Global Change Biology (2007) **13**, 761–775, doi: 10.1111/j.1365-2486.2007.01333.x

Source components and interannual variability of soil CO_2 efflux under experimental warming and clipping in a grassland ecosystem

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Abstract

Partitioning soil CO_2 efflux into autotrophic (R_A) and heterotrophic (R_H) components is crucial for understanding their differential responses to climate change. We conducted a long-term experiment (2000–2005) to investigate effects of warming 2 °C and yearly clipping on soil CO_2 efflux and its components (i.e. R_A and R_H) in a tallgrass prairie ecosystem. Interannual variability of these fluxes was also examined. Deep collars (70 cm) were inserted into soil to measure R_H. R_A was quantified as the difference between soil CO_2 efflux and R_H. Warming treatment significantly stimulated soil CO_2 efflux and its components (i.e. R_A and R_H) in most years. In contrast, yearly clipping significantly reduced soil CO_2 efflux only in the last 2 years, although it decreased R_H in every year of the study. Temperature sensitivity (i.e. apparent Q_{10} values) of soil CO_2 efflux was slightly lower under warming ($P > 0.05$) and reduced considerably by clipping ($P < 0.05$) compared with that in the control. On average over the 4 years, R_H accounted for approximately 65% of soil CO_2 efflux with a range from 58% to 73% in the four treatments. Over seasons, the contribution of R_H to soil CO_2 efflux reached a maximum in winter ($\sim$90%) and a minimum in summer ($\sim$35%). Annual soil CO_2 efflux did not vary substantially among years as precipitation did. The interannual variability of soil CO_2 efflux may be mainly caused by precipitation distribution and summer severe drought. Our results suggest that the effects of warming and yearly clipping on soil CO_2 efflux and its components did not result in significant changes in R_H or R_A contribution, and rainfall timing may be more important in determining interannual variability of soil CO_2 efflux than the amount of annual precipitation.

Keywords: clipping, global warming, heterotrophic respiration, interannual variability, partitioning, root respiration, soil respiration, tallgrass prairie

Received 12 October 2006; revised version received 18 December 2006 and accepted 19 January 2007

Introduction

Global warming induced by elevated atmospheric greenhouse gases has increased Earth's surface temperature by 0.6 °C in the past century and the temperature is predicted to continue to increase by 1.4–5.8 °C by the end of this century (IPCC, 2001). In the Great Plains, air temperature is predicted to increase by 2–4 °C with the doubling of the current CO_2 concentration (Long & Hutchin, 1991). This projected warming is probably altering ecosystem carbon (C) cycling, causing positive feedback if warming increases soil CO_2 efflux more than plant production (Cox *et al*., 2000). At a global scale, climate warming of 1 °C would result in an extra 11–34 $\mathrm{Pg\,C\,yr^{-1}}$ release to the atmosphere due to enhanced decomposition, equivalent to as much as five times the annual CO_2 release from all fossil fuel burning (Jenkinson *et al*., 1991; Schimel *et al*., 1994; IPCC, 2001).

Soil CO_2 efflux, commonly referred to as soil respiration, is the second largest C flux (68–80 $\mathrm{Pg\,C\,yr^{-1}}$) between terrestrial ecosystems and the atmosphere in the global C cycle (Raich & Schlesinger, 1992; Raich *et al*., 2002), and is, therefore, an important regulator of climate change, as well as determinant of net ecosystem C balance. It is largely influenced by soil temperature

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(Lloyd & Taylor, 1994; Boone *et al.*, 1998; Rustad *et al.*, 2001), water content (Davidson *et al.*, 2000; Liu *et al.*, 2002), nutrient availability (Raich & Tufekcioglu, 2000), and current photosynthetic rates (Högberg *et al.*, 2001). Both autotrophic respiration (R_A) from plant roots and rhizosphere microbes and heterotrophic component (R_H) during litter and soil organic matter (SOM) decomposition contribute to CO_2 efflux from soils (Hanson *et al.*, 2000; Wan & Luo, 2003; Kuzyakov, 2006; Subke *et al.*, 2006).

The relative contribution of R_A or R_H generally accounts for approximately one half of the total soil CO_2 efflux according to three recent reviews (Hanson *et al.*, 2000; Bond-Lamberty *et al.*, 2004; Subke *et al.*, 2006). However, the average estimates mask considerable variation because of the diversity of ecosystems and potential biases of different techniques and time scales. Hanson *et al.* (2000) synthesized 50 studies published in the literature, suggesting a mean contribution of 48% and 37% from autotrophic sources for forest and nonforest ecosystems with a wide range of 10–90%. In addition, the contribution of R_A exhibits large seasonality, usually being low during the dormant season and high during the active growing season as autotrophic respiration mainly depends on supply of carbohydrates from canopy photosynthesis (Rochette *et al.*, 1999; Lin *et al.*, 2001). Owing to year-to-year changes in climate variables and consequently indirect changes in physiological and ecological processes and nutrient availability, soil CO_2 efflux and its components usually exhibit the interannual variability (Savage & Davidson, 2001; Scott-Denton *et al.*, 2003; King *et al.*, 2004; Luo & Zhou, 2006). Understanding the seasonal and interannual variability and their responses to climate change is urgently needed to improve the prediction of ecosystem C cycling.

The dynamics of the two components, R_A and R_H, may be controlled by different abiotic and biotic factors, such as temperature, water availability, photosynthetic activity, or plant phenological development. Heterotrophic processes control soil C storage and nutrient dynamics, while autotrophic respiration reflects plant activity and the supply of organic compounds to roots from the canopy (Högberg *et al.*, 2001; Bhupinderpal-Singh *et al.*, 2003; Binkley *et al.*, 2006). In addition, the responses of R_A and R_H to temperature largely differ, exhibiting different Q_{10} values (Boone *et al.*, 1998; Rey *et al.*, 2002). The potential change in soil CO_2 efflux associated with global warming will largely depend on the relative contribution of autotrophic and heterotrophic components (Buchmann, 2000). Therefore, quantifying the components of soil CO_2 efflux is imperative to understand the nature and extent of feedbacks between climate change and soil processes and to predict ecosystem responses to climate change (Melillo *et al.*, 2002; Ryan & Law, 2005).

Although warmer temperature has been found to cause significant increases in the efflux of CO_2 from soils in various biomes (Rustad *et al.*, 2001), little information is available on how various components of soil CO_2 efflux respond differently to increasing temperature, especially in natural ecosystems. The results from modeling, mesocosm experiments, and transect studies are highly controversial (Lin *et al.*, 1999, 2001; Lavigne *et al.*, 2003; Eliasson *et al.*, 2005). For example, Lin *et al.* (1999, 2001) observed that litter decomposition and SOM oxidation were more sensitive to elevated temperature than rhizosphere respiration (R_A) in experimental forest mesocosms. However, a transect study by Lavigne *et al.* (2003) indicated that the response of soil CO_2 efflux to temperature are controlled more by autotrophic than heterotrophic respiration in balsam fir ecosystems. To date, we did not find any published results for warming effects on the source components of soil CO_2 efflux. It is essential that, at a long-term scale, warming responses of source components of soil CO_2 efflux are investigated in natural ecosystems.

Land use practices such as mowing or clipping for hay in grasslands, which account for about 20% of the global terrestrial ice-free surface, may also have considerable effects on soil CO_2 efflux and its components, especially in the short term (Bahn *et al.*, 2006). Clipping usually reduces soil CO_2 efflux by 21–49% despite the fact that it increases soil temperature (Bremer *et al.*, 1998; Wan & Luo, 2003). Craine *et al.* (1999) found that R_A and R_H also responded to a decrease of assimilate supply after clipping in a C_4-dominated grassland. However, Bahn *et al.* (2006) suggested that autotrophic respiration was little affected by clipping due to carbohydrate reserves which sustained root metabolism for several days, and heterotrophic respiration strongly responded to short-term changes in assimilate supply. The long-term response of soil CO_2 efflux and its components to clipping remains uncertain.

In this study, we investigated the responses of soil CO_2 efflux and its components to experimental warming and yearly clipping over a period of 6 years in a tallgrass prairie ecosystem. The interannual variability of these fluxes was also examined. Deep PVC collars (70 cm in depth) were used to exclude roots, so measured CO_2 efflux in these collars represents R_H. R_A was quantified by comparing soil CO_2 efflux with R_H. We hypothesized that warming would increase soil CO_2 efflux and its components in most years but yearly clipping would decrease them, with large interannual variability.

Materials and methods

Site description

The study was conducted at the Kessler Farm Field Laboratory (KFFL) in McClain County, Oklahoma (34°59′N, 97°31′W), approximately 40 km southwest of the Norman campus of the University of Oklahoma, USA. The field site is an old-field tallgrass prairie abandoned from agriculture 30 years ago and without grazing during the past 20 years. The grassland is dominated by three C_4 grasses: *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Eragrostis curvula*, and two C_3 forbs: *Ambrosia psilostachyia* and *Xanthocephalum texanum*. Mean annual temperature is 16.3 °C, with monthly air temperature ranging from 3.3 °C in January to 28.1 °C in July. Mean annual precipitation is 915 mm, with monthly precipitation ranging from 30 mm in January to 135 mm in May (average values from 1948 to 1998, data from Oklahoma Climatological Survey). In the study period (1999–2005), daily and annual rainfall data are shown in Fig. 1a and b. A silt loam soil includes 35.3% sand, 55.0% silt, and 9.7% clay (A. Subedar & Y. Luo, unpublished data, 2003). Soil carbon content is

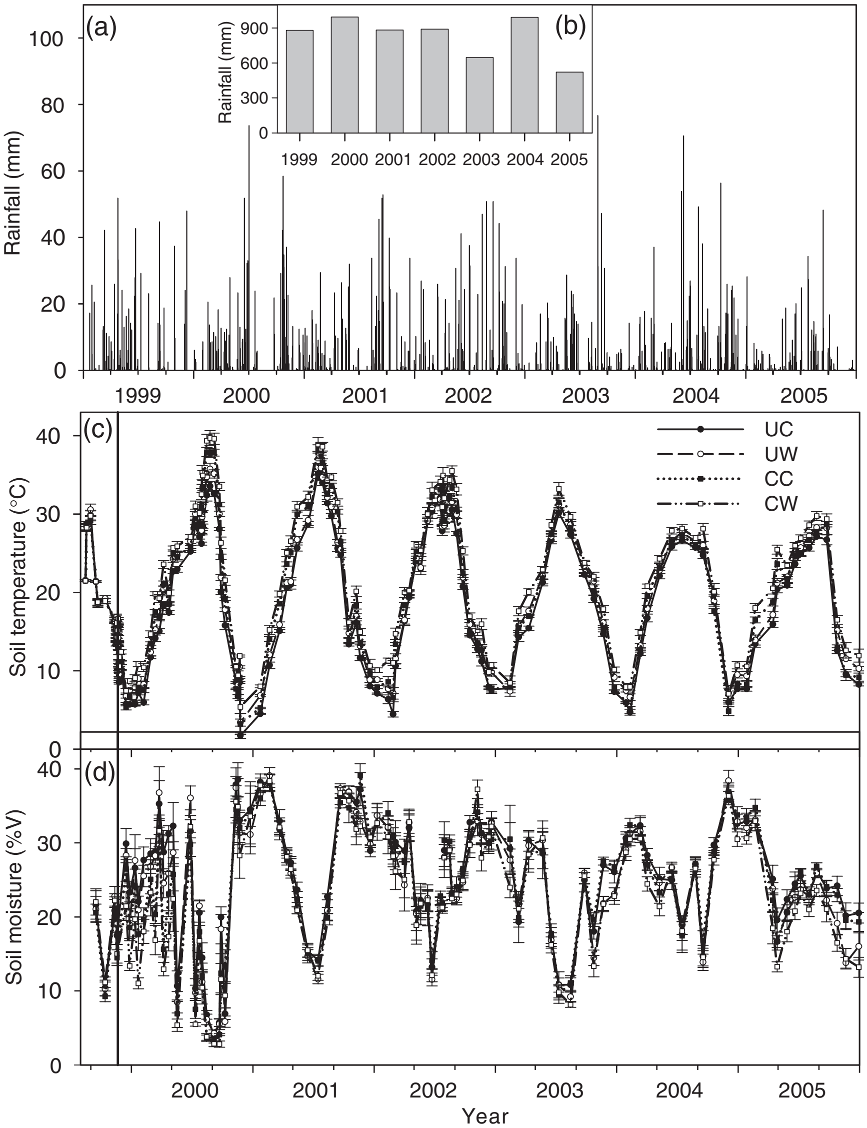

Fig. 1 Daily (a) and annual (b, inserted figure) rainfall at the experimental site, and seasonal and interannual variability of soil temperature at the depth of 5 cm (c) and soil moisture of 0–15 cm (d) from 1999 to 2005 in the long-term warming and clipping experiment. Yearly clipping was usually conducted in July. Vertical bars represent the standard error of the mean ($n = 6$). The dashed vertical line in c and d indicates the day when warming treatment started (November 21, 1999). UC, unclipped control; UW, unclipped warmed; CC, clipped control; CW, clipped warmed.

1.42% on a mass basis (Luo *et al*., 2001). The soil belongs to part of the Nash-Lucien complex with neutral pH, low permeability rate, high available water capacity, and a deep, moderately penetrable root zone (US Department of Agriculture, 1979).

Experimental design

The experiment used a paired nested design with warming as the main factor and clipping as a secondary factor. Twelve 2 m × 2 m plots were divided into six pairs of control (i.e. unwarmed) and warmed plots. In each warmed plot, one 165 m × 15 cm infrared heater (Kalglo Electronics Inc., Bethlehem, PA, USA) was suspended in the middle of each plot at the height of 1.5 m above the ground with a radiation output of 100 Watt m^{-2}. The heating has been operated year round, 24 h day^{-1} and 365 days yr^{-1} in the field since November 21, 1999. A previous study found that the effects of infrared heaters on soil temperature were spatially uniform in the warmed plots (Wan *et al*., 2002). To simulate shading effects of heaters, we installed one 'dummy' heater made of metal flashing with the same shape and size as the heating device over each control plot. For each paired plot, the distance between the control and the warmed plots was approximately 5 m to avoid heating the control plot by the infrared heater. The distances between the individual sets of 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 two diagonal subplots were clipped at the height of 10 cm above the ground yearly, usually in July. The other two were the unclipped subplots. Clipping in the manner effectively mimics hay mowing, a widely practiced land use in the southern Great Plains. Usually farmers and ranchers in the southern Great Plains mow grass pasture once or twice per year, depending on rainfall. Our study site is rather dry, yearly clipping mimics hay mowing once a year. After clipping, plants were allowed to grow until the next clipping. The four treatments in the experiment were unclipped control (UC), unclipped warmed (UW), clipped control (CC), and clipped warmed (CW) with six replicates. Further details of the study site were described in Wan *et al*. (2002, 2005).

Measurement protocols

To measure soil CO_2 efflux, PVC collars (80 cm^2 in area and 5 cm in height) was inserted 2–3 cm into the soil permanently at the center of each subplot. Small living plants inside the soil collars were clipped at the soil surface at least 1 day before the measurement to eliminate aboveground plant respiration. The clipped plant material was left in the collars to decompose. To detect the responses of heterotrophic respiration (R_H) to warming and yearly clipping, the original soil collars in one clipped and one unclipped subplots in each plot were replaced with deep PVC tubes (80 cm^2 in area and 70 cm in depth) in October 2001. The 70 cm long PVC tubes cut off old plant roots and prevented new roots from growing inside the tubes. The measurements of CO_2 efflux above these PVC tubes began immediately after installation to examine the transient response of dead root decomposition. After a specific period (5 months), CO_2 efflux measured above these PVC tubes represents R_H. Autotrophic respiration (R_A) is calculated as their difference. R_S and R_H were measured once or twice a month between 10 : 00 and 15 : 00 hours (local time), using a LI-COR 6400 portable photosynthesis system attached to soil CO_2 flux chamber (LI-COR Inc., Lincoln, NE, USA). A measurement consisted of placing the chamber on PVC collars, scrubbing the CO_2 to sub-ambient levels, and determining soil CO_2 efflux over the periods. Data were recorded at a 5 s interval by the datalogger in the LI-COR 6400 console. Each of the measurements usually took 1–3 min after placing the chamber over the collar.

Soil temperature at the depth of 5 cm was monitored adjacent to each PVC collar using a thermocouple probe (LI-COR 6000-09TC) connected to the LI-COR 6400 at the same time when soil CO_2 efflux was measured. Data were also logged at a 5 s interval. Soil moisture content was measured gravimetrically twice a month from September 1999 to December 2000. Soil samples at the top 5 cm were taken from one clipped and one unclipped subplots in each plot and oven dried at 105 °C for 24 h and weighed. Soil moisture was expressed as a percent of dry soil on a mass basis. Beginning from January 2001, volumetric soil water content (%V) was measured using manual Time Domain Reflectometry (TDR) equipment (Soilmoisture Equipment Corp., Santa Barbara, CA, USA) at the depth interval of 0–15 cm. To be consistent for analysis, those gravimetric soil moisture data taken before December 2000 were calibrated to volumetric soil moisture according to their relationship between mass-based and volumetric soil moisture. The measurement frequency of soil temperature and volumetric soil water content was same as soil CO_2 efflux, once or twice a month.

Estimation of annual CO_2 efflux

Annual soil CO_2 efflux for each treatment was estimated by summing the products of soil CO_2 efflux and the number of days between samples. It was corrected further for diurnal patterns in efflux. Our measurements, collected between 10 : 00 and 15 : 00 hours, were assumed to represent daytime averages based on diurnal patterns observed by Wan & Luo (2003) at a similar site. The calculated average daily efflux was 96.5% of the observed daytime average. The corrected daily flux was then multiplied by the number of days between measurements to compute the cumulative flux over the period (Bremer *et al*., 1998; Zhou *et al*., 2006).

Modeling soil CO_2 efflux and heterotrophic respiration

Soil temperature and soil moisture content are two main abiotic factors influencing soil CO_2 efflux. We used a reverse exponential decay function to simulate moisture effects and an exponential function to simulate temperature effects (Hui & Luo, 2004)

$$R = R_{0(\theta_v)} e^{bt} (1 - e^{(-c\theta_v + d)}) \quad (1)$$

$$R_{0(\theta_v)} = a + f\theta_v, \quad (2)$$

where R is the measured soil CO_2 efflux or heterotrophic respiration (μmol CO_2 m^{-2} s^{-1}); R_0 is the base respiration when soil temperature is 0 °C and changes with soil moisture; T is soil temperature (°C); and θ_v is volumetric soil moisture (%); a, b, c, d, and f are parameters related to soil temperature and moisture. When $\theta_v \leq d/c$, R = 0. When $\theta_v \geq (2\ln(10) + d)/c$, soil CO_2 efflux is hardly limited by soil moisture and largely controlled by soil temperature. The reverse exponential decay function fitted our observations better than other moisture functions (Luo & Zhou, 2006).

Data analysis

Each plot was an experimental unit, so replicate measurements were averaged by plot for analysis. In addition, monthly means of soil CO_2 efflux, R_H, R_A, soil temperature, and soil moisture were used to keep consistent in statistical analysis and calculation of annual mean values. Owing to paired design of experiment, we used paired sample *t*-test to examine annual statistical significance of warming, yearly clipping, and their interactive effects on soil CO_2 efflux, R_H, R_A, soil temperature, and soil moisture. The effects were considered to be significantly different if $P < 0.05$. The statistical analyses were performed in SPSS 11.0.1 for windows (SPSS Inc., Chicago, IL, USA, 2001).

We assessed sensitivity of mean soil CO_2 efflux, R_H, and R_A to soil temperature by fitting exponential functions to the data from individual treatments.

$$R = ae^{bT}, \quad (3)$$

where R is mean soil CO_2 efflux, R_H, and R_A (μmol m^{-2} s^{-1}), T is soil temperature (°C) at the depth of 5 cm, a is the intercept of soil CO_2 efflux when temperature is zero (i.e. basal respiration rate), and b represents the temperature sensitivity of soil CO_2 efflux, R_H, and R_A. The b values were used to calculate a respiration quotient (Q_{10}), which describes the change in fluxes over a 10 °C increase in soil temperature, by

$$Q_{10} = e^{10b}. \quad (4)$$

Values of parameters (i.e. a, b, and Q_{10}) derived from seasonal data sets reflect effects of temperature and other covarying factors on soil CO_2 efflux and its components (Boone *et al*., 1998; Högberg *et al*., 2001). Thus, an apparent Q_{10} value is used to denote the derived temperature sensitivity of soil CO_2 efflux, R_H, and R_A. In the analyses of temperature sensitivity and modeling, four data points of soil CO_2 efflux per treatment during the summer severe drought period (Fig. 2) were excluded when volumetric soil moisture was below 10% (Luo *et al*., 2001).

The significance of the effects of regression coefficients a and b among the treatments was examined by a *t*-test method as described by Zhou *et al*. (2006). Because the heterotrophic flux is recorded directly from measurements on deep collars, we decided to show R_H/R_S ratio as the relative contribution of R_H rather than R_A/R_S ratio as R_A contribution in the paper (Subke *et al*., 2006).

Results

Microclimate

Soil temperature at the depth of 5 cm exhibited pronounced seasonal variations over the 6 years, with a decrease in maximum values from 2001 to 2004 (Fig. 1c). Annual mean soil temperature ranged from 17.0 °C (2004) to 19.3 °C (2001) with an average of 17.8 °C in the control plots based on monthly daytime measurements (Table 1). The main effects of both warming and yearly clipping on annual mean soil temperature were statistically significant in every year of the study ($P < 0.001$). However, no significant interactive effects of warming and yearly clipping were found except in 2000 ($P < 0.05$). Specifically, warming significantly increased annual mean soil temperature by 1.4 ± 0.1 °C in the unclipped plots and by 2.0 ± 0.1 °C in the clipped plots from 2000 to 2005 (Table 1). Yearly clipping also increased soil temperature by 1.4 ± 0.3 °C relative to that in the control plots (Table 1).

Unlike soil temperature, volumetric soil moisture at the depth of 0–15 cm fluctuated greatly over the season (Fig. 1d). Usually the lowest soil moisture was observed in summer (July and August) and the highest in winter. Throughout the duration of the experiment, warming

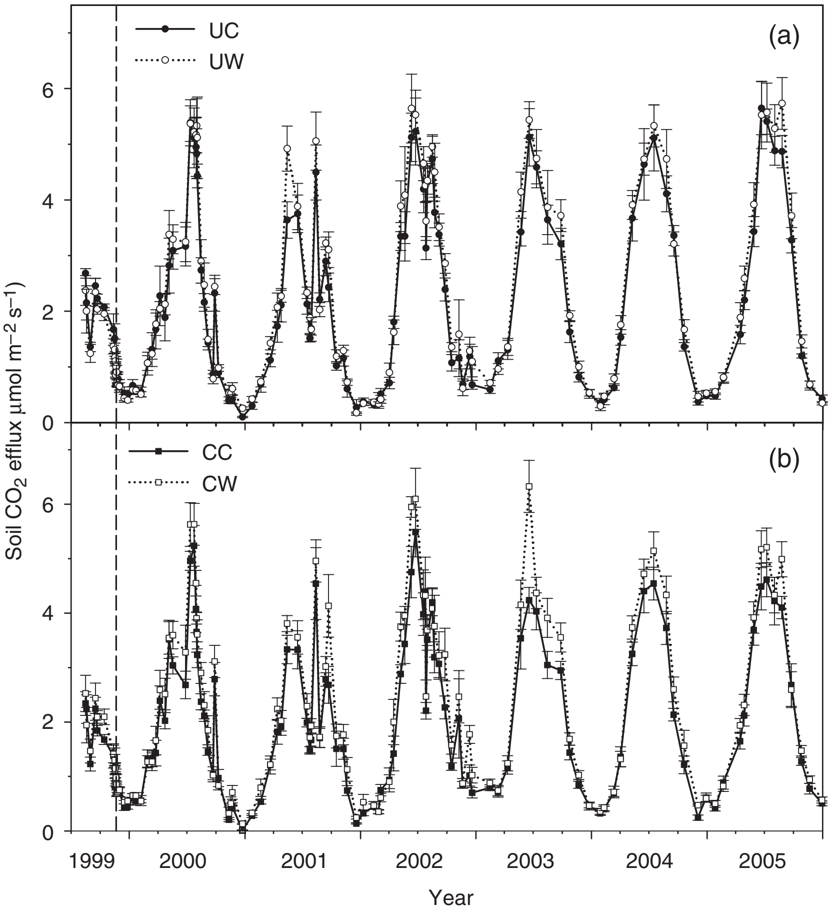

Fig. 2 Seasonal and interannual variability of soil CO_2 efflux from August 1999 to December 2005 under: (a) unclipped and (b) clipped treatments in the long-term warming experiment. See Fig. 1 for notes and abbreviations.

and yearly clipping significantly reduced soil moisture ($P<0.05$), although, in 2001 and 2003, effects of yearly clipping were not significant ($P>0.05$).

Soil CO_2 efflux

The temporal dynamics of soil CO_2 efflux followed the distinct seasonal pattern of soil temperature in all 6 years, which was high during summer and low in winter (Figs 1c and 2). However, long droughts in summer (August–September 2000, August 2001, July 2002, and July 2003) suppressed soil CO_2 efflux irrespective of the higher soil temperature (Figs 1d and 2). From year to year, there were also observable variations. For example, the summer peak of soil CO_2 efflux reached nearly 6 μmol m^{-2} s^{-1} in 2002 and was <4 μmol m^{-2} s^{-1} in 2001 in the control plots (Fig. 2). Soil CO_2 efflux in the winter is as low as nearly 0 μmol m^{-2} s^{-1} in 2002 but 0.3–0.5 μmol m^{-2} s^{-1} in other years. Annual mean soil CO_2 efflux ranged from 1.85 μmol m^{-2} s^{-1} (2001) to 2.50 μmol m^{-2} s^{-1} (2005) with an average of 2.18 μmol m^{-2} s^{-1} in the control plots (Table 1).

The stimulation of soil CO_2 efflux by warming was statistically significant for 5 years out of the 6-year study period (except 2000). On average, warming increased annual mean soil CO_2 efflux by 9.0 ± 1.5% in the unclipped plots and by 15.6 ± 1.5% in the clipped plots from 2000 to 2005 (Table 1). Effects of yearly clipping on soil CO_2 efflux were significant only in the last 2 years ($P<0.05$), while no interactions of warming and yearly clipping were found in any of the 6 years ($P>0.05$).

On the basis of the temperature relationship with soil CO_2 efflux in Eqn (3), soil temperature accounted for 81% of variation in the unclipped plots and nearly 70% in the clipped plots across the 6-year period (Fig. 3). The apparent Q_{10} values were slightly lower under warming ($P>0.05$) and reduced considerably by clipping ($P<0.05$) compared with that in the control, ranging from 1.70 to 3.62 for all four treatments (Table 2). There were higher Q_{10} values for the four treatments in 2004

Table 1 Annual mean soil CO$_2$ efflux (μmol m^{-1} s^{-1}), heterotrophic respiration (μmol m^{-1} s^{-1}), autotrophic respiration (μmol m^{-1} s^{-1}), soil temperature (°C) at the depth of 5 cm, and volumetric soil moisture (%V) at the depth of 0–15 cm from January 2000 to December 2005

	2000	2001	2002	2003	2004	2005
Soil CO$_2$ efflux						
UC	2.08	1.85	2.10	2.20	2.36	2.50
UW	2.16	2.13	2.31	2.41	2.54	2.71
CC	1.95	1.83	2.04	1.97	1.96	2.27
CW	2.18	2.12	2.36	2.35	2.30	2.51
Heterotrophic respiration						
UC			1.43	1.57	1.42	1.61
UW			1.55	1.73	1.72	1.74
CC	/	/	1.35	1.44	1.25	1.31
CW			1.42	1.48	1.44	1.67
Autotrophic respiration						
UC	/	/	0.67	0.63	0.94	0.89
UW			0.76	0.68	0.82	0.97
CC			0.69	0.53	0.71	0.96
CW			0.94	0.87	0.86	0.84
Soil temperature						
UC	17.6	19.3	17.7	17.9	17.0	17.4
UW	19.4	20.4	18.8	19.3	18.2	19.0
CC	19.8	21.9	19.1	18.6	17.6	18.5
CW	21.8	24.3	20.8	20.3	19.2	20.6
Soil moisture						
UC	23.3	29.8	27.6	22.1	27.5	24.8
UW	21.8	28.8	26.8	20.5	26.8	21.6
CC	19.5	28.7	27.5	22.1	27.8	23.6
CW	17.2	28.3	26.8	20.5	26.7	20.8

UC, unclipped control; UW, unclipped warmed; CC, clipped control; CW, clipped warmed.

than that in the other years, probably resulting from the effects of abundant rainfall or less drought stress.

Heterotrophic (R_H) *and autotrophic respiration* (R_A)

R_{H} also showed a distinct seasonal pattern and followed the changes in soil temperature across the 4 years of the study (2002–2005), although R_{H} had larger variability than soil CO$_2$ efflux (Fig. 4a). There were dips in the measured R_{H} during each summer due to the combined effects of low soil moisture and high temperature. Annual mean R_{H} ranged from 1.42 to 1.61 μmol m^{-2} s^{-1} with an average of 1.51 μmol m^{-2} s^{-1} in the control plots (Table 1). The effects of warming on R_{H} were statistically significant for 3 years of the 4-year study period (except 2003). Yearly clipping significantly reduced R_{H} in all the 4 years ($P < 0.05$). However, no interactions of warming and yearly clipping on R_{H} were found in any of the 4 years, as well as its temperature sensitivity ($P > 0.05$).

R_{H} contribution to soil CO$_2$ efflux and its annual mean values are displayed in Fig. 4b and c. Immediately after collar installation, decomposition of dead roots by deep-collar insertion contributed considerably to this efflux, which was larger than soil CO$_2$ efflux, but this phenomenon disappeared after 5 months. Thereafter, an opposite seasonal pattern occurred on the relative contribution of R_{H} compared with soil temperature (Fig. 4b). On average, annual mean R_{H} contributed to approximately 65% of soil CO$_2$ efflux across the 4 years (Fig. 4c). Warming and yearly clipping did not significantly affect R_{H} contribution to soil CO$_2$ efflux.

Annual mean R_{A} was calculated from the difference between soil CO$_2$ efflux and R_{H}, ranging from 0.53 to 0.96 μmol m^{-2} s^{-1} for the four treatments across the 4-year period (Table 1). Warming treatment also significantly stimulated R_{A} for 3 years of the 4-year study period (except 2004). Neither yearly clipping nor the interactions of warming and yearly clipping significantly affected R_{A} and its temperature sensitivity ($P > 0.05$). The temperature sensitivity of R_{A} (i.e. apparent Q_{10}) was higher than that of R_{H} (Table 2).

Seasonal and interannual variability

We calculated coefficient of variation (CV) from monthly and annual means to represent seasonal and interannual variability, respectively, in soil CO$_2$ efflux, R_{H}, R_{A}, soil temperature, soil moisture, and rainfall (Table 3). The seasonal variability was distinctly much greater than interannual variability for all the variables. It appeared that yearly clipping decreased the interannual variability of soil CO$_2$ efflux and increased that of soil temperature, while warming did not affect them. Interestingly, the highest mean soil CO$_2$ efflux occurred in 2005 when seasonal variability of precipitation during the growing season was lowest, indicating the importance of precipitation distribution (Tables 1 and 3). In addition, there was the larger seasonal variability in autotrophic respiration than that of other variables because estimates of R_{A} combined uncertainties of both R_{S} and R_{H} measurements.

Modeled soil CO$_2$ efflux and R_H

The inclusion of both soil temperature and moisture slightly improved model fitting of observed soil CO$_2$ efflux and R_{H} for the four treatments over seasons compared with the exponential model only using temperature (Figs 3 and 5). Although soil temperature and moisture often covary, the comparison between the two models suggests that soil temperature is the dominant environmental factor in regulating seasonal dynamics of soil CO$_2$ efflux and R_{H} across the whole study period.

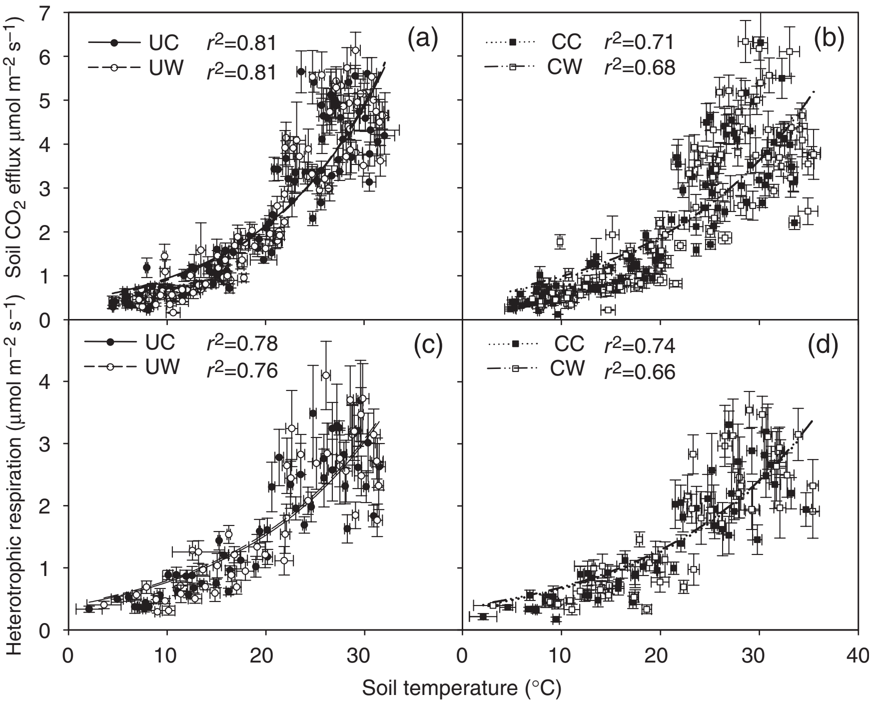

Fig. 3 Exponential relationships between soil CO_2 efflux and soil temperature under unclipped (a) and clipped (b) treatments and between heterotrophic respiration and soil temperature under unclipped (c) and clipped (d) treatments. Vertical and horizontal bars represent the standard error of the mean ($n = 6$). See Fig. 1 for abbreviations.

Table 2 Q_{10} values of soil CO_2 efflux, heterotrophic respiration, and autotrophic respiration from 2000 to 2005 calculated from Eqns (1) and (2)

	2000*	2001	2002	2003	2004	2005	All data
Soil CO_2 efflux							
UC	2.74	2.21	2.13	2.33	3.62	2.64	2.23
UW	2.66	2.09	2.10	2.22	3.18	2.62	2.28
CC	1.94	1.92	1.85	2.13	3.62	2.19	1.93
CW	1.94	1.82	1.70	2.13	3.20	2.39	1.89
Heterotrophic respiration							
UC			1.94	1.98	2.66	2.69	1.99
UW			1.85	1.85	2.68	2.83	1.96
CC	/	/	1.84	2.07	2.68	2.21	1.90
CW			1.82	2.16	3.10	2.55	1.88
Autotrophic respiration							
UC			2.23	4.06	4.37	2.82	2.35
UW			2.39	3.86	4.98	2.81	2.65
CC	/	/	2.01	2.75	5.22	2.62	2.18
CW			1.91	2.34	3.23	2.16	2.24

*Q_{10} in paper by Luo et al. (2001) was based on data in both 1999 and 2000.

UC, unclipped control; UW, unclipped warmed; CC, clipped control; CW, clipped warmed.

Unfortunately, the combined function of soil temperature and moisture did not fit the data well under severe water stress, where soil moisture was <10%, and we decided to exclude the four points in model fitting (see 'Materials and methods'). Therefore, biological factors such as biomass or net primary productivity (NPP) may be other important components controlling soil CO_2 efflux and R_H and should be included in future studies. In addition, we did not predict R_A with confidence because R_A only contributed a small proportion of soil CO_2 efflux with larger uncertainties than R_S and R_H, and seasonal changes in plant roots and closely associated organisms may have confounded the response to environmental soil variables (Trumbore *et al.*, 1996), making it more difficult to find clear relationships with environmental variables.

Estimated annual soil CO_2 efflux and its components

Annual soil CO_2 emissions ranged from 682 to 968 $g\,C\,m^{-2}\,yr^{-1}$ across the 6 years for the four treatments (Fig. 6). On average, warming treatment increased annual soil CO_2 efflux by 9.4 ± 1.4% in the unclipped plots and by 15.1 ± 1.6% in the clipped plots from 2000 to 2005. In contrast, yearly clipping decreased annual soil CO_2 efflux by 6.1 ± 1.6% compared with that in the control. Lower annual soil CO_2 efflux occurred in 2000 and 2001 than in the other years (Fig. 6), largely owing to the long drought and high temperature.

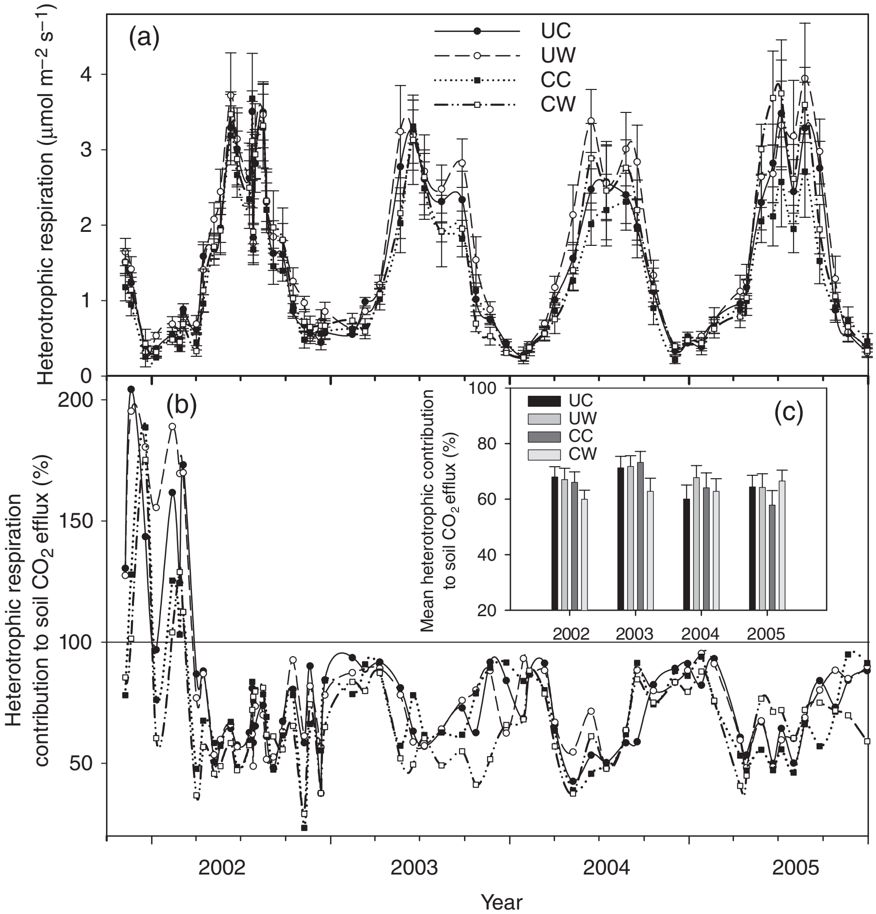

Fig. 4 Seasonal and interannual variability of heterotrophic respiration (a) and its contribution to total soil CO$_2$ efflux (b) under four different treatments from October 2001 to December 2005. Annual mean values of heterotrophic contribution to soil CO$_2$ efflux are shown in inserted figure (c). Vertical bars represent the standard error of the mean ($n = 6$). See Fig. 1 for abbreviations.

Annual R_H contributed 56.0–71.7% to total annual soil CO$_2$ efflux, ranging from 427 to 657 g C m^{-2} yr^{-1} across the 4 years (2002–2005) for the four treatments. On average, warming increased annual R_H by 14.5% in the unclipped plots and by 13.3% in the clipped plots across the 4 years, and yearly clipping decreased annual R_H by 12.5%. For annual R_A, which contributed 28.3–44.0% to total annual soil CO$_2$ efflux, warming increased annual R_A by 2.3% and yearly clipping increased it by 21.9% compared with that in the control.

Discussion

Partitioning soil CO$_2$ efflux

In our study, the surface CO$_2$ efflux measured in deep soil collars (70 cm), which were inserted beyond the main rooting zone to exclude roots, was used to represent heterotrophic flux component after severed roots caused by deep-collar insertion have been decomposed. On average over the 4 years, the relative contribution of R_H to soil CO$_2$ efflux was 66% in the control (Fig. 4), very close to the mean contribution in nonforest ecosystems (63%, Hanson *et al.*, 2000) and in temperate grassland (67%, Subke *et al.*, 2006), and well within the range of 60–88% in grasslands and croplands (Raich & Tufekcioglu, 2000).

Results from this and previous studies indicate that the deep-collar insertion is a useful technique to estimate relative contributions of R_H and R_A to soil CO$_2$ efflux after collars were installed several months (Buchmann, 2000; Wan *et al.*, 2005). Buchmann (2000), for example, compared results from the deep-collar insertion with those from trenching methods and found similar partitioning of soil respiration to R_A vs. R_H (~30% vs. ~70%). The insertion method is simple, cost effective, and easy to maintain over a long time. However, insertion of deep collars cut roots and stimulated decomposition of dead roots in the first several months (Fig. 4b), and thus the data during the disturbance

Table 3 Seasonal and interannual variability (IAV) of soil CO_2 efflux, heterotrophic respiration, autotrophic respiration, soil temperature, soil moisture, and annual precipitation as coefficient of variation from January 2000 to December 2005

	2000	2001	2002	2003	2004	2005	IAV
Soil CO_2 efflux							
UC	0.69	0.65	0.82	0.76	0.79	0.80	0.11
UW	0.69	0.67	0.82	0.76	0.76	0.78	0.09
CC	0.65	0.60	0.79	0.74	0.84	0.71	0.07
CW	0.65	0.59	0.74	0.83	0.80	0.73	0.06
Heterotrophic resp.							
UC			0.70	0.64	0.64	0.72	0.07
UW			0.64	0.64	0.67	0.72	0.05
CC	/	/	0.56	0.63	0.64	0.62	0.06
CW			0.56	0.65	0.70	0.80	0.07
Autotrophic resp.							
UC			1.18	1.17	1.03	1.07	0.20
UW			1.22	1.19	1.12	1.00	0.17
CC	/	/	1.06	1.13	1.34	0.91	0.25
CW			0.86	1.21	1.16	0.69	0.05
Soil temperature							
UC	0.50	0.50	0.53	0.43	0.51	0.42	0.04
UW	0.46	0.46	0.47	0.40	0.46	0.37	0.04
CC	0.50	0.47	0.52	0.42	0.51	0.40	0.08
CW	0.44	0.40	0.43	0.38	0.45	0.34	0.07
Soil moisture							
UC	0.44	0.28	0.19	0.32	0.23	0.17	0.11
UW	0.47	0.30	0.18	0.36	0.24	0.26	0.14
CC	0.47	0.32	0.17	0.33	0.22	0.22	0.15
CW	0.58	0.30	0.18	0.36	0.22	0.29	0.19
Precipitation	0.86	0.76	0.51	0.94	0.77	0.76	0.24
Precipitation in growing season	0.96 (60%)	0.83 (62%)	0.37 (68%)	0.79 (72%)	0.78 (62%)	0.31 (78%)	0.16 (66%)

Percentages in brackets of the bottom row are precipitation contribution in growing season to annual precipitation.
UC, unclipped control; UW, unclipped warmed; CC, clipped control; CW, clipped warmed.

period should be excluded from analysis. The insertion method may cause biases in estimated R_H in a few sources. First, there may be still some roots that grew underneath the 70 cm collars. In temperate grasslands, 83% of root biomass is grown in the upper 30 cm depth (Jackson *et al*., 1996). Our own data from ingrowth cores also showed that roots were very rare below 60 cm (data not shown). Usually, deep soil CO_2 production (including both R_A and R_H) is quite small relative to soil horizons nearer to the surface (Davidson & Trumbore, 1995; Hui & Luo, 2004; Davidson *et al*., 2006). Second, a small quantity of severed roots may slowly decompose for a long time after the collar insertion, possibly contributing to overestimation of heterotrophic respiration. Third, the inserted deep collars excluded root exudates and root litter and thus decreased organic matter input. As a consequence, measured R_H was supposed to gradually decline in comparison with the surrounding soil. Our 4 years of observation showed that the gradual decline was very minor. Lastly, the deep-collar insertion potentially resulted in different soil moisture content and possibly different temperature from those in soil outside of collars. The impacts of the differential environment on estimation of R_H are yet to be assessed.

Seasonal and interannual variability

The range of soil CO_2 efflux measured in the control plots over the 6 years is comparable with that in other studies (e.g. Davidson *et al*., 1998; Law *et al*., 1999; Xu & Qi, 2001; Bremer & Ham, 2002; Wan & Luo, 2003). Similar seasonal trends in soil CO_2 efflux have also been observed in a variety of ecosystems (e.g. Conant *et al*., 2000; Xu & Qi, 2001; Wan & Luo, 2003) except for arid ecosystems, where soil moisture dominates CO_2 efflux from soil (Davidson *et al*., 2000). In our study, seasonal variation in soil CO_2 efflux and its components considerably followed the temporal dynamics of soil temperature with some dips due to summer severe drought (Figs 1, 2 and 4).

The significant year-to-year variability in soil CO_2 efflux has been reported in various ecosystems such

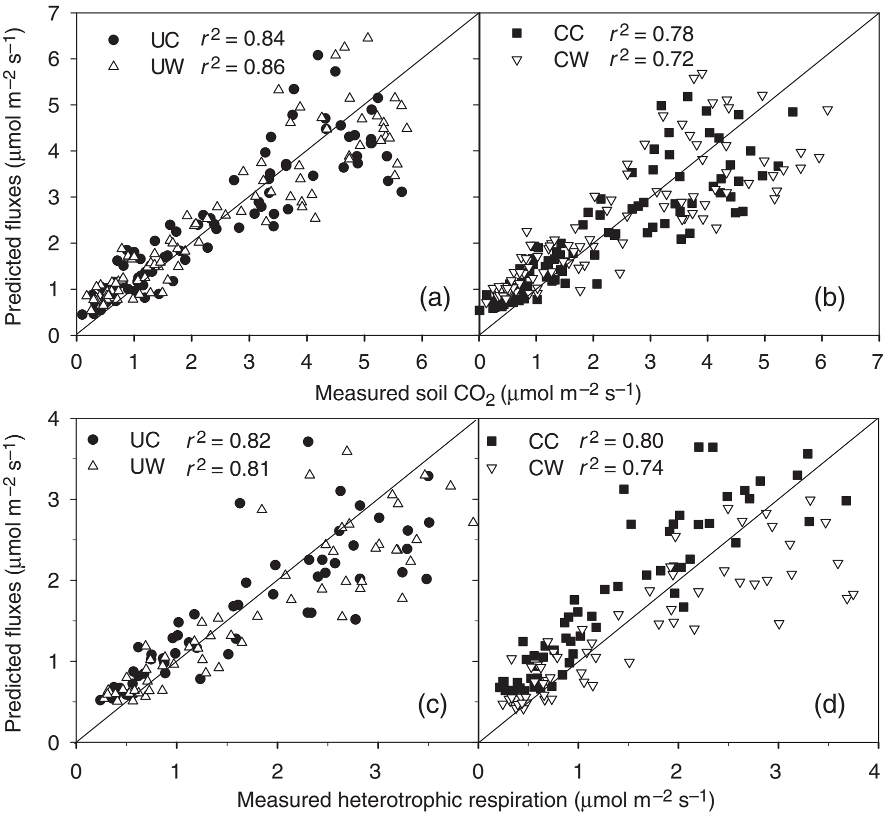

Fig. 5 Measured vs. modeled soil CO_2 efflux (a and b) and heterotrophic respiration (c and d) under the four treatments. See Fig. 1 for abbreviations.

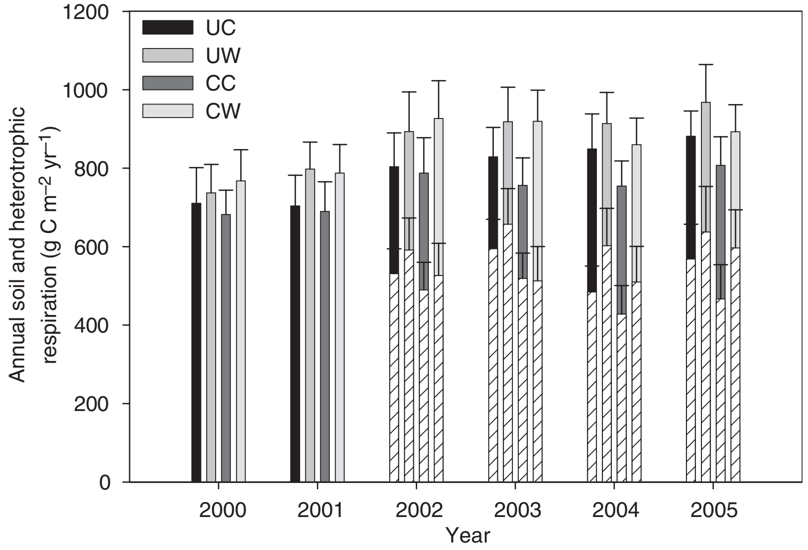

Fig. 6 Annual soil CO_2 efflux and heterotrophic respiration (g C m^{-2} s^{-1}) under the four treatments. Vertical bars represent the standard error of the mean ($n = 6$). The hatched columns represent annual heterotrophic respiration.

as grasslands (Frank *et al.*, 2002), a beech forest (Epron *et al.*, 2004), mixed temperate forests (Savage & Davidson, 2001), a mixed hardwood forest (Melillo *et al.*, 2002), ponderosa pine forests (Irvine & Law, 2002), and forest plantations (King *et al.*, 2004). Compared with those studies, the observed interannual variability in this study was relatively low for both soil CO_2 efflux and its components. Surprisingly, the year-to-year variation in soil CO_2 efflux did not follow the interannual pattern of precipitation at our site (Figs 1b and 6). For example, the highest annual soil CO_2 efflux occurred in 2005 when annual precipitation was lowest but a large proportion (78%) was present in the growing season and was evenly distributed (Table 3, Fig. 1a and b). In the first 2 years of the study, annual rainfall was relatively high while annual soil CO_2 efflux was lower than that in other years, largely resulting from high seasonal variability of precipitation with the long period of drought in the growing season of 2000 (55 days without rain) and 2001 (41 days without rain) and the negative effects of extremely high temperature in July of 2001 (Tables 1 and 3, Fig. 1). A general negative correlation between summer rainfall and high temperatures was also found throughout the tallgrass prairie (Rose, 1936). We carefully checked soil moisture pattern and found that some dips in soil CO_2 efflux corresponded with those points, where volumetric soil moisture was lower than around 12% (Fig. 1c). In a water manipulation experiment, Liu *et al.* (2002) observed that soil CO_2 efflux dropped very quickly when gravimetric soil moisture was below around 8%, which was very close to 12% of volumetric one, while there was little response of soil CO_2 efflux above this point. Evenly distributed precipitation during the growing season of 2005 caused intermediate soil moisture and then the highest soil CO_2 efflux. Therefore, the interannual variability of soil CO_2 efflux was controlled by precipitation distribution or soil moisture dynamics instead of annual precipitation. Similar results have been observed in other ecosystems (Davidson *et al.*, 2000; Savage & Davidson, 2001). Linear relationship between annual soil CO_2 efflux and precipitation, which occurred at the global scale (Raich & Schlesinger, 1992), may not work at a specific site.

Effects of warming and yearly clipping

Numerous studies have observed increases in soil CO_2 efflux in response to warming (Peterjohn *et al.*, 1994; McHale *et al.*, 1998; Rustad *et al.*, 2001; Melillo *et al.*, 2002; Niinistö *et al.*, 2004). The warming-induced responses in soil CO_2 efflux may be regulated by acclimatization of respiration (Luo *et al.*, 2001), physiological and phenological adjustments of plants and microbes (Melillo *et al.*, 2002), extensions of growing seasons (Dunne *et al.*, 2003; Wan *et al.*, 2005), changes in net N mineralization (Wan *et al.*, 2005), and stimulated C_4 plant productivity (Wan *et al.*, 2005). In our study, warming significantly increased the mean soil CO_2 efflux for 5 years out of the 6-year study period (except 2000). The warming-induced increases in soil CO_2 efflux likely resulted from extensions of growing season and increased plant productivity (Wan *et al.*, 2005). A positive linear correlation between soil CO_2 efflux and aboveground biomass across the first 3 years indicated that increase in soil CO_2 efflux largely enhanced belowground C allocation and R_A (Wan *et al.*, 2005). The magnitude of warming effects on soil CO_2 efflux was lower than the 20% mean increase found in 17 ecosystem warming experiments (Rustad *et al.*, 2001), likely due to low soil organic C content in our experimental site (Luo *et al.*, 2001). We did not observe a decline trend in warming stimulation of soil CO_2 efflux as shown by Rustad *et al.* (2001), mainly because soil CO_2 efflux is tightly coupled with carbon uptake through plant growth.

Few studies have examined the effects of warming on components of soil CO_2 efflux in the field (Melillo *et al.*, 2002). Our study found that warming significantly increased both R_H and R_A except for R_H in 2003 and R_A in 2004. The increased respiration likely resulted from enhanced oxidation of soil carbon compounds on warmed plots for R_H (Lin *et al.*, 2001; Eliasson *et al.*, 2005) and from an increase in root biomass for R_A (Wan *et al.*, 2005). Similarly, Lin *et al.* (1999, 2001) also observed the significant increases in soil CO_2 efflux and its components in response to warming in sun-lit controlled-environment terracosms.

The removal of aboveground biomass by clipping temporarily reduces the supply of current photosynthates to roots and mycorrhizal fungi, usually resulting in a decrease in soil CO_2 efflux by 19–49% at a short-term period (i.e. several days to months) (Bremer *et al.*, 1998; Craine *et al.*, 1999; Craine & Wedin, 2002; Zhou *et al.*, 2006). In our study, yearly clipping significantly reduced soil CO_2 efflux in the last 2 years and R_H for all the 4 years ($P < 0.05$), while there was no significant effect on R_A. At a yearly scale, the reduction in assimilate supply by clipping may strongly decrease R_H (Bahn *et al.*, 2006) and this trend enlarged with time from 2002 to 2005. Although R_A was slightly stimulated by clipping due to an increase in root biomass (Wan *et al.*, 2005) and offset the reduction in R_H, resulting in no significant effects on soil CO_2 efflux in the first 4 years, the compensation of R_A was not enough in the last 2 years. However, frequent clipping to keep the ground bare over the whole study period of 1 year significantly decreased soil CO_2 efflux by 33% at a similar grassland (Wan & Luo, 2003). Thus, frequency of clipping and duration of study can be sources of variable results for different studies.

Temperature sensitivity

The apparent Q_{10} values of soil CO_2 efflux was slightly lower under warming ($P > 0.05$) and reduced considerably by clipping ($P < 0.05$) compared with that in the control, while there was not consistent trends on the apparent Q_{10} values of R_H and R_A. The decrease in Q_{10} values in response to warming had been observed in other studies (McHale *et al.*, 1998; Luo *et al.*, 2001; Strömgren, 2001; Niinistö *et al.*, 2004; Zhou *et al.*, 2006), suggesting that temperature acclimation could have occurred, although the magnitude largely varied. Clipping not only affected the supply of current photosynthates to roots and their associated symbionts but also changed microclimate variables such as soil temperature and moisture (Wan *et al.*, 2002), resulting in the decrease in temperature sensitivity of soil CO_2 efflux.

The apparent Q_{10} values for R_A were higher than those for R_H and soil CO_2 efflux (Table 2). Similar results have been observed in other studies (Boone *et al.*, 1998; Epron *et al.*, 1999; Jiang *et al.*, 2005). The higher Q_{10} values for R_A than R_H may result not only from higher sensitivity of the specific root respiration to soil temperature, but also from seasonal variation in root biomass, which is usually high when temperature is high (Boone *et al.*, 1998; Rey *et al.*, 2002). The different Q_{10} values for R_A and R_H suggest that temperature sensitivity of soil CO_2 efflux depends on the relative root contribution. An ecosystem in which roots contribute the largest portion of soil CO_2 efflux should be most sensitive to warming.

Conclusions

This study showed that heterotrophic respiration accounted for approximately 66% of soil surface efflux over the 6 years in a grassland ecosystem. Throughout the duration of experiment, warming significantly stimulated soil CO_2 efflux and its components. However, warming did not change relative contributions of R_A and R_H to soil CO_2 efflux. Yearly clipping significantly reduced soil CO_2 efflux in the last 2 years and heterotrophic respiration in all the 4 years, while there was no significant clipping effect on R_A. The apparent Q_{10} values of soil CO_2 efflux was slightly lower under warming ($P > 0.05$) and reduced considerably by clipping ($P < 0.05$) compared with that in the control.

We found that the seasonal variability was distinctly much greater than interannual variability for soil CO_2 efflux and its components. Yearly clipping decreased the interannual variability of soil CO_2 efflux, while warming did not affect it. The interannual variability of annual soil CO_2 efflux was not related to fluctuations in precipitation, suggesting that rainfall distribution over seasons, especially growing season, is more important than annual precipitation.

Acknowledgements

The authors would like to thank Rebecca A. Sherry and Nancy A. Zehrbach for maintaining the experimental infrastructure and for assistance with field measurement as well as William Snodgrass and Ensheng Weng. This research was financially supported by US National Science Foundation (NSF) under DEB 0078325 and DEB 0444518, and by the Office of Science (BER), Department of Energy, Grants No.: DE-FG03-99ER62800 and DE-FG02-006ER64319.

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