

Article

# Stability of Ecosystem CO<sub>2</sub> Flux in Response to Changes in Precipitation in a Semiarid Grassland

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**Abstract:** Carbon dioxide (CO<sub>2</sub>) flux provides feedback between C cycling and the climatic system. There is considerable uncertainty regarding the direction and magnitude of the responses of this process to precipitation changes, hindering accurate prediction of C cycling in a changing world. We examined the responses of ecosystem CO<sub>2</sub> flux to ambient precipitation and experimentally decreased (−35%) and increased precipitation (+20%) in a semiarid grassland in China between July 2013 and September 2015. The measured CO<sub>2</sub> flux components included the gross ecosystem productivity (GEP), net ecosystem CO<sub>2</sub> exchange (NEE), ecosystem respiration (Re), and soil respiration (Rs). The results showed that the seasonal and diurnal patterns of most components of ecosystem CO<sub>2</sub> flux were minimally affected by precipitation treatments, with less than 4% changes averaged across the three growing seasons. GEP and NEE had a quadratic relationship, while Re and Rs increased exponentially with soil temperature. GEP, RE, and Rs, however, decreased with soil moisture. Decreased precipitation reduced the dependence of CO<sub>2</sub> flux on soil temperature but partly increased the dependence on soil moisture; in contrast, increased precipitation had the opposite influence. Our results suggested a relatively stable CO<sub>2</sub> flux in this semiarid grassland across the tested precipitation regimes.

**Keywords:** ecosystem respiration; net ecosystem exchange; response function; soil moisture; soil respiration; soil temperature

## 1. Introduction

Semiarid grassland ecosystems are among the most vulnerable ecosystems and are highly susceptible to global climate change [1,2]. Semiarid grassland ecosystems are also increasingly important drivers of the inter-annual variability of the global carbon (C) cycle [3]. Precipitation and the availability of soil water are the major limiting factors in semiarid ecosystems [4]. Precipitation directly affects soil moisture, which plays a prominent role in terrestrial ecosystems by affecting plant productivity and soil processes [5,6]. In turn, soil moisture modulates the impacts of other drivers of global change, such as elevated atmospheric CO<sub>2</sub> levels, temperature, and nitrogen deposition [7–9]. Therefore, the responses of ecosystem processes to variations in soil moisture have become a focus of current ecological and environmental research.

Photosynthesis and plant and soil respiration, which are the main components of the ecosystem CO<sub>2</sub> flux, are the major processes determining the productivity and C cycling in terrestrial ecosystems.

Although the responses of these processes to precipitation changes (both increasing and decreasing precipitation) have been studied in various ecosystems, considerable uncertainty remains regarding the direction and magnitude of the responses [3,4,10,11]. Studies in arid and semiarid regions, where precipitation is expected to decrease [12,13], are particularly lacking. Such uncertainties and lack of knowledge make it difficult to accurately predict the responses to future scenarios of precipitation change [14,15].

The CO<sub>2</sub> flux at various levels (from leaf to ecosystem) may acclimate to changes in temperature [16–18], which is characterized by a downward or upward regulation in the shape of long- or short-term response functions of CO<sub>2</sub> flux to temperature at different thermal environments [18]. Such shifts in the response function can modulate the feedback between C cycling in terrestrial and climate systems [18,19]. For example, shifts in the response function of plant respiration due to warming are predicted to have the potential to reduce the annual CO<sub>2</sub> release by 35–80%, in comparison to a theoretical case without shifts in the response function [18,19]. However, the shift in the components of CO<sub>2</sub> flux to soil moisture has rarely been examined. This information is urgently needed because such a shift in CO<sub>2</sub> flux would have important implications for ecosystem C cycling, which would be potentially similar to acclimation to temperature on ecosystem C cycling. This effect is particularly important for ecosystems limited by water, as changes in precipitation regimes can affect C dynamics and fluxes and are expected to have significant feedback on the terrestrial C cycle [20].

We investigated the components of ecosystem CO<sub>2</sub> flux (photosynthesis and plant and soil respiration) in plots with manipulated levels of precipitation in a *Stipa capillata* L. grassland in a semiarid region of the northwestern China. The *S. capillata* is a dominant native species adapted to the highly variable precipitation in this semiarid region [21,22]. We hypothesized that CO<sub>2</sub> flux components in this *S. capillata* grassland would not vary widely across precipitation regimes (H1). We also hypothesized that increased precipitation would enhance the dependence of CO<sub>2</sub> flux components (photosynthesis and respiration) on temperature, but decreased precipitation would weaken such dependence (H2) and that increased precipitation would weaken the dependence of CO<sub>2</sub> flux components on soil moisture, but decreased precipitation would enhance the dependence on soil moisture (H3). Hypotheses H2 and H3 were generated because long-term changes in precipitation might significantly change soil temperature and moisture, which in turn would lead to the shifts in the response curves of CO<sub>2</sub> flux components to the altered environment. The specific objectives of this study were to understand the following questions: (1) How does precipitation change influence components of ecosystem CO<sub>2</sub> flux? (2) Is the dependence of CO<sub>2</sub> flux components on soil temperature or moisture affected by precipitation? In our study, the precipitation treatments included ambient precipitation (AP), decreased precipitation (DP, 35% decreased), and increased precipitation (IP, 20% increased). Each CO<sub>2</sub> flux component was measured during the growing seasons from 2013 to 2015. We analysed the changes in the response functions of each CO<sub>2</sub> flux component to soil temperature or moisture to determine whether the dependence of these components on soil temperature or moisture shifted with precipitation manipulation.

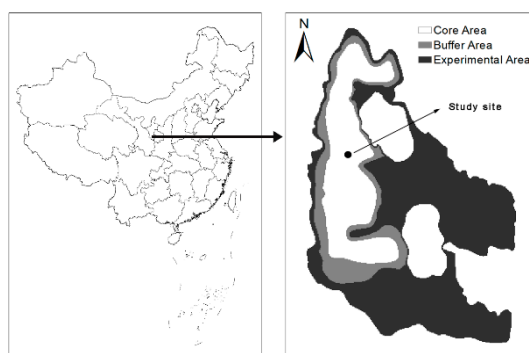
## 2. Materials and Methods

### 2.1. 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 centre of the Loess Plateau (Figure 1). The grassland protection zone was established in 1984, with an area of 4000 km<sup>2</sup> and elevation ranging from 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 448 mm (from 1957 to 2011). The growing season (May to September) precipitation accounts for 81% of the total annual precipitation. The soil in the study area is a mountain grey-cinnamon soil classified as

a Calci-Orthic Aridisol according to the Chinese taxonomic system, which is equivalent to a Haplic Calcisol in the FAO/UNESCO system.

This experiment was established in an *S. capillata* grassland derived from farmland that was abandoned 30 years ago. The grassland has been protected from mowing and grazing by the Yunwushan Natural Grassland Management Bureau since the farmland was abandoned. In the experiment, a random block design was used with four replicates and 1.0–2.0 m between blocks. Each block contained three 4.0 m × 5.0 m plots randomly arranged with 1.0 m between plots. The three plots in each block received one of the following three precipitation treatments: ambient precipitation (AP), decreased precipitation (DP), or increased precipitation (IP). Soil properties were the same among the plots. 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 the rain, and they were removed after approximately one-third of the duration of the rain. The amount of precipitation excluded was calculated from the measurement of rainfall over time and recorded with an automatic rain gauge at the site every 10 min. Water, equivalent to approximately 20% of the precipitation event, was added manually and evenly to the IP plots immediately after the end of the rain over both plants and soil; thus, the rate of application was similar to the rate of infiltration into the soil. Snowfall, accounting for <5% of the total annual precipitation, was not manipulated in this experiment. The precipitation was manipulated from July 2013 to September 2015.



**Figure 1.** Location of the study site.

## 2.2. Measurement of Ecosystem CO<sub>2</sub> Flux and Soil Temperature and Moisture

The seasonal pattern of ecosystem CO<sub>2</sub> flux, including net ecosystem CO<sub>2</sub> exchange (NEE), ecosystem respiration (Re), and soil respiration (Rs), was measured 2–8 times per month between 09:00 and 11:00 during the growing season (from July 2013 to September 2015) using a revised chamber system described by Chen et al. [23]. The diurnal pattern of CO<sub>2</sub> flux (NEE, Re, and Rs) was measured between 07:00 and 18:00 on 17 August and 25 September 2013; 15 July, 14 August, and 29 September 2014; and 28 July and 15 August 2015. NEE and Re were measured by an infrared gas analyser (LI-840, LI-COR Inc., Lincoln, NE, USA) attached to a cubic transparent chamber (50 cm × 50 cm × 50 cm) placed over a square PVC base (50 cm × 50 cm and 10 cm in height) that was inserted 7 cm into the soil in each plot. Two small fans in the top of the chamber mixed the air during the measurement, and a temperature probe was inserted into the chamber to determine the air temperature. A pump (6262-04, LI-COR Inc.) transported air from the chamber to the LI-840 to measure the CO<sub>2</sub> concentration. The chamber was lifted and vented after each NEE measurement. The chamber was then replaced on the base, covered by a lightproof cloth mantle, and the CO<sub>2</sub> flux (Re) was measured. Rs was measured using the same infrared gas analyser attached to a cylindrical chamber (20 cm in diameter and 20 cm in height) placed over a PVC base (20 cm in diameter and 10 cm in height) and inserted 7 cm into the soil in each plot. The plant in the PVC base was removed by hand a week prior the start of the experiment to exclude the effects of plant respiration and photosynthesis on the Rs measurement. A small fan in

the top of the chamber mixed the air during the measurement, and a temperature probe was inserted into the chamber to determine the air temperature. The same pump was used to pump air from the chamber to the LI-840 for measuring the CO<sub>2</sub> concentration.

The data for measurements of NEE, Re, and Rs were logged into a computer using the LI-840 data-acquisition software. The CO<sub>2</sub> concentrations inside the chamber were recorded every second for 2.5 min after the chamber was placed on the base. Our measurement showed that change in air temperature inside the chamber was less than 0.2 °C during the 2.5 min measurement, and thus the change in air temperature could be neglected. The attenuation of PAR by the chamber was less than 5%. There was no fog on the chamber during the measurement. Only data for the last 120 s were used to calculate NEE, Re, and Rs according to the following equation [23,24]:

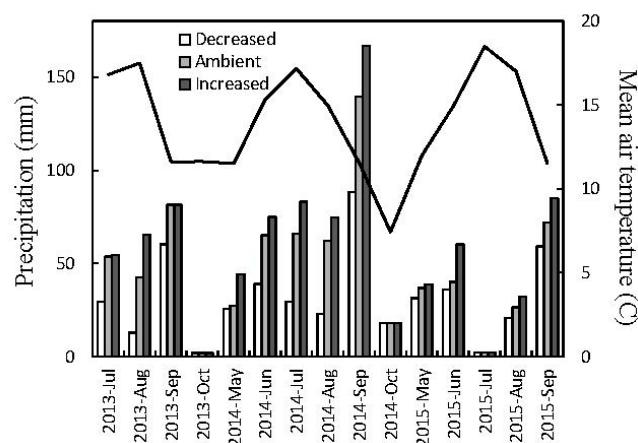
$$F = \frac{V \times P_{av} \times (1000 - W_{av})}{R \times S \times (T_{av} + 273)} \times \frac{dc}{dt} \quad (1)$$

where F is the CO<sub>2</sub> flux components (NEE, Re, or Rs,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), V is the volume of the chamber ( $\text{m}^3$ ), P<sub>av</sub> is the average pressure (kPa) during measurement, W<sub>av</sub> is the average water vapor mole fraction ( $\text{mmol mol}^{-1}$ ) during measurement, R is the ideal gas constant ( $8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ ), S is the surface area covered by the chamber ( $\text{m}^2$ ), T<sub>av</sub> is the average temperature (°C) during measurement, and dc/dt is the slope of the fitted equation between CO<sub>2</sub> and time.

The gross ecosystem productivity (GEP) was calculated as

$$\text{GEP} = -\text{NEE} + \text{Re} \quad (2)$$

Soil temperature and volumetric moisture content at a depth of 0–10 cm were measured with time-domain transmission sensors (Acclima, Meridian, ID, USA) in each plot every 10 min during the experimental period with a Campbell Scientific CR1000 data logger (Campbell Scientific, Logan, UT, USA). The climatic data, including rainfall and air temperature, were recorded by a weather station at the study site. The monthly mean precipitation in each treatment and the air temperature during the experimental period are presented in Figure 2.



**Figure 2.** Monthly precipitation (columns) and mean air temperature (solid line) during the experimental period (July 2013 to September 2015) in a semiarid grassland of the northwest China.

### 2.3. Data Analysis

A quadratic equation was used to fit the response function of GEP or NEE to soil temperature [25]:

$$F = a \times T^2 + b \times T + c \quad (3)$$

where  $F$  is GEP or NEE;  $T$  is soil temperature at a depth of 0–10 cm; and  $a$ ,  $b$ , and  $c$  are parameters. The values of  $a$  and  $b$  indicate the quadratic and linear slopes of the response function.

The optimal temperature ( $T_0$ ) at which NEE and GPP were the smallest and greatest, respectively, was calculated from the parameters of the temperature–response curve Equation (3) as follows:

$$T_0 = -\frac{b}{2a} \quad (4)$$

An exponential equation was used to fit the response function of  $R_e$  or  $R_s$  to soil temperature [17,18]:

$$F = a \times e^{b \times T} \quad (5)$$

where  $F$  is  $R_e$  or  $R_s$ , and  $a$  and  $b$  are the parameters. The value of  $b$  indicates the slope of the response function.

The temperature sensitivity ( $Q_{10}$ ) of the respiration rate ( $R_e$  or  $R_s$ ), a metric that describes the proportional increase in the respiration rate for a 10 °C increase in temperature, was calculated from the slope ( $b$ ) of the temperature–response curve by Equation (5) as follows:

$$Q_{10} = e^{10 \times b} \quad (6)$$

A linear equation was used to fit the response function of  $CO_2$  flux component to soil moisture [26–28]:

$$F = a + b \times M \quad (7)$$

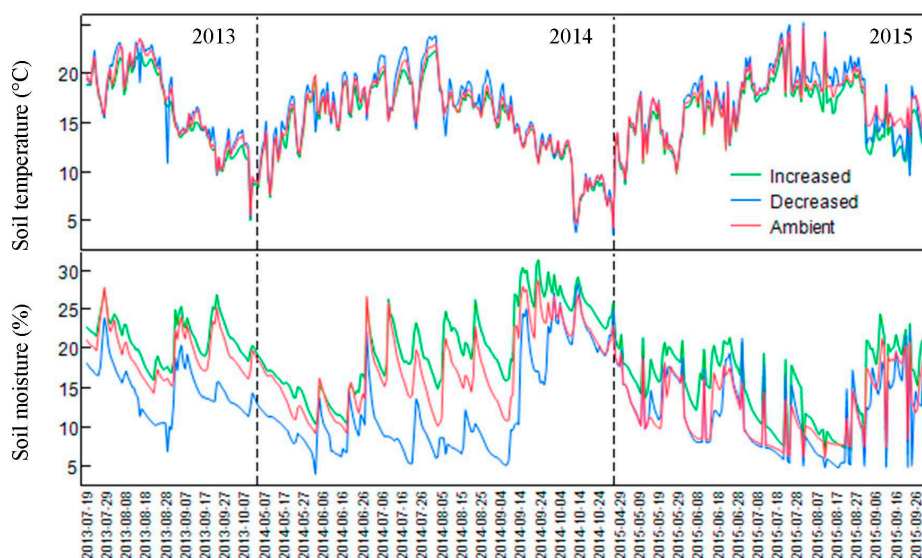
where  $F$  is the  $CO_2$  flux,  $M$  is soil moisture at a depth of 0–10 cm, and  $a$  and  $b$  are parameters. The value of  $b$  indicates the slope of the response function.

A repeated measure of ANOVA was conducted to compare the  $CO_2$  flux components among the precipitation treatments, stages of the season (early, middle, or late), and interactions between the precipitation treatments and stages of the season through 2013 to 2015. Linear and nonlinear regression analyses were conducted to fit the equations. We tested normal distribution (Shapiro-Wilk test) and homogeneity of variances (Levene test) for each metric prior to statistical analysis. All data were analysed with JMP 10.0 (SAS Institute, Cary, NC, USA). In this study, although there are lots of scatters in soil moisture, nearly all the fittings of  $CO_2$  flux to soil moisture were significant at  $p < 0.05$ . Therefore, our fittings reflected the general response pattern of  $CO_2$  flux to soil moisture. However, we recommended that such measurements should be intensified to avoid scatters.

### 3. Results

#### 3.1. Changes in Microclimate

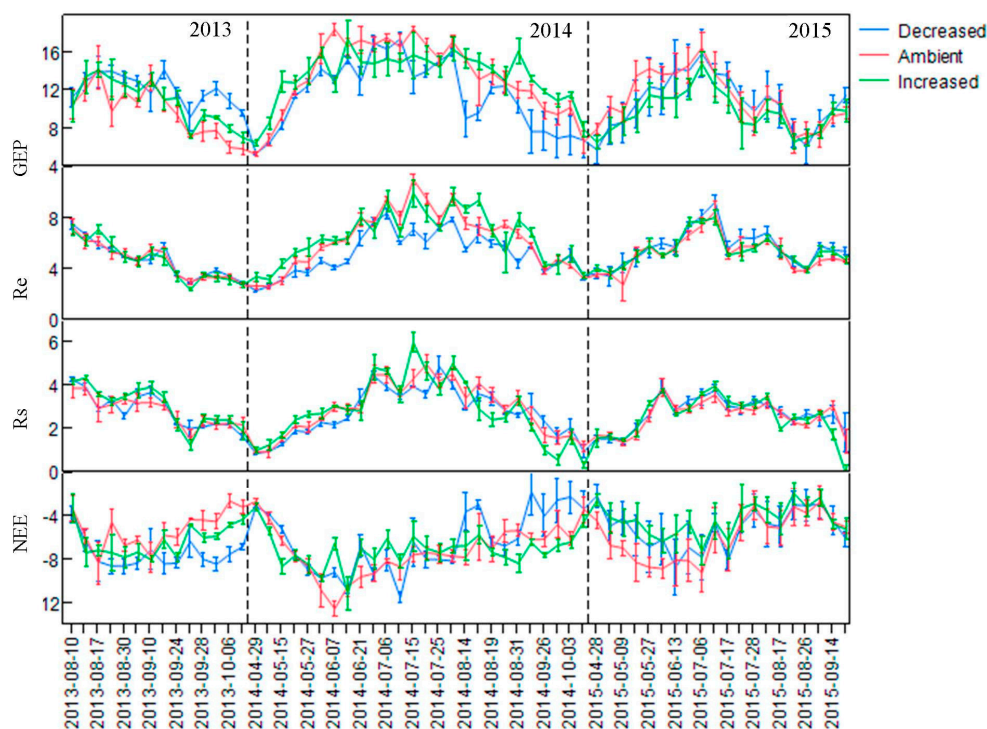
When averaged across the experimental period (July 2013 to September 2015), the mean rainfall for AP, DP, and IP plots during the growing season were 291 mm, 191 mm, and 354 mm, respectively (Figure 2). The rainfall for AP, DP, and IP corresponded to 55%, 10% and 90%, respectively, of the percentile in the 1957–2011 growing season rainfall distribution, presenting a normal year, drier year, and wetter year, respectively. The precipitation treatments significantly changed soil temperatures during the growing season ( $p = 0.0091$ ), with a 0.26 °C increase in DP and a 0.59 °C decrease in IP relative to AP (Figure 3). The averaged soil moisture was 21% higher in IP but 16% lower in DP ( $p < 0.0001$ ) compared to AP (Figure 3).



**Figure 3.** Daily mean soil temperature and moisture at 0–10 cm depth for each treatment during the experimental period (July 2013 to September 2015) in a semiarid grassland of northwest China. Values are means of the replicates. Vertical dashed lines separate different years.

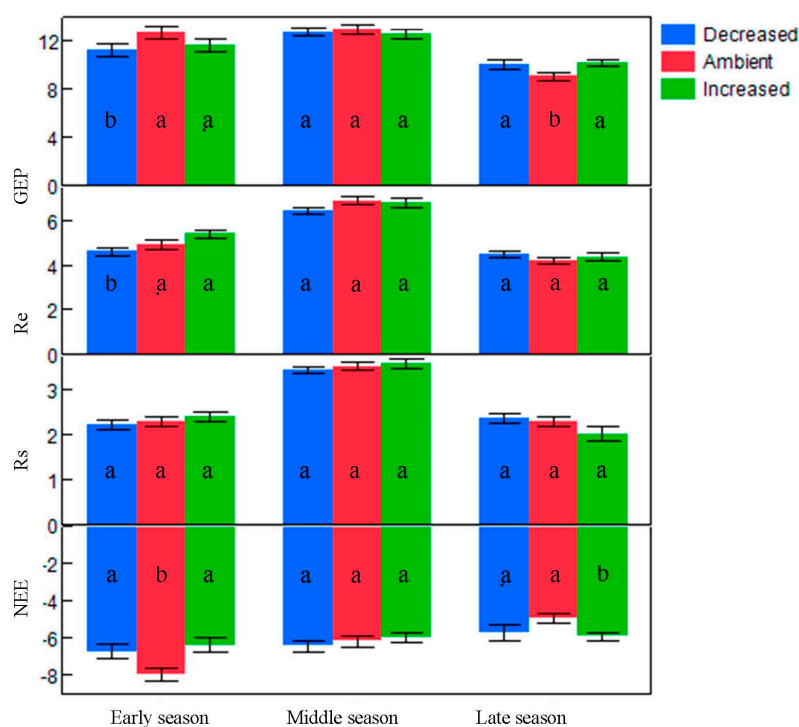
### 3.2. Seasonal and Diurnal Changes in Ecosystem $\text{CO}_2$ Flux

The components of ecosystem  $\text{CO}_2$  flux varied significantly with the stage of the growing season. There were relatively higher GEP and respiration rates ( $R_e$  and  $R_s$ ) during the mid-season (July and August) but more negative NEE and, thus, a high rate of C sequestration in the early season (May and June) (Figures 4 and 5, Table 1).



**Figure 4.** Seasonally dynamics of ecosystem  $\text{CO}_2$  flux through 2013 to 2015 of each precipitation treatment in a semiarid grassland of northwest China. GEP,  $R_e$ ,  $R_s$ , and NEE are gross ecosystem productivity, ecosystem respiration, soil respiration, and net ecosystem  $\text{CO}_2$  exchange, respectively. Values are mean  $\pm$  standard error. The unit of  $\text{CO}_2$  flux is  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Vertical dashed lines separate different years. The sampling size for each treatment is 4.

The precipitation treatment did not significantly affect the rate of most CO<sub>2</sub> flux component across the three growing seasons, with less than 4% changes in these components compared with ambient treatment. When tested within each stage of the growing season, DP showed a trend to decrease GEP and Re in the early stage of the season. Furthermore, both DP and IP increased GEP in the late stage of the season (Figure 5). NEE decreased (less negative) in the early stage of the season (+15 and +19%) but increased (more negative) in the late stage of the season (−15 and −19%) in both precipitation treatments. The Rs was not affected at any stage of the season (Figure 5).



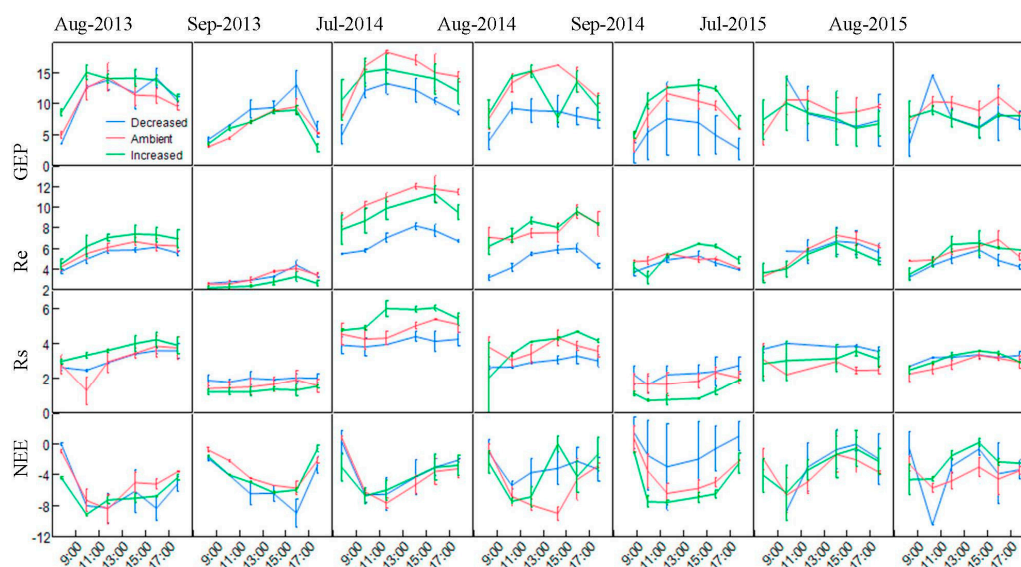
**Figure 5.** Averaged ecosystem CO<sub>2</sub> flux at early, middle, and late part of the growing season through 2013 to 2015 of each precipitation treatment in a semiarid grassland of the northwest China. GEP, Re, Rs, and NEE are gross ecosystem productivity, ecosystem respiration, soil respiration, and net ecosystem CO<sub>2</sub> exchange, respectively. Values are mean  $\pm$  standard error. The unit of CO<sub>2</sub> flux is  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . For each stage of the growing season, bars with different lowercase are significantly different at  $p < 0.05$ .

**Table 1.** ANOVA results of precipitation treatment and stage of season on gross ecosystem productivity (GEP), ecosystem respiration (Re), soil respiration (Rs), and net ecosystem CO<sub>2</sub> exchange (NEE) in a semiarid grassland of northwest China.

		GEP	Re	Rs	NEE
SS	Stage of season	1321.0	741.2	286.9	332.7
	Treatment	6.2	12.5	0.1	7.6
	Interaction	120.5	19.8	6.0	114.3
	Date	346.9	5.6	26.9	440.4
F	Stage of season	51.3	153.3	175.4	21.9
	Treatment	0.2	2.6	0.0	0.5
	Interaction	2.3	2.1	1.8	3.8
	Date	27.0	2.3	32.9	58.1
P	Stage of season	<0.0001	<0.0001	<0.0001	<0.0001
	Treatment	0.785	0.0755	0.9674	0.6047
	Interaction	0.0538	0.0857	0.1187	0.0048
	Date	<0.0001	0.1292	<0.0001	<0.0001

Degree of freedoms of the model, date, season, treatment, and interaction were 8, 1, 2, 2, and 4, respectively. Degree of error was 679.

Most diurnal patterns of CO<sub>2</sub> flux components were unaffected by precipitation treatments (Figure 6). Among the seven measurements of diurnal patterns, NEE was unaffected, and only one measurement of GEP was affected (decreased by DP in August 2014). The Re was unaffected in five measurements but decreased by DP in two measurements (July and August 2014). The Rs was unaffected in 2013, 2015, and August 2014, increased by IP in July 2014 but decreased in September 2014.



**Figure 6.** Diurnal pattern of CO<sub>2</sub> flux as affected by precipitation treatments at different stages of the growing season in a semiarid grassland of the northwest China. GEP, Re, Rs, and NEE are gross ecosystem productivity, ecosystem respiration, soil respiration, and net ecosystem CO<sub>2</sub> exchange, respectively. Values are mean  $\pm$  standard error. The unit of CO<sub>2</sub> flux is  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

### 3.3. Dependence of Ecosystem CO<sub>2</sub> Flux Components on Soil Temperature and Moisture

The GEP and NEE had a quadratic relationship with soil temperature. The rate of respiration (Re and Rs) increased exponentially with soil temperature (Figure 7, Table 2). These components of ecosystem CO<sub>2</sub> flux, however, decreased with soil moisture (Figure 7, Table 3). This was mainly due to decreased rates of these components in the late growing season when soil moisture was significantly higher, but the temperature was significantly lower than in the early and middle stages of the season (Figure 3). When averaged across each growing season, mean GEP and Re increased with precipitation during each season (Figure 8), indicating that CO<sub>2</sub> flux was dependent on growing season precipitation in this semiarid grassland.

The dependence of GEP on soil moisture and temperature was affected by the precipitation treatments. The GEP decreased with soil moisture, and the absolute value of the slope for the decreasing function (parameter b) increased by 9% in DP but decreased by 15% in IP relative to AP (Table 3). The dependence of GEP on soil temperature (the value of parameter b for the quadratic function) decreased by 41.1% in DP ( $p < 0.05$ ) but increased by 7.0% in IP ( $p > 0.05$ ). The  $T_0$  of this quadratic function increased by 1.24 °C in DP but decreased by 0.95 °C in IP (Table 2).



**Table 2.** Parameters for the relationships between CO<sub>2</sub> flux and soil temperature in a semiarid grassland of northwest China.

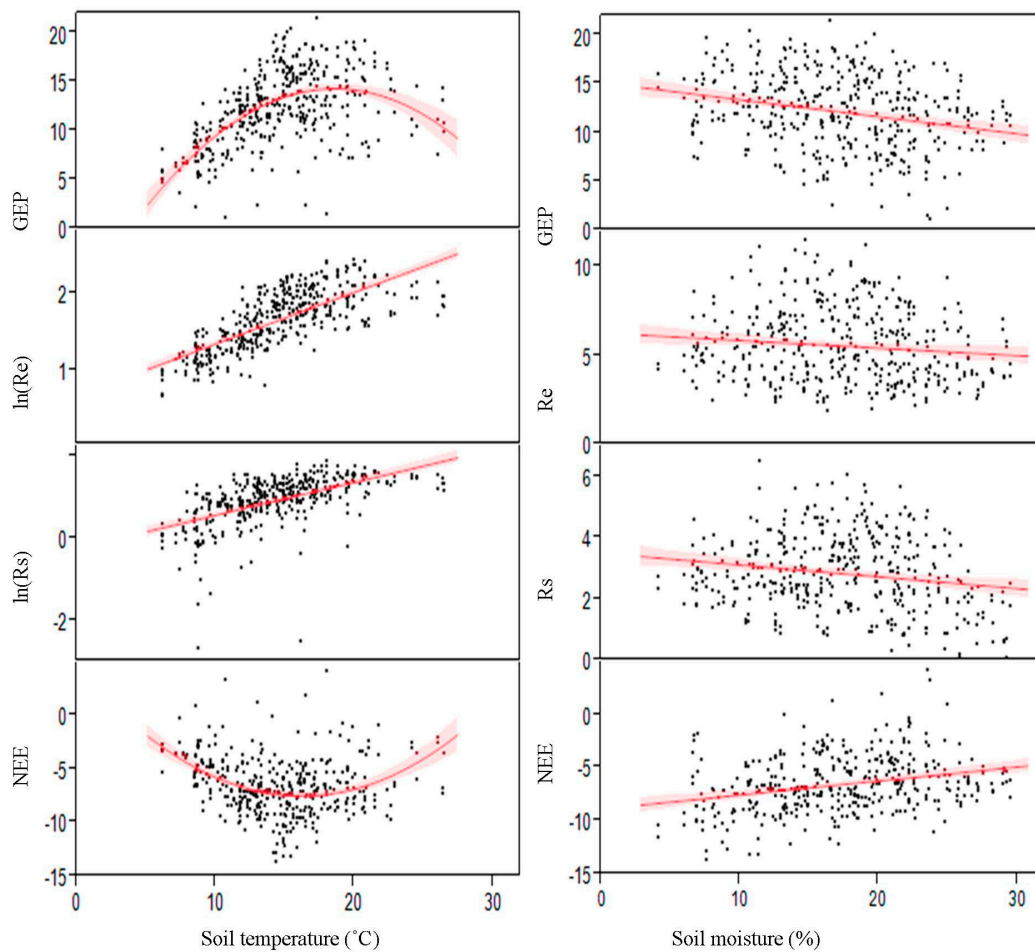
GEP = a × T <sup>2</sup> + b × T + c										
	a	SE(a)	b	SE(b)	c	SE(c)	T <sub>0</sub> (°C)	RMSE	R <sup>2</sup>	P
Across treatments	-0.065	0.006	2.419	0.198	-8.190	1.478	18.61	2.943	0.386	<0.01
Ambient precipitation	-0.078 a	0.014	2.861 a	0.398	-11.555 a	2.782	18.34	3.003	0.476	<0.01
Decreased precipitation	-0.043 b	0.010	1.684 b	0.325	-3.321 b	2.571	19.58	3.152	0.250	<0.01
Increased precipitation	-0.088 a	0.016	3.060 a	0.458	-11.862 a	3.175	17.39	2.488	0.452	<0.01
Re = a × e <sup>b×T</sup>										
	a	SE(a)	b	SE(b)	Q <sub>10</sub>	SE(Q <sub>10</sub> )		RMSE	R <sup>2</sup>	P
Across treatments	2.575	0.134	0.052	0.003	1.682	0.050		1.548	0.429	<0.01
Ambient precipitation	2.293 ab	0.208	0.064 a	0.005	1.896 a	0.095		1.516	0.517	<0.01
Decreased precipitation	2.401 a	0.158	0.046 b	0.004	1.584 b	0.063		1.048	0.566	<0.01
Increased precipitation	2.024 b	0.194	0.073 a	0.006	2.075 a	0.125		1.437	0.554	<0.01
Rs = a × e <sup>b×T</sup>										
	a	SE(a)	b	SE(b)	Q <sub>10</sub>	SE(Q <sub>10</sub> )		RMSE	R <sup>2</sup>	P
Across treatments	1.242	0.078	0.055	0.004	1.733	0.069		0.961	0.364	<0.01
Ambient precipitation	1.098 a	0.113	0.067 a	0.006	1.954 a	0.117		0.867	0.472	<0.01
Decreased precipitation	1.204 a	0.105	0.050 b	0.005	1.649 b	0.082		0.740	0.486	<0.01
Increased precipitation	1.017 a	0.151	0.072 a	0.009	2.054 a	0.185		1.100	0.330	<0.01
NEE = a × T <sup>2</sup> + b × T + c										
	a	SE(a)	b	SE(b)	c	SE(c)	T <sub>0</sub> (°C)	RMSE	R <sup>2</sup>	P
Across treatments	0.045	0.005	-1.469	0.161	4.443	1.199	16.32	2.388	0.175	<0.01
Ambient precipitation	0.058 a	0.011	-1.889 a	0.309	7.725 a	2.160	16.28	2.331	0.254	<0.01
Decreased precipitation	0.036 b	0.009	-1.207 b	0.300	2.671 b	2.370	16.76	2.905	0.122	<0.01
Increased precipitation	0.070 a	0.012	-2.077 a	0.341	7.647 a	2.363	14.84	1.851	0.215	<0.01

GEP, Re, Rs, and NEE are gross ecosystem productivity, ecosystem respiration, soil respiration, and net ecosystem CO<sub>2</sub> exchange, respectively. T is soil temperature at 0–10 cm depth, a, b, and c are parameters for each equation, respectively. T<sub>0</sub> is optimal temperature at which CO<sub>2</sub> flux is greatest. SE is the standard error for each parameter. RMSE is root mean square error. Temperature sensitivity (Q<sub>10</sub>) is calculated as e<sup>10×b</sup>. Standard error for Q<sub>10</sub> is calculated as Q<sub>10</sub> × 10 × SE(b). Values of the same parameters with the same lower-case letter were not statistically significant among precipitation treatments. The differences of parameters among treatments were identified as significant when the SE did not overlap. The sampling size for each treatment is 232.

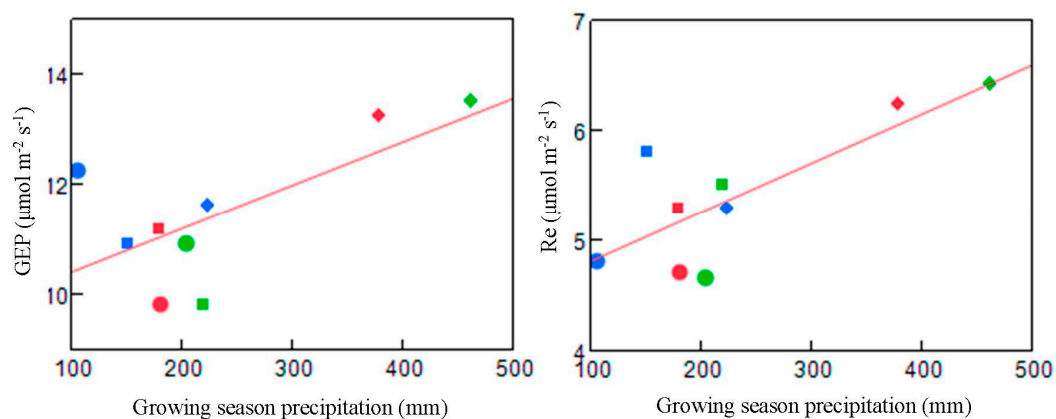
**Table 3.** Parameters for the relationships between CO<sub>2</sub> flux and soil moisture in a semiarid grassland of northwest China.

GEP = a + b × M							
	a	SE(a)	b	SE(b)	RMSE	R <sup>2</sup>	P
Across treatments	15.151	0.574	-0.175	0.032	3.616	0.070	<0.01
Ambient precipitation	17.845 a	1.236	-0.313 ab	0.066	3.843	0.137	<0.01
Decreased precipitation	15.769 b	0.800	-0.341 a	0.057	3.186	0.227	<0.01
Increased precipitation	18.124 a	1.129	-0.267 b	0.055	3.095	0.145	<0.01
Re = a + b × M							
	a	SE(a)	b	SE(b)	RMSE	R <sup>2</sup>	P
Across treatments	6.293	0.323	-0.043	0.018	2.033	0.014	0.02
Ambient precipitation	7.976 a	0.675	-0.121 a	0.036	2.100	0.074	<0.01
Decreased precipitation	5.528 b	0.395	-0.048 b	0.028	1.572	0.023	0.09
Increased precipitation	8.973 a	0.737	-0.154 a	0.036	2.021	0.117	<0.01
Rs = a + b × M							
	a	SE(a)	b	SE(b)	RMSE	R <sup>2</sup>	P
Across treatments	3.497	0.188	-0.039	0.010	1.185	0.033	<0.01
Ambient precipitation	3.863 b	0.375	-0.052 b	0.020	1.166	0.045	0.01
Decreased precipitation	3.084 c	0.255	-0.035 b	0.018	1.017	0.029	0.06
Increased precipitation	5.200 a	0.448	-0.114 a	0.022	1.227	0.165	<0.01
NEE = a + b × M							
	a	SE(a)	b	SE(b)	RMSE	R <sup>2</sup>	P
Across treatments	-8.858	0.399	0.132	0.022	2.516	0.081	<0.01
Ambient precipitation	-9.869 a	0.811	0.192 b	0.044	2.522	0.121	<0.01
Decreased precipitation	-10.240 a	0.680	0.293 a	0.049	2.707	0.231	<0.01
Increased precipitation	-9.151 a	0.733	0.113 c	0.036	2.011	0.067	<0.01

GEP, Re, Rs, and NEE are gross ecosystem productivity, ecosystem respiration, soil respiration, and net ecosystem CO<sub>2</sub> exchange, respectively. M is soil moisture at 0–10 cm depth, a and b are parameters for the linear equation, respectively. SE is the standard error for each parameter. RMSE is root mean square error. Values of the same parameters with the same lower-case letter were not statistically significant among precipitation treatments. The differences of parameters among treatments were identified as significant when the SE did not overlap. The sampling size for each treatment is 232.



**Figure 7.** Relationships between ecosystem CO<sub>2</sub> flux and soil temperature or soil moisture across all the treatments during the measuring period (July 2013 to September 2015). GEP, Re, Rs, and NEE are gross ecosystem productivity, ecosystem respiration, soil respiration, and net ecosystem CO<sub>2</sub> exchange, respectively. Ln(Re) or Ln(Rs) is the natural log transformed Re or Rs. The unit of CO<sub>2</sub> flux or natural log transformed CO<sub>2</sub> flux is  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .  $p < 0.05$  for all relationships.



**Figure 8.** Relationship between precipitation and gross ecosystem productivity (GEP) or ecosystem respiration (Re) during growing season. Values were averaged across each treatment in each year. Blue is decreased precipitation treatment, red is ambient precipitation treatment, green is increased precipitation treatment. Square was measured in 2013, diamond was measured in 2014, circle was measured in 2015.  $p < 0.05$  for both relationships.

In this study, NEE accounted for nearly 60% of GEP and was mainly determined by GEP ( $NEE = 1.662 - 0.666 \times GEP$ ,  $RMSE = 1.381$ ,  $R^2 = 0.777$ ,  $p < 0.01$ ). The effects of the precipitation treatments on dependence of NEE on soil temperature and moisture were similar to the effects on dependence of GEP. The DP decreased the slope for the NEE-temperature response function but increased the slope for the NEE-moisture response function; IP had the opposite effect on these dependencies (Tables 2 and 3).

The response functions of respiration ( $R_e$  and  $R_s$ ) to soil moisture and temperature also varied with treatments. The DP generally decreased the dependence of respiration on soil moisture (absolute values of the slope for the response function) and soil temperature (slope for the response function and temperature sensitivity ( $Q_{10}$ )) relative to AP, but IP increased these dependences (Tables 2 and 3). The effects of DP were greater than those of IP, probably due to larger changes in precipitation in DP (−35%) than in IP (+20%). For example, the  $Q_{10}$ s of  $R_e$  and  $R_s$  decreased by 16.5 and 15.6% in DP but increased by 9.4 and 5.1% in IP, respectively (Table 2).

## 4. Discussion

### 4.1. Response of $CO_2$ Flux to the Precipitation Treatments

Our results showed a seasonal pattern of  $CO_2$  flux in this semiarid grassland (Figures 4 and 5), which was mainly due to variations in plant growth throughout the growing season. A previous study at the same site showed that *S. capillata* is characterized by a higher growth rate early in the season and higher aboveground biomass accumulation at mid-season [29]. High growth rates often produce more negative NEEs and, thus, high rates of ecosystem C sequestration [30–32]. High above-ground biomass accumulation corresponds to a high GEP and, thus, high  $R_e$  and  $R_s$  because respiration is driven by photosynthesis-provided substrate in most ecosystems [33,34]. In our study,  $R_e$  and  $R_s$  were positively correlated with GEP ( $r = 0.683$  and  $0.419$ , respectively,  $p < 0.01$ ). The growth and accumulation of biomass in the ecosystem was lowest in the late stage of the growing season, resulting in a lower rate of each  $CO_2$  flux component (Figure 4). Our results are consistent with the dependence of the seasonal pattern of  $CO_2$  flux on plant growth observed in various grasslands [30,35–39].

We demonstrated that the seasonal and diurnal patterns of most  $CO_2$  flux component were not affected by increased or decreased precipitation in this study (Figures 4 and 5, Table 1). These results indicated that most components of  $CO_2$  flux were relatively stable in this semiarid grassland across the various precipitation scenarios, supporting our first hypothesis. The response of ecosystem  $CO_2$  flux to precipitation treatments was mainly manifested by changes in ecosystem productivity [40–42]. Ecosystem productivity generally increases with increasing precipitation [43–45] and decreases with decreasing precipitation [46,47]. In our study, however, above-ground biomass averaged across 2013 to 2015 was not affected by changes in precipitation, with mean aboveground biomass (post-experiment biomass) of 87.2, 88.0, and 88.9  $g\ m^{-2}$  in AP, DP, and IP plots, respectively. The most direct effect of the precipitation treatments on plant growth was the changes in the availability of soil water to plants [44]. However, soil water availability to plants remained constant at levels of 40–80% field capacity in the same region as this study [48], corresponding to 10.4–20.8% volumetric soil moisture at the same site of this study [49]. Soil moisture in our study was within this range in the three precipitation treatments during the early and middle stages of the growing season (Figure 3), indicating that the treatments did not affect the availability of soil water to plants. Soil moisture in DP was sometimes less than this range and, thus, may have influenced the stomatal performance of the leaves [50,51]. Furthermore, the little response of available soil moisture further indicated that soil water recharge from non-growing season precipitation might be important for determining the main processes of this ecosystem. Soil temperature in DP, however, was relatively higher than in AP, which may have partly enhanced the photosynthetic rate in this temperature-limited ecosystem [25,52], thus, may have offset the decreases in  $CO_2$  flux due to stomatal limitation. A lack of an effect of precipitation treatments on GEP was expected because the adaptation of plants would decrease the response to

environments [18,19,53]. This indicated that productivity in the semiarid grassland was relatively stable to variation in precipitation.

The Re and Rs were not affected by precipitation treatments, primarily due to the lack of response of GEP (−1% across three seasons), which drives ecosystem and soil respiration, as proposed by previous studies [33,34,54] and suggested by the linear relationship between the variables in our study (Re =  $1.662 + 0.334 \times \text{GEP}$ ,  $R^2 = 0.467$ , RMSE = 1.381,  $p < 0.0001$ ; Rs =  $1.381 + 0.121 \times \text{GEP}$ ,  $R^2 = 0.175$ , RMSE = 1.016,  $p < 0.0001$ ). Our results further showed significant changes in GEP and NEE in the early and late seasons and significant changes in Re in the early season with the precipitation treatments (Figure 5). This result indicated an asynchronous response of ecosystem respiration and assimilation to treatments, which is consistent with observations in *Eucalyptus saligna* [55] and in a Mediterranean species with different growth forms [56].

Alternatively, Rs may have acclimated to changes in soil temperature and moisture resulting from the treatments, which can decrease the sensitivity of soil CO<sub>2</sub> flux to precipitation treatments (Figure 5). Soil temperature and moisture regulate the availability of substrates, the activities of roots and microbes, and thus soil respiration [27,57]. However, soil temperature and moisture respond sensitively to precipitation regimes (Figure 3), while long term changes in soil temperature or moisture would result in acclimation in Rs. Acclimation of Rs to temperature changes due to grassland management in the semiarid grassland of the Loess Plateau has been demonstrated [58], but acclimation to soil moisture changes needs further examination.

The response of NEE to precipitation treatments was determined by the trade-off between GEP and Re [52,59] and was dominated by GEP (60%) in our study. Across the three seasons, both precipitation treatments did not affect GEP and Re and, thus, did not affect NEE (Table 1). Furthermore, NEE and GEP had a similar response pattern to precipitation changes in the early and late season (Figure 5).

#### 4.2. Dependence of CO<sub>2</sub> Flux on Soil Temperature

Our results demonstrate that decreased precipitation reduced the dependence of CO<sub>2</sub> flux components (GEP, Re, Rs, NEE) on temperature, while increased precipitation enhanced these dependencies (Table 2). The DP increased soil temperature by 0.26 °C and the range of soil temperature (difference between maximum and minimum values) by 1.35 °C during the growing season, which partly decreased the temperature limitation at the study site and thus weakened the dependencies of ecosystem processes on temperature. This occurred because the change in CO<sub>2</sub> flux per degree change in temperature in an ecosystem unlimited by temperature would be less than in a low-temperature limited ecosystem. This result was consistent with other findings that increases in temperature weakened the temperature limitation in temperate ecosystems, or those at high latitude or altitude [60–62]. In our study, IP decreased the mean value and range of soil temperature by 0.59 and 1.23 °C, respectively, during the growing season. The IP also enhanced the temperature limitation and, thus, increased the dependence of CO<sub>2</sub> flux on temperature. Our observation was consistent with results by Jia et al. [63] that water addition increased the temperature sensitivity of soil respiration in three of four communities in the semiarid region of northern China. It was also consistent with previous findings that there is lower temperature sensitivity of soil respiration during dry periods than during wet periods [28,54,64,65].

In this study, the influencing patterns of precipitation regimes on the dependence of each CO<sub>2</sub> flux component on temperature further indicated an interaction between soil temperature and moisture on these components (Table 4). In other words, CO<sub>2</sub> flux components depended more on temperature (higher slope for the response function) when soil moisture was higher (in IP treatment) but less on temperature (lower slope for the response function) when soil moisture was lower (in DP treatment), compared with AP treatment (Table 2). This interaction could be due to the co-limitation of temperature and moisture in the ecosystem.

**Table 4.** ANOVA results of soil temperature and moisture on gross ecosystem productivity (GEP), ecosystem respiration (Re), soil respiration (Rs), and net ecosystem CO<sub>2</sub> exchange (NEE) in a semiarid grassland of the northwest China.

		GEP	Re	Rs	NEE
SS	Moisture	10	67	5	25
	Temperature	856	982	246	4
	Interaction	863	126	46	330
F	Moisture	1	34	6	3
	Temperature	68	504	309	1
	Interaction	69	65	57	41
P	Moisture	0.3647	<0.0001	0.0124	0.0808
	Temperature	<0.0001	<0.0001	<0.0001	0.4658
	Interaction	<0.0001	<0.0001	<0.0001	<0.0001

Degree of freedoms of the model and error were 3 and 646, respectively.

#### 4.3. Dependence of CO<sub>2</sub> Flux on Soil Moisture

The rate of each CO<sub>2</sub> flux component was expected to increase with soil moisture in semiarid regions [1,41], but our results demonstrated decreased CO<sub>2</sub> flux with soil moisture (Table 3). This decreased CO<sub>2</sub> flux was mainly due to the asynchrony between soil moisture and plant growth or soil temperature during the growing season (Figure 3). Plants grew quickly in the early and middle stages of the season [29], and they had relatively high rates of assimilation and respiration, and more negative NEE (Figures 4 and 5). The air and soil temperatures were both higher, but soil moisture was lower at these stages, compared with the late stage of the growing season (Figure 3). In contrast, the plants stopped growing later in the season with lower (or less negative) GEP, NEE, and Re (Figures 4 and 5). The air and soil temperatures were lower, but soil moisture was higher at this stage (Figure 3). This asynchronous pattern between plant growth and soil moisture during the growing season results in a declining trend of CO<sub>2</sub> flux with soil moisture (Figure 7, Table 3). These results indicate that the ecosystem in the study region was more limited by soil moisture during the early and middle stages of the growing season but was more limited by temperature in the late stage of the season. This asynchrony was consistent with findings by Wan et al. [66] in a grassland in Tennessee and implied that the dependence of CO<sub>2</sub> flux on soil moisture was modulated by this asynchrony.

The precipitation treatments significantly changed the dependence of CO<sub>2</sub> flux on soil moisture. The DP resulted in 16% decrease in soil moisture, strengthening the limitation of soil moisture. In contrast, IP resulted in a 21% increase in soil moisture, which weakened the limitation of soil moisture and, thus, the dependence of GEP on soil moisture (Table 3). The dependence of respiration (Re and Rs) on soil moisture, however, decreased in DP (Table 3), which was consistent with results from a study in a piñon-juniper woodland [67]. The opposite influencing patterns of precipitation treatments on the dependence of GEP and Re to soil moisture may be due to differences in the mechanism between GEP and respiration in response to soil moisture conditions. Precipitation can directly affect GEP by changing stomatal performance, which is directly modulated by soil moisture [50,51]. On the other hand, respiration response is mainly determined by the availability of substrates, which is indirectly affected by soil moisture. In comparison to wet conditions, drought affects the allocation of assimilates in the plant-soil system by transferring a larger proportion of assimilates to the roots [68] and increasing microbial biomass and enzymatic activities in the rhizosphere [69]. Therefore, it has a contrasting effect on soil respiration, in comparison to effects on GEP.

Since long-term changes in precipitation might significantly change soil temperature and moisture (Figure 3), which determine ecosystem CO<sub>2</sub> flux, we hypothesized that increased precipitation would enhance the dependence of CO<sub>2</sub> flux components on temperature but weaken the dependence on soil moisture, while decreased precipitation would have opposite effects on such dependencies. The changes in the dependence of GEP, Re, and Rs on temperature (Table 2), and the changes in the

dependence of GEP and NEE on soil moisture (Table 3), supported these hypotheses. These results indicated shifts in the response functions of CO<sub>2</sub> flux to soil temperature or moisture resulting from precipitation treatments, which is consistent with the acclimation of foliar gas exchange to different precipitation regimes in a piñon-juniper woodland [67]. Such shifts in the response functions could be a mechanism underlying the relatively stable ecosystem CO<sub>2</sub> flux in this semiarid grassland and should be incorporated in current models that do not consider such shifts in the response functions to better predict ecosystem processes at various precipitation change scenarios.

## 5. Conclusions

Precipitation change is one of the most important global change factors. It is often interrelated with other factors (e.g., global warming and CO<sub>2</sub> elevation) in influencing ecosystem processes and leads to feedback between C cycling and climate systems [7–9]. Moreover, the effects of precipitation change on C cycling are particularly important in water-limited ecosystems [11,70]. Our results show relatively stable ecosystem CO<sub>2</sub> flux in a semiarid grassland over three years across various precipitation scenarios, implying that the dominant native species is adapted to the highly variable precipitation in this semiarid region. The response function of CO<sub>2</sub> flux to temperature and/or moisture changes was the basis for predicting C cycling [71,72]. However, we demonstrated the shifts in these response functions with precipitation treatments, which were rarely considered previously. We recommend that these shifts should be considered or incorporated into current models for predicting ecosystem processes at various precipitation change scenarios. Our field results suggest that CO<sub>2</sub> flux in semiarid grasslands may be less affected by precipitation changes. Such a response would weaken the feedback between C cycling and the climate system and simplify future modelling in semiarid environments.

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