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

Ben Wang[1,2], TianShan Zha[*1], Xin Jia[1,2], JinNan Gong[2], Charles Bourque[3], Wei Feng[1], Yun Tian[1], Bin Wu[1], YuQing Zhang[1], Heli Peltola[2]

[1]Yanchi Research Station, School of Soil and Water Conservation, Beijing Forestry University. Beijing 100083, PR China.
[2]School of Forest Sciences, University of Eastern Finland. PO Box 111, FIN-80101 Joensuu, Finland.
[3]Faculty of Forestry and Environmental Management, University of New Brunswick, PO Box 4400, 28 Dineen Drive, Fredericton, New Brunswick, E3B 5A3, Canada

*Correspondence to*: TianShan Zha (tianshanzha@bjfu.edu.cn)

**Abstract.** No consensus has been reached on the causes of diel hysteresis between soil respiration ($R_s$) and temperature. 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 investigated. 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 over an entire year in 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 $SWC > 0.08$ m$^3$ m$^{-3}$. However, as $SWC$ decreased below $0.08$ m$^3$ m$^{-3}$ (ratio of $SWC$ to soil porosity = 0.26), 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 shown that $SWC$ was responsible for regulating the relative control between photosynthesis and temperature on diel $R_s$, resulting in seasonal variation in hysteresis. Our findings highlight the importance of biological mechanisms and the role of $SWC$ in regulating diel hysteresis between $R_s$ and temperature. We recommend further studies to explore the actual mechanisms involved in explaining changes in the relative contribution of autotrophic and heterotrophic respiration to total $R_s$. These studies may help elucidate the role of $SWC$ in affecting seasonal variation in diel hysteresis.

# 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 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 $CO_2$ fluxes and their responses to climate change, it is necessary to understand the biophysical mechanisms that play 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; Phillips et al., 2011; Zhang et al., 2015). Generally, soil $CO_2$ fluxes are measured at the soil surface and 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 peaks in the afternoon (e.g., 14:00-16:00). These studies point out the need 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). Physical and biological processes that relate to the production and transport of $CO_2$ gas in soils are not mutually exclusive and 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 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 consistent. Based on the Millington-Quirk model, high $SWC$ block $CO_2$ 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 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 hysteresis, the role of $SWC$ needs to be studied.

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). 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) and, in general, conclude that diel hysteresis can result from physical processes alone. In contrast, 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 diel 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). Therefore, 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 porosity, the influence of $SWC$ on gas diffusion is likely minimized. In general, most 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 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 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 has a role in controlling hysteresis between $R_s$ and $T_s$; and (2) $SWC$ regulates the control of photosynthesis 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 $SWC$ influences diel hysteresis. To undertake this work, we measured $R_s$, $SWC$, $T_s$, and photosynthesis continuously in a desert-shrub ecosystem over an entire year in 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 $1.4 \times 10^{-5}$ MJ m$^{-2}$ and annual potential evaporation was on average $5.5 \times 10^{-3}$ kg m$^{-2}$ d$^{-1}$. 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 cm and 5-25 cm depth 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). At the study site, over 80% of soil organic matter and soil nitrogen was concentrated in the first 10 cm of the soil. The vegetation was regenerated from aerial seeding that took place in 1998 and is currently dominated by a semi-shrub cover of

5  *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

10  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 ($\mu$mol $CO_2$ m$^{-2}$ s$^{-1}$) was directly estimated from $CO_2$-flux measurements obtained with the opaque-chamber system. Photosynthetic rates ($\mu$mol $CO_2$ m$^{-2}$ s$^{-1}$) of the selected plants were determined as the difference in $CO_2$ fluxes between the transparent- and the opaque-chamber.

Continuous measurements of $CO_2$ fluxes ($\mu$mol $CO_2$ m$^{-2}$ s$^{-1}$) were made *in situ* over an entire year with a Li-8100 $CO_2$

15  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 $CO_2$-flux data collected over 2013 were used in our analysis.

20  ## 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 $EC_{H2O}$ 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 flux tower approximately 800 m from our soil $CO_2$-flux measurement site. Air temperature ($T_a$, $^{o}$C)

25  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 gauges (Model TE525MM, Campbell Scientific Inc., USA) placed 50 m from the flux tower (see Jia et al., 2014).

30  ## 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)). The instantaneous relative importance (*RI*) of photosynthesis to temperature in controlling $R_s$ over the growing season is calculated with a correlation-based ratio (Eq. (3)). As *RI* increases, the more important photosynthesis is to $R_s$:

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

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

$$RI = \frac{\rho_p}{\rho_t} \tag{3}$$

where $R_{10}$ is the respiration at $10^\circ C$, $Q_{10}$ is the temperature sensitivity of respiration, $T$ is temperature, $P$ is photosynthesis ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$), $a$ and $b$ are regression coefficients, and $\rho_p$ and $\rho_t$ 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 $> 15\ \mu mol$ $CO_2\ m^{-2}\ s^{-1}$ were considered to be anomalous as a result of, for instance, gas leakage or plant damage by insects and 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 equally 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 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 temperature-$R_s$ hysteresis. Furthermore, 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

5

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 the environmental factors, diel patterns in $R_s$ remained constant over the non-growing part of the year, peaking at 11:00 AM-13:00 PM, and being highly variable during the rest of the year, peaking between 10:00 AM-16:00 PM (Fig. 1f). Similar to $R_s$ during the growing season, diel patterns in photosynthesis were also highly variable, peaking between 10:00 AM-16:00 PM (Fig. 1e). Diel patterns in monthly mean $R_s$ were similar to those in $T_{surf}$ during the wet month and similar to those in photosynthesis during the dry month (Fig. 2g, h).

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

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 $R_s$ correlated fairly well 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 the variation (Fig. 3a, Table 2). However, during the dry 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 the variation (Fig. 3b, Table 2). Over the growing season, $RI$ of photosynthesis and temperature to $R_s$ was significantly affected by $SWC$ (Fig. 4), decreasing 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), 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, having similar timing to $T_{surf}$ (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 $SWC$ when $SWC$ < 0.08 m$^3$ m$^{-3}$ (ratio of $SWC$ to soil porosity = 0.26; Fig. 5a). No hysteresis was observed when $SWC$ > 0.08 m$^3$ m$^{-3}$ (Fig. 5a). In contrast, diel hysteresis between $R_s$ and photosynthesis was linearly related to $SWC$ when $SWC$ < 0.08 m$^3$ m$^{-3}$ (Fig. 5b), but ceased to be related when $SWC$ > 0.08 m$^3$ m$^{-3}$ ($p$ = 0.439; Fig. 5b).

### 4 Discussion

### 4.1 Physical vs. biological controls of diel hysteresis

In our study, we found that the diurnal pattern in temperature ($T_a$, $T_{surf}$, and $T_s$) lagged behind that in $R_s$ by several hours, which resulted in a counterclockwise loop in the relationship between $R_s$ and temperature. Although the magnitude of diel hysteresis between $R_s$ and temperature differed among the three temperature measurements, their seasonal variation was generally consistent. Among the temperature measurements, $T_{surf}$ was more closely related to diel $R_s$, resulting in weaker hysteresis. The magnitude of hysteresis between $R_s$ and $T_{surf}$ was 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 propensity to affect within-soil gas transport, resulting in physical properties of the soil having greater control on diel hysteresis. High $SWC$ tends to block gas transport, leading to greater hysteresis than under low $SWC$. However, at our site, sandy soils with high porosity, $SWC$ was lower ($< 0.15$ m$^3$ m$^{-3}$, Fig 1). According to the Millington-Quirk model (Millington and Quirk, 1961), changes in $SWC$ may have minor influences on within-soil gas transport processes. As a result, 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 patterns in $R_s$ generally followed those of photosynthesis under low $SWC$, resulting in a large hysteresis between $R_s$ and temperature (Fig. 2). Our results confirm the importance of biological processes in regulating diel hysteresis addressed in other studies (e.g., Högberg et al., 2001; Tang et al., 2005; Sampson et al., 2007; Kuzyakov and Gavrichkova, 2010; Mencuccini and Höltta, 2010). This relationship is consistent with our first hypothesis.

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

Earlier studies report that the rate of photosynthate transport, along with plant height, are important factors in determining the level of seasonal variation in diel hysteresis (Kuzyakov and Gavrichkova, 2010). Plant height is shown by other researchers to correlate fairly well to differences in diel hysteresis in various ecosystems (Kuzyakov and Gavrichkova, 2010). Height growth in *Artemisia ordosica* is generally slow, at about 3-4 cm yr$^{-1}$ for our site. This suggests that plant height potentially played a minor role in affecting seasonal variation in diel hysteresis. Moreover, phloem transport rates vary from 0.2 to 2 m h$^{-1}$ (Kuzyakov and Gavrichkova, 2010), suggesting that maximum delay in hysteresis by photosynthate transport alone should be about 30 min. This is clearly incompatible with our own findings, where lag times could be as large as 5 h (Table 1).

In our study, 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 $SWC$ regulation of hysteresis 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 $SWC$. For example, the birth effect, which claims there is a burst of decomposition of soil organic matter and corresponding $CO_2$ gas release after soil re-wetting by precipitation (Jarvis et al., 2007). In our study, the periods with $SWC > 0.08$ m$^3$ m$^{-3}$ only lasted several days (Fig. 1g, h). Resource pool accumulation on the surface of the soil may have resulted from microbial growth and nutrient mineralization between successive precipitation events (Fisher et al., 1987). Most organic material and microbes decomposing the material tend to concentrate in the upper part of the soil (Ciais et al., 2011; Thomas, 2012; Gao et al., 2014), whereas plant roots are found much deeper. Consequently, wet periods with $SWC > 0.08$ m$^3$ m$^{-3}$ can be responsible for heightened 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 $R_s$ should co-varied much more strongly with $T_{surf}$, eliminating hysteresis altogether when $SWC > 0.08$ m$^3$ m$^{-3}$. By contrast, dry periods with $SWC < 0.08$ m$^3$ m$^{-3}$ often occurred between successive precipitation events (Fig. 1g, h). Heterotrophic respiration is 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 strongly associated with photosynthesis (Liu et al., 2006; Baldocchi et al., 2006; Högberg and Read, 2006; Kuzyakov and Gavrihkova, 2010), it is not surprising that $R_s$ 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 as an indirect confirmation of 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 $R_s$, which is also consistent with our findings.

Our work provides urgently needed new information 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 m$^3$ m$^{-3}$ (ratio of SWC to soil porosity = 0.26). 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 commonly in practise. This would involve more complex, iterative methods, than what is currently being used because of the implied feedbacks that would be involved.

## 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$^{-3}$ (ratio of $SWC$ to soil porosity = 0.26), 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.

## References

Austin, A. T.: Has water limited our imagination for aridland biogeochemistry?, Trends Ecol. Evol., 26, 229-235, 2011.

Baldocchi, D., Tang, J. and Xu, L.: How switches and lags in biophysical regulators affect spatial-temporal variation of soil respiration in an oak-grass savanna, J. Geophys. Res-Biogeo., 111, G2, doi:10.1029/2005JG000063, 2006.

Barron-Gafford, G. A., Scott, R. L., Jenerette, G. D. and Huxman, T. E.: The relative controls of temperature, soil moisture, and plant functional group on soil $CO_2$ efflux at diel, seasonal, and annual scales, J. Geophys. Res-Biogeo., 116, G1, doi:10.1029/2010JG001442, 2011.

Bahn, M., Schmitt, M., Siegwolf, R., Richter, A. and Brüggemann, N.: Does photosynthesis affect grassland soil-respired $CO_2$ and its carbon isotope composition on a diurnal timescale?, New Phytol., 182, 451-460, 2009.

Borken, W., Savage, K., Davidson, E. A. and Trumbore, S. E.: Effects of experimental drought on soil respiration and radiocarbon efflux from a temperate forest soil, Global Change Biol., 12, 177-193, 2006.

Ciais, P., Bombelli, A., Williams, M., Piao S. L., Chave, J., Ryan, C. M., Henry, M., Brender, P. and Valentini, R.: The carbon balance of Africa: synthesis of recent research studies, Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences, 369 (1943), 2038-2057, 2011.

Carbone, M. S., Winston, G. C. and Trumbore, S. E.: Soil respiration in perennial grass and shrub ecosystems: Linking environmental controls with plant and microbial sources on seasonal and diel timescales, J. Geophys. Res-Biogeo., 113, G2, doi:10.1029/2007JG000611, 2008.

Casals, P., Lopez-Sangil, L., Carrara, A., Gimeno, C. and Nogués, S.: Autotrophic and heterotrophic contributions to short-term soil $CO_2$ efflux following simulated summer precipitation pulses in a Mediterranean dehesa, Global Biogeochem., Cy., 25, doi:10.1029/2007JG000611, 2011.

Davidson, E. A., Janssens, I. A. and Luo, Y. Q.: On the variability of respiration in terrestrial ecosystems: moving beyond $Q_{10}$, Global Change Biol., 12, 154-164., 2006.

Darenova, E., Pavelka, M. and Acosta, M.: Diurnal deviations in the relationship between $CO_2$ efflux and temperature: A case study, Catena, 123, 263-269, 2014.

Feng, W., Zhang, Y., Wu, B., Qin, S. and Lai, Z.: Influence of environmental factors on carbon dioxide exchange in biological soil crusts in desert areas, Arid Land Res. Manag., 28, 186-196, 2014.

Fisher, F. M., Parker, L. W., Anderson, J. P. and Whitford, W. G.: Nitrogen mineralization in a desert soil: interacting effects of soil moisture and nitrogen fertilizer, Soil Sci., Soc., Am. J., 51, 1033-1041, 1987.

Gao, G. L., Ding, G. D. Zhao, Y. Y., Wu, B., Zhang Y. Q., Qin S. G., Bao, Y. F., Yu, M. H. and Liu, Y. D.: Fractal approach to estimating changes in soil properties following the establishment of *Caragana Korshinskii* shelterbelts in Ningxia, NW China, Ecological indicators, 43, 236-243, 2014.

Gaumont-Guay, D., Black, T. A., Griffis, T. J., Barr, A. G., Jassal, R. S. and Nesic, Z.: Interpreting the dependence of soil respiration on soil temperature and water content in a boreal aspen stand, Agr. Forest Meteorol., 140, 220-235, 2006.

Gaumont-Guay, D., Black, T. A., Barr, A. G., Jassal, R. S. and Nesic, Z.: Biophysical controls on rhizospheric and heterotrophic components of soil respiration in a boreal black spruce stand, Tree Physiol., 28, 161-171, 2008.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Löfvenius, M. and Read, D. J.: Large-scale forest girdling shows that current photosynthesis drives soil respiration, Nature, 411, 789-792, 2001.

Högberg, P. and Read, D. J.: Towards a more plant physiological perspective on soil ecology, Trends Ecol. Evol., 21, 548-554, 2006.

Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J., Miglietta, F., Borghetti, M., Manca, G., Valentini, R.: Drying and wetting of Mediterranean soil stimulates decomposition and carbon dioxide emission: the "Birch effect", Tree physiology, 27, no. 7: 929, 2007.

Jia, X., Zhan, T., Wu, B., Zhang, Y., Chen, W., Wang, X., Yu, H. and He, G.: Temperature response of soil respiration in a Chinese pine plantation: hysteresis and seasonal vs. diel $Q_{10}$, PLoS ONE, 8, e57858. doi:10.1371/journal.pone.0057858, 2013.

Jia, X., Zha, T. S., Wu, B., Zhang, Y. Q., Gong, J. N., Qin, S. G., Chen, G. P., Qian, D., Kellomäki, S. and Peltola, H.: Biophysical controls on net ecosystem $CO_2$ exchange over a semiarid shrubland in northwest China, Biogeosciences, 11, 4679-4693, 2014.

Kuzyakov, Y. and Gavrichkova, O.: Review: Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls, Global Change Biol., 16, 3386-3406, 2010.

Lange, O. L.: Photosynthesis of soil-crust biota as dependent on environmental factors. In: Belnap J, Lange OL, Eds. Biological soil crusts: structure, function, and management. Berlin: Springer. p 217-40, 2003.

Liu, Q., Edwards, N. T., Post, W. M., Gu, L., Ledford, J. and Lenhart, S.: Temperature independent diel variation in soil respiration observed from a temperate deciduous forest, Global Change Biol., 12, 2136-2145, 2006.

Lloyd, J. and Taylor, J. A.: On the temperature dependence of soil respiration, Funct. Ecol., 8, 315-323, 1994.

Mencuccini, M. and Hölttä, T.: The significance of phloem transport for the speed with which canopy photosynthesis and belowground respiration are linked, New Phytol., 185, 189-203, 2010.

Noy-Meir, I.: Desert ecosystems: environment and producers, Annu. Rev. Ecol. Syst., 25-51, 1973.

Oikawa, P. Y., Grantz, D. A., Chatterjee, A., Eberwein, J. E., Allsman, L. A. and Jenerette, G. D.: Unifying soil respiration pulses, inhibition, and temperature hysteresis through dynamics of labile soil carbon and $O_2$, J. Geophys. Res-Biogeo., 119, 521-536, 2014.

Phillips, C. L., Nickerson, N., Risk, D. and Bond, B. J.: Interpreting diel hysteresis between soil respiration and temperature, Global Change Biol., 17, 515-527, 2011.

Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., Broquet, G., Canadell, J. G., Chevallier, F., Liu, Y. Y., Running, S. W., Sitch, S. and Van der Werf, G. R.: Contribution of semiarid ecosystems to interannual variability of the global carbon cycle, Nature, 509, 600-603, 2014.

Riveros-Iregui, D. A., Emanuel, R. E., Muth, D. J., McGlynn, B. L., Epstein, H. E., Welsch, D. L., Pacific, V. J., and Wraith, J. M.: Diurnal hysteresis between soil $CO_2$ and soil temperature is controlled by soil water content, Geophys. Res. Lett, 34, L17404, doi:10.1029/2007GL030938, 2007.

Ruehr, N. K., Offermann, C. A., Gessler, A., Winkler, J. B., Ferrio, J. P., Buckmann, N. and Barnard, R. L.: Drought effects on allocation of recent carbon: from beech leaves to soil $CO_2$ efflux, New Phytol., 184, 950-961, 2009.

Safriel, U. and Adeel, Z.: Dryland ecosystems, II, in: Ecosystems and human well-being: current state and trends, Vol 1, edited by: Hassan, R., Scholes, R., and Neville, A., Island Press, Washington, DC, 623–662, 2005.

Sampson, D. A., Janssens, I. A., Curiel-Yuste, J. and Ceulemans, R.: Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest, Global Change Biol., 13, 2008-2017, 2007.

Song, W., Chen, S., Zhou, Y., Wu, B., Zhu, Y., Lu, Q. and Lin, G.: Contrasting diel hysteresis between soil autotrophic and heterotrophic respiration in a desert ecosystem under different rainfall scenarios, Scientific reports, 5, doi:10.1038/srep16779, 2015.

Song, W., Chen, S., Wu, B., Zhu, Y., Zhou, Y., Lu, Q. and Lin, G.: Simulated rain addition modifies diurnal patterns and temperature sensitivities of autotrophic and heterotrophic soil respiration in an arid desert ecosystem, Soil Biol. Biochem., 82, 143-152, 2015.

Sponseller, R. A.: Precipitation pulses and soil $CO_2$ flux in a Sonoran Desert ecosystem, Global Change Biol., 13, 426-436, 2007.

Stoy, P. C., Palmroth, S., Oishi, A. C., Siqueira, M. B. S., Juang, J-Y., Novick, K. A., Ward, E. J., Katul, G. G., Oren, R.: Are ecosystem carbon inputs and outputs coupled at short time scales? A case study from adjacent pine and hardwood forests using impulse-response analysis, Plant, Cell and Environment, 30, 700-710, 2007.

Tang, J., Baldocchi, D. D. and Xu, L.: Tree photosynthesis modulates soil respiration on a diurnal time scale, Global Change Biol., 11, 1298-1304, 2005.

Thomas, A. D.: Impact of grazing intensity on seasonal variations of soil organic carbon and soil $CO_2$ efflux in two semi-arid grasslands in southern Botswana, Philosophical Transactions of the Royal Society of London B: Biological Sciences, 367(1606), 3076-3086, 2012.

Vargas, R. and Allen, M. F.: Environmental controls and the influence of vegetation type, fine roots and rhizomorphs on diel and seasonal variation in soil respiration, New Phytol., 179, 460-471, 2008.

Vargas, R., Baldocchi, D. D., Bahn, M., Hanson, P. J., Hosman, K. P., Kulmala, L., Pumpanen, J. and Yang, B.: On the multi-temporal correlation between photosynthesis and soil $CO_2$ efflux: reconciling lags and observations, New Phytol., 191, 1006-1017, 2011.

Wang, B., Zha, T. S., Jia, X., Wu, B., Zhang, Y. Q. and Qin, S. G.: Soil moisture modifies the response of soil respiration to temperature in a desert shrub ecosystem, Biogeosciences, 11, 259-268, 2014.

Wang, B., Zha, T. S., Jia, X., Gong, J. N., Wu, B., Bourque, C. P. A., Zhang, Y. Q., Qin, S. G., Chen, G. P. and Peltola, H.: Microtopographic variation in soil respiration and its controlling factors vary with plant phenophases in a desert-shrub ecosystem, Biogeosciences, 12, 5705-5714, 2015.

West, N. E., Stark, J. M., Johnson, D. W., Abrams, M. M., Wight, J. R., Heggem, D. and Peck, S.: Effects of climatic-change on the edaphic features of arid and semiarid lands of western North America. Arid Land Res. Manag., 8, 307-355, 1994.

Winkler, J. P., Cherry, R. S. and Schlesinger, W. H.: The $Q_{10}$ relationship of microbial respiration in a temperate forest soil, Soil Biol. Biochem., 28, 1067-1072, 1996.

Zhang, Q., Katul, G. G., Oren, R., Daly, E., Manzoni, S. and Yang, D.: The hysteresis response of soil $CO_2$ concentration and soil respiration to soil temperature, J. Geophys. Res-Biogeo., 120, 1605-1618, 2015.

**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 |
| | $r$ | **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 models 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.

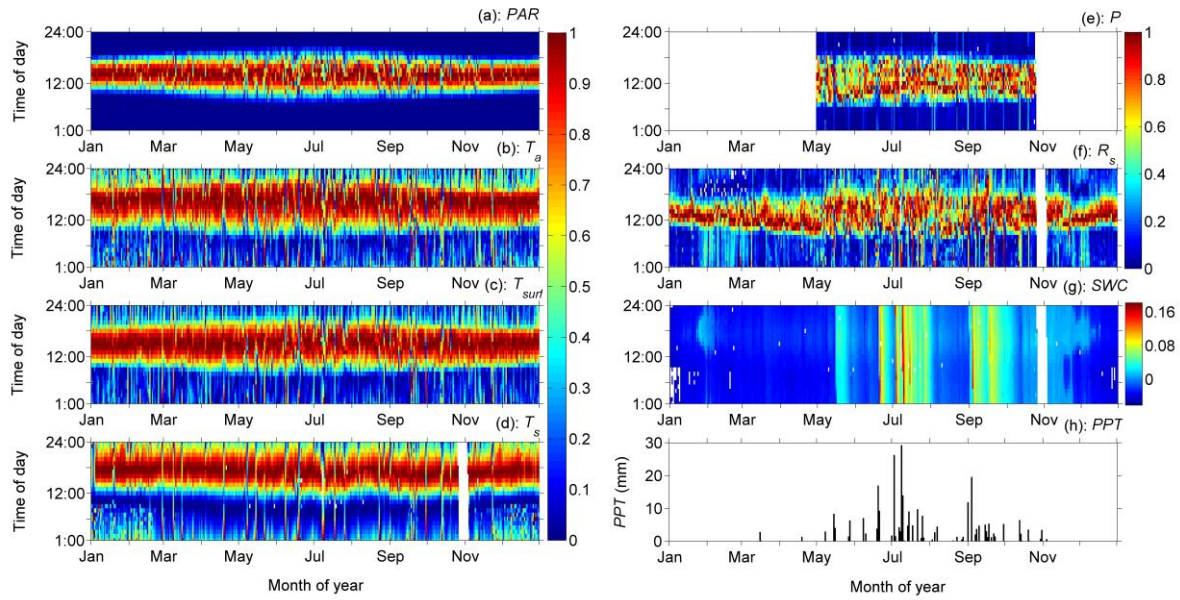| | Model | Wet month: July | Dry month: August |
|---|---|---|---|
| $T_{surf}$-$R_s$ | $Q_{10}$ | $R_s = 1.13 \times 1.4^{\frac{T_{surf}-10}{10}}$ | $R_s = 1.12 \times 1.1^{\frac{T_{surf}-10}{10}}$ |
| | | $R^2 = 0.97$ | $R^2 = 0.76$ |
| | | $RMSE = 0.0521$ | $RMSE = 0.0796$ |
| $P$-$R_s$ | Linear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

**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 a given day and 0, the daily minimum.
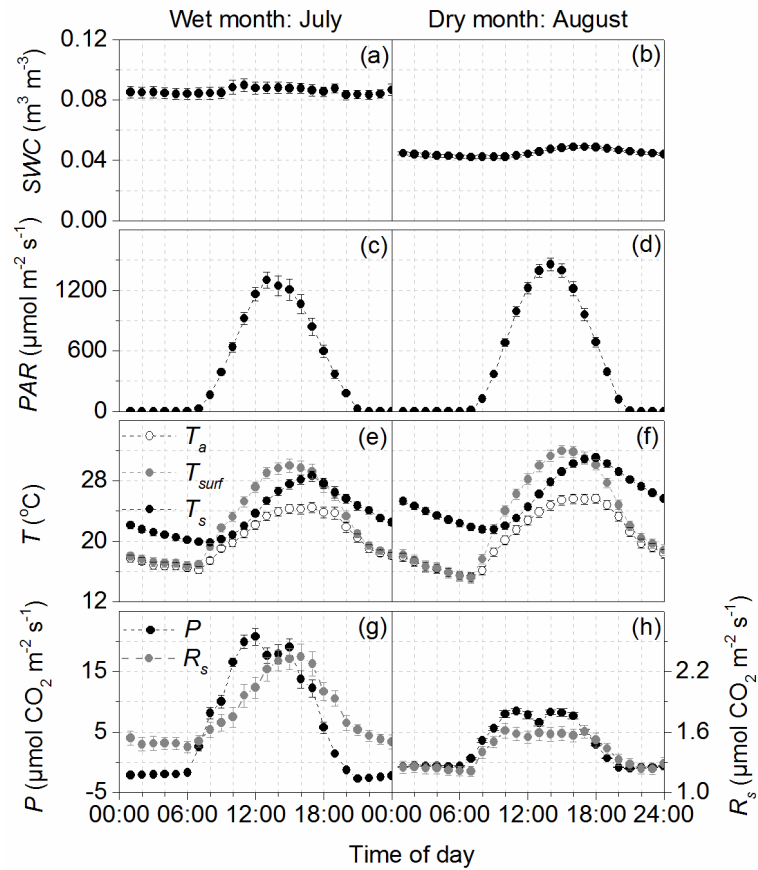
**Figure 2.** Mean monthly diel cycle of soil water content (*SWC*), incident photosynthetically active radiation (*PAR*), temperature [air temperature ($T_a$), soil surface temperature ($T_{surf}$), soil temperature ($T_s$)], soil respiration ($R_s$), and photosynthesis (*P*) in *Artemisia ordosica* during a wet (July) and dry (August) month. Each point is the monthly mean for a particular time of day. Bars represent standard errors.
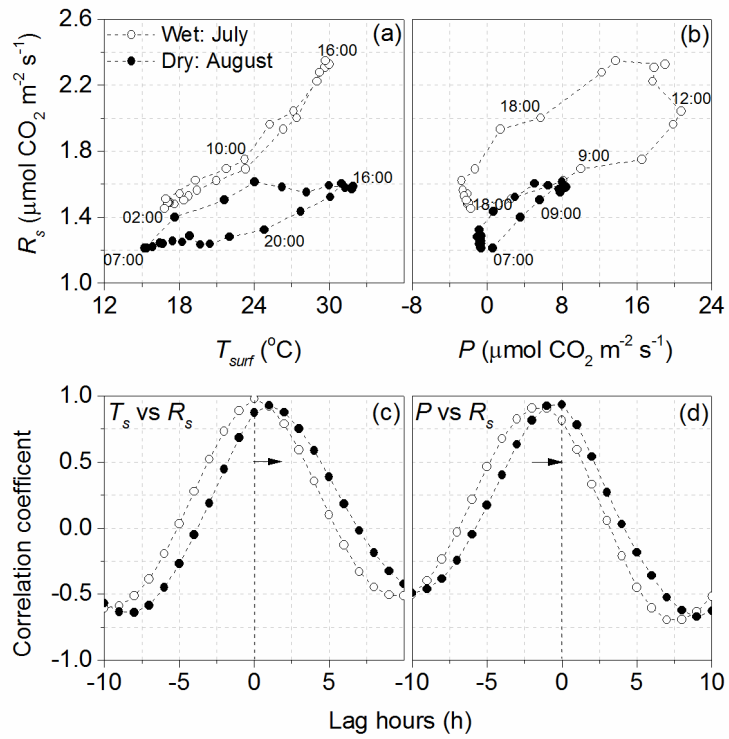
5

**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.
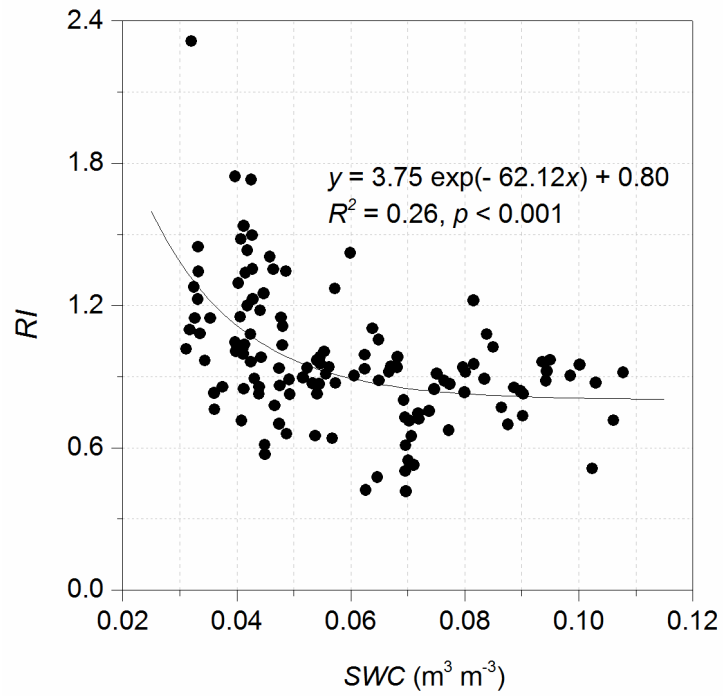
**Figure 4.** Relationship between soil water content (*SWC*) and the relative importance (*RI*) of soil surface temperature and photosynthesis in *Artemisia ordosica* with respect to diel soil respiration.
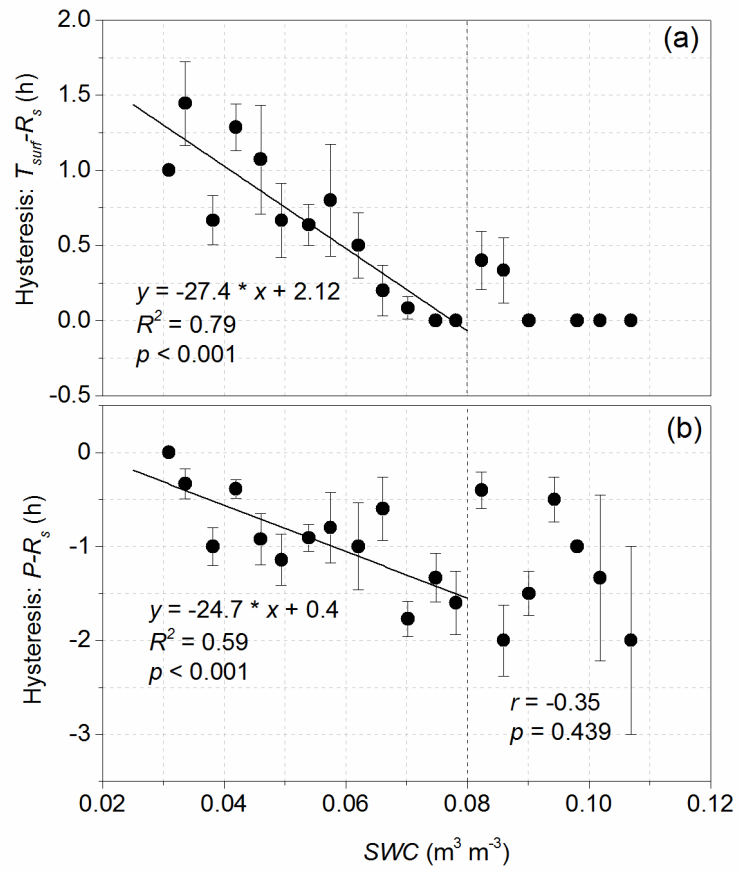
**Figure 5.** Lag time between soil respiration ($R_s$) and soil surface temperature ($T_{surf}$), $R_s$, and photosynthesis in *Artemisia ordosica*, and in relation to soil water content (*SWC*). Lag time were bin-averaged using *SWC*-intervals of 0.004 m$^3$ m$^{-3}$.