Response to editor's comments

We appreciate the editor's thoughtful and constructive comments. We have fully considered the editor's comments in the revised manuscript. Responses to the editor's comments appear below in blue.

Comments to the Author:
The manuscript represents an improvement, but the authors still seem to be affixed to the idea that there is a discrepancy in the literature regarding physical vs. biological controls over soil respiration and erroneously describe manuscripts in the literature as 'contradictory' when no contradiction exists. Physical and biological controls are both important, and their degree of control will differ in different ecosystems. By reframing the manuscript to actually describe the findings of the manuscripts that the authors incorrectly identify as 'contradictory' (see for example page 9 line 5. Eight citations without describing a single one!!!), the authors will be able to contribute to the literature rather than create an artificial debate where little debate exists. There is still an alarming lack of mechanistic reasoning for key passages in the manuscript as described in more detail below. Please note the approach and conclusions of Detto et al. (doi: 10.1086/664628) as it applies to photosynthesis/respiration coupling as you see fit.

Response: We agree that both biological and physical processes are important in the control of hysteresis between R_s and T_s. The manuscript has been reframed to reflect this point.

Our manuscript mainly focuses on the relative degree of control between physical and biological processes on hysteresis. After this study, our next work is to study the coupling of photosynthesis and respiration in desert shrubland. Thanks for the suggestion of Nonparametric Spectral Granger Causality Approach (Detto et al., 2012), which is better than classical correlation analysis with detecting causality in time series data. A second approach, Convergent Cross Mapping (CCM, Sugihara et al., 2012, DOI: 10.1126/science.1227079), may also be useful with detecting causality in complex dynamic systems. Both approaches will be considered in a new paper.

In the title write 'desert shrubland'.
Response: We agree. We have changed 'desert-shrub land' to 'desert shrubland' in the revised manuscript (line 2-3).

I basically disagree with line 12. The implications of Stoy et al. (2007) and other manuscripts is that physical and biological mechanisms cannot be fully separated from photosynthesis / soil respiration measurements because the time scales of biological and physical transport processes are concomitant (see also page 3 line 12). That being said, I agree that there is a substantial role for biology in determining hysteresis. In other words, when you write "Currently, it is not clear whether physical or biological processes (or their combination) dominate the control of diel hysteresis in drylands" it is in fact clear. Both do. The relative degree of control of each is what is of more interest.

By framing the manuscript with respect to the degree of control of physical and biological processes, rather than trying to find out which is the control when both are important, would lead to a much less questionable argument to motivate the analysis.
Response: We agree. The second paragraph in the introduction was reframed (lines 37-53). The sentence was changed to 'it is not clear to what degree physical and biological processes control hysteresis in drylands.' (line 67-68)

On page 2 line 16 (from here on out please always only use continuous line numbering when preparing manuscripts) one might argue that substrate in addition to temperature are equally important for determining soil respiration.
Response: Continuous line numbering has been used in the revised manuscript. We agree that substrate in addition to temperature are important for determining soil respiration. We changed 'but are for the most part' to 'and are' to reduce the argument (line 40). The influences of substrates to R_s has been described as photosynthate supply in the text (line 42-50).

There is no information to support the following statement: "At our study sites, it is likely that R_s-effluxes at the surface originated from biogeochemical processes in the deep soil." There is also no reason to frame the references in the previous sentence (p9 L5) to be 'contradictory'. The authors still seem like they are trying to solve some challenge in science with respect to physical vs. biological controls over soil respiration. Because both are important, this isn't a particularly useful way of thinking about the processes at hand.
Response: We agree, both sentences have been deleted from the text (line 203-206).

On page 9 line 20, please describe how these processes could occur on the order of minutes in sandy soils.
Response: We agree. Based on our latest revision, the manuscript focuses on the degree of control of photosynthesis on hysteresis. Thus, we have deleted discussion on the control of physical processes, due to lack of data and analysis (line 214-219).

Please cite Jorge's name as "Curiel Yuste" correctly on page 11 line 20.
Response: We agree. Jorge's name has been correctly revised in the manuscript (line 255 and 302).

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

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Abstract. Explanations for the occurrence of hysteresis (asynchronicity) between diel soil respiration (R_s) and soil temperature (T_s) have evoked both biological and physical mechanisms. The specifics of these explanations, however, tend to vary with the particular ecosystem or biome being investigated. So far, the ~~cause of such~~relative degree of control of biological and physical processes on hysteresis is not ~~properly addressed~~clear for drylands. This study examined the seasonal variation in diel hysteresis and its biological control ~~controlling factors~~ in a desert-shrub ecosystem in northwest (NW) China. The study was based on continuous measurements of R_s, air temperature (T_a), temperature at the soil surface and below (T_{surf} and T_s), volumetric soil water content (SWC), and photosynthesis in a dominant desert shrub (i.e., *Artemisia ordosica*) over an entire year in 2013. Trends in diel R_s were observed to vary with SWC over the growing season (April to October). Diel variations in R_s were more closely associated with variations in T_{surf} than with photosynthesis as SWC increased, leading to R_s being in phase with T_{surf}, particularly when $SWC > 0.08$ m^3 m^{-3} (ratio of SWC to soil porosity = 0.26). However, as SWC decreased below 0.08 m^3 m^{-3}, diel variations in R_s were more closely related to variations in photosynthesis, leading to pronounced hysteresis between R_s and T_{surf}. Incorporating photosynthesis into a Q_{10}-function eliminated 84.2% of the observed hysteresis, increasing the overall descriptive capability of the function. Our findings highlight ~~the~~ a ~~importance~~ high degree of control by photosynthesis and ~~the role of~~ SWC in regulating seasonal variation in diel hysteresis between R_s and temperature.

1 Introduction

27 Diel hysteresis (asynchronicity) between soil respiration (R_s) and soil temperature (T_s) is widely documented for forests

28 (Tang et al., 2005; Gaumont-Guay et al., 2006; Riveros-Iregui et al., 2007; Stoy et al., 2007; Vargas and Allen, 2008; Jia et

29 al., 2013), grasslands (Carbone et al., 2008; Barron-Gafford et al., 2011), and desert ecosystems (Wang et al., 2014; Feng et

30 al., 2014). Diel hysteresis, which appears as an elliptical loop in the relationship between R_s and T_s, is difficult to model with

31 theoretical functions, such as the Q_{10}, Lloyd-Taylor, Arrhenius, or van't Hoff functions (Lloyd and Taylor, 1994; Winkler et

32 al., 1996; Davidson et al., 2006; Phillips et al., 2011; Oikawa et al., 2014). ~~Diel hysteresis is also not currently addressed in~~

33 ~~the Q_{10} function for low soil water conditions~~, leading to an inadequate understanding of temperature-sensitivity in R_s

34 (Gaumont-Guay et al., 2008; Phillips et al., 2011; Darenova et al., 2014). Therefore, in order to accurately predict soil carbon

35 dioxide (CO_2) fluxes and their responses to climate change, it is necessary to understand the biophysical mechanisms that

36 have a role in controlling seasonal variation in diel hysteresis.

37 Over decades of research, two main processes have been reported to relate to ~~lines of reasoning have been proposed to~~

38 ~~explain the causes of~~ diel hysteresis between R_s and T_s. One ~~line~~ is associated with ~~based on~~ the physical processes of heat

39 and gas transport in soils (Vargas and Allen, 2008; Phillips et al., 2011; Zhang et al., 2015). Generally, soil CO_2 fluxes are

40 measured at the soil surface, ~~but are~~ and are ~~for the most part~~ related to temperatures in the soil. Transport of CO_2 gas to the

41 soil surface takes time to occur, which may cause delays to appear in observed respiration rates, causing hysteretic loops to

42 form between R_s and T_s (Zhang et al., 2015). The other is associated with the biological process of ~~However, in recent years,~~

43 ~~a second line of reasoning has emerged, which puts more importance on the role of biological initiators associated with~~

44 photosynthate supply (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011; Wang et al., 2014). Beyond

45 the control of temperature, ~~Aboveground~~ soil CO_2 fluxes have been associated with plant photosynthesis~~,~~. ~~which~~

46 Photosynthesis usually peaks at midday (e.g., 11:00-13:00), ~~provides~~ providing substrate for belowground roots and

47 rhizosphere-microbe respiration, but oscillates out of phase with T_s, usually peaking in the afternoon (e.g., 14:00-16:00).

48 Such influences of current photosynthesis could lead to the formation of hysteretic loops in the relationship between R_s and

49 T_s. These studies highlight the need to consider the inherent role of photosynthesis for a more accurate interpretation of R_s

50 (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011). Physical and biological processes that relate to

51 substrates and production-transport of carbon (C) in plants and soils are not mutually exclusive and both likely play crucial

52 roles in affecting diel variation in R_s (Stoy et al., 2007; Phillips et al., 2011; Zhang et al., 2015; Song et al., 2015a, b).

53 ~~Currently, causes of diel hysteresis between R_s and soil temperature remain largely unexplained.~~

54 Diel hysteresis between R_s and T_s has been shown to vary seasonally with soil water content (SWC; Tang et al., 2005;

55 Riveros-Iregui et al., 2007; Carbone et al., 2008; Vargas and Allen, 2008; Ruehr et al., 2009; Wang et al., 2014). However,

56 the influences of SWC on diel hysteresis are not uniform. Based on the Millington-Quirk model, high SWC blocks CO_2 gas

57 and thermal diffusion (Millington and Quirk, 1961), resulting in large hysteresis loops (Riveros-Iregui et al., 2007; Zhang et

58 al., 2015). In contrast, other studies have reported that low SWC and high water vapor pressure deficits (VPD) can promote

59 partial stomata closure, which leads to higher photosynthesis in the morning (e.g., 9:00-10:00) and supressed photosynthesis

60 in mid-afternoon, leading to pronounced hysteresis during dry periods (Tang et al., 2005; Vargas and Allen, 2008; Carbone

61 et al., 2008; Wang et al., 2014). Clearly to understand the causes of diel hysteresis, the role of *SWC* needs to be closely

62 ~~scrutinized~~evaluated.

63   Drylands cover a quarter of the earth's land surface and play an important role in the global C cycle (Safriel and Adeel,

64 2005; Austin, 2011; Poulter et al., 2014). Many studies in forest ecosystems are based on the application of physical soil CO_2

65 and heat transport models and evaluate the influences of *SWC* on CO_2-gas and thermal diffusion (Riveros-Iregui et al., 2007;

66 Phillips et al., 2011; Zhang et al., 2015). In general, many of these studies conclude that diel hysteresis is the result of

67 physical processes alone. Few studies have evaluated the causes of diel hysteresis in drylands. Currently, it is not clear to

68 what degree ~~whether~~ physical ~~or~~ and biological processes ~~(or their combination) dominate the~~ control ~~of~~ hysteresis in

69 drylands.

70   Drylands are characterized with low productivity. As weak organic C-storage pools (West et al., 1994; Lange, 2003),

71 drylands are noted for their large contribution of autotrophic production of CO_2. The autotrophic component of R_s occurs as a

72 direct consequence of root respiration, which is firmly coupled (within several hours) to recent photosynthesis (Liu et al.,

73 2006; Baldocchi et al., 2006; Högberg and Read, 2006; Bahn et al., 2009; Kuzyakov and Gavrichkova, 2010). Consequently,

74 photosynthesis may govern the level of variation in asynchronicity between R_s and T_s in drylands. In drylands, especially in

75 desert ecosystems characterized by sandy soils ~~of~~ with high soil porosity, the influence of *SWC* on gas diffusion is likely

76 ~~minimized~~nominal. As a rule, most of the available water is used directly in sustaining biological activity in drylands (Noy-

77 Meir, 1973). Under drought conditions, stomata closure in plants at midday reduces water losses, resulting in a

78 corresponding suppression of photosynthesis (Jia et al, 2014). Such changes in diel patterns of photosynthesis likely result in

79 modifications of patterns in R_s, leading to hysteresis between R_s and T_s. Soil water content likely regulates photosynthesis

80 and, in so doing, causes hysteresis between R_s and T_s to vary over the growing season.

81   In this study, we hypothesize that: (1) photosynthesis has a ~~role~~ high degree of ~~in controlling~~ control in the formation of

82 ~~hysteresis~~ hysteretic loops between R_s and T_s; and (2) *SWC* regulates ~~that~~ this control and its variation over the growing

83 season. The main objectives of this research were to: (1) ~~identify the physical and~~assess biological controls on diel hysteresis

84 between R_s and T_s; (2) explore the causes that lead to variation in seasonal variation in diel hysteresis; and (3) understand

85 *SWC*'s role in influencing ~~diel~~ hysteresis. To undertake this work, we measured R_s, *SWC,* T_s, and photosynthesis in a

86 dominant desert-shrub on a continuous basis for 2013.

87 **2 Materials and Methods**

88 **2.1 Site description**

89 The study was conducted at Yanchi Research Station of Beijing Forestry University, Ningxia, northwest China (37°42'31" N,

90 107°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

91 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 8.1ºC and the mean annual total precipitation was 292 mm (ranging between 250 to 350 mm), 63% of which fell in late summer (i.e., July-September; Wang et al., 2014; Jia et al., 2014). Annual potential evaporation was on average 5.5 kg m^{-2} d^{-1} (Gong et al., 2016). The soil at the research station was of a sandy type, with a bulk density of 1.6 g cm^{-3}. The total soil porosity within 0-2 and 5-25 cm depths was 50% and 38%, respectively. Soil organic matter, soil nitrogen, and pH were 0.21-2.14 g kg^{-1}, 0.08-2.10 g kg^{-1}, and 7.76-9.08, respectively (Wang et al., 2014; Jia et al, 2014). The vegetation was regenerated from aerial seeding applied in 1998 and is currently dominated by a semi-shrub species cover of *Artemisia ordosica*, averaging about 50-cm tall with a canopy size of about 80 cm × 60 cm (for additional site description, consult Jia et al. 2014 and Wang et al. 2014 ~~and~~, 2015).

2.2 Soil respiration and photosynthesis measurement

Two permanent polyvinyl chloride soil collars were initially installed on a small fixed sand dune in March, 2012. Collar dimensions were 20.3 cm in diameter and 10 cm in height, with 7 cm inserted into the soil. One collar was set on bare land with an opaque chamber (LI-8100-104, Nebraska, USA) and the other over an *Artemisia ordosica* plant (~10 cm tall) with a transparent chamber (LI-8100-104C). Soil respiration (µmol CO_2 m^{-2} s^{-1}) was directly estimated from CO_2-flux measurements obtained with the opaque-chamber system. Photosynthetic rates (µmol CO_2 m^{-2} s^{-1}) of the selected plants were determined as the difference in CO_2 fluxes obtained with the transparent and opaque chambers.

Continuous measurements of CO_2 fluxes (µmol CO_2 m^{-2} s^{-1}) were made *in situ* with a Li-8100 CO_2-gas analyzer and a LI-8150 multiplexer (LI-COR, Nebraska, USA) connected to each chamber. Instrument maintenance was carried out bi-weekly during the growing season, including removing plant-regrowth in the opaque-chamber installation, and cleaning to avoid blackout conditions associated with the transparent chamber. Measurement time for each chamber was 3 minutes and 15 seconds, including a 30-second pre-purge, 45-second post-purge, and 2-minute measurement period.

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

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

2.4 Data processing and statistical analysis

In this study, CO_2-flux measurements were screened by means of limit checking, i.e., hourly CO_2-flux data < -30 or > 15 µmol CO_2 m^{-2} s^{-1} were considered to be anomalous as a result of, for instance, gas leakage or plant damage by insects, and removed from the dataset (Wang et al., 2014, 2015). After limit checking, hourly CO_2 fluxes greater than three times the standard deviation from the calculated mean of 5 days' worth of flux data were likewise removed. Quality control and instrument failure together resulted in 5% loss of hourly fluxes for all chambers, 4% for temperatures, and 8% for *SWC* (Fig. 1). Differences in mean annual T_s and *SWC* between the two chambers were 0.01 °C and 0.003 m^3 m^{-3}, respectively.

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

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

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

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

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

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

Pearson correlation analysis was used to calculate the correlation coefficient between temperature or photosynthesis and R_s. Cross-correlation analysis was used to estimate hysteresis in the relationship between temperature- and R_s and photosynthesis- and R_s relationships. We used root mean squared error (*RMSE*) and the coefficient of determination (R^2) as criteria in evaluating function performance. To evaluate seasonal variation in diel hysteresis, the mean monthly diel daily cycles of R_s, T_a, T_{surf}, T_s, and photosynthesis were generated by averaging their hourly means at a given hour over a particular month (Table 1). Exponential and linear regression was used to evaluate the influence of *SWC* on the control of photosynthesis on temperature-R_s hysteresis. Likewise, influences of *SWC* on diel hysteresis was examined during a wet month with high rainfall and adequate *SWC* (July, *PPT* = 117.9 mm) and a dry month with low rainfall and inadequate *SWC* (August, *PPT* = 10.9 mm; Wang et al., 2014). In order to evaluate the influence of photosynthesis on diel hysteresis in the temperature-R_s relationship, we compared the time 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

153 ~~were~~ was calculated using the fitted parameters of each function and the measured hourly T_{surf} and photosynthesis for each

154 day. All statistical analyses were performed in MATLAB, with a significance level of 0.05 (R2010b, Mathworks Inc., Natick,

155 MA, USA).

3 Results

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

158 Incident photosynthetically active radiation, T_a, T_{surf}, and T_s exhibited distinctive daily patterns over the year (Fig. 1a-d),

159 peaking at ~12:00 PM (Local Time, LT), ~16:00 PM, ~14:00 PM, and ~17:00 PM, respectively (Fig. 1a-d). Unlike the

160 environmental factors, daily patterns in R_s remained constant over the non-growing part of the year, peaking at 11:00 AM-

161 13:00 PM, and highly variable during the growing season of the year (April to October), peaking between 10:00 AM-16:00

162 PM (Fig. 1f). Similar to R_s during the growing season, diel patterns of photosynthesis were also highly variable, peaking

163 between 10:00 AM-16:00 PM (Fig. 1e).

164 Diel patterns of monthly mean R_s were similar to those of T_{surf} during the wet month and similar to those of

165 photosynthesis during the dry month (Fig. 2g, h). During the wet month (July), monthly mean diel R_s was out of phase with

166 photosynthesis, but in phase with T_{surf} (Fig. 2g). Soil respiration peaked at 16:00 PM, exhibiting similar timing to T_{surf} (i.e.,

167 15:00 PM), but four hours later than photosynthesis (peaking at 12:00 PM; Fig. 2g). During the dry month (August), diel R_s

168 was generally in phase with photosynthesis, but out of phase with T_{surf} ~–~(Fig. 2h). Both photosynthesis and R_s plateaued

169 between 10:00 AM-16:00 PM, whereas T_{surf} peaked at 15:00 PM (Fig. 2h).

3.2 Control of photosynthesis and temperature on diel soil respiration

171 Among temperatures at the three levels, T_{surf} correlated the strongest with R_s, due to the high R^2's with monthly mean diel R_s

172 (Table 1). Over the growing season, monthly mean diel R_s correlated fairly well with photosynthesis (Table 1). The response

173 of R_s to temperature and photosynthesis was shown to be affected by SWC (Table 2, Fig. 3). During the wet month, T_{surf}

174 alone explained 97% of the variation in diel R_s (via Eq. 1), whereas photosynthesis explained 67% of ~that same~ the variation

175 (Table 2, Fig. 3a). However, during the dry month, photosynthesis explained 88% of the variation in diel R_s (via Eq. 2),

176 whereas T_{surf} explained 76% of the variation (Fig. 3b, Table 2). Irrespective of dry~/~ or wet periods, T_{surf} and photosynthesis

177 together explained over 90% of the diel variation in R_s (via Eq. 3; see Fig 3 and Table 2). ~Altogether~On the whole, RI varied

178 as a function of SWC, decreasing whenever SWC increased (Fig. 4).

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

180 During the wet month, hysteresis was not observed to occur in the monthly mean T_{surf}-R_s relationship, whereas two-hour lag~s~

181 ~times~ were found to occur in the photosynthesis-R_s relationship (Table 1; Fig. 3a). During the dry month, the opposite was

6

182   observed, where one-hour lags ~~times~~ were found to occur in the T_{surf}-R_s relationship (Table 1, Fig. 3b). Over the growing

183   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

184   (Fig. 5c). This led to ~~lag~~ time lags between measured and modeled R_s regardless of the variable, T_{surf} or photosynthesis,

185   resulting in about 26% of the days of the growing season (accounting for 184 days, in total) having no time lag ~~time~~ (Fig. 5e,

186   f). However, taking into account both T_{surf} ~~and~~ and photosynthesis as input variables ~~to~~ in the definition of R_s (via Eq. 3), ~~lag~~

187   time lags between measured and modeled R_s were mostly eliminated (Fig. 5a, d), with 84% of the days of the growing

188   season displaying no time lag ~~time~~.

189   Diel hysteresis in both relationships (i.e., T_{surf}-R_s and photosynthesis-R_s) was shown to be affected by SWC (Fig. 6).

190   Over the growing season, diel hysteresis between R_s and T_{surf} was linearly related to SWC in a downward manner, when SWC

191   < 0.08 m³ m⁻³ (ratio of SWC to soil porosity = 0.26; Fig. 6a). Hysteresis was not evident, when SWC > 0.08 m³ m⁻³ (Fig. 6a).

192   In contrast, diel hysteresis between R_s and photosynthesis was linearly related to SWC in an upward manner, when SWC <

193   0.08 m³ m⁻³ (Fig. 6b), but ceased to be related, when SWC > 0.08 m³ m⁻³ (Fig. 6b).

194   **4 Discussion**

195   **4.1 Degree of control of ~~Physical~~ photosynthesis ~~vs. biological controls~~ on diel hysteresis**

196   In our study, we found that the diurnal pattern in temperature (T_a, T_{surf}, and T_s) lagged behind R_s by 0-4 hours, which resulted

197   in a counterclockwise loop in the relationship between R_s and temperature. Although the magnitude of hysteresis between R_s

198   and temperature differed among the three temperature measurements, their seasonal variation was generally uniform. Among

199   the temperature measurements, T_{surf} was more closely related to diel R_s, resulting in weaker hysteresis. Magnitude of

200   hysteresis between R_s and temperature was comparable to those in other plant systems, e.g., 3.5-5 h in a boreal aspen stand

201   (Gaumont-Guay et al., 2006) and 0-5 h in a Chinese pine plantation (Jia et al., 2013). However, the direction of hysteresis

202   was unlike that reported by Phillips et al. (2011), who had reported R_s lagging behind soil temperature.

203   ~~Contradictory understanding exists on the causes of diel hysteresis between R_s and temperature (Tang et al., 2005;~~

204   ~~Riveros Iregui et al., 2007; Vargas and Allen, 2008; Carbone et al., 2008; Kuzyakov and Gavrichkova, 2010; Philips et al.,~~

205   ~~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~~

206   ~~biogeochemical processes in the deep soil.~~ In general, transfer of heat (downward) and gases (upward) through the soil

207   complex by simple diffusion would take time to occur. Increased SWC would serve to impede this transfer (Millington and

208   Quirk, 1961). If physical processes alone controlled hysteresis, you would expect R_s to lag behind T_{surf} and hysteresis to

209   increase with increasing SWC. However, such rationalization is not supported by our observations, which show T_{surf} to lag

210   behind R_s and hysteresis to decrease with increasing SWC. As a result, physical processes alone cannot account for the

211   observed patterns in hysteresis between R_s and temperature. Combining photosynthesis and T_{surf} as explanatory variables of

212   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,

213   relative to 27% of the days when T_{surf} alone was used (~~specific~~ associated with ~~to~~ Eq. 2), suggesting that photosynthesis has

214 a~~n greater~~ important role ~~in~~ governing hysteresis in ~~drylands~~desert shrubland. ~~Differences in soil properties between sandy~~

215 ~~soils at our study site and loamy and clayey soils at many of the forested sites may be responsible for disparity in explanation~~

216 ~~(Millington and Quirk, 1961; Hillel, 1998; Nickerson and Risk, 2009). Unlike higher clay/silt content soils in forests, sandy~~

217 ~~soils have lower heat and water-holding capacity and higher water and air permeability. Properties of sandy soils tend to~~

218 ~~make thermal and CO_2 gas transport much faster (e.g., within a few minutes), resulting in minor influences on hysteresis.~~

219 ~~Our observations lend support to an explanation of hysteresis based on a relationship with photosynthesis.~~ Along with other

220 studies, including those of Tang et al. (2005), Vargas and Allen (2008), Carbone et al. (2008), Kuzyakov and Gavrichkova

221 (2010), and Wang et al. (2014), our findings provide increasing evidence of the role of photosynthesis in regulating diel

222 hysteresis between R_s and temperature.

223 **4.2 Photosynthesis control of soil respiration and diel hysteresis**

224 The 0-4 h lag between R_s and photosynthesis observed are consistent with those observed in earlier studies, e.g., 0-4 h lag

225 between ecosystem-level photosynthesis and R_s in a coastal wetland ecosystem (Han et al., 2014) and 0-3 h lag between

226 plant photosynthesis and R_s in a steppe ecosystem (Yan et al., 2011). Short time lag~~s times~~ suggest rapid response between

227 recent photosynthesis and R_s (Kuzyakov and Gavrichova, 2010). This response is significantly faster than suggested in

228 earlier studies, when approached from an isotopic or canopy/soil flux-based methodology (Howarth et al., 1994; Mikan et al.,

229 2000; Jonson et al., 2002; Högberg et al., 2008; Kuzyakov and Gavrichova, 2010; Mencuccini and Hölttä, 2010; Kayler et al.,

230 2010; Han et al., 2014).

231 According to the "goodness-of-fit" of Eq. 3 to the field data, the time lag ~~time~~ between diel photosynthesis and R_s was

232 likely caused by variations in temperature, regardless of *SWC*. Photosynthesis provide substrates to roots and rhizosphere

233 microbes (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011; Han et al., 2014). Temperature directly

234 drives enzymatic kinetics of respiratory metabolism in organisms (Van't Hoff, 1898; Lloyd and Taylor, 1994).

235 Photosynthesis is directly driven by radiation (specifically, photosynthetically active radiation). Temperature is also driven

236 by radiation, but through heating of the surface and subsequent air and soil layers. Thus, diel patterns in temperature

237 continuously lagged behind those of photosynthesis by a few hours (as indicated in Fig. 2). The interactions between

238 photosynthesis and temperature lea~~d~~ R_s to lag behind photosynthesis~~,~~. but temperature lag~~ged~~ behind R_s (Fig. 2). This

239 sequence of events may explain the difference in the direction of hysteresis observed here, in contrast to that reported in

240 Phillips et al. (2011). Such explanation is different from the explanations for forest ecosystems, where the transport of

241 photosynthates and influence of turgor and osmotic pressure may be responsible for the specific coupling observed between

242 current photosynthesis and R_s (Steinmann et al., 2004; Högberg et al., 2008; Hölttä et al., 2006, 2009; Mencuccini and Hölttä,

243 2010). Variations in coupling dynamics may occur because of differences in vegetation height among ecosystems (Kuzyakov

244 and Gavrichova, 2010; Mencuccini and Hölttä, 2010). Unlike forest ecosystems, low-statured vegetation in shrub systems

245 (~0.5 m), may elicit a few minutes of delay in the transportation of photosynthates and influence of turgor and osmotic

246   pressure (Kuzyakov and Gavrichkova, 2010). Such small time lags ~~times~~ cannot be easily identified in hourly measurements,

247   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

249   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

250   decreased from this value, diel R_s varied more closely with photosynthesis, leading to increased diel hysteresis between R_s

251   and T_{surf}. These results suggest that SWC played a more important role in regulating the relative control of photosynthesis

252   and temperature on diel R_s over the growing season, supporting our second hypothesis.

253   A possible explanation for SWC regulating hysteresis might be associated with changes in substrate supply. During the

254   wet period with $SWC > 0.08$ m^3 m^{-3}, increases in SWC ameliorates diffusion of soil C substrates and its access to soil

255   microbes (Curiel Yuste et al., 2003; Jarvis et al., 2007). Amount of substrate to roots and rhizosphere microbes is also

256   expected to be high as a result of high current photosynthesis (Baldocchi et al., 2006). As a result, diel R_s is not limited by C

257   substrates provided by current photosynthesis and soil organic matter. Consequences of diel R_s may vary repeatedly in

258   synchrony with diel temperature, with no indication of hysteresis when $SWC > 0.08$ m^3 m^{-3} (Fig. 6a). By contrast, during dry

259   and hot phases, with $SWC < 0.08$ m^3 m^{-3}, inadequate soil water limits diffusion of soil C substrates and its access to soil

260   microbes (Jassal et al., 2008) and also suppresses photosynthesis (supported by Fig. 2g, h). As a result, R_s may be limited by

261   C substrates under dry conditions. It has been reported current photosynthesis can account for about 65-70% of total R_s over

262   the growing season (Ekblad and Högberg et al., 2001; Högberg et al., 2001). Thus, diel R_s may vary more closely to

263   photosynthesis during dry and hot phases over the growing season (Fig. 2h), resulting in increased hysteresis with decreasing

264   SWC below 0.08 m^3 m^{-3} (Fig. 6b).

265   The 0.08 m^3 m^{-3} SWC threshold of this study was consistent with an earlier study by Wang et al. (2014) that reported

266   that seasonal R_s decoupled from soil temperature as SWC fell below 0.08 m^3 m^{-3}. Earlier studies have reported similar

267   responses of R_s to temperature (Palmroth et al., 2005; Jassal et al., 2008). For example, R_s in an 18-year-old temperate

268   Douglas-fir stand decoupled from T_s when SWC fell below 0.11 m^3 m^{-3}. Our results suggest that the decoupling of R_s from

269   temperature for low SWC was due to a shift in control from temperature to photosynthesis. Our work provides urgently

270   needed new knowledge concerning causes/mechanisms involved in defining variation in diel hysteresis in desert- shrubland

271   ~~ecosystems~~. Based on our work, we suggest that photosynthesis should be considered in simulations of diel R_s in drylands,

272   especially when SWC falls below 0.08 m^3 m^{-3}.

5 Conclusions

274   Soil water content regulated the relative control between photosynthesis and temperature on diel R_s by changing the relative

275   contribution of autotrophic and heterotrophic respiration to total R_s, causing seasonal variation in diel hysteresis between R_s

276   and temperature. Hysteresis was not observed between R_s and T_{surf}, when $SWC > 0.08$ m^3 m^{-3}, but the lag-hours increased as

277 *SWC* decreased below this *SWC* threshold. Incorporating photosynthesis into R_s-temperature-based models reduces diel

278 hysteresis and increases the overall level of goodness-of-fit. Our findings highlight the importance of biological mechanisms

279 in diel hysteresis between R_s and temperature and the importance of *SWC* in plant photosynthesis-soil respiration dynamics

280 in dryland ecosystems.

281

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421

Table 1. Analysis of mean monthly diel cycles of soil respiration (R_s), air temperature (T_a), ~~soil~~ 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 <u>time</u> lag<u>s</u> times in R_s vs. T_a, T_{surf}, T_s, and P cycles. Statistically significant Pearson's correlation coefficients (r; $p < 0.05$) are denoted in bold.

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

427　**Table 2.** Regressions based on the Q_{10}, linear, and Q_{10}-linear functions of soil respiration (R_s) for both a wet (July) and ~~a~~ dry month

428　(August) in 2013. Variables T_{surf} (°C) refers to the ~~soil~~ soil-surface temperature; P photosynthesis in the dominant shrub layer; R^2 the

429　coefficient of determination; and *RMSE* the root mean squared error.

|	Model	Wet month: July	Dry month: August
R_s-T	Q_{10}	$R_s = 1.13 \times 1.4^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.97$ $RMSE = 0.0521$	$R_s = 1.12 \times 1.1^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.76$ $RMSE = 0.0796$
R_s-P	Linear	$R_s = 0.03 \times P + 1.61$ $R^2 = 0.67$ $RMSE = 0.1889$	$R_s = 0.04 \times P + 1.29$ $R^2 = 0.88$ $RMSE = 0.05752$
R_s-P-T	Linear$\times Q_{10}$	$R_s = (0.002 \times P + 1.16) \times 1.38^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.98$ $RMSE = 0.0491$	$R_s = (0.024 \times P + 1.20) \times 1.08^{\frac{T_{surf}-10}{10}}$ $R^2 = 0.94$ $RMSE = 0.0408$

430

431
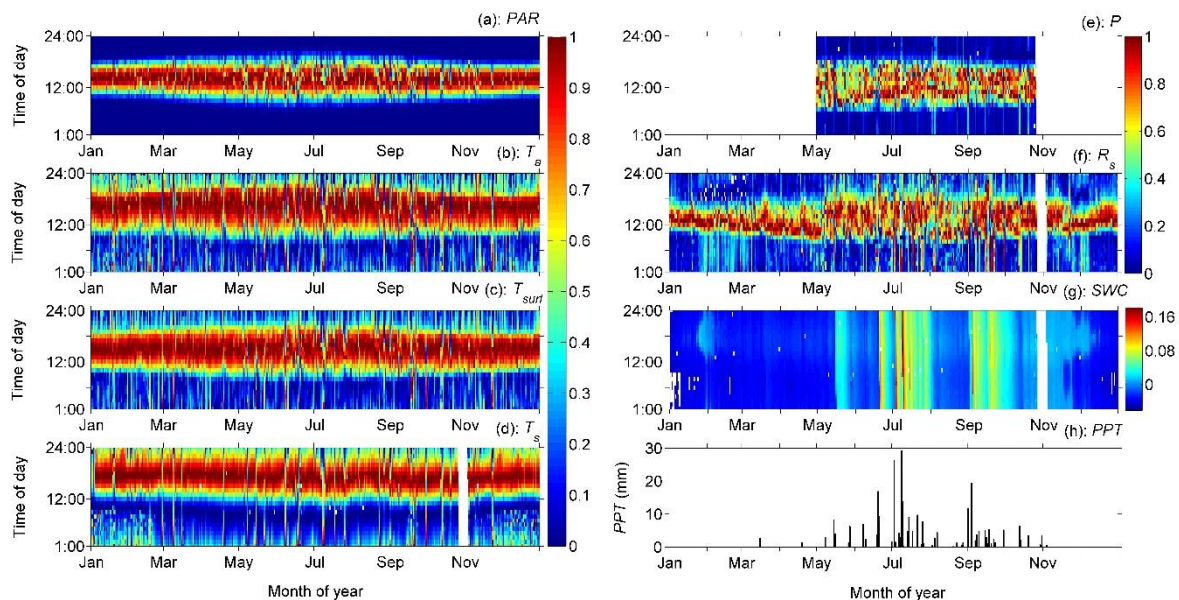
Figure 1. Seasonal variation in incident photosynthetically active radiation (*PAR*), temperature [i.e., air temperature (*T_a*), soil soil-surface

433 temperature (*T_surf*), and soil temperatures (*T_s*)], photosynthesis (*P*), and soil respiration (*R_s*) at an *Artemisia ordosica*-dominated site, and

434 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

435 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

436 given day and 0, the daily minimum value.

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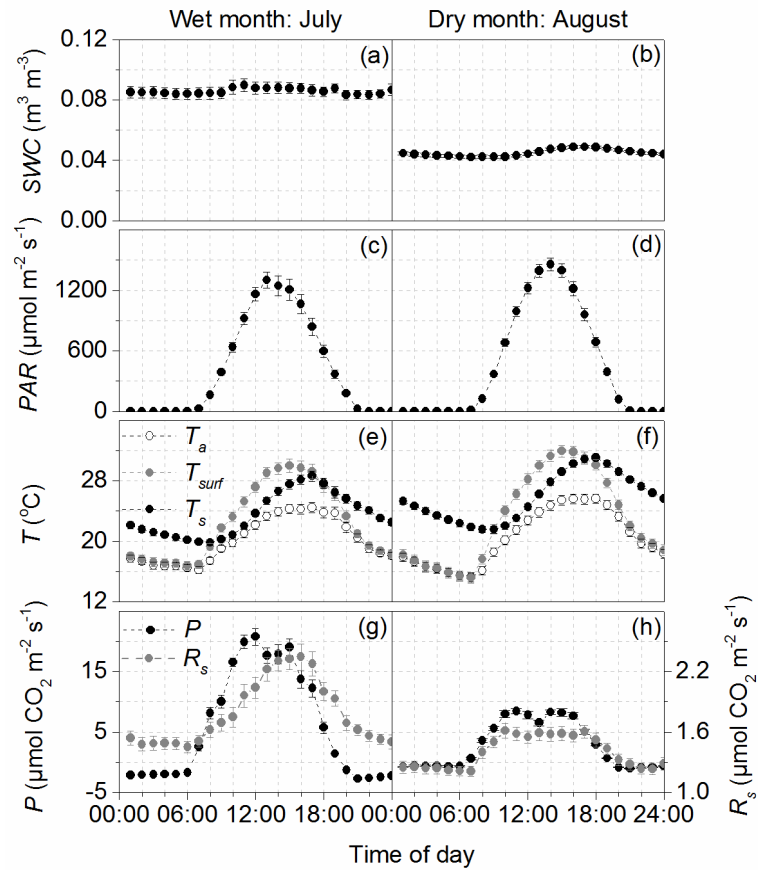
438

439 **Figure 2.** Mean monthly diel cycle of soil water content (*SWC*), incident photosynthetically active radiation (*PAR*), temperature [i.e., air

440 ~~temperature~~ (T_a), ~~soil~~ soil-surface ~~temperature~~ (T_{surf}), and soil temperatures (T_s)], soil respiration (R_s), and photosynthesis (*P*) at an

441 *Artemisia ordosica*-dominated site during a wet and dry month. Each point is the monthly mean for a particular time of day. Bars represent
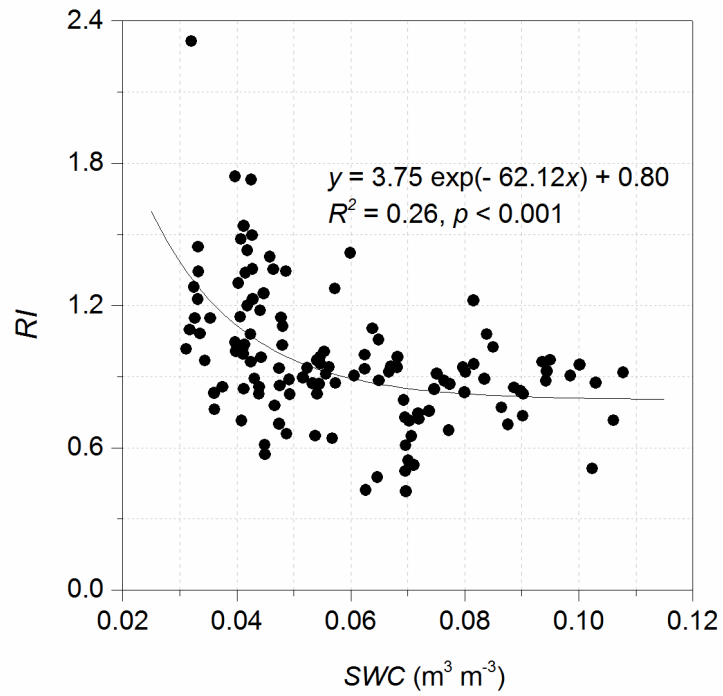
442 standard errors.

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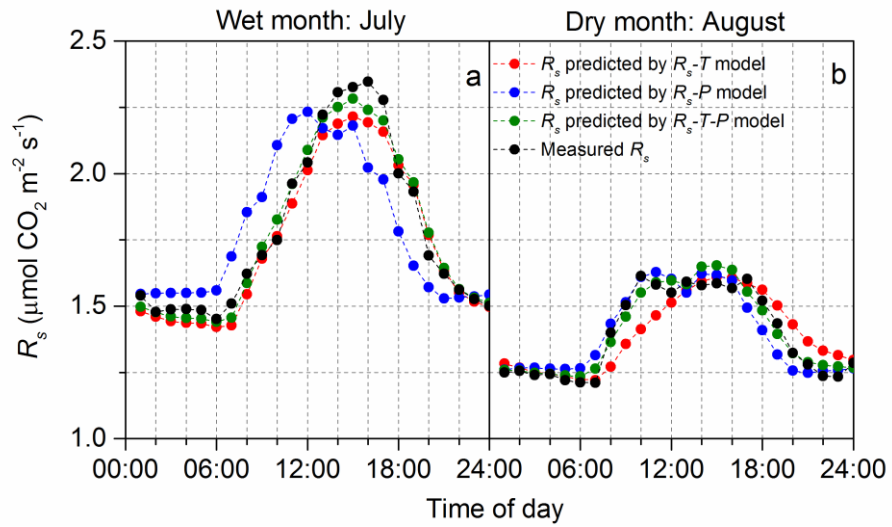
444
445 **Figure 3.** Diel variation of measured soil respiration (R_s) and modeled R_s by using temperature and photosynthesis as input variables in the
446 calculation of R_s for both a wet and dry month (i.e., July and August, respectively); R_s-T function (Eq. 1), R_s-P function (Eq .2), and R_s-T-P
447 function (Eq. 3).
448

$$y = 3.75 \exp(-62.12x) + 0.80$$
$$R^2 = 0.26,\ p < 0.001$$

449
450 **Figure 4.** Relationship between soil water content (*SWC*) and the relative importance (*RI*) of ~~soil~~ soil-surface temperature and

451 photosynthesis at an *Artemisia ordosica*-dominated site as a function of ~~diel~~ soil respiration (R_s).

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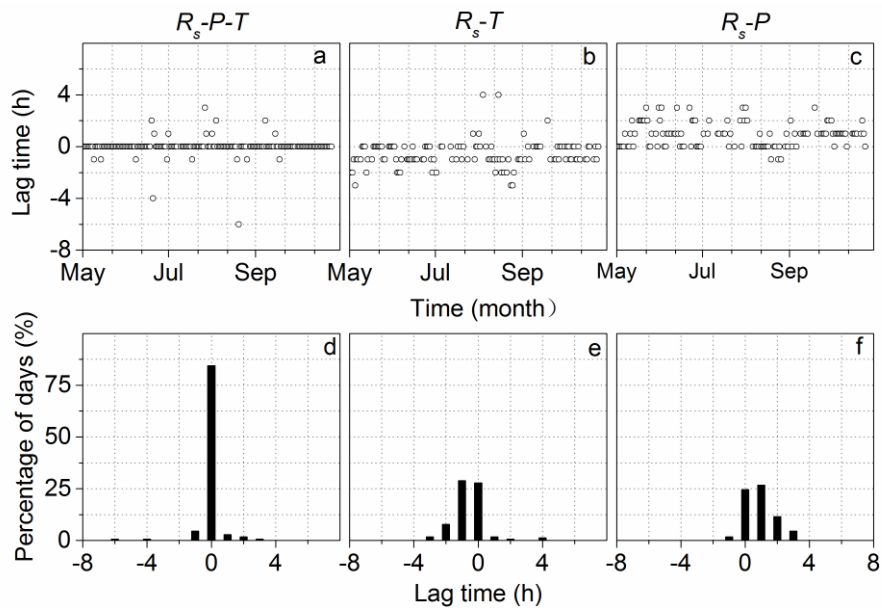
453
454 **Figure 5.** Time lags ~~Lag times~~ between measured and modeled soil respiration by means of ~~soil~~ soil-surface temperature and
455 photosynthesis over the growing season; R_s-T function (Eq. 1), R_s-P function (Eq. 2), and R_s-P-T function (Eq. 3).
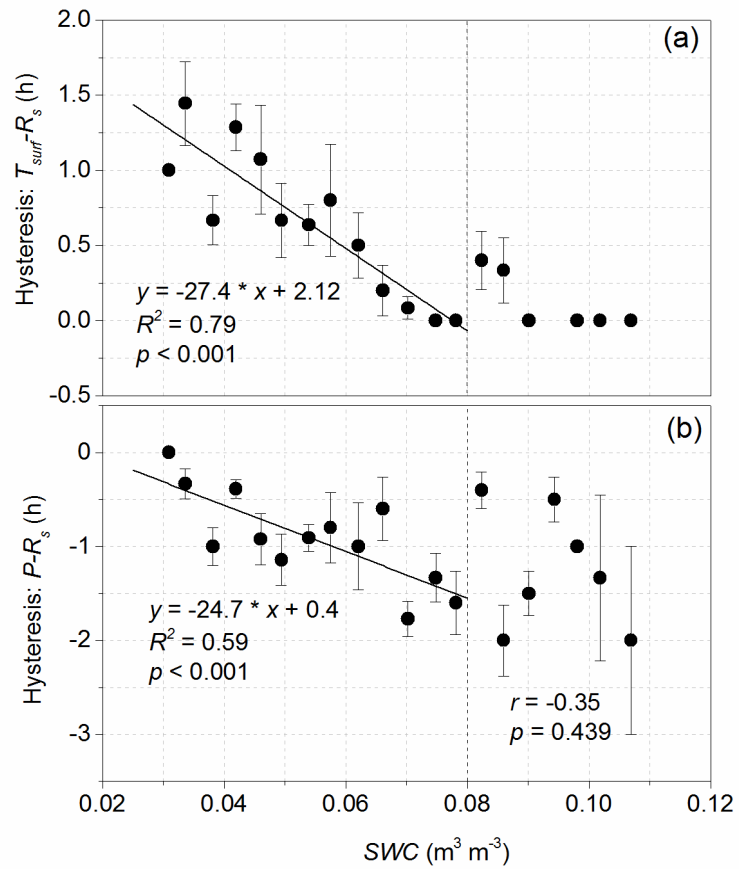
Figure 6. ~~Lag times~~Time lags between soil respiration (R_s) and ~~soil~~ soil-surface temperature (T_{surf}), R_s, and photosynthesis at an *Artemisia ordosica*-dominated site with respect to soil water content (*SWC*). ~~Lag times~~ Time lags were bin-averaged using *SWC*-intervals of 0.004 m^3 m^{-3}