri* (Christian Bay, personal communication, and our data). Underneath the sedges a dense moss cover is found, e.g., species of *Tomenthypnum*, *Scorpidium*, *Aulacomnium* and *Drepanocladus* (Ström et al. 2012). The peat layer at the measured site is between 18 and 20 cm deep (Falk and Ström unpublished results).

The muskox *Ovibos moschatus* is the only large herbivore in Northeast Greenland and is present in the Zackenberg area all year-round. During summer, muskoxen predominantly feed in the grasslands and mires mainly eating graminoids (Kristensen et al. 2011), in winter they prefer areas with thin snow-cover, where it is easier for them to access the vegetation (Berg et al. 2008). When muskoxen feed on graminoids, they press the incisors against the pad and pull, leaving the vegetation cut just a couple of centimeters above the surface (Kristensen et al. 2011). Bliss (1986) estimates that muskoxen in general consumes 1–2 % of the sedge dominated meadow cover per year, but may in some areas consume up to 20 % of the available vegetation (Jefferies et al. 1994).

Experimental setup

In 2008, five replicate blocks with three experimental treatments were established in the mire. The replicate blocks were placed closely in a homogeneous part of the mire. The habitat was determined as homogeneous based on a previous study by Ström et al. (2012) that showed very low variation in active layer, soil temperature and water-table depth between 15 plot replicates positioned in the same part of the mire. The three treatments are described below.

- One plot in each block served as an un-manipulated control, the plot was however still exposed to ambient muskox grazing and trampling.
- A second plot in each block had the vegetation cut approximately 3–4 cm above the surface twice each summer using a scissor, thus mimicking muskox grazing in the mire (see Kristensen et al. 2011). The vegetation was first cut when it reached a stabled height in the beginning of the growing season, whereas the second cut was made when the grazed vegetation had reached the surrounding vegetation height again. The plots were cut 2 July and 17 July in 2010, 15 July and 1 August in 2011 and 19 July and 13 August in 2012.
- A third plot in each block had all vascular plants removed in 2008, leaving only the mosses. New shoots were thereafter removed each summer. The vascular plants and their roots were gently pulled from the plots as soon as they became visible. These plots thus mimic the herbivore-induced change into moss-dominated plant communities observed by Sjögersten et al. (2008). No vascular plants (NV) plots represent extreme grazing and were initially established to investigate what happens with the CH_4 emission and the OA concentration when vascular plants are absent.

Muskoxen are moving freely in the area and all plots are exposed to both grazing and trampling. By clipping one-third of the plots twice each summer, we increase the grazing pressure substantially.

Before the muskox grazing simulation experiment was initiated, the plots were measured twice in 2009 and twice in 2010 in order to get an indication of the pre-experimental difference between control and clipped plots (later selected through randomization).

Each plot consisted of an aluminum base (39.5 × 39.5 cm) permanently installed (in 2008) 15 cm into the ground. Following the initiation of the simulated grazing in 2010 CH_4 and CO_2 fluxes and ecosystem parameters were measured on these plots approximately twice per week over the main part of the growing season and in the autumn in 2012. The measurements took place between 10 am and 5 pm, the specific time of the measurement varied each measuring day. No measurements were performed under windy conditions (when wind speed exceeded around 10 m s^{-1}). In 2010 the blocks were measured on 10 occasions between 21 June to 7 August and in 2011 on 13 occasions between 23 June and 5 August. In 2010 and 2011 we observed that the growing season was far from over in the beginning of August (see Figs. 3, 7). Consequently, in 2012 we prolonged our measurement period and the blocks were measured on 23 occasions between 1 July and 18 October.

Flux measurements

The fluxes of CO_2 and CH_4 were measured using a closed chamber technique (Christensen et al. 2000; Ström and Christensen 2007). For each measurement, a light and a dark measurement was made to establish NEE and the ecosystem respiration (R_{eco}) respectively. Measurements were performed with a transparent Plexiglas chamber equipped with a metal frame with a rubber list, to ensure an airtight seal against the aluminum base. The chamber had a volume of 0.041 m^3, and the area of the aluminum base was 0.156 m^2. The Plexiglas chamber reduced PAR by <10 % (Christensen et al. 2003). Dark measurements were conducted with the same chamber covered by a non-transparent plastic hood. Immediately before the start of a measurement the chamber was carefully placed on the aluminium base to avoid disturbance and each measurement lasted between 3 and 7 min. Chamber was equipped with a small fan to assist with the circulation and therefore mixing of the chamber air during the measurements. Air pressure inside the chamber was equalized by a small hole in the chamber, which was closed with a rubber stopper as soon as the measurement began.

In 2010 CH_4 fluxes were measured by a LGR RMT-200 Fast Methane Analyser (DLT200, Los Gatos Research, USA) and an infrared CO_2 gas analyser (PP-systems SBA-4, EGM-4, Hitchin, Hertfordshire, UK), the accuracy of both instruments are 1 %. The air from the chamber was pumped with a rate of 0.4 L min^{-1} to an analytical box containing the analyzers before it was non-destructively returned to the chamber. In 2011 and 2012, gas concentrations of CO_2 and CH_4 were simultaneously measured by a portable Fourier transform infrared (FTIR) spectrometer (Gasmet Dx 40-30, Gasmet Technologies Oy). The air from the chamber was pumped at a rate of 3.4 L m^{-1}. Both instruments was set up to record the CH_4 and CO_2 concentration every second. The FTIR was calibrated with a zero gas every second week. Stable high quality measurements with minimal baseline drift require a cell temperature of the FTIR between 20 and 35 °C. During summer optimal conditions were kept by the internal heating system of the FTIR and during the cold conditions in September and October 2012 the instrument was warmed with heating cables. To validate that the measurements from the two instruments were comparable, a control of the concentration of CH_4 measured in ambient air was performed prior to the field season of 2011 under controlled laboratory conditions. The results showed a small offset ranging from 0.08 to 0.23 ppm and a very small difference in calculated flux between the instruments.

The CO_2 and CH_4 fluxes were calculated from the changes in gas concentration as a function of time using linear fitting according to procedures by Crill et al. (1988), data has been corrected for the ambient air temperature and air pressure. As the replicate measurements (for each day) were all performed under stable and similar weather conditions we did not do any further corrections for environmental conditions. Release of gas from the ecosystem to the atmosphere is denoted by positive values and uptake by negative. Gas fluxes are expressed as mg m^{-2} h^{-1} of CH_4 or CO_2. Since we found a strong significant correlation ($R = 0.967$, $p < 0.0001$) between CH_4 fluxes measured during light and dark measurement for individual plots, the mean of these two measurements were calculated and used in the CH_4 flux calculations. NEE was the CO_2 flux measured within the transparent chamber, while R_{eco} were the dark measurement. GPP was calculated as the difference between NEE and R_{eco}.

Pore-water analysis

Pore-water was sampled shortly after each gas flux measurement, for subsequent analysis of organic acids. Pore-water samples were drawn from stainless steel tubes (3 mm in diameter), which were permanently installed in 5, 10 and 15 cm below the peat surface. Five cm above the moss surface, each tube was closed by a three-way valve that enabled sampling without air penetration into the soil. From each plot a 9 ml mixed pore-water sample was drawn using a syringe, if it was not possible to retrieve 9 ml of sample, an equal amount from each depth was drawn. The sample was immediately filtered through a low protein binding non-pyrogenic sterile pre-rinsed filter (Acrodisc PF 0.8/0.2 μm diameter 32 mm) and frozen as soon as possible. Subsequently, the pore-water samples were analyzed for OA using a liquid chromatography-ionspray tandem mass spectrometry system. The system consisted of a Dionex (Sunnyvale, CA, USA) ICS-2500 liquid chromatography (LC) system and an Applied Biosystems (Foster City, CA, USA) 2000 Q-trap triple quadrupole mass spectrometer (MS). The LC–MS method and instrumental set-up is described in more detail in Ström et al. (2012). Due to the relatively high pH values in the mire the prevailing form of acetic acid is acetate (it is however termed as acetic acid throughout the paper).

Ecosystem variables

As a measure of the environmental conditions, in connection with each flux measurement and in close proximity to each plot replicate, we determined the water table depth (WtD, cm below moss surface), the active layer thickness (AL, cm below moss surface), photosynthetically active radiation (PAR) and soil temperature at 10 cm below surface (T_s), using a 150 mm digital temperature probe (Viking, Eskilstuna, Sweden). PAR (μmol m^{-2} s^{-1}) was measured inside the chamber at 25 cm from the surface every minute, using a Minikin QTi data-logger (EMS Brno). Additionally, ambient incoming PAR and air temperature (Ta) were logged hourly (Minikin QTi) at 1 m from the ground surface throughout the growing season in 2011 and 2012. PAR and Ta data from 2010 were provided from the monitoring program ClimateBasis (Jensen and Rasch 2011). These, data were collected automatically about 1 km from the study site and measured at 2 m height. The WtD was measured at each block but to minimize disturbance not in individual plots. WtD was measured using a water permeable tube (2.5 cm in diameter) that was permanently installed in ground fitted with a float (made of cork). In 2011, the density and species composition of vascular plants was non-destructively estimated in each plot by counting the number of shoots of the three dominant vascular plant species.

Statistical analysis

To determine statistically significant differences between control, clipped and NV plots, with respect to gas fluxes, total OA and acetic acid concentration in pore water, Ts and AL, a general linear model repeated-measures analysis was performed (confidence interval adjustments were LSD). The model was made for each measuring year and took temporal development within seasons and the differences between blocks into account, as blocks and dates were random factors. Measurements earlier in the season with values around zero, due to an unproductive system, would render comparisons of the effects of the treatments on the carbon balance impossible. Therefore only fluxes measured after the onset of photosynthesis and with a negative NEE were included in the CO_2 data analyses. Following the same reasoning, CH_4 fluxes were included in the data treatment as long as the ecosystem was emitting measurable fluxes. The use of different time periods for CO_2 and CH_4 fluxes in 2012 should therefore be noted. Repeated-measures required gap filling of any data that were missing. Gap-filling was performed by computing a mean of the two measurements taken, on that particular plot, before and after the missing data point. Gap-filling was required in 2, 1.5 and 0 % cases for NEE, and R_{eco} and CH_4 respectively. Some OA data had to be removed due to contamination of the samples (one sampling date in 2010 and 2012 and two in 2011), in total 89.5 % of data was included in the data analyses. Gap filling was needed in 0.9 % of the cases for total OA and acetic acid.

To determine the variables that best could explain the plot scale variation in gas fluxes and any relationships between environmental variables a bivariate correlation (pearson 2-tailed test for significance) analysis was performed on the mean fluxes and ecosystem parameters (T_s, T_a, WtD, AL and PAR). To test the differences between the three vascular plant species in control and clipped plots data were first tested for normality and then an independent *t* test was performed.

Results

CH_4 and CO_2 fluxes

CH_4

For each individual measurement year (2010–2012) a clear significant difference ($p \leq 0.001$) between the CH_4 fluxes in control and NV plots were seen. The flux was on average 84 % lower in NV than in control plots, with fluxes in NV plots ranging between 0.1–3.1, 0.0–4.6 and 0.0–3.5 mg CH_4 m^{-2} h^{-1} for 2010, 2011 and 2012, respectively. Before the initiation of the increased grazing experiment (2 July 2010) the control plots and those that later were clipped were measured on four occasions (two times in August 2009 and two times in 2010). Here there were no significant differences ($p \geq 0.710$) in CH_4 flux between the plots (Fig. 1). Additionally, there was no significant difference ($p = 0.571$) in the mean CH_4 flux between control and clipped plots after the initiation of simulated increased grazing in 2010. However, one year after the start of the experiment (2011), the mean CH_4 flux was significantly lower in clipped than in control plots ($p = 0.010$) and this difference persisted during 2012 ($p = 0.045$). On average (2011 and 2012) the CH_4 fluxes were 26 % lower in clipped plots compared to control plots (Fig. 1) and the difference was visible throughout the seasons (Fig. 7). The highest CH_4 fluxes were measured around the 15 July (DOY 196–198). A late start of the growing season in 2012 is clearly seen in Fig. 7. That year the rapid increase of CH_4 emission normally seen following the onset of the growing season started on DOY 190 while it the previous years started around DOY 170.

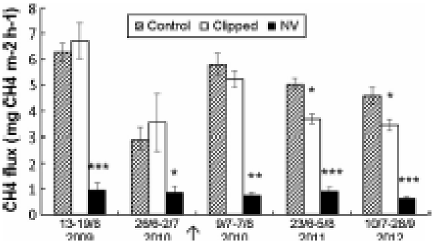

Fig. 1 The mean measured CH_4 fluxes (mg CH_4 m^{-2} h^{-1} ± SE, 2009 $n = 10$, 2010 (before clipping experiment) $n = 15$, 2010 (after clipping experiment) $n = 35$, 2011 $n = 60$, 2012 $n = 85$) for control (*stripped squares*), clipped (*open squares*) and no vascular plants (NV) (*closed squares*) plots. Significant differences (repeated measures ANOVA) between control and treatment plots are indicated with *asterisks* above the *bars*, ***$p \leq 0.001$, **$p \leq 0.01$ and *$p \leq 0.05$. Note the varying time periods between the years. The arrow indicates the start of clipping experiment on the 02/07/2010

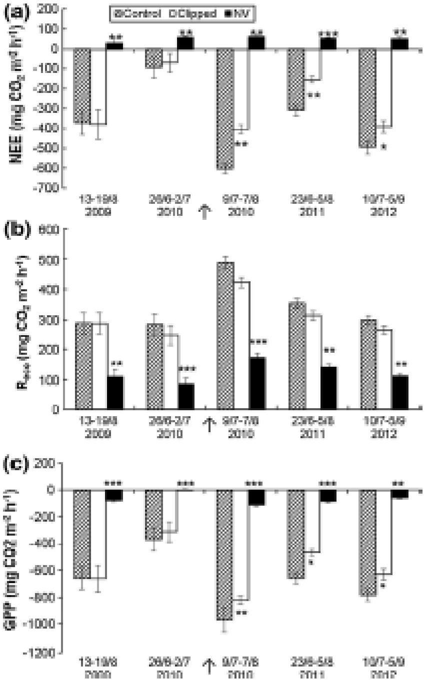

Fig. 2 The mean measured NEE (a), R_{eco} (b) and GPP (c) (mg CO_2 m^{-2} h^{-1} ± SE, 2009 $n = 10$, 2010 (before clipping experiment) $n = 15$, 2010 (after clipping experiment) $n = 35$, 2011 $n = 60$, 2012 $n = 60$) for control, clipped and no vascular plants (NV) plots. Significant differences (repeated measures ANOVA) between control and treatment plots are indicated with *asterisks* above *bars*, ***$p \leq 0.001$, **$p \leq 0.01$ and *$p \leq 0.05$. Note the varying time periods between the years. The *arrow* indicates the start of clipping experiment on the 02/07/2010

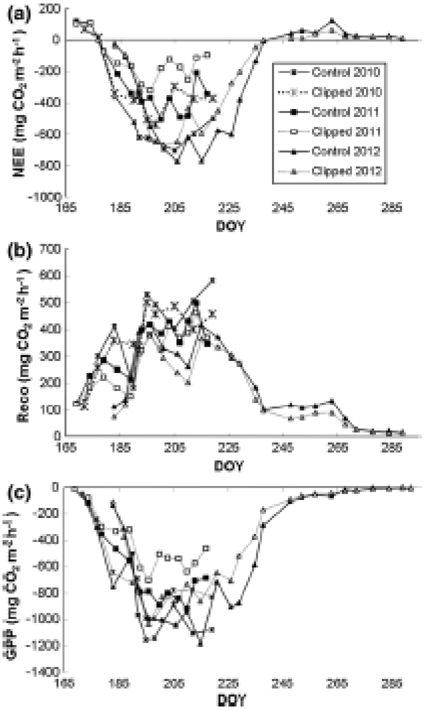

Fig. 3 NEE (a), R_{eco} (b) and GPP (c) (mg CO_2 m^{-2} h^{-1}) for control and clipped plots from the whole measuring period in 2010, 2011 and 2012. The time is shown as day of year (DOY). Each data point is an average of each treatment (five plots). The clipping was performed in 2010 on DOY 183 and 198, in 2011 on DOY 196 and 213 (DOY) and in 2012 on DOY 201 and 226

NEE

For each individual measurement year (2010–2012), a clear significant difference ($p \leq 0.001$) between NEE in control and NV plots was seen (Fig. 2). On average NV plots were 113 % lower, with fluxes ranging between −52 to 218, −43 to 183 and −71 to 310 mg CO_2 m^{-2} h^{-1} for 2010, 2011 and 2012, respectively. Before the initiation of the increased grazing experiment, there was no significant differences ($p \geq 0.724$) in NEE between control and plots that later were clipped. However, after initiation of clipping there was an immediate and significant decrease in NEE which persisted throughout the years (Fig. 3; $p = 0.003$, $p = 0.002$ and $p = 0.040$ for 2010, 2011 and 2012, respectively). For all 3 years NEE was on average 35 % lower in clipped plots (Fig. 2a) compared to control plots. The lower uptake of CO_2 in the clipped plots was mainly seen after the onset of the clipping each year. Consequently, the NEE values for the control and clipped plots were very similar before the first clipping of each season (Fig. 3a). In general, the mire acted as a net carbon sink for the main part of the measurement period in both control and clipped

Table 1 The percentile distribution of the organic acid for the three measuring years for control, clipped and plots with no vascular plants (NV)

Organic acid	Control			Clipped			NV		
	2010	2011	2012	2010	2011	2012	2010	2011	2012
Acetic (%)	57	63	49	50	61	44	44	54	41
Lactic (%)	14.3	7	30	20	8.5	31	20	9	36
Formic (%)	16.1	16	12	17	15.5	11.4	19.3	23	13
Glycolic (%)	10.4	6	2.4	9.8	6	3	11.8	6.5	2.5
Oxalic (%)	0.6	3.4	4.3	0.6	3.9	6	1.4	3	5.5
Succinic (%)	1.1	2.6	1.2	1.2	2.8	1.2	2.5	2.5	1.3
Malic (%)	0.2	2	0.2	0.7	1.7	0.2	0.3	2	0.2
Citric (%)	0.4	0	0.4	0.4	0	0.9	0.2	0	0.7
Tartaric (%)	0.01	0	0	0	0	0.1	0	0	0.1

The percentile is the mean value for each year and for all treatments ($n = 5$)

plots (NEE, Fig. 3a). 2011 was the least productive year with the lowest maximum uptake, while 2012 was the most productive year.

R_{eco}

For each individual measurement year (2010–2012) a clear significant difference ($p \leq 0.001$) between mean R_{eco} in control and NV plots was seen (Fig. 2b). On average R_{eco} in NV plots were 62 % lower, with fluxes ranging between 49–399, 27–465 and 0–217 mg CO_2 m^{-2} h^{-1} for 2010, 2011 and 2012, respectively. Before initiation of the increased grazing experiment there were no significant differences ($p \geq 0.577$) in R_{eco} between control plots and those plots that were later clipped (Fig. 2b). Following the initiation of increased grazing there was a slight tendency towards lower R_{eco}. This, however, was not significant and only seen in 2010 ($p = 0.116$, $p = 0.222$, $p = 0.248$ for 2010, 2011 and 2012, respectively). Maximum R_{eco} was highest in 2010 and lowest in 2011. Again the late start of the growing season in 2012 is clearly seen in Fig. 3b.

GPP

For each individual measurement year (2010–2012) a clear significant difference ($p \leq 0.001$) between GPP in control plots and NV plots were seen (Fig. 2c). The fluxes measured in NV plots was in general 89 % lower and ranged between 0–301, 0–465 and 0–234 mg CO_2 m^{-2} h^{-1} for 2010, 2011 and 2012, respectively. Before initiation of the grazing experiment there were no significant differences ($p \geq 0.567$) in GPP between control plots and those plots that later were clipped. Immediately after the start-up of the increased grazing simulation GPP decreased in clipped plots. The lower GPP was consistent throughout the years ($p = 0.009$, $p = 0.015$ and $p = 0.019$ for 2010, 2011 and 2012, respectively). The GPP in clipped plots were on average 21 % lower than control plots for all three years (Fig. 2c). The difference in GPP was consistent through the main part of the measurement periods (Fig. 3c). 2011 had consistently lower GPP than 2010 and 2012, while these years had very similar GPP ranges. Again the late start of the growing season in 2012 (DOY 190 compared to DOY 170 the previous years) is clearly seen in Fig. 3c.

Pore-water chemistry

The OA pool was dominated by acetic acid and additionally included citric acid, formic, glycolic, lactic, malic, oxalic, succinic, and tartaric (Table 1). The concentration of OA ranged between, 48–2796, 9–2590 and 17–524 µg C l^{-1} in control plots, 16–3652, 40–2569 and 25–726 µg C l^{-1} in clipped plots and 28–2888, 30–2579 and 15–537 µg C l^{-1} in NV plots, for 2010, 2011 and 2012, respectively. A strong significant correlation between OA and acetic acid was found ($R = 0.990$, $p < 0.0001$). The concentrations of acetic acid measured in NV plots ranged between $0 \geq 2402$, $4.1 \geq 2402$ and 2.7–342.6 for 2010, 2011 and 2012, respectively.

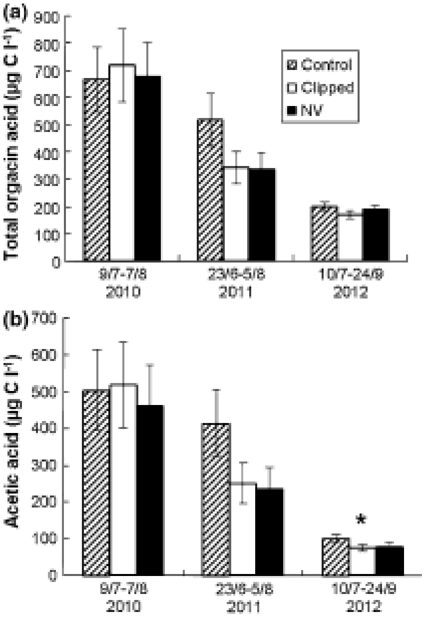

Fig. 4 The mean concentration (µg C l^{-1} ± SE, 2010 $n = 45$, 2011 $n = 60$, 2012 $n = 65$) of organic acid (a) and acetic acid (b) in control, clipped and plots with no vascular plants (NV). Significant differences (repeated measures ANOVA) between control and treatment plots are indicated with asterisks above the *bars*, ***$p \leq 0.001$, **$p \leq 0.01$ and *$p \leq 0.05$. Note the varying time periods between the years

No significant difference was found in the total OA concentration between control and treatment plots for any of the measurement years (Fig. 4a) (clipped plots $p = 0.759$, $p = 0.119$ and $p = 0.227$, and NV plots $p = 0.943$, $p = 0.105$ and $p = 0.643$ for 2010, 2011 and 2012, respectively). However in 2012, the third year after the experiment was initiated, a significantly ($p = 0.044$) lower (−27 %) mean acetic acid concentration was found in clipped plots compared to control plots and a strong tendency for NV plots ($p = 0.066$) was also found (Fig. 4b). The first 2 years no significant differences were seen in the acetic acid concentration between treatments (clipped plots $p = 0.929$, $p = 0.136$ and NV plots $p = 0.767$, $p = 0.106$ for 2010 and 2011, respectively). The difference between treatments in acetic acid concentration tended to decline later in the season and was, irrespective of treatment and year substantially higher in the beginning of the growing season (Fig. 5).

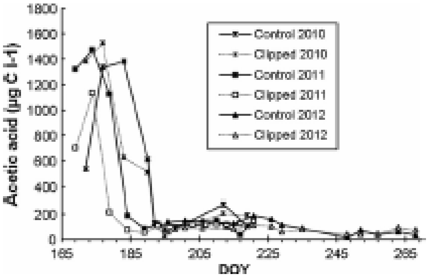

Fig. 5 The measured acetic acid concentration (µg C l^{-1}) in control and clipped plots, for the whole measuring period in 2010, 2011 and 2012. The time is shown as day of year (DOY). Each data point is an average of five plots. The clipping was performed in 2010 on DOY 183 and 198, in 2011 on DOY 196 and 213 (DOY) and in 2012 on DOY 201 and 226

Species composition

During the vegetation survey, the main vascular plant species within the plots were *Carex stans* 42 ± 2.5 (% ± SE), *Dupontia psilosantha* 32.7 ± 2.1 and *Eriophorum scheuchzeri* 24.3 ± 2.6. There was no significant effect of increased grazing on the vegetation composition after 1 year of grazing. However a strong tendency ($p = 0.07$) towards a higher total number of vascular plants in the control plots were seen (Fig. 6). Additionally, the number of *Eriophorum* shoots tended to be lower ($p = 0.096$) in clipped compared to control plots. For *Carex* and *Dupontia* the differences were less pronounced ($p = 0.231$ and 0.589, respectively, Fig. 6).

Environmental variables

Since all plots were situated in close proximity and in the same vegetation type there was no difference between blocks or plots in Ta, PAR, AL, peat layer depth or WtD. In 2010 T_s at 8–10 cm was however significantly lower (mean 0.7 °C) in NV plots compared to control and clipped plots ($p = 0.031$). In 2011 and 2012 no significant differences were observed $p = 0.280$ and $p = 0.444$ for 2011 and 2012, respectively. There was no significant difference in T_s ($p \geq 0.103$) between control and clipped plots

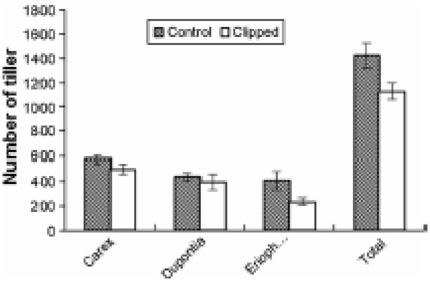

Fig. 6 Vegetation analyses from the experiment plots in NE Greenland, analyses are made in 2011. The dominating species in the plots were: *Carex stans*, *Dupontia psilosantha* and *Eriophorum scheuchzeri*. The figure shows the mean number of tiller of the three dominating vascular plant species and the total number of tillers ± SE, for control and clipped plots. No significant differences between the controlled and clipped plots for any of the species

for any of the years. The date of snow melt differed between the years, in 2012 it melted more than 10 days later than the previous years (Table 2), due to the large amount of snow that fell in the beginning of 2012. Since WtD mainly depends on the amount of snow precipitation, the level decreases over the summer. In 2012 the maximum WtD was not reached until the end of autumn, which correspondences with the high amount of water input from melting snow that summer. No significant differences ($p \geq 0.550$) between the mean measured AL were found for the three treatments.

Comparing the monthly mean environmental variables for 2010, 2011 and 2012 we found a significant correlation between PAR and Ts ($R = 0.888$, $p = 0.001$) and between WtD and AL ($R = 0.780$, $p = 0.013$). There were, however, no significant correlations between any of the other measured environmental variables; T_a and T_s ($R = 0.489$, $p = 0.182$), Ta and PAR ($R = 0.296$, $p = 0.440$), Ta and WtD ($R = -0.162$, $p = 0.678$), Ta and AL ($R = -0.232$, $p = 0.548$), WtD and T_s ($R = -0.285$, $p = 0.457$), WtD and PAR ($R = 0.129$, $p = 0.741$), AL and T_s ($R = -0.144$, $p = 0.713$) or Al and PAR ($R = 0.100$, $p = 0.798$).

Controls of fluxes

In order to identify the likely controls of fluxes in the plots, a correlation analysis between the measured mean fluxes, OAs and environmental soil variables was performed.

The analysis showed highly significant correlations between all flux measurements; CH_4 and NEE ($R = -0.926$, $p \leq 0.001$), CH_4 and R_{eco} ($R = 0.957$, $p \leq 0.001$), CH_4 and GPP ($R = -0.976$, $p \leq 0.001$) and NEE and R_{eco} ($R = -0.868$, $p = 0.002$). No correlation was found between gas fluxes and OA or acetic acid concentration, OA and CH_4 ($R = 0.322$, $p = 0.399$), OA and NEE ($R = -0.157$, $p = 0.688$), OA and R_{eco} ($R = 0.528$, $p = 0.144$), acetic acid and CH_4 ($R = 0.385$, $p = 0.306$), acetic acid and NEE ($R = -0.192$, $p = 0.621$), acetic acid and R_{eco} ($R = 0.580$, $p = 0.101$). No significant correlations between the seasonal mean CO_2 and CH_4 fluxes and the measured soil properties (AL and T_s) ($p \geq 0.4$) were found.

Discussion

The magnitude of CO_2 and CH_4 fluxes and the patterns during the growing season varied between the three

Table 2 Measured ecosystem parameters for the different measuring periods in the mire in NE Greenland, Zackenberg

Parameters	Abbreviation	2010	2011	2012
Air temperature (°C) mean/(range)	T_a	6.4 (−0.6 to 16.9)[a]	7.5 (−0.4 to 20.9)	5.7 (−11.1 to 24.9)
Soil temperature (°C) mean	T_s	6.6	7.6	6.5
Photosynthetically active radiatio (μmol^{-1} m^{-2} s^{-1}) mean/(range)	PAR	486.9 (10.9–1,515)[a]	470.4 (3.5–1,340)	286.7 (0.0–1,231)
Water table depth (max cm/date)	WtD	12 (31 July)	9.5 (26 July)	9 (24 September)
Active layer depth (range in cm)	AL	34–58	23–53	29–60
Date of snow melt[a]		18 June	16 June	28 June

[a] *Source* Climatebasis Zackenberg—monitoring program (www.zackenberg.dk)

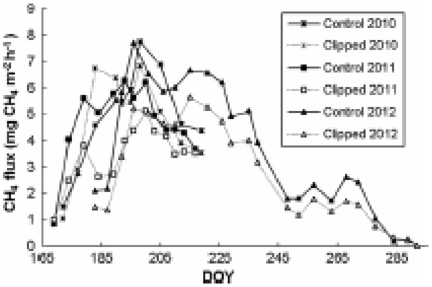

Fig. 7 CH_4 fluxes (mg CH_4 m^{-2} h^{-1}) for control and clipped plots from the whole measuring period in 2010, 2011 and 2012. The time is shown as day of year (DOY). Each data point is an average of each treatment (five plots). The clipping was performed in 2010 on DOY 183 and 198, in 2011 on DOY 196 and 213 (DOY) and in 2012 on DOY 201 and 226

measurement years (Figs. 1, 2, 3 and 7). The differences between the mean values (CH_4, NEE, GPP and R_{eco}, Figs. 1 and 2) for the three years is largely due to the different length of the measurement period each season and to the inter-annual variation in WtD. The measured flux magnitudes during the measurement periods were consistent with fluxes previously measured in the same mire (Mastepanov et al. 2008; Ström et al. 2012).

Grazing effects on CO_2 fluxes

The magnitude of the ecosystems responses to herbivory depends on type of ecosystem as well as grazing pressure (Mulder 1999). However, in many studies conducted in the Arctic have reported the same trends as found in this study, with a decrease in NEE with grazing (Cahoon et al. 2012; Elliott and Henry 2011; Sjögersten et al. 2008, 2011; Van der Wal et al. 2007). Over the 3 years we found a 35 % reduction in mean seasonal NEE in clipped plots compared to control plots (Fig. 2). The reduction can most likely be explained by the removal of photosynthetically active biomass and hereby less carbon uptake, as studies have shown a strong relationship between NEE, GEP (gross ecosystem photosynthesis) and the living plant biomass (Sjögersten et al. 2008; Ström and Christensen 2007). Additionally, the large differences in NEE just after the plots have been cut (Fig. 3) supports the hypothesis that reduced biomass leads to reduced CO_2 uptake. In a study from west Greenland, grazing induced a decrease in NEE by 190 %, and a change in the vegetation composition from being graminoid dominated when grazed to becoming shrub dominated when un-grazed (Cahoon et al. 2012). A vegetation alteration between graminoids and shrubs will result in a much larger NEE decrease and therefor their percentile is not fully comparable to our findings. NEE was 113 % lower in our NV plots, which were expected as most of the photosynthetic biomass (all vascular plants) was removed.

Sjögersten et al. (2011) and Van der Wal et al. (2007) found a strong reduction in above-ground biomass, below-ground biomass and C storage following grazing. Their studies were made in areas dominated by geese that are both grazing and grubbing, which may disturb the ecosystem hugely. In some cases it leads to exposed organic layer, which can result in erosion and huge losses of carbon. Speed et al. (2010) estimated that goose grazing and grubbing in some areas of Svalbard could result in a 75 % loss of carbon from vegetation and organic soil pools. The muskoxen graze the vegetation a couple of centimeters above the surface in the mire (Kristensen et al. 2011), which is much less invasive for the vegetation than geese grazing. It is therefore most likely that the below-ground biomass and the carbon stock are less disturbed in areas dominated by large herbivores than by geese. On the other hand a factor that is not considered in this study is the loss of accumulated CO_2 and CH_4 from the mire due to trampling, which may have substantial impact on the vegetation and pattern of gas flux emissions, but not directly on its production.

The much lowered respiration (mean of −62 % for all years, Fig. 2) found in plots with no vascular plants was expected, as the autotrophic respiration should be strongly reduced following removal of both above- and below-ground vascular vegetation. Several studies on arctic ecosystems have found a decrease in respiration with herbivory (Cahoon et al. 2012; Sjögersten et al. 2011; Stark and Grellmann 2002; Van der Wal et al. 2007). A likely explanation to the often observed reduction in R_{eco} may be that graminoids in the arctic are able to reduce their carbon allocation to below-ground structures such as roots when grazed (Chapin 1980). This would most likely lead to lower R_{eco}, as the root density and the below-ground carbon concentration in general are related to respiration from the soil (Chapin and Ruess 2001;

Hanson et al. 2000; Hogberg et al. 2001). In a study by Richards (1984) defoliation resulted in a 50 % reduction in root growth (Richards 1984). Our study could however not confirm these findings since we found no significant differences in R_{eco} between control and clipped plots, although a small but not significant tendency towards a reduction in R_{eco} was observed in 2010 (Fig. 2b). In wet arctic mires CO_2 respiration is to a high degree controlled and reduced by high WtD; this may explain the differences seen in this study in comparison to other studies that are performed in drier habitats.

Grazing effects on methane emissions

Many previous studies have shown a correlation between CH_4 emissions and net ecosystem production (NEP) or GPP (Bubier 1995; Christensen et al. 2000; Joabsson and Christensen 2001; Ström and Christensen 2007; Waddington et al. 1996). The commonly suggested explanation for these relationships is the effect of productivity and photosynthesis on methanogenesis, as a higher carbon uptake would result in more supply of methanogenic substrates to the root zone and subsequently to higher CH_4 emissions (Joabsson et al. 1999). Offering support to these studies we found a strong correlation between ecosystem productivity (NEE/NEP and GPP) and CH_4 emission. One might hypothesis that a lower CH_4 emission could be expected from a grazed ecosystem, since grazing is found to decrease GPP and NEP. Indeed, our study supports this hypothesis as we found that CH_4 emission was 26 % lower in clipped plots compared to control plots (Fig. 1). This contrast the only other study (to our knowledge) that is made on herbivory and CH_4 fluxes in an wet high arctic habitat, that reported no changes in the CH_4 fluxes between grazed and un-grazed plots (Sjögersten et al. 2011). Their study was, based on a 4 years old exclosure experiment in an area with geese and very low CH_4 fluxes (-0.046 to 0.025 mg CH_4 m^{-2} h^{-1}), and CH_4 fluxes were only measured a few times over one growing season. Consequently, responses on CH_4 fluxes may not be expected to the same extent as in our productive mire.

The large differences between plots that were clipped and NV plots, indicates the importance of the presence of vascular plants, which are known to mediate methane transport directly from anoxic peat depth to the atmosphere, thereby decreasing methane oxidation in oxic upper peat layers (Bellisario et al. 1999; Frenzel and Karofeld 2000; Greenup et al. 2000; King et al. 1998; Schimel 1995; Whalen 2005). Whalen (2005) showed that the absence of vascular plants could reduce CH_4 emission by 50–85 %, which is in line with our findings. In particular, *Eriophorum* species are often mentioned as being important for methane emissions (Frenzel and Rudolph 1998; Greenup et al. 2000; Joabsson and Christensen 2001; Schimel 1995; Ström and Christensen 2007; Ström et al. 2005, 2012). Offering some further support to the importance of vascular plant presence and composition to the CH_4 flux, we found a strong tendency towards a higher total number of vascular plant in the control plots. Additionally, the number of *Eriophorum* shoots tended to be lower (Fig. 6) in clipped compared to control plots. See below for further discussions on grazing effects on vegetation composition.

Grazing effects on plant community

In a study by Ström et al. (2012) a strong linkage between density of *Eriophorum* tillers, acetic acid concentration in pore water and a CH_4 emission was demonstrated. As mentioned above, we found a tendency towards a higher number of *Eriophorum* shoots in control plots (Fig. 6). A linkage between high CH_4 fluxes, high acetic acid concentration in the control plots, and a higher number of *Eriophorum* shoots corresponds well to the findings by Ström et al. (2012). The tendency towards a lower number of *Eriophorum* shoots in clipped plots may indicate that this species is more sensitive to higher grazing pressure than others. Additionally we found a strong tendency ($p = 0.07$) towards a higher total number of vascular plant in the control plots (Fig. 6). It might be speculated that the short arctic summer may also be too short for plants to fully recover from the loss of above ground tissue (Elliott and Henry 2011), which makes these ecosystems more sensitive towards grazing than others. The vegetation survey in our study was, however, performed already 1 year after the start of simulated grazing experiment and it is not unlikely that the vegetation composition has continued to change in clipped plots. Further studies are therefore necessary to confirm all the speculations above.

Grazing effects on substrate availability

The pore-water concentration of easily available substrates for methanogens and the magnitude of CH_4 emissions are closely linked (Christensen et al. 2003; Ström and Christensen 2007; Ström et al. 2005, 2012). The dominating organic substrate for methane production in wetlands is acetic acid (Ström and Christensen 2007; Ström et al. 2003, 2005, 2012), which alone have been found to account for 3.9 % of DOC (Ström et al. 2012). Not many studies on how grazing influence substrate availability has been conducted over longer periods of time and at in situ field conditions. A limited number of short time studies have, however, shown an increase in root exudation shortly after the vegetation has been "grazed" (Butenschoen et al. 2008; Hamilton Iii et al. 2008; Paterson et al. 2005). In contrast to these studies we found that after 3 years of increased grazing pressure substrate availability decreased with 27 % (Fig. 4b), thus stressing the importance of long-term studies before any generalization considering ecosystem responses to grazing can be made. Herbivory-induced changes in the growth pattern of sedges and graminoids include increased shoot production, increased leaf length and more leaves per shoot (Beaulieu et al. 1996; Chapin 1980). Graminoids generally preserve a larger reserve of below-ground carbon and nutrients than woody plants, which supports the fast regrowth of shoots after they have been grazed (Bryant et al. 1983; Chapin 1980; Green and Detling 2000; Mulder 1999). In a study by Chapin (1980) a decrease in root growth was found with defoliation of *Eriophorum* and *Carex*. In a high arctic area with high goose grazing pressure, *Dupontia fisheri* and *Eriophorum Scheuchzeri* were able to produce new shoots on the expense of below-ground reserves (Beaulieu et al. 1996). This is consistent with our findings of less available substrate in form of acetic acid in clipped plots. Subsequently, the equally low concentrations of acetic acid in NV plots are not surprising since the main producers of "fuel" for acetic acid production in the root zone are removed. It is important to mention that we in our study cannot discriminate between acetic acid or organic acids in general that are produced by fermentation or by root exudation, as our samples are taken from the peat layer where both processes are active.

Climate warming and grazing

Climate warming is proceeding faster in the Arctic than elsewhere on Earth (ACIA 2005). One of the evidence and predictions for a warmer Arctic is a greening and a transformation in plant composition towards a higher density of shrubs (Hill and Henry 2011; Hudson and Henry 2009; Myers-Smith et al. 2011; Tagesson et al. 2010). Several studies with combined warming and grazing have showed that grazing in the Arctic can have a larger effect on the carbon uptake than higher temperatures. Grazing by vertebrate herbivores may mitigate the increase in biomass production or the change toward more shrubs that predicted and observed with increasing temperatures in the Arctic (Cahoon et al. 2012; Klein et al. 2007; Olofsson et al. 2009; Post and Pedersen 2008; Rinnan et al. 2009; Sjögersten et al. 2008). Though an expansion of shrubs often is found in response to warming there is currently no indications of such a trend in the Zackenberg area (Schmidt et al. 2012), which is likely due to high density of muskoxen in the area (Myers-Smith et al. 2011). This delicate interplay between muskoxen and shrubs (Post and Pedersen 2008) makes muskoxen an important component for the function of this high arctic mire. During the last decade the moss density in the Zackenberg mire has increased and the ecosystem has become drier (Schmidt et al. 2012). Our study plots with no vascular plants had a much higher density of mosses and additionally much lower methane emission compared to control plots.

Conclusion

In our study we found that increased grazing in a high arctic mire plays a significant role for the carbon cycle and the CH_4 emission. We found that net ecosystem uptake decreased immediately after the initiation of the clipping experiment, for the following 3 years the total mean decrease was 35 %. The third year into the clipping experiment significantly lower substrate (acetic acid) availability for CH_4 production was found, the concentration was 27 % lower that year. This reduction indicates that these vascular plants, when exposed to a high grazing pressure, to a higher degree allocate the carbon to above-ground regrowth then to the root system. The second year into the experiment a vegetation analysis showed a strong tendency ($p = 0.07$) that clipped plots had lower number of vascular plants. The lower substrate availability, number of vascular plants and together with a decrease in CO_2 uptake explain the significant reduction we found in CH_4 emission the second year into the experiment, at the clipped plots. The following 2 years the mean decrease in CH_4 emission was 26 %. If the grazing pressure becomes so high that mosses become by far the most dominating vegetation type, we can expect a large decrease of CO_2 uptake and CH_4 emission. In our plots with no vascular plants (NV) we found a reduction in CO_2 uptake and CH_4 emission by 113 and 84 %, respectively. This study shows what an important role herbivores play in the ecosystem and that their influence should not be overlooked, when discussing the carbon balance of the arctic.

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References

ACIA (2005) Arctic climate impact assessment. Cambridge University Press, New York

Arndal M, Illeris L, Michelsen A, Albert K, Tamstorf M, Hansen B (2009) Seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five high arctic vegetation types. Arct Antarct Alp Res 41(2): 164–173. doi:10.1657/1938-4246-41.2.164

Bagchi S, Ritchie ME (2010) Introduced grazers can restrict potential soil carbon sequestration through impacts on plant community composition. Ecol Lett 13(8):959–968. doi:10.1111/j.1461-0248.2010.01486.x

Beaulieu J, Gauthier G, Rochefort L (1996) The growth response of graminoid plants to goose grazing in a high arctic environment. J Ecol 84(6):905–914. doi: 10.2307/2960561

Bellisario LM, Bubier JL, Moore TR, Chanton JP (1999) Controles on CH_4 emissions from a northern peatland. Glob Biogeochem Cycles 13:81–91

Berg TB, Schmidt NM, Høye TT, Aastrup PJ, Hendrichsen DK, Forchhammer MC, Klein DR (2008) High-arctic plant–herbivore interactions under climate influence. Adv Ecol Res 40:275. doi:10.1016/S0065-2504(07)00012-8

Bliss LC (1986) Arctic ecosystems: their structure, function and herbivore carrying capacity. In: Gudmundsson O (ed) Grazing research at northern latitudes, vol 108. NATO ASI Series. Springer, New York, pp 5–25. doi: 10.1007/978-1-4757-5338-7_2

Bryant JP, Chapin FS III, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40(3):357–368. doi: 10.2307/3544308

Bubier JL (1995) The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. J Ecol 3:403. doi:10.2307/2261594

Butenschoen O, Marhan S, Scheu S (2008) Response of soil microorganisms and endogeic earthworms to cutting of grassland plants in a laboratory experiment. Appl Soil Ecol 38(2):152–160. doi:10.1016/j.apsoil.2007.10.004

Cahoon SMP, Sullivan PF, Post E, Welker JM (2012) Large herbivores limit CO_2 uptake and suppress carbon cycle responses to warming in West Greenland. Glob Change Biol 18(2):469–479. doi:10.1111/j.1365-2486.2011.02528.x

Cargill SM, Jefferies RL (1984) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. J Appl Ecol 21(2):669–686. doi:10.2307/2403437

Chapin FS (1980) Nutrient allocation and responses to defoliation in tundra plants. Arct Alp Res 12(4):553–563. doi:10.2307/1550500

Chapin FS, Ruess RW (2001) Carbon cycle: the roots of the matter. Nature 411(6839):749–752. doi:10.1038/35081219

Charlatchka R, Cambier P (2000) Influence of reducing conditions on solubility of trace metals in contaminated soils. Water Air Soil Pollut 118(1–2):143–168. doi: 10.1023/A:1005195920876

Christensen TR, Friborg T, Sommerkorn M, Kaplan J, Illeris L, Soegaard H, Nordstroem C, Jonasson S (2000) Trace gas exchange in a high-arctic valley: 1. Variationsin CO_2 and CH_4 flux between tundra vegetation types. Glob Biogeochem Cycles 14(3):701–713. doi:10.1029/1999gb001134

Christensen TR, Ekberg A, Ström L, Mastepanov M (2003) Factors controlling large scale variations in methane emissions from wetlands. Geophys Res Lett 30(7):61–67. doi:10.1029/2002GL016848

Christiansen HH, Sigsgaard C, Humlum O, Rasch M, Hansen BU (2008) Permafrost and periglacial geomorphology at Zackenberg. Adv Ecol Res 40. doi: 10.1016/S0065-2504(07)00007-4

Cicerone RJ, Oremland RS (1988) Biogeochemical aspects of atmospheric methane. Glob Biogeochem Cycles 2(4):299–327. doi:10.1029/GB002i004p00299

Crill PM, Bartlett KB, Harriss RC, Gorham E, Verry ES, Sebacher DI, Madzar L, Sanner W (1988) Methane flux from Minnesota peatlands. Glob Biogeochem Cycles 2(4):371–384. doi:10.1029/GB002i004p00371

Elberling B, Tamstorf MP, Michelsen A, Arndal MF, Sigsgaard C, Illeris L, Bay C, Hansen BU, Christensen TR, Hansen ES, Jakobsen BH, Beyens L (2008) Soil and plant community-characteristics and dynamics at Zackenberg. Adv Ecol Res 40:223–248

Elliott TL, Henry GHR (2011) Effects of simulated grazing in ungrazed wet sedge tundra in the high Arctic. Arct Antarct Alp Res 2:198. doi:10.2307/41240416

Fischer H, Meyer A, Fischer K, Kuzyakov Y (2007) Carbohydrate and amino acid composition of dissolved organic matter leached from soil. Soil Biol Biochem 39(11):2926–2935

Frenzel P, Karofeld E (2000) CH_4 emission from a hollow-ridge complex in a raised bog: the role of CH_4 production and oxidation. Biogeochemistry 51(1):91–112. doi:10.1023/a:1006351118347

Frenzel P, Rudolph J (1998) Methane emission from a wetland plant: the role of CH_4 oxidation in *Eriophorum*. Plant Soil 202(1):27–32. doi:10.1023/A:1004348929219

Gounou C, Bousserrhine N, Varrault G, Mouchel J-M (2010) Influence of the iron-reducing bacteria on the release of heavy metals in anaerobic river sediment. Water Air Soil Pollut 212(1–4):123–139. doi:10.1007/s11270-010-0327-y

Green RA, Detling JK (2000) Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. Oikos 91(2):280–284. doi:10.1034/j.1600-0706.2000.910208.x

Greenup AL, Bradford MA, McNamara NP, Ineson P, Lee JA (2000) The role of *Eriophorum vaginatum* in CH_4 flux from an ombrotrophic peatland. Plant Soil 227(1–2):265–272. doi:10.1023/A:1026573727311

Hamilton Iii EW, Frank DA, Hinchey PM, Murray TR (2008) Defoliation induces root exudation and triggers positive rhizospheric feedbacks in a temperate grassland. Soil Biol Biochem 40(11):2865–2873. doi:10.1016/j.soilbio.2008.08.007

Hansen BU, Sigsgaard C, Rasmussen L, Cappelen J, Hinkler J, Mernild SH, Petersen D, Tamstorf MP, Rasch M, Hasholt B (2008) Present-day climate at Zackenberg. In: Meltofte H, Christiansen TR, Elberling B, Forchhammer MC, Morten R (eds) Advances in ecological research, vol 40. Academic Press, London, pp 111–149. doi:10.1016/S0065-2504(07)00006-2

Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48(1):115–146. doi:10.1023/a:1006244819642

Hill GB, Henry GHR (2011) Responses of High Arctic wet sedge tundra to climate warming since 1980. Glob Change Biol 17(1):276–287. doi:10.1111/j.1365-2486.2010.02244.x

Hogberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Hogberg MN, Nyberg G, Ottosson-Lofvenius M, Read DJ (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411(6839):789–792. doi:10.1038/35081058

Hudson JMG, Henry GHR (2009) Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology 10:2657. doi:10.2307/25592800

Jefferies RL, Klein DR, Shaver GR (1994) Vertebrate herbivores and northern plant communities: reciprocal influences and responses. Oikos 71(2):193–206. doi:10.2307/3546267

Jensen LM, Rasch M (2011) Zackenberg ecological research operations, 16th Annual Report, 2010. Zero Annual Report, p 117

Joabsson A, Christensen TR (2001) Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. Glob Change Biol 7:919–932

Joabsson A, Christensen TR, Wallen B (1999) Vascular plant controls on methane emissions from northern peatforming wetlands. Trends Ecol Evol 14(10):385–388

Killham K (1994) Soil ecology. Cambridge University Press, Cambridge

King JY, Reeburgh WS, Regli SK (1998) Methane emission and transport by arctic sedges in Alaska: results of a vegetation removal experiment. J Geophys Res 103(D22):29083–29092. doi:10.1029/98JD00052

Klein JA, Harte J, Zhao X-Q (2007) Experimental warming, not grazing, decreases rangeland quality on the Tibetan Plateau. Ecol Appl 2:541. doi:10.2307/40061876

Kristensen DK, Kristensen E, Forchhammer MC, Michelsen A, Schmidt NM (2011) Arctic herbivore diet can be inferred from stable carbon and nitrogen isotopes in C_3 plants, faeces, and wool. Can J Zool 89(10):892–899. doi:10.1139/z11-073

Kuzyakov Y, Domanski G (2000) Carbon input by plants into the soil. Rev J Plant Nutr Soil Sci 163:421–431

Mastepanov M, Sigsgaard C, Dlugokencky EJ, Houweling S, Ström L, Tamstorf MP, Christensen TR (2008) Large tundra methane burst during onset of freezing. Nature 456(7222):628–630

McGuire AD, Anderson LG, Christensen TR, Dallimore S, Guo L, Hayes DJ, Heimann M, Lorenson TD, Macdonald RW, Roulet N (2009) Sensitivity of the carbon cycle in the Arctic to climate change. Ecol Monogr 79(4):523–555. doi:10.1890/08-2025.1

Mikaloff Fletcher SE, Tans PP, Bruhwiler LM, Miller JB, Heimann M (2004) CH_4 sources estimated from atmospheric observations of CH_4 and its 13C/12C isotopic ratios: 2. Inverse modeling of CH_4 fluxes from geographical regions. Glob Biogeochem Cycles 18(4):GB4005. doi:10.1029/2004GB002224

Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol Monogr 63(4):327–366. doi:10.2307/2937150

Mulder CPH (1999) Vertebrate herbivores and plants in the Arctic and subarctic: effects on individuals, populations, communities and ecosystems. Perspect Plant Ecol Evol Syst 2(1):29–55. doi:10.1078/1433-8319-00064

Myers-Smith IH, Hik DS, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Sass-Klaassen U, Tape KD, Macias-Fauria M, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Ménard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environ Res Lett 6(4):045509. doi:10.1088/1748-9326/6/4/045509

Olff H, Ritchie ME, Prins HHT (2002) Global environmental controls of diversity in large herbivores. Nature 415(6874):901–904. doi:10.1038/415901a

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(1):13–24. doi:10.1034/j.1600-0587.2001.240103.x

Olofsson J, Stark S, Oksanen L (2004) Reindeer influence on ecosystem processes in the tundra. Oikos 105(2):386–396. doi:10.1111/j.0030-1299.2004.13048.x

Olofsson J, Oksanen L, Callaghan T, Hulme PE, Oksanen T, Suominen O (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. Glob Change Biol 15(11):2681–2693

Ouellet J-P, Boutin S, Heard DC (1994) Responses to simulated grazing and browsing of vegetation available to caribou in the Arctic. Can J Zool 72(8):1426–1435. doi:10.1139/z94-189

Paterson E, Thornton B, Midwood Andrew J, Sim A (2005) Defoliation alters the relative contributions of recent and non-recent assimilate to root exudation from *Festuca rubra*. Plant Cell Environ 28(12):1525–1533

Ping CL, Michaelson GJ, Jorgenson MT, Kimble JM, Epstein H, Romanovsky VE, Walker DA (2008) High stocks of soil organic carbon in the North American Arctic region. Nature Geosci 1(9):615–619. doi: 10.1038/ngeo284

Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. Proc Natl Acad Sci USA 105(34):12353–12358. doi:10.1073/pnas.0802421105

Post WM, Emanuel WR, Zinke PJ, Stangenberger AG (1982) Soil carbon pools and world life zones. Nature (Lond) 298(5870):156–159

Richards JH (1984) Root growth response to defoliation in two Agropyron bunchgrasses: field observations with an improved root periscope. Oecologia 64(1):21–25. doi:10.1007/BF00377538

Rinnan R, Stark S, Tolvanen A (2009) Responses of vegetation and soil microbial communities to warming and simulated herbivory in a subarctic heath. J Ecol 97(4):788–800. doi:10.1111/j.1365-2745.2009.01506.x

Schimel J (1995) Plant transport and methane production as controls on methane flux from arctic wet meadow tundra. Biogeochemistry 28(3):183–200. doi:10.1007/BF02186458

Schmidt NM, Kristensen DK, Michelsen A, Bay C (2012) High Arctic plant community responses to a decade of ambient warming. Biodiversity 13(3–4):191–199. doi:10.1080/14888386.2012.712093

Sjögersten S, Van der Wal R, Woodin SJ (2008) Habitat type determines herbivory controls over CO_2 fluxes in a warmer arctic. Ecology (Wash DC) 89(8):2103–2116

Sjögersten S, Van der Wal R, Loonen MJE, Woodin SJ (2011) Recovery of ecosystem carbon fluxes and storage from herbivory. Biogeochemistry 106(3):357–370. doi:10.1007/s10533-010-9516-4

Sjögersten S, Yanez-Serrano A, Llurba R, Ribas A, Sebastià MT (2012) Temperature and moisture controls of C fluxes in grazed subalpine grasslands. Arct Antarct Alp Res 44(2):230–246. doi:10.1657/1938-4246-44.2.239

Speed JDM, Woodin SJ, Tommervik H, van der Wal R (2010) Extrapolating herbivore-induced carbon loss across an arctic landscape. Polar Biol 33(6):789–797. doi:10.1007/s00300-009-0756-5

Stark S, Grellmann D (2002) Soil microbial responses to herbivory in an arctic tundra heath at two levels of nutrient availability. Ecology (Wash DC) 83(10):2736–2744

Stark S, Strommer R, Tuomi J (2002) Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. Oikos 97(1):69–78

Ström L, Christensen TR (2007) Below ground carbon turnover and greenhouse gas exchanges in a sub-arctic wetland. Soil Biol Biochem 39(7):1689–1698. doi: 10.1016/j.soilbio.2007.01.019

Ström L, Ekberg A, Mastepanov M, Christensen TR (2003) The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Glob Change Biol 9(8):1185–1192

Ström L, Mastepanov M, Christensen TR (2005) Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. Biogeochemistry (Dordr) 75(1):65–82

Ström L, Tagesson T, Mastepanov M, Christensen TR (2012) Presence of *Eriophorum scheuchzeri* enhances substrate availability and methane emission in an Arctic wetland. Soil Biol Biochem 45:61–70. doi: 10.1016/j.soilbio.2011.09.005

Susiluoto S, Rasilo T, Pumpanen J, Berninger F (2008) Effects of grazing on the vegetation structure and carbon dioxide exchange of a Fennoscandian fell ecosystem. Arct Antarct Alp Res 2:422. doi:10.2307/20181805

Tagesson T, Mastepanov M, Tamstorf MP, Eklundh L, Schubert P, Ekberg A, Sigsgaard C, Christensen TR, Ström L (2010) Satellites reveal an increase in gross primary production in a greenlandic high arctic fen 1992–2008. Biogeosci Discuss 7(1):1101–1129

Tanentzap AJ, Coomes DA (2012) Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? Biol Rev 87(1):72–94. doi:10.1111/j.1469-185X.2011.00185.x

Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, Zimov S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. Glob Biogeochem Cycles 23(2):GB2023. doi:10.1029/2008gb003327

Torn MS, Chapin FS III (1993) Environmental and biotic controls over methane flux from Arctic tundra. Chemosphere 26(1–4):357–368. doi: 10.1016/0045-6535(93)90431-4

Van der Wal R (2006) Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. Oikos 114(1):177–186. doi:10.1111/j.2006.0030-1299.14264.x

Van der Wal R, Bardgett RD, Harrison KA, Stien A (2004) Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. Ecography 2:242. doi:10.2307/3683835

Van der Wal R, Sjögersten S, Woodin SJ, Cooper EJ, Jonsdottir IS, Kuijper D, Fox TAD, Huiskes AD (2007) Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. Glob Change Biol 13(2):539–545

Waddington JM, Roulet NT, Swanson RV (1996) Water table control of CH_4 emission enhancement by vascular plants in boreal peatlands. J Geophys Res 101(D17):22775–22785. doi:10.1029/96JD02014

Welker J, Fahnestock J, Povirk K, Bilbrough C, Piper R (2004) Alpine grassland CO_2 exchange and nitrogen cycling: grazing history effects, medicine bow range, Wyoming, USA. Arct Antarct Alp Res 36(1):11–20

Whalen SC (2005) Biogeochemistry of methane exchange between natural wetlands and the atmosphere. Environ Eng Sci 22(1):73–94

Paper III

^{14}C allocation pattern and carbon balance of a high arctic mire – effect of simulated grazing

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Abstract

Understanding of the carbon (C) allocation pattern is important when discussing the C balance, and it has been found to vary a lot depending on the habitat, despite that is the knowledge about the arctic mires limited. In a pulse labelling experiment with eight monoliths from a high arctic mire, where the allocation pattern and greenhouse gas fluxes studied. 30 days after $^{14}CO_2$ labelling were the ^{14}C amount analyzed in the different biomass fractions and in the pore-water throughout the measuring period. Furthermore were the a more detailed C budget studied, by enclosing two of the labelled monoliths for additionally measuring the emitted $^{14}CO_2$ and $^{14}CH_4$ thorough the 30 days. Herbivory are known to change the C allocation pattern and the greenhouse gas fluxes and because a large number of muskoxen are found in the mire where the monoliths were collected an additional experiment were performed on the grazing effect, where half of the monoliths were clipped to simulate grazing.

30 days after labelling were 62% of the captured ^{14}C in the biomass allocated to above-ground, with the remaining 38% found below-ground where a majority of that were found in the peat and roots. In the closed C study, the C allocation pattern were somewhat different as more than 10% were respired as CO_2 and CH_4. No significant differences were found between control and clipped monoliths, several tendencies pointed however, towards an increase in root exudation following grazing, higher CH_4 emission, higher GPP and more C allocated to above-ground biomass. Further studies on the closed C budget are needed to verify the indication

seen here and to get a better understanding on C allocation patterns in grazed and un-grazed habitats. To better understand the C allocation pattern and how much of the assimilated C that potential could be stored below-ground longer studies are needed.

Introduction

The carbon cycle and greenhouse gas exchange of CO_2 and CH_4 in boreal and arctic wetlands are having an important impact on the global climate (IPCC, 2013). The arctic tundra are at current time estimated to hold half of the global below-ground carbon (C) (Tarnocai et al., 2009) and arctic wetlands store a large portion of that C, as the decomposition rate of the organic matter is slow under anoxic and cold conditions (Tarnocai et al., 2009). Many studies have measured the C balance in different arctic environments, however, to not many with the emphasis to get an understanding of how C is allocated to the different plant fractions and hereby how much of the newly assimilated C that potentially could be stored in arctic soils. Consequently, we need more studies on C allocation and on the closed C-budget. In general annual plants have been found to allocate 30-60% of the net assimilated through photosynthetic to below-ground, whereof 16-76% were lost to root respiration, 4-70% were deposited in the rhizosphere (Marschner, 1995). In a ^{14}C-labelling experiment on material collected at a subarctic wetland Christensen et al., (2003b) found that 69% of the total assimilated C remained in the living biomass after 35 day whereas only 12% was emitted as CO_2 and 0.5% as CH_4 (Christensen et al., 2003b).

The soil C stock is controlled by C input and outputs, where the abiotic factors: climate and hydrology are having a large effect on the C budget. Plant species composition has been recognized to play an important role for C assimilation and emission. Plant species differs in physiology, morphology, and the properties of their living and dead tissue, differences that will affected C and nutrient cycling (Dorrepaal, 2007). The C allocation pattern in addition differs between ecosystems; arctic wetlands have been shown to allocate a larger percentile of C to the above-ground living biomass (Christensen et al., 2003b, Woodin et al., 2009), while a warmer and drier habitat e.g. have been shown to have a higher percentile of the allocated C below-ground (Warembourg and Estelrich, 2000).

The C allocated below-ground are used for building biomass, root respiration and for root exudation of organic compounds to the rhizosphere (Amos and Walters, 2006). The quality and quantity of root exudation is affected by plant species composition, their physiological state, environmental conditions (Curl and Truelove, 1986, Jones, 1998, Rovira, 1969) and by herbivory (Butenschoen et al., 2008, Hamilton et al., 2008, Holland et al., 1996, Paterson et al., 2005). The many controlling factors makes it difficult to predict how much of the allocated C that is used for root exudation, in general root exudation have been found to vary from 4-70% (Marschner, 1995). In a study from 1969, the general root exudation was rarely found to exceed more than 0.4% of the total assimilated C in the plants (Rovira, 1969). A more recent study on C allocation in Maize, have however, shown that the net rhizosphere-deposition of the total assimilated C to the roots on average was 29%, ranging from 5% to 62% (Amos and Walters, 2006). Root exudation is important for the soil microorganism and the plant nutrient availability (Rovira, 1969). The amount of organic acid exuded have also been found to play an important role for the C emission in wet habitats, as a strong correlation between organic acid concentration in pore water and methane fluxes have been found (Christensen et al., 2003a, Joabsson et al., 1999, Ström et al., 2003, Ström et al., 2012).

Herbivory is influencing approximately half of Earths land surface (livestock or native) (Olff et al., 2002) which affects pant productivity, growth and reproduction (Batzli et al., 1980). Soil-plant-herbivore interactions have in several studies been found to have an substantial effect on the C balance in the arctic (Cahoon et al., 2012, Falk et al., 2014a, Falk et al., 2014b, Sjögersten et al., 2008, Sjögersten et al., 2011, Speed et al., 2010, Van der Wal et al., 2007). This effect can be both positive and negative. Grazing is especially known to change the growth and C allocation pattern of sedges and graminoids by increasing shoot production, leaf length and leaves per shoot (Beaulieu et al., 1996, Chapin, 1980) which can lead to an increase in NPP (e.g., Falk et al., 2014a, Olofsson et al., 2004, Van der Wal and Brooker, 2004). Long-term effects of herbivory have resulted in changes in root biomass and morphology and short-term effects changed C allocation patterns and root exudation

(Bardgett et al., 1998). In a grazing simulation study in a high arctic mire, increased grazing pressure resulted in a decrease in root exudation (organic acids) (Falk et al., 2014b), as the number of vascular plants decreased. Several short-term studies have however found an increase in root exudation following defoliation (Butenschoen et al., 2008, Hamilton et al., 2008, Paterson et al., 2005). Two studies from a high arctic mire in NE Greenland have shown that herbivory can have a substantial effect on both CO_2 and CH_4 fluxes. By increasing the grazing pressure $CH_{4,}$ emissions were found to decrease in line with the decreasing organic acid concentration in pore water (Falk et al., 2014b). By excluding the large grazing animals, CH_4 emission was found to decrease as the density of vascular plants decreased (Falk et al., 2014a). These results are pointing towards the delicate interplay between herbivory, plants and the ecosystem.

For better understanding of the C balance and C allocation patterns in an arctic mire, an in-depth laboratory study was performed on monoliths collected from a high arctic mire in NE Greenland. A pulse ^{14}C-labelling approach was used, as it is an good way to study the dynamics of C transfer from CO_2 assimilation to C fixed in biomass, flow of root C to pore-water and finally to CO_2 and CH_4 emission. Additionally, a study of herbivore effect on the C balance and C allocation patterns was conducted as half of the monoliths were clipped to simulate grazing. We hypothesized that: 1) more C would be allocated to above-ground than below as found in other wetland studies and that the C allocation pattern would change with herbivory. 2) We expect to find a positive correlation between root exudation and CH_4 fluxes in a closed C budget study. 3) In the closed C budget we believe to find most C allocated in the active biomass than to CO_2 emission, root exudation and lastly to CH_4 emission. 4) Finally, the Net Ecosystem Exchange (NEE), Gross Primary Production (GPP) and CH_4 fluxes may change with grazing simulation. Since previous results have given ambiguous rests the change may be either a decrease, as seen in Falk et al., 2014b where increased simulated grazing pressure led to a decrease in vegetation density and in gas fluxes. Or alternatively, an increase as seen in Falk et al., 2014a where grazing and trampling were stimulating vegetation growth which subsequently increased gas fluxes.

Materials and methods

Site description

Peat-plant monoliths were collected from a mire in the Zackenberg valley, situated in the National Park of NE Greenland (74°30’N 20°30W). The area is defined as being high arctic, with an annual mean air temperature around -9˚C and a highest mean monthly summer temperature of 5.8˚C. The mean annual precipitation was 260 ml in the period 1996-2005, with only 10% falling as rain during summer (Hansen et al., 2008). The average photosynthetically active radiation (PAR) during the growing season in Zackenberg was 300-490 µmol m^{-2} s^{-1} (Falk et al., 2014b). The vegetation in the mire is dominated by a few vascular plant species, e.g., the grass *Arctagrostis latifolia* and the sedges *Carex sp*, *Dupontia fisheri ssp. psilosantha*, *Eriophorum scheuchzeri* and *Equisetum sp* (Falk et al., 2014a). Underneath this plant cover a dense moss cover is found, dominated by *Tomenthypnun, Scorpidium, Aulacomnium* and *Drepanoclaudus* (Ström et al., 2012). The area has relatively high pH-values around 6.5 and the peat layer depth was measured to be between 18-20 cm, in the area where monoliths were collected (Falk et al., 2014b). The valley is influenced by large herbivores, as the muskox *Ovibos moschatus* are a natural part of the ecosystem and is found at Zackenberg in very high numbers (unpublished results Schmidt). During summer they are mainly feeding in grassland and mires, and approximately 80% of their graminoid-dominated summer forage is obtained in the mire areas (Kristensen et al., 2011).

Monolith collection and experimental set-up

Six monoliths were collected on the 8th of August 2010 and an additional two on the 10th of August 2011. The monoliths were transferred to plastic containers (13 cm diameter, 13 cm high) directly after removal from the peat. The monoliths were brought back to Lund, Sweden, shortly after sampling and placed in a dark cold room (5˚C). On February the 1st in 2012, the eight monoliths were transferred to a climate chamber (E15, Conviron, Canada) where temperature, light and moisture were regulated. To simulate spring the temperature and light level was slowly raised over a one-month period. On the 1st of March, the climate conditions were set to approximately imitate the summer conditions in Zackenberg. From 6 am to 11pm the light level was kept at chamber maximum (PAR = 552±1.4 µmol m^{-2} s^{-1}) and during night at to zero. Temperatures were a little high in comparison to field conditions and kept at 10˚C during night and at 13˚C in daytime. Air moisture was set to 80% throughout the measuring period simulating the naturally moist condition in the wetland ecosystem. The monoliths were additionally sprayed with 4 ml very weak nutrient solution simulating rainwater (<1 mg N l^{-1}) every second day and the water level depth was kept a couple of cm below the moss surface, which corresponds to the water table depth in the beginning of the growing season in the field. Prior to the experiment (in 2011) the six monoliths that were collected in 2010 were kept in the climate chamber (same growing conditions as described above) where half of them were clipped a 2-3 cm above surface, to simulate grazing (Falk et al., 2014b). On the 22 of March 2012, the vascular plant "spring" growth had leveled out and at that time the monoliths that were clipped in 2011 and one of the monoliths sampled in 2012 were again clipped 2-3 cm above the peat surface.

^{14}C experiment

Pulse labelling of monoliths

To study the plant allocation patterns to the different biomass fractions, pore-water, CO_2 respiration and CH_4 flux, the monoliths were pulse labelled with $^{14}CO_2$ on the 14 and 15 of March. ^{14}C has a long life half time and low toxicity (Warembourg and Paul, 1973), which makes ^{14}C suitable for determining the allocation and respiration patterns. Each monolith was labelled with 46 MBq of $^{14}CO_2$ over a period of 90 minutes. The $^{14}CO_2$ was created by adding 10% H_2SO_4 to sodium bicarbonate ($NaH^{14}CO_3$, Specific Activity: 40-60mCi (1.48-2.22GBq)/mmol, Perkin Elmer) resulting in a release of $^{14}CO_2$ according to the formula “$NaH^{14}CO_3 + H_2SO_4 \rightarrow Na_2SO_4 + {}^{14}CO_2 + H_2O$“. To determine the efficiency of the $^{14}CO_2$ uptake during labelling airsamples were taken repeatedly, shaken with NaOH and subsequently counted for radioactivity by the standard scintillation technique. Hionic-Flour™ (CIAB) was used as scintillation cocktail and counting was done on a Packard Tri-Carb 21000TR liquid scintillation analyser (USA).

Respired $^{14}CO_2$ and $^{14}CH_4$

Two of the labelled monoliths were kept in hermetically sealed Plexiglas chambers to measure the continuously emitted $^{14}CO_2$ and $^{14}CH_4$ over the following 30 days. A schematic illustration showing the experimental set-up can be seen in Figure 1. Ambient air was pumped through the chamber by a rate of 1 L min^{-1}. Approximately 10% of this air was passed through a sequence of four gas traps two $^{14}CO_2$ traps; containing 80 ml of NaOH solution (0.1M), a furnace (850° C) to oxidize $^{14}CH_4$ to $^{14}CO_2$, which subsequently was trapped in the last two traps (so called $^{14}CH_4$ traps). The first $^{14}CO_2$ and $^{14}CH_4$ traps were changed 23 times over the 30 days, the second $^{14}CO_2$ and $^{14}CH_4$ traps were only changed three times shortly after labeling and once in the end of the experiment, as the first $^{14}CO_2$ cylinders captured 99.6% of the $^{14}CO_2$. One ml of the NaOH solution from the cylinders was counted for radioactivity by the standard scintillation technique. The flow rate and time interval between each time the traps were changed was used to calculate the emission rate of $^{14}CO_2$ and $^{14}CH_4$. When traps were changed the sealed chamber was temporarily removed to enable measurements of CO_2 and CH_4 fluxes and for pore-water sampling. During the 30 days following labelling, 18 flux measurements were performed (see flux measurement in materials and method) and 14 pore-water samples were taken.

^{14}C in pore-water

Pore-water was sampled shortly after most of the gas flux measurement (n=14), for analysis of ^{14}C in pore-water. Eight ml of pore-water were drawn from stainless steel tubes (3 mm in diameter), which were permanently installed in the middle of the monoliths. Five cm above the moss surface each tube was closed by a three-way valve that enabled sampling without air penetration into the soil. Pore-water sample was drawn using a syringe and immediately filtered through a sterile pre-rinsed filter (Acrodisc PF 0.8/0.2 µm diameter 32 mm) and counted for radioactivity by the standard scintillation technique. The ^{14}C in pore-water are interpreted as being the organic carbon compounds, originated from the roots, i.e, root exudation.

^{14}C in biomass

At the end of the experiment the monoliths were harvested and sorted into vascular plant species (*Dupontia fisheri ssp. psilosantha*, *Eriophorum scheuchzeri* and *Equisetum sp)*, mosses (fresh and old), stems, roots, litter and peat, without large roots that could be visualy sorted from the peat. Only ¼ of the peat were sorted for roots and analysied. The different fractions were weighed, dried at 60˚C for 48 h and re-weighed to obtain the dry weight of biomass. The dried biomass fractions from each monolith was grained and five replicates (approxmiatly 0.1 gram) were taken and oxidized in a Packard sample oxidiser and the released CO_2 trapped in Carbo-Sorb scinttilation cocktail. Since the radioactivy of the 0.1 gram biomass was to high for the scintillator counter a second dilution step was required, 1 ml of the trapped sample was mixed with 5 ml Permaflour and 2 ml Carbo-Sorb, whereafter the biomass samples was counted for radioactivity by the standard scintillation technique.

Flux measurements

The carbon exchange between monoliths and atmosphere were measured using a closed chamber technique (Livingston and Hutchinson, 1995). Measurements were performed with a transparent Plexiglas chamber (9 L), equipped with a small fan to mix the air and a rubber list, to ensure an airtight seal against the monoliths. For each measurement, a light and a dark measurement was made to establish NEE and the ecosystem respiration (R_{eco}), respectively. For dark measurements, a non-transparent hood was covering the chamber. Measurement lasted between 2 to 4 minutes depending on flux magnitude.

Gas concentrations of CO_2 and CH_4 were simultaneously recorded every second by a portable Fourier Transform Infrared (FTIR) spectrometer (Gasmet Dx 40-30, Gasmet Technologies Oy). The air from the chamber was pumped at a rate of 3.4 L min^{-1} to the analytical box before it was non-destructively returned to the chamber. The FTIR was calibrated with a zero gas before and after the experiment; no baseline drift was found in data. Stable cell temperature of the FTIR between 20 and 32˚C are required for high quality measurements, this could be retained by the internal heating system.

Data treatment

Gas fluxes

CO_2 and CH_4 fluxes were calculated from changes in gas concentration in the chamber as a function of time using linear fitting (Crill et al., 1988), and were calculated with the 10°C, that were kept inside the climate box. Release of gas from the ecosystem to the atmosphere is denoted by positive values and uptake by negative. Gas fluxes are expressed as mg m^{-2} h^{-1} of CH_4 or CO_2. Due to a strong significant correlation ($R=0.971$, $p=0.000$) between light and dark CH_4 fluxes for individual plots, the mean of these two measurements were calculated and used in the CH_4 flux analysis. GPP was calculated as the difference between NEE and R_{eco}. To determine statistically significant differences in fluxes between control and clipped monoliths, a general linear model repeated-measures analysis was performed (confidence interval adjustment were LSD), as data were normally distributed. The analysis was preformed on the measuring period before half of the monoliths were clipped ($n=12$) and after ($n=9$). The temporal development within the two measuring periods were taken into account as the dates were random factors. Repeated-measures require gap-filling if any data were missing. Gap-filling was performed by computing a mean of the two measurements taken, on that particular plot, before and after the missing data point. Gap-filling was required in control monoliths before they were clipped (2%) and after they were clipped both control and clipped monoliths needed gap-filing (1%).

^{14}C in pore-water

^{14}C in the pore-water was normally distributed, and to determine a potential significant differences between control and clipped monoliths, a general linear model repeated-measures analysis was performed (confidence interval adjustment were LSD). The model input were the measuring period before half of the monoliths were clipped (16-22 April) (n=5), after the cut (26 March-4 April) (n=5) and the end period (8-16 April) (n=4). The temporal development within the three measuring periods was taken into account, as dates were random factors. No gap-filling were required as all data existed.

^{14}C in biomass

The ^{14}C recaptured in the different biomass samples were all normally distributed except for *Equisetum sp* as it was only present in one monolith. To test the differences in the total amount of ^{14}C allocated to the different fraction in control (n=4) and clipped (n=4) monoliths an independent t-test were performed, where homogeneity of variance were assumed. Because only ¼ of the peat were analyzed, the root and peat results were multiplied with four to get an estimate of the total ^{14}C and weight in those fractions. Denote that the fraction peat without sorted roots will throughout the paper be mentioned as peat.

Total ^{14}C allocation - closed budget

The C allocation budget following the ^{14}C labelling was estimated. The total emitted $^{14}CO_2$ and $^{14}CH_4$ for the 30 days were calculated as the sum of the trapped $^{14}CO_2$ and $^{14}CH_4$ for each measuring period and including the time when the chambers were temporarily removed. Unfortunately, a leakage was found in one of the two enclosed monoliths after two days and the results from those days had to be removed. The ^{14}C in the biomass fractions were multiplied with the exact amount of dried biomass. The ^{14}C in the pore-water should be seen more as an estimate, as the exact water volume in the monoliths are unknown, the monoliths were however estimated to hold approximately 500 ml water. For the budget, the last pore-water sample collected was used in the two monoliths.

Dry weight biomass

The dry weight of the different biomass fractions were all normally distributed except for *Equisetum sp* as it was only present in one monolith. To test the differences in dry weight between control and clipped monoliths an independent t-test were performed, where homogeneity of variance were assumed.

Results

^{14}C-labelling

Within 92 minutes, after the ^{14}C-labelling, the vegetation within the monoliths had assimilated 99% of the injected ^{14}C, and more than 90% of this were taken up within the first two minutes (Fig. 2).

The recaptured ^{14}C in the monoliths 30 days after labelling had on average allocated 53% of the ^{14}C to the above-ground active biomass (vascular plants, fresh mosses and the cut biomass from clipped monoliths), whereas 38% was found below-ground (roots, stems and peat) and 9% in the inactive biomass (old mosses and litter) (Table 1). Figure 3 is showing the mean ^{14}C that was allocated to the different biomass fractions for control and clipped monoliths. The variation between the monoliths irrespective of treatment was large and no significant differences for any of the biomass fractions or litter $p>0.300$ were found. However, looking at the sum of vascular plants and the cut biomass a trend of increased ^{14}C were found in clipped monoliths compared to control monoliths ($p=0.114$). In addition, peat in the clipped monoliths tended to contain more ^{14}C compared to controls ($p=0.077$).

The mean maximum ^{14}C content in the pore-water was measured 5-7 days after labelling (Fig.4). No significant differences were found between control and clipped monoliths during any of the sampling periods, before or after clipping ($p\geq0.498$). We additionally performed a single pilot study where we collected the ^{14}C-acetic and ^{14}C-lactic acid fraction in the pore-water by separating organic acids using high pressure liquid chromatography (see method description in Ström et al. 2012) and collecting a sample from the column outlet during the minutes when these two acids were known to emerge from the column. The pilot study showed that the radioactivity in these lactic and acetic acid accounted for 23 and 37% (n=2) of the total ^{14}C in pore water (Ström and Jackowicz-Korczynski unpublished results).

In an attempt to quantify how the labelled ^{14}C had been allocated after 30 days a budget of total emitted $^{14}CO_2$, $^{14}CH_4$, ^{14}C in biomass and an estimate of ^{14}C in pore-water was made for the two monoliths that had been enclosed (Table 2). Out of the 46 MBq injected ^{14}C around 70% were recaptured after 30 days, where the majority was found in above-ground green leaves and mosses. The second largest fraction of ^{14}C was found below-ground in roots, while peat contained almost the same percent (Table 2). The emitted $^{14}CO_{2,}$ from two days after labelling and the following 28 days were 11.3 and 10.5% of the total amount of recaptured ^{14}C, for control and clipped monoliths, respectably. The monolith that had been completely enclosed (no leakage) throughout the experiment emitted 2.8 MBq as $^{14}CO_2$ during the first two days, corresponding to 44% of the total emitted $^{14}CO_2$ increasing the recovery of the 46MBq to 75%. The respired $^{14}CO_2$ was emitted exponentially, with a rapid decline shortly after labelling. The percent emitted as $^{14}CH_4$ was low, 0.4% and 0.6% for control and clipped, respectively. The maximum $^{14}CH_4$ emission was found 10-15 days after ^{14}C labelling. For the two fully enclosed monoliths where we can attempt a full ^{14}C budget the clipped monolith had a higher percent ^{14}C allocated to above-ground and more ^{14}C were found in the peat, while the allocation to roots was lower than in the un-clipped monolith (Table 2), note the lack of replication.

Dry weight

The dry weights of both fresh and old mosses are the most dominating biomass fractions in the monoliths, while roots are accounting for the smallest part of the dry weight (Fig.5). The dominating vascular plants *Dupontia* and *Eriophorum* had approximately the same dry weight. There is no significant difference between the dry weight of control and clipped monoliths for any of the biomass fractions ($p \geq 0.254$). The sum of all vascular plants (including cut biomass) was however significantly higher (43%) in clipped monoliths compared to control monoliths ($p=0.033$).

Fluxes

CO₂

All monoliths acted as a C sinks over the measuring period and the mean CO_2 fluxes were before clipping slightly higher than after (Fig. 6). There were no significant differences in NEE between control and clipped monoliths in the period before ($p=0.154$) or after ($p=0.472$) the monoliths were clipped (Fig. 6a). R_{eco} were significantly higher in the clipped monoliths ($p=0.019$) compared to control before they were clipped, while no differences were found after clipping ($p=0.160$) (Fig.

6b). The differences in GPP between control and clipped monoliths showed a tendency of being higher in clipped monolith both before ($p=0.081$) and after ($p=0.094$) they were clipped (Fig. 6c) than in control monoliths.

CH_4

The mean CH_4 fluxes were slightly higher after clipping. There were no significant differences in CH_4 fluxes between control and clipped monolith, either before ($p=0.191$) or after ($p=0.574$) they were clipped (Fig.7).

Flux, biomass and C-allocation controls

In order to identify the controls of fluxes in all of the monoliths a correlation analysis was performed including the dry-biomass and C-allocation results (Table 3). The correlation analysis between fluxes shows a significant correlation between CH_4 emission and GPP ($R=-0.824$, $p=0.044$) and as GPP were calculated from NEE and R_{eco} a strong correlation between GPP and R_{eco} were found ($R=-0.955$, $p=0.003$). The dry weight of the biomass fractions; vascular plant, roots and stems, active biomass (vascular plant, roots and stems) and biomass (active biomass, litter and mosses) were all significantly correlated ($p\leq0.046$) (Table 3). The correlation analysis between ^{14}C-fractions shows a significant correlation between ^{14}C in roots/stems and in active biomass ($R=0.959$, $p=0.002$) and to biomass ($R=0.892$, $p=0.017$). The correlation between active biomass and total biomass was also significant ($R=0.916$, $p=0.010$). A tendency of a correlation between ^{14}C-allocated to vascular plants and to the pore-water was furthermore found (R=0.699, p=0.122). When looking at the controlling factors across fluxes, dry weight and allocated ^{14}C no significant correlations were found. However, tendencies of significant correlations were observed between CH_4 flux and several ^{14}C biomass fractions, e.g., CH_4 to roots/stems (R=0.789, p=0.062), CH_4 to active biomass (R=0.803, p=0.054) and CH_4 to biomass (R=0.680, p=0.138). Furthermore, R_{eco} and ^{14}C in total biomass had a tendency of being correlated (R=0.699, p=0.122).

Discussion

^{14}C biomass distribution

Most trace isotope gas experiments studies on C allocation have been made on cereals; wheat and barley, which in general show that approximately 30% of the total assimilated C is transported to below-ground (Kuzyakov and Domanski, 2000, Warembourg and Paul, 1973). A difference between annual cereals and perennial plants could be expected as perennials have a well develop root system, which stores C between years and has less need for yearly regrowth. However, a larger demand for C below-ground could be expected in our experiment, as cereals often are fertilized, leading to less release of organic substrates for nutrient tradeoff (Kuzyakov and Domanski, 2000). In this study we found a much higher percentile of ^{14}C in above-ground biomass with approximately 62% in this fraction. In accordance with our results, Christensen et al. (2003b) found that 68% of ^{14}C

assimilated into monoliths collected at a subarctic mire had been allocated to living biomass above-ground and 31% to below-ground. Still with good agreement we found that 38% of ^{14}C was allocated below-ground with the highest percentile of the total below-ground fraction found in peat followed by roots and finally in stems (Table 1). We assume that the high percent found in the peat fractions was ^{14}C allocated to fine and hair roots (impossible to visually sort from the peat), assimilated by microorganism or in pore-water remaining in the peat since a full drainage is impossible. In contrast to our findings two labelling experiments, with perennial grass from an artic meadow, found that a higher percentile of the assimilated C were allocated below-ground compared to above-ground (Warembourg and Estelrich, 2000, Woodin et al., 2009).

Most ^{14}C (35%) of the total ^{14}C assimilated in the monoliths was allocated to fresh mosses while all the vascular plants only counted for approximately 18% (Table 1). Woodin et al (2009) found that samples only containing mosses retain 70% of assimilated C, while samples with vascular plants only retained 40% a month after ^{13}C labelling in a an arctic wet meadow (Woodin et al., 2009). The large percentile allocated and retained C in mosses may partly be explain by their rapid C uptake and their slow nutrient release as decomposition of mosses is very slow (Oechel and Van Cleve, 1986). There were no differences in how much ^{14}C that was allocated to mosses in control and clipped monoliths (Fig. 3). The result may however be different in a natural habitat influenced by herbivores, as mosses in general are very sensitive towards trampling (Liddle, 1997). The moss cover tends to be much thinner in areas influenced by herbivory (Falk et al., 2014a, Olofsson et al., 2001, Van der Wal and Brooker, 2004, Van der Wal et al., 2001). Subsequently, in habitats with herbivores, this may lead to a reduction of assimilated C in the moss layer.

The mean ^{14}C found in the pore-water, show that the maximum translocation time from $^{14}CO_2$ to pore-water were approximately 5-7 days (Fig.4). In an experiment on wheat the translocation time to the root zone was found to be between 1-5 days depending on the root depth, with the highest rate of translocation in the upper 10-25 cm root (within 24 hours) (Warembourg and Paul, 1973). In the correlation analysis, we found a tendency of ^{14}C in the vascular plants being correlated to the ^{14}C found in pore-water (Table 3), which may indicate that the density of vascular plants plays a role for root exudation.

No significant differences in allocated ^{14}C or dry weight in any of the biomass fractions were found between clipped and control monoliths (Fig. 3&5). A trend of the total active above-ground biomass, which include the “cut biomass”, having higher ^{14}C in clipped monoliths were however, found. This corresponds to that more assimilated C is needed above-ground for regrowth after grazing (Chapin, 1980, Detling et al., 1979, Paterson et al., 2005). In the end of the experiment, the peat fraction in clipped monoliths had a tendency ($p=0.077$) of having more ^{14}C, which could indicate that root exudation increases with grazing, which has been found in several short time studies (Butenschoen et al., 2008, Hamilton et al., 2008, Holland et al., 1996, Paterson et al., 2005). Looking at the mean ^{14}C in pore-water (Fig. 4), no significant differences between control and clipped monoliths can however verify this. It might be speculated that the increase in standard error in clipped monoliths after clipping may indicate an increase in root exudation as the increase in SE is due to a number of high values which continued to be high approximately 10 days after clipping, where after SE stabilized. Paterson et al., (2005) showed that the increased root exudation after defoliation was time limited, but in their experiment, it only lasted for two days, the same period as they had reduced net CO_2 assimilation (Paterson et al., 2005). The increase in root exudation following defoliation is explained by an increase in C flow to the roots and increasing root respiration which will provide the energy needed for the higher nutrient uptake required to stimulate regrowth following grazing (Holland et al., 1996, Paterson, 2003). The increased root exudation following defoliation has been shown to originate from C assimilated prior to the defoliation (Paterson et al., 2005). In our study, no change in ^{14}C allocated to the roots were observed between controls and clipped monoliths. An increase in ^{14}C in the clipped monolith roots might however not be expected as, the ^{14}C allocated to the root were measured three weeks after clipping. Studies with more replicates are needed to verify the indications seen with increased ^{14}C in pore-water after clipping in high arctic peat monoliths, and to better understand the effect grazing has on root exudation.

Gas fluxes

The gas fluxes (NEE, GPP and CH_4) in our laboratory experiment were much higher (twice as large) compared to fluxes measured *in-situ* in the Zackenberg mire (Falk et al., 2014a, 2014b). An explanation could be the higher average air temperatures in the climate chamber (mean 11.5˚C) compared to the summer month's temperatures in Zackenberg (mean warmest month 5.8˚C (Hansen et al., 2008)). The average light level in the climate chamber was comparable to the average PAR found in the growing season in Zackenberg and cannot explain the differences. The monoliths are both before and after clipping acting as a C sink as more C is taken up than emitted. The respiration of CO_2 is in contrast to NEE and GPP within the same magnitude as what was found in the field (Falk et al., 2014a, 2014b). In our previous *in-situ* study from the Zackenberg mire, removal of vascular plants resulted in a 62% decrease in CO_2 respiration (Falk et al., 2014b). This could indicate that the small amount of C allocated to the vascular plants (18% (Table 1)) is accounting for a large percent of the emitted CO_2. Most of the emitted $^{14}CO_2$ is respired shortly after labelling (see results ^{14}C labelling) which indicates a short C turnover time. The turnover time below-ground seems much longer as ^{14}C released to pore-water were highest 5-7 days after labelling (Fig.4) long after the $^{14}CO_2$ emission rate had decreased substantially.

In accordance with many we found a significant correlation between CH_4 fluxes and GPP (e.g., Bubier, 1995, Falk et al., 2014b, Joabsson and Christensen, 2001, Ström and Christensen, 2007). The relationships is partly explained by the effect of productivity and photosynthesis on methanogenesis, as a higher C uptake results in more supply of methanogenic substrates to the root zone and subsequently to higher CH_4 emissions (Joabsson et al., 1999). In line with the close relationship between organic acids and CH_4 emission that has been found in many previous studies (Christensen et al., 2003a, Joabsson et al., 1999, Ström et al., 2003,2012) we found a strong tendency of a correlation between CH_4 flux and the amount of ^{14}C allocated to roots/stems, active biomass and biomass (Table 3). Acetic acid has been found to be an organic acid of particular interest in respect to methane production in the soils (e.g., Ström et al., 2003, 2005), which in our pilot study accounts for a high percentage of the total ^{14}C in pore-water. The results indicate that an increase in CO_2 assimilation leads to higher C allocation to active biomass and hereby to stems, roots and root exudation thereby, increasing the substrate availability (acetic acid) for CH_4 production and subsequently emission. This reasoning is further strengthened by the tendency of ^{14}C found in vascular plant being correlated to ^{14}C found in pore-water.

The tendency of higher GPP in clipped monoliths in our experiment (Fig.5) is in line with our previous *in-situ* field study (Falk et al., 2014a), where areas exposed to grazing had significantly higher NEE, GPP and CH_4 fluxes compared to areas inside three years old exclosures (Falk et al., 2014a). The differences before the monoliths were cut (Fig.5) in 2012 may be due to that we see an effect of the clipping from 2011. The tendency towards lower differences after clipping, were expected, as removal of biomass will create a strong reduction in the photosynthesis and thereby in GPP. The higher CO_2 uptake and CH_4 emission was mainly explained by a decrease in density of vascular tillers inside exclosures due to increased moss layer (Falk et al., 2014a). Unfortunately, no thorough vegetation density analysis was performed after harvesting, as the dry weight only is a rough estimate of the number of tillers. In general release of root exudates increases the microbial activity in the rhizosphere causing an increase in the microbial respiration, subsequently increasing CO_2 emission (Cheng et al., 1996). Root exudates have been shown to contribute with 17-24% of total respired CO_2 from northern peatland (Crow and Wieder, 2005). The increase in R_{eco} in clipped monoliths in our experiment may partly be explained by the indications of increased root exudation (see section "^{14}C biomass distribution" and "Closed ^{14}C budget").

A close relationship between organic acids and CH_4 emission have been found in previous studies (e.g., Christensen et al., 2003a, Joabsson et al., 1999, Ström et al., 2003). There was a slight indication of higher CH_4 fluxes from clipped monoliths, this was however not significant (Fig.6). A higher flux could have been expected if there were an increase in root exudation, as a clear connection between grazing and methane has been found in two previous in-situ field studies from the same mire (Falk et al., 2014a, 2014b). One might also hypotheses that an increase in CH_4 emission could be expected from clipped monoliths since they seems to have slight increase in GPP and root exudation, which would be in line with the findings by Falk et al., 2014a.

Closed ^{14}C budget - enclosed monoliths

In the closed ^{14}C budget, 70% of the injected ^{14}C was captured 30 days after labeling. The low recovery may partly be explained by that the total emitted $^{14}CO_2$ and $^{14}CH_4$ were much higher than listed in Table 1 as the first two days had to be removed due to leakage in one of the monoliths. These first two days accounted for 44% of total emitted $^{14}CO_{2,}$ increasing the total recovery to 75%. Another factor of uncertainty in the closed budget relates to how much ^{14}C that was excuded in the pore-water as the total water volume in the monoliths was only roughly estimated. In addition it should be noted that the closed ^{14}C budget could only be calculated form the two enclosed monoliths, consequently there are no replicates to verify our results and they should strictly be seen as indications.

The photosynthetic activity is often tightly coupled to the rhizospheric respiration. Kuzyakov and Cheng (2001) found that photosynthetically assimilated C were transported to the roots and metabolized by root and rhizosphere microorganism within a few hours, corresponding to the high percent of $^{14}CO_2$ within the first two days. The maximum release of ^{14}C in pore-water in our experiment was found 7 days after labeling, pointing towards that much of $^{14}CO_2$ emitted within the first days results from above-ground biomass or plant respiration. The rapid decline in respired $^{14}CO_2$ can be explained by the dilution of ^{14}C in the aerobic plant and microbial respiration (Christensen et al., 2003b). In accordance with Christensen et al (2003b) we found a time difference between maximum release of labelled $^{14}CO_2$ and $^{14}CH_4$ of 10-15 days. This points towards a slow pathway from C assimilation through photosynthesis via root exudation, fermentation and ultimately production of methanogenic substrate. It also indicates a between 3 to 8 day timelag between release to the root zone and CH_4 emission.

The allocation patterns found in several studies on cereals were review by Kuzyakov and Domanski (2000) and pointed to that roughly about half of the C allocated below-ground was found in the root, while one third was through roots exudation and fine roots respired as CO_2 within a few days. The remaining C was found “stored” in the soil and microorganism. In our closed C budget experiment, approximately 57% of the recaptured ^{14}C were allocated above-ground (Table 2), while the remaining 43% were allocated to below-ground and emitted as CO_2 and CH_4. When including the emitted $^{14}CO_2$ from the two first days after labelling (n=1, the monolith that was properly enclosed), we see that ^{14}C emitted as $^{14}CO_2/CH_4$ and found in roots and stems both counted for approximately 20% of the recaptured ^{14}C, increasing the below-ground fraction to 49%. The higher percent found in the peat fraction compared to the experiments done on cereals, may be explained by a higher demand for root exudation as the nutrient availability is low. Supporting a somewhat different allocation pattern between sub-arctic and arctic wetland plants and cereals Christensen et al. (2003b) showed that of the ^{14}C allocated below ground 32% was recovered in CO_2 and CH_4 emission, 23% in the roots, 23% in dead below ground biomass and 21% in the peat, in a subarctic wetland closed budget study.

We see no indication of any clear effects of clipping on total respired $^{14}CO_2$, as the difference between control (3.5 MBq) and clipped (3.6 MBq) monolith were very small compared to the total emitted $^{14}CO_2$ (3%). The differences between control (0.2 MBq) and clipped (0.3 MBq) monoliths are in contrast noticeable (50%) as the total emitted $^{14}CH_4$ was very small. The lack of replication in this full budget part of the study does however render any real conclusions as to the existence of a “true” difference impossible. It might be speculated that the higher percent emitted as $^{14}CH_4$ in the clipped monolith correspond to higher GPP (Fig.6), increased ^{14}C in pore-water and peat (Table 2) and the relationship described in the “Gas fluxes” section. The enclosed clipped monolith also had more C allocated to above-ground green leaves and mosses than the control monolith (Table 2), which supports the trends seen in all monoliths and the demand for C for regrowth following grazing (see ^{14}C biomass distribution section). Additionally, less ^{14}C were allocated to the root and stem faction in the clipped enclosed monolith compared to the control, 11.7% and 20.7%, respectively. A reduction in root biomass (Bardgett et al., 1998, Chapin, 1980) and below ground reserves (Beaulieu et al., 1996, Detling et al., 1979) following defoliation have been found by other studies and is explained by a rapid regrowth of above-ground biomass after grazing. Despite the decrease in C allocation to the roots we found a slight increase in C allocation to pore-water and peat (Table 2 and Fig. 4). Fig. 4 also shows that the variation (SE) increases after clipping. These increases possibly indicate that defoliation also leads to disturbances in the root zone and an increased leakage of C from the roots following defoliation. This might also offer an alternative explanation for the increased R_{eco} in clipped monoliths.

In conclusion, our results all point towards a positive correlation between GPP, substrate availability and CH_4 fluxes. The results further showed that approximately half of the captured $^{14}CO_2$ was translocated to below-ground structures irrespective of treatment. It is difficult to say how much of the assimilated C that potentially could be stored below-ground, as our experiment is a short-time study and any conclusions in this respect would require a full year budget. Despite the lack of replication our results indicate that the C-allocation pattern changed after simulated grazing. The results point towards the importance of considering herbivore influences when C balance and C storage below-ground is discussed. Further studies are however needed to verify this and to enable a full understanding of the exact mechanism following grazing.

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References

AMOS, B. & WALTERS, D. 2006. Maize root biomass and net rhizodeposited carbon. *Soil Science Society of America Journal,* 70**,** 1489-1503.

BARDGETT, R. D., WARDLE, D. A. & YEATES, G. W. 1998. Linking above-ground and below-ground interactions: How plant responses to foliar herbivory influence soil organisms. *Soil Biology & Biochemistry,* 30**,** 1867-1878.

BATZLI, G., WHITE, R., MACLEAN, S., PITELKA, F. & COLLIER, B. 1980. The herbivore-based trophic system. *An arctic ecosystem: The coastal tundra at Barrow, Alaska***,** 335-410.

BEAULIEU, J., GAUTHIER, G. & ROCHEFORT, L. 1996. The Growth Response of Graminoid Plants to Goose Grazing in a High Arctic Environment. *Journal of Ecology,* 84**,** 905-914.

BUBIER, J. L. 1995. The Relationship of Vegetation to Methane Emission and Hydrochemical Gradients in Northern Peatlands. *Journal of Ecology***,** 403.

BUTENSCHOEN, O., MARHAN, S. & SCHEU, S. 2008. Response of soil microorganisms and endogeic earthworms to cutting of grassland plants in a laboratory experiment. *Applied Soil Ecology,* 38**,** 152-160.

CAHOON, S. M. P., SULLIVAN, P. F., POST, E. & WELKER, J. M. 2012. Large herbivores limit CO2 uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology,* 18**,** 469-479.

CHAPIN, F. S. 1980. Nutrient Allocation and Responses to Defoliation in Tundra Plants. *Arctic and Alpine Research,* 12**,** 553-563.

CHENG, W., ZHANG, Q., COLEMAN, D. C., RONALD CARROLL, C. & HOFFMAN, C. A. 1996. Is available carbon limiting microbial respiration in the rhizosphere? *Soil Biology and Biochemistry,* 28**,** 1283-1288.

CHRISTENSEN, T. R., EKBERG, A., STRÖM, L. & MASTEPANOV, M. 2003a. Factors controlling large scale variations in methane emissions from wetlands. *Geophysical Research Letters,* 30**,** 67-1 - 67-4.

CHRISTENSEN, T. R., PANIKOV, N., MASTEPANOV, M., JOABSSON, A., STEWART, A., ÖQUIST, M., SOMMERKORN, M., REYNAUD, S. & SVENSSON, B. 2003b. Biotic controls on CO2 and CH4 exchange in wetlands – a closed environment study. *Biogeochemistry,* 64**,** 337-354.

CRILL, P. M., BARTLETT, K. B., HARRISS, R. C., GORHAM, E., VERRY, E. S., SEBACHER, D. I., MADZAR, L. & SANNER, W. 1988. Methane flux from Minnesota Peatlands. *Global Biogeochemical Cycles,* 2**,** 371-384.

CROW, S. E. & WIEDER, R. K. 2005. Sources of CO2 emission from a northern peatland: Root respiration, exudation, and decomposition. *Ecology,* 86**,** 1825-1834.

CURL, E. A. & TRUELOVE, B. 1986. *The rhizosphere,* Springer-Verlag.

DETLING, J. K., DYER, M. I. & WINN, D. T. 1979. Net photosynthesis, root respiration, and regrowth of Bouteloua gracilis following simulated grazing. *Oecologia,* 41**,** 127-134.

DORREPAAL, E. 2007. Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? *Journal of Ecology,* 95**,** 1167-1180.

FALK, J. M., SCHMIDT, N. M., CHRISTENSEN TORBEN, R. & STRÖM, L. 2014a. Large herbivore grazing alters vegetation structure and greenhouse gas balance in a high arctic mire. *Manuscript submitted for publication*.

FALK, J. M., SCHMIDT, N. M. & STRÖM, L. 2014b. Effects of simulated increased grazing on carbon allocation patterns in a high arctic mire. *Biogeochemistry,* 119**,** 229-244.

HAMILTON, E. W., FRANK, D. A., HINCHEY, P. M. & MURRAY, T. R. 2008. Defoliation induces root exudation and triggers positive rhizospheric feedbacks in a temperate grassland. *Soil Biology and Biochemistry,* 40**,** 2865-2873.

HANSEN, B. U., SIGSGAARD, C., RASMUSSEN, L., CAPPELEN, J., HINKLER, J., MERNILD, S. H., PETERSEN, D., TAMSTORF, M. P., RASCH, M. & HASHOLT, B. 2008. Present-Day Climate at Zackenberg. *Advances in Ecological Research.* San Diego: Elsevier Academic Press Inc.

HOLLAND, J. N., CHENG, W. & CROSSLEY, D. A. J. 1996. Herbivore-induced changes in plant carbon allocation: Assessment of below-ground C fluxes using carbon-14. *Oecologia (Berlin),* 107**,** 87-94.

IPCC 2013. Working group I contribution to the IPCC fifth Assessment, Report (AR5), Climate Change 2013: The Physical Science Basis. WMO, UNEP.

JOABSSON, A. & CHRISTENSEN, T. R. 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. *Global Change Biology,* 7**,** 919-932.

JOABSSON, A., CHRISTENSEN, T. R. & WALLEN, B. 1999. Vascular plant controls on methane emissions from northern peatforming wetlands. *Trends in Ecology and Evolution,* 14**,** 385-388.

JONES, D. L. 1998. Organic acids in the rhizosphere – a critical review. *Plant and Soil,* 205**,** 25-44.

KRISTENSEN, D. K., KRISTENSEN, E., FORCHHAMMER, M. C., MICHELSEN, A. & SCHMIDT, N. M. 2011. Arctic herbivore diet can be inferred from stable carbon and nitrogen isotopes in C3 plants, faeces, and wool. *Canadian Journal of Zoology,* 89**,** 892-899.

KUZYAKOV, Y. & DOMANSKI, G. 2000. Carbon input by plants into the soil. Review. *Journal of Plant Nutrition and Soil Science,* 163**,** 421-431.

LIDDLE, M. 1997. *Recreation ecology: the ecological impact of outdoor recreation and ecotourism,* Chapman & Hall Ltd.

LIVINGSTON, G. & HUTCHINSON, G. 1995. Enclosure-based measurement of trace gas exchange: applications and sources of error. *Biogenic trace gases: measuring emissions from soil and water.* Oxford UK: Blackwell Sciences.

MARSCHNER, H. 1995. Mineral nutrition of higher plants. *Academic Press, London*.

OECHEL, W. C. & VAN CLEVE, K. 1986. The Role of Bryophytes in Nutrient Cycling in the Taiga. *In:* VAN CLEVE, K., CHAPIN, F. S., III, FLANAGAN, P. W., VIERECK, L. A. & DYRNESS, C. T. (eds.) *Forest Ecosystems in the Alaskan Taiga.* Springer New York.

OLFF, H., RITCHIE, M. E. & PRINS, H. H. T. 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., STARK, S. & OKSANEN, L. 2004. Reindeer influence on ecosystem processes in the tundra. *Oikos,* 105**,** 386-396.

PATERSON, E. 2003. Importance of rhizodeposition in the coupling of plant and microbial productivity. *European Journal of Soil Science,* 54**,** 741-750.

PATERSON, E., THORNTON, B., MIDWOOD ANDREW, J. & SIM, A. 2005. Defoliation alters the relative contributions of recent and non-recent assimilate to root exudation from Festuca rubra. *Plant, Cell & Environment,* 28**,** 1525-1533.

ROVIRA, A. 1969. Plant root exudates. *The Botanical Review,* 35**,** 35-57.

SJÖGERSTEN, S., VAN DER WAL, R., LOONEN, M. J. E. & WOODIN, S. J. 2011. Recovery of ecosystem carbon fluxes and storage from herbivory. *Biogeochemistry,* 106**,** 357-370.

SJÖGERSTEN, S., VAN DER WAL, R. & WOODIN, S. J. 2008. Habitat type determines herbivory controls over CO2 fluxes in a warmer arctic. *Ecology (Washington D C),* 89**,** 2103-2116.

SPEED, J. D. M., WOODIN, S. J., TOMMERVIK, H. & VAN DER WAL, R. 2010. Extrapolating herbivore-induced carbon loss across an arctic landscape. *Polar Biology,* 33**,** 789-797.

STRÖM, L. & CHRISTENSEN, T. R. 2007. Below ground carbon turnover and greenhouse gas exchanges in a sub-arctic wetland. *Soil Biology & Biochemistry,* 39**,** 1689-1698.

STRÖM, L., EKBERG, A., MASTEPANOV, M. & CHRISTENSEN, T. R. 2003. The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. *Global Change Biology,* 9**,** 1185-1192.

STRÖM, L., MASTEPANOV, M. & CHRISTENSEN, T. R. 2005. Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. *Biogeochemistry (Dordrecht),* 75**,** 65-82.

STRÖM, L., TAGESSON, T., MASTEPANOV, M. & CHRISTENSEN, T. R. 2012. Presence of Eriophorum scheuchzeri enhances substrate availability and methane emission in an Arctic wetland. *Soil Biology and Biochemistry,* 45**,** 61-70.

TARNOCAI, C., CANADELL, J. G., SCHUUR, E. A. G., KUHRY, P., MAZHITOVA, G. & ZIMOV, S. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochem. Cycles,* 23**,** GB2023.

VAN DER WAL, R. & BROOKER, R. W. 2004. Mosses Mediate Grazer Impacts on Grass Abundance in Arctic Ecosystems. *Functional Ecology***,** 77.

VAN DER WAL, R., SJÖGERSTEN, S., WOODIN, S. J., COOPER, E. J., JONSDOTTIR, I. S., KUIJPER, D., FOX, T. A. D. & HUISKES, A. D. 2007. Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. *Global Change Biology,* 13**,** 539-545.

VAN DER WAL, R., VAN LIESHOUT, S. M. J. & LOONEN, M. J. J. E. 2001. Herbivore impact on moss depth, soil temperature and arctic plant growth. *Polar Biology,* 24**,** 29-32.

WAREMBOURG, F. R. & ESTELRICH, H. D. 2000. Towards a better understanding of carbon flow in the rhizosphere: a time-dependent approach using carbon-14. *Biology and Fertility of Soils,* 30**,** 528-534.

WAREMBOURG, F. R. & PAUL, E. A. 1973. The use of C14O2 canopy techniques for measuring carbon transfer through the plant-soil system. *Plant and Soil,* 38**,** 331-345.

WOODIN, S. J., VAN DER WAL, R., SOMMERKORN, M. & GORNALL, J. L. 2009. Differential allocation of carbon in mosses and grasses governs ecosystem sequestration: a 13C tracer study in the high Arctic. *New Phytologist*, 184**,** 944-949.

Figures

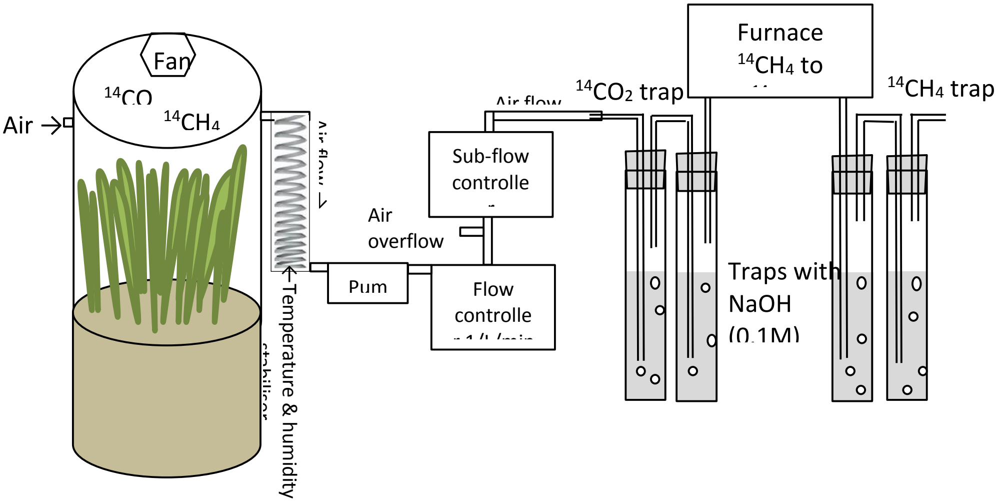


Figure 1. A schematic drawing of the experimental set-up for determination of emitted $^{14}CO_2$ and $^{14}CH_4$

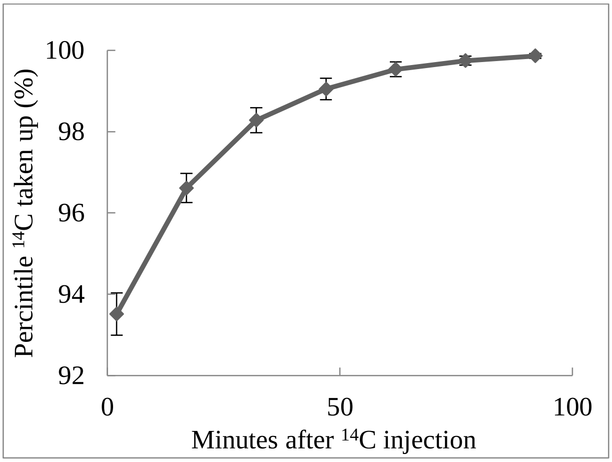


Figure 2. The mean percentile uptake of the injected 14C (% ± SE) (n=8) the first 90 minutes after injection

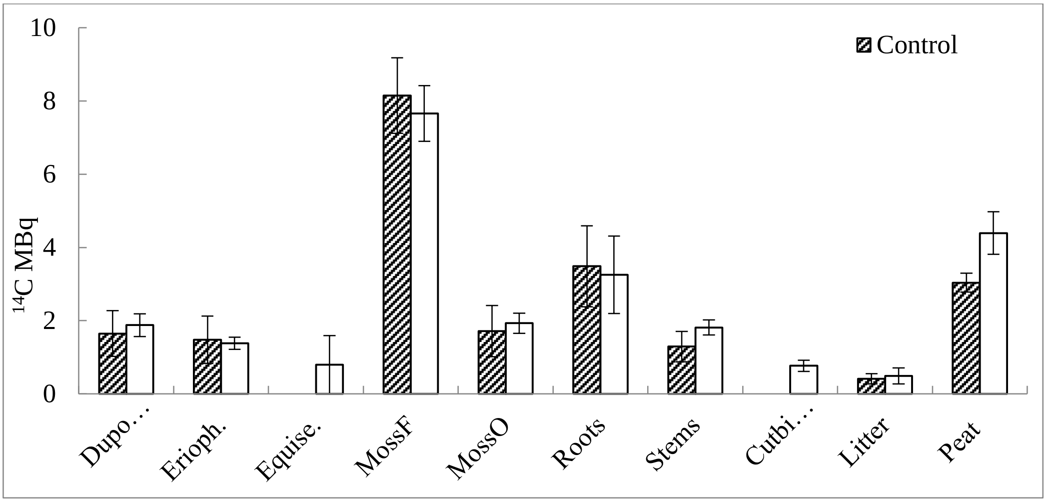


Figure 3. The mean total 14C (MBq) in the different vegetation fractions for each monolith, which are grouped into the two treatments control (striped squares) and clipped (open squares). The biomass was fractionated into the vascular plants: Dupontia fisheri ssp. Psilosantha , Eriophorum scheuchzeri (Erioph.) and Equisetum sp.(Equise.)(n=1), and roots, stems, fresh mosses (MossF), old mosses (MossO), the biomass that were cut (Cutbio), litter and peat where roots were removed

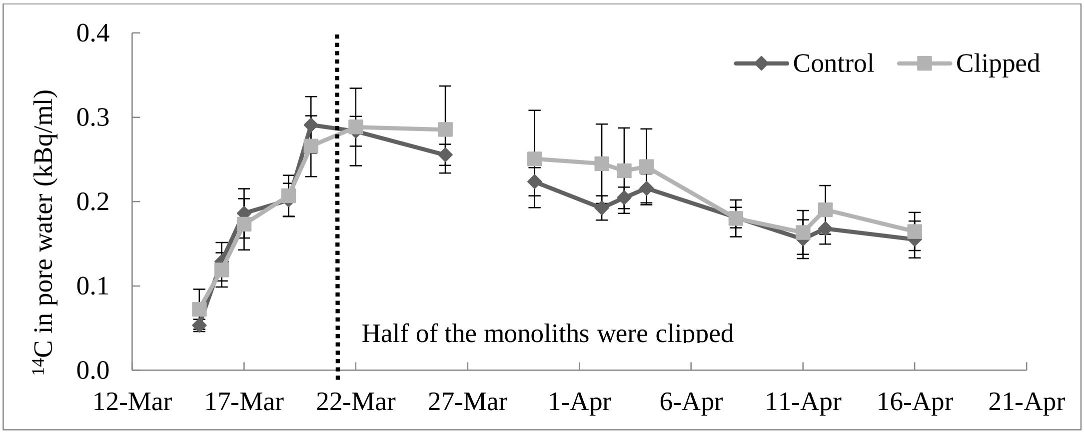


Figure 4. The mean 14C (±SE) kBq/ml in pore-water for control and clipped plots (n=4)

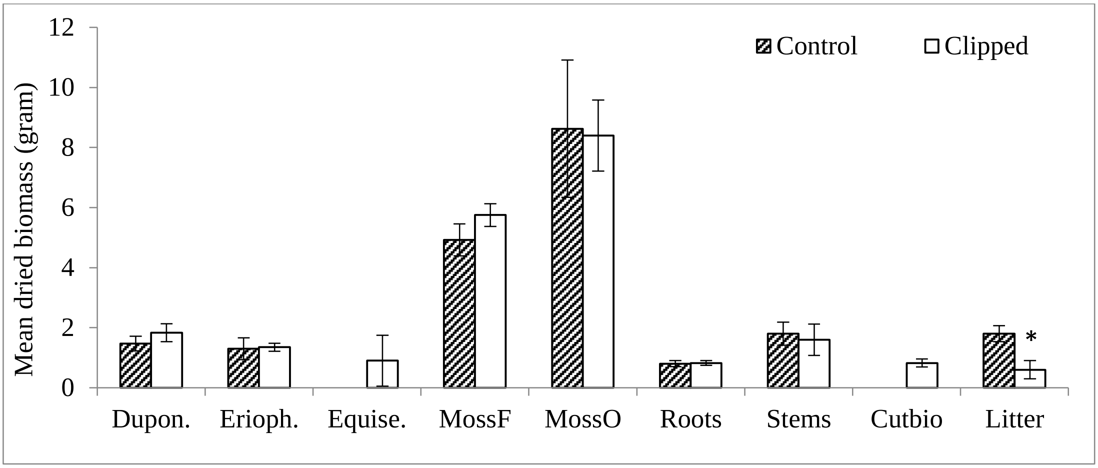


Figure 5. The mean dry weight of control (stripped squares) (n=4) and clipped (open squares) (n=4). The biomass was fractionated into the vascular plants: Dupontia fisheri ssp. Psilosantha (Dupon.), Eriophorum scheuchzeri (Erioph.) and Equisetum sp.(Equise.)(n=1) and fresh mosses (MossF), old mosses (MossO), roots, stems, the biomass that were cut (Cutbio) and litter. *significant different at the 0.05 level (2-tailed)

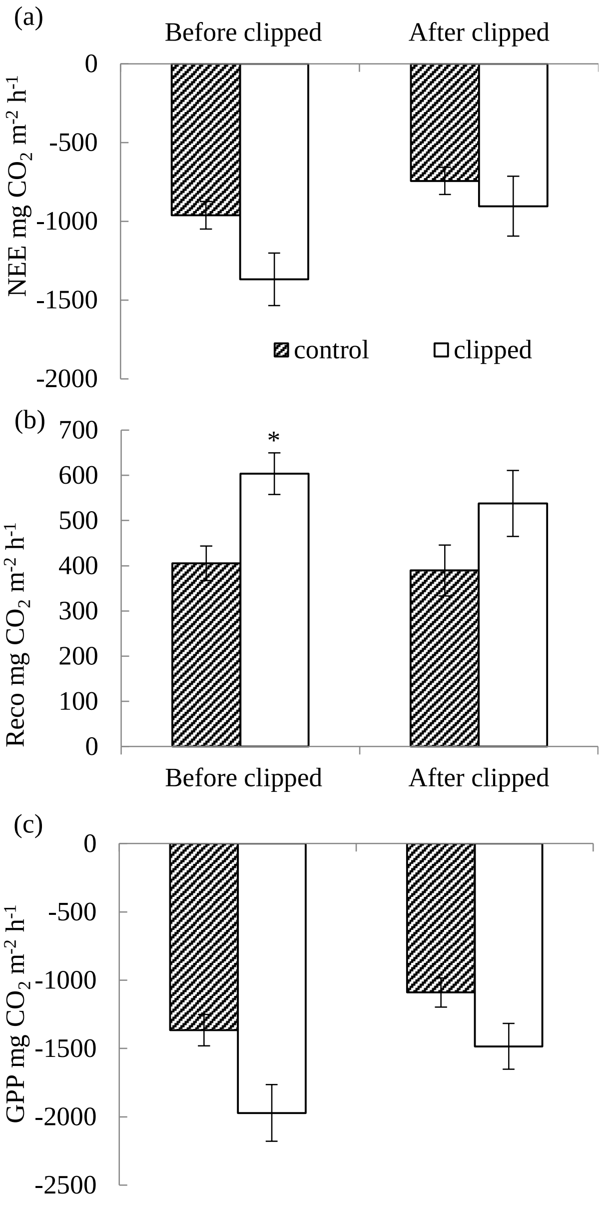


Figure 6. Mean CO_2 flux (mg m^{-2}h^{-1}) for the two treatments control (n=4) and cut (n=4) before and after the monoliths were cut. a= net ecosystem exchange (NEE), b= respiration (R_{eco}), c= gross primary production (GPP). *significant different at the 0.05 level

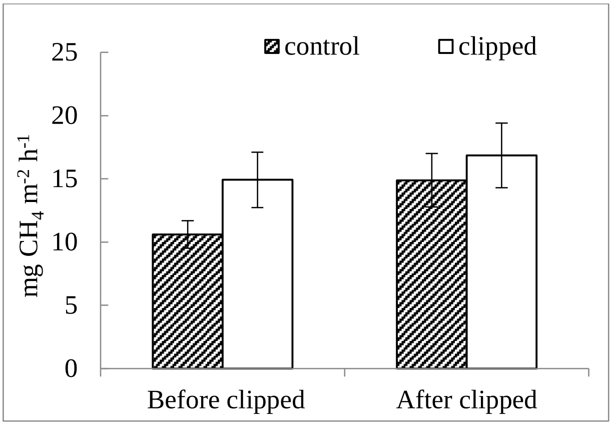


Figure 7. Mean CH_4 flux (mg $m^{-2}h^{-1}$) for the two treatments control (n=4) and cut (n=4) before and after the monoliths were

Tables

	^{14}C distributed kBq	**^{14}C distributed %**	**Above and below-ground %**
Dupontia	2349 ± 181	8.6 ± 2.2	
Eriophorum	1431 ± 310	6.1 ± 1.2	
Equisetum	389 ± 389	1.4 ± 1.4	
Moss - fresh	7903 ± 602	35.2 ± 2.3	
Cut-biomass	768 ± 108	1.6 ± 0.7	52.8
Moss - old	1822 ± 351	7.6 ± 1.1	
Litter	454 ± 122	1.9 ± 0.5	9.5
Roots	3371 ± 710	14.4 ± 2.5	
Stems	1555 ± 236	6.7 ± 1.0	
Peat without biomass	3716 ± 390	16.6 ± 1.5	37.7
sum	23766 ± 1834	100	100

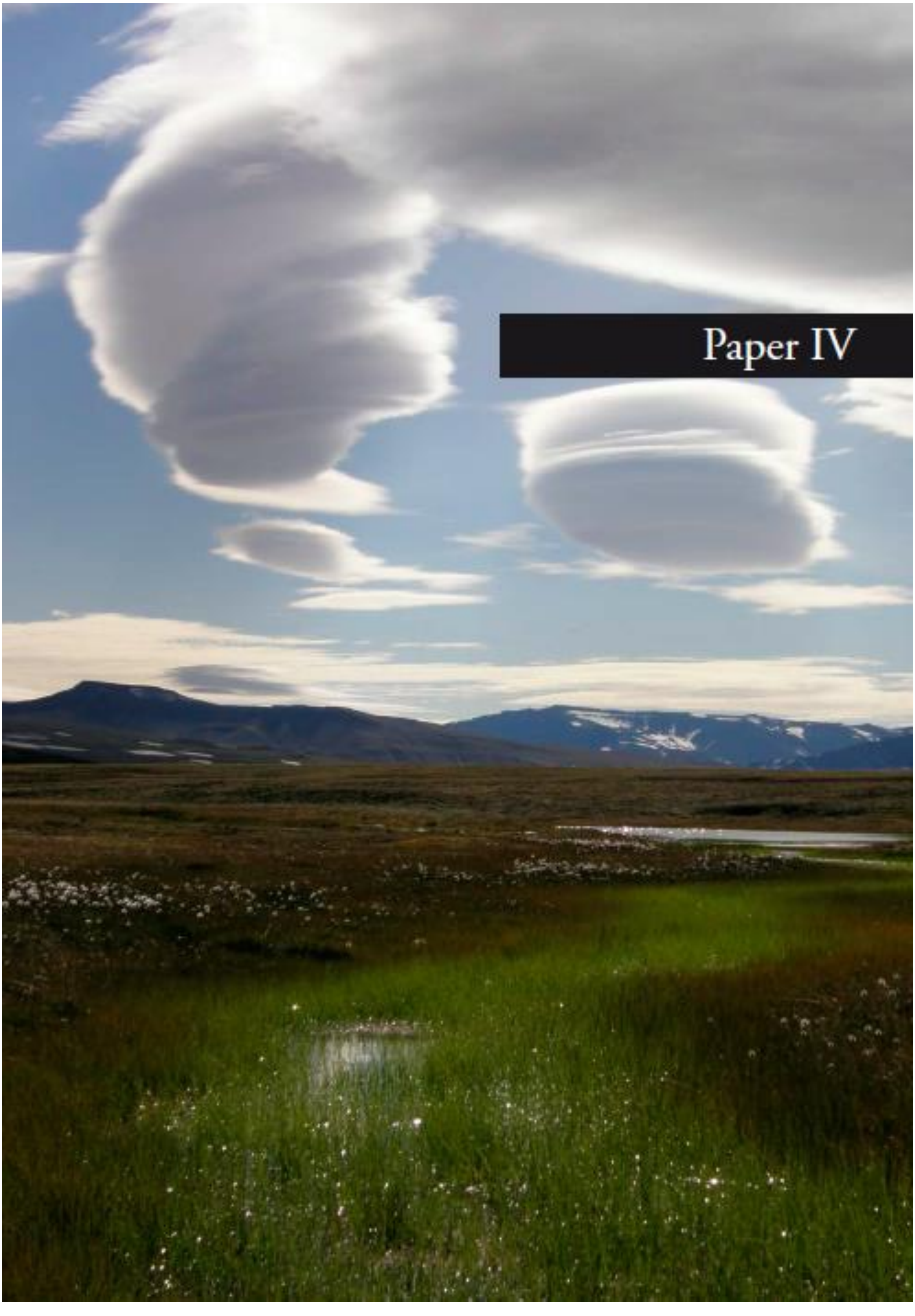
Table 1. The average ^{14}C (± SE) distribution recovered in monoliths (n=8), 30 days after labelling.

	Control		**Clipped**	
	MBq	%	MBq	%
Above-ground				
Green leaves + mosses	13.6	42.6	16.1	48.3
Withered leaves + mosses	4.1	12.9	3.6	10.8
Below-ground				
Roots	6.6	20.7	3.9	11.7
Peat	3.7	11.6	5.8	17.4
Emitted $^{14}CO_2$	3.6	11.3	3.5	10.5
Emitted $^{14}CH_4$	0.2	0.6	0.3	0.8
Estimated ^{14}C emitted in pore-water	0.1	0.3	0.1	0.3
Sum	31.9	100	33.3	100

Table 2. The distribution of ^{14}C in the end of the experiment, given as total MBq and the percent of the total recovered ^{14}C 30 days after labelling. Data is from the two enclosed monoliths control (n=1) and clipped (n=1)

		Mean flux				Weight of biomass				^{14}C				
		CH_4	NEE	R_{eco}	GPP	Vascular	Roots stems	Active biomass	Biomass	Vascular	Roots stems	Active biomass	Biomass	Pore water
CH_4	Sig.	1	-.613	.764	**-.824***	-.503	-.159	-.430	-.354	-.157	.789	.803	.680	-.425
	Corr.		.196	.077	.044	.309	.764	.395	.491	.767	.062	.054	.138	.401
NEE	Sig.	-.613	1	-.516	.660	.595	.618	.622	.388	-.206	-.115	-.187	-.105	.455
	Corr.	.196		.295	.154	.212	.191	.187	.447	.695	.829	.723	.844	.364
R_{eco}	Sig.	.764	-.516	1	**-.955****	-.068	-.046	-.064	-.225	-.164	.557	.550	.699	-.183
	Corr.	.077	.295		.003	.899	.930	.904	.668	.756	.251	.258	.122	.729
GPP	Sig.	**-.824***	.660	**-.955****	1	.246	.188	.239	.280	.295	-.569	-.523	-.609	.453
	Corr.	.044	.154	.003		.639	.721	.648	.590	.570	.238	.287	.199	.367
Vascular	Sig.	-.503	.595	-.068	.246	1	**.827***	**.989****	**.820***	-.055	-.471	-.527	-.316	.437
	Corr.	.309	.212	.899	.639		.043	.000	.046	.917	.346	.283	.542	.386
Roots stems	Sig.	-.159	.618	-.046	.188	**.827***	1	**.901***	**.854***	-.201	-.102	-.173	-.147	.253
	Corr.	.764	.191	.930	.721	.043		.014	.030	.702	.848	.743	.780	.629
Active biomass	Sig.	-.430	.622	-.064	.239	**.989****	**.901***	1	**.857***	-.096	-.390	-.452	-.282	.404
	Corr.	.395	.187	.904	.648	.000	.014		.029	.857	.445	.369	.588	.427
Biomass	Sig.	-.354	.388	-.225	.280	**.820***	**.854***	**.857***	1	-.102	-.520	-.594	-.597	.088
	Corr.	.491	.447	.668	.590	.046	.030	.029		.847	.291	.214	.211	.868
Vascular	Sig.	-.157	-.206	-.164	.295	-.055	-.201	-.096	-.102	1	-.395	-.118	-.157	.699
	Corr.	.767	.695	.756	.570	.917	.702	.857	.847		.438	.823	.767	.122
Roots stems	Sig.	.789	-.115	.557	-.569	-.471	-.102	-.390	-.520	-.395	1	**.959****	**.892***	-.282
	Corr.	.062	.829	.251	.238	.346	.848	.445	.291	.438		.002	.017	.589
Active biomass	Sig.	.803	-.187	.550	-.523	-.527	-.173	-.452	-.594	-.118	**.959****	1	**.916***	-.088
	Corr.	.054	.723	.258	.287	.283	.743	.369	.214	.823	.002		.010	.868
Biomass	Sig.	.680	-.105	.699	-.609	-.316	-.147	-.282	-.597	-.157	**.892***	**.916***	1	.053
	Corr.	.138	.844	.122	.199	.542	.780	.588	.211	.767	.017	.010		.921
Pore water	Sig.	-.425	.455	-.183	.453	.437	.253	.404	.088	.699	-.282	-.088	.053	1
	Corr.	.401	.364	.729	.367	.386	.629	.427	.868	.122	.589	.868	.921	

Table 3. The Pearson correlation between; mean fluxes over the measuring season for each monolith, the weight of the different fractions of each monoliths and the ^{14}C (MBq) amount of the different fractions in each monolith (n=6). The fractions were divided into: vascular plants (*Dupontia fisheri ssp. Psilosantha*, *Eriophorum scheuchzeri* and *Equisetum sp*.), Roots and stems, Active biomass (Vascular plants, roots and stems) and Biomass (Active biomass, litter and mosses) and the mean ^{14}C found in pore-water. *correlation is significant at the 0.05 level, ** is significant at the 0.01 level



Paper IV

Controls of spatial and temporal variability in CH_4 flux in a high arctic fen over three years

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Abstract

The aim of this study was to establish the main drivers of the spatial variability in growing season CH_4 flux within an arctic wetland ecosystem. During three years (2011-2013) we measured CH_4 flux and potential drivers, e.g., CO_2 fluxes (net ecosystem exchange (NEE), gross primary productivity (GPP) and ecosystem respiration), temperature, water table depth, pore-water concentration of organic acids (e.g., acetate) and the vascular plant composition and density. The study included 16-20 main plots (Cmain) and in 2013 also 29 “treated” plots (excluded muskoxen grazing, snow fence and automated chamber) distributed over 0.2 km^2. The results show a 1.8 times inter-annual and a 9-35 times spatial variability (depending on year and treatment) in CH_4 flux. All three years GPP was a consistently strong driver of the variability in Cmain plots. In accordance the plant productivity related variables NEE, GPP and acetate were singled out as the strongest drivers of the variability in 2013 when all variables were measured on a majority of the plots. All these variables were equally good predictors of the spatial variability in CH_4 flux whether “treated” plots were included in the analysis or not. The density of *Eriophorum scheuchzeri* was the strongest driver of the spatial variability in NEE, GPP and acetate. In conclusion, changes in vegetation composition or productivity of wet arctic ecosystems will have large impacts on their carbon balance and CH_4 flux, irrespective of whether these changes are driven directly by climate change or by indirect effects of for instance grazing pressure.

Introduction

Arctic ecosystems are an important global carbon sink and despite that the northern permafrost region covers only about 16% of the global land surface approximately 50% of the Earth's below-ground organic carbon is stored in this area (McGuire et al. 2009; Ping et al. 2008; Post et al. 1982; Tarnocai et al. 2009). Arctic wetlands, in particular, hold a large amount of this carbon, as the decomposition rate of organic matter is slow under cold and anoxic conditions (Tarnocai et al. 2009). The anoxic conditions at the same time favor anaerobic decomposition and methanogenesis. Combined, natural and agricultural wetlands contribute with over 40% of the annual atmospheric emissions of CH_4 and are considered the largest single contributor of this gas to the troposphere (Mikaloff Fletcher et al. 2004; Cicerone and Oremland 1988).

The spatial variability in CH_4 emissions can be large. Zhu et al. (2014) showed large spatial variations in CH_4 emissions from Antarctic tundra depending on local hydrological regimes, where dry/upland sites all had an uptake of CH_4 while waterlogged sites emitted between 0.03 and 2.4 (mg CH_4 m^{-2} h^{-1}). In a study performed in the high arctic valley Zackenberg in NE Greenland we found high spatial variability in CH_4 flux, with a range in mean (30th June to 4th July) CH_4 flux (mg CH_4 m^{-2} h^{-1}) from 9.1 in continuous fen to -0.03 in elevated heath areas (Tagesson et al. 2013).

Several variables have been identified as controls of methane production and ultimately of net CH_4 emission. These include soil temperature, water table depth (Torn and Chapin 1993; Waddington et al. 1996; Ström and Christensen 2007), plant composition and ecosystem productivity (i.e., Whiting and Chanton 1992, 1993; Bubier 1995; Chanton et al. 1995; Thomas et al. 1996; Waddington et al. 1996; Christensen et al. 2000; Joabsson and Christensen 2001; Ström and Christensen 2007; Ström et al. 2012), substrate type and quality (Bellisario et al. 1999; Joabsson et al. 1999a; Ström et al. 2003, 2012). Much of the easily decomposable carbon in soil is derived from roots, root residues and root exudates (Kuzyakov and Domanski 2000) and the production of labile substrates, e.g., AA, for CH_4 production is often found to be high in the root zone of vascular plants (Ström et al. 2003, 2005, 2012; Ström and Christensen 2007). The effect of vascular plants can be highly species specific and presence of *Eriophorum* species (*E. scheuchzeri*, *E. angustifolium* and *E. vaginatum*) are often found to increase substrate production and CH_4 flux, while other species have less pronounced effects (Ström et al. 2003, 2005, 2012; Ström and Christensen 2007). Additionally, we have recently shown that increased grazing pressure decreased CH_4 emission and net ecosystem uptake of CO_2 in an arctic wetland The effects could be attributed to suppressed plant growth of in particular *E. scheuchzeri* that resulted in decreased plant density and productivity and production of labile substrates in the root zone (Falk et al. 2014).

The primary aim of this study was to get a detailed understanding of the spatial variability in CH_4 flux and the main driving forces behind this variance. The study was conducted over a time period of three years (2011-2013), and therefore also includes an element of temporal variation. During the main part of the growing season we measured CH_4 flux and potential drivers (see material and method for details) on 16-20 main plots and in 2013 also on 29 “treated” plots (excluded muskoxen grazing, snow fence and automated chamber) distributed over 0.2 km^2 area in a high arctic mire complex situated in Zackenberg, NE Greenland. In accordance with previous studies we hypothesize that the main drivers of the spatial variability of CH_4 flux are vegetation composition and productivity, substrate availability and in addition physical parameters such as water table depth (WtD) and temperatures. With high productivity and substrate availability in combination with high WtD, and consequently a larger anoxic zone, and temperatures leading to high CH_4 flux.

Materials and method

Site description

The study took place in the freshwater lowland mire complex *Rylekæret* situated in the high arctic valley Zackenberg in NE Greenland (74°30’N 20°30W). Mires cover approximately 4% of the valley (Arndal et al. 2009). The mire ecosystem is normally water-saturated far into the growing season and wet continuous fen areas are dominated by sedges *Carex* sp. *(C. stans etc), Dupontia psilosantha* and *E. scheuchzeri* (Bay 1997). Underlying the sedge community is a dense moss cover, e.g., species of *Tomenthypnun, Scorpidium, Aulacomnium* and *Drepanoclaudus* (Ström et al. 2012).

The area is within the continuous permafrost zone and has an active layer thickness (AL) between 45 and 80 cm (Christiansen et al. 2008). The warmest month is July, which has a mean air temperature of 5.8˚C and 90% of the mean annual precipitation (261 mm in the period 1996-2005) falls as snow (Hansen et al. 2008). The valley is influenced by large herbivores and muskoxen (*Ovibos moschatus*) are a natural part of the ecosystem and found in very high numbers (Schmidt personal communication). During summer muskoxen mainly feed in the fen and grassland areas in the valley. Their summer forage is dominated by graminoids and around 80% of this is obtained in the mire areas (Kristensen et al. 2011). The site is described in further detail in, e.g., Falk et al. (2014), Ström et al. (2012) and Tagesson et al. (2013).

Experimental setup

The plots were distributed in parts of the mire complex that was classified as wet continuous fen based on the vascular plant composition (Bay 1997). The WtD varied between the plots due to landscape hydrology. In 2011 the set-up included 16 untreated plots (hereafter denoted Cmain) and in 2012 four additional plots were added to the set-up (n=20). In 2013 we also included data from 10 automated chamber plots (AC) to the analysis and from an experiment installed in August 2013 which included 10 plots where muskoxen grazing was excluded (EX) and 9 plots which were fenced in the main wind direction (SC). As a selection criteria for the added EX and SC plots we only included plots from this set-up that had a measurable CH_4 flux as some of the plots in the full set-up (EX, n=14 and SC, n=10) of these treatments were positioned in drier soil. The auto-chambers were installed in August 2005 and are described in further detail in Mastepanov et al. (2008 and 2013). The Cmain, EX and SC plots all consisted of aluminum base (40×40 cm) permanently installed 15 cm into the ground and protruding 5 cm. On, within or in close proximity to these bases manual measurements of CH_4 and CO_2 fluxes and additional variables were conducted approximately twice per week over the main part (1 July to 10 August) of the growing season and in the autumn in 2012. The measurements took place between 10 am and 5 pm (all plots measured at various times of day). For further details of the manual measurement set-up see Falk et al. (2014).

Flux measurements

Flux measurements of CO_2 and CH_4 on the main, exclosure and snow control plots were conducted using a closed chamber technique (Christensen et al. 2000; Ström and Christensen 2007). Gas concentrations of CO_2 and CH_4

were recorded simultaneously by a portable FTIR (Fourier Transform Infrared) spectrometer (Gasmet Dx 40-30, Gasmet Technologies Oy) within a transparent Plexiglas chamber (41 L). The concentration change of CO_2 in the chamber during light conditions was used to estimate net ecosystem exchange (NEE) and during dark to estimate ecosystem respiration (R_{eco}). The details of these measurements are further described in Falk et al. (2014). Auto-chamber measurements of CH_4 and CO_2 fluxes were conducted using a closed chamber technique adapted from Goulden and Crill (1997) and Mastepanov et al. (2008, 2013). The concentrations of CO_2 and CH_4 (and H_2O) were measured continuously with off-axis cavity integrated output spectroscopy (off-axis ICOS) (Gupta 2012) using a fast greenhouse gas analyzer (GGA-24EP, Los Gatos Research, USA).

Additional variables

Simultaneously to each flux measurement we also measured several other variables, including; air temperature (T_{Air}, °C) and photosynthetically active radiation (PAR, μmol $m^{-2}s^{-1}$) which were logged hourly using a Minikin QTi data-logger (EMS Brno), soil temperature (T_{Soil}, °C, 10 cm below moss surface) which was determined using a 150 mm digital temperature probe (Viking, Eskilstuna, Sweden) and the WtD and AL (cm below moss surface). Additionally, the vascular plant species composition and density (number of tillers m^{-2}) was non-destructively estimated by counting the number of tillers of the dominant species in each of the Cmain, EX and SC plots in 2011 and 2013 and in one quarter of the 0.36 m^2 AC plots in 2013.

In 2012 and 2013 pore-water was sampled from the main root zone (5-15 cm) directly after gas flux measurements in the Cmain, EX and SC plots from stainless tubes (3 mm in diameter), which were permanently installed within each plot. Pore water was drawn from three depths (5, 10 and 15 cm, 3 ml per depth) in plots with a peat layer >15 cm and from two depths (5 and 10 cm, 4 ml per depth) in plots with lower peat depths. The pore-water samples were subsequently analyzed for organic acids using a liquid chromatography-ionspray tandem mass spectrometry system. The system consisted of a Dionex (Sunnyvale, CA, USA) ICS-2500 liquid chromatography system and an Applied Biosystems (Foster City, CA, USA) 2000 Q-trap triple quadrupole mass spectrometer. The pore-water sampling and OA analysis is described in further detail in Ström et al. (2012).

Data treatment

On all plots the CO_2 and CH_4 fluxes were calculated from the change in gas concentration as a function of time using linear fitting, including corrections for ambient air temperature and pressure, according to procedures by Crill et al. (1988). Gas fluxes were expressed as mg m^{-2} h^{-1} of CH_4 or CO_2 where positive values denote a release of gas from the ecosystem to the atmosphere and negative an uptake. Gross Primary Production (GPP) was calculated as the difference between NEE and R_{eco}.

Statistical analyses were performed on the 1st July to 10th August means and on the vegetation analyses done in August. All data was tested for normal distribution using one-sample Kolmogorov-Smirnov test before further analyses. To determine statistically significant differences between the three years in gas fluxes and all measured ecosystem variables in the Cmain plots a general linear model analysis of variance with plot number as covariate was performed. To determine the variables that best could explain the plot scale variation in CH_4 flux a bivariate correlation (pearson 2-tailed test for significance) analysis was performed on the mean fluxes and additional parameters measured during that year. In 2011 (n=16) and 2012 (n=20) the matrix included all variables measured on the Cmain plots and in 2013 all variables measured in the Cmain, EX, SC and AC plots. For correlations performed only on Cmain plots the correlation coefficient is denoted R^m and the variable name with a superscript m (for example CH_4^m).

To make an attemt to determine the drivers of the temporal variability in CH_4 flux we also included data of a limited number of variables measured on five of the Cmain plots in 2010, see Falk et al. (2014) for details. A bivariate correlation (pearson 2-tailed test for significance) analysis was subsequently performed on the annual means of these 5 plots 2010-2014. It should however be noted that the correlation was performed on an insufficient number of replicate years (n=4) to achieve a fully statistically sound analysis. Additionally we made a bivariate correlation (pearson 2-tailed test for significance) analysis on the daily Cmain means and the other variables measured simultaneously to that measurement both within a year and for all years, note a certain degree of pseudo-replication since measurements from three years are included in the analysis.

All statistical analyses were done using SPSS 21 for Mac. Results of the statistics were regarded as significant if p-values were lower than 0.05.

Results

Spatial and temporal variability

The results show a high spatial and temporal variability in CH_4 emission between the Cmain plot means (table 1) with a 9-, 10- and 19-times higher flux from max than from min plots for 2011, 2012 and 2013 respectively. The difference between max and min in the treated AC (treated in the sense that 0.3 m high plexiglas frame is permanently installed on the plot), EX and SC plots in 2013 were for SC and AC in the same order of magnitude as for Cmain plots (14- and 16-times for SC and AC respectively) whereas EX plots had a much higher spatial variability with a 35-times difference between max and min (table 1). Other variables with high spatial variability were number of *Dupontia* tillers, which varied from ≥1000 to 0 (number of tillers not times due to 0 values), AA from 51- to 140-times, OAs from 5- to 28-times and number of *Eriophorum* tillers from 3- to 139-times (table 1).

There was a quite high (1.8-times) inter-annual variability in the CH_4 flux. In general the highest fluxes in Cmain plots were measured in 2012, which had a significantly higher CH_4 flux ($p \leq 0.044$), net ecosystem uptake of CO_2 (NEE, $p<0.001$) and GPP ($p \leq 0.005$) than 2011 and 2013 (table 1). 2012 was also clearly wetter (WtD, $p<0.001$) and warmer (T_{Soil}, $p<0.001$) than 2011 and 2013 and had a higher the AA concentration in pore water than 2013 ($p=0.024$) (not measured in 2011). R_{eco} ($p=0.010$) was significantly lower in 2012 than in 2013 and the number of vascular plant tillers was lower in 2013 than in 2011 (Fig. 1). For the variables that were measured repeatedly over the season the differences between the years were consistent throughout most of the measurement periods (Fig. 2). Further, there was a clear treatment effect and the CH_4 fluxes in EX, SC and AC was significantly lower ($p \leq 0.027$) than the Cmain plots, which can be considered as controls. The plant productivity related variables NEE and GPP in treated plots were also significantly lower (NEE: $p \leq 0.014$ and GPP: $p \leq 0.017$, not measured in AC) than in Cmain plots and the concentration of acetate in pore-water was significantly lower ($p=0.042$) in EX than in Cmain plots in 2013 (table 1).

Drivers of variability

The variables that explained the spatial variability in CH_4 flux varied somewhat between the years. The one variable that was consistent throughout the years was GPP. In the two years that it was measured OAs and AA concentration in pore water were also good predictors of the variability of CH_4 flux. The two years that the plant composition was measured the best predictor of GPP was *Eriophorum* coverage (table 2 and 3). In 2013 when all variables were measured several variables related to plant productivity was singled out as good explanatory variables for the CH_4 flux magnitude. In Cmain plots these were in order of strength NEE, GPP and AA concentration in pore-water. NEE, GPP and AA in Cmain plots were in turn best explained by the number of *Eriophorum* tillers (table 3 and for AA R=0.850, $p \leq 0.001$). The number of *Eriophorum* tillers was best explained by WtD (R=0.451, $p=0.046$), AL (R=0.486, $p=0.030$ and T_{Soil} (R=0.553, $p=0.011$), assuming that *Eriophorum* is an explanatory variable for productivity related variables and not vise versa. All the above mentioned relationships were equally good predictors of the spatial variability in CH_4 flux when EX, SC and AC plots were included in the correlation (table 3, Fig. 4).

The multiple stepwise regressions on all the 2013 plots singled out NEE and AA combined as the predictors of the spatial variation in CH_4 flux (R=0.845, $R^2=0.715$, $p<0.001$). The co-linearity problem between NEE and AA (table 3) should however be noted. The regression also singled out that the best predictors of NEE and GPP were *Eriophorum* and WtD combined (NEE: R=0.854, $R^2=0.729$, $p<0.001$, GPP: R=0.843, $R^2=0.711$, $p<0.001$). For R_{eco}, OA and AA the best predictor was *Eriophorum* alone and for number of *Eriophorum* tillers T_{Soil} (for R- and *p*-values see table 3).

The bivariate correlation performed on the annual means 2010-2014 (n=4) of the five Cmain plots measured also in 2010 (Falk et al. 2014) indicated a relationship between the magnitude of the inter-annual CH_4 flux and WtD (R=0.969, p=0.031). The other measured variables (R_{eco}, AL, T_{Soil} and NEE) were not significantly correlated to the CH_4 flux, although for NEE nearly significant (R=0.916, p=0.084). Additionally R_{eco} (p=0.010) was significantly lower in the wettest and presumably most anoxic year (2012) than in the driest year (2013).

The difference in plant species composition and density between 2011 and 2013 seemed to be somewhat related to environmental conditions since it was significantly lower in 2013 the coldest (T_{Soil} and lower AL) and driest (WtD) year (Fig. 1, table 1).

The temporal variation in CH_4 flux within each season was highly correlated to NEE and GPP in 2012 and 2013 (NEE: 2012, R=-0.955, p=0.011 and 2013, R=-0.976, p=0.004; GPP: 2012, R=-0.972, p=0.006 and 2013, R=-0.896, p=0.039) all other variables were insignificant as was all variables for 2011. When the temporal variation (Fig. 2) for all years combined was correlated several variables were significantly related to the CH_4 flux (note a certain degree of pseudo-replication), these were in order of magnitude; NEE: R=-0.947, p<0.001, GPP: R=-0.905, p<0.001, AA: R=0.750, p=0.012, OAs: R=0.772, p=0.009, WtD: R=0.556, p=0.032 and T_{Soil}: R=0.525, p=0.045. In addition correlations were found between AA-WtD: R=0.706, p=0.007, AA-T_{Soil}: R=0.755, p=0.012 and WtD-T_{Soil}: R=0.794, p<0.001.

Discussion

Spatial and temporal variability

The spatial variability in CH_4 emissions can be large. Zhu et al. (2014) showed large spatial variations in CH_4 emissions from Antarctic tundra depending on local hydrological regimes, where dry/upland sites all had an uptake of CH_4 up to -0.09 (mg CH4 m^{-2} h^{-1}) while waterlogged sites emitted up to 2.4 (mg CH4 m^{-2} h^{-1}). In a previous study performed in *Rylekæret* we found a high spatial variability in CH_4 flux between continuous fen and heath areas (9.1 to -0.03 mg CH_4 m^{-2} h^{-1}) (Tagesson et al. 2013). The Tagesson et al. (2013) study differed from our study in the sense that it included a range of ecosystem types and hydrological regimes from wet continuous fen to very dry heath, as did the Zhu et al. (2014) study. In comparison to these studies the spatial variability in our study is relatively low. We however focused our study to wet continuous fen and therefore a lower variation could be expected.

Positive correlations between plant productivity, i.e. GPP, NEE or net ecosystem productivity and CH_4 emissions have been found in several other studies (Whiting and Chanton 1992, 1993; Bubier 1995; Chanton et al. 1995; Thomas et al. 1996; Waddington et al. 1996; Joabsson et al. 1999b; Christensen et al. 2000; Joabsson and Christensen 2001, Ström and Christensen 2007). The relationship has been attributed to either a close linkage between: provision of methanogenic substrate and vascular plant production, a connection between plant biomass and CH_4

transport capacity, interactions between NEE and the environment, or finally a combined affect of them all (Joabsson et al. 1999a). In our study the variables singled out as drivers of the spatial variability in CH_4 flux varied somewhat between the years. The one variable that was a consistent explanatory factor for CH_4 flux throughout the years was GPP. In support of the proposed importance of productivity as a driver several variables related to plant productivity were singled out as good explanatory variables for the spatial variability in CH_4 flux magnitude in 2013, when all variables were measured on a majority of the plots. These were in order of strength NEE, GPP and AA concentration in pore-water. Providing a link between plant productivity and CH_4 flux the density of *Eriophorum* was singled out as the best driver of the spatial variability in NEE, GPP and AA both in 2011 and 2013, despite the lack of a direct correlation between CH_4 flux and *Eriophorum* in 2011. Indicating that the treatment effect on the CH_4 flux was driven by its effect on vegetation composition and productivity the drivers of the spatial variability in CH_4 flux was the same whether "treated" plots were included in the analysis or not.

We have previously demonstrated that species composition, and in particular *Eriophorum* species (*E. scheuchzeri*, *E. angustifolium* and *E. vaginatum*) can have a strong effect on CH_4 flux (Ström et al. 2003, 2005, 2012; Ström and Christensen 2007). Recently we showed that continuous fen plots dominated by *Eriophorum* in *Rylekæret* had a significantly higher CH_4 flux than plots dominated by *Carex* or *Dupontia* (Ström et al. 2012). The results from this study confirm our previous finding that CH_4 flux is affected by *Eriophorum* coverage at least in 2013. In 2011 we see no direct correlation between *Eriophorum* and CH_4 flux but an indirect relationship is apparent since CH_4 flux is correlated to GPP and GPP to *Eriophorum*. It may be suggested that *Eriophorum* is the primary driver of the spatial variability in NEE and GPP and that a higher productivity in plots dominated by this plant subsequently leads to higher CH_4 production capacity and subsequently flux in *Eriophorum* dominated plots.

In addition to plant composition and ecosystem productivity substrate type and quality is often suggested as an important control of CH_4 flux (Bellisario et al. 1999; Joabsson et al. 1999a; Ström et al. 2003, 2012). Roots, root residues and root exudates are the major source of easily decomposable carbon in soil (Kuzyakov and Domanski 2000). Consequently the production of low molecular organic acids such as acetic acid/acetate (acetate dominates at pH>4.76) that is a substrate of major importance for acetoclastic methanogenesis is often found to be high in the root zone of vascular plants (Ström et al. 2003, 2005, 2012; Ström and Christensen 2007). Stable isotope techniques have shown that a significant fraction of emitted CH_4 is derived from recently fixed carbon (Chanton et al. 1995). It has also been suggested that the acetate fermentation pathway dominate over CO_2 reduction when fresh organic material such as OAs and AA is the major substrate for methanogenesis (Chasar et al. 2000; Bellisario et al. 1999). In Ström et al. (2003) we showed that ^{14}C–acetic acid added to a continuous fen monolith collected at

Rylekæret was emitted as $^{14}CH_4$ within 4 hours. In this study we found that the concentration of OAs and especially AA in pore-water was one of the variables that best explained the spatial variability in CH_4 flux both years that OAs were measured ($R \geq 0.647$). A very likely explanation for the level of AA input to the pore water is the density of *Eriophorum*. Offering support to this reasoning we have previously shown that plots dominated by *Eriophorum* have higher concentration of AA in pore-water (Ström et al. 2012) and also that the production of AA is higher in the root vicinity of this species than in *Dupontia* and *Carex* (Ström et al. 2003). Subsequently, the results from this study give even further support to the importance of *Eriophorum* species as suppliers of substrate for acetoclastic methanogenesis (Ström and Christensen 2007, Ström et al. 2003, 2012; Greenup et al. 2000; Joabsson et al. 1999a; Chanton et al. 1995; Jackson and Caldwell 1992; Whiting and Chanton 1992; van Veen et al. 1989).

In addition to the above discussed productivity related variables several environmental variables have been identified as controls of CH_4 production and flux. The most commonly mentioned are T_{Soil} and WtD (e.g. Dise et al. 1993; Torn and Chapin 1993; Waddington et al. 1996; Ström and Christensen 2007; Elberling et al. 2008; Glaser and Chanton 2009). The effect is commonly attributed to higher methanogenic CH_4 production at higher temperatures and larger anoxic zone and less methanotrophic CH_4 oxidation at higher WtDs. The results from studies of the relationship between T_{Soil}, WtD and CH_4 flux are however somewhat ambiguous.

While some studies find clear relationships others fail to do so. In a study with sites ranging from Antarctic upland tundra to tundra marsh Zhu et al. (2014) found no correlations between CH_4 flux and environmental conditions such as T_{Soil} and T_{Air}. Tagesson et al. (2013) found clear correlations between the plot scale CH_4 flux and T_{Soil} (R^2=0.79) and WtD (R_2=0.81) within the continuous fen area in *Rylekæret*. In contrast to Tagesson et al. (2013) we, in this study, found no indications of T_{Soil} or WtD as important drivers of the plot scale variation in CH_4 flux within either of the three years. We, however found indications that T_{Soil} and WtD to some extent affected the temporal variation in CH_4 flux. However, only if data from all three seasons were included and in addition the correlation coefficients were comparably low ($R \leq 0.556$). Offering support to these results Mastepanov et al. (2013) found, in a 5-years study in *Rylekæret*, that neither temperature nor WtD offered any explanation to the inter-annual differences in flux during the first part of the growing season. While weak correlations between T_{Soil}, WtD and CH_4 flux could be found within individual years and offer some explanation to the seasonal trend in flux. The somewhat contradictory results from Ström et al. (2012), Mastepanov et al. (2013) and Tagesson et al. (2013) in combination to the findings from this study makes it hard to draw any definite conclusions regarding the importance of WtD and T_{Soil} as drivers of the spatial variability in CH_4 flux. However the results from this study is based on many more plot replicates (n=49 in 2013) than previous studies (Mastepanov et al. (2013), n=6 and Tagesson et al. (2013), n=11) and might therefore give a more comprehensive understanding of the relationship. Based on the results from the current study we conclude that WtD and T_{Soil} are relatively weak drivers of the spatial variability in CH_4 flux in a fairly homogeneous site such as *Rylekæret.*

Treatment effects

In 2013 we included three sets of treated plots to the analysis, i.e., EX, SC and AC. All these treatments had lower CH_4 fluxes than the Cmain plots which can be considered as controls. In agreement with previous findings and the reasoning presented above the lower productivity in treated plots also resulted in lower CH_4 flux. We also see a strong correlation between NEE, GPP and CH_4 flux as well as between NEE, GPP and *Eriophorum* density. Several reasons for the lower productivity in treated plots can be suggested. Rhizomatous graminoids species such as *Carex aquatilis stans, Eriophorum angustifolium, Eriophorum scheuchzeri, Dupontia fisheri* and *Alopecurus alpinus* are known to be well adapted to grazing (Henry 1998). The species composition in *Rylekæret* thus supports an ecosystem that is heavily influenced by grazing and that is likely to respond when the grazing pressure changes. In support of this reasoning we also found a significantly lower density of total vascular plant tillers and *Eriophorum* in EX compared to Cmain plots. In early spring 2012 the effects of the snow depth from the EX and SC treatments and no effects of the fences were found (Schmidt unpublished data). Consequently the reason for the difference between Cmain and SC plots is not likely due to differences in snow depth. An alternative explanation could be found in the foraging behavior of muskoxen around the fences, which may affect the vegetation composition in these areas and offer some explanation to the lower plant productivity in EX or SC plots.

Also in AC plots we found an indication of vegetation change with a significantly lower number of *Eriophorum* tillers than in Cmain plots. In consistence with other results these plots also had lower NEE and CH_4 flux. If we perform a correlation analysis for only AC plots we find a very strong correlation between CH_4 flux-NEE (R=-0.894, *p*<0.001), CH_4-*Eriophorum* (R=0.770, *p*<0.009) and NEE-*Eriophorum* (R=-0.764, *p*<0.010). We speculate that also the change in AC plots may be related to decreased grazing within the plots due to the protruding chamber and lid. Supporting this speculation the AC plots with highest emission were installed several years later than the other AC plots and would thus have been influenced by decreased grazing for a longer period. The difference in mean CH_4 flux was 5-times higher in the newly installed plots and NEE and *Eriophorum* were 3-times higher. The water-table depth was somewhat higher in the new AC plots (1.4-times), which might also offer some explanation to the higher flux. We however found no significant correlation between WtD and CH_4 flux for AC plots. Mastepanov et al. (2013) also tested the relationship between the 5 original AC plots and found no clear relationship and CH_4 flux. We conclude that irrespective of treatments the common driving forces behind the lower CH_4 flux are lower plant productivity and substrate availability for acetoclastic methanogenesis in treated plots.

Conclusions

The main result from this study is the establishment of a very strong dependence of the spatial variability in CH_4 flux on plant productivity and carbon input of labile substrates for acetoclastic methanogenesis in pore water. The main driver of productivity and carbon input to the ecosystem is the vegetation composition, with high number of *Eriophorum* tillers leading to high input. The results also show that the main reason for decreased CH_4 flux in treated plots is decreased productivity and substrate availability due to suppressed growth of *Eriophorum* following treatment. The results indicate that future environmental changes in wet arctic ecosystems that affect the vegetation composition and productivity will have large impacts on their carbon balance and CH_4 flux, irrespective of whether these changes are driven directly by climate change or by indirect effects on for instance grazing pressure.

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References

Arndal M, Illeris L, Michelsen A, Albert K, Tamstorf M, Hansen B (2009) Seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five high arctic vegetation types. Arct Antarct Alp Res 41: 164–173. doi:10.1657/1938-4246-41.2.164

Bay C (1997) Floristic division and vegetation zonation of Greenland of relevance to a circumpolar arctic vegetation map. In: Proceedings of The Second Circumpolar Arctic Vegetation Mapping Workshop, Arendal, Norway, 19-25 May 1996, Occasional paper No. 52, Institute of Arctic and Alpine Research, University of Colorado, pp. 27-31.

Bellisario LM, Bubier JL, Moore TR, Chanton JP (1999) Controls on CH_4 emissions from a northern peatland. Glob Biogeochem Cycles 13:81-91.

Bubier JL (1995) The relationship of vegetation to methane emission and hyrdochemical gradients in northern peatlands. J Ecol 83:403-420.

Chanton JP, Bauer JE, Glaser PA, Siegel DI, Kelley CA, Tyler SC, Romanowicz EH, Lazrus A (1995) Radiocarbon evidence for the substrates supporting methane formation within northern Minnesota peatlands. Geochim Cosmochim Ac 59:3663-3668.

Chasar LS, Chanton JP, Glaser PH, Siegel DI, Rivers JS (2000) Radiocarbon and stable carbon isotopic evidence for transport and transformation of dissolved organic carbon, dissolved inorganic carbon, and CH_4 in a northern Minnesota peatland. Glob Biogeochem Cycles 14:1095-1108.

Christensen TR, Friborg T, Sommerkorn M, Kaplan J, Illeris L, Soegaard H, Nordstroem C, Jonasson S (2000) Trace gas exchange in a high arctic valley 1: Variations in CO_2 and CH_4 flux between tundra vegetation types. Glob Biogeochem Cycles 14:701-713.

Christiansen HH, Sigsgaard C, Humlum O, Rasch M, Hansen BU (2008) Permafrost and periglacial geomorphology at Zackenberg. Adv Ecol Res 40. doi:10.1016/S0065-2504(07)00007-4

Cicerone RJ, Oremland RS (1988) Biogeochemical aspects of atmospheric methane. Glob Biogeochem Cycles 2:299-327.

Dise NB, Gorham E, Verry ES (1993) Environmental factors controlling CH_4 emissions from peatlands in northern Minnesota, J Geophys Res 98:583–594.

Elberling B, Nordstrøm C, Grøndahl L, Søgaard H, Friborg T, Christensen TR, Ström L, Marchand F, Nijs I (2008) Higharctic soil CO_2 and CH_4 production controlled by temperature, water, freezing and snow, Elsevier Academic Press Inc, San Diego, Adv Ecol Res 40:441–472.

Falk JM, Schmidt NM, Ström L (2014) Effects of simulated increased grazing on carbon allocation patterns in a high arctic mire. Biogeochemistry 119:1-16.

Glaser PH, Chanton, JP (2009) Methane accumulation and release from deep peat: measurements, conceptual models, and biogeochemical significance, in: Carbon Cycling in Northern Peatlands-Baird. In: AJ, Belyea LR, Comas X, Reeve AS, Slater LD (ed), Washington DC, USA, American Geophysical Union, Geophys Mono Series 184:145–158.

Goulden ML, Crill PM (1997) Automated measurements of CO_2 exchange at the moss surface of a black spruce forest. Tree Physiol 17:537–542.

Greenup A, Bradford LM, McNamara AN, Ineson PP, Lee JA (2000) The role of *Eriophorum* vaginatum in CH_4 flux from an ombotrophic peatland. Plant Soil 227:265-272.

Gupta M (2012) Cavity-Enhanced Laser Absorption Spectrometry for Industrial Applications. Gases and Instrumentation. May/June 2012, pp 23-28.

Hansen BU, Sigsgaard C, Rasmussen L, Cappelen J, Hinkler J, Mernild SH, Petersen D, Tamstorf MP, Rasch M, Hasholt B (2008) Present-Day Climate at Zackenberg. Advances in Ecological Research, Elsevier Academic Press Inc, San Diego, pp 111-149.

Henry GR (1998) Environmental influences on the structure of sedge meadows in the Canadian High Arctic. Plant Ecol 134:119-129.

Jackson RB, Caldwell MM (1992) Shading and the capture of localized soil nutrients: nutrient contents, carbohydrates, and root uptake kinetics of a perennial tussock grass. Oecologia 91:457-462.

Joabsson A, Christensen TR (2001) Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. Global Change Biol 7:919-932.

Joabsson A, Christensen TR, Wallén B (1999a) Vascular plan controls on methane emissions from northern peatforming wetlands. Trends Ecol Evol 14:385-388.

Joabsson A, Christensen TR, Wallén B (1999b) Influence of vascular plant photosynthetic rate on CH_4 emission from peat monoliths from southern boreal Sweden. Polar Res 18:215-220.

Kristensen DK, Kristensen E, Forchhammer MC, Michelsen A, Schmidt NM (2011) Arctic herbivore diet can be inferred from stable carbon and nitrogen isotopes in C3 plants, faeces, and wool. Can J Zool 89:892-899.

Kuzyakov Y, Domanski G (2000) Carbon input by plants into the soil. Review. J Plant Nutr Soil Sc 163:421-431.

Mastepanov M, Sigsgaard C, Dlugokencky EJ, Houweling S, Ström L, Tamstorf MP, Christensen TR (2008) Large tundra methane burst during onset of freezing, Nature 456:628–631.

Mastepanov M, Sigsgaard C, Tagesson T, Ström L, Tamstorf MP, Lund M, Christensen TR (2013) Revisiting factors controlling methane emissions from high-Arctic tundra. Biogeosciences 10:5139-5158.

McGuire AD, Anderson LG, Christensen TR, Dallimore S, Guo L, Hayes DJ, Heimann M, Lorenson TD, Macdonald RW, Roulet N (2009) Sensitivity of the carbon cycle in the Arctic to climate change. Ecol Monogr 79:523–555.doi:10.1890/08-2025.1

Mikaloff Fletcher SE, Tans PP, Bruhwiler LM, Miller JB, Heimann M (2004) CH_4 sources estimated from atmospheric observations of CH_4 and its $^{13}C/^{12}C$ isotopic ratios: 2. Inverse modeling of CH_4 fluxes from geographical regions. Glob Biogeochem Cycles 18(4):GB4005. doi:10.1029/2004GB002224

Ping CL, Michaelson GJ, Jorgenson MT, Kimble JM, Epstein H, Romanovsky VE, Walker DA (2008) High stocks of soil organic carbon in the North American Arctic region. Nature Geosci 1:615–619. doi:10.1038/ngeo284

Post WM, Emanuel WR, Zinke PJ, Stangenberger AG (1982) Soil carbon pools and world life zones. Nature 298:156-159.

Ström L, Christensen TR (2007) Below ground carbon turnover and greenhouse gas exchanges in a sub-arctic wetland. Soil Biol Biochem 39:1689-1698.

Ström L, Ekberg A, Mastepanov M, Christensen TR (2003) The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Global Change Biol 9:1185-1192.

Ström L, Mastepanov M, Christensen TR (2005) Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. Biogeochemistry 75:65-82.

Ström L, Tagesson T, Mastepanov M, Christensen TR (2012) Presence of *Eriophorum* scheuchzeri enhances substrate availability and methane emission in an Arctic wetland. Soil Biol Biochem 45:61-70.

Tagesson T, Mastepanov M, Mölder M, Tamstorf MP, Eklundh L, Smith B, Sigsgaard C, Lund M, Ekberg A, Falk JM, Friborg T, Christensen TR, Ström L (2013) Modelling of growing season methane fluxes in a high-Arctic wet tundra ecosystem 1997-2010 using in situ and high-resolution satellite data. Tellus B 65:1-21.

Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, Zimov S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. Glob Biogeochem Cycles 23:GB2023. doi:10.1029/2008gb003327

Thomas KL, Benstead J, Davies KL, Lloyd D (1996) Role of wetland plants in the diurnal controls of CH_4 and CO_2 fluxes in peat. Soil Biol Biochem 28:17-23.

Torn MS, Chapin FS (1993) Environmental and biotic controls over methane flux from arctic tundra. Chemosphere 26:357-368.

Van Veen A, Merckx R, Van De Geijn SC (1989) Plant- and soil related controls of the flow of carbon from roots through the soil microbial biomass. Plant Soil 115:179-188.

Waddington JM, Roulet NT, Swanson RV (1996) Water table control of CH_4 emission enhancement by vascular plants in boreal peatlands. J Geophys Res 101:775-785.

Whiting GJ, Chanton JP (1992) Plant-dependent CH_4 emission in a subarctic Canadian fen. Glob Biogeochem Cycles 6:225-231.

Whiting GJ, Chanton JP (1993) Primary production control of methane emission from wetlands. Nature 364:794-795.

Zhu RB, Ma DW, Xu H (2014) Summertime N_2O, CH_4 and CO_2 exchanges from a tundra marsh and an upland tundra in maritime Antarctica. Atmos Environ 83:269-281. doi: 10.1016/j.atmosenv.2013.11.017

Figures and Tables

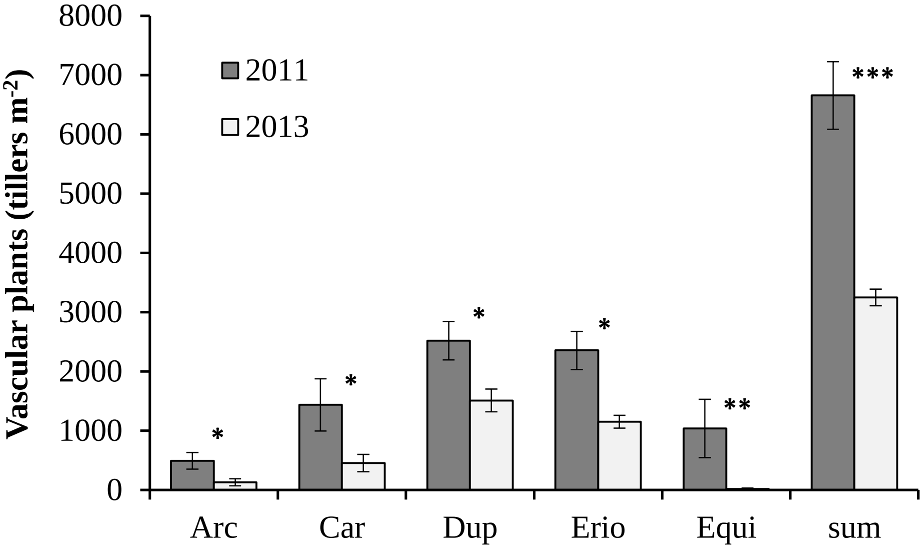

Fig. 1. The number of vascular plant tillers per m^2 (mean ± SE) of the vascular plant species, e.g., *Arctagrostis latifolia* (Arc), *Carex stans* (Carr), *Dupontia philosanta* (Dup), *Eriophorum scheuchzeri* (Erio), *Equisetum* spp. (Equi) and the sum of all plant tillers, in the Cmain plots in August 2011 (n=16) and 2013 (n=20). Asterisks indicate significant differences between 2011 and 2013, *** at the 0.001 level, ** at the 0.01 level and * at the 0.05 level.

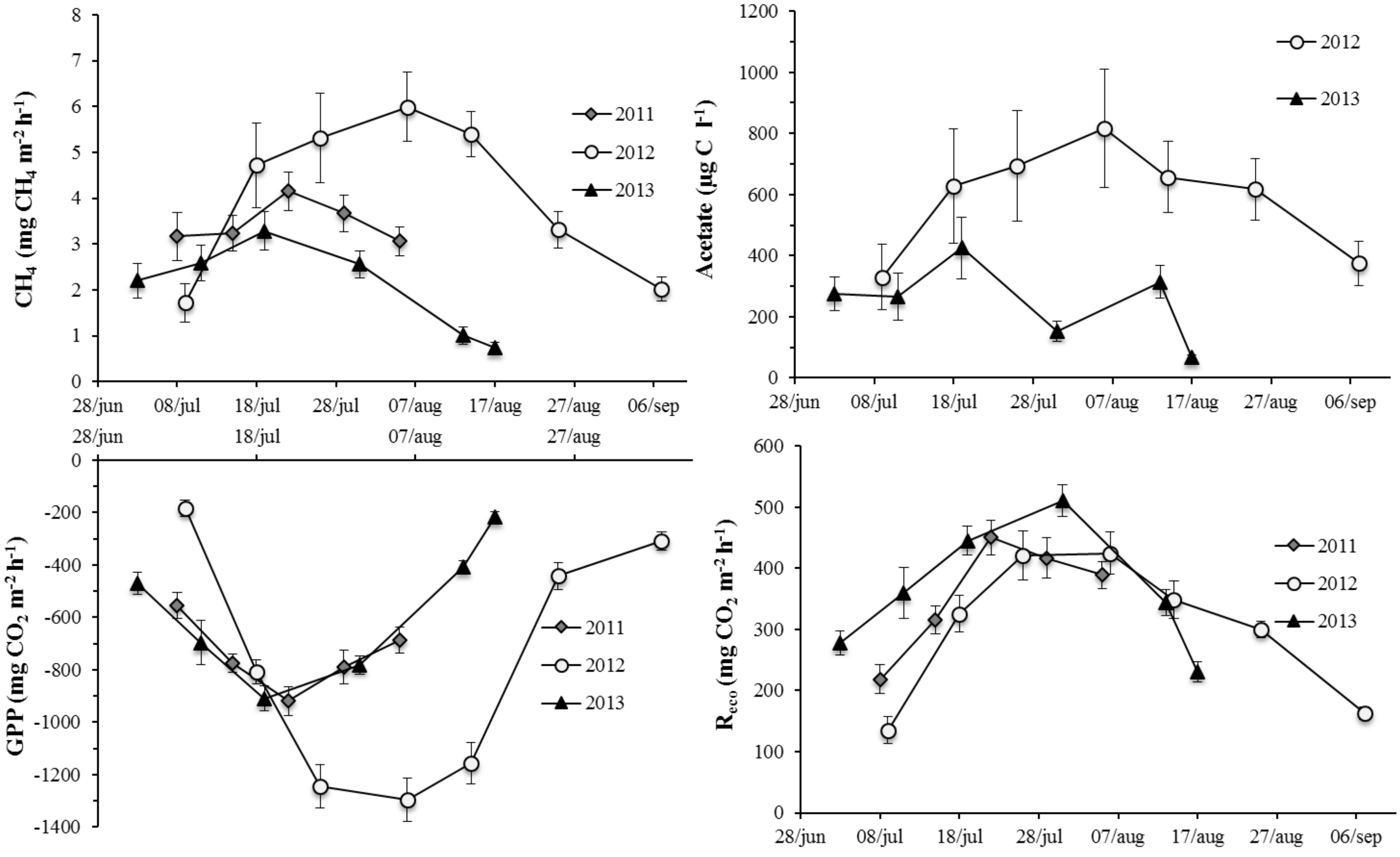

Fig. 2. The 2011 (n=16) , 2012 (n=20) and 2013 (n=20) full measurement period (mean ± SE) fluxes of CH_4 and CO_2 and the pore-water concentration of acetate (µg C l^{-1}) in the Cmain plots. The panels show; CH_4 flux, B) acetate, C) respiration (R_{eco}) and D) Gross Primary Production (GPP).

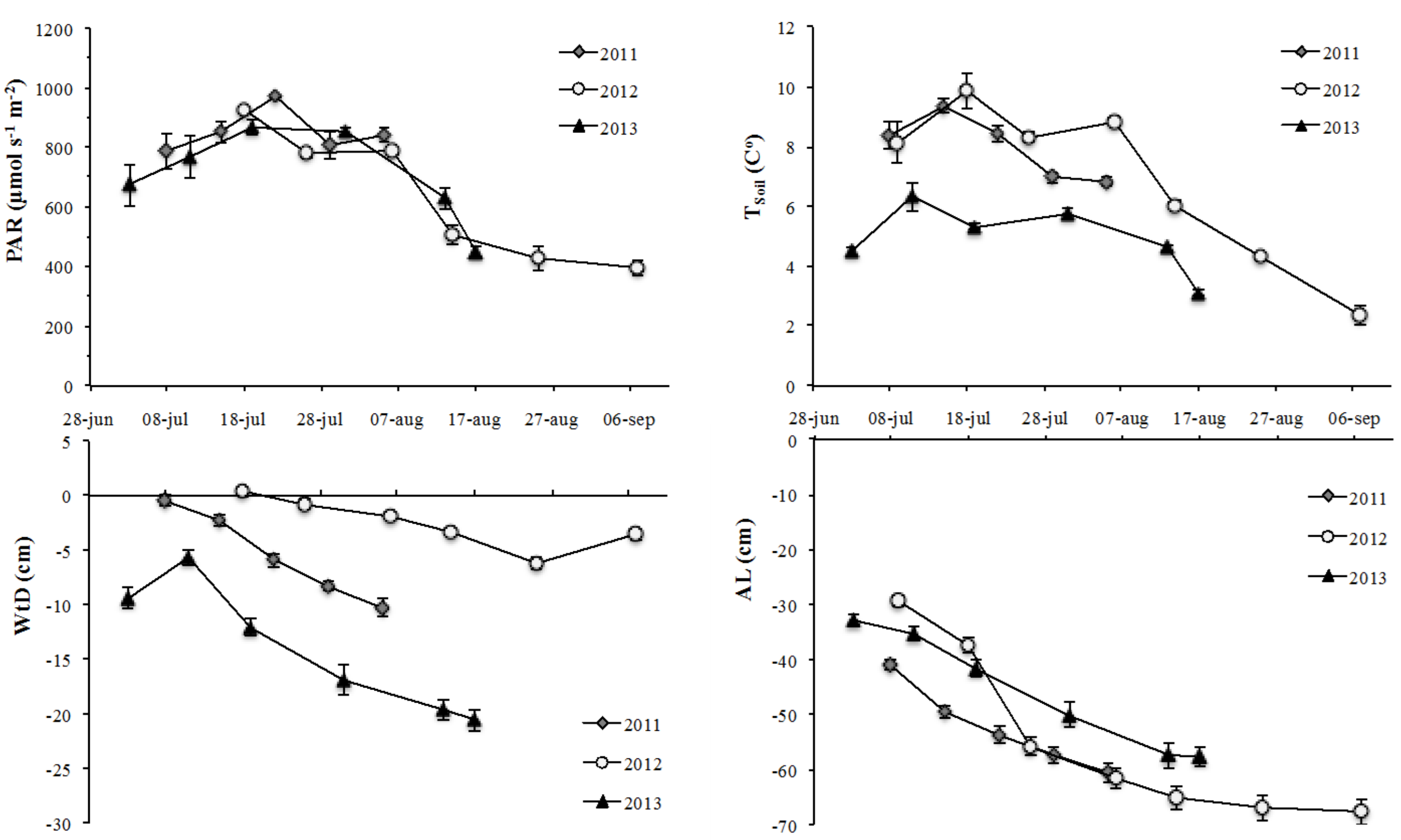

Fig. 3. The 2011 (n=16), 2012 (n=20) and 2013 (n=20) full measurement period (mean ± SE) environmental variables measured in the Cmain plots. The panels show; A) photosynthetically active radiation (PAR), B) soil temperature (T_{Soil}), C) active layer depth (AL, from peat surface) and D) water table depth (WtD, from peat surface).

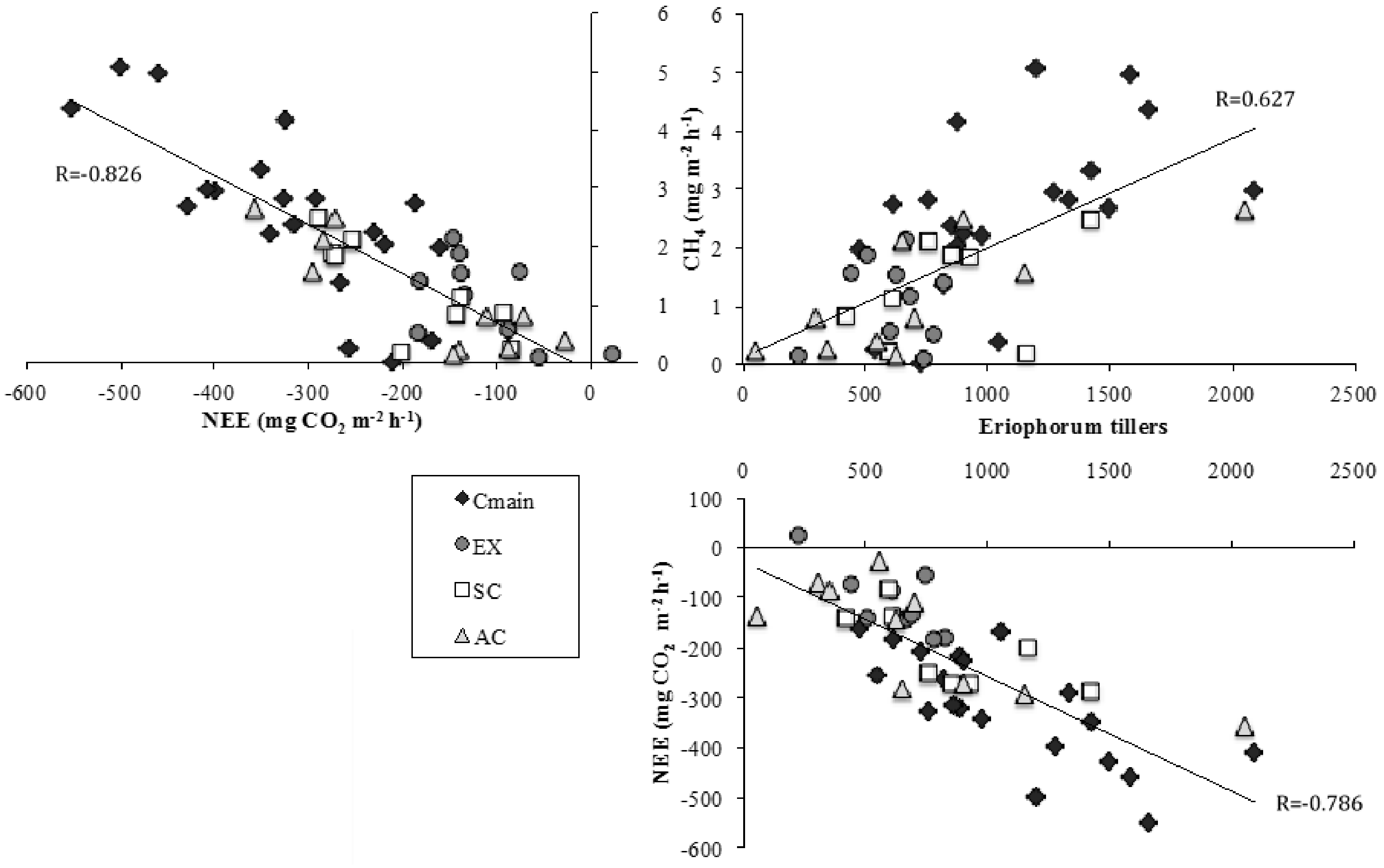

Fig. 4. The relationship between the mean measurement period flux of CH_4 and Net Ecosystem Exchange (NEE, panel A), CH_4 and number of *Eriophorum* tillers (panel B) and NEE and number of *Eriophorum* tillers (panel C) measured in Cmain (n=20), EX (n=10), SC (n=9) and AC (n=10) plots in 2013. The correlation lines and R-values represents all data points.

		CH_4	NEE	R_{eco}	GPP	OAs	Acetate	Wtd	AL	PAR	T_{Air}	T_{Soil}	Eriop	Dupon	Sum
Cmain plots:															
2011	max	6.15	-554	495	-959			8.7	62	824	9.9	8.8	4350	4131	11638
	mean	*3.21 b*	*-355 b*	*346 bc*	*-701 b*			*5.7 a*	*53 a*	*812 a*	*9.0 b*	*7.7 a*	*2355 a*	*2520 a*	*6657 a*
	min	0.72	-203	248	-497			2.2	39	792	8.5	6.9	31	0	2969
	SE	0.07	5	4	7			0.1	0.3	1	0.03	0.03	64	65	114
2012	max	11.58	-755	591	-1115	2692	2391	4.0	54	876	13.6	15.6			
	mean	*4.46 a*	*-546 a*	*325 ac*	*-871 a*	*816 a*	*674 a*	*0.8 b*	*44 b*	*801 a*	*12.3 a*	*10.2 b*			
	min	1.21	-371	225	-642	97	0	-2.3	32	656	10.6	6.6			
	SE	0.15	6	5	8	43	42	0.1	0.3	4	0.1	0.1			
2013	max	5.06	-552	562	-568	1239	919	16.5	51	969	11.5	6.6	2094	2813	4319
	mean	*2.58 b,A*	*-319 b,A*	*397 b,A*	*-310 b,A*	*557 a,B*	*369 a,B*	*11.9 c,A*	*41 b,A*	*793 a*	*9.4 b*	*5.4 c.A*	*1078 b,B*	*1572 b,A*	*3168 b,B*
	min	0.26	-160	227	-166	149	7	7.0	28	681	7.1	4.4	475	0	2406
	SE	0.07	6	4	6	16	14	0.2	0.2	6	0.1	0.04	21	35	28
EX plots:															
2013	max	2.12	22	453	-377	538	440	12.7	49			4.9	825	2019	2844
	mean	*1.09 B*	*-112 B*	*347 A*	*-459 B*	*247 AC*	*135 AC*	*11.7 A*	*42 A*			*4.4 B*	*611 AC*	*1599 A*	*2246 AC*
	min	0.06	-184	275	-600	115	9	10.7	35			3.9	225	406	1506
	SE	0.07	6	6	7	15	16	0.1	0.5			0.0	18	46	41
SC plots:															
2013	max	2.48	-84	485	-314	1121	521	19.0	60			6.8	1425	3013	4075
	mean	*1.22 B*	*-185 B*	*334 A*	*-527 B*	*416 BC*	*227 BC*	*15.1 B*	*47 B*			*5.3 A*	*827 BC*	*1506 A*	*2567 BC*
	min	0.17	-288	190	-773	83	9	12.3	27			4.2	419	0	988
	SE	0.08	8	10	17	33	20	0.3	0.9			0.1	31	124	108
AC plots:															
2013	max	2.45	-358					19.4					2050	1000	3175
	mean	*1.08 B*	*-179 B*					*13.2 AB*					*733*	*708 A*	*1843 BC*
	min	0.15	-28					9.5					50	450	975
	SE	0.28	36					1.0					176	59	259

Table 1. The maximum, mean (italic), minimum and standard error (SE) of the parameters measured (1 July to 10 August mean) in the Cmain plots in 2011 (n=16), 2012 (n=20) and 2013 (n=20) and in the EX (n=10), SC (n=9) and AC (n=10) plots in 2013. The table include; gas fluxes of CH_4 (mg CH_4 m^{-2} h^{-1}) and CO_2 (mg CO_2 m^{-2} h^{-1}), e.g., Net Ecosystem Exchange (NEE), respiration (R_{eco}) and photosynthesis (GPP), pore water concentration (µg C l^{-1}) of total organic acids (OAs) and acetate, air (T_{Air}) and soil (T_{Soil}, measured at 10 cm) temperature (°C), water table (WtD) and active layer (AL) depth (cm from peat surface), photosynthetically active radiation (PAR, µmol s^{-1} m^{-2}) and tillers of *Eriophorum scheuchzeri* (Erio) and all vascular plant species (tillers m^{-2}). Different lowercase letters indicate significant differences between the years in the Cmain plot means and different capital letters indicate significant differences between the Cmain, EX, SC and AC plots in 2013.

2011		CH_4^m	NEE^m	R_{eco}^m	GPP^m	**2012**		CH_4^m	NEE^m	R_{eco}^m	GPP^m
NEE^m	R	**-0.633**	1			NEE^m	R	-0.174	1		
	p	*0.004*					*p*	*0.477*			
R_{eco}^m	R	0.249	-0.388	1		R_{eco}^m	R	**0.672**	0.123	1	
	p	*0.304*	*0.101*				*p*	*0.002*	*0.615*		
GPP^m	R	**-0.559**	**0.880**	**-0.779**	1	GPP^m	R	**-0.587**	**0.759**	**-0.552**	1
	p	*0.013*	*0.000*	*0.000*			*p*	*0.008*	*0.000*	*0.014*	
Acetate^m	R	-	-	-	-	Acetate^m	R	**0.680**	0.038	**0.647**	-0.393
	p						*p*	*0.001*	*0.878*	*0.003*	*0.096*
OAs^m	R	-	-	-	-	OAs^m	R	**0.677**	0.022	**0.667**	-0.419
	p						*p*	*0.001*	*0.928*	*0.002*	*0.074*
WtD^m	R	0.171	-0.332	-0.084	-0.182	WtD^m	R	0.349	-0.458	0.314	**-0.590**
	p	*0.485*	*0.166*	*0.733*	*0.455*		*p*	*0.143*	*0.049*	*0.191*	*0.008*
AL^m	R	**0.740**	-0.287	0.124	-0.259	AL^m	R	0.231	0.384	-0.091	0.382
	p	*0.000*	*0.234*	*0.612*	*0.284*		*p*	*0.341*	*0.104*	*0.712*	*0.106*
PAR^m	R	**-0.692**	0.253	-0.335	0.345	PAR^m	R	0.143	-0.387	0.387	**-0.579**
	p	*0.001*	*0.295*	*0.160*	*0.148*		*p*	*0.559*	*0.102*	*0.101*	*0.009*
T_{air}^m	R	-0.393	0.454	-0.446	**0.539**	T_{air}^m	R	0.283	-0.348	0.491	**-0.615**
	p	*0.096*	*0.051*	*0.055*	*0.017*		*p*	*0.240*	*0.144*	*0.033*	*0.005*
T_{soil}^m	R	-0.199	0.252	-0.102	0.224	T_{soil}^m	R	0.344	0.079	-0.100	0.132
	p	*0.415*	*0.297*	*0.677*	*0.356*		*p*	*0.149*	*0.748*	*0.683*	*0.590*
Erioph.^{m}	R	0.211	**-0.516**	**0.643**	**-0.738**	*Erioph.*^{m}	R	-	-	-	-
	p	*0.449*	*0.049*	*0.010*	*0.002*		*p*				
Dupont.^{m}	R	-0.092	0.046	0.367	-0.176	*Dupont.*^{m}	R	-	-	-	-
	p	*0.744*	*0.871*	*0.179*	*0.530*		*p*				
Carex^m	R	0.387	0.055	0.074	-0.003	*Carex*^{m}	R	-	-	-	-
	p	*0.154*	*0.847*	*0.793*	*0.991*		*p*				
Arctagr.^{m}	R	-0.084	-0.255	0.442	-0.462	*Arctagr.*^{m}	R	-	-	-	-
	p	*0.807*	*0.449*	*0.173*	*0.153*		*p*				
Plants^m	R	0.289	-0.264	**0.677**	**-0.576**	Plants^m	R	-	-	-	-
	p	*0.297*	*0.342*	*0.006*	*0.025*		*p*				

Table 2. The correlation matrix between the parameters measured (1 July to 10 August mean) on the Cmain plots (main denoted by superscript m) in 2011 (n=16) and 2012 (n=20). The matrix include; gas fluxes of CH_4 (mg CH_4 m^{-2} h^{-1}) and CO_2 (mg CO_2 m^{-2} h^{-1}), e.g., Net Ecosystem Exchange (NEE), respiration (R_{eco}) and photosynthesis (GPP) and, air (T_{Air}) and soil (T_{Soil}) temperature (°C), photosynthetically active radiation (PAR, µmol s^{-1} m^{-2}) and water table (WtD) and active layer (AL) depth. In 2011 the matrix also include the number of tillers per m^2 of the dominant vascular plant species, e.g., *Eriophorum scheuchzeri*, *Dupontia philosanta*, *Carex sp.*, and the sum of all plant tillers and in 2012 the total concentration (µg C l^{-1}) of organic acids (OAs) and acetate in pore-water. Values represent the correlation coefficient (R) and significance level of the correlation (*p*), $R \geq 0.5$ in bold formatting.

2013		CH_4^m	NEE^m	R_{eco}^m	GPP^m	Acetate^m	OAs^m	**2013**		CH_4	NEE	R_{eco}	GPP	Acetate	OAs
NEE^m	R	**-0.759**	1					NEE	R	**-0.826**	1				
	p	*0.000*							*p*	*0.000*					
R_{eco}^m	R	**0.685**	**-0.816**	1				R_{eco}	R	**0.711**	**-0.646**	1			
	p	*0.001*	*0.000*						*p*	*0.000*	*0.000*				
GPP^m	R	**-0.762**	**0.963**	**-0.941**	1			GPP	R	**-0.847**	**0.940**	**-0.867**	1		
	p	*0.000*	*0.000*	*0.000*					*p*	*0.000*	*0.000*	*0.000*			
Acetate^m	R	**0.737**	**-0.764**	**0.700**	**-0.772**	1		Acetate	R	**0.704**	**-0.648**	**0.528**	**-0.658**	1	
	p	*0.000*	*0.000*	*0.001*	*0.000*				*p*	*0.000*	*0.000*	*0.001*	*0.000*		
OAs^m	R	**0.661**	**-0.692**	**0.565**	**-0.667**	**0.966**	1	OAs	R	**0.595**	**-0.564**	0.353	**-0.526**	**0.952**	1
	p	*0.002*	*0.001*	*0.009*	*0.001*	*0.000*			*p*	*0.000*	*0.000*	*0.027*	*0.001*	*0.000*	
WtD^m	R	0.017	-0.045	0.126	-0.032	0.355	0.367	WtD	R	-0.172	0.158	-0.162	0.105	-0.268	-0.262
	p	*0.943*	*0.852*	*0.596*	*0.893*	*0.124*	*0.112*		*p*	*0.252*	*0.295*	*0.323*	*0.526*	*0.099*	*0.107*
AL^m	R	0.032	-0.315	**-0.561**	0.445	-0.425	-0.314	AL	R	0.108	-0.152	0.014	0.085	0.117	0.134
	p	*0.895*	*0.175*	*0.010*	*0.050*	*0.062*	*0.178*		*p*	*0.474*	*0.315*	*0.935*	*0.605*	*0.479*	*0.417*
PAR^m	R	0.490	-0.453	**0.664**	**-0.573**	0.453	0.221								
	p	*0.028*	*0.045*	*0.001*	*0.008*	*0.045*	*0.350*								
T_{air}^m	R	0.282	-0.396	**0.590**	**-0.505**	0.474	0.271								
	p	*0.228*	*0.084*	*0.006*	*0.023*	*0.035*	*0.247*								
T_{soil}^m	R	0.404	-0.334	0.473	-0.415	**0.663**	**0.613**	T_{soil}	R	0.374	-0.427	0.194	-0.365	**0.611**	**0.659**
	p	*0.077*	*0.150*	*0.035*	*0.069*	*0.001*	*0.004*		*p*	*0.019*	*0.007*	*0.236*	*0.022*	*0.000*	*0.000*
Erioph.^{m}	R	**0.536**	**-0.741**	**0.718**	**-0.767**	**0.850**	**0.834**	*Erioph.*	R	**0.627**	**-0.786**	**0.549**	**-0.774**	**0.715**	**0.732**
	p	*,015*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*		*p*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*
Dupont.^{m}	R	0.141	-0.256	0.189	-0.237	-0.151	-0.291	*Dupont.*	R	0.170	-0.137	0.065	-0.069	-0.144	-0.228
	p	*0.552*	*0.276*	*0.426*	*0.314*	*0.524*	*0.214*		*p*	*0.249*	*0.352*	*0.700*	*0.680*	*0.387*	*0.168*
Carex^m	R	-0.151	0.377	-0.472	0.440	-0.335	-0.167	*Carex*	R	0.156	-0.129	-0.027	-0.040	-0.105	0.014
	p	*0.525*	*0.101*	*0.036*	*0.052*	*0.148*	*0.482*		*p*	*0.318*	*0.408*	*0.870*	*0.813*	*0.529*	*0.934*
Arctagr.^{m}	R	0.151	-0.393	0.499	-0.461	0.472	0.457	*Arctagr.*	R	0.121	-0.315	0.369	-0.404	0.486	0.488
	p	*0.525*	*0.087*	*0.025*	*0.041*	*0.035*	*0.043*		*p*	*0.445*	*0.042*	*0.023*	*0.012*	*0.002*	*0.002*
Plants^m	R	**0.518**	**-0.685**	**0.516**	**-0.640**	0.317	0.286	Plants	R	**0.642**	**-0.696**	0.440	**-0.626**	0.274	0.275
	p	*0.019*	*0.001*	*0.020*	*0.002*	*0.173*	*0.221*		*p*	*0.000*	*0.000*	*0.006*	*0.000*	*0.096*	*0.095*

Table 3. The correlation matrix between the parameters measured in an arctic fen in 2013 (1 July to 10 August) on the Cmain (n= 20) plots (main denoted by superscript m, left part of table) and in the full data set (right part of table) including Cmain, EX (n=10), SC (n=9) and AU (n=10) plots. The matrix include; gas fluxes of CH_4 (mg CH_4 m^{-2} h^{-1}) and CO_2 (mg CO_2 m^{-2} h^{-1}), e.g., Net Ecosystem Exchange (NEE), respiration (R_{eco}) and photosynthesis (GPP) and pore-water concentration (µg C l^{-1}) of total organic acids (OAs) and acetate, air (T_{Air}) and soil (T_{Soil}) temperature (°C), water table (WtD) and active layer (AL) depth, photosynthetically active radiation (PAR, µmol s^{-1} m^{-2}) and number of tillers per m^2 of the dominant vascular plant species, e.g., *Eriophorum scheuchzeri*, *Dupontia philosanta*, *Carex sp.*, and the sum of all plant tillers. Values represent the correlation coefficient (R) and significance level of the correlation (*p*). R≥0.5 in bold formatting.

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