

Plant community structure regulates responses of prairie soil respiration to decadal experimental warming

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Abstract

Soil respiration is recognized to be influenced by temperature, moisture, and ecosystem production. However, little is known about how plant community structure regulates responses of soil respiration to climate change. Here, we used a 13-year field warming experiment to explore the mechanisms underlying plant community regulation on feedbacks of soil respiration to climate change in a tallgrass prairie in Oklahoma, USA. Infrared heaters were used to elevate temperature about 2 °C since November 1999. Annual clipping was used to mimic hay harvest. Our results showed that experimental warming significantly increased soil respiration approximately from 10% in the first 7 years (2000–2006) to 30% in the next 6 years (2007–2012). The two-stage warming stimulation of soil respiration was closely related to warming-induced increases in ecosystem production over the years. Moreover, we found that across the 13 years, warming-induced increases in soil respiration were positively affected by the proportion of aboveground net primary production (ANPP) contributed by C₃ forbs. Functional composition of the plant community regulated warming-induced increases in soil respiration through the quantity and quality of organic matter inputs to soil and the amount of photosynthetic carbon (C) allocated belowground. Clipping, the interaction of clipping with warming, and warming-induced changes in soil temperature and moisture all had little effect on soil respiration over the years (all $P > 0.05$). Our results suggest that climate warming may drive an increase in soil respiration through altering composition of plant communities in grassland ecosystems.

Keywords: ecosystem production, plant community composition, soil respiration, tallgrass prairie, warming

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Introduction

Global mean temperature is projected to increase 2–7 °C by the end of this century (Allison *et al.*, 2009). Despite much research, however, how terrestrial carbon (C) cycling responds to climate warming is still a major uncertainty because of gaps in basic understanding of terrestrial ecosystem processes (e.g., Melillo *et al.*, 2002; Heimann & Reichstein, 2008; Friedlingstein *et al.*, 2014). For example, most C-climate models predict a positive feedback between terrestrial C cycle and climate warming due to enhanced C release (Friedlingstein *et al.*, 2014). On the other hand, field studies show that warming has substantially altered ecosystem C processes, but that the sign and magnitude of C-climate feedbacks are highly uncertain (e.g., Day *et al.*, 2008; Schuur *et al.*, 2009). Such controversy is partially due to the lack of a mechanistic understanding of the long-term feedback

responses of soil CO₂ efflux (commonly referred to as soil respiration) to climate warming.

In the global C cycle, soil respiration is the second largest C flux between terrestrial ecosystems and atmosphere (Raich & Schlesinger, 1992; Raich & Tufekcioglu, 2000). Concerns about climate change and its subsequent long-term impact on the global C cycle have intensified research interest in soil respiration (e.g., Rustad *et al.*, 2001; Zhou *et al.*, 2007; Schuur *et al.*, 2009). Soil respiration is strongly regulated by temperature (e.g., Rustad *et al.*, 2001; Schuur *et al.*, 2009), as seen in the observations of soil respiration in manipulative warming experiments (Melillo *et al.*, 2002; Zhou *et al.*, 2007). Warming usually increases soil respiration rates in the short term due to warming-accelerated decay of soil organic matter (Rustad *et al.*, 2001; Melillo *et al.*, 2002). Long-term responses of soil respiration to warming, however, are less clear because most manipulative experiments are too short to establish a clear trajectory of change with time (Rastetter, 1996; Rustad *et al.*, 2001; Luo *et al.*, 2011). Several long-term studies

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in forest ecosystems show that soil respiration rates returned to prewarming levels within a few years mainly due to decreased substrate availability in soils (Rustad *et al.*, 2001; Melillo *et al.*, 2002). In grasslands, plant productivity usually increases under warming (Xu *et al.*, 2012a; Lu *et al.*, 2013), leading to increased litter input and partial counteraction of the substrate loss from organic C pools. This may create different temporal patterns in the response of soil respiration to warming with the possible scenario that respiration response to warming will continue to increase as the experiment continues.

Ecosystem C processes are mediated through the plant community present within the system (Rastetter, 1996; Luo *et al.*, 2011). Although impacts of plant community structure on a range of ecosystem processes have been studied over the last two decades (e.g., Hooper & Vitousek, 1998; Schulze, 2006; de Deyn *et al.*, 2008; Johnson *et al.*, 2008; Martin *et al.*, 2014), little is known about the plant community as a driver of soil respiration. Obviously, plant community influence on the quantity of organic matter input to soil is the principal mechanism (Raich & Schlesinger, 1992; Metcalfe *et al.*, 2011). Plant production regulates soil respiration through impacts on autotrophic respiration and through indirect impacts of litter production and root exudates on heterotrophic belowground respiration (Raich & Schlesinger, 1992). In addition, the plant community may influence soil respiration via altering the quality of detrital inputs to soil (Metcalfe *et al.*, 2011). Plant tissue of high nitrogen (N) concentration is always associated with high respiration rates and easily attacked by macrofauna and microorganisms in soil (González & Seastedt, 2001; de Deyn *et al.*, 2008). Furthermore, the plant community regulates soil respiration by controlling the amount of photosynthate channeled belowground (Metcalfe *et al.*, 2011). In grasslands, C₃ and C₄ species compete for soil resources and competition usually increases root:shoot ratio (Wilson & Tilman, 1995; Xu *et al.*, 2014). Warming-induced dry conditions, on the other hand, may indirectly stimulate C₃ species to invest more in roots due to the competition with C₄ grasses which are favored under high temperatures (Xu *et al.*, 2014). Plant community composition is likely to change in response to climate shifts (Neilson *et al.*, 2005). So, do changes in plant community composition confound the effect of climate warming on soil respiration?

Interactions between soil respiration and climate change are likely to be confounded by land practices. In the southern Great Plains of the US, mowing for hay is a widely practiced land use. Hay harvest has the potential to considerably alter soil respiration because it alters microclimate, lowers the amount of aboveground

litter, breaks down inherent allocation rules between aboveground and belowground organs, and stimulates root growth through the removal of aboveground plant biomass (Niu *et al.*, 2010; Xu *et al.*, 2012a). Previous studies have shown contradictory results, with a decrease (Craine & Wedin, 2002) or little change (Zhou *et al.*, 2007) in soil respiration under clipping to simulate mowing being reported. Thus, further studies are needed to investigate the effects of land practices on the terrestrial C cycle.

Grassland ecosystems, which account for approximately 25% of the global land cover (Scurlock *et al.*, 2002), play an essential role in the global C cycle. Grasslands are potentially sensitive to climate change and land use practices (Sherry *et al.*, 2008; Niu *et al.*, 2010). A projected increase in air temperature between 2 and 8 °C for the Great Plains could substantially accelerate or slow climate change over this century (Christensen *et al.*, 2007). Here, we used a 13-year field warming experiment to evaluate the impacts of warming and clipping on soil respiration in a tallgrass prairie in the North American Great Plains. Specifically, we addressed the following questions: (i) Does plant community composition influence responses of soil respiration to experimental warming and clipping over the 13 years? (ii) What are the key mechanisms underlying plant community regulation on soil respiration in response to warming and clipping?

Materials and methods

Experimental site and design

The experimental site is located on the Kessler Atmospheric and Ecological Field Station (KAEFS) in Oklahoma, USA (34°59'N, 97°31'W). The grassland is dominated by C₄ grasses (*Schizachyrium scoparium* and *Sorghastrum nutans*) and C₃ forbs (*Ambrosia psilostachya*, *Solidago rigida*, and *Solidago nemoralis*). C₄ and C₃ grasses accounted for 70% and <1% of the total aboveground biomass, respectively (Niu *et al.*, 2010). Mean annual temperature is 16.3 °C, with monthly air temperature ranging from 3.3 °C in January to 28.1 °C in July. The mean annual precipitation is 914 mm (Oklahoma climatological survey, Norman, OK, USA). The soil is part of the Nash–Lucien complex with neutral pH, high available water holding capacity (around 37%), and a moderately penetrable root zone (US Department of Agriculture, 1979). This experiment uses a split-plot design with warming as the main factor, within which is nested a clipping factor. We have six replicates (i.e., six pairs of plots), and each pair has two plots of 2 m × 2 m. One plot has been subjected to continuous warming since November 21, 1999 while the other serves as the control with ambient temperature. Infrared heaters (165 cm × 15 cm; Kalglo Electronics, Bethlehem, PA, USA) having a radiation output of 100 W m⁻² are suspended 1.5 m above the ground in each warmed plot. The control plot has a 'dummy' heater with

same dimensions as the infrared heater suspended at a similar height to mimic the shading effects of the heater. For each pair of plots, the distance between warmed and control plots is approximately 5 m from centers to avoid heating of the control plots. The distances between the paired plots vary from 20 to 60 m.

Each 2 m × 2 m plot is divided into four 1 m × 1 m subplots. Plants in two diagonal subplots are clipped at a height of 10 cm above the ground once a year to mimic hay harvest while the other two subplots are unclipped. Clipped materials are removed and not returned to the plots. Thus, the experiment has four treatments: unclipped and control (ambient) temperature (UC), unclipped and warming (UW), clipped and control temperature (CC), and clipped and warming (CW).

Microclimate and NPP measurements

Precipitation data were obtained from an Oklahoma Mesonet Station (Washington Station) located approximately 200 m away from our experimental site. Soil temperature was monitored by thermocouples at a depth of 2.5 cm in the centers of one clipped and one unclipped subplot in each plot. Volumetric soil water content in the top 15 cm was measured once or twice a month using portable Time Domain Reflectometry (TDR) equipment (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Aboveground NPP (ANPP, separated into C₃ forbs and C₄ grasses) was directly measured by clipping in clipped subplots and indirectly estimated by pin-contact counts in unclipped subplots at peak biomass (usually August, Frank & McNaughton, 1990; Sherry *et al.*, 2008). From 2005 to 2010, the root ingrowth-core (0–45 cm) method was applied to estimate belowground NPP (BNPP, Xu *et al.*, 2012a). In 2000–2004 and 2011–2012, BNPP was indirectly estimated based on the correlation between ANPP and BNPP from 2005 to 2010 ($BNPP = 1.01 * ANPP + 160.64$, $r^2 = 0.40$, $P = 0.001$, $n = 24$).

Soil respiration

To measure soil respiration, PVC collars (10.16 cm in diameter and 5 cm in height) were installed 2–3 cm into the ground at the centers of the two 1 m × 1 m subplots in each 2 m × 2 m plot at the beginning of the experiment. 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 manually carried out monthly between 10:00 and 15:00 (local time), using a LI-COR 6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE, USA) from 2000 to 2009 and a LI-COR 8100 soil CO₂ flux system (LI-COR Inc.) from 2010 to 2012. Measurements of the two LI-COR machines are comparable with each other because the two machines have the same size CO₂ flux chambers. Standard procedures recommended by LI-COR were applied to measure soil respiration. Annual soil respiration (g C m⁻² yr⁻¹) for each treatment was estimated by calculating average soil respiration per day and then multiplying by 365 days.

Statistical analysis

We performed repeated-measures split-plot analysis of variance (ANOVA) to examine the main and interactive effects of experimental warming, clipping, and year on soil temperature and moisture, aboveground and belowground productivity, and soil respiration. Linear regression analysis was conducted to evaluate the relationships of warming-induced changes in annual soil respiration with warming-induced changes in ecosystem production, plant community composition (expressed as the proportion of ANPP contributed by C₃ forbs), and soil temperature and moisture and the relationship between warming-induced changes in BNPP and warming-induced changes in plant species. All above-mentioned statistical analyses were conducted using SPSS 17.0 for windows (SPSS Inc., Chicago, IL, USA). Additionally, confirmatory analyses of structural equation modeling (SEM) were applied to quantify direct and indirect impacts of warming on soil respiration. We created a conceptual model of hypothetical relationships based on a prior and theoretical knowledge. Five major pathways were constructed to explore the effect of warming on soil respiration. Among them were warming-induced changes in environmental variables (soil temperature and moisture), plant community composition (C_{3%}, the proportion of ANPP contributed by C₃ forbs), and plant production (ANPP and BNPP). Data were fitted to the model using the maximum likelihood estimation method. Adequate model fit was indicated by a nonsignificant chi-squared test ($P > 0.05$). SEM analysis was performed using AMOS 21.0 software (IBM, SPSS, Armonk, NY, USA).

Results

Microclimate and NPP

Annual precipitation (AP) varied from 515 mm in 2005 to 1307 mm in 2007 with a mean of 882 mm across the 13 years (Table S1). Warming increased soil temperature and decreased soil moisture by an average of 1.4 °C and 1.50% in the unclipped subplots and 2.3 °C and 1.7% in the clipped subplots, respectively (Tables 1 and S1). Warming also significantly stimulated ecosystem production (both ANPP and BNPP, all $P < 0.01$, Table 1) and the increases in ANPP and BNPP under warming varied greatly across the years (all $P < 0.01$, Table 1, Figs S1–S3). For example, experimental warming on average stimulated ANPP by 18 g m⁻² yr⁻¹ from 2000 to 2006 and 83 g m⁻² yr⁻¹ from 2007 to 2012 (Fig. S1c,d). In addition, clipping elevated soil temperature and lowered moisture by an average of 0.3 °C and 0.5% in the un-warmed subplots and 1.3 °C and 0.7% in the warmed subplots, respectively (Tables 1 and S1). Clipping decreased ANPP ($P < 0.05$) but increased BNPP ($P < 0.01$), leading to smaller changes in ecosystem production in comparison with the changes under warming alone. For instance, clipping on average

Table 1 Results of split-plot repeated-measures ANOVA (*P* values) for responses of soil temperature and moisture (T_{soil} , W_{soil}), ANPP, BNPP, and soil respiration (R_s) to warming (W), clipping (CL), year (Y), and their interactions from 2000 to 2010 (Table S1, Figs S1–S3)

	Warming	Clipping	Year	W×CL	W×Y	CL×Y	W×CL×Y
T_{soil}	<0.001	<0.001	<0.001	0.032	<i>0.062</i>	<0.001	0.001
W_{soil}	<0.001	<0.001	<0.001	0.445	<0.001	0.356	0.873
ANPP	<0.001	0.010	0.232	0.574	<0.001	<0.001	0.852
BNPP	<0.001	<0.001	<0.001	0.001	0.002	0.339	0.645
R_s	0.004	0.451	<0.001	0.616	<0.001	0.154	0.976

P values smaller than 0.05 and 0.10 are in bold and italic, respectively. ANPP, aboveground net primary production; BNPP, belowground net primary production. Statistical results of BNPP were based on data from 2005 to 2010.

decreased ecosystem production by $3 \text{ g m}^{-2} \text{ yr}^{-1}$ from 2005 to 2010 without warming.

Soil respiration

The temporal dynamics of soil respiration under the four treatments and the warming-induced increases in soil respiration followed a distinct seasonal pattern, which were high in summer and low in winter across the years (Fig. S4). The long-term warming induced two-stage stimulations of annual soil respiration (Fig. 1). Experimental warming on average stimulated annual soil respiration by $90 \text{ g C m}^{-2} \text{ yr}^{-1}$ from 2000 to 2006 and $206 \text{ g C m}^{-2} \text{ yr}^{-1}$ from 2007 to 2012. The relative effect of warming on soil respiration indicated, from 2000 to 2012, approximately a 22% increase in soil respiration in the warmed vs. un-warmed plots. Multiple regression analysis excluded the changes in soil temperature and moisture under warming as the dominant factors that regulated the variation in annual soil respiration (Fig. S5).

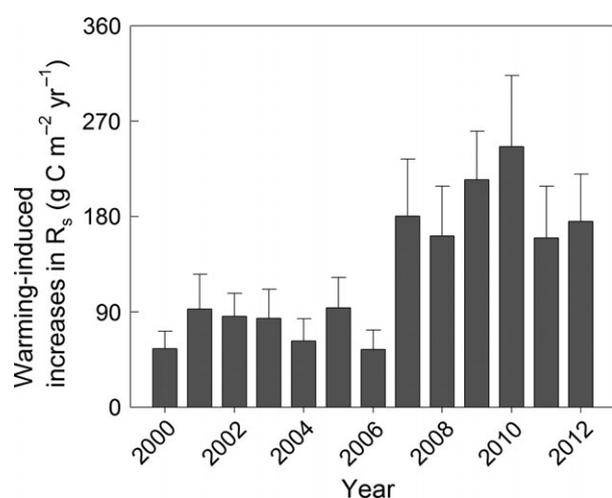


Fig. 1 Warming-induced increases (warmed minus unwarmed) in soil respiration per year across the 13 years. Values are mean \pm SE with 12 replicates.

SEM models adequately fitted the data, with interactive networks of environmental factors, plant community composition, and production regulating soil respiration ($\chi^2 = 5.75$, $df = 7$, $P = 0.57$, Fig. 2). Results of SEM showed that functional changes in the composition of plant communities (i.e., C_3 forbs vs. C_4 grasses) regulated warming-induced changes on soil respiration through plant production across the years (Figs 2–3 and S6). Responses of soil respiration were strongly coupled with ecosystem production in response to experimental warming across the 13 years (all $P < 0.01$, Figs 4 and S1–S3). Both C_3 forbs and C_4 grasses positively contributed to the increases in soil respiration (Fig. 4a,b). Moreover, we found changes in ANPP and BNPP under warming increased with the increasing proportional contribution of C_3 forbs to ANPP ($C_{3\%}$, Fig. 5, $P = 0.023$, $P < 0.05$, and $P = 0.057$, respectively) (and thus decreased with increasing proportion of C_4 to ANPP, $C_{4\%}$, Fig. S7). We did not observe statistically significant effects of clipping nor interactions with clipping and warming on soil respiration across years (all $P > 0.05$, Table 1). Clipping stimulated C allocation to roots (Xu *et al.*, 2012a), which may increase root respiration and thus balance the effect of aboveground biomass removal in the clipped subplots, leading to little change in soil respiration.

Discussion

Two-stage responses of soil respiration to warming

We found that stimulation of soil respiration under experimental warming was long lived and even enhanced across the 13 years (Fig. 1). Proportionally, increases in soil respiration averaged about 10% over the first 7 years of the study. Over the next 6 years of the study, the ‘stimulatory’ effect of experimental warming on soil respiration substantially increased (Fig. 1). Abrupt nonlinear changes in ecosystem structure and function are expected under chronic alterations of environment (Smith *et al.*, 2009). The two-stage

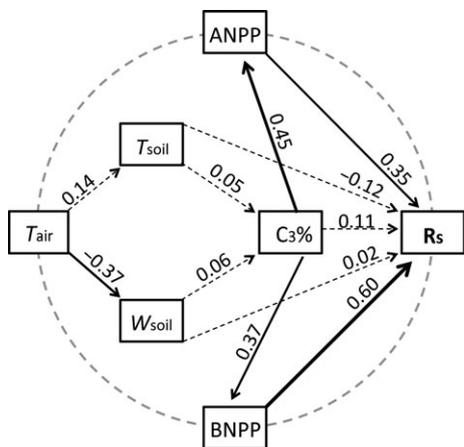


Fig. 2 Path analysis of the effects of warming-induced changes in abiotic and biotic factors on warming-induced changes in soil respiration. Solid and dashed arrows represent significant ($P < 0.05$) and nonsignificant ($P > 0.05$) paths in a fitted structural equation model depicting impact of variables on soil respiration. T_{air} : air temperature; T_{soil} : soil temperature; W_{soil} : soil moisture; ANPP & BNPP: aboveground and belowground net primary production; $C_3\%$: the proportion of ANPP contributed by C_3 forbs; R_s : soil respiration. Yearly data are used to perform the path analysis.

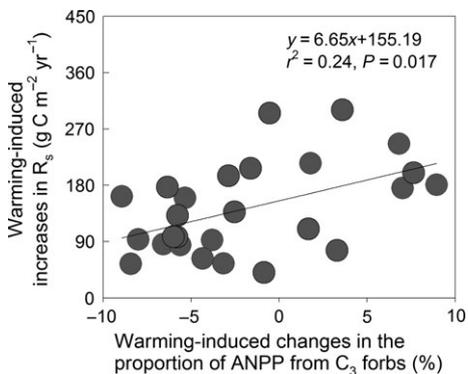


Fig. 3 Changes in soil respiration positively affected by the proportion of ANPP contributed by C_3 forbs under warming across the 13 years. ANPP: aboveground net primary production. Yearly data are used in this figure.

soil respiration stimulations were accompanied with changes in plant community composition but not related to changes in physical environment (Figs 3, S5, and S8) or unchanged soil C content (Xu *et al.*, 2012b). Chronic temperature increases in the warmed plots triggered a hierarchy of mechanisms with a temporal pattern of responses beginning with small physiological changes followed by large changes due to plant species reorganization (Smith *et al.*, 2009). Extreme precipitation in 2005–2007 facilitated the nature and pace of ecological changes under chronic warming through its

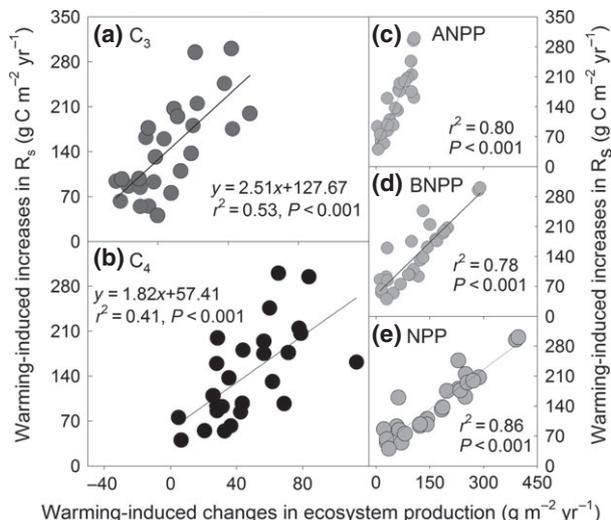


Fig. 4 Positive relationships of warming-induced changes in soil respiration with changes in the biomass of C_3 forbs (a), C_4 grasses (b), aboveground NPP (ANPP, c), belowground NPP (BNPP, d), and NPP (e). NPP: net primary production. Yearly data are used in this figure.

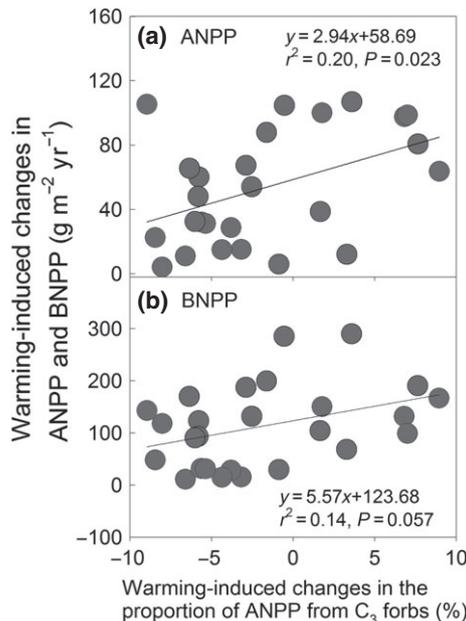


Fig. 5 Positive impact of the proportion of ANPP contributed by C_3 forbs on aboveground net primary production (ANPP, a) and belowground net primary production (BNPP, b) under warming. Yearly data are used in this figure.

interaction with increased temperatures. Responses of C_3 forbs to warming might have been accelerated by the extreme wet year as natural disturbances often interact with climate change to affect ecosystem structure and function (Jentsch & Beierkuhnlein, 2003; Smith

et al., 2009), leading to higher soil respiration. Chronic changes in temperature in global change experiments could lead to amplifying responses in ecosystems over time.

In contrast to our results, however, a previous field experiment showed that increases in soil respiration under soil warming (by the use of buried heating cables) diminished within a few years in a temperate forest (Melillo *et al.*, 2002). A possible reason for the discrepancy may be the availability of substrate to microbes under warming is very different in these two ecosystems. A study by Bradford *et al.* (2008) in the same forest demonstrated that the ephemeral response of soil respiration to warming could be attributed to substrate depletion and reductions in microbial biomass. However, enhanced responses of soil respiration to warming in our study were due to increased ecosystem production, litter input, and microbial biomass (Figs S1–S3, Zhou *et al.*, 2012). This controversy suggests the importance of plant controls on the quantity of C inputs on microbial mediation of C-cycle feedbacks to warming, which may overshadow the effects of microbial thermal adaptation to elevated temperature on respiration (Janssens *et al.*, 2001; Bradford *et al.*, 2008; Zhou *et al.*, 2012). However, further studies are needed to resolve the mechanistic linkages among plant C input, microbial community composition, and acclimation of soil respiration in different ecosystems.

Plant community regulation of soil respiration

Warming may alter ecosystem C cycling, such as soil respiration, by changing plant community structure and species composition because plants are the primary pathways through which C enters soil (Chapin *et al.*, 1995; Metcalfe *et al.*, 2011; Xu *et al.*, 2012b). Our analyses revealed that warming-induced increases in soil respiration were positively and negatively regulated by warming-induced changes in the proportion of C₃ forbs and C₄ grasses contributing to ANPP, respectively, over the years (all $P = 0.017$, Figs 2–3, S6), indicating the importance of functional composition of plant communities in determining soil respiration (Johnson *et al.*, 2008; Ward *et al.*, 2009). This is in line with a previous grassland mesocosm study that found consistent differences in soil respiration driven by plant functional types (Johnson *et al.*, 2008). As such, the C₃ forb communities were associated with the highest soil respiration rates while the lowest soil respiration rates were observed in the C₄ sedge communities (*Carex* species, Cyperaceae). We demonstrated here that responses of soil respiration to warming were

driven by changes in the functional composition of plant communities' control on the quantity and quality of organic matter (litter) input to soil and the amount of photosynthate allocated belowground as BNPP (Figs 2–4). Here, we define litter quality using C:N ratio, which was much higher in C₄ grasses (Niu *et al.*, 2010; Zhou *et al.*, 2012).

Plant control on the amount of C inputs. The two-stage responses of soil respiration to warming were positively coupled with the increases in ecosystem production (including biomass of C₃ forbs and C₄ grasses, ANPP, and BNPP) under warming over the years (all $P < 0.01$, Figs 4, S1–S3). It has long been recognized that on annual time scale, soil respiration positively correlates with ecosystem production (Raich & Schlesinger, 1992). Our results suggest that this mechanism holds true under long-term experimental warming since the close 'coupling' between soil respiration and ecosystem production persisted over the years (Fig. 4). Importantly, changes in the amount of photosynthetic C channeled belowground could substantially alter soil respiration because root respiration is a primary contributor to soil respiration, and hence, the amount of BNPP is a major factor influencing *in situ* soil respiration (Zhou *et al.*, 2007; Metcalfe *et al.*, 2011). Warming greatly stimulated belowground production ($P < 0.01$, Table 1, Fig. S3), leading to increases in soil respiration. Undoubtedly, the rise in grassland production under warming could drive a greater increase in soil respiration.

Plant control on the chemical composition of aboveground C inputs. Chemical properties of plant litter of different functional types vary greatly within plant communities. Changes in functional composition of plant communities under warming could thus serve as powerful drivers of soil respiration by controlling litter decomposition rates (Fig. S8, Metcalfe *et al.*, 2011). In comparison with C₄ grasses, C₃ forbs generally produce easily decomposable litter that is richer in N but poorer in C due to different photosynthetic pathways (Edwards & Still, 2008; Niu *et al.*, 2010; Martin *et al.*, 2014). Decomposition of herbaceous forb litter is faster than that from graminoids (Cornwell *et al.*, 2008), leading to enhanced soil respiration with increasing contribution of C₃ forbs to the community (Fig. 5). In contrast, recalcitrant litter of C₄ grasses is more beneficial for soil C sequestration (de Deyn *et al.*, 2008). At our study site, the C:N ratio of C₄ grasses was significantly higher than that of C₃ forbs (63 vs. 35, Zhou *et al.*, 2012). C₃ forbs' high litter quality is preferentially targeted by decomposers, which further promote soil respiration through mechanisms that decomposers'

excretion of plant materials in labile C and N forms and their physically mixing and breaking apart litter that facilitates microbial respiration (González & Seastedt, 2001; Bardgett & Wardle, 2003).

Plant control on the belowground C allocation. Allocation of biomass to BNPP relative to ANPP is a specialized survival strategy of plants, through which plants respond to environmental changes to maximize their growth (Bloom *et al.*, 1985; Chapin *et al.*, 1987). Our results showed that at the community level, warming enhanced the amount of biomass allocated to roots (Xu *et al.*, 2012a) and warming-induced increases in BNPP were positively regulated by the proportional contribution of C₃ forbs to ANPP (and thus negatively regulated by the proportional contribution of C₄ grasses) over the years. These results indicate that the mechanism is plant community control on soil respiration through belowground C allocation and different biomass allocation strategies for C₃ forbs and C₄ grasses under warming. In comparison with C₄ grasses, C₃ forbs may allocate proportionally more biomass to roots in response to the dryer conditions under warming. Warming favors the growth of C₄ grasses because the C₄ photosynthetic pathway confers a strong competitive advantage to plants in drought-prone environment (Edwards & Still, 2008). To compete with C₄ grasses for resources and root territories, C₃ forbs may inevitably invest more belowground (Bloom *et al.*, 1985; Chapin *et al.*, 1987). Moreover, C₃ forbs of high N concentration stimulate soil respiration because root respiration rates positively relate to N concentration of plant tissues (de Deyn *et al.*, 2008). On the other hand, activities of root herbivores (e.g., excretion) enhance the accessibility of organic matter for microorganisms and thus higher microbial respiration as discussed above (González & Seastedt, 2001; Bardgett & Wardle, 2003).

In summary, results from our long-term warming experiment in a tallgrass prairie suggest that warming-induced increases in soil respiration are positively coupled with changes in ecosystem production through the control of the plant community on (i) the quantity and quality of organic matter inputs to soil and (ii) the amount of photosynthetic C allocated belowground. Annual clipping as a land use may have little impact on soil respiration because the removal of aboveground biomass is counteracted by increased C allocation belowground. Changes in plant species composition are just as important as temperature in determining soil respiration. A comprehensive understanding for linking climate changes with variation in soil respiration via plant community characteristics is urgently

required to inform model simulations of climate–vegetation interactions.

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Authorship

XX analyzed the data and wrote the article. XX, ZS, and YL conceived the idea. YL designed the experiment. XX, DL, and XZ conducted the measurements. RAS performed canonical correspondence analysis.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Annual precipitation (AP), soil temperature and moisture (T_{soil} , W_{soil}) under different treatments at the experimental site

Figure S1. Variation in ANPP under the four treatments (a–b) and warming-induced changes in ANPP (c–d) and C₄ grasses (e–f) from 2000 to 2012.

Figure S2. Variation in ANPP contributed by C3 forbs under the four treatments (a–b) and warming-induced changes in C₃ forbs (c–d) from 2000 to 2012.

Figure S3. Variation in BNPP under the four treatments (a–b), the absolute (c–d) and the relative (e–f) warming-induced changes in BNPP from 2000 to 2012.

Figure S4. Seasonal variation in soil respiration under the four treatments (a–b) and warming-induced changes in soil respiration (c) from 2000 to 2012.

Figure S5. Relationships of warming-induced changes in annual soil respiration with warming-induced changes in soil temperature (a) and soil moisture (b) from 2000 to 2012.

Figure S6. Warming-induced changes in soil respiration negatively affected by the proportion of ANPP contributed by C₄ grasses across the 13 years. Yearly data are used in this figure.

Figure S7. Negative impact of the proportion of ANPP contributed by C₄ grasses on aboveground net primary production (ANPP, a) and belowground net primary production (BNPP, b) under warming. Yearly data are used in this figure.

Figure S8. Effects of warming and clipping on plant community structure.