

Long-term experimental warming decreased labile soil organic carbon in a tallgrass prairie

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Abstract

Aims Climate warming has been hypothesized to influence dynamics of soil organic carbon (SOC), especially labile SOC due to its rapid response to changes in temperature and carbon (C) supply. In this study, we examined impacts of experimental warming on the labile and whole SOC pools in association with warming-induced vegetation changes from 2000 to 2008 in a tallgrass prairie in Oklahoma, USA.

Methods Infrared heaters were used to elevate soil temperature by approximately 2°C since November 1999. The modified potassium permanganate (KMnO₄, 0.02 mol L⁻¹) procedure was used to estimate chemically labile organic C (LOC).

Results Warming significantly decreased chemically labile organic C (LOC) by an average of 15.56 %, but had little effect on SOC content. The decrease in LOC was probably attributable to increased soil respiration, enhanced soil erosion, and possibly stimulated

C₄ dominance under warming. Warming did not induce an instantaneous decrease in LOC. A 2-stage variation in LOC response to warming was observed, with no significant changes from 2000 to 2004 and significant decreases from 2005 to 2008. Lagged temporal dynamics of LOC (2 yrs) asynchronously correlated with warming-increased C₄ proportion of aboveground biomass (AGB).

Conclusions Our findings suggest that staged decrease in LOC under warming may potentially relate to the increase in C₄ biomass through detrital inputs, making it complex to predict the effect of warming on C cycling in this region.

Keywords Soil organic carbon (SOC) · Experimental warming · Labile organic carbon · C₃–C₄ composition · Tallgrass prairie

Introduction

Global mean temperature is expected to increase substantially (2–7°C) by the end of this century in response to rising concentrations of greenhouse gases in the atmosphere (Allison et al. 2009). Potential consequences of such warming for soil organic carbon (SOC) have received considerable attention because how SOC may respond to warming is still not clearly understood (Luo et al. 2001; Fang et al. 2005; Davidson and Janssens 2006; Craine et al. 2010). Soil is the largest terrestrial carbon (C) pool, storing approximately 2 times the

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amount of C present in atmospheric CO₂ (Dixon et al. 1994). A slight change in SOC may greatly stimulate buildup of atmospheric CO₂ concentration due to the huge fluxes between soil and atmosphere (Marin-Spiotta et al. 2009). Though soil is considered to be an important potential C sink to retard the greenhouse effect (Cheng et al. 2011), warmer temperatures may stimulate SOC mineralization, leading to a positive feedback to future climate warming (Conant et al. 2008; Hartley and Ineson 2008). Therefore, understanding the response of SOC decomposition to warming is particularly important because it partially determines whether we will have a positive or negative feedback to current global warming in the future (Hartley and Ineson 2008; Craine et al. 2010).

Undoubtedly, increasing temperature has prompted many studies investigating the response of SOC to warming (e.g. Luo et al. 2001; Fang et al. 2005; Craine et al. 2010). However, understanding responses of SOC to warming can be difficult because SOC is composed of a continuum of materials with varying chemical complexity (Marin-Spiotta et al. 2009) and minor changes are difficult to detect against the high background of SOC in soil (Weil et al. 2003). Fast-cycling labile soil organic C (LOC) has captured much more attention because of its fast response to warming (Zhang et al. 2005; Bradford et al. 2008; Carrillo et al. 2011) and its control over CO₂ fluxes between terrestrial ecosystems and the atmosphere (Trumbore et al. 1990). In the long term, LOC can influence terrestrial C storage through its impact on nutrient supply to plants (Zhang et al. 2005; Luo et al. 2009). Despite much research, however, the effect of warming on SOC remains unclear. For example, warming may have little effect on SOC (Marchand et al. 2004; Luo et al. 2009; Cheng et al. 2011) and LOC as measured by microbial biomass C (Zhang et al. 2005; Schindlbacher et al. 2011) or, it may increase SOC through great increase in plant biomass inputs (Day et al. 2008; Sardans et al. 2008; Carrillo et al. 2011). Conversely, other studies show that LOC and SOC may decrease in response to continuous warming (Fontaine et al. 2004; Eliasson et al. 2005; Bradford et al. 2008). An accurate quantitative prediction of C storage in soil is highly dependent on the assumed temperature sensitivity of SOC decomposition (Cox et al. 2000; Conant et al. 2008), but debate continues regarding whether LOC decomposition is more (Giardina and Ryan 2000; Reichstein et al. 2000), similar (Fang et al. 2005; Conen et al. 2006), or less

(Conant et al. 2008; Wetterstedt et al. 2009) sensitive to that of recalcitrant organic C. The lack of consensus is not surprising given that the various responses of SOC to warming depend on many factors, such as soil moisture, precipitation, microbial activity, and plant species composition (Sollins et al. 1996; Fissore et al. 2008; Schmidt et al. 2011).

One way that changes in plant species composition under warming may alter LOC and SOC is through altering the quantity and quality of detrital inputs to soil (Day et al. 2008; Fissore et al. 2008). Because SOC is almost exclusively derived from detrital inputs of plants growing on the site (Cheng et al. 2006), the magnitude of the warming effect on soil-stored C may largely depend on the quantity and quality of litter inputs. In grasslands, for example, warming significantly increases recalcitrant litter derived from C₄ species (Luo et al. 2009; Cheng et al. 2011), which may increase SOC storage. Alternatively, increases in the relative abundance of recalcitrant C compounds input to soil is expected to regulate responses of LOC and SOC to warming by altering soil chemical and physical processes (Fissore et al. 2008). Warmer temperatures may accelerate microbial utilization of labile compounds during litter decomposition (Hobbie 1996; Prescott et al. 2000), leaving behind SOC characterized by low C quality (Conant et al. 2008; Hartley and Ineson 2008). Although shifts in plant species composition under warming have been reported (Harte and Shaw 1995; Wan et al. 2005; Walker et al. 2006; Luo et al. 2009), we still have little understanding of how LOC and SOC may respond to changes in plant community structure, particularly under warming. The amount of soil-stored C is likely to change under global warming, especially with alteration in plant community structure and composition (Hobbie 1996; Cheng et al. 2011).

In a tallgrass prairie in central Oklahoma, we have conducted a warming experiment since November 1999 (Luo et al. 2001). The experimental site is dominated by C₄ grasses and C₃ forbs. Previous studies at this site have shown that warming significantly increases above-ground biomass through warming-enhanced C₄ dominance (Wan et al. 2005; Luo et al. 2009). Warming also increased C₄ species litter (low quality, high recalcitrance) inputs to soil by 47.20 % and decreased C₃ species litter input to soil by 19.10 % (Cheng et al. 2011). Long-term experimental warming and simultaneously shifting C₃–C₄ composition thus provide us with an ideal opportunity to evaluate variation in soil-

stored C and SOC decomposition. The specific objectives of this study were to evaluate warming effects on LOC and SOC from 2000 to 2008 and to examine the potential impacts of observed shifting of C₃–C₄ species composition on variations in LOC and SOC.

Materials and methods

Experimental site and design

The experimental site is located on the Kessler Farm Field Laboratory in 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 C₄ grasses (*Schizachyrium scoparium* and *Sorghastrum nutans*) and C₃ forbs (*Ambrosia psilostachya*, *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 water holding capacity (around 37 %), and a moderately penetrable root zone (USDA 1979).

The experiment uses a paired factorial design with warming as the main factor and clipping as a nested factor (Luo et al. 2001; Wan et al. 2005). 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 from 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 Wm⁻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. Detailed information can be found in Luo et al. (2009). 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. The soil experiment described in this paper was carried out only in the unclipped subplots, giving two treatments: control (C) and warmed (W).

Microclimate and aboveground biomass measurements

Soil temperature was measured by thermocouples installed 2.5 cm deep in the soil at the center of one unclipped subplot in each plot. Hourly average data were stored in a SM192 Storage Module (Campbell Scientific, Logan, Utah, USA). Volumetric soil 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 a soil depth of 0–15 cm. Precipitation data were obtained from an Oklahoma Mesonet Station (Washington Station) located approximately 200 m away from our experimental site (Oklahoma Climatological Survey). Total aboveground biomass (AGB), and C₃ and C₄ biomass was indirectly estimated by the pin-contact method (Frank and McNaughton 1990). A detailed description of the biomass estimation technique was provided by Sherry et al. (2008). In 2000, 2001, and 2002, the amount of C₃ biomass is obtained based on the correlation between C₃/C₄ cover ratio and C₃ biomass in clipped subplots each year (all $P < 0.01$, $n = 12$) because we did not separate AGB into C₃ and C₄ when measuring AGB during those three years. C₄ biomass is calculated as the difference between AGB and C₃.

Soil sampling

From 2000 to 2008 (except 2006), one soil core (4 cm in diameter, 0–15 cm in depth) was taken once a year from one unclipped subplot in each plot. 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, then air-dried, further inspected to remove rocks and fine roots, finely ground, and sieved (<0.25 mm) to measure SOC and LOC. In 2006, we did not archive soil samples.

LOC and SOC analyses

Given that only limited air-dried soil samples were archived, the modified potassium permanganate (KMnO₄,

0.02 mol L⁻¹) procedure (Weil et al. 2003; Mirsky et al. 2008) was used to measure LOC of the soil samples. Slightly alkaline KMnO₄ has been demonstrated to oxidize simple and active forms of soil C, such as carbohydrates, amino acids, and amine/amide sugars (Stanford 1978; Loginow et al. 1987), simulating the *in situ* enzymatic digestion of labile C of microbial decomposition (Mirsky et al. 2008). KMnO₄ solution (0.02 mol L⁻¹ KMnO₄ and 0.1 mol L⁻¹ CaCl₂) and standard KMnO₄ solutions ranging from 0 to 0.02 mol L⁻¹ were prepared. Soil samples (5 g) were added to 50 ml plastic screw-top centrifuge tubes. Then 20 ml KMnO₄ solution was added to each tube to react with soil samples. The soil suspension was shaken on a reciprocating shaker for 10 min at 180 rpm and then allowed to settle for 10 min. A 1 ml aliquot of the solution supernatant was diluted to 50 ml and absorbance was measured on a Spectronic Genesys 5 spectrophotometer (Thermo Fisher Scientific Inc. Waltham, MA, USA) at 550 nm. The amount of C oxidized after digestion was determined by the change in the concentration of the KMnO₄ solution. It was assumed that 9 gC was oxidized by 1 mol L⁻¹ KMnO₄ changing from Mn⁷⁺ to Mn²⁺. SOC was measured at Oklahoma State University, Stillwater.

Statistical analysis

Before ANOVA analysis, the datasets were tested for normality to meet the assumptions for statistical analysis. Repeated-measures ANOVAs were used to examine the effects of experimental warming, year, and their interaction on LOC, SOC, and the proportion of LOC to SOC. Paired *t*-tests were performed to analyze warming effects on AGB and the parameters mentioned above in each year. Linear regression analyses were used to evaluate the relationships of warming-induced changes in LOC with C₃–C₄ composition in the current year, 1 year later, and 2 years later. All statistical analyses were conducted using SPSS 16.0 for windows (SPSS Inc., Chicago, IL, USA).

Results

Microclimate

Warming significantly increased soil temperature every year from 2000 to 2008 (Table 1, $P < 0.05$). On average, it elevated soil temperature by 1.60°C. Warming also lowered volumetric soil moisture by an average of 1.47 %, but this effect was not significant (Table 1, $P > 0.05$). Annual precipitation (AP) varied from 515 mm in 2005 to 1307 mm in 2007 with a mean of 870 mm from 2000 to 2008 (Table 1).

Soil C pool and AGB

Warming significantly influenced LOC and its proportion to SOC, but had little effect on SOC from 2000 to 2008 in the soil layer of 0–15 cm (Table 2, Fig. 1a–f). Overall, warming decreased LOC, and the proportion of LOC to SOC by an average of 15.56 % ($P < 0.05$, Fig. 1d) and 14.94 % ($P < 0.01$, Fig. 1f), respectively. Warming did not induce an instantaneous decrease in LOC and a 2-stage variation in LOC was found. For example, the warming effect on LOC was not significant in the first several years of treatment (2000–2004), but warming decreased LOC from 2005 to 2008 (Fig. 1a). Similarly, experimental warming increased AGB (Fig. 2a) and the warming effect on C₄ biomass was significant in the second stage (2007–2008, Fig. 2b).

Relationships of changes in LOC with C₃–C₄ composition

Linear regression showed that C₃–C₄ composition, as expressed by C₄/AGB, was significantly related to 2-year-lagged changes in LOC ($P < 0.05$, Fig. 3a). Temporal variation in LOC was asynchronous with changes in the proportion of C₄ to aboveground biomass

Table 1 Precipitation (AP) and changes (W-C) in soil temperature and moisture (T_{soil} , W_{soil}) under warming from 2000 to 2008

Variable	Warming effect	2000	2001	2002	2003	2004	2005	2007	2008	Avg.
AP (mm)	n/a	995	883	890	647	991	522	1307	726	870
T_{soil} (°C)	W-C	2.05*	1.73*	1.33*	1.47*	1.72*	2.05*	1.37*	1.08*	1.60*
W_{soil} (%)	W-C	-3.77	-1.00	-0.78	-1.01	-0.1	-2.18*	-1.20	-1.75	1.47

W warming; C control. Asterisks (*) represent significant warming effect, *: $P < 0.05$

(C_4/AGB), lagging the biomass changes by 2 years (Fig. 3b).

Discussion

Variation in LOC is substantially influenced by changes in non-biological and biological environmental conditions (Garten Jr. et al. 1999; Fissore et al. 2008). Our results showed that warming significantly decreased LOC in the soil layer of 0–15 cm (Table 2, Fig. 1a, d), probably due to accelerated decomposition of LOC and the warming-increased soil erosion. At the same site, for example, both soil respiration and heterotrophic respiration significantly increased under warming (Wan et al. 2005; Zhou et al. 2007; Luo et al. 2009), which largely originates from LOC decomposition. The reduction in LOC is in line with a previous study that long-term soil warming significantly decreased the fast-cycling LOC, as measured by mineralizable C, substrate-induced respiration (SIR), and microbial biomass C (MBC) (Bradford et al. 2008). Also, increased soil erosion under warming at the same site led to preferential removal of labile SOC from the soil, both in the form of dissolved organic carbon (DOC) and in particulate organic carbon (POC) (Ludwig and Probst 1999; Xue et al. 2010). Though different labile SOC pools were measured and reported, they all represent a fast-cycling proportion of SOC and positive correlations of chemically LOC with SIR, MBC, and POC were found (Weil et al. 2003; Mirsky et al. 2008). Moreover, both model studies and laboratory incubation studies have suggested a faster depletion of LOC under higher temperatures (e.g. Eliasson et al. 2005; Conant et al. 2008; Hartley and Ineson 2008). But our results that warming decreased LOC were limited to the surface soils (0–15 cm), how the deep soils respond to warming may need further exploration.

Table 2 Results of repeated-measures ANOVA (P values) for responses of LOC, SOC, and the proportion of LOC to SOC ($n=6$) to warming (W) and year (Y)

	LOC	SOC	LOC/SOC
Warming	0.061	0.869	0.002
Year	0.006	0.397	0.024
W×Y	0.014	0.634	0.026

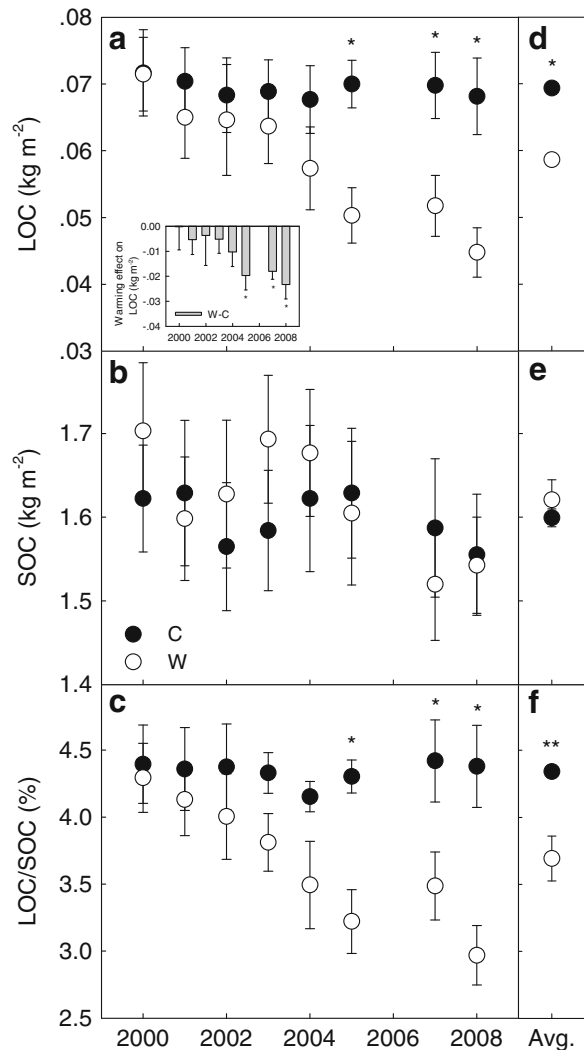


Fig. 1 LOC (a), SOC (b), and proportion of LOC to SOC (c) from 2000 to 2008 and their averages (d, e, f) under control (C) and warming (W) treatments. The inserted figure in panel a shows the warming-induced decrease in LOC over the years. LOC: chemically labile soil organic carbon; SOC: soil organic carbon. Values are mean \pm SE ($n=6$). Asterisks (*) represent significant warming effect, *: $P<0.05$; **: $P<0.01$

Additionally, a warming-driven community shift from C_3 to C_4 species at our site (Wan et al. 2005; Luo et al. 2009) may be another potentially possible factor in regulating the decrease in LOC because LOC responds rapidly to changes in C supply (Zhang et al. 2006). Hobbie (1996) suggested that changes in plant species composition are just as important as direct warming effects in determining SOC decomposition. At our site, for example, a SOC study based on ^{13}C showed that warming increased C_4 -derived C input to

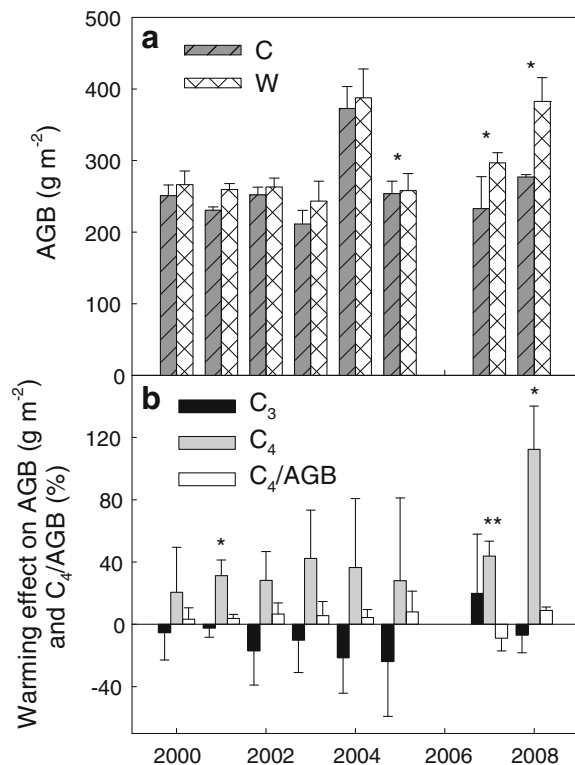


Fig. 2 Variation in AGB under control (C) and warming (W) treatments (a) and warming-induced changes in AGB (C₃ and C₄, b) from 2000 to 2008. AGB: aboveground biomass. Values are mean \pm SE ($n=6$). Asterisks (*) represent significant warming effect, *: $P<0.05$; **: $P<0.01$. In order to be consistent, we did not plot the biomass data in 2006 because soil samples in 2006 were not archived

soil by 18.77 % after 9 years' warming (Cheng et al. 2011). Compared to C₃ species, C₄ species have lower quality litter that eventually incorporates into soil with important consequences for biogeochemical processes and reduced SOC quality (Cheng et al. 2006; Fissore et al. 2008). LOC originating from C₄ species was found to decompose faster than whole SOC in mixed C₃/C₄ soils (Wynn and Bird 2007). Therefore, enhanced recalcitrant C₄-derived litter input to soil under warming may eventually stimulate LOC decomposition, lowering LOC content and its proportion to SOC in spite of the fact that warmed soils received more detrital inputs (Fig. 2). Although plant species change has been one of the important factors in influencing soil C dynamics (Hobbie 1996; Fissore et al. 2008), it was considered as a potential factor in leading to the LOC decrease in this study because our experimental design could not isolate warming effect from plant

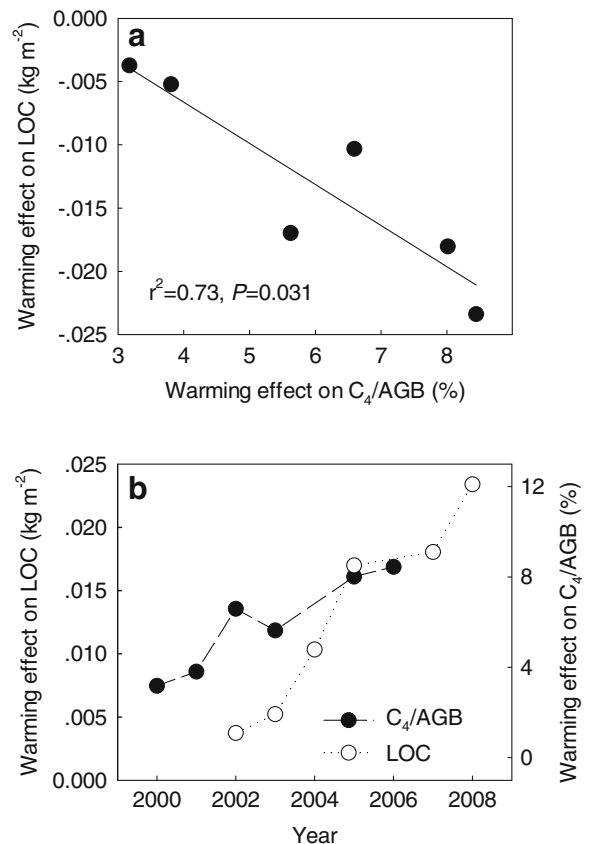


Fig. 3 Relationship of warming-induced changes in C₄/AGB (from 2000 to 2006) with 2-years lagged changes in LOC (from 2002 to 2008, a) and asynchronous variation of LOC and C₄/AGB under warming (b). LOC data showed in panel b was transformed by timing -1 . AGB: aboveground biomass

species composition effect on LOC. Further studies may be needed to compare plant composition effect with warming effect on SOC.

One unexpected result from our study was that despite higher inputs due to stimulated plant productivity over the years (Fig. 1b, Wan et al. 2005; Luo et al. 2009), SOC content appeared to be constant under warming (Table 2, Fig. 1b, e). SOC storage is mainly determined by the balance between detrital inputs and respiratory loss. The non-significant changes in SOC may arise from the great loss of fresh C back into the atmosphere as CO₂ through warming-induced increase in soil respiration observed at the same site (Luo et al. 2009; Cheng et al. 2011). Additionally, higher plant litter inputs to soil may be offset by warming increased SOC loss through soil erosion at a rate of 69.6 gm⁻² yr⁻¹, three times higher than that of the control at 22.5 gm⁻² yr⁻¹ (Xue et al. 2010). No changes in C storage under warming were also reported

in other studies (e.g. Marchand et al. 2004). Changes in the amount of SOC are particularly hard to detect (Kirschbaum 2006) due to the high background C levels in soil and to the small fraction of SOC that responds to warming over a long time period. It may take many centuries to observe the very slow changes in SOC (Kirschbaum 1993). However, it is important to note that the composition of SOC has changed, as evidenced by the significant decrease in the proportion of LOC to SOC (Fig. 1c). Moreover, ^{13}C -SOC signatures showed that relative abundance of C_4 -derived fraction in SOC significantly increased (Cheng et al. 2011), which lowered SOC quality and may impact the decomposition of SOC in response to warming.

We observed a 2-stage variation in the response of LOC to warming. In the first stage, from 2000 to 2004, the warming effect on LOC was not significant, but warming did significantly decrease LOC in the second stage from 2005 to 2008 (Fig. 1a). Plant litter input and root exudates are the major sources of LOC (Catovsky et al. 2002). Therefore, unlike laboratory incubation of soil samples with no continuous fresh C input (e.g. Fang et al. 2005; Craine et al. 2010; Xu et al. 2010), it may take years to detect *in situ* decrease in LOC. Interestingly, we also observed a similar warming effect on C_4 biomass as in LOC, with non-significant differences from 2000 to 2005 and significant differences from 2007 to 2008 (Fig. 2b). Moreover, the 2-year lagged decrease in LOC under warming significantly correlated with the increase in C_4 biomass (Fig. 3a). Previous studies have suggested that warming may alter C cycling by changing plant community structure and species composition (Johnson 1992; Chapin et al. 1995). In comparison to C_3 species, C_4 species may have smaller root systems, different root surface areas, or some other traits that could lower their contribution of C to the LOC. The staged variation in LOC over the years may thus be partly attributable to indirect warming stimulation via alterations in C_4 litter inputs and perhaps rhizodeposition. ^{13}C -SOC signatures showed that warming increased C_4 species litter by 47.20 % and increased C_4 -derived litter incorporated into soil by 11.87 % in 2008 (Cheng et al. 2011), which undoubtedly intensified C_4 species' control on LOC variation. Plant species influence LOC content via control over litter decomposition (Hobbie 1996), with byproducts eventually incorporated into soil. The variation in LOC and in plant species composition (C_4/AGB) was asynchronous (Fig. 3b), lagging the biomass change by

2 years (Fig. 3b). Given the time needed for plant-derived fresh C integrating into soil organic matter through a series of soil processes, the lagged changes in LOC is reasonable.

To conclude, our results from a long-term warming experiment in the tallgrass prairie in the US suggest that warming will have substantial and staged effect on LOC. Across the years, warming significantly decreased LOC through enhanced decomposition and increased soil erosion. In addition, warming-induced shift in C_3 – C_4 plant species composition perhaps also contributed to the decrease in LOC. SOC content under warming was not significantly different from that under control conditions, likely due to the balance between increased C input and increased C loss. It is important to note that the proportion of LOC to SOC was much lower under the warming treatment, which may influence soil C quality and decomposition in the long term. Warming may decrease LOC and simultaneously increase C_4 biomass. The 2-year lagged changes in LOC and changes in C_4 biomass potentially related to each other through detrital inputs, making predictions of warming effects on C cycling in grasslands more complex due to the impossibility in separating warming effect apart from plant species composition effect on LOC.

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