

Responses to editor's comments

We appreciate the editor's thoughtful and constructive comments. We have fully considered the editor's comments in the revision of the manuscript. Response to the editor's questions appear in blue.

Comments to the Author:

I thank the authors for their careful responses. The edited manuscript was difficult to read in places due to the pdf markup used (I couldn't figure out how some changes were being resolved nor read added text). A draft in which additions to the text can be identified would be appreciated.

Response: Sorry for that error, a draft with clear track changes has been submitted with corresponding response. Hopefully, this will make the reading easier.

My concern with the manuscript is that I still don't agree with equation 2 given the necessary lag between photosynthesis and respiration, which is likely to increase under drought stress depending on the response of phloem velocity to changes in xylem velocity. These terms will change as a function of drought stress. There is also of course the argument root-to-soil carbon flux occurs shortly after photosynthetic inputs to the plant due to osmoregulatory constraints, but it is unclear how large this effect is. Work by Mencuccini and others may add insight into time lags of transport between photosynthesis and respiration; the response in the letter regarding these dynamics was too terse. In brief, I feel that this manuscript is confirmatory and makes some interesting points regarding seasonal changes in photosynthesis/respiration coupling. At the same time, it is far less rigorous than many manuscripts that address similar issues, hence my concern that it is not sufficiently advancing the science. In summary, I would appreciate it if the authors could send a draft in which changes to the manuscript were more clear, and cite more relevant literature on photosynthesis/respiration coupling, which they might have but again these additions from the pdf that was uploaded is unclear.

Response: we agree with you that Eq. 2 may incorporate some bias in the description of the relationship between photosynthesis and soil respiration due to lag. However, we still found Eq. 2 to fit 24% of the days with diel R_s with no observable lag over the growing season. Thus, in order to improve Eq. 2, we needed to understand the lag that existed between photosynthesis and soil respiration. This is one of the aims of the study. Further analysis shows that the R_s -function with photosynthesis and temperature as explanatory variables (Eq. 3 in the text) was able to fit 84% of the days with no observable hysteresis. In addition, the calculated hysteresis between photosynthesis and soil respiration using Eq. 2 is the same as that based on the observed data. Therefore, we think Eq. 2 can be used.

More details about the influence of *SWC* on photosynthate transport in phloem has been added to the second part of the discussion of this manuscript.

In order to provide greater support for our conclusions, new results and discussion related to the influence of photosynthesis on diel R_s and seasonal variation in diel hysteresis have been added to the manuscript.

Relevant literature on photosynthesis-soil respiration coupling has been added to the manuscript and reference list.

A couple of minor notes:

Regarding the statement ‘rather than rely on relating daytime simulations of R_s to night-time respiration-temperature relationship’, note that many partitioning approaches don’t, but I agree that it is the normal course of affairs.

Response: we deleted the statement “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.”

‘No consensus has been reached’ implies that there is a single cause of hysteresis. But there are many, and different ecosystems should behave somewhat differently with respect to this hysteresis.

Response: we delete the sentence “Causes for diel hysteresis between soil respiration (R_s) and temperature remain highly controversial”, we added the sentence “So far, the cause of such hysteresis is not properly addressed for drylands” however, tend to vary with the particular ecosystem or biome being investigated”.

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

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10 **Abstract.** ~~Causes for diel hysteresis between soil respiration (R_s) and temperature remain highly controversial.~~ Explanations for the occurrence of hysteresis (asynchronicity) between diel soil respiration (R_s) and soil temperature (T_s) have ~~involved~~ evoked both biological and physical mechanisms. The specifics of these explanations, however, tend to vary with the particular ecosystem or biome being ~~studied~~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), ~~soil~~ 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 a-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 $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ (ratio of SWC to soil porosity = 0.26). 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} . Incorporating photosynthesis into a Q_{10} -function eliminated 84% of the observed hysteresis, increasing the overall descriptive capability of the function. ~~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 photosynthesis and the role of SWC in regulating diel hysteresis between R_s and temperature.

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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 ~~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 ~~an inadequate 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 ~~carbon dioxide (CO_2)~~ CO_2 -fluxes and their responses to climate change, it is necessary to understand the biophysical mechanisms that ~~have a role in controlling seasonal 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 [line](#) 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). ~~Generally, Soil 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 CO_2 -production (Phillips et al., 2011) 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., 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 peak~~ings in the afternoon (e.g., 14:00-16:00). These studies ~~point out that it is necessary to take highlight the need to consider the inherent role of~~ 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 p~~Physical and biological processes-~~are not mutually exclusive and both likely play important roles in affecting diel variation in R_s .~~ ~~that relate to substrates and production-transport of carbon (C) in plants and soils are not mutually exclusive and likely play crucial roles in affecting diel variation in R_s .~~ (Phillips et al., 2011; Zhang et al., 2015; Song et al., 2015a, b). 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 ~~uniformeconsistent, 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 CO_2 -gas and thermal diffusion.~~ ~~Based on the Millington-Quirk model, high SWC blocks CO_2 -gas 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 ~~vapour-vapor~~ pressure deficits (VPD) ~~can~~ 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~~ Clearly to understand the causes of diel hysteresis, ~~it is clear that the role of SWC needs to be considered~~ the role of SWC needs to be closely scrutinized.

Drylands cover a quarter of the earth's land surface and play an important role in the global carbon (~~C~~)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 CO₂ and heat transport models and evaluate the influences of SWC on CO₂-gas and thermal diffusion (Riveros-Iregui et al., 2007; Phillips et al., 2011; Zhang et al., 2015) ~~and, in.~~ In general, many of these studies conclude that diel hysteresis is the result of a 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~~C-storage pools (West et al., 1994; Lange, 2003), ~~which may result in drylands are noted for their~~ large contributions of autotrophic production of CO₂ ~~(increasing R_s) in drylands.~~ The Autotrophic-autotrophic components ~~to of~~ R_s occurs as a direct consequence of root respiration, which ~~has been shown to be~~ 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). ~~Therefore, Consequently, biologically photosynthesis related processes photosynthesis~~ may dominate the control of the 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, likely minimizes the influence of SWC on gas diffusion~~ is likely minimized. ~~In addition, As a rule, most of the available water is the primary driver of 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 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 photosynthesis~~ have has a role in controlling hysteresis between R_s and T_s; and (2) SWC regulates ~~the that control of photosynthesis related processes on hysteresis~~ and its variation over the growing season. The main objectives of this research were to: (1) ~~investigate identify the physical and biological controls on seasonal variation in~~ 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 ~~how SWC influences SWC's role in influencing~~ diel hysteresis. To undertake this work, we measured R_s, SWC, T_s, and photosynthesis ~~continuously~~ in a dominant desert-shrub ~~ecosystem over a year 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). ~~Radiation and evaporative demand were high at the station, i.e., annual incoming shortwave radiation was 1.4×10^5 MJ m⁻² and a~~ Annual potential evaporation was on average ~~5.5×10^3 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 ~~that took place~~ 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 ~~detail~~ site description, ~~see 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. ~~The~~ eCollars 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 CO₂-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 CO₂ fluxes ~~between~~ obtained with the transparent ~~and~~ the opaque ~~chambers~~.

Continuous measurements of CO₂ fluxes ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) were made *in situ* ~~over an entire year~~ with a Li-8100 CO₂-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 CO₂ 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 (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 EC_{H2O} soil-moisture sensor (LI-COR, Nebraska, USA; see Wang et al., 2014). Other environmental factors-variables were recorded every half hour using sensors mounted on a 6-m-tall flux-eddy-covariance tower approximately 800 m from our soil CO₂-flux measurement site.

5 Air temperature (T_a , °C) was measured with a thermohygrometer (HMP155A, Vaisala, Finland). Soil surface temperature (T_{surf} , °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 gauges (Model TE525MM, Campbell Scientific Inc., USA) placed 50 m from the flux tower (see Jia et al., 2014).

10 2.4 Data processing and statistical analysis

In this study, CO₂-flux measurements were screened by means of limit checking, i.e., hourly CO₂-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 plant damage by insects, and removed from the dataset (Wang et al., 2014, 2015). After limit checking, hourly CO₂ 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 °C and 0.003 $\text{m}^3 \text{m}^{-3}$, respectively.

~~the-The~~ Q_{10} function (e.g., Eq. (1)) ~~is-was~~ used here 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)). 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. Correlation coefficient, magnitude of hysteresis, and model performance are used to evaluate whether photosynthesis or temperature dominate diel R_s .-The instantaneous Relative-relative importance (RI) of temperature and photosynthesis-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 : ~~in~~ defining R_s over the growing season was calculated with a ratio of $\rho_p : \rho_t$ (Eq. (3)), where ρ_p is the correlation coefficient between photosynthesis and R_s , and ρ_t is the correlation coefficient between temperature and R_s .-The greater the RI value, the more important photosynthesis is to R_s .

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

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

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

$$RI = \frac{\rho_p}{\rho_t} \quad (34)$$

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. 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.

Measurements of CO_2 fluxes were screened by means of limit checking, i.e., hourly 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 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~~ generated 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 on~~ temperature- R_s hysteresis. ~~Further on~~ Likewise, influences of SWC on diel hysteresis was examined ~~in during~~ 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). 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 ~~showed clear and stable diel~~ 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 environmental factors, diel patterns in R_s remained ~~stable-constant~~ over the non-growing ~~season~~ part of the year, peaking at 11:00 AM-13:00 PM, and ~~being~~ 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 ~~Relative control~~ Control of photosynthesis and temperature on diel soil respiration

Among temperatures at the three ~~soil depths~~ levels, T_{surf} correlated best-the strongest 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 fairly well with photosynthesis (Table 1). The response of R_s to temperature and photosynthesis was shown to be 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 via Eq. 1), whereas photosynthesis explained 67% of ~~it that~~ same variation (Fig. 3a, Table 2). However, during the dry ~~season-month, with precipitation of 10.9 mm~~, photosynthesis explained 88% of the variation in diel R_s , ~~(by way of via Eq. 2), whereas whereas~~ T_{surf} explained 76% of ~~it 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). ~~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 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) ~~relationships were~~ shown to be affected by SWC (Fig. 5b). ~~In 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, 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 growing season, ~~the~~ diel hysteresis between R_s and T_{surf} was linearly related to SWC in a downward manner, when $SWC < 0.08 \text{ m}^3 \text{ m}^{-3}$ (ratio of SWC to soil porosity = 0.26; Fig. 6a~~Fig. 5a~~). Hysteresis was not evident. No hysteresis was observed when $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ (Fig. 5a6a). In contrast, diel hysteresis between R_s and photosynthesis was linearly related to SWC in an upward manner, when $SWC < 0.08 \text{ m}^3 \text{ m}^{-3}$ (Fig. 5b6b), but ceased to be related, when $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ ($p = 0.439$; Fig. 5b6b).

4 Discussion

4.1 Physical- vs. biological-~~processes in the controls~~ of on diel hysteresis

In our study, we found that the diurnal pattern in temperature (T_a , T_{surf} , and T_s) lagged behind ~~that in R_s , 0-4 hours~~ 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 depth temperature measurements, their seasonal variation was generally uniformeconsistent. Among the temperatures ~~measured~~ measurements, at the three depths, T_{surf} was more closely related to diel R_s , resulting in weaker hysteresis. ~~The m~~ Magnitude of hysteresis between R_s and ~~T_{surf} temperature~~ 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). However, the direction of hysteresis was unlike that reported by Phillips et al. (2011), who had reported R_s lagging behind soil temperature.

~~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.

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 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_g . Heterotrophic respiration has been reported to respond primarily to soil surface temperature (Lloyd and Taylor, 1994; Winkler et al., 1996). Therefore, diel R_g 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_g . Since root respiration has been reported to be firmly associated with photosynthesis (Liu et al., 2006; Baldocchi et al., 2006; Högberg and Read, 2006; Kuzyakov and Gavrihkova, 2010), it is not surprising that R_g 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_g , 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_g 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_g 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_g to night time respiration temperature relationships. This would involve more complex, iterative methods than are currently used because of the implied feedback.

The 0-4 h lag between R_g and photosynthesis observed are consistent with those observed in earlier studies, e.g., 0-4 h lag between ecosystem-level photosynthesis and R_g in a coastal wetland ecosystem (Han et al., 2014) and 0-3 h lag between plant photosynthesis and R_g in a steppe ecosystem (Yan et al., 2011). Short lag times suggest rapid response between recent photosynthesis and R_g (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; 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_g 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 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 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; Hödtä et al., 2006, 2009; Mencuccini and Hödtä 2010). Variations in coupling dynamics may occur because of differences in vegetation height among ecosystems (Kuzyakov and Gavrichova, 2010; Mencuccini and Hödtä 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

Diel R_s varied consistently with T_{surf} , with no observable signs of hysteresis, 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 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 $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$, 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 (Balocchi 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 $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ (Fig. 6a). By contrast, during dry and hot phases, with $SWC < 0.08 \text{ m}^3 \text{ m}^{-3}$, 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 $0.08 \text{ m}^3 \text{ m}^{-3}$ (Fig. 6b).

The $0.08 \text{ m}^3 \text{ m}^{-3}$ 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 $0.08 \text{ m}^3 \text{ m}^{-3}$. 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 $0.11 \text{ m}^3 \text{ m}^{-3}$. 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 $0.08 \text{ m}^3 \text{ m}^{-3}$.

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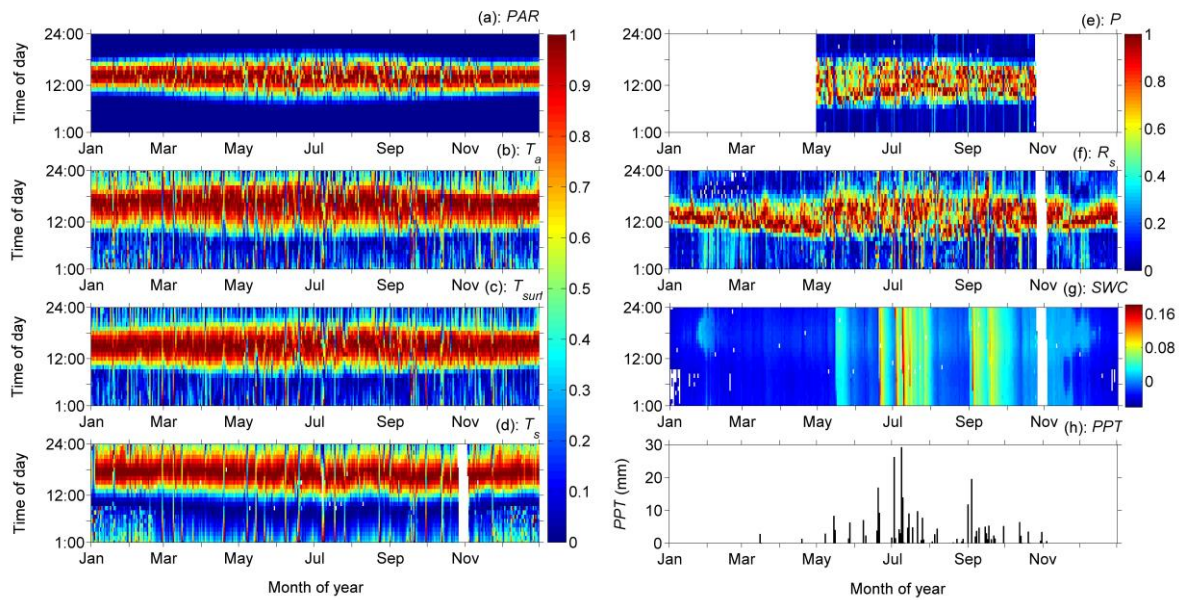
Table 1. Analysis of mean monthly diel cycles of soil respiration (R_s), air temperature (T_a), soil surface temperature (T_{surf}), soil temperature at a 10-cm depth (T_s), and photosynthesis (P) in a dominant desert-shrub ecosystem, including correlation coefficients and lag times in R_s vs. T_a ,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

5

		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} -~~and~~, linear, and Q_{10} -linear functions 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}-R_s-R_s-T	Q_{10}	$R_s = 1.13 \times 1.4^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.97$ $RMSE = 0.0521$	$R_s = 1.12 \times 1.1^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.76$ $RMSE = 0.0796$
P-R_s-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	<u>Linear</u> \times <u>Q_{10}</u>	$R_s = (0.002 \times P + 1.16) \times 1.38^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.98$ $RMSE = 0.0491$	$R_s = (0.024 \times P + 1.20) \times 1.08^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.94$ $RMSE = 0.0408$



5 **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 at an *Artemisia ordosica*-dominant 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 the a given day and 0, the daily minimum value.

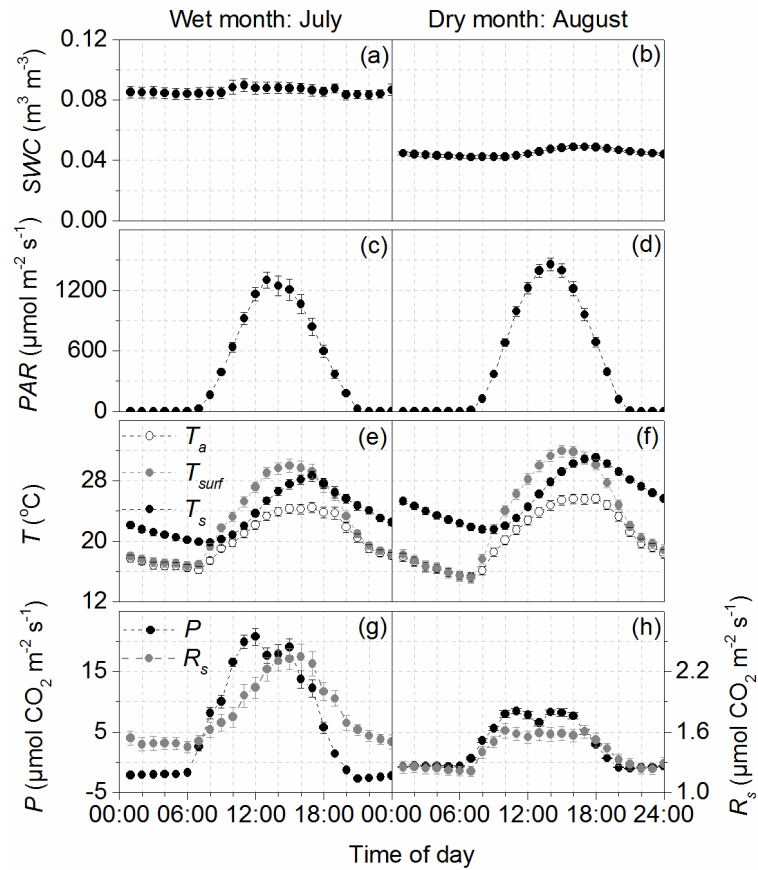


Figure 2. Mean monthly diel cycle of soil water content (SWC), incident photosynthetically active radiation (PAR), temperature [air temperature (T_a), soil surface temperature (T_{surf}), soil temperature (T_s)], soil respiration (R_s), and photosynthesis (P) in at Artemisia ordosica-dominated site during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

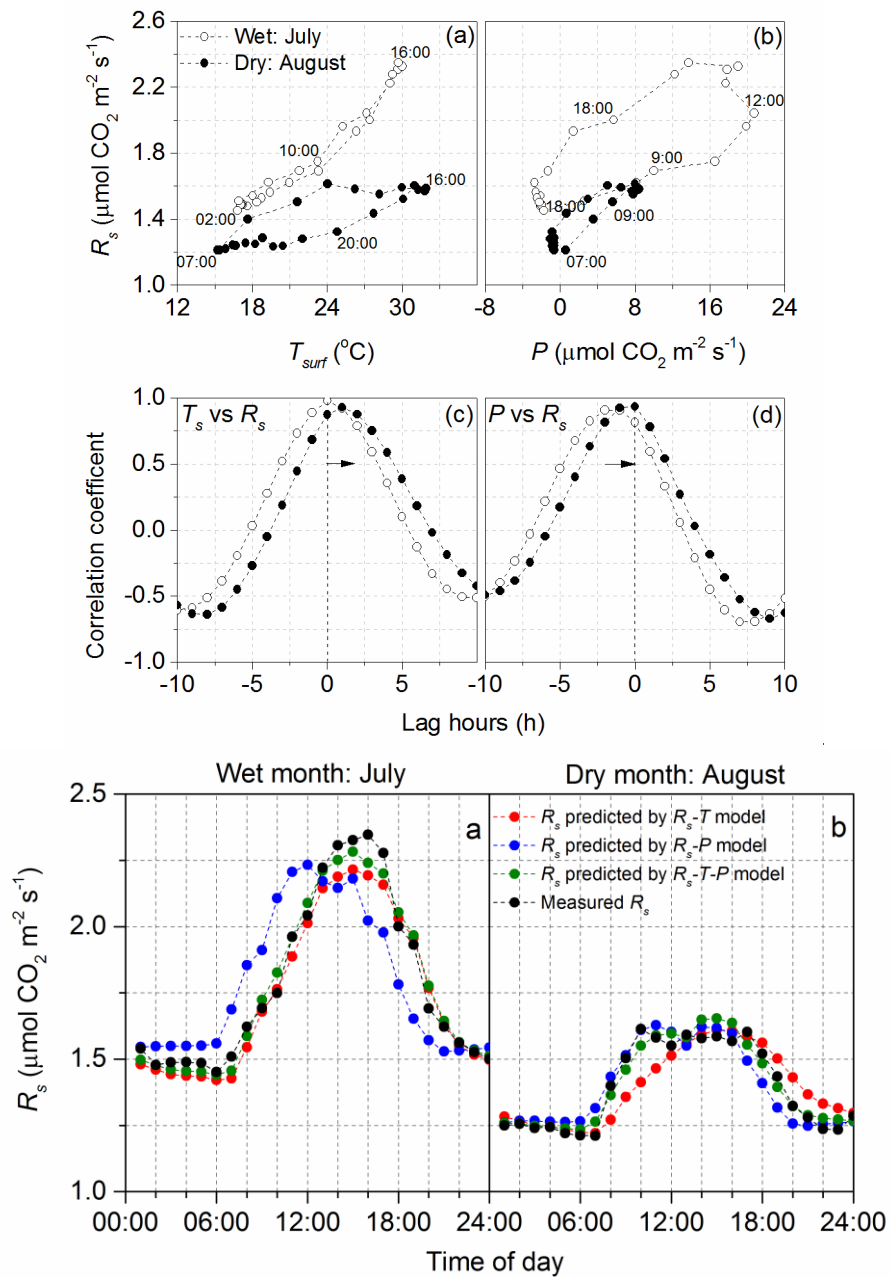


Figure 3. Diel variation of measured soil respiration (R_s) and modeled R_s by using temperature and photosynthesis as input variables in the calculation of R_s for both a wet and dry month (i.e., July and August, respective); R_s - T function (Eq. 1), R_s - P function (Eq. 2), and R_s - T - P function (Eq. 3), 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.

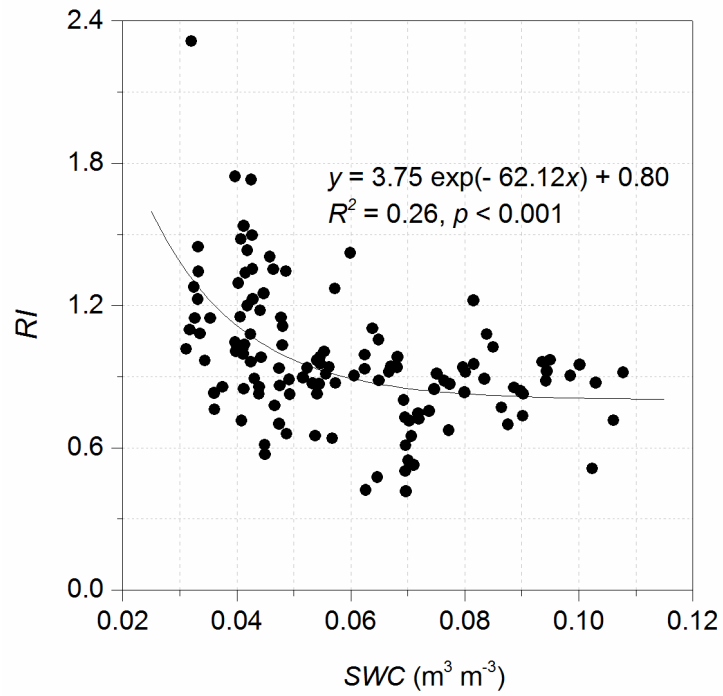


Figure 4. Relationship between soil water content (SWC) and the relative importance (RI) of soil surface temperature and photosynthesis ~~in~~ at an *Artemisia ordosica*-dominated site -as a function of ~~with respect to~~ diel soil respiration (R_d).

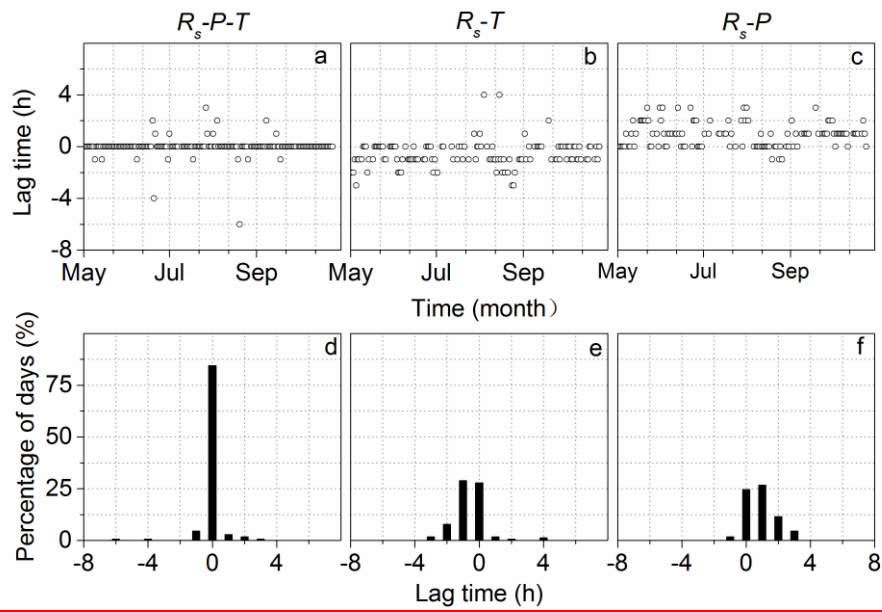


Figure 5. Lag times between measured and modeled soil respiration by means of soil surface temperature and photosynthesis over the growing season; R_s-T function (Eq. 1), R_s-P function (Eq. 2), and R_s-P-T function (Eq. 3).

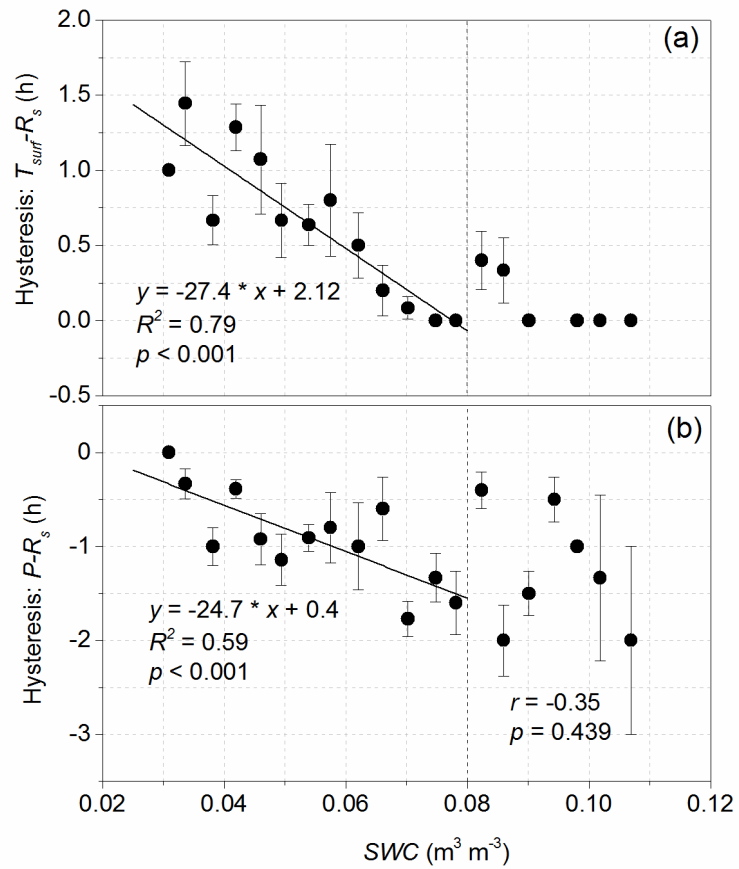


Figure 65. Lag times between soil respiration (R_s) and soil surface temperature (T_{surf}), R_s , and photosynthesis ~~in at an~~ *Artemisia ordosica*-~~dominated site with respect and in relation~~ to soil water content (SWC). Lag times were bin-averaged using SWC-intervals of $0.004 \text{ m}^3 \text{m}^{-3}$.