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Soil moisture modifies the response of soil respiration to temperature in a desert shrub ecosystem

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Abstract

The response of soil respiration (R_s) to soil temperature and moisture have been well documented in forests, but data and information from desert shrub ecosystems are limited. Soil CO_2 efflux from a desert shrub ecosystem was measured continuously with automated chambers in Ningxia, northwest China, from June to October 2012. The responses of R_s to T_s was strongly affected diurnally by soil moisture, with the diel variation in R_s being strongly related to 10 cm soil temperature (T_s) at moderate and high soil volumetric water content (VWC), but less related to T_s at low VWC. T_s typically lagged R_s by 3–4 h, however, the lag time varied in relation to VWC, with increased lag times at low VWC. Over the seasonal cycle, daily mean R_s was positively correlated with T_s when VWC exceeded $0.08 \text{ m}^3 \text{ m}^{-3}$, but became decoupled from T_s when VWC dropped below this threshold. The annual temperature sensitivity of R_s (Q_{10}) was 1.5. The short-term sensitivity of R_s to T_s , computed using three-day windows, varied significantly over the seasonal cycle; the short-term Q_{10} was negatively correlated with T_s and positively correlated with VWC. These results suggest the potential for a negative feedback to climate warming in desert ecosystems, related to the impact of low soil moisture on R_s . The results highlight the biological causes of diel hysteresis between R_s and T_s and the need for carbon cycle models to account for the interacting effects of T_s and VWC as joint determinants of R_s in desert ecosystem.

1 Introduction

Soil respiration (R_s) is receiving widespread attention as a key component of the global C cycle (Schimel, 1995). R_s accounts for 60–90 % of total ecosystem respiration (Raich et al., 2002; Schimel et al., 2001) and its global integral is an order of magnitude larger than anthropogenic CO_2 releases from burning fossil fuels and land-use change (Marlan et al., 2008). Soil chamber measurements are contributing to our knowledge and understanding of R_s in many ecosystems. However, R_s is not well documented for

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semi-arid and desert ecosystems, due in part to their low productivity which has caused them to be overlooked (Chen and Tian, 2005). Drylands cover a quarter of the earth's land surface (Reynolds, 2001) and are rapidly expanding due to human population growth and global climate change (Geist and Lambin, 2004). Carbon-cycle measurements from arid and semi-arid ecosystems are thus critical to ensure the accurate representation of these ecosystems in large-scale carbon models. Carbon cycling in deserts may be particularly vulnerable to climate and land-use changes (Feng et al., 2001; Wang et al., 2006). The carbon dynamics of desert ecosystems and their response to environmental factors are critical knowledge gaps in the global carbon budget (Cable et al., 2011).

Soil water content (VWC) is of primary importance for predicting the evolution of soil carbon stock and fluxes, because it strongly controls the decomposition of soil organic matter (Jassal et al., 2008; Liu et al., 2009; Moyano et al., 2012), root respiration (Palta and Nobel, 1989; Bouma et al., 1997), microbial activity (Linn and Doran, 1984; Skopp et al., 1990; Hallett and Yong, 1999; Drenovsky et al., 2004). VWC is predicted to change at global scales in the following decades (Wetherald and Manabe, 2002). Global climate change has been predicted to increase temperature, precipitation variability and potentially exacerbate aridity in some desert ecosystems (Lioubimtseva and Henebry, 2009). The associated impacts on the hydrological cycle of desert ecosystems include shorter wet periods and longer intervals of periodic drought. During the dry and warm portions of the year in desert ecosystem, VWC may have a greater influence than temperature on R_s (Conant et al., 2004). Although soil temperature (T_s) is the major control of soil respiration (R_s) through its influence on the kinetics of microbial decomposition and root respiration and the diffusion of enzymes and substrate (Jassal et al., 2008), low VWC limits microbial respiration by restricting access to C substrates, reducing the diffusion of C substrate and extra-cellular enzymes, and limiting microbial mobility (Yuste et al., 2003). The temporal variation in R_s for desert ecosystems, and its response to T_s and VWC, are expected to differ from other ecosystems due to differences in variation of environment conditions. In desert ecosystem, however, the

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seasonal dependence of R_s on both T_s and VWC is still poorly understood (Raich, 2002).

The sensitivity of R_s to T_s is often described by the Q_{10} model, where Q_{10} is the factor by which R_s increases for a 10 °C increment in temperature (Van't Hoff, 1898).

Q_{10} is reduced by low substrate availability, low VWC and high T_s (Geist, 2004), all of which are characteristic of desert ecosystems. However, desert ecosystems are also characterized by temporal extremes in T_s and VWC, and little is known about the related temporal variation in Q_{10} or its response to environmental factors.

R_s is usually highly correlated with shallow T_s (Jassal et al., 2005). However, studies have reported significant hysteresis in the seasonal cycles of R_s and T_s (Xu and Qi, 2001; Parkin and Kaspar, 2003; Subkem et al., 2003; Jia et al., 2013), and shown a decoupling of R_s from T_s during drought. Low VWC may increase the degree of hysteresis between R_s and T_s (Tang et al., 2005; Vargas and Allen, 2008; Carbone et al., 2008; Phillips et al., 2011) or, in some cases, decrease it (Riveros-Iregui et al., 2007). Both biological and physical explanations have been suggested for the hysteresis patterns (Phillips et al., 2011), however, no consensus has been reached. Phillips et al. (2011) and Riveros-Iregui et al. (2007) demonstrated that the diel phase lags between R_s and T_s may result from differences in the heat and CO₂ transport processes in forest ecosystems. However, in desert ecosystems with sandy soils, the low VWC and high soil porosity may maximize these lags. The magnitude and the causes of hysteresis and its variation remain unclear for desert ecosystems.

Therefore, we hypothesized: (1) desert soil respiration is highly limited by soil moisture and less sensitive to soil temperature; (2) the soil moisture in desert ecosystem affect R_s responses to T_s not only seasonally, but also diurnally. This study reports continuous R_s measurements from a desert shrubland ecosystem in northwest China. The objectives were: (1) to quantify the temporal variations of R_s and its impact factors; (2) to understand the influence of VWC on the sensitivity of R_s to T_s ; and (3) to explore the effects of VWC on hysteresis in the R_s – T_s relationship over the seasonal cycle.

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2 Materials and method

2.1 Site description

The research was conducted on a sand dune at the Yanchi Research Station (106°30' to 107°41' N and 37°04' to 38°10' E) of Beijing Forest University, Ningxia, northwest China. The site is located at the edge of the Maowusu desert in the transition between the arid and semi-arid climatic zones, at an elevation of 1550 m.a.s.l. The sandy soil has a bulk density of 1.6 gcm⁻³. The prevailing climate is of the temperature arid and semi-arid type. The mean annual precipitation is 292 mm, of which 62 % falls between July to September. The mean annual total of potential evapotranspiration is 2024 mm. the mean annual temperature was 8.1 °C. All meteorological data were provided by the meteorological station of Yanchi County and represent 51 yr averages (1954–2004). The vegetation has been recovered for 10 yr. The dominant vegetation is *Artemisia songarica* Schrenk, with sparse *Hedysarum fruticosum*.

2.2 Soil respiration measurements

Continuous measurements of soil surface CO₂ efflux (Rs) were made in situ using an automated soil respiration system (model LI-8100A fitted with a LI-8150 multiplexer, LI-COR, Nebraska, USA). Measurements were made on a typically-sized fixed sand dune, along two 26 m line transects that originated at the center of the dune. Eleven permanent PVC collars were installed at ~ 3 m spacing in March 2012, three months before the first Rs measurements. The collars were 20.3 cm in diameter and 10 cm in height, with ~ 7 cm inserted into the soil. The collar locations represented four positions (top, upper-slope, lower-slope, and inter-hill) and two aspects (windward and leeward) along the dune slope.

Hourly Rs was continuously measured from June to December 2012. A permanent opaque chamber (model LI-104, LI-COR, Nebraska, USA) was set on each collar. The measurement time for each chamber was 3 min and 15 s, including a 30 s pre-purge,

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a 45 s post-purge, and a 2 min observation period. Any plant re-growth within the measurement collar was manually removed.

Hourly Ts and VWC at 10 cm depth were measured outside of each chamber using the 8150–203 soil temperature sensor and EC_{H₂O} soil moisture sensor (LI-COR, Nebraska, USA), respectively. Rainfall was measured about 1 km away, using a manual rain gauge before 22 July 2012, and a tipping-bucket rain gauge (model TE525MM, Campbell Scientific, UT, USA) after 22 July 2012.

2.3 Data processing and analysis

The Rs data were screened using limit checking. Hourly CO₂ effluxes out the range of -1 to $15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ were considered abnormal and were removed from the data set. Instrument failure and quality control procedures resulted in 3 % missing data from 4 June to 22 October 2012. Hourly means were computed as the mean of the 11 chambers, and daily means were computed as the average of the hourly means. The mean diel cycles of Rs and Ts were computed for each month by averaging the hourly means for each time of day; the cycles were then used to analyze the diel variation in Rs and identify hysteresis in the Rs–Ts relationship. For a better understanding of the diel variation in Rs in response to Ts and VWC, we selected three-day periods with contrasting VWC. Daily mean values were used to examine the seasonal responses of Rs to Ts and VWC. In evaluating the Rs response to Ts, the measurements during rainfall were excluded to minimize the effects of the rain pulse.

Correlation analysis was used to evaluate the relationships between Rs and Ts and VWC. Normalized daily mean Rs (Rs_N), computed as the ratio of observed Rs to the value predicted by the best-fit Rs–Ts model, was used to analyze the seasonal dependence of Rs on VWC (Fig. 7). Three commonly-used models (Table 2), all of which fit the data well, were used to analyze the response of Rs to Ts. Three different bivariate models with Ts and VWC as independent variables were developed to represent the combined effect of both variables (Table 3). Akaike information criterion (AIC) was used

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to evaluate the goodness of the Rs models (Posada and Buckley, 2004).

$$ACI = n \times \ln(SSE) + 2 \times (p + 1) - n \times \ln(n)$$

Where, ACI represents Akaike information criterion, SSE is sum of squares for error, n is sample capacity, p is amount of independent variables used in regression analysis.

Seasonal changes in the sensitivity of Rs to Ts at 10 cm depth (Q_{10}) were analyzed using short-term Q_{10} derived from fitting the Q_{10} model to synchronized data from a three-day moving window with a one-day step (Fig. 8). Cross-correlation analysis was used to detect hysteresis between Rs and Ts at diel time scales, and to synchronize the values before regression analysis was performed. All analyses were processed in Matlab 7.11.0 (R2010b, The Mathworks Inc., Natick MA, USA).

3 Results

3.1 Hysteresis between Rs and Ts

Over the diel cycle, hourly Rs was out of phase with Ts at the 10 cm depth (Fig. 1), as seen in the hysteresis in the Rs–Ts relationship (Fig. 1 and Fig. 2). The mean time lag between Rs and Ts was 3 h during July, September and October, and 4 h during June and August (Table 1), with Rs peaking earlier than Ts. The time lag between Rs and Ts (Fig. 2 and Fig. 3) was negatively and linearly related to VWC (Fig. 3; Lag = $-41 \text{ h} \cdot \text{VWC} + 7.3 \text{ h}$, $R^2 = 0.71$, RMSE = 0.56). Hysteresis was smaller when VWC was higher (Fig. 2c), and larger when VWC was lower (Fig. 2a). For all models, including both bivariate models (Ts and VWC) and models with Ts only, the R^2 values derived from the data set with synchronized Rs and Ts were 12–20 % higher than that without synchronization (Table 3).

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3.2 Diel variation of Rs and its response to Ts and VWC

Over the daily cycle, minimum and maximum hourly Rs occurred at ~6:00 (GMT+8) and 13:00 (Fig. 1), respectively, while minimum and maximum Ts at 10 cm depth occurred at ~7:00 and 16:00. The diel variation of Rs was strongly influenced by Ts and VWC, as seen in contrasting 3 day time series (Fig. 2). At low VWC and high Ts (Fig. 2a), maximum Rs occurred at 9:00 coinciding with the Ts minimum, then sharply decreased as Ts rose, with a subtle, secondary Rs peak at 16:00. At moderate VWC and high Ts (Fig. 2b), Rs rose in response to rising Ts in the early morning but then plateaued at high Ts during the midday before declining with declining Ts. When VWC was high and Ts was low (Fig. 2c), Rs rose in response to rising Ts, with Rs peaking (at 12:00) earlier than Ts and no evidence of a midday plateau.

The mean diel cycles of hourly Rs and Ts, estimated for each month, showed significant positive correlations between Rs and Ts for all months except August (Table 1). The Q_{10} , quadratic and logistic models all fit the mean diel variation data poorly. However, when Rs and Ts data were synchronized to remove the time lag, all three models fit the data well, with the best fit from the Q_{10} model (Fig. 4; $R^2 = 0.89$ in August, $R^2 > 0.95$ for other months).

3.3 Seasonal variations in Rs and its response to Ts and VWC

Daily mean Ts was high during June to August (20 to 25°C), then gradually declined during September to a mean of 10°C in October (Fig. 5a). Daily mean VWC ranged from 0.046 to 0.170 m³ m⁻³, with higher values following periods of precipitation, and lower values at the end of drought (Fig. 5). The seasonal variations in VWC and Ts reflected typical desert climatic conditions, with a series of short wet periods followed by longer intervals of drought, and large differences in temperature between day and night (Fig. 5a). Daily mean Rs showed strong seasonality, peaking in July and declining in autumn, similar to the Ts seasonal cycle but tempered by the VWC seasonal cycle (Fig. 5c). Daily Rs was highest (2.56 μmol CO₂ m⁻² s⁻¹) on 29 July when VWC and Ts

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were high, and lowest ($0.23 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) on 22 October (Fig. 5b) when T_s was low. In general, R_s pulses followed precipitation events (Fig. 5c).

Over the measurement period, daily mean R_s was significantly and positively ($P < 0.01$) related to T_s when VWC was greater than $0.08 \text{ m}^3 \text{ m}^{-3}$ (Fig. 6, closed circles).

The logistic and quadratic models gave the lowest ACI, RMSE and highest R^2 (Fig. 6; Table 2), with T_s explaining $\sim 76\%$ of the seasonal variation in daily R_s . In contrast, R_s became decoupled from T_s when VWC was less than $0.08 \text{ m}^3 \text{ m}^{-3}$ (open circle on Fig. 6, Table 2, $r = 0.307$, $P = 0.69$). Normalized respiration R_{sN} , derived from the logistic model and excluding days with rainfall, was significantly and positively related to VWC (Fig. 7; $R_{sN} = 8.94 \cdot \text{VWC} + 0.08$, $R^2 = 0.78$, $P < 0.01$).

Table 3 lists the parameters from three empirical models. Overall, the bivariate models with T_s and VWC as independent variables produced a better fit than the T_s -only models. Data synchronization, removing the diel lag between R_s and T_s , improved the performance in terms of ACI, R^2 and RMSE for all models.

3.4 Q_{10} and its response to T_s and VWC

The annual sensitivity of R_s to T_s (parameter b from the Q_{10} model in Table 3) was 1.5. Short-term Q_{10} estimated from a 3 day moving window showed strong seasonality and ranged from 0.63 to 10 (Fig. 8a, Q_{10} during rainfall event has been excluded), being lower in June–August than September–October. Periods with rainfall had elevated Q_{10} .

After removing the data during rainfall, the Q_{10} was significantly and negatively related to T_s (Fig. 8b; $Q_{10} = -0.42 \cdot T_s + 12.4$, $R^2 = 0.86$, RMSE = 0.91), but positively related to VWC (Fig. 8c; $Q_{10} = 18\,010 \cdot \text{VWC}^{3.721} + 1.604$, $R^2 = 0.42$, RMSE = 3.165).

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4.1 Diel response of Rs to VWC

Our finding that the diel variation of Rs was constrained by VWC is opposite from the published conclusion for some of other ecosystems. For example, Tang et al.'s (2005) study of an oak-grass savanna reported that the diel variation in Rs was largely controlled by Ts. VWC had no influence on the diel Rs cycle but controlled the Rs seasonal pattern. Generally, diel variation of VWC can be small or constant over a day while Rs has an obvious diel variation (Gaumont-Guay et al., 2006). In forest ecosystems with high rainfall and high soil moisture, soil respiration may be less limited by VWC and the effect of VWC to diel Rs may be weak. In desert ecosystem, however, soil water content was usually low. Plant may suffer from water stress and be very sensitive to VWC, with leaf stomata being closed to reduce water loss when temperature was high in the midday and leading to a reduction in plant photosynthesis and root activity (Chaves et al., 2002), thus autotrophic respiration being constrained or becoming plateaued as showed in Fig. 2b. However, soil temperature in the morning was lower than air temperature, condensation water happened on the ground (Agam and Berliner, 2006), root activity being increased and inducing higher root respiration. As a result, Rs may peak in the morning when temperature was lower and become low in the midday when temperature was higher as showed in Fig. 2a. When temperature was low and VWC was high, diel variation in Rs corresponded with Ts with several hours lag (Fig. 2c). All these results strongly suggested that VWC affected the diel response of Rs to Ts in desert ecosystem. Rs peaked when Ts was low under low soil water content or when Ts was high under high soil water content. This coincided with the result that hysteresis between Rs and Ts was negatively affected by VWC.

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4.2 Seasonal R_s variation in relation to T_s and VWC

The seasonal variation in R_s was controlled primarily by T_s (Fig. 6), with secondary influence by VWC (Fig. 7). T_s explained 76 % of the variation in R_s for VWC values above $0.08 \text{ m}^3 \text{ m}^{-3}$, but was uncorrelated with R_s for VWC below $0.08 \text{ m}^3 \text{ m}^{-3}$ (Table 2). Many previous studies have reported a similar response. For example, Palmroth et al. (2005) found that R_s was dependent on both T_s and VWC when the soil was dry ($\text{VWC} < 0.20$) but depended on T_s alone when the soil was moist ($\text{VWC} > 0.20$). Jassal et al. (2008) reported that R_s became decoupled from T_s when VWC dropped below $0.11 \text{ m}^3 \text{ m}^{-3}$. The reduction in R_s with decreasing VWC mostly likely resulted from the suppression of plant growth, root and microbial activities, and the decay of soil organic matter at low VWC (Gaumont-Guay et al., 2006; Sotta et al., 2007; Jassal et al., 2008; Liu et al., 2009). Substrate availability and the diffusion of substrates and extracellular enzymes is reduced when VWC is low (Jassal et al., 2008). Unlike previous studies, however, our results do not show a distinct VWC threshold above which R_s decreased. Similar to other desert sites, the reason that the R_{sN} –VWC relationship does not show a threshold is that our site's low VWC (0.04 – $0.16 \text{ m}^3 \text{ m}^{-3}$) and high soil porosity did not restrict CO_2 transport out of soil and CO_2 production due to a lack of O_2 .

The result that bivariate R_s models, with T_s and VWC as independent variables, outperformed models with T_s only (Table 3), highlights the need to include soil moisture effects on R_s in carbon cycle models of desert ecosystems. Among bivariate models, the logistic-power model performed best, with higher R^2 and lower RMSE and AIC. This result is similar to that found for a temperate forest stand (Yu et al., 2011). Thus we recommend the use of the logistic-power model with VWC and T_s as independent variables for the estimation of soil respiration.

4.3 The response of Q_{10} to VWC

The overall Q_{10} of 1.5 from the desert shrubland in this study is at the lower end of the range of 1.25 to 1.63 from moss-dominated biological soil crusts to lichen-dominated

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biological soil crusts (He, 2012), 1.43 to 2.03 with the mean annual temperature from a global synthesis (Zhou et al., 2009), and 1.28 to 4.75 with the 5 cm depth T_s spanning alpine, temperate, and tropical ecosystems across China (Zheng et al., 2009). Among the diverse biomes in the global synthesis, deserts were found to have the lowest Q_{10} values, similar to the value in this study. The low Q_{10} values of desert shrub ecosystems result from their low soil organic matter, small microbial community, and dry soil conditions (Conant et al., 2004; Gershenson et al., 2009; Cable et al., 2011).

The negatively linear relationship between Q_{10} and T_s is consistent with many previous studies (Reichstein et al., 2003; Gaumont-Guay et al., 2006; Chen et al., 2010; Jia et al., 2013). The Q_{10} dependence on temperature may simply result from the fact that enzymatic processes respond differently over different temperature ranges. The analysis revealed a limitation in the Q_{10} model that use a fixed or universal Q_{10} value while temperature varied large range. The effects of temperature on Q_{10} should not be overlooked. Therefore, we agree with Jia's suggestion that a seasonally-varying, environmentally-controlled Q_{10} should be used for modeling short-term R_s (Jia et al., 2013).

The positive correlation between short-term Q_{10} and VWC over the seasonal cycle (Fig. 8c) agrees with previously published results (Chen and Tian, 2005; Gaumont-Guay et al., 2006; Zhang et al., 2010). Q_{10} declined from 2.5 to 1.0 with increasing drought severity in three Mediterranean evergreen stands (Reichstein et al., 2002a). Decreased Q_{10} with decreasing VWC may be due to switch in carbon pool of labile substrate to recalcitrant substrates in carbon pool being respired, or to an inactivation of the rhizosphere (Reichstein et al., 2002). The negative correlation of short-term Q_{10} with T_s and its positive correlation with VWC indicate negative feedbacks by R_s to projected climate change with rising temperature and decreasing soil moisture in desert ecosystem.

4.4 The response of diel hysteresis to VWC

Our results show a significant lag between Ts at 10 cm depth and Rs over the diel cycle, and that the lag time increased as VWC decreased. Similar lags between hourly Rs and Ts have been observed in many other ecosystems and found to vary seasonally with soil moisture (Tang et al., 2005; Gaumont-Guay et al., 2006; Riveros-Iregui et al., 2007; Vargas and Allen, 2008). The reason for the lag, however, is unclear. It may be caused by a mismatch between the depth of the Ts measurement and the depth of CO₂ production, or by a diurnal variation in the photosynthetic carbon supply which affects the rhizospheric respiration (Parkin and Kaspar, 2003; Subke et al., 2003; Xu and Qi, 2011), or attributed to the different responses of autotrophic and heterotrophic respiration to environmental factors (Riveros-Iregui et al., 2007). Autotrophic respiration responds to photosynthetically-active radiation (Liu et al., 2006) and air temperature, whereas heterotrophic respiration responds primarily to soil temperature (Lloyd and Taylor, 1994; Winkler et al., 1996). However, our finding that the lag time between Rs and Ts was negatively related to VWC is contrary to the findings of Riveros-Iregui et al. (2007).

Plant photosynthate has proven to be a factor influencing diel hysteresis between Rs and Ts (Tang et al., 2005). Photosynthate may be an explanation of diel hysteresis under relatively high soil water content as showed in Fig. 2b and c, but failed to explain that under lower soil water content as showed in Fig. 2a. We attribute the increased lag times at low VWC at our site to the decoupling of Rs from Ts when VWC is low, which reflects the sensitivity of root activity to soil water content. The timing of the diurnal Rs peak is highly sensitive to VWC, with progressively earlier peaks as the soil VWC declines. At low VWC, Rs peaks in the early morning because of root activity may strongly increased with condensation water, leading to pronounced hysteresis between Rs and Ts (Fig. 2).

Diel hysteresis between Rs and Ts was controlled by both physical and physiology effects. In desert ecosystem, we attribute the variations of the diurnal hysteresis be-

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tween Rs and Ts to biological effects (root activity and plant photosynthesis) in relation to different soil water conditions.

5 Conclusions

This study reports soil respiration measurements from a desert shrub ecosystem in northwest China, and analyzes its temporal variation in relation to soil temperature and moisture over diel and seasonal cycles. Over the diel cycle, Rs was mainly controlled by Ts, but the response of diel Rs to Ts was adjusted by soil water content, which reflected in the negative correlation between diel hysteresis and soil water content. Over the seasonal cycle, the control of Ts over Rs was modified by VWC, Rs became decoupled from Ts when VWC fell below than $0.08 \text{ m}^3 \text{ m}^{-3}$. Our results highlight the necessity for desert ecosystem carbon-cycle models to account for both temperature and moisture dependencies. At our site, the logistic-power model is suggested as a simple but effective model for desert shrub ecosystems. The positive correlation between Q_{10} and VWC indicates a potential negative feedback to climate warming, which is often associated with decreasing soil moisture in desert ecosystem.

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Table 1. Analysis of the mean monthly diel cycles of soil respiration (Rs), soil temperature at 10 cm depth (Ts), and soil water content at 10 cm depth (VWC), including Rs–Ts correlation coefficients, Rs–VWC correlation coefficients, and lag times in the Rs versus Ts diel cycles. r is the Pearson correlation coefficient. P is the significance level.

Time	Jun		Jul		Aug		Sep		Oct	
	r	P	r	P	r	P	r	P	r	P
Ts–Rs	0.488	0.016	0.629	0.010	0.338	0.106	0.634	0.001	0.491	0.015
lag time	4 h		3 h		4 h		3 h		3 h	

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Table 2. Regression parameters (a , b , c) from temperature-only models of soil respiration, based on the analysis of daily means. R_s ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), T_s ($^{\circ}\text{C}$) and VWC ($\text{m}^3 \text{ m}^{-3}$) are soil respiration, soil temperature at 10 cm depth, and soil volumetric water content at 10 cm depth, respectively. R^2 is the coefficient of determination. RMSE is the root-mean-square error. AIC is Akaike AIC criterion.

Name	Equation	VWC > 0.08 m ³ m ⁻³					VWC < 0.08 m ³ m ⁻³					Total data						
		<i>a</i>	<i>b</i>	<i>c</i>	AIC	<i>R</i> ²	RMSE	<i>a</i>	<i>b</i>	<i>c</i>	<i>R</i> ²	RMSE	<i>a</i>	<i>b</i>	<i>c</i>	AIC	<i>R</i> ²	RMSE
<i>Q</i> ₁₀	<i>R</i> _s = <i>a</i> · <i>b</i> ^{(<i>T</i>_s-10)/10}	0.69	1.9		-213.62	0.75	0.2376	0.51	1.73		0.09	0.2533	0.76	1.5		-239.28	0.36	0.3373
Quadratic	<i>R</i> _s = <i>a</i> · <i>T</i> _s ² + <i>b</i> · <i>T</i> _s + <i>c</i>	0.002	0.011	0.37	-215.09	0.76	0.237	-0.3	1.54	-18.3	0.14	0.2504	-0.001	0.1	0.01	-242.44	0.37	0.3341
Logistic	<i>R</i> _s = <i>a</i> / (1 + exp(<i>b</i> · (<i>c</i> - <i>T</i> _s)))	3.4	0.10	23.78	-215.47	0.76	0.2362	1.2	1.07	21.1	0.13	0.2515	1.56	0.2	11.8	-243.36	0.38	0.3372

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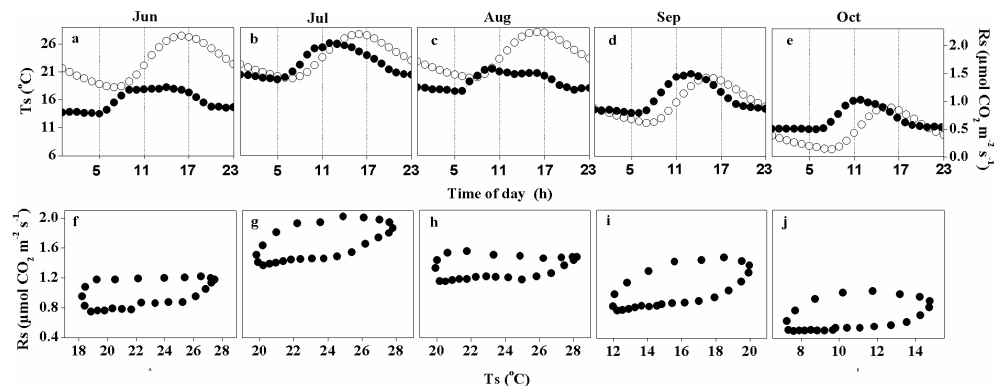


Fig. 1. Mean monthly diel cycles of soil respiration (Rs), soil temperature (Ts) and soil water content (VWC). Each point is the monthly mean for a particular time of day.

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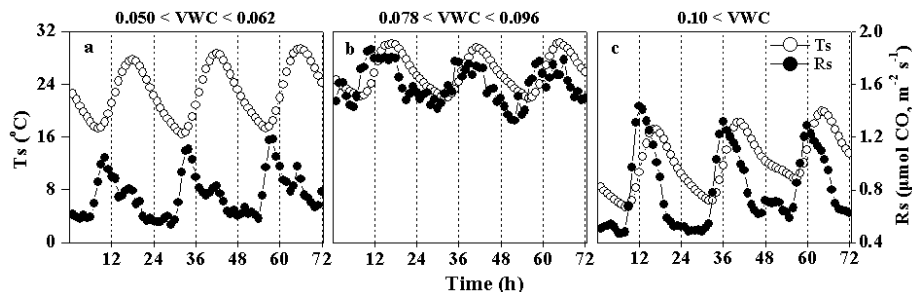


Fig. 2. Hourly soil respiration (R_s), soil temperature (T_s) and soil water content (VWC) over three continuous days under low ($0.05\text{--}0.06\text{ m}^3\text{ m}^{-3}$), moderate ($0.08\text{--}0.10\text{ m}^3\text{ m}^{-3}$), and high VWC ($0.10\text{--}0.11\text{ m}^3\text{ m}^{-3}$) conditions.

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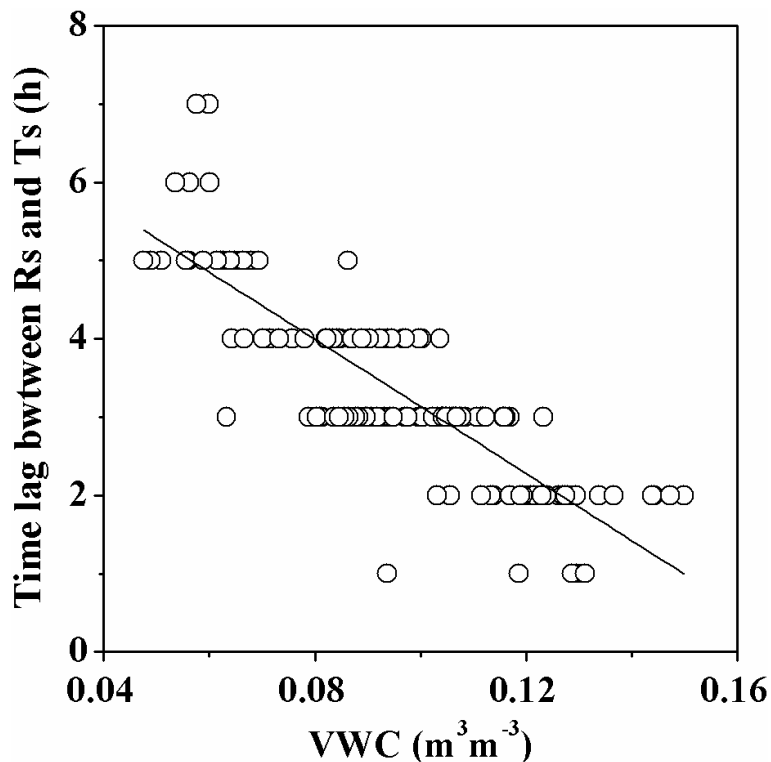


Fig. 3. Lag time between soil respiration and soil temperature over the diel cycle, in relation to soil volumetric water content (VWC) at 10 cm soil depth. The lag times were calculated by a cross-correlation analysis using a three-day moving window with one-day step. The solid line is fitted using linear regression.

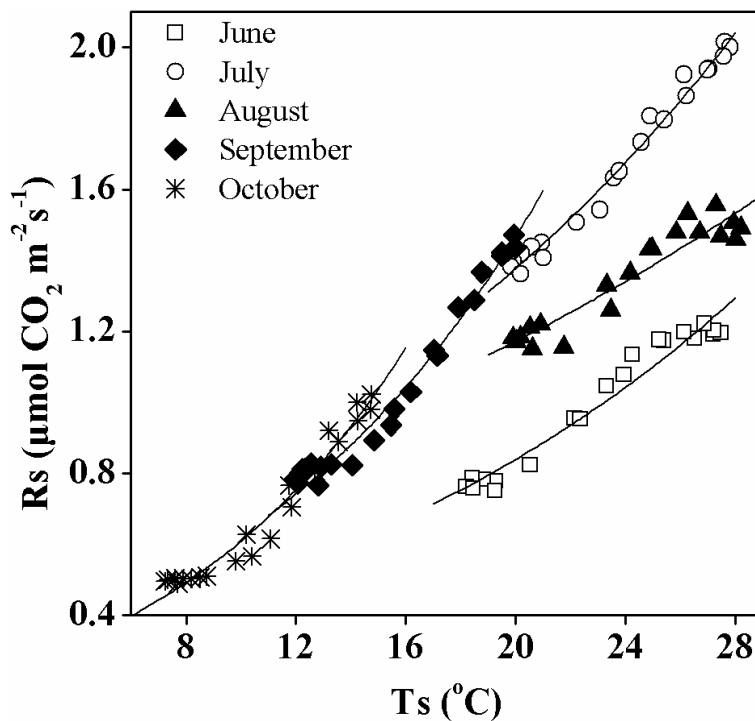


Fig. 4. Mean monthly diel cycles of R_s and T_s (from Fig. 1), but replotted in relation to each other. The solid line is fitted by the Q_{10} model.

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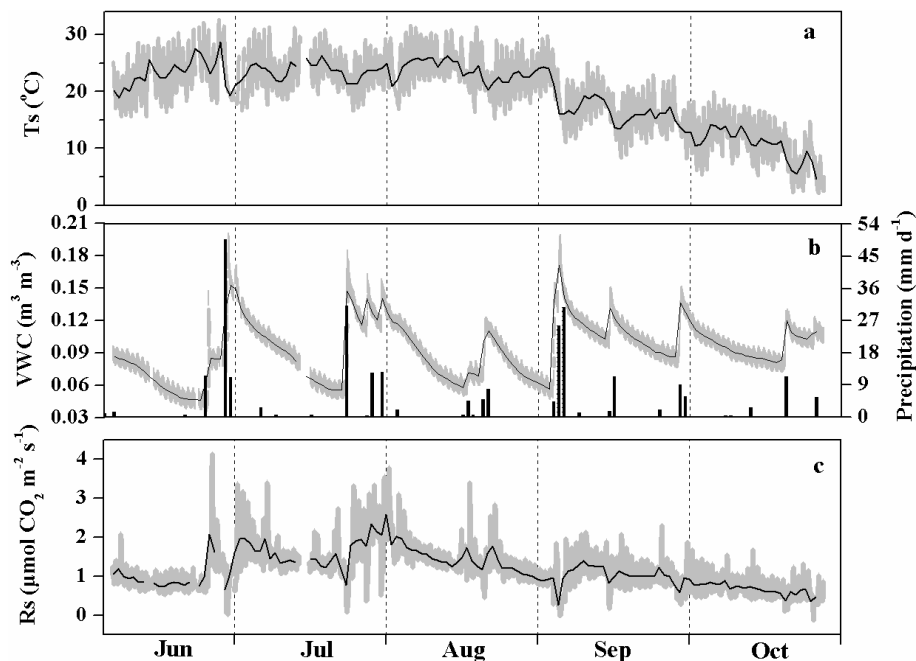


Fig. 5. Seasonal cycles of soil temperature (Ts), soil water content (VWC), precipitation, and soil respiration (Rs). Ts and VWC were measured at 10 cm depth. Hourly values are plotted in light grey; the solid line is the daily mean. The precipitation bar plot shows the daily totals.

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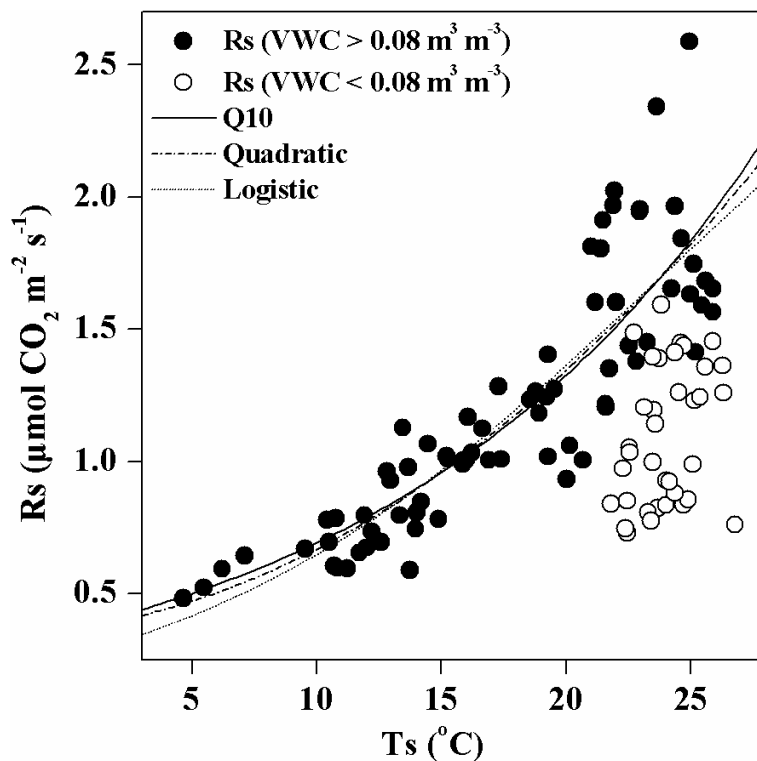


Fig. 6. Relationship between daily mean soil respiration (R_s) and soil temperature (T_s). The lines were fitted using the Q_{10} , quadratic, and logistic models.

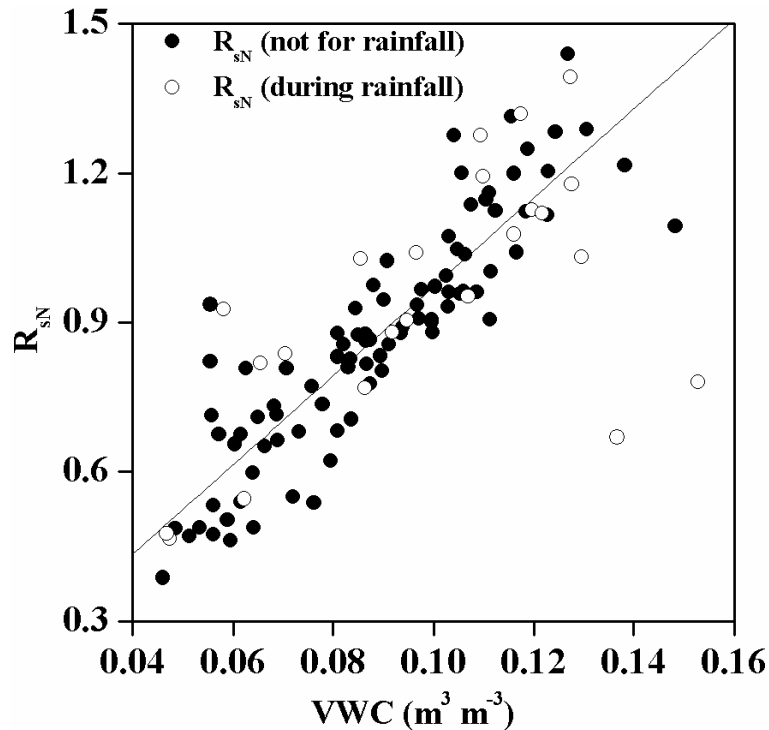


Fig. 7. Relationship between normalized daily mean soil respiration (R_{sN}) and soil water content (VWC). R_{sN} is the ratio of the observed R_s value to the value predicted by the logistic model. The solid line is fitted using linear regression.

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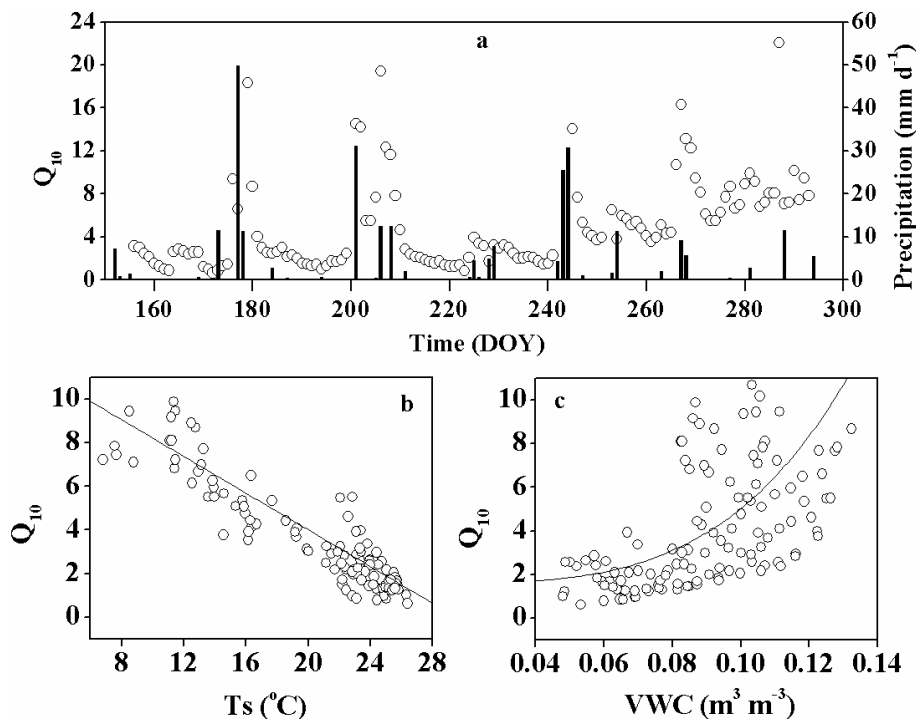


Fig. 8. Short-term Q_{10} as a function of (a) day of year, (b) soil temperature (T_s) and (c) soil water content (VWC). The Q_{10} values were derived by fitting the Q_{10} model to synchronized data using a three-day moving window with a one-day step. T_s and VWC are three-day means.

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