Biogeosciences Discuss., 7, 8381–8407, 2010
www.biogeosciences-discuss.net/7/8381/2010/
doi:10.5194/bgd-7-8381-2010

Biogeosciences Discussions

Soil organic matter dynamics in a North America tallgrass prairie after 9 years of experimental warming

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Received: 1 October 2010 – Accepted: 10 November 2010 – Published: 15 November 2010

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

The influence of global warming on soil organic matter (SOM) in terrestrial ecosystems remains unclear. In this study, we combined soil fractionation with isotope analyses to examine SOM dynamics after nine years of experimental warming in a North America tallgrass prairie. Soil samples from the control plots and the warmed plots were separated in four aggregate sizes (>2000 µm, 250–2000 µm, 53–250 µm and <53 µm), and three density fractions (free light fraction (LF), intra aggregate particulate organic matter (iPOM) and mineral-associated organic matter (mSOM)). All fractions were analyzed for their C and N contents, and δ^{13}C and δ^{15}N values. Warming did not significantly affect soil aggregate distributions and stability but increased C_4-derived C input into all fractions with the greatest one in LF. Warming also stimulated decay rates of C in whole soil and all aggregate sizes. C in the LF turned over faster than that in iPOM in the warmed soils. The δ^{15}N values of soil fractions were more enriched in the warmed soils than those in the control, indicating that warming accelerated loss of soil N. The δ^{15}N values changed from low to high while C:N ratios from high to low in order of LF, iPOM, and mSOM due to increased degree of decomposition and mineral association. Overall, warming increased the input of C_4-derived C by 11.6%, which was negated by the accelerated loss of soil C. Our results suggest that global warming simultaneously stimulated C input via shift in species composition and decomposition of SOM, resulting in negligible net change in soil C.

1 Introduction

The recent Intergovernmental Panel on Climate Change report (IPCC, 2007) predicts temperature to increase by 1.1–6.4 °C during current century. Climate warming affects most biological and chemical processes of terrestrial ecosystems (e.g., Davidson and Janssens, 2006), it can profoundly impact ecosystem processes such as soil organic matter (SOM) dynamics (e.g., Von Fischer et al., 2008). Carbon (C) in SOM accounts

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for 80% of the terrestrial C pools and is regarded as important potential C sink to retard the greenhouse effect. Small changes in SOM under global change have the potential to greatly affect atmospheric CO_2 concentrations (e.g., Batjes and Sombroek, 1997; Marin-spiotta et al., 2009). On the other hand, SOM also is a significant component of the global terrestrial nitrogen (N) pools. Warming-induced changes in the SOM regulate the availability of N to plant growth and ultimately influence the net primary productivity of terrestrial ecosystems. Hence, it is imperative for us to understand how global warming will affect SOM dynamics.

Effects of warming on SOM dynamics remain a widely debated topic (e.g., Pendall et al., 2004). For example, climatic warming increases soil temperature and hence accelerate organic matter decomposition rates, leading to loss of soil C and N (e.g., Rustad et al., 2001; Fontaine et al., 2004). Conversely, some studies have reported warming leads to increases in soil C and N because of great increases in biomass and litter inputs in tundra ecosystems (e.g., Welker et al., 2004; Day et al., 2008). These differences are not surprising given response of soils to warming depends on many factors, such as the soil moisture and temperature, particularly, on the plant species that provide carbon inputs to soils (e.g., Shaw and Harte, 2001; 2007; Fissore et al., 2008). Most SOM derives exclusively from the material of plants growing on the site. The changes in vegetation type are thus expected to alter the quality and quantity of SOM (Cheng et al., 2006; Fissore et al., 2008). Recent climatic warming has already led to dramatic shifts in plant functional groups (e.g., C_3 litter with high quality and C_4 litter with low quality), and this can cause appreciable changes in SOM by altering the quantity and quality of plant material entering into the soil (Day et al., 2008; Fissore et al., 2008).

Detecting changes in the SOM of terrestrial ecosystem under global change can be difficult, because SOM has a complex composition that consists of different fractions characterized by different physical and chemical stability (Van Groenigen et al., 2002; Del Galdo et al., 2003; Marin-spiotta et al., 2009). Numerous studies have been done to separate the bulk soil fractions that differ in chemical and/or physical composition

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(e.g., Jastrow, 1996; Six et al., 2000; Marin-Spiotta et al., 2009). These fractions are characterized by significant difference in microbial degradability and turnover time. For instance, aggregate size separations have shown that SOM associated with larger aggregates has higher turnover rates than SOM associated with smaller aggregates (Jastrow, 1996; Six et al., 2000). Density separation results in a light fraction, which is composed of decomposing plant tissues and it is generally thought to have a rapid turnover, and a heavy and mineral associated fraction, which remained as more recalcitrant fraction has a long-term turnover (Balesdent, 1996).

The stable isotopes are useful for evaluating the ecosystem C and N biogeochemical processes (Robinson, 2001; Jones and Donnelly, 2004; Billings and Richter, 2006; Auerswald et al., 2009). Combining SOM physical fractionation techniques with natural abundance stable C and N isotope offers an approach to better quantify SOM dynamics when global change induces a shift in the dominant plant species composition between C_4 and C_3 (López-Ulloa et al., 2005; John et al., 2005; Marin-Spiotta et al., 2009). Differences in the natural stable C isotope signature between C_3 (average δ^{13}C value of −27‰) and C_4 (average δ^{13}C value of −11‰) plants result in SOM with distinct isotopic signatures. Such as, the changes in δ^{13}C values of soil organic C over time following the change in vegetation can be used to quantify SOM decomposition rates (e.g., Liao et al., 2006). Furthermore, the soil δ^{15}N values reflect the net effect of N-cycling processes as influenced by the biotic and abiotic factors such as temperature, precipitation, and quantity and quality of organic matter inputs (Robinson, 2001; Dawson et al., 2002; Bai and Houlton, 2009). For instance, increased soil temperature enhanced rates of N cycling and loss of N, resulting in ^{15}N enrichment (Bijoor et al., 2008). The δ^{15}N values of soil fractions can also be related to the degree of decomposition and humification of SOM (Kramer et al., 2003; Liao et al., 2006; Templer et al., 2007; Marin-Spiotta et al., 2009).

In Central Oklahoma of US Great Plains, a long-term, ongoing experimental warming and clipping experiment was initiated on 21 November 1999 in a tallgrass prairie (Luo et al., 2001). Our study ecosystem is primarily dominated by mixture of C_4 grasses

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and a few C_3 forbs. Previous studies in this field experiment have shown that warming increased production of C_4 litter with low quality (i.e. recalcitrant C_4 plant) by 47.2% and decreased production of C_3 litter with high quality by 19.1%, and hence resulted in significant increases in litter input (An et al., 2005; Wan et al., 2005; Luo et al., 2009; Cheng et al., 2010). These changes provide a unique opportunity to utilize the natural abundance of $\delta^{13}C$ and $\delta^{15}N$ to evaluate changes in SOM dynamics after nine years of experimental warming. To guide this paper, we hypothesized that nine years of warming would significantly increase SOM storage due to warming-induced increases in production of recalcitrant C_4 plant, changes in litter input and litter quality (An et al., 2005; Cheng et al., 2010). To test this hypothesis, we measured the $\delta^{13}C$, $\delta^{15}N$, C and N concentrations in all SOM aggregates and density fractions in the tallgrass prairie. The specific objectives of this study were to: (1) evaluate the impact of the long-term experimental warming on the C and N pools in SOM fractions; (2) quantify amounts of C derived from C_4 vs. C_3 sources in SOM fractions after nine years of experimental warming; and (3) estimate the turnover of the SOM fractions in warmed soils.

2 Materials and methods

2.1 Site description

The experiment was located at the Great Plain Apiaries (34°58′54″ N, 97°31′14″ W), 40 km from the Norman campus of the University of Oklahoma, USA. Detailed description of the site characteristics and design of the experiment have been reported elsewhere (See Luo et al., 2001). Briefly, the site is a tallgrass prairie primarily dominated by C_4 grasses including *S. scoparium* (Michx.) Nash-Gould, and *Sorghastrum nutans* (L.) Nash., and a few C_3 forbs, including *A. psilostachya* DC., *Hemiachyris dracunuloides*, *Solidago rigida, Solidago nemoralis,* and *Aster ontarionis* Wieg. *S. scoparium* comprise over 80% of the cover and *A. psilostachya* was the most dominant C_3 forb in this community. Mean annual temperature is 16.0 °C with monthly mean temperature

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of 3.1 °C in January and 28.0 °C in July. Mean annual precipitation is 911.4 mm (Oklahoma Meteorological Survey). The soil is a silt loam with 36% sand, 55% silt, and 10% clay in the top 15 cm. The proportion of clay increases with depth. The soil is part of the Nash-Lucien complex, which is characterized by a low permeability, high available water capacity, and deep, moderately penetrable root zone (USDA Soil Conservation Service and Oklahoma Agricultural Experiment Station, 1963).

2.2 Experimental design

This experiment used a paired factorial design with warming as the main factor nested by clipping factor. Each treatment had six replicates (i.e., six pairs). Each pair had two plots of 2 m×2 m. One plot had been subjected to continuous warming since 12 November 1999 to present while the other was the control with ambient temperature. One 165 cm×15 cm radiant infrared heater (Kalglo Electronics Inc., Bethlehem, PA, USA) with an output of 100 Watt m^{-2} was suspended at 1.5 m above the ground in each warmed plot as the heating device. Reflector surface of the heaters were adjusted so as to generate evenly distributed radiant input to soil surface (Kimball, 2005). As a result, temperature increments generated by the infrared heaters were relatively even over the entire areas of plots and similar at different soil depths. Infrared heaters have been used to elevate soil temperature by approximately 2 °C continuously since November 1999 (Luo et al., 2009). A "dummy heater" with the same shape and size as the infrared heater was suspended at the same height in the control plots to simulate the shading effect of the heater on the plant canopy. For each paired plot, the distance between warmed and control plots was approximately 5 m to avoid heating of the control plots. The distance between the paired plots varied from 20 to 60 m.

Each 2 m×2 m plot was divided into four 1 m×1 m subplots. Plants in the two diagonal subplots were clipped at the height of 10 cm above the ground yearly to remove biomass, usually in August. Clipping in manner effectively mimics agricultural hay mowing, a widely practiced land use in the southern Great Plains. Usually farmers and ranchers in the southern Great Plains mow pasture once or twice per year, depending

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on rainfall. Clipping also simulates biomass harvest for biofuel feedstock production although the study was not originally designed to study bioenergy production. The other two diagonal subplots were unclipped. The four treatments in the experiment were unclipped control (UC), clipped control (CC), unclipped warming (UW), and clipped warming (CW).

2.3 Soil sampling and fractionations

Soil samples were collected at a depth of 0–20 cm with a 4 cm diameter soil corer from the experimental plots in the fall of 2008, nine years after the warming. Soil samples were air-dried, after which large roots and stone were removed by hand. The method for separation of aggregate size and isolation of free fraction (LF), intra aggregate particulate organic matter (iPOM) and mineral-associated organic matter (mSOM) was adapted from Six et al. (1998).

Four aggregate sizes were separated using wet sieving through a series of sieves (2000, 250, and 53 µm). A 100 gm air dried sample was submerged for 5 minutes in room temperature de-ionized water, on top of the 2000 µm sieve. Aggregate separation was achieved by manually moving the sieve up and down 3 cm with 50 repetitions during a period of 2 min. After the 2-min cycle, the stable >2000 µm aggregates were gently back-washed off the sieve into an aluminum pan. Floating organic material (>2000 µm) was discarded as this is by definition not considered as SOM. Water and soil that passed through the sieve was poured onto the next two sieves (one at a time) and the sieving was repeated in a similar fashion, but floating material was retained. Thus four size fractions of materials were obtained (>2000 µm, 250–2000 µm, 53–250 µm and <53 µm). The aggregates were oven dried at (50°C), weighed and stored in glass jars at room temperature.

The density fractionation was carried out by using solution of 1.85 g cm−3 sodium polytungstate (SPT), following the method described in Six et al. (1998). A subsample (5 g) of oven-dried (110°C) aggregate size fractions was suspended in 35 mL of SPT and slowly shaken by hand. The material remaining on the cap and sides of the

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centrifuge tube were washed into suspension with 10 mL of SPT. After 20 min of vacuum (138 kPa), the samples were centrifuged (1250 g) at 20 °C for 60 min. The floating material (light fraction-LF) was aspirated onto a 20 µm nylon filter, subjected to multiple washings with deionized water to remove SPT, and dried at 50°C. The heavy fraction (HF) was rinsed twice with 50 mL of deionized water and dispersed in 0.5% sodium hexametaphosphate by shaking for 18 h on a reciprocal shaker. The dispersed heavy fraction was then passed through a 53 µm sieve and the material remaining on the sieve, i.e. the intra-aggregate particulate organic matter (iPOM) was dried (50°C) and weighed.

2.4 Carbon, nitrogen and isotope analyses

The C and N concentrations and $\delta^{13}C$ and $\delta^{15}N$ were measured for all fractions. Subsamples from all fractions were treated with 1N HCL for 24 h at room temperature to remove any soil carbonates (Cheng et al., 2006). The C and N concentrations, $\delta^{13}C$ and $\delta^{15}N$ were determined at University of Arkansas Stable Isotope Laboratory on a Finnigan Delta^{+} mass spectrometer (Finnigan MAT, Germany) coupled to a Carlo Erba elemental analyzer (NA1500 CHN Combustion Analyzer, Carlo Erba Strumentazione, Milan, Italy) via a Finnigan Conflo II Interface. Carbon and nitrogen contents of SOM fractions were calculated on an areal basis, correcting for soil depth and density.

The carbon and nitrogen isotope ratio of the soil fractions was expressed as:

$$\delta^h X = \left[\left(\frac{X^h}{X^l}\right)_{\text{sample}} \Big/ \left(\frac{X^h}{X^l}\right)_{\text{standard}} - 1 \right] \times 1000 \quad (1)$$

where X is either carbon or nitrogen, h is the heavier isotope, l is the lighter isotope. Both CO_2 and N_2 samples were analyzed relative to internal, working gas standards. Carbon isotope ratios (^{13}C) are expressed relative to Pee Dee Belemnite ($\delta^{13}C$ = 0.0‰); nitrogen stable isotope ratios (^{15}N) are expressed relative to air ($\delta^{15}N$ =

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0.0‰). Standards (acetanilide and spinach) were analyzed after every ten samples; analytical precision of the instrument was ± 0.13 for δ^{13}C and ± 0.21 for δ^{15}N.

Differences in δ^{13}C isotope composition due to photosynthetic pathways allow for the proportion of soil C derived form C_3 or C_4sources to be calculated using a two-compartment mixing-model (Del Galdo et al., 2003; Cheng et al., 2006);

$$f_A = \frac{\delta_X - \delta_B}{\delta_A - \delta_B} \times 100\% \tag{2}$$

Where δ_X is the δ^{13}C of a given fraction isolated from the warmed or control plots, δ_A and δ_B are the isotope values of C_3 and C_4 plants from these plots, f_A is the fraction of C_3 vegetation and $f_B(1-f_A)$ is the proportion derived from C_4 grasses.

The fraction of new C, $f_{\text{new},}$ derived from the current vegetation in the warmed soils after nine years of warming is calculated by using the isotope mass balance method (Marin-Spiotta et al., 2009):

$$f_{\text{new}} = \frac{\delta_2 - \delta_0}{\delta_1 - \delta_0} \times 100\% \tag{3}$$

where δ_2 and δ_0 are δ^{13}C values for SOM pools in the warmed and control plots and $\delta_1$is the average δ^{13}C value of plant inputs to the SOM pool in the warmed plots, on the assumption that in the past 9 years, no shift in ratio between C_3/C_4 input in the control soil occurred.

Furthermore, decomposition rate constants (k) for old C of different fraction of SOM in the warmed plots were calculated using the following equation (Del Galdo et al., 2003):

$$\ln(f_{\text{old}}) = -kt \tag{4}$$

where f_{old}=$(1-f_{\text{new}})$ is the proportion of old C, k is the net relative decomposition rate constant of old C, and t is the age of warming.

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2.5 Statistics

Analysis of variance (ANOVA) of paired plot design (one pair of plots being considered a block) was conducted to examine the effects of warming on the soil organic C and N contents, the $\delta^{13}C$ and $\delta^{15}N$ values, C: N ratios in all soil fractions and the weight distribution. The differences in the soil organic C and N contents, the $\delta^{13}C$ and $\delta^{15}N$ values, C: N ratios between aggregate sizes and density fractions were analyzed using one-way ANOVA. All statistical analyses were performed using Stat Soft's Statistica, statistical software for Windows (Version 6.0, StatSoft, Inc., 2001).

3 Results

3.1 Whole soil C and N dynamics

Total soil organic C and N contents ranged from 2371 to 2707 $g\,C\,m^{-2}$ and 284 to 312 $g\,N\,m^{-2}$, respectively, across all treatments. No significant differences in C and N contents, or C:N ratios among treatments were found (Table 1). Nine-year warming significantly increased the $\delta^{13}C$ signature of SOM for both clipped and unclipped plots. On average, the warmed plot soils were 1.3‰ more enriched in ^{13}C and 0.58‰ more enriched in ^{15}N than the control plots. Thus, warming significantly increased the fraction of C_4-derived C by average 11.6% and the $\delta^{15}N$ values of organic soils by 0.93‰ in clipped plots (Table 1).

3.2 Size distribution, C and N contents, and $\delta^{13}C$ and $\delta^{15}N$ of soil aggregates

The aggregate distribution was not significantly affected by warming or clipping (Table 2). Warming significantly decreased soil organic C and N contents in microaggregate (<250 µm) in clipped plots but not in any other aggregate size classes (Table 2). Macroaggregates (>250 µm) contained significantly more C and N (78–84%) than microaggregates (Table 2). No significant differences in C:N ratios were found across aggregate size and treatments (Table 2).

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The $\delta^{13}C$ values of all aggregate sizes were more enriched in the warmed plots compared to the control plots (Table 3), indicating that warming stimulated input of C_4-derived C (Fig. 1a). Warming-induced increases in the fraction of C_4-derived C ranged from 5.3% to 10.8% among aggregate size classes, with the highest one in the >2000 µm macroaggregates (Fig. 1b).

The $\delta^{15}N$ values of all aggregate sizes were significantly more enriched in the warmed plots than the control (Table 3). There were no significant differences in $\delta^{15}N$ values between aggregates sizes, but microaggregates (<53 µm) had a significant higher $\delta^{15}N$ value than all other aggregate size classes (Table 3).

3.3 Density fraction: C and N contents, and ^{13}C and ^{15}N in LF, iPOM and mSOM

The LF accounted for the smallest fraction of total SOM, whereas the mSOM accounted for the highest (74–79%) fraction of total SOM in all aggregate size classes across all treatments (Table 2). The C and N contents in the mSOM and iPOM significantly decreased with size classes, whereas the highest C and N contents in LF were found in the 2000–250 µm macroaggregates (Table 2). Warming significantly decreased soil organic C and N contents in iPOM in macroaggregates (>2000 µm) in clipped plots but not in any other SOM classes. C:N ratio significantly increased in LF of the 250–53 µm microaggregate but not in any other SOM classes under warming in comparison with that under control (Fig. 2). C:N ratios decreased from LF to iPOM to mSOM in all aggregates across treatments (Fig. 2).

Warming resulted in an increase trend in $\delta^{13}C$ values across all the density fractions in all aggregate sizes (Table 3). The warming-induced increase was significant for $\delta^{13}C$ values of LF in the >2000 µm macroaggregate in clipped plots. The $\delta^{13}C$ values were generally more enriched in mSOM than LF and iPOM across aggregate sizes and the treatments (Table 3). The warming-induced increase in C_4-derived C was highest for LF in the >2000 µm macroaggregates among all aggregates and density fractions (Fig. 3b). In general, warming stimulated more C_4-derived C input into LF than iPOM

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and mSOM across all aggregate sizes, and more into larger than smaller aggregate sizes (Fig. 3b).

In general, warming significantly increased $\delta^{15}N$ values of LF, iPOM and mSOM across aggregate sizes (Table 3). mSOM had the highest $\delta^{15}N$ value and LF had the lowest $\delta^{15}N$ value among density fractions in all aggregate sizes across treatments (Table 3).

3.4 Soil C turnover

Experimental warming stimulated both new C input from C_4 photosynthesis and decay rate for old C (Table 4). The new C inputs in the whole soil were greater than other aggregate sizes. New C inputs were greater in LF than iPOM with the greatest one in the >2000 µm macroaggregate. Overall, new C inputs in soil fractions decreased for smaller aggregates except for mSOM (Table 4). Accordingly, the decay rates for old C in the whole soil were faster than other aggregates. The fastest decay rates were found in LF in the >2000 µm macroaggregate and LF had greater decay rate than iPOM for all SOM classes (Table 4).

4 Discussion

Warming effects at our study site are characterized by increased biomass growth, shift toward more C_4 species dominance, increased litter input, and increased soil respiration (Wan et al., 2005, Zhou et al., 2007; Luo et al., 2009; Cheng et al., 2010). It was originally hypothesized that soil C and N storage would increase with the increases in litter production of recalcitrant plant (C_4) under warming (Cheng et al., 2010). Our stable isotopic analysis confirmed that the $\delta^{13}C$ abundance in SOM in the warmed soils was more enriched than that in the control soils (Table 1), resulting from more contribution from C_4 residuals. Indeed, warming-induced increases in C_4 plant and decreases in C_3 plant led to increases in the fraction of C_4-derived C by average 11.6% (Table 1).

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However, differences in C inputs and changes in species dominance after 9-year warming did not significantly increase total soil organic C and N contents (Table 1; Niu et al., 2010). The response of SOM to warming is determined by a balance between litter input and soil C respiration (e.g., Shaw and Harte, 2001; Fissore et al., 2008). The unchanged SOM in our warming experiment resulted from concurrent increases in litter input to soil and decomposition. Our previous study found warming increased soil respiration (Zhou et al., 2007), similar to other studies under warming (e.g., Rustad et al., 2001; Fontaine et al., 2004). Furthermore, Wynn and Bird (2007) have found that the active pool of SOM derived from C_4 plants decomposes faster than the total pool of SOM. Warming-induced increased C_4-derived C in SOM pool likely accelerates decay rates of SOM in the warmed soils. Thus, the increased litter input (Cheng et al., 2010) was possibly offset by increased C loss through soil respiration under warming.

Additionally, the total soil C is also related to soil type (e.g., Hassink, 1997). For example, high clay soil can relatively resistant to change, leading to the increase in total soil C content (Hassink, 1997; Van Groenigen et al., 2002). No significant change in soil bulk density (unpublished data) and soil aggregates (Table 2) likely contributed to minimal soil disturbance and little net C change. The change in plant functional types (e.g., woody plant invasion on grassland) was shown to alter soil aggregate formation by affecting root growth and associated rhizosphere (e.g., Liao et al., 2006). Although warming induced plant shift from C_3 to C_4 species (Luo et al., 2009; Cheng et al., 2010), warming did not affect the level of soil aggregation (Table 2). These results are in agreement with Scott (1998), who reported grass species had no effect on size-distribution of soil aggregates or organic matter concentrations.

Similarly, the aggregate fractionation did not reveal significant effects of warming on soil organic C and N contents (Table 2). However, the C and N content on the different size fractions is primarily controlled by the amount of each aggregate size (Elliott, 1986; Van Groenigen et al., 2002). Generally, we found that macroaggregates (>250 µm) contained significantly more C and N than microaggregates (Table 2). This finding supports a conceptual model that organic C and N generally decrease with

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decrease in aggregate size (Elliott, 1986, Puget et al., 1995). Isotopic methods indicated that warming-induced increases in C_4-derived C in all aggregate size with the highest C_4-derived C in the >2000 µm macroaggreates (Fig. 1b). This is in accordance with other studies where new C is incorporated more rapidly in coarse SOM than fine SOM fraction (Desjardins et al., 2004; Schwendenmann and Pendall, 2006).

It is well known that the LF, iPOM and mSOM have different chemical make-ups and turnover times (Trumbore, 2000; Wynn and Bird, 2007). The higher C:N ratios of the LF reflected more recent litter inputs, while the mSOM had much lower C:N ratios (Fig. 2). Decreasing C:N ratios in soil C fractions have been associated with increasing SOM decomposition and mineral association (John et al., 2005; Marin-spiotta et al., 2009). Moreover, patterns in δ^{15}N of soil fractions provided further evidence to support the degree of decomposition and humification of SOM. We found the δ^{15}N values in the <53 µm microaggreates were higher than other aggregates (Table 3), which is similar to results of other studies (Liao et al., 2006; Marin-Spiotta et al., 2009). In general,.the low δ^{15}N values are related to recent matter inputs (litter, root) whereas high^{15}N values in silts +clays (<53 µm) are associated with older and more organic matter.

The δ^{15}N values of soil fractions were more enriched in the warmed soil than those in the control soil (Table 3). It suggests that the natural abundance of δ^{15}N in soil becomes enriched in δ^{15}N in the warmed soil by the processes of N losses from soil through increased soil mineralization and possibly nitrate leading compared to control sites (Rustad et al., 2001; Bijoor et al., 2008). Indeed, warming resulted in decreases in the total soil N pools by 14% in the unclipped plots in our study (Wan et al., 2005). The decrease in soil N pools may result partly from the more redistribution of N to C_4 plants (Niu et al., 2010) and partly from increased N mineralization and N availability (Wan et al., 2005; Zhou et al., unpublished data) leading to soil N losses under warming. The evidence that the soil in the warmed plots were enrich in δ^{15}N relative to control plots as showed in this study, further indicating the great N losses from soil. Thus, the N loss in the warmed soil would likely balance increased SOM input, resulting in no significant warming impact on soil organic C and N pools.

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Even though there were no significant increases in SOM pools after 9-year warming, isotopic measurements and turnover time estimates suggest different C decay rates of SOM fraction in the warmed soils. The increased new C inputs from plant residue could result in faster decomposition of SOM (Dijkstra and Cheng, 2007). The decay rates for old C in the whole soil were faster than other aggregate sizes due to greater new C inputs (Table 4). This finding also supports the evidence that soil aggregates physically protect certain SOM fractions, resulting in pools with longer turnover times (Six et al., 1998). Although LF generally represent only a small proportion of total SOC in biologically active soils (Gregorich et al., 2006), changes in carbon stocks following changes in species can be more pronounced in LF compared with bulk soil (Schwendenmann and Pendall, 2006). Our results showed that warming increased higher C_4-derived C in LF than iPOM and mSOM in all aggregate sizes (Fig. 3). The organic matter in LF fractions is not protected as within aggregates or associated with clay minerals, it is readily accessible to microbes as reflected by their initial rapid loss (Fontaine et al., 2004; Pendall et al., 2004). Because warming caused a rapid loss of labile substrates in the LF (Table 4), warming resulted in no significant decreases in organic C and N content in LF in all SOM density fractions except in aggregates 2000–250 µm in clipped plots (Table 2). As stated earlier, new C was incorporated more rapidly in coarse than fine SOM fraction (Desjardins et al., 2004; Schwendenmann and Pendall, 2006), significantly higher fraction of C_4-derived C for LF was observed in macroaggregates >2000 µm (Fig. 3b). With increasing degree of decomposition, organic matter may be transferred to more stabilized soil fractions. In contrast to the rapid decomposition of C_4-derived C from unprotected soil fractions, part of C_4-derived C remained in iPOM fractions with slower turnover rates and better physical protection mechanisms (Table 4). The iPOM and mSOM accounted for the large fraction of SOM of all aggregates (Table 2), no significant warming effects were detected for these fractions, supporting the view that the heavy and mineral associated fractions remain recalcitrant and stable in nature (e.g., Six et al., 1998).

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To conclude, we found that nine years of experimental warming caused no significant increases in soil organic C and N content in any soil fraction at our site. Warming did not significantly affect soil aggregate distribution and stability. However, warming did increase C_4-derived C input into all fractions with the highest C in LF across all aggregate classes. The significant C loss of the whole soil and the labile components of LF under warming likely offset increased SOM inputs. The δ^{15}N values of soil fractions were more enriched in the warmed soil than those in the control, indicating the increased N loss from the warmed soils. The C:N ratios and differences in natural abundance δ^{13}C and δ^{15}N in SOM fractions are associated with an increasing degree of decomposition across density fractions with increasing mineral association. Turnover times based on natural abundance stable isotope methods tend to be more related to recent C inputs and C pools associated with the C_3/C_4 vegetation type conversion (Six and Jastrow, 2002). Physical fractionation methods combined with isotope analyses in our study attempted to better understand SOM dynamics in responses to global warming by acknowledging that SOM consists of a continuum of substrate with different turnover times. The shifts in species composition under warming could potentially modify SOM quality and decomposition and consequently affect ecosystem functions.

Acknowledgements. This research was financially supported by National Science Foundation (NSF) under grants DEB 0078325 and DEB 0743778; by the Office of Science (BER), Department of Energy, grants no. DEFG02-006ER64319 and through the Midwestern Regional Center of the National Institute for Climatic Change Research at Michigan Technological University, under award number DE-FC02-06ER64158. We thank Meng Lu, Shenfei Fei, Xiaolei Yan for assistance in the field, Thomas L. Millican for assistance with laboratory analyses.

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Table 1. Soil organic C and N contents, ^{13}C- and ^{15}N signature, fraction of C_4-derived C (f_B) and the C: N ratio of the whole soils in a tallgrass prairie (0–20 cm depth) after nine years of warming and clipping. Data are expressed as mean ± SE, $n = 6$. Letters indicate statistical significance at $P < 0.05$ among the four treatments.

Treatment	C ($g\,C\,m^{-2}$)	$\delta^{13}C$ (‰)	f_B (%)	N ($g\,N\,m^{-2}$)	C:N	$\delta^{15}N$ (‰)
UC	2529 ± 478^a	-18.48 ± 3.1^b	60.2 ± 7.3^b	299 ± 55^a	8.4 ± 0.7^a	2.70 ± 1.0^a
UW	2693 ± 655^a	-17.26 ± 3.0^a	71.5 ± 6.9^a	303 ± 56^a	8.9 ± 2^a	2.93 ± 0.7^a
CC	2371 ± 352^a	-18.08 ± 2.8^b	62.8 ± 5.7^b	312 ± 41^a	7.6 ± 0.6^a	2.6 ± 0.6^b
CW	2707 ± 536^a	-16.79 ± 2.6^a	74.7 ± 8.3^a	284 ± 48^a	9.5 ± 1^a	3.53 ± 0.7^a

UC, unclipped control; CC, clipped control; UW, unclipped warming; CW, clipped warming

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Table 2. Soil organic C and N contents of soil fractions under four treatments after nine years of warming and clipping. Data are expressed as mean ± SE, $n = 6$. Letters indicate statistical significance at $P < 0.05$ among the four treatments. See Table 1 for abbreviations.

Fractions	C ($g\,C\,m^{-2}$)				N ($g\,N\,m^{-2}$)			
	UC	UW	CC	CW	UC	UW	CC	CW
>2000 µm	1214 ± 306[a]	1399 ± 268[a]	1171 ± 318[a]	1210 ± 277[a]	145.9 ± 36.1[a]	156.4 ± 33.2[a]	149.7 ± 32.7[a]	117.5 ± 19.3[a]
LF	56 ± 7[a]	43 ± 5[a]	31 ± 4[b]	20 ± 3[b]	2.4 ± 0.4[a]	1.6 ± 0.3[a]	2.2 ± 0.4[a]	1.31 ± 0.3[a]
iPOM	162 ± 24[a]	142 ± 23[a]	105 ± 13[a]	65 ± 11[b]	11.1 ± 1.4[a]	11.7 ± 1.4[a]	11.6 ± 2.3[a]	6.34 ± 1.1[b]
mSOM	990 ± 142[a]	1213 ± 290[a]	1032 ± 122[a]	1122 ± 116[a]	136.5 ± 20.2[a]	139.6 ± 23.3[a]	137.3 ± 30.3[a]	112.3 ± 19.2[a]
2000–250 µm	1022 ± 273[a]	979 ± 265[a]	806 ± 207[a]	1160 ± 303[a]	104.5 ± 25.4[a]	113.5 ± 32.3[a]	106.7 ± 14.9[a]	120.1 ± 22.7[a]
LF	88 ± 9.4[a]	79 ± 10[a]	85 ± 9[a]	88 ± 10[a]	5.6 ± 0.7[a]	4.6 ± 0.5[a]	4.4 ± 0.6[a]	5.5 ± 0.8[a]
iPOM	51 ± 9[a]	73 ± 12[a]	55 ± 8[a]	64 ± 12[a]	5.8 ± 1.1[a]	10.4 ± 1.5[a]	5.0 ± 0.9[a]	5.3 ± 1.1[a]
mSOM	879 ± 215[a]	812 ± 212[a]	663 ± 103[a]	1005 ± 136[a]	94.7 ± 10.2[a]	95.3 ± 11.3[a]	98.77 ± 15.3[a]	111.3 ± 21.2[a]
250–53 µm	266 ± 57[b]	286 ± 73[b]	344 ± 77[a]	307 ± 63[b]	37.4 ± 8.3[b]	33.8 ± 10.1[b]	44.4 ± 7.3[a]	37.7 ± 7.2[b]
LF	19 ± 3 [a]	11 ± 4[a]	20 ± 3[a]	19 ± 3[a]	2.1 ± 0.3[a]	0.7 ± 0.3[a]	1.34 ± 0.5[a]	1.20 ± 0.4[a]
iPOM	25 ± 5[a]	31 ± 6[a]	25 ± 7[a]	19 ± 4[a]	2.18 ± 0.4[a]	2.0 ± 0.6[a]	2.0 ± 0.5[a]	1.4 ± 0.4[a]
mSOM	218 ± 32[a]	240 ± 29[a]	295 ± 32[a]	262 ± 33[a]	33.7 ± 5.2[a]	31.3 ± 3.3[a]	42.0 ± 4.2[b]	33.8 ± 3.2[a]
<53 µm	36.4 ± 13[b]	45.5 ± 16[b]	58.5 ± 13[a]	40.1 ± 12[b]	5.5 ± 1.2[b]	5.8 ± 0.9[b]	7.4 ± 1.4[a]	5.9 ± 0.8[b]

LF=Light fraction; POM=Particle organic matter; iPOM=intra-aggregate POM; mSOM=mineral associated SOM

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Table 3. The $\delta^{13}C$ and $\delta^{15}N$ values of soil fractions under four treatments after nine years of warming and clipping. Data are expressed as mean ± SE, $n = 6$. Letters indicate statistical significance at $P < 0.05$ among the four treatments. See Table 1 for abbreviations.

Fractions	$\delta^{13}C$ (‰)				$\delta^{15}N$ (‰)			
	UC	UW	CC	CW	UC	UW	CC	CW
>2000 µm	-18.3 ± 3.3^{a}	-17.1 ± 3.4^{a}	-18.4 ± 3.1^{a}	17.3 ± 1.8^{a}	2.51 ± 0.7^{b}	3.06 ± 1.1^{a}	2.82 ± 0.9^{b}	3.37 ± 1.1^{a}
LF	-19.1 ± 2.6^{b}	-17.1 ± 2.4^{a}	-18.1 ± 2.9^{b}	-16.2 ± 2.1^{a}	-1.35 ± 1.1^{b}	-1.19 ± 1.2^{b}	-0.96 ± 0.9^{b}	-0.72 ± 0.7^{a}
iPOM	-19.5 ± 2.3^{a}	-19.1 ± 3.2^{a}	-20.1 ± 2.6^{a}	-18.2 ± 2.9^{a}	1.37 ± 0.6^{b}	2.07 ± 0.8^{a}	1.46 ± 0.6^{b}	2.21 ± 0.7^{a}
mSOM	-17.8 ± 3.4^{a}	-17.1 ± 3.6^{a}	-17.4 ± 3.2^{a}	-17.1 ± 3.3^{a}	4.74 ± 1.1^{a}	4.94 ± 1.5^{a}	4.63 ± 3.2^{a}	4.82 ± 0.8^{a}
2000–250 µm	-17.9 ± 4.3^{a}	-17.2 ± 2.7^{a}	-17.8 ± 2.8^{a}	-17.4 ± 2.9^{a}	2.73 ± 0.7^{b}	3.40 ± 1.1^{a}	2.47 ± 0.9^{b}	3.50 ± 0.7^{a}
LF	-19.6 ± 3.1^{a}	-18.4 ± 2.4^{a}	-18.7 ± 3.3^{a}	-18.0 ± 1.8^{a}	-1.82 ± 0.9^{b}	-1.85 ± 0.7^{b}	-1.96 ± 1.0^{b}	-0.62 ± 1.2^{a}
iPOM	-18.9 ± 2.7^{a}	-18.0 ± 2.1^{a}	-19.2 ± 3.3^{a}	-18.9 ± 2.7^{a}	1.14 ± 0.9^{b}	1.11 ± 1.1^{b}	1.11 ± 1.0^{b}	2.61 ± 0.8^{a}
mSOM	-17.9 ± 3.0^{a}	-17.0 ± 3.3^{a}	-17.8 ± 3.2^{a}	-17.2 ± 3.6^{a}	4.02 ± 0.6^{b}	3.93 ± 0.7^{b}	3.92 ± 0.9^{b}	4.92 ± 0.8^{a}
250–53 µm	-17.7 ± 2.2^{a}	-17.3 ± 3.2^{a}	-17.8 ± 1.8^{a}	-17.1 ± 2.8^{a}	2.98 ± 0.8^{b}	3.53 ± 0.8^{a}	3.39 ± 1.1^{a}	3.81 ± 0.8^{a}
LF	-19.4 ± 1.3^{a}	-19.0 ± 1.4^{a}	-19.8 ± 1.6^{a}	-19.1 ± 1.0^{a}	-0.12 ± 0.4^{a}	-0.11 ± 0.2^{a}	-0.32 ± 0.8^{a}	-0.11 ± 0.7^{a}
iPOM	-19.4 ± 2.0^{a}	-19.2 ± 2.5^{a}	-19.5 ± 2.1^{a}	-19.3 ± 2.4^{a}	0.76 ± 0.9^{b}	1.03 ± 1.3^{b}	1.13 ± 0.9^{b}	2.86 ± 1.0^{a}
mSOM	-17.2 ± 1.9^{a}	-16.8 ± 2.8^{a}	-17.2 ± 2.0^{a}	-17.0 ± 2.9^{a}	3.72 ± 0.7^{b}	4.08 ± 0.6^{b}	3.79 ± 0.7^{b}	5.13 ± 0.9^{a}
<53 µm	-17.3 ± 1.9^{a}	-17.0 ± 2.7^{a}	-17.5 ± 1.9^{a}	-17.3 ± 2.1^{a}	3.85 ± 1.0^{a}	4.21 ± 0.8^{a}	3.81 ± 0.9^{b}	4.54 ± 0.8^{a}

LF=Light fraction; POM=Particle organic matter; iPOM=intra-aggregate POM; mSOM=mineral associated SOM

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Table 4. The new C input ($f_{new,}$), and decay rate (k, yr^{-1}) of old C of soil fractions (0–20 cm) in the warmed soils after nine years of experimental warming.

Fraction	$f_{new,}$ (%)	Decay rate (k) of old C
Whole soil	33.7 ± 2.6	0.046 ± 0.003
>2000 µm	30.1 ± 3.4	0.040 ± 0.003
LF	36.3 ± 4.1	0.144 ± 0.02
iPOM	20.4 ± 1.7	0.025 ± 0.003
mSOM	16.0 ± 2.3	0.019 ± 0.002
2000–250 µm	17.3 ± 19	0.021 ± 0.002
LF	20.0 ± 2.7	0.025 ± 0.003
iPOM	12.4 ± 1.5	0.015 ± 0.001
mSOM	22.4 ± 2.8	0.028 ± 0.002
250–53 µm	16.2 ± 1.3	0.02 ± 0.001
LF	11.0 ± 0.9	0.013 ± 0.001
iPOM	4.9 ± 0.6	0.006 ± 0.001
mSOM	11.7 ± 1.3	0.014 ± 0.001
<53 µm	10.7 ± 0.8	0.012 ± 0.001

LF=Light fraction; POM=Particle organic matter; iPOM=intra-aggregate POM; mSOM=mineral associated SOM

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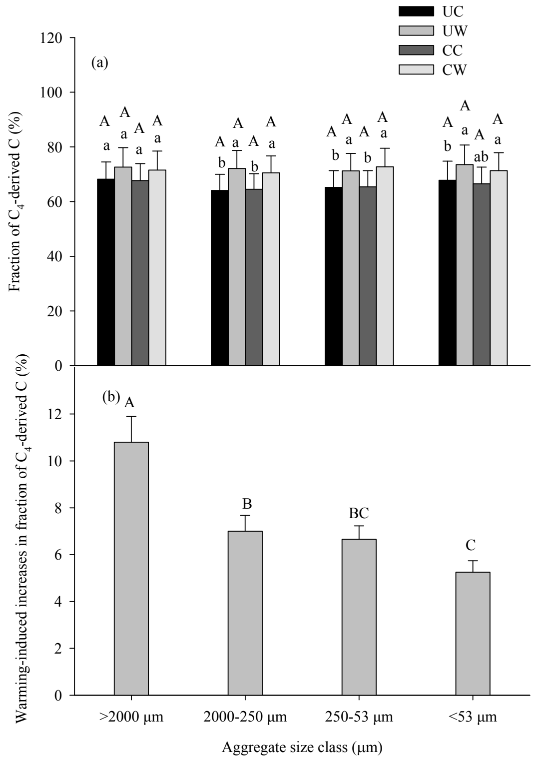

Fig. 1. Fraction of C_4-derived C of aggregate size classes under four treatments after nine years of warming and clipping **(a)**, and warming-induced increases in the fraction of C_4-derived C of aggregate size classes in the warmed soils **(b)**. Vales followed by a different lowercase letter are significantly different within aggregate size among treatments. Vales followed by a different capital are significantly different among aggregate size under treatments. Abbreviations: UC, unclipped control; CC, clipped control; UW, unclipped warming; CW, clipped warming.

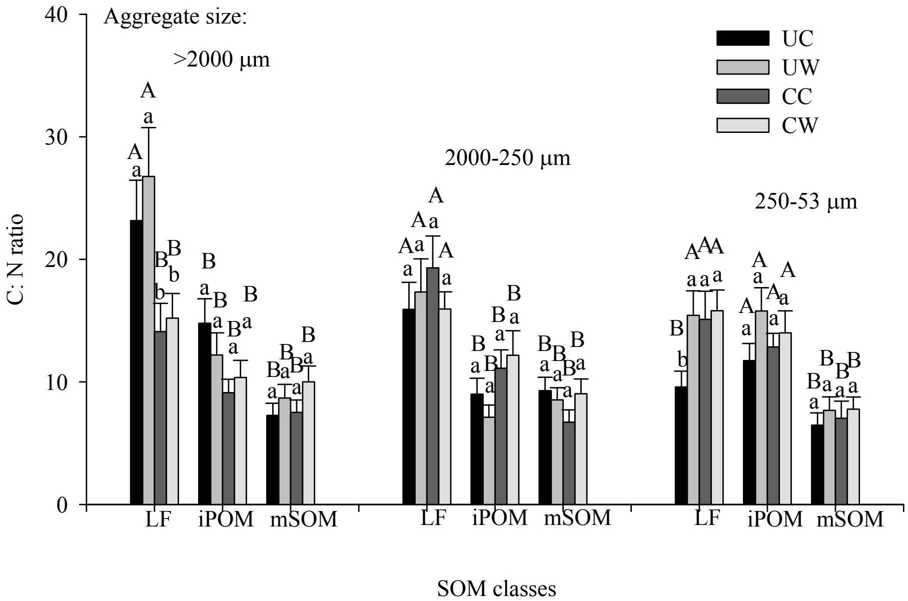

Fig. 2. C: N ratios of LF, iPOM and mSOM of aggregate size classes under four treatments after nine years of warming and clipping. Vales followed by a different lowercase letter are significantly different within SOM class among treatments of each aggregate size. Vales followed by a different capital are significantly different among SOM class under treatments of each aggregate size. See Fig. 1 for abbreviations.

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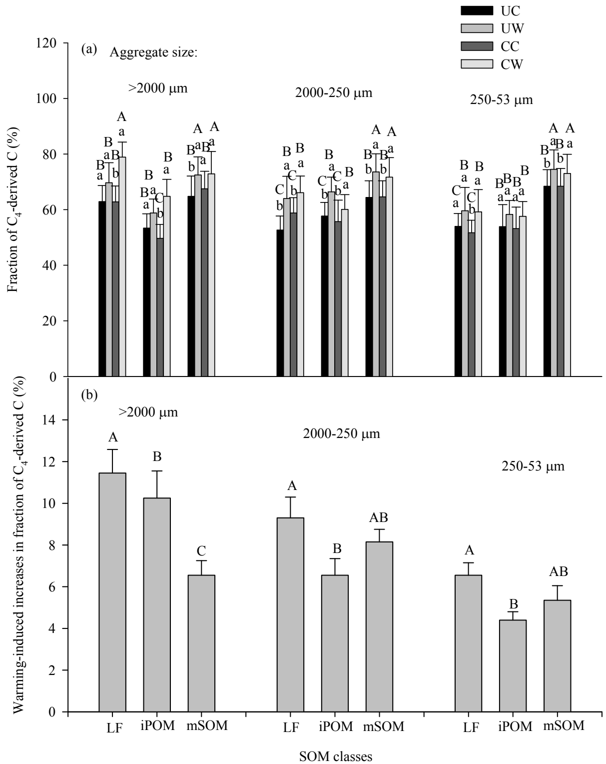

Fig. 3. Fraction of C_4-derived C in LF, iPOM and mSOM of aggregate size classes under four treatments after nine years of warming and clipping **(a)**, and warming-induced increases in the fraction of C_4-derived C in LF, iPOM and mSOM of SOM classes in the warmed soils **(b)**. See Fig. 2 for the explanation of the symbols.

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