

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

Julie Maria Falk · Niels Martin Schmidt ·
Lena Ström

Received: 3 October 2013 / Accepted: 23 January 2014 / Published online: 7 February 2014
© The Author(s) 2014. This article is published with open access at Springerlink.com

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 CO₂ decreased in clipped plots (mean total decrease for the three following years was 35 %). One year into the experiment a significantly lower CH₄ 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 CH₄ production was observed (27 % reduction). NV plots had a mean decrease in CO₂ uptake of 113 %, a 62 % decrease in ecosystem respiration and an 84 % decrease in CH₄ 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 CO₂ uptake leading to lower production of substrate for CH₄ formation and in lower CH₄ emission.

Responsible Editor: E. Matzner.

J. M. Falk (✉) · L. Ström
Department of Physical Geography and Ecosystem
Science, Lund University, Sölvegatan 12, 223 62 Lund,
Sweden
e-mail: julie_maria.falk@nateko.lu.se

N. M. Schmidt
Department of Bioscience, Aarhus University,
Frederiksborgvej 399, 4000 Roskilde, Denmark

N. M. Schmidt
Arctic Research Centre, Aarhus University, C.F. Møllers
Allé 8, 8000 Aarhus C, Denmark

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 (Olf et al. 2002), which makes it important to consider the influence they have on the ecosystem. Removal of

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 CH₄ production prevails under wet conditions. Arctic wetland ecosystems produce approximately 40 % of the natural global emissions of CH₄ (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 CH₄ production and emission, only few studies have focused on the effects of herbivory on CH₄ fluxes in the arctic and sub-alpine regions (Sjögersten et al. 2011, 2012, respectively). These studies showed no effect of herbivory on CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CO₂ fluxes, CH₄ 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 CH₄ 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 CH₄ and CO₂ 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 CO₂ and CH₄ 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 m³, and the area of the aluminum base was 0.156 m². 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 CH₄ fluxes were measured by a LGR RMT-200 Fast Methane Analyser (DLT200, Los Gatos Research, USA) and an infrared CO₂ 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 CO₂ and CH₄ were simultaneously measured by a portable Fourier transform infrared (FTIR) spectrometer (Gasmeter Dx 40-30, Gasmeter 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 CH₄ and CO₂ 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 CH₄ 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 CO₂ and CH₄ 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 CH₄ or CO₂. Since we found a strong significant correlation ($R = 0.967$, $p < 0.0001$) between CH₄ fluxes measured during light and dark measurement for individual plots, the mean of these two measurements were calculated and used in the CH₄ flux calculations. NEE was the CO₂ 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 QT_i data-logger (EMS Brno). Additionally, ambient incoming PAR and air temperature (T_a) were logged hourly (Minikin QT_i) at 1 m from the ground surface throughout the growing season in 2011 and 2012. PAR and T_a 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 CO₂ data analyses. Following the same reasoning, CH₄ fluxes were included in the data treatment as long as the ecosystem was emitting measurable fluxes. The use of different time periods for CO₂ and CH₄ 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 CH₄ 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

CH₄ and CO₂ fluxes

CH₄

For each individual measurement year (2010–2012) a clear significant difference ($p \leq 0.001$) between the

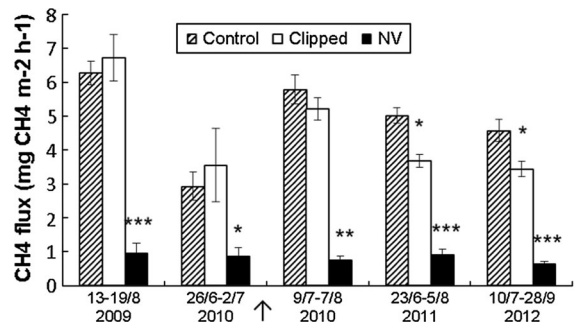


Fig. 1 The mean measured CH₄ fluxes (mg CH₄ m⁻² h⁻¹ ± SE, 2009 *n* = 10, 2010 (before clipping experiment) *n* = 15, 2010 (after clipping experiment) *n* = 35, 2011 *n* = 60, 2012 *n* = 85) for control (*striped squares*), clipped (*open squares*) and no vascular plants (NV) (*closed squares*) plots. Significant differences (repeated measures ANOVA) between control and treatment plots are indicated with *asterisks* above the *bars*, ****p* ≤ 0.001, ***p* ≤ 0.01 and **p* ≤ 0.05. Note the varying time periods between the years. The arrow indicates the start of clipping experiment on the 02/07/2010

CH₄ 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 CH₄ 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 CH₄ flux between the plots (Fig. 1). Additionally, there was no significant difference ($p = 0.571$) in the mean CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ emission normally seen following the onset of the growing season started on DOY 190 while in the previous years started around DOY 170.

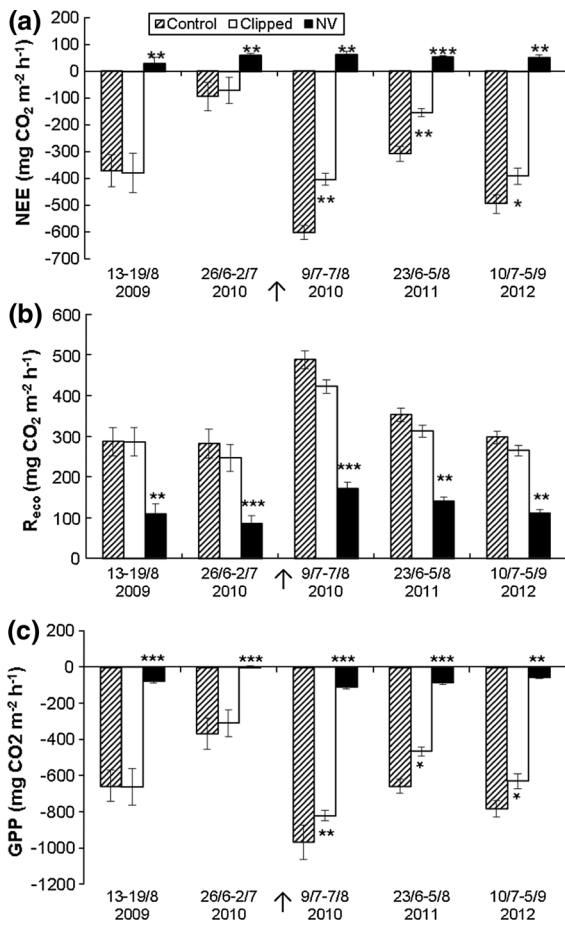


Fig. 2 The mean measured NEE (a), R_{eco} (b) and GPP (c) ($\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1} \pm \text{SE}$, 2009 $n = 10$, 2010 (before clipping experiment) $n = 15$, 2010 (after clipping experiment) $n = 35$, 2011 $n = 60$, 2012 $n = 60$) for control, clipped and no vascular plants (NV) 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

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 $310 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ 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

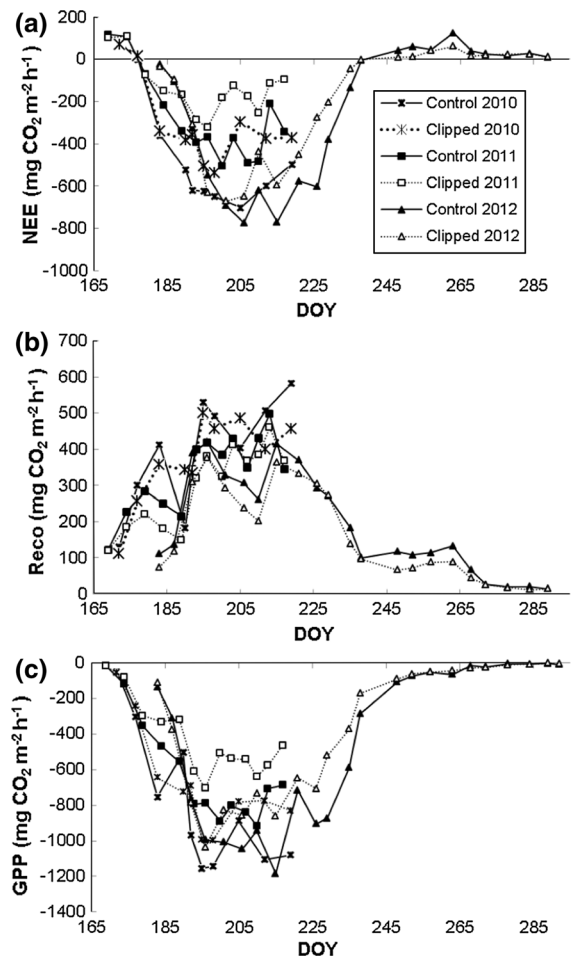


Fig. 3 NEE (a), R_{eco} (b) and GPP (c) ($\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) for control and clipped plots from the whole measuring period in 2010, 2011 and 2012. The time is shown as day of year (DOY). Each data point is an average of each treatment (five plots). The clipping was performed in 2010 on DOY 183 and 198, in 2011 on DOY 196 and 213 (DOY) and in 2012 on DOY 201 and 226

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 CO₂ 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 CO₂ 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 0–2402, 4.1–2402 and 2.7–342.6 for 2010, 2011 and 2012, respectively.

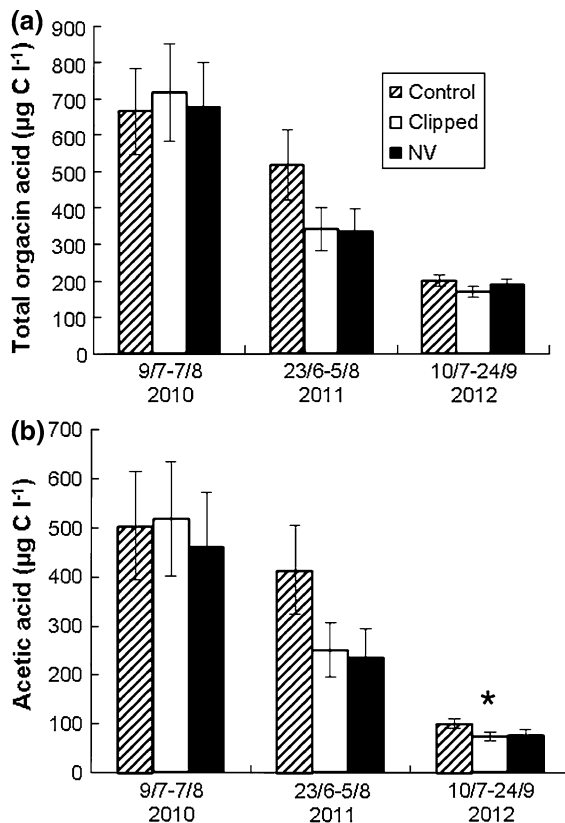


Fig. 4 The mean concentration ($\mu\text{g C l}^{-1} \pm \text{SE}$, 2010 $n = 45$, 2011 $n = 60$, 2012 $n = 65$) of organic acid (a) and acetic acid (b) in control, clipped and plots with no vascular plants (NV). Significant differences (repeated measures ANOVA) between control and treatment plots are 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

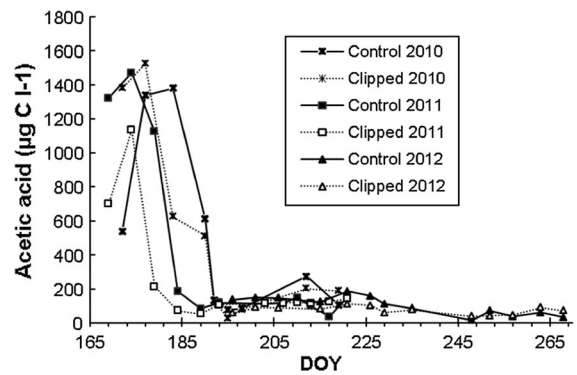


Fig. 5 The measured acetic acid concentration ($\mu\text{g C l}^{-1}$) in control and clipped plots, for the whole measuring period in 2010, 2011 and 2012. The time is shown as day of year (DOY). Each data point is an average of five plots. The clipping was performed in 2010 on DOY 183 and 198, in 2011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

treatment and year substantially higher in the beginning of the growing season (Fig. 5).

Species composition

During the vegetation survey, the main vascular plant species within the plots were *Carex stans* 42 ± 2.5 (% \pm 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 $0.7\text{ }^\circ\text{C}$) 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

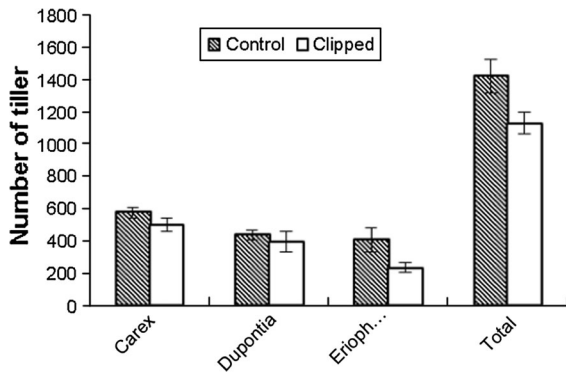


Fig. 6 Vegetation analyses from the experiment plots in NE Greenland, analyses are made in 2011. The dominating species in the plots were: *Carex stans*, *Dupontia pilosantha* and *Eriophorum scheuchzeri*. The figure shows the mean number of tiller of the three dominating vascular plant species and the total number of tillers \pm 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 T_s ($R = 0.888, p = 0.001$) 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 ($R = 0.489, p = 0.182$), T_a and PAR ($R = 0.296, p = 0.440$), T_a and WtD ($R = -0.162, p = 0.678$), T_a 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 ($^{\circ}\text{C}$) 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 ($^{\circ}\text{C}$) mean	T_s	6.6	7.6	6.5
Photosynthetically active radiatio ($\mu\text{mol}^{-1} \text{m}^{-2} \text{s}^{-1}$) 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)

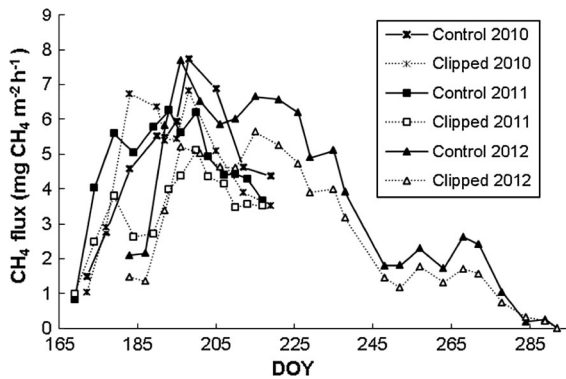


Fig. 7 CH_4 fluxes ($\text{mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$) for control and clipped plots from the whole measuring period in 2010, 2011 and 2012. The time is shown as day of year (DOY). Each data point is an average of each treatment (five plots). The clipping was performed in 2010 on DOY 183 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 therefore 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 Rues 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 hypothesize 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 enclosure experiment in an area with geese and very low CH_4 fluxes (-0.046 to $0.025 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$), 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 CH₄ 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 CH₄ 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 CH₄ 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 than 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.

Acknowledgments This study was carried out as part of the strategic research program: Biodiversity and Ecosystem services in a Changing Climate (BECC), Lund University and the Lund University Center for Studies of Carbon Cycle and Climate Interactions (LUCCI). The research was financed by BECC and INTERACT (International Network for Terrestrial Research and Monitoring in the Arctic). We are also grateful to Aarhus University, Denmark and personnel at Zackenberg field station for logistical support, to Marcin Jackowicz-Korczyński for support with the organic acid analysis and to Caroline Jonsson for field and laboratory assistance in 2012.

Open Access This article is distributed under the terms of the Creative Commons Attribution License which permits any use, distribution, and reproduction in any medium, provided the original author(s) and the source are credited.

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) Controls 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. Variations in 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](https://doi.org/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) CH₄ emission from a hollow-ridge complex in a raised bog: the role of CH₄ production and oxidation. *Biogeochemistry* 51(1):91–112. doi:[10.1023/a:1006351118347](https://doi.org/10.1023/a:1006351118347)
- Frenzel P, Rudolph J (1998) Methane emission from a wetland plant: the role of CH₄ oxidation in *Eriophorum*. *Plant Soil* 202(1):27–32. doi:[10.1023/A:1004348929219](https://doi.org/10.1023/A:1004348929219)
- Gounou C, Bousserhine 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](https://doi.org/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](https://doi.org/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 CH₄ flux from an ombrotrophic peatland. *Plant Soil* 227(1–2):265–272. doi:[10.1023/A:1026573727311](https://doi.org/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](https://doi.org/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, Elbering 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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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 C₃ plants, faeces, and wool. *Can J Zool* 89(10):892–899. doi:[10.1139/z11-073](https://doi.org/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](https://doi.org/10.1890/08-2025.1)
- 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. *Glob Biogeochem Cycles* 18(4):GB4005. doi:[10.1029/2004GB002224](https://doi.org/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](https://doi.org/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](https://doi.org/10.1078/1433-8319-00064)
- Myers-Smith IH, Hik DS, Forbes BC, Wilmsking M, Hallinger M, Lantz T, Blok D, Sass-Klaassen U, Tape KD, MacIsaac-Fauria M, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaeppman-Strub G, Wipf S, Rixen C, Ménard CB, Venn S, Goetz S, Andreu-Hayles L, Elmen-dorf 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](https://doi.org/10.1088/1748-9326/6/4/045509)
- Oloff H, Ritchie ME, Prins HHT (2002) Global environmental controls of diversity in large herbivores. *Nature* 415(6874):901–904. doi:[10.1038/415901a](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/10.1080/14888386.2012.712093)
- Sjögersten S, Van der Wal R, Woodin SJ (2008) Habitat type determines herbivory controls over CO₂ 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](https://doi.org/10.1007/s10533-010-9516-4)
- Sjögersten S, Yanez-Serrano A, Llorba 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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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](https://doi.org/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 CH₄ emission enhancement by vascular plants in boreal peatlands. *J Geophys Res* 101(D17):22775–22785. doi:[10.1029/96JD02014](https://doi.org/10.1029/96JD02014)
- 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, 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