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RESPONSES OF SOIL RESPIRATION AND ECOSYSTEM PRODUCTIVITY TO CLIMATE CHANGE IN SOUTHERN GREAT PLAINS

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RESPONSES OF SOIL RESPIRATION AND ECOSYSTEM PRODUCTIVITY TO CLIMATE CHANGE IN SOUTHERN GREAT PLAINS

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF BOTANY AND MICROBIOLOGY

BY

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To my lovely daughter, LUCY ZHOU

and her generation

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ABSTRACT

Terrestrial carbon processes, such as soil respiration and its components, net primary production (NPP), net ecosystem carbon exchange (NEE), and litterfall, are the important global change issues, which are related to carbon sequestration and ecosystem carbon-cycle feedback to climate change. This dissertation summarized four independent projects using experimental and modeling approaches. In the first study, I took advantage of two manipulative experiments – one long-term with a 2^{o}C increase and yearly clipping (Experiment 1) and one short-term with a 4.4^{o}C increase and doubled precipitation (Experiment 2) – to investigate main and interactive effects of warming, clipping, and doubled precipitation on soil respiration in a tallgrass prairie ecosystem. The transient responses to clipping were also studied in Experiment 2 (referred to as the transient study). On average, warming increased soil respiration 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. Doubled precipitation resulted in an increase of 9.0% (p < 0.05) in soil respiration in Experiment 2. Yearly clipping did not significantly affect soil respiration (p = 0.66) in Experiment 1, while clipping decreased soil respiration by 16.1% (p < 0.05) in the transient study. No significant interactive effects among the experimental factors were statistically found on soil respiration or their temperature sensitivities except for the warming×clipping interaction (p < 0.05) in the transient study. The 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 respiration to multi-factor global change, at least in our ecosystem.

In the second experiment, a long-term experiment was conducted to investigate effects of warming and yearly clipping on soil respiration and its components (autotrophic and heterotrophic respiration, R_A and R_H) in a tallgrass prairie ecosystem. Interannual variability of these fluxes was also examined. Using the deep-collar insertion to partition soil respiration, heterotrophic respiration accounted for approximately 66% of soil respiration over the six years. Warming treatment significantly stimulated soil respiration and its components (i.e., R_A and R_H) in most years. In contrast, yearly clipping significantly reduced soil respiration only in the last two years, although it decreased R_H in every year of the study. Temperature sensitivity (i.e., apparent Q_{10} values) of soil respiration was slightly lower under warming ($p>0.05$) and reduced considerably by clipping ($p<0.05$) compared to that in the control. However, warming did not change relative contributions of R_A or R_H to soil respiration. In addition, the apparent Q_{10} values for R_A were higher than those for R_H and soil respiration. Annual soil respiration did not vary substantially among years as precipitation did. The interannual variability of soil respiration may be mainly caused by precipitation distribution and summer severe drought. Our results suggest that the effects of warming and yearly clipping on soil respiration 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 respiration than the amount of

annual precipitation.

The third is to investigate the role of precipitation on ecosystem carbon processes (i.e., biomass, litterfall, and soil respiration) along a natural precipitation gradient in southern Great Plains. Our results show that aboveground biomass (AGB), standing litter (ST), surface litter (SU), and soil respiration often linearly increased with an increase in precipitation along the gradient, although belowground biomass (BGB) and total biomass did not largely change. BGB to AGB ratio and rain use efficiency (RUE) linearly decreased with increasing precipitation due to less plant allocation to roots and high biogeochemical constraints (e.g., nutrients or light), respectively, at mesic sites of the gradient. The one-year precipitation before samplings (OYP) had better correlations with biomass, litterfall, and soil respiration than mean annual precipitation (MAP). Soil respiration was not only affected by precipitation, but also regulated by litterfall in fall and winter and by AGB in spring, which were mainly controlled by precipitation. The results suggest that precipitation is an important driver in shaping ecosystem functioning by controlling soil water dynamics, which directly affects vegetation production and litterfall, and indirectly regulates soil respiration.

In the fourth study, a terrestrial ecosystem (TECO) model was used to examine nonlinear patterns of ecosystem responses to changes in temperature, CO_2, and precipitation individually or in combination. The TECO model was calibrated against experimental data obtained from a grassland ecosystem in central USA and ran for 100 years with gradual change at 252 different scenarios. The 100th-year results of

ecosystem responses were presented. Variables examined in this study are net primary productivity (NPP), Rh (heterotrophic respiration), net ecosystem carbon exchange (NEE), runoff, and evapotranspiration (ET). The modeling results show that nonlinear patterns were parabolic, asymptotic, and threshold-like in response to temperature, CO_2, and precipitation anomalies, respectively, for NPP, NEE, and Rh. Runoff and ET exhibited threshold-like pattern in response to both temperature and precipitation anomalies but were less sensitive to CO_2 changes. The combined two- or three-factor changes in temperature, CO_2, and precipitation considerably influenced nonlinearity of ecosystem responses by either changing patterns and/or shifting points of abrupt changes. Our results suggest that nonlinear patterns in response to multiple global change factors were diverse and considerably affected by combined climate anomalies on ecosystem carbon and water processes.

Keywords: global change, warming, precipitation, elevated CO_2, clipping, grassland, interaction, nonlinear, soil respiration, Q_{10}, heterotrophic respiration, net primary production, net ecosystem carbon excachange, litterfalll, runoff, evapotranspiration.

Chapter 1

Introduction

Global atmospheric concentrations of greenhouse gases such as CO_2, CH_4, and N_2O have increased dramatically since the industrial revolution at the end of the 18th century largely due to fossil fuel combustion and land use change (IPCC 2001). As a consequence of rising CO_2 and other greenhouse gases, the Earth's surface temperature has increased by 0.6°C in the 20th century and is expected to increase by 1.4 ~ 5.8°C by the end of this century due to the enhanced downward infrared radiation reflected by the earth's surface (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). Such rising CO_2 and warming are likely to alter patterns of global air circulation and hydrologic cycling that will change global and regional precipitation regimes (DelGenio *et al.* 1991, Trenberth 1999, Huntington 2006). Precipitation is anticipated to increase by about 0.5 to 1% per decade in this century globally as it happened in the last century (IPCC 2001). More importantly, heavy rainfall events may increase by 16-22% per decade in the southern Great Plains (Kunkel *et al.* 1999). The unprecedented changes in CO_2 concentration, temperature, and precipitation could profoundly alter ecosystem structure and function.

Land use practice such as mowing or clipping for hay in grasslands, which account for more than 20% of the global terrestrial ice-free surface (White *et al.* 2000) and 54% of the conterminous United States (USDA 1972), has widely been applied in the southern Great Plains. It may also have considerable effects on ecosystem processes (Leriche *et al.* 2003, Wan and Luo 2003, Bahn *et al.* 2006). Corresponding changes in air and soil temperature, atmospheric CO_2 concentration, and precipitation will co-occur with ongoing changes in land use and land cover, which are likely to alter ecosystem carbon cycling in terrestrial environments.

Soil respiration, also referred to as soil CO_2 efflux, represents CO_2 release at the soil surface from heterotrophic respiration during organic matter decomposition (R_H) and autotrophic respiration by live roots and their symbionts (R_A, Boone *et al.* 1998, Högberg *et al*. 2001, Wan and Luo 2003). This flux is the largest terrestrial source of

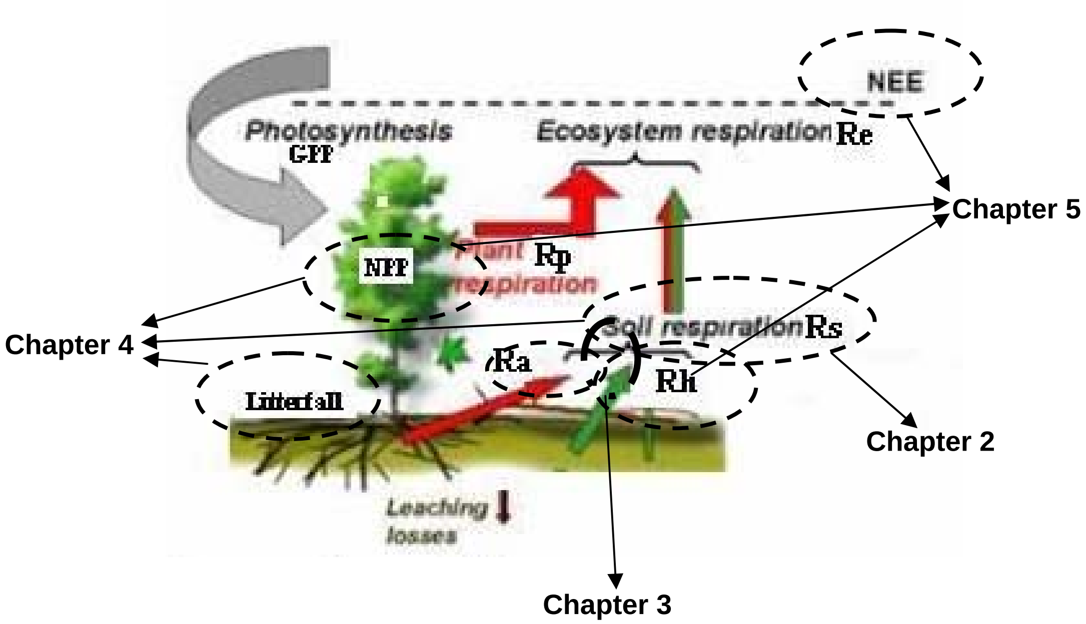

Fig. 1.1 Schematic diagram of ecosystem carbon processes. Circled are the processes focused in each chapter. GPP: gross primary production, NPP: net primary production, R_p: aboveground plant respiration, Ra: autotrophic root respiration, R_h: heterotrophic respiration, Rs: soil respiration, Re: ecosystem respiration, and NEE: net ecosystem exchange of CO_2.

CO_2 to the atmosphere, which is about 68 to 80 Pg C yr^{-1} on a global scale (Schlesinger 1977, Raich and Schlesinger 1992, Raich and Potter 1995, Raich *et al*. 2002). This is more than 10 times the current rate of fossil fuel combustion (Schlesinger 1997). Global modeling studies have demonstrated that even a small change in soil respiration could significantly exacerbate or mitigate the buildup of this greenhouse gas in the atmosphere (Cramer *et al.*, 2001), with consequent feedbacks to climate change (Kirshbaum 1995, 2000, Woodwell *et al*., 1998; Cox *et al*., 2000, Luo *et al.* 2001a). Furthermore, soil respiration is an integral part of the ecosystem carbon cycle and is closely related to various components of ecosystem production such as net primary production (NPP), net ecosystem exchange of CO_2 (NEE), and litterfall (Fig. 1.1, Luo and Zhou 2006). Global climate change can also potentially alter these ecosystem processes according to coupled carbon-climate models and manipulative experiments (Shave *et al.* 2000, Cramer *et al.* 2001, Weltzin *et al.* 2003). Therefore, understanding regulations of soil respiration and other terrestrial carbon processes by global environmental factors is a critical step toward projecting climate change in the future.

Concern about climate change and associated long-term impact on the earth has intensified research interest in the flux of carbon between terrestrial ecosystem and the atmosphere (Woodwell and Mackenzie 1995, IPCC 2001). Previous studies have shown that CO_2 efflux from soil varied largely with temperature (Peterjohn *et al.* 1993, McHale *et al.* 1998, Shaver *et al.* 2000, Rustad *et al*. 2001, Melillo *et al.* 2002, Verburg *et al.* 2005), moisture availability (Knapp *et al.* 2002, Liu *et al*. 2002, Lee *et al.* 2004, Xu *et al.* 2004, Harper *et al.* 2005), and substrate supply (Bremer *et al*. 1998, Craine *et al*. 1999, Craine and Wedin 2002). The majority of those studies that investigated responses of soil respiration to the above-mentioned variables have been carried out in single-factor experiments, although those results have considerably advanced our understanding of ecosystem responses to climate change. However, global change involves simultaneous changes in multiple factors, which could potentially have complex interactive influences on ecosystem structure and processes. Thus, understanding how ecosystems respond to multiple global change factors and how they interactively affect soil respiration are imperative.

Autotrophic root respiration (R_A) and heterotrophic component (R_H) contribute to soil respiration (Hanson *et al.* 2000, Kuzyakov 2006, Subke *et al.* 2006). 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 respiration respond differently to increasing temperature, especially in natural ecosystems. Partitioning soil respiration into R_A and R_H components becomes crucial for understanding their differential responses to climatic change. In contrast to climate warming, effects of land use practice on soil respiration have rarely been investigated (Davidson *et al.* 2000), and virtually nothing is known on how they influence components of grassland soil respiration (Hanson *et al*. 2000, Bond-Lamberty *et al*. 2004, Subke *et al.* 2006). Additionally, it is also not well known how climate warming and clipping would affect interannual variability of soil respiration and its components (i.e., R_A and R_H).

As we know, considerable research has been conducted to examine the effects of elevated temperature and CO_2 concentration on ecosystem structure and function (Koch and Mooney 1996, Shaver *et al.* 2000, Ainsworth and Long 2005). However, shifts in precipitation regimes may have an even greater impact on ecosystem dynamics than the singular or combined effects of rising CO_2 and temperature, especially in grassland ecosystems (Weltzin *et al.* 2003). How precipitation affects ecosystem carbon gain, reservoir, and loss (i.e., productivity, litterfall, and soil respiration) and how they are interactively regulated are largely limited.

In global change research, it is commonly acknowledged that ecosystem responses to global changes in temperature, CO_2 concentration, and precipitation are nonlinear. However, patterns of the nonlinearity have not been well characterized on ecosystem carbon and water processes. Currently, the majority of the experiments conducted at two discrete treatment levels were inadequate to examine nonlinearity. It is impossible to conduct manipulative experiments to examine nonlinear responses to simultaneous changes in multiple factors due to cost limitation and ecosystem complexities. Thus, it is urgently needed to examine nonlinear patterns in response to a range of potential future climates (e.g., temperature, CO_2, and precipitation) using modeling approach. These questions form the focus of this research shown in Fig. 1.1.

This dissertation is an attempt to address the effects of global change factors and land use practice on ecosystem carbon cycling (mainly soil respiration) in grassland ecosystems using three different approaches: warming manipulation, transect study, and modeling. More specifically, four objectives will be explored in this research. The first objective is to investigate how multifactor global change factors interactively affect soil respiration. To achieve this objective, two experiments, one long-term with a 2^{o}C increase and one short term with a 4.4^{o}C increase were conducted to investigate main and interactive effects of warming, clipping, and doubled precipitation on soil respiration and its temperature sensitivity. The second objective is to study effects of warming and clipping on soil respiration and its components (i.e., R_A and R_H) and on interannual variability of these fluxes. In this study, we will conduct a long-term warming and yearly clipping experiment to investigate effects on soil respiration and its components and interannual variability. The third objective is to evaluate the role of precipitation on ecosystem carbon processes along a natural precipitation gradient. A transect study will be conducted to investigate patterns of biomass, litterfall, and soil respiration along the gradient with the precipitation from 430 to 1200 mm. The fourth objective is to examine nonlinear patterns in response to changes in temperature, CO_2 concentration, and precipitation individually and in combination. To achieve this objective, we will use a terrestrial ecosystem (TECO) model to simulate 252 climate change scenarios with individual and combined changes in temperature, CO_2, and precipitation, and then present the nonlinear patterns.

The results from this research will help scientists and public to better understand effects of global change factors and land use practice (i.e., clipping) on the flux of carbon between grassland ecosystem and the atmosphere. The results may provide theoretical results that can serve as a guide for ecosystem service in a changing world. This work can be applicable for management of natural terrestrial carbon sinks and calculating CO_2 emission to trade carbon in the carbon mitigation market in the future. It is also important to feed this research back into the policy process.

This dissertation includes six chapters. Chapter 1 of the dissertation lays out the problem and significance of this research. Chapter 2 examines the main and interactive effects of warming, clipping, doubled precipitation on soil respiration. Chapter 3 addresses the study on source components and interannual variability of soil respiration under experimental warming and clipping. Chapter 4 explores patterns of biomass, litterfall, and soil respiration along a precipitation gradient in southern Great Plains. Chapter 5 presents nonlinear patterns of ecosystem carbon and water dynamics in response to gradual changes in temperature, CO_2 concentration, and precipitation using model approach. Chapter 6 of this dissertation provides conclusions of this research and implications for future work on global change research.

Chapter 2

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

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ABSTRACT

It is well documented that temperature, moisture, and substrate supply are three major factors affecting soil respiration. However, few studies have rigorously examined their interactive effects. We conducted two experiments – one long-term with a 2^{o}C increase (Experiment 1) and one short-term with a 4.4^{o}C increase (Experiment 2) – to investigate main and interactive effects of warming, clipping, and doubled precipitation on soil respiration and its temperature sensitivity in a tallgrass prairie of the US Great Plains. Infrared heaters were used to simulate climatic warming and clipping to mimic hay mowing. A 'rainfall collection pan' device was used to double precipitation in Experiment 2. Additionally, responses of soil respiration to abrupt reduction in substrate supply by clipping were studied in Experiment 2 (referred to as the transient study). On average, warming increased soil respiration 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. Doubled precipitation resulted in an increase of 9.0% ($p < 0.05$) in soil respiration in Experiment 2. Yearly clipping did not significantly affect soil respiration ($p = 0.66$) in Experiment 1, while clipping decreased soil respiration by 16.1% ($p < 0.05$) in the transient study. Temperature sensitivity of soil respiration 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 respiration 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 respiration to multi-factor global change, at least in our ecosystem. No matter if this conclusion can be generalized across ecosystems, this study poses testable hypotheses to be examined in other experiments.

***Keywords**:* Carbon cycle, global change, soil respiration, Q_{10}, interaction, warming, precipitation, clipping, substrate supply, tallgrass prairie.

2.1. Introduction

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 (Houghton *et al.* 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 (Houghton *et al.* 2001) and heavy rainfall events may increase by 16-22% per decade in the southern Great Plains, USA (Kunkel *et al.* 1999). Warmer temperature and increased precipitation would likely alter the fluxes of carbon from soil to the atmosphere (i.e., soil respiration).

Soil respiration, also referred to as soil CO_2 efflux, 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 *et al*. 2002). 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 respiration by major environmental factors is a critical step toward projecting climate change in the future.

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

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 multi-factor 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 respiration were not observed in other studies (Edwards and Norby 1998, Lin *et al*. 2001, Niinistö *et al*. 2004). Thus, evaluating multi-factor 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 multi-factor global change.

In this study, we took advantage of two on-going experiments to evaluate main and interactive effects of three factors – warming, clipping, and doubled precipitation – on soil respiration 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*. 2001a, Wan *et al*. 2005). Experiment 2 was to examine ecosystem responses to short-term (i.e., one-year) warming and doubled precipitation. To examine transient responses of soil respiration 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 respiration and clipping would decrease it. We also hypothesized that interactive effects of the three factors would occur on soil respiration and its temperature sensitivity. To test these hypotheses, we measured soil respiration at monthly intervals and derived basal respiration rates and temperature sensitivity coefficients by fitting an exponential equation to measured soil respiration and soil temperature. Repeated measures analysis of variance (RM-ANOVA) was applied for significance tests of treatment effects on soil respiration. T-tests of regression coefficients were performed to examine adjustments in temperature-respiration relationships under different treatments.

2.2. Materials and Methods

Site description

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, USA. 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). 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). Soil carbon content is 1.42% on a mass basis (Luo *et al*. 2001a). The soil belongs to part of the Nash-Lucien complex with neutral pH, high available water capacity, and a deep, moderately penetrable root zone (USDA 1979).

Experimental design

We used two on-going experiments to examine main and interactive effects of warming, clipping, and doubled precipitation on soil respiration and its temperature sensitivity. Experiments 1 examined the long-term warming/yearly clipping effects on ecosystem processes, whereas experiment 2 investigated ecosystem responses to one-

Table 2.1 Comparison of Experiment 1, Experiment 2, and the transient study

	Experiment 1[a]	Experiment 2[b]	The transient study [c]
Treatments	Warming and yearly clipping	Warming and doubled precipitation	Clipping, warming, and doubled precipitation
Warming period	21 Nov 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% (0-15cm)	_	-2.47% (0-15cm)
Hourly record	–	-5.68% (0-15 cm)	–

Notes: The measurement depths of soil temperature and moisture are shown in parentheses.

[a] the long-term experiment with warming and yearly clipping treatments

[b] the short-term (one-year) experiment with warming and doubled precipitation treatments

[c] conducted in Experiment 2 from 16 September to 21 November 2003

year warming/doubled precipitation and subsequent-year lag effects on biogeochemical processes (Table 2.1). 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.

Experiment 1: 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, USA) 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 1.5m 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^{o}C and soil temperature at the 2.5-cm depth by 2.0^{o}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 6 replicates.

Experiment 2: The experiment was situated approximately 500 meters 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 1.5m 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.

The transient study: We studied transient responses of soil respiration 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.

Measurement protocols

To measure soil respiration, 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 respiration were taken monthly between 10:00 and 15:00 (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, USA). Standard procedures recommended by LI-COR were applied to measure soil respiration. Data were recorded at a 5 second interval by the datalogger in LI-COR 6400 console. Each of the measurements usually took 1 – 3 minutes 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 we measured soil respiration. Data were also logged at a 5 second interval.

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, USA) 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 datalogger (Campbell scientific, Inc., Logan, Utah). However, due 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 0-15cm were used because this depth is more closely associated with soil surface CO_2 efflux.

In Experiment 1, soil respiration, 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 respiration and soil temperature were performed in the southwest and northeast quarters from January 2002 to February 2004 except February and March 2003 (three times per month), while soil moisture was monitored hourly at the center of each plot. In the transient study, soil respiration, 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.

Estimation of annual soil respiration

Annual soil respiration for each treatment was estimated by summing the products of monthly mean soil respiration and the number of days between samples. It was corrected further for diurnal patterns in fluxes. Our measurements, collected between 10:00 and 15:00, 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).

Data analysis

In Experiment 2, each plot was an experimental unit, so replicate measurements were averaged by plot for analysis. In addition, means of soil respiration 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 respiration, 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, USA 2001).

We assessed the sensitivity of soil respiration to soil temperature by fitting exponential functions to the data from individual treatments.

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

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

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 $p < 0.05$.

2.3. Results

Warming and yearly clipping effects in Experiment 1

Soil respiration 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 (Fig. 2.1a). Soil respiration 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, Fig. 2.1a, Table 2.2). However, no significant effects of yearly clipping and warming×yearly clipping interaction were found on soil respiration. Significant interactions occurred between warming and sampling dates and between yearly clipping and sampling dates (W×D and CL×D, Table 2.2).

Soil temperature at the depth of 5 cm showed a similar seasonal trend as soil respiration (Fig. 2.1b). Warming increased soil temperature by 1.23^{o}C over the whole year in unclipped plots and by 1.73^{o}C in clipped plots based on monthly daytime measurements ($p<0.0001$, Fig. 2.1, Table 2.1,). Yearly clipping increased soil temperature by 0.80^{o}C relative to that in the control plots in the daytime ($p < 0.001$, Fig. 2.1b). Soil moisture (0-15 cm) fluctuated greatly over the season (Fig. 2.1c). The lowest soil moisture was observed in summer (July and August) and the highest in winter.

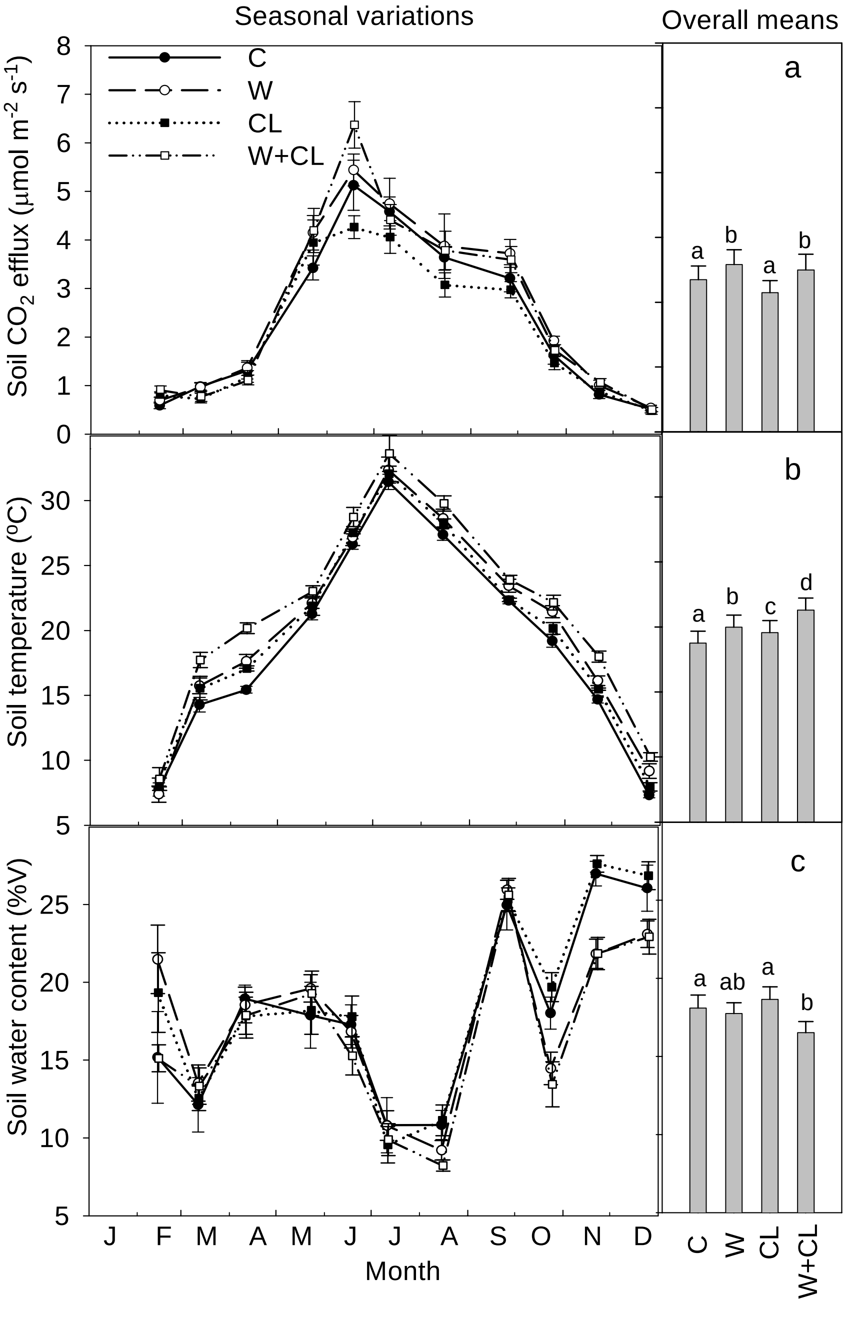

Fig. 2.1 Seasonal variations and overall means of soil respiration (a), soil temperature at the depth of 5 cm (b), and soil water content of 0-15 cm (c) in Experiment 1 in 2003. Clipping was conducted on September 26, 2003. Vertical bars represent the standard error of the mean (n=6). C: control; W: warmed; CL: clipped; W+CL: clipped plus warmed.

Warming had a marginally significant negative effect on soil moisture (p=0.06), while yearly clipping did not affect soil moisture (p=0.6, Fig. 2.1c).

Our analysis with equation 1 showed that soil temperature accounted for more than 60% of the variation on soil respiration in the four treatments (Fig. 2.2). 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 2.3).

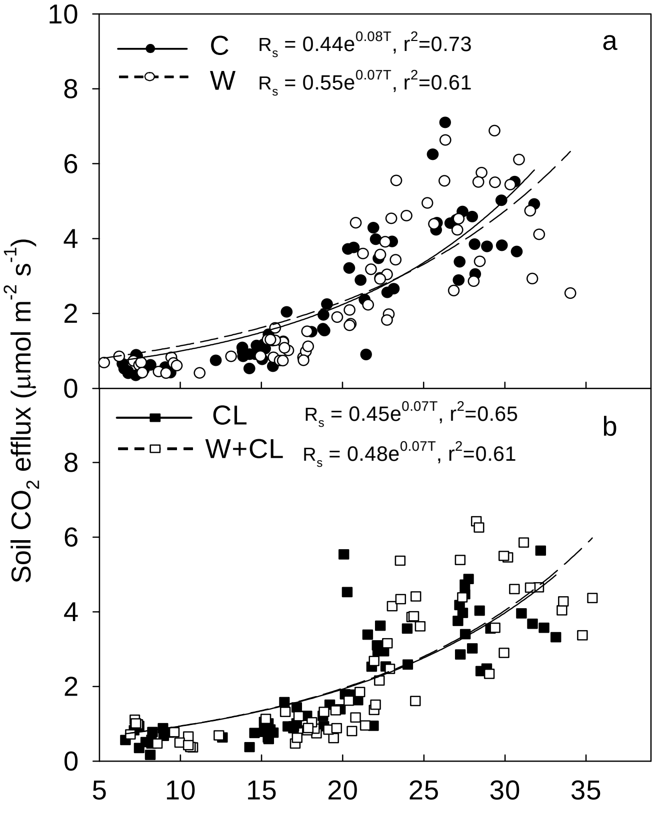

Fig. 2.2 The exponential relationships between soil respiration and soil temperature under unclipped (a) and clipped (b) treatments in Experiment 1 in 2003. See Fig. 2.1 for abbreviations.

Table 2.2 Results of RM-ANOVA showing the F values and levels of significance for responses of soil respiration to warmed (W), doubled precipitation (PPT), clipped (CL) treatments and sampling dates (D). * p≤0.05, ** p≤0.01, ***p≤0.0001

Experiment 1			Experiment 2			The transient study		
Factor	df	F values	Factor	df	F values	Factor	df	F values
W	1	9.32**	W	1	26.93***	W	1	34.85***
CL	1	0.20	PPT	1	4.70*	PPT	1	0.06
D	10	164.2***	D	12	107.4***	CL	1	7.93*
W×CL	1	1.39	W×PPT	1	2.68	D	7	155.4***
W×D	10	3.63*	W×D	12	12.40**	W×PPT	1	0.24
CL×D	10	4.05*	PPT×D	12	1.05	W×CL	1	6.25*
W×CL×D	10	0.85	W×PPT×D	12	0.32	PPT×CL	1	0.93
						W×D	7	1.85
						PPT×D	7	0.65
						CL×D	7	4.18*
						W×PPT×CL	1	0.13
						W×PPT×D	7	0.75
						W×CL×D	7	0.55
						PPT×CL×D	7	3.60
						W×PPT×CL×D	7	0.48

Warming and precipitation effects in Experiment 2

Soil respiration closely tracked the seasonal changes in soil temperature, with average values ranging from 0.54 to 7.64 μmol m^{-2} s^{-1} between Jan 2002 and Feb 2004 in the control plots (Fig. 2.3a). Warming and doubled precipitation caused significant increases in soil respiration (Fig. 2.3a, Table 2.2). Soil respiration 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, Fig. 2.3a). Doubled precipitation increased soil respiration by an average of 9.0% compared to those without extra precipitation treatments (Fig. 2.3a, Table 2.2). No significant interaction was

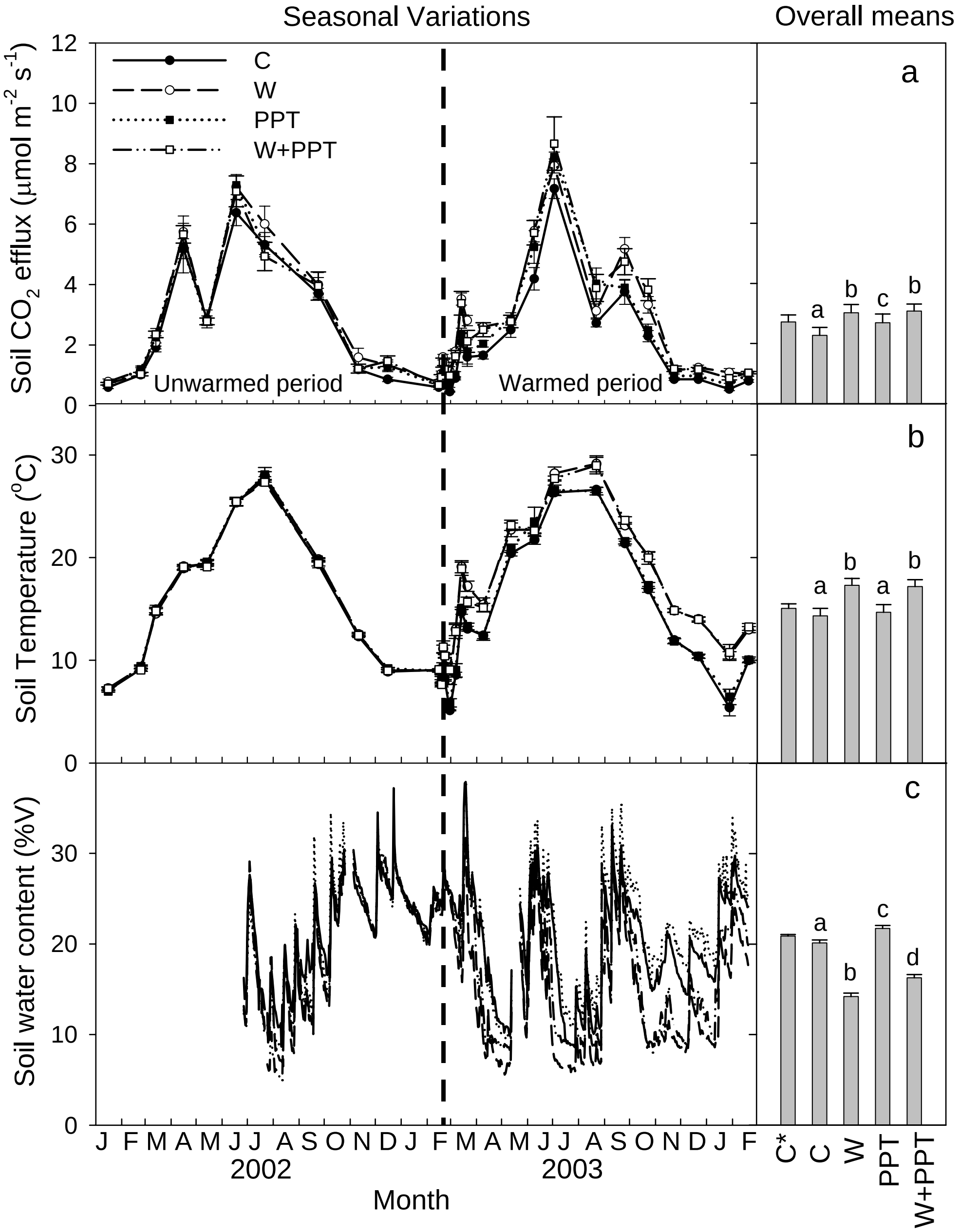

Fig. 2.3 Seasonal variations and overall means of soil respiration (a), soil temperature at the depth of 5 cm (b), and soil water content of 0-15 cm (c) in Experiment 2 from Jan 2002 to Feb 2003. Vertical bars represent the standard error of the mean (n=5). The dashed vertical line indicates the day 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 Feb 2003.

detected between warming and doubled precipitation ($p=0.121$).

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 with doubled precipitation based on monthly daytime measurements ($p<0.0001$, Fig. 2.3b). Our continuous measurements showed that warming increased daily mean soil temperature by 4.4°C at the depth of 2 cm (Table 2.1). Soil moisture (0-15 cm) fluctuated greatly due to highly variable rainfall (Fig. 2.3c). 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 (Fig. 2.3c).

On the basis of the temperature relationship of soil respiration in equation 1, soil temperature accounted for more than 57% of variation in soil respiration (Fig. 2.4). The apparent Q_{10} values decreased from 2.51 in unwarmed plots to 2.02 in warmed plots

Table 2.3 Results of T-test showing *t* values and levels of significance for response of coefficients *a* and *b* to warmed (W), doubled precipitation (PPT), and clipped (CL) treatments. * p<0.05, **p<0.01

Experiment 1			Experiment 2			The transient study		
Factor	t_a	t_b	Factor	t_a	t_b	Factor	t_a	t_b
W	0.614	-0.588	W	2.175*	-2.476**	W	0.239	-0.616
CL	-0.244	-0.506	PPT	-0.456	0.848	PPT	1.767	-1.484
W×CL	-0.354	0.524	W×PPT	-0.836	0.508	CL	0.514	-2.076*
						W×PPT	-0.126	-0.429
						W×CL	-2.482*	2.024*
						PPT×CL	1.044	-1.224
						W×PPT×CL	-1.341	1.348

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 2.3).

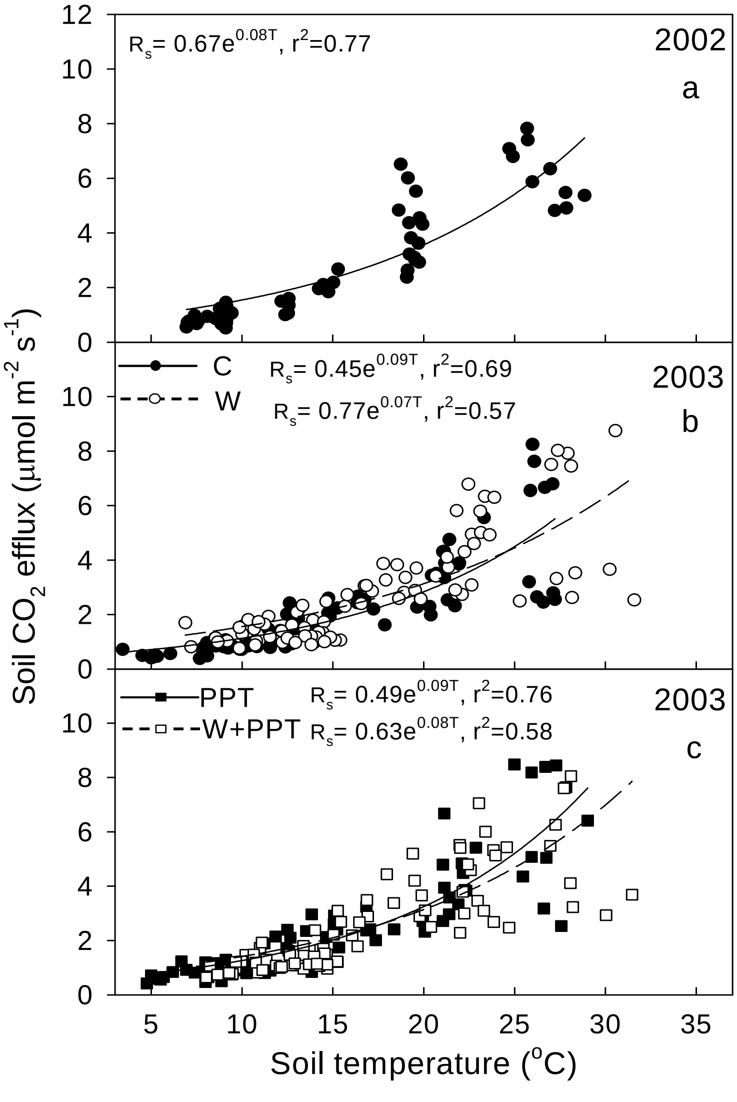

Fig.2. 4 The exponential relationships between soil respiration and soil temperature in Experiment 2 in 2002 (a), without extra precipitation in 2003 (b), and with doubled precipitation in 2003 (c). See Fig. 2.3 for abbreviations.

Substrate effects in the transient study

Clipping significantly reduced average soil respiration 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, Fig. 2.5). During the period of the transient study, warming significantly increased soil respiration 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, $p < 0.001$, Fig. 2.5c). Doubled precipitation did not alter soil respiration in either unclipped or clipped subplots. Interactive effects of warming×clipping and clipping×sampling dates were statistically significant on soil respiration (Table 2.2).

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 ($p < 0.001$, Fig. 2.5d,e,f,g,h,i), whereas doubled precipitation had no effects on either soil temperature or moisture ($p > 0.1$).

Clipping significantly decreased the temperature sensitivity of soil respiration (Fig. 2.6). 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 2.3).

Estimated annual soil respiration

In Experiment 1, annual soil CO_2 emissions ranged from 782 to 927 g C m^{-2} yr^{-1} for the four treatments (Table 2.4). Warming increased annual soil respiration by 10.9% in unclipped plots and by 17.0% in clipped plots. In Experiment 2, warming increased annual soil respiration by 28.7% without extra precipitation and by 15.1% with doubled

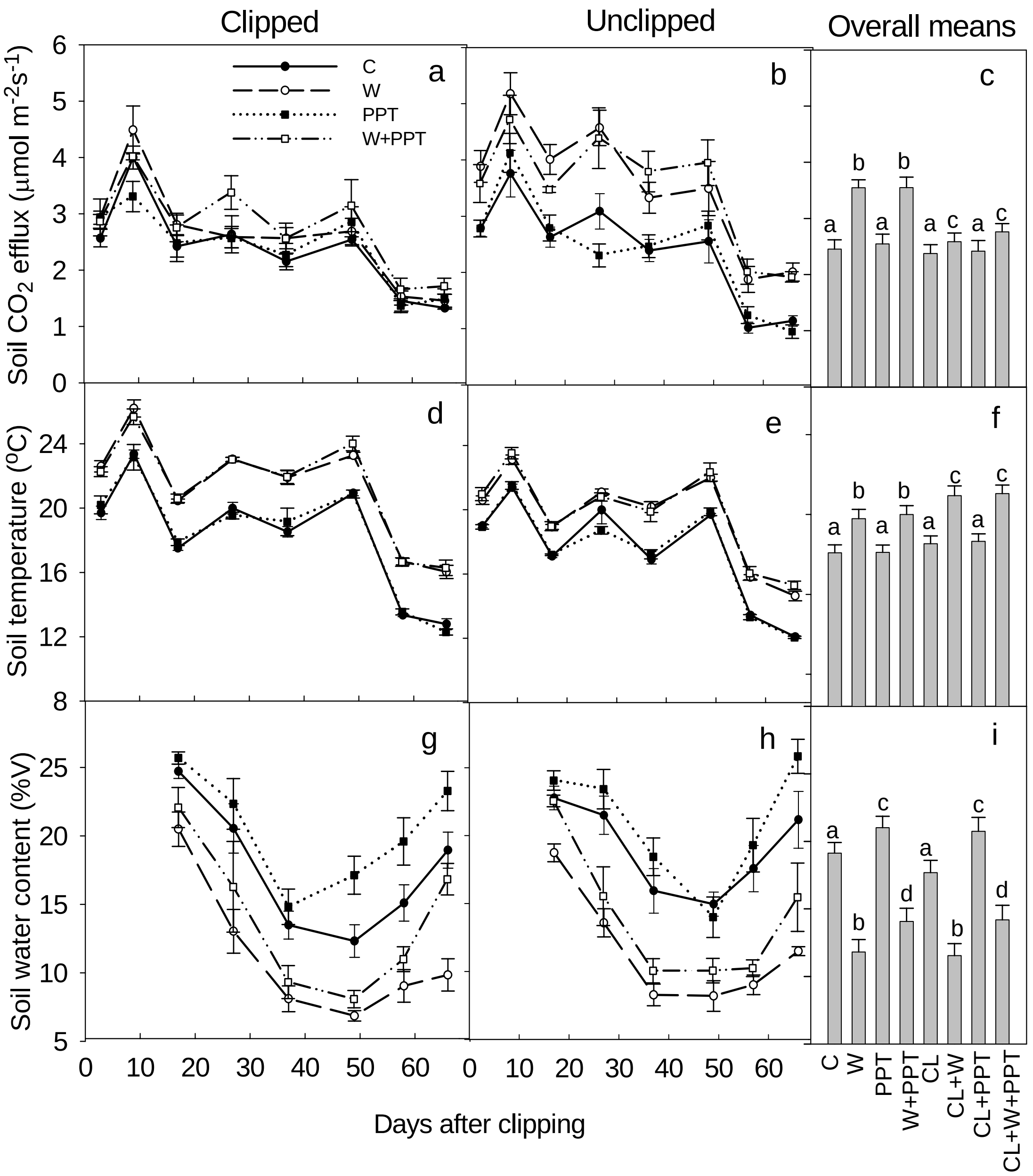

Fig. 2.5 Variations and overall means of soil respiration (a, b, and c), soil temperature at the depth of 5 cm (d, e, and f), and soil water content of 0-15 cm (g, h, and i) after clipping in the transient study. Vertical bars represent the standard error of the mean (n=5). C: control, W: warmed; PPT: doubled precipitation, CL: clipped.

precipitation. Doubled precipitation also increased annual soil respiration 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 2.4), largely due to differences in precipitation between the two years.

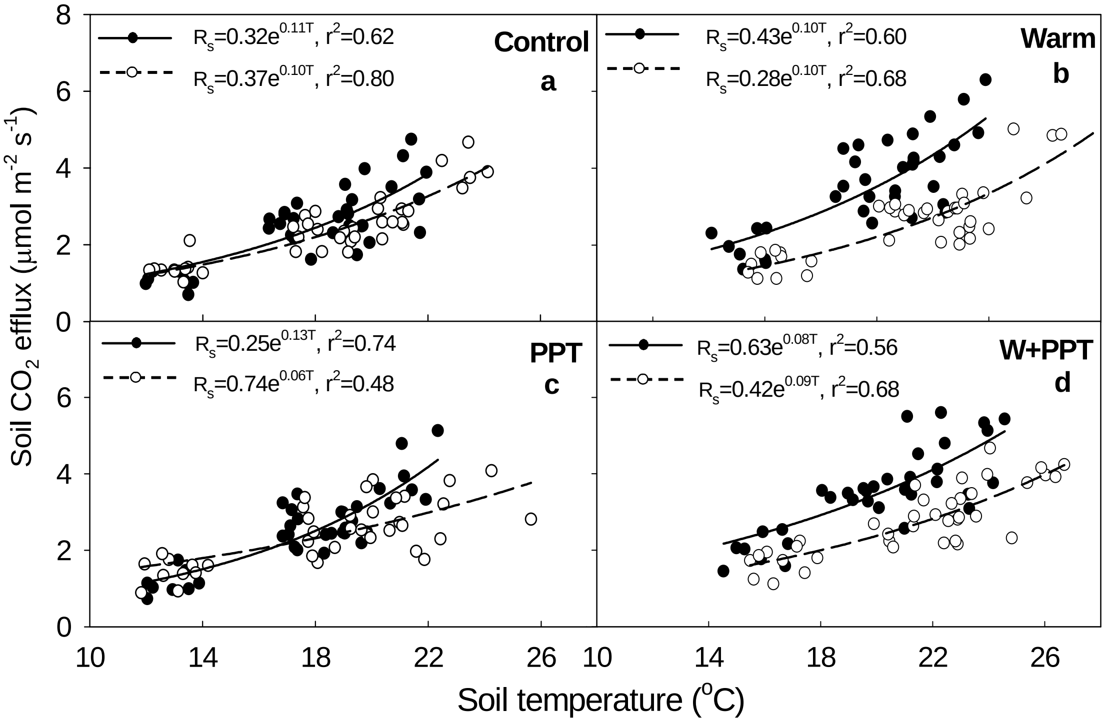

Fig. 2.6 The exponential relationships between soil respiration and soil temperature for unclipped (—●—) and clipped (-○-·) treatments in control (a), warmed (b), doubled precipitation (c), and warmed plus doubled precipitation (d) treatments in the transient study. See Fig. 2.5 for abbreviations.

2.4. Discussion

Prediction of ecosystem responses to multi-factor 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 respiration, 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 respiration significantly decreased under the warming treatment in Experiment 2 and under the clipping treatment in the transient study. Below we discuss magnitude of soil respiration, main effects of single factors, and interactive effects of multiple factors.

Table 2.4 Annual soil respiration (g C m^{-2} yr^{-1}) in Experiment 1 with warmed (W) and clipped (CL) treatments and Experiment 2 with warmed (W) or doubled precipitation (PPT) treatments. Data are shown by mean ± 1SE.

Experiment 1			Experiment 2		
Year	Treatments	Annual soil respiration	Year	Treatments	Annual soil respiration
			2002	Control*	1131±93
2003	C	835±73	2003	C	877 ± 69
2003	W	927±87	2003	W	1129±70
2003	CL	782±67	2003	PPT	1013±85
2003	W+CL	915±80	2003	W+PPT	1166±107

Control*: refers to the result calculated from the average in all pretreatment plots.

Magnitude of soil respiration

Soil respiration measured in the control plots ranged from 0.52 to 7.64 μmolm^{-2} s^{-1}, which is comparable to previous measurements in grasslands (Bremer *et al*. 1998, Wan and Luo 2003). Although annual soil respiration 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 respiration between 2002 and 2003 in the control plots of Experiment 2 (Table 2.4).

Main effects of single factors on soil respiration

The increase in soil respiration 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 respiration 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).

The long-term response of soil respiration to warming is regulated by acclimatization (Luo *et al*. 2001a), 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 respiration increased by 9.9% in the fourth year (Fig. 2.2), 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*. 2001a). The increases in soil respiration 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 respiration observed in Experiment 1 likely resulted from changes in productivity (Wan *et al*. 2005) and other abiotic factors such as drought. The lower response of soil respiration 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*. 2001a).

This study demonstrated that warming significantly increased basal respiration rate (coefficients *a*) and decreased temperature sensitivity of soil respiration (coefficient *b*) in Experiment 2, whereas neither of the parameters was significantly altered by warming in Experiment 1 (Table 2.3). The different responses of the two parameters to warming between the experiments may be due to a few reasons. First, the temperature increase was ~ 2^{o}C in Experiment 1 and 4.4^{o}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 three-year warming in Experiment 1, labile carbon could be in a steady state between supply and depletion (A. Tedla and Y. Luo, unpublished data). In addition, the shift in soil microbial community structure toward more fungi (Zhang *et al*. 2005) likely resulted in lower sensitivity of soil respiration to temperature because fungi are more tolerant to higher soil temperature and drying due 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).

Doubled precipitation significantly increased soil respiration in Experiment 2 (Table 2.2), greatly due to stimulation of soil respiration in the dry growing season of 2003 (Fig. 2.3). Similar effects of additional water on soil respiration 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 due to the absence of water stress. Although the basal respiration rate and temperature sensitivity were not affected by doubled precipitation (Table 2.3), 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. But 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 respiration to water availability.

A large portion of soil respiration 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 respiration 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 respiration in the fourth year of Experiment 1 and clipping significantly reduced soil respiration in the transient study within two months (Figs. 2.1, 2.5; Table 2.2). In Experiment 1, we evaluated the effect of yearly clipping against monthly measurements of soil respiration over a whole year. The treatment of yearly clipping in our study likely has less impact on soil respiration than mowing several times per year. However, the transient effects of clipping were examined within two 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 respiration. 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 2.3), 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).

Interactive effects of warming, precipitation, and clipping

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 respiration were minor except for the warming × clipping interaction in the transient study. Minor interactive effects among multiple global change factors on soil respiration 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 respiration statistically significant. Similarly, there were no significant interactions among elevated CO_2, nitrogen supply, and plant diversity on soil respiration (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.

The lack of significant interactive effects in Experiment 1 suggests that soil respiration was determined by warming and yearly clipping treatments in a statistically independent manner. Warming increased soil respiration 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 respiration by 9.0% relative to those without extra precipitation treatments, high 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 respiration to individual rainfall events (Liu *et al*. 2002). Thus, we do expect that soil water content and temperature interactively regulate soil respiration under different circumstances in spite of the fact that we did not detect significant interactions between them in this particular study.

An interactive response to warming and clipping was observed on soil respiration and its temperature sensitivity in the transient study (Tables 2.2 and 2.3). 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 respiration 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 respiration 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 respiration 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.

2.5. Conclusions

This study investigated the main and interactive effects of warming, doubled precipitation, and clipping on soil respiration and its temperature sensitivity in a tallgrass prairie of Central Oklahoma. The main effects of warming and doubled precipitation were significant on soil respiration. Clipping significantly decreased soil respiration 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 respiration 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 respiration to multi-factor 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 multi-factor experiments.

2.6. Acknowledgments

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Appendix A: Statistical tests of regression coefficients

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). Below is an array of coefficients *a* or *b* and standard errors for calculating *t* values of main and interactive effects between two factors: warming vs. precipitation and warming vs. clipping:

		Treatment level of Factor 1		
		1	2	Ave.-Factor 2
Treatment level of Factor 2	1	$x_{11}\pm S_{11}$	$x_{21}\pm S_{21}$	$\overline{x_{.1}}$
	2	$x_{12}\pm S_{12}$	$x_{22}\pm S_{22}$	$\overline{x_{.2}}$
	Ave.-Factor 1	$\overline{x_{1.}}$	$\overline{x_{2.}}$	

where x_{ij} are values of coefficients *a* or *b* (*i, j*=1, 2), S_{ij} are standard errors of coefficients *a* or *b* in different treatments, $\overline{x_{i.}}$ is a mean of treatment level *i* of factor 1, $\overline{x_{.j}}$ is a mean of treatment level *j* of factor 2.

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:

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

For the 3-way factorial experiment with warming, precipitation (ppt), and clipping, coefficients *a* or *b* and their standard errors can be arranged as follows to calculate *t* values of main and interactive effects:

		Treatment level of Factor 1				
		1-Unclipped		2-Clipped		
		Treatment level of Factor 2		**Treatment level of Factor 2**		Ave.-Factor3
		1-Ambient ppt	2-Double ppt	1-Ambient ppt	2-Double ppt	
Treatment level of Factor 3	1-Unwarmed	$x_{111} \pm S_{111}$	$x_{121} \pm S_{121}$	$x_{211} \pm S_{211}$	$X_{221} \pm S_{221}$	$\overline{x}_{..1}$
	2-Warmed	$x_{112} \pm S_{112}$	$x_{122} \pm S_{122}$	$x_{212} \pm S_{212}$	$X_{222} \pm S_{222}$	$\overline{x}_{..2}$
Ave.-Factor1		$\overline{x}_{1..}$		$\overline{x}_{2..}$		
Ave.-Factor2		$\overline{x}_{.1.}$			$\overline{x}_{.2.}$	

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

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:

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

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.

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

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

Chapter 3

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

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ABSTRACT

Partitioning soil respiration 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 and yearly clipping on soil respiration 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 respiration and R_H. Warming treatment significantly stimulated soil respiration and its components (i.e., R_A and R_H) in most years. In contrast, yearly clipping significantly reduced soil respiration only in the last two years, although it decreased R_H in every year of the study. Temperature sensitivity (i.e., apparent Q_{10} values) of soil respiration was slightly lower under warming ($p>0.05$) and reduced considerably by clipping ($p<0.05$) compared to that in the control. On average over the four years, R_H accounted for approximately 65% of soil respiration with a range from 58 to 73% in the four treatments. Over seasons, the contribution of R_H to soil respiration reached a maximum in winter (~90%) and a minimum in summer (~35%). Annual soil respiration did not vary substantially among years as precipitation did. The interannual variability of soil respiration may be mainly caused by precipitation distribution and summer severe drought. Our results suggest that the effects of warming and yearly clipping on soil respiration 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 respiration than the amount of annual precipitation.

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

3.1. 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 by1.4 – 5.8°C by the end of this century (IPCC 2001). In the Great Plains, air temperature is predicted to increase by 2 to 4°C with the doubling of the current CO_2 concentration (Long and Hutchin 1991). This projected warming is probably altering ecosystem carbon (C) cycling, causing positive feedback if warming increases soil respiration more than plant production (Cox *et al.* 2000). At a global scale, climate warming of 1°C would result in an extra 11-34 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 respiration, also referred to as soil CO_2 efflux, is the second largest C flux (68 to 80 Pg C yr^{-1}) between terrestrial ecosystems and the atmosphere in the global C cycle (Raich and 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 (Lloyd and Taylor 1994, Boone *et al.* 1998, Rustad *et al.* 2001), water content (Davidson *et al.* 2000, Liu *et al.* 2002), nutrient availability (Raich and 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 and 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 respiration 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 non-forest 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 since autotrophic respiration mainly depends on supply of carbohydrates from canopy photosynthesis (Rochette *et al.* 1999, Lin *et al.* 2001). Due to year-to-year changes in climate variables and consequently indirect changes in physiological and ecological processes and nutrient availability, soil respiration and its components usually exhibit the interannual variability (Savage and Davidson 2001, Scott-Denton *et al.* 2003, King *et al.* 2004, Luo and 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 respiration associated with global warming will largely depend on the relative contribution of autotrophic and heterotrophic components (Buchmann 2000). Therefore, quantifying the components of soil respiration 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 and 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 respiration 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 respiration 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 respiration. It is essential that, at a long-term scale, warming responses of source components of soil respiration 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 respiration and its components, especially in the short term (Bahn *et al.* 2006). Clipping usually reduces soil respiration by 21 – 49% despite the fact that it increases soil temperature (Bremer *et al.* 1998, Wan and 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 respiration and its components to clipping remains uncertain.

In this study, we investigated the responses of soil respiration and its components to experimental warming and yearly clipping over a period of six 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 respiration with R_H. We hypothesized that warming would increase soil respiration and its components in most years but yearly clipping would decrease them, with large interannual variability.

3.2. 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. 3.1a,b. A silt loam soil 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.* 2001a). 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 (U.S. 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 × 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, 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 hours per day and 365 days per year in the field since 21 November, 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 × 2 m plot was divided into four 1m × 1m subplots. Plants in two diagonal subplots were clipped at the height of 10cm 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 respiration, PVC collars (80 cm^2 in area and 5 cm in height) were 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 (see above) 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 several 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 (local time), using a LI-COR 6400 portable photosynthesis system attached to soil CO_2 flux chamber (LI-COR. Inc., Lincoln, Nebraska, USA). A measurement consisted of placing the chamber on PVC collars, scrubbing the CO_2 to sub-ambient levels, and determining soil respiration over the periods. Data were recorded at a 5-second interval by the datalogger in the LI-COR 6400 console. Each of the measurements usually took 1 – 3 minutes 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 respiration was measured. Data were also logged at a 5 second interval. Soil moisture content was measured gravimetrically twice a month from September 1999 to December 2000. Soil samples from the top 5 cm were taken from one clipped and one unclipped subplots in each plot and oven dried at 105°C for 24 hours 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, California, 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 the same as soil respiration, once or twice a month.

Estimation of annual CO_2 efflux

Annual soil respiration for each treatment was estimated by summing the products of soil respiration 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, 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, See Chapter 2).

Modeling soil respiration and heterotrophic respiration

Soil temperature and soil moisture content are two main abiotic factors influencing soil respiration. We used a reverse exponential decay function (Equation 1) to simulate moisture effects and an exponential function (Equation 2) to simulate temperature effects (Hui and Luo 2004):

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

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

where R is the measured soil respiration or heterotrophic respiration (μmol CO_2 m^{-2} s^{-1}); R_0 is the base respiration when soil temperature is 0^oC and changes with soil moisture; T is soil temperature (^oC); and θ_v is volumetric soil moisture (%); a, b, c, d, and f are parameters related to soil temperature and moisture. When $\theta_v \le \frac{d}{c}$, R = 0. When $\theta_v \ge \frac{2\ln(10) + d}{c}$, soil respiration is hardly limited by soil moisture and largely controlled by soil temperature. The reverse exponential decay function fits our observations better than other moisture functions (Luo and 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 respiration, R_H, R_A, soil temperature, and soil moisture were used to keep consistent in statistical analysis and calculation of annual mean values. Due 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 respiration, 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, USA 2001).

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

$$R = ae^{bT} \tag{3}$$

where R is mean soil respiration, R_H, and R_A (µmol m^{-2} s^{-1}), T is soil temperature (^oC) at the depth of 5 cm, *a* is the intercept of soil respiration when temperature is zero (i.e., basal respiration rate), and *b* represents the temperature sensitivity of soil respiration, 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:

$$Q_{10} = e^{10b} \tag{4}$$

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 respiration 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 respiration, R_H, and R_A. In the analyses of temperature sensitivity and modeling, four data points of soil respiration per treatment during the summer severe drought period (Fig. 3.2) were excluded when volumetric soil moisture was below 10% (Luo *et al.* 2001a).

The significance of the effects of regression coefficients *a* and *b* among the treatments was examined by a t-test method as described in Chapter 2. 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 (Subke *et al.* 2006).

3.3. Results

Microclimate

Soil temperature at the depth of 5 cm exhibited pronounced seasonal variations over the six years, with a decrease in maximum values from 2001 to 2004 (Fig. 3.1c). Annual

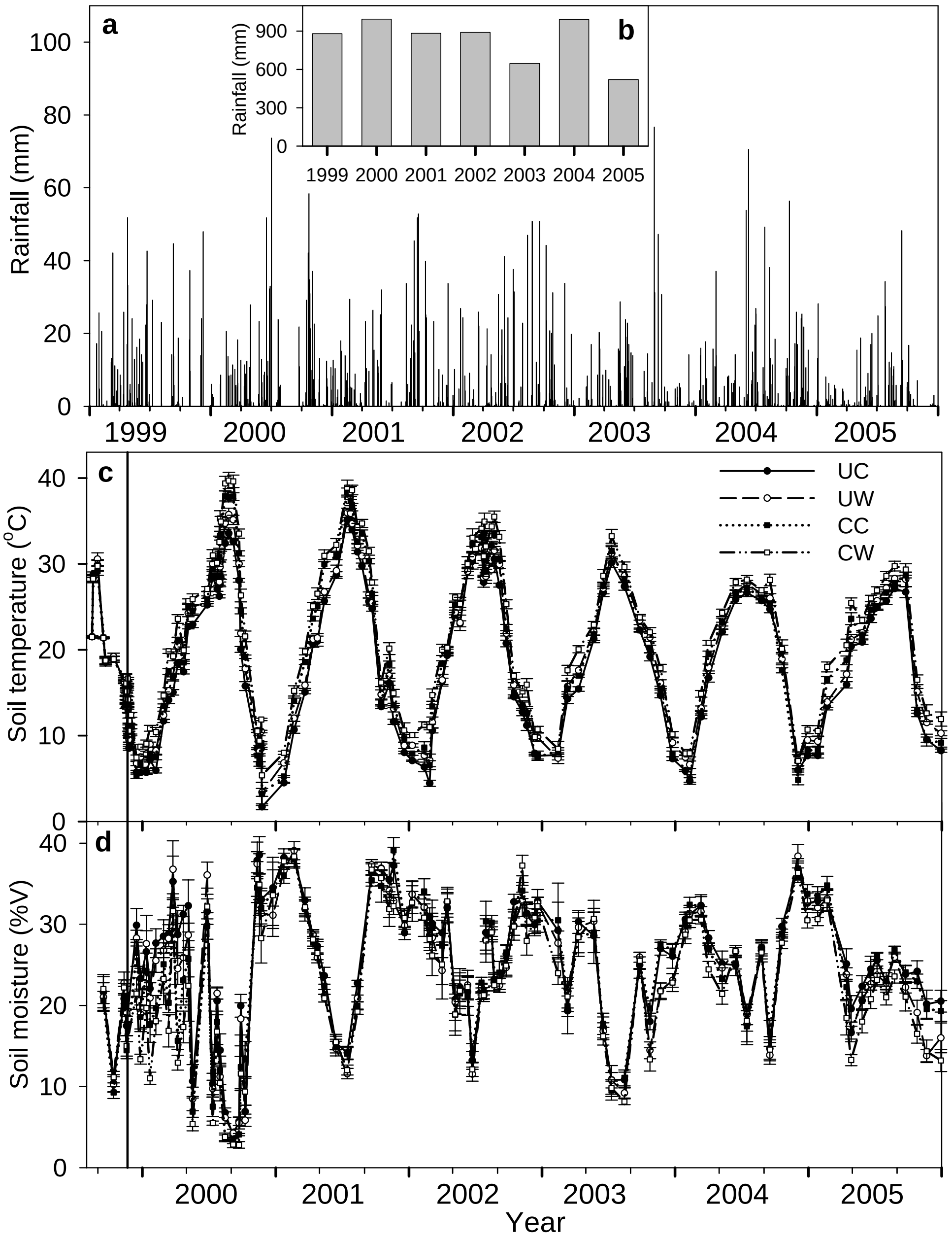

Fig. 3.1 Daily (a) and annual (b, inserted figure) rainfall at the experimental site, and seasonal and interannual variability of soil temperature at the depth of 5 cm (c) and soil moisture of 0-15 cm (d) from 1999 to 2005 in the long-term warming and clipping experiment. Yearly clipping was usually 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 (Nov 21, 1999). UC: unclipped control; UW: unclipped warmed; CC: clipped control; CW: clipped warmed.

Table 3.1 Annual mean soil respiration (μmol m^{-1} s^{-1}), heterotrophic respiration (μmol m^{-1} s^{-1}), autotrophic respiration (μmol m^{-1} s^{-1}), soil temperature (^{o}C) at the depth of 5 cm, and volumetric soil moisture (%V) at the depth of 0-15cm from Jan 2000 to Dec 2005.

	2000	2001	2002	2003	2004	2005
Soil respiration						
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.

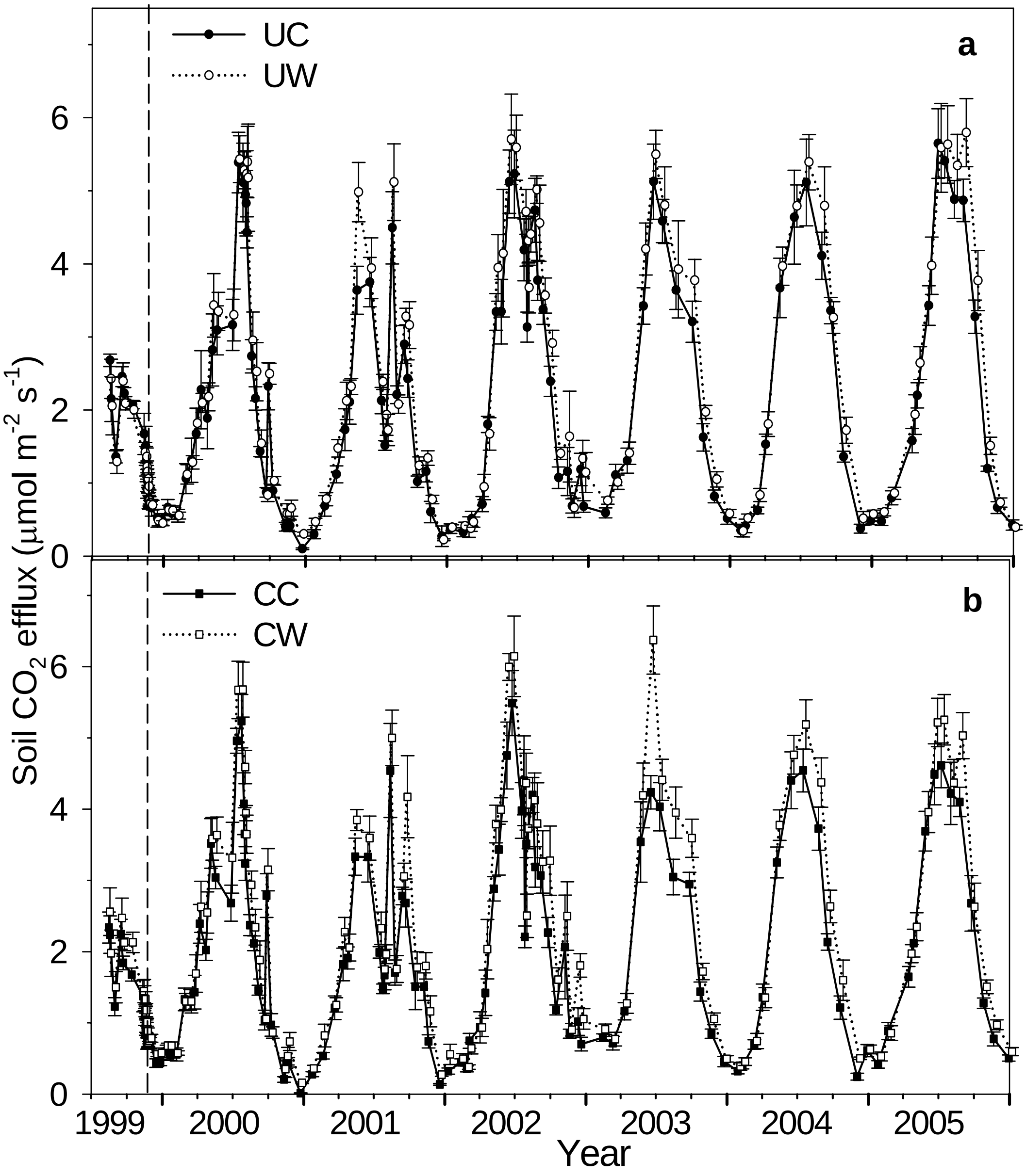

Fig. 3.2 Seasonal and interannual variability of soil respiration from Aug 1999 to Dec 2005 under: (a) unclipped and (b) clipped treatments in the long-term warming experiment. See Fig. 3.1 for notes and abbreviations.

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 3.1). 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 by1.4 ± 0.1 °C in the unclipped plots and by 2.0 ± 0.1 °C in the clipped plots from 2000 to 2005 (Table 3.1). Yearly clipping also increased soil temperature by 1.4 ± 0.3 °C relative to that in the control plots (Table 3.1).

Unlike soil temperature, volumetric soil moisture at the depth of 0-15 cm fluctuated greatly over the season (Fig. 3.1d). Usually the lowest soil moisture was observed in summer (July and August) and the highest in winter. Throughout the duration of the experiment, warming 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 respiration

The temporal dynamics of soil respiration followed the distinct seasonal pattern of soil temperature in all six years, which was high during summer and low in winter (Figs.3.1c and 3.2). However, long droughts in summer (August – September 2000, August 2001, July 2002, and July 2003) suppressed soil respiration irrespective of the higher soil temperature (Figs. 3.1d and 3.2). From year to year, there were also observable variations. For example, the summer peak of soil respiration reached nearly 6 μmol m^{-2} s^{-1} in 2002 and was less than 4 μmol m^{-2} s^{-1} in 2001 in the control plots (Fig.

3.2). Soil respiration 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 respiration 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 3.1).

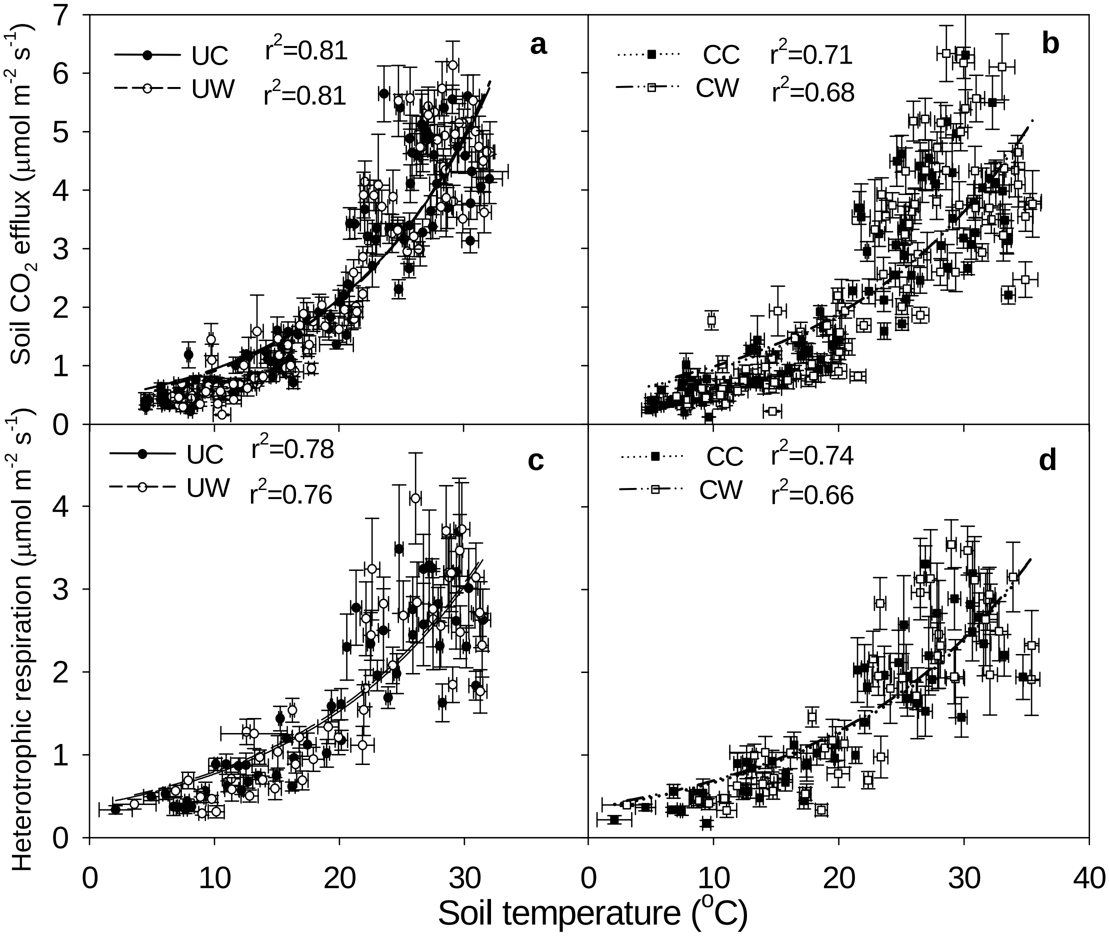

Fig. 3.3 Exponential relationships between soil respiration and soil temperature under unclipped (a) and clipped (b) treatments and between heterotrophic respiration and soil temperature under unclipped (c) and clipped (d) treatments. Vertical and horizontal bars represent the standard error of the mean (n=6). See Fig. 3.1 for abbreviations.

Table 3.2 Q_{10} values of soil respiration, heterotrophic respiration, and autotrophic respiration from 2000 to 2005 calculated from equation 1 and 2.

	2000*	2001	2002	2003	2004	2005	All data
Soil respiration							
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

* Note: Q_{10} in paper by Luo *et al.* (2001a) was based on data in both 1999 and 2000. UC: unclipped control; UW: unclipped warmed; CC: clipped control; CW: clipped warmed.

The stimulation of soil respiration by warming was statistically significant for 5 years out of the 6-year study period (except 2000). On average, warming increased annual mean soil respiration by 9.0±1.5 % in the unclipped plots and by 15.6±1.5 % in the clipped plots from 2000 to 2005 (Table 3.1). Effects of yearly clipping on soil respiration were significant only in the last two years ($p<0.05$), while no interactions of warming and yearly clipping were found in any of the six years ($p>0.05$).

On the basis of the temperature relationship with soil respiration in equation (3), soil temperature accounted for 81% of variation in the unclipped plots and nearly 70% in the clipped plots across the six-year period (Fig. 3.3). The apparent Q_{10} values were slightly lower under warming ($p>0.05$) and reduced considerably by clipping ($p<0.05$) compared to that in the control, ranging from 1.70 to 3.62 for all four treatments (Table 3.2). There were higher Q_{10} values for the four treatments in 2004 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 four years of the study (2002 - 2005), although R_H had larger variability than soil respiration (Fig. 3.4a). 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 3.1). 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 four years ($p<0.05$). However, no interactions of warming and yearly clipping on R_H were found in any of the four years as well as its temperature sensitivity ($p>0.05$).

R_H contribution to soil respiration and its annual mean values are displayed in Fig. 3.4b,c. Immediately after collar installation, decomposition of dead roots by deep-collar insertion contributed considerably to this efflux, which was larger than soil respiration, but this phenomenon disappeared after 5 months. Thereafter, an opposite seasonal pattern occurred on the relative contribution of R_H compared to soil temperature (Fig. 3.4b). On average, annual mean R_H contributed to approximately 65% of soil respiration across the four years (Fig. 3.4c). Warming and yearly clipping did not significantly affect R_H contribution to soil respiration.

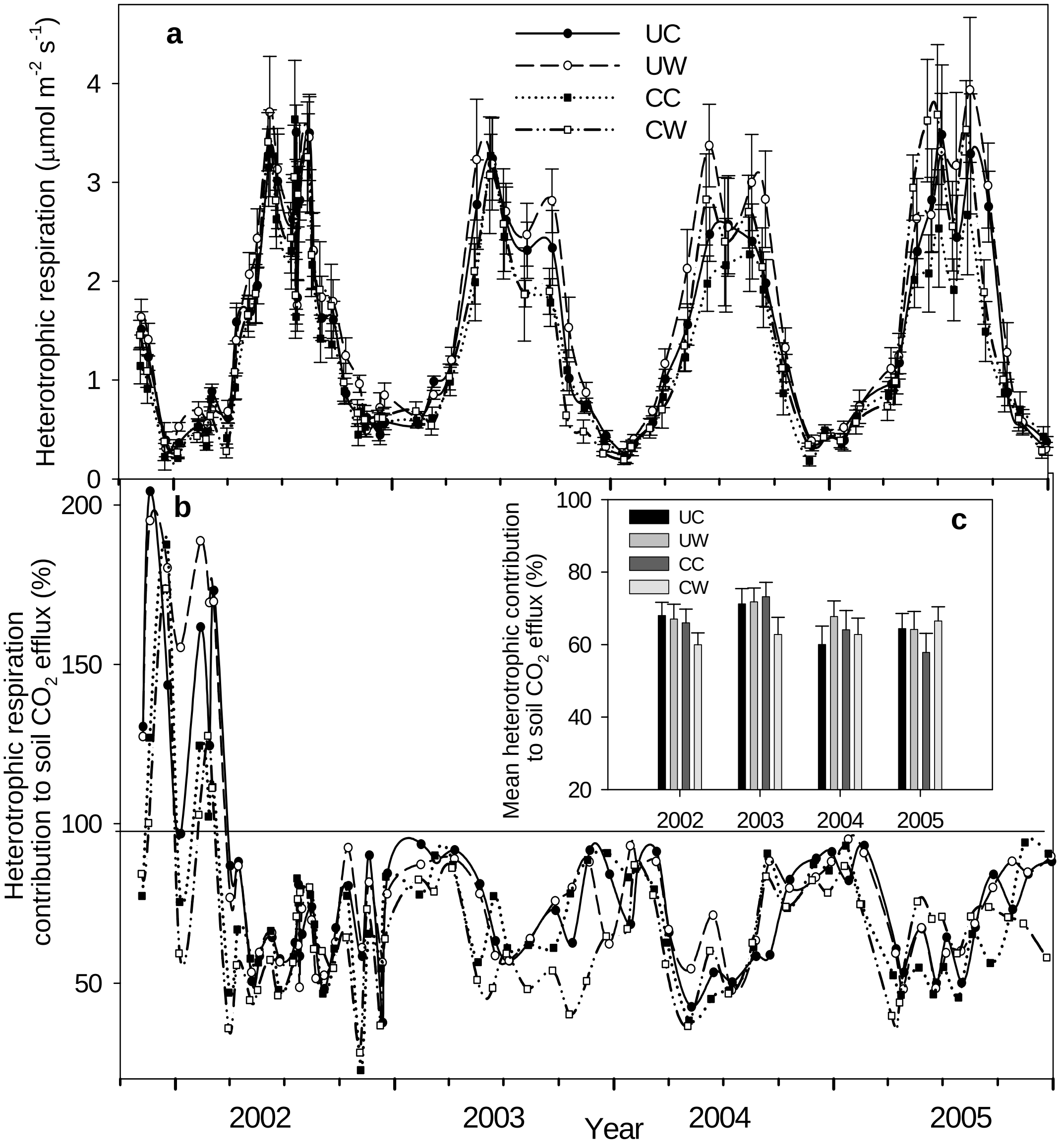

Fig. 3.4 Seasonal and interannual variability of heterotrophic respiration (a) and its contribution to total soil respiration (b) under four different treatments from Oct 2001 to Dec 2005. Annual mean values of heterotrophic contribution to soil respiration are shown in inserted figure (c). Vertical bars represent the standard error of the mean (n=6). See Fig. 3.1 for abbreviations.

Annual mean R_A was calculated from the difference between soil respiration and R_H, ranging from 0.53 to 0.96 μmol m^{-2} s^{-1} for the four treatments across the four-year period (Table 3.1). 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 3.2).

Seasonal and interannual variability

We calculated coefficient of variation (CV) from monthly and annual means to represent seasonal and interannual variability, respectively, in soil respiration, R_H, R_A, soil temperature, soil moisture, and rainfall (Table 3.3). 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 respiration and increased that of soil temperature, while warming did not affect them. Interestingly, the highest mean soil respiration occurred in 2005 when seasonal variability of precipitation during the growing season was lowest, indicating the importance of precipitation distribution (Tables 3.1 and 3.3). In addition, there was 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.

Table 3.3 Seasonal and interannual variability (IAV) of soil respiration, heterotrophic respiration, autotrophic respiration, soil temperature, soil moisture, and annual precipitation as coefficient of variation from Jan 2000 to Dec 2005

	2000	2001	2002	2003	2004	2005	**IAV**
Soil respiration							
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%)**

Note: 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.

Modeled soil respiration and R_H

The inclusion of both soil temperature and moisture slightly improved model fitting of observed soil respiration and R_H for the four treatments over seasons compared to the exponential model only using temperature (Figs. 3.3 and 3.5). Although soil temperature and moisture often co-vary, the comparison between the two models suggests that soil temperature is the dominant environmental factor in regulating seasonal dynamics of soil respiration and R_H across the whole study period. Unfortunately, the combined function of soil temperature and moisture did not fit the data well under severe water stress, where soil moisture was less than 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 respiration 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 respiration 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 respiration and its components

Annual soil CO_2 emissions ranged from 682 to 968 g C m^{-2} yr^{-1} across the six years for the four treatments (Fig. 3.6). On average, warming treatment increased annual soil respiration 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 respiration by 6.1±1.6 % compared to that in the control. Lower annual soil respiration occurred in

2000 and 2001 than in the other years (Fig. 3.6), largely owing to the long drought and high temperature.

Annual R_H contributed 56.0 -71.7% to total annual soil respiration, ranging from 427 to 657 g C m^{-2} yr^{-1} across the four 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 four 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 respiration, annual R_A increased 2.3 % by warming and 21.9% by yearly clipping compared to that in the control.

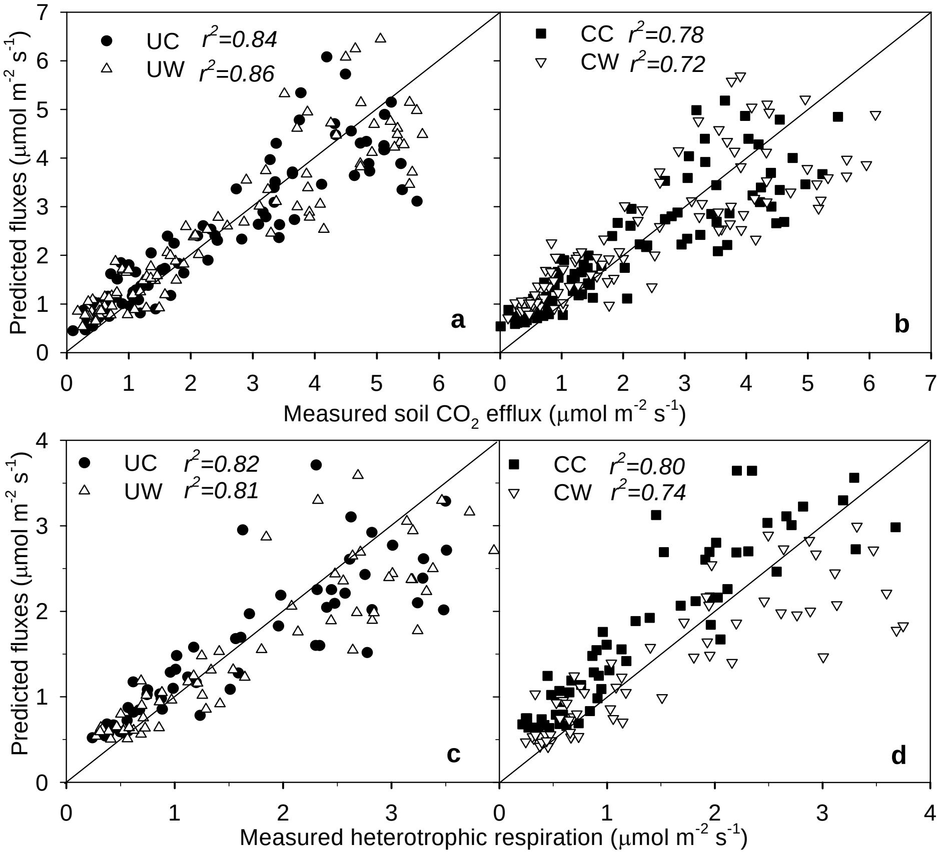

Fig. 3.5 Measured vs. modeled soil respiration (a and b) and heterotrophic respiration (c and d) under the four treatments. See Fig. 3.1 for abbreviations.

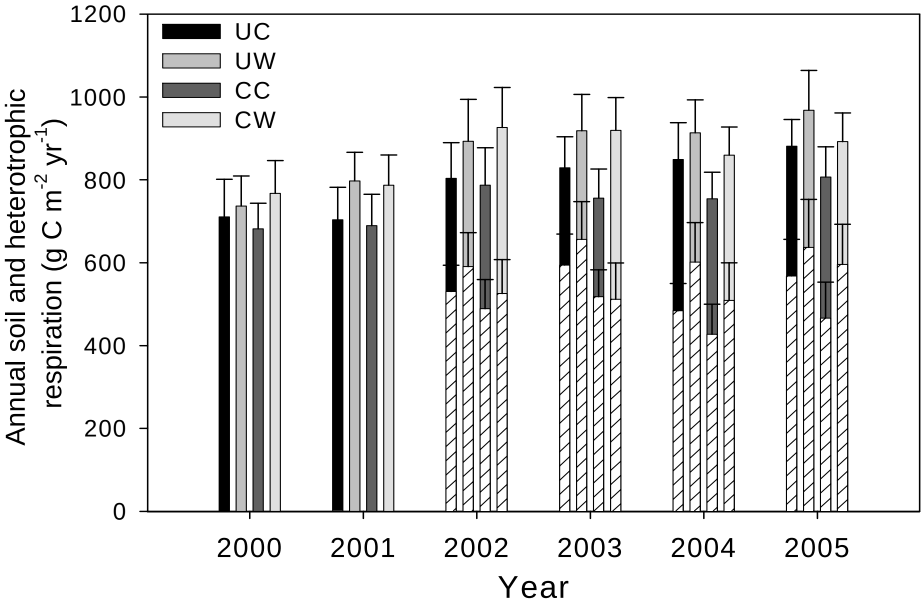

Fig. 3.6 Annual soil respiration and heterotrophic respiration (g C m^{-2} s^{-1}) under the four treatments. Vertical bars represent the standard error of the mean (n=6). The hatched columns represent annual heterotrophic respiration.

3.4. Discussion

Partitioning soil respiration

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 four years, the relative contribution of R_H to soil respiration was 66% in the control (Fig. 3.4), very close to the mean contribution in non-forest 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 and 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 respiration 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. 3.4b), and thus the data during the disturbance 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 and Trumbore 1995, Hui and 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 to the surrounding soil. Our four 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 respiration measured in the control plots over the six years is comparable to that in other studies (e.g., Davidson *et al.* 1998, Law *et al.* 1999, Xu and Qi 2001, Bremer and Ham 2002, Wan and Luo 2003). Similar seasonal trends in soil respiration have also been observed in a variety of ecosystems (e.g., Conant *et al.* 2000, Xu and Qi 2001, Wan and 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 respiration and its components considerably followed the temporal dynamics of soil temperature with some dips due to summer severe drought (Figs. 3.1, 3.2, and 3.4).

The significant year-to-year variability in soil respiration has been reported in various ecosystems such as grasslands (Frank *et al.* 2002), a beech forest (Epron *et al.* 2004), mixed temperate forests (Savage and Davidson 2001), a mixed hardwood forest (Melillo *et al.* 2002), ponderosa pine forests (Irvine and Law 2002), and forest plantations (King *et al.* 2004). Compared to those studies, the observed interannual variability in this study was relatively low for both soil respiration and its components. Surprisingly, the year-to-year variation in soil respiration did not follow the interannual pattern of precipitation at our site (Figs. 3.1b and 3.6). For example, the highest annual soil respiration occurred in 2005 when annual precipitation was lowest but a large proportion (78%) was present in the growing season and was evenly distributed (Table 3.3, Fig. 3.1a,b). In the first two years of the study, annual rainfall was relatively high while annual soil respiration 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 3.1 and 3.3, Fig. 3.1). 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 respiration corresponded with those points, where volumetric soil moisture was lower than around 12% (Fig. 3.1c). In a water manipulation experiment, Liu *et al.* (2002) observed that soil respiration dropped very quickly when gravimetric soil moisture was below around 8%, which was very close to 12% of volumetric moisture, while there was little response of soil respiration above this point. Evenly distributed precipitation during the growing season of 2005 caused intermediate soil moisture and then the highest soil respiration. Therefore, the interannual variability of soil respiration 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 and Davidson 2001). The linear relationship between annual soil respiration and precipitation, which occurred at the global scale (Raich and Schlesinger 1992), may not work at local scale.

Effects of warming and yearly clipping

Numerous studies have observed increases in soil respiration 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 respiration may be regulated by acclimatization of respiration (Luo *et al.* 2001a), 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 respiration for 5 years out of the 6-year study period (except 2000). The warming-induced increases in soil respiration likely resulted from extensions of growing season and increased plant productivity (Wan *et al.* 2005). A positive linear correlation between soil respiration and aboveground biomass across the first three years indicated that increase in soil respiration largely enhanced belowground C allocation and R_A (Wan *et al.* 2005). The magnitude of warming effects on soil respiration 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.* 2001a). We did not observe a decline in warming stimulation of soil respiration as shown by Rustad *et al.* (2001), mainly because soil respiration is tightly coupled with carbon uptake through plant growth.

Few studies have examined the effects of warming on components of soil respiration 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 significant increases in soil respiration and its components in response to warming in sun-lit controlled-environment terracosms.

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 respiration by 19 – 49% at a short-term period (i.e., several days to months) (Bremer *et al.* 1998, Craine *et al.* 1999, Craine and Wedin 2002). In our study, yearly clipping significantly reduced soil respiration in the last two years and R_H for all the four 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 increased through time from 2002 to 2005. R_A was slightly stimulated by clipping due to an increase in root biomass (Wan *et al.* 2005). This increase offset the reduction in R_H, resulting in no significant effects on soil respiration in the first four years. In the last two years, however, the compensation of R_A was not enough to offset declining R_H. However, frequent clipping to keep the ground bare over the whole study period of one year significantly decreased soil respiration by 33% at a similar grassland (Wan and Luo 2003). Thus, frequency of clipping and duration of study can be sources of variation among studies.

Temperature sensitivity

The apparent Q_{10} values of soil respiration were slightly lower under warming ($p>0.05$) and reduced considerably by clipping ($p<0.05$) compared to the control, while there was no consistent trends among 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.* 2001a, Strömgren 2001, Niinistö *et al.* 2004), 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 a decrease in temperature sensitivity of soil respiration.

The apparent Q_{10} values for R_A were higher than those for R_H and soil respiration (Table 3.2). 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 (Boon *et al.* 1998, Rey *et al.* 2002). The different Q_{10} values for R_A and R_H suggest that temperature sensitivity of soil respiration depends on the relative root contribution. An ecosystem in which roots contribute the largest portion of soil respiration should be most sensitive to warming.

3.5. Conclusions

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

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

3.6. Acknowledgements

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Chapter 4

Patterns of biomass, litterfall, and soil respiration along a precipitation gradient in southern Great Plains

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This part has been prepared for *Ecology*.

ABSTRACT

Precipitation is a key driver in influencing ecosystem structure and function, especially in grassland ecosystems, and its regional control along natural gradients is thought to mirror long-term climate change. Along precipitation gradients, aboveground production is positively correlated with precipitation. However, how precipitation affects ecosystem belowground carbon gain, reservoir of litterfall, and loss of soil respiration and how they are interactively regulated are largely unknown. To address the role of precipitation in controlling ecosystem C gain, reservoir, and loss and their interaction, we measured aboveground and belowground biomass (AGB and BGB), standing and surface litter (ST and SU), and soil respiration for three seasons along a natural precipitation gradient from southeast to northwest Oklahoma in southern Great Plains. Our results show that AGB, ST, SU, and soil respiration often linearly increased with an increase in precipitation along the gradient, although belowground biomass (BGB) and total biomass varied little. BGB to AGB ratio and rain use efficiency (RUE) linearly decreased with increasing precipitation due to less plant allocation to roots and high biogeochemical constraints (e.g., nutrients or light), respectively, at mesic sites of the gradient. The one-year precipitation before samplings (OYP) had better correlations with biomass, litterfall, and soil respiration than mean annual precipitation (MAP). Soil respiration was not only affected by precipitation, but also regulated by litterfall in fall and winter and by AGB in spring, which were mainly controlled by precipitation. Our results suggest that precipitation controls soil water dynamics, which directly affects vegetation production and litterfall, and indirectly regulates soil respiration.

***Keywords**:* aboveground biomass, belowground biomass, litterfall, standing litter, surface litter, soil respiration, precipitation gradient, grassland

4.1. Introduction

Precipitation is a dominant environmental driver in influencing ecosystem structure and function, especially in grassland ecosystems (Webb *et al.* 1978, Sala *et al.* 1988, Lane *et al.* 2000, Epstein *et al.* 2002, Zerihun *et al.* 2006), and its availability could mediate the responsiveness of communities and ecosystems to global changes (Smith *et al.* 2000, Shaw *et al.* 2002, Huxman *et al.* 2004). The IPCC (2001) has projected a probable increase in precipitation of 0.5 to 1% per decade in this century, globally. However, predictions from the Vegetation-Ecosystem Modeling and Analysis (VEMAP) suggest that the Great Plains region of the North America would experience an approximate 30% decrease in annual precipitation by the end of this century (USGCRP 2003). Changes in precipitation may be of great consequence for ecosystem carbon cycling process because precipitation drives both biotic and abiotic processes and has the potential to affect grassland types, productivity, and decomposition rates (Lauenroth and Sala 1992, Milchunas *et al.* 1994, Knapp *et al.* 2001, 2002, Fay *et al.* 2002, Santiago and Mulkey 2005). Furthermore, Weltzin *et al.* (2003) suggested that shifts in precipitation regimes may have an even greater impact on ecosystem dynamics than the singular or combined effects of rising CO_2 and temperature, respectively. Therefore, understanding the role of precipitation is imperative to improve the prediction of ecosystem carbon cycling in the changing climate.

Regional controls on ecosystem structure and function have been explored through the use of spatial variation of key climatic factors (e.g., temperature and precipitation). Rgional analyses have elucidated control of precipitation on species assemblages (Epstein *et al.* 1996), primary production (Sala *et al.* 1988, Austin and Sala 2002, Epstein *et al.* 2002, Zerihun *et al.* 2006), litter decomposition (Meentemeyer *et al.* 1982, Austin 2002), and trace gas flux (Matson and Vitousek 1987, Simmons *et al.* 1996, McCulley *et al.* 2005). Those results are crucial for assessing the potential response to long-term global climate change (decades to centuries), and have thus been incorporated into statistical and simulation models (Burke *et al.* 1997), when experimental manipulation provides short-term responses (annual to decadal scales) (Shaver *et al.* 2000). In Oklahoma of the USA, annual precipitation shows a strong northwest-southeast gradient from 430 to 1200 mm, with a shift in grassland types from short grass steppe to mixed grass and tallgrass prairie. This precipitation gradient provides a unique opportunity to examine ecosystem carbon processes in different grassland types occurring in close proximity.

Along spatial precipitation gradients, the majority of previous studies have evaluated the control of precipitation on aboveground net primary production (ANPP), which often linearly increased with increasing precipitation from deserts to grasslands, but not all biomes (Webb *et al.* 1978, Sala *et al.* 1988, McNaughton *et al.* 1993, Paruelo *et al.* 1998, 1999, Austin and Sala 2002, Epstein *et al.* 2002, Zhou *et al.* 2002, Huxman *et al.* 2004, Santiago and Mulkey 2005, McCulley *et al.* 2005, Zerihun *et al.* 2006). However, ANPP represents only one-half or less of NPP of grasslands (Sims and Singh 1978, Milchunas and Lauenroth 2001), although it determines forage availability for herbivores In contrast, belowground compartment of the vegetation likely contributes to a more important source of soil C than aboveground one. Due to methodological difficulties (Medina and Klinge 1983, Olson *et al.* 2001), few studies have quantified belowground production, and even fewer were made along natural precipitation gradients (Sims and Singh 1978, McCulley *et al.* 2005). Thus, quantifying belowground response to regional precipitation patterns becomes necessary to better understand ecosystem functioning in the changing world.

The litter of an ecosystem is one of the reservoirs of carbon and nutrients. It is an important transfer station of material and energy from plant to soil (Yin and Huang 1996). This reservoir is an input-output system, which receives dead vegetation input, loses biomass by decomposition, and storesorganic matter in soil until released by decomposing organisms. The CO_2 flux from the last two parts is called heterotrophic respiration, which approximately contributes to 70% of soil respiration, and another component is root respiration (~30%) in grasslands (Hanson *et al.* 2000, See Chapter 3). At the global scale, litter decomposition and soil respiration are strongly influenced by precipitation (Raich and Schlesinger 1992). Along precipitation gradients, increasing primary production may largely enhance litterfall production (Read and Lawrence 2003, Lawrence 2005), and then stimulate soil respiration (Gärdenäs 2000, McCulley *et al.* 2005). However, ecosystem carbon gain, reservoir, and loss (i.e., productivity, litterfall, and soil respiration) may be interactively constrained by the magnitude of precipitation. In addition, standing (ST) and surface (SU) litter may have different responses to precipitation along the gradient compared to total litterfall. Therefore, it is essential to examine how ST and SU respond differentially to change in precipitation and how biomass, litterfall, and soil respiration are interactively regulated along the precipitation gradient.

In gradient studies, nearly all analyses have used mean annual precipitation (MAP) to describe response patterns of ecosystem processes (e.g., Sala *et al.* 1988, Lane *et al.* 2000, Austin and Sala 2002, Huxman *et al.* 2004, Santiago and Mulkey 2005, Zerihun *et al.* 2006). However, measurements in the field were usually conducted in a simple snapshot of long-term responses to precipitation. MAP may not reflect the snapshot measurements compared to one-year precipitation before sampling (OYP). Therefore, in this study, we compared relationships between measured variables and MAP or OYP to determine which one better represents ecosystem functioning.

In this study, our objectives were to examine spatial controls of precipitation on biomass, litterfall, and soil respiration and how they are interactively regulated, and to attempt to identify how well MAP and OYP reflect these processes along a precipitation gradient in southern Great Plains grasslands. We hypothesized that biomass, litterfall, and soil respiration all would increase along the precipitation gradient and litterfall and soil respiration would be regulated by biomass. We also hypothesized that OYP would better reflect ecosystem carbon processes than MAP.

4.2. Materials and methods

Site descriptions

This transect study was conducted in temperate grasslands of Oklahoma along a precipitation gradient through the southern Great Plains region of the USA (Fig. 4.1). Nine grassland sites were selected to represent three grassland types which differ substantially in physiognomy: short-grass steppe, mixed-grass prairie, and tallgrass prairie (Sims 1988). We chose sites with the minimum amount of disturbance and land-use impact possible based on conversations with site owners and managers of government organization, although light to intermediate grazing had or was occurring. Mean annual precipitation (MAP) across these sites varied from 430 mm in northwest Oklahoma to 1200 mm in southeast Oklahoma (Table 4.1). Across this precipitation gradient, mean annual temperature (MAT) had a relatively little change. Table 4.1 shows location (Latitude and Longitude), elevation, MAP, MAT, and soil types of nine

Table 4.1 Location (latitude and longitude), elevation, mean annual precipitation (MAP), mean annual temperature (MAT), and soil type at nine grassland sites from southeastern to northwestern Oklahoma.

Site	**Latitude**	**Longitude**	**Elevation (m)**	**MAP (mm)**	**MAT (°C)**	**Soil Type**
HU	34°01'50" N	95°25'24" W	174	1203	16.5	Fine sandy loam
PR	34°30'05" N	96°36'59" W	309	1048	16.2	Silt loam
KF	34°58'54" N	97°31'14" W	340	915	16.3	Silt loam
HP	35°14'53" N	98°51'41" W	480	806	15.3	Clay loam
HL	35°37'50" N	98°30'24" W	493	760	15.4	Fine sandy loam
CL	36°07'30" N	98°37'55" W	485	735	14.4	Fine sandy loam
UW	36°26'04" N	99°23'58" W	579	660	13.6	Loam fine sand
OL	36°38'45" N	101°13'18" W	913	465	13.8	Loam
RB	36°31'43" N	102°50'01" W	1263	434	13.0	Fine sandy loam

Notes: **HU**- Hugo Lake **PR**-Pontotoc Ridge preserve
KF- Kessler’s farm field laboratory **HP**-Hulsey’s private land
HL- American Horse Lake **CL**- Canton Lake
OL- Optima Lake **RB**-Rita Blanca national grassland
UW- USDA southern plains range research station in Woodward

Elevation, MAP, and MAT are NOAA monthly normals of the nearest weather station from each site (http://cdo.ncdc.noaa.gov/climatenormals/clim81/OKnorm.pdf). Soil type is from Soil Conservation Services (SCS), State Soil Geographic Datatbase (STATSGO) http://www.xdc.arm.gov/data_viewers/sgp_surfchar/Oklasoil_new.html grassland sites from southeastern to northwestern Oklahoma. Species composition and phonological habit changed across this precipitation gradient (X. Zhou and Y. Luo, unpublished data, 2005).

Sampling design

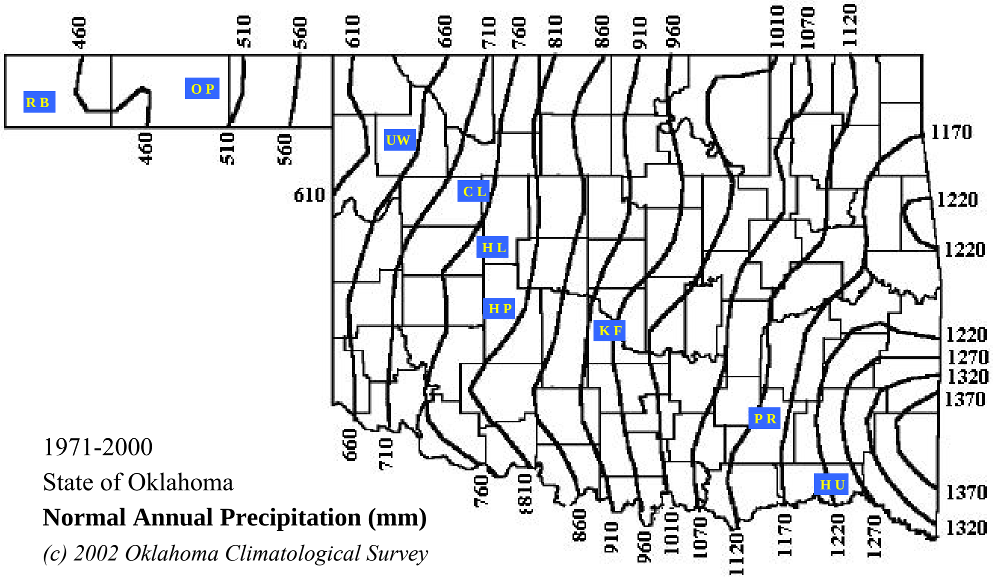
Samples were collected within one week in fall (August 2003) and spring (May 2005) to reduce effects of temperature variation. In winter (February 2004), sampling was extended to two weeks. In fall and winter, only seven sites were selected (excluding CL

and UW, Table 4.1), and measured variable included aboveground biomass (AGB), standing litter (ST), surface litter (SU), soil respiration, soil moisture, and soil temperature. In May 2005, we also measured belowground biomass (BGB), leaf area index (LAI), field capacity, pH, total C and N besides those variables measured in fall and winter.

At each sampling site, five randomly selected plots were investigated on 0.5 m × 0.5 m quadrants. Within the selected plot, we firstly measured LAI using LAI-2000 and soil respiration and temperature by LiCor 6400 connected with soil CO_2 efflux chamber and thermocouple probe, respectively. Then all vegetation including AGB, ST, and SU was harvested. Finally, we collected one soil core with two increments (0-15 and 15-30 cm, diameter = 4.0 cm) for root biomass and one core (diameter =3.5 cm, height=5 cm) for field capacity at each plot. Soil moisture, pH, total C and N contents were measured in 0-15-cm soil core after picking roots. We stored soil samples in an ice chest until they were brought back to the laboratory stored in a freezer (-4^{o}C).

Biomass and litterfall measurements

Aboveground biomass (AGB) and standing litter (ST) were determined by the harvest method. All vegetation within a 0.5 × 0.5 m^2 quadrant was clipped at 5 cm above the soil surface at each plot. Once return to the laboratory, samples were oven dried at 60^oC for 48 h right away, and then separated into categories of live and dead biomass (i.e., AGB and ST) and weighted.



1971-2000
State of Oklahoma
Normal Annual Precipitation (mm)
(c) 2002 Oklahoma Climatological Survey

Fig. 4.1 Map showing location of grassland sites and normal annual precipitation (1971-2000) over state of Oklahoma from Oklahoma Climatological Survey. See Table 4.1 for abbreviations.

Belowground biomass (BGB): One soil core sample was collected at the two increments: 0-15 and 15-30 cm using 4 cm diameter steel corer in each sampling plot. After washing soil through 0.25 mm mesh sieve, roots were oven dried at 60^oC for 48 h and weighted.

Surface litter (SU) was removed with a hand rake in a 0.5 m × 0.5 m quadrant prior to soil sampling at each plot. The litter samples were cleaned, oven dried at 60^{o}C for 48 h and weighted.

Measurements of other variables

Leaf area index (LAI) is the total cone-sided foliage area per unit ground surface area. LAI was measured using LiCor plant canopy analyzer (Model LAI-2000, LI-COR. Inc., Lincoln, Nebraska, USA). LAI-2000 measures the transmitted blue sky light (400-490 nm) under the canopy. A single above-canopy radiation measurement with five below-canopy readings each plot was used to compute the LAI. A 90^{o} view restrictor was used in all measurements to prevent direct sunlight from reaching the sensor and to occlude the operator from the field of view.

S*oil respiration* was measured using a LI-COR 6400 portable photosynthesis system attached to soil CO_2 flux chamber (LI-COR. Inc., Lincoln, Nebraska, USA). A measurement consisted of placing the chamber on soil, scrubbing the CO_2 to sub-ambient levels, and determining soil CO_2 efflux over the periods. Data were recorded at a 5-second interval by the datalogger in the LI-COR 6400 console.

Soil temperature at the depth of 5 cm was monitored 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.

Soil moisture was measured gravimetrically. Soil samples at the top 15 cm were taken from each plot and oven dried at 105°C for 48 hours and weighed. Gravimetric soil moisture was expressed as a percent of dry soil on a mass basis.

Field capacity (FC) was measured by soaking the soil for 12 h in a plastic cylinder (diameter =3.5 cm, height=5 cm) with a 0.3 mm nylon mesh in the bottom. After the soil was drained for 1h, the soil was emptied into a container and the FC was determined as for gravimetric soil moisture.

Soil pH was measured at a 1:10 soil-to-water ratio with a pH meter (Model 420A+Thermo Orion, Beverley, MA). Samples were mixed end-over-end for 1h.

Total C and N content: On prior analysis, it was found that the soil contains carbonates. To avoid misinterpretation of soil C and N data, soils were acid-treated based on a procedure used by Subedar (2005). Briefly, 5 ml of 6N H_2SO_3 was added to 0.5 g of soil in clean glass vials. The samples were agitated for a few seconds to suspend the soil in the solution. The presence of carbonates was indicated by formation of bubbles. The samples were let to sit at room temperature for approximately 6 hours and then dried overnight at 60° C. The analysis of soil samples for total C and N content was done using a Finnigan DELTA plus Advantage gas isotope-ratio mass spectrometer (Thermo Finnigan MAT GmbH, Barkhausenstr, Germany), which is configured through the CONFLO III for automated continuous-flow analysis of solid inorganic/organic samples using a Costech ECS 4010 elemental analyzer (Costech Analytical Technologies Inc., Valencia, CA).

Data analysis

The statistical effects of MAP or OYP on biomass, litterfall, and soil respiration were examined using regression analysis with MAP or OYP as an independent continuous variable. Comparisons of biomass, litterfall, and soil respiration were performed with 1-way analysis of variance (ANOVA). Stepwise multiple linear regression analysis was also applied to examine the control factor(s) of AGB, litterfall, and soil respiration using all other measured variables. Differences within the factor (site) were analyzed with a post-hoc Duncan's multiple range test. The effects were considered to be significantly different if $p<0.05$ in all cases. All statistical analyses were performed using SPSS 11.0.1 for windows (SPSS Inc., Chicago, IL USA, 2001).

4.3. Results

Soil characteristics along the precipitation gradient

Soil characteristics measured in this study are field capacity, pH, bulk density, C and N contents, and C:N ratio (Fig. 4.2). Along the precipitation gradient, distinct trends were only shown in pH and C:N ratio (Fig. 4.2b,d). Decreasing trend of pH was due to the existence of calcium carbonate at low precipitation sites based on simple test of HCl

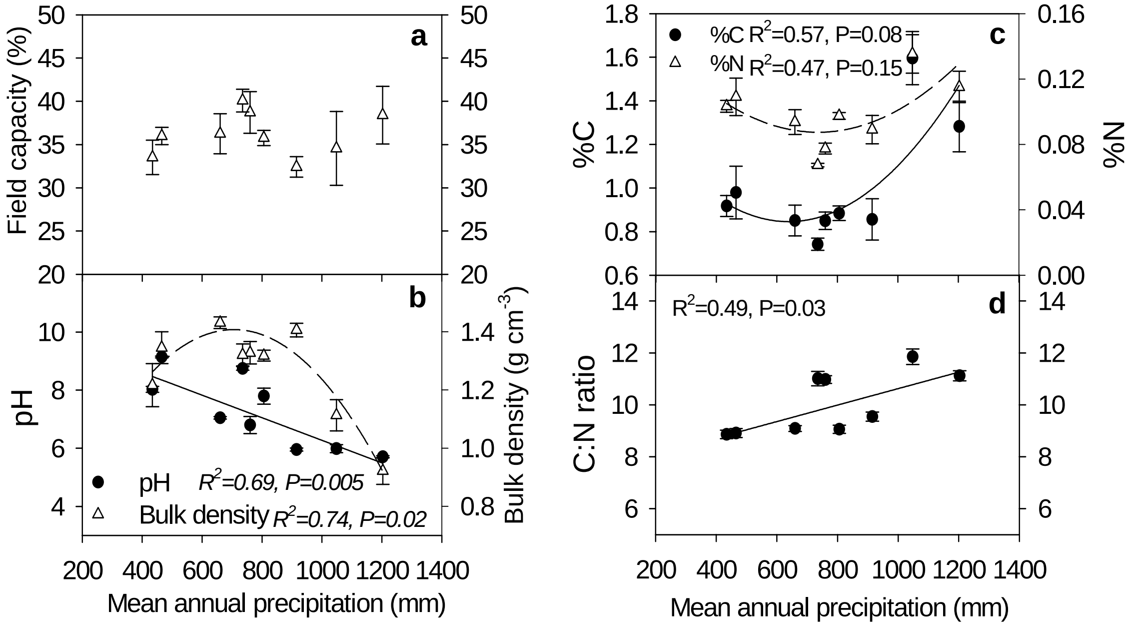


Fig. 4.2 Soil characteristics along the precipitation gradient: Field capacity (%, a), pH and soil bulk density (g cm^{-3}, b), %C and %N (c), and C:N ratio (d). Data are shown as mean ± SE (n=5).

(Fig. 4.2b). %C and %N contents and bulk density did not significantly change with increasing precipitation except the wettest site (Hugo Lake, Fig. 4.2b,c). If %C and %N contents were transferred to volume contents (g m^{-3}), C and N contents were similar for all sites (Data not shown) as well as field capacity (Fig. 4.2a).

Comparison of relationships for MAP and OYP

There was considerable difference between the one-year precipitation before measurements (OYP) and mean annual precipitation (MAP), especially in Aug 2003 and Feb 2004, which largely regulate short-term and long-term processes, respectively (Fig. 4.3). Biomass, litterfall, and soil respiration may be affected by both MAP and OYP. However, better correlations occurred between measured variables and OYP than those between measured variables and MAP (Table 4.2), suggesting the larger regulation of biomass, litterfall, and soil respiration from OYP than MAP. Thus, we stated our results using relationships between measured variables and OYP instead of MAP thereafter, which were usually showed in the literature (e.g., Sala *et al.* 1988, Epstein *et al.* 2002, Lane *et al.* 2000, Austin and Sala 2002, Zerihun *et al.* 2006).

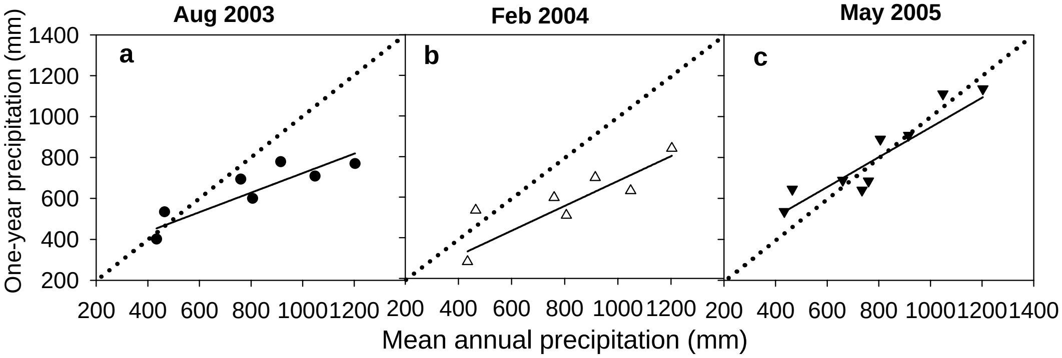


Fig. 4.3 Discrepancy between mean annual precipitation (MAP) and one-year precipitation before measurements (OYP) in Aug 2003 (a), Feb 2004 (b), and May 2005 (c). Data are shown as mean ± SE (n=5).

Table 4.2 Comparison of relationships between measured variables and one-year precipitation before measurements (OYP) and between measured variables and mean annual precipitation (MAP) in Aug 2003, Feb 2004, and May 2005. R^2 is the determinant coefficient. P values represent the significance of regression.

Time	Parameters	One-year precipitation (OYP)		Mean annual precipitation (MAP)	
		R^2	P	R^2	P
Aug 2003	AGB	0.85	0.009	0.62	0.06
	ST	0.79	0.007	0.75	0.01
	SU	0.65	0.03	0.48	0.08
	ST/SU ratio	0.45	0.09	0.44	0.10
	Soil respiration	0.88	0.006	0.80	0.02
	Soil moisture	0.73	0.01	0.64	0.04
Feb 2004	ST	0.52	0.07	0.65	0.03
	SU	0.62	0.06	0.67	0.05
	ST/SU ratio	0.63	0.03	0.61	0.04
	Soil respiration	0.79	0.008	0.60	0.04
	Soil moisture	0.70	0.03	0.79	0.02
May 2005	AGB	0.75	0.006	0.63	0.02
	AGB/BGB ratio	0.50	0.03	0.41	0.06
	ST	0.12	0.37	0.14	0.32
	SU	0.57	0.02	0.56	0.02
	ST/SU ratio	0.43	0.05	0.42	0.06
	Soil respiration	0.66	0.01	0.65	0.01
	Soil moisture	0.67	0.007	0.51	0.05

Pattern of biomass along a precipitation gradient

Green aboveground biomass (AGB) linearly increased along the precipitation gradient in both August 2003 and May 2005 as well as leaf area index (LAI) in May 2005 (Fig. 4.4a,b,c), although there was one outlier at each measurement, both resulting from drought stress. In August 2003, the outlier site was in Kessler farm field laboratory (KFFL) due to the long period of no rain in June and July (34 days). In May 2005, the outlier occurred in Pontotoc ridge preserve (PR) because of a low proportion of rainfall

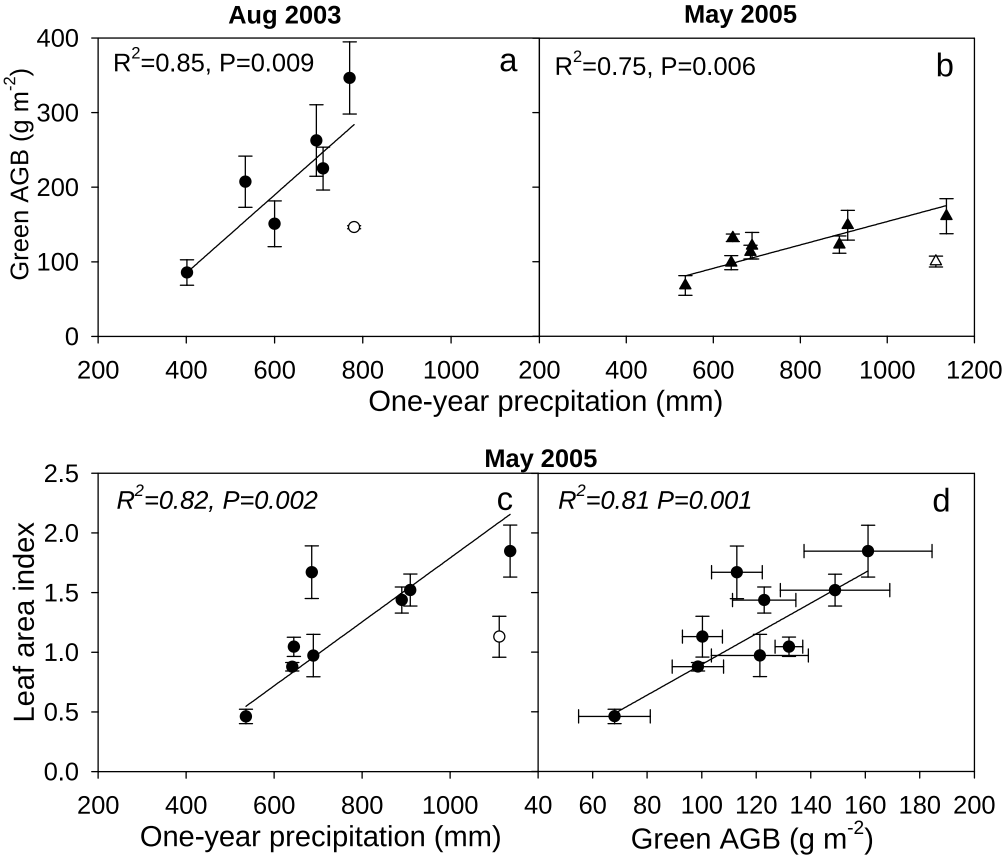


Fig. 4.4 Changes in green aboveground biomass (AGB) in Aug 2003 (a) and May 2005 (b) and leaf area index (LAI) in May 2005 (c) with one-year precipitation before measurements (OYP) along the precipitation gradient. Panel d shows the relationship between green AGB and LAI in May 2005. Data are shown as mean ± SE (n=5).

in the period from Jan to May 2005 (20%). Leaf area index (LAI) controls light interception of plant canopies, and affects carbon exchange between vegetation and the atmosphere. Thus, a good relationship occurred between green AGB and LAI without outliers in May 2005 (Fig. 4.4d).

Interestingly, root or belowground biomass (BGB) at the depth intervals of 0-15, 15-30, and 0-30cm did not show distinct changes with increasing precipitation as well as total biomass (AGB+BGB) (Fig. 4.5a,b,c). However, BGB to AGB ratios linearly decreased along a precipitation gradient (Fig. 4.5d) as well as rain use efficiency (RUE), which was calculated from total biomass divided by OYP (Fig. 4.6).

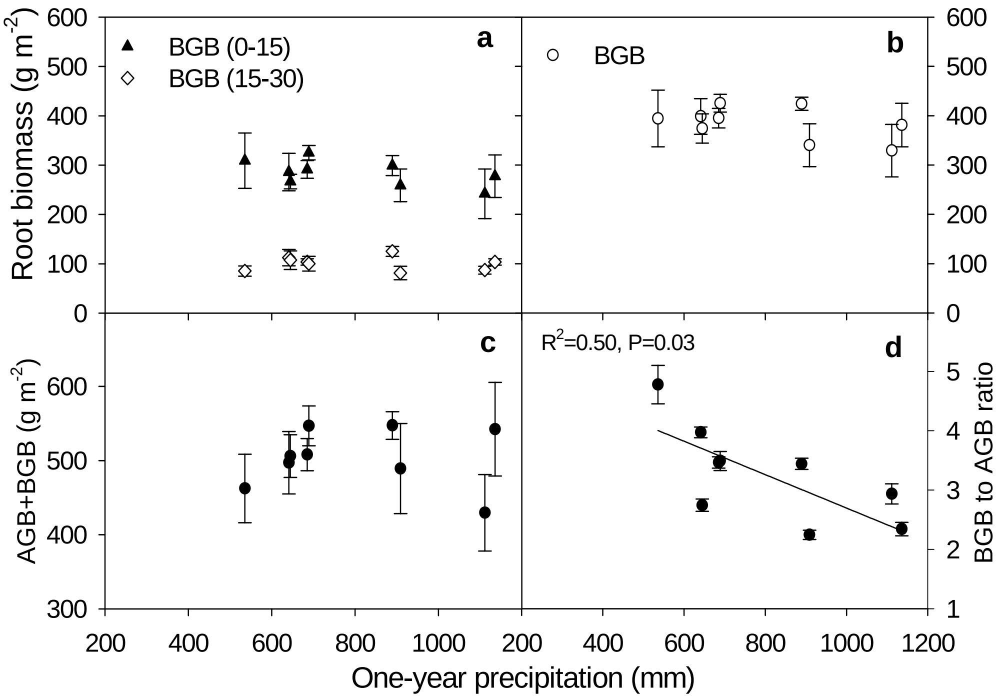


Fig. 4.5 Changes in belowground biomass (BGB) at the depth of 0-15 cm and 15-30 cm (a), total measured BGB at the depth of 0-30 cm (b), total biomass including AGB and BGB (c), and AGB:BGB ratio (d) along a precipitation gradient. Data are shown as mean± SE (n=5).

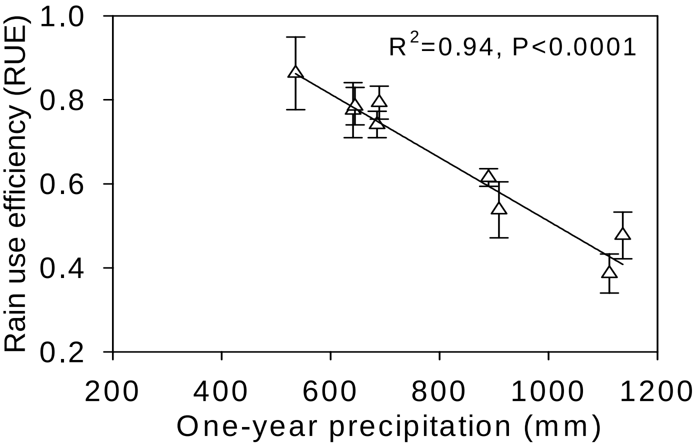


Fig. 4.6 Pattern of rain use efficiency (RUE, ratio of total biomass (AGB+BGB) to OYP) along a precipitation gradient. Data are shown as mean ± SE (n=5).

Pattern of litterfall and soil respiration along a precipitation gradient

Litterfall was separated into standing litter (ST) and surface litter (SU). Different patterns of ST, SU, total litter (ST+SU), and ST to SU ratio occurred in three seasons along the precipitation gradient (Fig. 4.7). Both ST and SU linearly increased with increasing precipitation except ST in May 2005 (no change, Fig. 4.7c) and SU in February 2004 (decrease, Fig. 4.7e). Total litter and ST to SU ratios also linearly increased along the precipitation gradient except ST+SU in February 2004 due to a decrease in SU (Fig. 4.7b) and ST:SU ratio in May 2005 (decrease, Fig. 4.7i).

Soil respiration and soil moisture linearly increased along the precipitation gradient in all three seasons, while there were not significant changes in soil temperature (Fig. 4.8). An outlier occurred in May 2005 for soil respiration largely due to a significant low rainfall from January to May 2005 (Fig. 4.8c,f).

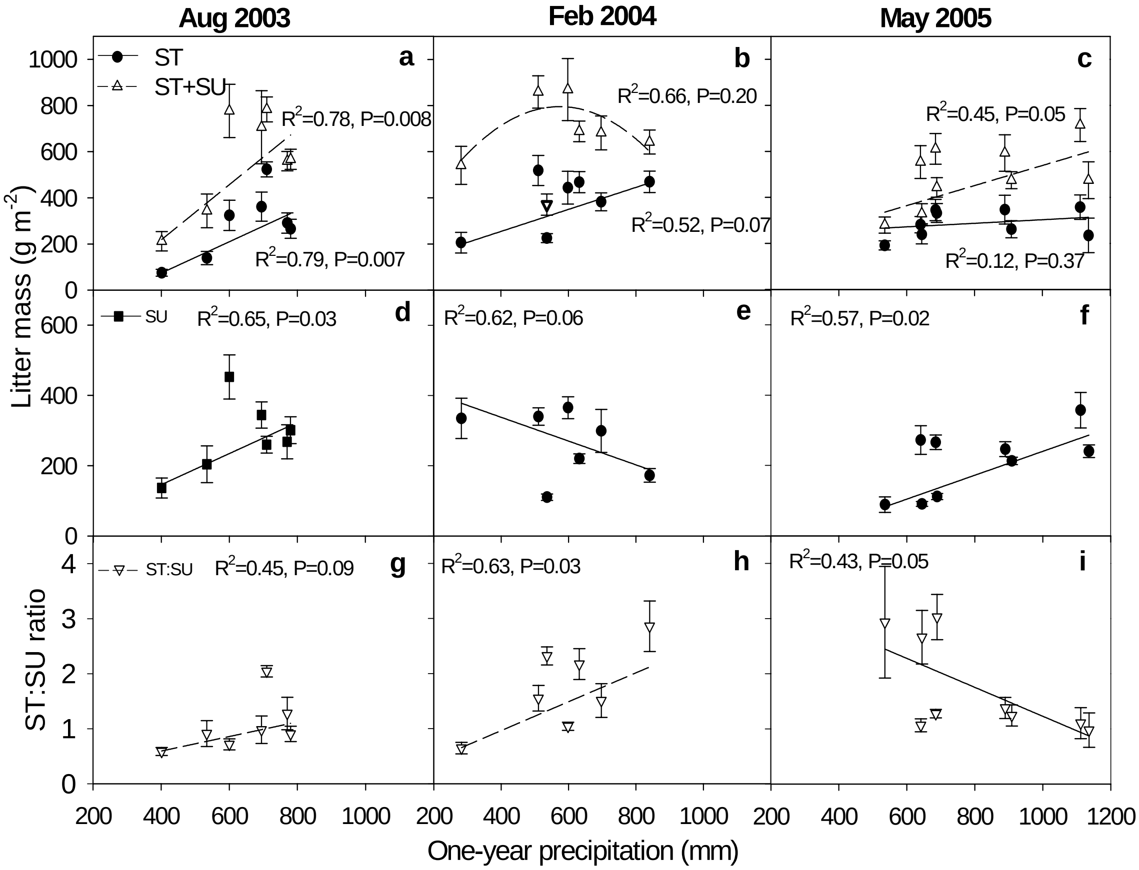


Fig. 4.7 Changes in standing litter (ST), surface litter (SU), total litter (ST+SU), and ST:SU ratio in Aug 2003 (a, d, g), Feb 2004 (b, e, h), and May 2005 (c, f, i) along a natural precipitation gradient. Data are shown as mean ± SE (n=5).

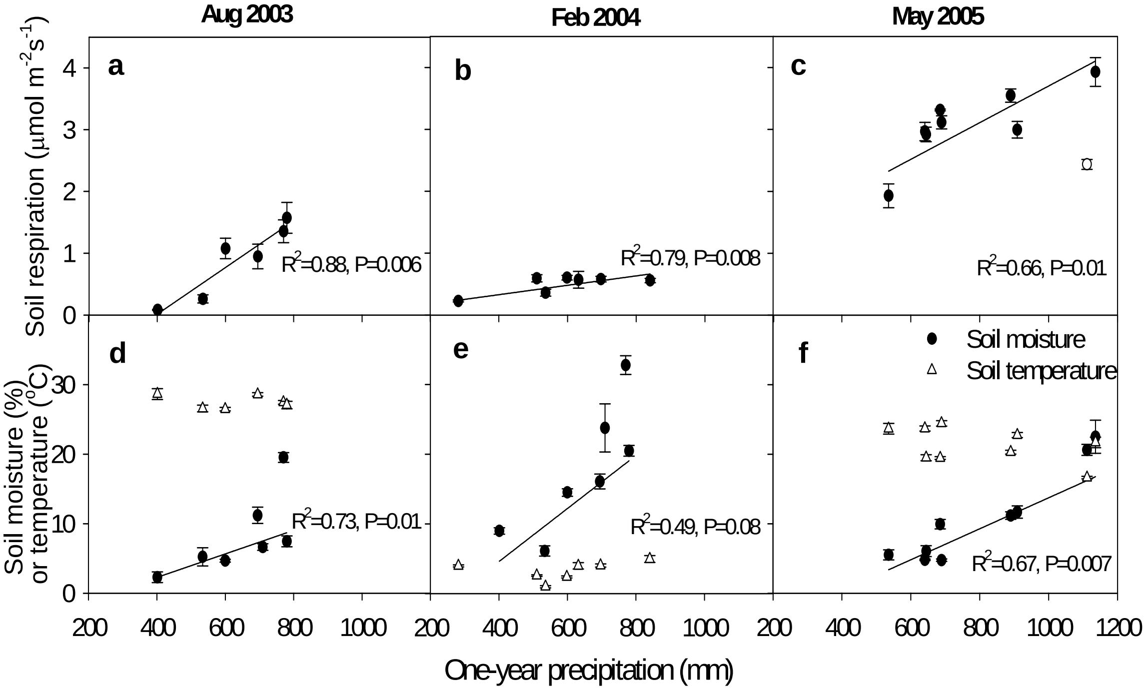


Fig. 4.8 Changes in soil respiration (μmol m^{-2} s^{-1}), soil moisture (%g), and soil temperature (°C) in Aug 2003 (a, d), Feb 2004 (b, e), and May 2005 (c, f) along the precipitation gradient. Data are shown as mean ± SE (n=5).

Relationships between biomass, litterfall, and soil respiration

Table 4.3 shows relationships between biomass, litterfall, and soil respiration in the three seasons. Soil respiration was significantly linearly correlated with SU and ST in Aug 2003 and February 2004 and with AGB in May 2005, while AGB was mainly controlled by precipitation. Similarly, ST and SU were also not related to other processes besides between each other. Using all measured variables, stepwise multiple linear regression analysis also showed the similar results above-stated for AGB, litterfall, and soil respiration (data not shown).

Table 4.3 Relationships between soil respiration, aboveground (AGB) and belowground (BGB) biomass, standing litter (ST), and surface litter (SU) in three seasons.

	Aug 2003			**Feb 2004**			**May 2005**		
	Variable	R^2	P	Variable	R^2	P	Variable	R^2	P
Rs	AGB	0.50	0.12	**ST**	0.82	**0.005**	**AGB**	0.73	**0.003**
	ST	0.87	**0.006**	**SU**	0.51	**0.07**	BGB	0.04	0.61
	SU	0.80	**0.02**				ST	0.23	0.19
							SU	0.12	0.37
ST	AGB	0.56	0.09	**SU**	0.72	**0.02**	AGB	0.01	0.85
	SU	0.78	**0.008**				BGB	0.15	0.31
							SU	0.53	**0.03**
AGB	ST	0.53	0.10				BGB	0.01	0.77
	SU	0.26	0.30		/		SU	0.11	0.38
							ST	0.21	0.21

4.4. Discussion

Our study demonstrated that linear relationships often occurred between biomass, litterfall, or soil respiration and precipitation along the precipitation gradient in southern Great Plains grasslands (Figs. 4.4, 4.7, and 4.8), although BGB did not greatly change (Fig. 4.5). BGB:AGB ratio and rain use efficiency (RUE) linearly decreased with increasing precipitation. The one-year precipitation before samplings (OYP) had a better correlation with biomass, litterfall, and soil respiration than mean annual precipitation (MAP, Table 4.2). In addition, biomass, litterfall, and soil respiration are interactively regulated by the magnitude of precipitation (Table 4.3). This transect study provides an effective tool to gain insight and allows us to evaluate trends and regulation in biomass, litterfall, and soil respiration as a function of precipitation without the confounding effect of drastic changes in vegetation type and soil characteristics.

Comparison of relationships for MAP and OYP

Ecosystem carbon cycling processes are the outcome of combined effects of long- and short-term environmental drivers (Bloom *et al.* 1985, Burke *et al.* 1998, Zerihun *et al.* 2006). Along the precipitation gradient, these processes are not only influenced by mean annual precipitation (MAP) but also regulated by one-year precipitation before sampling (OYP). Our results show that biomass, litterfall, and soil respiration often had better correlations with OYP than MAP in three seasons (Table 4.2). The snapshot measurements in each of three seasons largely reflect effects of OYP more than MAP in this transect study, especially aboveground biomass (AGB). AGB was mainly controlled by current-year precipitation while litterfall and soil respiration were interactively regulated by both OYP and MAP (Tables 4.2 and 4.3). The study of interannual variation in primary production supports our results that ANPP was correlated with both current-year and previous-year precipitation in grassland ecosystems (Oesterheld *et al.*'s 2001, Nippert *et al.* 2006). Thus, cautions should be taken when we explained the data from snapshot measurement. Current-year precipitation and MAP both should be considered to evaluate the responses of ecosystem processes to precipitation.

Pattern of biomass along a precipitation gradient

Vegetation dynamics are tightly coupled with hydrologic processes (Saco *et al.* 2006). Precipitation has served as a powerful predictor of plant productivity and other ecological attributes (Sala *et al.* 1988, Knapp *et al.* 2002, Austin and Sala 2002, Breshears 2005). Our results show the similar trend for AGB, which linearly increased with increasing precipitation along the gradient (Fig. 4.4). The positive relationships between ANPP and precipitation also have been observed in the central grassland region of the USA (Sala *et al.* 1988, Lane *et al.* 1998, 2000) and Siberian grasslands (Titlyanova *et al.* 1999) as well as other regions (Webb *et al.* 1978, Austin and Sala 2002, Zhou *et al.* 2002, Huxman *et al.* 2004, Santiago and Mulkey 2005, Zerihun *et al.* 2006). However, BGB did not show distinct changes along the precipitation gradient as well as total biomass (Fig. 4.5), largely resulting from a decrease in the proportion of primary production allocated to roots and an increase in turnover of roots with increasing precipitation (Comeau and Kimmins 1989, Pietikäinen *et al.* 1999, Kahmen *et al.* 2005).

Difference between the patterns of AGB and BGB resulted in a decreased trend in BGB to AGB ratio along the precipitation gradient (Fig. 4.5d), indicating marked ecosystem-level adjustments in relative balances of BGB and AGB stocks. The trend of BGB to AGB ratio in our study is consistent with other studies (Comeau and Kimmins 1989, Chapin *et al.* 1993, Schulze *et al.* 1996, Zerihun *et al.* 2006) and prediction of resource balance/optimality theory (Bloom *et al.* 1985, Friedlingstein *et al.* 1999) largely due to the difference of the limiting source or plant strategy (Tilman 1988, Vinton and Burke 1997, Craine 2005). In semi-arid short-grass steppe, water is the primary limitation with physiological stress on plant production (Lauenroth *et al.* 1978), whereas production is limited by water as well as light and nutrient (mainly competition stress) in the tallgrass prairie (Knapp and Seastedt 1986, Schimel *et al.* 1991, Lane *et al.* 1998, 2000). Plant biomass distribution is adjusted to facilitate the acquisition of growth-limiting resources.

As a consequence, rain use efficiency (RUE) decreased with increasing precipitation along the gradient (Fig. 4.6), largely resulting from a decrease in vegetational constraints associated with response of dominant plants to changes in resource availability (i.e., water) and an increase in biogeochemical constraints related to the magnitude of nutrient or light limitation (Paruelo *et al.* 1999). Specifically, at the driest extreme of the gradient, plants with low relative growth rates (RGR) constrain the response of ANPP to precipitation with high BGB:AGB ratio (Fig. 4.5d), low LAI (Fig. 4.4c,d), low stomatal conductance, and low photosynthetic rates (Tilman 1988, Santiago and Mulkey 2005). At the wettest extreme of the gradient, high biomass or LAI reduce vegetational constraints and may result in an increase in nutrient (or light) limitation due to high nitrogen use efficiency or plant shading (Vitousek 1982, Vinton and Burke 1995), that is to say, biogeochemical constraints. Our results were remarkably similar to other studies for different areas of the world (Sala *et al.* 1988, McNaughton *et al.* 1993, Paruelo *et al.* 1998, 1999, Huxman *et al.* 2004).

Pattern of litterfall along a precipitation gradient

Litterfall represents an essential link between plant production and CO_2 release from soil. Our results show that standing litter (ST), surface litter (SU), total litterfall, and ST to SU ratio increased linearly along the precipitation gradient in fall (Fig. 4.7a,d,g), while, in winter and spring, this trend was not followed by all variables (Fig. 4.7b,c,e,i). The positive relationships between litterfall and precipitation result from different mechanisms along the gradient. At low rainfall, low input of production results in low accumulation of detritus when litter decomposition is also slow. As precipitation increases, litterfall input increases at a higher rate than mass loss, and then accumulates the larger litters at soil surface and in the air (Austin 2002). Slower decomposition of ST in the air than that of SU at the soil surface results in an increase in ST to SU ratio along the precipitation gradient due to low water availability of litter in the air (Kuehn *et al.*

1998). The trends were consistent with regional and global patterns of detritus for ecosystems in the same precipitation regimes (Schlesinger 1977, Austin 2002).

However, SU decreased along the precipitation gradient in February 2004 (Fig. 4.7e), largely resulting from enhanced physical leaching (Swift *et al.* 1979) and confounding effect of temperature (Read and Lawrence 2003). Along the precipitation gradient, the proportion of annual precipitation from September 2003 to February 2004 increased from 25% to 50% in despite of increasing rainfall, too. The greater rainfall accelerates the breakdown of surface litter through physical process of leaching, which is controlled by precipitation (Swift *et al.* 1979, Austin and Vitousek 2000). In addition, mean annual temperature (MAT) varied from 13.0 to 16.5^{o}C along the precipitation gradient (Table 4.1). A larger response to the small change in temperature may occur in winter compared to summer along the gradient due to higher temperature sensitivity of litter decomposition at low temperature range than high range (Kirschbaum 1995, Janssens and Pilegaard 2003, Chen and Tian 2005). In winter, thus, litter decomposition was faster in mesic than xeric sites, resulting in an opposite trend for SU along the gradient. This trend did not occurred on ST because low water availability of litter largely slow down decomposition in the air (Kuehn *et al.* 1998).

In May 2005, ST did not show distinct change along the precipitation gradient (Fig. 4.7c, i) because the snapshot measurement of ST represented those amounts of previous-year recalcitrant litter, which was difficult for microbial decomposition (e.g., stem). The previous-year ST were easier to fall down and decompose at mesic than xeric sites due to high temperature and wet climate along the gradient, although plant C:N ratio increased (Swift *et al.* 1979, Vitousek *et al.* 1994, Murphy *et al.* 2002). The relatively constant trend for ST led to a decreased trend of ST to SU ratio along the precipitation gradient (Fig. 4.7i). Our results suggest that patterns of ST, SU, total litterfall, and ST to SU ratio were not constant in different seasons along the precipitation gradient (Fig. 4.7).

Litterfall is generally related to vegetation biomass as an interesting index of ecosystem productivity (Olson 1963). However, our correlative analysis did not show this relationship, largely resulting from that these grassland sites may be not in equilibrium due to light or intermediate grazing. Usually, the amount of litter input is also served as a parameter determining the size of soil C pools and soil respired CO_2 (Cotrufo 2006). Our study did show the relationship between soil respiration and ST or SU (Table 4.3). However, Sayer *et al.* (2006) found that roots responded rapidly to changes in fresh leaf litter input and appeared to closely follow the patterns of litter decomposition in increasing litterfall experiments. That is to say, quantity of standing litter is a driving factor of root dynamics. Although we did not carefully examine root dynamics and no correlation between root biomass and either ST or SU was found along the precipitation gradient, such different effects may reflect differences in litter quantity, litter quality, or distribution of detritus.

Pattern of soil respiration along a precipitation gradient

Soil respiration linearly increased along a precipitation gradient in the study (Fig. 4.8). Temperature and moisture are the two major factors influencing soil respiration (Luo and Zhou 2006). To reduce temperature effects, our sampling was conducted within one week in fall and spring and within two weeks in winter. Precipitation is the primary input of soil moisture and often important to predict the regional and global variability in soil respiration (Raich and Schlesinger 1992, Conant *et al.* 1998, Gärdenäs

2000, Epstein *et al.* 2002). Thus, this trend occurred along the gradient. Other studies also found this trend that soil respiration and decomposition rates both increased with MAP across the Great Plains of North America (McCulley *et al.* 2005). In addition, leaf litter mass and CO_2 fluxes from leaf litter decomposition both were positively correlated with MAP in northern hardwood ecosystems in Maine, USA (Simmons *et al.* 1996).

Soil respiration includes autotrophic root respiration and heterotrophic component during litter and soil organic matter (SOM) decomposition. Usually, root respiration is tightly related to root biomass with a linear relationship (Kucera and Kirkham 1971, Edwards and Sollins 1973, Behara *et al.* 1990). Our results show that root biomass did not change largely along the precipitation gradient (Fig. 4.5), and thus autotrophic root respiration also did not vary greatly. This results in that the contribution of heterotrophic to total soil respiration decreased along the precipitation gradient. Thus, the regional increase in soil respiration along the gradient is largely the result of increasing litter and soil organic matter decomposition. Unfortunately, we still can not determine the exact proportion of root or heterotrophic respiration to soil respiration.

Soil respiration was not only affected by precipitation, but also regulated by litterfall in fall and winter and by AGB in spring, which were mainly controlled by precipitation (Table 4.3). In the growing season (May 2005), roots were very active, resulting in root respiration contributing a large proportion of total soil respiration because autotrophic component reflects plant activity and the supply or organic compounds to root from the canopy (Högberg *et al.* 2001, Bhupinderpal-Singh *et al.* 2003, Binkley *et al.* 2006, Also see Chapter 3). In non-growing season, the relationship between soil respiration and ST or SU suggests that litter decomposition may contribute a considerable amount to soil respiration. Thus, precipitation directly affects vegetation production and litterfall, and indirectly regulates soil respiration.

4.5. Conclusion

This transect study examined patterns of biomass (AGB and BGB), litterfall (ST and ST), and soil respiration in southern Great Plains grasslands along a precipitation gradient (430 – 1200 mm). The results show that AGB, litterfall (ST and SU), and soil respiration were often linearly related to precipitation, although BGB and total biomass did not largely change. BGB to AGB ratios and rain use efficiency (RUE) linearly decreased with increasing precipitation due to less plant allocation to roots and high biogeochemical constraints (e.g. nutrients and light), respectively, at the wet sites of the gradient. The one-year precipitation before samplings (OYP) was a better predictor on biomass, litterfall, and soil respiration, than mean annual precipitation (MAP). Our results indicate that precipitation is an important driver in shaping ecosystem functioning by controlling soil water dynamics, which directly affects vegetation production and litterfall, and indirectly regulates soil respiration in grassland ecosystems. It is suggested to incorporate our findings into current biogeochemical models as this will improve the predictions of long-term climate change effects (decades to centuries) on grassland ecosystems' carbon balances.

4.6. Acknowledgements

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Chapter 5

Patterns of Nonlinearity in Ecosystem Carbon and Water Dynamics in response to Gradual Changes in Temperature, CO_2, and Precipitation: Modeling Analysis

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This part has been submitted to *Ecological Applications* (In review).

ABSTRACT

It is commonly acknowledged that ecosystem responses to global climate change are nonlinear. However, patterns of nonlinearity have not been well characterized on ecosystem carbon and water processes. We used a terrestrial ecosystem (TECO) model to examine nonlinear patterns of ecosystem responses to changes in temperature, CO_2, and precipitation individually or in combination. The TECO model was calibrated against experimental data obtained from a grassland ecosystem in central USA and ran for 100 years with gradual change in 252 different scenarios. The 100th-year results of ecosystem responses were presented. Variables examined in this study are net primary productivity (NPP), Rh (heterotrophic respiration), net ecosystem exchange of CO_2 (NEE), runoff, and evapotranspiration (ET). Our modeling results show that nonlinear patterns were parabolic, asymptotic, and threshold-like in response to temperature, CO_2, and precipitation anomalies, respectively, for NPP, NEE, and Rh. Runoff and ET exhibited threshold-like pattern in response to both temperature and precipitation anomalies but were less sensitive to CO_2 changes. The combined two- or three-factor changes in temperature, CO_2, and precipitation considerably influenced nonlinearity of ecosystem responses by either changing patterns and/or shifting points of abrupt changes. Our results suggest that nonlinear patterns in response to multiple global change factors are diverse and were considerably affected by combined climate anomalies on ecosystem carbon and water processes.

Key Words: Nonlinear pattern, global change, temperature, CO_2, precipitation, net primary production, net ecosystem exchange, heterotrophic respiration, runoff, evapotranspiration, grassland

5.1. Introduction

Global climate change usually involves simultaneous and continuous changes in atmospheric CO_2 concentration, earth surface temperature, and precipitation over a time of decades and centuries (IPCC 2001). Changes in the climate forcing variables likely cause nonlinear responses of ecosystem structure and functioning, and alter ecosystem services to human society. Research has been done mostly with two discrete treatment levels of one or two factors to quantify effects of global change on ecosystem processes and mechanisms (Shaver *et al.* 2000, Weltzin *et al.* 2003, Ainsworth and Long 2004, Rustad 2006). However, considerable uncertainty occurs in the IPCC (2001) projections for future global changes, making it difficult to predict how ecosystems might respond to future atmospheric conditions. Thus, it is important to understand how ecosystems could respond to a range of potential future climates (e.g., temperature, CO_2, and precipitation).

It is commonly acknowledged that ecosystem responses to global climate change are nonlinear (Ackerly and Bazzaz 1995, Gill *et al.* 2002, Burkett *et al.* 2005). Ecosystem nonlinearity is now becoming an increasingly important focus on global change research (Pielke *et al.* 2003, Mayer and Rietkerk 2004), which were identified as high-priority research across the federal government of USA (Lucier *et al.* 2006). Several international programs have focused on nonlinear and threshold responses to climate change (Körner 2000, Pielke *et al.* 2003), such as International Geosphere-Biosphere Programme (IGBP) workshop entitled “Non-linear responses to global environmental change: critical thresholds and feedbacks” at Duke University, North Carolina, USA in May 2001. In addition, nonlinear responses may explain some of the apparent contradictory results observed in climate change studies (Zak *et al.* 1993, Rustad *et al.* 2001). Therefore, ecosystem nonlinearity is a vital and challenging component of global change science, which may impact on how we design experiments, build models, and perceive ecosystem dynamics in a changing world (Reynolds 2002).

Most previous research on nonlinearity in response to global change factors was focused on the level of plant individual processes (e.g., photosynthesis and production) and identified a diversity of response patterns for various plant species (Körner 1995, Reddy *et al.* 1999, Xiong *et al.* 2000), even in a single CO_2 gradient (Ackerly and Bazzaz 1995, Luo *et al.* 1998). However, those results may not provide a sufficient basis to extrapolate from plant to ecosystem scales. Only a few studies have examined nonlinear responses to global change factors (mainly single global change scenario) on ecosystem carbon and water processes. For example, soil carbon storage and net N mineralization in an intact C_3/C_4 grassland of central Texas responded nonlinearly to a subambient to superambient CO_2 gradient (Mielnick *et al.* 2001, Gill *et al.* 2002). Responses to three levels of soil gradient warming (i.e., 2.5, 5.0, and 7.5°C) in a northern hardwood forest were also nonlinear on soil respiration and leaf litter decomposition (Mchale *et al.* 1998). Although a few experimental studies with multiple levels of individual temperature, CO_2, and precipitation changes have been conducted in the field (Mchale *et al.* 1998, Mielnick *et al.* 2001, Gill *et al.* 2002, Yahdjian and Sala 2006), their overall objectives were not to examine patterns and mechanisms of nonlinearity, limiting their applications in ecosystem services. In addition, ecosystem responses to multiple global change factors, which were often conducted at two discrete treatment levels, were inadequate to examine nonlinearity. To date, a range of treatment levels of simultaneous changes in temperature, CO_2, and precipitation have not been investigated by experiments, because, in the real world, it is impossible to conduct manipulative experiments to examine nonlinear responses to simultaneous changes in multiple factors due to cost limitation and ecosystem complexities.

The use of models can be of particular importance to simulate multiple global change factors, examine response patterns, and then deliver an idea of possibilities to decision makers (Millennium Ecosystem Assessment 2005, Groffman *et al.* 2006). Vegetation model simulations revealed potential nonlinearity in response to global change factors at the community or ecosystem level based on competition between plant species or various plant functional types (Ackerley and Bazzaz 1995, Cowling and Shin 2006). However, patterns and mechanisms underlying nonlinearity in responses to simultaneous changes in temperature, CO_2, and precipitation remain largely uncertain in natural ecosystems. We are aware of only one modeling study to examine ecosystem nonlinear responses to individual and simultaneous changes in temperature, precipitation, and CO_2 (only two levels) using a dynamic global vegetation model (DGVM) within a region of Amazonia (Cowling and Shin 2006). However, this study mainly focused on threshold responses in tropical rainforest ecosystems and the results that temperature thresholds increased with decreasing precipitation were arguable. It is not clear how other ecosystems may respond to a range of levels of multiple global change factors.

In the present modeling study, we used a terrestrial ecosystem (TECO) model to examine nonlinear patterns of ecosystem carbon and water dynamics in response to a range of individual and simultaneous changes in temperature, CO_2, and precipitation in a grassland ecosystem of central USA. Climate change scenarios varied gradually within 100 years. Variables of carbon and water cycles examined in the study are net primary productivity (NPP), heterotrophic respiration (Rh), net ecosystem carbon exchange (NEE=NPP-Rh), runoff, and evapotranspiration (ET). We also discussed implications of experimental studies and model assumptions.

Response dynamics from 2000 to 2100 to gradual changes under different scenarios were similar as other studies (Fig. 5.3, Campbell *et al.* 1997, Ollinger *et al.* 2002, Hanson *et al.* 2005), which were not the main focus of this study. Thus, we only show the results of one level of three global change factors (i.e., +4^{o}C of temperature, double CO_2, and +30% of precipitation) and their combinations. Mostly, the 100th-year results of ecosystem responses were presented for NPP, Rh, NEE, runoff, and ET.

5.2. Materials and methods

Model description

Terrestrial ecosystem (TECO) model evolves from a terrestrial carbon sequestration (TCS) model (Luo and Reynolds 1999) and is designed to examine ecosystem responses to perturbations in global change factors. The model has been extensively applied to the modeling study at the Duke Forest CO_2 enrichment experiment (Luo *et al.* 2001b,c, 2003, Xu *et al.* 2005). It has three major components: a canopy photosynthesis model, a soil water dynamic model, and a carbon dynamics model that describes plant and soil carbon transfer processes (Fig. 5.1). The canopy photosynthesis and soil moisture dynamics models were simulated at the hourly time step, while the plant growth and the soil carbon dynamics were simulated at the daily step. Temperature-driven changes in pehnology and the length of growing seasons were simulated on a carbon-gain based scheme (Arora and Boer 2005). Acclimation of physiological and ecological processes to warming and elevated CO_2 was not imposed on model runs unless it was simulated internally via changes in nutrient dynamics or water stress. The detailed description of TECO model refers to Gerten *et al.* (2007), and Luo *et al.* (2007).

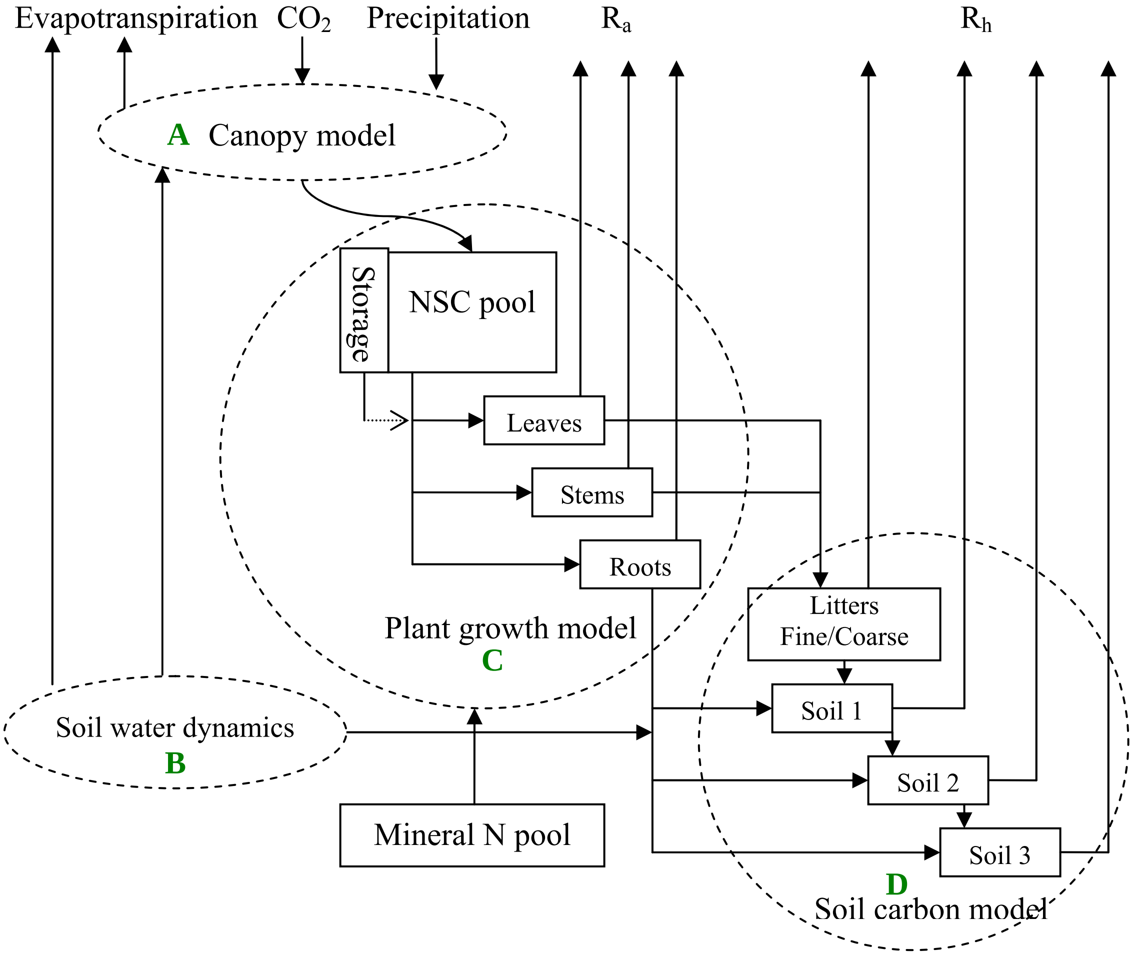

Fig. 5.1 Schematic diagram of Structure of terrestrial ecosystem (TECO) model. Boxes represent pools and dashed cycles stand for four submodels. NSC is non-structural carbon, R_a is autotrophic respiration including leaf, stem, and root respiration, and R_h is heterotrophic respiration including litter and SOM decomposition.

The canopy model is a multi-layer process-based model to simulate canopy conductance, photosynthesis, and energy partitioning by calculating radiation transmission based on Beer's law. For each layer, foliage is divided into sunlit and shaded leaf area index (LAI) to separately simulate canopy conductance, photosynthesis, and energy partitioning as described by Wang and Leuning (1998). Carbon uptake (i.e., leaf photosynthesis) and transpiration is based on the coupled Farquhar photosynthesis model and the Ball-Berry stomatal conductance model as described by Harley *et al.* (1992). The coupled leaf-level model of stomatal conductance, photosynthesis, and transpiration for the sunlit leaf (i=1) or shaded leaf (i=2) is:

$$\text{Photosynthesis: } A_{c,i} = b_{sc} \cdot G_{s,i} \cdot (C_{s,i} - C_i) = G_{c,i}(C_a - C_i) \qquad (1)$$

$$\text{Stomatal conductance: } G_{s,i} = G_{0,i} + \frac{a_l f_w A_{c,i}}{(C_{s,i} - \Gamma)(1 + D_{s,i} / D_0)} \qquad (2)$$

$$\text{Transpiration: } E_{c,i} = G_{s,i} \cdot D_{s,i} = G_{w,i}(D_a + s \cdot \Delta T_i) \qquad (3)$$

where $A_{c,i}$ is the net photosynthesis rate; $E_{c,i}$ is transpiration rate; $G_{s,i}$ and $G_{0,i}$ are the bulk stomatal and residual ($G_{s,i}$ when $A_{c,i}$=0) conductance for water vapour, respectively; D_a and $D_{s,i}$ are water vapour mol fraction deficits (VPD) in the ambient air and at the leaf surface, respectively; $G_{w,i}$ and $G_{c,i}$ are the total conductance from the intercellular space of the leaves to the reference height above the canopy for H_2O and CO_2, respectively; s is the slope of the function relating saturated water vapor mol fraction to temperature; ΔT_i is the temperature difference between the surface of the big leaf and that of the air at the reference height; b_{sc} is the ratio of diffusivity of CO_2 and H_2O through the stomata; C_a, $C_{s,i}$, and C_i are CO_2 mol fractions in the air, at the leaf surface, and intercellular spaces, respectively; Γ is the CO_2 compensation point; D_0 is a parameter for stomatal sensitivity to VPD; a_l is related to the intercellular CO_2 concentration by $C_i/Cs_{,i}=1-1/a_l$ at maximal stomatal opening (when both D_s,i and $G_{0,i}$ are zero and $f_w=1$); and f_w describes the sensitivity of stomata to soil water content. Canopy photosynthesis and transpiration were closely approximated by integrating values of individual leaves as below.

$$\begin{aligned} Y_i &= \int_0^L y_i(\xi) w_i(\xi) d\xi \\ Y &= Y_1 + Y_2 \end{aligned} \tag{4}$$

where y_i is flux of CO_2 or transpiration of individual sunlit or shaded leaf within the canopy; Yi is the flux value for the big leaves; ξ is the cumulative leaf area index from the canopy top, L is the total canopy leaf area index, Y represents the total flux of the whole canopy, w_i is the fraction of sunlit (i=1) or shaded (i=2) leaf area within the canopy.

The carbon dynamic model considers plant growth, plant respiration and soil carbon transfers among pools. Allocation of assimilates over the plant components depends on the growth rate of leaves, stems and roots, and varies with phenology. The soil profile is divided into three layers with water and carbon movement between the layers. Carbon inputs to the soil from plant residues are partitioned into these three layers. Plant growth model contains a non-structural carbon pool and growth equations of leaves, stems and roots:

$$G_i = G_{\max i} \cdot BM_i \cdot S_{r/s} \cdot S_{nsc} \cdot S_{LAI} \tag{5}$$

where i= leaf, stem or root. G_i is growth rate, $G_{\max}$ is the maximum relative growth rate, BM_i is biomass of leaves, stems or roots. $S_{r/s}$, S_{nsc} and S_{LAI} are scaling factors of root/shoot ration, non-structural carbon pool, and LAI, respectively. NPP is the difference between canopy photosynthesis and autotrophic respiration (R_a). The latter is dependent on biomass amounts, specific respiration rates, and regulated by temperature as below:

$$R_a = b \cdot BM \cdot e^{a \cdot T} \tag{6}$$

where BM is biomass, T is air temperature, and a and b is empirical parameters.

Soil carbon model is partly from the soil carbon transfer part of VAST (Barret *et al.* 2002) by simulating carbon transfer from plant to soil and then to atmosphere. The model has multiple plant, litter and soil carbon pools. Heterotrophic respiration (R_h) includes decomposition of litter and soil organic matter, which is regulated by soil temperature and moisture. At steady state, R_h from each litter and soil pool is given by:

$$R_k = -P_n f_k \tag{7}$$

where f_k is the fraction of NPP arriving at the k^{th} pool after traversing upstream pools. For each pool the functions for f_k are

$$\begin{aligned}
f_F &= [\alpha_L + \eta\alpha_W](1-\theta_F) \\
f_C &= \alpha_W(1-\eta-\theta_C) \\
f_{S1} &= [\zeta_1\alpha_R + \theta_F(\alpha_L+\eta\alpha_W) + \theta_C\alpha_W](1-\theta_{S1}) \\
f_{S2} &= [\zeta_2\alpha_R + \theta_{S1}(\zeta_1\alpha_R + \theta_F(\alpha_L+\eta\alpha_W) + \theta_C\alpha_W)](1-\theta_{S2}) \\
f_{S3} &= [\zeta_3\alpha_R + \theta_{S2}(\zeta_2\alpha_R + \theta_{S1}(\zeta_1\alpha_R + \theta_F(\alpha_L+\eta\alpha_W) + \theta_C\alpha_W))]
\end{aligned} \tag{8}$$

where *F, C, S1,S2,* and *S3* are litterfall, wood, and soil layer 1, 2, and 3. α_L, α_W, and α_R are the allocation coefficients of NPP to leaf, wood, and root, θ is carbon partitioning coefficient of C pools, η is the fragmentation coefficient of coarse woody debris by mechanical breakdown, and ξ is proportion of C-allocated to fine roots in the j^{th} soil layer. Thus, annual heterotrophic respiration from each litter and soil pool at steady state was obtained directly from f_k in equation (7) and (8). Net ecosystem exchange of CO_2 (NEE) can be calculated as the difference between NPP and R_h.

The soil moisture dynamics is determined by precipitation (P), evapotranspiration (ET), and runoff. ET includes soil evaporation and plant transpiration. Transpiration is coupled in canopy model (Equation 3) and evaporation of soil surface is from the following equation:

$$E_s = \frac{e^*(T_{soil}) - e_a}{r_{soil} + r_d} \frac{\rho c_p}{\gamma} \frac{1}{\lambda} \qquad (10)$$

where E_S is soil evaporation, e* (T_{soil}) is the saturation vapor pressure at the temperature of the soil, e_a is the atmospheric vapor pressure, r_{soil} is a soil resistance term, r_d is the aerodynamic resistance between the ground and the canopy air space, ρ is the density of air, c_p is the specific heat of air, γ is the psychrometric constant, λ is the latent heat of sublimation. Runoff is calculated from ecosystem water balance among precipitation, soil evaporation, canopy transpiration, and changes in soil water content in soil layers.

Study site

The study was conducted at the Kessler's Farm Field Laboratory (KFFL) in McClain County, Oklahoma (34^{o}59' N, 97^{o}31' W), approximately 40 kilometers southwest of Norman campus of the University of Oklahoma, USA. The field site is an old-field tallgrass prairie abandoned from agriculture 30 years ago without grazing for 25 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^{o}C, with monthly air temperature ranging from 3.3^{o}C in January to 28.1^{o}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 & Y. Luo, unpublished data, 2003). Soil carbon content is 1.42% on a mass basis (Luo *et al*. 2001a). 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 1979).

Input data

Daily climate variables used in this study were from the MESONET station of Washington, Oklahoma (1994 to 2005), including air temperature, soil temperature, vapor pressure deficit, relative humidity, precipitation, and incident photosynthetically active radiation. Equilibrium state was accomplished by running the model using repeated cycles of the 12-year climate set. Simulations were run from bare ground for 1000 years, at which time climate change scenarios were imposed.

Modelling scenarios

Our experimental simulations involved each climate anomaly individually and in combination (i.e., temperature, CO_2, and precipitation). Temperature anomaly influences all ecosystem processes by soil and air temperature. CO_2 anomaly affects them by stomatal conductance. Precipitation anomaly affects ecosystem processes by soil water

Table 5.1 Scenarios examined in this study

Global change factors	Treatment levels
Temperature	-2, 0, +2, +4, +6, +8, +10°C
CO_2 concentration	-20, 0, +30, +60, +100, +140%
Precipitation	-40, -20, 0, +30, +60, 100%

Note: Zero (0) represents the current condition of temperature and precipitation (i.e., control), while CO_2 concentration was set to 350 ppm.

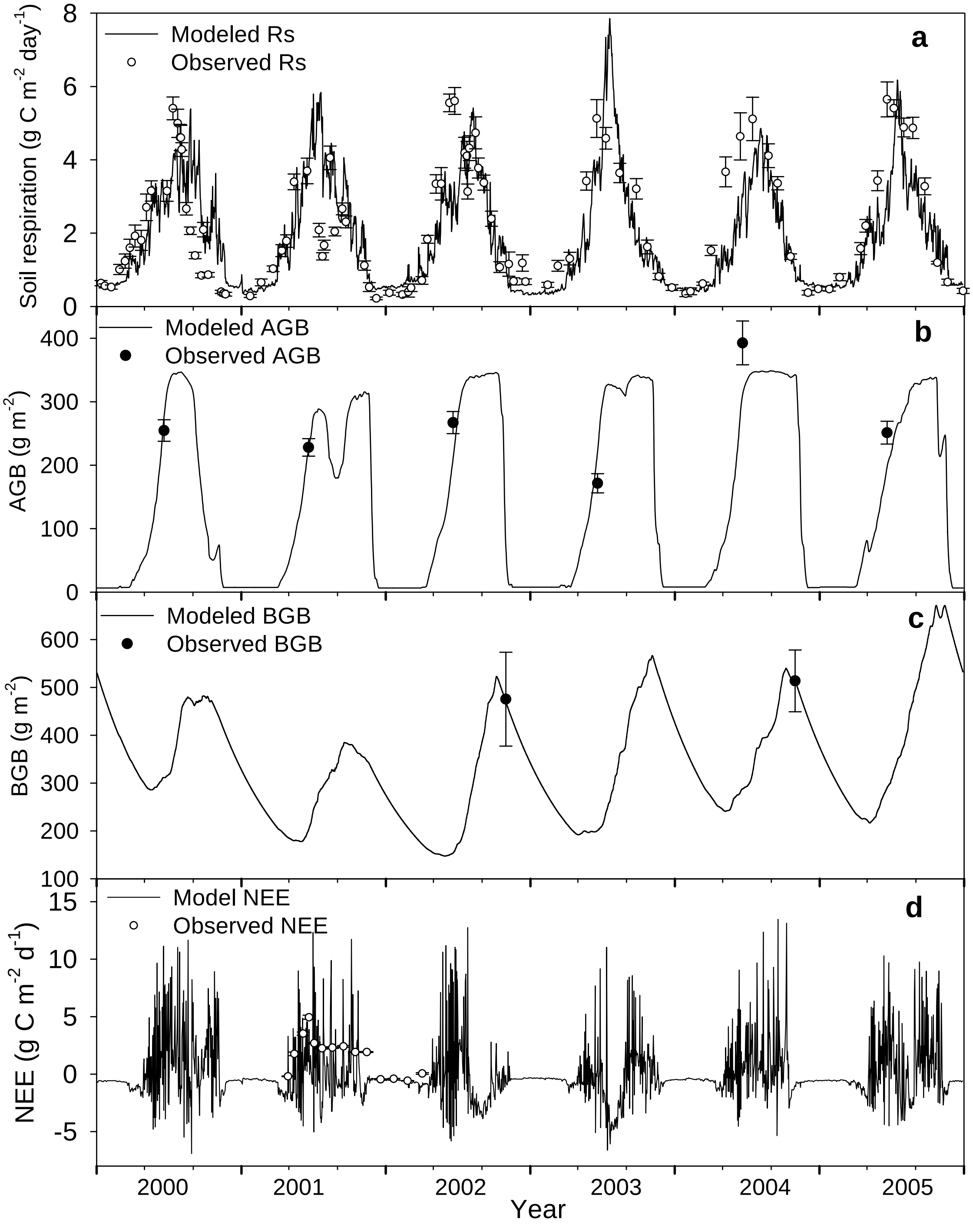

Fig. 5.2 Observed vs. simulated daily soil respiration (a), aboveground biomass (AGB, b), belowground biomass (BGB, c), and net ecosystem exchange (NEE, d) in Oklahoma grassland

dynamics. To evaluate the individual and combined effects of temperature, CO_2, and precipitation, we conducted a total of 252 simulations (including all possible crosses of the climate anomalies and control) (Table 5.1). All anomalies were changed gradually (mean changes within 100 years) starting in 2000 and ending by 2100. Because dynamic responses from 2000 to 2100 to changes in different scenarios were not the main focus of this study, we only presented the results of dynamic responses to one level of three global change factors (i.e., 4°C increase in temperature, doubling CO_2 concentration, and 30% increase in precipitation) and their combinations. Mostly, we present modelling results of ecosystem responses at the 100th-year data for NPP, Rh, NEE, runoff, and ET.

Model validation

In this grassland, we used soil respiration, aboveground (AGB) and belowground (BGB) biomass, and NEE to validate the simulated values. Observed soil respiration was measured approximately once a month using LiCor 6400 with soil CO_2 flux chamber (Luo *et al.* 2001a, Wan *et al.* 2005, Also see Chapter 2 and 3). Observed aboveground biomass was measured once a year and belowground biomass was only in October 2002 and 2004 (Wan *et al.* 2005, X. Zhou and Y. Luo, unpublished data, 2004). NEE was measured monthly in 2001 (X. Liu and Y. Luo, unpublished data, 2001). For all these variables, the simulated results are in good agreement with observational data except an overprediction of soil respiration in summer 2001 (Fig. 5.2). However, paired *t* tests between simulated and observed soil respiration ($p>0.10$) indicate no significant difference.

5.3. Results

Response dynamics to different scenarios

Simulated NPP, NEE, R_h, Runoff, and ET dynamics within 100 years in response to individual and simultaneous increases in temperature (+4°C), CO_2 (doubling), and precipitation (+30%) are shown in Fig. 5.3. Usually, multifactor scenarios have greater responses than single-factor ones. For example, combinations of temperature and CO_2, temperature and precipitation, and the three factors linearly increased NPP and R_h by about 60, 50, and 75%, respectively, from 2000 to 2100 (Fig. 5.3a, c). In contrast, individual temperature, CO_2, and precipitation nonlinearly increased NPP and R_h by about 5 to 27% from 2000 to 2100. The response dynamics of NEE to all scenarios are nonlinear with the largest carbon loss under temperature alone (-50 g C m^{-2}) and the largest carbon gain under the combination of CO_2 and precipitation (60 g C m^{-2}) from 2000 to 2100 (Fig. 5.3b).

Runoff and evapotranspiration (ET) responded largely to precipitation changes in comparison to temperature and CO_2. Our modeling analysis shows that both precipitation alone and its combination with CO_2 doubling increased by approximately 400% for runoff and by 22% for ET from 2000 to 2100 (Fig. 5.3d, e). Combinations of temperature and precipitation and the three factors also largely increased ET by about 30%. However, temperature increase and its combination with CO_2 doubling reduced runoff by 44 and 61%, respectively, from 2000 to 2100.

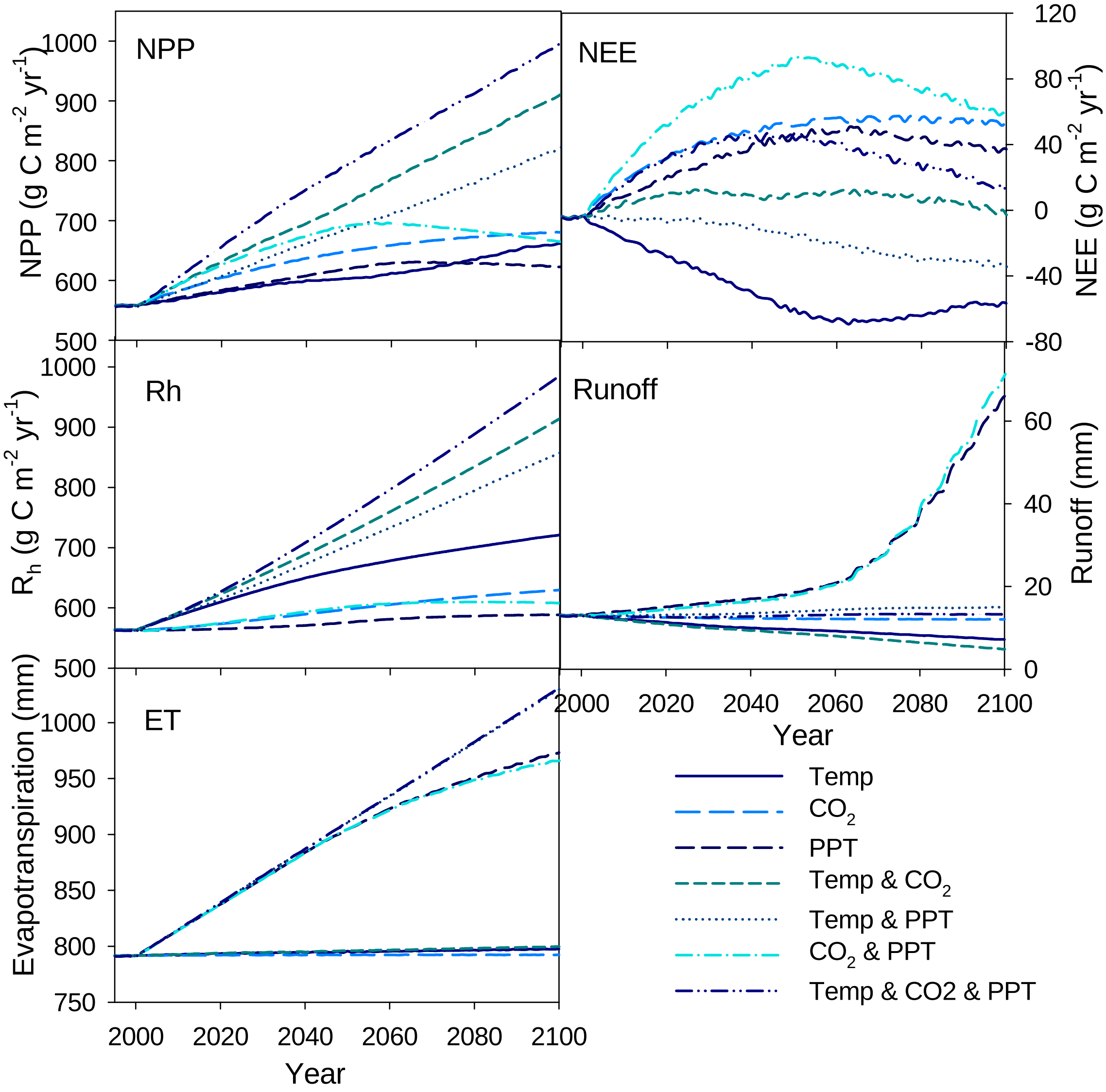

Fig. 5.3 Simulated net primary productivity (NPP, a), NEE (b), heterotrophic respiration (Rh, c), runoff (d), and evapotranspiration (ET, e) dynamics from 2000 to 2100 in response to gradual changes in one level of temperature (4°C increase), CO_2 (doubling-700 ppmv), and precipitation (30% increase) and their combinations.

Nonlinear responses to single factor changes

Simulated NPP, R_h, and NEE all show parabola-curve responses to temperature anomalies from -2°C to +10°C compared to current condition (Fig. 5.4a, b). NPP and R_h increased with rising temperature, reached a peak at +5°C (NPP) or +6°C (R_h), and then declined, while NEE had an adverse trend with a lowest value at +7°C. Increases in CO_2 concentration from 280 to 840 ppmv stimulated NPP, R_h, and NEE with an asymptotic curve (Fig. 5.4c, d). However, responses of NPP, R_h, and NEE to precipitation changes from -40% to +100% compared to current condition display threshold-like curves (Fig. 5.4e, f), which increased with precipitation increase at the beginning and then reached a plateau around +30% (NPP and NEE) or current condition (R_h). If we define 'threshold' as a point at which there is an abrupt change in response to external stimuli, our

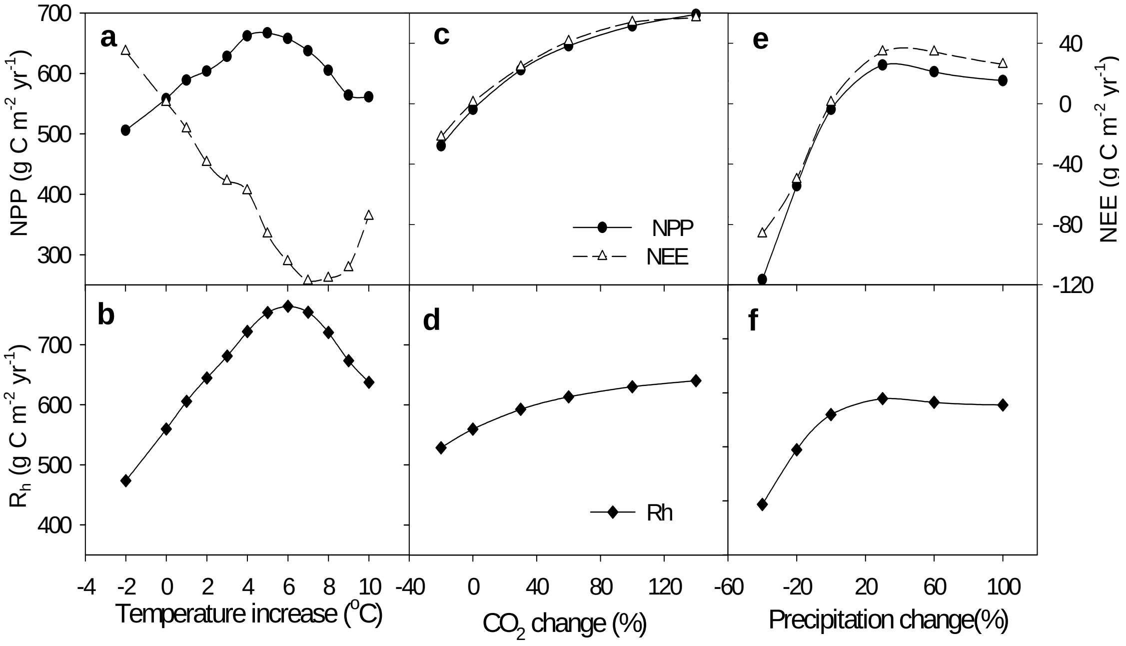

Fig. 5.4 Responses of NPP, Rh, and NEE to single-factor changes in temperature (a, b), CO_2 (c, d), and precipitation (e, f)

modeling results indicate that NPP and NEE had precipitation threshold values in about +30% and R_h had a threshold value near current condition.

For runoff and ET of water cycle, response patterns to individual temperature and precipitation changes were threshold-like, while runoff and ET were less sensitive to CO_2 changes (Fig. 5.5). Runoff decreased in response to increasing temperature while ET increased, but both with similar threshold values near current condition. Runoff and ET responded positively to precipitation changes but with different threshold values, which were near current condition for runoff and +30% for ET.

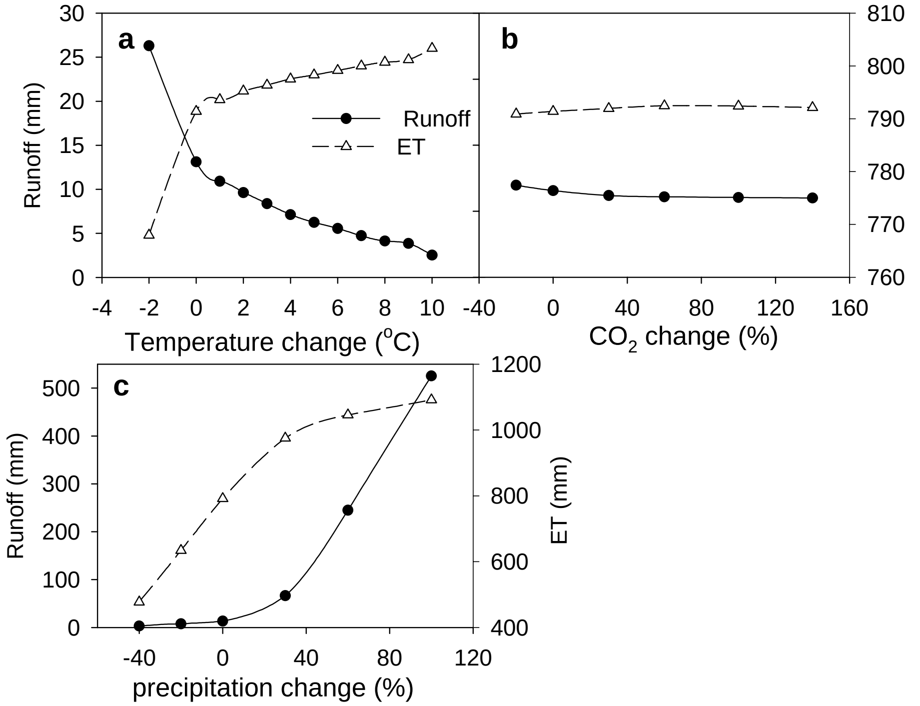

Fig. 5.5 Responses of runoff and ET to single-factor changes in temperature (a, b), CO_2 (c, d), and precipitation (e, f)

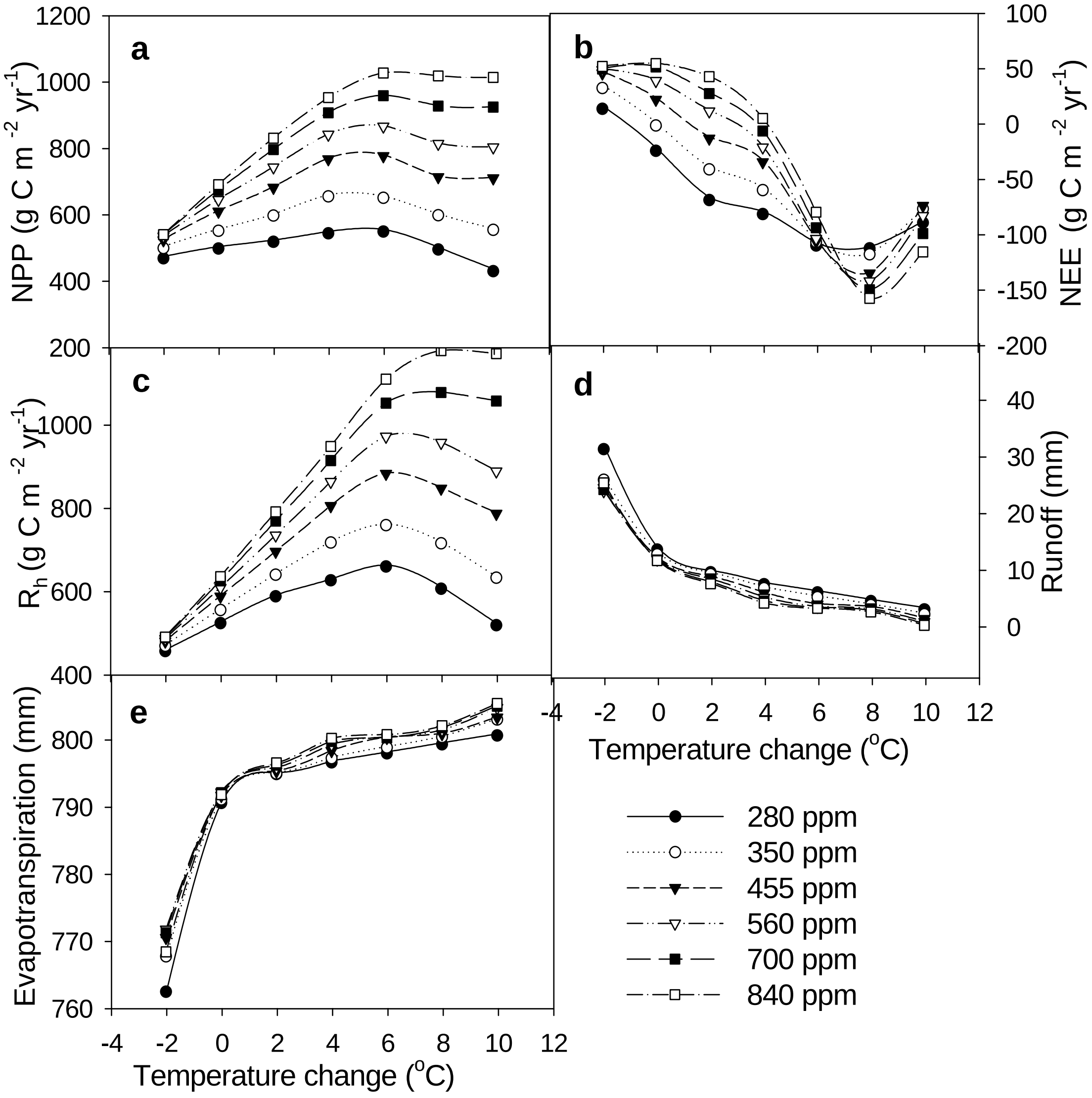

Fig. 5.6 Responses of NPP (a), NEE (b), Rh (c), runoff (d), and ET (e) to simultaneous changes in temperature and CO_2.

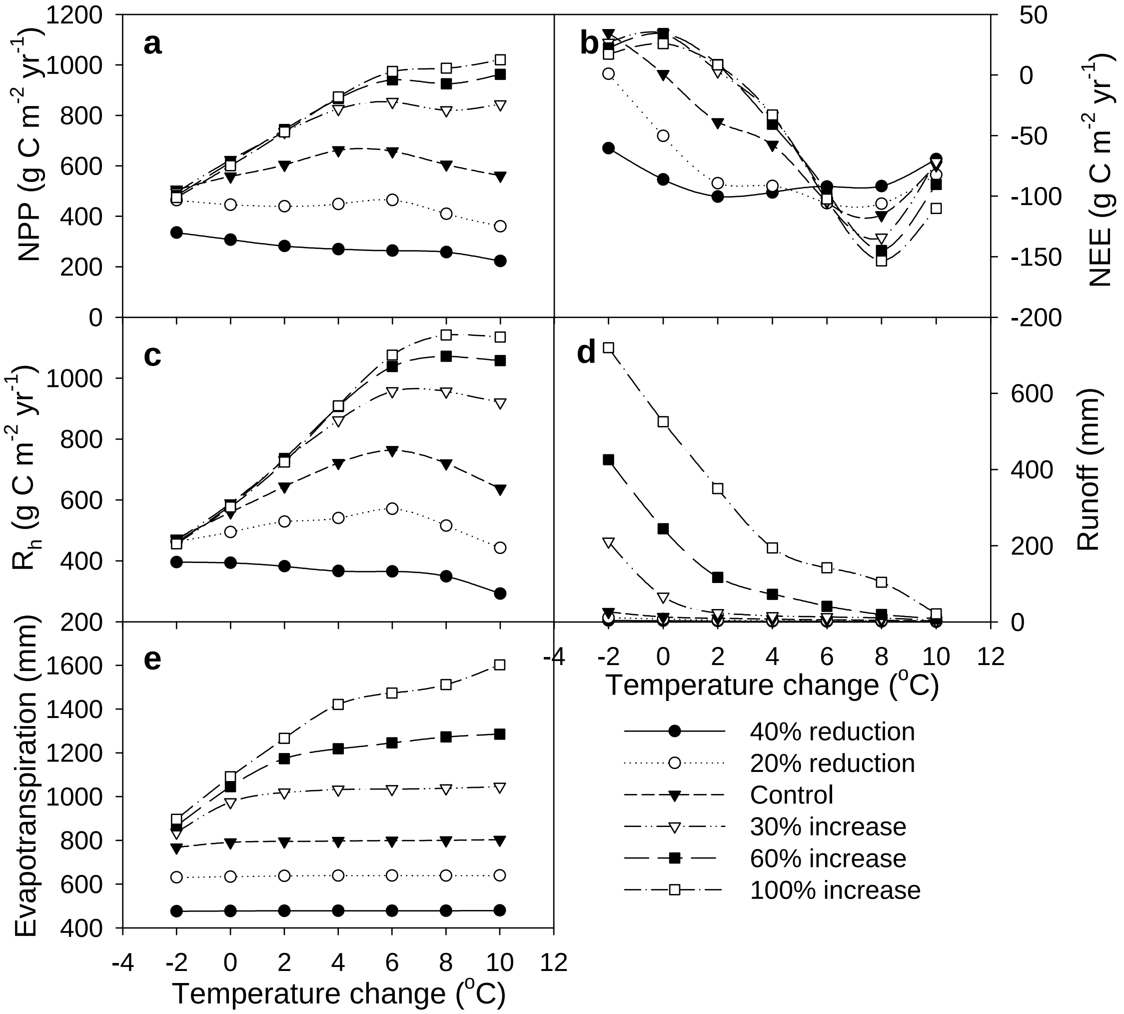

Fig. 5.7 Responses of NPP (a), NEE (b), Rh (c), runoff (d), and ET (e) to simultaneous changes in temperature and precipitation

Nonlinear responses to simultaneous changes in multiple factors

Simultaneous changes in temperature and CO_2 not only affected optimum or threshold points of temperature responses but also varied nonlinear response curves for NPP, Rh, and NEE, while there were no interactive effects on runoff and ET (Fig. 5.6). Specifically, with increasing CO_2 concentration from 280 to 840 ppmv, temperature optimum values increased by 1°C from +5 to +6°C for NPP and from +6 to +7°C for R_h, and nonlinear patterns of responses changed from parabolic (below 560 ppmv) to threshold-like (above 700 ppmv) curves (Fig. 5.6a, c). The lowest values of NEE were in +6°C under 280 ppmv of CO_2 concentration and +8°C above 560 ppmv compared to +7°C in the control (CO_2=350 ppmv) (Fig. 5.6b).

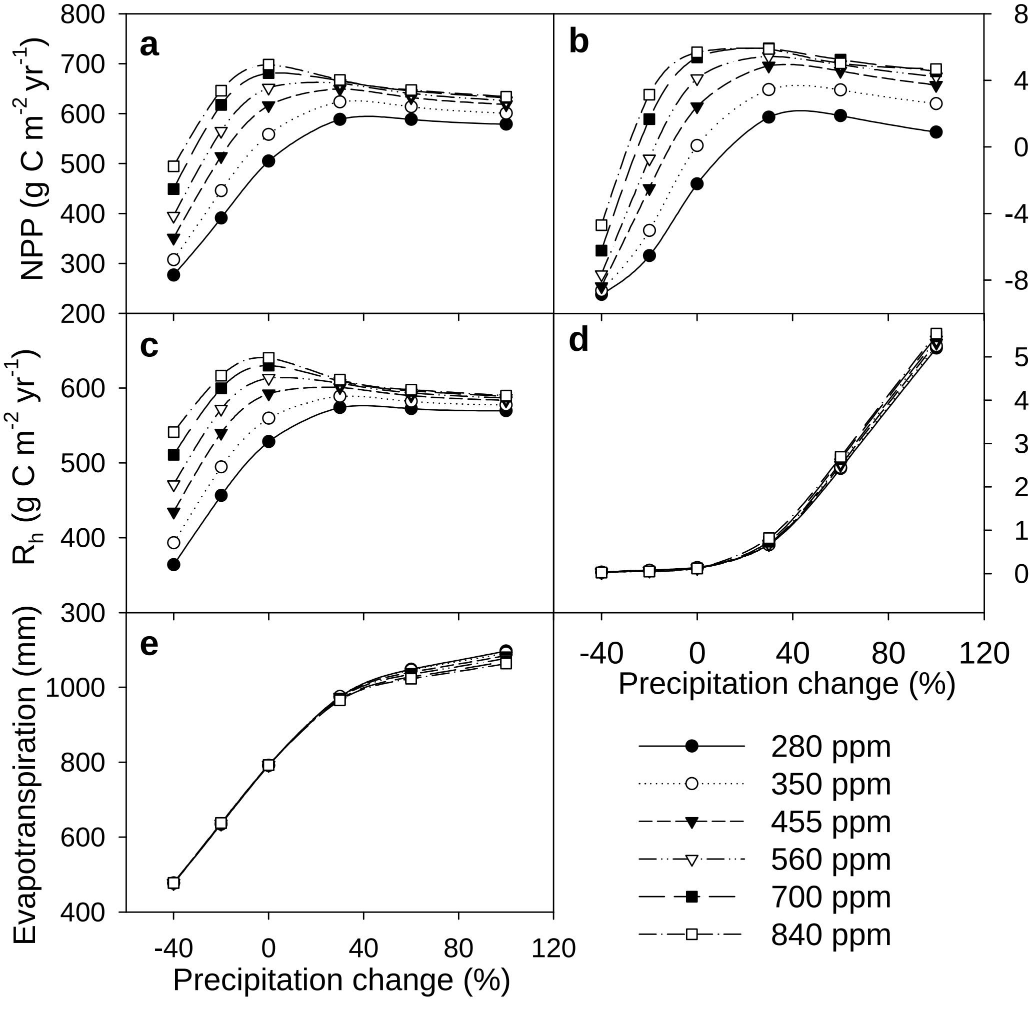

Fig. 5.8 Responses of NPP (a), NEE (b), Rh (c), runoff (d), and ET (e) to simultaneous changes in precipitation and CO_2

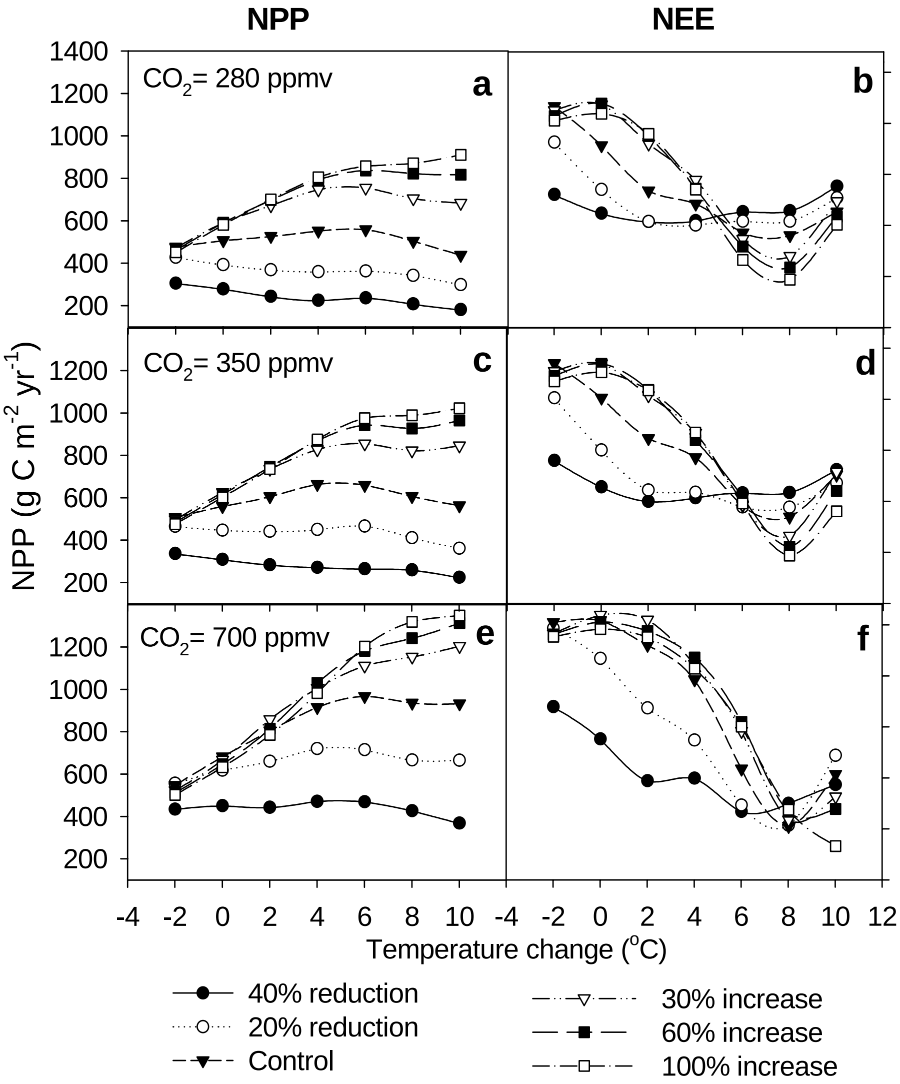

Fig. 5.9 Responses of NPP (a, c, e) and NEE (b, d, f) to simultaneous changes in temperature, CO_2, and precipitation

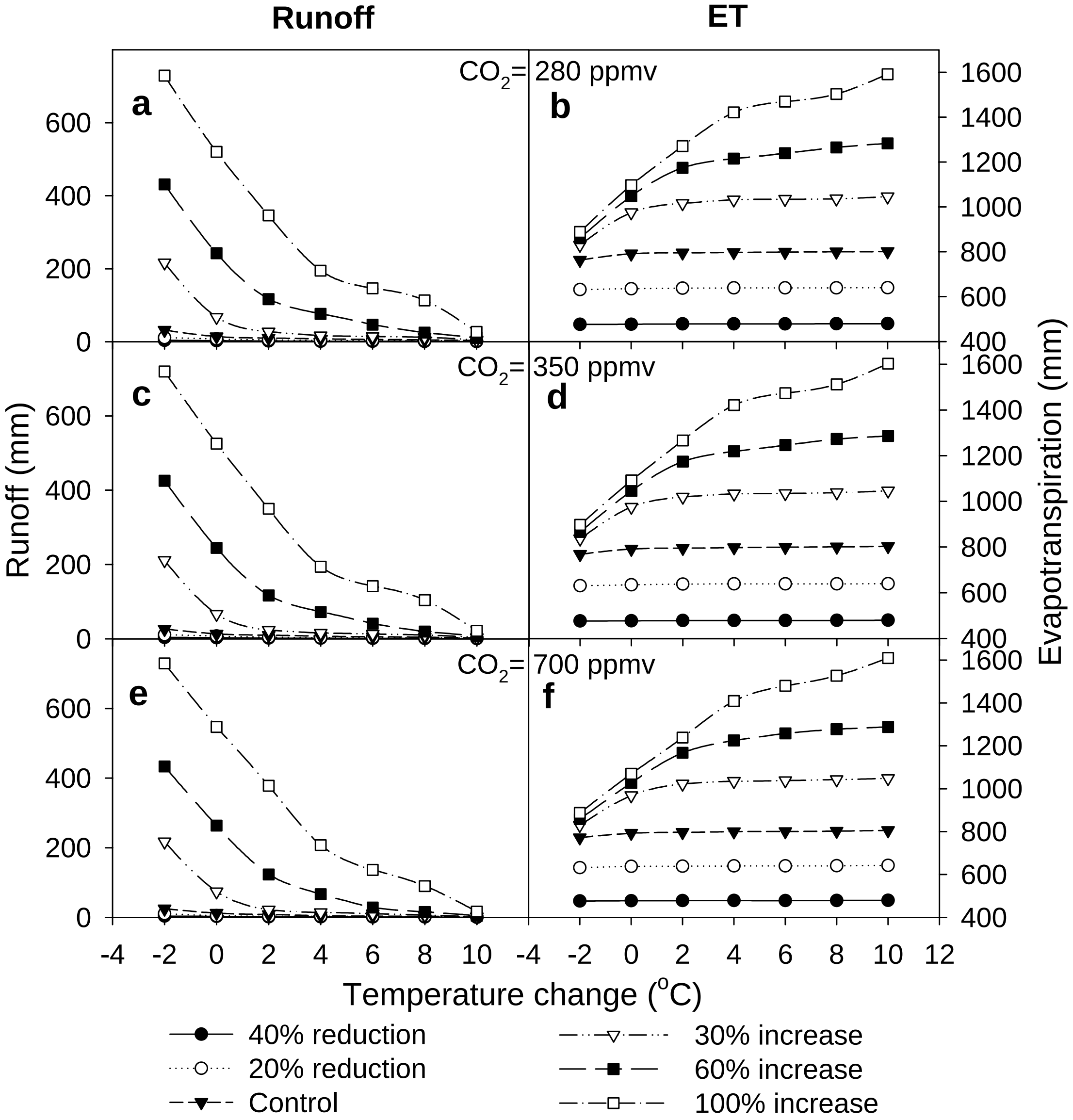

Fig. 5.10 Responses of runoff (a, c, e) and ET (b, d, f) to simultaneous changes in temperature, CO$_2$, and precipitation

Similarly, with increasing precipitation from -40 to +100%, both response curves and threshold points were also affected (Fig. 5.7). Temperature response curves were relatively insensitive under -40% of precipitation, were parabolic under -20% and current condition, and became threshold-like above +30% for NPP and R_h (Fig. 5.7a, c).

The lowest values of NEE are in +2^{o}C under -40 and -20% of precipitation and +8^{o}C above +30% compared to +7^{o}C in the control (Fig. 5.7b). Response magnitude of runoff and ET to temperature anomalies increased largely with increasing precipitation (Fig. 5.7d, e). Specifically, temperature responses were relatively insensitive under -40, -20%, and current condition of precipitation and show threshold-like patterns above +30% for NPP and R_h. Temperature threshold values increased from 0^{o}C under current condition to 4^{o}C under +100% of precipitation for both runoff and ET. With increasing CO_2 concentration, precipitation response curves did not vary, while their threshold values decreased from +30% of precipitation under 280 ppmv to current condition under 840 ppmv for NPP, NEE, and R_h (Fig. 5.8a,b,c), while there were no effects on runoff and ET (Fig. 5.8e,d).

For simultaneous changes in temperature, CO_2, and precipitation, we only show NPP and NEE for carbon cycle due to similar trend between NPP and R_h under three CO_2 concentrations, representing preindustrial, current, and future conditions. The three factors interactively changed response patterns and optimum or threshold points for NPP and NEE (Fig. 5.9). For example, temperature optimum or threshold values of NPP did not change with increasing precipitation under 280 ppmv of CO_2 concentration, increased from +5 to 6^{o}C under 350 ppmv, and increased from 5 to 8^{o}C under 700 ppmv (Fig. 5.9a, c, e). The lowest values of NEE were +2^{o}C at -40% of precipitation under 280 and 350 ppmv, while was 6^{o}C under 700 ppmv (Fig. 5.9b, d, f). However, CO_2 concentration did not significantly affect responses of runoff and ET to simultaneous changes in temperature and precipitation (Fig. 5.10).

5.4. Discussion

Our modeling analysis demonstrates diverse nonlinear patterns of ecosystem carbon and water dynamics in response to global change factors. Response patterns of NPP, R_h, and NEE were in parabola, asymptotic, and threshold-like shapes to individual changes in temperature, CO_2, and precipitation, respectively (Fig. 5.4). Runoff and ET also responded nonlinearly to temperature and precipitation anomalies with a threshold-like pattern but were less sensitive to changing CO_2 (Fig. 5.5). Combinations of temperature, CO_2, and precipitation anomalies interactively affected nonlinearity by changing response patterns (Figs. 5.6, 5.7, 5.9, and 5.10) and/or shifting points of abrupt changes (e.g., threshold values, Figs. 5.6, 5.7, 5.8 and 5.9). The nonlinear dynamics and multifactor interactions on ecosystem carbon and water processes greatly complicate the interpretation and predictability of ecosystem level responses.

Nonlinear responses to single factor changes

Our results of model simulations exhibit different patterns of nonlinear responses to individual changes in temperature, CO_2, and precipitation for NPP, R_h, NEE, runoff, and ET. A parabolic pattern in response to temperature change was observed in NPP and R_h (Fig. 5.4a,b). At a low temperature range, warming stimulated plant biomass growth and soil respiration and extended the growing season (Rustad *et al.* 2001, Wan *et al.* 2005), resulting in increases of the two fluxes with increasing temperature. At a high temperature range, the stimulation of warming declined with increasing temperature due to soil moisture limitation (Drake *et al.* 1997), because the effects of climate warming on production and decomposition were strongly dependent on interactions with soil moisture (Ise and Moorcraft 2006). Our results were consistent with that under three levels of soil gradient warming in a northern hardwood forest, which soil respiration and leaf litter decomposition were less in +7.5^{o}C than +2.5 and +5^{o}C (Mchale *et al.* 1998). However, R_h was more responsive to warming than NPP, resulting in a decrease in NEE with increasing warming at a low temperature range and slight recovery at a high temperature range.

The responses of NPP, NEE, and R_h to a gradient of CO_2 levels were in an asymptotic shape (Fig. 5.4c,d). The stimulated effects were similar to observed results from a manipulative experiment in central Texas for a continuous gradient of CO_2 from 200 to 550 μmol mol^{-1} (Mielnick *et al.* 2001, Gill *et al.* 2002, Polley *et al.* 2003, 2007). Along that gradient, CO_2 enrichment increased photosynthesis (Mielnick *et al.* 2001), biomass production (Polley *et al.* 2003), net carbon uptake (Gill *et al.* 2002), and ecosystem respiration (Polley *et al.* 2006). A further enhancement of CO_2 supply may reduce the stimulated effects on the rate of uptake due to CO_2 saturation to photosynthesis and the diminishing CO_2 sensitivity (Körner 1995, Lamber *et al.* 1998). However, the compiled response patterns of plant growth and reproduction along CO_2 gradients were diverse with the positive, negative, non-monotonic, and non-significant (flat) responses due to photosynthetic acclimation (Ackerley and Bazzaz 1995, Luo *et al.* 1998).

Threshold-like response patterns to climate change are not uncommon in ecosystems. Our results show the threshold-like responses to precipitation change for NPP, NEE, Rh, runoff, and ET (Figs. 5.4e,f and 5.5a,c). Precipitation threshold values are about +30% for NPP, NEE, and ET and near current condition (+0%) for Rh and runoff. The threshold response curves indicate that the carbon and water fluxes are relatively insensitive above the threshold values, while the large response occurs below the values. Little information was available in manipulative precipitation experiments, although the similar threshold response patterns have been reported along natural rainfall gradients (Austin 2002, Austin and Sala 2002). Under water interception, Yahdjian and Sala (2006) showed that aboveground NPP and plant density linearly increased with increasing precipitation, which were consistent with our results at the low precipitation range. Unfortunately, their study did not conduct the experiments of increased precipitation and our results can not be further verified. Runoff and ET also have a threshold response pattern to temperature change. These threshold values were invaluable when we apply this concept to manage and restore ecosystem after perturbation (Groffman *et al.* 2006). The strategies for sustainable management should focus on maintaining resilience and disturbance, which should not exceed the threshold values (Scheffer *et al.* 2001).

Nonlinear response to simultaneous changes in multiple factors

Combined temperature, CO_2, and precipitation anomalies considerably changed nonlinear responses compared to individual factor, resulting in changes in either response patterns or points of abrupt changes (Figs. 5.6, 5.7, 5.8, 5.9, and 5.10). For example, values of abrupt changes in temperature anomalies for NPP, NEE, and R_h increased with rising CO_2 concentration (Fig. 5.6), probably resulting from reduced stomatal conductance and increased water-use efficiency (WUE), and then minimizing the deleterious effects of soil drying and alleviating water stress under high temperature (Drake *et al.* 1997, Lilley *et al.* 2001, Ainsworth and Long 2004, Wall *et al.* 2006). Similarly, increasing precipitation certainly mitigated water stress under high temperature, resulting in higher values of abrupt changes (Fig. 5.7). However, a reduction in precipitation caused large changes in response curves and became more flat with increasing temperature because it enhanced water stress irrespective of climate warming (Ise and Moorcraft 2006). With rising CO_2 concentration, precipitation threshold values of NPP, NEE, and R_h decreased because of the effects of CO_2 enrichment on stomatal conductance and WUE (Drake *et al.* 1997). The interaction of combined temperature, CO_2, and precipitation anomalies was complicated through both changing response patterns and threshold points (Figs. 5.9 and 5.10). The mechanisms discussed above (i.e., one- or two-factor changes) guided us to understand these changes in response patterns of carbon and water fluxes and points of abrupt points in this grassland.

To date, there has been no experimental evidence on ecosystem nonlinear patterns in response to multiple treatment levels of combined climate change anomalies, although several mesocosm experiments (e.g., chamber and tunnel) have exposed specific plants to three levels of both temperature and CO_2 (Hadley *et al.* 1995, Horie *et al.* 1995, Lee *et al.* 2001, Usami *et al.* 2001, He *et al.* 2005). Those results only showed that the interactive effects of warming and elevated CO_2 resulted in a larger growth enhancement than warming alone in the one-year experiment. The short-term results could bring out large uncertainty in predicting long-term ecosystem responses to climate change based on leaf- or plant-level response (Körner 1995). Currently, the Boston-Area Climate Experiment (BACE) is designed to characterize ecosystem responses (linear vs. nonlinear) to simultaneous climate change with five levels of warming across each of three precipitation treatments in a New England old-field ecosystem, but it is still under construction by Jeffrey Dukes in Waltham, MA. The only model study by Cowling and Shin (2006) showed that temperature threshold values increased with decreasing precipitation in Amazonia tropical rainforests. We argue that, due to increasing water stress, temperature threshold values were supposed to decrease as illustrated in this study (Ise and Moorcraft 2006, Wall *et al.* 2006). With very limited data sets, it is too early to rigorously evaluate consistency between model simulations and between modeling and experimental results.

Implications for experimental studies

Our modeling results from numerous scenarios reflect effects of a range of future climates compared to that from manipulative experiments with limited treatment levels and global change factors. Thus, our study will offer suggestions for experimental studies on ecosystem response to multiple global change factors at least in three aspects. First, as expected, our results exhibit ecosystem nonlinearity in response to global change factors. However, the majority of experiments were currently manipulated in two treatment levels of the gradients for one or two factors. Although those results provided single-factor pulse response under climate change and/or two-factor interaction, there was no information on ecosystem nonlinearity along the gradients. Thus, cautions should be taken on interpretation of results. Linear insertion or extrapolation was inappropriate to explain the results under other conditions of the same climate change factor. For example, if nonlinear pattern was parabolic in response to temperature (Fig. 5.4a), the same response magnitude occurred under two treatments (e.g., 3 and 7°C for NPP), resulting in misinterpretation.

Second, the nonlinear patterns of ecosystem carbon and water dynamics in response to individual changes in temperature, CO_2, and precipitation were different. The diverse patterns indicate that it is necessary to conduct experimental studies with individual gradient of temperature, CO_2, and precipitation changes. Although some experiments have been manipulated in the field, for example, a continuous gradient of CO_2 from 200 to 550 ppmv in central Texas (Gill *et al.* 2002), the range under experimental manipulation was narrower compared to IPCC projection (668~734 ppmv in 2100, IPCC 2001). Furthermore, the differential responses may occur between the low-range and high-range of climate change factors (Figs. 5.4 and 5.5).

Third, the combined two- or three-factor anomalies substantially changed nonlinear patterns and/or shifted points of abrupt changes on ecosystem carbon and water processes compared to single-factor changes. The substantial changes would make it very difficult to infer ecosystem responses to multifactor global change from single-factor experimental results. It is also impossible to conduct multisite, multifactorial experiments with a range of treatment levels due to ecosystem complexities and cost limitation. However, some experiments need to be manipulated, such as the Boston-Area Climate Experiment (BACE) in a New England old-field ecosystem (under construction), to verify part of the modeling results and provide technical input to future experimental design and theoretical development. For example, how many treatment levels are needed for two-factor changes to reveal nonlinear responses? What is the interval of treatment levels? Furthermore, new experiments are needed that explicitly account for nonlinear patterns generated from feedback mechanisms and threshold behavior.

Model assumptions

Model simulation results show diverse nonlinear patterns in response to individual and simultaneous global changes on ecosystem carbon and water processes. The diversity of nonlinear responses reflect the fact that the natural ecosystems may have different responses to multiple global change factors (Scheffer *et al.* 2001, Burkett *et al.* 2005), which were well simulated by the structure of TECO model. However, ecosystem biogeochemical models share a similar structure of carbon and water flows but have different functions to relate the rate variables that control the flows to temperature, CO_2, and precipitation, resulting in large simulation uncertainties of ecosystem response to global change (Burke *et al.* 2003). Thus, the results may change with incorporated function in various models. It is critical to examine and improve various response functions.

Although global climate change largely affects ecosystem structure and function and impacts the natural resources on which humans depend, it has to be considered that vegetation may acclimate and adapt to changing climate conditions (Luo *et al.* 1998, 2001a, Hanson *et al.* 2005, Rustad 2006). In addition, changes in community composition would be expected because plant species exhibit markedly different response patterns to climate change (Ackerly and Bazzaz 1995). However, the acclimation mechanisms and the changes in vegetation composition were left out from our present study, which was complicated to multiple treatment levels of multiple global change factors. The further research is needed to incorporate them into our TECO model. The expected results will improve ecological forecasting and inform decision makers on managing the conditions leading to nonlinear responses and subsequent changes to ecosystem services. (Carpenter *et al.* 1999, Scheffer *et al.* 2001).

5.5. Conclusions

Using the TECO model, we assessed nonlinear patterns in response to individual and simultaneous changes in temperature, CO_2, and precipitation on ecosystem carbon and water dynamics of a grassland ecosystem. Our results show different patterns of ecosystem nonlinearity, which were parabola, asymptotic, and threshold-like in response to individual changes in temperature, CO_2, and precipitation, respectively, for NPP, NEE, and Rh. For runoff and ET, threshold-like shape was found in response to both temperature and precipitation anomalies, while the response to changing CO_2 was less sensitive. The combinations of two- or three-factor changes in temperature, CO_2, and precipitation interactively affected nonlinear curves by changing response patterns (Figs. 5.6 and 5.7) and/or shifting points of abrupt changes (i.e., threshold values, Figs. 5.6, 5.7, and 5.8). Our modeling study indicates that a diversity of nonlinear patterns in response to different global change factors and effects of combined climate anomalies should be concerned with choosing scenarios of climate change to predict ecosystem responses and to set up new experiments.

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Chapter 6

Conclusions and implications

6.1. Conclusions

In this work, several ecosystem processes of carbon and water cycling (mainly soil respiration) in response to global climate change and land use practice (i.e., clipping) were studied using experimental and modeling approaches (Chapter 1, Fig. 1.1). Some major findings are listed as follows:

- Based on two multifactor manipulative experiments – one long-term with warming (2°C) and yearly clipping and one short-term with warming (4.4°C) and doubled precipitation (The transient response to clipping was also studied) – in a tallgrass prairie ecosystem, the main effects of warming and doubled precipitation were significant on soil respiration. Clipping significantly decreased soil respiration in the transient study but not in the long-term experiment. No significant interactive effects among the experimental factors were statistically found on soil respiration or their temperature sensitivities except for the warming×clipping interaction ($p < 0.05$) in the transient study. As a consequence, the interactive effects of warming, clipping, and doubled precipitation were minor relative to main effects on soil respiration.

- Using the deep-collar insertion to partition soil respiration into autotrophic (R_A) and heterotrophic (R_H) components, heterotrophic respiration accounted for approximately 66% of soil respiration over the six years in a grassland ecosystem. Warming significantly stimulated soil respiration and its components throughout the duration of experiment. Yearly clipping significantly reduced soil respiration in the last two years and heterotrophic respiration in all the four years, while there was no significant clipping effect on R_A. However, the effects of warming and yearly clipping on soil respiration and its components did not result in significant changes in R_H or R_A contribution. The apparent Q_{10} values of soil respiration was slightly lower under warming ($p>0.05$) and reduced considerably by clipping ($p<0.05$) compared to that in the control. In addition, the apparent Q_{10} values for R_A were higher than those for R_H and soil respiration.

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

- The transect study examined patterns of biomass, litterfall, and soil respiration in southern Great Plains grasslands along a precipitation gradient. Our results show that aboveground biomass (AGB), standing litter (ST), surface litter (SU), and soil respiration often linearly increased with an increase in precipitation along the gradient, although belowground biomass (BGB) and total biomass did not largely change. BGB to AGB ratio and rain use efficiency (RUE) linearly decreased with increasing precipitation due to less plant allocation to roots and high biogeochemical constraints (i.e., nutrients or light), respectively, at mesic sites of the gradient. The one-year precipitation before samplings (OYP) had better correlations with biomass, litterfall, and soil respiration than mean annual precipitation (MAP). Soil respiration was not only affected by precipitation, but also regulated by litterfall in fall and winter and by AGB in spring, which were mainly controlled by precipitation.

- Using a terrestrial ecosystem (TECO) model, I examined nonlinear patterns of ecosystem responses to changes in temperature, CO_2, and precipitation individually or in combination. The modeling results show that nonlinear patterns were parabolic, asymptotic, and threshold-like in response to temperature, CO_2, and precipitation anomalies, respectively, for net primary production (NPP), net ecosystem exchange of CO_2 (NEE), and heterotrophic respiration (Rh). Runoff and evapotranspiration (ET) exhibited threshold-like pattern in response to both temperature and precipitation anomalies but were less sensitive to CO_2 changes. The combined two- or three-factor changes in temperature, CO_2, and precipitation considerably influenced nonlinearity of ecosystem responses by either changing patterns and/or shifting points of abrupt changes.

6.2. Implications for future work

- 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 respiration to multi-factor global change, at least in grassland ecosystems. It is yet to be examined whether the 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 multi-factor experiments.

- The higher apparent Q_{10} values for R_A than R_H and soil respiration were found in our study as well as some other studies. However, the Q_{10} values came from the field experiments, which were often confounded by other co-varying factors, and have not been carefully examined for intrinsic Q_{10} values. To clearly understand the mechanisms, it is imperative to carefully design manipulative experiments in both field and laboratory to eliminate the effects of confounding factors.

- The significant effects of warming and yearly clipping on soil respiration and its components did not result in considerable changes in R_H or R_A contribution. The results suggest that R_H or R_A contribution to soil respiration will not change largely in the changing climate. Although our results may largely simply the prediction of R_H or R_A contribution in the future, it remains unknown how other ecosystems responded to global change on R_H or R_A contribution, Therefore, the further studies should be conducted to verify whether the conclusion could be generalized across ecosystems.

- The linear relationships between precipitation, biomass, litterfall, and soil respiration indicate that precipitation is an important driver in shaping ecosystem functioning by controlling soil water dynamics, which directly affects vegetation production and litterfall, and indirectly regulates soil respiration. If our findings were incorporated into current biogeochemical models, this will improve the predictions of long-term climate change effects (decades to centuries) on grassland ecosystems' carbon balances.

- Ecosystem nonlinearity in response to global change factors suggests that cautions should be taken on interpretation of results. Currently, the majority of experiments were manipulated in two treatment levels of the gradients for one or two factors and there was no information on ecosystem nonlinearity along the gradients. Linear insertion or extrapolation was inappropriate to explain the results under other conditions of the same climate change factor.

- Diverse nonlinear patterns of ecosystem carbon and water dynamics in response to individual changes in temperature, CO_2, and precipitation indicate necessary to conduct experimental studies with individual gradient of temperature, CO_2, and precipitation changes. Although some experiments have been manipulated in the field, for example, a continuous gradient of CO_2 from 200 to 550 ppmv in central Texas (Gill *et al.* 2002), the range was narrower compared to IPCC projection (668~734 ppmv in 2100, IPCC 2001). Furthermore, the differential responses may occur between the low-range and high-range of climate change factors (Figs. 5.4 and 5.5).

- The combined two- or three-factor anomalies substantially changed nonlinear patterns and/or shifted points of abrupt changes on ecosystem carbon and water processes compared to single-factor changes. The substantial changes would make it difficult to infer ecosystem responses to multifactor global change from single-factor experimental results. However, it is impossible to conduct multisite, multifactorial experiments with a range of treatment levels due to ecosystem complexities and cost limitation, but some experiments still should be manipulated, such as the Boston-Area Climate Experiment (BACE) in a New England old-field ecosystem (under construction), to verify part of the modeling results, provide technical input to future experimental design and theoretical development, and improve ecological forecasting and inform decision makers on managing the conditions leading to nonlinear responses and subsequent changes to ecosystem services.

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