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# Drought-induced shift from a carbon sink to a carbon source in the grasslands of Inner Mongolia, China

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A R T I C L E I N F O

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A B S T R A C T

Precipitation has an impact on both gross ecosystem productivity (GEP) and ecosystem respiration (Reco), which ultimately influences net ecosystem productivity (NEP). A positive NEP denotes an ecosystem functioning as a carbon sink; whereas, a negative NEP denotes an ecosystem functioning as a carbon source. Therefore, drought plays an important role in the carbon balance of an ecosystem. However, little is known about the point at which the ecosystem converts from a carbon sink to a carbon source in extreme droughts. Such knowledge is crucial for predicting terrestrial carbon cycling under climate change, and consequently, was the subject of this study. We imposed two types of drought treatments on desert-grassland: (1) press-drought, in which the quantity of natural precipitation was reduced by 66% from May to August; and (2) pulse-drought, in which the quantity of natural precipitation was reduced by 100% during June and July. Reco and NEP were measured and GEP was calculated and then regression analyses were employed to determine the point at which the carbon sink shifts to a carbon source. The regression equation of NEP ($\mu mol \cdot m^{-2} \cdot s^{-1}$) on Reco ($\mu mol \cdot m^{-2} \cdot s^{-1}$) took the form: NEP = 0.504 Reco – 0.086 and, consequently, when Reco equaled 0.171 $\mu mol \cdot m^{-2} \cdot s^{-1}$, there was zero change in the carbon sink and GEP also equaled 0.171 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Below this value, the ecosystem functioned as a carbon source, whereas above this value, the ecosystem functioned as a carbon sink. Structural equation models (SEM) demonstrated that coverage, standing biomass, pH, soil water content and total soil carbon were the main driving factors on desert grassland ecosystem carbon fluxes.

## 1. Introduction

Precipitation plays a central role in the carbon balance of an ecosystem (Wu et al., 2011). Drought decreases not only gross ecosystem production (GEP), due to suppressed photosynthesis (Granier et al., 2007; Chaves et al., 2009), but also ecosystem respiration (Reco), due to reduced decomposition of plant biomass (Schwalm et al., 2012; Doughty et al., 2015). A change in GEP and/or Reco could affect net ecosystem productivity (NEP), if the difference between GEP and Reco is altered. Both GEP and Reco increase with an increase in precipitation, but GEP more so than Reco, resulting in an increase in NEP. In contrast, both GEP and Reco decrease with a decrease in precipitation, but again, more so in GEP than in Reco, resulting in a decrease in NEP (Schwalm et al., 2010; Shi et al., 2014). In the former scenario, the ecosystem sequesters carbon; whereas in the latter scenario, the ecosystem loses carbon (Craine et al., 2012; Ma et al., 2012; Frank et al., 2015).

The desert grasslands of Northern China have a long term (1953–2013) mean annual precipitation of less than 200 mm (Wang et al., 2018; Zhang et al., 2019b). The area, which covers about $6 \times 10^4$ $km^2$, accounting for 6% of the grasslands in China (Wang et al., 2018), has been experiencing an extended drought during the last 70 years (John et al., 2016), as climate change has induced an uneven distribution of precipitation, especially in summer. It is predicted that precipitation patterns will shift from frequent, small size events, with relatively short intervals, to larger events, with longer dry intervals, particularly in the arid and semi-arid areas (Heislerwhite et al., 2008; Cook et al., 2015; Liu et al., 2017). Small precipitation events could enhance ecosystem carbon emissions through increased microbial

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respiration; whereas large precipitation events could enhance ecosystem carbon sequestration by triggering photosynthesis (Huxman et al., 2004). In contrast, under desiccating conditions, microbial activity is limited and net primary productivity is reduced (Frank et al., 2015; Murray-Tortarolo et al., 2016).

It has been predicted that future precipitation, especially in extreme drought areas, will be reduced substantially and, therefore, aboveground net primary productivity will be reduced and push grassland ecosystem beyond the threshold of recovery (Zhang et al., 2017). Consequently, precipitation distribution and variation are highly likely to affect plant and ecosystem processes and, thus, carbon fluxes and balance. With this in mind, being able to predict at which point a carbon sink converts to a carbon source during extreme drought would be important in assessing the vulnerability of desert grassland ecosystems to possible future climate change. In this study, we employed controlled, manipulated precipitation regimes to determine the effects of extreme droughts on patterns of ecosystem carbon fluxes during the growing season in a desert-grasslands. By the use of regression analyses, we determined at which point of Reco does the ecosystem function convert from a carbon sink to a carbon source. In addition, by using structural equation models (SEM), we determined the direct and indirect driving factors of NEP and Reco and of GEP under extreme droughts. Results could enhance our understanding of how extreme droughts affect ecosystem carbon fluxes in desert-grasslands and could enable us to predict carbon balance of the ecosystem under anticipated future climate change.

## 2. Materials and methods

### 2.1. Site description

The study site was located in the Urat Desert Grassland Research Station (106°58′E, 41°25′N, 1650 m a. s. l., Fig. 1A), a desert-grassland in western Inner Mongolia, China, which has a typical temperate continental monsoon climate. The long-term mean annual precipitation (1987–2017) is 145 mm and rainfall in July and August accounts for about 70% of the total (Liu et al., 2016). During the study, daily precipitation records were obtained from the weather station at the Urat Desert Grassland Research Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences. The average annual temperature is 5.3 °C, average annual wind speed is up to 5 m/s, and the frost-free period totals about 130 days. The main plant species are *Stipa glareosa* P. A. Smirn. *(Graminae); Peganum* harmala L. *(Zygophyllaceae); Asparagus gobicus* Ivan. ex Grubov*, Allium mongolicum* Regel and *Allium polyrhizum* Turcz. ex Regel *(Liliaceae); Reaumuria songarica* (Pall.) Maxim. *(Tamaricaceae); Salsola pellucida* Litv. and *Bassia dasyphylla* (Fisch. et C. A. Mey) Kuntze *(Chenopodiaceae); Artemisia frigida* Willd and *Ajania achilloides* (Turcz) Poljak *(Compositae)*. The soil types in the study area consist mainly of brown soil and grey brown desert soil according to the Chinese soil classification system (National Soil Survey Office, 1998).

### 2.2. Experimental design

Three treatments were applied from May 1 to August 31, 2015, that is, during the growing season, as follows: two extreme drought treatments (press-drought: chronic, but long term and pulse-drought: extreme, but short term) and a control treatment. For the press-drought treatment, the quantity of natural precipitation was reduced by 66% from May 1 to August 31 (4 months) using shelters, which were partially covered with strips of clear polycarbonate plastic (95% light transmission). For the pulse-drought treatment, the natural precipitation was reduced by 100% from June 1 to July 31 (2 months) using completely covered clear polycarbonate plastic shelters (Fig. 1B). A control treatment (CK) was not covered and received 100% natural precipitation. A randomized block design was used with 6 blocks and 3 treatments in each block. There were 18 plots, each 6 m × 6 m, in total. To avoid edge effects, all measurements were made in the central area (5 m × 5 m). Tin sheets were inserted into the ground to a depth of 60 cm around each plot to minimize lateral movement of soil water. All plots were fenced to avoid grazing disturbances on carbon fluxes.

### 2.3. Measurements of vegetation and soil characteristics

The number of plants were determined in August, at which time coverage, height and frequency were measured and used to calculate their importance value (Zhang et al., 2019a) and the Shannon-Wiener index, Simpson dominance index and Pielou evenness index of the desert-grassland (Ge et al., 2017). In each plot, 5 quadrats of 1 m × 1 m were used, in which four quadrats were used to determine plant characteristics and one quadrat was used to measure vegetation biomass. Above-ground biomass in each quadrat was harvested in August, standing biomass and litter separated, oven-dried at 65 °C for 48 h (Zhao et al., 2016) and weighed.

Soil bulk density (SBD) was calculated using the volumetric ring method, soil pH was determined in a soil: water ratio of 1:2.5 using a PHS-3C pH meter and soil water content (SWC) was measured twice a month throughout the growing season from June to September by the oven drying method (Institute of Soil Science, Chinese Academy of Sciences (ISSCAS), 1978). Topsoil samples (0–10 cm) were collected with a soil auger from each quadrat in August and, after removal of visible roots and debris (small stones and animal material), air-dried at room temperature for measuring soil characteristics. Total soil carbon and nitrogen were measured by an elemental analyzer (Costech ECS4010, Milan, Italy). A soil depth of 10 cm was sampled because the targeted community, *Stipa glareosa*, has a root depth of less than 15 cm (Fig. S1).

### 2.4. Measurements of ecosystem carbon fluxes

All measurements were made in the growing season of 2017 and 2018, two years after the drought treatments were initially applied. The measured ecosystem carbon fluxes included net ecosystem $CO_2$ exchange (NEE, NEP = −NEE, a positive value represents emission, a negative value represents absorption.) (Randerson et al., 2002, Ye et al., 2016, Li et al., 2017) between grassland ecosystem and atmosphere, and ecosystem respiration (Reco). NEE was measured with a transparent chamber (0.5 × 0.5 × 0.5 $m^3$), made of polytetrafluoroethene (6 mm in thickness) with 99% light transmittance, which was attached to an infrared gas analyzer (IRGA) (LI-6400 Portable Photosynthesis System; Li-Cor, Lincoln, NE, USA). The chamber was secured on an aluminum frame that was inserted into the soil to a depth of 5 cm. There were two small fans fixed at opposite top corners of the chamber to mix the air inside the chamber. Concentration of $CO_2$ in the chamber was analyzed by the infrared gas analyzer every 10 s and recorded in the flash card of LI-6400 during a 90 s period. Following the measurements of NEE, the chamber was opened for more than 30 s, and then covered with an opaque cloth (to keep out light from going through) for Reco measurement.

Seasonal dynamics of NEE and Reco were measured between 9:00 and 12:00 twice a month on clear, sunny days from May to September (once in May). This static-chamber method has been used successfully to evaluate plot level fluxes of $CO_2$ in grassland ecosystems (Niu et al., 2007; Xia et al., 2010; Zhang et al., 2019b). GEP (μmol $CO_2$ $m^{-2}$ $s^{-1}$) was calculated as Reco + NEP (μmol $CO_2$ $m^{-2}$ $s^{-1}$) (Oberbauer et al., 2007; Xia et al., 2010; Luo et al., 2015; Liu et al., 2017).

### 2.5. Statistical analysis

Seasonal average values of ecosystem carbon fluxes were calculated from the monthly average values, which were averaged from two measurements per month. Repeated-measures ANOVA analyses were

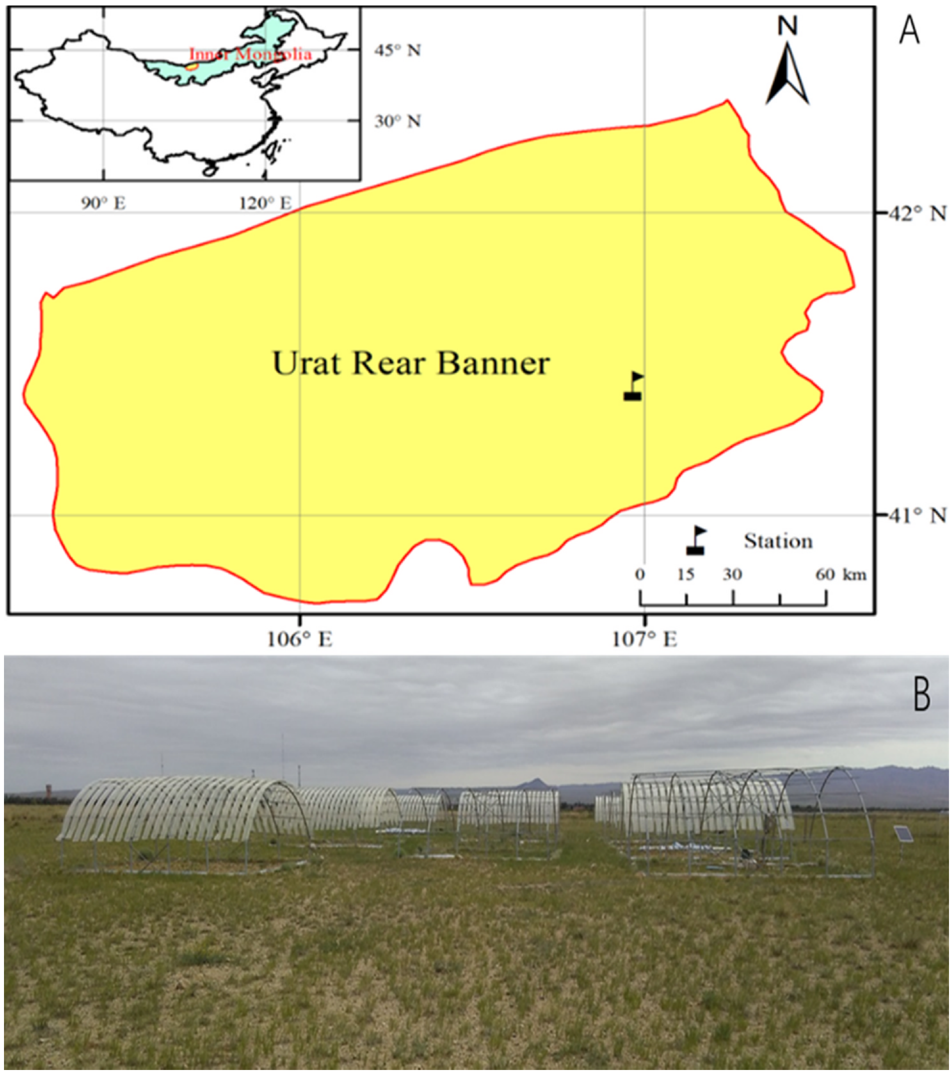


**Fig. 1.** Location of the Urat Desert Grassland Research Station (A). The extreme drought experiment was established in 2015 in a desert grassland in Inner Mongolia, China. During the growing season, twelve shelters were used to impose two drought treatments: press-drought: shelters reduced natural precipitation by 67% from 1st May to 31st August; pulse-drought: shelters reduced natural precipitation by 100% from 1st June to 31st July. Controls (CK) with 100% natural precipitation had no shelter (B).

used to test the effects of treatment, sampling date and their interactions on net ecosystem productivity (NEP), gross ecosystem productivity (GEP) and ecosystem respiration (Reco). Two-way ANOVA was used to test the effects of drought and year, and their interactions on vegetation and soil characteristics. One-way analysis of variance (ANOVA) was used for multi-comparison of the effect of treatment on vegetation and soil characteristics, monthly and growing seasonal average values of ecosystem carbon fluxes, followed by Duncan's post hoc tests ($P < 0.05$). Linear regression analysis was used to examine the relationship between the growing seasonal average NEP and Reco and the point of Reco at zero NEP was taken as the Reco at no change in the ecosystem carbon pool. Data are presented as means ± standard error. All statistical analyses were done using SPSS 18.0 for Windows (SPSS Inc., Chicago, Illinois, USA).

Confirmatory analysis of structural equation model (SEM) was applied to the data to determine direct and indirect impacts of drought on ecosystem carbon fluxes. The model was applied separately for NEP and Reco together in one and for GEP in another. GEP could not be tested together with either NEP or Reco as it was the sum of the two measurements. Consequently, GEP was not an independent variable and together with either NEP and/or Reco would introduce bias due to self-correlation. Data were fitted to the model using the maximum likelihood estimation method. SEM analysis used lavaan packages in R version 3.5.2 (https://www.r-project.org/). Measurements of coverage, standing biomass, pH and total soil carbon were collected in August, while SWC, NEP, Reco and GEP were the growing seasonal average values in each plot in the model.

## 3. Results

### 3.1. Air temperature and precipitation in the study area

The air temperature (Tair) did not differ among treatments in both 2017 and 2018 (Fig. S2) and, therefore, there was no heat induction in the drought treatments. Precipitation from January to October in 2018 was 250 mm, of which 247 mm fell during the growing season (May to September). Precipitation from January to April totaled 22 mm, 4 mm, 25 mm and 3 mm in 2015 to 2018. Although the precipitation in the first four months of 2016 almost equaled that in 2018, the precipitation in May and June 2016 (77 mm) was 4.3 times that in 2018 (18 mm). Therefore, the first six months in 2018 were driest of the four years. Precipitation from January to June was 39.8 mm and 21.4 mm in 2017 and 2018, respectively. Precipitation during the growing season from May to August in the press-drought, pulse-drought plots and CK were

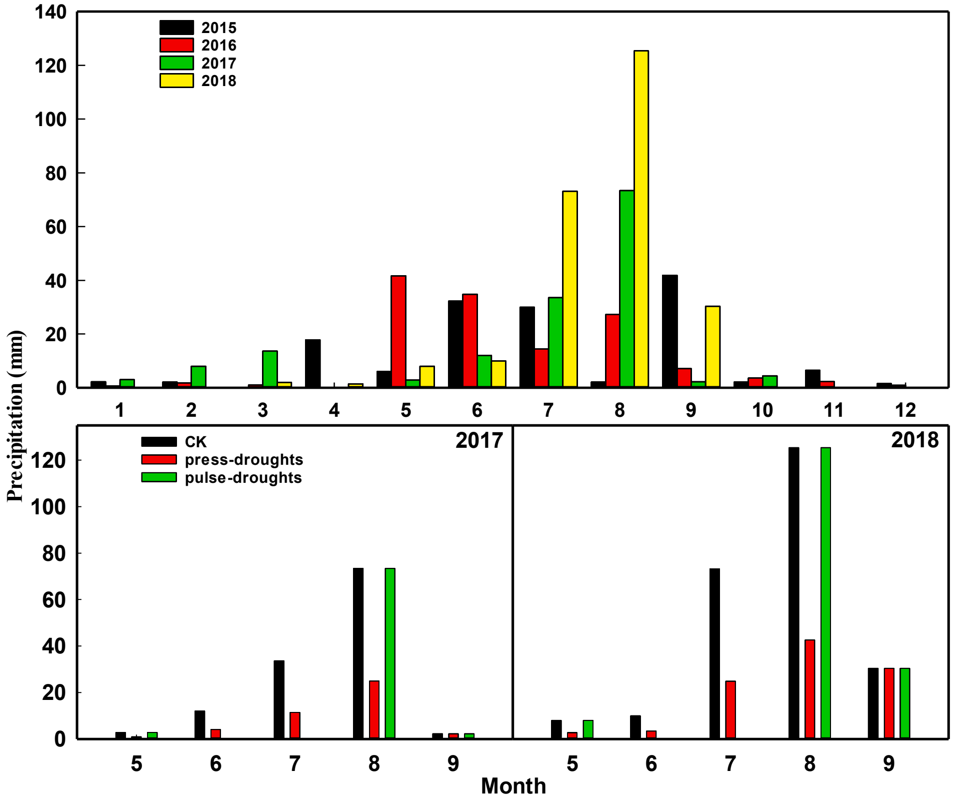


**Fig. 2.** Monthly precipitation at the study site in 2015, 2016, 2017 and 2018 (January-October) and manipulated precipitation in drought treatments from May to September in 2017 and 2018.

41 mm, 76 mm and 122 mm in 2017 and 74 mm, 133 mm and 217 mm in 2018, respectively (Fig. 2).

### 3.2. Vegetation parameters and soil properties

*Stipa glareosa, Allium polyrhizum* and *Peganum harmala* were the dominant plant species in all treatment plots according to the species importance value and the dominance of *Allium polyrhizum* and *Peganum harmala* increased in drought treatments. *Setaria viridis*, *Torularia humilis* and *Corispermum macrocarpum* occurred only in CK in 2018 and *Lagochilus ilicifolius* only in the drought treatments (Table S1 in supporting information). Plant coverage, standing biomass and litter were greater in the control treatment than the two drought treatments, and the pulse drought treatment was greater or tended to be greater than the press-drought treatment (Table 1). The number of plant species was higher in the control treatment than in the two drought treatments. The Shannon-Weiner and Simpson indices did not differ among treatment in 2017, but was greater in the controls than the two drought treatments in 2018. The Pielou index did not differ among groups in either 2017 or 2018 (Table 1).

Soil pH and soil bulk density exhibited fluctuations between years, but there was no difference among treatments. Total soil carbon and soil nitrogen were not affected by drought treatments and sampling time (Tables 1 and S2). Soil water content in the two drought treatments were lower than in CK in both 2017 and 2018 (Table 1).

### 3.3. Dynamics in net ecosystem productivity (NEP), ecosystem respiration (Reco) and gross ecosystem productivity (GEP)

Generally, NEP, Reco, and GEP were affected significantly by treatment and sampling date in both 2017 and 2018 (Table 2). Ecosystem carbon fluxes showed marked seasonal patterns which were similar in the two drought treatments. NEP and GEP exhibited unimodal patterns which were similar in 2017 and 2018; whereas Reco exhibited an inconspicuous partial bimodal in CK and press-drought, but which differed between 2017 and 2018 in the early growing season, and a unimodal pattern in the pulse-drought treatment. The ecosystem carbon fluxes reached their highest values at the end of August (Figs. 3–5).

NEP in May, June, July 2017 and June 2018 were negative under both drought treatments and were also negative under the press-drought treatment in September 2017 and July 2018 (Fig. 6A, B). The highest NEP, Reco, and GEP occurred in August in all treatments (Fig. 6) and, in August, NEP, Reco, and GEP in the press-drought and pulse-drought treatments were significantly lower than in the CK. The Reco in June 2017 and July 2018 were significantly lower in both drought treatments than in the CK (Fig. 6C, D), while NEP in September 2018 and GEP in September 2017 and July 2018 were significantly lower in the press-drought than in CK plots (Fig. 6B, E, F).

### 3.4. Responses of net ecosystem productivity (NEP), ecosystem respiration (Reco), gross ecosystem productivity (GEP) to drought treatments

Drought treatments had significant effects on NEP, Reco, and GEP in the growing season in 2017 and 2018 (Fig. 7). Seasonal mean NEP decreased by 161% ($-0.08$ μmol·m$^{-2}$·s$^{-1}$, 2017) and 100% ($-0.003$ μmol·m$^{-2}$·s$^{-1}$, 2018) in the press-drought treatment, and by 22% (0.10 μmol·m$^{-2}$·s$^{-1}$, 2017) and 58% (0.13 μmol·m$^{-2}$·s$^{-1}$, 2018) in the pulse-drought treatment, when compared with CK (0.13 μmol·m$^{-2}$·s$^{-1}$, 2017 and 0.31 μmol·m$^{-2}$·s$^{-1}$, 2018). Seasonal mean Reco decreased significantly by 31% (0.45 μmol·m$^{-2}$·s$^{-1}$, 2017) and 57% (0.18 μmol·m$^{-2}$·s$^{-1}$, 2018) in the press-drought treatment, and by 29% (0.46 μmol·m$^{-2}$·s$^{-1}$, 2017) and 41% (0.25 μmol·m$^{-2}$·s$^{-1}$, 2018) in the pulse-drought treatment, when compared with CK (0.65 μmol·m$^{-2}$·s$^{-1}$, 2017 and 0.42 μmol·m$^{-2}$·s$^{-1}$, 2018). Seasonal mean GEP decreased significantly by 53% (0.37 μmol·m$^{-2}$·s$^{-1}$, 2017)

**Table 1**
Coverage, biomass, plant diversity indices and soil characteristics in control (CK) and press-drought (Pr-D) and pulse drought (Pu-D) treatments during 2017 and 2018.

| Variables | 2017 | | | 2018 | | |
|---|---|---|---|---|---|---|
| | CK | Pr-D | Pu-D | CK | Pr-D | Pu-D |
| *Vegetation Parameters* | | | | | | |
| Coverage (%) | 21.7 ± 3.89a | 13.7 ± 2.85b | 17.0 ± 0.65ab | 19.0 ± 179a | 5.40 ± 1.65c | 10.8 ± 1.02b |
| Species No. | 8.80 ± 0.58a | 7.20 ± 1.02ab | 6.40 ± 0.40b | 9.40 ± 1.03a | 4.80 ± 1.2b | 4.40 ± 0.24b |
| SBM ($g\ m^{-2}$) | 29.6 ± 3.73a | 10.4 ± 3.86b | 12.9 ± 1.46b | 27.5 ± 3.83a | 8.74 ± 1.19b | 11.3 ± 1.37b |
| Litter ($g\ m^{-2}$) | 15.2 ± 2.83a | 6.04 ± 2.50b | 12.2 ± 0.81ab | 7.66 ± 0.89a | 4.38 ± 0.60b | 5.35 ± 0.34b |
| S-W index | 1.81 ± 0.08 | 1.65 ± 0.11 | 1.54 ± 0.07 | 1.84 ± 0.09a | 1.19 ± 0.23b | 1.21 ± 0.05b |
| Pielou index | 0.84 ± 0.01 | 0.86 ± 0.02 | 0.84 ± 0.02 | 0.83 ± 0.02 | 0.82 ± 0.02 | 0.82 ± 0.02 |
| Simpson Index | 0.80 ± 0.01 | 0.77 ± 0.02 | 0.78 ± 0.02 | 0.79 ± 0.02a | 0.61 ± 0.06b | 0.65 ± 0.02b |
| *Soil Parameters* | | | | | | |
| pH | 9.27 ± 0.02 | 9.21 ± 0.02 | 9.27 ± 0.02 | 9.03 ± 0.03 | 8.95 ± 0.04 | 9.04 ± 0.02 |
| SWC (%) | 2.78 ± 0.17a | 1.66 ± 0.28b | 1.86 ± 0.38b | 3.57 ± 0.39a | 1.61 ± 0.21b | 2.84 ± 0.42a |
| SBD ($g{\cdot}cm^{-3}$) | 1.22 ± 0.07 | 1.43 ± 0.06 | 1.21 ± 0.08 | 1.64 ± 0.05 | 1.58 ± 0.05 | 1.67 ± 0.07 |
| TC ($g\ kg^{-1}$) | 9.86 ± 1.55 | 7.27 ± 0.67 | 7.70 ± 0.9 | 9.73C ± 1.72 | 8.48 ± 0.73 | 8.25 ± 0.81 |
| TN ($g\ kg^{-1}$) | 0.50 ± 0.04 | 0.47 ± 0.06 | 0.40 ± 0.03 | 0.53 ± 0.06 | 0.49 ± 0.03 | 0.47 ± 0.03 |

Note: Species No. = number of species; SBM = standing biomass; S-W index = Shannon-Wiener index; Pielou index = Pielou evenness index; Simpson index = Simpson dominance index; SWC = average soil water content in June to September; SBD = Soil bulk density; TC = total soil carbon; TN = total soil nitrogen. Different lowercase letters denote significant differences ($p < 0.05$) among treatments within one year. Data are presented as mean ± standard error (n = 5).

and 75% (0.18 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, 2018) in the press-drought treatment, and by 28% (0.56 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, 2017) and 48% (0.38 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, 2018) in the pulse-drought treatment, when compared with CK (0.78 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, 2017 and 0.73 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, 2018).

The seasonal mean NEP of the press-drought treatment was negative, but in the pulse-drought treatment was positive in both 2017 and 2018 (Fig. 7A), indicating that during the growing season, the desert-grassland ecosystem changed from a carbon sink to a carbon source in the press-drought treatment but not in the pulse-drought treatment. The seasonal mean Reco was significantly higher in 2017 than in 2018 in all treatments (CK, $P = 0.000$; press-drought, $P = 0.000$; pulse-drought, $P = 0.000$; Fig. 7B), while the seasonal mean GEP was significantly higher in 2017 than in 2018 in the press-drought treatment ($P = 0.044$; Fig. 7C).

The regression equation of NEP ($\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$) on Reco ($\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$) took the form (Fig. 8):

$$NEP = 0.504\ (\pm 0.199) Reco\ --\ 0.086\ (\pm 0.088),$$

where n = 30; $S_{x.y}$ (SE of estimate) = 0.21; $r^2 = 0.186$; and $P = 0.017$. Therefore, when Reco equaled 0.171 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, there was zero change in the carbon sink and GEP also equaled 0.171 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$

### *3.5. Relationships among soil water content, coverage, standing biomass and ecosystem carbon fluxes*

The final SEM for predicting the direct and indirect effects of drought on net ecosystem productivity (NEP) and ecosystem respiration (Reco) emerged when soil water content (SWC), pH, total soil carbon (TC), coverage (COV) and standing biomass (SBM) were the variables ($\chi^2 = 3.28$, $df = 12$, $P = 0.993$; CFI = 1.000; RMSEA = 0.000, $P = 0.995$). The final model explained 66% of the variance of Reco, 28% of NEP, 59% of SBM, 61% of coverage, 13% of SWC, 9% of TC and 3% of pH (Fig. 9). Drought (Dr) had a negative indirect impact on NEP (−0.37, through SBM, SWC, COV and Reco) and on Reco (−0.18, through SWC, COV, SBM and NEP) and a negative direct impact on Reco (−0.27), soil water content (SWC, −0.36) and standing biomass (SBM, −0.51). Coverage (COV) had a positive direct effects on Reco (0.45) and SBM (0.45) and a positive indirect effect (0.40, through standing biomass and Reco) on NEP; SWC had a positive direct effect on NEP (0.34) and a positive indirect effect (0.41, through COV and NEP) on Reco; and, SBM had a positive direct effect on NEP (0.37) and a positive indirect effect (0.19, through NEP) on Reco. Soil pH emerged as having positive direct effects on Reco (0.40) and a positive indirect effect (0.45, through COV, standing biomass and Reco) on NEP; whereas, total soil carbon (TC) had a significant positive indirect effect on NEP (0.10, through COV, SBM and Reco) and on Reco (0.14, through COV, SBM and NEP). TC (0.26), SWC (0.52) and pH (0.60) were directly related to COV. These results implied that a decrease in SWC, plant coverage, standing biomass and TC due to drought resulted in a decrease in Reco and NEP in the growing season.

The final SEM for predicting the direct and indirect effects of drought on GEP also included soil water content, pH, total soil carbon, coverage and standing biomass as the variables ($\chi^2 = 3.00$, $df = 8$, $P = 0.935$; CFI = 1.000; RMSEA = 0.000, $P = 0.947$). The final model explained 42% of the variance of GEP, 59% of SBM, 61% of COV and 13% of SWC (Fig. 10). The SEM model demonstrated that drought had a significant negative indirect effect (−0.12, through SWC) on GEP, significant negative direct effects on SWC (−0.36) and SBM (−0.50) and an insignificant negative direct effect on TC (−0.28). Coverage had a positive direct effect (0.45) on SBM and indirect effect (0.12, through

**Table 2**
Repeated measures (ANOVA) of treatment and sampling date, and their interactions on ecosystem carbon fluxes in the growing seasons in 2017 and 2018.

| Variance source | df | 2017 | | | 2018 | | |
|---|---|---|---|---|---|---|---|
| | | NEP | Reco | GEP | NEP | Reco | GEP |
| Treatment (T) | 2 | 5.67** | 20.33*** | 10.81*** | 9.26*** | 11.07*** | 13.78*** |
| Date (D) | 8 | 17.78*** | 16.21*** | 20.96*** | 8.81*** | 4.84*** | 6.52*** |
| T × D | 16 | 1.58 | 1.93* | 1.76* | 4.13*** | 0.89 | 2.84** |

Note. Significance: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. NEP = net ecosystem productivity, Reco = ecosystem respiration and GEP = gross ecosystem productivity.

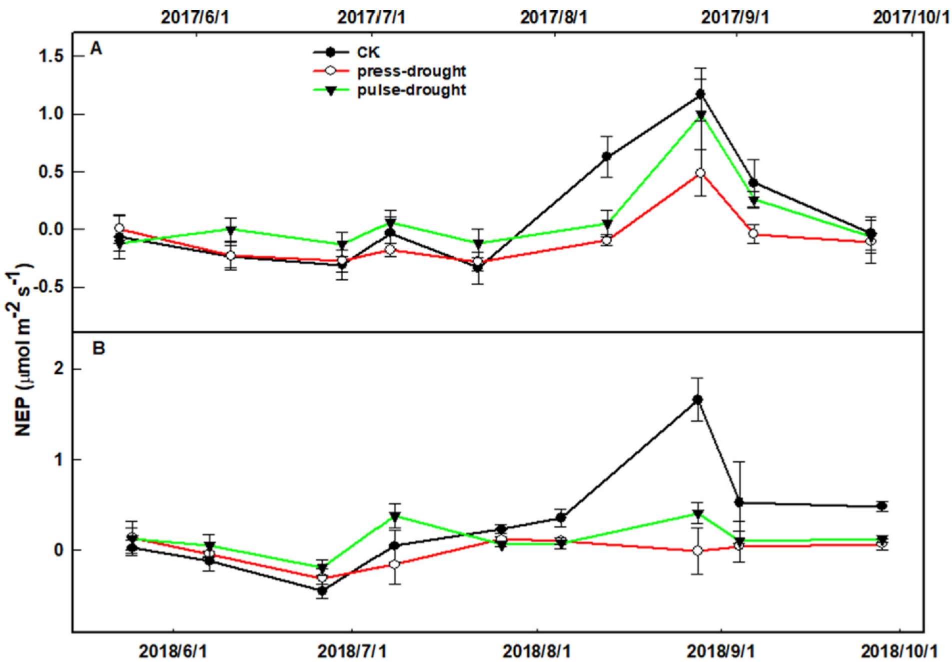


**Fig. 3.** Seasonal variations of NEP in the growing seasons of 2017 (A) and 2018 (B) for different treatments (n = 6; bars indicate SE).

standing biomass) on GEP. SWC (0.32) and pH (0.27) had significant positive direct effects while SBM (0.27) and TC (0.23) had insignificant positive direct effects on GEP. These results also implied that a decrease in SWC, plant coverage, standing biomass and TC due to drought resulted in a decrease in GEP in the growing season.

## 4. Discussion

### *4.1. Dynamics of carbon fluxes in the semi-arid and arid ecosystems*

Mongolian grasslands fall within semi-arid and arid regions and have the potential to act as a huge carbon sink in the growing season in the terrestrial ecosystem. Consequently, global grassland carbon sequestration could be influenced by the Mongolian grassland ecosystem carbon fluxes and possible future precipitation variations should be considered (Zhang et al., 2019b). The ecosystem carbon fluxes reached their highest values at the end of August, which agreed with the findings in a temperate steppe (Niu et al., 2007and in desert grasslands (Li et al., 2017; Zhang et al., 2019b). These observations can be explained by the precipitation in July and August, which increased soil water content and stimulated the rapid growth of plants in the middle stage of the growing season (Niu et al., 2007; Bahn et al., 2009). Thereafter NEP, Reco, and GEP decreased with plant senescence in the last stage of the growing season. The dynamic characteristics of NEP and GEP were similar between drought treatments, exhibiting a unimodal pattern, whereas Reco exhibited an inconspicuous partial

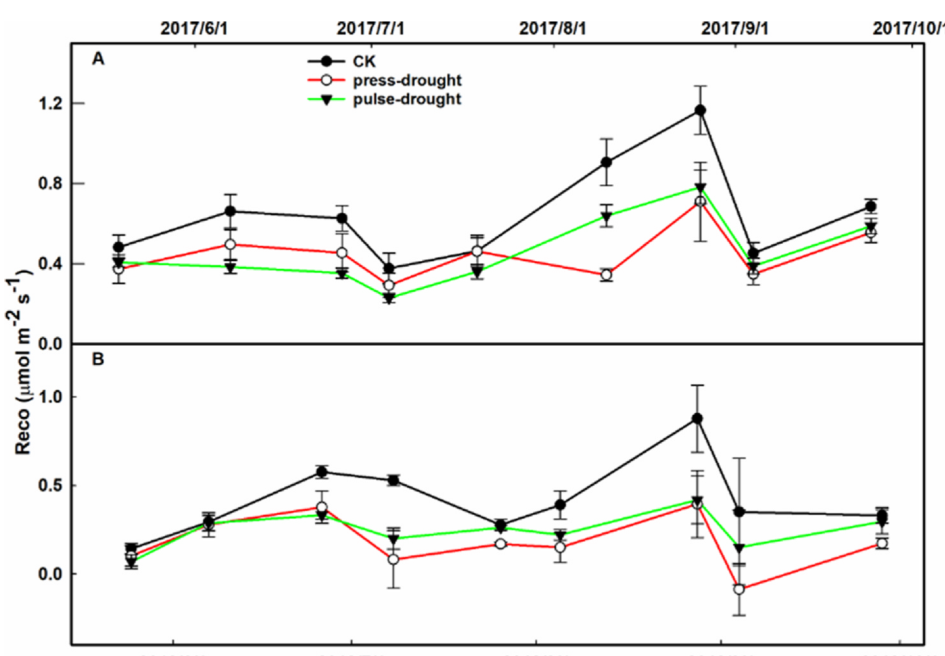


**Fig. 4.** Seasonal variations of Reco in the growing seasons of 2017 (A) and 2018 (B) for different treatments (n = 6; bars indicate SE).

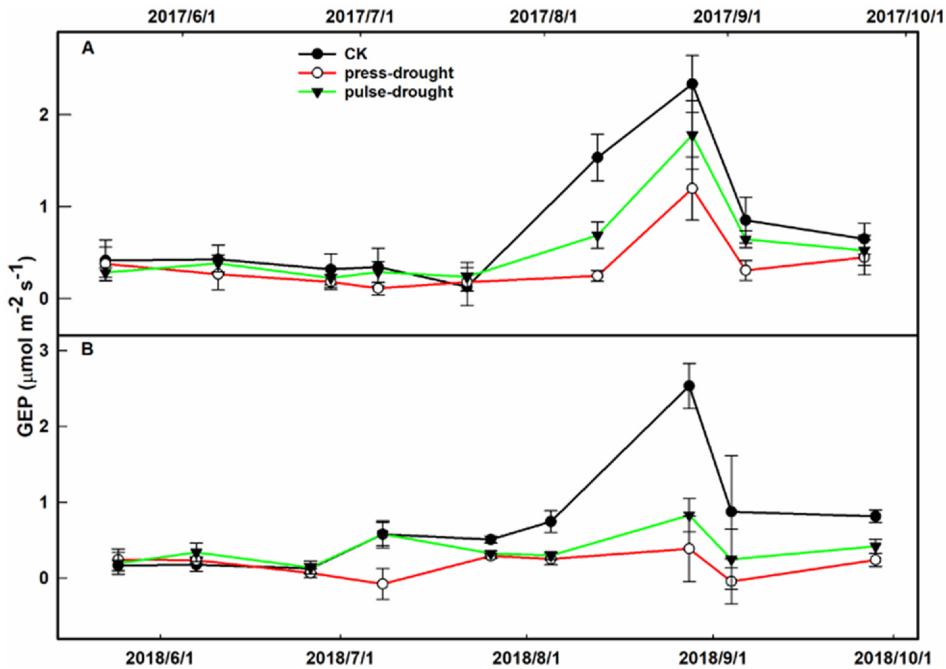


**Fig. 5.** Seasonal variations of GEP in the growing seasons of 2017 (A) and 2018 (B) for different treatments (n = 6; bars indicate SE).

bimodal pattern in the CK and press-drought treatments. These patterns were also described under conditions of a manipulated increase or decrease of total rainfall by 60% for three years in the desert grasslands of Inner Mongolia (Zhang et al., 2019b). In the pulse-drought treatment, Reco exhibited a unimodal pattern as there was no rainfall in June and July in this treatment.

Low rainfall can stimulate soil respiration, as was illustrated in the present study. It was reported that as little as 3–5 mm rainfall can effectively affect soil moisture in drylands (Xia et al., 2010), which can then influence Reco (Wei and Guo 2008; Yue et al., 2016). In the present study, there was an 8-mm rainfall event between 22 and 23 June 2017, and a 10-mm rainfall event between 21 and 24 June 2018 which led to the first Reco peak in the CK and press-drought treatments. The total rainfall of 73 mm between 1 and 20 August, 2017, and 125 mm between 3 and 27 August 2018, led to the higher Reco peak. Therefore, the distribution of precipitation (Fig. S3 in the supporting information) explained the partial bimodal peak of Reco in the CK and press-drought treatments in the growing season. The different patterns of Reco, GEP, and NEP indicated that seasonal dynamics of Reco were more responsive to rainfall distribution than either GEP or NEP, as was also reported in a long-term study on the reduction of rainfall (Zhang et al., 2019b).

The responses of GEP to both increased and decreased precipitation were greater than those of Reco, as has been reported in earlier studies on desert grasslands (Li et al., 2017; Zhang et al., 2019b). Both GEP and Reco increased with an increase in precipitation, but GEP did so to a greater extent and, therefore, there was an increase in NEP. Similarly, both GEP and Reco decreased with a decrease in precipitation, but again, GEP to a greater extent, and therefore, there was a decrease in NEP. Consequently, the ecosystem functioned as a carbon sink even though there was a loss of soil carbon through an increase in Reco with an increase in precipitation, and as a carbon source even though there was gain of soil carbon through a decrease in Reco with a decrease in precipitation. According to the regression equation of NEP on Reco in this study, when Reco equaled 0.171 $\mu mol \cdot m^{-2} \cdot s^{-1}$, there was zero change in the carbon sink. Below this value, the ecosystem functioned as a carbon source, whereas above this value, the ecosystem functioned as a carbon sink. A close examination of the points around the regression line revealed a tight cluster at low Reco and a larger variation at higher Reco. This would imply greater variation in carbon fluxes with an increase in precipitation, or a more variable relationship between GEP and Reco with an increase in precipitation. Since GEP = NEP + Reco, then, when NEP = zero, GEP also = 0.171 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Also, since GEP = NEP + Reco, and NEP = 0.504 Reco – 0.086, then GEP = Reco + 0.504 Reco – 0.086; or GEP = 1.504 Reco – 0.086. And when Reco = zero, both GEP and NEP = −0.086 (Fig. 11).

Seasonal droughts reduced carbon uptake, release and sequestration and decreased ecosystem productivity in a tropical rainforest (Aguilos et al., 2018). Similar observations occurred in the present study, where NEP, Reco, and GEP in the press-drought and pulse-drought treatments were lower than in the CK treatment in the middle and late stages of the growing season, and were lower in the press-drought than in the pulse-drought treatment. Consequently, the drought conditions in the desert-grassland and the seasonal droughts in tropical rainforests both led to reduced carbon fluxes. Negative NEP in the press-drought treatment in the present study was supported by Wang et al. (2018) and Zhang et al. (2018) who reported a negative NEP in an Inner Mongolian desert-grassland and an alpine meadow of the Tibetan Plateau when rainfall was very low during the growing season. The negative NEP in the press-drought treatment during the growing season in the present study demonstrated that the ecosystem converted from a carbon sink into a carbon source. However, NEP remained positive and as a carbon sink in the pulse-drought treatment.

### 4.2. Effect of drought on ecosystem carbon fluxes

In semi-arid and arid ecosystems, precipitation after a prolonged, dry period stimulates large Reco pulses (i.e. the Birch Effect), while a sequence of events is often required to upregulate plants and stimulate GEP (Birch 1958, Huxman et al., 2004). Therefore, low precipitation frequency enhances Reco to a greater extent than GEP, thereby reducing the magnitude of NEP. It was demonstrated that decreasing the frequency of precipitation, with longer dry intervals, impacted the ecosystem similarly to drought, that is, in a reduction in gross and net $CO_2$ uptake and in above-ground net primary productivity (Liu et al., 2017).

Diurnal variability in GEP was reported to be affected by incident

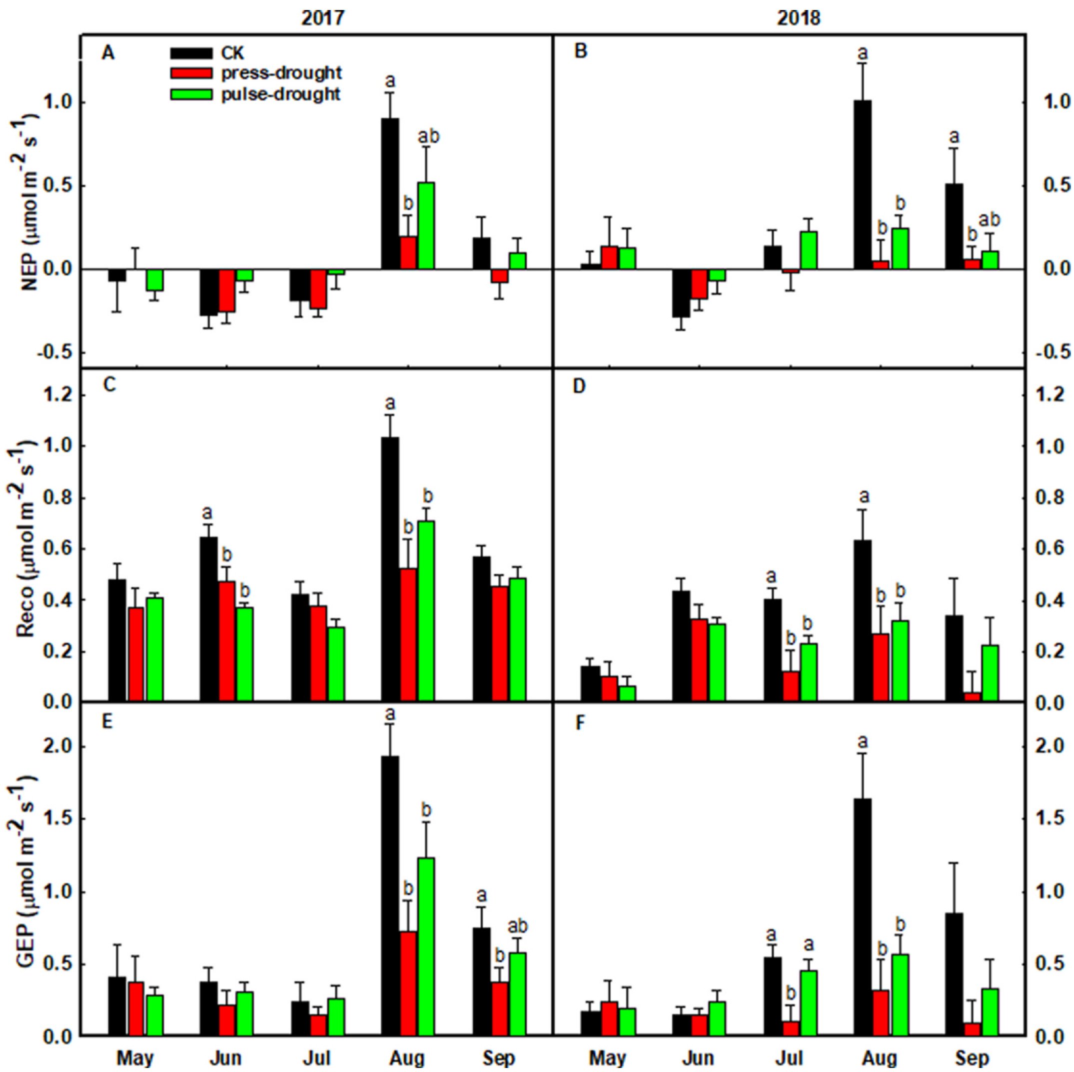


**Fig. 6.** Monthly average NEP (A, B), Reco (C, D) and GEP (E, F) in 2017 (left) and 2018 (right) in different treatments (n = 12, but n = 6 in May; bars indicate SE). Different lowercase letters denote significant differences ($p < 0.05$) among treatments within a month.

radiation, whereas seasonal dynamics were affected by plant phenology and precipitation, which subsequently affected soil water content (Tagesson et al., 2016). In this study, we manipulated precipitation which affected soil water content and, ultimately, carbon fluxes. The findings in the present study were in agreement with others which reported that ecosystem carbon fluxes in arid and semi-arid grasslands were sensitive to precipitation variation (Knapp et al., 2002; Weltzin et al., 2003), as the seasonal mean NEP, Reco and GEP decreased with drought treatments. The main reason for the decreases in GEP and NEP was that plant growth was reduced with the lower precipitation, which led to smaller and sparser canopies and presented a smaller area for photosynthesis (Ye et al., 2016). Ecosystem carbon fluxes were decreased to a greater extent by press-drought than by pulse-drought treatment. This occurred even though the press-drought treatment received more rain events than the pulse-drought treatment. However, the press-drought treatment had less total rainfall than the pulse-drought treatment. In addition, precipitation in August was greater in the pulse- than the press-drought treatment, which stimulated plant growth and enhanced soil microbial activity, and thus ameliorated the effect of drought in June and July. Consequently, the effect of drought on carbon fluxes can be mitigated by subsequent precipitation in the desert grassland. Drought treatments reduced GEP more so than Reco, leading to a reduced NEP, which is in line with findings across the Sahel that GEP was more variable than Reco (Tagesson et al., 2016).

### 4.3. *Driving factors of carbon fluxes*

Previous studies have shown that productivity and carbon fluxes of different ecosystems responded differently to precipitation change (Fay et al., 2003, Arper and Han 2005, Heislerwhite et al., 2009, Thomey et al., 2011; Liu et al., 2020). Therefore, there are complicated processes modifying ecosystem carbon fluxes in response to precipitation regimes (Niu et al., 2017; Goncharova et al., 2020). According to the SEM in the present study, drought did not affect GEP, or NEP directly in the growing season, but did so indirectly by reducing standing biomass, SWC and total soil carbon. Drought, coverage and pH were the main direct driving factors for Reco, whereas SWC was the main direct driving factor for NEP and for GEP. Reco is the $CO_2$ produced by the biological activity of soil organisms, including plant biomass, microbes, and soil animals and, consequently, is affected mainly by plant biomass (Phillips and Nickerson 2015).

Soil pH, the main driving factor of soil inorganic carbon (SIC) and soil organic carbon (SOC) (Shi et al., 2012), explained more of the variation in Reco (16%) than in GEP (7.3%). Of the variables examined in the present study, coverage had the greatest direct influence on Reco. In addition, total carbon had a significant effect on coverage and, consequently, an indirect effect on Reco. Total carbon decreased numerically in the two drought treatments in both years (by approximately 24% in 2017 and 14% in 2018), which suggested a reduction in

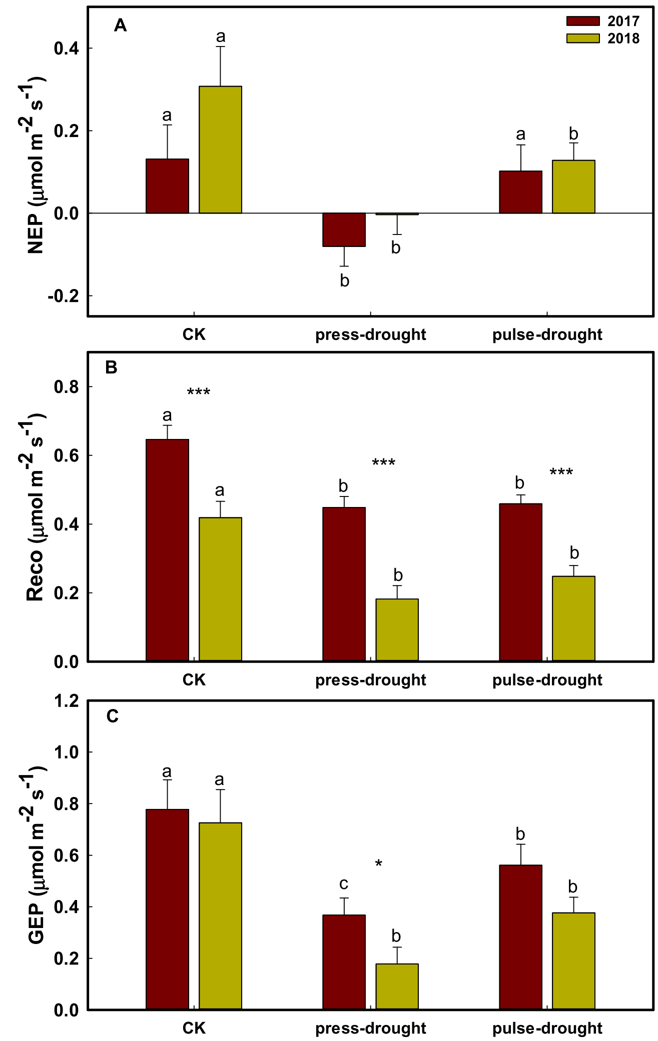


**Fig. 7.** Ecosystem carbon fluxes (NEP: A, Reco: B, GEP: C) during the growing season for different treatments. (n = 54; bars indicate SE). Different lowercase letters denote significant differences ($P < 0.05$) in treatments within a year. ***, $P < 0.001$; *, $P < 0.05$.

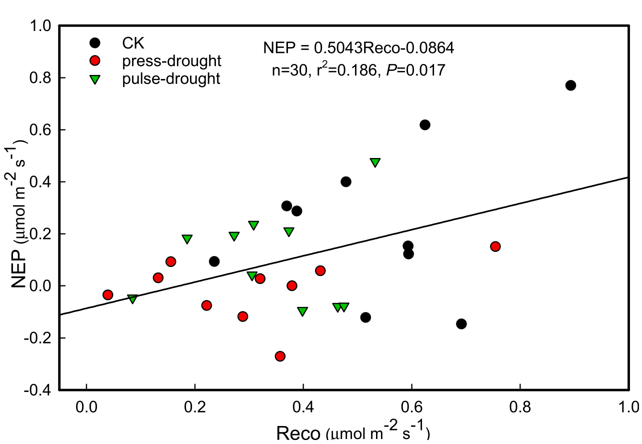


**Fig. 8.** Regression of the growing seasonal average NEP on Reco.

TC with the drought treatments, albeit the differences in TC were not significant statically. Both SIC and SOC are affected by precipitation and air temperature. The effect of air temperature was minimized as a factor among treatments, as all treatments were exposed to the same temperature. It was reported that with a decrease in precipitation, there

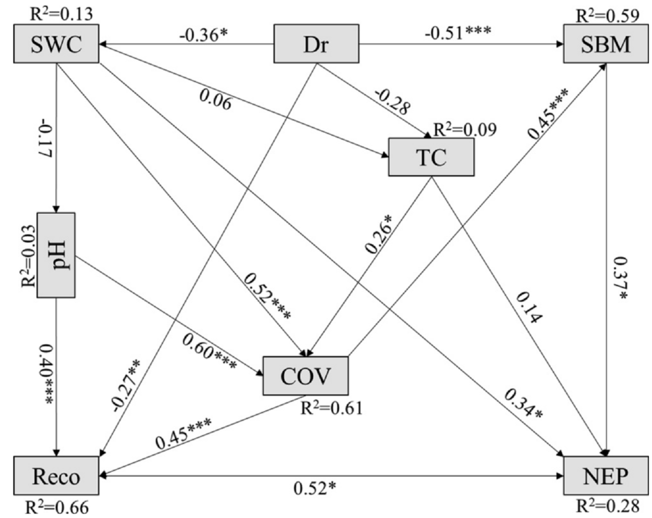


**Fig. 9.** Effects of abiotic and biotic factors on NEP and Reco in the growing season calculated by the structural equation model of path analysis based on data during 2017–2018. The values on the arrows are standardized path coefficients, asterisks following the numbers denote significant relationships (***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$), and the $R^2$ values at the rectangles represent the proportion of the variance explained by relationships with other variables. The $\chi^2$ and P value refer to a model fit test statistic ($\chi^2 = 3.28$, $df = 12$, $P = 0.993$; RMSEA = 0.000, $P = 0.995$). The $\chi^2$ test (the model has a good fit when $P$ value of $\chi^2$ test: $0.05 < P \leq 1.00$) and the root mean square error of approximation (the model has a good fit when $0 \leq$ RMSEA $\leq 0.05$ and $0.10 < P \leq 1.00$) suggested that there was a good fit for the data by the SEM. Dr, drought treatments; SWC, soil water content; COV, coverage; SBM, standing biomass; TC, total soil carbon, NEP, net ecosystem productivity; Reco, ecosystem respiration.

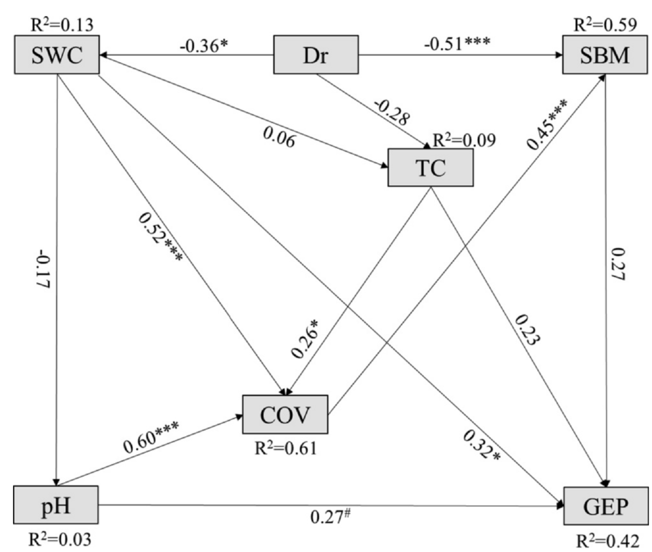


**Fig. 10.** Effects of abiotic and biotic factors on GEP in the growing season calculated by the structural equation model of path analysis based on data during 2017–2018. The values on the arrows are standardized path coefficients, asterisks following the numbers denote significant relationships (***$P < 0.001$, *$P < 0.05$ and # < 0.1), and the $R^2$ values at the rectangles represent the proportion of the variance explained by relationships with other variables. The $\chi^2$ and P value refer to a model fit test statistic ($\chi^2 = 3.00$, $df = 8$, $P = 0.935$; RMSEA = 0.000, $P = 0.947$). The $\chi^2$ test (the model has a good fit when $P$ value of $\chi^2$ test: $0.05 < P \leq 1.00$) and the root mean square error of approximation (the model has a good fit when $0 \leq$ RMSEA $\leq 0.05$ and $0.10 < P \leq 1.00$) suggested that there was a good fit for the data by the SEM. Dr, drought treatments; SWC, soil water content; COV, coverage; SBM, standing biomass; TC, total soil carbon, GEP, gross ecosystem productivity.

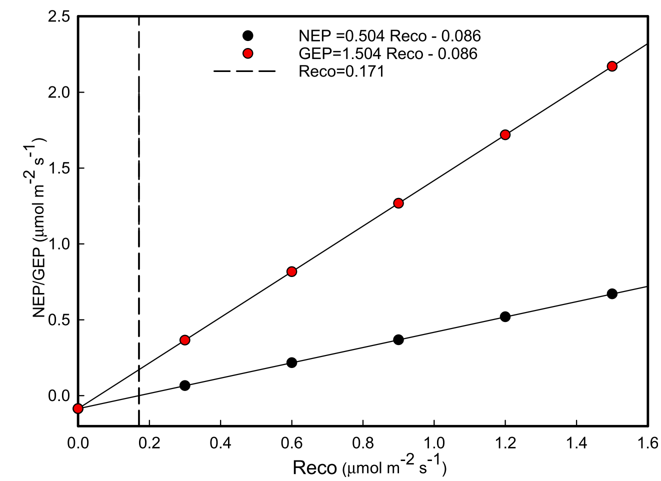


**Fig. 11.** Regression line of NEP on Reco from data in this study and calculated regression of GEP on Reco. The space between GEP and NEP represents Reco. The Y-intercept of both GEP and NEP is at −0.086 μmol·m$^{-2}$·s$^{-1}$. The line at 0.171 μmol·m$^{-2}$·s$^{-1}$ Reco passes through zero μmol·m$^{-2}$·s$^{-1}$ NEP and 0.171 μmol·m$^{-2}$·s$^{-1}$ GEP. The ecosystem functions as a carbon sink at values above 0.171 μmol·m$^{-2}$·s$^{-1}$ Reco and as a carbon source at values below 0.171 μmol·m$^{-2}$·s$^{-1}$ Reco.

was an increase in SIC but a decrease in SOC in arid and semi-arid regions in Inner Mongolia (Mi et al., 2008; Shi et al., 2012). This would indicate that with the decrease in TC in this the present study, SOC decreased to a greater extent than the increase in SIC and also that the ratio of SIC:TC actually increased in the drought treatments. This premise was further supported as SOC of the topsoil was approximately nine times that of SIC across sites in Inner Mongolia (Shi et al., 2012); consequently, a small change in SOC could cause a considerable change in TC.

Soil pH was reported to be the main driver of SIC and the SIC:TN ratio. It was reported that SIC increased linearly but SOC decreased linearly with an increase in pH (Shi et al., 2012). In the present study, pH was above 7.0 and was similar among the treatments, which would indicate that pH had a similar effect on the treatments and that SIC was relatively high in all treatments. However, the assumed increase in SIC in the drought treatments would infer a greater abundance of carbonates and salts content in the soil in these treatments than in the control (Maki et al., 2007). The calcium carbonate accumulates in the upper soil layer and, subsequently, the carbonate dissolves with $Ca^{+}$ and $HCO_3^-$ moving to lower soil layers, causing a decrease in below ground biomass, SOC and micro-organisms (Driessen et al., 2001). The higher salt contents and lower microbial activity would affect primary production negatively and could have contributed, at least in part, to the lower coverage, number of plant species, standing biomass and litter in the drought treatments than in the controls observed in this study. As Reco explained only about 27% of the variation in NEP, it is reasonable to assume that GEP would explain a greater proportion of the variation of NEP than Reco, a premise which was supported by Li et al. (2017). These findings indicated that ecosystem function was affected by precipitation variation and water availability through altering the ecosystem structure, and that the carbon sink capacity was reduced by drought treatments in the desert-grasslands to the point where a carbon sink could be converted to a carbon source.

## 5. Conclusions

Understanding the response of ecosystem carbon fluxes to drought is crucial to predict the effect of future intra- and inter-annual drought on ecosystem structure and function processes in desert-grasslands. During the growing season, it emerged that: (1) the seasonal dynamics of NEP and GEP exhibited a single peak across both drought treatments, whereas Reco exhibited a partial bimodal peak in the press-drought treatment; (2) drought treatments decreased GEP more so than Reco, resulting in a reduced NEP; and (3) the desert-grassland ecosystem was converted from a carbon sink into a carbon source in the press-drought treatment, but not in the pulse-drought treatment. The press-drought treatment had more rain events but less total rainfall than the pulse-drought treatment. From the regression equation of NEP on Reco, when Reco equaled 0.171 μmol·m$^{-2}$·s$^{-1}$, there was no change in the carbon sink and GEP also equaled 0.171 μmol·m$^{-2}$·s$^{-1}$. Below this value, the ecosystem functioned as a carbon source, whereas above this value, the ecosystem functioned as a carbon sink. The structural equation models demonstrated that drought did not have a direct effect on either NEP or GEP, but had a direct negative effect on Reco, standing biomass and on SWC. Coverage and pH had direct positive effects on Reco; SWC and pH had direct positive effects on GEP; and SWC and SBM had direct positive effects on NEP. Our findings provide some insight into the response of ecosystem carbon fluxes to extreme drought in desert-grasslands and provide data for assessing terrestrial ecosystem assimilation and respiration with climate change.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2020.104845.

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