

Ephemeral plants mediate responses of ecosystem carbon exchange to increased precipitation in a temperate desert



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ABSTRACT

The ecological consequences of increased precipitation on ecosystem carbon (C) exchange are gaining increasing concern, especially in the context of ongoing climate change in temperate deserts. In this study, a field manipulative experiment was conducted to assess the effects of increased precipitation and nitrogen (N) addition on net ecosystem C exchange (NEE) in a temperate desert in northwestern China during two years with contrasting precipitation patterns (2011 and 2012). Increased precipitation decreased ecosystem C release by nearly 50% in the wet year of 2011, whereas ecosystem C release was increased in the dry year of 2012 because of the disproportional stimulation of gross ecosystem productivity (GEP) and ecosystem respiration (ER) by increased precipitation. N addition had no impact on NEE because of the slight responses of both GEP and ER to N addition. During the wet year, most of the precipitation occurred during the growing season of ephemeral plants, which profoundly stimulated plant growth and led to a higher response of GEP than ER to increased precipitation. As a result, positive effects of increased precipitation on NEE occurred in this year. During the dry year, the majority of the precipitation fell post the ephemeral growing season and only a small increase in herb biomass was observed. However, the response of ER to increased precipitation was larger than that of GEP, leading to a more negative NEE in 2012, as compared to 2011. C release was thus stimulated by increased precipitation in 2012. Irrespective of precipitation treatment, N addition weakly decreased C release because of the negligible stimulation of GEP and ER, as well as the slight response of ephemeral biomass. The responses of NEE to increased precipitation showed no difference between interplant spaces and beneath the dominant shrubs because of the similar responses of plant growth, GEP and ER between sites. Overall, this study shows that the responses of NEE to projected increasing precipitation depend on the coupling of precipitation timing and plant growing season.

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1. Introduction

The terrestrial ecosystems are experiencing simultaneous changes in temperature, atmospheric CO₂ concentration, precipitation and nitrogen deposition (IPCC, 2007), and concerns on the ecological consequences of climate change differ among terrestrial ecosystems (Grimm et al., 2013). Precipitation and nitrogen (N) are co-limiting factors in temperate deserts in central Asia (Hooper and Johnson, 1999; Yahdjian et al., 2011). However, climate models predict increasing precipitation (Cholaw et al., 2003; IPCC, 2007) and N deposition (Li et al., 2013; Liu et al., 2013) in these regions. Short-term experiments have shown that both increased precipitation

and N deposition can alter vegetation growth and plant community structure (Xia and Wan, 2008; Yahdjian et al., 2011). However, the responses of ecosystem carbon (C) exchange and C budget, as well as their feedbacks to climate change in desert ecosystems, remain unclear because of the few experimental and modeling studies.

Net ecosystem C exchange (NEE) represents the balance between gross ecosystem productivity (GEP) and ecosystem respiration (ER) (Chapin et al., 2002). The responses of GEP and ER to increased precipitation and N are largely dependent on soil moisture and nutrient status in arid and semiarid regions (Huxman et al., 2004; Sponseller, 2007). Increased precipitation can promote GEP by increasing photosynthesis (Yan et al., 2011; Hamerlynck et al., 2012), while its effects on NEE rely on whether ER responds proportionally with GEP. At present, synchronized observations of GEP and ER in temperate deserts are still rare. In addition, the role of desert ecosystems has long been underestimated in the scenario of

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climate change. Therefore, considering the large area and potential C fixation pathways (Evans et al., 2014), further studies are needed to assess their ecological significance.

N deposition due to excessive application of N fertilizers and fossil fuel combustion has become an important subject in global climate change (Tilman et al., 2012). Positive impacts of N addition on individual plant growth are well evidenced in greenhouse experiments (LeBauer and Treseder, 2008), while its effects on plant community and carbon cycling at the ecosystem level are debated in arid and semiarid ecosystems (Hooper and Johnson, 1999; Harpole et al., 2007). The inconsistencies primarily originate from the following three points. First, because of the different directions or divergent magnitudes of responses between GEP and ER to N addition, NEE does not always respond in the same direction as GEP (Hooper and Johnson, 1999). Second, the alteration of plant community structure and composition under N addition can cause complex variations of GEP and ER (LeBauer and Treseder, 2008; Xia and Wan, 2008), leading to uncertain NEE responses to N addition (Xia et al., 2009; Niu et al., 2010). Third, because the degree of N saturation differs among ecosystems, equal amount of N addition may generate contrasting effects on NEE (Fang et al., 2012). In addition, soil N availability usually varies with the precipitation pulse in desert ecosystems (Austin et al., 2004), and N addition effects are dependent on soil moisture (Harpole et al., 2007). Thus, more studies are required to understand the effects of N addition, alone and interactively with increased precipitation, on ecosystem C exchange in desert ecosystems.

GEP and mean annual precipitation are well correlated at the regional scale (Sala et al., 1988; Knapp and Smith, 2001; Reichmann et al., 2013), while their relationship is uncertain at the local scale in arid and semiarid ecosystems (Scott et al., 2009). In addition, soil resources show great variations in interplant spaces and beneath perennial plants (Sponseller, 2007; Cable et al., 2008; Su et al., 2013). Results from manipulative experiments show the rainfall pulses can exert different effects on plants, having no effect on deep-rooted plants and obvious influences on shallow-rooted plants (Snyder et al., 2004; Sponseller et al., 2012; Baez et al., 2013). Thus, vegetation structure may differ in interplant spaces and beneath shrubs, which can generate inconsistent GEP responses to environmental cues. Besides, the relationship between ER and soil moisture also varies in arid ecosystems (Wang et al., 2014). The patchy distribution of shrubs elicits spatial heterogeneities in soil C and N (Jackson and Caldwell, 1993; Aguiar and Sala, 1999). Nutrients accumulate under shrubs, while soil fertility decreases in interplant spaces due to wind erosion and litter movement (Ludwig et al., 2000). The accumulation of nutrients benefits microbial growth under shrubs. Thus, given the close correlation of soil respiration with substrates (Herman et al., 1995; Kieft et al., 1998), ER responses to increased precipitation or N addition may differ between interplant spaces and beneath shrubs. Therefore, incorporating the spatial heterogeneity generated by 'shrub islands' into C cycling and budget estimation can increase the prediction accuracy of climate change in desert ecosystems.

The effects of precipitation and N on ecosystem C exchange largely depend on how the dominant functional group responds to changing precipitation and N decomposition and its relative contribution to the ecosystem C exchange (Weltzin et al., 2003; Henry et al., 2006; Suttle et al., 2007). Desert plants have developed different life history strategies to adapt to the highly variable and unpredictable precipitation. For instance, a long life history and slow growth rate are widely observed in perennials and summer annuals, whereas a short life history and fast growth rate occurs in ephemerals and spring annuals, and the two types of plants differ temporally in dominance and biomass in the community. However, the carbon cycling models that consider the relationship of temporal variation in precipitation with plant phenology are still

rare (D'Odorico et al., 2003; Moyano et al., 2013; Porporato et al., 2003). In fact, some studies have demonstrated that the ecological consequences of climate change strongly rely on the effects of environmental cues on dominant plant growth (Chou et al., 2008; Heisler-White et al., 2009; Parton et al., 2012; Jongen et al., 2013). Thus, the spatial variation in soil resources between sites and the temporal variation in precipitation may generate complex effects on C exchange in deserts.

Ephemerals (spring annuals) and annual plants (summer and autumn annuals) are two major components of vegetation in the Gurbantunggute Desert, center of the Eurasian Continent (Angert et al., 2010; Fan et al., 2012). Desert ephemerals reach their growth peak within two months after snowmelting, and this peak is a critical phase for herbaceous community in terms of cover and biomass. Annuals exhibit a slow growth rate during ephemeral growing and arrive at the peak growth in late August (Fan et al., 2013). Therefore, herbaceous growth shows apparent ephemeral growing and post ephemeral growing phases (Fig. S1). A field experiment was conducted to investigate the effects of increased precipitation and N addition on NEE and its two components, GEP and ER, in this region in 2011 and 2012. Given the shallow plant roots in this study site, we hypothesized that (1) increased precipitation would increase GEP, imposing positive influences on NEE (smaller CO₂ loss); (2) N addition would increase NEE because of the fertilization effect on plant growth; (3) given that soil moisture can promote plant N uptake, combined increased precipitation and N addition would generate synergistic effects on NEE; (4) both microsite ('shrub islands' effect) and the inter- and intra-annual variation of precipitation would regulate the responses of NEE to increased precipitation and N addition.

2. Materials and methods

2.1. Study site description

The field site was in the vicinity of the Fukang Station of Desert Ecology, Chinese Academy of Sciences, on the southern edge of the Gurbantunggut Desert (44°17'N, 87°56'E and 475 m a.s.l.). This region has an arid temperate continental climate, with a hot, dry summer and cold winter. The annual mean temperature is 6.6°C and the annual mean precipitation is 160 mm, of which 70–80% is distributed in the plant growth season from April to September. Soils are desert solonetz, with aeolian sandy soil at the top (0–100 cm). The shrubs and semishrubs are primarily *Tamarix ramosissima*, *Haloxylon ammodendron*, and *H. persicum*, with a coverage of ca. 30%. The herbaceous layer is composed of ephemerals and annuals, with a coverage reaching 40% (Fan et al., 2012). Based on life history, herbs are comprised of two groups: ephemerals (spring-annuals) and annuals (summer-annuals). The dominant ephemerals include *Alyssum linifolium*, *Schismus arabicus*, *Lactuca undulata*, and *Erodium oxyrrhynchum*, accounting for more than 85% of the herbaceous layer biomass. Annuals includes *Salsola subcrassa*, *Ceratocarpus arenarius*, *Orostachys spinosus*, *Euphorbia turczaninowii*, *Descurainia sophia*, *Hyalea pulchella*, *Astragalus arpilobus*, *Trigonella arcuata* and *Agriophyllum squarrosum*, and they are accompanying species from late-March to June, but dominate in the community after the death of ephemerals. Moreover, herbaceous growth season can be divided into two periods in terms of community phenology (Fig. S1). The first period, termed as 'ephemeral growing season', is usually before mid-June, and the plant community is dominated by ephemerals. The second period, termed as 'post ephemeral growing season', is after ephemeral death, and the plant community is dominated by annuals. According to the phenological protocol (Price and Waser, 1998), the duration of the ephemeral growing season was set from the date

on which the germination frequency reached 80% (for the beginning) to the data on which senescence reached 80% (for the end). The ephemeral growing season began on April 4 and ended on July 2 in 2011, while it began on 1 April and ended on 21 June in 2012.

2.2. Experimental design

The experiment used a completely randomized block design with four treatments, control (CK), nitrogen addition (N), precipitation addition (P), and nitrogen plus precipitation addition (NP), with each treatment replicated six times. A total of 24 plots were arranged in a 4×6 matrix, each plot was 10×10 m, with a 10 m wide buffer zone between adjacent plots. In the P and NP treatments, precipitation was increased by 30%, according to predictions for northern China over the next 30 years (Liu et al., 2010). The 30% extra precipitation was collected using “rainfall collection pans”. The pans were constructed from galvanized iron sheets, with an area of 1.9×1 m, totally 18 pans were installed in each plot, the total area of pans was equivalent to 30% of the plot area. The pan was erected at a slight angle, and the rainfall intercepted was collected in a bucket that was buried in the soil. Immediately after a rainfall event, the collected rain was evenly sprayed onto the plots during the late afternoon to prevent excessive evaporation. Moreover, given the ecological significance of snow in our study site (Fan et al., 2012), snow fallen in the pan was also evenly added to the corresponding plot in early spring. Given that snow usually melts within 1–2 days, snow addition had no significant warming effects in the trial test. In the N and NP treatments, N was applied in liquid form, 1667-g NH_4NO_3 was diluted in 15-L distilled water and evenly sprayed (equal to 0.15 mm rainfall) onto the corresponding plots (10×10 m) in early-April and mid-July to meet the growth requirements of ephemerals and annuals. The same amount of distilled water was added in the CK and P treatments. N addition (corresponding to $5 \text{ gN m}^{-2} \text{ year}^{-1}$) was based upon the real mean airborne N deposition rate ($3.6 \text{ gN m}^{-2} \text{ year}^{-1}$) registered in Xinjiang, northern China over the past 10 years (He et al., 2007). In addition, all samplings and measurements were conducted beneath shrubs and in interplant spaces in each plot. The experiment was set up in 2010, and a previous investigation showed no heterogeneity among plots or blocks.

2.3. Meteorological data and soil moisture, soil temperature, and soil inorganic N measurements

Soil moisture (θ) and soil temperature (T_s) were measured simultaneously with ecosystem C exchange measurements. θ was measured using time domain reflectometry (HH2-Delta T Device moisture meter, UK) to a depth of 0–5 cm beneath shrubs and in interplant spaces. T_s at 0–5 cm was measured by placing a thermocouple (JM424 soil temperature measurement system, the Tianjin Electronic Company, Tianjin, China) near the carbon exchange chamber. In addition, soil at 0–5 cm was collected in each plot monthly, and soil inorganic N (IN) was measured with an Auto Analyzer 3 (AA3, BRAN-LUEBBE Ltd., Hamburger, Germany). Air temperature (T_a) and precipitation were monitored hourly using an automatic meteorological station (Campbell Scientific Corporation, Logan, UT, USA).

2.4. Carbon exchange measurements

The closed static chamber method was used to measure C exchanges. The chamber dimension was 0.5×0.5 m at the base and 0.3 m in height. This method is widely used and provides valuable information that cannot be obtained easily in other ways (Risch and Frank, 2007; Xia et al., 2009). The chamber walls were constructed of clear polyethylene sheeting, which allows 90% of

photosynthetically active radiation to pass. Two electric cooling fans were installed to circulate air in the chamber during measurements. Aluminum collars (ca. 3 cm deep) with a groove for chamber placement were installed in each plot one month prior to the first measurement (late March 2011) to minimize the disturbance of collar insertion.

We measured C exchange using three Li-Cor 840 portable photosynthesis systems (IRGA; LI-840, LiCor Inc., Lincoln, NE, USA) simultaneously to decrease the temporal variation of the measurements. C exchange measurements were conducted between 9:30 and 11:30 h at two-week intervals from mid-April to October in 2011 and 2012. Two measurements, at ambient radiation ($\text{PPFD} > 1200\text{--}1600 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and dark condition, were conducted at each collar location. NEE was estimated by collecting twelve consecutive recordings of CO_2 under ambient radiation during a 120 s period at 10 s intervals, as the CO_2 concentration steadily increased or decreased. ER was measured following the same procedure, with the chamber being covered with an opaque cloth to eliminate photosynthesis (usually 15–20 min after covering opaque cloth, in the preparative test). The difference between NEE and ER represents GEP within the chamber. Specifically, positive and negative NEE values represent net carbon uptake by and release from the ecosystem, respectively. NEE and ER were both calculated using the following calculation procedure:

$$F_c = \frac{10VP_0(1 - W_0)}{RS(T_0 + 273.15)} \frac{\partial C}{\partial t}$$

where F_c is the C exchange rate ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), V is the volume of the assimilation chamber and the base ($76,200 \text{ cm}^3$), P_0 is the initial pressure (kPa), W_0 is the initial water vapor mole fraction ($\mu\text{mol mol}^{-1}$), R is the universal gas constant ($8.312 \text{ kJ mol}^{-1} \text{ K}^{-1}$), S is the inner surface area of the chamber base (2401 cm^2), T_0 is the initial air temperature ($^{\circ}\text{C}$), and $\partial C/\partial t$ is the slope of least squares linear regression of CO_2 concentration on time ($r^2 > 0.98$). For data validity and conformity, we completed measurement in 120 s, and all r^2 values for the relationship between CO_2 internal concentration and time were higher than 0.98.

2.5. Peak aboveground biomass measurement

Five 1×1 m quadrats (three in interplant spaces, two beneath shrubs) were sampled in each plot in mid-May 2011 and 2012, respectively. Given that the peak aboveground biomass of the herbaceous layer occurred during this phase, all living biomass was clipped, sorted into ephemerals and annuals, and weighed after drying in an oven at 65° for 48 h.

2.6. Statistical analysis

To analyze the inter-annual differences in response variables of ecosystem C exchange, soil moisture, soil inorganic N, and peak aboveground biomass, the seasonal mean values from April to October of response variables were calculated from the monthly values, which were first averaged from all measurements within the same month. The general linear model (GLM) routine was used to generate a four-way ANOVA with the year, precipitation, N, and site as fixed factors. Bonferroni pairwise comparisons were used to test for pairwise differences. To detect treatment and site effects on C exchange over the experimental period in 2011 and 2012, data based on monthly values were analyzed with a repeated-measures ANOVA model. Factors in the model included precipitation, N and site as between-subject factors; time of season as within-subject factor; and interaction terms for all treatment combinations. A GLM command routine was used to estimate the model and perform hypothesis tests for the effects of each factor and each

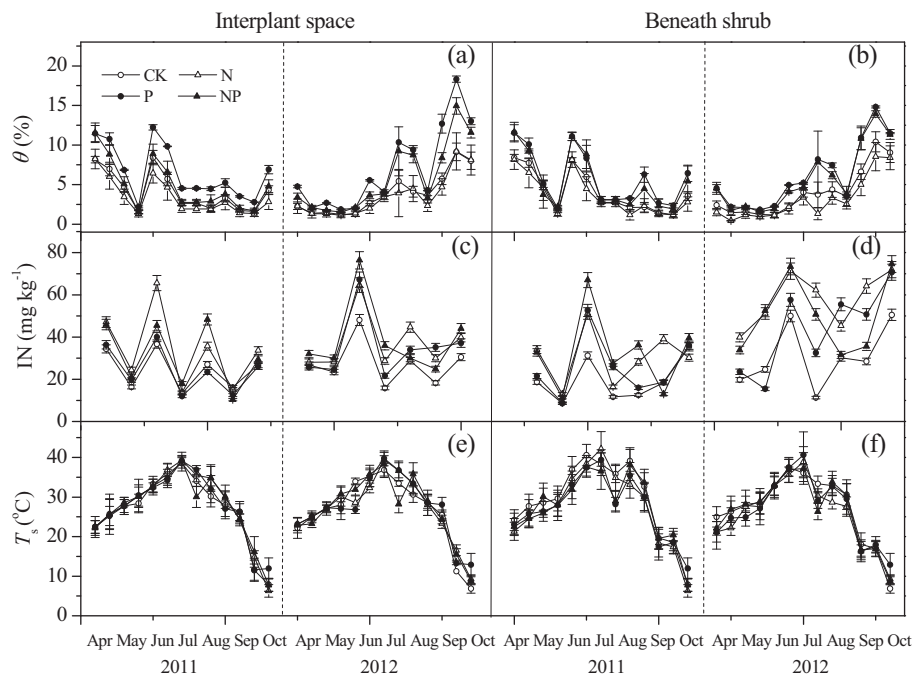


Fig. 1. Soil volumetric water content (θ), soil inorganic nitrogen content (IN), and soil temperature (T_s) in the control (CK), nitrogen addition (N), precipitation addition (P) and nitrogen plus precipitation addition (NP) treatments in interplant space and beneath shrub in 2011 and 2012. All values are mean $\pm$ S.E.

interaction of factors. Regression with correction for autocorrelation and stepwise multiple linear analyses were used to examine the relationships of C exchange with soil temperature, soil moisture, soil inorganic N, peak ephemeral biomass, and peak annual biomass. All statistical analyses were conducted with SPSS software (SPSS 13.0 for Windows, SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Treatment effects on soil moisture, soil inorganic nitrogen and soil temperature

Precipitation was 167.4 mm and 102 mm in 2011 and 2012, respectively, and exhibited different seasonalities, with 63.2% and 32.7% falling in the ephemeral growing season in 2011 and 2012, respectively (Fig. S2). Soil volumetric water content (θ) followed the precipitation pattern; in the control plots, the averaged θ

during the growing period (April–October) at 0–5 cm was 3.8% and 4.0% in 2011 and 2012, respectively (Fig. 1a and b). Increased precipitation significantly increased θ , on average, by 2.0% in 2011 and 2.7% in 2012 (Fig. 1a and b, Table 1).

Soil inorganic nitrogen (IN) showed a significant inter-annual difference. In the control plots, averaged IN over the two years was 21.9 mg kg^{-1} and 28.9 mg kg^{-1} in the interplant spaces and beneath shrubs, respectively, showing a profound difference between sites (Fig. 1c and d). N addition significantly increased soil IN by 28% and 76% in 2011 and 2012, respectively (Fig. 1c and d). Soil temperature showed no difference between treatments and between sites (Fig. 1e and f).

3.2. Treatment effects on ecosystem C exchange

NEE and GEP showed significant inter-annual variations (Table 1). NEE and GEP exhibited a high peak in April–May and

Table 1
Results (F values) of four-way ANOVA on the effects of nitrogen addition (N), increased precipitation (P), site (S), year (Y) and their interactions on net ecosystem carbon exchange (NEE), gross ecosystem carbon production (GEP), ecosystem respiration (ER), soil volumetric water content (θ), soil inorganic nitrogen content (IN), ephemeral aboveground biomass (EB), annual aboveground biomass (AB) and total aboveground biomass (TB).

Effect	NEE	GEP	ER	θ	IN	EB	AB	TB
Y	104.7**	70.8**	1.9	5.8*	7.0*	92.8**	32.3**	93.3**
Y $\times$ P	13.6**	3.420*	1.3	2.2	8.9*	4.3*	3.7 [^]	6.0*
Y $\times$ N	0.74	0.094	0.201	1.25	2.5	0.464	3.4 [^]	2.0
Y $\times$ S	1.8	0.004	2.253	0.51	0.815	3.1 [^]	0.1	1.9
Y $\times$ P $\times$ N	1.1	0.643	0.003	0.25	0.006	3.6 [^]	2.215	4.4*
Y $\times$ P $\times$ S	0.03	0.118	0.455	0.13	4.5*	1.227	0.404	1.2
Y $\times$ P $\times$ S	1.7	0.161	0.643	0.24	0.325	0.138	0.399	0.3
Y $\times$ P $\times$ N $\times$ S	0.2	0.016	0.091	0.00	0.208	0.665	2.372	0.1
P	1.8	28.1**	18.5**	27.4**	0.04	19.2**	16.1**	25.1**
N	0.3	0.407	1.3	1.48	30.1**	0.166	6.9**	2.9
S	1.9	5.7*	1.6	0.21	69.9**	0.834	0.102	0.6
P $\times$ N	0.001	1.009	1.1	0.24	1.8	2.94	3.05	3.01
P $\times$ S	0.005	0.227	0.31	0.10	0.091	1.515	2.693	2.7
N $\times$ S	0.051	0.024	0.13	0.69	0.142	0.014	0.357	0.146
P $\times$ N $\times$ S	0.031	0.109	0.035	0.27	2.339	0.572	2.618	0.093

**, *, and [^] represent significant differences at $p < 0.01$, $p < 0.05$ and $p < 0.1$, respectively.

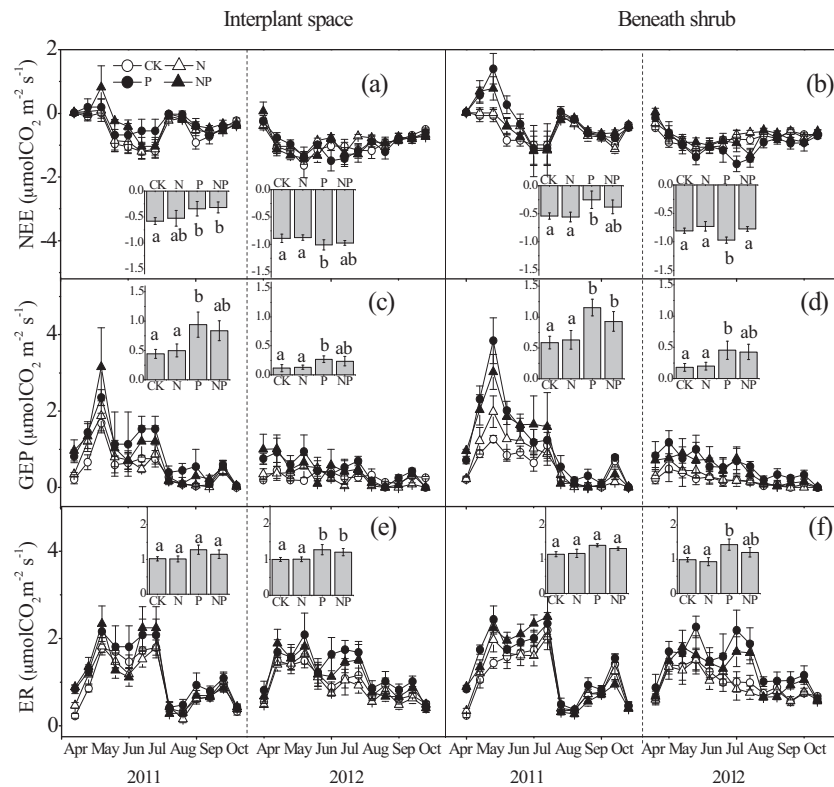


Fig. 2. Seasonal dynamics (symbols and lines) and means (bars) ($\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of net ecosystem carbon exchange (NEE) (a, b), gross ecosystem production (GEP) (c, d), and ecosystem respiration (ER) (e, f) in the control (CK), nitrogen addition (N), increased precipitation (P) and combined increased precipitation and nitrogen addition (NP) treatments in interplant space and beneath shrub in 2011 and 2012. All values are mean $\pm$ S.E. ($n=6$). Inset figures show the mean values of NEE, GEP and ER during growing season, and different small letters indicate significant differences between treatments at $p < 0.05$.

a small peak in August 2011, and one peak in May 2012 (Fig. 2a–d). ER exhibited no significant inter-annual fluctuations (Fig. 2e and f).

Precipitation and year exerted a significant interactive effect on NEE (Table 1, Fig. 2a and b). In 2011, increased precipitation increased NEE by 41.2%, from $-0.58 \mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in CK to $-0.34 \mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the P plots, whereas in 2012, increased precipitation decreased NEE by 13.3%, from $-0.88 \mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in CK to $-1.01 \mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the P plots. Increased precipitation significantly increased GEP by more than two times as compared to the control (from

$0.44 \mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ to $0.93 \mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in 2011; from $0.11 \mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ to $0.26 \mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in 2012) (Fig. 2c and d). Increased precipitation significantly stimulated ER by 27.0% in 2012, but exerted no influence on ER in 2011 (Table 2, Fig. 2e and f).

N addition imposed no significant effects on NEE, GEP and ER (Tables 1 and 2). In addition, combined increased precipitation and N addition showed no interactive effects on NEE, GEP and ER (Fig. 2, Tables 1 and 2). In both years, NEE and GEP were higher beneath shrubs than in interplant spaces, irrespective of the treatment, but

Table 2

Results (F values) of repeated-measures ANOVA on the effects of nitrogen addition (N), increased precipitation (P), site (S), measurement time (T), and their interactions on soil volumetric water content (θ), net ecosystem carbon exchange (NEE), gross ecosystem carbon exchange (GEP) and ecosystem respiration (ER) during the growing season of 2011 and 2012.

Effect	2011				2012			
	NEE	GEP	ER	θ	NEE	GEP	ER	θ
T	28.6**	45.2**	99.4**	180.0**	19.7**	11.01**	34.7**	112.4**
T $\times$ P	1.9	3.6**	3.3**	6.7**	2.3**	2.5**	4.5**	4.0**
T $\times$ N	0.40	0.25	0.31	1.11	1.51	1.27	0.62	0.35
T $\times$ S	1.62	1.16	0.69	0.46	1.07	1.48	0.30	1.73
T $\times$ P $\times$ N	0.35	0.47	0.70	0.87	0.98	1.25	0.83	2.8*
T $\times$ P $\times$ S	1.16	1.04	0.33	1.19	0.79	0.43	0.94	0.29
T $\times$ N $\times$ S	0.47	0.17	0.19	0.92	1.26	0.77	0.77	0.87
T $\times$ P $\times$ N $\times$ S	1.20	1.29	0.38	1.11	1.27	1.41	0.62	1.07
P	7.7**	11.4**	2.61	12.45**	4.4*	10.9**	14.3**	22.0**
N	0.009	0.201	0.335	2.69	2.295	0.099	1.226	0.00
S	0.011	1.352	2.68	0.00	8.4*	5.0*	0.013	0.35
P $\times$ N	0.293	0.736	0.570	0.40	1.141	0.033	0.561	0.04
P $\times$ S	0.003	0.004	0.001	0.02	0.067	0.637	0.594	0.06
N $\times$ S	0.328	0.070	0.028	1.22	2.443	0.060	0.487	0.32
P $\times$ N $\times$ S	0.127	0.047	0.001	0.27	0.068	0.038	0.091	0.38

**, and * represent significant differences at $p < 0.01$, and $p < 0.05$, respectively.

Table 3
Means of ephemeral plant biomass (g m^{-2}), annual plant biomass and total plant biomass in four treatments: control (CK), nitrogen addition (N), increased precipitation (P), and combined increased precipitation and nitrogen addition (NP) in 2011 and 2012. Values represent the mean $\pm$ S.E ($n=6$). Different small letters indicate significant differences between treatments within each site at $p=0.05$.

	Interplant space				Beneath shrub			
	CK	N	P	NP	CK	N	P	NP
2011								
Ephemeral	35 $\pm$ 3.6a	51 $\pm$ 3.4ab	65 $\pm$ 6.2b	45 $\pm$ 9.7ab	26 $\pm$ 3.8a	30 $\pm$ 2.8a	61 $\pm$ 15.1b	48 $\pm$ 9.4ab
Annual	20 $\pm$ 4.5ab	13 $\pm$ 4.1b	29 $\pm$ 6.9a	20 $\pm$ 4.7b	9 $\pm$ 2.2a	11 $\pm$ 3.5a	43 $\pm$ 10.5b	14 $\pm$ 5.1a
Total	55 $\pm$ 5.3a	65 $\pm$ 6.5a	95 $\pm$ 11.0b	66 $\pm$ 7.9a	35 $\pm$ 5.6a	41 $\pm$ 5.0a	105 $\pm$ 22.6b	62 $\pm$ 14.1a
2012								
Ephemeral	12 $\pm$ 0.8a	14 $\pm$ 3.4a	18 $\pm$ 2.5a	17 $\pm$ 3.2a	12 $\pm$ 1.7a	15 $\pm$ 2.6ab	22 $\pm$ 2.1b	20 $\pm$ 4.4ab
Annual	4 $\pm$ 1.9a	5 $\pm$ 1.2a	8 $\pm$ 1.9a	5 $\pm$ 0.8a	4 $\pm$ 1.4a	8 $\pm$ 0.9b	12 $\pm$ 4.5b	15 $\pm$ 8.1a
Total	16 $\pm$ 1.6a	20 $\pm$ 2.4ab	27 $\pm$ 2.1b	22 $\pm$ 3.6ab	17 $\pm$ 2.5a	24 $\pm$ 2.9a	34 $\pm$ 5.6b	36 $\pm$ 9.9b

the difference was only significant in 2012. ER did not differ significantly between microsites (Table 2, Fig. 2e and f).

3.3. Treatment effects on the peak aboveground biomass

Substantial inter-annual variations were observed in the ephemeral, annual, and total community biomass (Table 1). For example, in the control plots, the ephemeral, annual, and total biomass in 2011 was nearly three times of that in 2012 (Table 3). Increased precipitation significantly increased the ephemeral, annual and whole community biomass (Tables 1 and 3). N addition did not have any significant effects on ephemeral biomass (Tables 1 and 3). However, for annual plants, although all over ANOVA showed N addition had a significant effect (Table 1), the

significant stimulative effect of N addition on annual biomass was only found beneath shrubs in 2012. Combined increased precipitation and N addition did not impose influence on community biomass, except beneath shrubs in 2012 (Table 3).

3.4. Temporal and spatial controlling factors on ecosystem C exchange

NEE and ER increased linearly with increasing soil temperature in the ephemeral growing season, whereas no relationship was found between NEE or ER with soil temperature in the post ephemeral growing season in 2011 (Fig. 3). Both NEE and GEP increased linearly with increasing soil moisture across the ephemeral and post ephemeral growing seasons, with a

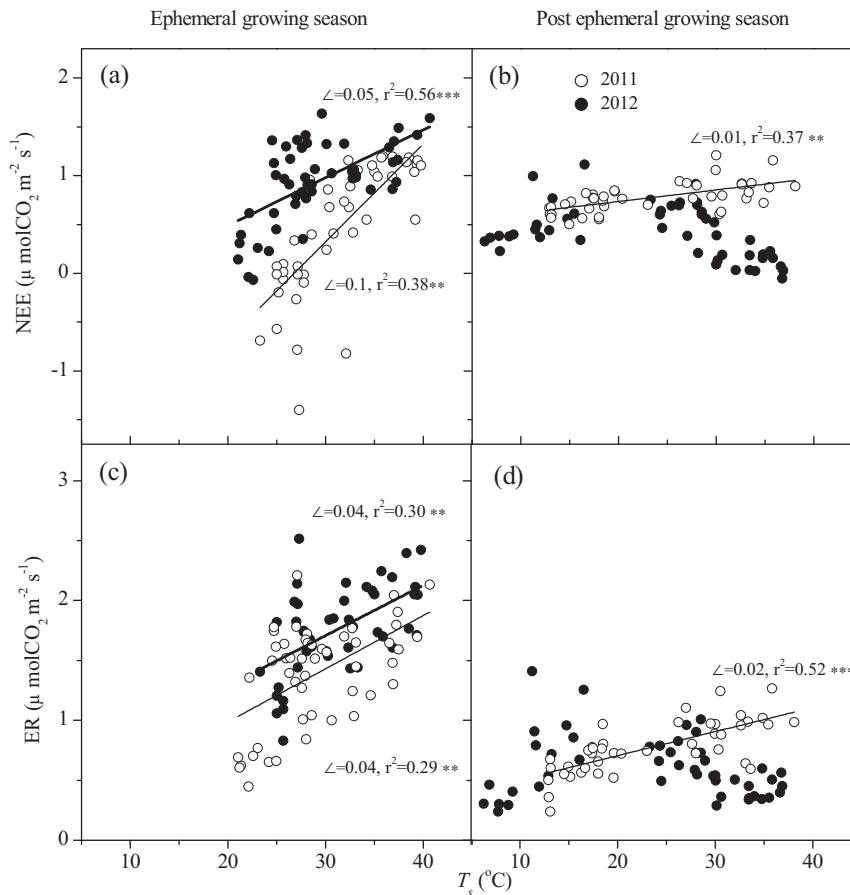


Fig. 3. Temporal dependence of net ecosystem carbon exchange (NEE), and ecosystem respiration (ER) in interplant space and beneath shrub on soil temperature (T_s) across different plots at the ephemeral (left panel) and post ephemeral growing season (right panel) in 2011 (solid circles and thick lines) and 2012 (open circles and slim lines). Dot represents the mean of our treatments.

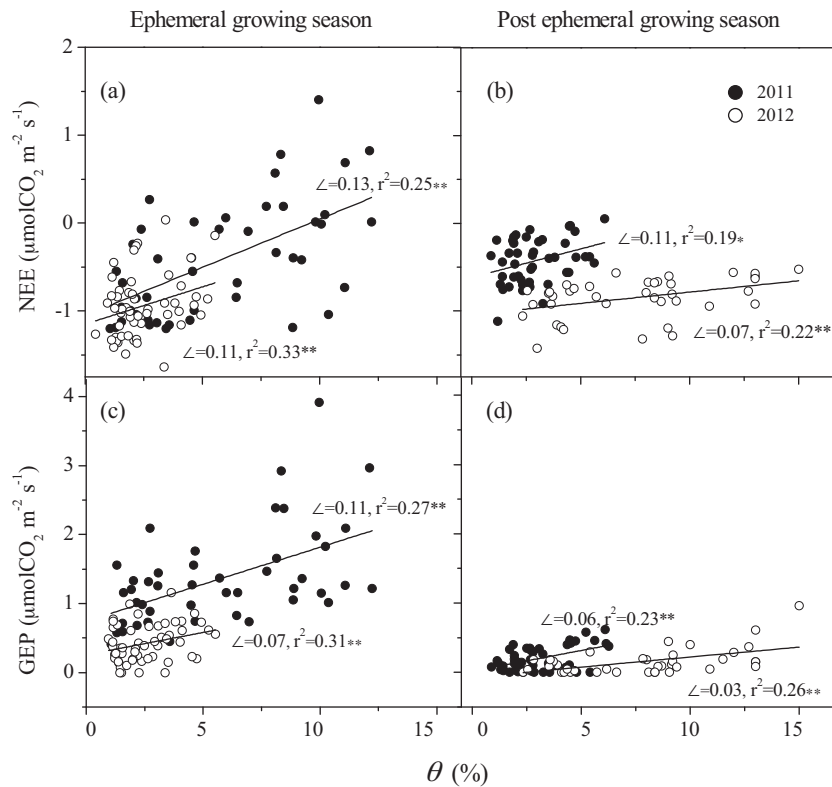


Fig. 4. Temporal dependence of net ecosystem carbon exchange (NEE), gross ecosystem productivity (GEP) on soil moisture (θ) across different plots at the ephemeral (left panel) and post ephemeral (right panel) growing season in 2011 (solid circles and thick lines) and 2012 (open circles and slim lines). Dot represents the mean of our treatments.

steeper slope in ephemeral than in the post ephemeral growing season (Fig. 4). Positive relationship between ER and soil moisture was only observed in 2011 (Fig. 5). Stepwise multiple regression analyses demonstrated that soil temperature and moisture explained 64% ($\text{NEE} = -0.05\theta + 0.08T_s - 1.78$) and 45% ($\text{NEE} = -0.02\theta + 0.05T_s - 0.49$) of the temporal variation in NEE, and 34% ($\text{GEP} = 0.09\theta - 0.03T_s + 1.65$) and 37% ($\text{GEP} = 0.14\theta - 0.02T_s + 0.61$) of the temporal variation in GEP, at the ephemeral growing season in 2011 and 2012, respectively. In the post ephemeral growing season, soil temperature and moisture together explained 19% ($\text{NEE} = -0.05\theta + 0.08T_s - 1.78$)

and 40% ($\text{NEE} = -0.01\theta + 0.01T_s + 0.66$) of the temporal variation in NEE, and 35% ($\text{GEP} = 0.06\theta + 0.01T_s + 0.19$) and 31% ($\text{GEP} = 0.01\theta + 0.01T_s - 0.18$) of the temporal variation in GEP, in 2011 and 2012, respectively. Soil temperature alone explained 36% ($\text{ER} = 0.03T_s + 0.26$) and 39% ($\text{ER} = 0.04T_s + 0.03$) of the temporal variation in ER when combining the ephemeral and post ephemeral growing seasons, in 2011 and 2012, respectively.

In 2011, seasonal mean NEE showed a positive linear dependence on mean soil moisture, peak ephemeral biomass, and peak annual biomass (Figs. 6a and 7a and b). Soil IN did not influence NEE (Fig. 6b). The stepwise multiple regression analysis showed that in 2011, 56% of the variation in NEE was explained by ephemeral biomass (Fig. 7a). In 2012, none of these variables were related to NEE (Figs. 6a, b and 7a, b). Seasonal mean GEP was mainly related to ephemeral biomass and soil moisture (Figs. 6c, d and 7c, d), and the peak ephemeral biomass (B_e), together with soil moisture accounted for 76.8% ($\text{GEP} = 0.012B_e + 0.098\theta - 0.195$) and 38.0% ($\text{GEP} = 0.013B_e + 0.035\theta - 0.140$) of the spatial variation of GEP in 2011 and 2012, respectively.

Seasonal mean ER showed a linear positive correlation with θ , soil IN, and peak ephemeral biomass in 2011 (Figs. 6e, f and 7e, f), and was positively correlated only with θ and peak ephemeral biomass (B_e) in 2012 (Figs. 6e and 7e). θ combined with peak ephemeral biomass (B_e) explained 34% ($\text{ER} = 0.002B_e + 0.087\theta + 0.739$) and 36% ($\text{ER} = 0.016B_e + 0.063\theta + 0.557$) of the variation in ER in 2011 and 2012.

4. Discussion

4.1. Effects of increased precipitation on C exchange

Increased precipitation exerted opposite effects on NEE in the wet (2011) and dry (2012) year. In 2011, 63% of the annual

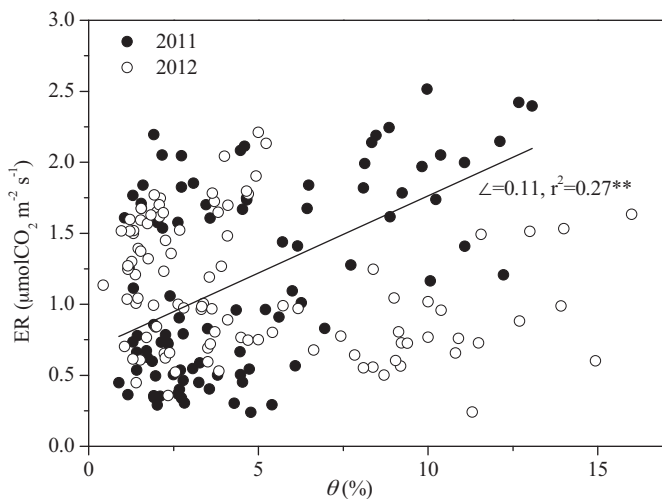


Fig. 5. Temporal dependence of ecosystem respiration (ER) on soil moisture (θ) across different plots in 2011 (solid circles and thick line) and 2012 (open circles and slim lines). Dot represents the mean of all four treatments.

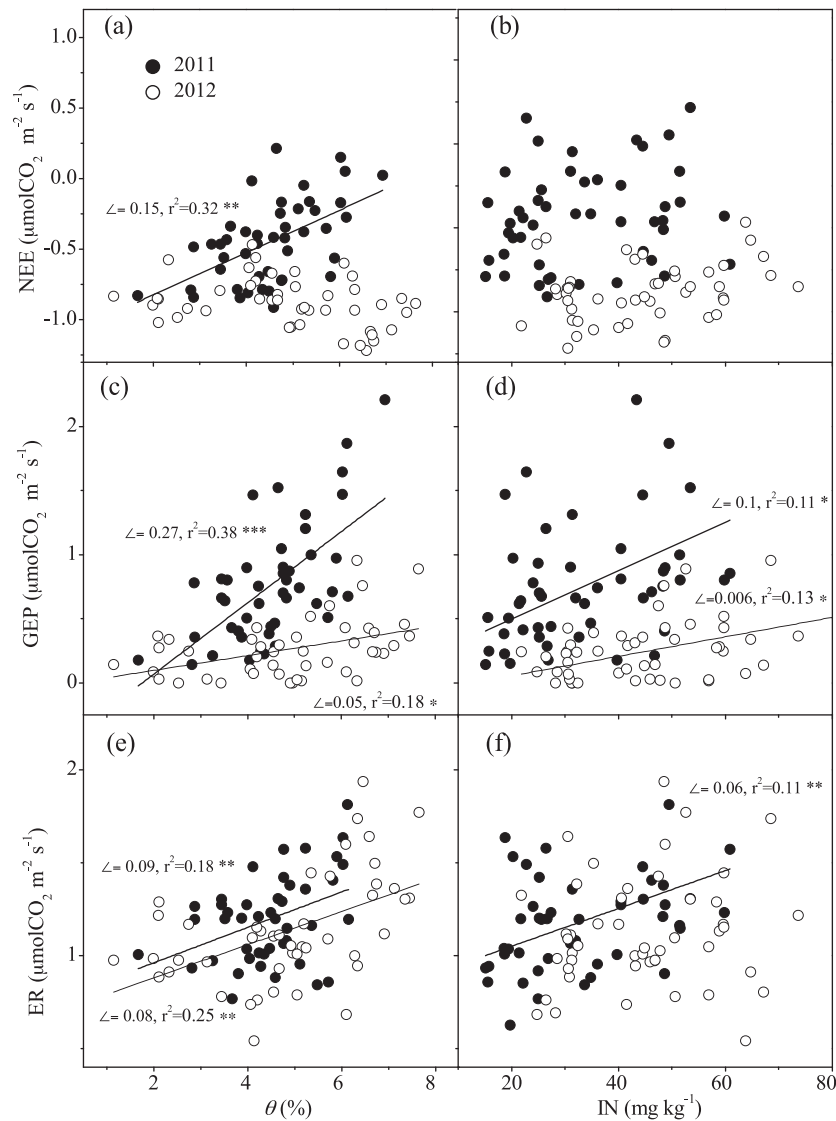


Fig. 6. Spatial dependence of seasonal mean net ecosystem carbon exchange (NEE), gross ecosystem productivity (GEP), and ecosystem respiration (ER) on soil moisture (θ) and inorganic nitrogen (IN), respectively, across different plots in 2011 (solid circles and bold lines) and 2012 (open circles and thin lines). Data are the mean of each treatment for six replicates.

precipitation fell in the ephemeral growing season. Increased precipitation significantly increased community biomass (both of ephemerals and annuals), leading to an increased GEP. Although ER was also stimulated by increased precipitation, the magnitude of the increase was relatively small. Therefore, the larger positive response of GEP as compared to ER to increased precipitation resulted in a positive impact on NEE (a smaller CO_2 loss). Positive NEE responses to increased precipitation have also been observed in arid and semiarid regions (Parton et al., 2012). Consistent with our study, the plant growth is the critical determinant of the NEE response to increased precipitation. For example, increased precipitation increased NEE in a sotol grassland of the Chihuahuan Desert by promoting grass growth and density, despite no impacts on shrubs and succulents (Robertson et al., 2010). Moreover, a greater increase in GEP than ER under increased precipitation generally relies on a higher photosynthetic capacity and faster relative growth rate of ephemerals in this desert (Qin and Tan, 2007; Huxman et al., 2008; Gremer et al., 2012).

The precipitation pattern in the dry year (2012) differed profoundly from that in the wet year (2011), with only 32.7% of total precipitation falling in the ephemeral growing season. In this dry

year, increased precipitation had a negative effect on NEE (a greater CO_2 loss), and this resulted from the larger response of NEE than that of GEP to increased precipitation, as evidenced by the lower slope for the correlation of GEP vs. θ as compared to that of ER vs. θ . The relative importance to ER shifted from precipitation in 2011 to temperature in 2012. In 2011, the stimulation of plant growth with increased precipitation exerted an indirect effect on decomposition by increasing litter availability. Thus, ER was related to θ in this year. However, there was no correlation between ER and T_s , and this is because of the decreased T_s in autumn. In the autumn of 2012, the controlling effect of T_s on ER surpassed that of θ , leading to a decoupling of ER with θ , and T_s became the most important influencing factor of ER.

Overall, the disproportional increases in GEP and ER were responsible for the opposite responses of NEE to increased precipitation between years. The magnitude of the responses of GEP and ER to increased precipitation is mediated by the differential plant growth responses of ephemerals and annuals to precipitation, which emphasizes the critical role of precipitation timing in determining the responses of NEE to increased precipitation. This conclusion has also been found by other studies (Wu et al.,

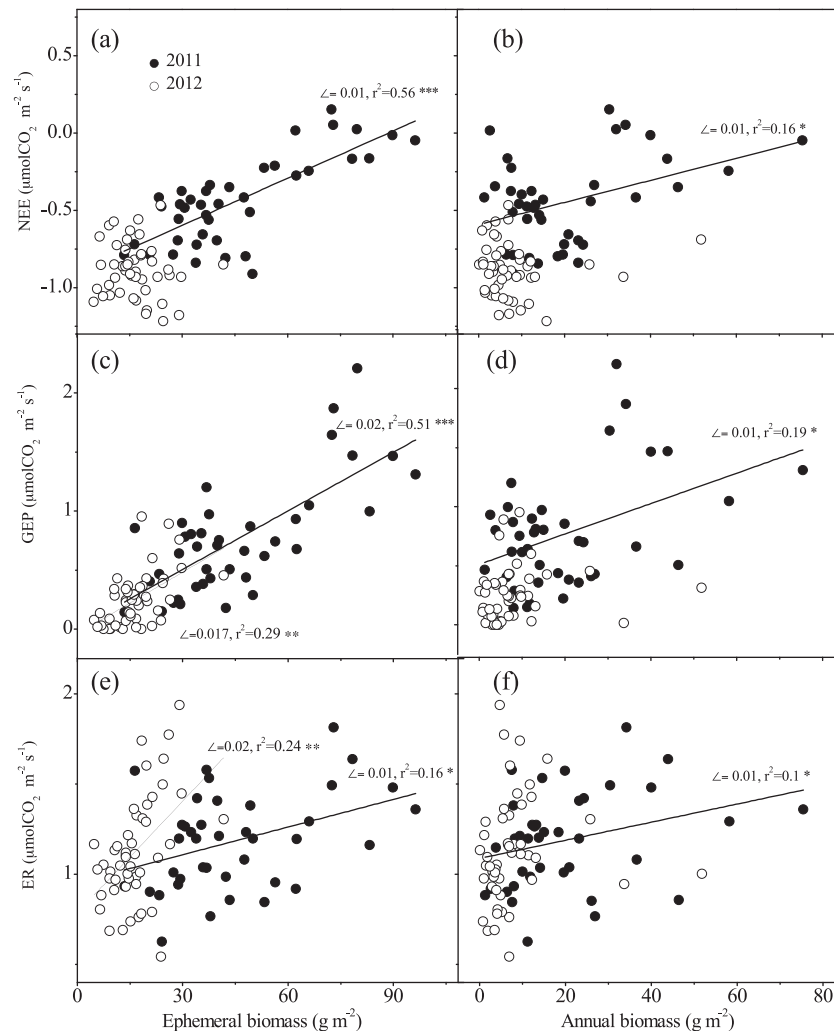


Fig. 7. Spatial dependence of seasonal mean net ecosystem carbon exchange (NEE), gross ecosystem productivity (GEP), and ecosystem respiration (ER) on ephemeral and annual biomass, respectively, across different plots in 2011 (solid circles and thick lines) and 2012 (open circles and slim lines). Data are the mean of each treatment for six replicates.

2011; Richardson et al., 2013). For instance, a recent review found that plant-available water is a key factor driving the C exchange responses to the variation of precipitation (Zeppel et al., 2014), and the absent response of NEE to increased precipitation in a shortgrass in northeastern Colorado was caused by the mismatch of precipitation with plant biomass accumulation (Levine et al., 2011).

4.2. N addition effects on C exchange

Although N addition usually stimulates plant growth and increases productivity because of its tight linkage with photosynthesis (Elser et al., 2007; LeBauer and Treseder, 2008; Treseder, 2008), the effects of N addition on GEP and ER vary among studies because of the different impacts on plant community and soil biota (Arens et al., 2008; Treseder, 2008). For instance, N addition exerted no impacts in a boreal mire in eastern Finland (Saarnio et al., 2003) and negative impacts on NEE in a California grassland (Harpole et al., 2007), whereas positive N addition effects on NEE were observed in a temperate steppe adjacent to our study site (Xia et al., 2009). The present results showed that N addition had no significant influences on NEE because of the lack of responses of GEP and ER to N addition.

Previous studies have emphasized the importance of plant functional group in regulating the responses of ecosystem C exchange

to N addition (Xia et al., 2009). The present study showed that N addition slightly increased community biomass by promoting ephemeral growth in the wet year (2011). Given the higher photosynthetic rate and larger biomass proportion of ephemerals in the herbaceous layer, GEP and ER were slightly and proportionally stimulated by N addition, as evidenced by the positive relation between IN and GEP, and IN and ER. Therefore, no NEE responses to N addition in 2011 resulted from the proportional increase in GEP and ER. In the dry year (2012), N addition only slightly stimulated ephemeral growth in interplant spaces because of the low precipitation in the ephemeral growing season. As a result, N addition did not induce an increase in GEP and responses of NEE were thus negative (greater CO_2 loss) in interplant spaces. While benefiting from the nursing effects and the stemflow of shrubs (Li et al., 2009, 2010), annual plants beneath shrubs could survive in the dry year and increase their biomass. As a result, N addition generated a positive response of GEP beneath shrubs in the dry year. Moreover, consistent with some studies (Saarnio et al., 2003; Bubier et al., 2007), N addition did not have any significant effects on ER in the dry year. So, N addition positively impacted NEE (smaller CO_2 loss) beneath shrubs in 2012, although not significant. In summary, our results showed that the inter-annual variation of precipitation could generate discrepant responses to N addition between annuals and ephemerals, and thus modulated the response regime of NEE to N addition in the desert.

Combined increased precipitation and N addition exhibited no interactive influences on C exchange in this study. This is consistent with some studies conducted in drylands (Bubier et al., 2007; Harpole et al., 2007). The non-synergistic effects of increased precipitation and N addition on NEE can be the result of the increased N availability with increasing precipitation (by 14% in 2011 and 38% in 2012) (Reichmann et al., 2013). This result may suggest that the effects of increased precipitation on C exchange would not be constrained by N availability in this temperate desert.

4.3. Site effects on the responses of C exchange

Throughout the two observational years, ER in interplant spaces and beneath shrubs was comparable, while in 2012, GEP was significantly higher beneath shrubs than interplant spaces, because of the increased plant growth of annuals beneath shrubs. Thus, CO₂ loss was reduced beneath shrubs. Our results differ from other studies with regard to the effects of 'shrub islands' on C exchange in arid lands. Those studies have shown a close dependence of ER on the size of SOM pool, and C production was much greater beneath plants than in interplant spaces because of the higher microbial activity beneath shrubs. However, although soil substrates for microbial respiration were significantly higher beneath shrubs (Li et al., 2011), soil microbial biomass showed no significant difference between the two sites due to the unfavorable soil pH beneath shrubs (Li et al., 2011). Meanwhile, because of the poor shading of shrubs, soil temperature also had no difference between sites. Thus, similar soil microbial biomasses and temperatures might be responsible for the comparable ER between sites. This result highlights the critical role of GEP in determining the difference of NEE between sites. In detail, although plant community composition differed between the two sites, the plant life-history and functional group are similar. For instance, the life history of *S. arabis* beneath shrubs is similar to *E. oxyrhinchum* and *A. linifolium* in interplant spaces (Fig. S1). Also, the dominant annual *S. passerina* beneath shrubs functionally resembles *S. nitraria* in interplant spaces. Therefore, both GEP and ER responded similarly in magnitude to precipitation and N addition, leading to the independent NEE response to increased precipitation and N addition between microsites. This result suggests that soil substrates may not constrain C exchange responses to increased precipitation and N deposition in this temperate desert.

4.4. Potential ecological roles of ephemeral plant community in desert C exchange

Although increased precipitation and N addition increased GEP, the positive effects on GEP did not offset ER because of the extremely short growing season for ephemerals; as a result, ecosystem showed a net carbon release even under increased precipitation. In addition, a clear inter-annual variation in ecosystem C exchange was observed, with a reduction in C release in the wet year (61% less than that in the dry year), which mainly resulted from the boosted growth of ephemeral plants. Thus, the effects of increased precipitation were dependent on the ephemeral growth, with ca. 84% and 86% of GEP from the ephemeral growing season in 2011 and 2012. Ephemeral plants are complementary to shrubs and perennials with regard to ecosystem carbon uptake in this desert ecosystem (Liu et al., 2012). In addition, the interaction between site and plant functional group has two key implications for ecosystem C exchanges. First, although our result is not in line with the 'resource islands' concept in arid lands (Jackson and Caldwell, 1993; Aguiar and Sala, 1999), our study highlights the important role of active vegetation in desert C exchange, suggesting soil resource heterogeneity does not always result in a variation of ecosystem function. Second, the limited observational duration (two years) is

a shortage in our study. If increased precipitation and N addition lead to more resources accumulating beneath shrubs and becoming available to annuals, the dominance of annuals in plant community may increase and lead to inconsistent NEE seasonalities and responses to environmental cues. A similar process occurred in the Great Basin, North America, where the invasion of some alien annuals, including *Erodium cicutarium*, *Bromus rubens*, and *Schismus spp.*, altered the ecosystem C exchange (Brooks, 1999).

5. Conclusions

Our results support the idea that the spring herbaceous plant community in the temperate desert is important for C exchange. These species can change their growth responses, thereby mediating the NEE responses to increased precipitation and N addition. Inconsistent with the first hypothesis, increased precipitation decreased ecosystem C release in the wet year, but increased it in the dry year, due to the disproportional stimulations of gross ecosystem productivity (GEP) and ecosystem respiration (ER). Also, contrary to our prediction, NEE was independent of N availability, as no changes in NEE were observed with N addition, and NEE in interplant space and beneath shrub was comparable. There were no synergistic effects between increased precipitation and N addition, and the responses of NEE to increased precipitation showed no difference between interplant space and beneath the dominant shrub. In sum, this study highlights the critical role of precipitation in the responses of NEE of desert ecosystems to climate change.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2014.11.011>.

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