



Thermal acclimation of organic matter decomposition in an artificial forest soil is related to shifts in microbial community structure



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ABSTRACT

Thermal acclimation of soil organic matter (SOM) decomposition is frequently observed and has often been attributed to substrate depletion under warming, but other mechanisms, such as changes in microbial community structure and functioning, have received less attention. In order to determine whether shifts in microbial community structure and functioning are involved in thermal acclimation of SOM decomposition, a laboratory incubation experiment was conducted using an artificial forest soil. Samples were first subjected to different temperatures of 5, 15, and 25 °C during a 72-day pre-incubation period and then half of the microcosms from each pre-incubation temperature were incubated at 5 or 25 °C for a period of 11 days. Substantial thermal acclimation of SOM decomposition was observed, with the SOM decomposition in soils pre-incubated at higher temperatures being less sensitive to temperature. Along with the reduced temperature sensitivity in response to warming, significant changes in microbial community PLFAs, microbial biomass carbon (MBC), and the potential activities of 11 enzymes were also observed. Nevertheless, shifts in microbial community PLFAs and particular enzyme activities provided the most explanatory power for the decreased temperature sensitivity with warming, as revealed by a multivariate regression analysis. The microbial community structure shifts were mainly manifested as an increase in the relative abundance of Gram-positive bacteria and decreases in the relative abundances of Gram-negative bacteria and fungi. Microbial communities pre-incubated under lower temperatures experienced greater shifts in their structure. Substrate depletion did not occur in this short-term incubation experiment, since neither total organic carbon (TOC) nor dissolved organic carbon (DOC) decreased with increasing temperature. Our results suggest that shifts in microbial community structure and functioning may underlie the thermal acclimation of SOM decomposition and should be taken into account when predicting the response of soil CO₂ efflux to global warming.

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1. Introduction

The decomposition of soil organic matter (SOM), approximated by soil heterotrophic respiration in most publications, is affected by numerous factors such as temperature, moisture, vegetation and soil type (Jenkinson et al., 1991; Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Kirschbaum, 1995; Shen et al., 2009; Schmidt et al., 2011). In the majority of studies, temperature is reported to

enhance SOM decomposition rate quasi-exponentially, and therefore an exponential index of temperature sensitivity, termed Q_{10} , is widely used to describe the thermal response of SOM decomposition. This Q_{10} reflects the synoptic response of SOM decomposition to temperature and is assumed constant previously (~ 2.0 ; e.g., Jenkinson et al., 1991). Although the decomposition rate increases exponentially with increasing temperature in the short-term, warming does not necessarily increase SOM decomposition to a similar extent. Indeed, SOM decomposition has been frequently observed to acclimate in response to warming (Hartley et al., 2007; Allison et al., 2010; Bradford et al., 2010; Crowther and Bradford, 2013), yielding lower-than-expected decomposition rates under prolonged warmer conditions. Such thermal acclimation may thus

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render current predictions of future carbon cycling that do not take into account thermal acclimation uncertain.

Although thermal acclimation of SOM decomposition is often observed (Dieleman et al., 2012), the underlying mechanisms are still a matter of scientific debate (Luo, 2007; Hartley et al., 2008; Vicca et al., 2009; Bradford et al., 2010; Conant et al., 2011; Crowther and Bradford, 2013), and it remains particularly unclear how warming affects the Q_{10} of SOM decomposition (Bradford et al., 2008). On the one hand, substrate depletion due to faster microbial consumption under warmer conditions may reduce the temperature sensitivity of SOM decomposition at higher temperatures (Eliasson et al., 2005; Hartley et al., 2007, 2008), especially over long timescales. On the other hand, it has also been suggested that the temperature sensitivity of SOM decomposition increases with increasing molecular complexity of substrates (Knorr et al., 2005; Davidson and Janssens, 2006; Hartley and Ineson, 2008; Craine et al., 2010; Conant et al., 2011). A rapid depletion of labile substrate and an increase of recalcitrant substrate during the initial stages of experimental warming (Hartley et al., 2007, 2008; Ziegler et al., 2013), without any microbial adjustment, could therefore lead to increased temperature sensitivity of SOM decomposition by warming, as observed by Rinnan et al. (2009). These contrasting observations indicate that alterations in the temperature sensitivity of SOM decomposition with warming cannot be fully explained by substrate depletion.

Alternatively, reduced temperature sensitivity at higher temperatures may also result from shifts in the composition of soil microbial communities (Luo et al., 2001; Zhang et al., 2005; Hartley et al., 2007; Luo, 2007; Malcolm et al., 2008; Vicca et al., 2009; Conant et al., 2011; Crowther et al., 2012). Although several authors have reported that soil microorganisms do not experience detectable shifts in community composition after minor experimental warming (Biasi et al., 2008; Schindlbacher et al., 2011; Kuffner et al., 2012), shifts in soil microbial communities, in addition to the frequently observed reduction in microbial biomass induced by increasing temperature (Bradford et al., 2008; Frey et al., 2008; Rousk et al., 2012; Weedon et al., 2012), have also been documented. For instance, Zogg et al. (1997) showed that within 16 weeks, the soil microbial communities shifted significantly in composition at higher temperature. Using $\delta^{13}\text{C}_{\text{CO}_2}$ and phospholipid fatty acids (PLFAs) analyses, Biasi et al. (2005) also found that the soil microbial community composition changed with rising temperature. Altered microbial communities may exhibit different temperature dependencies (Frey et al., 2008; Malcolm et al., 2008; Balsler and Wixon, 2009), and consequently result in the observed thermal acclimation of SOM decomposition (Luo, 2007). Although it has been shown that soil microbial community composition can shift with temperature, there is still a lack of direct experimental evidence relating the thermal acclimation of SOM decomposition to shifts in soil microbial community structure and functioning (Conant et al., 2011).

Global temperatures are rising and this trend is likely to continue with the continuing increase of greenhouse gas concentrations in the atmosphere (IPCC, 2007). Increasing temperature could result in a positive feedback on the SOM decomposition, and therefore tend to upset the dynamic equilibrium of the terrestrial carbon cycling (Luo and Weng, 2011). However, thermal acclimation of SOM decomposition may reduce this positive feedback effect and thus yield lower carbon emission from soils than what has been predicted previously (Allison et al., 2010).

In this study, we conducted a laboratory incubation experiment to test the role of microbial community structure and functioning in the thermal acclimation of SOM decomposition. The experiment contained two periods: a 72-day pre-incubation period during which soil samples were incubated at temperatures of 5, 15, and

25 °C, and an 11-day incubation period during which half of the samples from each pre-incubation temperature were incubated at 5 °C and the other half at 25 °C. By comparing the temperature sensitivity of SOM decomposition corresponding to the three pre-incubation temperatures, we aimed to test the hypothesis that the temperature sensitivity would be lower for soils that had experienced high pre-incubation temperatures than for soils that had experienced low pre-incubation temperatures (i.e., thermal acclimation would occur as observed in many previous studies). By analyzing soil microbial community PLFAs, microbial biomass carbon, dissolved organic carbon, and enzyme activities related to SOM decomposition at the end of both periods, we also aimed to analyze the relative contributions of these factors to the thermal acclimation of SOM decomposition.

2. Materials and methods

2.1. Artificial soil mixture

We composed an artificial soil for incubation by mixing clay (15%), sand (60%), and organic matter (25%) to ensure the homogeneity of the samples incubated. Artificial soils can be used in laboratory incubations to eliminate the confounding effects of factors other than the factor of interest (Guenet et al., 2011), although it differs from natural soils in its aggregate structure and resultant sorption-adsorption dynamics of substrates. By using the artificial soil, we also aimed to minimize potential variation resulting from oxygen and water limitations. The organic matter was collected from the surface humus horizon of a Scots pine forest in the Belgian Campine region (see details in Janssens et al., 1999). Since this humus was not sterilized, it was also the source of microorganisms. The organic matter was air-dried, ground and passed through a sieve with a mesh of 1 mm. The clay used was commercial bentonite (Sigma–Aldrich), a 2/1 clay type with high cation exchange capacity (Guenet et al., 2011). The sand was inert, acid-washed white sand with particle sizes ranging from 63 μm to 365 μm . The final organic carbon content in the composed soil amounted to 6%.

2.2. Soil incubations and CO_2 efflux measurements

Twenty-four samples, each consisting of 100 g oven-dried artificial soil, were placed into 200 ml glass Erlenmeyer flasks. The soil water content was adjusted to 60% WHC by adding deionized water before the beginning of the incubation. The water holding capacity (WHC) of the artificial soil ($0.98 \pm 0.01 \text{ g g}^{-1}$ soil) was determined by waterlogging 35 g-subsamples for 24 h in Whatman #42 filter papers placed in plastic funnels, and then draining them for another 24 h before determining the water content by drying for 48 h in an oven at 60 °C. The 24 flasks were then separated into three batches (8 flasks in each batch) and incubated at three constant temperatures (5, 15, and 25 °C) for 72 days (the pre-incubation period). After the pre-incubation period, half of the samples in each batch (i.e., 4 samples) were further incubated at 5 °C and the other half at 25 °C for another 11 days (the incubation period). Prior to the change in temperature, the CO_2 efflux rate was measured to ensure that samples subsequently incubated at 5 °C did not differ significantly from those subsequently incubated at 25 °C ($P = 0.780$ for groups pre-incubated at 5 °C, $P = 0.367$ for groups at 15 °C, and $P = 0.693$ for groups at 25 °C, Fig. 1c). The lowest temperature (5 °C) used in our incubation study is similar to the average temperature (3 °C) of the coldest month at the Scots pine forest where the organic matter and soil microbes originated from, while the highest temperature (25 °C) was higher than the highest monthly average temperature (18 °C) in the forest (Janssens

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