



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

Xia Xu<sup>a,\*</sup>, Yiqi Luo<sup>a</sup>, Jizhong Zhou<sup>a,b</sup>

<sup>a</sup>Department of Botany & Microbiology, 101 David L. Boren Blvd., University of Oklahoma, Norman, OK 73019, USA

<sup>b</sup>Institute for Environmental Genomics, University of Oklahoma, Norman, OK 73019, USA

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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  $\pm 5$  °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.

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### 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<sub>2</sub> 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

\* Corresponding author. Tel.: +1 405 325 6519.

E-mail addresses: [xuxia.1982@yahoo.com](mailto:xuxia.1982@yahoo.com), [xia.xu-1@ou.edu](mailto:xia.xu-1@ou.edu) (X. Xu).

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 tall-grass prairie with changing temperatures (low-high-low) at a  $\pm 5^\circ C$  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

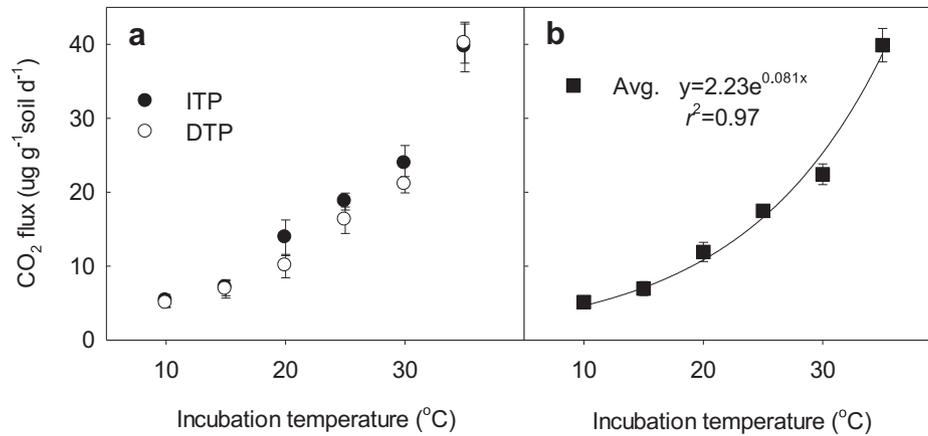
The experimental site is located on the Kessler Farm Field Laboratory in central Oklahoma, USA ( $34^\circ 59'N$ ,  $97^\circ 31'W$ ). The site has never been cultivated and has been ungrazed for the past 40 years. The grassland is dominated by  $C_4$  grasses (*Schizachyrium scoparium* and *Sorghastrum nutans*) and  $C_3$  forbs (*Ambrosia psilostachya*, *Solidago rigida*, and *Solidago nemoralis*). Mean annual temperature is  $16.3^\circ C$  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  $2\text{ m} \times 2\text{ m}$ . 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 ( $165\text{ cm} \times 15\text{ cm}$ ; Kalglo Electronics, Bethlehem, PA, USA) having a radiation output of  $100\text{ W m}^{-2}$  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  $2\text{ m} \times 2\text{ m}$  plot is divided into four  $1\text{ m} \times 1\text{ m}$  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



**Fig. 1.** An example of  $Q_{10}$  value calculation of SOC decomposition by curve fitting. No statistically significant differences were found at any specific incubation temperature between increasing temperature period (ITP) and decreasing temperature period (DTP) (a), we thus averaged the respiration values at each temperature when fitting the curve to get  $Q_{10}$  values (b, Fang et al., 2005). Values are mean  $\pm$  SE ( $n = 6$ ) from the first incubation cycle under control treatment.  $Q_{10}$  values based on the fitted curves with respiration rates from ITP, DTP, and averaged values were not significantly different from each other (all  $P > 0.05$ ).

water content (%V) was measured once or twice a month using Time Domain Reflectometry (TDR) equipment (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) at soil depths of 0–15 cm.

### 2.3. Soil sampling and C pool measurements

On October 4th, 2010, we took two soil cores from the subplot with no deep tube and one soil core from deep tube in the other subplot in each plot. Soil cores were 5 cm in diameter and 0–20 cm in depth. The holes in subplots without deep tubes were immediately filled with root-free soils originated from the same depth outside of the plots. In deep tubes, we filled the holes by installing PVC pipes (same size as soil cores) full of soils. Soil samples were packed in polyethylene bags, immediately stored in coolers, and transported to the Ecolab at the University of Oklahoma, Norman. The soil samples were sieved (<2 mm) to remove soil fauna, rocks, and fine roots and kept fresh at 5 °C before incubation. A small proportion of soil samples were air-dried, finely ground, and sieved (<0.25 mm) to measure soil organic carbon (SOC) and chemically labile SOC (LOC). SOC and total nitrogen (TN) were measured at the Environmental and Agricultural Testing Service at North Carolina State University. LOC content before and after lab incubation was estimated using the modified potassium permanganate (KMnO<sub>4</sub>, 0.02 N) procedure (Weil et al., 2003; Mirsky et al., 2008).

### 2.4. Laboratory incubation

During the 170 d incubation, fresh soil samples (100 g) were incubated in quart jars in a low temperature incubator (Model 2020, Sheldon Manufacturing Inc. Oregon, USA) after a 20-day pre-incubation at 20 °C starting on October 5th, 2010. We had 5 single incubation cycles in total and during each single cycle, temperature was continuously increased by 5 °C of each 24 h period, beginning

at 5 °C up to 35 °C (increasing temperature period, ITP) and then, at 35 °C down to 5 °C (decreasing temperature period, DTP). Six controls, with no soil, were prepared and incubated at the same time. After each cycle, soils were kept at 20 °C for 10, 20, and 30 days, respectively. Small vials (30 ml, with lids removed) containing 5 ml of 1 M NaOH solution were placed in each Mason jar to trap respired CO<sub>2</sub> (Liu and Zou, 2002). Samples were taken every 24 h by removing the NaOH vials. The amount of CO<sub>2</sub> was determined by titration of the NaOH with 1 M HCl to pH 8.3 in the presence of BaCl<sub>2</sub>. Quart jars were flushed with compressed air to allow replenishment of O<sub>2</sub> after each interval and deionized water was added to maintain moisture at 60% of water holding capacity. No measurements were carried out at 5 °C because of low respiratory rates.

### 2.5. Statistical analysis

To describe the relationship between decomposition rates of SOC across the temperature range (10–35 °C), Eq. (1) was used (Fig. 1, Mikan et al., 2002; Fierer et al., 2005):

$$R_T = Ae^{kT} \quad (1)$$

where  $R_T$  is the decomposition rate (ug CO<sub>2</sub>-C g<sup>-1</sup>soil d<sup>-1</sup>) at a given temperature  $T$  (°C),  $A$  and  $k$  are the exponential fit parameters. Throughout this paper,  $Q_{10}$  is used to describe the temperature sensitivity of SOC decomposition, calculated as:

$$Q_{10} = e^{10k} \quad (2)$$

As in other studies (Bosatta and Ågren, 1999; Mikan et al., 2002; Fierer et al., 2005), we hypothesized that C quality (the availability and lability) of SOC equals  $A$  in Eq. (1), which relates decomposition rate to temperature. The parameter  $A$  is considered to be a simple

**Table 1**  
Microclimate and soil properties under four treatments in field conditions.

Treatment	$T_{soil}$ (°C)	$W_{soil}$ (%)	SOC (mg g <sup>-1</sup> )	TN (mg g <sup>-1</sup> )	C:N	LOC <sub>b</sub> (mg g <sup>-1</sup> )	LOC <sub>a</sub> (mg g <sup>-1</sup> )
C	16.30 $\pm$ 0.18 <sup>b</sup>	29.78 $\pm$ 1.15 <sup>a</sup>	12.42 $\pm$ 1.65 <sup>a</sup>	1.13 $\pm$ 0.14 <sup>a</sup>	10.95 $\pm$ 0.47 <sup>a</sup>	0.30 $\pm$ 0.03 <sup>a</sup>	0.08 $\pm$ 0.01 <sup>a</sup>
W	18.00 $\pm$ 0.15 <sup>a</sup>	28.62 $\pm$ 1.31 <sup>a</sup>	9.72 $\pm$ 1.07 <sup>ab</sup>	0.90 $\pm$ 0.10 <sup>ab</sup>	10.84 $\pm$ 0.52 <sup>a</sup>	0.22 $\pm$ 0.04 <sup>ab</sup>	0.06 $\pm$ 0.01 <sup>ab</sup>
FI	16.30 $\pm$ 0.18 <sup>b</sup>	33.59 $\pm$ 4.11 <sup>a</sup>	10.50 $\pm$ 2.14 <sup>ab</sup>	0.98 $\pm$ 0.16 <sup>ab</sup>	10.61 $\pm$ 1.27 <sup>a</sup>	0.16 $\pm$ 0.01 <sup>bc</sup>	0.05 $\pm$ 0.01 <sup>b</sup>
WFI	18.00 $\pm$ 0.15 <sup>a</sup>	27.30 $\pm$ 1.38 <sup>a</sup>	7.47 $\pm$ 0.93 <sup>b</sup>	0.72 $\pm$ 0.09 <sup>b</sup>	10.54 $\pm$ 0.70 <sup>a</sup>	0.11 $\pm$ 0.03 <sup>c</sup>	0.04 $\pm$ 0.01 <sup>b</sup>

Note: C: control (ambient) temperature and normal litter input; W: warming and normal litter input; FI: control temperature and field incubation (9 years' litter exclusion); and WFI: field warming and field incubation.  $T_{soil}$ : soil temperature;  $W_{soil}$ : volumetric soil moisture; LOC<sub>b</sub>: labile soil organic carbon content before lab incubation; LOC<sub>a</sub>: labile soil organic carbon content after lab incubation. The base of mg g<sup>-1</sup> is soil mass (mg g<sup>-1</sup> soil). Values are mean  $\pm$  SE ( $n = 6$ ). For  $T_{soil}$  and  $W_{soil}$ , values are mean  $\pm$  SE from 2010. Different letters indicate statistical significance at  $P < 0.05$ .

**Table 2**

Results of repeated-measures ANOVA ( $P$  values) for the response of  $\text{CO}_2$  release and  $Q_{10}$  values to field warming (W), field incubation (FI), each single incubation cycle (cycle), and their interactions ( $n = 6$ ). A single incubation cycle is composed of an increasing temperature period (ITP) and a decreasing temperature period (DTP).  $P$  values smaller than 0.05 are bold.

Factor	W	FI	Cycle	W × FI	W × cycle	FI × cycle	W × FI × cycle
$\text{CO}_2$	0.767	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.843	<b>0.041</b>	<b>&lt;0.001</b>	0.727
$Q_{10}$	0.300	0.227	<b>0.006</b>	0.881	0.793	0.381	0.509
SOC quality	0.192	<b>0.001</b>	<b>&lt;0.001</b>	0.247	0.082	<b>&lt;0.001</b>	0.961

index of the overall C quality of SOC that is being utilized by microbes at a specific time point.

Repeated-measures ANOVA were used to examine the effects of field warming, field incubation (litter exclusion), incubation cycle, and their interactions on  $\text{CO}_2$  release,  $Q_{10}$  values, and SOC quality. One-way ANOVA was performed to test the significance of the amount of  $\text{CO}_2$  respired and  $Q_{10}$  values between increasing and decreasing temperature periods. A  $t$ -test method was used to examine the significance of regression coefficients  $A$  and  $k$  in Eq. (1) between different treatments. Detailed description of the  $t$ -test method can be found in Toutenburg (2002) and Zhou et al. (2006). Regression analyses were used to evaluate the relationships between substrate quality ( $A$ ) and  $Q_{10}$  values and the relationships of changes in SOC quality with changes in  $Q_{10}$  values under different treatments and under different incubation cycles. All statistical analyses were conducted using SPSS 16.0 for windows (SPSS Inc., Chicago, IL, USA).

### 3. Results

#### 3.1. Microclimate and soil properties

Field experimental warming elevated soil temperature by an average of 1.70 °C and lowered volumetric soil moisture in 2010 (Table 1). The amount of LOC was significantly lower in the soils subjected to field incubation in comparison to that in the control both before and after lab incubation. Warming or field incubation alone had little effects on SOC and TN, but their interactions significantly decreased SOC and TN (Table 1). C:N ratios of the soils were little affected by either field warming or field incubation.

#### 3.2. SOC decomposition rates

During the whole laboratory incubation, field incubation treatment (litter exclusion) and lab incubation cycles significantly influenced SOC decomposition (all  $P < 0.05$ , Table 2). The

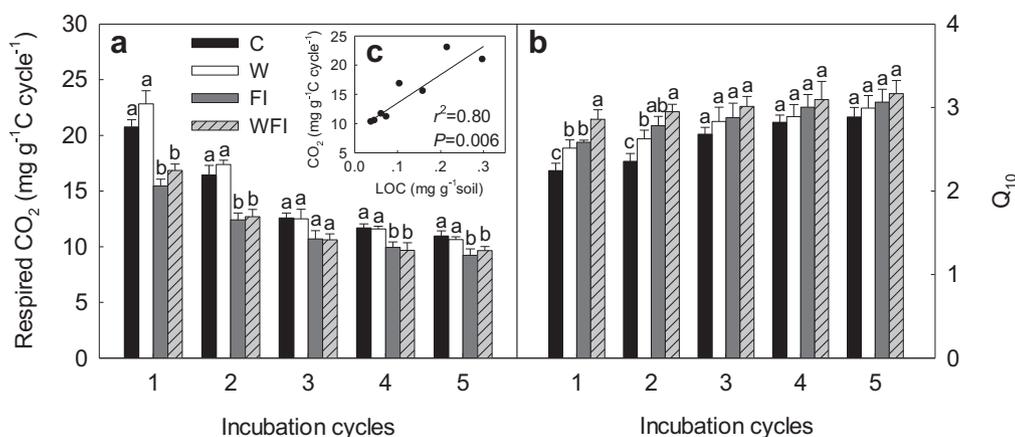
decomposition rates of SOC of soils subjected to 9 years' field incubation were significantly lower than those of control and warmed soils (Fig. 2a), indicating the depletion of LOC with no fresh C input under litter exclusion treatment. SOC decomposition decreased with increasing lab incubation cycles under four treatments. For example, the respired  $\text{CO}_2$  decreased from  $20.75 \pm 0.66 \text{ mg g}^{-1}$  in the 1st cycle to  $10.95 \pm 0.46 \text{ mg g}^{-1}$  in the 5th cycle under control treatment (Fig. 2a). The decomposition of SOC followed a two-phase variation with a rapid decrease in the 1st two cycles and leveling off in the last three cycles (Fig. 2a). LOC content in the soils under four treatments were positively correlated with the amount of  $\text{CO}_2$  released ( $P = 0.006$ , Fig. 2c insert).

#### 3.3. $Q_{10}$ of SOC decomposition

The temperature sensitivity of SOC decomposition increased with increasing lab incubation cycles ( $P = 0.006$ , Table 2). Under the control treatment, for example, the estimated mean  $Q_{10}$  values based on respired  $\text{CO}_2$  for SOC decomposition were significantly higher in the 5th cycle than that in the 1st cycle ( $2.89 \pm 0.12$  vs.  $2.24 \pm 0.09$ , Fig. 2b). The trend in  $Q_{10}$  values was the same among different treatments during the whole lab incubation cycle (Fig. 2b). Within each lab incubation cycle, soils with low LOC content under the four treatments exhibited high sensitivity to changes in temperature (Table 1, Fig. 2b). Significant treatment effects of field warming or field incubation on  $Q_{10}$  values were only observed in the 1st two incubation cycles, probably due to the progressively increased contribution of recalcitrant C and closer similarity in SOC quality among incubated soils under different treatments.

#### 3.4. SOC quality and its relationship with $Q_{10}$

Both field incubation and lab incubation cycles had significant influence on SOC quality (all  $P < 0.01$ , Table 2). After the 2nd, 3rd, 4th, and 5th cycle of lab incubation, there was a 30.59%, 62.94%, 70.62%, and 74.01% decrease, respectively, in SOC quality ( $A$ ) in



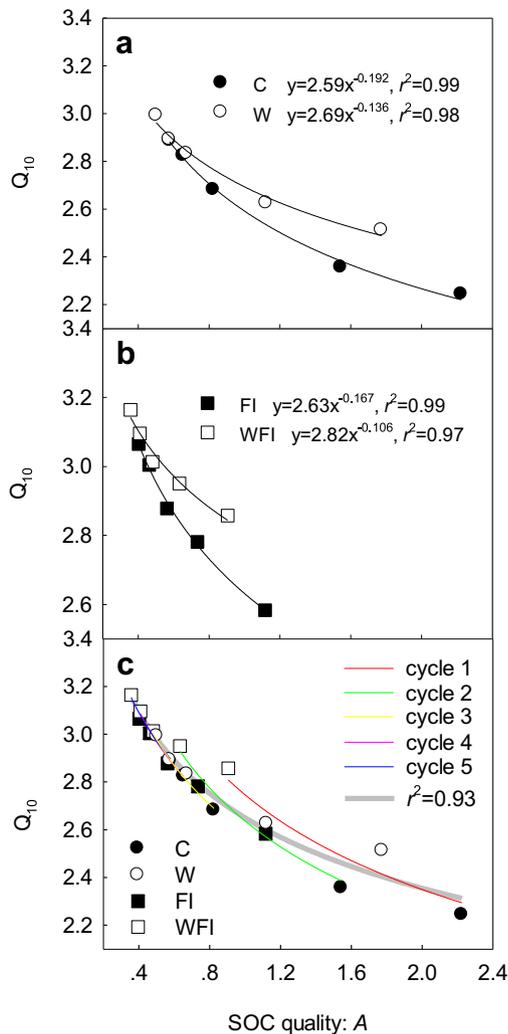
**Fig. 2.** Variation in SOC decomposition (expressed as respired  $\text{CO}_2$ , a) and  $Q_{10}$  values (b) over lab incubation cycles under four treatments. The insert panel (c) shows a correlation between LOC content (before and after lab incubation) and respired  $\text{CO}_2$  in the 1st and 5th incubation cycles ( $n = 8$ ). C: control (ambient) temperature and normal litter input; W: field warming and normal litter input; FI: control temperature and field incubation (9 years' litter exclusion); WFI: field warming and field incubation.

comparison to that of the 1st cycle under the control treatment. SOC quality was negatively correlated with  $Q_{10}$  values both under different treatments over all incubation cycles (Fig. 3a, b) and under different incubation cycles over all treatments (Fig. 3c), regardless of whether the differences in SOC quality resulted from inherent differences in SOC chemistry or from differences in the extent of SOC decomposition. Changes in the temperature sensitivity of SOC decomposition ( $Q_{10}$ ) under field warming, field incubation, and different laboratory incubation cycles were largely regulated by the changes in SOC quality induced by field warming, field incubation, and lab incubation cycles, respectively (Fig. 4). Larger decrease in SOC quality led to higher increase in  $Q_{10}$  values.

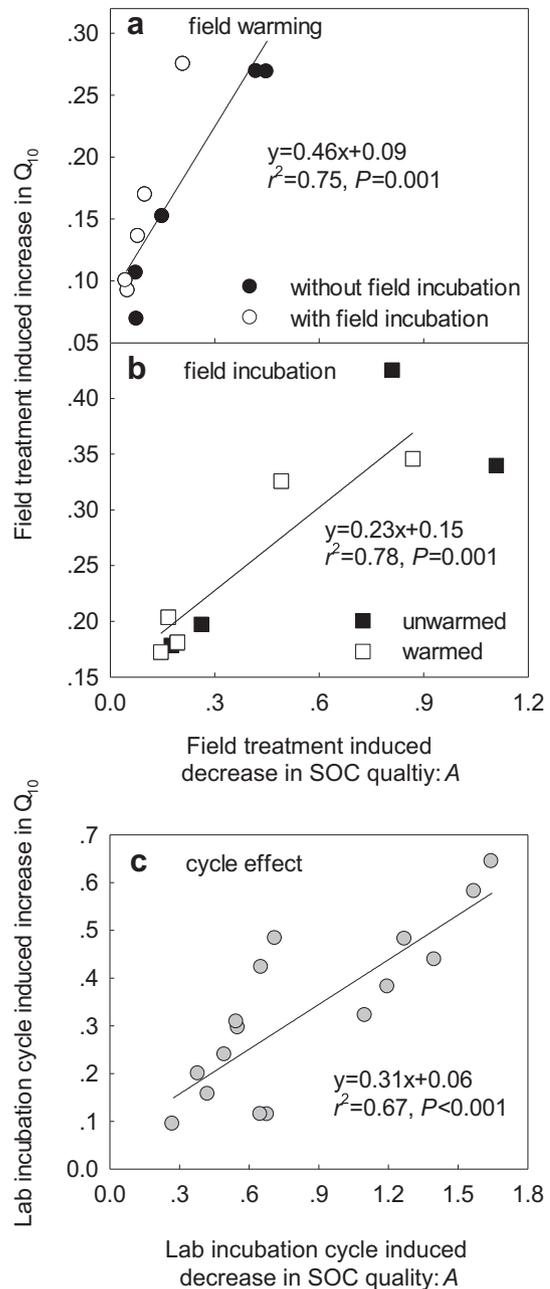
## 4. Discussion

### 4.1. Comparisons of SOC decomposition rates

Overall, the rates of SOC decomposition of the soils subjected to 9 years' field incubation were significantly lower in comparison to those without field incubation (Fig. 2a). This probably resulted from



**Fig. 3.** The negative relationships between SOC quality (A) and the  $Q_{10}$  of SOC decomposition under different treatments over all incubation cycles (a, b) and under different incubation cycles over all treatments (c). Different color lines in panel (c) represent curves fit within each lab incubation cycles ( $n = 4$ ). The gray line shows an overall relationship between SOC quality and the  $Q_{10}$  values across all treatments and incubation cycles ( $n = 20$ ). Data were fit using the two-parameter power equation:  $Q_{10} = a \times A^k$ . See Fig. 2 for acronyms (C, W, FI, and WFI).



**Fig. 4.** Relationships of the changes in SOC quality (A) and  $Q_{10}$  values under field warming (a,  $n = 10$ ), field incubation (b,  $n = 10$ ), and different laboratory incubation cycles across all treatments (c,  $n = 16$ ). Incubation-cycle effects in panel c represent the differences of the 1st incubation cycle with the following four (2nd–5th) cycles.

low LOC content in the soils under field incubation with no fresh C input (Table 1). Low-quality SOC is generally accepted to limit the availability of energy for soil microbes, leading to low rates of SOC decomposition (Paul and Clark, 1989). Additionally, we observed a two-phase pattern for SOC decomposition under different treatments, with decomposition rates dropping substantially in the 1st two incubation cycles and remaining relatively low and constant in the last three cycles (Fig. 2a). A decline in SOC decomposition rates was widely observed with increasing incubation time (e.g. Fang et al., 2005; Conant et al., 2008; Wetterstedt et al., 2010). The rapid drop in the 1st phase may be attributable to the depletion of LOC of soils being incubated (Eliasson et al., 2005). Microbes decomposed LOC relatively quickly under controlled lab conditions

due to the cutting off of fresh C supply from plants. With the progressive increase in the contribution of recalcitrant compounds, SOC decomposition leveled off in the 2nd phase (Vanhala et al., 2007; Xu et al., 2010). Changes in LOC or SOC quality were believed to be the major factors influencing the decline in SOC decomposition (Fig. 2c, Kirschbaum, 2006; Conant et al., 2008).

#### 4.2. Comparisons of $Q_{10}$ estimates

How the sensitivity of SOC decomposition responds to temperature changes has received considerable interest due to its importance in projecting future climate change (e.g. Fang et al., 2005; Davidson and Janssens, 2006; Conant et al., 2008; Craine et al., 2010). In line with many previous incubation studies (e.g. Fierer et al., 2005; Conant et al., 2008; Wetterstedt et al., 2010; Xu et al., 2010), our results showed that soils subjected to field warming or field incubation had higher temperature sensitivity than the control soils (1st two cycles, Fig. 2b). Since soil samples were incubated under controlled moisture and temperature conditions, this may arise from the low LOC content (low SOC quality) in warmed or field incubated soils (Table 1). In grasslands, warming has been reported to largely increase  $C_4$ -derived litter input to soil organic matter and decreased SOC quality without influencing SOC content (Cheng et al., 2011), suggesting SOC decomposition was quality-dependent. It is a reasonable supposition given high temperature sensitivity and low C quality are usually coupled across multiple scales and soil types (Craine et al., 2010).

The differences in the response of SOC decomposition to temperature indicated a shift to the decay of biochemically recalcitrant C, especially in the soils with the 9-year field incubation treatment. As decomposition progressed over time with increasing contribution of recalcitrant C, however, differences in  $Q_{10}$  values of different soils became much smaller (the last two cycles, Fig. 2b). Due to the high temperature sensitivity of the large amount of recalcitrant C stored in soil (50–90%, Trumbore, 1997), climate warming may stimulate loss of soil-stored C and cause a positive feedback to climate change.

#### 4.3. Relationship between SOC quality and $Q_{10}$

We observed strong negative relationships between SOC quality and  $Q_{10}$  values across soils under different treatments and incubation cycles (Fig. 3). Many laboratory studies also found that temperature sensitivity of SOC decomposition increases with decreasing substrate quality (e.g. Mikan et al., 2002; Fierer et al., 2005; Vanhala et al., 2007; Wetterstedt et al., 2010). These results support the enzyme kinetics that temperature sensitivity of SOC decomposition is inversely proportional to the complexity of the C substrates being decomposed by microbes (Bosatta and Ågren, 1999; Davidson and Janssens, 2006). With increasing incubation time, the quality of the decomposed C substrates decreased, as evidenced by the decrease in the  $A$  values (Fig. 3). Though temperature sensitivity of SOC decomposition is regulated by several factors, such as substrate availability (Davidson and Janssens, 2006), inhibition of microbial activity (Balsler and Firestone, 2005), and physico-chemical protection (Oades, 1988; Six et al., 2002), the intrinsic C quality responds most to changes in temperature (Craine et al., 2010).

#### 4.4. Relationship of treatment- or incubation cycle-effects between SOC quality and $Q_{10}$

Since the degree of treatment and lab incubation-cycle effects on  $Q_{10}$  values largely depended on the changes in SOC quality

(Fig. 4), it becomes clear that accurate estimates of C storage and turnover will require an understanding of the factors controlling SOC quality under global climate change. Warming is hypothesized to influence SOC quality through directly affecting organic C composition or indirectly influencing plant community structure (Fissore et al., 2008; Cheng et al., 2011). Warming may affect the composition of SOC by accelerating LOC decomposition, which was found in forest and grassland ecosystems subjected to long-term warming (Bradford et al., 2008; Xu et al., unpublished data). Additionally, changes in plant community structure under warming may also play an important role in determining the magnitude of changes in SOC quality (Hobbie, 1996), because SOC is almost exclusively derived from detrital input of plants growing on the site (Cheng et al., 2011). Given the high temperature sensitivity of large-amount, low-quality SOC, changes in its dynamics have the highest potential to impact long-term C stocks. Moreover, how C quality influences SOC decomposition in relation to warming may potentially become a prominent determinant of whether we will have a positive or negative feedback of SOC to current global warming in the future.

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