

Recovery of ecosystem carbon fluxes and storage from herbivory

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Abstract The carbon (C) sink strength of arctic tundra is under pressure from increasing populations of arctic breeding geese. In this study we examined how CO₂ and CH₄ fluxes, plant biomass and soil C responded to the removal of vertebrate herbivores in a high arctic wet moss meadow that has been intensively used by barnacle geese (*Branta leucopsis*) for ca. 20 years. We used 4 and 9 years old grazing exclosures to investigate the potential for recovery of ecosystem function during the growing season (July 2007). The results show greater above- and below-ground vascular plant biomass within the grazing exclosures with graminoid biomass being most responsive to the removal of herbivory whilst moss

biomass remained unchanged. The changes in biomass switched the system from net emission to net uptake of CO₂ (0.47 and $-0.77 \mu\text{mol m}^{-2} \text{s}^{-1}$ in grazed and exclosure plots, respectively) during the growing season and doubled the C storage in live biomass. In contrast, the treatment had no impact on the CH₄ fluxes, the total litter C pool or the soil C concentration. The rapid recovery of the above ground biomass and CO₂ fluxes demonstrates the plasticity of this high arctic ecosystem in terms of response to changing herbivore pressure.

Keywords Carbon · Geese · Herbivory · Methane · Recovery · Tundra · Vegetation

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Introduction

Tundra ecosystems can store substantial amounts of carbon (Ping et al. 2008; Tarnocai et al. 2009). Across the landscape, wet areas have the greatest CO₂ assimilation (Giblin et al. 1991; Sjögersten et al. 2006) due to low decomposition resulting in the greatest C storage in wet areas (Tarnocai et al. 2009). Although climate change is considered the greatest threat to arctic ecosystems and the arctic C store (ACIA 2005), herbivory has been shown to impact the C uptake more strongly than elevated temperature, particularly in wet ecosystems (Sjögersten et al. 2008). Indeed, herbivores have been found to impact many aspects of arctic ecosystem function e.g. net

primary productivity, litter decomposition and nutrient cycling through inputs from faeces (Stark et al. 2003; Semmartin et al. 2004; Jefferies et al. 2006; Bråthen et al. 2007; Sjögersten et al. 2008).

Geese are currently one of the most abundant groups of herbivores in the Arctic (Van der Wal 2005) and goose populations continue to increase due to changes in both land use and climate in their temperate overwintering and migration areas as well as in their breeding areas in the North (Abraham et al. 2005; Fox et al. 2005; Gauthier et al. 2005; Kéry et al. 2006).

Increases in the number of arctic breeding geese have dramatically reduced ecosystem productivity of coastal marshes along the Hudson Bay area in Canada (Jefferies et al. 2006). Here grubbing by geese has caused complete loss of the vegetation cover and organic horizon and although the impact of this degradation on C storage has not been studied it is likely to be severe. In the case of ecosystems that have been severely degraded as a consequence of overgrazing a new stable state might establish (Jefferies et al. 2006), with recovery of the vegetation being a slow process even if the grazing pressure is reduced (Handa and Jefferies 2000; Handa et al. 2002). However, in areas where the impact of herbivory does not result in an alternative stable state devoid of vegetation but merely a shift from one vegetation state to another (e.g. from grass dominated to moss dominated), the ecosystem might be able to change relatively quickly in response to reduced grazing pressure (Van der Wal 2006).

Such long-term and large-scaled ecosystem degradation as witnessed along the Hudson Bay coast has not yet been observed in the European Arctic (Jefferies and Drent 2006). However, on a smaller scale, ecosystem degradation caused by grubbing by geese is also evident on Spitsbergen, linked to the increase in pink-footed geese (*Anser brachyrhynchus*) in the area (Speed et al. 2009). Furthermore, in studies on Spitsbergen grazing by barnacle geese (*Branta leucopsis*) has been found to reduce the CO₂ uptake of wet tundra (Sjögersten et al. 2008) and grubbing for below ground plant tissue by pink-footed geese during spring reduced the CO₂ uptake of wet tundra as well as the C storage in both plant biomass and the soil organic horizon (Van der Wal et al. 2007).

A key issue not yet addressed is the recovery capacity of the C fluxes of arctic tundra if grazing

was removed through for example predation or density dependent population dynamics. In relation to goose grazing it is plausible that the recovery of the C uptake rate will be closely related to the extent the vegetation recovers since the above ground biomass appears to be the strongest driver of the CO₂ uptake (Sjögersten et al. 2008; Van der Wal et al. 2007). If the vegetation recovers quickly in response to reduced grazing pressure then the CO₂ sink strength could potentially be restored over a relatively short time period should grazing pressure drop. If the grazing or grubbing on the other hand is associated with substantial C loss from the soil through erosion processes (McLaren and Jefferies 2004; Van der Wal et al. 2007), recovery of the soil C storage is likely to be slow.

In this study, we use Ny-Ålesund, Spitsbergen, as a model system to quantify the recovery potential of ecosystem function, compared to ungrazed areas on Spitsbergen, following long term intensive goose grazing. This site has been heavily grazed by geese for more than 20 years (Tombre et al. 1998), over which period the vegetation has changed substantially and hence provides an ideal location to investigate the recovery of C uptake rates following goose removal and explore the mechanisms by which the presence or absence of geese drives C dynamics in arctic ecosystems.

Only limited information exists on grazing impacts on methane (CH₄) fluxes in arctic ecosystems despite the importance of CH₄ for the balance of sinks and sources of radiatively active trace gases in tundra ecosystems. In temperate wetland, grazing by swans has been found to reduce CH₄ production and increase CH₄ uptake in response to bioturbation and increased aeration of the soil surface (Bodelier et al. 2006) indicating that herbivores may be important drivers of CH₄ fluxes in wetland systems. Additionally, herbivores may also impact on CH₄ fluxes indirectly through their impact on the vegetation (Torn and Chapin 1993; Joabsson et al. 1999; Kutzbach et al. 2004).

In this study we tested the following overarching hypothesis: Removing herbivores from grazed moss meadows will increase the C uptake during the growing season and ecosystem C storage in standing biomass to levels similar to ungrazed moss meadow areas. We also hypothesise that increased below ground C inputs resulting from greater plant biomass

stimulate the microbial biomass and dissolved organic C (DOC) in the soil. In contrast, we expect that the total soil C concentrations remain unchanged since we anticipate this pool to respond only over longer time scales. In order to test these hypotheses we measured CO₂ and CH₄ fluxes, standing biomass and litter C pools, microbial biomass and DOC and soil C concentrations in established (4 and 9 years old) grazing exclosures and their adjacent controls.

Materials and methods

Site description

This research was carried out on high arctic Svalbard, Norway, in and near the small settlement of Ny-Ålesund on the island of Spitsbergen. The Ny-Ålesund area, situated on the shores of Kongsfjorden on the west coast (78°55'N, 11°56'E), has supported a breeding population of barnacle geese (*Branta leucopsis*) for more than 20 years. Over this period the number of breeding geese increased from the first pair in 1980 to a peak of 329 nests in 1997 (Tombre et al. 1998). Most birds breed on small islands in the fjord but both families and non-breeding birds rely heavily on the Ny-Ålesund area throughout summer for foraging. We focussed our research on two locations, Solvatnet and Thiisbukta, which are on either side of Ny-Ålesund and highly favoured by geese; both locations represent wet tundra with similar ecosystem characteristics and goose utilisation levels. The growth of the goose population has strongly impacted the vegetation in the area, leading to the suppression of both grasses and herbs i.e. the preferred forage species (van der Wal and Hessen 2009). In the wetter areas preferentially used by geese the vegetation now consists predominantly of mosses.

The climate in the area is oceanic and hence relatively mild given the latitude. The mean annual temperature in the region is −6.3°C. The January mean temperature is −14.7°C and the July mean temperature is around 4.7°C. The mean annual precipitation is 370 mm. The landscape is underlain by permafrost and surface soils start thawing in June reaching maximum thaw depths in late summer (August).

The wet moss-dominated vegetation in the study areas is largely composed of *Calliergon* sp. with the

grass *Poa arctica* as the dominant vascular plant; herbs are very low in abundance. The depth of the soil organic horizon is variable (ranging from 10 to more than 300 mm in the wettest areas) and at Thiisbukta it contained layers of silt, or was washed through with silt, indicating that the area is fed with silt during snowmelt through overland flow. The soil organic horizon was composed of largely poorly decomposed moss tissue.

Experimental design

To assess the recovery of C uptake rates of the ecosystem we utilized long term grazing exclosures. Exclosures were set up at the two study sites within the Ny-Ålesund area, i.e. Solvatnet and Thiisbukta, in 1998 ($n = 5$) and 2003 ($n = 6$), respectively. These consisted of ca. 0.5 m high wire netting with string across the top to prevent geese from entering the plots. Grazed controls were staked out within 1–2 m of the exclosures. Within each of the two wetlands, the plot pairs were spaced ca. 20–30 m apart across a 0.5–1 ha area. The exclosures measured 0.7 m × 0.7 m and 2 m × 2 m at Solvatnet and Thiisbukta, respectively. At both sites care was taken to sample in the central part of the plots to avoid problems with edge effects leaving a buffer zone of ca. 20 cm. The two study areas are ca. 0.5 km apart.

In the summer of 2007 a sampling campaign was undertaken to determine how the vegetation and total soil C concentrations responded to the removal of herbivores at both sites. We also quantified the effect of herbivore removal on dissolved organic C, microbial biomass, fluxes of CO₂ and CH₄ during the growing season at the Thiisbukta site. The data collection during July took place under a range of light and temperature conditions. The field based C flux measurements were done at the 4 year old exclosures at Thiisbukta only and formed the basis for the investigation of links between C fluxes and grazing. The specific methods used for determining the C pools and fluxes are outlined below.

Vegetation sampling and C pools

To quantify the response of the vegetation to the exclusion of geese, plant biomass data were collected from the exclosures in July 2007. For each exclosure and control plot, two 7 cm × 7 cm turves for

biomass and vegetation C pool determination were collected at the end of July. From Thiisbukta two additional turves were collected 1 and 2 weeks prior to the end of July sampling (i.e. a total of three sampling points over time, ca. 1 week apart) to provide a biomass sample that temporally closely corresponded to the CO₂ flux measurement (which are outlined below) to account for the rapid development of the vegetation during the short growing season. The turves were collected down to the mineral horizon (depth of the soil organic horizon was 71 mm (3–142) and 54 mm (15–98), mean, minimum and maximum, at Thiisbukta and Solvatnet, respectively). The above ground vegetation was sorted into the live fractions of functional groups (namely: grasses, herbs, *Equisetum* sp., deciduous shrubs and mosses) and the litter fraction was separated into the non-photosynthesising part of the moss (here after denoted ‘brown’ moss) and vascular plant litter. Root biomass for each enclosure and control plot was determined in one of the turves collected at the end of July. Each separate vegetation fraction from the final harvest in July 2007 was subsequently analyzed for its C and N content using a Carlo Erba NA 1500 elemental analyser and the C and nitrogen (N) pool in each biomass fraction was calculated. In addition to the biomass determinations the depth of the green and brown (litter) parts of the moss mat were measured when the turves were collected.

Soil C and microbial biomass

Soil samples for determination of treatment responses of soil organic horizon C concentration were collected from all plots as described above and the depth of the soil organic horizon was measured. The C and N content was determined using a Carlo Erba NA 1500 elemental analyser. To explore if the grazing treatment impacted on the soil microbial community, soil microbial biomass was determined in the soil organic horizon (down to 5 cm below the moss mat) at the Thiisbukta site. Since temporal variation in soil microbial biomass is known to be strong in arctic environments (Bardgett et al. 2007), microbial biomass was estimated in the temporally (i.e. all three sampling occasions) replicated turves collected for biomass determination. The turves to be used for microbial biomass determination were frozen on the

day of collection and were kept frozen during transport (ca. 2 weeks in total) prior to analysis. Subsequently, soils were thawed and microbial biomass C was estimated using the chloroform fumigation extraction method (Vance et al. 1987). Briefly ca. 20 g of fresh soil were exposed to a chloroform atmosphere for 24 h and extracted in 100 ml 0.5 M K₂SO₄ whilst a parallel unfumigated sample of soil was extracted directly. Total organic C in the extracts was analysed using a Shimadzu TOC-V carbon analyser (Shimadzu Corp, Kyoto, Japan). Soil microbial biomass was calculated as the difference between fumigated and unfumigated samples (Vance et al. 1987).

Dissolved organic C in the soil solution

The dissolved organic carbon (DOC) was collected from the soil organic horizon (under the moss litter layer) using Rhizon samplers which are 10 cm long thin probes made from a hydrophilic porous polymer tube with a pore diameter of ca. 0.1 µm (Rhizosphere research products, Wageningen, the Netherlands). The Rhizon samplers were inserted parallel with the ground surface in the top part of the soil organic horizon and left to settle for 1 week prior to sampling. A 20 ml sample of the soil solution was collected by applying a gentle vacuum using a syringe. The samples were collected in parallel with the biomass sampling at Thiisbukta (i.e. once a week over a 3-week period). Samples were frozen directly after collection. The samples were thawed prior to analysis and the organic C content in the soil solution was analysed the same day using a Shimadzu TOC-V carbon analyser (Shimadzu Corp, Kyoto, Japan).

Fluxes of CO₂

Ecosystem CO₂ fluxes were measured with custom-built flux measurement chambers (30 cm diameter, 12 l volume) clamped to steel rings inserted into the soil, and each attached to an EGM-4 Infra Red Gas Analyzer using an open dynamic system with a through flow of 11 l min⁻¹ (to avoid CO₂, temperature and pressure build up within the chambers), which collected data continuously (switching between reference and chamber air every 30 s) from the plots with an average record of the CO₂ flux taken every 2 min (IRGA; PP Systems, Hitchin, UK—see Sjögersten

et al. (2006) for details). CO₂ fluxes were measured on five separate days per plot to estimate treatment effects; all measurement took place between 10:00 and 17:00 h. Each enclosure and grazed plot pair were measured concurrently and the measurements were spread evenly across the day for the plot pairs to ensure that data collected from all plots reflected the full range of light and temperature conditions. During the midday measurements throughout July both net ecosystem exchange (NEE) and ecosystem respiration (R_e) were measured on each plot in the following sequence: the system was allowed to equilibrate for 5–10 min, NEE data were collected for 20 min, a hood was placed over the chamber to exclude light and stop photosynthesis, the system was allowed 5–10 min to equilibrate, and then R_e was measured for 15 min (the difference in measurement time was to reflect to greater variation in NEE as light conditions varied). After the initial period of equilibration, temperature or humidity did not increase within the chamber during the measurement period. From each measurement period mean values were determined for NEE and R_e . To obtain an estimation of gross ecosystem photosynthesis (GEP) the mean plot R_e fluxes were subtracted from the mean plot NEE fluxes for each measurement period. The midday measurements illustrate maximum uptake rates; negative CO₂ flux values indicate uptake of CO₂ while positive values represent an efflux of CO₂ to the atmosphere. To assess the effects of treatment on diurnal fluctuations in net ecosystem exchange of CO₂, 24 h measurements were carried out on three occasions per plot in July 2007; for these measurements the chambers were placed on the plots for 24 h allowing CO₂ fluxes to be measured continuously. To quantify night time fluxes, NEE, R_e and GEP fluxes were measured at midnight on two occasions in all of the plots in mid to late July 2007 using the same sequence of measurements as for the midday data collection.

Photosynthetically active radiation (PAR) and air temperature (ca. 10 cm above the ground surface) were recorded simultaneously with the CO₂ fluxes within the chambers.

Fluxes of CH₄

CH₄ fluxes were sampled on four occasions in July from the plots in Thiisbukta using the closed chamber technique. The head spaces were transparent with a volume of 7.8 dm³ and the surface area was

0.062 m². In the wetter plots, the head spaces were very gently placed onto the wet moss mat and in the drier plots, they were inserted carefully to ca. 5 cm depth to ensure that a good seal between the ground and the headspaces was achieved. Gas samples were collected at $T = 0$ min and again at $T = 20$ min through suba seals using hypodermic needles. Each 30 ml gas sample was injected onto a 12 ml evacuated exetainer, the over pressure in the exetainers allowed us to check for leaks. Gas samples were subsequently analysed on a Shimadzu Gas Chromatograph with a 1 ml sample loop, a molecular sieve column and a flame ionisation detector. Note that the two sampling times did not allow us to check for linearity of the change in CH₄ concentration in the head spaces so our data might be a slight over or under estimation of the actual fluxes.

Soil moisture and temperature measurements

Soil temperature at 5 cm depth and volumetric and gravimetric soil moisture content were measured in parallel with the gas flux measurements and the biomass harvest. Three measurements were taken in each plot to incorporate some of the spatial variation. Additionally, the soil temperature and the volumetric soil moisture content were determined in the immediate vicinity of where biomass samples were collected at the time of the final harvest. Soil temperature was measured using temperature probes (RS components, UK), and volumetric soil moisture using a hand-held Theta probe and meter (ΔT devices, Burwell, UK). Gravimetric soil moisture content was measured by drying 5 g subsamples at 105°C.

Data analysis

All data analyses were performed using Genstat vs. 10 (www.genstat.com). The Treatment, Site and Site \times Treatment effects were analysed using mixed linear models (REML—residual maximum likelihood) with ‘block’ as the random effect. To test for treatment effects on biomass and C pools we used the end of July sampling point. Since the CO₂, CH₄ fluxes, DOC and soil microbial biomass were collected on several occasions we used a repeated measures mixed model for analysis of treatment effects. Testing for how much of the variance in the

dependent variable, previously attributed to the treatment effect, was absorbed by covariates was done by fitting the covariate in the model first. For these two types of analysis we used the default methods for calculating the F statistic, AI optimisation and a maximum of 20 iterations. Note that the mixed model repeated measures block structure gives rise to variable denominator degrees of freedom depending on the strength of the random effect.

The linear regressions were carried out using plot means. Moss depth was log transformed prior to regressing it against soil temperature to meet to normality assumption of the residuals.

Results

Plant biomass and standing litter

Total above ground live biomass in the exclosures was nearly double that of the grazed controls in both short-term (4 years: 391.5 ± 91.3 vs. 221.9 ± 30.4 g m⁻², mean and \pm SE shown throughout) and longer-term (9 years: 322.2 ± 36.0 vs. 196.9 ± 30.0 g m⁻²) exclosures, which is reflected by the significant overall treatment effect: $F_{1,9} = 8.63$, $P < 0.05$; Fig. 1. Root biomass and vascular litter biomass were also substantially (12 and 28 times, respectively) higher in exclosures (Fig. 1; $F_{1,9} = 11.28$, $P < 0.01$ and $F_{1,9} = 6.24$, $P < 0.05$, respectively). It was clear that some plant groups were more responsive to the absence of grazers than others. Notably grasses, but

also herbs, showed a strong increase in biomass following herbivore exclusion (Treatment effects: $F_{1,9} = 8.98$, $P < 0.01$ and $F_{1,9} = 6.52$, $P < 0.05$, respectively). The apparent positive effect of grazer exclusion on *Equisetum arvense* was not statistically significant ($P > 0.1$). However, it is worth noting that the grazing exclosures at Thiisbukta (*Equisetum* was not visible in the plots at the start of the experiment) was the only obvious occurrence of this plant species in the Ny-Ålesund area. Contrary to expectation, the biomass of neither green nor brown moss differed between exclosure and grazed control ($P > 0.3$). Overall, the exclosures resulted in a shift from a system nearly completely dominated by mosses towards a system with an overstorey of vascular plants above the moss mat. The absence of any significant site or site \times treatment effects indicates that the removal of grazing leads to a relatively rapid (≤ 4 years) response in plant vascular biomass with little further change as judged from the pattern in the longer term (9 years) exclosures (76 and 63% increase of biomass in the 4 and 9 years exclosures, respectively).

C pools

Vegetation and litter

The increase in vascular plant biomass in the exclosures was reflected in increased C storage in the vegetation at the two sites (110 and 94% at Thiisbukta and Solvatnet, respectively, $F_{1,9} = 12.53$, $P < 0.01$; Table 1). The increased C pool in the

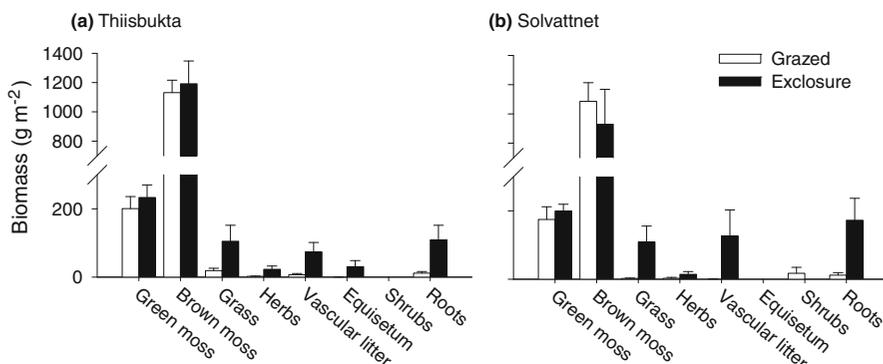


Fig. 1 Biomass of plant functional groups and standing litter in grazed (white bars) and ungrazed exclosure (black bars) plots measured at peak biomass at the two wet moss tundra study sites: Thiisbukta (4 year old exclosures) and Solvatnet

(9 year old exclosures). *Brown moss* refers to below ground non-photosynthesising brown moss tissue. Mean and SE are shown ($n = 6$ and 5 at Solvatnet and Thiisbukta, respectively)

Table 1 C pools (g m^{-2}) in different components of the ecosystem

	Thiisbukta		Solvatnet	
	Grazed	Exclosure	Grazed	Exclosure
Forbs	0.8 ± 0.5	9.9 ± 4.0	1.2 ± 1.2	7.7 ± 4.6
Grasses	8.0 ± 3.1	44.5 ± 18.2	1.0 ± 0.5	47.2 ± 20.8
<i>Equisetum</i>	0.0 ± 0.0	12.6 ± 5.1	NP	NP
Deciduous shrubs	NP	NP	9.0 ± 9.0	NP
Roots	4.8 ± 2.1	45.8 ± 18.7	4.8 ± 3.3	64.4 ± 24.7
Moss	90.3 ± 17.6	109.7 ± 44.8	87.2 ± 17.8	101.8 ± 8.5
Total vegetation	103.9 ± 17.3	218.2 ± 89.1	103.2 ± 12.4	200.7 ± 24.9
Vascular litter	7.4 ± 0.7	33.2 ± 13.5	0.0 ± 0.0	53.5 ± 30.1
Moss litter ^a	465.6 ± 34.3	541.8 ± 221.2	450.5 ± 62.0	325.7 ± 75.9
Total litter	468.1 ± 33.3	574.9 ± 234.7	450.5 ± 62.0	379.2 ± 90.9

Based on C pool data collected at peak biomass in the end of July 2007. Data shown are mean values \pm SE for grazed and exclosure plots at Thiisbukta and Solvatnet (4 and 9 years old exclosures, respectively)

NP not present

^a Below ground non-photosynthesising brown moss tissue

vegetation in the exclosures was due to an increase of the vascular C pool ($F_{1,9} = 18.17$, $P < 0.01$) rather than moss C pool which did not increase in the exclosures ($P > 0.3$). Similarly, with respect to C inputs to the soil system, vascular litter C inputs tended to be increased ($F_{1,8} = 3.97$, $P = 0.08$) in the exclosures but not the total litter C input to the soil ($P > 0.7$) which was composed largely of moss litter. Despite the different times (4 and 9 years) the treatment plots had been protected from grazing, the treatment effect was similar at the two sites (i.e. no significant site \times treatment interaction). This suggests that within 4 years most of the recovery from grazing of the vegetation C pool had already taken place and after this point further changes in the standing C pool in the biomass are more gradual as already indicated by the biomass data in the previous section.

The plant tissue C to N ratio was differentially affected by the exclosures: In grasses the C to N ratio was significantly lower in grazed plots (12.7 ± 2.0 and 20.1 ± 1.5 in grazed and exclosure plots respectively; $F_{1,20} = 8.76$, $P < 0.01$) and there was a tendency for lower C to N ratios also in the root biomass (which is mainly composed of grasses) (24.3 ± 1.4 and 30.7 ± 3.1 in grazed and exclosure plots, respectively; $F_{1,16} = 3.08$, $P = 0.098$). In contrast, there were no significant effects of the treatment on the C to N ratios in either herbs (16.5 ± 3.6 and

17.4 ± 1.7 in grazed and exclosure plots, respectively; $P > 0.7$, mean 17.1 ± 1.6) or green moss tissue ($P > 0.6$, mean 27.6 ± 1.2). The grazing exclosures did not impact on either moss ($P > 0.8$) or vascular ($P > 0.4$) litter C to N ratios. Additionally, the moss and vascular leaf litter C to N ratios were similar, at 28.25 ± 1.18 and 27.60 ± 1.37 , respectively.

Soil and microbial biomass C and N

As expected, grazer exclusion did not measurably alter the total concentration of C in the soil organic horizon ($P > 0.3$; Fig. 2a) or the depth of the soil organic horizon ($P > 0.4$, 72 ± 20 mm vs. 70 ± 22 mm at Thiisbukta and 46 ± 12 mm vs. 62 ± 13 mm at Solvatnet for grazed and exclosure plots, respectively). However, N levels in the soil organic horizon were slightly lower in the exclosures ($F_{1,9} = 6.93$, $P < 0.05$): $0.54 \pm 0.13\%$ vs. $0.41 \pm 0.16\%$ at Thiisbukta and $2.09 \pm 0.33\%$ vs. $1.50 \pm 0.38\%$ at Solvatnet for grazed and exclosure plots, respectively. With respect to the more labile pools of C, DOC were not affected by the treatment ($P > 0.1$) however, DOC concentrations decreased significantly ($F_{2,13} = 7.64$, $P < 0.01$) over the measurement period (Fig. 2b). The size of the microbial biomass C pool appeared resilient to the exclusion of geese as

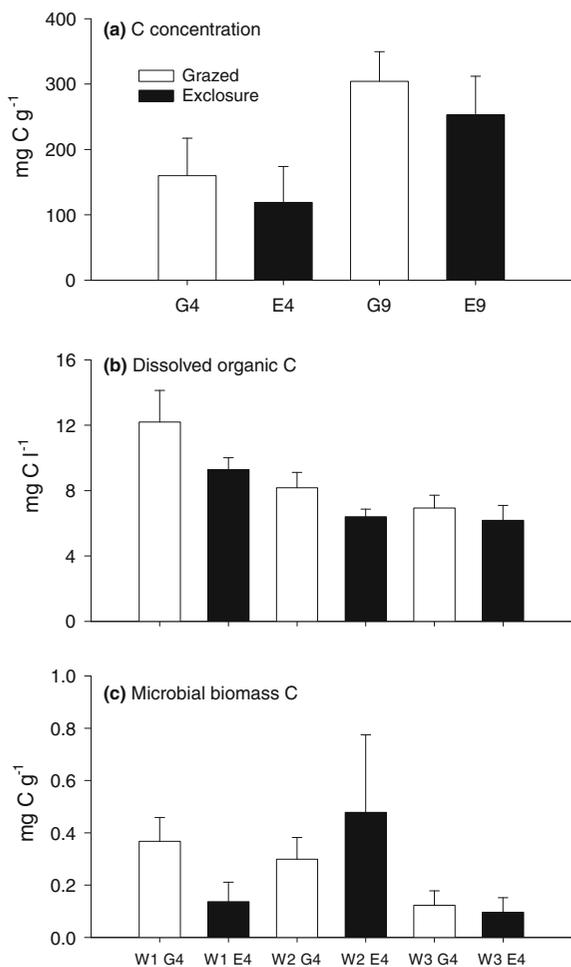


Fig. 2 **a** Soil total C concentrations in the soil organic horizon, **b** dissolved organic carbon (DOC) in the soil pore water in the soil organic horizon and **c** microbial biomass C in the soil organic horizon. *G4* and *E4* and *G9* and *E9* represent the 4 and 9 years old grazed (G) and enclosure (E) plots at Thiisbukta and Solvatnet, respectively. *W1*, *W2* and *W3* indicated the three consecutive weeks in July 2007 when the DOC and microbial biomass measurements were carried out. Mean and SE are shown ($n = 6$ and 5 at Solvatnet and Thiisbukta, respectively)

there was no effect of the treatment ($P > 0.6$) and there were no significant variation in microbial biomass over time ($P > 0.1$) (Fig. 2c).

Fluxes of C in the field

CO₂ fluxes

The light conditions (ranging between 200 and 1,200 μmol of photons $\text{m}^{-2} \text{s}^{-1}$) were a good

predictor of the variation in NEE and GEP whilst air temperature (ranging between 9 and 25°C) predicted variation in R_e (Fig. 3) but the fit depended on the grazing treatment: Light conditions were related to GEP in enclosure plots whilst air temperature mainly impacted on R_e in grazed plots. This suggests that the presence or absence of herbivores (and hence vascular plants) controls the response of the CO_2 fluxes to abiotic controls.

Grazed areas showed net losses ($0.46 \mu\text{mol} \text{m}^{-2} \text{s}^{-1}$) of CO_2 to the atmosphere whilst the enclosures showed net uptake ($-0.77 \mu\text{mol} \text{m}^{-2} \text{s}^{-1}$) of CO_2 in July (period of maximum photosynthesis based on sampling occasions at midday; Fig. 4). Both gross ecosystem photosynthesis (GEP) and ecosystem respiration (R_e) rates were greater (i.e. more negative in the figure for GEP) in enclosures than in grazed plots with the effect being larger for GEP than for R_e .

The strongest effect of herbivore exclusion on C fluxes was observed during daytime (10 am to 5 pm); there was no significant treatment effect on NEE at night (despite the relatively high light levels due to the midnight sun) (Fig. 5a). The NEE in enclosure plots tended to follow the daily pattern in PAR and air temperature (Fig. 5b, c) whilst grazed plots showed no pronounced daily cycle in NEE. Interestingly, although no significant treatment effect was found for NEE during night time (11 pm to 1 am) it was clear that R_e rates were still somewhat elevated in the enclosures ($F_{1,4} = 17.71$, $P < 0.05$), being 1.4 ± 0.1 and $1.9 \pm 0.2 \mu\text{mol}$ of photos $\text{m}^{-2} \text{s}^{-1}$ in grazed and enclosure plots respectively, whilst no significant treatment effect was apparent for GEP at midnight ($P > 0.2$). Interestingly, although substantially (ca. 40%) lower than daytime fluxes, GEP was still measurable at midnight (e.g. $-1.0 \pm .01 \mu\text{mol} \text{m}^{-2} \text{s}^{-1}$ in control plots). Photosynthetically active radiation at midnight was $140 \mu\text{mol}$ of photons $\text{m}^{-2} \text{s}^{-1}$ when averaged over the measurement period. This indicates that the large day time differences in GEP between grazing treatments are likely to be driven by species with greater light demand, since the grazing effect on GEP disappears at midnight when light levels are low.

Both components of NEE, R_e and GEP, appeared to be linked to above ground vascular biomass (Fig. 6). Indeed, above ground biomass was a significant covariate ($F_{1,15} = 14.29$, $P < 0.01$ and $F_{1,11} = 14.13$, $P < 0.01$ for R_e and GEP, respectively) which absorbed the variation previously predicted by the

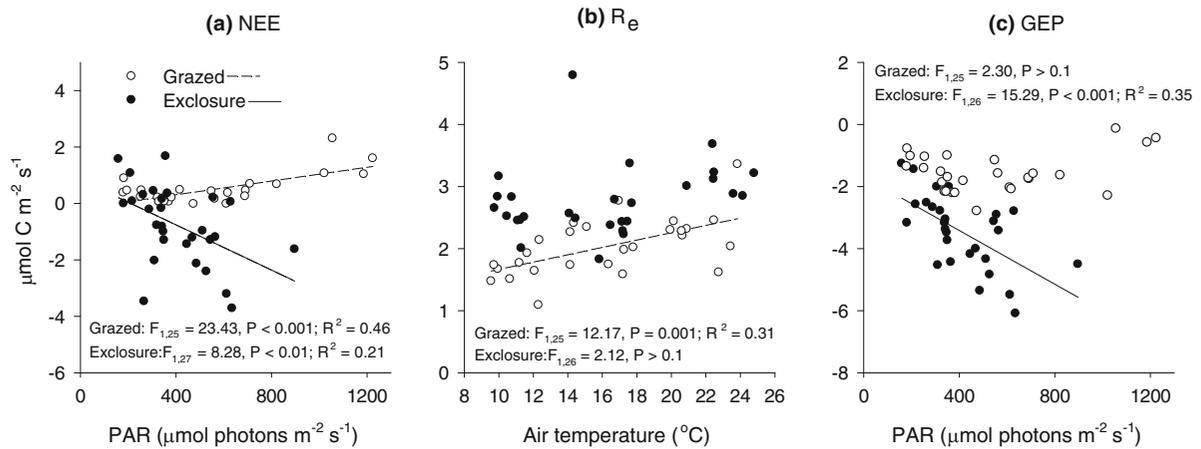


Fig. 3 CO₂ fluxes in relation to changes in the most significant abiotic predictor **a** photosynthetically active radiation (PAR) versus net ecosystem exchange of CO₂ (NEE), **b** air temperature versus ecosystem respiration (R_e) and **c** PAR versus gross ecosystem photosynthesis (GEP) measured in July at Thiisbukta in grazed wet moss tundra (*open circle*) and 4 year old

exclosures (*filled circle*). The data are from the five occasions CO₂ fluxes were measured over a 3-week period in July. Significant regression for the two treatments is shown. Positive fluxes represent an efflux of CO₂ whilst negative values indicate uptake of CO₂ from the atmosphere

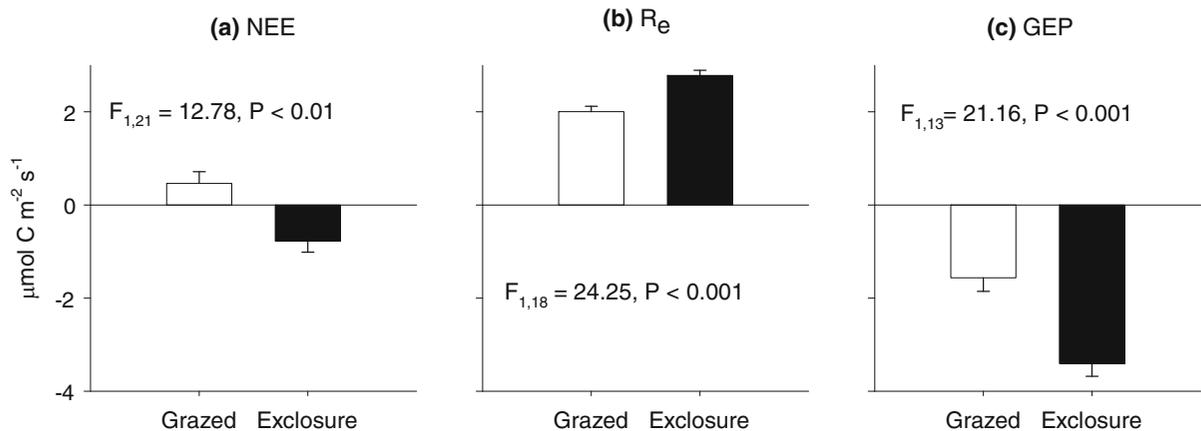


Fig. 4 **a** Net ecosystem exchange of CO₂ (NEE), **b** ecosystem respiration (R_e) and **c** gross ecosystem photosynthesis (GEP) measured in July at Thiisbukta in grazed wet moss tundra (*open bars*) and 4 year old exclosures (*closed bars*). Mean and SE are given of 5 day-time measurements in July. Positive fluxes represent an efflux of CO₂ whilst negative values

indicate uptake of CO₂ from the atmosphere. Significant differences are indicated by F statistics; the variable denominator degrees of freedom are related to the strength of the random (block) effect within the repeated measures mixed model structure

grazing treatment for both R_e and GEP such that the treatment effect was no longer significant. This was not the case for NEE itself. No other measured environmental (soil temperature and soil moisture) or soil biological parameter (below ground biomass, DOC C and N content, microbial biomass) accounted for variation in CO₂ fluxes in relation to the treatment.

CH₄ fluxes

The variation in CH₄ fluxes could be partially explained by the volumetric soil moisture content in the soil organic horizon ($R^2 = 0.52, F_{1,8} = 10.66, P < 0.05$) with CH₄ uptake dominating in plots with drier surface conditions and CH₄ efflux dominating in wet plots (fluxes ranged between

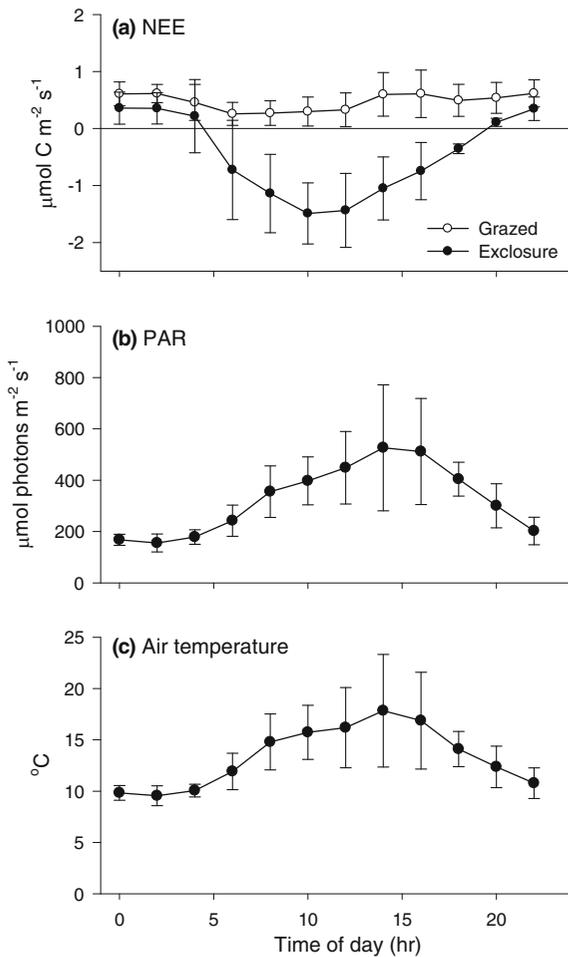


Fig. 5 Diurnal variation in **a** net ecosystem exchange (NEE) of CO₂ in grazed and ungrazed plots at Thiisbukta (4 year old exclosures), **b** photosynthetically active radiation (PAR) and **c** air temperature. Positive fluxes represent an efflux of CO₂ whilst negative values indicate uptake of CO₂ from the atmosphere. Significant treatment effects were between 8.00 and 20.00 h. For NEE means (two hourly) were first calculated on the treatment level and the means and standard deviations over the tree sampling periods were calculated to demonstrate the temporal (between weeks) variability in CO₂ fluxes and the abiotic conditions (PAR and air temperature)

–46 and 25 μg CH₄ m⁻² h⁻¹). However, there was no significant difference between grazed and ungrazed plots throughout July ($P > 0.4$, 0.18 ± 4.6 and -0.35 ± 2.1 μg CH₄ m⁻² h⁻¹, in control and exclosure plots, respectively) suggesting that grazing does not exert a strong control over the net CH₄ fluxes at these sites, at least not over the time frame of our study.

Soil temperature and moisture content

As expected, soils were found to be colder below deep moss mats as described by a significant negative regression between soil temperature and moss depth ($R^2 = 0.22$, $F_{1,20} = 6.90$, $P < 0.05$). There was a trend for increased moss depth in exclosures (overall for Thiisbukta and Solvatnet: 20 ± 3 and 31 ± 7 mm in grazed and exclosure plots, respectively), but this was not significant ($P = 0.16$) possibly due to the relatively short time that the exclosures at Thiisbukta were present. The volumetric moisture content of the surface moss was lower in the exclosures (0.73 and 0.46 m³ m⁻³ in grazed and exclosure plots, respectively; $F_{1,6} = 8.19$, $P = 0.03$) due to the reduced compaction. The drier moss surface was associated with higher temperatures in surface moss mat (5 cm below the surface) in exclosures (8.9 vs. 8.2°C ; $F_{1,10} = 35.57$, $P < 0.001$) than in grazed plots. However, in the soil organic horizon the moisture content (below the moss mat) did not vary between treatments ($P > 0.2$). As noted above neither changes in soil temperature nor soil moisture appeared to drive the changes seen in CO₂ fluxes.

Discussion

In this study we have demonstrated that the exclusion of herbivores from wet moss meadows which had been grazed intensively by geese for the previous 20 years allowed a relatively fast increase in vascular plant biomass, vascular plant C storage and C uptake rates. Interesting comparisons can be made between the extent of recovery observed in the grazing exclosures and the characteristics of a naturally ungrazed moss meadow in Adventdalen, a valley further south on Spitsbergen. This demonstrates that after only 4 years, the removal of herbivores from the wet meadow tundra at Ny-Ålesund led to the restoration of the vascular biomass, and C storage in that biomass, to levels that exceed those at the ungrazed site in Adventdalen where the total C storage in the vascular biomass was 18.0 ± 3.1 g m⁻² (Sjögersten et al. unpublished data). Consequently, the C uptake rates in the ungrazed plots in Ny-Ålesund attained a magnitude similar to that observed in the ungrazed meadow in Adventdalen (-0.68 μmol m⁻² s⁻¹; Sjögersten et al. 2008). This indicates that recovery from heavy grazing to what

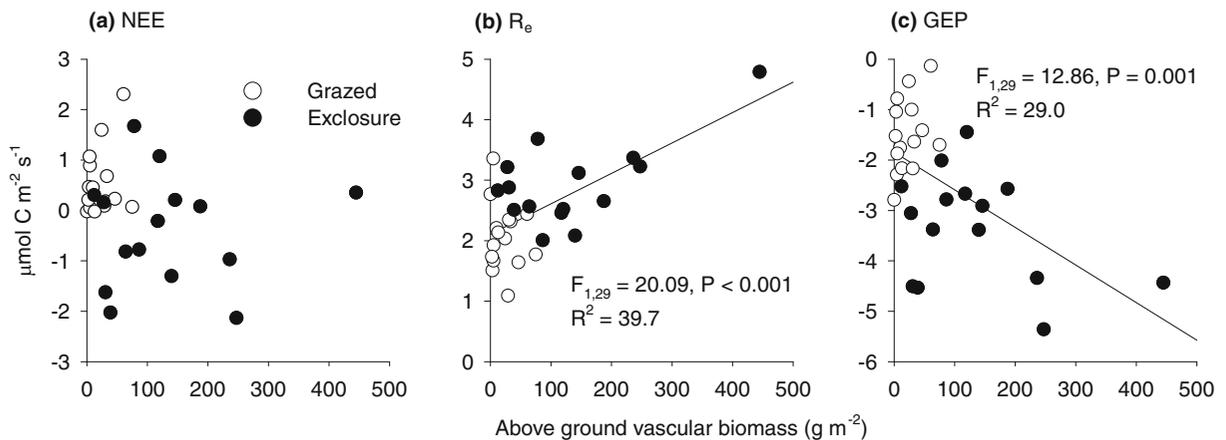


Fig. 6 Above ground vascular plant biomass in relation to changes in **a** net ecosystem exchange of CO₂ (NEE), **b** ecosystem respiration (R_e) and **c** gross ecosystem photosynthesis (GEP) measured in July at Thiisbukta in grazed wet moss tundra (*open circle*) and 4 year old exclosures (*filled*

circle). The data are from three biomass harvests from all plots in three consecutive weeks concurrent with the CO₂ flux measurements. Positive fluxes represent an efflux of CO₂ whilst negative values indicate uptake of CO₂ from the atmosphere

might be expected for an ungrazed wet tundra system can be rapid. A similar rapid increase in above ground biomass in heavily grazed moss meadows following the exclusion of geese has been found also on Bylot Island, Canada (Gauthier et al. 2004). This increased C uptake in the exclosures contrasts to long term grazing exclosures on shrub dominated moorlands where grazing actually enhances the C sink strength of the ecosystem (Ward et al. 2007). This shows that herbivores impact on the C uptake differently in contrasting habitats either through the herbivores impact on the relative proportions on plant functional groups within the ecosystem (De Deyn et al. 2008) and/or the grazing intensity (Zacheis et al. 2001).

The exclusion of the herbivores had the greatest effect on CO₂ fluxes during day time, when CO₂ uptake was substantially greater under ungrazed conditions, most likely due to the greater vascular plant biomass (mainly grasses) and its greater photosynthetic activity compared to mosses (Otieno et al. 2009; Ward et al. 2009). In fact, whilst the grazed vegetation showed little diurnal variation in NEE, the ungrazed plots exhibited the same diurnal pattern as observed in the ungrazed moss meadows in Adventalen (Sjögersten et al. 2008). There was no significant effect of grazer exclusion on NEE during the night. Yet, R_e was higher in exclosure plots both during the day and at midnight, suggesting that the increased above and below ground plant biomass gave rise to

increased respiration rates throughout the diurnal cycle. The similar levels of GEP in grazed and exclosure plots at midnight indicate that only the mosses, which had comparable biomass in exclosures and grazed plots and completely dominated the vegetation in grazed plots, are able to maintain photosynthesis rates right through the 24 h cycle. Mosses have been shown to have low light requirements compared to grasses (Uchida et al. 2002; Douma et al. 2007; Otieno et al. 2009) and our results suggests that during the period of midnight sun at this high arctic site, the light levels in the night are sufficient for their photosynthesis.

It is possible that the magnitude of response to the grazing treatment would vary between years given that the CO₂ fluxes are strongly influenced by light levels and temperature. The 2007 growing season were within the max and min values for both temperature and precipitation (Table 2) but were on the warmer end so the effect by herbivores on the net uptake of CO₂ might have been more pronounced in years when lower temperatures suppresses R_e .

CH₄ efflux was generally low compared to other wet high arctic sites (Mastepanov et al. 2008; Wille et al. 2008), whilst the CH₄ consumption rate in the drier plots compared to rates measured from mineral soil along the Yenisej river, northern Russia (Flessa et al. 2008) and tundra heath in northern Scandinavia (Sjögersten and Wookey 2002). The exclosures had

Table 2 Variation in summer climate in the Ny-Ålesund area

	Precipitation (mm)	Temp (°C)	Temp anomaly (°C)	Min temp (°C)	Max temp (°C)	Heat sum (°C)
2007	52.4	6.6	1.7	2.9	11.4	204.1
Mean	31.2	5.7	0.8	1.0	12.9	177.8
Max	58.8	6.7	1.8	2.9	18.7	206.5
Min	0.0	4.6	-0.3	-2.7	10.1	143.6

Data shown is mean, max and min values for July over the period 1999–2009 and the values for 2007. Data from www.met.no

no impact on the net CH₄ fluxes despite the fact that the treatment altered many aspects of the ecosystem, which have the potential to impact on CH₄ fluxes e.g. graminoid and root biomass, temperature and moisture in the moss surface. This suggests that after 4 years neither the shifts in vegetation in the exclosures (e.g. through increases in root exudates with larger grass biomass (Trinder et al. 2008), nor the reduced C inputs from faeces, substantially altered the belowground production of labile C which is the precursor to CH₄ production (Wagner et al. 2003). Furthermore, this also suggests that the changes in nutrient inputs from the faeces did not have a strong impact on net CH₄ fluxes.

There was no significant effect of herbivore removal (either after 4 or 9 years) on the soil organic matter C storage despite the pronounced effects on biomass and CO₂ fluxes, suggesting that any changes in the soil C concentration in response to ecosystem recovery from grazing would be slow. A similar lack of increased below ground C storage, despite a substantial increase in aboveground biomass after 2 years of removal of herbivores was noted in grazed marshes in Louisiana (Ford and Grace 1998). However, the substantial increases of below ground biomass following the removal of the herbivore might be an important factor that in the future could impact on quality and quantify of the C input to the soil organic matter given the recalcitrance and size of the root C pool in ungrazed tundra systems (Loya et al. 2004; Woodin et al. 2009).

With respect to litter chemistry, the moss litter C to N ratio (28.25 ± 1.18 , average for grazed and exclosure plots, note that these were not significantly different) was lower compared to that of moss litter in the ungrazed moss meadows in Adventdalen on Spitsbergen (42.4 ± 4.1 , S. Sjögersten unpublished

data), and was comparable to that of vascular litter in the grazed and exclosure plots. This low moss litter C to N ratio indicates that N inputs from geese would increase moss litter decomposition given that this tends to be N limited (Quested et al. 2003). The fact that the C to N ratio is comparable in both exclosures and grazed plots is likely to be linked to persistence of N in the moss mat (i.e. old goose N is still held in the moss mat in the exclosures (Gornall et al. 2009)). The lower soil N found in exclosures is likely to be due to (i) reduced N inputs from faeces, (ii) the result of the reallocation of N from the soil organic matter to plant tissue supporting the substantially greater growth of the vegetation or a combination of the two processes. This suggests that grazing in this high arctic system results in a larger component of the ecosystem N to be held in the soil. Despite the higher soil N in grazed plots we saw no indication of elevated decomposition rates (e.g. lower C concentrations, depth of the soil organic horizon) compared to in the exclosures. This contrasts with the rapid loss of C that has been found in response to experimentally increased N levels in Alaska (Nowinski et al. 2008) suggesting that N inputs will impact on decomposition differently in contrasting tundra habitats in relation to the SOM quality and the level of N inputs.

The recovery of the above ground biomass and CO₂ fluxes demonstrates the plasticity of this high arctic ecosystem in terms of response to changing herbivore pressure. Given that the study area had been heavily grazed for the previous 20 years, the relatively quick response (4 years) of the vegetation demonstrates that neither nutrient levels nor the seed bank (Kuijper et al. 2006) have been eroded over this period to a point from which recovery of ecosystem function is no longer possible. The rapid recovery

demonstrated in this study differs dramatically from the situation in subarctic Canada where geese have pushed the ecosystem to an alternate stable state dominated by exposed sediment (Jefferies et al. 2006) and the removal of the herbivore has been demonstrated not to be sufficient to restore the vegetation (Handa and Jefferies 2000). However, it is worth noting that in addition to grazing, which is the focus of this study, below ground feeding activities (or grubbing) by pink-footed geese, on a par with snow geese, have been observed to impact wet systems across Svalbard (Speed et al. 2009). Since grubbing is more disruptive than grazing, the ecosystems' ability to recover from this might be less rapid. In conclusion, our results suggests that at this point severe grazing pressure by geese in the Ny-Ålesund area has not resulted in a permanent ecosystem state change and that although grazing currently suppresses the C uptake of the ecosystem it is clear that if grazing pressure on the vegetation was reduced the C uptake during the growing season would recover.

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References

- Abraham KF, Jefferies RL, Alisauskas RT (2005) The dynamics of landscape change and snow geese in mid-continent North America. *Glob Chang Biol* 11:841–855
- ACIA (2005) The Arctic Climate Impact Assessment. Cambridge University Press, New York
- Bardgett RD, van der Wal R, Jonsdottir IS, Quirk H, Dutton S (2007) Temporal variability in plant and soil nitrogen pools in a high-Arctic ecosystem. *Soil Biol Biochem* 39: 2129–2137
- Bodelier PLE, Stomp M, Santamaria L, Klaassen M, Laanbroek HJ (2006) Animal–plant–microbe interactions: direct and indirect effects of swan foraging behaviour modulate methane cycling in temperate shallow wetlands. *Oecologia* 149:233–244
- Bråthen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T, Hausner VH (2007) Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems* 10:773–789
- De Deyn GB, Cornelissen JHC, Bardgett RD (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol Lett* 11:516–531
- Douma JC, Van Wijk MT, Lang SI, Shaver GR (2007) The contribution of mosses to the carbon and water exchange of arctic ecosystems: quantification and relationships with system properties. *Plant Cell Environ* 30:1205–1215
- Flessa H, Rodionov A, Guggenberger G, Fuchs H, Magdon P, Shibistova O, Zrazhevskaya G, Mikheyeva N, Kasansky OA, Blodau C (2008) Landscape controls of CH₄ fluxes in a catchment of the forest tundra ecotone in northern Siberia. *Glob Chang Biol* 14:2040–2056
- Ford MA, Grace JB (1998) Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation and soil elevation changes in a coastal marsh. *J Ecol* 86:974–982
- Fox AD, Madsen J, Boyd H, Kuijken E, Norriss DW, Tombre IM, Stroud DA (2005) Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. *Glob Chang Biol* 11:881–893
- Gauthier G, Bety J, Giroux J-F, Rochefort L (2004) Trophic interactions in a high arctic snow goose colony. *Integr Comp Biol* 44:119–129
- Gauthier G, Giroux J-F, Reed A, Béchet A, Bélanger L (2005) Interactions between land use, habitat use, and population increase in greater snow geese: what are the consequences for natural wetlands? *Glob Chang Biol* 11:856–868
- Giblin AE, Nadelhoffer KJ, Shaver GR, Laundre JA, McKerrrow AJ (1991) Biogeochemical diversity along a riverside topequence in arctic Alaska. *Ecol Monogr* 61:415–435
- Gornall JL, Woodin SJ, Jonsdottir IS, Van der Wal R (2009) Herbivore impacts to the moss layer determine tundra ecosystem response to grazing and warming. *Oecologia* 161:747–758
- Handa IT, Jefferies RL (2000) Assisted revegetation trials in degraded salt-marshes. *J Appl Ecol* 37:944–958
- Handa IT, Harmsen R, Jefferies RL (2002) Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands. *J Ecol* 90:86–99
- Jefferies RL, Drent RH (2006) Arctic geese, migratory connectivity and agricultural change: calling the sorcerer's apprentice to order. *Ardea* 94:537–554
- Jefferies RL, Jano AP, Abraham KF (2006) A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *J Ecol* 94:234–242
- Joabsson A, Christensen TR, Wallen B (1999) Vascular plant controls on methane emissions from northern peatforming wetlands. *Trends Ecol Evol* 14:385–388
- Kéry M, Madsen J, Lebreton J-D (2006) Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. *J Anim Ecol* 75: 1172–1181
- Kuijper DPJ, Bakker JP, Cooper EJ, Ubels R, Jónsdóttir IS, Loonen MJJE (2006) Intensive grazing by Barnacle geese depletes high Arctic seed bank. *Can J Bot* 84:995–1004
- Kutzbach L, Wagner D, Pfeiffer EM (2004) Effect of microrelief and vegetation on methane emission from wet

- polygonal tundra, Lena Delta, Northern Siberia. *Biogeochemistry* 69:341–362
- Loya WM, Johnson LC, Nadelhoffer KJ (2004) Seasonal dynamics of leaf- and root-derived C in arctic tundra mesocosms. *Soil Biol Biochem* 36:655–666
- 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
- McLaren JR, Jefferies RL (2004) Initiation and maintenance of vegetation mosaics in an Arctic salt marsh. *J Ecol* 92: 648–660
- Nowinski NS, Trumbore SE, Schuur EAG, Mack MC, Shaver GR (2008) Nutrient addition prompts rapid destabilization of organic matter in an arctic tundra ecosystem. *Ecosystems* 11:16–25
- Otieno DO, Waringer M, Nishiwaki A, Hussain MZ, Muhr J, Borken W, Liseid G (2009) Responses of CO₂ exchange of primary production of the ecosystem components to environmental changes in a mountain peatland. *Ecosystems* 12:590–603
- Ping C-L, 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. *Nat Geosci* 1:615–619
- Quested HM, Cornelissen JHC, Press MC, Callaghan TV, Aerts R, Trosien F, Riemann P, Gwynn-Jones D, Konradchuk A, Jonasson SE (2003) Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology* 84:3209–3221
- Semmartin M, Aguiar MR, Distel RA, Moretto AS, Ghersa CM (2004) Litter quality and nutrient cycling affected by grazing-induced species replacements along a precipitation gradient. *Oikos* 107:148–160
- Sjögersten S, Wookey PA (2002) Spatio-temporal variability and environmental controls of methane fluxes at the forest-tundra ecotone in the Fennoscandian mountains. *Glob Chang Biol* 8:885–894
- Sjögersten S, Van der Wal R, Woodin SJ (2006) Small-scale hydrological variation determines landscape CO₂ fluxes in the high Arctic. *Biogeochemistry* 80:205–216
- Sjögersten S, Van der Wal R, Woodin SJ (2008) Habitat type determines herbivory controls over CO₂ fluxes in a warmer arctic. *Ecology* 89:2103–2116
- Speed JDM, Woodin SJ, Tommervik H, Tamstorf MP, Van der Wal R (2009) Predicting habitat utilization and extent of ecosystem disturbance by an increasing herbivore population. *Ecosystems* 12:349–359
- Stark S, Tuomi J, Strommer R, Helle T (2003) Non-parallel changes in soil microbial carbon and nitrogen dynamics due to reindeer grazing in northern boreal forests. *Ecography* 26:51–59
- 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
- Tombre IM, Mehlum F, Loonen MJJE (1998) The Kongsfjorden colony of barnacle geese: nest distribution and the use of breeding islands 1980–1997. *Norsk Polarinstittut Skrifter* 200:57–65
- Torn MS, Chapin FS (1993) Environmental and biotic controls over methane flux from Arctic tundra. *Chemosphere* 26: 357–368
- Trinder CJ, Artz RRE, Johnson D (2008) Contribution of plant photosynthate to soil respiration and dissolved organic carbon in naturally recolonising cutover peatlands. *Soil Biol Biochem* 40:1622–1628
- Uchida M, Muraoka H, Nakatsubo T, Bekku Y, Ueno T, Kanda H, Koizumi H (2002) Net photosynthesis, respiration, and production of the moss *Sanionia uncinata* on a glacier foreland in the high Arctic, Ny-Alesund, Svalbard. *Arct Antarct Alp Res* 34:287–292
- Van der Wal R (2005) Plant-animal interactions. In: van der Wal Rene (ed) *Encyclopedia of the Arctic*. Routledge, New York, pp 1649–1650
- 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, Hessen DO (2009) Analogous aquatic and terrestrial food webs in the high Arctic: the structuring force of a harsh climate. *Perspect Plant Ecol Evol Syst* 11: 231–240
- Van der Wal R, Sjögersten S, Woodin SJ, Cooper EJ, Jónsdóttir IS, Kuijper D, Fox TAD, Huiskes AD (2007) Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. *Glob Chang Biol* 13:539–545
- Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass-C. *Soil Biol Biochem* 19:703–707
- Wagner D, Kobade S, Pfeiffer EM, Hubberten HW (2003) Microbial controls on methane fluxes from a polygonal tundra of the Lena Delta, Siberia. *Permafrost Periglac Process* 14:173–185
- Ward SE, Bardgett RD, McNamara NP, Adamson JK, Ostle NJ (2007) Long term consequences of grazing and burning on northern peatland carbon dynamics. *Ecosystems* 10: 1069–1083
- Ward SE, Bardgett RD, McNamara NP, Ostle NJ (2009) Plant functional groups identity influences short-term peatland ecosystem carbon flux: evidence from a plant removal experiment. *Funct Ecol* 23:454–462
- Wille C, Kutzbach L, Sachs T, Wagner D, Pfeiffer EM (2008) Methane emission from Siberian arctic polygonal tundra: eddy covariance measurements and modelling. *Glob Chang Biol* 14:1395–1408
- Woodin SJ, Van der Wal R, Sommerkorn M, Gornall JL (2009) Differential allocation of carbon in mosses and grasses governs ecosystem sequestration: a ¹³C tracer study in the high Arctic. *New Phytol* 184:944–949
- Zacheis A, Hupp JW, Ruess RW (2001) Effects of migratory geese on plant communities of an Alaskan salt marsh. *J Ecol* 89:57–71