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Western Palaearctic breeding geese can alter carbon cycling in their winter habitat

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Abstract. Changes in land use, implementation of protective measures and a warming climate have improved the survival rate of geese, resulting in considerable increases in the majority of Western Palaearctic goose populations during recent decades. To the best of our knowledge, this is the first study aiming to understand the impact of goose grazing on carbon cycling in their winter habitat. To this end, the impact of goose grazing pressure on biomass, litter decomposition and CO_2 fluxes (net CO_2 exchange partitioned into photosynthesis and ecosystem respiration) was studied in the coastal polders of Belgium, a wintering habitat for geese of international importance. Experimentally manipulated grazing by *Anser anser* (Greylag Geese) in grassland mimicked four different grazing pressures, including a control treatment from which geese were excluded. We found that grazing pressure by geese has a significant, but variable effect on carbon fluxes during the entire year. In winter, at the end of the grazing season, both plants' carbon assimilation and total ecosystem respiration were decreased with increasing grazing pressure, resulting in less carbon taken up during day time. Total ecosystem respiration was also reduced due to goose grazing in spring and autumn (i.e., outside the grazing season), while no significant difference in ecosystem CO_2 fluxes was detected in summer. These grazing effects on CO_2 fluxes can partly be explained by the effect of goose grazing on standing biomass. Decomposition rates were significantly reduced by higher grazing pressure during the winter season when geese were present, but on the long term grazing accelerated decomposition rates. Our data suggest that the rising numbers of Western Palaearctic breeding geese can alter the carbon balance of their winter habitat. The differences between short- and long-term effects observed in our study demonstrate the complexity of goose grazing effects on carbon cycling and indicate directions for future studies.

Key words: *Anser anser*; Belgian North Sea polders; biomass; carbon; decomposition; geese; grassland; herbivory.

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INTRODUCTION

Global temperatures have increased and recent simulations suggest that the global average surface temperature will increase even more in the coming decades (IPCC 2007). In addition to changes in land use and implementation of protective measures in Europe, the warming climate has improved geese's ability to survive during winter in Western Europe and to arrive in the Arctic breeding areas in good physical condition (Kéry et al. 2006, Jensen et al. 2008). As a result, population numbers for the majority of Western Palaearctic goose populations have increased considerably during recent decades (Madsen et al. 1999, Fox et al. 2010).

Recent research in the Arctic breeding sites has revealed that these birds influence the dynamics of CO_2 exchange between the biosphere and atmosphere by reducing carbon stocks and ecosystem sink strength (Sjögersten et al. 2008, Speed et al. 2010, Sjögersten et al. 2011), which in turn feed back to the climate (Chapin et al. 2008). However, this is only part of the story. Geese are migratory birds and thus likely to impact also on the carbon balance of their wintering habitats: temperate grasslands, which usually act as sinks for greenhouse gases (Soussana et al. 2007, Ostle et al. 2009, Schulze et al. 2009).

Research in the Arctic breeding sites revealed a strong decrease in aboveground plant biomass due to goose grazing (Loonen and Solheim 1998, Zacheis et al. 2001, Sjögersten et al. 2011) which is indicated as the principal mechanism of grazing impact on net ecosystem exchange of CO_2 (van der Wal et al. 2007, Sjögersten et al. 2008). This pattern of decreased aboveground biomass with increased goose grazing is also found in the temperate grasslands of the wintering habitat, albeit less pronounced (Groot Bruinderink 1989, Van Gils et al. 2010). How much CO_2 is taken up from, or released to, the atmosphere by ecosystems depends on the magnitude of photosynthetic inputs and respiration outputs (both autotrophic and heterotrophic), respectively.

Both photosynthesis and autotrophic respiration are positively correlated with aboveground biomass. However, in addition to aboveground biomass, also roots contribute to ecosystem autotrophic respiration. Research in Arctic breeding sites revealed a decrease in root biomass through increased goose grazing (Sjögersten et al. 2011). Thus far, the effect of goose grazing on root biomass in temperate grasslands remains uncertain; whereas in one study ungulate herbivory increased root productivity considerably (Frank et al. 2002), Bardgett and Wardle (2003) suggested a decrease in root productivity due to herbivory.

In addition to an effect on autotrophic respiration, there is ample evidence that herbivores, like geese, also affect the heterotrophic component of ecosystem respiration. In unproductive ecosystems with low consumption rates, such as the wetlands of the Arctic breeding sides, negative impacts of grazing on soil biota are probably most common (Bardgett and Wardle 2003). In contrast, in ecosystems of high soil fertility and high consumption rates, like most temperate grasslands, positive effects such as an increase in numbers of nematodes and springtails and in microbial biomass are observed (Bardgett et al. 1998, Bardgett and Wardle 2003).

The increase in decomposer abundance can accelerate the decomposition process (Swift et al. 1979, Bardgett et al. 1998), which is of crucial importance as the amount of carbon returned to the atmosphere by decomposition of dead organic matter is an important component of the global carbon budget (Shaver and Billings 1992, Coûteaux et al. 1995, Woodwell and Mackenzie 1995). Raich and Schlesinger (1992) estimated that decomposition of litter (including root litter) contributes about 70% to the total annual carbon flux from the soil. Furthermore, trampling by animals is also suggested to accelerate the decomposition process by fragmenting plant material and mingling of the litter in the soil (Ruess 1987, Zacheis et al. 2002). Reduction of particle size might indeed accelerate decomposition (Handayanto et al. 1997). Litter incorporated in the soil in turn is in closer contact with the microbial biomass in the soil and decomposes faster (Holland and Coleman 1987).

All this suggests that increased goose grazing could change the C balance in temperate grasslands. Changes in the exchange of CO_2 (the main constituent of the C balance) to the atmosphere are important because they can imply either a mitigation or a reinforcement of the greenhouse effect (Oechel et al. 1993). However, to the best of our knowledge the effect of goose grazing on the CO_2 exchange in temperate grasslands has not been studied so far. In order to contribute to a more complete understanding of the multiple pathways of ecosystem feedback on climate, the following hypotheses were tested in a field experiment with controlled grazing by *Anser anser* (Linnaeus 1758) (Greylag Geese), mimicking different grazing pressures.

We hypothesize that intensive goose grazing (1) decreases the input of CO_2 due to the removal of photosynthesizing above ground biomass, and (2) increases the output of CO_2 due to goose-induced stimulation of the decomposition and the heterotrophic soil communities.

Carry-over effects of goose grazing on CO_2 fluxes to the seasons after the geese have left (and

Table 1. Initial soil characteristics ($n = 36$).

Soil characteristic	Parameter	Mean ± SE
Soil texture† (%)	Sand (>53 μm)	17.2 ± 0.5
	Silt (2–53 μm)	73.3 ± 0.4
	Clay (<2 μm)	9.51 ± 0.15
	Organic matter	0.19 ± 0.00
Soil nutrient content‡	P	1.74 ± 0.04
(mg g^{-1} DW)	N	8.31 ± 0.14
Extractible soil nutrients§	PO_4^{3-}	98.9 ± 5.8
(mg kg^{-1} WW)	NH_4^+-N	15.8 ± 1.21
	$(NO_2^- + NO_3^-)$-N	3.9 ± 0.5
pH¶	pH-H_2O	5.79 ± 0.03
	pH-KCl	4.89 ± 0.00

Notes: Analysis protocols:

† Grain size: laser diffractometry (Malvern S, Malvern Instruments Ltd, Worcestershire, UK), Organic matter content: loss on ignition 6h, 550°C (Deutsche Einheitsverfahren zur Wasser- Abwasserund Schlammuntersuchung 1991).

‡ Total N and P concentrations: acid digestion (Walinga et al. 1989) followed by colorimetrically determination of concentrations using a SAN++ Flow Analyser (Skalar, FAS, SA 20/40, Skalar Analytical B.V., Breda, The Netherlands).

§ Soil extractable phosphorous (PO_4^{3-}): Ammonium acetate-EDTA extraction (Cottenie et al. 1982*b*), Soil extractable N (NH_4^+-N, $(NO_2^- + NO_3^-)$-N) potassium chloride Extraction (Cottenie et al. 1982*a*), followed by concentration determination as described for total N and P.

¶ pH: 1:5 WW vol^{-1} solution (Houba et al. 1989).

after the grassland is mown as is a common practice) are expected to reflect indirect grazing effects on biomass production and on decomposition rates. We hypothesize (3) no indirect grazing effect on biomass production and gross primary production, while we expect goose grazing to increase total ecosystem respiration by stimulating decomposition rates.

Methods

Study site

This study was conducted in the Uitkerkse polder (Flanders, Belgium 51°090 N, 04°240 E). Belgian climate is characterized by mild winters and cool summers. Average annual air temperature varies around 9.6°C; annual precipitation averages 780 mm, and is more or less equally distributed throughout the year. The selected study site lies in the coastal polders, a wintering area of international importance for geese, situated close to the North Sea (<10 km). This area is extremely important for *Anser albifrons* (Scopoli, 1769) (White-fronted Geese) and *Anser brachyrhynchus* (Baillon, 1834) (Pink-footed Geese). Nowadays, 2–3% of the Baltic-North Sea population of White-fronted Geese and 80% of the total Svalbard population of Pink-footed Geese spend the winter in the coastal polders. Further, the geese population of the coastal polders mainly exists of Greylag Geese, *Anser fabalis rossicus* (Latham, 1787) (Bean Geese) and *Branta leucopsis* (Bechstein, 1803) (Barnacle Geese). In total 71% of all goose days in Flanders occur in this area (Devos et al. 2005, Kuijken et al. 2005). As a result of the general increase in population size of most Western Palearctic breeding geese and some strong winters, the total amount of goose days spent in this area increased about five times from 1981 to 2004 (Madsen et al. 1999, Kuijken et al. 2005).

In a meadow in a nature reserve in the Uitkerkse polder, 800 m^2 was exclosed for wild geese in 2006 before the first goose arrived. Twice a year the exclosure was mown (July and October) to mimic one of the common land uses in this polder area: mowing and grazing. The meadow is a historical permanent grassland with as characteristic species *Cynosurus cristatus* L. (crested dogstail). However, following grass species were more dominant: *Dactylis glomerata* L. (Cock's-Foot), *Lolium perenne* L. (English ryegrass), *Poa trivialis* L. (rough bluegrass), *Hordeum secalinum* Schreb. (meadow barley), *Elymus repens* (L.) Gould (couch grass) and *Alopecurus geniculatus* L. (marsh foxtail). The vegetation consisted further of following forbs: *Ranunculus sardous* Crantz. (hairy buttercup), *Ranunculus repens* L. (creeping buttercup), *Ranunculus acris* L. (meadow buttercup), *Cirsium arvense* (L.) Scop. (creeping thistle), *Trifolium repens* L. (white clover) and *Cerastium fontanum* Baumg. (common mouse-ear). Table 1 summarizes the key soil characteristics.

Experimental design

Nine experimental blocks were embedded within the goose exclosure, with a buffer zone of 2 m. Each experimental block was divided in four plots of 3 m × 3 m, of which the middle 2 m × 2 m plot was subjected to one of the four specified grazing pressures (ungrazed, low, moderate and high), following a randomized design. Grazing pressure during the first experimental grazing season (2006–2007) was based on the carrying capacity of 9 goose days d^{-1} ha^{-1} for a period of ±120 days or 1080 goose days yr^{-1} ha^{-1} established for another nearby wintering area for goose in the coastal polders (Meire and

Kuijken 1991, Kuijken et al. 2005). In practice grazing succeeded by one couple of Greylag Geese in a cage (2 m × 2 m), which was transported from one plot to another, while geese were allowed to forage for 15, 30 or 60 minutes, corresponding with 625 goose days yr^{-1} ha^{-1}, 1250 goose days yr^{-1} ha^{-1} and 2500 goose days yr^{-1} ha^{-1} respectively. In the last plot no grazing occurred. The plots were grazed every two weeks in winter from November till February, the main time wild geese are present in the area (Kuijken et al. 2005). Grazing occurred periodically (not continuously) to reflect the habit of geese to cyclically revisit grasslands (Meire and Kuijken 1991). There was no grazing in summer and the first and the last grazing only lasted for half of the time to mimic the natural situation, where geese leave the coastal polders to breed in the North and where not all geese are arriving and leaving on the same day (Meire and Kuijken 1991, Kuijken et al. 2005).

Given that the impact of the high grazing pressure treatment during the first grazing season of the experiment was far less than the natural grazing impact surrounding the exclosure, we decided to double the experimental grazing pressure during the second grazing season (2007–2008) to better imitate reality. The ecological relevance of our study is reflected in the impact of the experimental grazing on the vegetation during the second year, which resembled closely the results of a study by Van Gils et al. (2010) on a broad range of agricultural grasslands in the coastal polders.

Biomass

Samples for the determination of above ground biomass, above ground necromass, roots, and macro-invertebrates were taken just after the peak of the grazing season (February 2008), during the peak of the subsequent growing season (July 2008) and just before next grazing season (November 2008). To determine aboveground mass we clipped three squares of 10 × 10 cm^2 (February and November), respectively 50 × 50 cm^2 (July) in each plot. Entire samples (February and November) and subsamples (July) were then sorted in dead and living plant material, dried at 70°C until constant mass and weighed. For the determination of belowground biomass and macro-invertebrates three soil cores with a diameter of 5.3 cm to a depth of 10 cm were taken in each plot with the aid of kopecky rings (Eijkelkamp, The Netherlands). Those samples were sieved over 500 μm. Hereafter bigger soil particles were picked up and roots and macro-invertebrates were carefully separated.

During CO_2 flux measurement periods (February, May, August, November 2008), vegetation height was measured using a foam disc of 40 cm diameter, weighing 100 g and moving along a stick with centimeter scale. Three measurements were taken per plot and the average was used for further calculations. As grass length has been found to correlate with dry weight of grass (Van Gils et al. 2010), we considered vegetation height as a proxy of the standing crop at that time.

At the end of the grazing season (February 2008) we took three additional soil samples per plot (Grass Plot Sampler, Eijkelkamp) to determine microbial C. Samples were pooled for analysis. Major roots were removed and three subsamples were taken. One sample was used to determine the ratio between wet and oven dry weight. Two other samples (10 g oven dry equivalent) were used to determine microbial C. Microbial biomass C in the soil was measured using the chloroform fumigation direct extraction (CFDE) protocol (Brookes et al. 1985). Extraction and fumigation were started within 24 h after sampling. Total dissolved carbon in the extracts was analyzed on a TOC analyzer (Shimadzu Total Organic Carbon Analyzer TOC-5000 with autosampler ASI-5000, Japan). Following Beck et al. (1997), kEC was estimated as 0.45.

Decomposition

Litterbags were used to test for effects of goose grazing on decomposition. The litterbags were made of polyester gauze with mesh width 0.3 mm, a mesh width which is a good compromise still allowing the majority of soil organisms to enter and preventing too much litter loss (Cornelissen 1996, Smith 2003). The dimensions of the litterbags were 6 cm x 6 cm between stitching (with borders: 7.5 cm × 7 cm) to minimize disturbance by placing. In each plot 16 litterbags were randomly fixed with pegs and all litterbags were individually labeled. Litterbags were filled with approximately 1 g of air-dried *Phragmites australis* (Cav.) Trin. ex Steud.

(reed) leaves which were previously cut into slivers of around 1 cm. Moisture content of the litter was determined by taking sub samples (5 g air-dried material) at the moment of weighing litterbag samples, which were dried at 70°C until constant mass and weighed again. The ratio between air-dry mass and oven-dry mass was used to express all data on a dry mass basis.

On two occasions eight litterbags were collected, namely after one grazing season (February 2008) and a year (November 2008) of incubation. In the laboratory extraneous litter, soil particles and organisms and roots were removed. The remaining litter was dried at 70°C and weighed. Corrections for inflow of nonorganic material were made after determining loss-on-ignitions of both litter and soil samples (Robertson et al. 1999). Incineration occurred by 550°C for 4 hours in a muffle furnace (Kendro Heraeus M110, Germany).

CO_2 fluxes

Carbon dioxide fluxes were measured at the end of the grazing season (February 2008), in spring before mowing (May 2008), in the summer, between both mowing periods (August 2008) and just before the start of the subsequent grazing season (November 2008). Each period lasted for approximately one week and at least five, but mostly more than seven measurements were made per plot, spread between sunrise and sunset.

Flux measurements and subsequent data analysis were performed as in Vicca et al. (2007). First, a transparent polymethyl pentene cuvette (60 cm high; 25 cm in diameter) was placed on equal-diameter 8 cm high soil collars, which were installed in the middle of each plot in November 2006, one year before measurements started. The collars rose 2 cm above the ground level and the lower 4 cm were perforated to impede root growth and water flow as less as possible. Airtightness between the cuvette and the collars was ensured by a gas tight seal. CO_2 fluxes were then measured using an infrared gas analyzer (IRGA; EGM-4; PP Systems, Hitchin, UK) which was coupled to the cuvette. Chambers were closed for two minutes (as is standard). In case Δ CO_2 started to rise over 50 ppm measurements were shortened to avoid our measurements to be influenced by too high CO_2 concentrations. During these measurements, a quantum sensor (JYP 1000, SDEC, France) inside the cuvette measured photosynthetic photon flux density (PPFD). Two aerators guaranteed well-mixed air. After placing the cuvette, net ecosystem exchange of CO_2 (NEE) was measured. Subsequently, measurements of total ecosystem respiration (TER) were performed in the dark, by covering the cuvette with a black cloth, preventing photosynthesis. Gross primary productivity (GPP) could then be calculated as: GPP = NEE − TER. We are aware of the fact that this calculation can cause a slight (max 5–10%) overestimate of GPP, because leaf respiration is partially inhibited in the light (Atkin et al. 2000). However, in this study our interest primarily lies in the relative differences in GPP among grazing treatments, not in absolute values of GPP. We therefore believe that the method used was suitable for our study.

Air temperature was derived from the weather station in the neighboring town (IVA MDK–afdeling Kust–Meetnet Vlaamse Banken).

Data analysis

The aim of our research was to determine whether geese were significantly influencing the carbon fluxes. Because air temperature was constantly fluctuating, we wanted to compare TER rates at a standard temperature of 10°C (TER_{10}). In order to estimate TER_{10} we fitted regressions for TER in Matlab 2010a (The MathWorks, Natick, MA, USA), using the following function:

$$\mathrm{TER} = \mathrm{BR} \times Q_{10}^{((T_{\mathrm{air}}-10)/10)} \quad (1)$$

in which BR is the basal rate, Q_{10} is the temperature sensitivity of TER, and T_{air} (in °C) is the recorded air temperature at the time of measurement. In order to obtain TER_{10} T_{air} in Eq. 1 was set at 10°C. TER_{10} is thus corresponding with BR. For every period, regressions were fitted to all measurements made in a particular plot. Regressions for GPP were calculated as a function of PPFD. Since light intensities fluctuated continuously as well, GPP_{300} (GPP at a PPFD value of 300 μmol photons m^{-2} s^{-1}) was estimated for each plot. For this purpose, we used the following function:

Table 2. Statistical comparison (ANOVA) of measured biomass parameters between different experimental grazing pressures (ungrazed, low, moderate and high).

Parameters	February 2008			July 2008			November 2008		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Aboveground plant biomass	3, 24	2.16	0.12	3, 24	2.37	0.096	3, 24	0.54	0.66
Aboveground plant necromass	3, 24	0.21	0.89	3, 24	0.50	0.68	3, 24	1.71	0.19
Plant roots	3, 24	0.05	0.99	3, 24	2.73	0.066	3, 24	1.55	0.23
Macro invertebrates	3, 24	1.25	0.31	3, 24	1.66	0.20	3, 24	0.84	0.49

$$\mathrm{GPP} = \frac{\mathrm{QE} \times \mathrm{PPFD} \times P_{\max}}{\mathrm{QE} \times \mathrm{PPFD} + P_{\max}} \quad (2)$$

in which QE is the quantum efficiency and $P_{\max}$ the maximum photosynthesis. In order to obtain GPP_{300} PPFD in Eq. 2 was set at 300 μmol photons m^{-2} s^{-1}. For every period regressions were fitted to all measurements made in a particular plot.

Analogous to GPP regressions for NEE were calculated as function of PPFD using following equation:

$$\mathrm{NEE} = \frac{\mathrm{QE} \times \mathrm{PPFD} \times P_{\max}}{\mathrm{QE} \times \mathrm{PPFD} + P_{\max}} + R \quad (3)$$

in which R is respiration. For calculation of NEE_{300}, PPFD in Eq. 2 was set at 300 μmol photons m^{-2} s^{-1}.

Additionally, we calculated for each plot an average of all NEE measurements ($NEE_{daytime}$), randomly taken at different times, and thus light intensities, between sunrise and sundown.

To test if differences in CO_2 fluxes between grazing treatments were related to plant cover only, a linear function was fitted to the data:

$$y = a + bx \quad (4)$$

in which y is GPP_{300}, or TER_{10} and x is vegetation height. Subsequently, we used the fitted functions to calculate $GPP_{300(pcl)}$, $TER_{10(pcl)}$, for the vegetation height measured in each plot. (To clarify: $GPP_{300(pcl)}$, $TER_{10(pcl)}$, are predicted flux rates based on the measured vegetation height and Eq. 4, whereas GPP_{300}, TER_{10}, are measured fluxes, albeit normalized for light or temperature). We then computed residuals as $GPP_{300} - GPP_{300(pcl)}$, $TER_{10} - TER_{10(pcl)}$ (residuals were termed $Resid_{GPP}$ and $Resid_{TER}$). To verify the validity of vegetation height as a measure of aboveground biomass linear regression analysis was performed using the reg procedure of the software program SAS (SAS Institute, Cary, NC, USA; Version 9.2, 2008), which was used for all further analysis.

Means and standard errors for the CO_2 fluxes and residuals of each treatment and period were weighted by the R^2 of the fitted curves using the means procedure. CO_2 fluxes and residuals (both weighted for the R^2 of the fitted curves), biomass of different ecosystem components, vegetation height and decomposition parameters were all compared using an (weighted) ANOVA. Grazing treatment and experimental block were set as fixed and random factor respectively. In case of significant differences, grazing treatments were compared pair-wise with a Tukey-Kramer correction. Therefore we used the mixed and univariate normal procedure. Data was log-transformed if needed to meet the prerequisite of normality and differences were considered significant at $P \leq 0.05$.

Results

Biomass

Aboveground plant biomass, aboveground plant necromass, plant roots and macro-invertebrates were not significantly affected by grazing pressure at any moment in our study, although at the peak of the growing season (July 2008) both aboveground and root biomass showed a borderline significant increase in response to grazing (Table 2, Fig. 1). At that time the total plant biomass (aboveground biomass + roots) was significantly increased under moderate and high grazing pressure compared to ungrazed plots ($F_{3,24} = 4.34$, $P = 0.014$; Fig. 1B).

Standing crop during CO_2-flux measurements, as measured by vegetation height, differed significantly between different grazing pressures in February and May ($F_{3,23} = 29.99$, $P < 0.0001$; $F_{3,24} = 3.69$, $P = 0.0257$; Fig. 2A, B). In August and

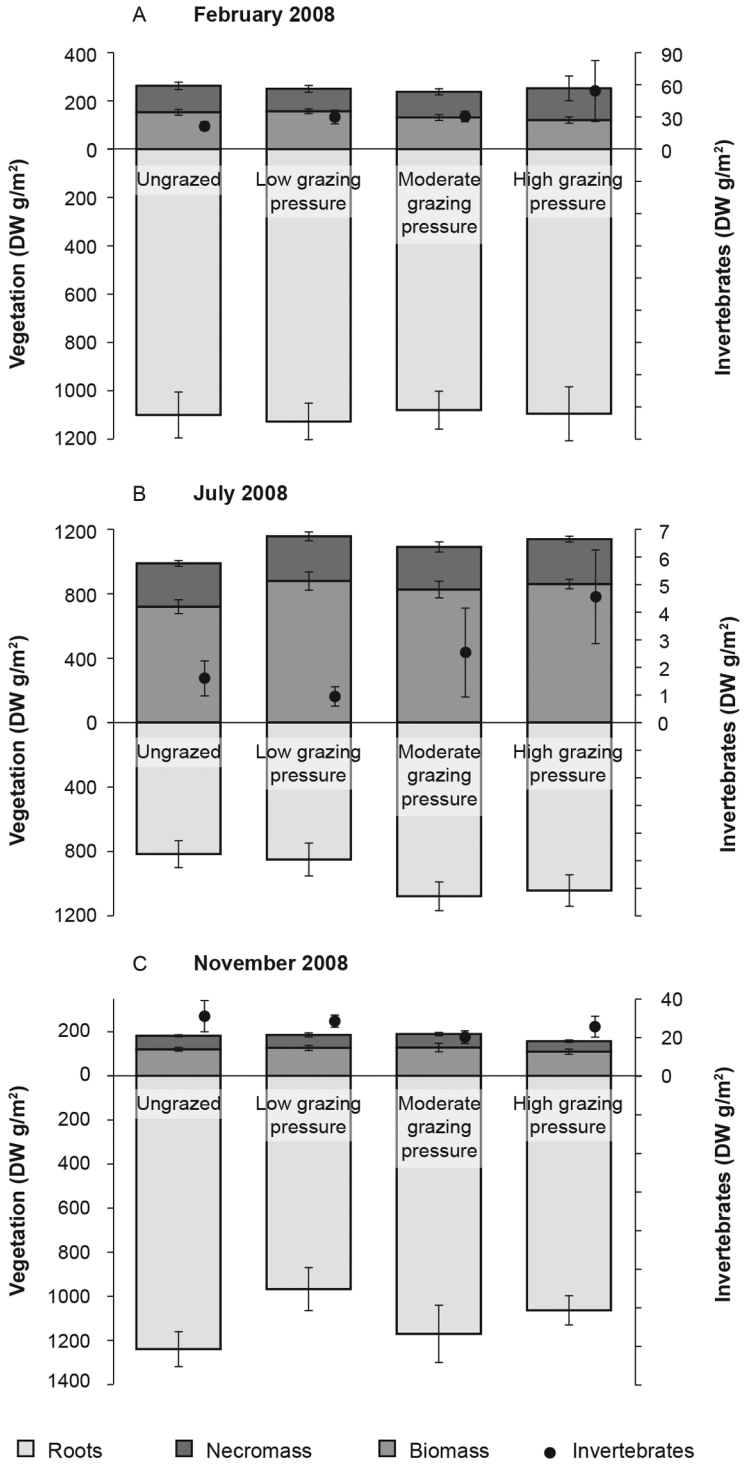

Fig. 1. Biomass in grassland plots under different experimental grazing pressures. Average belowground plant mass (roots), aboveground plant biomass (biomass), above ground plant necromass (necromass) and belowground macro-invertebrate biomass (invertebrates) just after the grazing season (A), at the peak of the growing season (B) and just before subsequent grazing season (C) are given. Error bars indicate the standard errors on the mean. Results of statistical analyses are presented in Table 2.

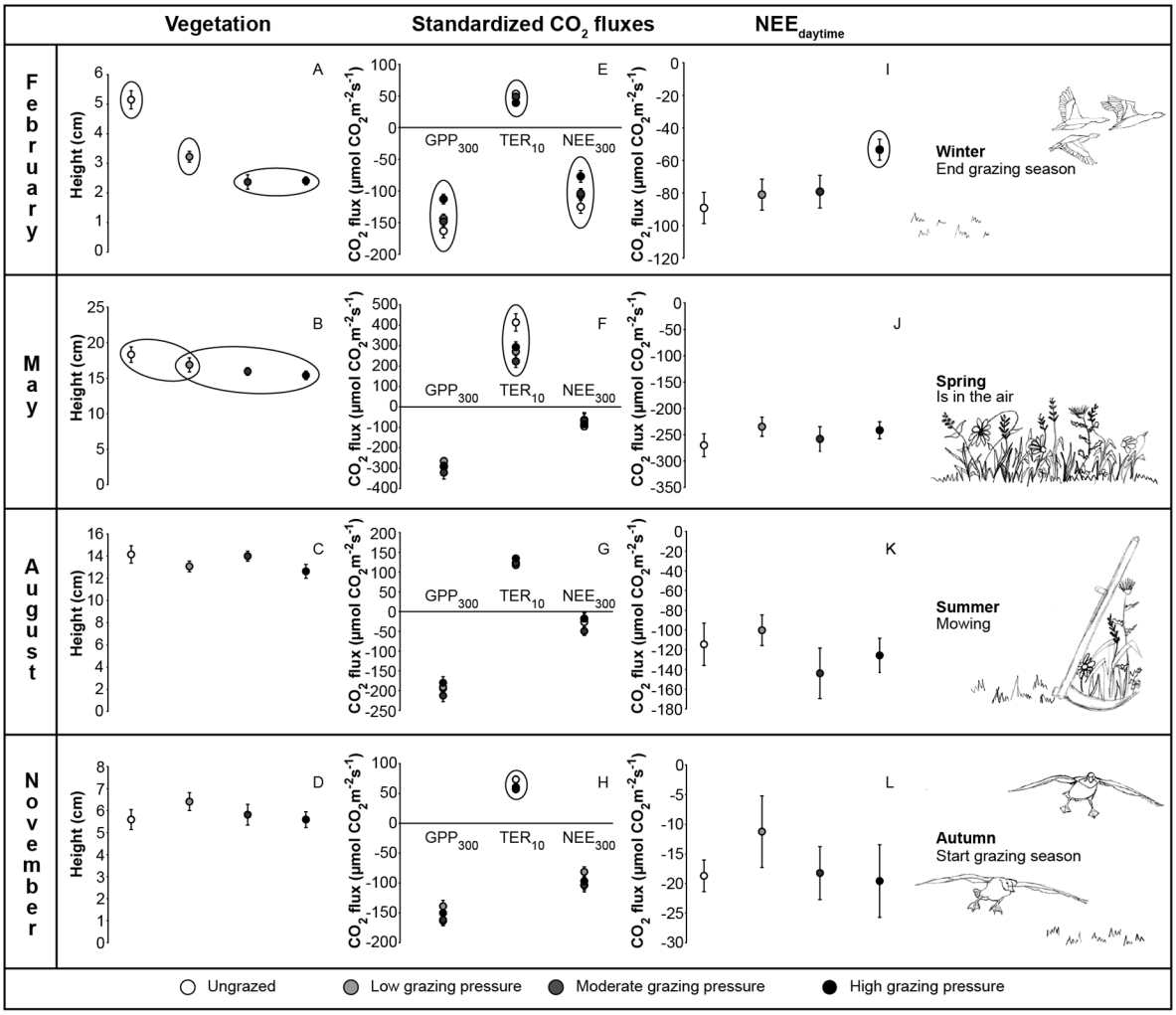

Fig. 2. Carbon fluxes and vegetation height in grassland plots subjected to different grazing treatments. The first column, vegetation, gives the vegetation height during measurements. The second column, standardized CO_2 fluxes, gives the weighted average per treatment of the gross primary production at PPFD 300 photons m^{-2} s^{-1} (GPP_{300}), the total ecosystem respiration at 10°C (TER_{10}) and net ecosystem exchange by PPFD 300 photons m^{-2} s^{-1} (NEE_{300}), calculated for each plot. The last column, $NEE_{daytime}$, gives the average per treatment of the mean net ecosystem exchange measured for each plot ($n = 5$–9, measurements random spread from sunrise to sunset). Error bars represent standard errors; circles represent significant differences ($P \leq 0.05$).

November this difference seemed to have disappeared ($F_{3,24} = 1.61$, $P = 0.2122$; $F_{3,24} = 0.94$, $P = 0.4355$; Fig. 2C, D). The linear regression between vegetation height and aboveground biomass (as determined from the two harvests just after measuring CO_2 fluxes in February and November 2008) was highly significant ($F_{1,33} = 6.90$, $P = 0.0129$; $F_{1,34} = 3.46$, $P = 0.0015$). However, only 17–26% of the variation in biomass was explained by vegetation height (R^2 between 0.17 and 0.26).

At the end of the grazing season (February 2008) microbial carbon amounted to 2.15 ± 0.05 mg C g^{-1}, averaged over all plots. We found no indications for a difference in microbial biomass among the treatments ($F_{3,24} = 0.63$, $P = 0.605$).

Decomposition

The first phase of litter breakdown—from autumn, when litter is shed and geese start to arrive (November 2007) until late winter when

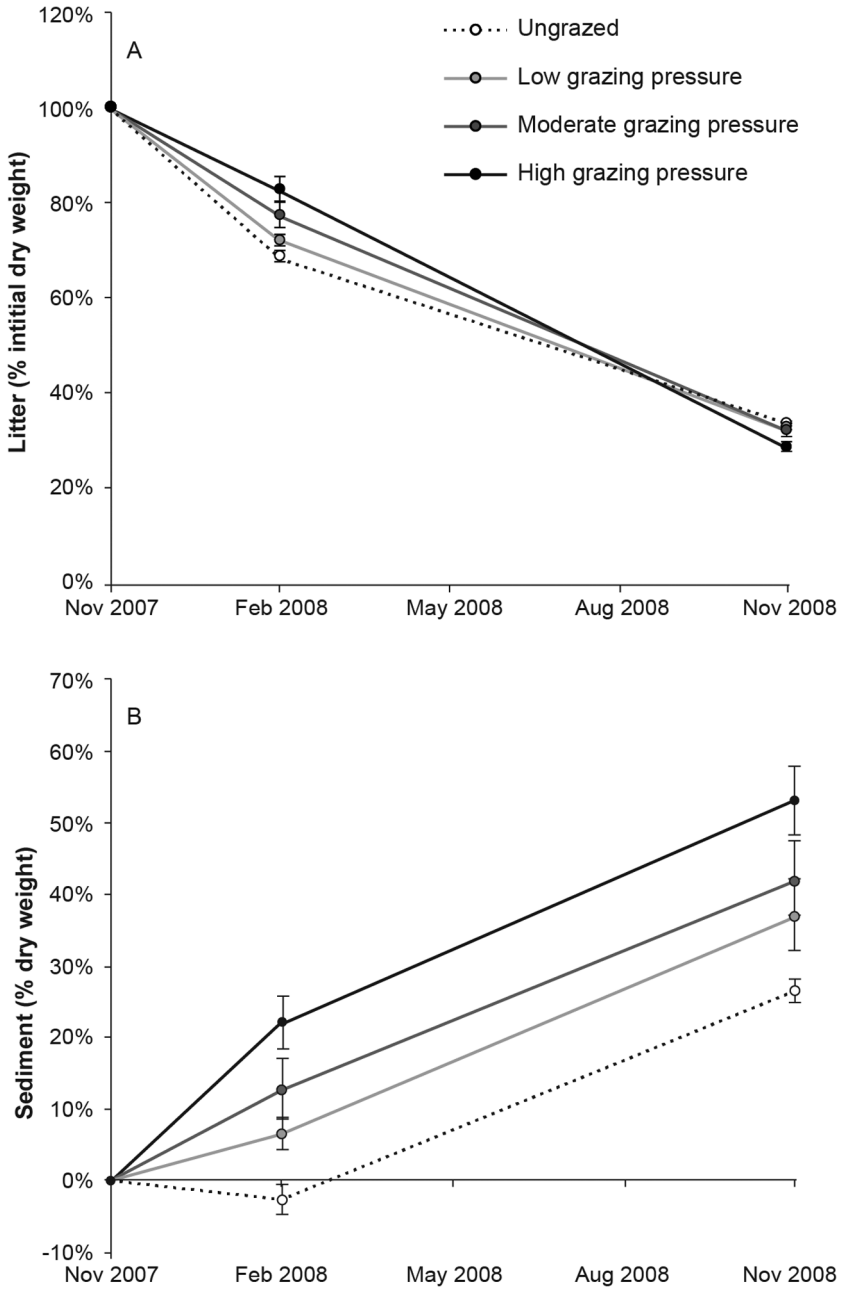

Fig. 3. Decomposition parameters derived from litterbags filled with *Phragmites australis* (Cav.) Trin. ex Steud. (reed) incubated in grassland plots under different experimental grazing pressures. Average litter breakdown (A) and sediment input in the litterbags (B) are given together with the standard error (error bars). Significant differences ($P \leq 0.05$) existed between grazing treatments for both parameters and both incubation times.

geese are leaving (February 2008)—was significantly slowed down with increasing grazing pressure ($F_{3,24} = 9.67$, $P = 0.0002$; Fig. 3A). Decomposition rate in ungrazed plots was significantly higher than in the plots under moderate and high grazing pressure. Decomposition in plots under high grazing pressure in turn was significantly lower than in plots under

Table 3. Carbon fluxes (μmol CO_2 m^{-2} s^{-1}) in grassland plots subjected to different grazing treatments.

Carbon fluxes	Statistic	February 2008	May 2008	August 2008	November 2008
GPP_{300}	df	**3, 24**	3, 24	3, 24	3, 24
	F	**7.72**	1.11	1.17	1.77
	P	**0.0009**	0.37	0.34	0.18
TER_{10}	df	**3, 24**	**3, 24**	3, 24	**3, 24**
	F	**7.63**	**4.79**	1.96	**6.11**
	P	**0.0009**	**0.009**	0.15	**0.003**
NEE_{300}	df	**3, 24**	3, 24	3, 24	3, 24
	F	**5.57**	0.31	1.69	1.48
	P	**0.0048**	0.82	0.20	0.25
$NEE_{daytime}$	df	**3, 24**	3, 24	3, 24	3, 24
	F	**5.66**	0.86	1.81	0.73
	P	**0.004**	0.47	0.17	0.55

Notes: Results of the statistical comparison (ANOVA) of the gross primary production at PPFD 300 photons m^{-2} s^{-1} (GPP_{300}), the total ecosystem respiration at 10°C (TER_{10}) and net ecosystem exchange at PPFD 300 photons m^{-2} s^{-1} (NEE_{300}), calculated for each plot; the mean net ecosystem exchange ($NEE_{daytime}$) measured for each plot (n = 5-9, measurements random spread from sunrise to sunset). Values for GPP_{300}, TER_{10}, NEE_{300}, $NEE_{daytime}$ are given in Fig. 2. Parameters which significantly differed between grazing pressures are indicated in boldface. Level of significance: $P \leq 0.05$.

low grazing pressure. In the same period the reverse pattern was found for sediment input in the litter bags ($F_{3,24} = 11.71$, $P < 0.0001$; Fig. 3B).

Long term decomposition (one year of incubation, November 2008) was also significantly affected by grazing pressure ($F_{3,24} = 5.36$, $P = 0.0057$; Fig. 3A), but the pattern of change was smaller and opposite to the short-term effect: the higher the grazing pressure, the higher the mass loss after one year (Fig. 3A). The highest grazing pressure indeed resulted in a significantly increased litter mass loss by about 15% compared to no and low grazing pressure, the difference with a moderate grazing pressure was borderline significant ($t_{24} = 2.62$, $P = 0.0665$). Long term sediment input, in contrast, was similar to short term sediment input and although still significantly different between grazing pressures this only counted for the difference between plots under high grazing pressure and the ungrazed plots ($F_{3,24} = 6.06$, $P = 0.0032$; Fig. 3B).

Carbon fluxes

Immediately after the grazing season (February 2008) a significant difference in gross primary production (GPP_{300}), total ecosystem respiration (TER_{10}) and net ecosystem exchange (NEE_{300}, $NEE_{daytime}$) existed between different grazing treatments (Table 3, Fig. 2E). Whereas an increase in grazing pressure resulted in a smaller uptake of CO_2 through photosynthesis (difference significant between high grazing pressures and the other treatments), also less CO_2 was returned to the atmosphere via respiration (difference significant between ungrazed plots at the one hand and plots with low and high grazing pressure at the other hand). The decrease in TER_{10}, however, was smaller than the decline in GPP_{300} and the resulting NEE_{300} was therefore less negative (i.e., the system was a smaller sink) at high versus low grazing pressure (significant difference between ungrazed and grazed; Table 3, Fig. 2E). $NEE_{daytime}$ showed a similar pattern as NEE_{300} (significant difference between the high grazing pressure treatment and all other treatments; Table 3, Fig. 2E, I).

During the subsequent spring (May), when geese had migrated north, the difference in GPP_{300} had disappeared but TER_{10} was still affected by the difference in grazing pressure during winter. Although all grazed plots had lower values of CO_2 release than the ungrazed plots, only the difference with the plots subjected to a moderate grazing pressure was significant (Table 3, Fig. 2F, J).

Shortly after mowing (August), the observed differences in CO_2 fluxes caused by grazing pressure vanished, and none of the measured variables showed a significant post-grazing effect (Table 3, Fig. 2G, K). One additional mowing later, i.e., just before the new grazing season (November), the effect of grazing pressure on the CO_2 fluxes was again noticeable: the TER_{10} was significantly lower in grazed plots compared to the ungrazed plot (Table 3, Fig. 2H, L).

In order to test if effects of different grazing pressure on GPP_{300} and TER_{10} were only caused by the differences in standing crop, linear

Table 4. Correlation parameters (linear regression) between vegetation height and carbon fluxes, namely the gross primary production at PPFD 300 photons m^{-2} s^{-1} (GPP_{300}), the total ecosystem respiration at 10°C (TER_{10}).

Parameter	Period	df	F	P	R^2
Vegetation height – GPP_{300}	February 2008	1, 33	12.31	0.001	0.27
Vegetation height – TER_{10}	February 2008	1, 33	7.48	0.010	0.18
	May 2008	1, 34	4.61	0.039	0.12

functions between vegetation height and GPP_{300} and TER_{10} were calculated (Eq. 4). This regression analysis revealed a significant correlation for both GPP_{300} and TER_{10}, with vegetation height explaining 12% and 27% of the variation in GPP_{300} and TER_{10}, respectively (Table 4). These linear functions were then used for residual analysis (see *Materials and Methods*). $Resid_{GPP}$ differed significantly between the moderate and high grazing pressure for GPP_{300} in February ($F_{3,23} = 4.80$, $P = 0.0097$). Differences in $Resid_{TER}$ between grazing pressures were marginally significant both in February and May ($F_{3,23} = 2.91$, $P = 0.0562$; $F_{3,24} = 2.46$, $P = 0.087$; Fig. 4).

Discussion

Western Palaearctic geese population densities have increased considerably during the past decades and climate warming is expected to result in a further growth of at least some of them (Jensen et al. 2008). In a field experiment with manipulated grazing by Greylag Geese imposing different grazing pressures, information was gathered on the biomass, decomposition rates and carbon fluxes of temperate grasslands to assess the consequences of winter grazing by geese for two key processes that contribute to the carbon balance of a temperate grassland ecosystem: photosynthesis and ecosystem respiration, and this in different seasons. Our findings should be considered as the result of a two-year grazing experiment of which the first year represented a rather poor goose year and the second year, when measurements occurred, was equivalent to a good goose year. Information on this matter is crucial to better understand the impact of geese on their wintering habitat and to gain knowledge about possible biotic feedbacks to climate change.

CO_2 uptake

How much CO_2 is taken up from the atmosphere by ecosystems depends on the magnitude of photosynthetic inputs by the aboveground biomass. The decrease in aboveground biomass in grasslands by goose grazing has since long been a point of interest, albeit typically in the context of agricultural damage. Local farmers can indeed suffer from crop damage caused by intensive goose foraging on their fields (Groot Bruinderink 1989, Van Gils et al. 2010), which is also confirmed by the reduction in vegetation height due to increased goose grazing. Nevertheless, we did not find a statistically significant reduction in aboveground biomass at the end of the grazing season. This is not only surprising because of the significant reduction in vegetation height, but also given the fact that it was possible to distinguish plots with different grazing pressure by eye. In July (the time of mowing), plant biomass even tended to be stimulated by wintertime goose grazing. This might indicate overcompensation, but the effect rapidly diminished and at the start of the subsequent grazing season (November 2008), plant biomass did no longer vary between the different grazing pressures.

In accordance with our first hypothesis, the reduced biomass due to goose grazing resulted in a decreased GPP_{300} in February. However, although the standing crop, measured as vegetation height, was reduced by goose grazing both in February and in May, CO_2 flux measurements revealed that only in February GPP_{300} was significantly affected. Analysis of the $RESID_{GPP}$, which differed significantly between the moderate and high grazing treatment, suggests that the difference in GPP_{300} between the moderate and high grazing pressure in February are not entirely explained by the difference in standing crop (Fig. 4). The difference in GPP_{300} between plots under high and moderate grazing pressure

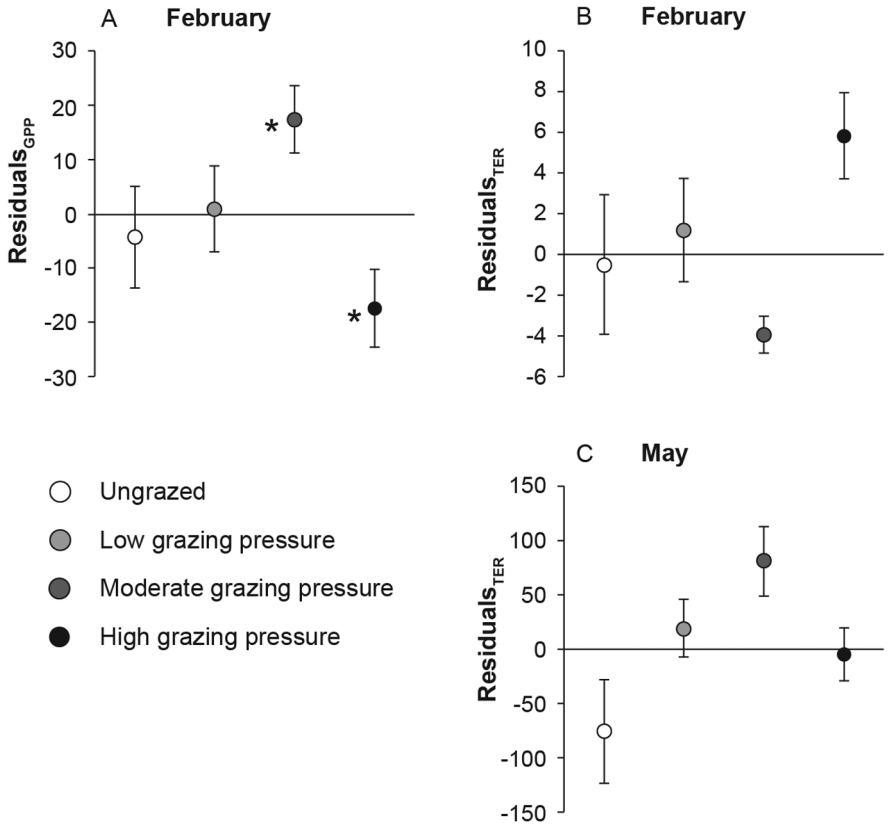

Fig. 4. Residuals between (A) gross primary production at PPFD 300 photons m^{-2} s^{-1} (GPP_{300}) and (B, C), the total ecosystem respiration at 10°C (TER_{10}) and the predicted values based on the observed vegetation height just after the grazing season (A, B) and in the subsequent spring (C). Error bars indicate the standard error on the mean. Residuals for GPP_{300} (A) differed significant between plots with moderate and high grazing pressure, which is indicated by an asterisk (* $P \leq 0.05$).

might be explained by the mechanical disturbance geese caused through trampling. The plants growing under high grazing pressure were of similar height as plant of moderate grazing pressure (i.e., ca. 2 cm, a typical minimum for a heavily grazed sward [Groot Bruinderink 1987]), but were covered more with mud, which hampers light penetration and thus photosynthesis.

In May, two months after the majority of geese had left and plants had started to grow again, photosynthesis rates (both GPP_{300} and GPP in general, data not shown) were higher than in February and differences in GPP_{300} between the treatments had disappeared. This trend persisted also during the rest of the year, suggesting that the geese's influence on GPP, is in accordance with hypothesis three only short-live, resulting in a rather small (if not negligible) impact on the annual total GPP.

CO_2 release

In contrast to GPP, TER was significantly affected by grazing intensity both in February at the end of the grazing season when the effect of goose grazing on the standing crop was most noticeable and in May when small differences in standing crop were still present. Analysis of $Resid_{TER}$, which revealed only marginally significant differences between treatments, did not give strong evidence for a parameter other than vegetation height to be responsible for differences in TER. Nevertheless, TER is not only determined by the respiration of the above ground biomass. Also soil respiration, including decomposition, contributes to a considerable

extent to the TER in grasslands (Bahn et al. 2008). Grazing effects on litter, roots, macro-invertebrates and microbial carbon were not statistically significant, but the lower CO_2 release by respiration in the plots under high grazing pressure is likely also partly explained by grazing slowing down the decomposition process during the winter season. It might also explain the borderline significant difference in TER in February between the plots with high and moderate grazing pressure, which had a similar standing crop.

The litterbag experiment indeed revealed that during the grazing season (the early stages of decomposition), the decomposition rate was decreased with increasing grazing pressure. This retardation of the decomposition process in response to goose grazing contrasts with our second hypothesis as well as with earlier research on herbivory effects on decomposition, where decomposition was stimulated rather than reduced in response to grazing (e.g., Sjögersten et al. 2012). The increase in sediment input into the litterbags with increasing grazing pressure does suggest trampling to be an important mechanism. We believe, however, that in this particular case the enhanced soil-litter contact hampered the decomposition process instead of increased as suggested by previous studies (e.g., Ruess 1987, Zacheis et al. 2002). The soil in the coastal polders is composed of very fine clay particles and in wintertime, when the soil is water-saturated, the wet clay might form an air-tight sealing around the litter. This could physically separate the litter from its decomposer community. Moreover, the resulting anaerobic conditions might further decrease the rate of decomposition, as anaerobic decomposition is thermodynamically unfavorable and hence much less efficient than aerobic decomposition (Stumm and Morgan 1981, Berg and McClaugherty 2008).

After mowing in August, TER was similar for all grazing treatments. Probably, vegetation height was at that time most influential on the CO_2 fluxes and the entire grassland was mown to the same height. However, in November, one month after the second mowing period and just before the geese arrived again, TER differed significantly among the treatments. Interestingly, this result was not yet present after the first poor goose year (November 2007, data not shown). In contrast with our third hypothesis, effects of goose grazing re-emerged with lower TER in grazed than in ungrazed plots. As neither vegetation height, nor plant biomass differed between the treatments at that moment, other mechanisms must have come into play. Given that our litter bag experiment revealed an increase in decomposition rates of standard litter in response to goose grazing (on the long term), decomposition seems unlikely responsible for the decrease in TER.

In contrast to short term decomposition rates at the time that geese were present, longer term (1 year of incubation) decomposition was accelerated by goose grazing. Our results on the long term effect of winter grazing by geese are thus in correspondence with earlier research on (geese) herbivory effects on decomposition (e.g., Sjögersten et al. 2012). Similar to the retardation of the first phase of decomposition during winter, the acceleration of decomposition in the long term might result from the higher sediment input by trampling as grazing pressure rises. After winter the soil becomes dryer and the sediment attached to the litter provides a larger surface area for microbes to grow upon and may help retaining water and avoiding drought. In contrast to what the early-stage decomposition rates suggested, goose grazing can therefore stimulate decomposition, which is in agreement with earlier studies (Ruess 1987, Zacheis et al. 2002). Such overall enhancement of decomposition rates due to wintertime goose herbivory in the temperate grasslands, is also found for summertime goose grazing in the Arctic breeding habitats of the geese (Zacheis et al. 2002, Sjögersten et al. 2011, Sjögersten et al. 2012).

However, it is worth mentioning that our litterbag experiment did not take into account indirect herbivory effects such as a change in litter quality, temporal variations throughout the year, or the full extent of trampling impact. Finally, grazing short-circuits the decomposition process by the production of feces (Bryant et al. 1983). This influences the time course of conversion of living plant tissue to dead organic matter and the form of dead organic matter: feces rather than dead leaves (Maclean 1974), which are more readily decomposed (Floate 1970, Bazely and Jefferies 1985). Our advice for future studies is therefore to measure soil respiration (or even

better, heterotrophic respiration) directly in the field (e.g., via soil respiration chambers) so that above- and belowground respiration can be separated to test whether the changes in TER are primarily plant-related or rather microbial mediated.

CO_2 balance

From the results and the above discussion about GPP and TER, we conclude that geese do impact ecosystem CO_2 fluxes. As geese numbers are projected to increase partially due to the change in climate (Kéry et al. 2006, Jensen et al. 2008), the described effect of grazing pressure on the CO_2 fluxes might contribute to a possible feedback loop to climate change. Within that framework, especially NEE, the resultant of GPP and TER, is of interest. At the end of the grazing season, when geese were leaving (February), both GPP and the TER were affected by grazing pressure and the resulting NEE was positively correlated with the grazing pressure (Fig. 2). After the grazing season, the difference in NEE disappeared. These results are analogous to the most probable scenario in the Arctic breeding sites, where during summer geese reduce the carbon sink strength of wetlands, their preferred habitat (Sjögersten et al. 2008, Speed et al. 2010, Sjögersten et al. 2011). Outside the grazing season, however, no difference in NEE was found in this habitat (Sjögersten et al. 2008).

It is, however, important to remark that our measurements in the temperate grasslands were only taken from sunrise to sunset and are therefore not completely comparable with the fore-mentioned studies in the Arctic breeding sites where measurements were taken over 24 h. As TER during the day may differ from nighttime TER (Lasslop et al. 2010), it is not possible to make any further predications about the general CO_2 balance over 24 h in this study. Indeed, factors driving TER, such as temperature, moisture regime, light-induced inhibition of foliar respiration and activity of biota, differ between day and night. Moreover, our measurements were not continuous over the entire year, but took place during four critical periods. As the grazing effect changes over the year, it is not opportune to extrapolate them over the entire year.

In contrast to the Arctic breeding sites, we can therefore not yet ascertain that the increased populations of Western Palearctic geese reduce the CO_2 uptake and thus carbon sink strength of the temperate grasslands from their winter habitat. Nonetheless, our study indicates that goose grazing may substantially impact the CO_2 fluxes of temperate grasslands, and that grazing effects are not restricted to a temporary reduction of the biomass. Future studies are needed to calculate the resulting effect on the CO_2 balance of temperate grasslands and to further unravel the legacy effect of goose grazing on ecosystem CO_2 fluxes.

Conclusions

This study demonstrated that grazing pressure by geese in their wintering habitat can significantly impact carbon cycling in these temperate grasslands. Similar to the results from studies on the northern breeding sites, a goose-induced decrease in uptake of CO_2 (the main constituent of the C balance) due to the removal of photosynthesizing aboveground biomass was found (corresponding to hypothesis 1). In contrast to previous studies in the northern breeding sites, decomposition was hampered due to goose presence together with a reduction in autotrophic respiration this resulted in a decreased emission of CO_2 when geese were present (contrasting to hypothesis two). We found carry-over effects of goose grazing to the seasons after the geese had left only on ecosystem respiration, not on GPP (corresponding to hypothesis 3). Surprisingly, eight months after the geese had left, effects of goose grazing were still detectable as a decrease of ecosystem respiration (contrasting to hypothesis 3). This effect was neither related to differences in standing crop (which were absent), nor to long-term decomposition rates. In contrast to the short term rates, grazing had increased rather than decreased decomposition rates after the geese had left. Further research is needed to unravel the indirect effects of goose grazing on ecosystem respiration in their wintering habitat. Such study should aim to separate TER in aboveground respiration and belowground (autotrophic and heterotrophic) respiration.

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Literature Cited

Atkin, O. K., J. R. Evans, M. C. Ball, H. Lambers, and T. L. Pons. 2000. Leaf respiration of snow gum in the light and dark: interactions between temperature and irradiance. Plant Physiology 122:915–924.

Bahn, M. et al. 2008. Soil respiration in European grasslands in relation to climate and assimilate supply. Ecosystems 11:1352–1367.

Bardgett, R. D., and D. A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84:2258–2268.

Bardgett, R. D., D. A. Wardle, and G. W. Yeates. 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. Soil Biology & Biochemistry 30:1867–1878.

Bazely, D. R., and R. L. Jefferies. 1985. Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. Journal of Applied Ecology 22:693–703.

Beck, T., R. G. Joergensen, E. Kandeler, F. Makeschin, E. Nuss, H. R. Oberholzer, and S. Scheu. 1997. An inter-laboratory comparison of ten different ways of measuring soil microbial biomass C. Soil Biology and Biochemistry 29:1023–1032.

Berg, B., and C. McClaugherty. 2008. Plant litter: decomposition, humus formation, carbon sequestration. Second edition. Springer-Verlag, Berlin, Germany.

Brookes, P. C., A. Landman, G. Pruden, and D. S. l. S. B. B. Jenkinson. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biology & Biochemistry 17:837–842.

Bryant, J. P., F. S. Chapin, III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357–368.

Chapin, F. S., J. T. Randerson, A. D. McGuire, J. A. Foley, and C. B. Field. 2008. Changing feedbacks in the climate–biosphere system. Frontiers in Ecology and the Environment 6:313–320.

Cornelissen, J. H. C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. Journal of Ecology 84:573–582.

Cottenie, A., M. Verloo, L. Kiekens, G. Velghe, and R. Camerlynck. 1982*a*. Extractable NH_4-N en (NO_2+NO_3)-N. Page 47 *in* Chemical analysis of plants and soils. State University of Ghent, Ghent, Belgium.

Cottenie, A., M. Verloo, L. Kiekens, G. Velghe, and R. Camerlynck. 1982*b*. Extractable P. Page 41 *in* Chemical analysis of plants and soils. State University of Ghent, Ghent, Belgium.

Coûteaux, M.-M., P. Bottner, and B. Berg. 1995. Litter decomposition, climate and litter quality. Trends in Ecology & Evolution 10:63–66.

Deutsche Einheitsverfahren zur Wasser- Abwasserund Schlammuntersuchung. 1991. Bestimmung des Glührückstandes und des Glühverlustes des Trockenmasse eines Schlammes, DIN 38414/S3, 1985. VCH Verlagsgesellschaft mbH, Weinheim, Germany.

Devos, K., E. Kuijken, C. Verscheure, P. Meire, L. Benoy, W. De Smet, and J. Gabriëls. 2005. Overwinterende wilde ganzen in Vlaanderen 1990/91-2003/04. Natuur.oriolus 71:4–20.

Floate, M. S. J. 1970. Decomposition of organic materials from hill soils and pastures. III. The effect of temperature on the mineralization of carbon, nitrogen and phosphorous from plant materials and sheep faeces. Soil Biology & Biochemistry 2:187–196.

Fox, A. D., et al. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and an assessment of trends. Ornis Svecica 20:115–127.

Frank, D. A., M. M. Kuns, and D. R. Guido. 2002. Consumer control of grassland plant production. Ecology 83:602–606.

Groot Bruinderink, G. W. T. A. 1987. Wilde ganzen en cultuurgrasland in Nederland (Wild geese and grassland in the Netherlands). Dissertation. Landbouwuniversiteit te Wageningen, Centrum voor Agrobiologisch Onderzoek (CABO), Wageningen, The Netherlands.

Groot Bruinderink, G. W. T. A. 1989. The impact of

wild geese visiting improved grasslands in The Netherlands. Journal of Applied Ecology 26:131–146.

Handayanto, E., G. Cadisch, and K. E. Giller. 1997. Regulating N mineralization from plant residues by manipulation of quality. Pages 175–185 *in* G. Cadisch and K. E. Giller, editors. Driven by nature: Plant litter quality and decomposition. CAB International, Wallingford, UK.

Holland, E. A., and D. C. Coleman. 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. Ecology 68:425–433.

Houba, V. J. G., J. J. van der Lee, I. Novazamsky, and I. Walinga. 1989. 7. Determination of pH. Pages 7–1 *in* Soil analysis procedures. Agricultural University, Wageningen, The Netherlands.

IPCC. 2007. Climate Change 2007: Synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Jensen, R. A., J. Madsen, M. O'Connell, M. S. Wisz, H. Tommervik, and F. Mehlum. 2008. Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. Global Change Biology 14:1–10.

Kéry, M., J. Madsen, and J.-D. Lebreton. 2006. Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. Journal of Animal Ecology 75:1172–1181.

Kuijken, E., C. Verscheure, and P. Meire. 2005. Ganzen in de Oostkustpolders: 45 jaar evolutie van aantallen en verspreiding. Natuur.oriolus 71:21–42.

Lasslop, G., M. Reichstein, D. Papale, A. D. Richardson, A. Arneth, A. Barr, P. Stoy, and G. Wohlfahrt. 2010. Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. Global Change Biology 16:187–208.

Loonen, M. J. J. E., and B. Solheim. 1998. Does arctic vegetation change when grazed by barnacle geese? A pilot study. Norsk Polarinstitutt Skrifter 200:99–103.

Maclean, S. F. J. 1974. Primary production, decomposition, and the activity of soil invertebrates in tundra ecosystems: a hypothesis. Pages 197–206 *in* A. J. Holding, O. W. Heal, S. F. J. Maclean, and P. W. Flanagan, editors. Soil organisms and decomposition in tundra. Tundra Biome Steering Committee, Stockholm, Sweden.

Madsen, J., G. Cracknell, and A. D. Fox, editors. 1999. Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International Publication Number 48. Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute. Rönde, Denmark.

Meire, P., and E. Kuijken. 1991. Factors affecting the number and distribution of wintering geese and some implications for their conservation in Flanders, Belgium. Ardea 79:143–157.

Oechel, W. C., S. J. Hastings, G. Vourlrtis, M. Jenkins, G. Riechers, and N. Grulke. 1993. Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. Nature 361:520–523.

Ostle, N. J., P. E. Levy, C. D. Evans, and P. Smith. 2009. UK land use and soil carbon sequestration. Land Use Policy 26, Supplement 1:S274–S283.

Raich, J. W., and W. H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus B 44:81–99.

Robertson, G. P., D. C. Coleman, C. S. Bledsoe, and P. Sollins, editors. 1999. Standard soil methods for long-term ecological research. Oxford University Press, Oxford, UK.

Ruess, R. W. 1987. Herbivory. The role of large herbivores in nutrient cycling of tropical savannas. Pages 67–91 *in* B. H. Walker, editor. Determinants of tropical savannas. Oxford University Press, Oxford, UK.

Schulze, E. D., et al. 2009. Importance of methane and nitrous oxide for Europe's terrestrial greenhouse-gas balance. Nature Geoscience 2:842–850.

Shaver, G. R., and W. D. Billings. 1992. Global change and the carbon balance of arctic ecosystems. BioScience 42:433–441.

Sjögersten, S., R. Van der Wal, M. J. J. E. Loonen, and S. J. Woodin. 2011. Recovery of ecosystem carbon fluxes and storage from herbivory. Biogeochemistry 106:357–370.

Sjögersten, S., R. van der Wal, and S. J. Woodin. 2008. Habitat type determines herbivory controls over CO_2 fluxes in a warmer arctic. Ecology 89:2103–2116.

Sjögersten, S., R. van der Wal, and S. J. Woodin. 2012. Impacts of grazing and climate warming on C pools and decomposition rates in Arctic environments. Ecosystems 15:349–362.

Smith, T. M. 2003. Elements of ecology. Fifth edition. Pearson Education, San Francisco, California, USA.

Soussana, J. F., et al. 2007. Full accounting of the greenhouse gas (CO_2, N_2O, CH_4) budget of nine European grassland sites. Agriculture, Ecosystems & Environment 121:121–134.

Speed, J. M., S. J. Woodin, H. Tømmervik, and R. van der Wal. 2010. Extrapolating herbivore-induced carbon loss across an arctic landscape. Polar Biology 33:789–797.

Stumm, W., and J. J. Morgan. 1981. Aquatic chemistry: an introduction emphasizing chemical equilibria in natural waters. Wiley, New York, New York, USA.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979.

Decomposition in terrestrial ecosystems. Blackwell Scientific, London, UK.

van der Wal, R., S. Sjörgersten, S. J. Woodin, E. J. Cooper, I. S. Jonsdottir, D. Kuijper, T. A. D. Fox, and A. D. Huiskes. 2007. Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. Global Change Biology 13:539–545.

Van Gils, B., F. Huysentruyt, J. Casaer, K. Devos, A. De Vliegher, and L. Carlier. 2010. Project winterganzen 2008-2009: onderzoek naar objectieve schadebepaling, INBO.R.2009.56. Instituut voor Natuur- en Bosonderzoek, Brussels, Belgium.

Vicca, S., P. Serrano-Ortiz, H. de Boeck, C. Lemmens, I. Nijs, R. Ceulemans, A. S. Kowalski, and I. Janssens. 2007. Effects of climate warming and declining species richness in grassland model ecosystems: acclimation of CO_2 fluxes. Biogeosciences 4:27–36.

Walinga, I., W. van Vark, V. J. G. Houba, and J. J. van der Lee. 1989. Plant analysis procedures. Pages 13–16 *in* Soil and plant analysis, Part 7. Agricultural University, Wageningen, The Netherlands.

Woodwell, G. M., and F. T. Mackenzie. 1995. Biotic feedbacks in the global climatic system: will the warming feed the warming? Oxford University Press, New York, New York, USA.

Zacheis, A., J. W. Hupp, and R. W. Ruess. 2001. Effects of migratory geese on plant communities of an Alaskan salt marsh. Journal of Ecology 89:57–71.

Zacheis, A., R. W. Ruess, and J. W. Hupp. 2002. Nitrogen dynamics in an Alaskan salt marsh following spring use by geese. Oecologia 130:600–608.

Supplemental Material

Appendix

Some examples of regressions fitted to standardize GPP, TER and NEE

Regressions were fitted for every period to all measurements made in a particular plot using Eq. 1 (TER), Eq. 2 (GPP) and Eq. 3 (NEE). Figs. A1, A2 and A3 show the raw data and the fitted regressions for one replicate of each treatment in August.

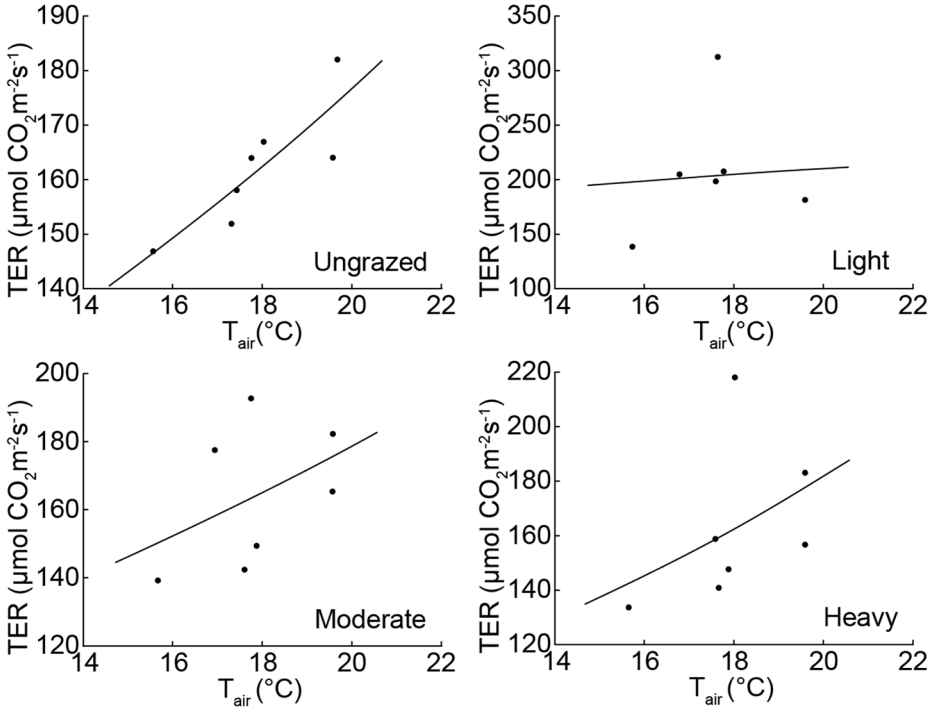

Fig. A1. Non-standardized fluxes of TER and regressions fitted for standardization per plot for one replicate of all treatments in August 2008. CO_2 fluxes are given in function of the variable used in the regressions; e.g., air temperature (T_{air}). Treatments were ungrazed (control) and light, moderate and heavy (grazing pressure).

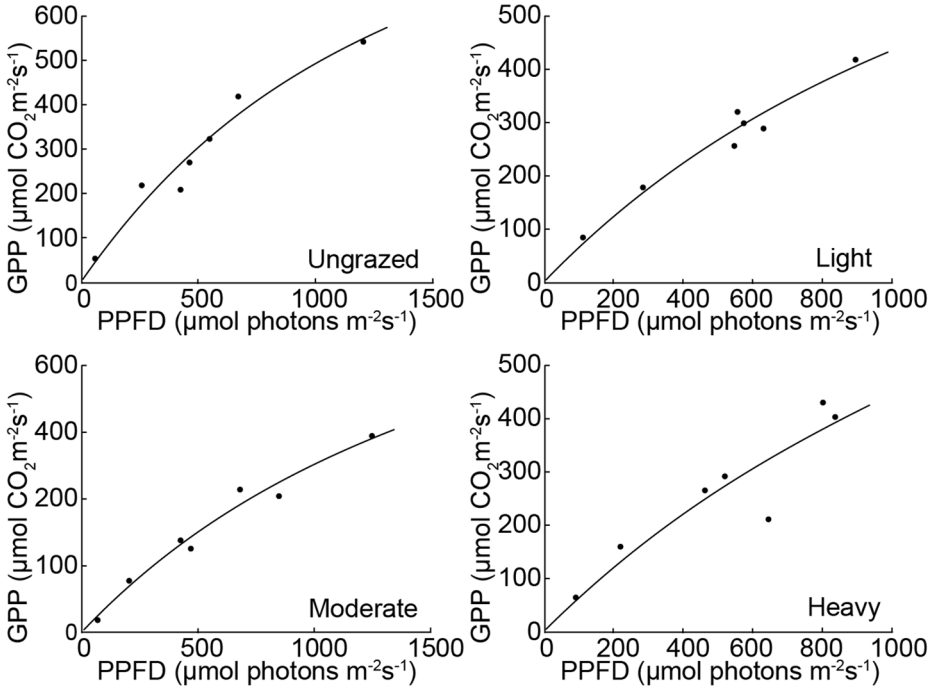

Fig. A2. Non-standardized fluxes of GPP and regressions fitted for standardization per plot for one replicate of all treatments in August 2008. CO_2 fluxes are given in function of the variable used in the regressions; e.g., photosynthetic photon flux density (PPFD). Treatments were ungrazed (control) and light, moderate and heavy (grazing pressure).

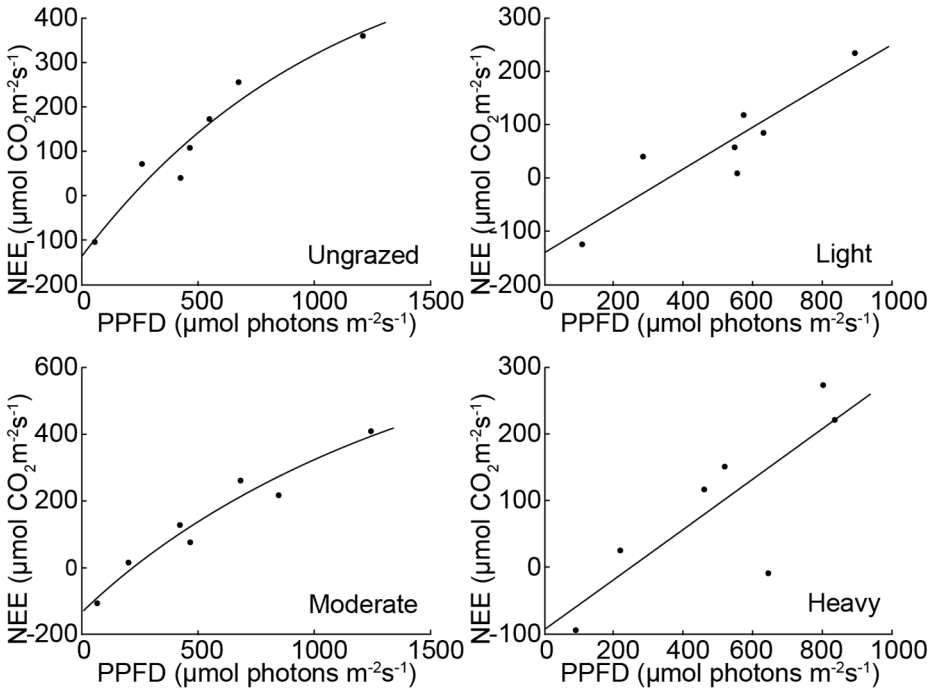

Fig. A3. Non-standardized fluxes of NEE and regressions fitted for standardization per plot for one replicate of all treatments in August 2008. CO_2 fluxes are given in function of the variable used in the regressions; e.g., photosynthetic photon flux density (PPFD). Treatments were ungrazed (control) and light, moderate and heavy (grazing pressure).