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Impact of future climatic conditions on the potential for soil organic matter priming

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ABSTRACT

Terrestrial carbon (C) storage and turnover are of major interest under changing climatic conditions. We present a laboratory microcosm study investigating the effects of anticipated climatic conditions on the soil microbial community and related changes in soil organic matter (SOM) decomposition. Soil samples were taken from a heath-land after six years of exposure to elevated carbon dioxide (eCO_2) in combination with summer drought (D) and increased temperature (T). Soil C-dynamics were investigated in soils from: (i) ambient, (ii) eCO_2, and (iii) plots exposed to the combination of factors simulating future climatic conditions ($TDeCO_2$) that simulate conditions predicted for Denmark in 2075. ^{13}C enriched glucose (3 atom% excess) was added to soil microcosms, soil CO_2 efflux was measured over a period of two weeks and separated into glucose- and SOM-derived C. Microbial biomass was measured using chloroform fumigation extraction, and compound-specific phospholipid fatty acid analysis was used to determine microbial community composition and substrate use. We observed that glucose additions induced SOM priming in ambient and eCO_2 treated soils, but not in soil exposed to future climatic conditions. Climate treatments and glucose additions did not affect relative abundances of microbial functional groups but the fate of glucose through the microbial community was changed by climate treatments as revealed by the incorporation of ^{13}C in PLFAs. Soil treated with eCO_2 showed a high flow of glucose through gram-positive bacteria whereas in ambient and future soils utilization of glucose by actinomycetes and fungi (putative SOM-decomposers) was greater. Our results suggest that individual climate change factors may influence pathways of C-flux through microbial communities and therefore affect soil processes; these factors may counterbalance each other and maintain ecosystem stability. This highlights the importance of studying climate change factors in combination to fully assess consequences of environmental change on plant–soil systems.

1. Introduction

Although the turnover of terrestrial soil carbon (C) stocks is relatively slow, the large size of these stocks (~2200 Pg C) means that the gross flux of CO_2 to the atmosphere is very large (~60 Pg C yr^{-1}). For soils in equilibrium, these losses are balanced by the inputs of plants, but under expected climate change scenarios this balance may be disrupted and soils may turn into net CO_2 sources (Carney et al., 2007). If this does occur, depletion of terrestrial C stocks would accelerate climate change.

During recent years, impacts of elevated carbon dioxide (eCO_2) on ecosystem processes have been investigated *in-situ* with Free-Air Carbon Enrichment (FACE) experiments (Leakey et al., 2009; Larsen et al., 2011). eCO_2 has been found to accelerate C turnover in terrestrial ecosystems (Martin-Olmedo et al., 2002; Carney et al., 2007; Carrillo et al., 2011), i.e. through increased plant CO_2 uptake (Leakey et al., 2009), plant belowground C exudation (Hagedorn et al., 2008; Phillips et al., 2011) and soil C effluxes (Martin-Olmedo et al., 2002; Hagedorn et al., 2008). To date it is of major debate if eCO_2 will lead to soil C sequestration (Lagomarsino et al., 2006; Iversen et al., 2012) or net soil C mineralization (Martin-Olmedo et al., 2002; Carney et al., 2007; Hagedorn et al., 2008; Phillips et al., 2011).

Soil C turnover is not only influenced by atmospheric CO_2 concentration. Soil temperature (Fierer et al., 2003), nutrient availability (Martin-Olmedo et al., 2002; Cheng and Kuzyakov, 2005; Paterson et al., 2008b; Phillips et al., 2011), hydrology (Xiang et al., 2008) and soil characteristics (Kemmitt et al., 2008; Dorodnikov et al., 2009) are also important internal and external drivers for

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soil C decomposition. Kemmitt et al. (2008) attempted to describe SOM dynamics solely by physical and chemical processes considering the soil microbial community as a constant soil parameter. However, subsequent discussions illustrate that soil C dynamics are intensely modulated by the soil microbial community (Brookes et al., 2009; Garcia-Pausas and Paterson, 2011).

Rhizosphere microbes are consumers of plant-derived C released into the soil matrix by root exudation and litter inputs. Between 5 and 25% of photosynthetically fixed CO_2 is exuded as rhizodeposits (Helal and Sauerbeck, 1984) and strongly impacts the microbial community structure, activity and SOM mineralization (Fontaine et al., 2011; Phillips et al., 2011). Increased SOM mineralization induced by labile C input to the soil (the 'priming effect') is increasingly recognized as quantitatively significant in soil C-dynamics (Fontaine et al., 2007; Kuzyakov et al., 2009).

The mechanisms and controls of SOM priming are still a matter of debate (Kemmitt et al., 2008; Paterson, 2009) and impacts of eCO_2 are difficult to anticipate (Billings et al., 2010). Elevated CO_2 has been reported to increase microbial biomass size (Martin-Olmedo et al., 2002; Paterson et al., 2008b) and to support SOM priming (Martin-Olmedo et al., 2002; Lagomarsino et al., 2006). However, eCO_2 and facilitated C turnover do not necessarily lead to net soil C loss because plant-derived C can also be stabilized within the soil matrix and immobilized within the microbial community (Lagomarsino et al., 2006; Gude et al., 2012). Microbial community composition is a determinant of the magnitude of priming (Garcia-Pausas and Paterson, 2011), and activities of fungi and actinomycetes have been implicated in increased rates of priming compared to those of the bacterial community (Carney et al., 2007; Garcia-Pausas and Paterson, 2011).

Here we present a laboratory incubation experiment to investigate long term impacts of eCO_2 in combination with drought and temperature on the soil microbial community and connected SOM mineralization. Potential priming was assessed by adding ^{13}C labelled glucose to soil samples from a temperate heath that has been exposed to climatic manipulations for six years. We hypothesize that (H1) microbial C turnover in soils treated with eCO_2 show an increased utilization of SOM-derived C in the presence of labile C (priming) and (H2) that eCO_2 induces a change in activity of different microbial functional groups associated with higher SOM mineralization rates.

2. Materials and methods

2.1. Soil collection and processing

Soil was collected in March 2012 from a temperate heath-land exposed to climatic manipulation for six consecutive years including elevated CO_2 (eCO_2 at 510 ppm) by Free-air carbon dioxide enrichment (FACE), extended summer drought (*D*, 4 weeks) and increased night time temperature (*T*, 1 °C) (Mikkelsen et al., 2008). The factorial combination of eCO_2, *D* and *T* simulates the climatic conditions predicted for Denmark in 2075 (Mikkelsen et al., 2008). Each treatment was replicated six times. Samples were taken from five different treatments (Table 1). Four soil cores (Ø 1.5 cm, 10 cm deep) were taken below the grass *Deschampsia flexuosa* L. and bulked together. Soils were transported to the UK (The James Hutton Institute, Aberdeen) within 24 h and stored at 4 °C until further processing within one week. Soil was sieved (2 mm) and the soil gravimetric water content (SWC) was determined by oven drying.

2.2. Microcosm incubation and treatments

In each microcosm (0.5 L glass jar) the soil was divided into 3 separate compartments of equivalent depths (2 × 15 g, 1 × 70 g soil) to facilitate sequential sampling during the experiment, without causing soil disturbance by sampling one compartment per harvest. Two sets of microcosms (treatment and control) were prepared from each field treatment sampled. All microcosm units were packed to a bulk density of 1 g dry soil cm^{-3} which is close to field bulk density. Samples were adjusted to the same SWC (16.4% on dry soil basis), which was maintained throughout the experiment by addition of deionized water (dH_2O). Microcosms were incubated at 8 °C within a controlled-environment room; all experimental manipulations and sampling were conducted at this temperature.

An acclimatisation period (addition of water only) of 18 d was imposed, during which soil CO_2 efflux rates stabilized following the disturbance of microcosm preparation. Following the acclimatisation period, glucose was applied to half of the microcosms (glucose treatment). Glucose was applied at a rate of 200 μg C g^{-1} dry soil per day (dissolved in 0.5 mL of dH_2O) on six consecutive days (3 atom% excess: APE, uniformly labelled ^{13}C-glucose, Sigma Aldrich), where day 1 was the first day of glucose addition. To maintain SWC (16.4%), the loss in excess of that replaced by addition of glucose solutions was balanced by gravimetric addition of dH_2O. Compensation for water loss in control microcosms was achieved by gravimetric addition of dH_2O only. Soil harvests took place at days 0, 6 and 14.

2.3. Soil CO_2 efflux

Measurements of soil CO_2 efflux rates were conducted at days 1, 2, 3, 4, 6, 7, 9, 11 and 14. Before CO_2 accumulation, microcosms were tightly sealed (plastic sealing strip, Terostat VII) and microcosm headspace was flushed with CO_2 free air to reduce the CO_2 concentrations to ≤10 ppm. Then, after 6 h incubation, CO_2 concentrations were immediately measured (EGM-4, PP-Systems, Amesbury, USA) and $\delta^{13}C$ isotopic values were determined from microcosm headspace samples stored in 12 mL N_2 flush-filled Exertainer® vials (GasBenchII, Delta^{PLUS} Advantage IRMS, Thermo Finnigan, Bremen, Germany). We determined respiration rates at specific time points and integrated these rates to determine the cumulative respiration for the whole period. The EGM-4 was not

Table 1
Overview of climate treatments: soil temperature (5 cm soil depth), soil water content (SWC) in the field and immediately prior to the experiment and the C contents of the experimental soils. Field data are from the day of soil sampling. Means ± SE.

Treatments	Abbreviations	Soil temp (°C)	SWC (vol %)		Soil C content (%)
		Field	Field	Experiment	Experiment
Ambient	Ambient	4.4 ± 0.1	19.1 ± 1.6	11.2 ± 0.4	1.3 ± 0.1
Elevated CO_2	eCO_2	4.5 ± 0.1	18.4 ± 1.7	11.7 ± 0.9	1.3 ± 0.1
Summer droughts*eCO_2	DCO_2	4.6 ± 0.1	20.4 ± 1.5	12.5 ± 0.5	1.4 ± 0.1
Increased temperature*eCO_2	TCO_2	4.7 ± 0.1	17.7 ± 0.4	12.3 ± 0.6	1.4 ± 0.1
Temperature*drought*eCO_2	Future	4.7 ± 0.1	18.8 ± 1.7	12.3 ± 1.0	1.4 ± 0.1