Response of soil CO_2 efflux to precipitation manipulation in a semiarid grassland

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ABSTRACT

Soil CO_2 efflux (SCE) is an important component of ecosystem CO_2 exchange and is largely temperature and moisture dependent, providing feedback between C cycling and the climate system. We used a precipitation manipulation experiment to examine the effects of precipitation treatment on SCE and its dependences on soil temperature and moisture in a semiarid grassland. Precipitation manipulation included ambient precipitation, decreased precipitation (−43%), or increased precipitation (+17%). The SCE was measured from July 2013 to December 2014, and CO_2 emission during the experimental period was assessed. The response curves of SCE to soil temperature and moisture were analyzed to determine whether the dependence of SCE on soil temperature or moisture varied with precipitation manipulation. The SCE significantly varied seasonally but was not affected by precipitation treatments regardless of season. Increasing precipitation resulted in an upward shift of SCE–temperature response curves and rightward shift of SCE–moisture response curves, while decreasing precipitation resulted in opposite shifts of such response curves. These shifts in the SCE response curves suggested that increasing precipitation strengthened the dependence of SCE on temperature or moisture, and decreasing precipitation weakened such dependences. Such shifts affected the predictions in soil CO_2 emissions for different precipitation treatments. When considering such shifts, decreasing or increasing precipitation resulted in 43 or 75% less change, respectively, in CO_2 emission compared with changes in emissions predicted without considering such shifts. Furthermore, the effects of shifts in SCE response curves on CO_2 emission prediction were greater during the growing than the non-growing season.

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Introduction

Semiarid grassland ecosystems are among the most vulnerable, and are highly susceptible to global climate change (Carbone et al., 2011; Morgan et al., 2011). They are also increasingly important drivers of the inter-annual variability of the global carbon (C) cycle (Poulter et al., 2014). Precipitation and the availability of soil water are the major limiting factors in

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semiarid ecosystems (Austin et al., 2004). Precipitation most directly affects soil moisture, which is a key driver of biological processes and plays a prominent role in terrestrial ecosystems by affecting plant productivity and soil processes (Ehrenfeld et al., 2005; Rodríguez-Iturbe and Porporato, 2005; Cruz-Martínez et al., 2012), which in turn modulate the impacts of other drivers of global change such as elevated atmospheric CO_2 levels, temperature, and nitrogen deposition (Wan et al., 2007; Jia et al., 2012). The responses of ecosystem processes to variations in soil moisture due to changes in precipitation have thus become the focus of current ecological and environmental research.

Responses of ecosystem processes to precipitation changes (both increasing and decreasing precipitation) have been studied in various ecosystems (Reichstein et al., 2002; Huxman et al., 2004; Lee et al., 2004; Xu and Baldocchi, 2004; Pereira et al., 2007; Chen et al., 2009), but considerable uncertainty remains about the directions and magnitude of the responses (Knapp et al., 2002; Hellmann, 2014), especially for arid or semiarid regions. This uncertainty complicates the accurate prediction of responses to future scenarios of precipitation change, which can impact C dynamics and fluxes in ecosystems (Doughty et al., 2015).

Soil CO_2 efflux (SCE) is the release rate of CO_2 from soil produced by autotrophs (roots) and heterotrophs (microbes and fauna), and is an important component of ecosystem CO_2 exchange (Monson et al., 2006; Carbone et al., 2011; Karhu et al., 2014). Soil CO_2 efflux thus provides feedbacks between C cycling and the climate system (Luo et al., 2001; Davidson and Janssens, 2006; Heimann and Reichstein, 2008). Soil CO_2 efflux increases with soil temperature, but has a quadratic relationship with soil moisture, i.e., is limited by extremely dry and wet conditions (Harper et al., 2005; Wan et al., 2007). Such dependences provide the scientific basis for accurately predicting CO_2 emission and have been incorporated into models of C cycling (Kim et al., 2014). Changes in precipitation will undoubtedly alter soil temperature and moisture and thus the dependence of CO_2 release on these variables (Luo et al., 2001; Harper et al., 2005). The effect of precipitation manipulation on the dependence of SCE on temperature or moisture, however, has received little attention, but this knowledge is essential for understanding the adaption of SCE to changes in precipitation and thus for predicting CO_2 emission in future scenarios of climate change, because changes in precipitation regimes in dry ecosystems are expected to have significant feedback effects on CO_2 flux and the terrestrial C cycle (Shen et al., 2009).

In this study, we investigated the SCE in plots with manipulated levels of precipitation in a semiarid grassland in northwestern China. The response curves of SCE to soil temperature and moisture were analyzed. The objectives were to examine the effects of precipitation manipulation on SCE and its dependence on soil temperature and moisture in semiarid grassland.

1. Materials and methods

1.1. Study site and experimental design

This study was performed in the Yunwushan natural grassland protection zone (36°13′–36°19′N, 106°24′–106°28′E) near Guyuan City, Ningxia Hui Autonomous Region, China, in the center of the Loess Plateau. The grassland protection zone was established in 1984, with an area of 4000 km^2 and elevations of 1800–2148 m a.s.l. The study area has a continental monsoon climate. The mean annual temperature is 6.9°C, and the annual maximum and minimum temperatures occur in July (24°C) and January (–14°C), respectively. The mean annual precipitation is 425 mm. The soil in the study area is a mountain grey-cinnamon soil classified as a Calci-Orthic Aridisol according to the Chinese taxonomic system, equivalent to a Haplic Calcisol in the FAO/UNESCO system. The growing season at the study site is from May to October.

This experiment was established in a *Stipa capillata* L. grassland succeeded from farmland abandoned 30 years ago. The grassland has been protected from clipping and grazing by the Yunwushan Natural Grassland Management Bureau since the abandonment of the farmland. The experiment used a random block design with four replicates and 1.0–2.0 m between blocks. Each block contained three 4.0 × 5.0 m plots randomly arranged, with 1.0 m between plots. The three plots in each block received one of three precipitation treatments: ambient precipitation (AP), decreased precipitation (DP), or increased precipitation (IP). A movable rainout shelter (6.0 m long × 5.0 m wide × 2.1 m high) consisting of a steel frame supporting a clear plastic roof was installed in each block to intercept precipitation in the plots with decreased precipitation. The rainout shelters were manually moved to cover the DP plots before a rain and removed after ca. 1/3 of the duration of the rain. The amount of precipitation excluded was calculated from the measurement of the rainfall over time, recorded with an automatic rain gauge at the site every 10 min. Water equivalent to ca. 15% of the precipitation was added manually and evenly to the IP plots immediately after the end of the rain over both plants and soil so that the rate of application was similar to the rate of infiltration into the soil. Snowfall was not manipulated in this experiment. The precipitation was manipulated starting in July 2013.

To assess the influence of variations in major soil properties on the response of SCE, we measured soil bulk density (BD) and the concentrations of organic carbon (OC) and nitrogen (N) in the top 20-cm depth for each plot before the start of the experiment. Soil bulk density was measured in each plot at 0–20 cm depth using a stainless steel cutting ring 5.0-cm high by 5.0-cm in diameter. The soil cores were dried at 105°C for 24 hr. Three representative soil samples were randomly collected from 0 to 20 cm depth in each plot for measuring soil OC and N concentrations. Visible pieces of organic material were removed, and the moist field soil samples were brought to the laboratory and air-dried for chemical analysis. Soil OC and N concentrations were measured by the Walkley–Black method and Kjeldahl method, respectively. The results showed that these soil properties did not vary among plots, with a range of 0.98–1.03 g/cm^3 for BD, 34.2–36.4 g/kg and 3.53–3.69 g/kg for OC and N concentrations, respectively. We therefore assume that soil properties did not influence the response of SCE to precipitation treatments.

To evaluate the effects of plant biomass on SCE, aboveground biomass was measured by sampling three 1 × 1 m^2 subplots in each plot at the end of each growing season. Five

soil cores with 9-cm diameter were also collected in each plot. Roots in soil cores were carefully separated and washed to measure belowground biomass. The plant and root samples were oven-dried at 65°C for 72 hr to calculate above- and belowground biomass.

1.2. Measurement of SCE and soil temperature and moisture

Soil CO_2 efflux was measured 2–8 times per month depending on the season from July 2013 to December 2014 using a modified chamber system described by Chen et al. (2009). Briefly, a PVC base 20 cm in diameter and 10 cm in height was inserted 7 cm into bare soil in each plot. Soil CO_2 efflux was measured between 9:00 and 11:00 with a cylindrical chamber (20 cm in diameter and 20 cm in length) placed over the base and attached to an infrared gas analyzer (LI-840, LI-COR Inc., Lincoln, USA). A small fan in the top of the chamber mixed the air during measurement, and a temperature probe was inserted inside the chamber to determine the air temperature. An air pump (6262-04, LI-COR Inc.) pumped air from the chamber to the LI-840 for measurement of CO_2 concentrations. The LI-840, air pump, and fan were battery (12 V, 20 Ah) operated. The data were logged to a computer using the LI-840 data-acquisition software. The CO_2 concentrations inside the chamber were recorded every second for 2.5 min after the chamber was placed on the base. Only the data for the last 120 sec were used to calculate SCE as Eq. (1) (Jasoni et al., 2005; Chen et al., 2009):

$$SCE = \frac{V \times P_{av} \times (1000 - W_{av})}{R \times S \times (T_{av} + 273)} \times \frac{dc}{dt} \tag{1}$$

where, SCE is soil CO_2 efflux ($\mu mol/(m^2 \cdot sec)$), V (m^3) is the volume of the chamber, P_{av} (kPa) is the average pressure during measurement, W_{av} (mmol/mol) is the average water mole fraction during measurement, R (8.314 J/(mol·K)) is the ideal gas constant, S (m^2) is the surface area covered by the chamber, T_{av} (°C) is the average temperature during measurement, and dc/dt is the slope of the fitted equation between CO_2 and time.

Soil temperature and volumetric moisture content at a depth of 0–10 cm were measured with time-domain transmission sensors (Acclima Inc., Meridian, USA) in each plot

Fig. 1 – Monthly precipitation (columns) and mean air temperature (line) during the experimental period (July 2013 to December 2014).

every 10 min with a Campbell Scientific CR1000 data logger (Campbell Scientific Inc., Logan, USA) during the experimental period. The climatic data were recorded by a weather station at the study site. Rainfall and air temperature at a height of 1.5 m were measured automatically at the weather station with an interval of 10 min. The monthly mean precipitation in each treatment and the air temperature during the experimental period are presented in Fig. 1.

1.3. Data analysis

Response curves of SCE to temperature or moisture were fitted by equations commonly used to examine the effects of the treatments on the dependence of SCE on soil temperature or moisture:

$$SCE = a \times e^{b \times T} \tag{2}$$

$$SCE = a \times M^2 + b \times M + c \tag{3}$$

where T (°C) and M (%) are the soil temperature and moisture at a depth of 0–10 cm, respectively, and a, b, and c are parameters for each equation.

The apparent temperature sensitivity (Q_{10}), a metric that describes the proportional increase of SCE with a 10°C increase in temperature, was calculated from the slope (b) of the temperature-response curve (Eq. (2)) as:

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

The optimal moisture (M_o) at which SCE is greatest was calculated from the parameters of the moisture-response curve (Eq. (3)) as:

$$M_o = -\frac{b}{2a}. \tag{5}$$

The response of SCE to both temperature and moisture was also fitted using the model:

$$SCE = a \times e^{b \times T} \times M^c \tag{6}$$

where a, b, and c are parameters of the equation.

These response functions were fitted using measured SCE, soil temperature and moisture for each treatment during the experimental period. Our fitting results showed that parameters of these functions were affected by precipitation manipulation (Table 1), indicating that SCE–temperature or –moisture response curves may shift with decreasing or increasing precipitation. We therefore used these parameters to generate the response curves of SCE and to illustrate how these curves shift with precipitation treatment.

A comparison of the fitted results from the three models indicated that Eq. 6 performed better than the others in predicting SCE (Table 1). We therefore used Eq. (6) to predict CO_2 emission and to assess the influence of shifts in the SCE response curve on CO_2 emission prediction. The CO_2 emissions in ambient treatment and in decreased or increased precipitation treatments with shifts in response curves were predicted, with parameters in each treatment and soil temperature and moisture measured in each
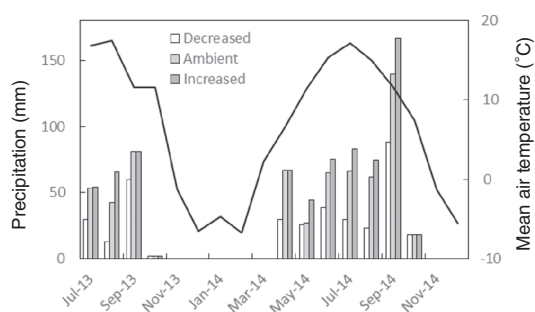
Table 1 – Parameters for the relationships between soil CO$_2$ efflux (SCE) and soil temperature (T) and/or moisture (M).

$SCE = a \times e^{b \times T}$

	a	SE (a)	b	SE (b)	Q$_{10}$	SE (Q$_{10}$)	RMSE	R^2	p
Across treatments	0.946	0.038	0.066	0.002	1.928	0.040	0.898	0.611	<0.01
Ambient precipitation	0.969a	0.071	0.065ab	0.004	1.919b	0.073	0.959	0.586	<0.01
Decreased precipitation	0.932a	0.053	0.062b	0.003	1.867b	0.054	0.722	0.697	<0.01
Increased precipitation	0.831a	0.065	0.077a	0.004	2.154a	0.091	0.938	0.616	<0.01

$SCE = a \times M^2 + b \times M + c$

	a	SE (a)	b	SE (b)	c	SE (c)	M$_o$	RMSE	R^2	p
Across treatments	−0.013	0.001	0.439	0.037	−0.727	0.289	16.88	1.351	0.126	<0.01
Ambient precipitation	−0.015ab	0.002	0.516ab	0.081	−1.347ab	0.671	17.20	1.407	0.110	<0.01
Decreased precipitation	−0.011b	0.002	0.330b	0.060	0.227b	0.401	15.00	1.219	0.091	<0.01
Increased precipitation	−0.019a	0.002	0.687a	0.074	−3.064a	0.667	18.08	1.354	0.211	<0.01

$SCE = a \times e^{b \times T} \times M^c$

	a	SE (a)	b	SE (b)	c	SE (c)	RMSE	R^2	p
Across treatments	1.046	0.087	0.066	0.002	−0.039	0.034	0.895	0.615	<0.01
Ambient precipitation	2.152a	0.312	0.067b	0.003	−0.293a	0.058	0.924	0.613	<0.01
Decreased precipitation	0.949b	0.095	0.062b	0.003	−0.013b	0.051	0.669	0.724	<0.01
Increased precipitation	3.529a	0.848	0.082a	0.003	−0.517a	0.08	0.872	0.670	<0.01

SE is the standard error for each parameter. RMSE is the root mean square error of the equation. T and M are the soil temperature and moisture at 0–10 cm depth, respectively, a, b and c are parameters for each equation, respectively. Temperature sensitivity (Q$_{10}$) is calculated as exp(10 × b). Standard error for Q$_{10}$ is calculated as Q$_{10}$ × 10 × SE(b). M$_o$ is the optimal moisture at which SCE is greatest. 95% confidence interval (95% CI) was used to assess the statistical differences in each parameter among treatments. 95% CI was calculated as 1.96 × SE. The difference between two treatments was identified as significant when the 95% CIs did not overlap. Parameters followed by different lower-case letters among different precipitation treatment are significantly different at $p < 0.05$.

treatment. The CO$_2$ emissions without shifts in response curves were predicted with parameters from the ambient treatment but soil temperature and moisture measured in the decreased or increased precipitation treatments. The measurements of soil temperature and moisture every 10 min from July 2013 to December 2014 were used for CO$_2$ emission prediction.

A mixed-effect analysis of variance was conducted to compare SCE, temperature, and moisture. The independent variables in the model were precipitation treatment, season (growing season vs. non-growing season), and their interaction. Nonlinear regression analysis was conducted to fit Eqs. (2), (3), and (6). All data were analyzed with JMP 10.0 (SAS Institute, Cary, USA).

2. Results

2.1. Changes in microclimate

The total rainfall for the AP, DP, and IP treatments during the experimental period were 625, 358, and 732 mm, respectively, 89%–91% of which fell during the growing season (Fig. 1). The rainfall for AP, DP, and IP corresponded to the 77.5th, 7.5th, and 92.5th percentiles of growing season precipitation during 1957–2011, presenting normal, drier, and wetter years, respectively. Soil temperature was not significantly affected by precipitation treatments across either season ($p > 0.05$), but was significantly changed during the growing season ($p = 0.0091$), with a 0.42°C increase in DP and a 0.61°C decrease in IP (Fig. 2a). Soil moisture

was significantly higher during the growing than during the non-growing season ($p < 0.0001$) and was significantly higher in IP but lower in DP ($p < 0.0001$) relative to AP regardless of season, indicated by the lack of an interaction between season and treatment ($p = 0.0866$) (Fig. 2b). Similarly, the effect of precipitation treatment on soil moisture was greater in the growing than the non-growing season.

2.2. Changes in soil CO$_2$ efflux

The SCE showed a significant seasonal pattern across the treatments, with higher SCE during the growing season (Fig. 2c). The mean SCE was 6-fold higher during the growing than during the non-growing season. Furthermore, SCE varied significantly with the stage of the growing season, with the SCE higher in middle season (July and August) than in the early (May and June) or late (September and October) stages (Fig. 3, $p < 0.0001$).

Precipitation treatments did not affect SCE either within or across seasons (Fig. 2c). The SCE were 2.6, 2.5, and 2.6 μmol/(m^2·sec) in AP, DP, and IP, respectively ($p = 0.51$), averaged across years and seasons. The mean SCE from 2013 to 2014 in AP, DP, and IP were 0.55, 0.49, and 0.53 μmol/(m^2·sec) ($p = 0.48$) during the non-growing season and 3.1, 2.9, and 3.1 μmol/(m^2·sec) ($p = 0.18$) during the growing season, respectively. Moreover, the effects of precipitation treatment were not significant during the early ($p = 0.06$), middle ($p = 0.06$), and late ($p = 0.68$) stages of the growing season. These results indicated that SCE in this semiarid grassland was not affected by precipitation manipulation (Fig. 3).
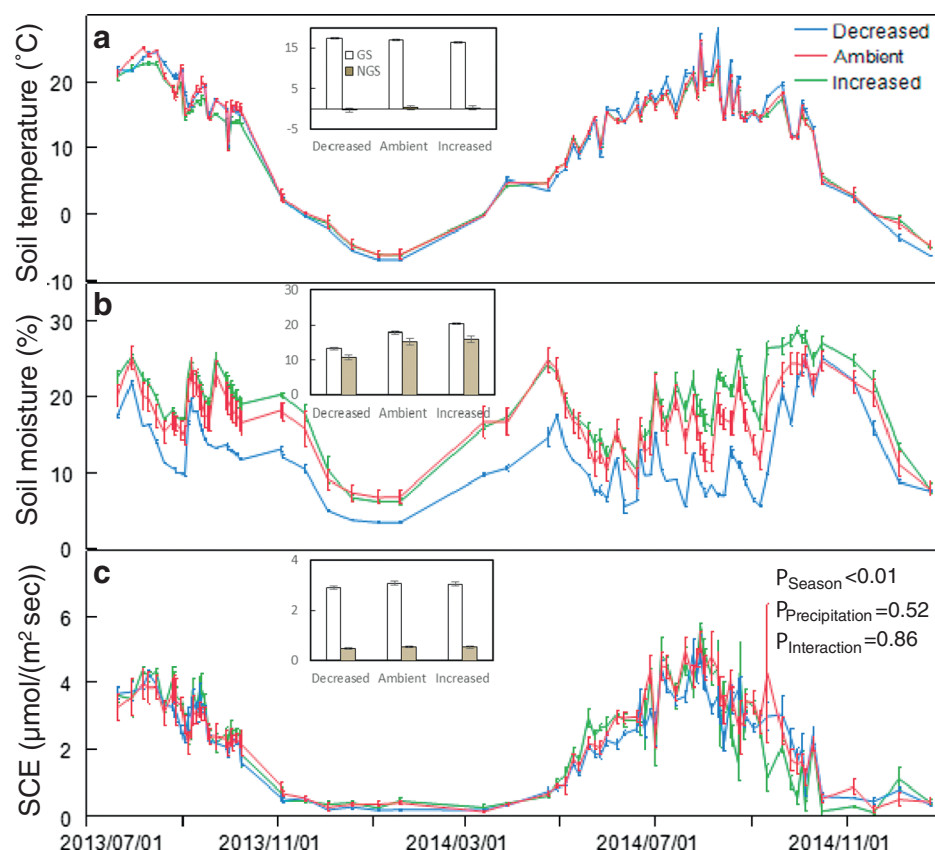
Fig. 2 – Soil temperature (a), moisture (b) and soil CO_2 efflux (SCE) (c) of each precipitation treatment in a semiarid grassland of northwest China. Measurement were made between July 2013 and December 2014. Values are means of replicate measurements. Error bars are standard errors of means. The inset graphs show mean value of soil temperature, soil moisture and SCE (μmol/(m^2·sec)), respectively, at each treatment during the growing season (GS) and non-growing season (NGS) through the whole experimental period.

2.3. Dependence of soil CO_2 efflux on soil temperature and moisture

The SCE was more dependent on soil temperature than on soil moisture across all treatments, indicated by the relatively lower root mean squared error and higher R^2 of the relationships (Table 1). Examinations within treatments showed that precipitation treatments altered the dependence of SCE on soil temperature and moisture. For example, the slope of the SCE–temperature response curve (b in Eq. (2)) and the Q_{10} of
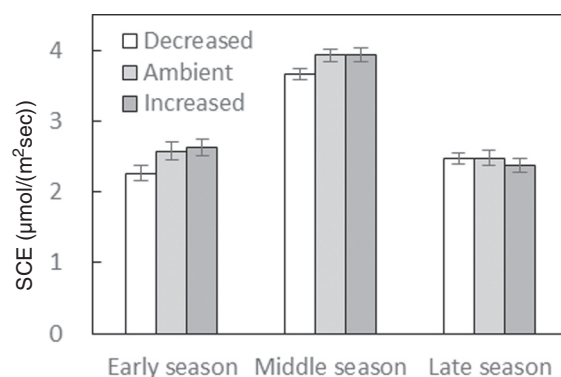

Fig. 3 – Soil CO_2 efflux (SCE) of each precipitation treatment at early (May and June), middle (July and August) and late (September and October) stage of growing season in a semiarid grassland of northwest China. Measurements were made between July 2013 and December 2014. Error bars are standard errors of means.

Table 2 – Predicted soil CO_2 emission (mol CO_2/m^2) with and without considering shifts in the response curves either across or within seasons.

Treatment		All seasons (531 days)	Non-growing season (242 days)	Growing season (289 days)
Ambient precipitation		91.1	22.1	69.0
Decreased precipitation	With shifts in response curves	83.4	19.8	63.6
	Without shifts in response curves	103.9	24.4	79.5
Increased precipitation	With shifts in response curves	89.3	20.1	69.3
	Without shifts in response curves	85.7	21.6	64.1

The CO_2 emission with shifts in response curves to precipitation treatment is predicted with parameters in each treatment and soil temperature and moisture measured in each treatment. The CO_2 emission without shifts in response curves to precipitation treatment is predicted with parameters from the ambient treatment but soil temperature and moisture measured in each treatment. The measurements of soil temperature and moisture every 10 min from July 2013 to December 2014 were used for CO_2 emission prediction.

the SCE were not affected in DP but were significantly higher in IP, indicating that increasing precipitation strengthened the dependence of SCE on temperature. These results further suggested the effect of the interaction between soil moisture and temperature on SCE, i.e., the rise in the SCE with temperature would be steeper when soil moisture was higher.

The slope of the SCE–moisture response curve (b in Eq. (3)) was significantly lower in DP (36%) but significantly higher in IP (33%), indicating that the decreased precipitation weakened and the increased precipitation enhanced the dependence of SCE on moisture. The optimal moisture (M_o), at which SCE is highest, was 17.2% for AP, similar to the mean soil moisture during the experimental period (17.4%) in the same treatment. M_o, however, was higher than the mean moisture in DP (14.9% vs. 12.7%) but lower in IP (18.1% vs. 19.6%). The changes in M_o were only 46% of the changes in mean soil moisture in DP and IP. These results suggested shifts in the SCE–moisture response curve to precipitation treatments.

2.4. Soil CO_2 emission

Total soil CO_2 emissions during the experimental period were 91.9, 83.4, and 89.3 mol CO_2/m^2 in AP, DP, and IP, respectively (Table 2). Emission occurred mainly in the growing season (May to October), accounting for 75%–78% of the total emission. The average daily rates of emission were 149%–189% higher in the growing than the non-growing season among the precipitation treatments.

The shifts in the response curves of SCE to changes in soil temperature and moisture due to precipitation treatment weakened the changes in CO_2 emission during the experimental period (Table 2). Without considering such shifts, CO_2 emission would be 103.9 and 85.7 mol CO_2/m^2 in DP and IP, respectively. Considering such shifts due to decreased or increased precipitation produced changes of 7.6 or 1.7 mol CO_2/m^2 in CO_2 emission, 59% or 32% of expected changes in emissions without considering such shifts, respectively. The effects of shifts of response curves on CO_2 emission were greater in the growing than the non-growing season. For instance, shifts to decreased or increased precipitation during the growing season reduced changes in emissions by 48% or 94%, respectively.

3. Discussion

The SCE and CO_2 emission varied strongly with season, with higher values in the growing season and lower values in the non-growing season. This seasonality of SCE and CO_2 emission was likely due mainly to changes in root and microbial respiration, which are determined by the seasonal patterns of soil temperature and moisture, consistent with the findings of other studies (Boone et al., 1998; Luo et al., 2001; Wan et al., 2007). Changes in precipitation can directly influence plant growth and root and microbial respiration by altering the availability of soil water (Rodríguez-Iturbe and Porporato, 2005; Wan et al., 2007; Cruz-Martínez et al., 2012). The effects of soil-water availability on SCE are particularly strong and important in arid and semiarid ecosystems that are limited by the availability of precipitation or soil water (Austin et al., 2004). The above- and belowground biomass averaged across 2013 and 2014 in our study, however, was not affected by precipitation treatment, with mean aboveground biomass of 94.4, 96.6, and 96.1 g/m^2, and mean belowground biomass of 247, 355, 204 g/m^2 across 0–20 cm depth in AP, DP, and IP, respectively. These results imply that root activity, and consequently root respiration, were likely not affected by precipitation treatments, although we did not measure root respiration in this study. The lack of significant differences in plant biomass can thus explain our observation that SCE was not affected by precipitation treatment, because plant growth strongly influences soil respiration and its response to environmental change (Boone et al., 1998; Bond-Lamberty et al., 2004).

Root and microbial respiration respond sensitively to changes in soil temperature and moisture, which change the availability of substrates and the activities of roots and microbes (Qi and Xu, 2001; Almagro et al., 2009). Changes in precipitation influence surface energy fluxes, and thus soil temperature (Dai et al., 1999). In our study, increased precipitation increased soil moisture but reduced soil temperature (Fig. 2), shifting the SCE–moisture response curve to the right and the SCE–temperature response curve upward (Fig. 4, Table 1). Similarly, decreased precipitation reduced soil moisture but increased soil temperature (Fig. 2), shifting the SCE–moisture response curve to the left and

the SCE–temperature response curve downward (Fig. 4, Table 1).

Current understanding of the shifts in the response of CO_2 efflux to temperature changes is mainly focused on plants, and the response is assumed to be associated with substrate and/or adenylate limitation (Atkin and Tjoelker, 2003). The SCE, however, is due to root and microbial respiration and the decomposition of organic matter. The shifts in the response function of SCE is thus more complex than that of plant CO_2 efflux and may include mechanisms such as nutrient and substrate availability (Atkin and Tjoelker, 2003; Kirschbaum, 2004), adaptation of roots to variable soil environments (Atkin and Tjoelker, 2003; Thorne and Frank, 2009), and changes in the composition and function of the microbial community (Monson et al., 2006; Castro et al., 2010; Karhu et al., 2014).

The shifts in the response of CO_2 efflux to moisture changes have not been well addressed. Our results provide evidence that the dependence of SCE on soil moisture can be altered by precipitation manipulation. Changes in soil moisture influences the allocation of assimilates in the plant–soil system, and alters microbial biomass and enzymatic activities in the rhizosphere (Sanaullah et al., 2011), thus feeding back to the shifts in the SCE–moisture response function.

The shifts in the SCE response curves have important implications in predicting SCE or CO_2 emission (Table 2). The flux of CO_2 from the soil to the atmosphere has been estimated at 76.5 Pg C/year in terrestrial ecosystems, 30%–60% higher than terrestrial net primary productivity (Raich and Potter, 1995). Soil CO_2 efflux thus plays an important role in regional and global C cycling and provides a feedback mechanism between C cycling and climate change (Luo et al., 2001; Davidson and Janssens, 2006; Heimann and Reichstein, 2008). According to the shifts in the SCE–temperature response curve, either decrease in temperature due to increased precipitation or increase in temperature due to decreased precipitation will result in less change in SCE compared with SCE predicted from ambient precipitation treatment (Fig. 4a). According to the quadratic response function of SCE to moisture, soil moistures either lower or higher than M_o would produce a relatively lower SCE compared to the SCE at M_o. Either an increase or decrease in precipitation would thus decrease SCE. The changes in the shape of the SCE–moisture function, however, weakened this decrease (Fig. 4b). Therefore, such shifts in the response curves to temperature or moisture due to precipitation manipulation could weaken the changes in SCE or CO_2 emission more than predicted without considering such shifts, and thus modulate the feedback between C cycling and climate change. Moreover, if our results prove to be general, any current predictions about CO_2 emission in response to precipitation changes associated with climate change need to be reexamined in semiarid grasslands because the shifts in the SCE response were not considered previously.
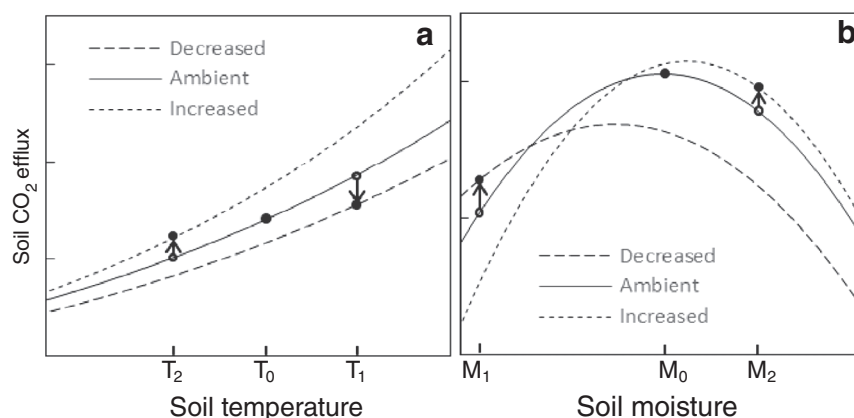
Fig. 4 – Conceptual illustration of the shift in soil CO_2 efflux (SCE) –temperature response curve (a) or SCE–moisture response curve (b) due to precipitation treatment. Arrow indicates the decrease in SCE change due to the shift of SCE response curves. T_0, T_1 and T_2 are the mean soil temperature, M_0, M_1 and M_2 are the mean soil moisture in ambient, decreased and increased precipitation treatments, respectively, during the experimental period. The open circle is the value without shifts in the SCE response curve and is predicted with parameters from the ambient treatment but mean soil temperature or moisture in the decreased or increased precipitation treatments. The filled circle is the value with shifts in the SCE response curve and is predicted with parameters and mean soil temperature or moisture in each decreased or increased precipitation treatment.

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