



# Different Effects of Spring and Summer Droughts on Ecosystem Carbon and Water Exchanges in a Semiarid Shrubland Ecosystem in Northwest China

Peng Liu,<sup>1,2,3</sup> Tianshan Zha,<sup>1,2\*</sup> Xin Jia,<sup>1,2</sup> T. Andrew Black,<sup>3</sup>  
Rachhpal S. Jassal,<sup>3</sup> Jingyong Ma,<sup>1,2</sup> Yujie Bai,<sup>1,2</sup> and Yajuan Wu<sup>1,2</sup>

<sup>1</sup>Yanchi Research Station, School of Soil and Water Conservation, Beijing Forestry University, 35 East Qinghua Road, Haidian District, Beijing 100083, China; <sup>2</sup>Key Laboratory of State Forestry Administration on Soil and Water Conservation, Beijing Forestry University, Beijing 100083, China; <sup>3</sup>Biometeorology and Soil Physics Group, University of BC, 2357 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada

## ABSTRACT

Extensive revegetation and conservation programs have been initiated in semiarid desert areas in northern China for over 10 years. However, our knowledge on how drought affects the desert ecosystem carbon (C) and water exchanges is limited. Based on eddy covariance measurements, we evaluated the effect of spring and summer droughts on ecosystem C and water exchanges over a semiarid *Artemisia ordosica* shrubland in Northwest China for 2014–2016. Over the 3 years, the ecosystem was a weak source of C ( $40 \pm 32 \text{ g C m}^{-2} \text{ y}^{-1}$ ) (mean  $\pm$  standard deviation) with evapotranspiration (ET) of  $310 \pm 65 \text{ mm y}^{-1}$ . Annual net ecosystem production was  $-76$ ,  $-25$  and  $-18 \text{ g C m}^{-2} \text{ y}^{-1}$  and

water use efficiency (WUE) [gross ecosystem production (GEP)/ET] was 0.92, 1.14 and 1.09  $\text{g C kg}^{-1} \text{ H}_2\text{O}$  in 2014, 2015 and 2016, respectively, indicating greater C loss and suppressed WUE in 2014. We found that GEP,  $R_e$  and ET were significantly suppressed in year 2014 when a severe spring drought occurred, as compared to the year 2016 with summer droughts. The differences in C and water fluxes between years 2014 and 2016 were greater than those between years 2015 and 2016, although the ecosystem suffered a severe summer drought in 2015. Interannual differences in GEP were likely due to differences in leaf area index and canopy conductance, both of which were decreased by drought. Our results indicated that spring drought appears to be more critical to the C balance than summer drought in this semiarid shrubland. This suggested that under future climate change with more variable precipitation and frequent droughts expected in northern China, the timing of drought may be critical to the C and water balances.

Received 22 August 2018; accepted 19 March 2019;  
published online 12 April 2019

**Author's Contributions** All authors made intellectual contributions to this research work. PL, TZ and XJ conceived and designed research; PL, XJ and YW helped perform the research and obtained the data; and PL, TAB, RSJ, YB and JM analyzed the data. PL wrote the paper. Together, all authors discussed and interpreted the results and approved the final manuscript.

\*Corresponding author; e-mail: tianshanzha@bjfu.edu.cn

**Key words:** drought; carbon flux; water use efficiency; gross ecosystem production; net ecosystem production; ecosystem respiration.

## HIGHLIGHTS

- Interannual differences in NEP were mostly due to the effects of drought on GEP
- Spring drought reduced ecosystem production and water use efficiency
- Spring drought is more critical to the C balance than summer drought

## INTRODUCTION

Climate projections forecast greater climatic variability and more frequent extreme events, increasing both the frequency and severity of droughts in the future (Ciais and others 2005). Many studies have demonstrated that droughts can greatly impact ecosystem carbon (C) and water fluxes, thereby affecting the global C and water cycles more strongly in the future (von Buttlar and others 2018). Arid and semiarid (drylands) areas account for over one-third of the global land surface and strongly influence the global C cycle due to the inherent variability of water status (Biederman and others 2018). Model-based results have shown that these areas have dominated the interannual variation and trend of the global land C sink over recent decades (Ahlström and others 2015). However, continuous, long-term measurements of CO<sub>2</sub> exchange in drylands are rarer than in mesic and humid regions (Biederman and others 2018). Knowledge of key factors controlling annual ecosystem C and water exchanges in drylands is less well understood (Xie and others 2015).

In drylands environments with low precipitation, high light availability and low vegetation cover, ecosystem C and water fluxes are usually limited by water availability (Li and others 2008; Scott and others 2015; Biederman and others 2016, 2017). Previous studies have reported that the dryland ecosystem response is relatively more dependent on variability of precipitation than on total precipitation (Ross and others 2012; Jia and others 2016b; Biederman and others 2016, 2018), and some of them have highlighted the importance of spring/winter precipitation in regulating ecosystem C and water fluxes (Jia and others 2016b; Biederman and others 2018). It was plausible to think spring drought is more critical than summer drought in regulating C fluxes in drylands ecosystems. But a number of studies on drylands implied that the direction (positive/negative) and the magnitude of the effect of spring/summer drought on C fluxes and water use depend on plant func-

tional type and vary among different ecosystems (Schwinning and others 2005; Heitschmidt and Vermeire 2006; Bowling and others 2010; Scott and others 2010; Correia and others 2014; Petrie and others 2015). Furthermore, the relative effects of spring and summer drought on ecosystem C fluxes are confounded by duration and severity of drought (van der Molen and others 2011). Also, the mode of the effect of drought on ecosystem C fluxes and water use may vary with the timing of drought (Noormets and others 2008). However, we lack a comparison between spring and summer droughts in natural drylands ecosystems in terms of their relative effects on ecosystem C and water exchanges. Improved understanding of the response of ecosystems to the timing of droughts is urgently needed for predicting the impact of climate variability and change on global terrestrial C exchange.

Drought can affect the ecosystem C balance through its different effects on GEP and ecosystem respiration ( $R_e$ ). Drought decreases both GEP and  $R_e$  in the majority of ecosystems (Biederman and others 2016, 2017). There is, however, still debate on whether GEP or  $R_e$  is more sensitive to drought in desert ecosystems. It has been reported that multi-year droughts decreased GEP more than  $R_e$  and caused net C losses in a semiarid cold desert ecosystem (Bowling and others 2010). Short-term drought may suppress  $R_e$  more than GEP, causing increased net C uptake (Yang and Zhou 2013). This range of effects may be due to the different levels of severity of soil moisture limitation and to different plant species (Welp and others 2007). Therefore, more studies are required to examine the sensitivity of GEP and  $R_e$  to seasonal drought in different ecosystems.

Drylands account for 52.5% of China's land surface of which 2.11 million km<sup>2</sup> (80.7%) are characterized as being impacted by desertification (State Forestry Administration of China 2015). Shrubland ecosystems at the southern edge of the Mu Us Desert are characterized by highly variable precipitation and frequent drought periods. Recent studies in this region have focused on the biophysical controls on seasonal and annual dynamics of ecosystem C exchange in a mixed shrubland ecosystem (Jia and others 2014, 2016b) and highlighted the carry-over effect of the previous year's autumn precipitation on current year's C fluxes. However, there is still a gap in our understanding of how timing of droughts impact annual C fluxes and water use in other shrubland desert ecosystems, and this information is essential to their adaptive management under changing climate.

In this study, we used the eddy covariance technique to measure C and water exchanges in an *Artemisia ordosica*-dominated shrubland ecosystem over 3 years (2014–2016) to estimate annual net ecosystem production (NEP) and evapotranspiration (ET). The anomalous distribution of precipitation in this area caused periods with persistently low soil moisture during spring in 2014 (canopy development period, day of the year (DOY) 111–150) and during summer in 2015 (flower-bearing period, DOY 170–211). In 2016, there are two short periods with slightly reduced soil moisture (DOY 170–185 and DOY 215–230) (see Figure 1D). This gave us the opportunity to examine how timing of droughts would impact C fluxes (that is, GEP,  $R_c$  and NEP), water use (that is, ET) and WUE in this shrubland ecosystem. We hypothesized that differences in the timing of drought would cause significantly different impacts on the C and water balances and the differences would be due more to the effects on GEP than on  $R_c$ . Specifically, the objectives of this study were (1) to quantify seasonal and annual C and water fluxes, and examine the effects of timing and extent of drought thereof and (2) to determine drought effects on the ecosystem responses to environmental controls.

## MATERIALS AND METHODS

### Site Description

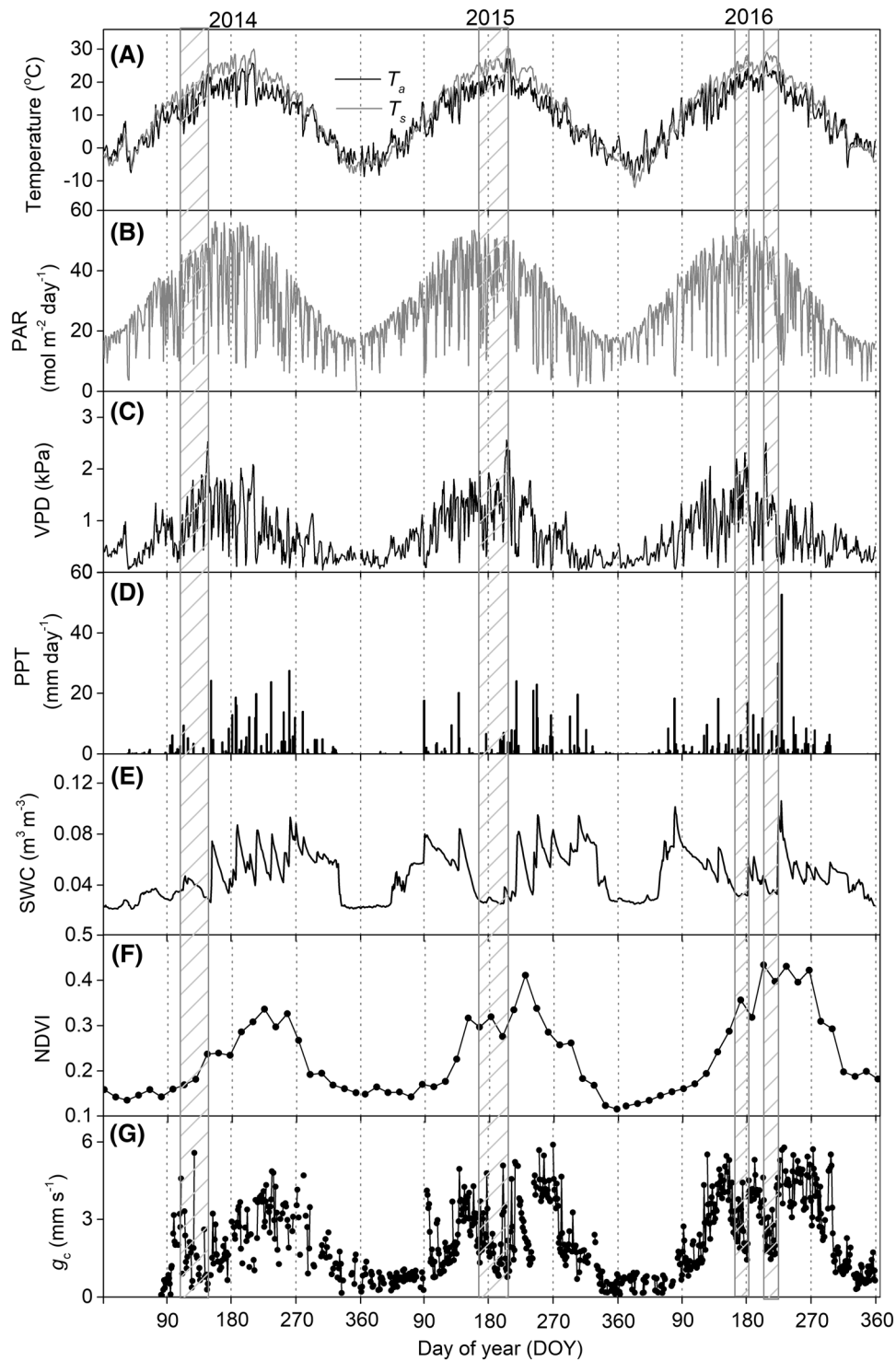
The study was conducted at the Yanchi Research Station (37°42'46"N, 107°13'57"E, 1530 m a.s.l.) of Beijing Forestry University, which is located in Ningxia Province, Northwest China. The site is located at the southern edge of the Mu Us Desert and is characterized by a semiarid continental monsoon climate with variable precipitation and frequent droughts (Xie and others 2015). *A. ordosica* is one of the most typical vegetation types in the Mu Us Desert and accounts for 31.2% of the desert area. From the mid-twentieth century, anthropogenic disturbances (for example, overgrazing) have caused severe vegetation degradation in this area (Chen and Duan 2009). Rehabilitation practices (for example, banning grazing) since late 1990s have promoted a dramatic expansion of the shrubland, which is considered a sign of desertification reversal. Increased organic matter, nutrient content and biodiversity indicate that this area is evolving toward a healthy state. This indicates that the shrubland ecosystem is becoming a stable biome. Available soil water depends entirely on PPT as the water table lies 8–10 m below the ground surface. The 30-year (1985–2016) mean

annual temperature and precipitation (PPT) are 8.1 °C and 292 mm, respectively. Because very little (14%) PPT falls in spring and winter, spring soil water storage is mainly a result of the previous year's autumn PPT (data provided by the Yanchi County Meteorological Station, Table 1 and Figure 1D, E). The site with a relative vegetation coverage of about 70% is dominated by *A. dosica*, a deciduous shrub, which is about 1 m in height, and is more than 3 km away from the intensively studied mixed species shrubland site (Jia and others 2014, 2016a, b). *A. ordosica* roots are distributed mainly in the upper 0.40 m of the soil. The summer maximum leaf area index is 1.2 m<sup>2</sup> m<sup>-2</sup>. The soil is fine sandy and has a bulk density of 1540 kg m<sup>-3</sup> in the upper 0.10 m of the soil profile.

The growing season defined following Xie and others (2016) (three consecutive days of GEP is > 5% of the summer maximum C uptake) was limited to DOY 111–304, 101–293 and 103–295 in 2014, 2015 and 2016, respectively. Based on in situ measurements of volumetric soil water content (SWC) and soil water matric potential, SWC at field capacity and permanent wilting point for the 0–0.20 m soil layer are 0.10 (soil water matric potential of – 10 kPa) and 0.02 (– 1500 kPa) m<sup>3</sup> m<sup>-3</sup>, respectively (Zhang and others 2004). Our analysis showed that when SWC in the 0–0.30 m layer was less than 0.04 m<sup>3</sup> m<sup>-3</sup> (soil water matric potential about – 160 kPa), GEP dropped significantly. The threshold was further verified using the technique used by Jia and others (2014). We defined drought periods as those days when SWC was less than 0.04 m<sup>3</sup> m<sup>-3</sup> in the 0–0.30-m layer during the growing season, and drought periods in each year are identified in Figure 1.

### Flux Measurements

Continuous eddy covariance (EC) measurements of CO<sub>2</sub> and H<sub>2</sub>O exchange were made from March 25, 2014, until December 31, 2016. Fluxes were measured at the 2.6 m height on a scaffold tower, 2 m × 3 m × 6 m tall, using an open-path CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyzer (model LI-7500, LI-COR Inc., Lincoln, NE, USA) and a three-dimensional ultrasonic anemometer (Windmaster Pro, Gill Instruments, Ltd., Lymington, UK), both providing 10 Hz measurements. The high-frequency data were stored in an analyzer interface unit (model LI-7550, LI-COR Inc.). The fetch was flat extending for over 300 m in all directions from the EC tower. The 90% cumulative flux footprint contour was usually within 150 m of the tower in the daytime



**Figure 1.** Seasonal variations in **A** daily mean air temperature ( $T_a$ ) at 6 m above the ground and soil temperature ( $T_s$ ) at 10 cm depth, **B** daily mean vapor pressure deficit (VPD), **C** daily integrated photosynthetically active radiation (PAR), **D** daily precipitation, **E** daily volumetric soil water content (SWC) for the 0–30 cm depth, **F** NDVI (normalized difference vegetation index) for 16-day intervals, **G** daily canopy conductance ( $g_c$ ) in shrubland at the Yanchi Research Station, China. The computation for  $g_c$  was limited to half-hourly values when PAR was greater than  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Hatched bands in the figure indicate drought periods during the spring (in 2014) and during the summer (in 2015 and 2016).

**Table 1.** Seasonal and Annual Precipitation Totals for 2014–2016 with Long-Term (1985–2016) Average Precipitation for the Yanchi Research Station

Year	Rainfall (mm)			
	Spring (Mar–May)	Summer (Jun–Aug)	Autumn (Sep–Nov)	Annual
1985–2016	41 (14)	145 (50)	104 (35)	292
2014	39 (11)	186 (54)	115 (34)	342
2015	67 (22)	87 (28)	148 (48)	306
2016	83 (24)	189 (55)	68 (20)	342

Numbers in the brackets are the proportions (%) of the annual rainfall totals.

but at night sometimes reached 350 m (Kljun and others 2004).

## Meteorological Measurements

Soil temperature ( $T_s$ ) and volumetric SWC were measured at four depths (0.10, 0.30, 0.70 and 1.2 m) 5–10 m from the EC flux tower in three directions (3 locations  $\times$  4 depths) using ECH<sub>2</sub>O-5TE sensors (Decagon Devices, Pullman, WA, USA). Other meteorological variables were measured at the 6 m height on another EC flux tower about 3200 m away. Photosynthetically active radiation (PAR) was measured using a quantum sensor (Par Lite, Kipp & Zonen, Delft, Netherlands). Air temperature ( $T_a$ ) and relative humidity (RH) were measured with a temperature and relative humidity probe (HMP155A, Vaisala, Helsinki, Finland). Vapor pressure deficit (VPD) was calculated from  $T_a$  and RH. PPT measurements started in 2012 using a tipping bucket (TE525WS, Campbell Scientific Inc. (CSI), Logan, UT, USA). All micrometeorological variables were measured every 10 s and stored in two CSI data loggers (CR200X for PPT and CR3000 for all other variables), and half-hourly averages were calculated by the logger. We used MODIS NDVI (normalized difference vegetation index) data products (MOD13Q1) obtained from the Earth Observing System (EOS) Data Gateway to characterize vegetation greenness. This product provides NDVI data at 16-day intervals with a 250 m spatial resolution. Four points in the 250  $\times$  250 m<sup>2</sup> grid cell subsets, where the EC flux tower was located, were chosen to calculate the average NDVI of the site.

## Data Processing and Analysis

### Flux Calculation and Quality Control

Raw data were processed using EddyPro 6.0.0 software (LI-COR Inc.). Data processing included

spike removal, tilt correction (double-axis rotation), spectral correction, sensor heating correction, block averaging, correction for density fluctuations and flux computation. If missing high-frequency data, removed spikes, and beyond limit measurements combined exceeded 10% of the half-hourly high-frequency data, the half-hourly CO<sub>2</sub> flux was rejected (Jia and others 2014). The calculated half-hourly values were then inspected for outliers following Papale and others (2006). The CO<sub>2</sub> storage term was not added in estimating net ecosystem exchange (NEE) because of the relatively short canopy that usually makes the term negligible (Jia and others 2014). Nighttime data were also excluded from the analysis when turbulent mixing was low on calm nights (friction velocity,  $u_* < 0.1 \text{ m s}^{-1}$ ). The  $u_*$  threshold was estimated following the China FLUX standard method (Zhu and others 2006).

Although 39% of the negative values in wintertime (when  $T_a$  at the 6 m height was  $< 5 \text{ }^\circ\text{C}$  and  $T_s$  at the 10 cm depth was  $< 1 \text{ }^\circ\text{C}$ ) were corrected using the sensor heating correction of Burba and others (2008), negative values still accounted for 24% (1361 data points) of wintertime data in 2014. When separated into daytime and nighttime data, 42% of the daytime data were negative, but only 11% of the nighttime data after the application of the sensor heating correction. We discarded these negative values. Burba and others (2008) also found that the wintertime CO<sub>2</sub> uptake phenomenon was more serious during daytime and attributed it to the absorption of solar radiation by the LI-7500 IRGA. They found wind velocities exceeding  $6 \text{ m s}^{-1}$  effectively reduced the difference between surface temperature of the detector housing and ambient air temperature. Thus, we followed the approach of Brown and others (2010) to examine the effect of average wind speed ( $V$ ) on our 2014 wintertime data by plotting the fraction of negative NEE values against  $V$ . The fraction of

negative NEE values showed a decreasing trend with increasing  $V$ , with the largest reduction (from 0.18% to 0.11%) occurring as  $V$  increased from 4 to 6  $\text{m s}^{-1}$ . We also checked the relationship between the fraction of negative NEE values and PAR and found that the fraction increased when PAR was high ( $> 600 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Consequently, we discarded all daytime data when  $V < 6 \text{ m s}^{-1}$  or  $\text{PAR} > 600 \mu\text{mol m}^{-2} \text{s}^{-1}$ , which removed an additional 35% of the daytime values, leaving 367 daytime winter values.

In the case of the nighttime data, the fraction of negative values was relatively constant at about 6% regardless of  $V$ , so we did not discard any remaining nighttime data (2296 values) based on wind speed. In total, there were 2623 (46% of the total possible values) acceptable half-hourly values in wintertime. The same screening procedure was applied to 2015 and 2016 wintertime data. Nighttime evapotranspiration data were rejected when  $u_* < 0.1 \text{ m s}^{-1}$ . During the winter, the screening procedure applied to NEE data was also applied to ET data.

Instrumentation random noise induced occasional small negative  $\text{CO}_2$  fluxes when respiration was small; thus, removing only wintertime negative NEE values might have caused a bias toward greater  $\text{CO}_2$  loss. Alternatively, wintertime respiration might have been greater than measured values because surface heating of the open-path array might have had the effect of reducing the measured ecosystem C exchange from its actual value.

#### Gap-Filling and Partitioning of NEP into GEP and $R_e$

NEP was calculated as  $-\text{NEE}$ . Gaps in NEP data for 2014 (including missing data in Jan–Mar), 2015 and 2016, respectively, accounted for 44, 39 and 33% during daytime and 43, 21 and 19% during nighttime. Gaps were relatively small (that is,  $< 4$  days) during the growing season. The rejected data ( $\sim 30\%$  of all data) were mostly during winter. We would expect the gaps in wintertime had limited effects on our results because the study site had little litterfall accumulation and was dominated by deciduous species with winter respiration of about 9% of annual total (Wang and others 2017). Gaps in NEP were filled following Xie and others (2016). In brief, gaps in  $R_e$  during nighttime ( $\text{PAR} < 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) were filled using the nighttime relationship between  $R_e$  and  $T_s$  as follows:

$$R_e = R_{10} Q_{10}^{(T_s - 10)/10} \quad (1)$$

where  $R_e$  is the nighttime NEE,  $T_s$  the soil temperature at the 10 cm depth,  $R_{10}$  the reference ecosystem respiration when  $T_s = 10 \text{ }^\circ\text{C}$ , and  $Q_{10}$  is the temperature sensitivity of ecosystem respiration. Equation (1) is only fit to the annual data set because short-term data points were too scattered to establish any valid short-term  $R_e - T_s$  relationships. The nighttime relationship between  $R_e$  and  $T_s$  was used to obtain daytime  $R_e$  ( $R_{e\_day}$ ). Gaps in NEP during the daytime ( $\text{PAR} \geq 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) were filled using the relationship between daytime NEP, PAR and  $R_{e\_day}$  as follows:

$$\text{NEP}_{\text{day}} = \frac{\alpha \text{PAR} P_{\text{max}}}{\alpha \text{PAR} + P_{\text{max}}} - R_{e\_day} \quad (2)$$

where  $\alpha$  is the apparent quantum yield in  $\mu\text{mol CO}_2 \mu\text{mol}^{-1}$  quanta and  $P_{\text{max}}$  is the maximum apparent photosynthetic capacity of the canopy in  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ . Seasonal variation was taken into account by fitting Eq. (2) to daytime data points every 2 weeks. To get a temperature-independent estimate of daytime  $R_e$ , another estimate of daytime  $R_e$  (i.e.  $R_d$ ) was determined using a 3-day-wide window moving 1 day at a time (for  $\text{PAR} < 300 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) in the 3 years. According to Jassal and others (2007), a PAR range of 0–300  $\mu\text{mol m}^{-2} \text{s}^{-1}$  was used here because: (a) a survey of a large number of leaf gas exchange experiments showed that the light inhibition effect does not increase above a PAR level of approximately 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Wohlfahrt and others 2005) and (b) inclusion of higher values of PAR might risk using data beyond the linear response region (Shapiro and others 2004) and violating the statistical assumption of normal distribution of  $\epsilon$  (random error in daytime  $R_e$  estimation). Gross ecosystem production (GEP) was calculated as the sum of NEP and  $R_e$  (that is,  $\text{GEP} = \text{NEP} + R_e$ ), and GEP was assumed to be zero during wintertime.

To obtain annual C and water fluxes for 2014, the nighttime  $R_e - T_s$  relationship was used to estimate the missing values of  $R_e$  and NEP ( $\text{NEP} = -R_e$ ) in January–March in 2014. We followed Jia and others (2016a) using the mean diurnal variation (MDV) approach with consecutive 15-day windows to fill gaps in ET during growing season. We used the linear relationship ( $R^2 > 0.75$ ) between ET of the EC flux tower and ET of an EC flux tower about 3200 m away (detailed description to see Jia and others 2014) to fill the missing ET values in January–March in 2014 and in wintertime.

Uncertainty in annual NEP, caused by gaps and gap-filling, was estimated according to Jia and others (2014). The uncertainty in annual fluxes was estimated by bootstrapping, in which the gap-

filled annual dataset of half-hourly values was sampled 2000 times with replacement, permitting calculation of the standard deviation (Table 3).

Daily canopy conductance ( $g_c$ ,  $\text{m s}^{-1}$ ) was estimated by inverting the Penman–Monteith equation as follows:

$$g_c = \frac{\lambda E \gamma g_a}{\Delta R_a + \rho_a c_p g_a \text{VPD} - \lambda E (\Delta + \gamma)} \quad (3)$$

where  $\lambda$  is the latent heat of vaporization ( $\text{J kg}^{-1}$ ),  $\gamma$  is the psychrometric constant ( $\text{kPa K}^{-1}$ ),  $g_a$  is the aerodynamic conductance calculated assuming a neutral wind profile using  $u_*$  and wind speed above the canopy (Monteith 1965) which were measured with the sonic anemometer,  $\Delta$  is the rate of change of the saturation  $\text{H}_2\text{O}$  vapor pressure with air temperature ( $\text{kPa K}^{-1}$ ),  $R_a$  is the available energy flux ( $\text{W m}^{-2}$ ) which was calculated as the sum of the latent and sensible heat fluxes since net radiation and soil heat flux were not measured at the site,  $\rho_a$  is the air density ( $\text{kg m}^{-3}$ ),  $c_p$  is the specific heat of air ( $\text{J kg}^{-1} \text{K}^{-1}$ ) and VPD is the vapor pressure deficit (kPa).

#### Data Analysis

The comparison of microclimatic conditions ( $T_a$ ,  $T_s$ , PAR, VPD and SWC), NDVI and  $g_c$  among years was done using a repeated measures ANOVA, with day of year as the repeated measure. GEP normalized by NDVI was also applied to the repeated measures ANOVA to examine the difference among years. For this purpose, daily integrated values of GEP were summed to obtain half-monthly values to match NDVI data. We also calculated the monthly standardized precipitation evapotranspiration index (SPEI) using long-term climate data (1985–2016) for Yanchi County using the R programming language based on the package “SPEI” (Vicente-Serrano and others 2010). Data analysis was performed at a significance level of 0.01 using MATLAB R2014a statistical software.

## RESULTS

### Comparison of Climatic and Biotic Conditions

The three study years (2014–2016) showed similar seasonal patterns and magnitudes in terms of  $T_a$ ,  $T_s$ , PAR and VPD ( $P > 0.01$ , Figure 1A–C). Daily values of  $T_a$ ,  $T_s$ , PAR and VPD reached their maximum in summer and the minimum in winter. In general, almost 80% of annual PPT fell in summer and

autumn with little falling in winter and spring (Table 1).

Annual PPT values in 2014, 2015 and 2016 were similar and were 13, 4 and 13% higher than the long-term mean (1985–2016, 292 mm), respectively. The timing of PPT, however, showed contrasting patterns with significantly different SWC distributions over the 3 years (Figure 1D, E). Summer SWC in 2014 was high ( $\sim 0.06 \text{ m}^3 \text{ m}^{-3}$ ) with PPT being 28% higher than the 30-year average (Table 1). Summer PPT in 2015, however, was 40% lower than the 30-year average and resulted in a corresponding low SWC period (DOY 170–211, Figure 1E). Although there was above average summer PPT in 2016, almost 45% of it fell during two single rainfall events in late August (on DOY 228 and 233, respectively). Low SWC periods were also evident in 2016 (DOY 170–185 and DOY 215–230). Despite the frequent small rainfall events during the canopy development period in 2014 (DOY 111–150), soils were drier in 2014 than in the corresponding periods in the other 2 years (Figure 1E). The moderately high SWC in spring in 2015 and 2016 was mainly a result of high mid- to late autumnal PPT during the preceding year.

On the basis of the number of consecutive low SWC days during the growing season, 2014 had one drought period (DOY111–150) during spring with a mean SWC of  $0.038 \text{ m}^3 \text{ m}^{-3}$  (Figure 1E). 2015 had one drought period (DOY 170–211) during summer with a mean SWC of  $0.028 \text{ m}^3 \text{ m}^{-3}$ . 2016 had two short drought periods (DOY 170–185 and 215–230) in summer with a mean SWC of  $0.032$  and  $0.033 \text{ m}^3 \text{ m}^{-3}$ , respectively. Monthly SPEI values showed that there was a moderate drought during spring period in May 2014 and a moderate drought during the summer period in July 2015, while there were two mild droughts in June and July in 2016 (Table 2). The drought period obtained using SPEI was generally consistent with low SWC periods (0–0.3 m depth,  $\text{SWC} < 0.04 \text{ m}^3 \text{ m}^{-3}$ ).

Both the seasonal maximum and mean values of NDVI and daily  $g_c$  increased over the 3 years (Figure 1 and Table 3). NDVI was significantly lower in 2014 than in 2016 ( $P < 0.01$  throughout the growing season). The mean growing season value of  $g_c$  was significantly lower in 2014 than in 2016 (Figure 1G,  $P < 0.01$ ).

### Seasonal and Interannual Variation in Carbon and Water Exchanges

Seasonal patterns of C and water fluxes were markedly different among years (Figure 2). Daily

NEP in 2014 reached its maximum ( $0.91 \text{ g C m}^{-2} \text{ day}^{-1}$ ) on DOY 224, whereas in 2015 and 2016, daily NEP peaked on DOY 161 ( $2.72 \text{ g C m}^{-2} \text{ day}^{-1}$ ) and DOY 148 ( $2.40 \text{ g C m}^{-2} \text{ day}^{-1}$ ), respectively (Figure 2A). Despite very similar growing season lengths (Table 3), C sink days (daily NEP > 0) were 92, 112, 113 days for 2014, 2015 and 2016, respectively. Maximum daily GEP was  $2.37 \text{ g C m}^{-2} \text{ day}^{-1}$  (DOY 231) in 2014,  $4.06 \text{ g C m}^{-2} \text{ day}^{-1}$  (DOY 161) in 2015 and  $4.34 \text{ g C m}^{-2} \text{ day}^{-1}$  (DOY 148) in 2016. Daily GEP was markedly lower in the 2014 drought period than that in the drought periods in 2016 (Figure 2B) and remained lower for 1 month after the drought. By contrast, in 2015 GEP decreased significantly in the last 2 weeks of the

**Table 2.** Drought Indices Based on the Standardized Precipitation Evapotranspiration Index (SPEI) Values for 2014, 2015 and 2016

SPEI	2014	2015	2016
Apr	0.9050	0.8233	0.1773
May	-1.3313	0.8282	0.1824
Jun	1.3504	0.0496	-0.4762
Jul	0.7674	-1.1499	-0.3724
Aug	0.5517	0.0523	1.1245
Sep	1.2658	1.4394	0.0638
Oct	0.7646	0.4021	0.0785

SPEI values were calculated monthly using long-term climatic data (1975–2016) from the Yanchi County Meteorological Station based on the R programming package SPEI. [-2, -1.5], severe drought; [-1.5, -1], moderate drought; [-1, 0] mild drought.

drought period but showed strong recovery within 2 weeks after the drought period ended. Daily  $R_e$  was low in winter ( $< 0.5 \text{ g C m}^{-2} \text{ day}^{-1}$ ) and peaked at 1.97, 2.24 and  $3.10 \text{ g C m}^{-2} \text{ day}^{-1}$  on DOY 210, 180 and 190 for 2014, 2015 and 2016, respectively (Figure 2C). Short-term response of  $R_e$  to drought was quite small compared to GEP. Annual GEP and  $R_e$  were both highest in 2016 and lowest in 2014, with greater interannual variability in GEP than in  $R_e$  (Table 3). The gap-filled annual values of NEP, associated with their uncertainties, indicated the site was clearly a C source in 2014 but switched to being virtually C neutral in 2015 and 2016.

Daily ET was close to zero during winter and reached its maximum values (2.8, 2.5 and  $3.4 \text{ mm day}^{-1}$ ) on DOY 155, 144 and 148 in 2014, 2015 and 2016, respectively (Figure 2D). It should be noted that an increase in ET in spring 2014 was caused by several small rain events (Figure 2D). The highest annual ET and GEP both occurred in 2016 (Table 3).

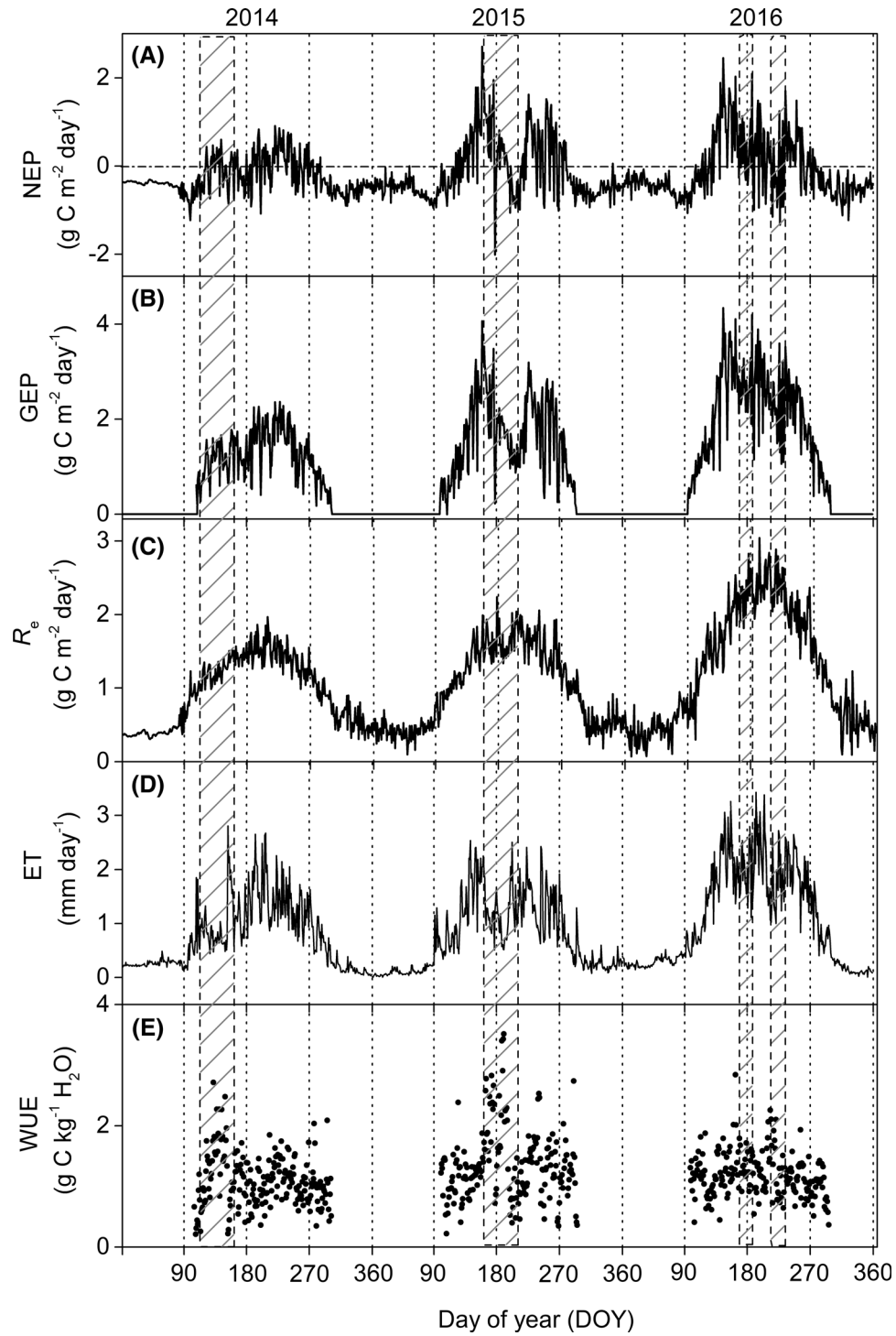
Annual WUE was lower in 2014 than the other 2 years (Table 3). Daily WUE was higher during the drought period in 2014, but was lower during the mid- to late growing season in 2014 compared with the corresponding periods in 2015 and 2016 (Figure 2E). Although daily WUE increased during the initial part of the drought period in 2015, it fell during the late stage of the drought period due to declining GEP. Daily WUE was relatively constant throughout the whole growing season in 2016.

**Table 3.** Annual Carbon and Water Fluxes, Indices and Physiological Parameters for a Shrubland Ecosystem at the Yanchi Research Station, China, during 2014, 2015 and 2016

Parameter	2014	2015	2016	Ratios
NEP ( $\text{g C m}^{-2} \text{ y}^{-1}$ )	$-76 \pm 19$	$-25 \pm 15$	$-18 \pm 12$	4.22:1.39:1
$R_e$ ( $\text{g C m}^{-2} \text{ y}^{-1}$ )	$322 \pm 22$	$345 \pm 17$	$439 \pm 14$	0.73:0.79:1
GEP ( $\text{g C m}^{-2} \text{ y}^{-1}$ )	$246 \pm 18$	$320 \pm 15$	$421 \pm 12$	0.58:0.76:1
ET ( $\text{mm y}^{-1}$ )	$266 \pm 5$	$280 \pm 4$	$386 \pm 4$	0.69:0.73:1
NDVI	0.24	0.27	0.31	0.77:0.87:1
$P_{\max}$ ( $\mu\text{mol C m}^{-2} \text{ s}^{-1}$ )	5.08	6.30	7.98	0.63:0.78:1
$\alpha$ ( $\mu\text{mol C } \mu\text{mol PAR}^{-1}$ )	0.013	0.018	0.025	0.56:0.72:1
$g_c$ ( $\text{mm s}^{-1}$ )	2.28	2.61	3.53	0.65:0.74:1
$R_e/\text{GEP}$	1.31	1.07	1.04	1.25:1.03:1
WUE ( $\text{g C kg}^{-1} \text{ H}_2\text{O}$ )	0.92	1.14	1.09	0.84:1.04:1
GSL	194	193	193	1.01:1:1

Uncertainties in fluxes represent  $\pm 1$  standard deviation of 2000 annual values derived from Monte Carlo simulations following Jia and others (2014). Physiological parameters are averages for the growing season. Also shown are the ratios of values for 2014 and 2015, respectively, to the value for 2016. Definitions of symbols and acronyms are: NEP net ecosystem production,  $R_e$  ecosystem respiration, GEP gross ecosystem productivity, NDVI normalized difference vegetation index,  $P_{\max}$  maximum apparent photosynthetic capacity of the canopy,  $\alpha$  apparent quantum yield,  $g_c$  canopy conductance, WUE water use efficiency (GEP/ET), GSL growing season length.





**Figure 2.** Seasonal variations in daily **A** net ecosystem production (NEP), **B** gross ecosystem production (GEP), **C** ecosystem respiration ( $R_e$ ), **D** evapotranspiration (ET) and **E** water use efficiency (WUE) from 2014 to 2016 of shrubland at the Yanchi Research Station. Hatched bands in the figure indicate drought periods during the spring in 2014 and during summer in 2015 and 2016.

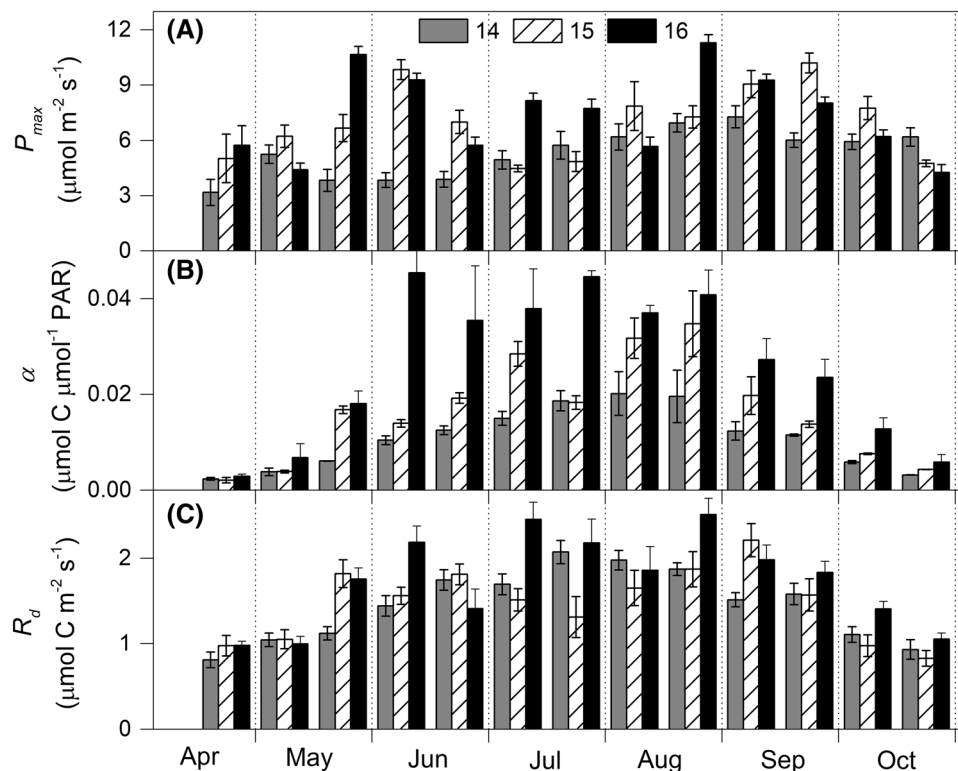
## Effects of Drought on GEP and $R_e$ Parameters

The differences in the magnitude of ecosystem C exchange among the years were reflected in the photosynthetic parameters (Figure 3). Maximum apparent photosynthetic capacity ( $P_{\max}$ ) was consistently lower in 2014 than the other 2 years, except during the summer period when  $P_{\max}$  decreased during the drought periods in 2015 and 2016 (Figure 3A). The mean value of  $P_{\max}$  over growing season was 5.08, 6.30 and 7.98  $\mu\text{mol C m}^{-2} \text{s}^{-1}$  in 2014, 2015 and 2016, respectively. Quantum yield ( $\alpha$ ) over the growing season was consistently higher in 2016 and lower in 2014 (Figure 3B), whereas it decreased in the summer drought periods in 2015 and 2016.  $R_d$  in 2016 was slightly higher than in 2014 and 2015 (Figure 3C).

$P_{\max}$  was linearly correlated with SWC in the upper 0.30-m soil layer, but neither  $\alpha$  nor  $R_d$  was statistically correlated with SWC (Figure 4). All

parameters increased linearly with increasing NDVI during the growing season in the 3 years ( $P < 0.05$ ) with the exception of  $P_{\max}$  in 2015 ( $P > 0.05$ ). We found that the relationship between monthly  $R_d$  and  $T_s$  was similar to that between monthly  $R_n$  and  $T_s$  (Figure 5) with comparable  $R_{10}$  and  $Q_{10}$  values. The similarity of the  $R_d$  and  $R_n$  values shows little effect of light inhibition of plant respiration in this shrubland ecosystem which might be due to the low LAI. The influence of drought on GEP was evident in 2014 when  $T_s$  was low and in 2015 and 2016 when  $T_s$  was high (Figure 6).

We also normalized GEP by NDVI (Figure 7). Normalized GEP plateaued after DOY 145 in 2014, whereas in 2015 and 2016, it increased during the initial part of the growing season and then decreased showing some indication of plateauing near the end of the growing season. Normalized GEP reached a higher maximum in 2016 than 2015 and was significantly lower in 2014 than 2015 and 2016 over the growing season ( $P < 0.01$ ). Bin-averaged



**Figure 3.** Half-monthly values of the GEP and  $R_e$  parameters obtained by fitting the light (PAR)-response curve (Eq. 2) to daytime half-hourly net ecosystem production (NEP) measurements during the 2014–2016 growing seasons.  $P_{\max}$  is the maximum apparent photosynthetic capacity of the canopy,  $\alpha$  is the apparent quantum yield, and  $R_d$  is the average daytime respiration.  $R_d$  was obtained as the average value of the intercept of the linear relationships between daytime NEP and PAR using 3-day-wide windows moving one day at a time (for  $\text{PAR} < 300 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Only  $R_d$  values obtained from relationships with  $P < 0.01$  were accepted. 88% of the values met this criterion and resulted in an average  $R^2$  of 0.62. Vertical bars are  $\pm 1$  standard deviation.

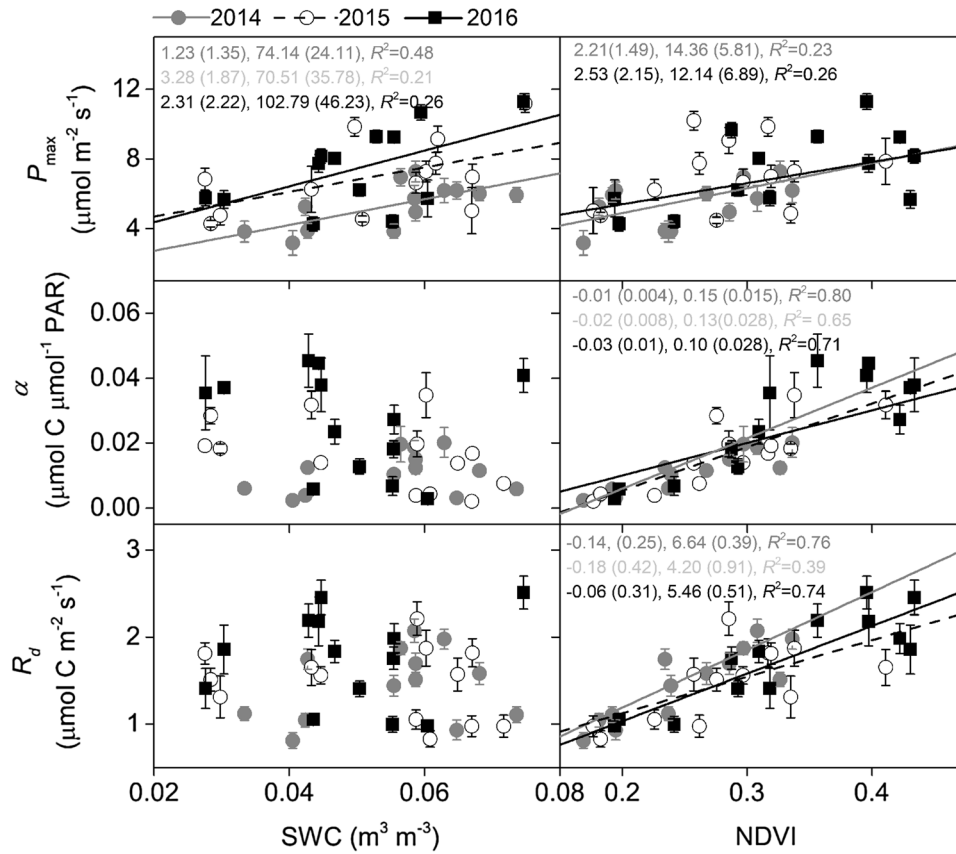


Figure 4. Relationships between GEP and  $R_e$  parameters ( $P_{max}$ ,  $\alpha$  and  $R_d$ ) from Eq. (2) with mean volumetric soil water content (SWC) in the upper 0.30 m of soil (left panels) and NDVI (right panels) for the growing seasons in 2014–2016. The lines are the linear regression fits to the data. The value outside the parentheses is the intercept and slope of the regression, and that inside is the standard error of the regression. All regression lines are significant at significance level of 0.01.

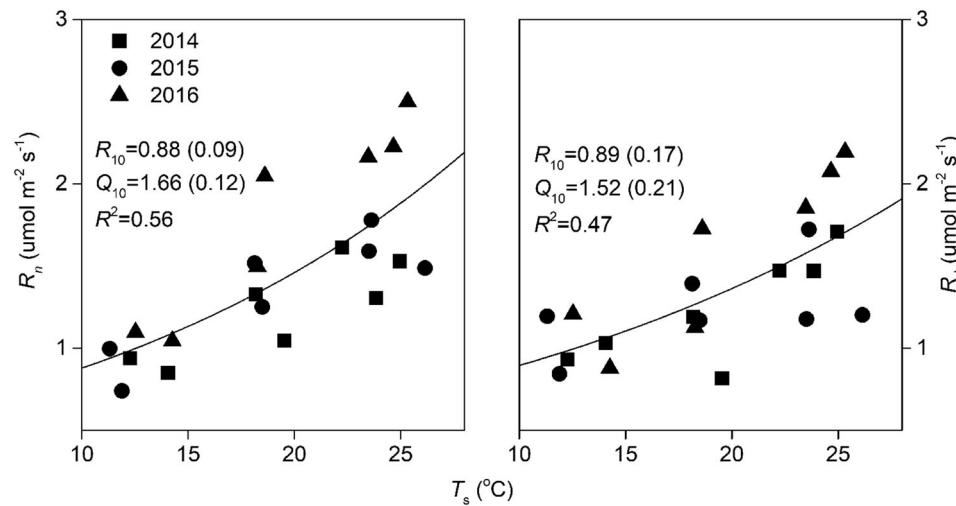
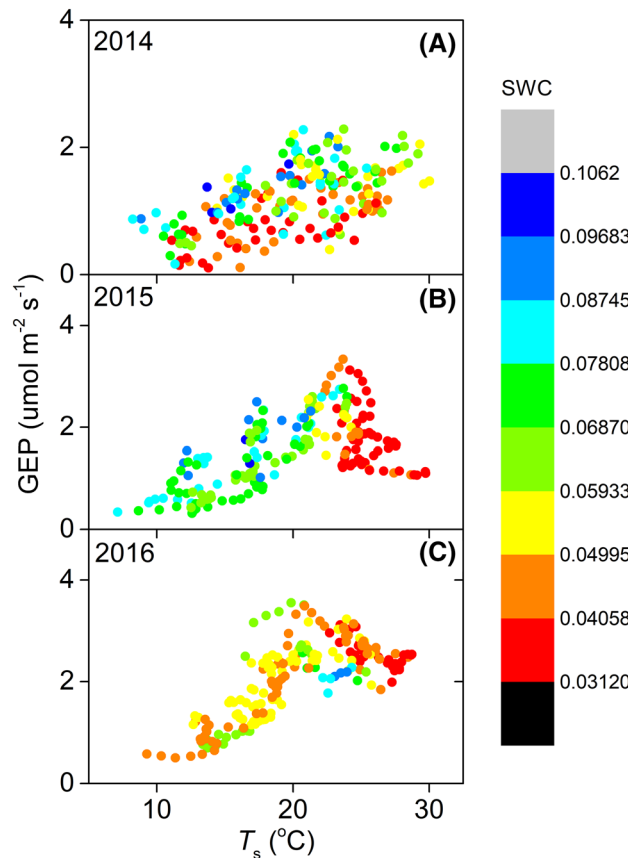
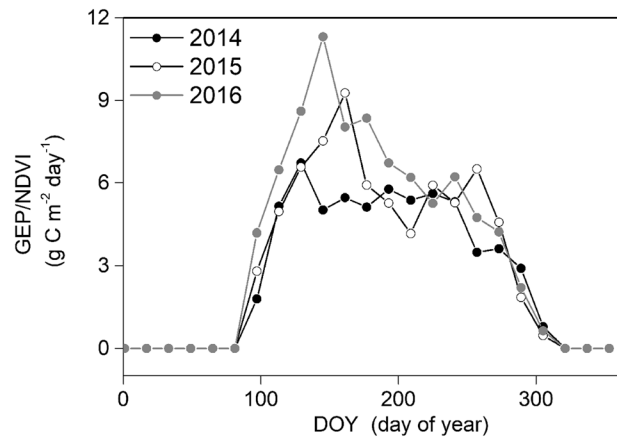


Figure 5. Monthly (April–October) daytime ( $R_d$ ) and nighttime ( $R_n$ ) respiration versus  $T_s$  for 2014, 2015 and 2016. The curves show the fits of Eq. (1) to the data with the parameters also shown. Bracketed values are  $\pm 1$  standard error.



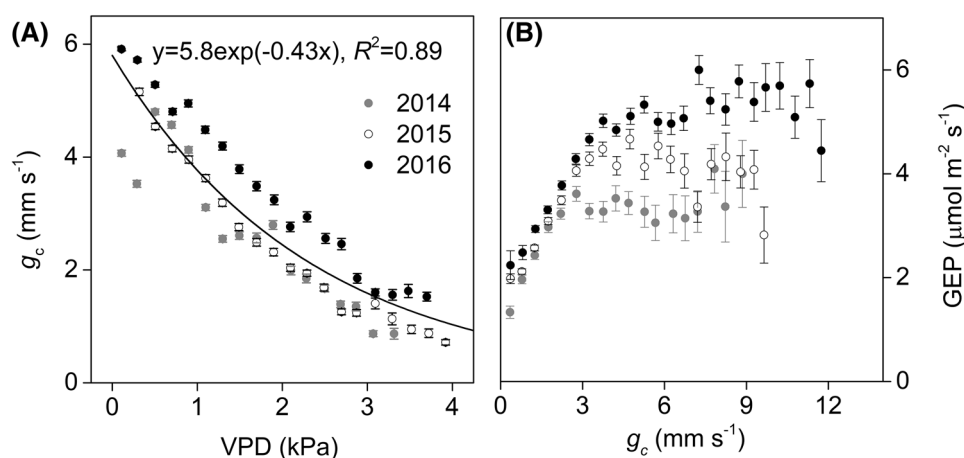
**Figure 6.** 5-day running means of gross ecosystem production (GEP) versus soil temperature ( $T_s$ ) at the 0.10 m depth over the growing season in 2014 (A), 2015 (B) and 2016 (C) sorted by 0–0.30 m volumetric soil water content (SWC) ( $\text{m}^3 \text{m}^{-3}$ ) with color scale shown on the right (Color figure online).



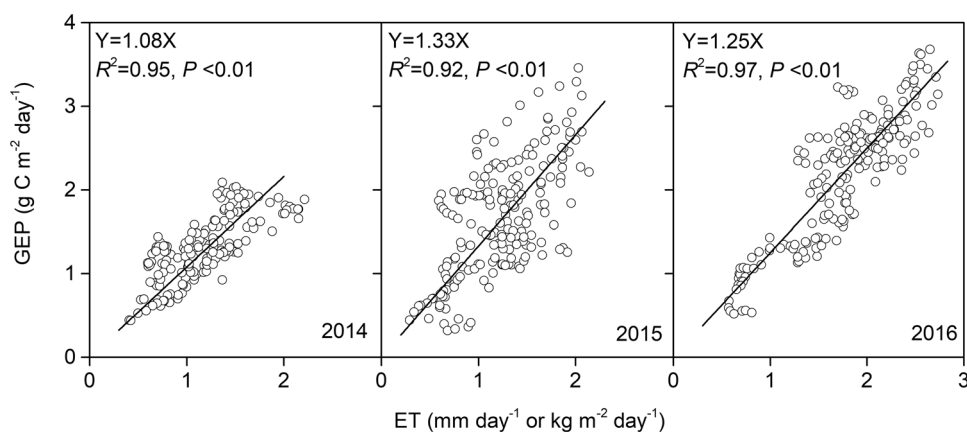
**Figure 7.** GEP normalized by NDVI from 2014 to 2016. GEP data were recalculated at half-monthly intervals to fit MODIS NDVI data.

half-hourly  $g_c$  declined with increasing VPD (Figure 8A). The  $g_c$ -VPD relationship was well described by an exponential function among the 3 years ( $R^2 = 0.89$ ). GEP increased with  $g_c$  before  $g_c$  reached a threshold and then GEP plateaued (Fig-

ure 8B). The threshold was lowest in 2014 and highest in 2016. Furthermore, we also determined the relationships between daily GEP and ET which showed a shallow slope in 2014 (Figure 9).



**Figure 8.** Relationships of canopy conductance ( $g_c$ ) to vapor pressure deficit (VPD) (**A**) and GEP to  $g_c$  (**B**) for growing season of 2014–2016. Half-hourly  $g_c$  values were bin-averaged into 0.2 kPa VPD increments, and half-hourly GEP values were bin-averaged into 0.5  $\text{mm s}^{-1}$   $g_c$  increments. All half-hourly data were limited to daytime when PAR was greater than 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The curve in (**A**) is a fit to the data for all 3 years.



**Figure 9.** Relationships between the 5-day running means of GEP and ET for 2014–2016. Units of the slopes are  $\text{g C (kg H}_2\text{O)}^{-1}$ . The regressions are forced through zero.

## DISCUSSION

### Source of NEP Difference

The interannual differences in NEP were mainly caused by greater suppression of GEP than  $R_e$  as a result of droughts (Table 3). Previous studies reported that annual GEP is jointly controlled by the maximum of GEP and growing season length which primarily correspond to plant physiology and phenology, respectively (Xia and others 2015). In the present study, because the growing season length was similar among years, differences in phenology were probably inconsequential. The interannual differences in GEP were attributed mainly to the differences in physiological processes among years. Physiological parameters ( $P_{\text{max}}$ ,  $\alpha$  and  $g_c$ ), which reflect the canopy photosynthetic

capacity (Liu and others 2016), were lowest in 2014 and highest in 2016 (Figures 1, 3, and Table 3). Furthermore, the very good relationship between NDVI and  $P_{\text{max}}/\alpha$  indicated that the NDVI was closely related to physiological processes of plant (Figure 4). NDVI is a metric of greenness which is indicative of the amount of green leaves which is quantified by the LAI. Thus, we concluded that the interannual differences in GEP were probably due to plant controls on  $g_c$  and LAI (as suggested by NDVI).

Both GEP and  $R_e$  declined in response to drought (Figure 2), resulting in small changes in annual NEP (Table 3). But GEP and  $R_e$  responded differently to changes in climatic variables.  $R_e$  was generally controlled by  $T_s$ , SWC and substrate availability (for example, recent photosynthetic

assimilates which are coupled to GEP). GEP was mainly controlled by PAR,  $T_a$ , SWC and the green part of the canopy (NDVI or leaf area index) (Jia and others 2014, 2016b). In addition to the potentially confounding direct effects of  $T_s$  and SWC, our data suggested that the SWC effect on  $R_e$  may have been mediated by GEP. The direct relationship between  $R_e$  and SWC was not significant in 2014 (not shown). Annual  $R_e$  showed similar value between 2014 and 2015, both of which were much lower than the annual  $R_e$  in 2016 (Table 3). But annual GEP in 2014 was much lower than that in 2015. Wang and others (2017) demonstrated that photosynthetic substrate supply was an important factor in regulating soil respiration on a daily timescale in a desert shrubland ecosystem and its effect on respiration increased when surface soil moisture content decreased. Autotrophic respiration (roots, stems and foliage) can account for about 60% of  $R_e$  (Law and others 2001), and short-term variations in  $R_e$  are largely determined by the supply of labile organic carbon compounds produced by photosynthesis (van der Molen and others 2011). The suppression of  $R_e$  in 2014 might have been mainly because of the limitation of substrate availability (for example, recent photosynthetic assimilates, coupled with GEP). The occurrence of maximum daily  $R_e$  in 2014 was later than in the other 2 years, and it appeared to be affected by the late maximum of GEP.

The observation that interannual variability in GEP among years exceeded interannual variability in  $R_e$  (Table 3) is consistent with previous findings (Biederman and others 2016; Scott and others 2015; Xie and others 2015; Jia and others 2016b). It supports our initial hypothesis that the differences in NEP would be due more to the effects on GEP than on  $R_e$ . It is important to note that GEP and  $R_e$  were almost simultaneously suppressed by the summer drought in 2015, but GEP was more depressed than  $R_e$  by the spring drought in 2014. We speculate that the ratio of heterotrophic respiration ( $R_h$ ) to  $R_e$  was relatively high in spring. The relatively wet surface soil due to the frequent small rainfalls in spring of 2014 (Figure 1D), might have eliminated the water limitation to  $R_h$ , causing similar values of  $R_e$  in the springs of 2014 and 2015. The higher  $R_e$  in the spring of 2016 than in the spring of 2015 along with the more spring rainfall in 2016 supports this speculation (Table 1). As discussed above, the reduction in  $R_e$  in 2014 was most likely related to the decline in GEP. Some published studies have reported greater interannual variation in  $R_e$  than GEP (Arain and others 2002; Morgenstern and others 2004). Sometimes,

similar changes in GEP and  $R_e$  may offset each other resulting in little change in NEP (Powell and others 2008). The sensitivity of GEP and  $R_e$  to drought is not only related to the duration and severity of the deficiency in soil moisture but also to the timing of its occurrence. For instance, Lund and others (2012) reported increased  $R_e$  with unaffected GEP in response to drought that occurred in mid-summer, whereas GEP was more suppressed than  $R_e$  due to drought that occurred during the canopy development period in a temperate peatland. Overall, our results revealed that photosynthetic and respiratory processes might be constrained differently by SWC during the growing season.

We compared our annual NEP in 2014 with the annual NEP of a nearby (less than 5 km) mixed shrubland ecosystem reported by Jia and others (2016). Our annual NEP ( $-76 \pm 19 \text{ g C m}^{-2} \text{ y}^{-1}$ ) was much lower than Jia and others' value ( $-22 \pm 5 \text{ g C m}^{-2} \text{ y}^{-1}$ ), indicating the current ecosystem was a larger C source under drought conditions. Difference in the species composition of ecosystems is relevant to effects of drought on carbon balance, and the ecosystem dominated by single species was less stable than the multiple species mixed ecosystem (van der Molen and others 2011; Lebourgeois and others 2013). Thus, the vegetation differences between the two sites likely contributed to the difference in annual NEP. But the mechanistic understanding of how species richness affects the response of the ecosystem C balance to drought is very limited and requires further study.

## Effects of Drought on Evapotranspiration and WUE

ET was substantially reduced in response to the droughts (Figure 2 and Table 3). Semiarid shrublands employ water saving strategies and reduce their ET early in a drought (Kurc and Small 2004; Jia and others 2016b). As ET responded earlier to drought than GEP (Figure 2), daily WUE tended to increase first and then decrease in the following dry days. But due to similar relative decreases in GEP and ET, annual WUE in 2015 was similar to that in 2016 (Table 3). Annual WUE of  $0.92 \text{ g C kg}^{-1} \text{ H}_2\text{O}$  was lowest in 2014, which compared to  $1.33 \text{ g C kg}^{-1} \text{ H}_2\text{O}$  for the same year observed by Jia and others (2016b) indicate an almost pure *A. dosica* ecosystem having lower WUE than a mixed ecosystem. Because the vegetation was sparsely distributed at our site, leaf area index was small (maximum LAI  $< 1.2 \text{ m}^2 \text{ m}^{-2}$ ), so soil evapora-

tion is expected to contribute considerably to ET. Unlike the long rain-free period during summer in 2015, PPT was evenly distributed in 2014 (Figure 1), which would have kept the soil surface relatively wet and maintained a high soil evaporation rate with reduced penetration of water into the root zone. This result was consistent with previous findings that surface soil layer is the primary reservoir for water storage and source for ET in semiarid shrublands (Kurc and Small 2004). That is likely why GEP was greatly decreased and ET was similar in 2014 relative to that in 2015 (Table 3). Thus, the PPT distribution (that is timing of drought) impacted GEP and ET differently and exerted a significant influence on WUE.

Another sign of changes in WUE among years is reflected in the GEP versus  $g_c$  relationships (Figure 8). The lower threshold in 2014 might indicate a lower intrinsic water use efficiency (that is, GEP/ $g_c$ ). The lower threshold as well as the smaller slope of GEP versus ET in 2014 (Figure 9) showed that the limitation of water for photosynthesis was more severe in 2014.

### Effects of Drought on GEP and $R_e$

We found that the lowest annual C and water fluxes in the 3 years occurred in 2014 which had the spring drought period (Table 3), whereas fluxes were less impacted by the summer drought period in 2015. GEP was markedly lower during the spring drought period in 2014 than in the same period in 2016 and remained lower for 1 month after the period. The same interannual differences were also observed in  $P_{max}$  and  $\alpha$  (Table 3). This might indicate that the ecosystem recovered from the summer drought after plentiful rainfall, whereas the drought in spring had a lasting effect on C uptake depressing GEP substantially during the remainder of the growing season. Noormets and others (2008) also found that drought during canopy development had a lasting effect on the annual C balance in a deciduous temperate forest. Spring drought has been reported to suppress canopy development and peak leaf area (Jia and others 2016b), as well as to induce stomatal closure (Noormets and others 2008). In the current study, both growing season NDVI and  $g_c$  were lower in 2014 than the other 2 years (Figure 1 and Table 3). As the photosynthetic structure in the leaf is determined by conditions at the time of leaf development (Kull and Tulva 2002), the sustained low SWC in the spring of 2014 might have had a detrimental effect on physiological parameters for the entire growing season, extending beyond the drought period. That

appears to be why  $P_{max}$  and  $\alpha$  were lower in 2014 during the entire growing season than the other 2 years (Figures 1, 3, and Table 3). NDVI-normalized GEP was higher in 2016 and 2015 than that in 2014, which is attributable to the higher spring SWC in 2015 and 2016 resulting from the considerable previous year's autumn PPT (Jia and others 2016b). Similarly, Biederman and others (2018) reported that C sink strength in the warm deserts of North America was determined by winter  $P$  rather than summer  $P$ . These observations together suggest that timing of droughts can affect GEP in different ways, and that spring drought affects GEP more than summer drought. This supports our hypothesis that timing of drought would exert a significant impact on C fluxes in this desert shrubland ecosystem. In the context of climate change, our results indicate that future studies should focus on the evaluation of the effect of timing of drought on dryland ecosystems. However, they are mainly based on only 3 years of observations and are therefore preliminary. Longer (decade scales) time series and a wider range of SWC and PPT conditions are needed for confirm or refine these findings of how timing of droughts affects ecosystem C uptake and water use in drylands.

### CONCLUSIONS

This *A. ordosica* shrubland ecosystem was a C source of  $40 \pm 32 \text{ g C m}^{-2} \text{ y}^{-1}$  and used  $310 \pm 65 \text{ mm y}^{-1}$  of water. Timing of drought had a large impact on ecosystem C and water fluxes. Compared to the reference year (2016), spring drought in 2014 reduced GEP more than  $R_e$  resulting in decreased NEP, whereas summer drought in 2015 reduced GEP and  $R_e$  by a similar amount resulting in almost no difference in NEP. In the case of WUE, the relative decrease in GEP caused by the 2014 spring drought was greater than that in ET resulting in a marked decrease in WUE compared to 2016, whereas in 2015 the relative decreases in GEP and ET were almost the same so that WUE was very similar to that in 2016. Differences in annual GEP among years were probably due to plant controls on  $g_c$  and LAI that were greatly suppressed due to drought.

Overall, this work emphasized the importance of the seasonality of rainfall pattern in controlling the temporal variation in ecosystem C sequestration in dryland ecosystems. The main findings highlight the importance of spring drought to the annual C balance in such ecosystems, mainly through its impact on GEP. On the other hand, although

summer droughts may impact both  $R_e$  and GEP, their contribution to the interannual variability of ecosystem carbon source/sink is less important than spring drought. These findings are valuable for future studies of the effects of climate change on such ecosystems and also to management practices aimed at enhancing ecosystem functionality under a changing climate.

## ACKNOWLEDGEMENTS

The research work has been supported by grants from the National Natural Science Foundation of China (NSFC: 31670710, 31670708), by the National Key Research and Development Program of China (No. 2016YFC0500905) and by the Fundamental Research Funds for the Central Universities (No. 2015ZCQ-SB-02). The U.S.–China Carbon Consortium (USCCC) supported this work by providing opportunity for instructive discussions and exchange of ideas. We also thank Cai Ren, Jiawei Mu, Ziqi Wang and Cai Zhang for their assistance with field measurements and instrument maintenance. The data analyzed in this manuscript are available through <https://drive.google.com/open?id=1YUF5iQu3KOY8Z2haNuQdgESJLnkpXo6f> and can also through e-mail request to the corresponding author Tianshan Zha (tianshanzha@bjfu.edu.cn).

## REFERENCES

- Ahlström A, Raupach MR, Schurgers G, Smith B, Arneth A, Jung M, Reichstein M, Canadell JG, Friedlingstein P, Jain AK. 2015. The dominant role of semi-arid ecosystems in the trend and variability of the land CO<sub>2</sub> sink. *Science* 348:895–9.
- Arain MA, Black TA, Barr AG, Jarvis PG, Massheder J, Verseghy DL, Nescic Z. 2002. Effects of seasonal and interannual climate variability on net ecosystem productivity of boreal deciduous and conifer forests. *Canad J For Res* 32:878–91.
- Biederman JA, Scott RL, Goulden ML, Vargas R, Litvak ME, Kolb TE, Yeepez E, Oechel W, Blanken P, Bell T, Garatuza-Payan J, Maurer G, Dore S, Burns S. 2016. Terrestrial carbon balance in a drier world: the effects of water availability in southwestern North America. *Global Change Biol* 22(5):1867–79.
- Biederman JA, Scott RL, Bell TW, Bowling DR, Dore S, Garatuza-Payan J, Kolb TE, Krishnan P, Krofcheck DJ, Litvak ME, Maurer GE. 2017. CO<sub>2</sub> exchange and evapotranspiration across dryland ecosystems of southwestern North America. *Global Change Biol* 23(10):4204–21.
- Biederman JA, Scott RL, Arnone JA, Jasoni RL, Litvak ME, Moreo MT, Papuga SA, Ponce-Campos GE, Schreiner AP, Vivoni ER. 2018. Shrubland carbon sink depends upon winter water availability in the warm deserts of North America. *Agric For Meteorol* 249:407–19.
- Bowling DR, Bethers-Marchetti S, Lunch CK, Grote E, Belnap J. 2010. Carbon, water, and energy fluxes in a semiarid cold desert grassland during and following multiyear drought. *J Geophys Res* 115:G04026.
- Brown M, Black TA, Nescic Z, Foord VN, Spittlehouse DL, Freedman AL, Grant NJ, Burton PJ, Trofymow JA. 2010. Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia. *Agric For Meteorol* 150:254–64.
- Burba GG, McDERMITT DK, Grelle A, Anderson D, Xu LK. 2008. Addressing the influence of instrument surface heat exchange on the measurements of CO<sub>2</sub> flux from open-path gas analyzers. *Global Change Biol* 14:1854–76.
- Chen X, Duan Z. 2009. Changes in soil physical and chemical properties during reversal of desertification in Yanchi County of Ningxia Hui autonomous region, China. *Environ Geol* 57:975–85.
- Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529–33.
- Correia AC, Costa e Silva F, Correia AV, Hussain MZ, Rodrigues AD, David JS, Pereira JS. 2014. Carbon sink strength of a Mediterranean cork oak understorey: how do semi-deciduous and evergreen shrubs face summer drought? *J Veg Sci* 25(2):411–26.
- Jassal RS, Black TA, Cai T, Morgenstern K, Li Z, Gaumont-Guay D, Nescic Z. 2007. Components of ecosystem respiration and an estimate of net primary productivity of an intermediate-aged Douglas-fir stand. *Agric For Meteorol* 144:44–57.
- Jia X, Zha T, Wu B, Zhang Y, Gong J, Qin S, Chen G, Qian D, Kellomäki S, Peltola H. 2014. Biophysical controls on net ecosystem CO<sub>2</sub> exchange over a semiarid shrubland in northwest China. *Biogeosciences* 11:4679–93.
- Jia X, Zha T, Gong J, Wang B, Zhang Y, Wu B, Qin S, Peltola H. 2016a. Energy partitioning over a semi-arid shrubland in northern China. *Hydrol Process* 30:972–85.
- Jia X, Zha T, Gong J, Wang B, Zhang Y, Wu B, Qin S, Peltola H. 2016b. Carbon and water exchange over a temperate semi-arid shrubland during three years of contrasting precipitation and soil moisture patterns. *Agric For Meteorol* 228:120–9.
- Heitschmidt RK, Vermeire LT. 2006. Can abundant summer precipitation counter losses in herbage production caused by spring drought? *Rangel Ecol Manag* 59(4):392–9.
- Kljun N, Calanca P, Rotach MW, Schmid HP. 2004. A simple parameterisation for flux footprint predictions. *Bound Layer Meteorol* 112:503–23.
- Kull O, Tulva I. 2002. Shoot structure and growth along a vertical profile within a *Populus-Tilia* canopy. *Tree Physiol* 22:1167–75.
- Kurc SA, Small EE. 2004. Dynamics of evapotranspiration in semiarid grassland and shrubland ecosystems during the summer monsoon season, central New Mexico. *Water Resour Res* 40(9):W09305.
- Law BE, Thornton PE, Irvine J, Anthoni PM, Van Tuyl S. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biol* 7:755–77.
- Lebourgeois F, Gomez N, Pinto P, Mérian P. 2013. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *For Ecol Manag* 303:61–71.
- Li SG, Eugster W, Asanuma J, Kotani A, Davaa G, Oyunbaatar D, Sugita M. 2008. Response of gross ecosystem productivity, light use efficiency, and water use efficiency of Mongolian steppe to seasonal variations in soil moisture. *J Geophys Res Biogeosci* 113:G01019.



- Liu R, Cieraad E, Li Y, Ma J. 2016. Precipitation pattern determines the inter-annual variation of herbaceous layer and carbon fluxes in a phreatophyte-dominated desert ecosystem. *Ecosystems* 19:601–14.
- Lund M, Christensen TR, Lindroth A, Schubert P. 2012. Effects of drought conditions on the carbon dioxide dynamics in a temperate peatland. *Environ Res Lett* 7:045704.
- Monteith JL. 1965. Evaporation and environment. In: Fogg GE, Ed. *The state and movement of water in living organisms*. New York: Academic Press. p 205–34.
- Morgenstern K, Black TA, Humphreys ER, Griggs TJ, Drewitt GB, Cai T, Nestic Z, Spittlehouse DL, Livingston N. 2004. Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Niño La Niña cycle. *Agric For Meteorol* 123:201–19.
- Noormets A, McNulty SG, DeForest JL, Sun G, Li Q, Chen J. 2008. Drought during canopy development has lasting effect on annual carbon balance in a deciduous temperate forest. *New Phytol* 179:818–28.
- Papale D, Reichstein M, Aubinet M, Canfora E, Bernhofer C, Kutsch W, Longdoz B, Rambal S, Valentini R, Vesala T. 2006. Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences* 3:571–83.
- Petrie MD, Collins SL, Swann AM, Ford PL, Litvak ME. 2015. Grassland to shrubland state transitions enhance carbon sequestration in the northern Chihuahuan Desert. *Global Change Biol* 21(3):1226–35.
- Powell TL, Gholz HL, Clark KL, Starr G, Cropper WP, Martin TA. 2008. Carbon exchange of a mature, naturally regenerated pine forest in north Florida. *Global Change Biol* 14:2523–38.
- Ross I, Misson L, Rambal S, Arneeth A, Scott RL, Carrara A, Cescatti A, Genesio L. 2012. How do variations in the temporal distribution of rainfall events affect ecosystem fluxes in seasonally water-limited northern hemisphere shrublands and forests? *Biogeosciences* 9(3):1007–24.
- Schwinning S, Starr BL, Ehleringer JR. 2005. Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part II: effects on plant carbon assimilation and growth. *J Arid Environ* 61(1):61–78.
- Scott RL, Hamerlynck EP, Jenerette GD, Moran MS, Barron-Gafford GA. 2010. Carbon dioxide exchange in a semidesert grassland through drought-induced vegetation change. *J Geophys Res* 115:G03026.
- Scott RL, Biederman JA, Hamerlynck EP, Barron-Gafford GA. 2015. The carbon balance pivot point of southwestern US semiarid ecosystems: insights from the 21st century drought. *J Geophys Res Biogeosci* 120(12):2612–24.
- Shapiro JB, Griffin KL, Lewis JD, Tissue DT. 2004. Response of *Xanthium strumarium* leaf respiration in the light to elevated CO<sub>2</sub> concentration, nitrogen availability and temperature. *New Phytol* 162:377–86.
- State Forestry Administration of China. 2015. The fifth bulletin on desertification in China. <http://www.forestry.gov.cn/main/65/20151229/835177.html>.
- van der Molen MK, Dolman AJ, Ciais P, Eglin T, Gobron N, Law BE, Meir P, Peters W, Phillips OL, Reichstein M. 2011. Drought and ecosystem carbon cycling. *Agric For Meteorol* 151:765–73.
- Vicente-Serrano SM, López-Moreno JJ, Beguería S. 2010. A multi-scalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index -SPEI. *J Clim* 23:1696–718.
- von Buttlar J, Zscheischler J, Rammig A, Sippel S, Reichstein M, Knohl A, Jung M, Menzer O, Arain MA, Buchmann N, Cescatti A, Gianelle D, Kiely G, Law BE, Magliulo V, Margolis H, McCaughey H, Merbold L, Migliavacca M, Montagnani L, Oechel W, Pavelka M, Peichl M, Rambal S, Raschi A, Scott RL, Vaccari FP, van Gorsel E, Varlagin A, Wohlfahrt G, Mahecha MD. 2018. Impacts of droughts and extreme-temperature events on gross primary production and ecosystem respiration: a systematic assessment across ecosystems and climate zones. *Biogeosciences* 15:1293–318.
- Wang B, Zha TS, Jia X, Gong JN, Bourque C, Feng W, Tian Y, Bin W, Zhang YQ, Heli Petola. 2017. Soil water regulates the control of photosynthesis on diel hysteresis between soil respiration and temperature in a desert shrubland. *Biogeosciences* 14:3899.
- Welp L, Randerson J, Liu H. 2007. The sensitivity of carbon fluxes to spring warming and summer drought depends on plant functional type in boreal forest ecosystems. *Agric For Meteorol* 147:172–85.
- Wohlfahrt G, Bahn M, Haslwanter A, Newsely C, Cernusca A. 2005. Estimation of daytime respiration to determine gross production of a mountain meadow. *Agric For Meteorol* 130:13–25.
- Xia J, Niu S, Ciais P, Janssens IA, Chen J, Ammann C, Afrain A, Blanken PD, Cescatti A, Bonal D, Buchmann N, Curtis PS, Chen S, Dong J, Flanagan LB, Frankenberg C, Georgiadis T, Gough CM, Hui D, Kiely G, Li J, Lund M, Magliulo V, Marcolla B, Merbold L, Montagnani L, Moors EJ, Olesen JE, Piao S, Raschi A, Rouspard O, Suyker AE, Urbaniak M, Vaccari FP, Varlagin A, Vesala T, Wilkinson M, Weng E, Wohlfahrt G, Yan L, Luo Y. 2015. Joint control of terrestrial gross primary productivity by plant phenology and physiology. *Proc Natl Acad Sci USA* 112:2788–93.
- Xie J, Zha T, Jia X, Qian D, Wu B, Zhang Y, Bourque CP-A, Chen J, Sun G, Peltola H. 2015. Irregular precipitation events in control of seasonal variations in CO<sub>2</sub> exchange in a cold desert-shrub ecosystem in northwest China. *J Arid Environ* 120:33–41.
- Xie J, Zha T, Zhou C, Jia X, Yu H, Yang B, Chen J, Zhang F, Wang B, Bourque CP-A, Sun G. 2016. Seasonal variation in ecosystem water use efficiency in an urban-forest reserve affected by periodic drought. *Agric For Meteorol* 221:142–51.
- Yang F, Zhou G. 2013. Sensitivity of temperate desert steppe carbon exchange to seasonal droughts and precipitation variations in Inner Mongolia, China. *PLoS ONE* 8:e55418.
- Zhang Q, Sun XY, Yu WP, Huang LQ. 2004. Studies on soil water characteristic curves and infiltration capability of Mu Us Sandland. *For Res* 17:9–14.
- Zhu Z, Sun X, Wen X, Zhou Y, Tian J, Yuan G. 2006. Study on the processing method of nighttime CO<sub>2</sub> eddy covariance flux data in China FLUX. *Sci China Earth Sci D* 49(supp. II):36–46.