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Carbon quality and the temperature sensitivity of soil organic carbon decomposition in a tallgrass prairie

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ABSTRACT

The temperature sensitivity of soil organic carbon (SOC) decomposition will influence the accuracy of the quantitative prediction of carbon (C) balance between ecosystem C fixation and decomposition in a warmer world. However, a consensus has not yet been reached on the temperature sensitivity of SOC decomposition with respect to SOC quality. The fundamental principles of enzyme kinetics suggest that temperature sensitivity of decomposition is inversely related to the C quality of the SOC. This "C quality-temperature" hypothesis was tested in a 170-day laboratory experiment by incubating soil samples with changing temperature (low-high-low) at a ±5 °C step every 24 h. Soil samples were collected from a long-term warming experiment in a tallgrass prairie. There were four treatments of soil samples before lab incubation: control (C), warmed (W), field incubation (FI, litter exclusion), and warmed plus field incubation (WFI). Results showed that SOC decomposition rates were influenced by labile organic C (LOC) content, which were low in the soils under field incubation and decreased with increasing lab incubation time. Field warming and field incubation increased the temperature sensitivity of SOC decomposition in the 1st two lab incubation cycles but the treatment effects diminished as decomposition proceeded, probably due to increased contribution of recalcitrant C. In line with the hypothesis, we found that the lower the SOC quality, the higher the Q_{10} values. This relationship held across treatments and lab incubation cycles, regardless of whether the differences in SOC quality resulted from inherent differences in SOC chemistry or from differences in the extent of SOC decomposition. Treatment effects of field warming and field incubation on SOC quality and Q_{10} values also negatively correlated with each other. Our results suggest that dynamics of low-quality SOC have the highest potential to impact long-term C stocks in soils. Potential decreases in SOC quality in response to warming and consequent shifting species composition may result in a positive feedback of SOC to climate change in the future.

1. Introduction

In response to rising concentrations of greenhouse gases in the atmosphere, global mean temperature is predicted to increase 2–7 °C by the end of this century (Allison et al., 2009). Rising concerns about global warming has led to increased emphasis on understanding the role of soil as a potential carbon (C) sink to buffer the greenhouse effect (Cheng et al., 2011). Because of large C stocks in soil (Schlesinger, 1995), warmer temperatures may increase atmospheric CO_2 concentration by accelerating soil organic C (SOC) decomposition, resulting in a positive feedback to future climate warming (Hartley and Ineson, 2008; Craine et al., 2010). Predictions from coupled climate-C models differed substantially in magnitude and in the direction of the potential response of stored soil-C to warming (Cox et al., 2000; Friedlingstein et al., 2006). A negative feedback may occur if the amount of plant-derived C incorporated into soil exceeds the C loss through decomposition. So far, the temperature sensitivity of SOC decomposition remains one of the major uncertainties in predicting climate- C cycle feedback (Lenton and Huntingford, 2003; Conant et al., 2011).

The accuracy of the quantitative prediction of the C balance between ecosystem C fixation and decomposition is highly dependent on the assumed temperature sensitivity of SOC decomposition (Cox et al., 2000; Conant et al., 2008). Much research has thus addressed the responses of SOC decomposition to warmer temperatures in the last few decades (e.g. Kirschbaum, 1995; Fang et al., 2005; Friedlingstein et al., 2006; Xu et al., 2010) using the temperature coefficient (Q_{10}) to measure the temperature sensitivity of SOC decomposition. In modeling studies, it is in

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general for simplicity assumed that all types of SOC respond equally to climate warming (i.e. constant Q_{10}), independent of the differences in the C quality of SOC (Cox et al., 2000; Ågren and Bosatta, 2002; Burke et al., 2003). In empirical studies, on the other hand, the temperature sensitivity of SOC decomposition varies greatly depending on the type of SOC and the extent of SOC decomposition. Such studies have reported increases (Fierer et al., 2005; Conant et al., 2008; Wetterstedt et al., 2010), no changes (Fang et al., 2005; Conen et al., 2006), and decreases (Giardina and Ryan, 2000; Reichstein et al., 2000) in the temperature sensitivity of SOC decomposition with decreasing C quality. Despite much research, information about how the contradictory Q_{10} values and how SOC decomposition will respond to changes in temperatures is still limited. To accurately predict feedbacks of C dynamics to future climate change, we need to better understand the role of C quality in influencing SOC decomposition.

The fundamental principles of enzyme kinetics suggest that temperature sensitivity of decomposition at any specific point is controlled by the C quality of the substrates being consumed by microbes (Bosatta and Ågren, 1999; Davidson and Janssens, 2006). Bosatta and Ågren (1999) suggested that more enzymatic steps (as expressed by activation energy) are required to release CO_2 from low-quality C substrates in comparison with that of high-quality C substrates. Therefore, temperature sensitivity of SOC decomposition should be inversely related to C quality, commonly referred to as the "C quality-temperature" hypothesis (Bosatta and Ågren, 1999; Mikan et al., 2002; Craine et al., 2010). Dozens of studies have tested this hypothesis using laboratory incubations. However, the majority have suffered from at least one of the following problems: (1) the samples were subjected to incubation/treatment for too short a time (e.g. several months) for the microbes to deplete high-quality C substrates, obscuring the temperature responses of different components of SOC; (2) a single constant incubation temperature could not well mimic the natural temperature changes in field conditions. Constant incubation temperatures may have caused microbial adaptation to different temperatures by producing new enzymes or changing membrane fatty acids (Mikan et al., 2002; Wetterstedt et al., 2010), leading to contradictory results about the temperature sensitivity of SOC decomposition (Davidson and Janssens, 2006).

To avoid those potential problems when testing the "C quality-temperature" hypothesis, we incubated soil samples from a tallgrass prairie with changing temperatures (low-high-low) at a ± 5 °C step every 24 h. Soil samples had previously been subjected to continuous experimental warming for 10 years and field incubation (litter exclusion) for 9 years. The field incubation treatment should have depleted the original high-quality C substrate in the soil samples and changing lab incubation temperatures to mimic diurnal/seasonal temperature changes in the field should prevent microbial thermal adaptation during the whole incubation period. By changing incubation temperatures, we could mimic what happens in the field as well as focus on the relationship between substrate quality and the temperature sensitivity caused by substrate properties rather than by the properties of decomposers (Bradford et al., 2008; Wetterstedt et al., 2010).

Grassland ecosystems play an important role in the global C cycling because they occupy approximately a quarter of the global land cover and contain 10% of the global C stock (Scurlock et al., 2002). Soils from grasslands with warming and field incubation treatments offer us a unique opportunity to address the "C quality-temperature" hypothesis and the potential responses of SOC decomposition to projected global warming. There were four treatments: control (ambient) temperature and normal litter input (C), field warming and normal litter input (W), control temperature and field incubation (FI, 9 years' litter exclusion), and field warming and field incubation (WFI). The specific questions addressed in this study were: (1) Are Q_{10} values of SOC decomposition relatively high with low C quality under different treatments? The four treatments represent a declining C quality that is hypothesized to be reflected by the Q_{10} of SOC decomposition. (2) Does temperature sensitivity of SOC decomposition differ during the initial and following stages as decomposition proceeds? (3) Does C quality regulate the temperature sensitivity of SOC decomposition under different treatments and different incubation cycles?

2. Materials and methods

2.1. Experimental site and design

The experimental site is located on the Kessler Farm Field Laboratory in central Oklahoma, USA (34°59′N, 97°31′W). The site has never been cultivated and has been ungrazed for the past 40 years. The grassland is dominated by C_4 grasses (*Schizachyrium scoparium* and *Sorghastrum nutans*) and C_3 forbs (*Ambrosia psilostachyia, Solidago rigida,* and *Solidago nemoralis*). Mean annual temperature is 16.3 °C and mean annual precipitation is 914 mm (Oklahoma climatological survey, Norman, OK, USA). The soil is part of the Nash–Lucien complex with neutral pH, high available water holding capacity (around 37%), and a moderately penetrable root zone (USDA, 1979).

The experiment uses a split-plot paired factorial design with warming as the main factor and clipping as the nested or split factor. Each treatment has six replicates (i.e. six pairs of plots). Each pair has two plots of 2 m × 2 m. One plot has been subjected to continuous warming since 21 November 1999 to the present while the other serves as the control with ambient temperature. Infrared heaters (165 cm × 15 cm; Kalglo Electronics, Bethlehem, PA, USA) having a radiation output of 100 W m^{-2} are suspended 1.5 m above the ground in each warmed plot. The control plot has a 'dummy' heater with same dimensions as the infrared heater suspended at a similar height to mimic the shading effects of the heater. Temperature increments generated by the infrared heaters are relatively even over the entire area of the plots and similar at different soil depths (Wan et al., 2002). For each pair of plots, the distance between warmed and control plots is approximately 5 m from centers to avoid heating of the control plots. The distances between the paired plots vary from 20 to 60 m.

Each 2 m × 2 m plot is divided into four 1 m × 1 m subplots. Plants in two diagonal subplots are clipped at a height of 10 cm above the ground once a year while the other two subplots are unclipped. In each plot, PVC tubes (10 cm in diameter, 70 cm in length) were permanently installed 67–68 cm into soil in two adjacent subplots (one clipped and one unclipped) in October 2001. The tubes cut off old plant roots and prevented new roots from growing into the tubes. Litter that fell into the tubes was manually removed once or twice a month. For incubation, soil samples were taken from two unclipped diagonal subplots. In the subplot with deep tube installation, soils samples were taken from the deep tube. Clipping treatment was not considered in this experiment. Thus, we had 4 treatments in total: control (ambient) temperature and normal litter input (C), field warming and normal litter input (W), control temperature and field incubation (FI, 9 years' litter exclusion), and field warming and field incubation (WFI).

2.2. Microclimate

Soil temperature was measured by thermocouples installed 2.5 cm deep in the soil at the center of one unclipped subplot in each plot. The hourly average data was stored in a SM192 Storage Module (Campbell Scientific, Logan, Utah, USA). Volumetric soil