Soil water regulates the control of photosynthesis on diel hysteresis between soil respiration and temperature in a desert-shrub land

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Abstract. Explanations for the occurrence of hysteresis (asynchronicity) between diel soil respiration (R_s) and soil temperature (T_s) have evoked both biological and physical mechanisms. The specifics of these explanations, however, tend to vary with the particular ecosystem or biome being investigated. So far, the cause of such hysteresis is not properly addressed for drylands. 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), temperature at the soil surface and below (T_{surf} and T_s), volumetric soil water content (SWC), and photosynthesis in a dominant desert shrub (i.e., *Artemisia ordosica*) over an entire year in 2013. Trends in diel R_s were observed to vary with SWC over the growing season (April to October). Diel variations in R_s were more closely associated with variations in T_{surf} than with photosynthesis as SWC increased, leading to R_s being in phase with T_{surf}, particularly when $SWC > 0.08$ m^3 m^{-3} (ratio of SWC to soil porosity = 0.26). However, as SWC decreased below 0.08 m^3 m^{-3}, diel variations in R_s were more closely related to variations in photosynthesis, leading to pronounced hysteresis between R_s and T_{surf}. Incorporating photosynthesis into a Q_{10}-function eliminated 84.2% of the observed hysteresis, increasing the overall descriptive capability of the function. Our findings highlight the importance of photosynthesis 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; Stoy 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 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 an inadequate understanding of temperature-sensitivity in R_s

5   (Gaumont-Guay et al., 2008; Phillips et al., 2011; Darenova et al., 2014). Therefore, in order to accurately predict soil carbon dioxide (CO_2) fluxes and their responses to climate change, it is necessary to understand the biophysical mechanisms that have a role in controlling seasonal 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 line is based on the physical processes of heat and gas transport in soils (Vargas and Allen, 2008;

10 Phillips et al., 2011; Zhang et al., 2015). Generally, soil CO_2 fluxes are measured at the soil surface, but are for the most part related to temperatures in the soil. Transport of CO_2-gas to the soil surface takes time to occur, which may cause delays to appear in observed respiration rates, causing hysteretic loops to form between R_s and T_s (Zhang et al., 2015). 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.,

15 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, usually peaking in the afternoon (e.g., 14:00-16:00). These studies highlight the need to consider the inherent role of photosynthesis for a more accurate interpretation of R_s (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011). Physical and biological processes that relate to substrates and production-transport of carbon (C) in plants and soils are not mutually exclusive and likely play crucial roles

20 in affecting diel variation in R_s (Phillips et al., 2011; Zhang et al., 2015; Song et al., 2015a, b). Currently, causes of diel hysteresis between R_s and soil 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 uniform. Based on the Millington-Quirk model, high *SWC* blocks CO_2-gas

25 and thermal diffusion (Millington and Quirk, 1961), resulting in large hysteresis loops (Riveros-Iregui et al., 2007; Zhang et al., 2015). In contrast, other studies have reported that low *SWC* and high vapor pressure deficits (*VPD*) can promote partial stomata closure, which leads to higher photosynthesis in the morning (e.g., 9:00-10:00) and supressed photosynthesis in mid-afternoon, leading to pronounced hysteresis during dry periods (Tang et al., 2005; Vargas and Allen, 2008; Carbone et al., 2008; Wang et al., 2014). Clearly to understand the causes of diel hysteresis, the role of *SWC* needs to be closely scrutinized.

30 Drylands cover a quarter of the earth's land surface and play an important role in the global C cycle (Safriel and Adeel, 2005; Austin, 2011; Poulter et al., 2014). Many studies in forest ecosystems are based on the application of physical soil CO_2 and heat transport models and evaluate the influences of *SWC* on CO_2-gas and thermal diffusion (Riveros-Iregui et al., 2007; Phillips et al., 2011; Zhang et al., 2015). In general, many of these studies conclude that diel hysteresis is the result of

physical processes alone. Few 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 hysteresis in drylands.

Drylands are characterized with low productivity. As weak organic C-storage pools (West et al., 1994; Lange, 2003), drylands are noted for their large contribution of autotrophic production of CO_2. The autotrophic component of R_s occurs as a direct consequence of root respiration, which is firmly coupled (within several hours) to recent photosynthesis (Liu et al., 2006; Baldocchi et al., 2006; Högberg and Read, 2006; Bahn et al., 2009; Kuzyakov and Gavrichkova, 2010). Consequently, photosynthesis may govern the level of variation in asynchronicity between R_s and T_s in drylands. In drylands, especially in desert ecosystems characterized by sandy soils of high soil porosity, the influence of *SWC* on gas diffusion is likely minimized. As a rule, most of the available water is used directly in sustaining biological activity in drylands (Noy-Meir, 1973). Under drought conditions, stomata closure in plants at midday reduces water losses, resulting in a corresponding suppression of photosynthesis (Jia et al, 2014). Such changes in diel patterns of photosynthesis likely result in modifications of patterns in R_s, leading to hysteresis between R_s and T_s. Soil water content likely regulates photosynthesis and, in so doing, causes hysteresis between R_s and T_s to vary over the growing season.

In this study, we hypothesize that: (1) photosynthesis has a role in controlling hysteresis between R_s and T_s; and (2) *SWC* regulates that control and its variation over the growing season. The main objectives of this research were to: (1) identify the physical and biological controls on diel hysteresis between R_s and T_s; (2) explore the causes that lead to variation in seasonal variation in diel hysteresis; and (3) understand *SWC*'s role in influencing diel hysteresis. To undertake this work, we measured R_s, *SWC*, T_s, and photosynthesis in a dominant desert-shrub on a continuous basis for 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°42'31" N, 107°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°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). Annual potential evaporation was on average 5.5 kg m^{-2} d^{-1} (Gong et al., 2016). The soil at the research station was of a sandy type, with a bulk density of 1.6 g cm^{-3}. The total soil porosity within 0-2 and 5-25 cm depths was 50% and 38%, respectively. Soil organic matter, soil nitrogen, and pH were 0.21-2.14 g kg^{-1}, 0.08-2.10 g kg^{-1}, and 7.76-9.08, respectively (Wang et al., 2014; Jia et al, 2014). The vegetation was regenerated from aerial seeding applied in 1998 and is currently dominated by a semi-shrub species cover of *Artemisia ordosica*, averaging about 50-cm tall with a canopy size of about 80 cm × 60 cm (for additional site description, consult 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. Collar dimensions 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 (μmol CO_2 m^{-2} s^{-1}) was directly estimated from CO_2-flux measurements obtained with the opaque-chamber system. Photosynthetic rates (μmol CO_2 m^{-2} s^{-1}) of the selected plants were determined as the difference in CO_2 fluxes obtained with the transparent and opaque chambers.

Continuous measurements of CO_2 fluxes (μmol CO_2 m^{-2} s^{-1}) were made *in situ* with a Li-8100 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. 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.

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

Hourly soil temperature (T_s, ^{o}C) and volumetric soil water content (SWC, m^3 m^{-3}) at a 10-cm depth were measured simultaneously about 10 cm from the chambers using a LI-8150-203 temperature sensor and EC_{H2O} soil-moisture sensor (LI-COR, Nebraska, USA; see Wang et al., 2014). Other environmental variables were recorded every half hour using sensors mounted on a 6-m tall eddy-covariance tower approximately 800 m from our soil CO_2-flux measurement site. Air temperature (T_a, ^{o}C) was measured with a thermohygrometer (HMP155A, Vaisala, Finland). Soil surface temperature (T_{surf}, ^{o}C) was measured with an infrared-emission sensor (Model SI-111, Campbell Scientific Inc., USA). Incident photosynthetically active radiation (PAR) was measured with a light-quantum sensor (PAR-LITE, Kipp and Zonen, the Netherlands) and precipitation (PPT, mm), with three tipping-bucket rain gages (Model TE525MM, Campbell Scientific Inc., USA) placed 50 m from the tower (see Jia et al., 2014).

2.4 Data processing and statistical analysis

In this study, CO_2-flux measurements were screened by means of limit checking, i.e., hourly CO_2-flux data < -30 or > 15 μmol CO_2 m^{-2} s^{-1} were considered to be anomalous as a result of, for instance, gas leakage or plant damage by insects, and removed from the dataset (Wang et al., 2014, 2015). After limit checking, hourly CO_2 fluxes greater than three times the standard deviation from the calculated mean of 5 days' worth of flux data were likewise 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). Differences in mean annual T_s and SWC between the two chambers were 0.01 ^{o}C and 0.003 m^3 m^{-3}, respectively.

The Q_{10}-function (e.g., Eq. 1) was used here to describe the response of R_s to temperature. Earlier studies have shown strong correlation between basal rate of R_s and photosynthesis (Irvine et al., 2005; Sampson et al., 2007). Response of R_s to changes in photosynthesis was, in turn, characterized as a linear function (Eq. 2). Interaction between photosynthesis and temperature on R_s was conveyed through Eq. 3. The instantaneous relative importance (*RI*) of photosynthesis and temperature on R_s over the growing season was calculated with a correlation-based ratio (see Eq. 4). The importance of photosynthesis on R_s increases with a corresponding increase in *RI*:

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

$$R_s = a \times P + b \tag{2}$$

$$R_s = (a \times P + b) \times c^{(T-10)/10} \tag{3}$$

$$RI = \frac{\rho_p}{\rho_t} \tag{4}$$

where R_{10} is the respiration at 10°C, Q_{10} is the temperature sensitivity of respiration, T is temperature, P is photosynthesis (μmol CO_2 m^{-2} s^{-1}), *a*, *b*, and c are regression coefficients, and ρ_p and ρ_t are the correlation coefficients between photosynthesis and R_s and temperature and R_s, respectively.

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 function 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 generated by averaging their hourly means at a given hour over a particular month (Table 1). Exponential and linear regression was used to evaluate the influence of *SWC* on the control of photosynthesis on temperature-R_s hysteresis. Likewise, influences of *SWC* on diel hysteresis was examined during a wet month with high rainfall and adequate *SWC* (July, *PPT* = 117.9 mm) and a dry month with low rainfall and inadequate *SWC* (August, *PPT* = 10.9 mm; Wang et al., 2014). In order to evaluate the influence of photosynthesis on diel hysteresis in the temperature-R_s relationship, we compared the lag time (in hours) between measured and modeled R_s by means of Eq.'s 1 through 3 with a one-day moving window and a one-day time step over the growing season (April to October). Modeled R_s were calculated using the fitted parameters of each function and the measured hourly T_{surf} and photosynthesis for each day. 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 exhibited distinctive daily 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 the environmental factors, daily patterns in R_s remained constant over the non-growing part of the year, peaking at 11:00 AM-13:00 PM, and highly variable during the growing season of the year (April to October), 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 those of T_{surf} during the wet month and similar to those of photosynthesis during the dry month (Fig. 2g, h). During the wet month (July), 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, exhibiting similar timing to T_{surf} (i.e., 15:00 PM), but four hours later than photosynthesis (peaking at 12:00 PM; Fig. 2g). During the dry month (August), diel R_s was generally 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).

3.2 Control of photosynthesis and temperature on diel soil respiration

Among temperatures at the three levels, T_{surf} correlated the strongest with R_s, due to the high R^2's with monthly mean diel R_s (Table 1). Over the growing season, monthly mean diel R_s correlated fairly well with photosynthesis (Table 1). The response of R_s to temperature and photosynthesis was shown to be affected by SWC (Table 2, Fig. 3). During the wet month, T_{surf} alone explained 97% of the variation in diel R_s (via Eq. 1), whereas photosynthesis explained 67% of that same variation (Table 2, Fig. 3a). However, during the dry month, photosynthesis explained 88% of the variation in diel R_s (via Eq. 2), whereas T_{surf} explained 76% of the variation (Fig. 3b, Table 2). Irrespective of dry/wet periods, T_{surf} and photosynthesis together explained over 90% of the diel variation in R_s (via Eq. 3; see Fig 3 and Table 2). Altogether, RI varied as a function of SWC, decreasing whenever SWC increased (Fig. 4).

3.3 Effects of soil water content and photosynthesis on diel hysteresis in temperature-R_s relationship

During the wet month, hysteresis was not observed to occur in the monthly mean T_{surf}-R_s relationship, whereas two-hour lag times were found to occur in the photosynthesis-R_s relationship (Table 1; Fig. 3a). During the dry month, the opposite was observed, where one-hour lag times were found to occur in the T_{surf}-R_s relationship (Table 1, Fig. 3b). Over the growing season, T_{surf} lagged behind R_s by about 0-4 hours (Fig. 5b), and R_s lagged behind photosynthesis by about the same amount (Fig. 5c). This led to lag times between measured and modeled R_s regardless of the variable, T_{surf} or photosynthesis, resulting in about 26% of the days of the growing season (accounting for 184 days, in total) having no lag time (Fig. 5e, f). However, taking into account both T_{surf} and photosynthesis as input variables to the definition of R_s (via Eq. 3), lag times between

measured and modeled R_s were mostly eliminated (Fig. 5a, d), with 84% of the days of the growing season displaying no lag time.

Diel hysteresis in both relationships (i.e., T_{surf}-R_s and photosynthesis-R_s) was shown to be affected by SWC (Fig. 6). Over the growing season, diel hysteresis between R_s and T_{surf} was linearly related to SWC in a downward manner, when SWC < 0.08 m^3 m^{-3} (ratio of SWC to soil porosity = 0.26; Fig. 6a). Hysteresis was not evident, when SWC > 0.08 m^3 m^{-3} (Fig. 6a). In contrast, diel hysteresis between R_s and photosynthesis was linearly related to SWC in an upward manner, when SWC < 0.08 m^3 m^{-3} (Fig. 6b), but ceased to be related, when SWC > 0.08 m^3 m^{-3} (Fig. 6b).

4 Discussion

4.1 Physical- vs. biological-controls on diel hysteresis

In our study, we found that the diurnal pattern in temperature (T_a, T_{surf}, and T_s) lagged behind R_s 0-4 hours, which resulted in a counterclockwise loop in the relationship between R_s and temperature. Although the magnitude of hysteresis between R_s and temperature differed among the three temperature measurements, their seasonal variation was generally uniform. Among the temperature measurements, T_{surf} was more closely related to diel R_s, resulting in weaker hysteresis. Magnitude of hysteresis between R_s and temperature was 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). However, the direction of hysteresis was unlike that reported by Phillips et al. (2011), who had reported R_s lagging behind soil temperature.

Contradictory understanding exists on the causes of diel hysteresis between R_s and temperature (Tang et al., 2005; Riveros-Iregui et al., 2007; Vargas and Allen, 2008; Carbone et al., 2008; Kuzyakov and Gavrichkova, 2010; Philips et al., 2011; Wang et al., 2014, Zhang et al., 2015). At our study sites, it is likely that R_s-effluxes at the surface originated from biogeochemical processes in the deep soil. In general, transfer of heat (downward) and gases (upward) through the soil complex by simple diffusion would take time to occur. Increased SWC would serve to impede this transfer (Millington and Quirk, 1961). If physical processes alone controlled hysteresis, you would expect R_s to lag behind T_{surf} and hysteresis to increase with increasing SWC. However, such rationalization is not supported by our observations, which show T_{surf} to lag behind R_s and hysteresis to decrease with increasing SWC. As a result, physical processes alone cannot account for the observed patterns in hysteresis between R_s and temperature. Combining photosynthesis and T_{surf} as explanatory variables of R_s (via Eq. 3), we found 84% of the days over the growing season had no observable lag between measured- and modeled-R_s, relative to 27% of the days when T_{surf} alone was used (specific to Eq. 2), suggesting that photosynthesis has a greater role governing hysteresis in drylands. Differences in soil properties between sandy soils at our study site and loamy and clayey soils at many of the forested sites may be responsible for disparity in explanation (Millington and Quirk, 1961; Hillel, 1998; Nickerson and Risk, 2009). Unlike higher-clay/silt-content soils in forests, sandy soils have lower heat and water-holding capacity and higher water and air permeability. Properties of sandy soils tend to make thermal and CO_2-gas transport much faster (e.g., within a few minutes), resulting in minor influences on hysteresis. Our observations lend support to an

explanation of hysteresis based on a relationship with photosynthesis. Along with other studies, including those of Tang et al. (2005), Vargas and Allen (2008), Carbone et al. (2008), Kuzyakov and Gavrichkova (2010), and Wang et al. (2014), our findings provide increasing evidence of the role of photosynthesis in regulating diel hysteresis between R_s and temperature.

4.2 Photosynthesis control of soil respiration and diel hysteresis

5   The 0-4 h lag between R_s and photosynthesis observed are consistent with those observed in earlier studies, e.g., 0-4 h lag between ecosystem-level photosynthesis and R_s in a coastal wetland ecosystem (Han et al., 2014) and 0-3 h lag between plant photosynthesis and R_s in a steppe ecosystem (Yan et al., 2011). Short lag times suggest rapid response between recent photosynthesis and R_s (Kuzyakov and Gavrichova, 2010). This response is significantly faster than suggested in earlier studies, when approached from an isotopic or canopy/soil flux-based methodology (Howarth et al., 1994; Mikan et al., 2000;

10 Jonson et al., 2002; Högberg et al., 2008; Kuzyakov and Gavrichova, 2010; Mencuccini and Hölttä, 2010; Kayler et al., 2010; Han et al., 2014).

According to the "goodness-of-fit" of Eq. 3 to the field data, the lag time between diel photosynthesis and R_s was likely caused by variations in temperature, regardless of *SWC*. Photosynthesis provide substrates to roots and rhizosphere microbes (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011; Han et al., 2014). Temperature directly drives

15 enzymatic kinetics of respiratory metabolism in organisms (Van't Hoff, 1898; Lloyd and Taylor, 1994). Photosynthesis is directly driven by radiation (specifically, photosynthetically active radiation). Temperature is also driven by radiation, but through heating of the surface and subsequent air and soil layers. Thus, diel patterns in temperature continuously lagged behind those of photosynthesis by a few hours (as indicated in Fig. 2). The interactions between photosynthesis and temperature lead R_s to lag behind photosynthesis but temperature lag behind R_s (Fig. 2). This sequence of events may explain

20 the difference in the direction of hysteresis observed here, in contrast to that reported in Phillips et al. (2011). Such explanation is different from the explanations for forest ecosystems, where the transport of photosynthates and influence of turgor and osmotic pressure may be responsible for the specific coupling observed between current photosynthesis and R_s (Steinmann et al., 2004; Högberg et al., 2008; Hölttä et al., 2006, 2009; Mencuccini and Hölttä, 2010). Variations in coupling dynamics may occur because of differences in vegetation height among ecosystems (Kuzyakov and Gavrichova,

25 2010; Mencuccini and Hölttä, 2010). Unlike forest ecosystems, low-statured vegetation in shrub systems (~0.5 m), may elicit a few minutes of delay in the transportation of photosynthates and influence of turgor and osmotic pressure (Kuzyakov and Gavrichkova, 2010). Such small lag times cannot be easily identified in hourly measurements, resulting in an apparent temperature-dominated control of photosynthesis and R_s.

4.3 Influences of soil water content on seasonal variation in diel hysteresis

30 Diel R_s varied consistently with T_{surf}, with no observable signs of hysteresis, when $SWC > 0.08$ m^3 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* played a more important role in regulating the relative control of photosynthesis and temperature on diel R_s over the growing season, supporting our second hypothesis.

A possible explanation for *SWC* regulating hysteresis might be associated with changes in substrate supply. During the wet period with $SWC > 0.08$ m^3 m^{-3}, increases in *SWC* ameliorates diffusion of soil C substrates and its access to soil microbes (Yuste et al., 2003; Jarvis et al., 2007). Amount of substrate to roots and rhizosphere microbes is also expected to be high as a result of high current photosynthesis (Baldocchi et al., 2006). As a result, diel R_s is not limited by C substrates provided by current photosynthesis and soil organic matter. Consequence of diel R_s may vary repeatedly in synchrony with diel temperature, with no indication of hysteresis when $SWC > 0.08$ m^3 m^{-3} (Fig. 6a). By contrast, during dry and hot phases, with $SWC < 0.08$ m^3 m^{-3}, inadequate soil water limits diffusion of soil C substrates and its access to soil microbes (Jassal et al., 2008) and also suppresses photosynthesis (supported by Fig. 2g, h). As a result, R_s may be limited by C substrates under dry conditions. It has been reported current photosynthesis can account for about 65-70% of total R_s over the growing season (Ekblad and Högberg et al., 2001; Högberg et al., 2001). Thus, diel R_s may vary more closely to photosynthesis during dry and hot phases over the growing season (Fig. 2h), resulting in increased hysteresis with decreasing *SWC* below 0.08 m^3 m^{-3} (Fig. 6b).

The 0.08 m^3 m^{-3} *SWC* threshold of this study was consistent with an earlier study by Wang et al. (2014) that reported that seasonal R_s decoupled from soil temperature as *SWC* fell below 0.08 m^3 m^{-3}. Earlier studies have reported similar response of R_s to temperature (Palmroth et al., 2005; Jassal et al., 2008). For example, R_s in an 18-year-old temperate Douglas-fir stand decoupled from T_s when *SWC* fell below 0.11 m^3 m^{-3}. Our results suggest that the decoupling of R_s from temperature for low *SWC* was due to a shift in control from temperature to photosynthesis. 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 photosynthesis should be considered in simulations of diel R_s in drylands, especially when *SWC* falls below 0.08 m^3 m^{-3}.

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 $SWC > 0.08$ m^3 m^{-3}, but the lag-hours increased as *SWC* decreased below this *SWC* threshold. Incorporating photosynthesis into R_s-temperature-based models reduces diel hysteresis and increases the overall level of goodness-of-fit. 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. Statistically significant Pearson's correlation coefficients (r; $p < 0.05$) 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	**0.64**	0.25	**0.49**	**0.46**	**0.85**	**0.85**	**0.93**	**0.76**	**0.94**	**0.89**	**0.78**	**0.77**
R_s-T_{surf}	Lag	1	2	2	2	0	0	0	1	0	0	1	1
	r	**0.82**	**0.57**	**0.75**	**0.72**	**0.96**	**0.96**	**0.98**	**0.87**	**0.98**	**0.97**	**0.89**	**0.87**
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	**0.54**	**0.58**	**0.80**	0.31	**0.77**	**0.65**	0.23	0.12
R_s-P	Lag					-1	-1	-2	0	-1	-1		
	r					**0.84**	**0.83**	**0.82**	**0.94**	**0.86**	**0.88**		

Table 2. Regressions based on the Q_{10}, linear, and Q_{10}-linear functions of soil respiration (R_s) for a wet and a dry month. Variables T_{surf} (°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
R_s-T	Q_{10}	$R_S = 1.13 \times 1.4^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.97$ $RMSE = 0.0521$	$R_S = 1.12 \times 1.1^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.76$ $RMSE = 0.0796$
R_s-P	Linear	$R_S = 0.03 \times P + 1.61$ $R^2 = 0.67$ $RMSE = 0.1889$	$R_S = 0.04 \times P + 1.29$ $R^2 = 0.88$ $RMSE = 0.05752$
R_s-P-T	Linear×Q_{10}	$R_S = (0.002 \times P + 1.16) \times 1.38^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.98$ $RMSE = 0.0491$	$R_S = (0.024 \times P + 1.20) \times 1.08^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.94$ $RMSE = 0.0408$
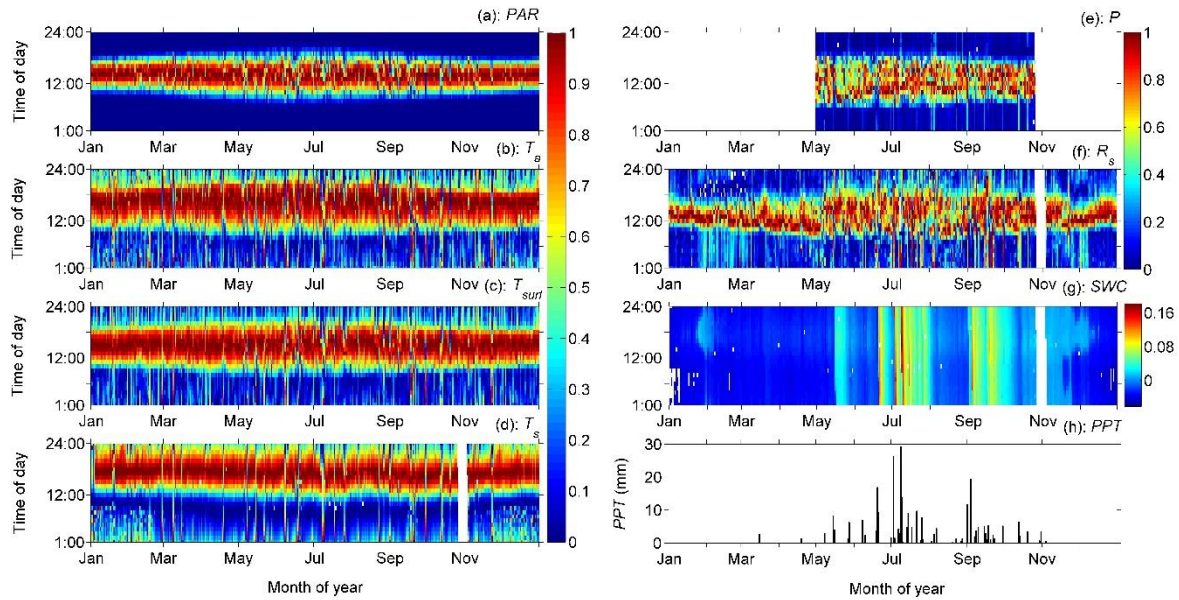
Figure 1. Seasonal variation in incident photosynthetically active radiation (*PAR*), temperature [i.e., air temperature (T_a), soil surface temperature (T_{surf}), soil temperature (T_s)], photosynthesis (*P*), and soil respiration (R_s) at an *Artemisia ordosica*-dominated site, and seasonal variation 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 a given day and 0, the daily minimum value.
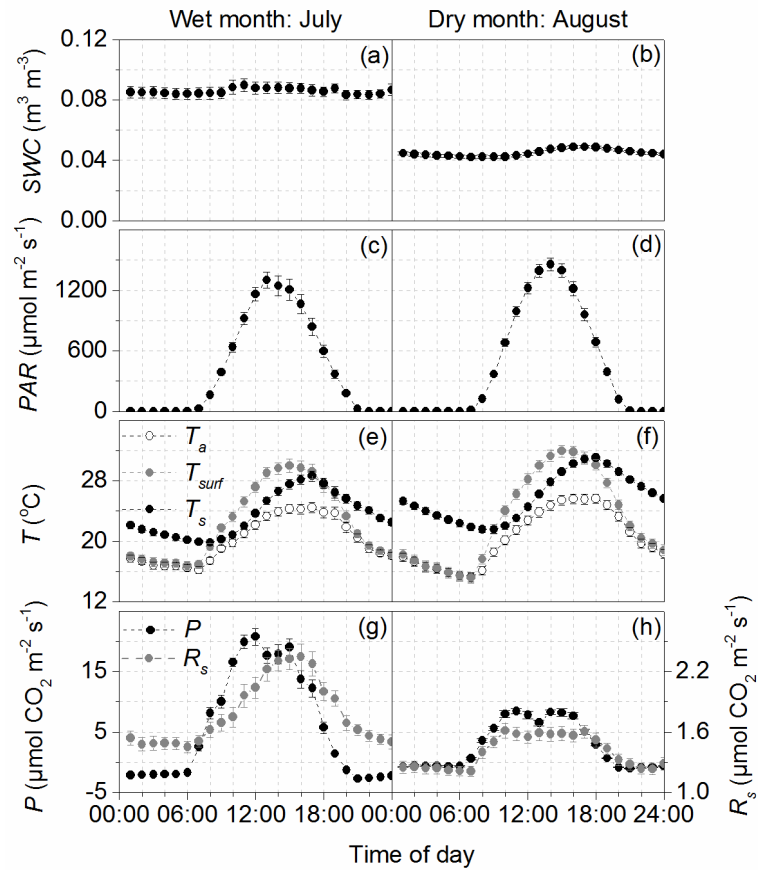
Figure 2. Mean monthly diel cycle of soil water content (*SWC*), incident photosynthetically active radiation (*PAR*), temperature [air temperature (T_a), soil surface temperature (T_{surf}), soil temperature (T_s)], soil respiration (R_s), and photosynthesis (*P*) at an *Artemisia ordosica*-dominated site during a wet and dry month. Each point is the monthly mean for a particular time of day. Bars represent standard errors.
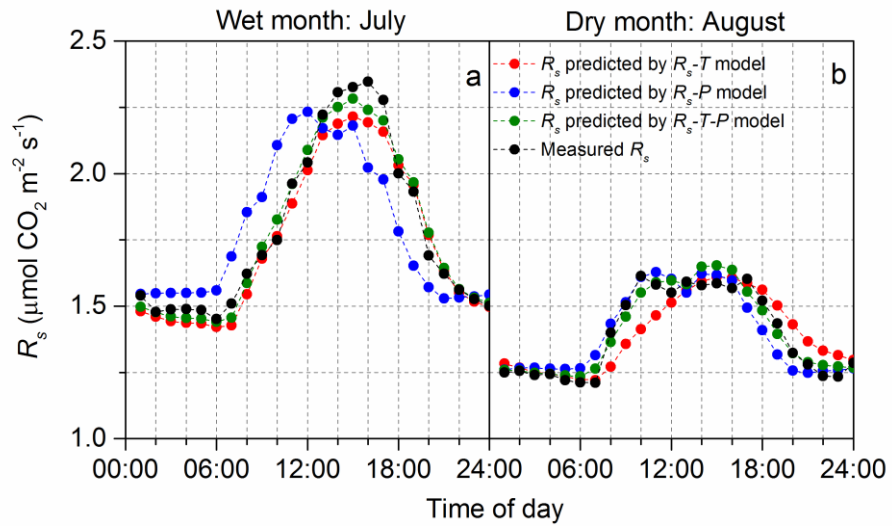
Figure 3. Diel variation of measured soil respiration (R_s) and modeled R_s by using temperature and photosynthesis as input variables in the calculation of R_s for both a wet and dry month (i.e., July and August, respective); R_s-T function (Eq. 1), R_s-P function (Eq .2), and R_s-T-P function (Eq. 3).
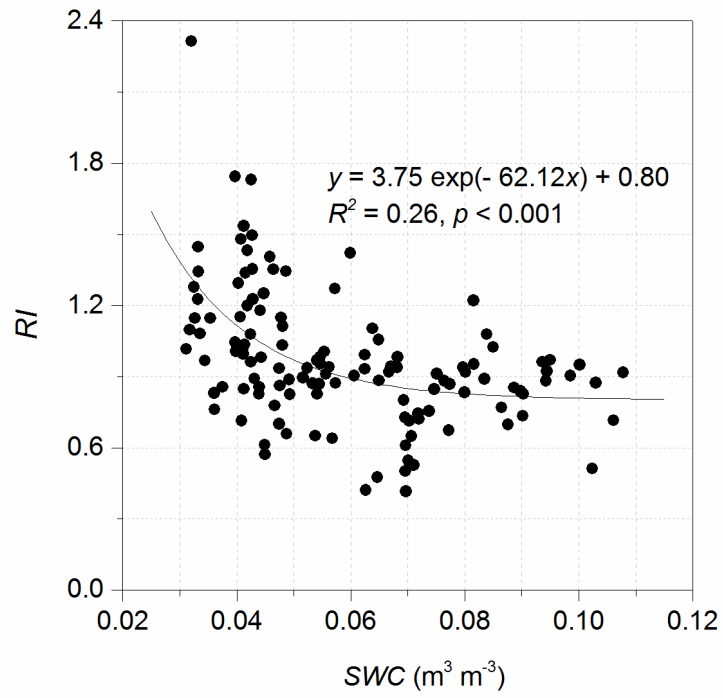
Figure 4. Relationship between soil water content (*SWC*) and the relative importance (*RI*) of soil surface temperature and photosynthesis at an *Artemisia ordosica*-dominated site as a function of diel soil respiration (*R$_s$*).
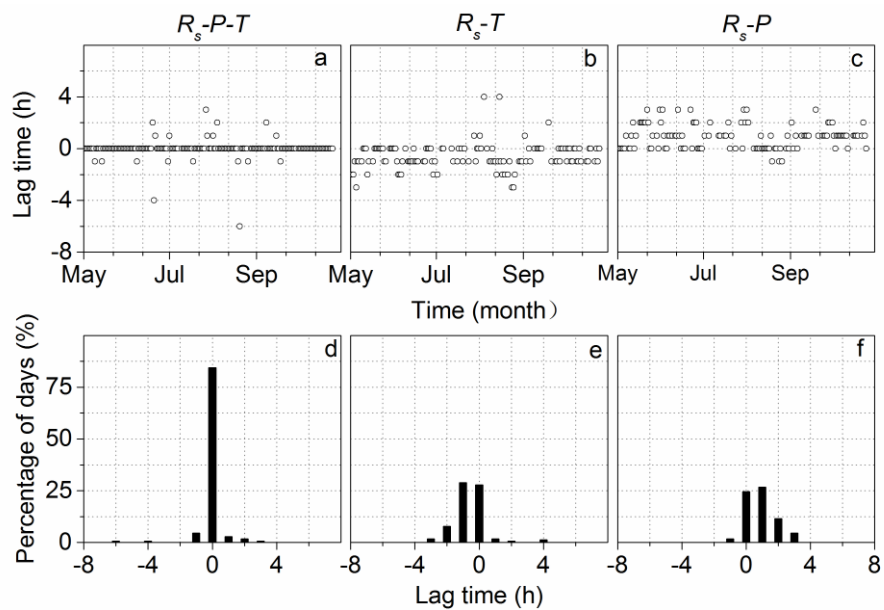
Figure 5. Lag times between measured and modeled soil respiration by means of soil surface temperature and photosynthesis over the growing season; R_s-T function (Eq. 1), R_s-P function (Eq. 2), and R_s-P-T function (Eq. 3).
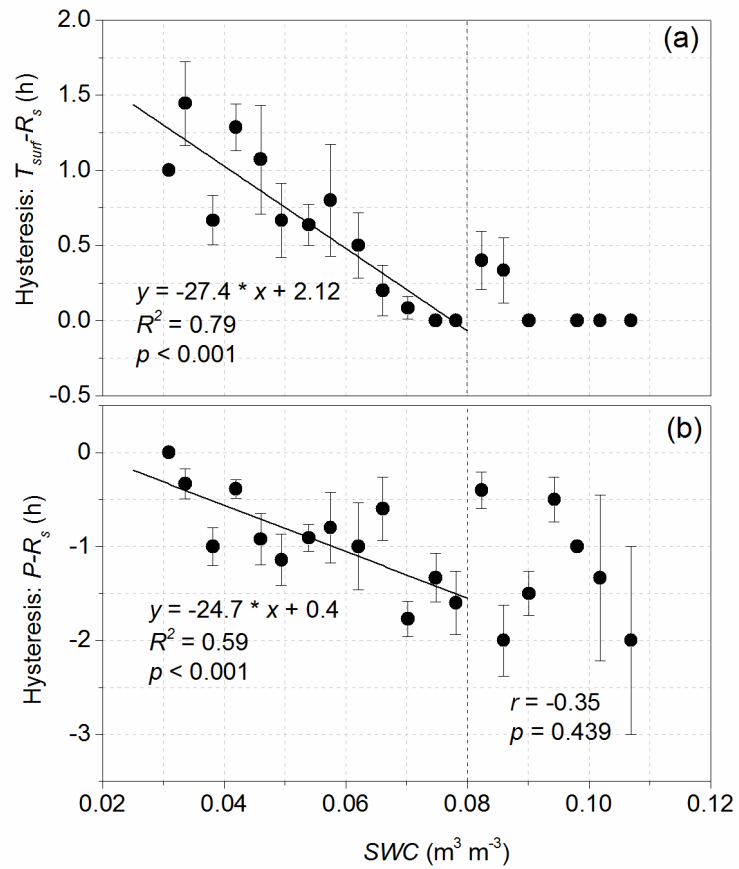
Figure 6. Lag times between soil respiration (R_s) and soil surface temperature (T_{surf}), R_s, and photosynthesis at an *Artemisia ordosica*-dominated site with respect to soil water content (*SWC*). Lag times were bin-averaged using *SWC*-intervals of 0.004 m³ m⁻³.