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Grazing increases the temperature sensitivity of soil organic matter decomposition in a temperate grassland

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Abstract
We tested the effects of ungulate grazing and nutrient availability on the temperature sensitivity of soil respiration (CO_2) and methane (CH_4) emissions in semi-natural temperate grassland. To do this, soil taken from long term grazed and ungrazed grassland was incubated at four temperatures (4, 10, 15 and 20 °C) with two levels of nutrient (NP) addition. The results showed that the variation in soil CO_2 and CH_4 emissions was explained by temperature and grazing, with grazing increasing the temperature sensitivity of CO_2 and CH_4 production by between 15 and 20 °C. This response was constrained by nutrient availability for CO_2, but not CH_4. These findings suggest that grazing could potentially have important impacts on the temperature sensitivity of greenhouse gas emissions in nutrient limited grasslands.

Keywords: grazing, Q_{10}, nutrients, CO_2 and CH_4 emissions

1. Introduction

The potential for soils under different land uses to sequester carbon (C) has been the subject of much recent discussion (Woodward *et al* 2009). Grasslands are an important part of the global C cycle as they cover approximately one quarter of Earth's land surface (Olson 1994) and act as a significant source and sink for greenhouse gases (Ostle *et al* 2009, Wohlfarht *et al* 2008). However, our understanding of the factors that control greenhouse gas emissions from grasslands is poor.

Temperature is considered to be a key factor controlling CO_2 emissions from soils, and there is considerable concern that warming will increase C mineralization and hence CO_2 loss from soil, causing a positive feedback on climate changes (Bardgett *et al* 2008). It is estimated that soil heterotrophic respiration doubles with every 10 °C increase in atmospheric temperature (Davidson and Janssens 2006). This implies a metabolic Q_{10} value of 2, which has been widely used in C cycle models to predict soil CO_2 emissions under different global warming scenarios (Davidson and Janssens 2006). However, there is much uncertainty surrounding this value due to differences in the temperature sensitivity of decomposition of organic C of varying chemical complexity and the potential influence of environmental constraints, such as physical and chemical protection of C, and nutrient limitation on microbial activity. Hence, the sensitivity of decomposition to temperature is likely to vary greatly across ecosystems and land use systems of differing organic matter and nutrient status. In fact, highly organic soils are relatively poorly described in current coupled carbon-cycle–climate (C4) models (Friedlingstein *et al* 2006).

With respect to methane, its importance lies in its high global warming potential (GWP) which is 25 times that of CO_2 on a 100 yr time horizon (IPCC 2007). As with CO_2, methane emissions depend chiefly on temperature (van Hulzen *et al* 1999, Tamai *et al* 2003). However, much more uncertainty than in the case of CO_2 surrounds the sensitivity of CH_4 emissions to temperature, with reported Q_{10} values ranging from 1.1 to 28 (Dalal *et al* 2008).

In grasslands, a major factor affecting soil organic matter quality and quantity, and hence its sensitivity to temperature, is ungulate grazing. Grazing animals affect organic matter quantity and quality via several mechanisms including the return of animal wastes to soil, alteration of plant productivity and vegetation composition which govern the quality and amount of plant-leaf–root litter and root exudates entering soil, and changes in the activity and composition of soil microbial communities. These changes, in turn, affect rates of nutrient cycling creating feedbacks to plant productivity that affect the amount of organic matter entering soil (Bardgett and Wardle 2003). Although grazing is known to influence soil greenhouse gas emissions, including CO_2, CH_4 and N_2O (Polley *et al* 2008, Wolf *et al* 2010), the consequences of grazing-induced changes for the temperature sensitivity of decomposition are unknown. In this study we tested in a laboratory incubation experiment how grazing-induced changes in soil properties influence the temperature sensitivity of CO_2 and CH_4 production, and whether this response is affected by nutrient limitation.

2. Materials and methods

Our study site was in the Ingleborough National Nature Reserve, northern England (54.18°N, 2.36°E; National Grid Reference Number SD 763762). The climate is temperate maritime, with a mean annual precipitation of 1840 mm (averaged for 10 yr, UK Meteorological Office 2010). Soils are derived from carboniferous sandstones in the Yoredale group with a pH of 4.5 and an organic surface horizon of 20–30 cm depth. This grassland type is representative of many parts of upland Britain where it forms the mainstay vegetation type of the sheep farming industry (Rodwell 1992). The site is part of a landscape-scale re-wilding experiment established in 2000. In 2007, we sampled two adjacent areas of this experiment with different histories of sheep grazing. Grazing exclusion was done at the landscape scale: the ungrazed area, of approximately 170 ha, was fenced in 2000 to exclude sheep, whereas the adjacent grazed area, of 58 ha, retained a stocking rate of 4 ewes ha^{-1}, imposed since 1996. Neither area has received any fertilizer or manure applications. Both areas had similar organic C and nitrogen (N) contents (42±7% and 1.96 ± 0.36% for the grazed and 45 ± 3% and 1.99 ± 0.18% for the ungrazed area, respectively), but differed in their soil biological properties: the grazed area had greater soil microbial biomass N (19.7 ± 2.1 and g N m^{-2} versus 14.1 ± 1.7 g N m^{-2}; $P = 0.001$) and a higher availability of inorganic N with a DON/DIN ratio of 3.21 ± 0.57 versus 3.33±0.25 ($P < 0.05$) in the ungrazed area. The vegetation of the grazed site was dominated by graminoids (*Nardus stricta* L., *Festuca ovina* L., *Agrostis capillaris* L., *Eriophorum vaginatum* L.), whereas the cessation of grazing caused a significant increase in dwarf shrubs, such as *Calluna vulgaris* Salib., and a build up of litter on the soil surface. More details about the management and properties of this studied area can be found in Medina-Roldán *et al* (2012).

Within each area, six randomly positioned plots (4 m × 4 m) were established along a north–south transect. Studies performed at large spatial scales such as ours often do not allow for truly replicated experimental designs. However, many authors argue that these types of studies are valid when caution is applied (Oksanen 2001). Thus, because our two areas studied (grazed and ungrazed) are large areas that share the same climatic conditions, soil type, parent material and topography, the potential differences can be attributed to grazing management. In fact, this approach has been used in other studies on grazer effects at the landscape level (Parfitt *et al* 2010, Meyer *et al* 2011).

In October 2007, soil cores were taken from the 12 plots (6 grazed and 6 ungrazed) for the laboratory incubations. The incubations retained the experimental design of the field experiment, with 6 replicates taken from the grazed and ungrazed areas. Cores were collected with PVC pipes (5 cm diameter, 10 cm depth) and 8 cores (5 cm diameter and 10 cm in depth) were sampled from each replicate plot, yielding a total of 96 soil cores. Surface vegetation was removed and cores were transported back to the laboratory at Lancaster University.

Intact soil cores were pre-incubated for 14 days at 4 °C in order to stabilize microbial activity after sampling. Afterwards, the 96 soil cores (6 field replicates × 2 differently managed areas × 4 temperatures × 2 nutrient addition levels) were enclosed in a series of 2 l capacity lock and lock containers. To measure the temperature sensitivity of CO_2 and CH_4 emissions, soil cores from each replicate plot of the grazed and ungrazed site were incubated in the dark in temperature-controlled rooms at 4, 10, 15 and 20 °C. To test how nutrient limitation affected the temperature sensitivity of CO_2 and CH_4, at each temperature room, half of the cores received a solution containing NH_4NO_3, NaH_2PO_4 and Na_2HPO_4 at a rate equivalent to 100 kg N ha^{-1} and 50 kg P ha^{-1}, while the other half of the cores were used as controls. The solution was prepared just before doing the addition and was added to the soil cores using a Pasteur pipette. Soils were weighed every two days to determine weight loss, and distilled water was sprayed evenly over the soil surface of the soils to compensate for moisture loss.

Measures of CO_2 and CH_4 fluxes were made 1 h, 2 h, 4 h, 1 week, 2 weeks, 4 weeks, 6 weeks, 8 weeks, 12 weeks and 16 weeks after fertilizer addition. At each sampling, containers were sealed for 1 h, and 5 ml of headspace gas was taken as a sample at the beginning and end of the incubation period. CO_2 and CH_4 concentrations were analysed using a gas chromatograph fitted with an FID, which incorporated a methaniser (AutoSystem XL, Perkin Elmer), and gas fluxes were expressed as μg CO_2–C g^{-1} dry soil day^{-1} and μg CH_4–C g^{-1} dry soil day^{-1}.

Repeated measures analysis of variance (RMANOVA) was used to test for grazing, fertilizer and temperature effects

on greenhouse gases. RMANOVA was performed in SPSS 15.0 using type III sum of squares. All data were tested for normality using the one-sample Kolmogorov–Smirnov test before running any parametrical statistical tests. Data were log transformed when necessary to ensure that the ANOVA assumptions of normality and homoscedasticity were met. Differences at the $P < 0.05$ level were considered significant.

The value of Q_{10} is the factor by which the respiration rate differs for a temperature interval of 10 °C. For the first-order exponential equation, which assumes Q_{10} is constant over the temperature range, the Q_{10} value can be calculated as:

$$Q_{10} = (R_2/R_1)^{10(T_2/T_1)}$$

where R_2 and R_1 are the respiration rates measured at temperatures T_2 and T_1. Q_{10} was calculated for the 4–15 and 10–20 °C temperature intervals.

Hourly data on soil temperature (0–10 cm) were obtained from Ingleborough National Nature Reserve Automatic Weather Station. The number of hours at which temperature was above 15 °C was calculated for the years for which a complete record was available (2006–8).

3. Results

Both areas were identical in terms of carbon stocks, with a value of 5889 ± 367 g m^{-2} for the grazed area and 6238 ± 444 g m^{-2} for the ungrazed area (Medina-Roldán *et al* 2012). However, rates of CO_2 respiration varied with temperature ($P < 0.001$; figure 1). The temperature response of soil respiration was greatest at 20 °C but did not vary across the 4–15 °C temperature interval. The soil respiration response to temperature was greater in grazed than ungrazed soil at 20 °C, with grazed soil respiring 1.37 times more CO_2 than ungrazed soil ($P < 0.001$ for the grazing × temperature interaction; figure 1). However, there was no difference in soil respiration between grazed and ungrazed soils at the lower temperatures. Nutrient addition influenced respiration in a similar way to grazing, with a significant interaction between temperature and nutrient addition ($P < 0.05$). Soil respiration was, in this way, higher at 20 °C for the soil that received nutrient addition.

Methane emissions increased significantly with temperature ($P < 0.001$) but, as with respiration, this response was restricted to the highest temperature: CH_4 emissions did not change between the temperature intervals 4–15 °C, but then almost doubled at 20 °C (figure 1). Methane emissions were also significantly greater ($P < 0.001$) in grazed than ungrazed soils, and unlike respiration there was no positive effect of nutrient addition.

We found no temperature sensitivity of organic matter decomposition in the 4–15 °C range of temperatures. However, Q_{10} values calculated on the basis of intervals between 10 and 20 °C were significantly greater in grazed than ungrazed cores, and in fertilized compared to unfertilized cores ($P < 0.05$; figure 2). The Q_{10} for methane emissions varied in a similar way to that for respiration, but it was only affected by grazing and not nutrient addition.

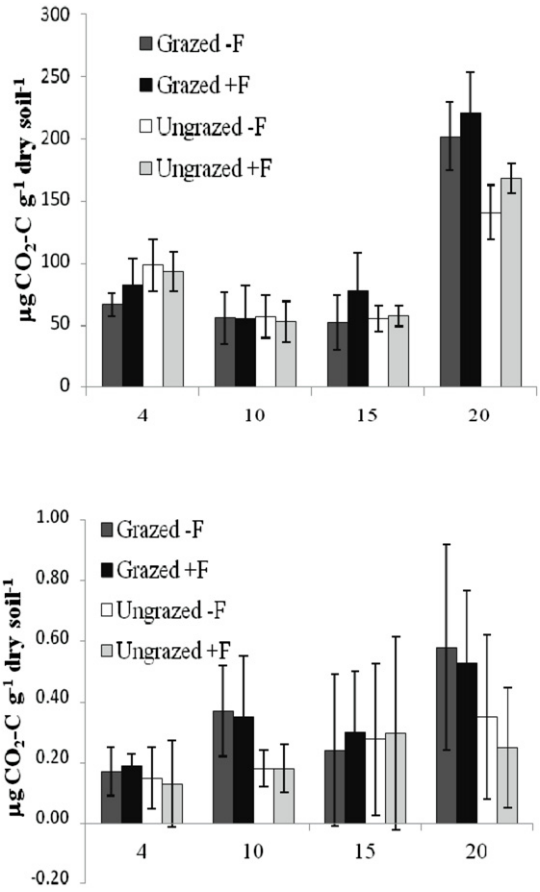

Figure 1. Effect of grazing and nutrient addition on CO_2 (upper graph) and CH_4 (lower graph) for different temperatures.

The amount of time, expressed as a percentage of the total hours within a year, when soil temperatures were over 15 °C varied greatly across years at the Colt Park study site, with a percentage values of 9.6% in 2006, 0.4% in 2007 and 5.4% in 2008.

4. Discussion

We found that soil from grazed plots had a greater temperature sensitivity of CO_2 production, as measured by Q_{10} across the 10–20 °C interval. This suggests that grazing enhances the temperature sensitivity of organic matter decomposition, especially at higher soil temperatures. We cannot be certain of the mechanism for this, but it is possibly due to greater nutrient availability in grazed soils as nutrient additions were found to increase soil respiration at warmer temperatures in grazed and ungrazed soils. It is well documented that grazing can stimulate soil N availability in temperate grasslands (Bardgett and Wardle 2003), and previous studies at the site used in our study confirm that this is the case (Medina-Roldán *et al* 2012). We also found a rapid increase in soil respiration at temperatures between 15 and 20 °C, although our experimental design did not allow us to discriminate the exact temperature. This type of temperature threshold at which considerable increases in respiration occur have been reported before (Chapman and Thurlow 1998), and could

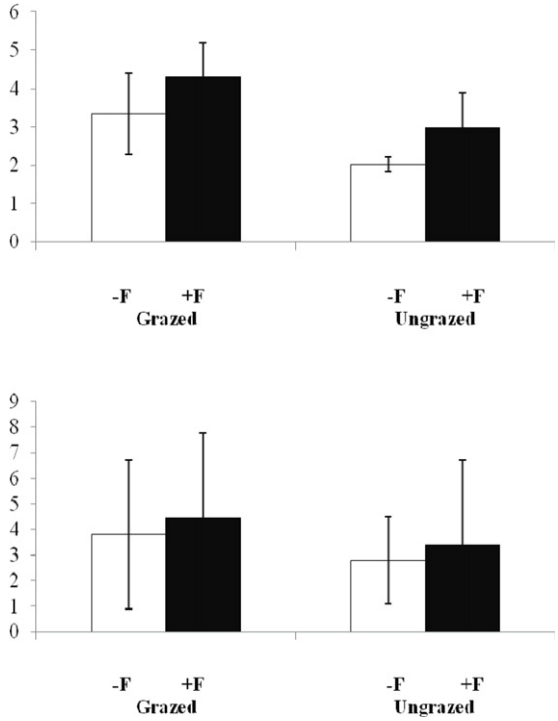

Figure 2. Q_{10} for respiration (upper graph) and CH_4 (lower graph) in the 10–20 °C interval (+F and −F indicate nutrient addition or absence of fertilizer, respectively).

depend on factors such as soil microbial community structure (i.e. the proportion of mesophiles to cryophiles) or the type of substrates being degraded at different temperatures. The absolute Q_{10} values for ungrazed soils (2.02 ± 0.19; figure 2) were similar than the median value of 2.0 given in the literature (Davidson and Janssens 2006), but were much greater for the grazed and fertilized soil (4.31 ± 0.87). However, organic soils have been reported to have Q_{10} values much greater than mineral soils, although the mechanisms involved remain unknown.

The influence of grazing on Q_{10} values for CO_2 could be due to many factors. Consistent with other studies (Bardgett and Wardle 2003), grazing significantly altered plant productivity and community composition in our study site (Medina-Roldán *et al* 2012), leading to a reduction in cover of dwarf shrubs and an increase in graminoids. Fast-growing plants, such as graminoids, allocate most of their carbon to photosynthetically active structures of low density and high nutrient content, yielding easily decomposable litter (De Deyn *et al* 2008). Thus, it is hypothesized that the traits that make plants palatable to herbivores (i.e. high nutrient concentrations) may promote their decomposability and root exudation. Fast-growing plants are characterized by a high litter quality and low C/N ratio thus, enhancing soil carbon loss. In contrast, shrubs, more abundant in the ungrazed area, produce nutrient poor, recalcitrant litter, incorporating lignin to soil, and potentially increasing soil carbon sequestration. This would result if differences in soil organic matter quality and its sensitivity to temperature (Davidson and Janssens 2006). Labile C pools have a higher temperature sensitivity than recalcitrant C pools, and can be altered by nutrient addition (Davidson *et al* 2006), and most likely grazing.

Grassland soil is generally a sink for CH_4, but it can also be a source as evidenced in our study. Grassland vegetation can affect CH_4 emissions with legume pastures generally showing net CH_4 emissions and grass pastures showing net CH_4 consumption (Veldkamp *et al* 2001). The Q_{10} value for CH_4 ranges from 1.1 and 28.0 (Dalal *et al* 2008), with an average of about 4.0. This variation has been attributed to differences in substrate type, availability of electron acceptors, and the thermal and temporal range of measurement. Our measures of Q_{10} for CH_4 were hence in the range of other studies, and were increased by grazing. However, unlike for respiration, the cause of this was not nutrient limitation; Q_{10} values for CH_4 were not affected by nutrient addition. Thus, we believe that grazing-induced differences in plant litter quality and/or alterations in the soil microbial community were more influential.

Previous studies show that Q_{10} can vary depending on the range of temperatures used for calculation and highlight that it can be subject to seasonal and annual fluctuations. Our study has shown that grazing, a common form of land management, can also affect the temperature sensitivity of CO_2 and CH_4 production and that this response is influenced by nutrient addition. Specifically, we have shown that grazing enhances the temperature sensitivity of CO_2 and CH_4 emissions from soil, suggesting that climate warming could, potentially, increases greenhouse gas emissions from grazed grassland soils. Our results highlight the importance of using appropriate Q_{10} values for climate modelling given that we demonstrate that they can vary substantially depending on land management. In drawing these conclusions we stress that further research is needed to properly incorporate into climate change models the impact of grazing on Q_{10} values given that our experiment was short term and the measured response was limited to the higher range of temperatures used in our study.

The validity of our results is constrained by our experimental design, which does not allow us to estimate the exact temperature threshold at which rapid increases in greenhouse gas emissions are produced. Also, caution is needed in generalizing our findings to other upland grasslands in the UK because the extent of global warming in UK uplands and the average temperatures for these ecosystems is uncertain (Burt and Holden 2010). There was a weather station near our research site and we calculated the proportion of hours per year when soil temperatures were above 15 °C, which varied greatly across years, but reached a maximum of 9.6% over the years recorded. Hence, the grazing-induced increase in temperature sensitivity of CO_2 and CH_4 production recorded in our study between 15 and 20 °C could potentially be of significance, especially given the extent that the uplands of Britain are grazed (Bardgett *et al* 2001) and the likelihood that future increases in average temperature in Britain and extreme weather events are forecast (IPCC 2007). As a result, our findings suggest that carbon fluxes from upland temperate grasslands will potentially be altered as a result of climate warming and that grazing might modify this response. However, given that our findings come from a

laboratory experiment based on soils from a single location in northern England, we suggest further research is needed to determine the exact thresholds for greenhouse gas emissions in temperate, semi-natural grasslands, and their response to grazing.

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