

# Soil CO<sub>2</sub> efflux in response to the addition of water and fertilizer in temperate semiarid grassland in northern China

Xiaoxu Jia · Ming'an Shao · Xiaorong Wei

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## Abstract

**Background and aims** Knowledge about the effects of water and fertilizer on soil CO<sub>2</sub> efflux (SCE) and  $Q_{10}$  is essential for understanding carbon (C) cycles and for evaluating future global C balance. A two-year field experiment was conducted to determine the effects of water, fertilizer, and temperature on SCE in semiarid grassland in northern China.

**Methods** SCE, as well as environmental factors was measured in two grasslands, one with bunge needlegrass (BNE, *Stipa bungeana*) and one with purple alfalfa (ALF, *Medicago sativa*), with four treatments: CK

(unwatered and unfertilized); W (50 mm water addition yr<sup>-1</sup>); F (50 kg phosphorus (P) fertilizer ha<sup>-1</sup> yr<sup>-1</sup> for ALF, 100 kg nitrogen (N)+50 kg P fertilizer ha<sup>-1</sup> yr<sup>-1</sup> for BNE); and W + F.

**Results** During the 11-month experimental period from July 2010 to October 2011, the addition of water consistently stimulated mean SCE in BNE and ALF, and the positive effects were relatively stronger during dry seasons. P fertilization consistently enhanced SCE in ALF, and the positive effect was strongly dependent on the availability of soil water. The effects of N plus P fertilization on SCE in BNE varied seasonally from significant increases to small reductions to no response. Water addition increased the  $Q_{10}$  of SCE in ALF by 11 % but had no effect in BNE. Fertilization, however, reduced the  $Q_{10}$  of SCE by 21 % and 13 % for BNE and ALF, respectively. Models that rely only on  $Q_{10}$  underestimated the emissions of soil CO<sub>2</sub> by 8–15 % at the study site, which was mediated by species and treatment.

**Conclusions** Responses of SCE and its temperature sensitivity to water and fertilizer may vary with species and depend on the period of measurement. Models of SCE need to incorporate the availability of ecosystemic water and nutrients, as well as species, and incorporate different environmental factors when determining the impact of water, nutrients, and species on SCE.

**Keywords** Soil CO<sub>2</sub> efflux · Water addition · Fertilization · Temperature sensitivity · Semiarid grassland

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## Abbreviations

AGB	Aboveground biomass
ALF	Alfalfa
BNE	Bunge needlegrass
C	Carbon
F	Fertilization
FRB	Fine root biomass
M	Soil moisture
N	Nitrogen
P	Phosphorus
Pr	Period
SCE	Soil CO <sub>2</sub> efflux
T	Soil temperature
W	Water addition

## Introduction

As the second largest flux of carbon (C) between terrestrial ecosystems and the atmosphere, soil CO<sub>2</sub> efflux (SCE) (mainly from soil respiration) plays an important role in global C cycling (Schlesinger and Andrews 2000; Lal 2004). The SCE represents CO<sub>2</sub> release at the soil surface from microbial respiration during the decomposition of organic matter and from rhizosphere respiration by living roots and their symbionts (Högberg et al. 2001) interacting with both biotic and abiotic factors (Buchmann 2000; Wan et al. 2007; Xu and Wan 2008; Yan et al. 2011). The manipulation of water and/or nutrients availability through irrigation and fertilization can induce changes in the structure of microbial communities, plant growth, soil properties, and soil microclimate, which can alter SCE (Cox et al. 2000), with consequent impacts on future ecosystemic and global C cycling (Harpole et al. 2007; Liu et al. 2009; Janssens et al. 2010). Elucidating the interactive effects and relative importance of water and fertilizer in regulating SCE will thus improve model simulations of C cycling in future global change and ecosystemic management scenarios.

Fertilization is expected to stimulate SCE by increasing plant growth, net primary productivity, and amount and decomposition rate of litter, resulting in an increased supply of C substrates for roots and microorganisms. However, a number of studies reported inconsistent effect of fertilization on SCE (Keith et al. 1997; Maier and Kress 2000; Tyree et al. 2006;

Xu and Wan 2008; Janssens et al. 2010). Other studies have shown a neutral or negative relationship between SCE and fertilization in terrestrial ecosystems (Vose et al. 1997; Bowden et al. 2004; Olsson et al. 2005). They ascribe the negative effect of fertilization on SCE to a decrease in the relative allocation of C belowground (Haynes and Gower 1995; Bowden et al. 2000; Craine et al. 2001). In addition, some studies suggested that fertilization may inhibit both root and lignin degrading fungi activities (Bowden et al. 2004; Burton et al. 2004). Similarly, SCE has been found to be both sensitive and insensitive to changes in amounts of water (Maier and Kress 2000; Maier et al. 2004). Soil moisture affects SCE by its direct influence on the processes of canopy photosynthesis and root and microbial activity or by its indirect influences on the physical (such as gas diffusivity and soil temperature) and chemical (such as decomposition of C) conditions of the soil (Harpole et al. 2007; Wan et al. 2007). For example, Wan et al. (2007) and Yan et al. (2011) showed that a higher availability of soil water significantly increased SCE in semiarid grassland because water stimulated the photosynthetic substrate supply. Although the effects of water and fertilizer on SCE have been studied in recent decades, little information on the response of SCE to alterations of water and nutrients availability on the Loess Plateau region have been presented.

In addition to the absolute responses of SCE to the addition of water and fertilizer, the temperature sensitivity (commonly referred to as  $Q_{10}$ , representing the respiration rate change over a temperature shift by 10 °C) is also of great concern for research on global change (Cox et al. 2000; Ryan and Law 2005). The sensitivity of SCE to temperature is an important index in quantifying and predicting the response of terrestrial C cycling to future climate change (Cox et al. 2000; Davidson et al. 2006; Davidson and Janssens 2006). The  $Q_{10}$  of SCE receives substantial interest but still remains controversial (Ryan and Law 2005; Davidson and Janssens 2006). Besides, most climatic researchers focus on the impacts of global warming and elevated levels of CO<sub>2</sub> on the  $Q_{10}$  of SCE (Luo et al. 2001; Davidson et al. 2006; Davidson and Janssens 2006; Wan et al. 2007). Changing soil water and/or nutrients availability may alter the microbial and root activity, and the rate of C decomposition (Bowden et al. 2000, 2004; Frey et al. 2004; Wan et al. 2007; Conant et al. 2011), which may impact the  $Q_{10}$  of SCE, but little information is known about whether added water and/or

fertilizer, and their possible interactions affect the  $Q_{10}$  of SCE in semiarid grassland. The  $Q_{10}$  relationship has been commonly used to predict SCE (Epron et al. 1999; Buchmann 2000). Recent studies, however, have shown that models that rely on  $Q_{10}$  may erroneously predict future soil CO<sub>2</sub> emissions under conditions of global warming (Yuste et al. 2004; Wan et al. 2007; Almagro et al. 2009). Few reports have addressed the performance of temperature-response functions applied to the grassland ecosystem under altered availabilities of water and nutrients on the Loess Plateau.

The grassland of the Loess Plateau, an important component of China's grassland, is mainly characterized by an arid and semiarid climate (Wang et al. 2011). Ecosystems in this region are mainly constrained by water during dry seasons and mediated by nutrients during wet seasons. Previous studies have predicted that future summer precipitation in North China would increase by 93–136 mm (Cholaw et al. 2003). In this study, we focused on how SCE would change in response to an increase in future precipitation early in the growing season, i.e. the dry period. Therefore, a manipulative experiment with treatments of water and fertilizer was conducted in two typical semiarid grasslands in northern China, one with bunge needlegrass and one with purple alfalfa, to test how water and fertilizer may influence SCE and its sensitivity to temperature. In the light of the above the following hypotheses are proposed. (1) Given the limitation of water on plant and microbial activities in semiarid ecosystems, we hypothesize that the addition of water will stimulate SCE by providing more C substrates for respiratory processes of plant roots and soil microbes, and the positive effects will be regulated by plant species and period of measurement. (2) Fertilization can stimulate evapotranspiration, consequently reducing soil moisture (Frey et al. 2004; Harpole et al. 2007), and aggravating soil water deficits in semiarid regions. We therefore hypothesize that reduced soil moisture under fertilization could constrain root and microbial activities, offset the positive effects of stimulated plant production, and will lead to inconsistent responses of SCE. (3) Since the microbial community and the quality and quantity of substrate regulate the responses of SCE to temperature (Giardina and Ryan 2000; Zhang et al. 2005), we hypothesize that water and fertilizer will have different effects on the  $Q_{10}$  of SCE due to different effects on the microbial community and the supply of C substrates.

## Materials and methods

### Site description

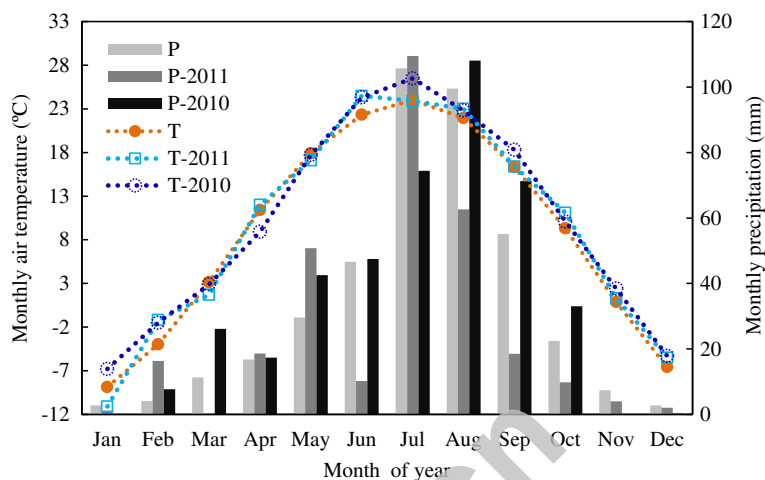
This study was conducted at the Shenmu Erosion and Environment Research Station (38°49' N, 110°23' E) on the northern Loess Plateau of China. The area is located at an altitude ranging from 1081 m to 1274 m above sea level. The region has a semiarid, continental climate. According to data available for the period 1971–2011 at the study site from the National Meteorological Information Center of China, the mean annual air temperature is 8.4 °C, the coldest being –9.7 °C in January and the warmest being 23.7 °C in July. The average annual precipitation is 400 mm, approximately 80 % of which falls between July and October (Fig. 1). The type of soil was Loessial, which belongs to the order Regosols according to FAO/ISRIC/ISSS Soil Taxonomy. The landscape is typically transitional and subject to severe erosion from both wind and water. Various efforts during the past decade have been made to prevent further erosion, including the widespread planting of arid-land perennial plants, such as purple alfalfa (*Medicago sativa*) and korshinsk peashrub (*Caragana korshinskii*), and the establishment of fallow land formerly used for crop production to allow the regeneration of natural vegetation. The dominant native species in the natural grassland is bunge needlegrass (*Stipa bungeana*).

### Experimental design and treatments

The experiments were conducted in two types of grassland; one is dominated by bunge needlegrass (BNE) and the other by purple alfalfa (ALF). BNE is a native perennial grass, and ALF is an exotic perennial leguminous grass which can fix N from the atmosphere. The ALF were planted with row spacing of 50 cm in 2000, and was harvested twice per year, in late August and October (cut near the soil surface), at the peak biomass for stock feeding. Additionally, the dominant species represented more than 95 % of the sum peak above-ground biomass of each grassland ecosystem during the experimental period. Neither grassland received irrigation or fertilization before our experiments.

The experiments used a nested design, with water addition manipulated at the plot level and

**Fig. 1** Monthly mean precipitation (P) and air temperature (T) between 1971 and 2011 and in 2010 and 2011 at the study site



fertilization manipulated at the subplot level. Three blocks of 43×11 m area were randomly selected for each type of grassland in spring 2010. In each block, there were two 21×11 m plots, with one assigned as ambient and the other as water addition treatment. Each 21×11 m plot was divided into four 10×5 m subplots with two fertilized subplots and two unfertilized subplots arranged randomly. The distance between any two subplots was 1 m. Therefore, the experimental design consisted of 24 subplots and four treatments (unfertilized and unwatered control (CK), water addition (W), fertilization (F), and water addition plus fertilization (W + F)) with six replicates for each treatment within each community.

The fertilizers for the BNE were nitrogen plus phosphorus (NP), using urea and P<sub>2</sub>O<sub>5</sub> as the sources of N and P, respectively. The ALF received only P fertilizer due to ALF's ability to fix N<sub>2</sub> from the atmosphere. Phosphorus was also applied in the form of P<sub>2</sub>O<sub>5</sub>. All fertilizers were manually added to the experimental subplots at rates of 100 kg N ha<sup>-1</sup> yr<sup>-1</sup> and 50 kg P ha<sup>-1</sup> yr<sup>-1</sup> at the end of May 2010 and 2011, respectively. In each of the watered plots, six sprinklers were arranged in three rows to cover the 21×11 m area evenly. To simplify the study, we wanted to induce water deficit conditions consistently, without causing fluctuations in the plant response to deficit-non-deficit conditions as a result of periodical watering. On 27 May 2010 and 18 May 2011, a total of 50 mm of water, which was about 13 % of the annual mean precipitation for this region, was added at once to the watered plots.

### Measurement of SCE and soil properties

SCE was measured three or four times monthly from 1 July to 20 October 2010 and from 10 April to 20 October 2011. All measurements of SCE were conducted between 9:00 and 11:00 h (local time). Measurements of SCE were performed with the CI-340 Photosynthesis System (CID Bio-Science, Inc., Camas, WA, USA) attached to a soil-respiration chamber (CI-301SR Soil Respiration Chamber, Inc., Camas, WA, USA). Air was allowed to flow through the chamber at a rate of 0.5 l min<sup>-1</sup> for 3 min before the start of logging to achieve an equilibrium efflux. Measurements were logged at 1 Hz. A measurement took approximately 2 min, depending on the flux rate.

The SCE was calculated from the change in CO<sub>2</sub> concentration over the measurement period and was computed using a linear function as follows:

$$F = \left( \Delta m / \Delta t \right) \times D \times \left( v / A \right) \\ = h \times D \times \left( \Delta m / \Delta t \right) \quad (1)$$

where  $F$  is the SCE ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $v$  is volume ( $\text{cm}^3$ ),  $\Delta m / \Delta t$  is the linear slope of concentration change with time over the measured period, which is thought to be effective only when the correlation coefficient ( $R^2$ ) is greater than 0.95,  $D$  is the gas density of the chamber ( $D = P_a / RT$ ,  $\text{mol m}^{-3}$ ,  $P_a$ : atmospheric pressure,  $T$ : temperature

and  $R$ : air constant),  $A$  is the surface area of the chamber, and  $h$  is the height of the chamber.

Two PVC collars (25 cm in diameter and 8 cm in height) were carefully pressed into the soil to a depth of about 3 cm at two randomly selected positions in each subplot about 2 weeks before the first measurement. Care was taken when inserting the collars to limit the severing of roots and the disturbance of soil structure. All collars were left at the site for the entire study period. Living plants inside the soil collars were removed by hand at least 1 day before the flux measurements to avoid the effects of plant leaf respiration. The clipped plant materials were left in the collars in order to include  $\text{CO}_2$  release from decomposition of aboveground litter. Respiration data were discarded if not in the 95 % confidence interval determined by all the observations for each measurement dataset. The soil temperature and moisture near each collar were measured at the same time as SCE. Soil temperature was measured using a digital thermometer (Omega HH509R, Stamford, CT) at a depth of 5 cm adjacent to each PVC collar. Soil moisture was measured using frequency domain reflectometry (FDR) with a handheld push probe (Theta probe type ML2X, Delta-T, UK) at a depth of 0–6 cm. Volumetric moisture was calculated using the following Theta-probe calibration curve:

$$Y = 0.9228 \times X - 1.3196 (R^2 = 0.91, RMSE = 3.2\%) \quad (2)$$

where  $X$  is the soil moisture measured by the Theta-probe (%) and  $Y$  is the soil moisture obtained by a gravimetric method (%). The calibration curve was obtained from the same area. More detailed information on the calibration procedure can be found elsewhere (Hu et al. 2011).

Before the first addition of water and fertilizer, one aluminum neutron probe access tube (5 cm in internal diameter and 100 cm in depth) was permanently installed in the soil at the center of each subplot. Slow neutron counting rates ( $CR$ ) were recorded at soil depths of 10, 20, 40, 60, 80 and 100 cm monthly in 2010 and twice a month in 2011 from April to October (the growing season) to calculate the soil water storage for different soil layers. Volumetric soil moisture,  $\theta$ , at each depth

was calculated from the slow-neutron counting rates,  $CR$ , using the following calibration curve (Hu et al. 2009):

$$\theta = 0.6483 \times CR - 0.0102 (R^2 = 0.90, P < 0.001) \quad (3)$$

The calibration curve was obtained from the same area and was considered valid for all depths.

#### Aboveground production and fine root biomass

In late August of 2010 and 2011, we sampled peak aboveground biomass (AGB) for both grasslands by clipping an area of  $1 \times 1$  m in each subplot. ALF was sampled again in mid-October to simulate the typical land use management of the study area. The total biomass sampled in August and October was taken as the annual aboveground production in ALF. The plant samples were dried at  $65^\circ\text{C}$  in an oven for 72 h to estimate dry weight. After aboveground plant residues were collected in August, one soil core (10-cm diameter) was collected from 0 cm to 40 cm soil layers and was divided into 0–10, 10–20 and 20–40 cm depths to estimate fine root biomass (FRB) in each subplot for both communities. All cores were transported to the laboratory as soon as possible and fine roots (<2 mm in diameter) in the soil cores were carefully separated by hand and washed on a 2-mm sieve. The washed roots were oven-dried at  $65^\circ\text{C}$  for about 72 h and then weighed as an estimate of FRB.

#### Data analyses

The response of SCE to temperature was modelled using the exponential function as follows:

$$R = \alpha \times \exp(\beta T) \quad (4)$$

where  $\alpha$  and  $\beta$  are two coefficients in the regression line,  $R$  is measured SCE and  $T$  is soil temperature.

To examine whether adding water and/or fertilizer influenced the temperature sensitivity of SCE, we calculated  $Q_{10}$  based on the data from the entire experimental period. The temperature ranges used to calculate  $Q_{10}$  within each treatment in both communities were all similar, from approximately 7.5 to  $28.8^\circ\text{C}$ .  $Q_{10}$  was calculated to describe the proportional

increase of SCE with a 10 °C increase in temperature as follows:

$$Q_{10} = \exp(\beta T) \quad (5)$$

Data of SCE for both years were analyzed using three-way ANOVAs (at  $P < 0.05$ ) to determine the main and interactive effects of species, water, and fertilizer (Table 1). Because of the significant influence of species and treatment (water addition or fertilization) on SCE, three-way ANOVAs (at  $P < 0.05$ ) were conducted to estimate the effects of water addition, fertilization, and measuring period for each grassland (Table 2). A one-way ANOVA followed by a least significant difference (LSD) test ( $P < 0.05$ ) was used to examine the effects of water addition, fertilization, and measuring period on soil moisture, soil temperature, and SCE. A one-way ANOVA followed by an LSD test ( $P < 0.05$ ) examined the effects of water and fertilizer on  $Q_{10}$ . Seasonal mean SCE across the experimental period was estimated using the simple temperature-response function [Eq. (4)] at the seasonal mean temperature within each treatment. Paired sample *t*-tests were used to analyze differences between measured and estimated SCE within each treatment for each community. To determine which variable was more important to SCE, simple and multiple linear and nonlinear regression analyses examined the relationships between SCE and soil temperature and soil moisture. All statistical analyses were performed with the Statistical Analysis System (SAS) software.

## Results

We examined the effects of species (S), water addition (W), fertilization (F) and their interactions on SCE over the 2 years (Table 1). ANOVAs indicated significant effects ( $P < 0.001$ ) on SCE with S, W, and F. Significant interactive effects ( $P < 0.001$ ) from S × W, S × F, and W × F were also detected (Table 1). These analyses indicated that the responses of SCE to water and fertilizer were dependent on plant species. We then therefore examined the effects of measuring period (Pr), W, and F on SCE, soil moisture, and soil temperature for each community (Table 2). Temporal variations of soil moisture (Figs. 2a and 3a), soil temperature (Figs. 2b and 3b), and SCE (Figs. 2c

and 3c) for both grasslands in response to these effects are discussed in the following sections.

### Microclimate and vegetative biomass

Precipitation during the growing season fluctuated widely (Fig. 1). The climate of the study area is characterized by low amounts of precipitation, with a clear separation of dry and wet seasons. We therefore subdivided the entire experimental period into three measuring periods (wet-2010, dry-2011, and wet-2011) to examine the main and interactive effects of Pr, W, and F on SCE. The early-growing stage (April to June) was recognized as the dry period, and July–October as wet period (Fig. 1). For BNE, W significantly increased mean soil moisture by 1.55 % v/v ( $P < 0.05$ ) in dry-2011 but had no effect in the two wet seasons ( $P > 0.05$ ). While F significantly decreased ( $P < 0.05$ ) mean soil moisture in all three measuring periods compared to the control plots (Fig. 4a). For ALF, mean soil moisture was significantly increased ( $P < 0.05$ ) by W treatment and significantly decreased ( $P < 0.05$ ) by F treatment during the three periods (Fig. 4b). Significant W × Pr and F × Pr interactive effects on soil moisture occurred in both grasslands. Significant interactions of W × F and W × F × Pr affected soil moisture for ALF ( $P < 0.001$ ) but not for BNE ( $P > 0.05$ ) (Table 2).

Soil temperature for BNE was relatively higher ( $P < 0.05$ ) in the watered plots than in the control plots during the two wet periods. In the fertilized plots, soil temperature was 0.62 °C higher ( $P < 0.05$ ) in wet-2010 but 1.38 °C lower ( $P < 0.01$ ) in dry-2011 compared to the control plots (Fig. 4c). For ALF, soil temperature was significantly lower ( $P < 0.05$ ) in the watered and fertilized plots than in the control plots during the three periods (Fig. 4d). W × F, W × Pr, and F × Pr interactions affected temperatures in both communities ( $P < 0.01$ ) (Table 2). Additionally, significant W × F × Pr interactive effects on soil temperature for ALF were detected ( $P = 0.035$ ) (Table 2).

W, F, and W + F significantly increased the AGB and FRB (0–10 cm,  $P < 0.05$ ) for BNE and ALF (Fig. 5). W significantly increased AGB and FRB for the 0–10 cm layer over the 2 years of the experiment, on average, by 35 % and 75 % for BNE and by 60 % and 73 % for ALF, respectively. F significantly increased AGB and FRB by 103 % and 160 % for BNE

**Table 1** ANOVA results of the effects of plant species (S), addition of water (W), and fertilization (F) on the measured efflux of soil CO<sub>2</sub> ( $n=6$ ). DF = degree of freedom and  $F$  =  $F$  statistic

	DF	$F$	$P$
Species (S)	1	789.31	< 0.001
Water addition (W)	1	240.11	< 0.001
Fertilization (F)	1	191.16	< 0.001
S × W	1	66.65	< 0.001
S × F	1	180.36	< 0.001
W × F	1	15.36	< 0.001
S × W × F	1	1.97	0.169

over the 2 years, respectively (Fig. 5). F had no significant effect on AGB for ALF during the first growing stage (April–August), but significantly increased AGB, on average, by 80 % during the second growing stage (September–October) in both seasons. In addition, F significantly increased FRB for the 0–10 cm layer for ALF by 120 % over the 2 years. W + F significantly increased AGB and FRB, on average, by 116 % and 133 % for BNE and by 104 % and 73 % for ALF over the 2 years of the experiment, respectively (Fig. 5).

**Table 2** ANOVA results of the effects of addition of water (W), fertilization (F), and measuring period (Pr) on soil moisture (M), soil temperature (T), and the measured efflux of soil CO<sub>2</sub> (SCE)

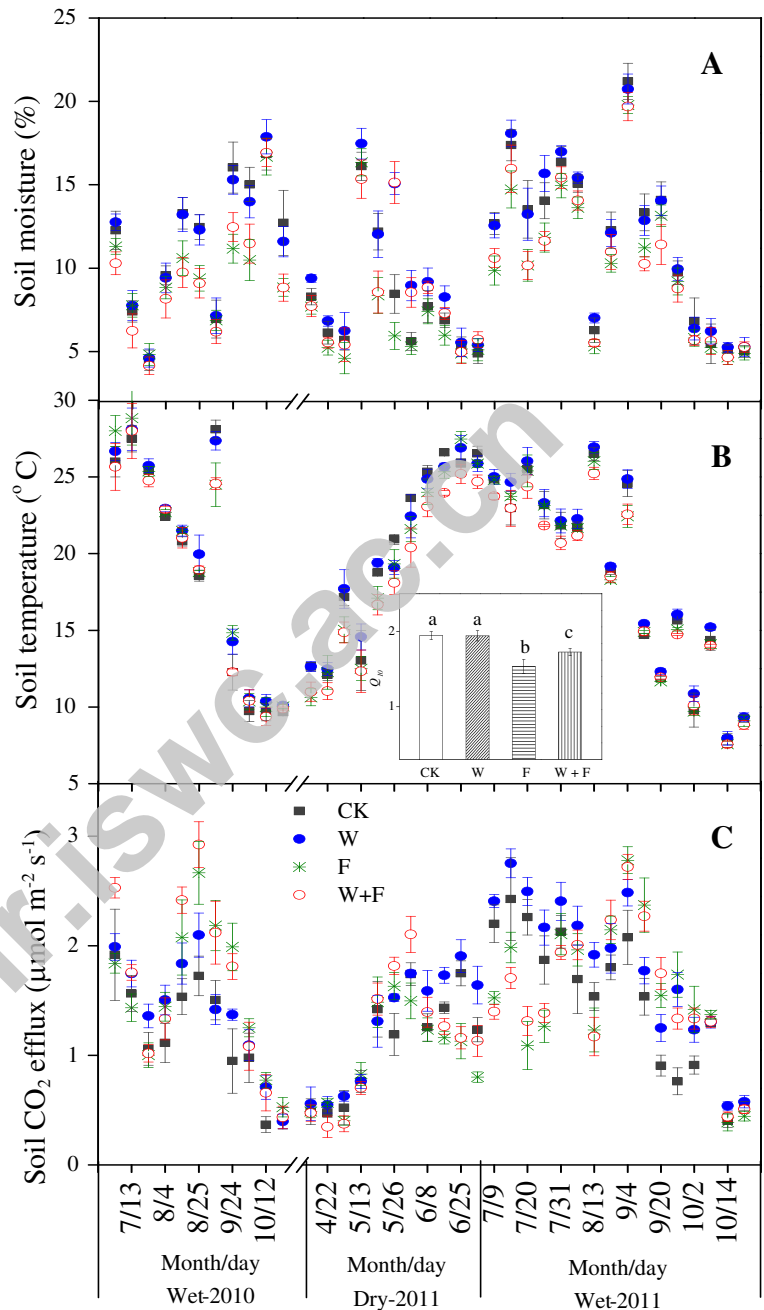
	DF	M (%)		T (°C)		SCE ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	
		$F$	$P$	$F$	$P$	$F$	$P$
<b>BNE</b>							
Water addition (W)	1	69.48	< 0.001	4.76	0.040	81.13	< 0.001
Fertilization (F)	1	701.33	< 0.001	88.81	< 0.001	3.48	0.067
Period (Pr)	2	968.41	< 0.001	41.63	< 0.001	490.67	< 0.001
W × F	1	2.35	0.129	33.69	< 0.001	35.19	< 0.001
W × Pr	2	82.47	< 0.001	9.26	0.001	0.46	0.636
F × Pr	2	25.85	< 0.001	27.54	< 0.001	87.65	< 0.001
W × F × Pr	2	0.01	0.991	1.30	0.292	7.76	0.001
<b>ALF</b>							
Water addition (W)	1	383.04	< 0.001	107.40	< 0.001	500.12	< 0.001
Fertilization (F)	1	272.26	< 0.001	337.06	< 0.001	588.06	< 0.001
Period (Pr)	2	2688.64	< 0.001	288.51	< 0.001	482.29	< 0.001
W × F	1	55.77	< 0.001	57.94	< 0.001	5.18	0.027
W × Pr	2	113.67	< 0.001	33.40	< 0.001	15.52	< 0.001
F × Pr	2	9.54	< 0.001	14.63	< 0.001	81.6	< 0.001
W × F × Pr	2	11.54	< 0.001	3.93	0.035	0.14	0.874

#### Dependence of SCE on soil moisture and soil temperature

The seasonal patterns of SCE generally followed those of soil moisture and temperature (Figs. 2 and 3). Simple linear regression functions were used to describe the relationships between SCE and soil moisture within the different treatments for BNE and ALF throughout the entire experimental period (Table 3). The equations were all significant at  $P < 0.01$ . Soil moisture explained 12–22 % of the variations in SCE

in bunge needlegrass (BNE) and purple alfalfa (ALF) ( $n=6$ ). DF = degree of freedom and  $F$  =  $F$  statistic

**Fig. 2** Seasonal dynamics of soil moisture (a), soil temperature (b), and soil CO<sub>2</sub> efflux (c) from July 2010 to October 2010 and April 2011 to October 2011 for bunge needlegrass (BNE) and the temperature sensitivity ( $Q_{10}$ ) of soil CO<sub>2</sub> efflux by fitting data collected over the whole period (inserts, mean  $\pm$  standard deviation,  $n=6$ ). Values of  $Q_{10}$  followed by different lower-case letters within different treatments are significantly different at  $P < 0.05$ . Treatments are control (CK), water addition (W), fertilization (F), and water addition plus fertilization (W + F). Soil moisture, soil temperature and soil CO<sub>2</sub> efflux are displayed as means  $\pm$  standard deviations with the sample size  $n=6$

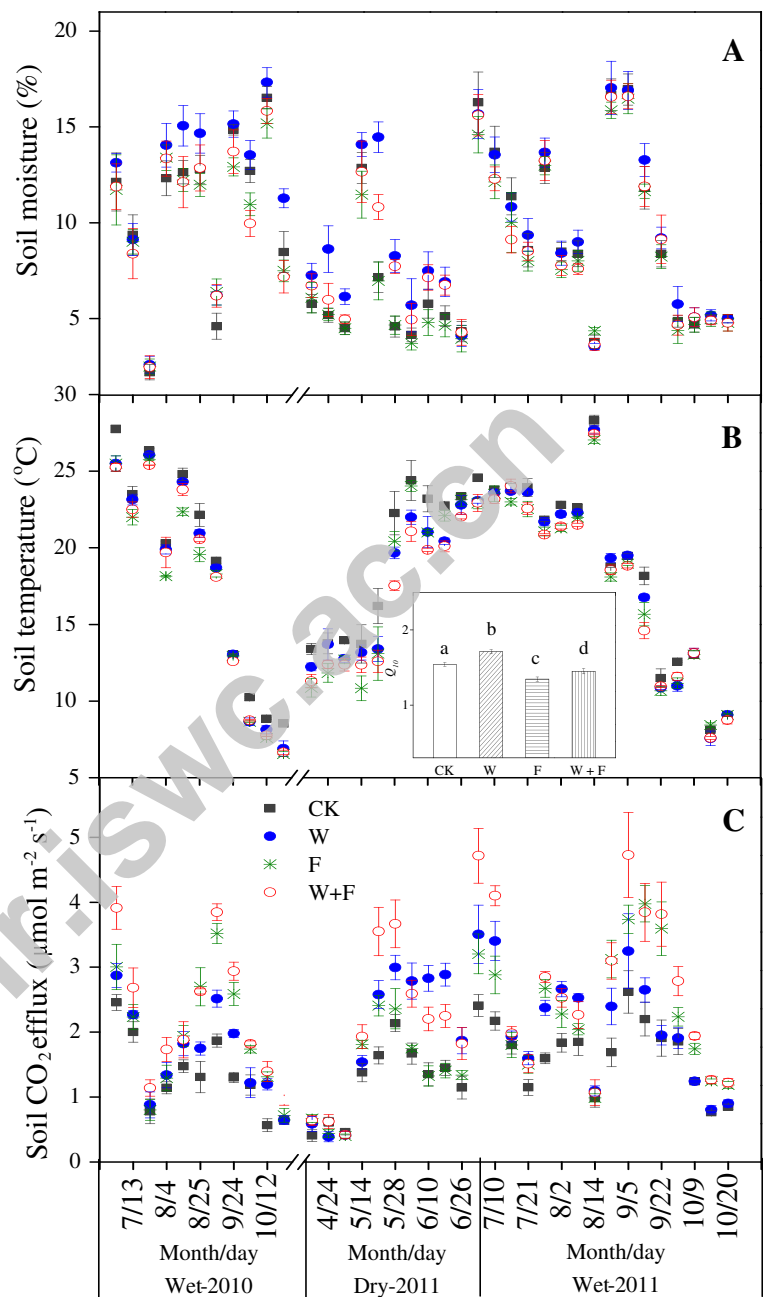


across treatments in BNE and 12–33 % in ALF. Furthermore, exponential functions were used to describe the relationships between SCE and soil temperature for BNE and ALF (Table 3). The equations were all significant at  $P < 0.01$ . Soil temperature explained 33–61 % of the variations in SCE across treatments in BNE and 11–40 % in ALF. We combined soil

moisture and temperature to examine their interactive effects on SCE ( $SCE = ae^{bT}M^c$ ). Soil moisture and temperature together contributed 42–77 % ( $P < 0.01$ ) of the seasonal variations in SCE across treatments for BNE and 36–46 % ( $P < 0.01$ ) for ALF (Table 3). These results indicated that soil temperature was more important than moisture in regulating the seasonal



**Fig. 3** Seasonal dynamics of soil moisture (a), soil temperature (b), and soil CO<sub>2</sub> efflux (c) from July 2010 to October 2010 and April 2011 to October 2011 for purple alfalfa (ALF) and the temperature sensitivity ( $Q_{10}$ ) of soil CO<sub>2</sub> efflux by fitting data collected over the whole period (inserts, mean  $\pm$  standard deviation,  $n=6$ ). Values of  $Q_{10}$  followed by different lower-case letters within different treatments are significantly different at  $P<0.05$ . Treatments are control (CK), water addition (W), fertilization (F), and water addition plus fertilization (W + F). Soil moisture, soil temperature and soil CO<sub>2</sub> efflux are displayed as means  $\pm$  standard deviations with the sample size  $n=6$



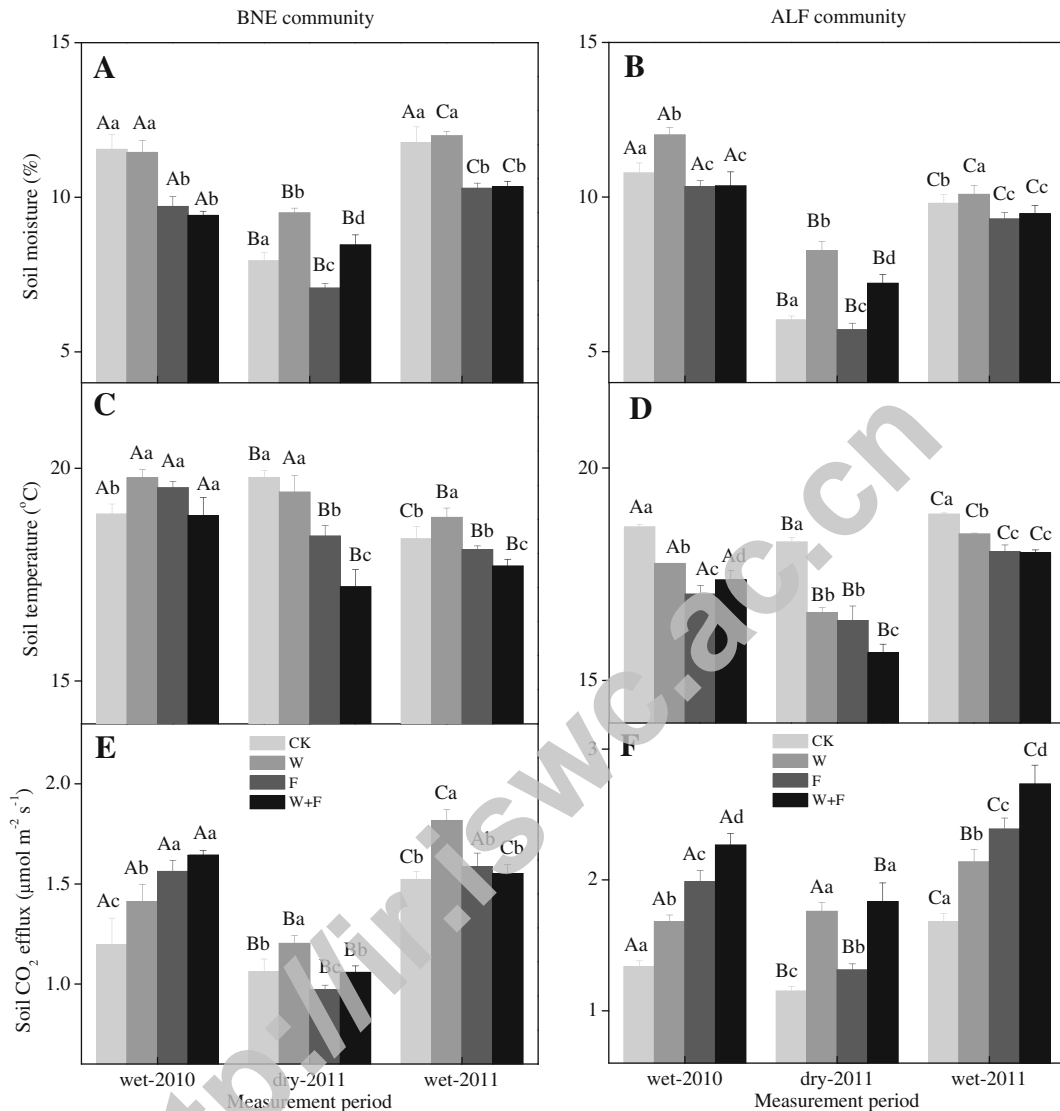
patterns of SCE for BNE. Similar results were found for the control and watered plots of ALF, but SCE was mainly regulated by moisture in the fertilized plots.

Effects of water and fertilizer on SCE varied with species and period

Positive effects of water addition on SCE varied not only with species, but also with measuring period. W increased

the SCE for BNE by 18.1 % ( $P<0.01$ ), 13.4 % ( $P<0.01$ ), and 19.4 % ( $P<0.01$ ) in wet-2010, dry-2011, and wet-2011, respectively (Fig. 4e). For ALF, W increased SCE by 25.5 % ( $P<0.01$ ), 53.1 % ( $P<0.01$ ), and 27.0 % ( $P<0.01$ ) in these three periods, respectively (Fig. 4f).

Changes in SCE induced by fertilization also varied with species and period. For BNE, fertilization increased SCE by 30.8 % ( $P<0.01$ ) in wet-2010, but the SCE was 8.5 % ( $P<0.05$ ) lower in the fertilized



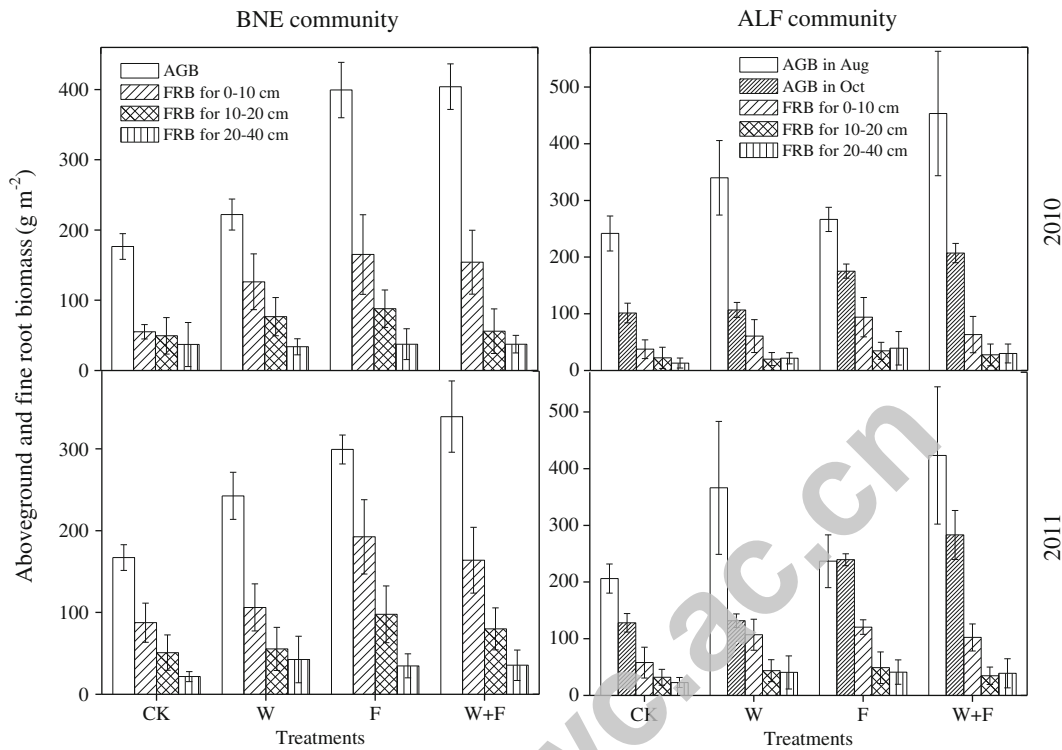
**Fig. 4** Mean values of soil moisture, soil temperature, and soil CO<sub>2</sub> efflux (means  $\pm$  standard deviations,  $n=6$ ) during measurement periods of July–October 2010 (wet-2010), April–June 2011 (dry-2011), and July–October 2011 (wet-2011) for bunge needgrass (BNE) and purple alfalfa (ALF). Treatments are control (CK), water addition (W), fertilization (F), and water

addition plus fertilization (W + F). Significant differences between treatments within each measurement period are labelled with different lowercase letters, while differences between measurement periods within each treatment are labelled with different capital letters ( $P<0.05$ )

plots in dry-2011 and was not significantly different in wet-2011 ( $P>0.05$ ), compared to the control plots (Fig. 4e). Fertilization consistently increased SCE for ALF by 48.3 % ( $P<0.01$ ), 14.1 % ( $P<0.01$ ), and 41.9 % ( $P<0.01$ ) in the wet-2010, dry-2011, and wet-2011 periods, respectively (Fig. 4f).

Consistent with the separate addition of water and fertilizer, the effects on SCE of W + F were

dependent on period and species. W + F increased the SCE of BNE by 37.6 % ( $P<0.01$ ) in wet-2010 but had no significant effect during the dry and wet seasons of 2011 ( $P>0.05$ ) (Fig. 4e). For ALF, W + F consistently increased SCE by 69.3 % ( $P<0.01$ ), 59.6 % ( $P<0.01$ ), and 62.3 % ( $P<0.01$ ) in the wet-2010, dry-2011, and wet-2011 periods, respectively (Fig. 4f).



**Fig. 5** Mean aboveground biomass and fine root biomass (means ± standard deviations,  $n=6$ ) for the 0–10, 10–20 and 20–40 cm soil layers under four treatments (CK, control, W, water addition; F, fertilization; W + F, water addition plus fertilization) for bunge needlegrass (BNE) and purple alfalfa (ALF) in 2010 and 2011, respectively

Effects of water and fertilizer on the  $Q_{10}$  of SCE

The effects of water and fertilizer on  $Q_{10}$  varied with species. The value of  $Q_{10}$  was not altered by

W for BNE ( $P>0.05$ ) (Fig. 2b, inserts). W, however, increased the  $Q_{10}$  of ALF by 11.1 % ( $P<0.01$ ) (Fig. 3b, inserts). F reduced  $Q_{10}$ , on average, by 21.0 % ( $P<0.01$ ) and 12.6 % ( $P<0.01$ ) for

**Table 3** Parameters of different models of soil CO<sub>2</sub> efflux (SCE) in relation to soil temperature (T) and soil moisture (M) within the different treatments for bunge needlegrass (BNE) and purple alfalfa (ALF) throughout the entire experimental period

Community	Treatment	$SCE = ae^{\beta T}$			$SCE = dM + f$			$SCE = ae^{bT}M^c$			
		$\alpha$	$\beta$	$R^2$	$d$	$f$	$R^2$	$a$	$b$	$c$	$R^2$
BNE	CK	0.322	0.066	0.61 <sup>a</sup>	0.045	0.813	0.12 <sup>a</sup>	0.139	0.059	0.459	0.77 <sup>a</sup>
	W	0.384	0.066	0.60 <sup>a</sup>	0.058	0.867	0.16 <sup>a</sup>	0.161	0.056	0.472	0.77 <sup>a</sup>
	F	0.552	0.043	0.34 <sup>a</sup>	0.079	0.671	0.22 <sup>a</sup>	0.249	0.027	0.551	0.42 <sup>a</sup>
	W + F	0.466	0.055	0.33 <sup>a</sup>	0.069	0.769	0.15 <sup>a</sup>	0.222	0.041	0.500	0.44 <sup>a</sup>
ALF	CK	0.571	0.043	0.37 <sup>a</sup>	0.054	0.943	0.20 <sup>a</sup>	0.349	0.036	0.342	0.43 <sup>a</sup>
	W	0.628	0.054	0.40 <sup>a</sup>	0.072	1.172	0.12 <sup>a</sup>	0.368	0.043	0.380	0.46 <sup>a</sup>
	F	1.009	0.030	0.11 <sup>a</sup>	0.135	0.802	0.33 <sup>a</sup>	0.413	0.021	0.570	0.36 <sup>a</sup>
	W + F	1.049	0.037	0.15 <sup>a</sup>	0.160	0.888	0.32 <sup>a</sup>	0.415	0.026	0.591	0.36 <sup>a</sup>

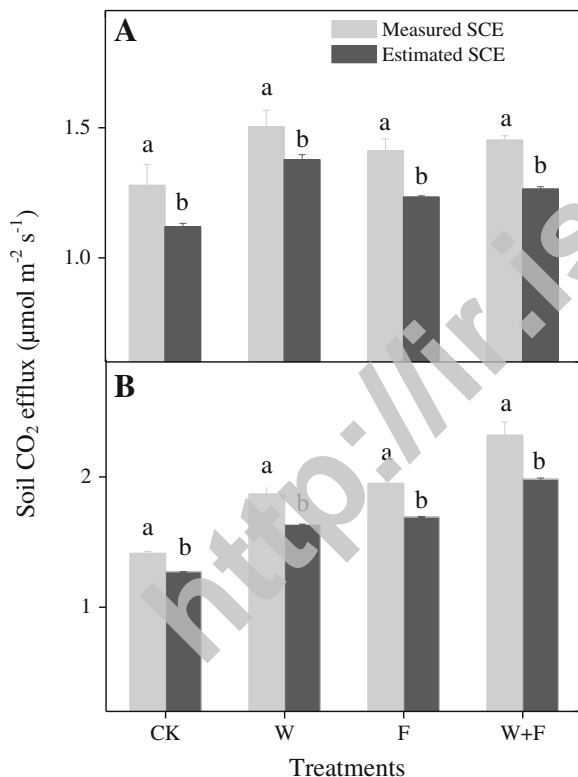
CK control; W water addition; F fertilization; W + F water addition plus fertilization

<sup>a</sup> Correlation is significant at  $P<0.01$

BNE and ALF, respectively. Additionally, W + F significantly decreased  $Q_{10}$  by 11.2 % ( $P < 0.01$ ) and 6.0 % ( $P < 0.01$ ) for BNE and ALF, respectively.

#### Estimation of SCE by a simple temperature-response function

Mean seasonal SCE for the entire experimental period was estimated using models as a simple temperature-response function for BNE (Fig. 6a) and ALF (Fig. 6b) at the mean seasonal temperature within each treatment. Generally, the estimated mean seasonal flux was significantly lower than the measured flux ( $P < 0.01$ ), indicating that the simple temperature-response function underestimated the SCE at the study site. For



**Fig. 6** Measured and estimated mean seasonal soil CO<sub>2</sub> efflux (means ± standard deviations,  $n=6$ ) by a simple temperature-response function at the seasonal mean temperature under four treatments (CK, control; W, water addition; F, fertilization; W + F, water addition plus fertilization) across the entire experimental period for bunge needlegrass (BNE) (a) and purple alfalfa (ALF) (b). Significant differences between measured and estimated mean soil CO<sub>2</sub> efflux within each treatment are labelled with different lowercase letters ( $P < 0.05$ )

BNE, the estimated mean seasonal SCE was underestimated by 12.4 %, 8.4 %, 12.6 %, and 12.9 % in the control, W, F, and W + F plots, respectively (Fig. 6a). For ALF, the estimated mean seasonal SCE was underestimated by 10.0 %, 12.6 %, 13.2 %, and 14.5 % in the control, W, F, and W + F plots, respectively (Fig. 6b).

## Discussion

### Microclimatic factors of SCE

The dependence of SCE on soil moisture and temperature has been reported in many ecosystems (Högberg et al. 2001; Wan et al. 2007), but their relative importance is still controversial for semiarid ecosystems (Huxman et al. 2004). In our study, the dependence of SCE on soil moisture and temperature varied with species and treatment. Soil temperature was more important than moisture in regulating the seasonal patterns of SCE in all treatments for BNE (Fig. 2 and Table 3) while only in the control and watered plots for ALF (Fig. 3 and Table 3). The SCE of ALF in the fertilized plots was mainly regulated by moisture (Fig. 3 and Table 3). Differences in plant activity, soil microbes, and substrate supply between communities and treatments may account for these observations. Our results were consistent with those of Wan et al. (2007) who found that soil temperature was more important than moisture in determining the seasonal dynamics of SCE in a grassland ecosystem. Fertilization can increase the dependence of SCE on soil moisture in both communities because fertilization can lead to a larger depletion of soil water in the rooting zone (Harpole et al. 2007). The addition of water generally increased the temperature dependence of SCE for ALF, supporting Riveros-Iregui et al. (2007) who found that the relationship between SCE and soil temperature was regulated by the availability of the soil water in a semiarid forest.

### Positive effects of water addition on SCE

SCE generally has positive linear correlations with moisture in arid and semiarid grassland ecosystems. The addition of water is thus often assumed to stimulate SCE in such ecosystems (Wan et al. 2007; Liu et al. 2009; Yan et al. 2011). Improved availability of water

would not only directly stimulate respiration and microbial and root activity, but also indirectly increase SCE via the stimulation of plant growth, allocation of below-ground C, and substrate availability (Williams 2007; Liu et al. 2009; Yan et al. 2011). Our study demonstrated that the addition of water consistently increased SCE by 13–53 % in the two grasslands over the 2 years (Fig. 4), similar to the 15.7–31.6 % increases of Wan et al. (2007) and Liu et al. (2009) in grassland ecosystems. The positive responses of SCE to the addition of water were dependent on plant species and measuring period, in agreement with our first hypothesis.

Adding water increased the SCE for ALF more than for BNE across the entire experimental period, indicating that the SCE of ALF was more sensitive to changes in the availability of water than the SCE of BNE (Fig. 4). This may be ascribed to the differences in the microbial compositions of the soils and the species-specific water sensitivity of plant growth and microbial activity. Leaves and stems from a N-fixing species had a lower C:N ratio and showed faster decomposition rates than species with relatively higher C:N ratio (Tateno et al. 2007; Shi et al. 2011). Plant material left in the collars in ALF may therefore produce more microbial respiration than those in BNE during the decomposition of organic matter. Furthermore, we found that the addition of water over the 2 years of the experiment increased AGB and FRB for the 0–10 cm layer, on average, by 60 % and 73 % for ALF and by 35 % and 75 % for BNE, respectively (Fig. 5), indicating greater response of AGB in ALF in response to the addition of water. In addition, different proportion of the root and microbial respiration within different communities also may have resulted in different responses of respiration to water (Chen et al. 2004). The SCE of ALF was stimulated more in dry seasons compared to wet seasons, suggesting that the effects of water on SCE was much stronger during dry periods, perhaps because soil moisture was a limiting factor and adding water stimulated more microbial and root respiration during the dry seasons. Gallardo and Schlesinger (1995) showed that microbial biomass could increase rapidly in wet soil after dry-wet cycles because the surviving microbes were able to use the C and nutrients released from the microbes killed by drought stress. Furthermore, precipitation was approximately 125 mm lower in 2011 than in 2010 (Fig. 1), which may have enhanced the responses of AGB and SCE to water in 2011 (Figs. 4 and 5). Increases in SCE

for BNE due to the addition of water, however, did not differ greatly between dry and wet seasons. These different responses of SCE to water may be ascribed to differences in the microbial compositions of the soils and to the root activities in BNE and ALF.

Contrary to the above positive direct and indirect effects, the addition of water can negatively influence SCE indirectly by reducing soil temperature (Wan et al. 2007). Lower soil temperature may suppress respiration and microbial and root activities. The negative relationship we observed between the changes in SCE induced by the addition of water and the changes in soil temperature (data not shown) for ALF is consistent with this proposition. The influence of the availability of soil water on SCE via changes in soil temperature, however, was not observed for BNE. In general, the positive direct and indirect effects on SCE of adding water were much stronger than the negative indirect effect from the reduction of soil temperature, so the two grasslands thus experienced a net enhancement of SCE. All these observations indicated that the addition of water could enhance SCE in semiarid grassland, and the positive effects of water were mediated by species and measuring period, also supporting our first hypothesis.

#### Effects of fertilization on SCE

The availability of nutrients influences SCE via microclimatic factors, ecosystemic productivity, the allocation of assimilated sugars belowground and litter decomposition, and consequently the supply of C substrates for roots, microbial activity, and respiration (Craine et al. 2001; Kim 2008; Xu and Wan 2008). In our study, SCE consistently increased for ALF with P fertilization (Fig. 4f), this can be explained by the stimulation of AGB (increased by 80 %) and FRB for the 0–10 layer (increased by 120 %) (Fig. 5), but also by an increase in P availability in a low-P system, which may result in an increase of microbial biomass and respiration. Under conditions of water deficit, the ALF allocates the P-fertilizer to develop a fine root system to access more of the soil water. Our results did not agree with those of Keith et al. (1997) who showed that P fertilization decreased SCE by 8 % in a forest dominated by *Eucalyptus pauciflora*, which however is a non-N-fixing plant. The net change in SCE depends on the balance between microbial and root respiration and on the total productivity and allocation

of above- and belowground biomass. Keith et al. (1997) ascribed the reduction of SCE to lower root activity resulting from a reduced allocation of assimilated belowground resources. Purple alfalfa is an N-fixing plant, the addition of P-fertilizer can stimulate its root activity and exudates production (Li et al. 2011), increasing SCE. This may explain the inconsistency of the effect of P on SCE between this study and Keith et al. (1997). Few reports have addressed the effects of P-fertilizer on SCE, more work is necessary to determine the different response mechanisms of SCE to P fertilization operating within different ecosystems. Also, fertilization increased SCE more during wet periods (Fig. 4f), potentially indicating an increased availability of nutrients due to higher levels of soil moisture.

The effects of NP fertilization on the SCE of BNE varied seasonally, from significant increases in wet-2010 to small reductions in dry-2011 to no response in wet-2011 (Fig. 4e). Such differences in SCE in response to fertilization represent the net result of many processes that involve microbial and root activity (Keith et al. 1997). During the first wet season, SCE increased primarily through enhanced plant growth, root and microbial activity. Fertilization stimulated AGB and FRB for the 0–10 cm layer by 126 and 199 % in 2010, respectively (Fig. 5). During the dry season of 2011, soil moisture, which may have suppressed respiration and root and microbial activity (Suseela et al. 2012), was significantly lower in the fertilized plots than in the control plots (Fig. 4a). Harpole et al. (2007) observed that increased plant growth and productivity with fertilization could result in greater evapotranspiration and a more rapid depletion of soil water in the rooting zone, which may in turn suppress plant growth and root activity. Morell et al. (2012) also showed that a reduced availability of water limited the positive response of plant growth and root respiration to fertilization. In support of this speculation, we found that increased plant growth and productivity under NP fertilization resulted in a significant depletion of soil water storage for 0–60 cm layer by 35 % for BNE (Fig. S1), which can constrain plant and microbial activity, belowground C allocation as well as decomposition of plant litter and soil organic matter (Davidson and Janssens 2006). As a consequence, this would result in reduced supply of C substrate for roots and microorganisms, leading to decreased respiration. Nevertheless, during the second

wet season, the positive effects from stimulated plant growth (Xu and Wan 2008) and increased decomposition of roots (Kim 2008) after fertilization may be offset by decreases in the relative allocation of belowground C by plants (Haynes and Gower 1995; Bowden et al. 2000; Craine et al. 2001), despite an increase in the availability of nutrients and enhanced plant production from relatively higher levels of soil moisture. Although we could not calculate the relative partitioning of C belowground, the SCE of BNE did not discernibly change in the fertilized plots during the wet season of 2011 (Fig. 4e). Furthermore, the long-term application and/or high amounts of N may induce the accumulation of toxic compounds and suppress the activity of soil microbes (Guo et al. 2010; Janssens et al. 2010) and thus decrease heterotrophic respiration. The different responses to fertilization of SCE for ALF and BNE may be attributed to the differences in fertilizers and the phenological patterns of the plants. In addition, the addition of P fertilizer to ALF did not cause more depletion of soil water storage for 0–60 cm layer compared to control plots (Fig. S2), which was inconsistent with that of BNE. Our observations suggested that P fertilization in ALF may cause net losses of soil C, whereas NP fertilization in BNE may lead to net gains of soil C.

The results generally indicated that the seasonal variation of SCE was mainly regulated by water in dry periods and by nutrients in wet periods. The SCE of BNE, however, showed no response to fertilization during the wet season of 2011 (Fig. 4e). Our results, then, highlight the inconsistent responses of SCE to fertilization, supporting our second hypothesis. Furthermore, we found a greater stimulation of SCE by the addition of water in the fertilized than the unfertilized plots as well as larger increases in SCE in the watered than the unwatered plots under fertilization treatment for ALF (Figs. 4e and f). These results indicated that water can intensify the positive effect of P fertilization on SCE of ALF. Similar patterns were also observed for BNE during the first wet season (Fig. 4e). The SCE of BNE was reduced in the fertilized plots due to reductions in soil water content during the dry season of 2011 (Fig. 4e); however, the addition of water in the fertilized plots may have compensated for the decrease in SCE by changing the availability of soil water (Williams 2007). No synergistic effects of water and fertilizer were observed during the wet

season of 2011 for BNE (Fig. 4e). All the above observations indicated that changes in SCE induced by fertilization were not only regulated by period and/or species, but also by the availability of soil water.

The  $Q_{10}$  of SCE and implications for estimating C fluxes

Climatic changes and/or anthropogenic perturbations can affect the  $Q_{10}$  of SCE. Irrespective of the stimulation of SCE by the addition of water, no effects on  $Q_{10}$  were observed for BNE (Fig. 2b). In contrast, adding water not only stimulated SCE of ALF, but also increased the  $Q_{10}$ , indicating that the effects of water on  $Q_{10}$  were dependent on species, possibly because differences in the microbial compositions of the soils (Suseela et al. 2012) and the species-specific water sensitivity of plant growth and root activity (Yuste et al. 2004). The changes in  $Q_{10}$  may have been the result of several mechanisms, including concurrent changes in substrate availability, root and microbial activity, and a shift in the structure of the soil microbial community (Luo et al. 2001; Zhou et al. 2006; Suseela et al. 2012). The addition of water can stimulate plant growth and the allocation of belowground C as well as the decomposition of soil organic matter, especially in arid and semiarid ecosystems. As a consequence, water would increase the supply of C substrates for roots and microorganisms, leading to an increased  $Q_{10}$  of SCE (Fig. 3b). The increase in  $Q_{10}$  in the water treatment for ALF confirmed the potential of the availability of soil water to modify the sensitivity to temperature. Our results are consistent with those reported in a previous study of an herbaceous community and tree seedlings (Suseela et al. 2012) in which the annual  $Q_{10}$  of heterotrophic respiration was positively correlated with moisture.

The F and W + F treatments decreased  $Q_{10}$  in both communities (Figs. 2b and 3b). Reductions in soil water storage in rooting zone after fertilization can suppress root and microbial activity, which should result in decreases in  $Q_{10}$  (Davidson and Janssens 2006). Previous studies have reported lower sensitivity to temperature due to dry soils, perhaps largely due to substrate limitation caused by the limited diffusion of solutes in thin films of water (Davidson et al. 2006; Carbone et al. 2008; Suseela et al. 2012). Moreover, such a decrease in  $Q_{10}$  with fertilization may be related

to the acclimatization of soil respiration, which may possibly result from changes in the composition of the microbial community (Zogg et al. 1997) and/or a reduced respiratory capacity of the soil (Davidson et al. 2006; Davidson and Janssens 2006). The addition of water in the fertilized plots, however, may have compensated for the decrease in moisture, thus the overall decrease in  $Q_{10}$  in the W + F treatment may largely be the result of a shift in the structure of the soil microbial community. These observations suggest that the addition of water may increase the temperature sensitivity of SCE, and fertilization may reduce the temperature sensitivity in semiarid grassland, mediated by species, supporting our third hypothesis. Changes in  $Q_{10}$  due to changes in climate and/or land-use management may have the potential to exacerbate or offset, at least partially, the additional release of C that would be stimulated by global warming.

SCE is often modelled as a simple temperature-response function due to its simplicity. Our results indicated an underestimation of SCE by the temperature-response functions over 2 years (Fig. 6). Furthermore, the degree of underestimation (8–15 %) was regulated by water and/or fertilizer for both communities, perhaps because the addition of water and/or fertilizer changes the relationship between belowground biological activity and temperature. We therefore conclude that the typical correlation between SCE and temperature observed on an annual scale does not imply a causal relationship. Models that rely on  $Q_{10}$  can thus produce erroneous results (underestimates in our study) when predicting future emissions of soil CO<sub>2</sub> under conditions of global warming (Yuste et al. 2004). Our results agreed with those of Wan et al. (2007) who suggested that simple temperature-response functions should not be used to represent future responses of SCE. Given that small changes in SCE can significantly intensify or mitigate current atmospheric increases of CO<sub>2</sub> (Xu and Qi 2001), with potential implications to climate change, the underestimation of SCE by a simple temperature-response function may confound the predictions of terrestrial C cycles.

## Conclusions

The addition of water significantly stimulated the mean seasonal SCEs of BNE and ALF throughout

the growing seasons. P fertilization consistently enhanced the SCE of ALF, but the effects of NP fertilization on SCE for BNE varied seasonally from significant increases to small reductions to no response. Water stimulated the  $Q_{10}$  of SCE in ALF but had no effect in BNE. Fertilization, however, reduced the  $Q_{10}$  of SCE in both communities. We therefore conclude that SCE and its sensitivity to temperature in response to water and fertilizer may be mediated by plant species and measuring period in semiarid grassland. Our study highlights the importance and complexity of both direct and indirect effects on the biotic (plant and microbial activity via substrate regulation) and abiotic (soil temperature and moisture) mechanisms associated with the activity of the two grassland communities subjected to different treatments. Models that rely on  $Q_{10}$  can underestimate the prediction of soil CO<sub>2</sub> emissions under conditions of global warming at the study site. Simple temperature-response functions should therefore not be used to represent future responses of SCE, and a more mechanistic representation that includes the availability of ecosystemic water and nutrients, vegetation, microbial dynamics, and substrate supply is needed.

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