Ecosystem Carbon Fluxes in Response to Warming and Clipping in a Tallgrass Prairie

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ABSTRACT

Global warming and land-use change could have profound impacts on ecosystem carbon (C) fluxes, with consequent changes in C sequestration and its feedback to climate change. However, it is not well understood how net ecosystem C exchange (NEE) and its components respond to warming and mowing in tallgrass prairie. We conducted two warming experiments, one long term with a 1.7°C increase in a C_4-dominated grassland (Experiment 1), and one short term with a 2.8°C increase in a C_3-dominated grassland (Experiment 2), to investigate main and interactive effects of warming and clipping on ecosystem C fluxes in the Great Plains of North America during 2009–2011. An infrared radiator was used to simulate climate warming and clipping once a year mimicked mowing in both experiments. The results showed that warming significantly increased ecosystem respiration (ER), slightly increased GPP, with the net outcome (NEE) being little changed in Experiment 1. In contrast, warming significantly suppressed GPP and ER in both years, with the net outcome being enhanced in NEE (more C

sequestration) in 2009–2010 in Experiment 2. The C_4-dominated grassland showed a much higher optimum temperature for C fluxes than the C_3-dominated grassland, which may partly contribute to the different warming effects in the two experiments. Clipping significantly enhanced GPP, ER, and NEE in both experiments but did not significantly interact with warming in impacting C fluxes in either experiment. The warming-induced changes in ecosystem C fluxes correlated significantly with C_4 biomass proportion but not with warming-induced changes in either soil temperature or soil moisture across the plots in the experiments. Our results demonstrate that carbon fluxes in the tallgrass prairie are highly sensitive to climate warming and clipping, and C_3/C_4 plant functional types may be important factor in determining ecosystem response to climate change.

Key words: climate warming; biofuel harvest; C_3; C_4; carbon fluxes; carbon sequestration; optimum temperature; plant functional types; feedback.

INTRODUCTION

The response of terrestrial carbon (C) cycling to climate warming constitutes a major uncertainty in predicting future atmospheric CO_2 concentrations and temperatures (Meir and others 2006; Heimann and Reichstein 2008). It has been well documented that warming has greatly changed both ecosystem

C uptake and release (Luo and others 2009, 2012), with a consequence of positive (Friedlingstein and others 2006; Heimann and Reichstein 2008) or negative (Welker and others 2004; Day and others 2008) feedback to atmospheric CO_2 concentrations, which in turn augments or diminishes climate warming. Despite substantial progress made in the past decade, large challenges and uncertainties still remain, partly due to our limited understanding of the complex impacting factors and regulatory mechanisms of ecosystem temperature sensitivity and also the contradictory results in previous studies (Cox and others 2000; Field and others 2007; Luo 2007; Heimann and Reichstein 2008).

Current coupled climate-C models all predict a positive feedback between terrestrial C cycle and climate warming, primarily due to the increased C release under warming (Friedlingstein and others 2006). However, experiments have shown contradictory results, with decrease (Schuur and others 2009), increase (Day and others 2008), or little change (Niu and others 2008; Luo and others 2009) in ecosystem carbon storage or sequestration all being reported. Although some manipulative studies have investigated warming effects on some of the C cycle processes, most measures are NPP, biomass, and soil respiration (Rustad and others 2001; Lin and others 2010; Wu and others 2011), based on which C sequestration changes were speculated. How net ecosystem C exchange (NEE), the direct measure of C sink/source, and its two major components, gross primary production (GPP) and ecosystem respiration (ER), respond to warming in field experiments (Lu and others 2012) has received less attention.

Climate warming can directly influence C fluxes by changing plant photosynthesis and plant and soil respiration and also indirectly regulate these by changing soil water content (Harte and others 1995; Niu and others 2008), species composition, and community structure (Saleska and others 2002; Luo and others 2009), and other factors and processes. For example, plant functional type is one important regulatory factor that may influence the response of ecosystem carbon cycling to climate change (Huxman and others 2004; Reich and others 2004; Polley and others 2007; Niu and others 2009; Langley and Megonigal 2010). It is well documented that different plant functional types with their characteristic ecophysiological traits (Chapin and others 1996; Reich and others 2007; Morgan and others 2011) can substantially differ in the way they regulate ecosystem functions (Hooper and Vitousek 1997; Tilman and others 1997; Hooper and others 2005; Gustafsson and Bostrom

2009). For example, a shift from forbs to shrubs decreased litter inputs and reduced soil organic C in an alpine meadow ecosystem (Saleska and others 2002) and the replacement of C_3 by C_4 plants increased primary production and litter accumulation in a tallgrass prairie (Luo and others 2009; Niu and others 2010a). So, plant functional types are often expected to influence ecosystem responses to climate change (Reich and others 2004; Harte and others 2006; Luo 2007; Polley and others 2007; Luo and others 2009; Langley and Megonigal 2010). However, we lack evidence and mechanistic understanding of how plant functional types modify ecosystem responses to climate change.

Land-use change is another important factor that could fundamentally change ecosystem carbon cycling and its response to climate warming (Caspersen and others 2000; Chapin and others 2008). Mowing is one of the most prevalent land uses in grasslands, and has the potential to substantially alter carbon cycling in those ecosystems by (1) altering microclimate and the availability of light, water, and nutrients; (2) changing photosynthetic activity and stimulating compensatory growth (Anten and Ackerly 2001; Zhao and others 2008); as well as (3) modifying the species composition (Derner and others 2006). Although these processes collectively appear to accelerate rates of C cycling, their impacts on ecosystem carbon sequestration are inconsistent (Derner and others 2006; Niu and others 2010a) and their influences on carbon-climate feedbacks are poorly understood.

In this study, we took advantage of two ongoing experiments to evaluate the main and interactive effects of warming and clipping on ecosystem C fluxes in tallgrass prairies in the USA Great Plains. Experiment 1 was designed to examine long-term warming and clipping on community structure and ecosystem functions in a C_4-dominated grassland (for example, Luo and others 2001; Wan and others 2005; Niu and others 2010a). Experiment 2 was to examine ecosystem responses to the main and interactive effects of warming, changing precipitation, and clipping in a C_3-dominated grassland. We hypothesized that (1) climate warming and clipping will largely impact ecosystem C sequestration by changing both GPP and ER in the tallgrass prairie in the Great Plains, (2) there will be different warming responses in ecosystem C fluxes in the two experiments because the dominant plant functional types were different. Warming will enhance ecosystem carbon fluxes in the C_4-dominated grassland but reduce them in the C_3-dominated grassland based on the higher optimum temperature of photosynthesis

in C_4 than C_3 plants (Pearcy and Ehleringer 1984), and (3) clipping will decrease ecosystem carbon fluxes and their responses to climate warming. In both experiments, we used an infrared radiator to simulate climate warming and mimicked mowing by yearly clipping aboveground plants at peak biomass. GPP, ER, and NEE were measured monthly to investigate C fluxes and sequestration of tallgrass prairie in response to climate warming and land-use change.

METHODS

The Experiments

The experiments were conducted in central Oklahoma on the Great Plains of the USA (34°58′54″N, 97°31′14″W). The mean annual precipitation at this site was 914 mm, with monthly precipitation ranging from 30 mm in January to 135 mm in May. The mean annual temperature was 16.3°C, with monthly air temperature ranging from 3.3°C in January to 28.1°C in July. The maximum and minimum temperatures were 44.4 and −23.8°C, respectively (average values from 1948 to 1998, Oklahoma Climatological Survey, Norman, Oklahoma, USA). There are two independent experiments in this study. Experiment 1 is in a C_4-dominated grassland (C_4 plants occupying 72.0% of total aboveground biomass) and Experiment 2 is in a C_3-dominated grassland (C_3 plants occupying 72.4% of the total aboveground biomass, Table 1). The distance between the two experimental sites is less than 500 m. Except for dominant plant functional types, climate and other environmental factors were similar between the two sites. Both sites had a silt loam soil, which belongs to part of the Nash–Lucien complex with neutral pH, high available water capacity, and a deep, moderately penetrable root zone (USDA 1979). In Experiment 1, the dominant C_4 species are *Sorghastrum nutans*, *Schizachryum scoparium*, and *Sporobolus asper*. In Experiment 2, the dominant C_3 species are *Vicia sativa*, *Bromus arvenis*, *Ambrosia trifida*, and *Cirsium altissimum* and the C_4 species is *Tridens flavus*. The variation of vegetation in the two experiments could have resulted from the legacy of site history. The site of Experiment 1 was closed to grazing since 1974, whereas the site of Experiment 2 has been closed to grazing since 2007.

Experiment 1 used a paired, nested design with warming as the main factor and clipping as a secondary factor. Six pairs of control and warming plots (2×2 m^2) were treated from November 1999. In each pair, one plot was warmed continuously

using infrared heaters (Kalglo Electronics Inc, Bethlehem, Pennsylvania, USA) suspended 1.5 m above the center of each plot and the other was the control. In the control plots, one dummy heater of the same size and shape as the heaters was suspended at the same height to mimic shading effects of the heaters. The heaters under the warming treatments were set at a radiation output of approximately 1,600 W. Each 2×2 m^2 plot was divided into four 1×1 m^2 subplots. Two diagonally opposed subplots in each plot were clipped 10 cm above the ground once a year at peak biomass (late August or early September). The clipped material was taken away and not returned to the plots. Detailed methods are described in (Wan and others 2002). We measured ecosystem C fluxes in one clipped and one unclipped subplot in each plot.

Experiment 2 used a randomized block design to manipulate temperature and precipitation. There were four 13×15.5 m^2 blocks. The distance between two adjacent blocks was 5 m. Within each block were six 2.5×3.5 m^2 plots, including a 25 cm buffer area around all sides. There were two levels of the temperature treatment (ambient and warming) and three levels of precipitation treatment (ambient, increased, and decreased precipitation), totaling six treatments randomly allocated to the six plots in each block. In this experiment, we also used infrared heaters with 2,000 W radiation output to warm the plots all year round. Two infrared heaters were suspended 1.5 m above the ground in each warmed plot to evenly distribute the heat. The warming treatment started in July 2009. In the control plots, two dummy heaters were suspended at the same height. Each plot was divided into two subplots, one clipped and the other unclipped. The clipping treatment in Experiment 2 was conducted in the same manner as that in experiment 1. So, for both experiments, there were four treatments in this study: unclipped with control (ambient) temperature (UC), unclipped warmed (UW), clipped with control temperature (CC), and clipped warmed (CW).

Soil Temperature and Moisture

Soil temperature was monitored by homemade thermocouples installed at the depth of 2.5 cm at the C_4 site and 7.5 cm at the C_3 site, in the center of one clipped and one unclipped subplot in each plot. The hourly average data were recorded by a CR10X datalogger (Campbell Scientific, Logan, Utah, USA). Volumetric soil water content (%V) was measured two or three times a month using manual Time Domain Reflectomery (TDR) equipment

Table 1. Results (*F* Values) of Repeated-Measurement ANOVA on the Effects of Warming (W), Clipping (Cl), Measurement Time (T), and Their Interactions on Net Ecosystem CO_2 Exchange (NEE), Ecosystem Respiration (ER), and Gross Primary Productivity (GPP)

	DF	2009–2010			DF	2010–2011		
		ER	GPP	NEE		ER	GPP	NEE
Experiment 1								
W	1	8.63**	0.0	2.34	1	3.53^	1.92	0.14
Cl (W)	2	37.21***	21.45***	5.5*	2	3.58*	16.92***	4.66*
T	15	84.76***	48.05***	9.59***	13	46.56***	46.83***	13.83***
T × *W*	15	1.09	1.59	1.74	13	1.64^	0.47	0.71
T × Cl (W)	30	3.22**	4.2***	2.11*	26	1.70^	2.53***	1.14
Experiment 2								
W	1	26.9***	4.6*	10.1**	1	7.4**	4.4*	0.9
Cl	1	35.9***	44.7***	11.8**	1	5.4*	11.5**	35.5***
W × Cl	1	0.01	0.10	0.3	1	0.5	0.1	2.2
T	12	16.8***	49.0***	79.2***	13	72.4***	60.1***	35.7***
T × *W*	12	2.81**	2.3**	3.9***	13	3.8***	3.5***	2.6***
T × Cl	12	3.1***	7.4***	5.7***	13	2.9***	1.4	1.3
T × *W* × Cl	12	0.2	0.3	0.2	13	1.1	0.7	1.3

DF degree of freedom
^,*,**,***Significance was at the level of P < 0.1, 0.05, 0.01, and 0.001, respectively.

(Soil Moisture Equipment Corp., Santa Barbara, California, USA) at 0–12 cm depth at the C_4 site. At the C_3 site, volumetric soil water content was measured automatically by TDR profiling probes (ESI Inc., Victoria, BC, Canada) at 0–15 cm depth and recorded every hour.

Warming on average increased soil temperature by 1.7°C at 2.5 cm depth at the C_4 site (Experiment 1) and by 2.8°C at 7.5 cm depth at the C_3 site (Experiment 2) over the study period (all $P < 0.05$, Table S1 in Electronic supplementary material). Soil moisture was reduced by an average of 1.76% at 12 cm depth at the C_4 site and 2.25% ($P < 0.05$) at 15 cm depth at the C_3 site in the warmed plots in comparison with the control plots.

Ecosystem Carbon Flux Measurements

We measured ecosystem C fluxes in one clipped and one unclipped subplot in each plot from July 2009 to June 2011 in both experiments. In each subplot, one square aluminum frame (0.5×0.5 m²) was permanently inserted into the soil at 3 cm depth. Each side of the frame was 3 cm wide and provided a flat base between the soil surface and the CO_2 sampling chamber. We measured ecosystem C exchange with an infrared gas analyzer (IRGA; LI-6400, LiCor Inc., Lincoln, Nebraska, USA) attached to a transparent chamber ($0.5 \times 0.5 \times 0.6$ m³, also see the detail information in the study of Niu and others 2010a, b), which covered all the vegetation within

the aluminum frame. The radiation is reduced by 8% within the chamber, which was measured by a Licor sensor (Licor-2003S). One small electric fan was running continuously to promote air mixing within the chamber during the measurement. Nine consecutive recordings of CO_2 and water vapor concentration were taken from each frame at 10-s intervals during a 90-s period after steady-state conditions were achieved within the chamber. During measurement, CO_2 concentration was allowed to build up or draw down over time, from which flux rates were determined from the time-course of the concentration to calculate net ecosystem CO_2 exchange (NEE). Increases in air temperatures within the chamber during the measuring time period were about 0.2°C. Details about these static-chamber flux calculations can be found in the soil-flux calculation procedure on the LI-6400 manual (LiCor Inc., 2004). This static-chamber method has been used and validated in previous studies (Huxman and others 2004; Welker and others 2004). Following measurement of NEE, the chamber was vented, replaced on each frame, and covered with an opaque cloth. Then the CO_2 exchange measurements were repeated. Because the second set of measurements eliminated light (and hence photosynthesis), the values obtained represented ER (Welker and others 2004). The difference between NEE and ER was considered to represent instantaneous GPP for the vegetation within the chamber. By convention, negative NEE and GPP

values refer to net C uptake by the ecosystem, whereas positive NEE values represent net C loss from the ecosystem. Ecosystem gas exchange was measured at 2- to 3-week intervals at 8:00–11:00 am from July 2009 to July 2011 in both experiments.

Biomass Measurements

Biomass in both experiments was estimated by clipping the clipped plots at peak biomass (Sept 6, 2009 and Aug 31, 2010) at 10 cm above the soil surface, then oven-drying the biomass at 65°C for 48 h and weighing. C_3 and C_4 plants were separated during clipping.

Data Analyses

A repeated-measures (RM) ANOVA was used in Experiment 2 and a nested RM ANOVA was used in Experiment 1 to examine warming and clipping effects on ecosystem C fluxes in 2009–2010 and 2010–2011. Between-subject effects were evaluated as warming or clipping treatment and within-subject effects were measurement times. The effects were considered to be significantly different if $P < 0.05$. Because there were no significant interactions of precipitation × warming (P = 0.15, 0.34, and 0.1 for NEE, ER, and GPP, respectively) or precipitation × clipping (P = 0.1, 0.11, and 0.24 for NEE, ER, and GPP, respectively) across 2009–2011 in Experiment 2, we merged all the precipitation treatments as replicates and only focused on warming and clipping impacts. Temperature response curves of carbon fluxes were constructed based on 1°C temperature bins across all the measurements. In practice, we pooled all the measurements of C fluxes and the corresponding air temperature together, then binned the C fluxes and air temperature based on 1°C bins. The air temperature and net ecosystem exchange were averaged through every temperature bin over all the measurements across plots and times. Because we expected to examine the overall temperature response of C exchange at ecosystem level, our methods may include seasonality/phenology changes and plant physiology. This approach of generating temperature response curves of ecosystem C exchange has been used in the previous studies (Huxman and others 2003; Niu and others 2011, 2012; Yuan and others 2011).

Linear regression analyses were used to evaluate relationships of warming-induced changes in carbon fluxes with C_3 and C_4 biomass proportion, soil temperature, and moisture changes. Warming-induced changes in carbon fluxes were calculated as the values in the warmed plots minus those in the unwarmed plots. We estimated warming effects only in the clipped plots because we only clipped the plants and estimated biomass in the clipped plots. In Experiment 2, in each block, we had three pairs of warmed and unwarmed plots, that is, plots with the treatment of ambient precipitation, increased, or decreased precipitation. So in each block, we had 3 data points of warming effects. Because there were 4 blocks, in total we had 12 data points for the warming effects in each year. Across both years, there were 24 points in Experiment 2 (C_3 grassland). Similarly, in Experiment 1 (C_4 grassland), we had 12 data points for the warming effects across both years. We normalized the warming-induced changes in C fluxes between the two sites using warming-induced changes in C fluxes divided by soil temperature changes. Although soil temperature was measured at different soil depths (2.5 and 7.5 cm for C_4 and C_3 site, respectively), based on Wan and others' study, warming-induced changes in soil temperature were parallel at different soil depths (Wan and others 2002). So, soil temperature being taken at different depths may not cause much uncertainty in the normalization. The relationship of warming sensitivity of C fluxes with C_4 biomass proportion was also analyzed using linear regression. All statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc., Chicago, Illinois, USA).

RESULTS

Warming Effects on Carbon Fluxes in C_4 Grassland (Experiment 1)

In Experiment 1, plants were actively taking up C from April to October but C fluxes were very low from November to March in both years (Figure 1A–D). The main effect of warming was positive for ER in 2009–2010 ($P < 0.05$) and 2010–2011 ($P < 0.1$), respectively, but not significantly for GPP or NEE in either year (Table 1). Averaged over a year, ER was significantly higher in the warmed than unwarmed plots by 12.3 and 24.9% for 2009–2010 and 2010–2011, respectively, across the clipping treatments (both $P < 0.05$, Figure 1A, B; Table 1). There was strong seasonal variation in ecosystem C fluxes and their responses to warming (Figure 1). For example, the main effect of warming significantly suppressed NEE (less negative) in August and early September 2009, and March 2010 (all $P < 0.05$), but did not change NEE at other times (Figure 1E, F). The significant main effects of warming on C fluxes were marked at each measurement point in Figure 1.
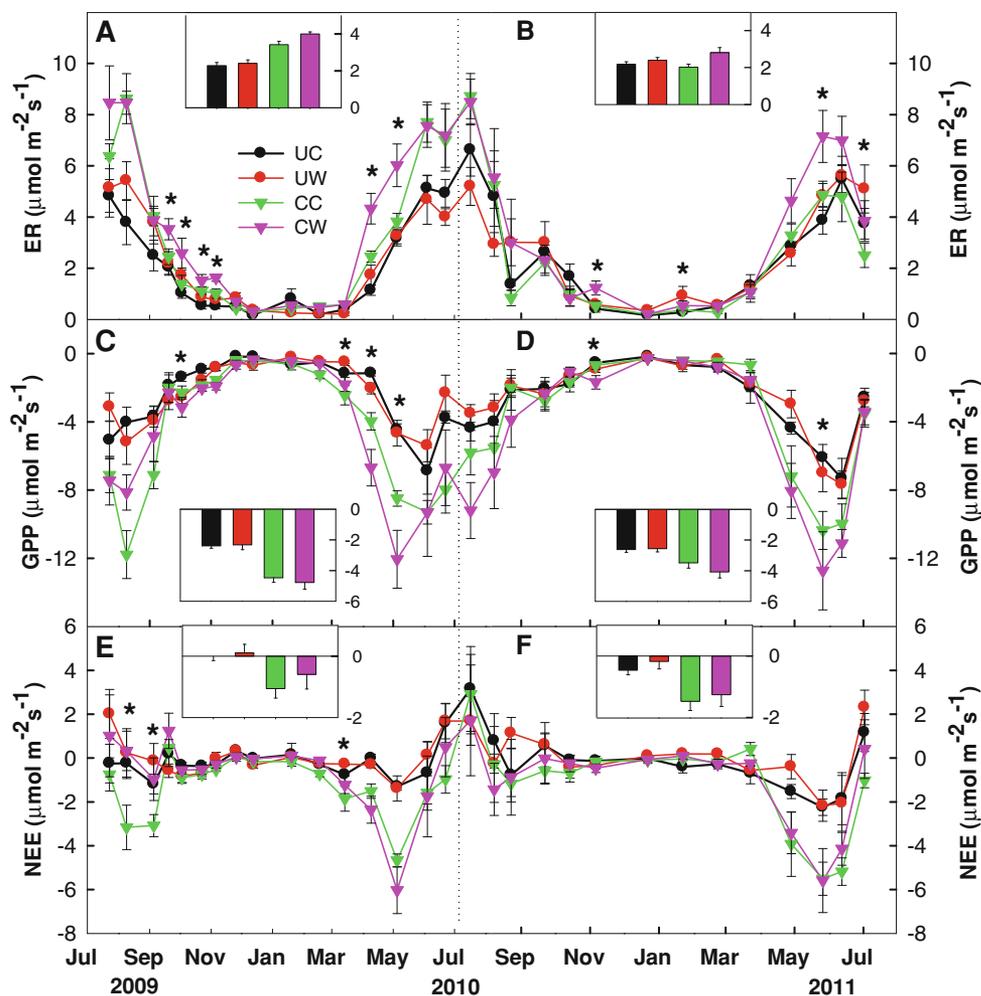
Figure 1. Seasonal dynamics and mean values of ecosystem respiration (ER, means ± 1 SE, **A**, **B**), gross primary productivity (GPP, **C**, **D**), net ecosystem carbon exchange (NEE, **E**, **F**), and their response to climate warming at the C_4-dominated grassland of Experiment 1. *Significant main effects of warming across the clipping treatments at the specific measurement time. *Insets* The means of carbon fluxes across the seasons. *UC* Unclipped control, *UW* unclipped warmed, *CC* clipped control, *CW* clipped warmed.

Warming Effects on Carbon Fluxes in C_3 Grassland (Experiment 2)

Plants were actively taking up C in winter in the C_3-dominated grassland (Figure 2) due to the growth of a C_3 winter grass, *B. arvensis*. The main effect of warming was significant for ER and GPP in both years and for NEE in 2009–2010 (Table 1). There were no significant warming × clipping interactions on any C flux in either year (Table 1). On average, ER and GPP were suppressed by 18 and 8% in 2009–2010, and 19 and 18% in 2010–2011, respectively, as the main effect of warming (all $P < 0.05$, Figure 2A–D). Warming enhanced NEE (more negative NEE) on average by 32% across the clipping treatments in 2009–2010 ($P < 0.05$, Figure 2E), but did not significantly change NEE in 2010–2011 ($P = 0.35$, Figure 2F). There were significant interactions between measurement time and warming on NEE, ER, and GPP in both years (Table 1). The significant warming effects on NEE were detected at most

measurement times in 2010. The main effect of warming significantly decreased ER in July and October 2009, and January, May–August 2010, as well as January, March–April 2011 (Figure 2A, B). GPP under warming decreased significantly in July and October 2009, and most times in 2010 and 2011 in comparison with those in the control (Figure 2C, D).

Clipping Effects on Carbon Fluxes and Their Responses to Climate Warming

The main effect of clipping was significant and similar for NEE, ER, and GPP in both experiments (Table 1). Specifically, in Experiment 1, clipping on average enhanced ER and GPP by 58 and 95% in 2009–2010 (both $P < 0.05$) and by 6 and 46% in 2010–2011($P < 0.05$ for GPP), respectively (Figures 1, 2). NEE was enhanced by 0.88 and 1.05 μmol m^{-2} s^{-1}, respectively, in 2009–2010 and 2010–2011 (all $P < 0.05$). In Experiment 2, clipping on average enhanced NEE, ER, and GPP by 30,
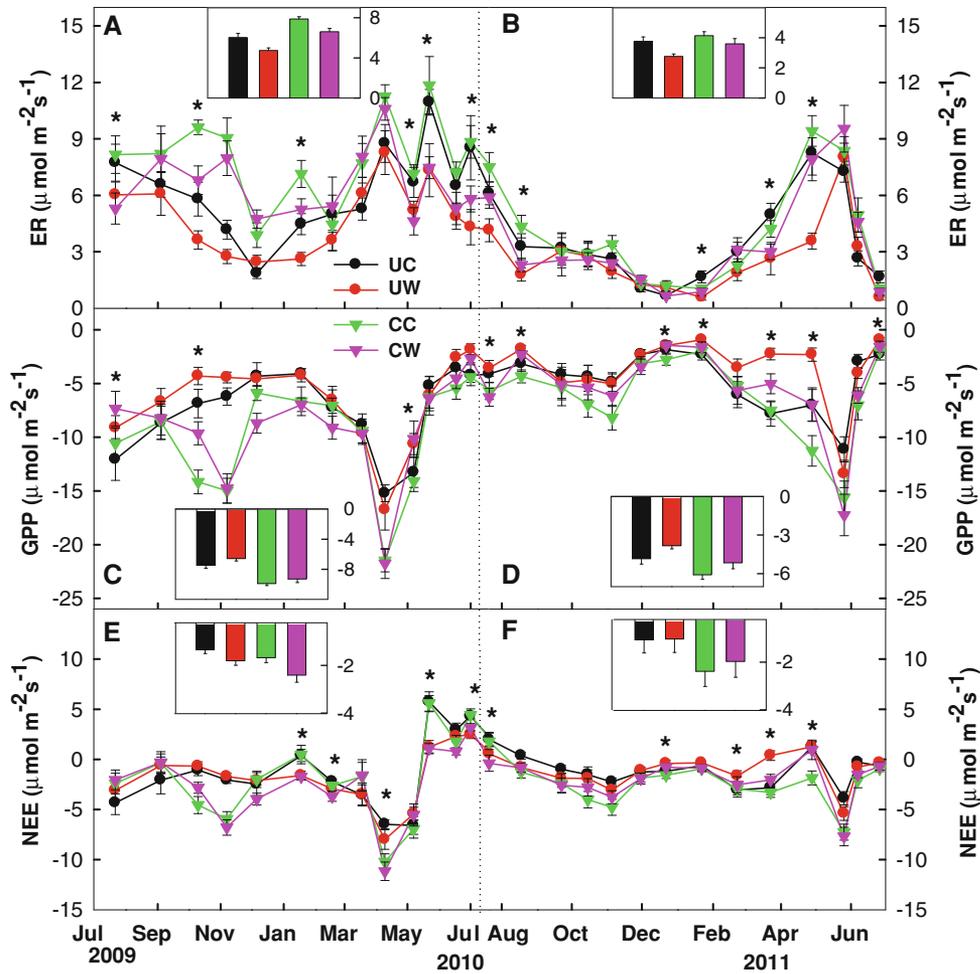
Figure 2. Seasonal dynamics and mean values of ecosystem respiration (ER, means ± 1 SE, **A**, **B**), gross primary productivity (GPP, **C**, **D**), net ecosystem carbon exchange (NEE, **E**, **F**), and their response to climate warming at the C_3-dominated grassland of Experiment 2. See Figure 1 for abbreviations and symbols.

32, and 37%, respectively, in 2009–2010 and by 70, 18, and 30%, respectively, in 2010–2011 (all $P < 0.05$, Figures 1, 2). Clipping did not significantly interact with warming in impacting any of the C fluxes in either experiment (Table 1).

Relationships between Warming Effects and Biotic or Abiotic Factors

We examined various potential causes of variable responses of ecosystem C fluxes to experimental warming in the experiments. Warming effects on C fluxes were not significantly correlated with warming-induced changes in soil moisture or soil temperature across the plots in either experiment (Figures S1, S2 in Electronic supplementary material), but were significantly dependent on C_4 and C_3 biomass proportions in the community (Figure 3). The multiple regressions showed that C_4 biomass proportion best explained warming effects on C fluxes. C_4 biomass proportion explained 67 and 34% in 2009–2010, 59 and 34% in 2010–2011 of the changes in ER and GPP, respectively, across

the grasslands (Figure 3). For NEE, there was an optimum C_4 biomass proportion (50%), at which NEE had the maximum net C sequestration. We normalized the warming effects by temperature changes under the treatments to calculate sensitivity of C fluxes to warming (that is, $\mu mol\ m^{-2}\ s^{-1}\ ^\circ C^{-1}$). The relationship between warming sensitivity and C_4 biomass proportion still held for both experiments in both years (Figure 4).

Temperature Response Curves of Carbon Fluxes in the Two Grasslands

Based on the seasonal changes, ER and GPP both followed a peak–curve pattern in response to temperature in both experiments. Their values increased with temperature in the lower temperature range, reaching a maximum at an optimal temperature, and then declined with temperature. The optimum temperatures for ER and GPP between the two grasslands were different. Specifically, in the C_4 grassland, GPP and ER attained the maximum values between 30 and 40°C (Figure 5A, B).
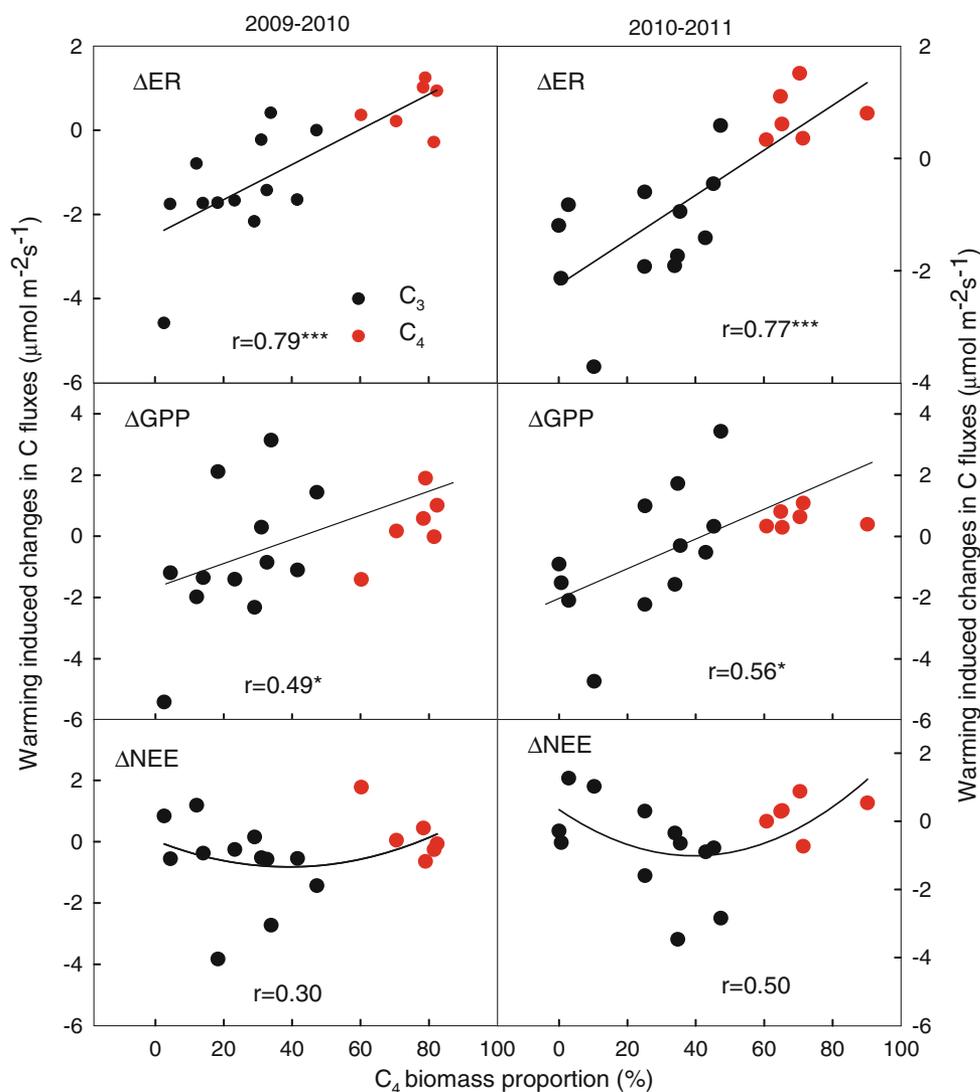
Figure 3. Relationships between warming-induced changes in carbon fluxes and C_4 biomass proportion. Negative ΔGPP values mean that warming enhanced gross ecosystem carbon uptake whereas a positive ΔGPP means that warming suppressed gross ecosystem carbon uptake. The *black circles* are for C_3 grassland (Experiment 1) and the *red circles* are for C_4 grassland (Experiment 2). Each point represents a warming effect calculated as a warmed plot minus the corresponding unwarmed plot (Color figure online).

Although in the C_3 grassland, the optimum temperatures for GPP and ER were much lower (less than 30°C) (Figure 5A, B). The steep decline in GPP between 10 and 15°C was mostly due to the fast growth of C_3 grass (*B. arvensis*) in the spring in Experiment 2, a period in which these temperatures are the normal. The optimum temperature of NEE also was lower in C_3 than in C_4 grassland (Figure 5C).

DISCUSSION

Carbon budgets of tallgrass prairie are perceived to be near equilibrium (Suyker and others 2003). However, there are limited data on the responses of NEE and its components (GPP and ER) to climate and land-use change in tallgrass prairie in the literature. By bringing together data from two different but still very similar experiments which are close to each other, we found that ecosystem level C exchanges are sensitive to climate and land-use change in tallgrass prairie. However, the two experiments showed different responses to climate warming but similar responses to clipping, suggesting the complexity of impacting factors and regulatory processes that influence the ecosystem's response to climate change.

Warming Effects on Ecosystem Carbon Fluxes

This study revealed various responses of ecosystem C fluxes to climate warming in a tallgrass prairie. As expected, ecosystem C fluxes are sensitive to warming, but respond differently between the two experiments, which are probably due to the following reasons.
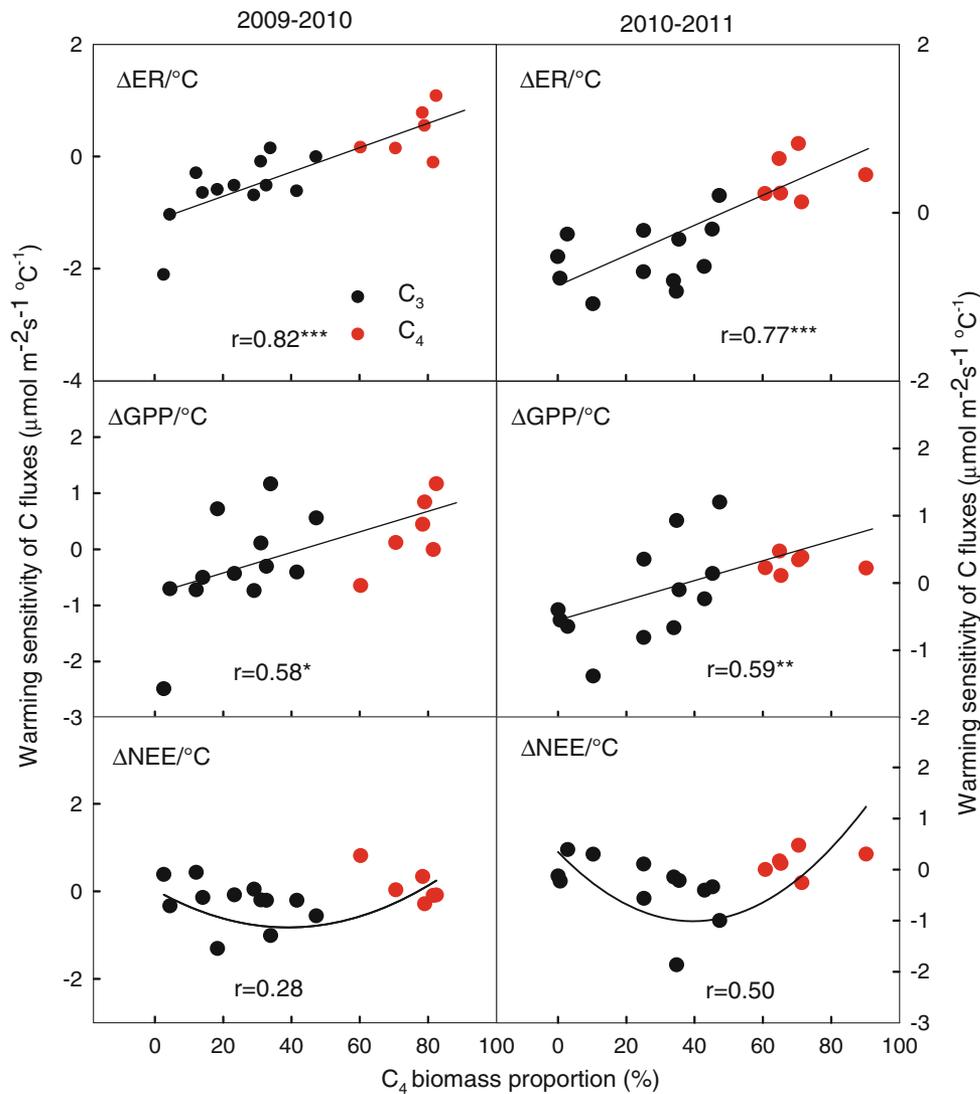
Figure 4. Relationships between warming sensitivity of carbon fluxes (changes in carbon fluxes per °C increase of soil temperature due to warming) and C_4 biomass proportion. Negative ΔGPP values mean that warming enhanced gross ecosystem carbon uptake whereas a positive ΔGPP means that warming suppressed gross ecosystem carbon uptake. The *black circles* are for C_3 grassland (Experiment 1) and the *red circles* are for C_4 grassland (Experiment 2). Each point represents a warming effect calculated as a warmed plot minus the corresponding unwarmed plot (Color figure online).

First, the different optimum temperature of C fluxes between C_3 and C_4 grasslands may contribute to the differential responses of ecosystem carbon fluxes in the two experiments. The C_4 grassland (Experiment 1) had much (around 10°C) higher optimal temperatures for ER, GPP, and NEE than the C_3 grassland (Figure 5), which is consistent with plant level responses (Pearcy and Ehleringer 1984; Collatz and others 1998). Due to the low optimal temperature, the C_3 grassland (Experiment 2) may suffer from high temperature stress under climate warming when the temperature surpasses the optimum temperature, leading to inhibited growth and increased mortality, especially for the winter annual plants (which are all C_3 species) (R. A. Sherry, unpublished data). Moreover, greater competitive ability for water resources and the higher water-use efficiency of C_4 plants (Niu and others 2003; Aires and others 2008) can alleviate warming-induced drought stress. On the contrary, C_3 species are more sensitive to water limitation (Nayyar and Gupta 2006). Warming-induced drought stress may thus also limit GPP and ER in the C_3 grassland (Experiment 2).

Due to the different temperature responses of C_3 and C_4 communities, warming-induced changes in ecosystem C fluxes were correlated with the relative abundance of C_4 plant functional types (Figure 3). Plots with more C_4 biomass proportion have higher warming-induced enhancements in GPP and ER, whereas plots with more C_3 biomass proportion have higher warming-induced reductions in GPP and ER. The relative changes in GPP and ER under warming over the long term indicate changes in C sequestration. In this study, ER was more sensitive to warming than GPP probably because of the more sensitive responses of soil respiration than plant photosynthesis in this ecosystem (Zhou and
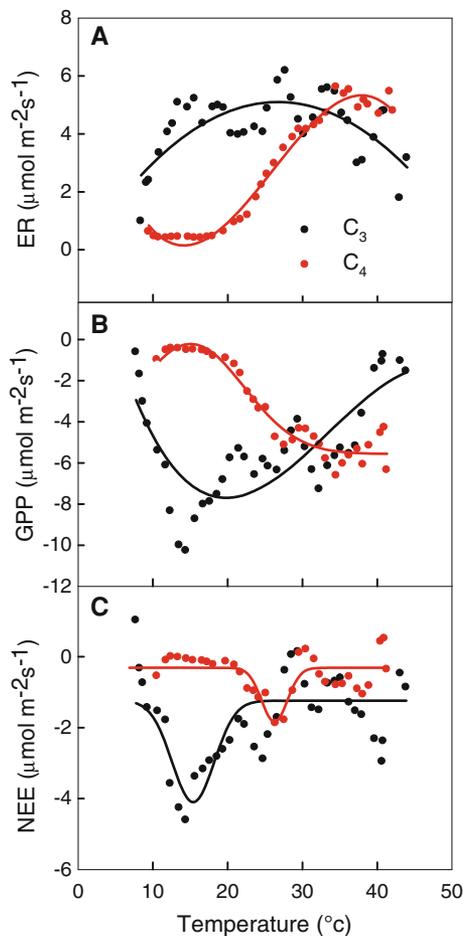
Figure 5. The seasonal temperature response curves of carbon fluxes at the C_3-(*black circle*) and C_4-(*red circle*) dominated grasslands. The *curves* were constructed based on 1°C temperature bins across all the measurements. Each point represents the average of air temperature/NEE within the corresponding temperature bin over all the measurements (Color figure online).

others 2006, 2007). Warming increased ER more than GPP, leading to less net C sequestration in the warmer environment in Experiment 1 (Figure 1E, F). However, in Experiment 2, warming induced C_3 grass mortality (Rebecca Sherry, unpublished data), reduced GPP, biomass, and litter production, thus decreasing soil respiration (Xuhui Zhou, unpublished data). The reduction in ER was larger than that in GPP, leading to more net C sequestration (Figure 2E, F). As a consequence, there was an optimum C_4 biomass proportion for NEE across all the measurements in the two experiments (Figure 3). The different dominant C_4 species between the two experiments may partly contribute to the different responses of NEE to C_4 biomass proportion. The fundamental mechanisms underlying the optimum C_4 species proportion for C

sequestration is relevant but beyond the scope of this study. A full investigation of the mechanism needs to be further pursued in the future study. A previous study in a mixed grassland reported that sensitivity of NEE in response to CO_2 concentration also varied with C_3–C_4 composition of vegetation (Polley and others 2007). These findings illustrate the potential role of C_3 and C_4 plant functional types in modifying ecosystem function in response to global change.

Second, the warming magnitude (delta soil temperature) was different between the two experiments in this study (1.7°C in Experiment 1 vs 2.8°C in Experiment 2), which might potentially contribute to the different warming impacts between the two experiments. However, our further analysis showed no significant correlations between soil temperature changes and warming effects on C fluxes across the plots in either grassland (Figure S2 in Electronic supplementary material), and the normalized warming effects on C fluxes still showed a significant relationship with C_4 biomass proportion (Figure 4). In addition, warming effects on C fluxes did not show a significant relationship with soil moisture changes across the plots in grasslands (Figure S1). These results together suggest that the different warming response between the two experiments is less likely attributed to the different magnitude of warming or its effects on soil moisture. Previous meta-analysis also shows that a warming magnitude between 1 and 3°C did not cause any differences of warming impacts on the terrestrial ecosystem C cycle (Lin and others 2010; Lu and others 2012), which is in agreement with our speculation.

Third, the two experiments have different warming treatment histories (12 vs 2 years), which may also lead to the different warming impacts. However, the long-term Experiment 1 showed that the warming effect on biomass and soil respiration in the C_4 grassland was always positive across the years, even in the first 2 years of the treatment (Luo and others 2009; Niu and others 2010a). Although the overall warming effect on GPP was not significant in this study, GPP was much larger in the warmed than unwarmed plots with the clipping treatment (Figure 1). Moreover, soil texture and nutrient content in both grasslands were almost identical (Table S1 in Electronic supplementary material). The similar responses of two grasslands to clipping also suggest a similarity at some extent between the grasslands. The warming effects on C fluxes was significantly related to C_4 biomass proportion, but not to other environmental factors, suggesting that dominant plant functional types are

probably the main factor whereas other potential factors contribute little to the varied warming effects in the grasslands.

Clipping Impacts on Carbon Sequestration and Warming Effects

Mowing for hay or biofuel harvest is a typical land-use type in tall grass prairie which substantially changes ecosystem C fluxes (Houghton and others 1999; Searchinger and others 2008). The enhancement of GPP, ER, and NEE with clipping (Figures 1, 2) is consistent with previous studies in a temperate steppe (Niu and others 2010b), but contrast with a Swiss grassland (Rogiers and others 2005). The negative impact of clipping on GPP in Rogers and others (2005) is due to grass being cut in June (mid growing season), which may reduce the green leaf area and thus C uptake. The positive clipping effect on gross and net carbon uptake may primarily result from improved light conditions with the removal of standing litter (Niu and others 2010b) and compensatory growth from clipping (Zhao and others 2008). In this study, clipping was conducted in early September when plants began to senescence, so clipping would not change GPP and NEE much in the later growing season. The results support the current hypothesis that grass harvest for biofuel after plant senescence may have less impact on ecosystem C stocks than in systems clipped while still growing (Heaton and others 2009). Our study indicates that appropriate harvest management is capable of avoiding negative effects on, or even improving, net carbon sequestration. Clipping at 10 cm above the ground surface once a year could be an effective management that does not reduce C sequestration in tallgrass prairie due to the stimulation of GPP as mentioned above.

Although the main effect of clipping was significant, the clipping treatment did not change the warming effects on C fluxes (no significant warming $\times$ clipping interactions), suggesting that warming and clipping impacted C fluxes in a statistically independent manner. The insignificant interactions between warming and clipping on C cycling were also reported in previous studies (Niu and others 2010a; Lin and others 2011). Nevertheless, in the tallgrass prairie, clipping tended to stimulate C_3 species but suppress C_4 species growth (Niu and others 2010a). So, in the long term, clipping may change ecosystem responses to warming through changing species composition.

Implications

Some meta-analysis studies on warming impacts on the terrestrial ecosystem C cycle have demonstrated various results among individual experiments in different ecosystem types or biomes (for example, Rustad and others 2001, Lu and others 2012). This study revealed that even in the same ecosystem with similar biomes, soil, and climates, ecosystem C fluxes also showed different responses to climate warming, which may be due to the different dominant C_3/C_4 plant functional types. This provides evidence of complex impact factors and regulatory mechanisms in influencing the terrestrial ecosystem C cycle and its response to climate change.

Our study has important implications for grassland response to climate warming. Previous studies have demonstrated great changes in the C_3–C_4 species composition of the grassland community under climate warming (White and others 2000; Luo and others 2009; Wittmer and others 2010). For example, an extreme heat event in a New Zealand grassland favored the expansion of C_4 species relative to C_3 species (White and others 2000). Manipulative warming markedly increased C_4 biomass but decreased C_3 biomass in a semi-arid grassland (Morgan and others 2011) and tallgrass prairie (Luo and others 2009; Niu and others 2010a). Over a long history of increasing temperature, C_4 species abundance increased in a temperate steppe (Wittmer and others 2010). For grasslands throughout the world that experience vegetation dynamics similar to our site, it is possible that they will respond to warming in a similar way. Because C_3–C_4 species composition strongly regulates, even reverses ecosystem responses to climate warming, any shift from C_3 to C_4 species in natural ecosystems will potentially cause an increase in ecosystem C sequestration under climate warming.

Our study also has implications for dynamic global vegetation models (DGVMs). Currently, most DGVMs considered the differences of C_3 and C_4 plant functional types based on Farquhar and others (1980) and Collatz and others (1992) formulations in simulating stomatal conductance and photosynthesis (Farquhar and others 1980; Collatz and others 1992). They treat C_3 and C_4 plants differently in their optimum temperature for photosynthesis, that is, C_4 species have higher temperature optima than C_3 species in photosynthesis (Cramer and others 2001; Sitch and others 2008). The temperature response curves of GPP in this study support the model simulations. Under climate change scenarios, some DGVMs simulate

vegetation changes and the corresponding changes in plant production and ecosystem C sequestration. For example, ORCHIDEE and Lund-Potsdam-Jena (LPJ) models simulated increasing woody coverage in the tundra under climate warming, which led to increased plant production, whereas JPJ simulated a replacement of boreal evergreen forest by deciduous woody and herbaceous plants, which led to a decrease in C storage (Sitch and others 2008). Some tropical regions became carbon sources under climate warming because simulated regional drought caused forest die-back and changed vegetation toward C_4-dominated grassland, which caused carbon loss (Cramer and others 2001). However, to the best of our knowledge, few DGVMs reported the C_3–C_4 shifts in grassland and the corresponding changes in carbon sequestration with climate change, which should be drawn attention to in future studies.

By taking advantages of two ongoing warming experiments, this study revealed the responses of C sequestration and the two major components, GPP and ER, to climate warming and clipping in the tallgrass prairie. Two experiments showed similar responses to clipping but different responses to warming, indicating the complexity of impacting factors and regulatory mechanisms in influencing the ecosystem's response to climate change. We suggest that changes in plant functional types may regulate the direct warming effects on ecosystem carbon fluxes. The findings highlight that the biotic link between warming and vegetation regulation of C fluxes could influence the response and feedback of grasslands to climate change. It is essential in the future to adequately quantify both the direct warming effects, which vary with species composition as shown in this study, and the indirect effects via species composition changes under climate warming. Currently, it is still difficult to evaluate complex interactions and feedbacks between warming-induced changes in species composition and species-regulated ecosystem responses to climate warming using either experimental or modeling approaches.

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