GLOBAL BIOGEOCHEMICAL CYCLES, VOL. 20, GB1003, doi:10.1029/2005GB002526, 2006

Main and interactive effects of warming, clipping, and doubled precipitation on soil CO_2 efflux in a grassland ecosystem

Xuhui Zhou, Rebecca A. Sherry, Yuan An,[1] Linda L. Wallace, and Yiqi Luo
Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma, USA

Received 4 April 2005; revised 23 August 2005; accepted 7 November 2005; published 14 January 2006.

[1] We conducted two experiments, one long term with a 2°C increase (Experiment 1) and one short term with a 4.4°C increase (Experiment 2), to investigate main and interactive effects of warming, clipping, and doubled precipitation on soil CO_2 efflux and its temperature sensitivity in a U.S. tallgrass prairie. On average, warming increased soil CO_2 efflux by 13.0% ($p < 0.01$) in Experiment 1, by 22.9% ($p < 0.0001$) in Experiment 2, and by 26.6% ($p < 0.0001$) in the transient study of Experiment 2. Doubled precipitation resulted in an increase of 9.0% ($p < 0.05$) in soil CO_2 efflux in Experiment 2. Yearly clipping did not significantly affect soil CO_2 efflux ($p = 0.66$) in Experiment 1, while clipping decreased soil CO_2 efflux by 16.1% ($p < 0.05$) in the transient study. Temperature sensitivity of soil CO_2 efflux significantly decreased from an apparent Q_{10} value of 2.51 in unwarmed plots to 2.02 in warmed plots without extra precipitation and from 2.57 to 2.23 with doubled precipitation in Experiment 2. No significant interactive effects among the experimental factors were statistically found on soil CO_2 efflux or their temperature sensitivities except for the warming × clipping interaction ($p < 0.05$) in the transient study. Our observed minor interactive effects relative to main ones suggest that results from single-factor experiments are useful in informing us of potential responses of soil CO_2 efflux to multifactor global change, at least in our ecosystem.

Citation: Zhou, X., R. A. Sherry, Y. An, L. L. Wallace, and Y. Luo (2006), Main and interactive effects of warming, clipping, and doubled precipitation on soil CO_2 efflux in a grassland ecosystem, *Global Biogeochem. Cycles*, *20*, GB1003, doi:10.1029/2005GB002526.

1. Introduction

[2] Global warming resulting from CO_2 and other greenhouse gases is expected to increase the mean global temperature by 1.4 ~ 5.8°C by the end of this century [*Intergovernmental Panel on Climate Change* (*IPCC*), 2001]. In the US Great Plains, air temperature is predicted to increase by 2° to 4°C with doubling of current CO_2 concentration [*Long and Hutchin*, 1991]. In addition, anthropogenic climate change likely will result in increasingly altered precipitation regimes. The anticipated increase in precipitation is about 0.5 to 1% per decade in this century globally [*IPCC*, 2001] and may occur in heavy rainfall events by 16–22% per decade in the southern Great Plains, United States [*Kunkel et al.*, 1999]. Warmer temperature and increased precipitation would likely alter the fluxes of carbon from soil to the atmosphere (i.e., soil CO_2 efflux).

[3] Soil CO_2 efflux, commonly referred to as soil respiration, represents CO_2 release at the soil surface from microbial respiration during organic matter decomposition and rhizosphere respiration by live roots and their symbionts [*Boone et al.*, 1998; *Högberg et al.*, 2001, *Wan and Luo*, 2003]. This flux is the largest terrestrial source of CO_2 to the atmosphere, which is about 68 to 80 Pg C yr^{-1} on a global scale [*Raich and Schlesinger*, 1992; *Raich and Potter*, 1995]. Global modeling studies have demonstrated that even a small change in soil CO_2 emissions could significantly exacerbate or mitigate the buildup of this greenhouse gas in the atmosphere [*Cramer et al.*, 2001], with consequent feedbacks to climate change [*Woodwell et al.*, 1998; *Cox et al.*, 2000]. Therefore understanding regulations of soil CO_2 efflux by major environmental factors is a critical step toward projecting climate change in the future.

[4] Past research has demonstrated that the rate of CO_2 production in the soil varies strongly with temperature [*Peterjohn et al.*, 1993; *Rustad et al.*, 2001], moisture availability [*Liu et al.*, 2002; *Xu et al.*, 2004], and substrate supply [*Bremer et al.*, 1998; *Craine et al.*, 1999]. The majority of the studies that investigated responses of soil CO_2 efflux to the above-mentioned variables have been carried out in single-factor experiments. These single-factor experiments have considerably advanced our understanding of ecosystem responses to climate change. For example,

---

[1] Now at College of Agriculture and Biology, Shanghai Jiaotong University, Shanghai, China.

0886-6236/06/2005GB002526$12.00

Table 1. Comparison of Experiment 1, Experiment 2, and the Transient Study[a]

	Experiment 1[b]	Experiment 2[c]	Transient Study[d]
Treatments	warming and yearly clipping	warming and doubled precipitation	clipping, warming, and doubled precipitation
Warming period	21 November 1999 to present	20 February 2003 to 20 February 2004	20 February 2003 to 20 February 2004
Warming effects on soil temperature			
Monthly measurement	1.48°C (5 cm)	2.73°C (5 cm)	2.63°C (5 cm)
Hourly record	2.0°C (2.5 cm)	4.4°C (2 cm)	4.3°C (2 cm)
Warming effects on soil moisture			
Monthly measurement	−1.24% (0–15 cm)	–	−2.47% (0–15 cm)
Hourly record	–	−5.68% (0–15 cm)	–

[a] Measurement depths of soil temperature and moisture given in parentheses.
[b] Long-term experiment with warming and yearly clipping treatments.
[c] Short-term (1 year) experiment with warming and doubled precipitation treatments.
[d] Conducted in Experiment 2 from 16 September to 21 November 2003.

warming experiments have indicated average increases of 20% in soil CO_2 efflux across a range of temperature increases, with greater increases in the first few years [*Rustad et al.*, 2001]. Clipping, instead, significantly reduces soil CO_2 efflux by 19–49% [*Bremer et al.*, 1998; *Wan and Luo*, 2003]. Increased rainfall variability and/or reduced rainfall amount usually decrease soil CO_2 efflux [*Harper et al.*, 2005].

[5] Unlike common single-factor experiments, global change involves simultaneous changes in multiple factors, which could potentially have complex interactive influences on ecosystem structure and processes. For example, data from a grassland site in California showed that elevated CO_2 suppressed the effects of increased temperature, precipitation, and N deposition on net primary production (NPP) in the third year of manipulations (2000–2001). That result indicates that the multifactor responses to global changes differed greatly from simple combinations of single-factor responses [*Shaw et al.*, 2002]. Conversely, interactive effects of warming with elevated atmospheric CO_2 on soil CO_2 efflux were not observed in other studies [*Edwards and Norby*, 1998; *Lin et al.*, 2001; *Niinistö et al.*, 2004]. Thus evaluating multifactor interactions in influencing ecosystem structure and processes is critical to understanding their response to global change in the real world. Indeed, when interactive effects dominate over the main effects of individual factors, results from single-factor experiments become less useful for understanding ecosystem changes. In the case that interactive effects are minor relative to main effects, results from single-factor experiments may become useful in informing us of potential changes of ecosystems in response to multifactor global change.

[6] In this study, we took advantage of two ongoing experiments to evaluate main and interactive effects of three factors, warming, clipping, and doubled precipitation, on soil CO_2 efflux and its temperature sensitivity in a grassland ecosystem. Experiment 1 was designed to examine effects of long-term warming plus yearly clipping on community structure and ecosystem processes [*Luo et al.*, 2001; *Wan et al.*, 2005]. Experiment 2 was to examine ecosystem responses to short-term (i.e., 1 year) warming and doubled precipitation. To examine transient responses of soil CO_2 efflux to substrate supply, we also clipped aboveground biomass in autumn of 2003 in Experiment 2. We hypothesized that warming and doubled precipitation would increase soil CO_2 efflux and clipping would decrease it. We also hypothesized that interactive effects of the three factors would occur on soil CO_2 efflux and its temperature sensitivity. To test these hypotheses, we measured soil CO_2 efflux at monthly intervals and derived basal respiration rates and temperature sensitivity coefficients by fitting an exponential equation to measured soil CO_2 efflux and soil temperature. Repeated measures analysis of variance (RM-ANOVA) was applied for significance tests of treatment effects on soil CO_2 efflux. T-tests of regression coefficients were performed to examine adjustments in temperature-respiration relationships under different treatments.

2. Materials and Methods

2.1. Site Description

[7] The experiments were conducted at the Great Plains Apiaries in McClain County, Oklahoma (34°59′N, 97°31′W), approximately 40 km southwest of the Norman campus of the University of Oklahoma. It is a 137.6-ha farm located in the Central Redbed Plains of Oklahoma [*Tarr et al.*, 1980]. The study site is an upland tallgrass prairie dominated by four C_4 grasses (*Schizachyrium scoparium*, *Sorghastrum nutans*, *Andropogon gerardii*, and *Panicum virgatum*), two C_3 forbs (*Ambrosia psilostachyia* and *Xanthocephalum texanum*), and one winter-dominant C_3 grass (*Bromus japonicus*). The four C_4 grasses represent approximately 75% of the total plant biomass (R. Sherry and Y. Luo, unpublished data, 2003). 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, Oklahoma Climatological Survey). A silt loam soil in the grassland includes 35.3% sand, 55.0% silt, and 9.7% clay (A. Subedar and Y. Luo, unpublished data, 2003). Soil carbon content is 1.42% on a mass basis [*Luo et al.*, 2001]. The soil belongs to part of the Nash-Lucien complex with neutral pH, high available water capacity, and a deep, moderately penetrable root zone [*U.S. Department of Agriculture (USDA)*, 1979].

2.2. Experimental Design

[8] We used two ongoing experiments to examine main and interactive effects of warming, clipping, and doubled precipitation on soil CO_2 efflux and its temperature sensi-

tivity. Experiment 1 examined the long-term warming/yearly clipping effects on ecosystem processes, whereas Experiment 2 investigated ecosystem responses to one-year warming/doubled precipitation and subsequent-year lag effects on biogeochemical processes (Table 1). In addition, the transient responses to clipping in Experiment 2 were studied in contrast with yearly clipping in Experiment 1. The two experiments and the transient study are described below.

2.2.1. Experiment 1

[9] The experiment was conducted at a site of old-field tallgrass prairie abandoned from crop field 30 years ago without grazing for 27 years. The field experiment used a paired, nested design with warming as the main factor and clipping as a secondary factor. Twelve 2 × 2 m plots were divided into six pairs of control (i.e., unwarmed) and warmed plots. In each warmed plot, one 165 × 15 cm infrared heater (Kalglo Electronics Inc., Bethlehem, Pennsylvania) has a radiation output of 100 Watts m^{-2} and was suspended in the middle of each plot at the height of 1.5m above the ground. The height of 1.5 m was determined by considerations of vegetation height and radiative energy output. The heating is on year around, 24 hours per day and 365 days per year in the field. 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. A previous study by *Wan et al.* [2002] has documented that warming increased daily mean air temperature at 25 cm above the ground by 1.1°C and soil temperature at the 2.5-cm depth by 2.0°C. Each 2 × 2 m plot was divided into four 1 × 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 control. Usually farmers and ranchers in the southern Great Plains mow grass pasture once to twice per year, depending on rainfall. Our study site is rather xeric, yearly clipping mimic hay mowing once a year. Each treatment, control (C), warmed (W), clipped (CL), and warmed plus clipped (W + CL), had six replicates.

2.2.2. Experiment 2

[10] The experiment was situated approximately 500 m away from Experiment 1. Twenty 3 × 2 m plots were established in two rows that were separated by approximately 3 m. Within one row, the distance between plots was 1.5 m. Half of the plots were randomly selected for warming treatments with two infrared heaters suspended in the middle of the plots at the height of 1.5 m above the ground. The other 10 plots had "dummy" heaters suspended at the same height as in the warmed plots. Five of both the warmed and unwarmed plots were randomly selected to receive doubled precipitation using a "rainfall collection pan" device, which is an angled catchment with the same size and shape as the plot. One rainfall collection pan was installed about 40 cm above the ground with a slope lower near the plot and 30 cm away from each doubled precipitation plot to funnel water onto these plots so that the amount of rainfall was doubled. The pan was connected to three 1.8-cm (inner diameter) polyvinyl chloride (PVC) pipes with 3.0-mm holes to distribute the collected water evenly over the plots. We also installed the PVC pipes in those plots without extra precipitation to have uniform effects of pipes if any. Thus, four treatments, control (C), warmed (W), doubled precipitation (PPT), and warmed plus doubled precipitation (W + PPT), had five replicates.

2.2.3. The Transient Study

[11] We studied transient responses of soil CO_2 efflux to abrupt reduction in substrate supply by clipping in Experiment 2. A half of each plot was clipped at 10 cm above the ground on 16 September 2003. Thus there were eight treatments, control (C), warmed (W), doubled precipitation (PPT), warmed plus doubled precipitation (W + PPT); clipped (CL), clipped plus warmed (CL + W), clipped plus doubled precipitation (CL + PPT), and clipped plus warmed plus doubled precipitation (CL + W + PPT), with five replicates.

2.3. Measurement Protocols

[12] To measure soil CO_2 efflux, PVC collars (80 cm^2 in area and 5 cm in height) were inserted 2–3 cm into the ground at the center of each subplot or quarter at the beginning of the experiments. 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 materials were left in the collars. Measurements of soil CO_2 efflux were taken monthly between 1000 and 1500 (local time), using a LI-COR 6400 portable photosynthesis system attached to a 6400-09 soil CO_2 flux chamber (LI-COR. Inc., Lincoln, Nebraska). Standard procedures recommended by LI-COR were applied to measure soil CO_2 efflux. Data were recorded at a 5-s interval by the data logger in LI-COR 6400 console. Each of the measurements usually took 1–3 min after placing the chamber over the collar.

[13] 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 we measured soil CO_2 efflux. Data were also logged at a 5-s interval.

[14] In Experiment 1 and the transient study, volumetric soil water content (%V) was measured using manual Time Domain Reflectometry (TDR) equipment (Soilmoisture Equipment Corp., Santa Barbara, California) at the depth interval of 0–15 cm. In Experiment 2, TDR probes (ESI Environmental Sensor Inc., Victoria, British Columbia, Canada) were used to automatically monitor soil moisture at depths of 0–15 cm, 15–30 cm, 30–60 cm, 60–90 cm, and 90–120 cm. Soil moisture data were logged hourly through a CR10X data logger (Campbell scientific, Inc., Logan, Utah). However, owing to shrinking and swelling of soils, nine TDR probes were partially damaged or malfunctioned in the middle of the study. Complete data sets of soil moisture were available only in 11 of the 20 plots. In this study, the readings at the depth of 0–15 cm were used because this depth is more closely associated with soil surface CO_2 efflux.

[15] In Experiment 1, soil CO_2 efflux, soil temperature, and soil moisture were monthly measured in one clipped and one unclipped subplot of each plot in 2003. In Experiment 2, each plot was divided into four quarters, and monthly measurements of soil CO_2 efflux and soil temperature were

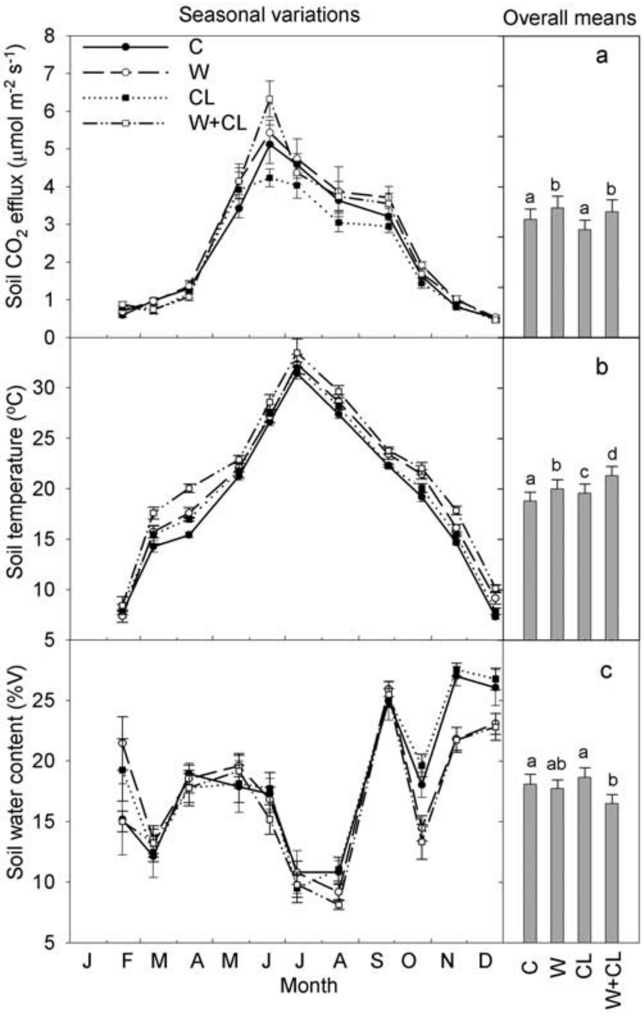

Figure 1. Seasonal variations and overall means of (a) soil CO_2 efflux, (b) soil temperature at the depth of 5 cm, and (c) soil water content of 0–15 cm in Experiment 1 in 2003. Clipping was conducted on 26 September 2003. Vertical bars represent the standard error of the mean (n = 6). C, control; W, warmed; CL, clipped; W + CL, clipped plus warmed.

performed in the southwest and northeast quarters from January 2002 to February 2004 except February and March 2003 (3 times per month), while soil moisture was monitored hourly at the center of each plot. In the transient study, soil CO_2 efflux, soil temperature, and soil water content (%V) were intensively measured at days 3, 9, 17, 27, 37, 49, 58, 66 after clipping until 21 November 2003 in both the clipped and unclipped half plots.

2.4. Estimation of Annual Soil CO_2 Efflux

[16] Annual soil CO_2 efflux for each treatment was estimated by summing the products of monthly mean soil CO_2 efflux and the number of days between samples. It was corrected further for diurnal patterns in fluxes. Our measurements, collected between 1000 and 1500 local time, were assumed to represent daytime averages based on diurnal patterns observed by *Wan and 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].

2.5. Data Analysis

[17] In Experiment 2, each plot was an experimental unit, so replicate measurements were averaged by plot for analysis. In addition, means of soil CO_2 efflux and soil temperature in February and March 2003 were applied to keep monthly consistent in statistical analysis. The main and interactive effects and temporal changes of warming, precipitation, and clipping treatments on soil CO_2 efflux, soil temperature, and soil moisture were determined with a repeated measures analysis of variance (RM-ANOVA). The statistical analyses were performed in SPSS 11.0.1 for windows (SPSS Inc., Chicago, 2001).

[18] We assessed the sensitivity of soil CO_2 efflux to soil temperature by fitting exponential functions to the data from individual treatments.

$$R_s = ae^{bT}, \qquad (1)$$

where R_s is soil CO_2 efflux (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. 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

$$Q_{10} = e^{10b}. \qquad (2)$$

Values of parameters (i.e., *a*, *b*, and Q_{10}) derived from seasonal data sets reflect effects of temperature and other co-varying factors on soil CO_2 efflux [*Boone et al.*, 1998; *Högberg et al.*, 2001]. Thus an apparent Q_{10} value is used to denote the derived temperature sensitivity of soil respiration hereafter.

[19] A T-test was used to assess the significance of main and interactive effects of regression coefficients *a* and *b* among the treatments as presented in Appendix A. The main and interactive effects were considered to be significantly different if $p < 0.05$.

3. Results

3.1. Warming and Yearly Clipping Effects in Experiment 1

[20] Soil CO_2 efflux exhibited pronounced seasonal variations with average values ranging from 0.52 μmol m^{-2} s^{-1} in December to 5.13 μmol m^{-2} s^{-1} in June in the control plots in 2003 (Figure 1a). Soil CO_2 efflux in warmed plots increased significantly by 9.9% in comparison to that in unwarmed plots without clipping, and by 16.4% with clipping (13.0% on average, Figure 1a, Table 2). However, no significant effects of yearly clipping and warming × yearly clipping interaction were found on soil CO_2 efflux.

Table 2. Results of RM-ANOVA Showing the F Values and Levels of Significance for Responses of Soil CO_2 Efflux to Warmed, Doubled Precipitation, and Clipped Treatments and Sampling Dates[a]

	Experiment 1		Experiment 2		Transient Study	
Factor	df	F Values	df	F Values	df	F Values
W	1	9.32^{b}	1	26.93^{c}	1	34.85^{c}
PPT	na	na	1	4.70^{d}	1	0.06
CL	1	0.20	na	na	1	7.93^{d}
D	10	164.23^{c}	12	107.44^{c}	7	155.42^{c}
W × CL	1	1.39	na	na	1	6.25^{d}
W × PPT	na	na	1	2.68	1	0.24
PPT × CL	na	na	na	na	1	0.93
W × D	10	3.63^{d}	12	12.40^{b}	7	1.85
CL × D	10	4.05^{d}	na	na	7	4.18^{d}
PPT × D	na	na	as	1.05	7	0.65
W × PPT × CL	na	na	na	na	1	0.13
W × PPT × D	na	na	12	0.32	7	0.75
W × CL × D	10	0.85	na	na	7	0.55
PPT × CL × D	na	na	na	na	7	3.60
W × PPT × CL × D	na	na	na	na	7	0.48

[a] W, warmed; PPT, doubled precipitation; CL, clipped; D, sampling dates; na, not applicable.
[b] Here $p \leq 0.01$.
[c] Here $p \leq 0.0001$.
[d] Here $p \leq 0.05$.

Significant interactions occurred between warming and sampling dates and between yearly clipping and sampling dates (W × D and CL × D, Table 2).

[21] Soil temperature at the depth of 5 cm showed a similar seasonal trend as soil CO_2 efflux (Figure 1b). Warming increased soil temperature by 1.23°C over the whole year in unclipped plots and by 1.73°C in clipped plots based on monthly daytime measurements ($p < 0.0001$, Figure 1 and Table 1). Yearly clipping increased soil temperature by 0.80°C relative to that in the control plots in the daytime ($p < 0.001$, Figure 1b). Soil moisture (0–15 cm) fluctuated greatly over the season (Figure 1c). The lowest soil moisture was observed in summer (July and August) and the highest in winter. Warming had a marginally significant negative effect on soil moisture ($p = 0.06$), while yearly clipping did not affect soil moisture ($p = 0.6$, Figure 1c).

[22] Our analysis with equation (1) showed that soil temperature accounted for more than 60% of the variation on soil CO_2 efflux in the four treatments (Figure 2). Warming and yearly clipping both slightly reduced the derived coefficient *b*, while basal respiration rate (i.e., coefficient *a*) was not affected. T-test analysis illustrated that those slight differences in coefficients either *a* or *b* among treatments were not significant (Table 3).

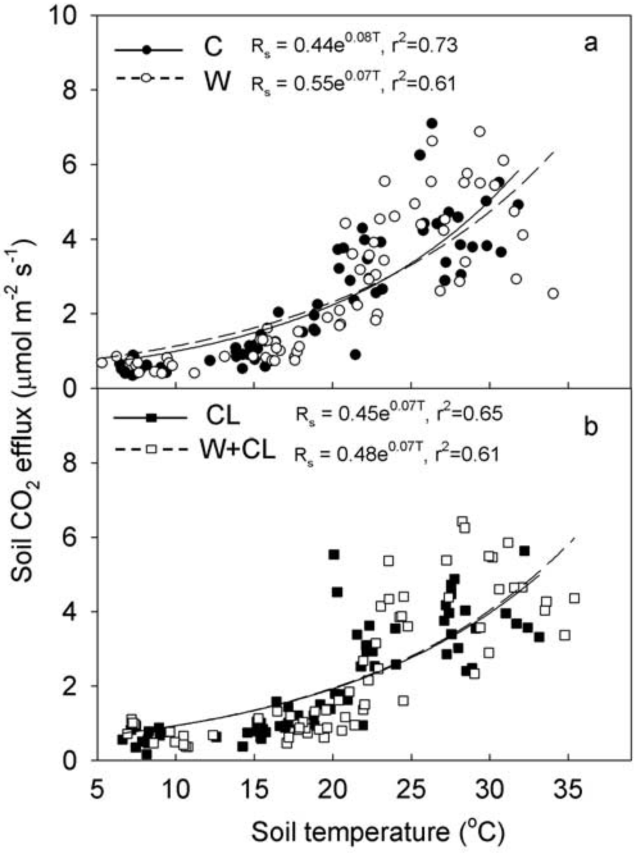

Figure 2. Exponential relationships between soil CO_2 efflux and soil temperature under (a) unclipped and (b) clipped treatments in Experiment 1 in 2003. See Figure 1 for abbreviations.

3.2. Warming and Precipitation Effects in Experiment 2

[23] Soil CO_2 efflux closely tracked the seasonal changes in soil temperature, with average values ranging from 0.54 to 7.64 μmol m^{-2} s^{-1} between January 2002 and February 2004 in the control plots (Figure 3a). Warming and doubled precipitation caused significant increases in soil CO_2 efflux (Figure 3a and Table 2). Soil CO_2 efflux in warmed plots increased by 32.9% in comparison to that in unwarmed plots without extra precipitation and by 14.5% with doubled precipitation (22.9% on average, Figure 3a). Doubled precipitation increased soil CO_2 efflux by an average of 9.0% compared to those without extra precipitation treatments (Figure 3a and Table 2). No significant interaction was detected between warming and doubled precipitation ($p = 0.121$).

[24] Soil temperature at the depth of 5 cm in warmed plots increased significantly by 2.97°C compared to that in unwarmed plots without extra precipitation and by 2.50°C

Table 3. Results of T-Test Showing *t* Values and Levels of Significance for Response of Coefficients *a* and *b* to Warmed, Doubled Precipitation, and Clipped Treatments[a]

	Experiment 1		Experiment 2		Transient Study	
Factor	t_a	t_b	t_a	t_b	t_a	t_b
W	0.614	−0.588	2.175^{b}	-2.476^{c}	0.239	−0.616
PPT	na	na	−0.456	0.848	1.767	−1.484
CL	−0.244	−0.506	na	na	0.514	-2.076^{b}
W × PPT	na	na	−0.836	0.508	−0.126	−0.429
W × CL	−0.354	0.524	na	na	-2.482^{b}	2.024^{b}
PPT × CL	na	na	na	na	1.044	−1.224
W × PPT × CL	na	na	na	na	−1.341	1.348

[a] W, warmed; PPT, doubled precipitation, CL, clipped; na, not applicable.
[b] Here $p < 0.05$.
[c] Here $p < 0.01$.

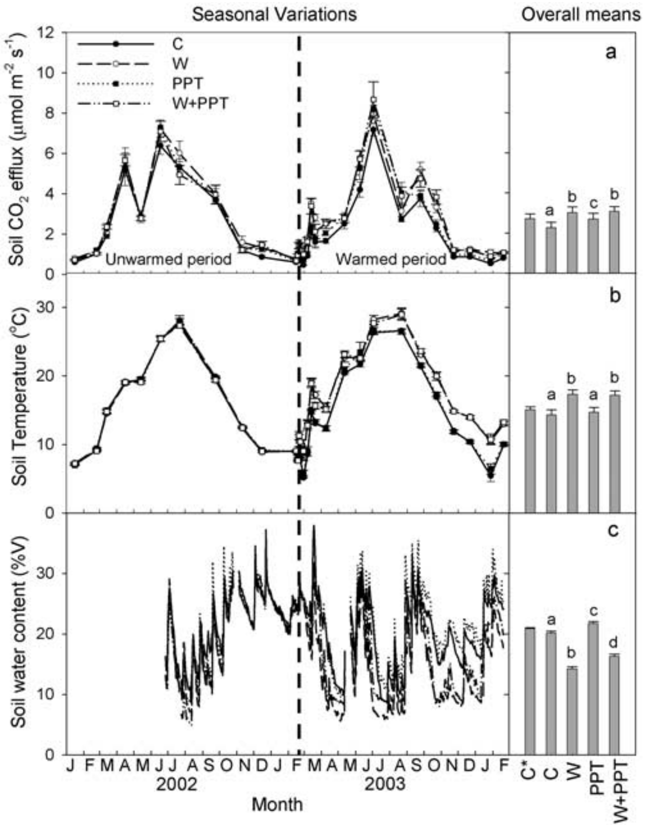

Figure 3. Seasonal variations and overall means of (a) soil CO$_2$ efflux, (b) soil temperature at the depth of 5 cm, and (c) soil water content of 0–15 cm in Experiment 2 from January 2002 to February 2003. Vertical bars represent the standard error of the mean (n = 5). The dashed vertical line indicates the day when warming and precipitation treatments started. C, control; W, warmed; PPT, doubled precipitation; W + PPT, warmed plus doubled precipitation. C* refers to overall means from all pretreatment plots before 20 February 2003.

with doubled precipitation based on monthly daytime measurements ($p < 0.0001$, Figure 3b). Our continuous measurements showed that warming increased daily mean soil temperature by 4.4°C at the depth of 2 cm (Table 1). Soil moisture (0–15 cm) fluctuated greatly owing to highly variable rainfall (Figure 3c). Warming significantly decreased soil moisture by 29.4% without extra precipitation and by 25.1% with doubled precipitation. Doubled precipitation increased soil moisture approximately by 2% volumetrically in both warmed and unwarmed plots (Figure 3c).

[25] On the basis of the temperature relationship of soil CO$_2$ efflux in equation (1), soil temperature accounted for more than 57% of variation in soil CO$_2$ efflux (Figure 4). The apparent Q_{10} values decreased from 2.51 in unwarmed plots to 2.02 in warmed plots without extra precipitation and from 2.57 to 2.23 with doubled precipitation. However, coefficient a had an opposite response to warming in comparison to the apparent Q_{10}, being higher under warming. T-test analysis indicated that warming significantly affected coefficients a or b in opposite directions, while doubled precipitation and its interaction with warming did not significantly affect coefficients a or b (Table 3).

3.3. Substrate Effects in the Transient Study

[26] Clipping significantly reduced average soil CO$_2$ efflux by 27.0% and 22.2% in warmed and warmed plus doubled precipitation treatments, respectively, but had no significant effect in the control and doubled precipitation (16.1% on average, Figure 5). During the period of the transient study, warming significantly increased soil CO$_2$ efflux by 44.5% and 39.3% without and with doubled precipitation, respectively, in unclipped subplots and by 9.0% and 14.1% in clipped subplots (26.6% on average, $p < 0.001$, Figure 5c). Doubled precipitation did not alter soil CO$_2$ efflux in either unclipped or clipped subplots. Interactive effects of warming × clipping and clipping × sampling dates were statistically significant on soil CO$_2$ efflux (Table 2).

[27] Soil temperature and soil moisture were not significantly affected by clipping in any of the four treatments ($p > 0.1$). Warming significantly increased soil temperature and reduced soil water content ($p < 0.001$, Figures 5d, 5e, 5f, 5g,

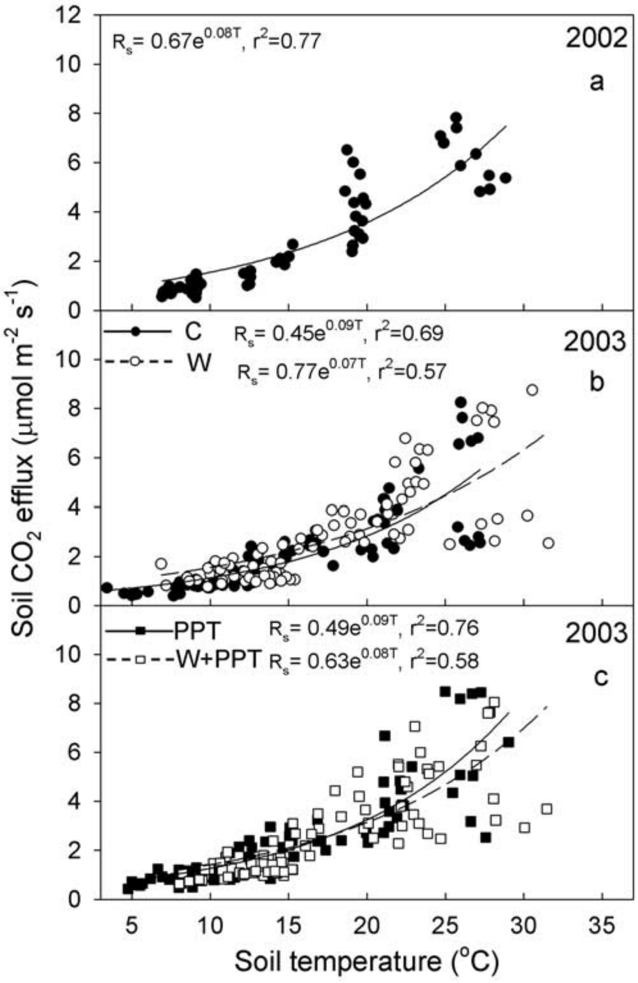

Figure 4. Exponential relationships between soil CO$_2$ efflux and soil temperature in Experiment 2 (a) in 2002, (b) without extra precipitation in 2003, and (c) with doubled precipitation in 2003. See Figure 3 for abbreviations.

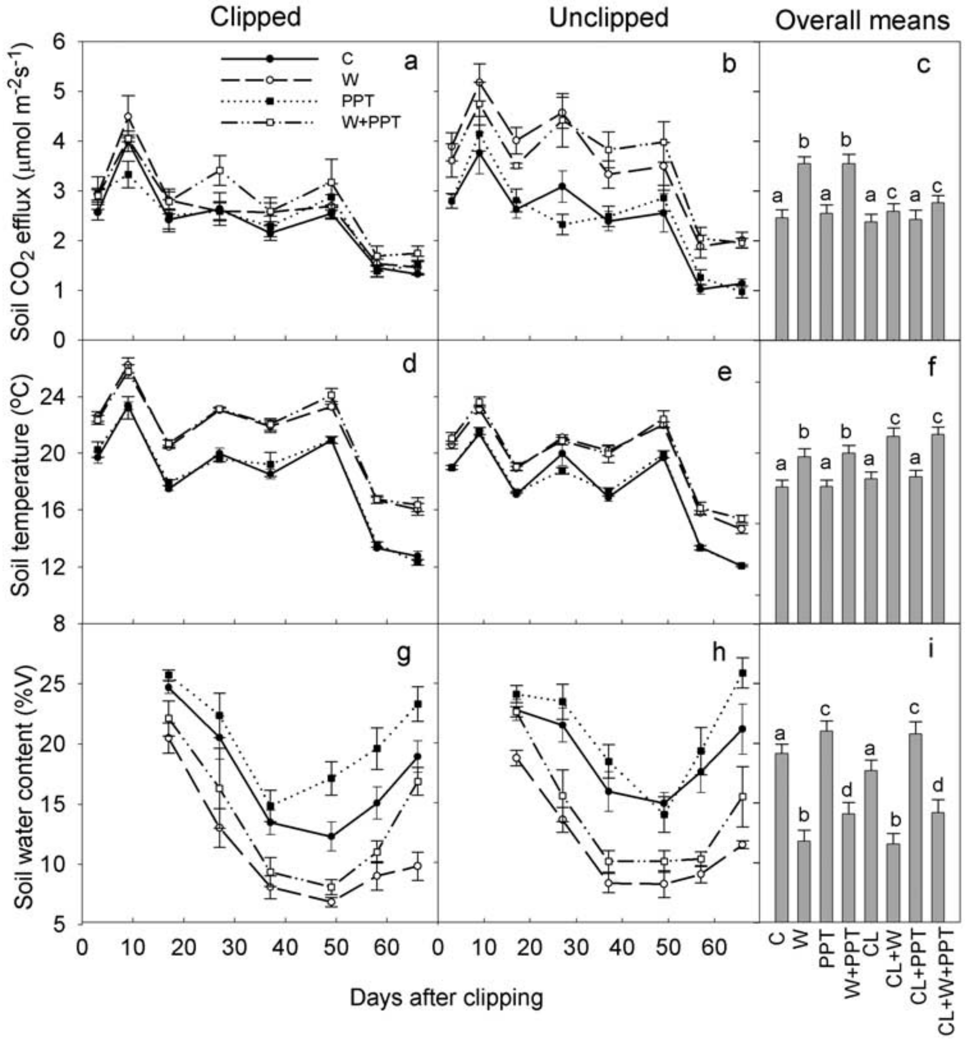

Figure 5. Variations and overall means of (a, b, and c) soil CO$_2$ efflux, (d, e, and f) soil temperature at the depth of 5 cm, and (g, h, and i) soil water content of 0–15 cm after clipping in the transient study. Vertical bars represent the standard error of the mean (n = 5). C, control; W, warmed; PPT, doubled precipitation; CL, clipped.

5h, and 5i), whereas doubled precipitation had no effects on either soil temperature or moisture ($p > 0.1$).

[28] Clipping significantly decreased the temperature sensitivity of soil CO$_2$ efflux (Figure 6). However, the clipping effects on the temperature sensitivity varied with warming treatments, leading to significant interactions between clipping and warming in influencing coefficient *b* (Tables 3).

3.4. Estimated Annual Soil CO$_2$ Efflux

[29] In Experiment 1, annual soil CO$_2$ emissions ranged from 782 to 927 g C m^{-2} yr^{-1} for the four treatments (Table 4). Warming increased annual soil CO$_2$ efflux by 10.9% in unclipped plots and by 17.0% in clipped plots. In Experiment 2, warming increased annual soil CO$_2$ efflux by 28.7% without extra precipitation and by 15.1% with doubled precipitation. Doubled precipitation also increased annual soil CO$_2$ efflux by 15.4% compared to that in the control. However, a large difference existed between 2002 and 2003 in the control plots of Experiment 2 (Table 4), largely owing to differences in precipitation between the two years.

4. Discussion

[30] Prediction of ecosystem responses to multifactor global changes in a future world strongly relies on our understanding of their interactions. Our study showed that among the three factors that we examined in our experiments, warming and doubled precipitation had significant main effects on soil CO$_2$ efflux, whereas the main effect of clipping was significant only in the transient study. The interactive effects of the three factors were not significant except for warming × clipping in the transient study. The temperature sensitivity of soil CO$_2$ efflux significantly decreased under the warming treatment in Experiment 2 and under the clipping treatment in the transient study. Below we discuss magnitude of soil CO$_2$ efflux, main effects of single factors, and interactive effects of multiple factors.

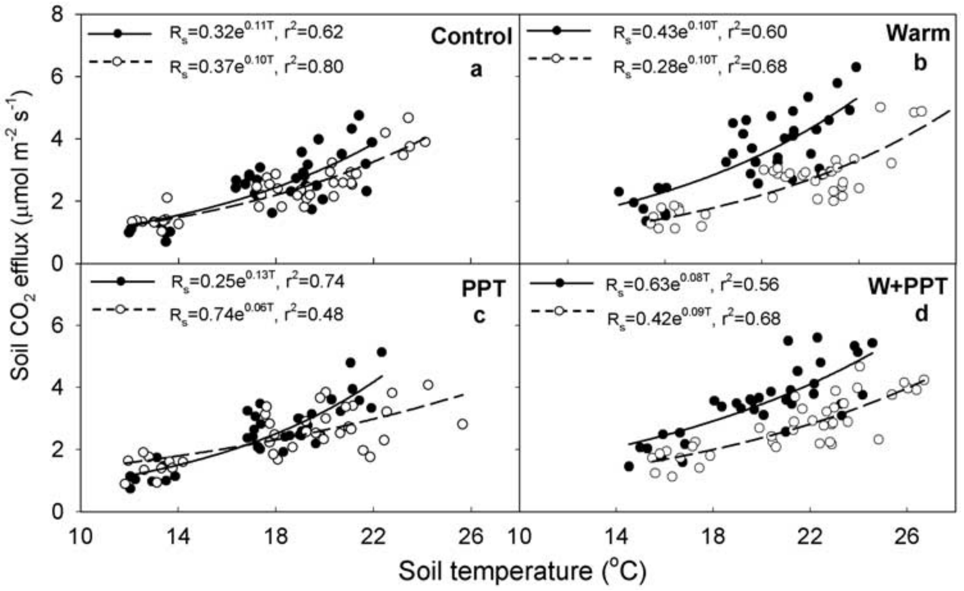

Figure 6. Exponential relationships between soil CO$_2$ efflux and soil temperature for unclipped (solid line with solid circles) and clipped (dashed line with open circles) treatments in (a) control, (b) warmed, (c) doubled precipitation, and (d) warmed plus doubled precipitation treatments in the transient study. See Figure 5 for abbreviations.

4.1. Magnitude of Soil CO$_2$ Efflux

[31] Soil CO$_2$ efflux measured in the control plots ranged from 0.52 to 7.64 μmol m^{-2} s^{-1}, which is comparable to previous measurements in grasslands [*Bremer et al.*, 1998; *Wan and Luo*, 2003]. Although annual soil CO$_2$ efflux is not the main focus of this study, our estimates are consistent with the studies on Konza Prairie [*Bremer et al.*, 1998] but greater than estimates of 340 to 480 g C m^{-2} yr^{-1} from less productive grasslands in California [*Luo et al.*, 1996]. Overall, our estimates fall within the upper limits of the estimates which range from 160 to 1060 g C m^{-2} yr^{-1} in North America and Europe [*Hanson et al.*, 1993]. The difference in annual precipitation (890 mm in 2002 and 647 mm in 2003) likely contributed to the significant difference in annual soil CO$_2$ efflux between 2002 and 2003 in the control plots of Experiment 2 (Table 4).

4.2. Main Effects of Single Factors on Soil CO$_2$ Efflux

[32] The increase in soil CO$_2$ efflux in response to warming has been observed in various ecosystems [*Rustad et al.*, 2001]. The short-term response to warming in Experiment 2 is similar to those observed in a temperate forest [*McHale et al.*, 1998] and a boreal pine forest [*Niinistö et al.*, 2004]. The observed increase of soil CO$_2$ efflux in our study is 0.74 μmol m^{-2} s^{-1}, which is slightly lower than the mean increase of 1.20 μmol m^{-2} s^{-1} in the first-year warming from a meta-analysis of 17 ecosystem warming experiments [*Rustad et al.*, 2001]. The increased respiration likely resulted from enhanced oxidation of labile soil carbon compounds on warmed plots [*Peterjohn et al.*, 1993; *Lin et al.*, 2001].

[33] The long-term response of soil CO$_2$ efflux to warming is regulated by acclimatization [*Luo et al.*, 2001], physiological adjustments to pool size changes by plants and microbes [*Melillo et al.*, 2002], extension of growing seasons [*Dunne et al.*, 2002; *Wan et al.*, 2005], and stimulated C$_4$ plant productivity [*Wan et al.*, 2005]. In Experiment 1, soil CO$_2$ efflux increased by 9.9% in the fourth year (Figure 2), by 8.0% and 15.6% in the third and second year, respectively [*Wan et al.*, 2005], and decreased by 5% in the first year [*Luo et al.*, 2001]. The increases in soil CO$_2$ efflux observed in this study are lower than the 20% mean increase reported from a meta-analysis [*Rustad et al.*, 2001]. The meta-analysis synthesized studies mainly from high latitude regions. The year-to-year variation in warming-induced changes in soil CO$_2$ efflux observed in Experiment 1 likely resulted from changes in productivity [*Wan et al.*, 2005] and other abiotic factors such as drought.

Table 4. Annual Soil CO$_2$ Efflux in Experiment 1 With Warmed (W) and Clipped (CL) Treatments and Experiment 2 With Warmed (W) or Doubled Precipitation (PPT) Treatments[a]

Year	Treatments	Annual Soil CO$_2$ Efflux, g C m^{-2} yr^{-1}
	Experiment 1	
2003	C	835 ± 73
2003	W	927 ± 87
2003	CL	782 ± 67
2003	W + CL	915 ± 80
	Experiment 2	
2002	Control[b]	1131 ± 93
2003	C	877 ± 69
2003	W	1129 ± 70
2003	PPT	1013 ± 85
2003	W + PPT	1166 ± 107

[a] Data shown by mean ±1 SE. W, warmed, CL, clipped; PPT, doubled precipitation.

[b] Refers to the result calculated from the average in all pretreatment plots.

The lower response of soil CO_2 efflux to warming observed in our experiments is likely related to the fact that our grassland has lower soil organic C content than other ecosystems [*Luo et al.*, 2001].

[34] This study demonstrated that warming significantly increased basal respiration rate (coefficients *a*) and decreased temperature sensitivity of soil CO_2 efflux (coefficient *b*) in Experiment 2, whereas neither of the parameters was significantly altered by warming in Experiment 1 (Table 3). The different responses of the two parameters to warming between the experiments may be due to a few reasons. First, the temperature increase was $\sim$ 2°C in Experiment 1 and 4.4°C in Experiment 2. Thus the experimental forcing was stronger in Experiment 2 than in Experiment 1. Second, Experiment 1 was in the fourth year. Ecosystem processes may adjust to warming treatment over time [*Melillo et al.*, 2002]. After 3-year warming in Experiment 1, labile carbon could be in a steady state between supply and depletion (A. Tedla and Y. Luo, unpublished data, 2003). In addition, the shift in soil microbial community structure toward more fungi [*Zhang et al.*, 2005] likely resulted in lower sensitivity of soil CO_2 efflux to temperature because fungi are more tolerant of higher soil temperature and drying owing to their filamentous nature. The opposite responses of coefficients *a* and *b* to warming could result from changes in root phenology and acclimation of roots and microbes to climate [*Janssens and Pilegaard*, 2003].

[35] Doubled precipitation significantly increased soil CO_2 efflux in Experiment 2 (Table 2), greatly owing to stimulation of soil CO_2 efflux in the dry growing season of 2003 (Figure 3). Similar effects of additional water on soil CO_2 efflux have been observed in other experiments [*Laporte et al.*, 2002; *Liu et al.*, 2002]. During the period of the transient study, CO_2 efflux from soils was not significantly affected by doubled precipitation owing to the absence of water stress. Although the basal respiration rate and temperature sensitivity were not affected by doubled precipitation (Table 3), the apparent Q_{10} value in the control was significantly higher in 2003 than 2002 ($p < 0.05$), largely resulting from differences in precipitation. *Dörr and Münnich* [1987] found that the apparent Q_{10} values were low in the wet years and high in the dry years in a multiyear study of a grassland and a beech-spruce forest in Germany. However, others found that the apparent Q_{10} values were lower in the well-drained sites than the wetter sites [*Davidson et al.*, 1998; *Xu and Qi*, 2001]. Complex interactions between soil water and temperature, which influence CO_2/O_2 diffusion, root and microbial activities, could result in these diverse responses of the temperature sensitivity of soil CO_2 efflux to water availability.

[36] A large portion of soil CO_2 efflux is derived from recently fixed carbon, thus making it responsive to changes in carbon supply due to clipping, girdling, and shading [*Craine et al.*, 1999; *Högberg et al.*, 2001; *Wan and Luo*, 2003]. Clipping reduces soil CO_2 efflux by 19% to 49% in grassland ecosystems [*Bremer et al.*, 1998; *Craine et al.*, 1999; *Wan and Luo*, 2003]. Our study showed that yearly clipping had no significant effects on soil CO_2 efflux in the fourth year of Experiment 1 and clipping significantly reduced soil CO_2 efflux in the transient study within two months (Figures 1 and 5 and Table 2). In Experiment 1, we evaluated the effect of yearly clipping against monthly measurements of soil CO_2 efflux over a whole year. The treatment of yearly clipping in our study likely has less impact on soil CO_2 efflux than mowing several times per year. However, the transient effects of clipping were examined within 2 months in the transient study. In addition, *Wan and Luo* [2003] kept clipping aboveground biomass to maintain bare ground in the clipped plots during the whole study period of one year, leading to a 33% decrease in mean soil CO_2 efflux. Thus frequency of clipping and durations of study can be sources of variable results. Our transient study showed that clipping significantly reduced respiratory sensitivity to temperature (Table 3), similar to the results in other studies both from the laboratory [*Townsend et al.*, 1997] and field experiments [*Boone et al.*, 1998; *Wan and Luo*, 2003].

4.3. Interactive Effects of Warming, Precipitation, and Clipping

[37] Global climate change in the real world involves changes in multiple factors [*Shaw et al.*, 2002; *Norby and Luo*, 2004]. Therefore the effects of warming on terrestrial ecosystems must be evaluated in combination with other factors. In this study, we found that interactive effects of warming, precipitation, and clipping on soil CO_2 efflux were minor except for the warming × clipping interaction in the transient study. Minor interactive effects among multiple global change factors on soil CO_2 efflux have been reported in the literature. For example, *Edwards and Norby* [1998] and *Niinistö et al.* [2004] did not find interactive effects of elevated CO_2 and temperature on soil CO_2 efflux statistically significant. Similarly, there were no significant interactions among elevated CO_2, nitrogen supply, and plant diversity on soil CO_2 efflux [*Craine et al.*, 2001] and between elevated CO_2 and O_3 [*Kasurinen et al.*, 2004]. However, significant interactive effects of elevated CO_2 and warming were found on "old" pool C decomposition in a warming-CO_2-N experiment in tunnels with ryegrass swards [*Loiseau and Soussana*, 1999]. The interaction was largely regulated by N supply.

[38] The lack of significant interactive effects in Experiment 1 suggest that soil CO_2 efflux was determined by warming and yearly clipping treatments in a statistically independent manner. Warming increased soil CO_2 efflux while yearly clipping decreased it. The effect size of the warming plus yearly clipping treatment was between that of the warming treatment and the one of the yearly clipping treatment. The insignificant interaction between warming and doubled precipitation in Experiment 2 resulted largely from the anomalously low precipitation in 2003. Precipitation was 647 mm, which was 29.3% less than the average (915 mm). The long period of drought in June and July (34 days without rain) negated the doubled precipitation treatment. A heavy rain of 108.0 mm in two days on 30–31 August 2003 resulted in substantial water loss through surface runoff. Although doubled precipitation increased soil water content by 10.6% and soil CO_2 efflux by 9.0% relative to those without extra precipitation treatments, high

Table A1. Coefficient *a* or *b* and Their Standard Errors for Calculating *t* Values of Main and Interactive Effects Between Two Factors[a]

	Treatment Level 1 of Factor 1	Treatment Level 2 of Factor 2	Average: Factor 2
Treatment level 1 of factor 2	$x_{11} \pm S_{11}$	$x_{21} \pm S_{21}$	$\overline{x_{.1}}$
Treatment level 2 of factor 2	$x_{12} \pm S_{12}$	$x_{22} \pm S_{22}$	$\overline{x_{.2}}$
Average: factor 1	$\overline{x_{1.}}$	$\overline{x_{2.}}$	

[a]Terms: x_{ijk}, values of coefficients *a* or *b* ($i, j = 1, 2$); S_{ij}, standard errors of coefficients *a* or *b* in different treatments; $\overline{x_{i..}}$, a mean of treatment level *i* of factor 1; $\overline{x_{.j.}}$, a mean of treatment level *j* of factor 2.

variability in rainfall events in our ecosystem did not generate statistically significant interaction. In addition, our monthly measurements may not detect fast transient responses of soil CO_2 efflux to individual rainfall events [*Liu et al.*, 2002]. Thus we do expect that soil water content and temperature interactively regulate soil CO_2 efflux under different circumstances in spite of the fact that we did not detect significant interactions between them in this particular study.

[39] An interactive response to warming and clipping was observed on soil CO_2 efflux and its temperature sensitivity in the transient study (Tables 2 and 3). Clipping immediately reallocated assimilate to regrowth of shoots [*Bremer et al.*, 1998; *Craine et al.*, 1999] and reduced supply of current photosynthates to roots and their mycorrhizal fungi [*Högberg et al.*, 2001]. As a consequence, soil respiration decreases. However, experimental warming accelerated plant regrowth in comparison with that in unwarmed plots after clipping either with or without doubled precipitation. Thus warming made soil CO_2 efflux more responsive to clipping, contributing to the observed significant interaction during the transient period. In addition, complex and unpredictable interactions do occur in regulating soil CO_2 efflux in other ecosystems [*Loiseau and Soussana*, 1999] or other ecosystem attributes such as biomass growth [*Shaw et al.*, 2002]. A mechanistic understanding of interactions of warming and other global change factors on soil CO_2 efflux also requires study of root and microbial processes, which may have different sensitivities to temperature and other factors in complex soil physical and chemical environments.

5. Conclusions

[40] This study investigated the main and interactive effects of warming, doubled precipitation, and clipping on soil CO_2 efflux and its temperature sensitivity in a tallgrass prairie of central Oklahoma. The main effects of warming and doubled precipitation were significant on soil CO_2 efflux. Clipping significantly decreased soil CO_2 efflux in the transient study but not in the long-term warming experiment. Our statistical analysis showed no significant interactive effects of the three factors on soil CO_2 efflux or its temperature sensitivity except for the warming × clipping in the transient study. The minor interactive effects observed in this study suggest that results from single-factor experiments are useful in informing us of potential responses of soil CO_2 efflux to multifactor global change, at least in our ecosystem. It is yet to be examined whether our conclusion on minor interactive effects could be generalized across ecosystems. Regardless, this study posed testable hypotheses, which can be examined in other ecosystems. Furthermore, the statistical methods used in this study to rigorously detect interactive effects of global change factors are useful for other multifactor experiments.

Appendix A: Statistical Tests of Regression Coefficients

[41] We tested the significance of coefficients *a* and *b* of equation (1) in the temperature-respiration relationship primarily according to methods presented by *Toutenburg* [2002]. Table A1 is an array of coefficients *a* or *b* and standard errors for calculating *t* values of main and interactive effects between two factors: warming versus precipitation and warming versus clipping.

[42] The *t* value of the main effects was calculated for factor 1 by

$$t = \frac{\overline{x_{2.}} - \overline{x_{1.}}}{\sqrt{\frac{\sum S_{ij}^2}{4}}} \qquad (i, j = 1, 2). \tag{A1}$$

Similarly, the *t* values for factor 2 was also calculated by equation (A1) with $\overline{x_{.1}}$ and $\overline{x_{.2}}$. The *t* value of the interactive effects of factor 1 and factor 2 on coefficients *a* and *b* was calculated by

$$t = \frac{\frac{x_{11} + x_{22} - x_{12} - x_{21}}{2}}{\sqrt{\frac{\sum S_{ij}^2}{4}}} \qquad (i, j = 1, 2). \tag{A2}$$

[43] For the three-way factorial experiment with warming, precipitation (ppt), and clipping, coefficients *a* or *b* and

Table A2. Coefficient *a* or *b* and Their Standard Errors for Calculating *t* Values of Main and Interactive Effects Between Three Factors[a]

	Treatment Level 1 of Factor 1: Unclipped		Treatment Level 2 of Factor 1: Clipped		
	Treatment Level 1 of Factor 2: Ambient, ppt	Treatment Level 2 of Factor 2: Double, ppt	Treatment Level 1 of Factor 2: Ambient, ppt	Treatment Level 2 of Factor 2: Double, ppt	Average: Factor 3
Treatment level 1 of factor 3: Unwarmed	$x_{111} \pm S_{111}$	$x_{121} \pm S_{121}$	$x_{211} \pm S_{211}$	$X_{221} \pm S_{221}$	$\overline{x_{..1}}$
Treatment level 2 of factor 3: Warmed	$x_{112} \pm S_{112}$	$x_{122} \pm S_{122}$	$x_{212} \pm S_{212}$	$X_{222} \pm S_{222}$	$\overline{x_{..2}}$
Average: factor 1	$\overline{x_{1..}}$		$\overline{x_{2..}}$		
Average: factor 2	$\overline{x_{.1.}}$			$\overline{x_{.2.}}$	

[a]Terms: x_{ijk}, values of coefficients *a* or *b* ($i, j, k = 1, 2$); S_{ijk}, standard errors of coefficients *a* or *b* in different treatments; $\overline{x_{i..}}$, a mean of treatment level *i* of clipping; $\overline{x_{.j.}}$, a mean of treatment level *j* of precipitation; $\overline{x_{.k.}}$, a mean of treatment level *k* of warming.

their standard errors can be arranged as follows to calculate t values of main and interactive effects, as shown in Table A2.

[44] The t values of the main effects of clipping, precipitation, and warming were calculated by equation (A1) with $\overline{x_{i..}}$, $\overline{x_{.j.}}$, or $\overline{x_{..k}}$, and $\sqrt{\frac{\sum S_{ijk}^2}{16}}$. The t value of the 2-way interactive effect of factor 1 (clipping) and factor 2 (precipitation) was calculated by

$$t = \frac{\dfrac{\sum x_{11k} + \sum x_{22k} - \sum x_{12k} - \sum x_{21k}}{4}}{\sqrt{\dfrac{\sum S_{ijk}^2}{16}}} \qquad (i,j,k = 1,2). \tag{A3}$$

Similarly, the t values of the interactive effects of clipping and warming, or of precipitation and warming were calculated by equation (A3) with $\sum x_{1j1} + \sum x_{2j2} - \sum x_{1j2} - \sum x_{2j1}$ or $\sum x_{i11} + \sum x_{i22} - \sum x_{i12} - \sum x_{i21}$, respectively.

[45] The t value of the 3-way interactive effects of clipping, precipitation, and warming on coefficients a or b was calculated by

$$t = \frac{\dfrac{x_{112} + x_{121} + x_{211} + x_{222} - x_{111} - x_{122} - x_{212} - x_{221}}{4}}{\sqrt{\dfrac{\sum S_{ijk}^2}{16}}} \qquad (i,j,k = 1,2). \tag{A4}$$

[46] **Acknowledgments.** The authors thank the two anonymous reviewers for their insightful comments, Nancy A. Zehrbach for maintaining the experimental infrastructure and for assistance with field measurements; and Jesse Bell for help with soil moisture data. This research was financially supported by US National Science Foundation (NSF) under DEB 0078325 and by the Terrestrial Carbon Program at the Office of Science, US Department of Energy, under DE-FG03-99ER62800.

References

Boone, R. D., K. J. Nadelhoffer, J. D. Canary, and J. P. Kaye (1998), Roots exert a strong influence on the temperature sensitivity of soil respiration, *Nature*, *396*, 570–572.

Bremer, J. D., J. M. Ham, C. E. Owensby, and A. K. Knapp (1998), Responses of soil respiration to clipping and grazing in a tallgrass prairie, *J. Environ. Qual.*, *27*, 1539–1548.

Cox, P. M., R. A. Betts, C. D. Jones, S. A. Spall, and I. J. Totterdell (2000), Acceleration of global warming due to carbon-cycle feedbacks in a coupled model, *Nature*, *408*, 184–187.

Craine, F. M., D. A. Wedin, and F. S. Chapin III (1999), Predominance of ecophysiological controls on soil CO_2 flux in a Minnesota grassland, *Plant Soil*, *207*, 77–86.

Cramer, W., et al. (2001), Global response of terrestrial ecosystem structure and function to CO_2 and climate change: Results from six dynamic global vegetation models, *Global Change Biol.*, *7*, 357–374.

Davidson, E. A., E. Belk, and R. D. Boone (1998), Soil water content and temperature as independent or confound factors controlling soil respiration in a temperature mixed hardwood forest, *Global Change Biol.*, *4*, 217–227.

Dörr, H., and K. O. Münnich (1987), Annual variation in soil respiration in selected areas of the temperate zone, *Tellus, Ser. B*, *39*, 114–121.

Dunne, J., J. Harte, and K. Taylor (2002), Response of subalpine meadow plant reproductive phenology to manipulated climate change and natural climate variability, *Ecol. Monogr.*, *73*, 69–86.

Edwards, N. T., and R. J. Norby (1998), Below-ground respiratory responses of sugar maple and red maple saplings to atmospheric CO_2 enrichment and elevated air temperature, *Plant Soil*, *206*, 85–97.

Hanson, P. J., S. D. Wullschleger, S. A. Bohlman, and D. E. Todd (1993), Seasonal and topographic patterns of forest floor CO_2 efflux from an upland oak forest, *Tree Physiol.*, *13*, 1–15.

Harper, C. W., J. M. Blair, P. A. Fay, A. K. Knapp, and J. D. Carlisle (2005), Increased rainfall variability and reduced rainfall amount decreases soil CO_2 efflux in a grassland ecosystem, *Global Change Biol.*, *11*, 322–334.

Högberg, P., A. Nordgren, N. Buchmann, A. F. S. Taylor, A. Ekblad, M. N. Högberg, G. Nyberg, M. Ottosson-Löfvenius, and D. J. Read (2001), Large-scale forest girdling shows that current photosynthesis drives soil respiration, *Nature*, *411*, 789–792.

Intergovernmental Panel on Climate Change (2001), *Climate Change 2001: The Scientific Basis*, edited by H. T. Houghton et al., Cambridge Univ. Press, New York, USA.

Janssens, I. A., and K. Pilegaard (2003), Large seasonal changes in Q_{10} of soil respiration in a beech forest, *Global Change Boil.*, *9*, 911–918.

Kasurinen, A., P. Kokko-Gonzales, J. Riikonen, E. Vapaavuori, and T. Holopainen (2004), Soil CO_2 efflux of two silver birch clones exposed to elevated CO_2 and O3 levels during three growing seasons, *Global Change Biol.*, *10*, 1654–1665.

Kunkel, K. E., K. Andsager, and D. R. Easterling (1999), Long-term trends in extreme precipitation events over the conterminous United States and Canada, *J. Clim.*, *12*, 2515–2527.

Laporte, M. F., L. C. Duchesne, and S. Wetzel (2002), Effect of rainfall patterns on soil surface CO_2 efflux, soil moisture, soil temperature and plant growth in a grassland ecosystem of northern Ontario, Canada: Implications for climate change, *BMC Ecol.*, *2*(10), 1–6.

Lin, G., P. T. Rygiewicz, J. R. Ehleringer, M. G. Johnson, and D. T. Tingey (2001), Time-dependent responses of soil CO_2 efflux components to elevated atmospheric [CO_2] and temperature in experimental forest mesocosms, *Plant Soil*, *229*, 259–270.

Liu, X., S. Wan, B. Su, D. Hui, and Y. Luo (2002), Response of soil CO_2 efflux to water manipulation in a tallgrass prairie ecosystem, *Plant Soil*, *240*, 213–223.

Loiseau, P., and J. F. Soussana (1999), Elevated CO_2, temperature increase and N supply effects on the turnover of belowground carbon in a temperate grassland ecosystem, *Plant Soil*, *210*, 233–247.

Long, S. P., and P. R. Hutchin (1991), Primary production in grasslands and coniferous forests with climate change: An overview, *Ecol. Appl.*, *1*, 139–156.

Luo, Y., R. B. Jackson, C. B. Field, and H. A. Mooney (1996), Elevated CO_2 increases belowground respiration in California grasslands, *Oecologia*, *108*, 130–137.

Luo, Y., S. Wan, D. Hui, and L. Wallace (2001), Acclimatization of soil respiration to warming in a tall grass prairie, *Nature*, *413*, 622–625.

McHale, P. J., M. J. Mitchell, and F. P. Bowles (1998), Soil warming in a northern hardwood forest: Trace gas fluxes and leaf litter decomposition, *Can. J. For. Res.*, *28*, 1365–1372.

Melillo, J. M., et al. (2002), Soil warming and carbon-cycle feedbacks to the climate system, *Science*, *298*, 2173–2176.

Niinistö, S. M., J. Silvola, and S. Kellomäki (2004), Soil CO_2 efflux in a boreal pine forest under atmospheric CO_2 enrichment and air warming, *Global Change Biol.*, *10*, 1363–1376.

Norby, R. J., and Y. Luo (2004), Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world, *New Phytol.*, *162*, 281–293.

Peterjohn, W. T., J. M. Melillo, and S. T. Bowles (1993), Soil warming and trace gas fluxes: Experimental design and preliminary flux results, *Oecologia*, *93*, 18–24.

Raich, J. W., and C. S. Potter (1995), Global patterns of carbon dioxide emissions from soils, *Global Biogeochem. Cycles*, *9*, 23–36.

Raich, J. W., and W. H. Schlesinger (1992), The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus, Ser. B*, *44*, 81–99.

Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, and J. Gurevitch (2001), A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming, *Oecologia*, *126*, 543–562.

Shaw, M. R., E. S. Zavaleta, and N. R. Chiariello (2002), Grassland responses to global environmental changes suppressed by elevated CO_2, *Science*, *298*, 1987–1990.

Tarr, E., J. G. Botkin, E. L. Rice, E. Carpenter, and M. Hart (1980), A broad analysis of fifteen sites in the tall-grass prairie of Oklahoma, *Proc. Okla. Acad. Sci.*, *60*, 39–42.

Toutenburg, H. (2002), *Statistical Analysis of Designed Experiments*, Springer, New York.

Townsend, A. R., P. M. Vitousek, D. J. Desmarais, and A. Tharpe (1997), Soil carbon pool structure and temperature sensitivity inferred using CO_2 and $^{13}CO_2$ incubation fluxes from five Hawaiian soils, *Biogeochemistry*, *38*, 1–17.

U.S. Department of Agriculture (1979), Soil survey of McClain County, Oklahoma, report, Okla. Agric. Exp. Stn., Stillwater.

Wan, S., and Y. Luo (2003), Substrate regulation of soil respiration in a tallgrass prairie: Results of a clipping and shading experiment, *Global Biogeochem. Cycles*, *17*(2), 1054, doi:10.1029/2002GB001971.

Wan, S., Y. Luo, and L. L. Wallace (2002), Changes in microclimate induced by experimental warming and clipping in tallgrass prairie, *Global Change Biol.*, *8*, 754–768.

Wan, S., D. Hui, L. L. Wallace, and Y. Luo (2005), Direct and indirect warming effects on ecosystem carbon processes in a tallgrass prairie, *Global Biogeochem. Cycles*, *19*, GB2014, doi:10.1029/2004GB002315.

Woodwell, G. M., F. T. Mackenzie, R. A. Houghton, M. Apps, E. Gorham, and E. Davidson (1998), Biotic feedback in the warming of the earth, *Clim. Change*, *40*, 495–518.

Xu, L., D. D. Baldocchi, and J. Tang (2004), How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature, *Global Biogeochem. Cycles*, *18*, GB4002, doi:10.1029/2004GB002281.

Xu, M., and Y. Qi (2001), Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California, *Global Change Biol.*, *7*, 667–677.

Zhang, W., K. Parker, Y. Luo, L. Wallace, and S. Hu (2005), Soil microbial responses to experimental atmospheric warming and clipping in a tallgrass prairie, *Global Change Biol.*, *11*, 266–277.

Y. An, College of Agriculture and Biology, Shanghai Jiaotong University, Shanghai 201101, China.

Y. Luo, R. A. Sherry, L. L. Wallace, and X. Zhou, Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA. (zxuhui14@ou.edu)