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Asymmetric sensitivity of ecosystem carbon and water processes in response to precipitation change in a semi-arid steppe

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Summary

1. Semi-arid ecosystems play an important role in regulating the dynamics of the global terrestrial CO_2 sink. These dynamics are mainly driven by increasing inter-annual precipitation variability. However, how ecosystem carbon processes respond to changes in precipitation is not well understood, due to a lack of substantial experimental evidence that combines increased and decreased precipitation treatments.

2. This study, a 3-year field manipulation experiment with five precipitation levels conducted in a semi-arid steppe, examined the impacts of increased and decreased precipitation on ecosystem CO_2 (GEP: gross ecosystem photosynthesis; ER: ecosystem respiration; NEE: net ecosystem CO_2 exchange), water exchange (ET: evapotranspiration), and resource use efficiency (CUE: carbon use efficiency; WUE: water use efficiency).

3. We found that decreased precipitation reduced ecosystem CO_2, water exchange and resource use efficiency significantly, while increased precipitation did not cause significant influence on them. That is, they responded more sensitively to decreased precipitation. Soil water availability was the most important driver determining changes in GEP, ER and ET. Changes in NEE, CUE and WUE were predominately regulated by soil temperature. Photosynthesis at leaf and ecosystem levels showed significantly greater sensitivity to changed precipitation than respiration and ET, and therefore determined the trends of net carbon uptake and resource use efficiency.

4. This study highlighted an asymmetric response of ecosystem carbon and water processes to altered precipitation. This is potentially important for improving our understanding of how possible future changes in precipitation will affect the carbon cycle. Taking this asymmetric response into consideration will inevitably reduce uncertainties in predicting the dynamics of the global carbon cycle.

Key-words: altered precipitation, carbon use efficiency, ecosystem CO_2 exchanges, evapotranspiration, nonlinear response, water use efficiency

Introduction

Terrestrial ecosystems make up about half of the global CO_2 sink (Ballantyne *et al.* 2012) and are a major cause of inter-annual variability and uncertainty in global CO_2 uptake (Ahlström *et al.* 2015). Recent studies have revealed that most of the variability and uncertainty arise from semi-arid ecosystems (Poulter *et al.* 2014; Ahlström *et al.* 2015). Ecosystem productivity in semi-arid areas is generally water-limited and strongly associated with inter-annual precipitation fluctuations (Knapp *et al.* 2008; Poulter *et al.* 2014; Ahlström *et al.* 2015; Bernacchi & VanLoocke 2015; Nielsen & Ball 2015). Therefore, understanding how ecosystem carbon (C) processes respond to

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precipitation change in semi-arid ecosystems can greatly improve our ability in predicting the global C cycle (Poulter *et al*. 2014).

Net ecosystem CO_2 exchange (NEE) is an index for ecosystem CO_2 uptake or release, which is the difference between gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER) (Niu *et al*. 2008; Chen *et al*. 2009; Sloat *et al*. 2015). Until now, most field experiments that manipulate precipitation have used either water addition or water reduction treatments (Niu *et al*. 2008; Chen *et al*. 2009; Yan *et al*. 2011a; Sloat *et al*. 2015). These studies have found that NEE is significantly suppressed by reduced precipitation, due to a greater decrease in GEP than ER under drought condition (Xu & Zhou 2008; Wu *et al*. 2011). However, NEE does not give a consistently positive response to increased precipitation, in spite of both increased GEP and ER. For example some studies have shown that with increased precipitation, GEP has a greater increase than the increase in ER in arid and semi-arid ecosystems, leading to increasing NEE (Niu *et al*. 2008; Yan *et al*. 2011a). Other studies report an increase in GEP that is offset by ER, resulting in no change in NEE with increased precipitation, an outcome mostly observed under mesic conditions (Verma *et al*. 2005; Risch & Frank 2007). Therefore, the response magnitude of the ecosystem CO_2 exchange to increased precipitation may not be the same as the response to reduced precipitation. This creates a compelling need to include increased and decreased precipitation in a single experiment, to have a broader understanding of the impacts of altered precipitation (Nielsen & Ball 2015).

Resource use efficiency is used to express the cost of carbon acquisition in terms of carbon, water and nutrients (Limousin *et al*. 2015), e.g. carbon use efficiency (CUE), the ratio of NEE to GEP (DeLucia *et al*. 2007; Maseyk *et al*. 2008; Zhu 2013). In many biogeochemical cycling models, CUE is set at a constant value of about 0·5 (DeLucia *et al*. 2007; Metcalfe *et al*. 2010; Zhu 2013). However, an increasing number of recent studies are challenging the idea that CUE is a constant and find variable CUE at different temporal and spatial scales (DeLucia *et al*. 2007; Maseyk *et al*. 2008; Piao *et al*. 2010; Zhang *et al*. 2014). For example CUE has been reported to increase with decreasing temperature, and increasing precipitation and nutrient supply in forest ecosystems (DeLucia *et al*. 2007; Metcalfe *et al*. 2010; Piao *et al*. 2010; Zhang *et al*. 2014). However, in semi-arid grasslands, where the ecosystem C cycle is highly sensitive to precipitation change (Knapp *et al*. 2008; Wu *et al*. 2011), how CUE would change under future precipitation patterns is as yet unknown.

Water use efficiency (WUE), the ratio of ecosystem CO_2 assimilation to water losses (Beer *et al*. 2009; Niu *et al*. 2011; Bernacchi & VanLoocke 2015), is a key index to couple terrestrial ecosystem C and water cycles and evaluate potential carbon sequestration under future precipitation change (Beer *et al*. 2009; Bernacchi & VanLoocke 2015). Previous studies have reported that ecosystem WUE is sensitive to climate change and enhanced with increasing annual precipitation (Beer *et al*. 2009; Niu *et al*. 2011; Yan *et al*. 2011a; Bernacchi & VanLoocke 2015). However, the underlying mechanisms for this are not clear yet.

The semi-arid steppe of Inner Mongolia is a water-limited ecosystem (Bai *et al*. 2008; Chen *et al*. 2009). To date, most studies have focused on the influence of varying precipitation on productivity and community composition (Bai *et al*. 2008; Yang *et al*. 2011). Limited information about the C exchange process hampers our understanding of the mechanisms underlying the response of ecosystem functions to future changed precipitation regimes. In this study, a manipulative experiment with a 5-level precipitation gradient was conducted in the steppe. Ecosystem CO_2 and water exchange were determined during the growing seasons of 2012–2014. In a water-limited ecosystem, plant growth is generally suppressed or even ceased under drought condition (Knapp *et al*. 2015), therefore, we hypothesized that: (i) the responses of ecosystem CO_2 and water exchange would be more sensitive to drought than to water addition; (ii) resource use efficiency (CUE and WUE) would exhibit a positive response to changes in precipitation, depending on the magnitude of variations in ecosystem photosynthesis and respiration or evapotranspiration.

Materials and methods

STUDY SITE

This study was conducted in a semi-arid natural grassland (44°22′N, 117°35′E, 1148 m), located in West Ujinmqin Banner, Inner Mongolia, China. The site was fenced in 2011 with no grazing or other disturbance thereafter. Before being fenced, the site was mown once every year during August. Based on long-term (1955–2011) meteorological records from a weather station located about 30 km from the site, the mean annual temperature is 1·5 °C, annual precipitation is 333 mm with 87% (288 mm) occurring during the growing season (May to September). Precipitation during the growing season fluctuated from 508 mm in 1998 (76% above the long-term mean) to 118 mm in 2007 (59% below the mean). It is a typical steppe plant community, dominated by C_3 perennial grasses and forbs, such as *Stipa grandis*, *Leymus chinensis* and *Anemarrhena asphodeloides*. These three species make up about 60% of the total above-ground biomass.

EXPERIMENTAL DESIGN

The experiment was established in June 2012 as a randomized block design with five precipitation levels. These were a 60% (P−60) and 30% (P−30) precipitation reduction, an ambient control (P), and a 30% (P+30) and 60% (P+60) precipitation addition. A total of 20 plots were assigned to four blocks as replicates. Each plot was 3 m × 4 m with 1 m spacing between plots. To avoid edge effects, all measurements were conducted in the central area (2 m × 3 m). We also inserted tin sheets into the ground to a depth of 100 cm around each plot to prevent any lateral movement of soil water.

Precipitation treatments were carried out from May (June in 2012) through August 2012–2014. For the P−30 and P−60 treatments, rainfall was removed by passive rainout shelters. Each shelter has a fixed metal structure (4 m in length, 3 m in width, 1·0–1·4 m in height), with the high end of the shelter (1·4 m) facing south. Eight and 16 V-shaped acrylic strips (15·6 cm in width and 300 cm in length; 95% light transmission; Beijing Plastics Research Institute, Beijing, China) were used to block 30% and 60% of the precipitation. This type of shelter was developed by (Yahdjian & Sala 2002), and has been replicated in many experiments around the world, due to the low cost and minimal influence on microclimate (Yahdjian & Sala 2002). In this experiment, the rainout shelters intercepted 6% and 11% of photosynthetically active radiation (PAR) in the P−30 and P−60 treatments, and did not significantly affect daytime canopy air temperature (Fig. S1, Supporting Information).

For the P+30 and P+60 treatments, 30% and 60% rainfall amount of each precipitation event was added immediately after the event that was >2 mm. The water addition was conducted with a handheld irrigation system. All the added water was taken from rainfall removed by the rainout shelters. This gave us five precipitation levels without modifying the seasonal precipitation pattern.

ECOSYSTEM CO_2 AND WATER EXCHANGE MEASUREMENT

Ecosystem CO_2 exchange was measured using the static chamber method according to (Chen *et al.* 2009). Briefly, before measurement, a square metal base rim (0·5 m × 0·5 m in area with 10 cm in height) was inserted into the soil leaving 3 cm above the ground. During the growing season, ecosystem CO_2 exchange was measured on sunny days every 10 days from 2012 to 2014. The measurements were conducted using a transparent chamber (0·5 m × 0·5 m × 0·5 m) attached to an infrared gas analyser (LI-840A; LI-COR Inc., Lincoln, NE, USA) and an air pump (LI-COR Inc.). During measurement, a transparent chamber was attached to the base to determine net ecosystem CO_2 exchange (NEE) and evapotranspiration (ET). Consecutive measures of CO_2 and H_2O concentrations were logged by a computer at 1 s intervals for 80 s. The chamber was then lifted, vented and replaced on the base rim, and covered with a lightproof cloth mantle to prevent sunlight entering the chamber. These steps were repeated to determine ER. All measurements were taken during 08:00–11:00 h (local time). NEE and ER were calculated from the time-courses of CO_2 concentrations following (Chen *et al.* 2009), and ET was calculated from H_2O. Gross ecosystem photosynthesis (GEP) was calculated as the difference between NEE and ER (GEP = −NEE + ER). The negative and positive NEE values represent net C uptake and release by the ecosystem respectively.

ENVIRONMENTAL FACTORS

Daily precipitation and air temperature (T_a) were collected from an automatic weather station about 100 m away from the experimental plots. At the same time as ecosystem CO_2 exchange measurements, volumetric soil water content (VSWC) at 0–10 cm soil depth was determined by a TDR-300 soil moisture probe (Spectrum Technologies Inc., Plainfield, IL, USA); soil temperature (T_s) at 10 cm was determined by a thermocouple probe (LI-8100-201) connected to the LI-8100 (LI-COR Inc.).

ABOVE-GROUND NET PRIMARY PRODUCTIVITY

During the peak growing season (10–15 August) in each year, above-ground plant biomass was harvested from a 0·2 m × 0·8 m strip in each plot. Current year biomass (including green tillers and current year litter) was separated from litter from the previous year, oven-dried at 65 °C for 48 h, and then weighed. Current year biomass was used to evaluate above-ground net primary productivity (ANPP) in each season.

CANOPY GREENNESS COVERAGE

Canopy greenness coverage (Cover) was determined by an improved digital camera method (Arnone *et al.* 2008). Briefly, after ecosystem CO_2 measurement, two digital photos of the area in each base rim were taken with a digital camera (DMC-LX7GK; Matsushita Electric Inc., Osaka, Japan). The photos were analysed in Photoshop (CS7.1; Adobe Inc., San Jose, CA, USA) to acquire the total number of pixels and a green pixel count. Cover was quantified by the percentage of green pixels to total pixels.

SOIL INORGANIC NITROGEN AND LEAF NITROGEN CONTENT

In August 2014, two soil cores (10 cm depth by 7 cm diameter) were collected from each plot and mixed as one sample to determine soil inorganic nitrogen content (SIN). After all visible roots had been excluded; soil samples were extracted with 0·5 m K_2SO_4. The solutions were filtered through 45 μm filters and analysed with a FIAstar 5000 Analyzer (Foss Tecator, Hillerod, Denmark). During the peak season, the leaves of the three dominant species (*S. grandis*, *L. chinensis* and *A. asphodeloides*) were collected, oven-dried and crushed to measure leaf nitrogen (N) content. Leaf N content was determined in the laboratory with a CHNOS Elemental Analyzer (Vario EL III, Elemental Inc., Hanau, Germany).

FOLIAR GAS EXCHANGE MEASUREMENT

In July 2014, foliar gas exchange in the three dominant species (*S. grandis*, *L. chinensis* and *A. asphodeloides*) in the P−60, P and P+60 treatments was measured using a portable photosynthesis system (LI-6400; LI-COR Inc.) with a 6-cm^2 (2 cm × 3 cm) clamp-on leaf cuvette. Leaves did not fully fill the cuvette so leaf area was determined by the width of a single leaf (for *L. chinensis* and *A. asphodeloides*) or 8–10 leaves abreast (for *S. grandis*) and the length of the cuvette. For example the leaf width of *L. chinensis* was 0·8 cm, therefore the leaf area was 2·4-cm^2 (0·8 cm × 3 cm). All measurements were taken from 07:30 to 11:00 h (local time) on a sunny day, when ambient PAR ranged from 660 to 1300 μmol m^{-2} s^{-1}. A light source was set to 1500 μmol m^{-2} s^{-1} to determine maximum leaf photosynthesis rate (A_{max}), transpiration rate (T) and stomatal conductance (g_s). Previous studies have shown that a light intensity of 1500 μmol m^{-2} s^{-1} is beyond the light saturation point of species in this region (Niu *et al.* 2008; Yan *et al.* 2011b). An airflow rate of 500 ml min^{-1} was used during the measurements. We did not control leaf temperature, water vapour or CO_2 concentrations.

STATISTICAL ANALYSES

Ecosystem carbon (CUE) and water (WUE) use efficiency were calculated as follows:

$$\mathrm{CUE} = 1 - \frac{\mathrm{ER}}{\mathrm{GEP}} = -\frac{\mathrm{NEE}}{\mathrm{GEP}} \qquad \text{eqn 1}$$

$$\mathrm{WUE} = \frac{\mathrm{GEP}}{\mathrm{ET}} \qquad \text{eqn 2}$$

Sensitivity is indicated by the relative change in response parameters to the relative change in precipitation in the manipulation plots compared with the control plots and calculated as follows:

$$\text{Sensitivity} = \frac{(X_{\mathrm{PPT}i} - X_{\mathrm{PPT}})/X_{\mathrm{PPT}}}{(\mathrm{PPT}i - \mathrm{PPT})/\mathrm{PPT}} \qquad \text{eqn 3}$$

where X indicates the response parameters, e.g. GEP, ER, NEE, ET, CUE and WUE; PPT is the ambient precipitation and PPT*i* indicates precipitation in the manipulation plots. A sensitivity of one indicates that a relative change in precipitation (e.g. 1%) induces the same relative change in response parameters (e.g. 1%) in the same direction (Hsu, Powell & Adler 2012). A negative value of sensitivity means the direction of change in the parameter is opposite to the precipitation manipulation. The parameter of sensitivity is dimensionless, which allows us to compare the differences in ecosystem processes in response to precipitation change.

In this study, seasonal mean values were calculated from all measurements during each growing season. Seasonal variability in VSWC ($\mathrm{CV_{VSWC}}$) was calculated by the ratio of standard deviation to mean VSWC. Repeated Measures ANOVA (RMANOVA) was applied to examine precipitation manipulation effects on VSWC, T_s, Cover, GEP, ER, NEE, ET, CUE and WUE over each growing season. Student's *t*-tests were used to compare the differences in sensitivity in response to increased and decreased precipitation. One-way ANOVA was applied to examine the effect of precipitation manipulation on leaf photosynthetic parameters. Partial correlation analysis was used to examine the relationship between abiotic and biotic factors, and ecosystem C cycle processes, in which T_a was used as the control variable. All statistical analyses were performed using SAS 9.1.3 (SAS Institute Inc., Cary, NC, USA). Structural equation modeling (SEM) was performed to analyse hypothetical pathways that may induce changes in C cycle processes in response to precipitation change, which was performed by AMOS 17.0 (Amos Development, Spring House, PA, USA).

Results

ABIOTIC AND BIOTIC FACTORS

During the growing season (May–September), natural precipitation in 2012–2014 was 429 mm, 261 mm and 260 mm (Fig. S2a,e and i) respectively. The amounts were 49% greater, and 9% and 10% less than the long-term (1955–2011) mean value (288 mm). After manipulation, we had a five-fold range in precipitation from 122 mm (P−60 in 2014) to 610 mm (P+60 in 2012), which was greater than the long-term natural fluctuation (118–508 mm).

Seasonal variations in VSWC were closely related to precipitation events and were significantly affected by precipitation manipulation in all seasons ($P < 0{\cdot}001$, Fig. S2b, f and j). Mean VSWC in the control plots (P) was 16%, 14% and 13% from 2012 to 2014 respectively (Fig. 1a). Over the whole experimental period, VSWC in the P−30 and P−60 treatments decreased by 19% and 37%, and increased by 11% and 26% in the P+30 and P+60 treatments. Therefore, VSWC increased logarithmically as precipitation increased, with a greater sensitivity to the decreased precipitation treatment (Fig. 1a). The seasonal variability in VSWC ($\mathrm{CV_{VSWC}}$) was found to be negatively related to precipitation change, especially in the latter two seasons (Fig. 1b).

Air and soil temperature (T_a and T_s) shared similar seasonal patterns, with a peak in August (Figs S1 and S2). Decreased precipitation increased T_s significantly ($P < 0{\cdot}05$), especially in the third season (Figs 1c and S2k). Canopy greenness coverage (Cover) developed with increasing temperature, with maximum values of 50–60% during the peak season (Fig. S2d,h and i). As precipitation increased, Cover increased nonlinearly, except during the first wet season (Fig. 1d).

ECOSYSTEM $\mathrm{CO_2}$ AND WATER EXCHANGE

Clear seasonal variations in ecosystem $\mathrm{CO_2}$ (GEP, ER and NEE) and water exchange (ET) were observed during the three seasons (Fig. S3). In the first two seasons, the pattern was similar, with a peak during July–August (Fig. S3). However, in the third season, a double-humped pattern was observed for GEP and NEE, and values peaked in June and August (Fig. S3m and o), whereas ER and ET retained the past seasonal dynamics (Fig. S3n).

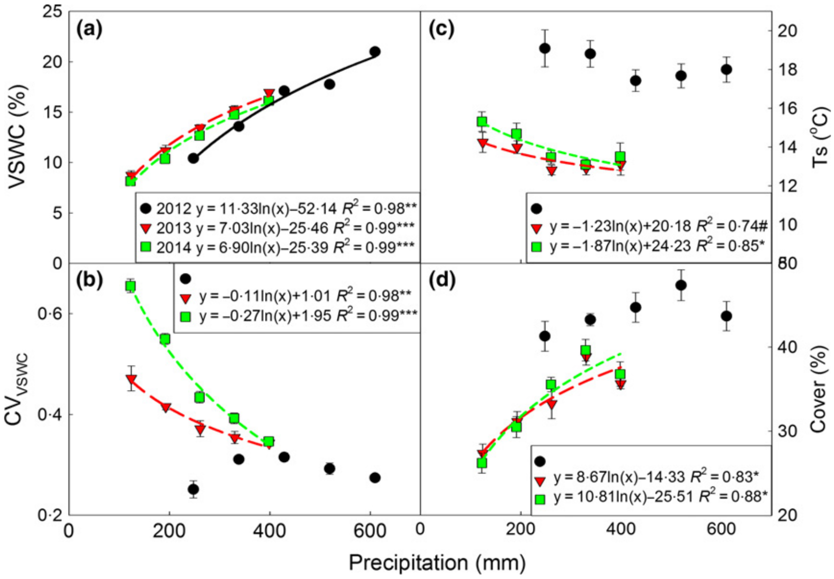

Fig. 1. Nonlinear response of abiotic and biotic factors to precipitation during 2012–2014. (a) Seasonal mean volumetric soil water content at 0–10 cm soil depth (VSWC, %), (b) seasonal variability of VSWC ($\mathrm{CV_{VSWC}}$), (c) soil temperature at 10 cm soil depth (T_s, °C) and (d) community canopy greenness coverage (Cover, %). All response curves are logarithmic. ***, **, * and # indicate the significant levels of $P < 0{\cdot}001$, $P < 0{\cdot}01$, $P < 0{\cdot}05$ and $P < 0{\cdot}1$ respectively.

Precipitation manipulation significantly influenced ecosystem CO_2 exchange throughout the measurement period, especially during the latter two seasons (Fig. S3). On average, decreased precipitation reduced GEP by 20% and 36% in P−30 and P−60 plots, ER by 11% and 26%, NEE by 27% and 44%, ET by 11% and 29% (Figs 2 and S3). There was no significant effect of water addition on these processes ($P > 0·1$; Figs 2 and S3). Overall, CO_2 and water fluxes showed significantly logarithmic relationships with increasing precipitation across three seasons ($P < 0·1$, Fig. 2a–d).

ECOSYSTEM RESOURCE USE EFFICIENCY

Seasonal variation in resource use efficiency in the control plots was relatively stable (0·5–0·7 for CUE and 4–6 μmol CO_2 $mmol^{-1}$ H_2O for WUE) over the first two seasons (Fig. S3e and f,k and l). However, in the third season, there was significant seasonal variation with lower values (0·14 for CUE and 2·4 for WUE) during the peak season (Fig. S3q–r), which induced relatively lower seasonal mean values. Mean CUE in the control plots was 0·57, 0·59 and 0·44, WUE was 5·55, 4·22 and 3·59 from 2012 to 2014 (Fig. S3q–r). During all three seasons, mean CUE and WUE showed positive and logarithmic increases as precipitation increased, except WUE in 2012 (Fig. 2e–f).

SENSITIVITY OF ECOSYSTEM C AND WATER PROCESSES IN RESPONSE TO PRECIPITATION CHANGE

On average, significantly greater sensitivity to decreased precipitation (0·80, 0·50, 1·06 and 0·50) than to increased precipitation (0·24, 0·24, 0·24 and 0·24) was observed for all CO_2 and water exchange components – GEP, ER, NEE and ET (all $P < 0·1$; Fig. 3). The response sensitivity of GEP to precipitation change was greater than that of ER and ET, especially in drought treatments. Similar asymmetric patterns were also observed in the response of CUE and WUE (0·56 and 0·39 for decreased precipitation vs. 0·05 and 0·00 for increased precipitation; $P < 0·1$, Fig. 3).

THE INFLUENCE OF ABIOTIC AND BIOTIC FACTORS ON ECOSYSTEM C AND WATER PROCESSES

Abiotic (VSWC, CV_{VSWC} and T_s) and biotic (Cover and ANPP) factors both showed close correlations with CO_2, water exchange and resource use efficiency (Table S1). The results of the SEM analyses indicated that precipitation change directly altered the soil environment (VSWC, CV_{VSWC} and T_s), and explained 95%, 32% and 47% of the variation in soil parameters (Fig 4). Both SEM and partial correlation analyses showed that changes in GEP, ER and ET were dominated by the direct pathway through VSWC (Fig. 4a and Table S1). However, changes in NEE, CUE and WUE under precipitation manipulation were mainly affected through the T_s pathway (Fig. 4b and Table S1). GEP, ER, NEE and ET also showed significant positive relationships with soil nitrogen supply (Fig. S4).

The variations in NEE, CUE and WUE were all more dependent on changes in GEP (Fig. 5a–c). A significant quadratic relationship was found between CUE and WUE (Fig. 5d). CUE approached 0·6 with increasing WUE (Fig. 5d).

LEAF GAS EXCHANGE

Leaf maximum photosynthetic rate (A_{max}), transpiration (T) and stomatal conductance (g_s) of the three dominant species (*S. grandis*, *L. chinensis* and *A. asphodeloides*) were

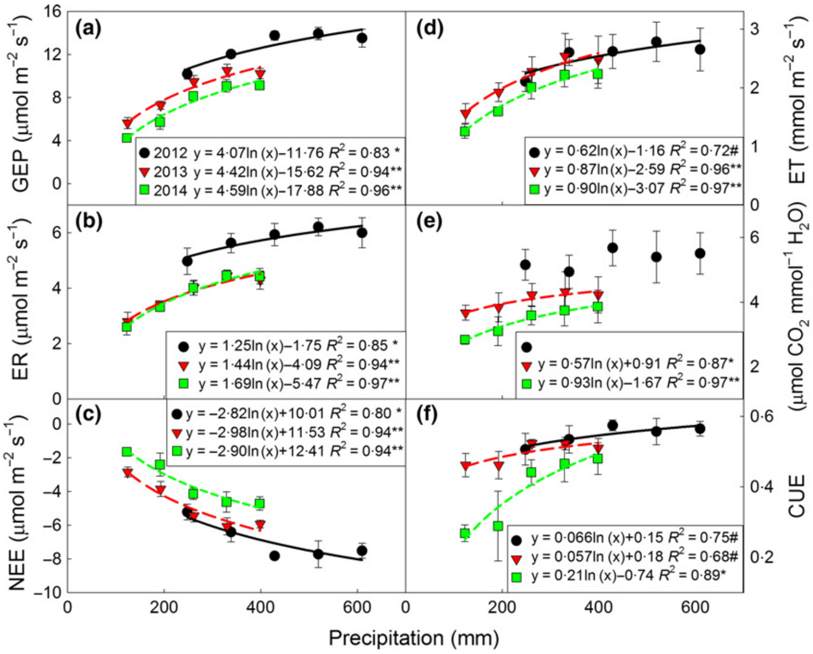

Fig. 2. Nonlinear responses of ecosystem C and water processes to changing precipitation during 2012–2014. (a) Seasonal mean gross ecosystem photosynthesis (GEP, μmol m^{-2} s^{-1}), (b) ecosystem respiration (ER, μmol m^{-2} s^{-1}), (c) net ecosystem CO_2 exchange (NEE, μmol m^{-2} s^{-1}), (d) evapotranspiration (ET, mmol m^{-2} s^{-1}), (e) water use efficiency (WUE, μmol CO_2 $mmol^{-1}$ H_2O) and (f) carbon use efficiency (CUE). **, * and $^{\#}$ indicate the significant levels of $P < 0·01$, $P < 0·05$ and $P < 0·1$ respectively.

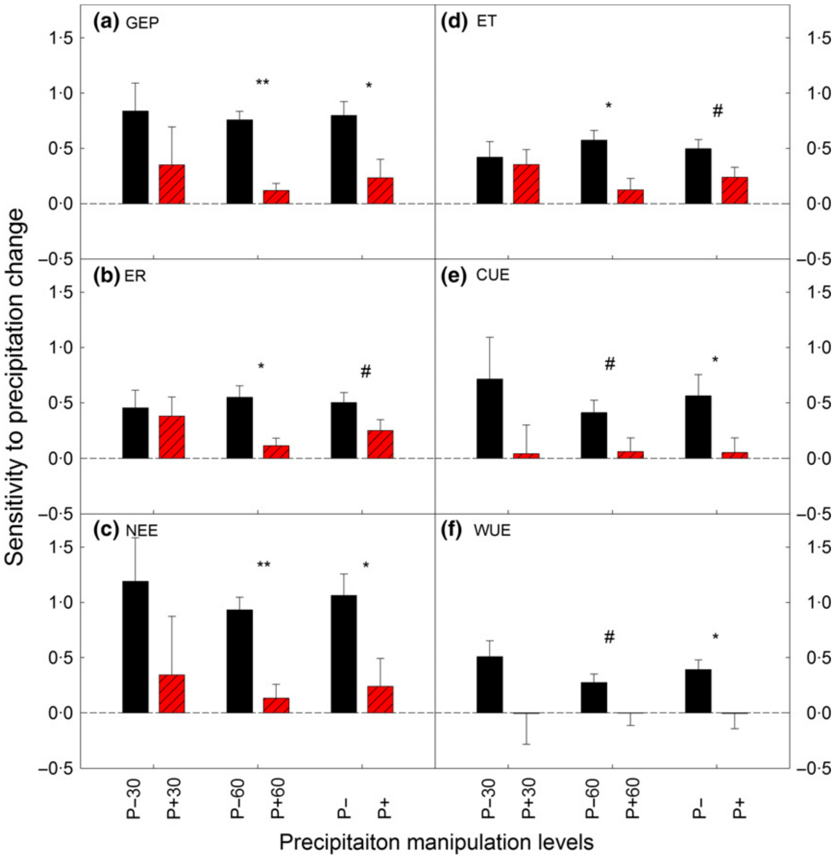

Fig. 3. Sensitivity of (a) gross ecosystem photosynthesis, (b) ecosystem respiration, (c) net ecosystem CO_2 exchange, (d) evapotranspiration, (e) carbon use efficiency and (f) water use efficiency in response to precipitation manipulation treatments. Sensitivity is a dimensionless parameter, calculated by the ratio of relative change in ecosystem C fluxes to the relative change in precipitation. P−30: 30% reduction in growing season precipitation; P+30: 30% increase in growing season precipitation; P−60: 60% reduction in growing season precipitation; P+60: 60% increase in growing season precipitation. P− represents the mean sensitivity to decreased precipitation and is averaged from sensitivity to P−30 and P−60; P+ represents the mean sensitivity to increased precipitation and is averaged from P+30 and P+60. **, * and # on each group of bars represents significant differences in *t*-test, at $P < 0{\cdot}01$, $P < 0{\cdot}05$ and $P < 0{\cdot}1$ levels respectively.

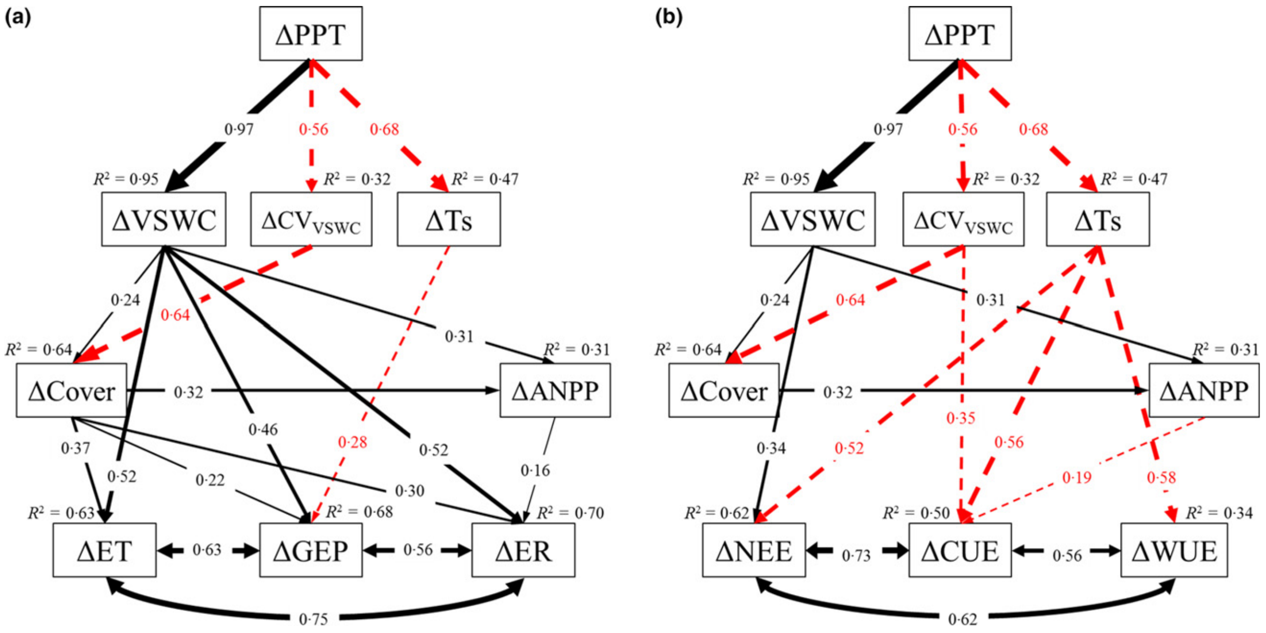

Fig. 4. Structural equation modeling (SEM) analysis of treatment effects on ecosystem C and water processes. Square boxes indicate variables included in the model. Results of model fitting: (a) gross ecosystem photosynthesis, ecosystem respiration and evapotranspiration, $\chi^2 = 22{\cdot}7$, $P = 0{\cdot}201$, d.f. = 18, $n = 48$; (b) net ecosystem CO_2 exchange, carbon use efficiency and water use efficiency, $\chi^2 = 23{\cdot}7$, $P = 0{\cdot}225$, d.f. = 20, $n = 48$ (a high P value associated with a chi-squared test indicates a good fit of the model to the data, i.e., no significant discrepancies). Black solid and red dashed arrows indicate significant ($P < 0{\cdot}05$) positive and negative effects. Values associated with the arrows represent standardized path coefficients. Arrow width indicates the strength of the relationship. R^2 values associated with response variables indicate the proportion of variation explained by relationships with other variables.

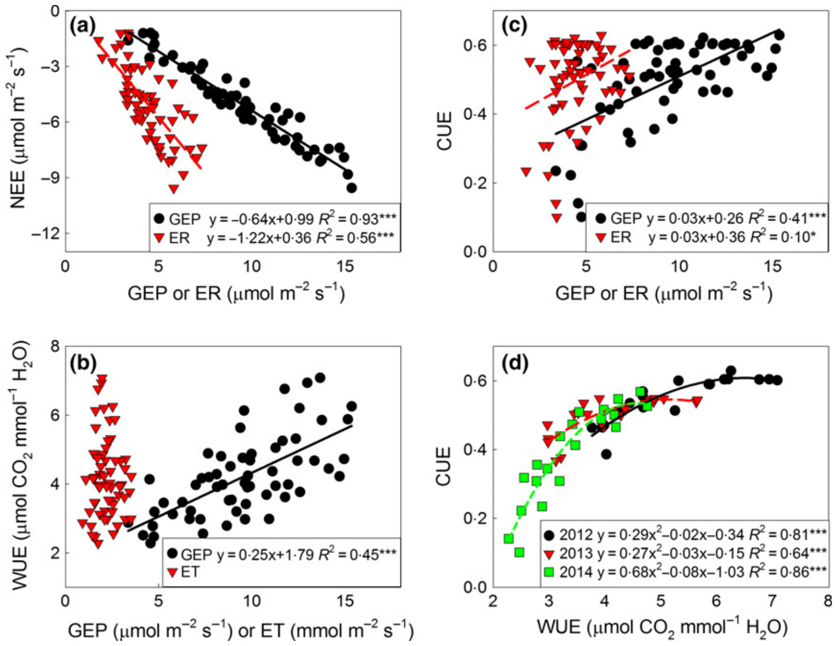

Fig. 5. Relationships among ecosystem C and water processes from 2012 to 2014. (a) The relative contribution of seasonal mean gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER) to net ecosystem CO$_2$ exchange, (b) GEP and ER to carbon use efficiency (CUE), (c) GEP and evapotranspiration to water use efficiency (WUE) and (d) Nonlinear relationship (quadratic curves) between CUE and WUE in each season. *** and * indicate the significant levels of $P < 0{\cdot}001$ and $P < 0{\cdot}05$ respectively.

all significantly reduced when precipitation was decreased (except for A_{max} of *L. chinensis*), but not affected by water addition (Fig. 6a,d and f). CO$_2$ and water exchange at leaf level were closely related to those at the ecosystem level (Fig. S5).

Discussion

ASYMMETRIC SENSITIVITY OF ECOSYSTEM CO$_2$ AND WATER EXCHANGE TO PRECIPITATION CHANGE

In this study, ecosystem CO$_2$ and water exchange were all reduced by decreased precipitation, but not significantly affected by increased precipitation, leading to the greater sensitivity to decreased than to increased precipitation. Therefore, significantly logarithmic relationships were observed among ecosystem carbon and water fluxes with the increase in precipitation amount. Such patterns have also been revealed in several model stimulations (Zhou, Weng & Luo 2008; Peng *et al.* 2013), although are still not confirmed by experimental evidence. This is largely due to a lack of studies that combine both reduced and enhanced precipitation (Nielsen & Ball 2015).

Volumetric soil water content was found to play a predominant role in determining the asymmetric sensitivity of ecosystem CO$_2$ and water exchange to variable precipitation (Fig. 4a and Table S1). In semi-arid regions, roots and microbial activities are mostly concentrated in the surface soil (Knapp *et al.* 2008; Bernacchi & VanLoocke 2015). A previous study in the same region demonstrated that the effect of increased precipitation on surface VSWC was reduced as the increase in event size due to water

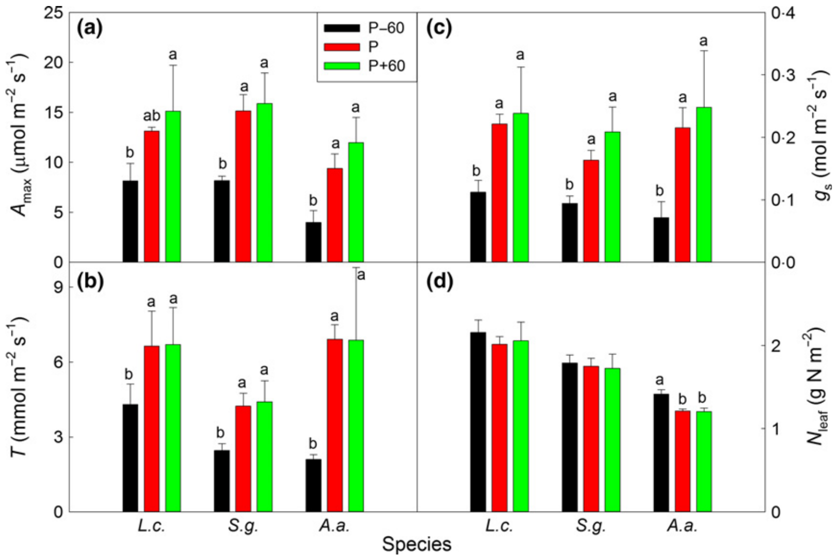

Fig. 6. Leaf gas exchanges of three dominant species in P−60, P and P+60 treatments. (a) Leaf maximum net photosynthesis (A_{max}, μmol m^{-2} s^{-1}), (b) transpiration (T, mmol m^{-2} s^{-1}), (c) stomatal conductance (g_s, mol m^{-2} s^{-1}) and (d) leaf nitrogen content (N_{leaf}, %). *L.c.*, *Leymus chinensis*, *S.t.*, *Stipa grandis*, *A.a.*, *Anemarrhena asphodeloides*. Different letters on the bars indicate a significant difference of $P < 0{\cdot}05$.

percolation, i.e. a rain event above 10 mm can trigger an increase in VSWC below the 10 cm soil layer (Chen *et al.* 2016). On the other hand, under decreased precipitation, reduction in VSWC could be strengthened greatly due to an increase in soil evaporation. In our study, plant growth and canopy cover were suppressed by drought, and as a consequence, soil temperature was enhanced (Fig. 1). These were found to be the main causes of increased soil evaporation and drying (Hu *et al.* 2009). Moreover, changes in soil water availability also altered soil nutrient supply (Fig. S4a). Soil inorganic nitrogen concentration was reduced significantly by decreased precipitation, and exacerbated further the depression of ecosystem CO_2 and water exchange under drought treatments (Fig. S4b). Therefore, a greater reduction in VSWC in the decreased precipitation plots leads to asymmetric change in ecosystem CO_2 and water exchange.

Similar asymmetric responses to precipitation change were also observed in leaf-level photosynthetic characteristics of the three dominant species (Fig. 6). To adapt to drought conditions, plants tend to decrease leaf stomatal conductance to prevent water loss, consequently suppressing leaf gas exchange (Xu & Zhou 2008; StPaul *et al.* 2012). The water addition treatment did not, however, improve leaf gas exchange in the dominant species. Similar results have been observed in other semi-arid studies (Niu *et al.* 2008, 2011). The insensitivity of leaf carbon assimilation to water addition might be due to limitations in the leaf photosynthetic capacity. Moreover, leaf nitrogen content, directly related to the leaf carbon assimilation rate (Evans 1989), was not changed by water addition. These results indicate that plant species that are adapted to limited water and N resources in semi-arid steppe systems tend to adopt a conservative resource-use strategy and may not be able to adjust their resource utilization in the short time (Zheng *et al.* 2012).

In addition, shelter artefact effects on microclimate (light, temperature and humidity, etc.) also potentially influence the physiological responses of plants to precipitation in manipulation experiments using permanently installed shelter infrastructure (Fay *et al.* 2000; Yahdjian & Sala 2002; Vogel *et al.* 2013; Power *et al.* 2016). Light interception, an unavoidable artefact, has shown substantial influences on plant responses (e.g. litter decomposition rate, plant metabolites and productivity) (Vogel *et al.* 2013; Power *et al.* 2016). In this study, light intensity was reduced 6% and 11% light interception by P−30 and P−60 shelters, which is comparable to other partially rainout shelters (Yahdjian & Sala 2002) and may cause overestimation of the drought effect on plant photosynthesis. However, the influence will be slight according to a previous shading experiment conducted in the same region, which found that light is not a limiting factor for plant growth in this area (Yan *et al.* 2011b). Moreover, the greater drought effects on leaf-level physiological responses (A_{max}, T and g_s, all measured at a fixed light intensity 1500 μmol m^{-2} s^{-1}; Fig. 6) of dominant species also suggested that the asymmetric ecosystem sensitivity to changing precipitation mainly resulted from the inherent responses of plants, but not the shading effect. Daytime air temperature was not affected significantly, likely due to the opened shelters to maximize air movement (Fay *et al.* 2000). We did not have data about other microclimate parameters, e.g. nighttime air temperature, humidity and vapour pressure deficit, which may also have some obscure effects on the responses of plants. However, in the absence of roof control and related data, their potential influences cannot be evaluated and completely dismissed in our study. Therefore, roof controls, the useful treatments to assess potential shelter effects, are strongly recommended in future manipulation experiments with rainout shelters.

DIFFERENT RESPONSES OF ECOSYSTEM CO_2 AND WATER EXCHANGE COMPONENTS TO PRECIPITATION CHANGE

The greater damping effect of drought on GEP than on ER suggests that CO_2 assimilation is more dependent than CO_2 release on water availability (Chen *et al.* 2009; Xia, Niu & Wan 2009; Sloat *et al.* 2015). GEP, resulting from plant photosynthesis, was greatly suppressed by drought stress through both direct (reduced photosynthetic area and capacity, Figs 1a and 6d) and indirect (constrained leaf stomatal conductance and nutrient supply, Figs 6c and S4a) pathways. Generally, ER is a combination of two components. One is heterotrophic respiration, which is sensitive to changes in water availability (Liu, Zhang & Wan 2009; Yan *et al.* 2010). But this only accounts for <40% of total ER (Chen *et al.* 2009; Yan *et al.* 2010, 2011a). The other major component is autotrophic respiration, dominated by plant maintenance respiration and highly sensitive to temperature rather than water condition (Ryan 1991; Lavigne & Ryan 1997; Yan *et al.* 2010). Therefore, increased T_s would enhance the maintenance respiration component and offset the decrease in heterotrophic respiration caused by drought (Metcalfe *et al.* 2010). This then leads to the greater reduction in GEP under the decreased precipitation treatments.

Evapotranspiration, the combination of canopy transpiration and soil evaporation, also showed the lower sensitivity to precipitation change than GEP. Predictably, canopy transpiration is reduced by lower leaf stomatal conductance (Fig. 6c) and canopy cover when precipitation decreases (Fig. 1d). Soil evaporation, which contributes up to 50% to total ET in the Inner Mongolian steppe, has been reported to increase in its proportion to ET with decreasing leaf area index or canopy coverage (Hu *et al.* 2009). Therefore, the reduced response sensitivity of ET to decreased precipitation is a trade-off between reducing canopy transpiration and increasing soil evaporation components.

CARBON BALANCE AND RESOURCE USE EFFICIENCY UNDER PRECIPITATION CHANGE

NEE and CUE are important parameters to indicate ecosystem C assimilation capacity and are determined by the relative magnitude of GEP and ER (DeLucia *et al.* 2007; Niu *et al.* 2008; Zhu 2013). In many global C cycle models, CUE is a fixed value of 0·5 (DeLucia *et al.* 2007; Metcalfe *et al.* 2010). However, increasing NEE and CUE were observed in this study as precipitation increased (Fig. 2). Similar trends in CUE have also been observed in forest ecosystems (DeLucia *et al.* 2007; Metcalfe *et al.* 2010; Limousin *et al.* 2015) and at a global scale (Zhang *et al.* 2014), indicating that changes in precipitation not only affect plant photosynthesis rates but also photosynthate partitioning into plant biomass (McDowell 2011; Limousin *et al.* 2015).

Our study also revealed that changes in NEE and CUE were more dependent on GEP than ER under precipitation manipulation (Fig. 5a and b). This is closely related to the greater sensitivity of GEP than ER in response to altered precipitation. Similar results were also reported by a multisite study in European forest ecosystems (Reichstein *et al.* 2007). As mentioned above, T_s is the key pathway regulating the outcome of net carbon assimilation and utilization. Increased T_s means greater plant respiration costs (Ryan 1991; Lavigne & Ryan 1997), therefore, less plant photosynthesis will be converted into net ecosystem CO_2 uptake, namely, lower NEE and CUE (McDowell 2011; Limousin *et al.* 2015).

WUE, the ratio of ecosystem photosynthesis to water loss, was also improved as precipitation increased and more dependent on GEP. This process was mainly regulated through variations in T_s (Fig. 4b), with higher T_s in the reduced precipitation plots playing a critical role in promoting soil evaporation and offsetting the suppressed transpiration (Hu *et al.* 2008; Tian *et al.* 2016). Consequently, the lower response of ET to precipitation change determines the greater dependency of WUE on GEP than ET (Hu *et al.* 2008; Niu *et al.* 2011; Tian *et al.* 2016).

We found that CUE presented a saturated response along with increasing WUE up to a threshold value of 0·6 (Fig. 5c), which is consistent with many other studies (DeLucia *et al.* 2007; Zhu 2013; Zhang *et al.* 2014). In this region, soil heterotrophic respiration is found to account for 15–30% of GEP, while plant respiration consumes about 25–40% of carbon assimilated by GEP (Chen *et al.* 2009; Yan *et al.* 2010, 2011a). That is, about 40–70% of photosynthetic carbon is returned to the atmosphere by hetero- and autotrophic respiration in this semi-arid grassland ecosystem. In our study, CUE was enhanced by increased precipitation and approached the maximum value (0·6) when precipitation was beyond 400 mm.

In summary, ecosystem C and water processes in response to increased and decreased precipitation were evaluated in a semi-arid steppe. We found: (i) an asymmetric sensitivity of ecosystem C and water processes in response to precipitation change. Therefore, the relative effects of increases or decreases in precipitation on ecosystem processes cannot be treated equally in any future data-assimilation and model analysis. (ii) Soil water content most strongly affects ecosystem photosynthesis, respiration and evapotranspiration, while soil temperature plays a more critical role in determining the responses of net C assimilation (NEE) and resource use efficiency (CUE and WUE). Therefore, in precipitation manipulation experiments, changes in temperature caused by precipitation treatments might be an important indirect pathway in regulating ecosystem C and water balance and should not be ignored. This study highlights the asymmetric responses of ecosystem processes to increased and decreased precipitation. Based on the asymmetric and nonlinear responses of the ecosystem to precipitation change (Zhou, Weng & Luo 2008), increasing global CO_2 concentration (Gill *et al.* 2002), nitrogen deposition (Tian *et al.* 2016) and warming (Wang *et al.* 2014), we suggest there is a widespread nonlinear ecological process taking place under climate change. Future manipulation experiments with multiple gradients should be encouraged to evaluate their influence on ecosystem productivity and processes, which are critical to our understanding and prediction of the global carbon cycle.

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Data accessibility

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.vf8d2 (Zhang *et al.* 2016).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Seasonal dynamics and mean values of daytime photosynthetically active radiation and air temperature.

Fig. S2. Seasonal variation in abiotic factors and biotic factors under different treatments from 2012 to 2014.

Fig. S3. Seasonal patterns of ecosystem C and water fluxes under different treatments from 2012 to 2014.

Fig. S4. Soil inorganic nitrogen content and its influence on ecosystem C processes.

Fig. S5. Relationships of net photosynthesis and transpiration between leaf and ecosystem levels.

Table S1. Results of partial correlation analysis among abiotic and biotic factors with ecosystem C processes.

Data S1. Raw data for analysis.