



# Soil water regulates the control of photosynthesis on diel hysteresis between soil respiration and temperature

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**Abstract.** Causes for diel hysteresis between soil respiration ( $R_s$ ) and temperature remain highly controversial. Explanations for the occurrence of hysteresis have involved both biological and physical mechanisms. The specifics of these explanations, however, tend to vary with the particular ecosystem or biome being studied. This study examined the seasonal variation in diel hysteresis and its controlling factors in a desert-shrub ecosystem in northwest (NW) China. The study was based on continuous measurements of  $R_s$ , air temperature ( $T_a$ ), soil temperature at the surface and below ( $T_{surf}$  and  $T_s$ ), volumetric soil water content (SWC), and photosynthesis over a year 2013. Trends in diel  $R_s$  were observed to vary with SWC over the growing season. Diel variations in  $R_s$  were more closely associated with  $T_{surf}$  than with photosynthesis as SWC increased, leading to  $R_s$  being in phase with  $T_{surf}$ , particularly when  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ . However, as SWC decreased below  $0.08 \text{ m}^3 \text{ m}^{-3}$ , diel variations in  $R_s$  were more closely related to variations in photosynthesis, leading to a pronounced diel hysteresis and asynchronicity between  $R_s$  and  $T_{surf}$ . It was indicated that SWC regulates the relative control between photosynthesis and temperature on diel  $R_s$  by changing the relative contribution of autotrophic and heterotrophic respiration to total  $R_s$ , and thus, causing seasonal variation in diel hysteresis between  $R_s$  and temperature. Our findings highlight the importance of biologically-based mechanisms and the role of SWC in regulating diel hysteresis between  $R_s$  and temperature.

## 1 Introduction

Diel hysteresis (asynchronicity) between soil respiration ( $R_s$ ) and soil temperature ( $T_s$ ) is widely documented for forests (Tang et al., 2005; Gaumont-Guay et al., 2006; Riveros-Iregui et al., 2007; Vargas and Allen, 2008; Jia et al., 2013), grasslands (Carbone et al., 2008; Barron-Gafford et al., 2011), and desert ecosystems (Wang et al., 2014; Feng et al., 2014). Diel hysteresis, which appears as an elliptical loop in the relationship between  $R_s$  and  $T_s$ , is difficult to model with theoretical



functions, such as with the  $Q_{10}$ , Lloyd-Taylor, Arrhenius, or van't Hoff functions (Lloyd and Taylor, 1994; Winkler et al., 1996; Davidson et al., 2006; Phillips et al., 2011; Oikawa et al., 2014). Diel hysteresis is also not currently addressed in the  $Q_{10}$  function for low soil water conditions, leading to a poor understanding of temperature-sensitivity in  $R_s$  (Gaumont-Guay et al., 2008; Phillips et al., 2011; Darenova et al., 2014). Therefore, in order to accurately predict soil  $\text{CO}_2$  fluxes and their responses to climate change, it is necessary to understand the biophysical mechanisms that control the variation in diel hysteresis.

Over decades of research, two main lines of reasoning have been proposed to explain the causes of diel hysteresis between  $R_s$  and  $T_s$ . One is based on the physical processes of heat and gas transport in soils (Vargas and Allen, 2008; Phillips et al., 2011; Zhang et al., 2015). Soil  $\text{CO}_2$  production is an integrated response to a non-uniform  $T_s$  profile (e.g., 0-1 m) at discrete soil depths (e.g., 5 cm, 10 cm), thus  $T_s$  used in models is likely different in both magnitude and phase from the average  $T_s$ , which is involved in forcing soil  $\text{CO}_2$  production (Phillips et al., 2011). However, in recent years, a second line of reasoning has emerged, which puts more importance on the role of biological initiators associated with photosynthate supply (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011; Wang et al., 2014). Aboveground photosynthesis, which usually peaks at midday (e.g., 11:00-13:00), provides substrate for belowground roots and rhizosphere-microbe respiration, but oscillates out of phase with  $T_s$ , which usually peaks in the afternoon (e.g., 14:00-16:00). These studies point out that it is necessary to take photosynthesis into consideration for a more accurate interpretation of  $R_s$  (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011). In addition, both physical and biological processes are not mutually exclusive and both likely play important roles in affecting diel variation in  $R_s$  (Phillips et al., 2011; Zhang et al., 2015; Song et al., 2015). Currently, the causes of diel hysteresis between  $R_s$  and temperature remain largely unexplained.

Diel hysteresis between  $R_s$  and  $T_s$  has been shown to vary seasonally with soil water content ( $SWC$ ; Tang et al., 2005; Riveros-Iregui et al., 2007; Carbone et al., 2008; Vargas and Allen, 2008; Ruehr et al., 2009; Wang et al., 2014). However, the influences of  $SWC$  on diel hysteresis are not consistent, and the mechanisms behind the influence of  $SWC$  on diel hysteresis remain also largely unexplained. Some studies have reported that high  $SWC$  tends to block  $\text{CO}_2$  gas and thermal diffusion, resulting in large hysteresis loops (Riveros-Iregui et al., 2007; Zhang et al., 2015). In contrast, other studies have reported low  $SWC$  and high vapour pressure deficits ( $VPD$ ) promote partial stomata closure, which leads to higher photosynthesis in the morning (e.g., 9:00-10:00) and suppressed photosynthesis in mid-afternoon, leading to pronounced diel hysteresis during dry periods (Tang et al., 2005; Vargas and Allen, 2008; Carbone et al., 2008; Wang et al., 2014). To understand the causes of diel hysteresis, it is clear that the role of  $SWC$  needs to be considered.

Drylands cover a quarter of the earth's land surface and play an important role in the global carbon (C) cycle (Safriel and Adeel, 2005; Austin, 2011; Poulter et al., 2014). However, compared to forest ecosystems, few previous studies address soil respiration dynamics in drylands. Many studies in forest ecosystems are based on the application of physical soil  $\text{CO}_2$  and heat transport models and evaluate the influences of  $SWC$  on  $\text{CO}_2$  gas and thermal diffusion (Riveros-Iregui et al., 2007; Phillips et al., 2011; Zhang et al., 2015) and, in general, conclude that diel hysteresis can result from physical processes



alone. In comparison, few previous studies have evaluated the causes of diel hysteresis in drylands. Currently, it is not clear whether physical or biological processes (or their combination) dominate the control of diel hysteresis in drylands.

Drylands are characterized with low productivity and as weak organic C storage pools (West et al., 1994; Lange, 2003), which may result in large contributions of autotrophic production of  $\text{CO}_2$  (increasing  $R_s$ ) in drylands. Autotrophic components to  $R_s$  occurs as a direct consequence of root respiration, which has been shown to be firmly coupled (within several hours) to recent photosynthesis (Liu et al., 2006; Baldocchi et al., 2006; Höglberg and Read, 2006; Bahn et al., 2009; Kuzyakov and Gavrichkova, 2010). Therefore, biologically photosynthesis-related processes may dominate the control of the asynchronicity between  $R_s$  and  $T_s$  in drylands. In drylands, especially in desert ecosystems characterized by sandy soils, high soil porosity, likely minimizes the influence of  $\text{SWC}$  on gas diffusion. In addition, water is the primary driver of biological activity in drylands (Noy-Meir, 1973). Under drought conditions, stomata closure in plants at midday reduces water losses, resulting in a suppression of photosynthesis (Jia et al., 2014). Such changes in diel patterns of photosynthesis likely result in modification of diel patterns in  $R_s$ , leading to hysteresis between  $R_s$  and  $T_s$ . Soil water content likely regulates photosynthesis-related processes and, in doing so, causes hysteresis between  $R_s$  and  $T_s$  to vary over the growing season.

In this study, we hypothesize that: (1) photosynthesis-related processes have a role in controlling hysteresis between  $R_s$  and  $T_s$ ; and (2)  $\text{SWC}$  regulates the control of photosynthesis-related processes on hysteresis and its variation over the growing season. The main objectives of this research were to: (1) investigate seasonal variation in diel hysteresis between  $R_s$  and  $T_s$ ; (2) explore the causes that lead to variation in diel hysteresis; and (3) understand how  $\text{SWC}$  influences diel hysteresis. To undertake this work, we measured  $R_s$ ,  $\text{SWC}$ ,  $T_s$ , and photosynthesis continuously in a desert-shrub ecosystem over a year 2013.

## 2 Materials and Methods

### 2.1 Site description

The study was conducted at Yanchi Research Station of Beijing Forestry University, Ningxia, northwest China ( $37^\circ 42' 31''$  N,  $107^\circ 13' 37''$  E, 1550 m a.s.l.). The station is located at the southern edge of the Mu Us desert in the transition between the arid and semi-arid climatic zones. Based on 51 years of data (1954-2004) from the Meteorological Station at Yanchi, the mean annual air temperature at the station was  $8.1^\circ\text{C}$  and the mean annual total precipitation was 292 mm (ranging between 250 to 350 mm), 63% of which fell in late summer (i.e., July-September; Wang et al., 2014; Jia et al., 2014). Radiation and evaporative demand were high at the station, i.e., annual incoming shortwave radiation was  $1.4 \times 10^5 \text{ MJ m}^{-2}$  and annual potential evaporation was on average  $5.5 \times 10^3 \text{ kg m}^{-2} \text{ d}^{-1}$ . The soil at the research station was of a sandy type, with a bulk density of  $1.6 \text{ g cm}^{-3}$ . Soil organic matter, soil nitrogen, and pH were  $0.21\text{--}2.14 \text{ g kg}^{-1}$ ,  $0.08\text{--}2.10 \text{ g kg}^{-1}$ , and  $7.76\text{--}9.08$ , respectively (Wang et al., 2014; Jia et al., 2014). The vegetation was regenerated from aerial seeding that took place in 1998



and is currently dominated by a semi-shrub species, *Artemisia ordosica*, averaging about 50 cm tall with a canopy size of about 80 cm × 60 cm (for additional details, see Jia et al. 2014 and Wang et al. 2014 and 2015).

## 2.2 Soil respiration and photosynthesis measurement

Two permanent polyvinyl chloride soil collars were initially installed on a small fixed sand dune in March, 2012. The collars were 20.3 cm in diameter and 10 cm in height, with 7 cm inserted into the soil. One collar was set on bare land with an opaque chamber (LI-8100-104, Nebraska, USA) and the other over an *Artemisia ordosica* plant (~10 cm tall) with a transparent chamber (LI-8100-104C). Soil respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) was directly estimated from  $\text{CO}_2$ -flux measurements obtained with the opaque-chamber system. Photosynthetic rates ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) of the selected plants were determined as the difference in  $\text{CO}_2$  fluxes between the transparent- and the opaque-chamber.

Continuous measurements of  $\text{CO}_2$  fluxes ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) were made *in situ* over an entire year with a Li-8100  $\text{CO}_2$  gas analyzer and a LI-8150 multiplexer (LI-COR, Nebraska, USA) connected to each chamber. Instrument maintenance was carried out bi-weekly during the growing season, including removing plant-regrowth in the opaque-chamber installation, and cleaning to avoid blackout conditions associated with the transparent-chamber installation. Measurement time for each chamber was 3 minutes and 15 seconds, including a 30-second pre-purge, 45-second post purge, and 2-minute measurement period. The  $\text{CO}_2$ -flux data collected over 2013 were used in our analysis, after an initial period of site disturbance stabilization from March, 2012 to June, 2012.

## 2.3 Measurements of temperatures, soil water content and other environmental factors

Hourly soil temperature ( $T_s$ , °C) and volumetric soil water content ( $\text{SWC}$ ,  $\text{m}^3 \text{ m}^{-3}$ ) at a 10-cm depth were measured simultaneously about 10 cm from the chambers using a LI-8150-203 temperature sensor and  $\text{EC}_{\text{H}_2\text{O}}$  moisture sensor (LI-COR, Nebraska, USA; see Wang et al., 2014). Other environmental factors were recorded every half hour using sensors mounted on a 6-m-tall flux tower approximately 800 m from our soil  $\text{CO}_2$ -flux measurement site. Air temperature ( $T_a$ , °C) was measured with a thermohygrometer (HMP155A, Vaisala, Finland). Soil surface temperature ( $T_{\text{surf}}$ , °C) was measured with an infrared-emission sensor (Model SI-111, Campbell Scientific Inc., USA). Incident photosynthetically active radiation ( $\text{PAR}$ ) was measured with a light-quantum sensor (PAR-LITE, Kipp and Zonen, the Netherlands) and precipitation ( $\text{PPT}$ , mm), with three tipping-bucket raingauges (Model TE525MM, Campbell Scientific Inc., USA) placed 50 m from the flux tower (see Jia et al., 2014).

## 2.4 Data processing and statistical analysis

In this study, the  $Q_{10}$  function (e.g., Eq. (1)) is used to describe the response of  $R_s$  to temperature. The response of  $R_s$  to changes in photosynthesis is characterized by a linear function (Eq. (2)). Correlation coefficient, magnitude of hysteresis, and model performance are used to evaluate whether photosynthesis or temperature dominate diel  $R_s$ . Relative importance



(*RI*) of temperature and photosynthesis in defining  $R_s$  over the growing season was calculated with a ratio of  $\rho_p : \rho_t$  (Eq. (3)), where  $\rho_p$  is the correlation coefficient between photosynthesis and  $R_s$ , and  $\rho_t$  is the correlation coefficient between temperature and  $R_s$ . The greater the *RI*-value, the more important photosynthesis is to  $R_s$ .

$$R_s = R_{10} \times Q_{10}^{(T-10)/10} \quad (1)$$

$$R_s = a \times P + b \quad (2)$$

$$RI = \frac{\rho_p}{\rho_t} \quad (3)$$

where  $R_{10}$  is the respiration at 10°C,  $Q_{10}$  is the temperature sensitivity of respiration,  $T$  is temperature, and  $P$  is photosynthesis ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), with  $a$  and  $b$  as regression coefficients.

Measurements of  $\text{CO}_2$  fluxes were screened by means of limit checking, i.e., hourly  $\text{CO}_2$ -flux data  $< -30$  or  $> 15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  were considered to be anomalous as a result of, for instance, gas leakage or insect assault and immediately removed from the dataset (Wang et al., 2014, 2015). After limit checking, hourly  $\text{CO}_2$  fluxes greater than three times the standard deviation from the calculated mean of 5 days' worth of flux data were also removed. Quality control and instrument failure together resulted in 5% loss of hourly fluxes for all chambers, 4% for temperatures, and 8% for *SWC* (Fig. 1).

Pearson correlation analysis was used to calculate the correlation coefficient between temperature or photosynthesis and  $R_s$ . Cross-correlation analysis was used to estimate hysteresis in temperature- $R_s$  and photosynthesis- $R_s$  relationships. We used root mean squared error (*RMSE*) and the coefficient of determination ( $R^2$ ) as criteria in evaluating model performance. To evaluate seasonal variation in diel hysteresis, the mean monthly diel cycles of  $R_s$ ,  $T_a$ ,  $T_{surf}$ ,  $T_s$ , and photosynthesis were calculated by averaging their hourly means at a given hour over a particular month (Table 1). Exponential and linear regression was used to evaluate influence of *SWC* on the control of photosynthesis over temperature- $R_s$  hysteresis. Further on, influences of *SWC* on diel hysteresis was examined in a wet month with highest rainfall and adequate *SWC* (July, *PPT* = 117.9 mm) and a dry month with low rainfall and inadequate *SWC* (August, *PPT* = 10.9 mm) during the growing season (see Wang et al., 2014). All statistical analyses were performed in MATLAB, with a significance level of 0.05 (R2010b, Mathworks Inc., Natick, MA, USA).

### 3 Results

#### 3.1 Diel patterns of soil respiration, photosynthesis, and environmental factors

Incident photosynthetically active radiation,  $T_a$ ,  $T_{surf}$ , and  $T_s$  showed clear and stable diel patterns over the year (Fig. 1a-d), peaking at ~12:00 PM (Local Time, LT), ~16:00 PM, ~14:00 PM, and ~17:00 PM, respectively (Fig. 1a-d). Unlike environmental factors, diel patterns in  $R_s$  remained stable over the non-growing season, peaking at 11:00 AM-13:00 PM, and being highly variable during the growing season, peaking between 10:00 AM-16:00 PM (Fig. 1f). Similar to  $R_s$  during the



growing season, diel patterns of photosynthesis were also highly variable, peaking between 10:00 AM-16:00 PM (Fig. 1e). Diel patterns of monthly mean  $R_s$  were similar to  $T_{surf}$  during the wet month and similar to photosynthesis during the dry month (Fig. 2g, h).

### 3.2 Relative control of photosynthesis and temperature on diel soil respiration

5 Among temperatures at the three soil depths,  $T_{surf}$  correlated best with diel  $R_s$ , due to the high  $R^2$ 's with monthly mean diel  $R_s$  throughout the year (Table 1). Over the growing season, monthly mean diel  $R_s$  was also significantly correlated with photosynthesis (Table 1). The response of  $R_s$  to temperature and photosynthesis was affected by SWC during the growing season (Table 2; Fig. 3). During the wet month (July) with precipitation of 117.9 mm,  $T_{surf}$  alone explained 97% of the variation in diel  $R_s$  ( $Q_{10}$  function), whereas photosynthesis explained 67% of it (Fig. 3a, Table 2). However, during the dry  
 10 season with precipitation of 10.9 mm, photosynthesis explained 88% of the variation in diel  $R_s$ , (by way of Eq. (2), whereas  $T_{surf}$  explained 76% of it (Fig. 3b, Table 2). Over the growing season,  $RI$  of photosynthesis and temperature on  $R_s$  was significantly affected by SWC (Fig. 4), and decreased with increasing SWC.

### 3.3 Effects of soil water content on diel hysteresis in temperature- $R_s$ relationship

Diel hysteresis in both  $T_{surf}$ - $R_s$  and photosynthesis- $R_s$  relationships were affected by SWC (Fig. 5). In the wet month (July),  
 15 monthly mean diel  $R_s$  was out of phase with photosynthesis, but in phase with  $T_{surf}$  (Fig. 2g). Soil respiration peaked at 16:00 PM, being very similar timing to that of  $T_{surf}$  (i.e., 15:00 PM), but four hours later than photosynthesis (peaking at 12:00 PM; Fig. 2g). In the dry month (August), however, diel  $R_s$  was in phase with photosynthesis, but out of phase with  $T_{surf}$  (Fig. 2h). Both photosynthesis and  $R_s$  plateaued between 10:00 AM-16:00 PM, whereas  $T_{surf}$  peaked at 15:00 PM (Fig. 2h). Over the  
 20 growing season, the diel hysteresis between  $R_s$  and  $T_{surf}$  was linearly related to SWC when  $SWC < 0.08 \text{ m}^3 \text{ m}^{-3}$  (Fig. 5a). No hysteresis was observed when  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$  (Fig. 5a). In contrast, diel hysteresis between  $R_s$  and photosynthesis was linearly related to SWC, when  $SWC < 0.08 \text{ m}^3 \text{ m}^{-3}$  (Fig. 5b), but ceased to be related, when  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$  ( $p = 0.439$ ; Fig. 5b).

## 4 Discussion

### 4.1 Physical- vs. biological-processes in the control of diel hysteresis

25 In our study, we found that the diurnal pattern in temperature ( $T_a$ ,  $T_{surf}$ , and  $T_s$ ) lagged behind that in  $R_s$  by several hours, which resulted in a counter-clockwise loop in the relationship between  $R_s$  and temperature. Although the magnitude of diel hysteresis between  $R_s$  and temperature differed among the three soil depths, their seasonal variation was generally consistent. Among the temperatures measured at the three depths,  $T_{surf}$  was more closely related to diel  $R_s$ , resulting in weaker hysteresis.



The magnitude of hysteresis between  $R_s$  and  $T_{surf}$  was in our study comparable to those in other plant systems, e.g., 3.5-5 h in a boreal aspen stand (Gaumont-Guay et al., 2006) and 0-5 h in a Chinese pine plantation (Jia et al., 2013).

Contradictory results exist on the effects of  $SWC$  on hysteresis between  $R_s$  and temperature. Some studies have reported that the greatest diel hysteresis in temperature and  $R_s$  occurs during dry months (Tang et al., 2005; Vargas and Allen, 2008; Carbone et al., 2008; Wang et al., 2014), which is consistent with our finding. Whereas, some studies have reported strong hysteresis-loops under high  $SWC$  (Riveros-Iregui et al., 2007; Zhang et al., 2015). These contrasting findings may be a result of differences in soil properties and biophysical processes. In montane-conifer forests (Riveros-Iregui et al., 2007) and pine plantations (Zhang et al., 2015), dense soils have a greater influence on within-soil gas transport, resulting in physical aspects of the soil having a greater control on diel hysteresis. High  $SWC$  tends to block gas transport, leading to larger hysteresis than under low  $SWC$ . However, sandy soils with high soil porosity, as on our site, have a minor influence on within-soil gas transport processes. As a result of this, biological processes become more important in controlling diel hysteresis. During dry months of the growing season, low  $SWC$  causes stomata closure (Tang et al., 2005; Vargas and Allen, 2008; Carbone et al., 2008; Jia et al., 2014; Wang et al., 2014), suppressing photosynthesis (Fig. 2). Diel  $R_s$  followed diel photosynthesis under low  $SWC$ , resulting in a large hysteresis between  $R_s$  and temperature (Fig. 2). Our results confirm the important role of biological processes in regulating diel hysteresis which has been suggested also in many previous studies (Högberg et al., 2001; Tang et al., 2005; Sampson et al., 2007; Kuzyakov and Gavrichkova, 2010; Mencuccini and Hölttä 2010). It also, thus is consistent with our first hypothesis.

#### 4.2 Causes and the influences of soil water content on seasonal variation in diel hysteresis

In our study, diel  $R_s$  varied consistently with  $T_{surf}$ , and no observable hysteresis was found when  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ . However, as  $SWC$  decreased from this value, diel  $R_s$  varied more closely with photosynthesis, leading to increased diel hysteresis between  $R_s$  and  $T_{surf}$ . These results suggest that  $SWC$  regulated the relative control of photosynthesis and temperature on diel  $R_s$  over the growing season, supporting our second hypothesis.

Possible reason for  $SWC$  regulation might be associated with changes in the relative contribution of autotrophic and heterotrophic respiration to total  $R_s$  in response to rainfall-induced changes in  $SWC$ . In our study, the periods with  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$  only lasted several days (Fig. 1g, h). Resource pool accumulation on the soil surface may have resulted from microbial growth and nutrient mineralization between successive precipitation events (Fisher et al., 1987). Most organic matter and microbes tend to concentrate in the upper part of the soil, whereas plant roots are found much deeper. Consequently, wet periods with  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$  drive heterotrophic activity, but not enough or long enough to elicit autotrophic activity (Sponseller 2007; Song et al., 2015), leading to a higher relative contribution of heterotrophic respiration to total  $R_s$ . Heterotrophic respiration has been reported to respond primarily to soil surface temperature (Lloyd and Taylor, 1994; Winkler et al., 1996). Therefore, diel  $R_s$  co-varied much more strongly with  $T_{surf}$ , eliminating hysteresis altogether when  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ . By contrast, dry periods with  $SWC < 0.08 \text{ m}^3 \text{ m}^{-3}$  often occurred between successive precipitation



events (Fig. 1g, h). Heterotrophic respiration was observed to be largely suppressed during these periods (Borken et al., 2006), giving opportunity for autotrophic respiration to contribute to total  $R_s$ . Since root respiration has been reported to be firmly associated with photosynthesis (Liu et al., 2006; Baldocchi et al., 2006; Höglberg and Read, 2006; Kuzyakov and Gavrihkova, 2010), it is not surprising that  $R_s$  is seen to co-vary with photosynthesis during dry periods. Although we could not directly show changes in relative contribution between autotrophic and heterotrophic respiration to total  $R_s$ , the changes in relative correlation and diel patterns during the dry and wet months could be used to indirectly confirm our inference. Casals et al. (2011) reported that the ratio of autotrophic components increased in response to drought, increasing the influence of recent photosynthate supply to  $R_s$  during drought, which is also consistent with our finding.

Our work provides urgently needed new knowledge concerning causes/mechanisms involved in defining variation in diel hysteresis in desert-shrub ecosystems. Based on our work, we suggest that diel photosynthesis should be considered in simulations of diel  $R_s$  in drylands, especially when  $SWC$  falls below  $0.08 \text{ m}^3 \text{ m}^{-3}$ . This information would be particularly useful when processing ecosystem fluxes obtained with eddy covariance measurements, rather than rely on relating daytime simulations of  $R_s$  to night-time respiration-temperature relationships. This would involve more complex, iterative methods than are currently used because of the implied feedback.

## 5 Conclusions

Soil water content regulated the relative control between photosynthesis and temperature on diel  $R_s$  by changing the relative contribution of autotrophic and heterotrophic respiration to total  $R_s$ , causing seasonal variation in diel hysteresis between  $R_s$  and temperature. Hysteresis was not observed between  $R_s$  and  $T_{surf}$ , when  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ , but lag-hours increased between the co-variation in the variables as  $SWC$  decreased below this threshold. Our findings highlight the importance of biological mechanisms in diel hysteresis between  $R_s$  and temperature and the importance of  $SWC$  in plant photosynthesis-soil respiration dynamics in dryland ecosystems.

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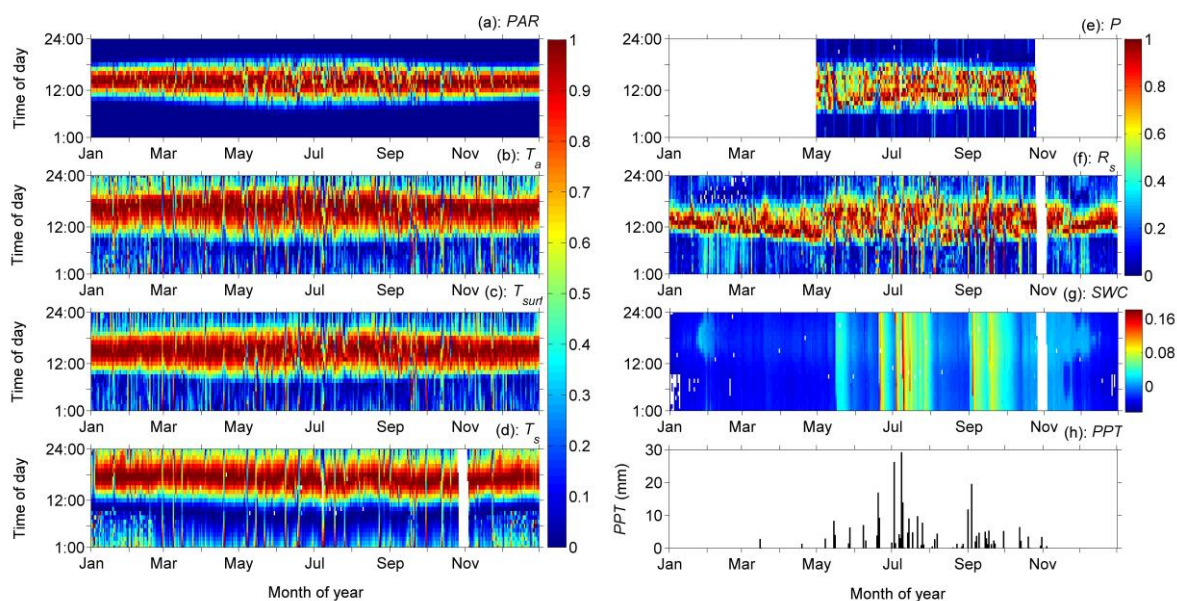
**Table 1.** Analysis of mean monthly diel cycles of soil respiration ( $R_s$ ), air temperature ( $T_a$ ), soil surface temperature ( $T_{surf}$ ), soil temperature at a 10-cm depth ( $T_s$ ), and photosynthesis ( $P$ ) in a dominant desert-shrub ecosystem, including correlation coefficients and lag times in  $R_s$  vs.  $T_a$ ,  $T_{surf}$ ,  $T_s$ , and  $P$  cycles. Pearson's correlation coefficients ( $r$ ) that are significant (i.e.,  $p < 0.05$ ) are denoted in bold.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
$R_s$ - $T_a$	Lag	2	4	3	3	1	1	1	2	1	1	1	1
	$r$	<b>0.64</b>	0.25	<b>0.49</b>	<b>0.46</b>	<b>0.85</b>	<b>0.85</b>	<b>0.93</b>	<b>0.76</b>	<b>0.94</b>	<b>0.89</b>	<b>0.78</b>	<b>0.77</b>
$R_s$ - $T_{surf}$	Lag	1	2	2	2	0	0	0	1	0	0	1	1
	$r$	<b>0.82</b>	<b>0.57</b>	<b>0.75</b>	<b>0.72</b>	<b>0.96</b>	<b>0.96</b>	<b>0.98</b>	<b>0.87</b>	<b>0.98</b>	<b>0.97</b>	<b>0.89</b>	<b>0.87</b>
$R_s$ - $T_s$	Lag	4	5	5	5	3	3	2	4	2	2	4	4
	$r$	-0.06	-0.31	-0.06	-0.07	<b>0.54</b>	<b>0.58</b>	<b>0.80</b>	0.31	<b>0.77</b>	<b>0.65</b>	0.23	0.12
$R_s$ - $P$	Lag					-1	-1	-2	0	-1	-1		
	$r$					<b>0.84</b>	<b>0.83</b>	<b>0.82</b>	<b>0.94</b>	<b>0.86</b>	<b>0.88</b>		

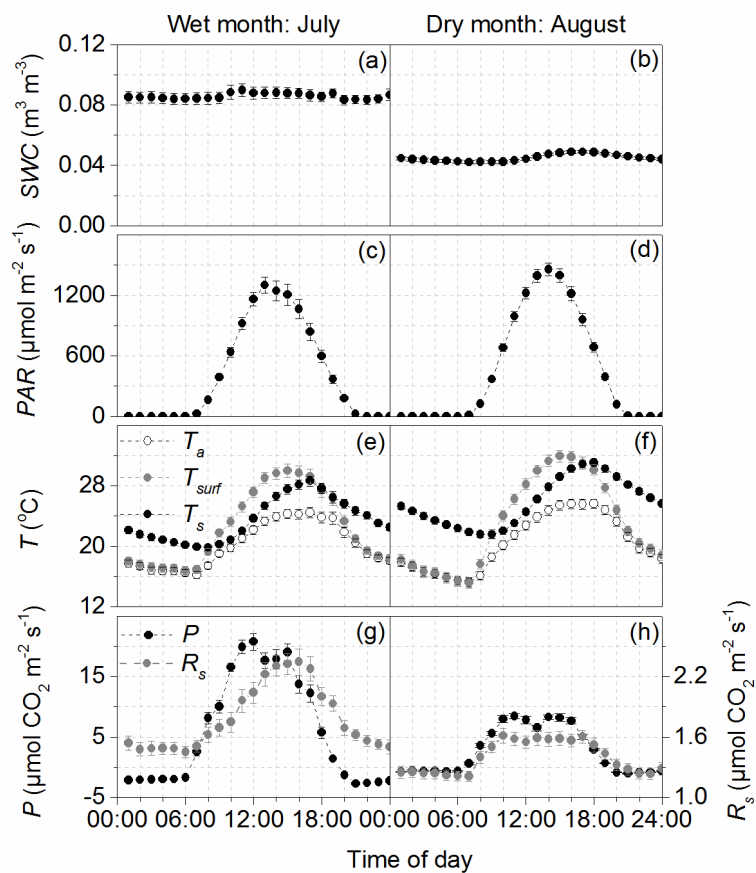


**Table 2.** Regressions based on the  $Q_{10}$  and linear models of soil respiration ( $R_s$ ) for a wet and a dry month. Variables  $T_{surf}$  ( $^{\circ}\text{C}$ ) refers to the soil surface temperature;  $P$  photosynthesis in the dominant shrub layer;  $R^2$  the coefficient of determination; and  $RMSE$  the root mean squared error.

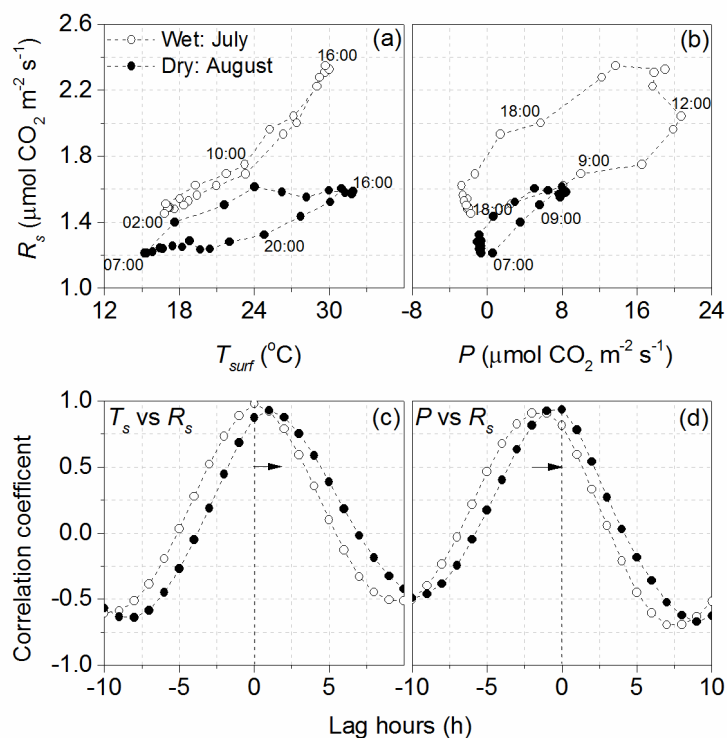
Model		Wet month: July	Dry month: August
$T_{surf} \sim R_s$	$Q_{10}$	$R_s = 1.13 \times 1.4^{\frac{T_{surf}-10}{10}}$	$R_s = 1.12 \times 1.1^{\frac{T_{surf}-10}{10}}$
		$R^2 = 0.97$	$R^2 = 0.76$
		$RMSE = 0.0521$	$RMSE = 0.0796$
$P \sim R_s$	Linear	$R_s = 0.03 \times P + 1.61$	$R_s = 0.04 \times P + 1.29$
		$R^2 = 0.67$	$R^2 = 0.88$
		$RMSE = 0.1889$	$RMSE = 0.05752$



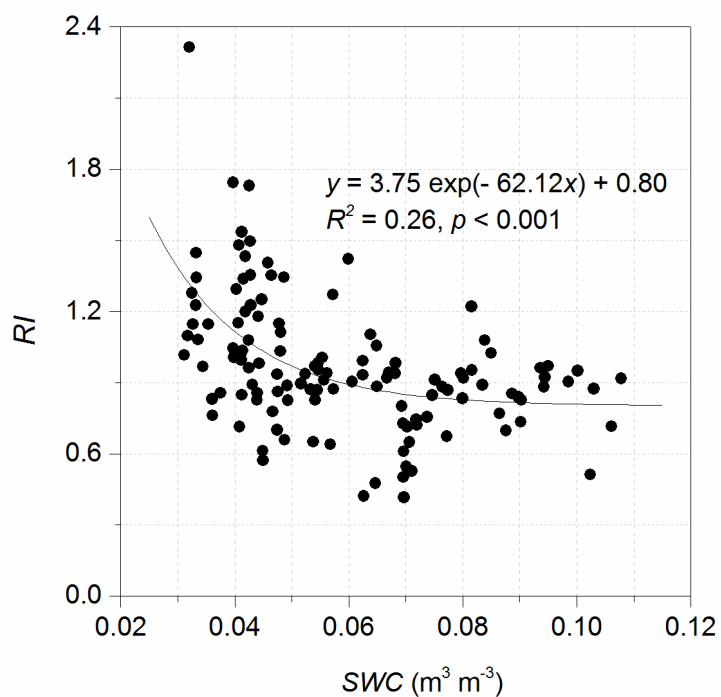
**Figure 1.** Seasonal variation in incident photosynthetically active radiation ( $PAR$ ), temperature [i.e., air temperature ( $T_a$ ), soil surface temperature ( $T_{surf}$ ), soil temperature ( $T_s$ )], photosynthesis ( $P$ ), and soil respiration ( $R_s$ ) in *Artemisia ordosica*, and seasonal variation in soil water content ( $SWC$ ) and precipitation ( $PPT$ ) for 2013. Hourly  $PAR$ ,  $T_a$ ,  $T_{surf}$ ,  $T_s$ ,  $R_s$ , and  $P$  are normalized against all values for each day. Each hourly value (y-axis) for each day (x-axis) is shown as a value of 1 through 0; 1 denotes the peak value for the day and 0, the daily minimum.



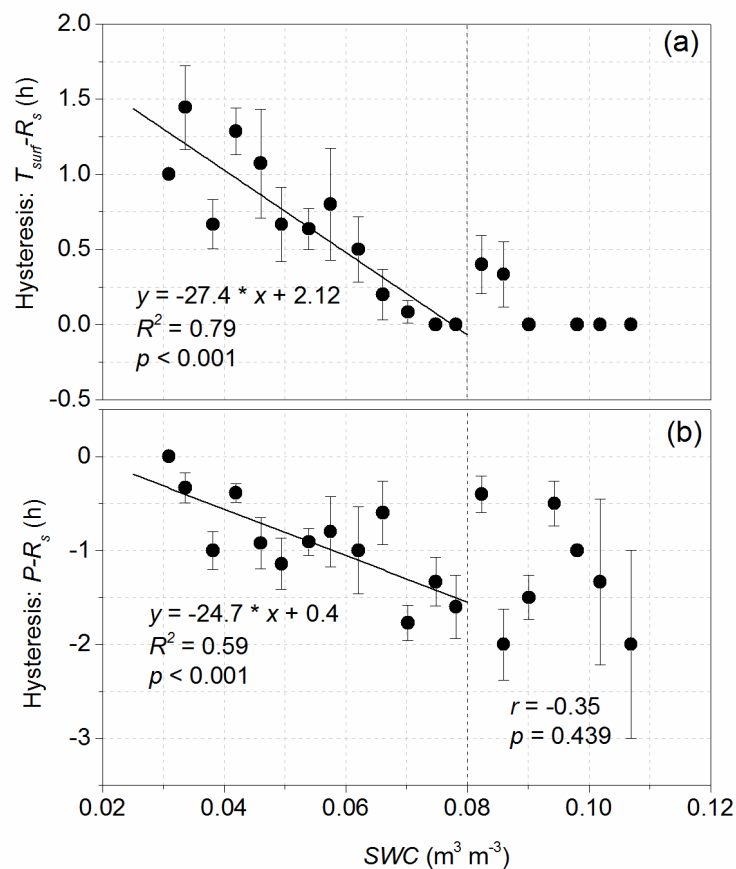
**Figure 2.** Mean monthly diel cycle of soil water content (SWC), incident photosynthetically active radiation (PAR), temperature [air temperature ( $T_a$ ), soil surface temperature ( $T_{surf}$ ), soil temperature ( $T_s$ )], soil respiration ( $R_s$ ), and photosynthesis ( $P$ ) in *Artemisia ordosica* during a wet (July) and dry (August) month. Each point is the monthly mean for a particular time of day. Bars represent standard errors.



**Figure 3.** Diel soil respiration ( $R_s$ ) vs. soil surface temperature ( $T_{surf}$ ), diel  $R_s$  vs. photosynthesis in *Artemisia ordosica* ( $P$ ), and their lag correlations during a wet (July) and dry (August) month.



**Figure 4.** Relationship between soil water content (SWC) and the relative importance (RI) of soil surface temperature and photosynthesis in *Artemisia ordosica* with respect to diel soil respiration.



**Figure 5.** Lag time between soil respiration ( $R_s$ ) and soil surface temperature ( $T_{surf}$ ),  $R_s$ , and photosynthesis in *Artemisia ordosica*, and in relation to soil water content (SWC). Lag time were bin-averaged using SWC-intervals of  $0.004 \text{ m}^3 \text{m}^{-3}$ .