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Higher assimilation than respiration sensitivity to drought for a desert ecosystem in Central Asia

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Abstract

Responses of ecosystem assimilation and respiration to global climate change vary considerably among terrestrial ecosystems constrained by both biotic and abiotic factors. In this study, net CO₂ exchange between ecosystem and atmosphere (NEE) was measured over a 4-year period (2013-2016) using eddy covariance technology in a desert ecosystem in Central Asia. Ecosystem assimilation (gross primary production, GPP) and respiration (R_{eco}) were derived from NEE by fitting light response curves to NEE data based on day- and nighttime data, and their responses to soil water content (SWC) and evaporative fraction (EF) were assessed during the growing season. Results indicated that both GPP and R_{eco} linearly decreased with declining SWC, with the sensitivity of GPP to SWC being 3.8 times higher than that of R_{eco} during the entire growing season. As a result, ecosystem CO₂ sequestration capacity decreased from 4.00 μmol m⁻² s⁻¹ to 1.00 μmol m⁻² s⁻¹, with increasing soil drought. On a seasonal scale, significant correlation between GPP and SWC was only found in spring while that between R_{eco} and SWC was found in all growing seasons with the sensitivity increasing steadily from spring to autumn. EF had a low correlation with SWC, GPP and R_{eco} (R² = 0.03, 0.02, 0.05, respectively), indicating that EF was not a good proxy for soil drought and energy partitioning was not tightly coupled to ecosystem carbon exchanges in this desert ecosystem. The study deepens our knowledge of ecosystem carbon exchange and its response to drought as well as its coupling with ecosystem energy partitioning in an extreme dry desert. The information is critical for better assessing carbon sequestration capacity in dryland, and for understanding its feedback to climate change.

Key words: Gross primary production, Drought sensitivity, Evaporative fraction, Desert ecosystem

1. Introduction

Carbon exchange between terrestrial ecosystems and the atmosphere is the basic process supporting ecosystem productivity and biodiversity, and has a considerable effect on ecosystem feedback to climate change (Pereira et al., 2007; Molen et al., 2011). Net ecosystem CO₂ exchange (NEE) is the balance between ecosystem CO₂ assimilation (i.e. gross primary production-GPP) and respiration (R_{eco}). While GPP and R_{eco} relate to not exactly the same biological processes, both are largely influenced by environmental factors and always tightly coupled to water cycle and energy partitioning (Gažovič et al., 2013; Doughty et al., 2015).

Soil moisture can strongly modulate hydrologic and climatic conditions and may act as a key factor driving CO₂ exchange in terrestrial ecosystems, especially in drylands (Ford et al., 2014; Wagle et al., 2017). Arid and semiarid regions (ASALs), accounting for nearly 1/3 of the global carbon sequestration are among the most climate change-sensitive ecosystems of the world (Li et al., 2015). In addition, ASALs are regarded as having high turnover rates of carbon pools and are increasingly becoming important in driving inter-annual variability of the global carbon cycle (Poulter et al., 2014). As a typically extreme arid and vulnerable ecosystem, deserts are regarded as having low magnitudes of CO₂ exchange. They are also highly sensitive to slight changes in soil moisture (Jiang et al., 2017). In the Chihuahuan desert in America, NEE decreased linearly with decreasing total summer precipitation, inducing a conversion from carbon sink to carbon source (Mielnick et al., 2005). Two hot deserts in New Mexico and Arizona in Northern America acted as carbon sources in most observed years and drought tended to enhance the period and magnitude of net ecosystem CO₂ release (Svejcar et al., 2008). In the Gurbantunggute desert in Northwest China, NEE depended largely on land cover type and had a significant positive linear correlation with soil water content in various land cover types when volumetric soil water content was less than 3% (Su et al., 2013). In the same study, both the mean ecosystem NEE and dark respiration increased during the first two days following rainfall addition treatment but the sensitivity of dark respiration to rainfall was higher than that of NEE.

Under drought, physiology and community structure of plants and the microbial

organisms and their habitat microclimatic conditions (e.g. temperature, radiation) change, with ramifications on terrestrial carbon fixation and release (Reichstein et al., 2002; Molen et al., 2011; Yang and Zhou, 2013). On a global perspective, the sensitivity of GPP to soil drought was found to be 50% higher than that of R_{eco} (Schwalm et al., 2010). Welp et al. (2007) however, reported that GPP decrease was less than the decrease of R_{eco} during summer drought in both evergreen and deciduous broadleaf forests in northwest America. The reported decrease in NEE under drought in this desert in previous studies may have resulted from higher sensitivity of GPP to drought than that of R_{eco} . Unfortunately, comparative researches are rare in deserts, hence there is large knowledge gap on the effects of drought on key processes related to CO_2 exchange processes in desert ecosystems.

Evaporative fraction (EF) is the ratio of latent heat flux and total available energy at the land surface, representing the fraction of incoming energy used for evapotranspiration. When the land surface is moist, most of the net radiation is used predictably to evaporate surface water and $EF \rightarrow 1$, while when the surface is moisture limited, more of the available energy loss is through heat conduction and convection (Kurc and Small, 2004), and hence $EF \rightarrow 0$. EF has, therefore, been viewed as a proxy for soil drought in natural ecosystems, ranging from 0 (completely dry) to 1 (fully wet), and is a valuable tool for describing drought effect on C-exchange processes (Kurc and Small, 2004; Schwalm et al., 2010). In croplands, EF was found showing significant positive correlation with SWC and GPP, and has been integrated into satellite-based ecosystem GPP simulation models as a drought proxy (Running et al., 2004; Yuan et al., 2015). Whether EF can act as a proxy for tracing drought effect on ecosystem carbon exchanges in desert ecosystems has not been explored.

In this study, we measured net ecosystem CO_2 exchange and energy fluxes during the growing seasons spanning four years (2013-2016) in a desert ecosystem in Central Asia using eddy-covariance technology to examine: (1) How ecosystem assimilation and respiration respond to soil drought in an extreme-drought desert; (2) The degree of coupling between ecosystem energy partitioning and soil water content and ecosystem carbon cycle process in a desert ecosystem. Based on these two objectives and previous

studies, two hypotheses were proposed and examined: (1) Sensitivity of carbon assimilation to soil drought is higher than of respiration in desert ecosystem; (2) EF couples well with soil water content and has a considerable effect on ecosystem carbon assimilation and respiration in this desert ecosystem.

2. Materials and Methods

2.1. Site description

This study was conducted in a relatively flat desert site (44°25'54"N, 87°54'9"E) on the southern edge of Gurbantünggüt desert located in Northwest China. The site is situated at around 600 m asl. The climate here is hot and dry in summer while cold, with snow-cover in winter. The mean annual air temperature was 7.5 °C, while the mean annual rainfall was 163 mm, much lower than mean annual pan evaporation of approximate 2000 mm (Liu et al., 2012). The soil is composed of homogeneous weathered sand soil, in which soil organic carbon and total salt content is 0.80 ~ 7.08 mg g⁻¹ and 0.25 ~ 0.69 mg g⁻¹, respectively.

The dominant vegetation is an appropriate 2-meter-high shrub, *Haloxylon ammodendron*. The density and mean canopy coverage of *H. ammodendron* in this study site is 584 stems ha⁻¹ and 16%, respectively (Zheng and Wang, 2014; Zheng and Wang, 2015). The mean basal diameter is 6.4 cm and coverage of sapwood area is appropriate 0.77 m² ha⁻¹ (Zheng and Wang, 2014). Under the canopy, there are some short-life herbaceous plants (e.g. *Erodium oxyrrhynchum*, *Ceratocarpus arenarius* and *Alyssum linifolium*) occurred in spring irrigated by melted snow water and died out in early summer when soil become dry. Photosynthetic organ (assimilation shoots) of *H. ammodendron* is photosynthetically active from the middle of spring but they become dormant by late autumn.

2.2. Measurement of environment variables and eddy fluxes

Air temperature (T_{air}), air relative humidity (RH), wind speed and direction were continuously measured from early spring to early winter for a period of four years (2013-2016) using a 2.5-m-high automatic weather station (Vantage Pro2™, Davis

Instruments, USA) installed on the study site. A quantum sensor (Li190SB, Campbell Scientific, Inc., Logan, USA) was used to measure photosynthetic photons flux density (PPFD) at the same height as climate sensors. Volumetric soil water content (SWC) at 20 cm depth was measured by soil moisture sensors (ThetaProbe, Delta-T Devices Ltd., Cambridge, UK). All the environment variables were measured every 1 min and 10 min averages were recorded by weather station logger and a standing alone data logger (DT80, Thermo Fisher Scientific Australia Pty Ltd, Australia) synchronously.

Net ecosystem CO₂, H₂O and energy flux were measured with an open-path eddy covariance system installed on an 11 m-high flux tower, which was 50 m away from the automatic weather station. This eddy covariance system included a 3D sonic anemometer (CSAT3, Campbell Scientific Inc., Logan, Utah, USA) which measures wind vector and air temperature, and an open-path infrared gas analyzer (Li-7500, Licor Inc., Lincoln, NE, USA) which measures CO₂ and H₂O concentration, at sampling rate of 10 Hz.

2.3. Data treatment and statistical analysis

Raw flux data were computed and calibrated using EddyPro™ software (www.licor.com/eddypro, Licor Inc., Lincoln, NE, USA), which were gone through coordinate rotation, sonic temperature correction, frequency and WPL correction (Fratini and Mauder, 2014). Outlier in half-hourly net ecosystem CO₂ exchange (NEE) were removed based on the method according to Papale et al. (2006). All rainy-day and night-time data under non-turbulent conditions were excluded based on a u*-threshold criterion which was determined according to Reichstein et al. (2002, 2005). Ecosystem assimilation and respiration were separated by fitting light response curves of NEE based on day- and nighttime hourly data according to Mcmurtrie et al. (1992):

$$NEE = \max(-QUE_{app} \times PPF D; GPP_{sat}) + R_{eco} \quad (1)$$

where QUE_{app} ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photons) was the apparent quantum use efficiency of ecosystem carbon uptake, GPP_{sat} ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) was the gross carbon uptake under

saturating photon flux density, and R_{eco} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was ecosystem respiration estimated as NEE when PPFD was 0. Those three parameters were fitted by scattering PPFD and NEE every 5 days with a 15-day window following Reichstein et al. (2005).

The fitted 5-day mean R_{eco} was described using a regression model in each year taking T_{air} and SWC as predictors similar to that of Reichstein et al. (2002):

$$R_{eco} = R_{ecoref} \times (a + b \times SWC) \frac{T_{air} - T_{ref}}{10} \times \frac{SWC - SWC_0}{(SWC_{1/2} - SWC_0) + (SWC - SWC_0)} \quad (2)$$

where R_{ecoref} was the ecosystem respiration at 15 °C and optimal soil moisture condition, and T_{ref} was fixed to 15 °C, and $SWC_{1/2}$ and SWC_0 were the SWC at which the half-maximal R_{eco} occurred and at which R_{eco} was 0, respectively. In addition to the measured hourly T_{air} and SWC, the established R_{eco} regression model was used to estimate hourly R_{eco} . Ecosystem gross primary production (GPP) was calculated as the sum of net CO₂ uptake and R_{eco} :

$$GPP = -NEE + R_{eco} \quad (3)$$

In keeping with micrometeorology, negative value of NEE indicate the carbon uptake by ecosystem while positive value means CO₂ release from ecosystem to atmosphere in this study. Evaporative fraction (EF) was described as a function of tower-based heat fluxes given by:

$$EF = \frac{LE}{H + LE} \quad (4)$$

where H was sensible heat flux (W m^{-2}) and LE was latent heat flux (W m^{-2}) above the canopy.

Seasons were determined by the calendar month and local phenology in this study site, i.e. climatic spring consists April, May and June, climatic summer consists July and August, and climatic autumn includes September and October. These three climatic

seasons constitute entire growing season in the study site. In order to avoid seasonal variation effect of daytime length, the systematic complexity and uncertainty associated with calm conditions during nighttime (Irvine et al., 2002) and be comparable with EF, daily average instead of accumulative flux data during daytime was used for the following analysis. Daytime was defined as $PPFD > 40 \mu\text{mol m}^{-2} \text{s}^{-1}$.

In order to compare general response of assimilation and respiration to soil drought, linear function was used to describe ecosystem GPP and R_{eco} response to SWC and the fitted slope was viewed as their general sensitivity to soil drought. All statistical analysis was conducted with $P < 0.05$ as a threshold for statistical significance. Avoiding limited repeated samples for the years when part data missed, relationships among GPP, R_{eco} , SWC and EF were analyzed based on all data from 2013 to 2016 other than did it each year.

3. Results

3.1 Environment variables

During the measurement period, from 2013 to 2016, daily average T_{air} increased from spring, peaked in middle summer and then decreased continuously, ranging from $-1.71 \text{ }^{\circ}\text{C}$ to $39.05 \text{ }^{\circ}\text{C}$ with an average of $22.19 \text{ }^{\circ}\text{C}$ (Fig. 1a). Daily average of PPFD reached maximum value (around $900 \mu\text{mol m}^{-2} \text{s}^{-1}$) in early summer (Fig. 1b). The mean daily PPFD for the four years was $650 \mu\text{mol m}^{-2} \text{s}^{-1}$. Seasonal pattern of daily average VPD and T_{air} were similar, with maximum values occurring in mid-summer. But VPD showed more steep seasonal increase and decrease rate than T_{air} (Fig. 1c). The maximum and mean daily VPD were approximate 6.00 kPa and 2.10 kPa , respectively. Volumetric SWC at 20 cm depth was highest in mid spring followed by continuous decreasing from late spring until the end of growing season (Fig. 1d). This pattern was repeated every year during the measurement period. Due to technical error, certain data missed during the period between 2013 and 2014. SWC in the study site ranged from 2% to 10% and the average was 4.34% during the studied four years.

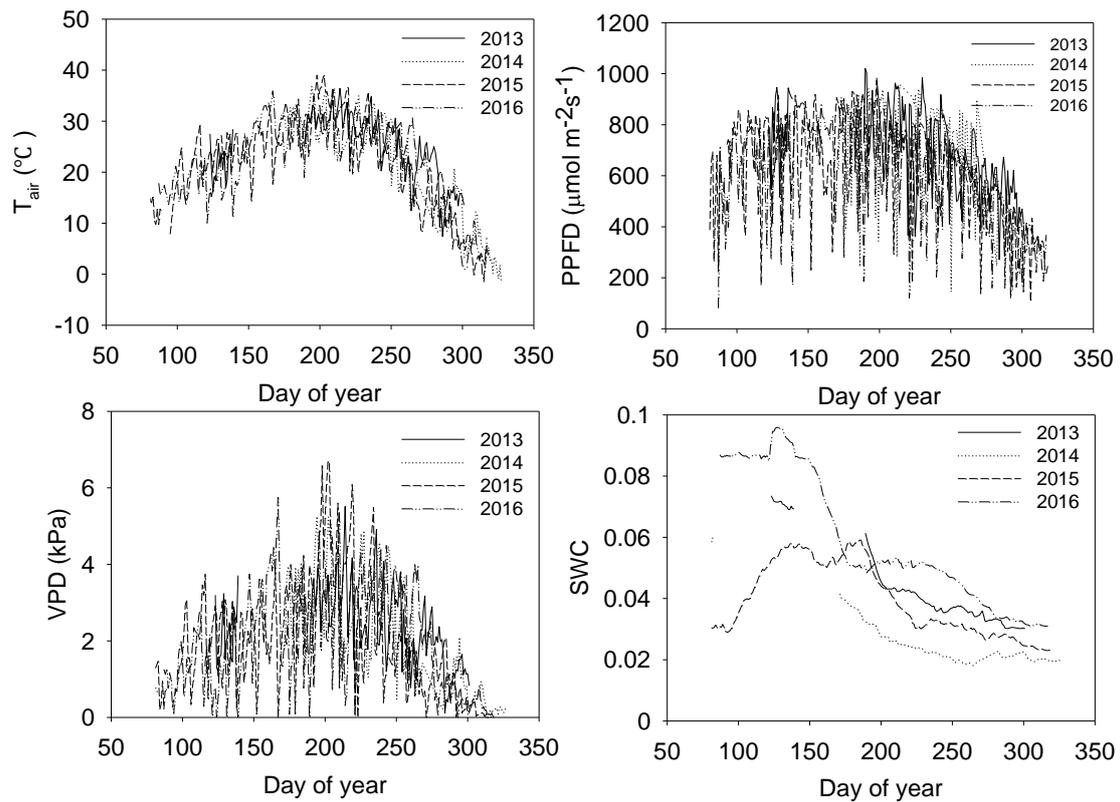


Fig.1 Seasonal variation in daily average T_{air} (a), PPFD (b), VPD (c) when PPFD > 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and SWC (d) during the growing season from 2013 to 2016. Missing data were due to power/equipment failure.

3.2. Response of assimilation parameters to SWC

During the growing season from 2013 to 2016, the fitted aggregate 5-day ecosystem apparent quantum use efficiency of carbon uptake (QUE_{app}) ranged from 0.001 to 0.009 $\mu\text{mol } \mu\text{mol}^{-1}$ and averaged 0.004 $\mu\text{mol } \mu\text{mol}^{-1}$ (Fig. 2a). The fitted 5-day aggregate gross primary productivity rate under saturating photon flux density (GPP_{sat}) ranged from 1.00 to 4.00 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and averaged 2.13 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2b). Both QUE_{app} and GPP_{sat} were significantly correlated with SWC ($P < 0.01$) and linearly increased with increasing SWC (Fig. 2a-b).

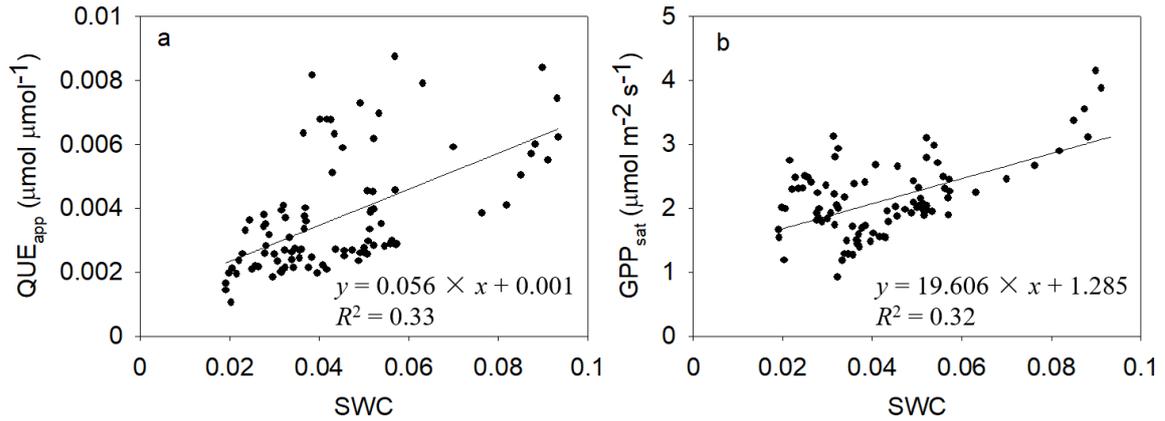


Fig.2 Responses of ecosystem QUE_{app} (a) and GPP_{sat} (b) to SWC during growing season from 2013 to 2016. Data points were 5-day aggregates.

3.3. Seasonal variation in CO_2 exchanges and their response to SWC

During the four-year study period, daily mean R_{eco} increased in spring and decreased in autumn, with peak rates of $2.00 \mu\text{mol m}^{-2} \text{s}^{-1}$ occurring in summer. The average R_{eco} during the period was $0.59 \mu\text{mol m}^{-2} \text{s}^{-1}$. The daily average GPP increased rapidly from early spring, reaching a maximum in mid spring, but then declining continuously until the end of the growing season. Daily GPP varied from 0.00 to $6.00 \mu\text{mol m}^{-2} \text{s}^{-1}$ and averaged $1.79 \mu\text{mol m}^{-2} \text{s}^{-1}$ over the entire growing season (Fig. 3a). Both ecosystem GPP and R_{eco} were positively and significantly correlated with SWC ($P < 0.001$). The sensitivity to soil drought (defined as the slope of regressed linear function between GPP/R_{eco} and SWC) of ecosystem GPP was approximately 3.8 times higher than that of R_{eco} (Fig. 3b). As a result, net ecosystem CO_2 uptake ($-NEE$) declined significantly ($P < 0.001$) from $4.00 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $1.00 \mu\text{mol m}^{-2} \text{s}^{-1}$ with decreasing SWC following a quadratic function (Fig. 4).

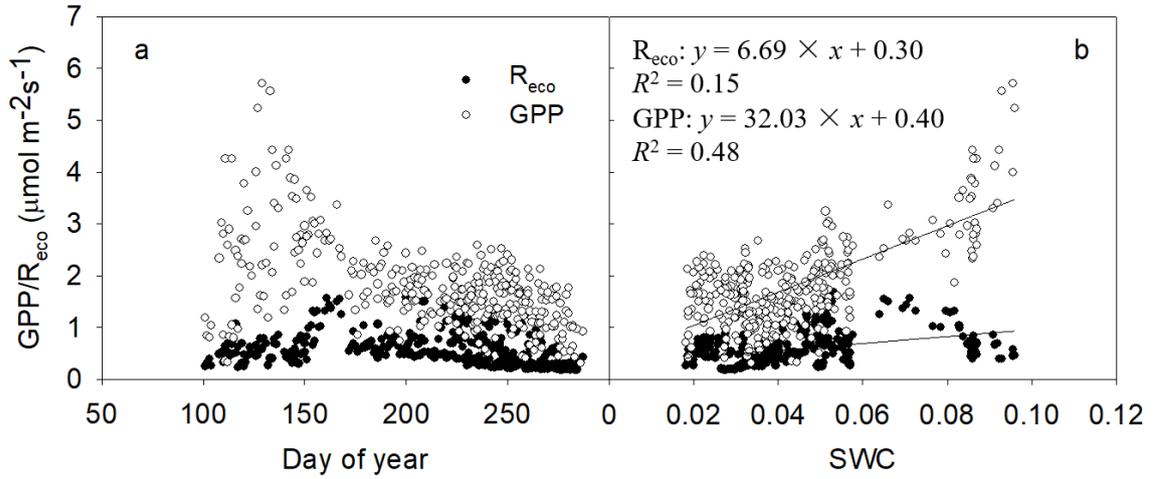


Fig.3 Seasonal variation of daily average ecosystem GPP and R_{eco} when PPFD > 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (a) and their response to SWC at 20 cm depth (b) during growing seasons from 2013 to 2016.

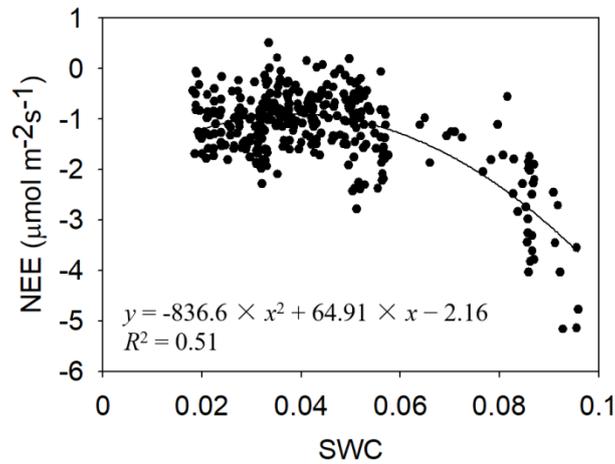


Fig.4 Response of daily average net ecosystem CO_2 exchange (NEE) to SWC during growing season from 2013 to 2016.

3.4. Seasonal variation in GPP and R_{eco} response to SWC

In spring, both GPP and R_{eco} were positively and significantly correlated with SWC ($P < 0.05$, Fig. 5a). The sensitivity of GPP to SWC was 11.32 times higher than that of R_{eco} (Fig. 5d). In both summer and autumn, R_{eco} and SWC were positively and significantly correlated ($P < 0.001$) while GPP was not ($P > 0.05$, Fig. 5b-c). Among the three seasons, the sensitivity of R_{eco} to SWC continually increased from spring to autumn. Sensitivity of GPP to SWC in spring was the highest in annual course, despite

the lack of significant correlation between GPP and SWC in both summer and autumn (Fig. 5d).

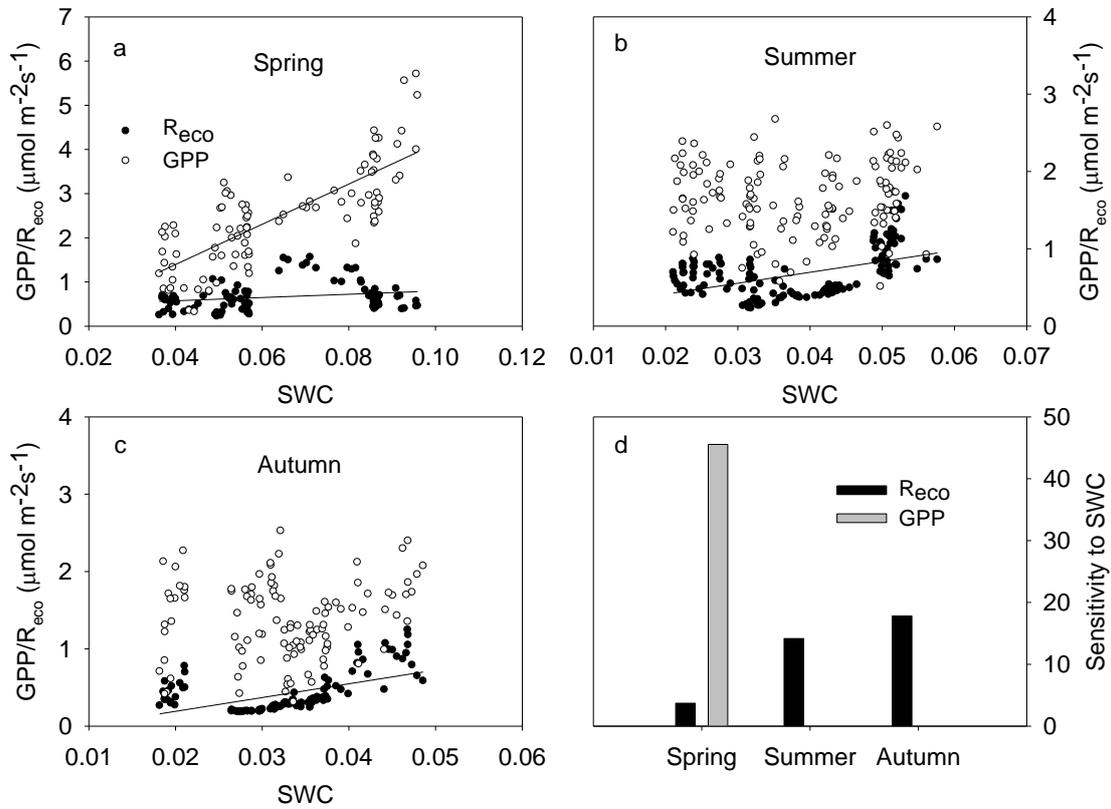


Fig.5 Response of daily average ecosystem GPP and R_{eco} when $PPFD > 40 \mu\text{mol m}^{-2} \text{s}^{-1}$ to SWC in spring (a), summer (b) and autumn (c), and the general sensitivity of GPP and R_{eco} to SWC (defined as the slope of linear regression between SWC and GPP, R_{eco}) in three seasons (d) during growing season from 2013 to 2016.

3.5. Seasonal variation in EF and its response to SWC, GPP and R_{eco}

During the growing season between 2013 and 2016, daily average evaporative fraction (EF) during daytime ranged from 0.04 to 0.65 and averaged at 0.20. Daily EF was higher in spring and then declined in summer and autumn, but with strong seasonal fluctuations (Fig. 6a). There was significant ($P < 0.01$) positive correlation between EF and SWC and EF could be described as a linear function of SWC (Fig. 6b). Daily EF was positively correlated with GPP, but negatively correlated with R_{eco} , and both relationships were poor but statistically significant ($P < 0.05$, Fig. 6c).

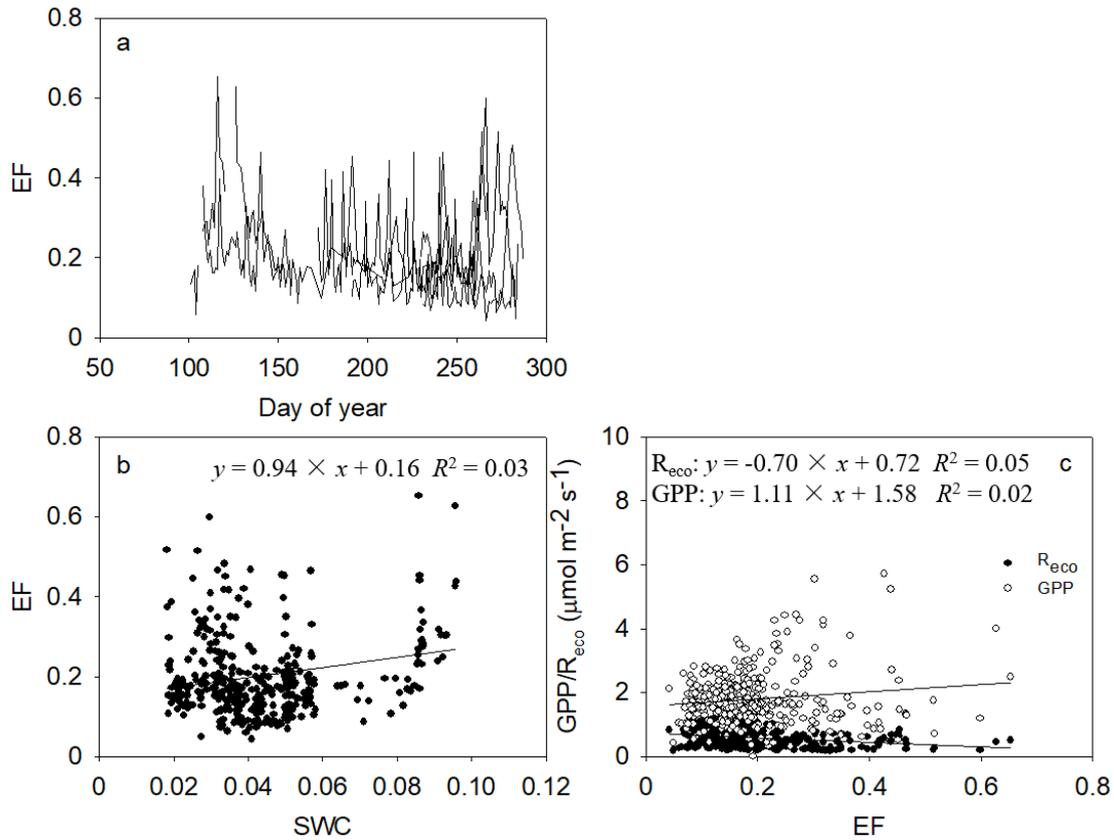


Fig.6 Seasonal variation of daily average EF during growing season from 2013 to 2016 (a), response of daily EF to SWC (b) and response of daily GPP and R_{eco} to EF (c).

4. Discussion

4.1. Soil drought effect on desert ecosystem assimilation and respiration

Soil water is the main water source for terrestrial ecosystems, hence in arid systems as well. Changes in SWC directly affect ecosystem processes, such as CO_2 exchanges (Jia et al., 2016). Significant correlation between GPP, R_{eco} and SWC at 20 cm depth were observed in this study. This indicated that soil moisture availability in the shallow soil layer was a critical water sources for this desert ecosystem and had non-ignorable effect on ecosystem C cycle. In addition to shallow-rooted herbaceous plants in the understory, root vertical distribution of the canopy shrub, *H. ammodendron*, contributed to the dependence of ecosystem on shallow soil water. A field excavation experiment conducted approximate 2 km-away from our study site showed that surface area of feeder roots of *H. ammodendron* decreased continually from ground surface to

deeper layer and that approximate 70% of the feeder roots were located within 0 to 50 cm soil layer (Xu et al. 2007). Furthermore, branch transpiration and leaf water potential of *H. ammodendron* were found to be sensitive to rain pulse events and precipitation-derived upper soil water (Xu and Li, 2006). The shallow root system of the dominant plants in this desert ecosystem demonstrate that shallow soil water is crucial in the regulation of ecosystem carbon cycle.

Under drought stress, plants usually lose part of turgor in guard cells and partially or fully close their stomata in order to lower leaf stomatal conductance and limit transpirational water loss. Consequently, there is also reduction in leaf assimilation. Leaf photosynthesis may also decline as a result of depressed enzymatic activity, which declines under water deficit. During the growing season of 2013 to 2016 in this study desert, both fitted aggregate 5-day ecosystem $Q_{E_{app}}$ and GPP_{sat} linearly decreased with declining SWC (Fig. 2), indicating a depressed ecosystem assimilation under soil drought. As a result, ecosystem GPP linearly decreased with increasing soil drought intensity during the entire growing season (Fig. 3b). Similarly, R_{eco} declined linearly with declining SWC, but its sensitivity to SWC was lower than that of GPP. Overall, there was a decline in carbon sequestration capacity (a factor of NEE, Fig. 4) under increasing drought intensity in this temperate desert ecosystem. Similar results had also been reported for a temperate dry grassland in the Inner Mongolia of China, where the ratio between sensitivities of GPP and R_{eco} to SWC varied from 1.96 to 4.10 times (Yang and Zhou, 2013), and for cold and warm desert grasslands in USA (Bowling et al., 2010; Anderson-teixeira et al., 2011). Similarly, GPP sensitivity to annual total precipitation was 0.6 ~ 2.7 times higher than that of R_{eco} in two sagebrush-steppe ecosystems in USA (Gilmanov et al., 2006). The results were also similar to those reported for a global-scale study (Schwalm et al., 2010). However, differences between sensitivities of GPP and R_{eco} to SWC in this study (3.8 times) were higher than that of global terrestrial average level (0.5 times). These results are in favor of the conclusion that the difference between sensitivity of ecosystem assimilation and respiration to drought increased as drought intensity increased, as derived from a synthesized analysis on published observational and experimental results (Shi et al., 2014). Our results

indicated that the sensitivity of carbon sequestration capacity to soil drought in this extreme drought desert was above the global average.

Ecosystem CO₂ exchange is closely influenced by air temperature. In this study, both GPP and R_{eco} showed positive correlations with T_{air} over the entire growing season. However, peak GPP rates were recorded during spring and did not coincide with the highest T_{air} during the year, indicating that phenology also had considerable effect on carbon cycle (Reichstein et al., 2003). The effect of temperature and phenology may further influence the response pattern of GPP and R_{eco} to soil drought. Thus, drought effects on GPP and R_{eco} were analyzed at varying times during the year, taking into account the integrated effect of air temperature and plant phenology.

During spring when short-life herbaceous plants were active, sensitivity of GPP to soil drought was higher than the growing season's average. GPP, however, showed no response to soil drought during summer and autumn when herbaceous plants dried out (Fig. 5b-c). The highest growing season's GPP was during spring when herbaceous plants were active. Thus, the herbaceous vegetation dominated ecosystem C uptake during spring in this desert ecosystem as a result of its high ground coverage (> 80%). The dominance of herbaceous understory in driving ecosystem GPP has also been reported for a humid savanna ecosystem in western Kenya (Otieno et al., 2015) and also in a seasonally dry Mediterranean oak woodland, with scattered trees and an herbaceous ground layer (Pereira et al., 2007). On the other hand, these results also indicated that assimilation of canopy shrub, *H. ammodendron*, had weak response to soil drought during summer and autumn, which were the driest periods of the entire growing season (Fig. 5b-c). This may be linked to its high adaptive capacity to extreme drought conditions during summer and autumn. Although most of feeder roots of *H. ammodendron* distributed in shallow soil layer, the deep roots could also extend to an average depth of 3.32 m (Xu et al., 2007), which may benefit from deep soil water and then maintain survival of *H. ammodendron* and loosen their response of assimilation to extreme shallow soil drought. Unlike GPP, sensitivity of R_{eco} to soil drought continually increased from spring to autumn associated with declining SWC (Fig. 5). Similar results were found in a cold desert grassland in USA where the highest sensitivity of GPP to

soil drought occurred during spring (Bowling et al., 2010). This seasonal pattern of GPP and R_{eco} sensitivity to soil drought was different from that of integrated global terrestrial ecosystem where the highest sensitivity of both GPP and R_{eco} to soil drought occurred in climatic summer (Schwalm et al., 2010). This may be resulted from unstable vegetation structure and special phenology of dominated vegetation among intra-annual growing seasons in this studied desert.

4.2. Suitability of EF as a soil drought index to trace carbon exchange in desert ecosystem

In this study, EF significantly correlated with SWC, GPP and R_{eco} but the correlation was not robust (Fig. 5). These results were similar to those reported for a cropland (Yuan et al., 2015) and from an analysis comparing 11 biomes and 238 tower sites at global scale (Schwalm et al., 2010). However, the correlation (R^2) between EF and GPP/ R_{eco} were much less than that between SWC and GPP/ R_{eco} , even EF and SWC had opposite effects on R_{eco} (SWC actively correlated with R_{eco} while EF negatively correlated with R_{eco} , Fig. 3b and Fig. 6c). Therefore, energy partitioning was not tightly coupled with carbon cycle, and EF was not a strong proxy of soil drought and failed to trace response of GPP/ R_{eco} to soil drought precisely in this desert ecosystem, and hence the second hypothesis in this study was rejected.

Besides available soil water, EF also correlated with other biological and abiotic processes which may decouple the correlations between ecosystem energy partitioning and available water source, carbon exchanges. In water-limited Southern Great Plains of United States, EF acted as a linear function of soil moisture only when soil moisture located between wilting point and critical value and when daily net radiation above the average level, and the relationship between them varied substantially from year to year (Ford et al., 2014). Similarly, Hunt et al. (2002) also found that EF decreased linearly with SWC only when SWC was less than approximate 50% of field capacity in a tussock grassland. In our study, short-life herbaceous plant broke out in the early spring and then died in early summer, most of ground surface was covered by dry herbaceous plants and woody debris in summer and autumn. The existence of withered grass layer

changed the ecosystem albedo and the proportion of available energy to evaporative surface water (Schwalm et al., 2010), and then tended to weaken the correlation between SWC and EF (Fig. 6b). In this context, EF had become a weak proxy for soil drought for the entire growing season and hence had poor correlation with ecosystem carbon exchange. Schwalm et al. (2010) found that relative low EF related with absence of new foliage during spring when soil moisture was abundant in an integrated analysis including 29 deciduous broadleaf forests, and concluded that it was not suitable to view EF as an index of soil water status. This integrated analysis, together with results found in our desert study commonly indicated that EF was not a good proxy for soil moisture status during periods when vegetation structure varied resulted from different phenology of various plant species in a mixed ecosystem. This was different from other ecosystems where vegetation structures were stable and the dominant species phenology were relative consistent during most of growing season and thus EF acted robust link to soil drought and ecosystem carbon exchange (Schwalm et al., 2010; Yuan et al., 2015).

Another reason for failure for EF to trace soil drought effect on carbon exchange in this desert was that EF and SWC showed opposing effects on ecosystem R_{eco} (Fig. 3b and Fig. 6c). In the temperate zone, air temperature is one of the dominant factors affecting ecosystem respiration (Flanagan and Johnson, 2005; Durocher et al., 2012). In this study site, both fitted 5-day aggregated and daily average ecosystem respiration significantly correlated with air temperature, increasing exponentially at higher temperature (unpublished data). Soil respiration was also found to be tightly correlated with air temperature in the same study site (Guan et al., 2015). During spring when herbaceous plants were active, EF was high while air temperature and related R_{eco} was at relative low level (Fig. 1a and Fig. 3a). On the contrary, during summer and autumn when herbaceous layer died, EF was limited to some extent by the coverage of dry grass, while air temperature and related ecosystem respiration in this period were at high level (Fig. 1a and Fig. 3a). The special seasonal regime of vegetation phenology, air temperature and related ecosystem respiration jointly induced the negative effect of EF on R_{eco} , which was in contrast to the effect of soil drought on R_{eco} . In tropical evergreen

broadleaf forests, decrease of EF during onset of dry season is linked to the number of rainy days and the level of solar radiation, which in turn promotes both assimilation and respiration of forests that commonly have deep root system to access deep soil water stores, leading to the same negative correlation between EF and R_{eco} as our study (Schwalm et al., 2010). These emphasized the complexity of interaction between energy partitioning and ecosystem carbon exchange. In addition, vegetation rooting depth, precipitation pulse, and canopy shrub also affect both energy partitioning and carbon cycle processes with different strategies, these together imposed the uncertainty in tracing drought effect on ecosystem carbon cycle using EF in this temperate desert ecosystem.

5. Conclusions

Both GPP and R_{eco} linearly decreased with declining SWC during the entire growing season. The sensitivity of GPP to SWC was 3.8 times higher than that of R_{eco} , inducing a decrease of carbon sequestration capacity under soil drought. At seasonal scale, GPP significantly correlated with SWC only in spring while R_{eco} significantly correlated with SWC in each growing season and the sensitivity increased continually from spring to autumn. Ecosystem CO_2 exchange and its response to soil drought was driven predominantly by short-lived herbaceous plants. The decoupling of EF from SWC was mainly due to death of the herbaceous plants in early summer. The seasonal regime of air temperature and activity of herbaceous plants jointly lead to a negative correlation between EF and R_{eco} that contrast with the relationship between R_{eco} and SWC. Energy partitioning was not tightly coupled to ecosystem carbon exchange in this desert, and EF was not a good proxy for soil drought and hence not suitable for tracing the response of ecosystem carbon exchange to soil drought as soil moisture did in this temperate desert ecosystem.

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