

1 Soil water regulates the control of photosynthesis on diel hysteresis 2 between soil respiration and temperature in a desert shrubland

3 Ben Wang^{1,2}, TianShan Zha^{*1}, Xin Jia^{1,2}, JinNan Gong², Charles Bourque³, Wei Feng¹, Yun Tian¹, Bin
4 Wu¹, YuQing Zhang¹, Heli Peltola²

5 ¹Yanchi Research Station, School of Soil and Water Conservation, Beijing Forestry University. Beijing 100083, PR China.

6 ²School of Forest Sciences, University of Eastern Finland. PO Box 111, FIN-80101 Joensuu, Finland.

7 ³Faculty of Forestry and Environmental Management, University of New Brunswick, PO Box 4400, 28 Dineen Drive,
8 Fredericton, New Brunswick, E3B 5A3, Canada

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

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

24 1 Introduction

25 Diel hysteresis (asynchronicity) between soil respiration (R_s) and soil temperature (T_s) is widely documented for forests
26 (Tang et al., 2005; Gaumont-Guay et al., 2006; Riveros-Iregui et al., 2007; Stoy et al., 2007; Vargas and Allen, 2008; Jia et
27 al., 2013), grasslands (Carbone et al., 2008; Barron-Gafford et al., 2011), and desert ecosystems (Wang et al., 2014; Feng et

28 al., 2014). Diel hysteresis, which appears as an elliptical loop in the relationship between R_s and T_s , is difficult to model with
29 theoretical functions, such as the Q_{10} , Lloyd-Taylor, Arrhenius, or van't Hoff functions (Lloyd and Taylor, 1994; Winkler et
30 al., 1996; Davidson et al., 2006; Phillips et al., 2011; Oikawa et al., 2014), leading to an inadequate understanding of
31 temperature-sensitivity in R_s (Gaumont-Guay et al., 2008; Phillips et al., 2011; Darenova et al., 2014). Therefore, in order to
32 accurately predict soil carbon dioxide (CO_2) fluxes and their responses to climate change, it is necessary to understand the
33 biophysical mechanisms that have a role in controlling seasonal variation in diel hysteresis.

34 Over decades of research, two main processes have been reported to relate to diel hysteresis between R_s and T_s . One is
35 associated with the physical processes of heat and gas transport in soils (Vargas and Allen, 2008; Phillips et al., 2011; Zhang
36 et al., 2015). Generally, soil CO_2 fluxes are measured at the soil surface, and are related to temperatures in the soil. Transport
37 of CO_2 -gas to the soil surface takes time to occur, which may cause delays to appear in observed respiration rates, causing
38 hysteretic loops to form between R_s and T_s (Zhang et al., 2015). The other is associated with the biological process of
39 photosynthate supply (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011; Wang et al., 2014). Beyond
40 the control of temperature, soil CO_2 fluxes have been associated with plant photosynthesis. Photosynthesis usually peaks at
41 midday (e.g., 11:00-13:00), providing substrate for belowground roots and rhizosphere-microbe respiration, but oscillates out
42 of phase with T_s , usually peaking in the afternoon (e.g., 14:00-16:00). Such influences of current photosynthesis could lead
43 to the formation of hysteretic loops in the relationship between R_s and T_s . These studies highlight the need to consider the
44 inherent role of photosynthesis for a more accurate interpretation of R_s (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010;
45 Vargas et al., 2011). Physical and biological processes that relate to substrates and production-transport of carbon (C) in
46 plants and soils are not mutually exclusive and both likely play crucial roles in affecting diel variation in R_s (Stoy et al., 2007;
47 Phillips et al., 2011; Zhang et al., 2015; Song et al., 2015a, b).

48 Diel hysteresis between R_s and T_s has been shown to vary seasonally with soil water content (SWC ; Tang et al., 2005;
49 Riveros-Iregui et al., 2007; Carbone et al., 2008; Vargas and Allen, 2008; Ruehr et al., 2009; Wang et al., 2014). However,
50 the influences of SWC on diel hysteresis are not uniform. Based on the Millington-Quirk model, high SWC blocks CO_2 -gas
51 and thermal diffusion (Millington and Quirk, 1961), resulting in large hysteresis loops (Riveros-Iregui et al., 2007; Zhang et
52 al., 2015). In contrast, other studies have reported that low SWC and high water vapor pressure deficits (VPD) can promote
53 partial stomata closure, which leads to higher photosynthesis in the morning (e.g., 9:00-10:00) and suppressed photosynthesis
54 in mid-afternoon, leading to pronounced hysteresis during dry periods (Tang et al., 2005; Vargas and Allen, 2008; Carbone
55 et al., 2008; Wang et al., 2014). Clearly to understand the causes of diel hysteresis, the role of SWC needs to be closely
56 evaluated.

57 Drylands cover a quarter of the earth's land surface and play an important role in the global C cycle (Safriel and Adeel,
58 2005; Austin, 2011; Poulter et al., 2014). Many studies in forest ecosystems are based on the application of physical soil CO_2
59 and heat transport models and evaluate the influences of SWC on CO_2 -gas and thermal diffusion (Riveros-Iregui et al., 2007;
60 Phillips et al., 2011; Zhang et al., 2015). In general, many of these studies conclude that diel hysteresis is the result of

61 physical processes alone. Few studies have evaluated the causes of diel hysteresis in drylands. Currently, it is not clear to
62 what degree physical and biological processes control hysteresis in drylands.

63 Drylands are characterized with low productivity. As weak organic C-storage pools (West et al., 1994; Lange, 2003),
64 drylands are noted for their large contribution of autotrophic production of CO₂. The autotrophic component of R_s occurs as a
65 direct consequence of root respiration, which is firmly coupled (within several hours) to recent photosynthesis (Liu et al.,
66 2006; Baldocchi et al., 2006; Högberg and Read, 2006; Bahn et al., 2009; Kuzyakov and Gavrichkova, 2010). Consequently,
67 photosynthesis may govern the level of variation in asynchronicity between R_s and T_s in drylands. In drylands, especially in
68 desert ecosystems characterized by sandy soils with high soil porosity, the influence of SWC on gas diffusion is likely
69 nominal. As a rule, most of the available water is used directly in sustaining biological activity in drylands (Noy-Meir, 1973).
70 Under drought conditions, stomata closure in plants at midday reduces water losses, resulting in a corresponding suppression
71 of photosynthesis (Jia et al, 2014). Such changes in diel patterns of photosynthesis likely result in modifications of patterns
72 in R_s , leading to hysteresis between R_s and T_s . Soil water content likely regulates photosynthesis and, in so doing, causes
73 hysteresis between R_s and T_s to vary over the growing season.

74 In this study, we hypothesize that: (1) photosynthesis has a high degree of control in the formation of hysteretic loops
75 between R_s and T_s ; and (2) SWC regulates this control and its variation over the growing season. The main objectives of this
76 research were to: (1) assess biological controls on diel hysteresis between R_s and T_s ; (2) explore the causes that lead to
77 variation in seasonal variation in diel hysteresis; and (3) understand SWC's role in influencing hysteresis. To undertake this
78 work, we measured R_s , SWC, T_s , and photosynthesis in a dominant desert-shrub on a continuous basis for 2013.

79 **2 Materials and Methods**

80 **2.1 Site description**

81 The study was conducted at Yanchi Research Station of Beijing Forestry University, Ningxia, northwest China (37°42'31" N,
82 107°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
83 and semi-arid climatic zones. Based on 51 years of data (1954-2004) from the Meteorological Station at Yanchi, the mean
84 annual air temperature at the station was 8.1°C and the mean annual total precipitation was 292 mm (ranging between 250 to
85 350 mm), 63% of which fell in late summer (i.e., July-September; Wang et al., 2014; Jia et al., 2014). Annual potential
86 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
87 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
88 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;
89 Jia et al, 2014). The vegetation was regenerated from aerial seeding applied in 1998 and is currently dominated by a semi-
90 shrub species cover of *Artemisia ordosica*, averaging about 50-cm tall with a canopy size of about 80 cm × 60 cm (for
91 additional site description, consult Jia et al. 2014 and Wang et al. 2014, 2015).

92 2.2 Soil respiration and photosynthesis measurement

93 Two permanent polyvinyl chloride soil collars were initially installed on a small fixed sand dune in March, 2012. Collar
94 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
95 with an opaque chamber (LI-8100-104, Nebraska, USA) and the other over an *Artemisia ordosica* plant (~10 cm tall) with a
96 transparent chamber (LI-8100-104C). Soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was directly estimated from CO_2 -flux
97 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
98 determined as the difference in CO_2 fluxes obtained with the transparent and opaque chambers.

99 Continuous measurements of CO_2 fluxes ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) were made *in situ* with a Li-8100 CO_2 -gas analyzer and a
100 LI-8150 multiplexer (LI-COR, Nebraska, USA) connected to each chamber. Instrument maintenance was carried out bi-
101 weekly during the growing season, including removing plant-regrowth in the opaque-chamber installation, and cleaning to
102 avoid blackout conditions associated with the transparent chamber. Measurement time for each chamber was 3 minutes and
103 15 seconds, including a 30-second pre-purge, 45-second post-purge, and 2-minute measurement period.

104 2.3 Measurements of temperatures, soil water content and other environmental factors

105 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
106 simultaneously about 10 cm from the chambers using a LI-8150-203 temperature and $\text{EC}_{\text{H}_2\text{O}}$ soil-moisture sensor (LI-COR,
107 Nebraska, USA; see Wang et al., 2014). Other environmental variables were recorded every half hour using sensors mounted
108 on a 6-m tall eddy-covariance tower approximately 800 m from our soil CO_2 -flux measurement site. Air temperature (T_a , °C)
109 was measured with a thermohygrometer (HMP155A, Vaisala, Finland). Soil-surface temperature (T_{surf} , °C) was measured
110 with an infrared-emission sensor (Model SI-111, Campbell Scientific Inc., USA). Incident photosynthetically active
111 radiation (PAR) was measured with a light-quantum sensor (PAR-LITE, Kipp and Zonen, the Netherlands) and precipitation
112 (PPT , mm), with three tipping-bucket rain gages (Model TE525MM, Campbell Scientific Inc., USA) placed 50 m from the
113 tower (see Jia et al., 2014).

114 2.4 Data processing and statistical analysis

115 In this study, CO_2 -flux measurements were screened by means of limit checking, i.e., hourly CO_2 -flux data < -30 or > 15
116 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ were considered to be anomalous as a result of, for instance, gas leakage or plant damage by insects, and
117 removed from the dataset (Wang et al., 2014, 2015). After limit checking, hourly CO_2 fluxes greater than three times the
118 standard deviation from the calculated mean of 5 days' worth of flux data were likewise removed. Quality control and
119 instrument failure together resulted in 5% loss of hourly fluxes for all chambers, 4% for temperatures, and 8% for SWC (Fig.
120 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.

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

$$127 R_s = R_{10} \times Q_{10}^{(T-10)/10} \quad (1)$$

$$128 R_s = a \times P + b \quad (2)$$

$$129 R_s = (a \times P + b) \times c^{(T-10)/10} \quad (3)$$

$$130 RI = \frac{\rho_p}{\rho_t} \quad (4)$$

131 where R_{10} is the respiration at 10°C, Q_{10} is the temperature sensitivity of respiration, T is temperature, P is photosynthesis
 132 ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), a , b , and c are regression coefficients, and ρ_p and ρ_t are the correlation coefficients between
 133 photosynthesis and R_s and temperature and R_s , respectively.

134 Pearson correlation analysis was used to calculate the correlation coefficient between temperature or photosynthesis and
 135 R_s . Cross-correlation analysis was used to estimate hysteresis in the relationship between temperature and R_s and
 136 photosynthesis- and R_s . We used root mean squared error ($RMSE$) and the coefficient of determination (R^2) as criteria in
 137 evaluating function performance. To evaluate seasonal variation in diel hysteresis, the mean monthly daily cycles of R_s , T_a ,
 138 T_{surf} , T_s , and photosynthesis were generated by averaging their hourly means at a given hour over a particular month (Table
 139 1). Exponential and linear regression was used to evaluate the influence of SWC on the control of photosynthesis on
 140 temperature- R_s hysteresis. Likewise, influences of SWC on diel hysteresis was examined during a wet month with high
 141 rainfall and adequate SWC (July, $PPT = 117.9$ mm) and a dry month with low rainfall and inadequate SWC (August, $PPT =$
 142 10.9 mm; Wang et al., 2014). In order to evaluate the influence of photosynthesis on diel hysteresis in the temperature- R_s
 143 relationship, we compared the time lag (in hours) between measured and modeled R_s by means of Eq.'s 1 through 3 with a
 144 one-day moving window and a one-day time step over the growing season (April to October). Modeled R_s was calculated
 145 using the fitted parameters of each function and the measured hourly T_{surf} and photosynthesis for each day. All statistical
 146 analyses were performed in MATLAB, with a significance level of 0.05 (R2010b, Mathworks Inc., Natick, MA, USA).

147 **3 Results**

148 **3.1 Diel patterns of soil respiration, photosynthesis, and environmental factors**

149 Incident photosynthetically active radiation, T_a , T_{surf} , and T_s exhibited distinctive daily patterns over the year (Fig. 1a-d),
150 peaking at ~12:00 PM (Local Time, LT), ~16:00 PM, ~14:00 PM, and ~17:00 PM, respectively (Fig. 1a-d). Unlike the
151 environmental factors, daily patterns in R_s remained constant over the non-growing part of the year, peaking at 11:00 AM-
152 13:00 PM, and highly variable during the growing season of the year (April to October), peaking between 10:00 AM-16:00
153 PM (Fig. 1f). Similar to R_s during the growing season, diel patterns of photosynthesis were also highly variable, peaking
154 between 10:00 AM-16:00 PM (Fig. 1e).

155 Diel patterns of monthly mean R_s were similar to those of T_{surf} during the wet month and similar to those of
156 photosynthesis during the dry month (Fig. 2g, h). During the wet month (July), monthly mean diel R_s was out of phase with
157 photosynthesis, but in phase with T_{surf} (Fig. 2g). Soil respiration peaked at 16:00 PM, exhibiting similar timing to T_{surf} (i.e.,
158 15:00 PM), but four hours later than photosynthesis (peaking at 12:00 PM; Fig. 2g). During the dry month (August), diel R_s
159 was generally in phase with photosynthesis, but out of phase with T_{surf} (Fig. 2h). Both photosynthesis and R_s plateaued
160 between 10:00 AM-16:00 PM, whereas T_{surf} peaked at 15:00 PM (Fig. 2h).

161 3.2 Control of photosynthesis and temperature on diel soil respiration

162 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 ,
163 (Table 1). Over the growing season, monthly mean diel R_s correlated fairly well with photosynthesis (Table 1). The response
164 of R_s to temperature and photosynthesis was shown to be affected by SWC (Table 2, Fig. 3). During the wet month, T_{surf}
165 alone explained 97% of the variation in diel R_s (via Eq. 1), whereas photosynthesis explained 67% of the variation (Table 2,
166 Fig. 3a). However, during the dry month, photosynthesis explained 88% of the variation in diel R_s (via Eq. 2), whereas T_{surf}
167 explained 76% of the variation (Fig. 3b, Table 2). Irrespective of dry or wet periods, T_{surf} and photosynthesis together
168 explained over 90% of the diel variation in R_s (via Eq. 3; see Fig 3 and Table 2). On the whole, RI varied as a function of
169 SWC , decreasing whenever SWC increased (Fig. 4).

170 3.3 Effects of soil water content and photosynthesis on diel hysteresis in temperature- R_s relationship

171 During the wet month, hysteresis was not observed to occur in the monthly mean T_{surf} - R_s relationship, whereas two-hour lags
172 were found to occur in the photosynthesis- R_s relationship (Table 1; Fig. 3a). During the dry month, the opposite was
173 observed, where one-hour lags were found to occur in the T_{surf} - R_s relationship (Table 1, Fig. 3b). Over the growing season,
174 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).
175 This led to time lags between measured and modeled R_s regardless of the variable, T_{surf} or photosynthesis, resulting in about
176 26% of the days of the growing season (accounting for 184 days, in total) having no time lag (Fig. 5e, f). However, taking
177 into account both T_{surf} and photosynthesis as input variables in the definition of R_s (via Eq. 3), time lags between measured
178 and modeled R_s were mostly eliminated (Fig. 5a, d), with 84% of the days of the growing season displaying no time lag.

179 Diel hysteresis in both relationships (i.e., T_{surf} - R_s and photosynthesis- R_s) was shown to be affected by SWC (Fig. 6).
180 Over the growing season, diel hysteresis between R_s and T_{surf} was linearly related to SWC in a downward manner, when SWC
181 $< 0.08 \text{ m}^3 \text{ m}^{-3}$ (ratio of SWC to soil porosity = 0.26; Fig. 6a). Hysteresis was not evident, when $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ (Fig. 6a).
182 In contrast, diel hysteresis between R_s and photosynthesis was linearly related to SWC in an upward manner, when $SWC <$
183 $0.08 \text{ m}^3 \text{ m}^{-3}$ (Fig. 6b), but ceased to be related, when $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ (Fig. 6b).

184 **4 Discussion**

185 **4.1 Degree of control of photosynthesis on diel hysteresis**

186 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
187 in a counterclockwise loop in the relationship between R_s and temperature. Although the magnitude of hysteresis between R_s
188 and temperature differed among the three temperature measurements, their seasonal variation was generally uniform. Among
189 the temperature measurements, T_{surf} was more closely related to diel R_s , resulting in weaker hysteresis. Magnitude of
190 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
191 (Gaumont-Guay et al., 2006) and 0-5 h in a Chinese pine plantation (Jia et al., 2013). However, the direction of hysteresis
192 was unlike that reported by Phillips et al. (2011), who had reported R_s lagging behind soil temperature.

193 In general, transfer of heat (downward) and gases (upward) through the soil complex by simple diffusion would take
194 time to occur. Increased SWC would serve to impede this transfer (Millington and Quirk, 1961). If physical processes alone
195 controlled hysteresis, you would expect R_s to lag behind T_{surf} and hysteresis to increase with increasing SWC . However, such
196 rationalization is not supported by our observations, which show T_{surf} to lag behind R_s and hysteresis to decrease with
197 increasing SWC . As a result, physical processes alone cannot account for the observed patterns in hysteresis between R_s and
198 temperature. Combining photosynthesis and T_{surf} as explanatory variables of R_s (via Eq. 3), we found 84% of the days over
199 the growing season had no observable lag between measured- and modeled- R_s , relative to 27% of the days when T_{surf} alone
200 was used (associated with to Eq. 2), suggesting that photosynthesis has an important role in governing hysteresis in desert
201 shrubland. Along with other studies, including those of Tang et al. (2005), Vargas and Allen (2008), Carbone et al. (2008),
202 Kuzyakov and Gavrichkova (2010), and Wang et al. (2014), our findings provide increasing evidence of the role of
203 photosynthesis in regulating diel hysteresis between R_s and temperature.

204 **4.2 Photosynthesis control of soil respiration and diel hysteresis**

205 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
206 between ecosystem-level photosynthesis and R_s in a coastal wetland ecosystem (Han et al., 2014) and 0-3 h lag between
207 plant photosynthesis and R_s in a steppe ecosystem (Yan et al., 2011). Short time lags suggest rapid response between recent
208 photosynthesis and R_s (Kuzyakov and Gavrichova, 2010). This response is significantly faster than suggested in earlier
209 studies, when approached from an isotopic or canopy/soil flux-based methodology (Howarth et al., 1994; Mikan et al., 2000;

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

212 According to the “goodness-of-fit” of Eq. 3 to the field data, the time lag between diel photosynthesis and R_s was likely
213 caused by variations in temperature, regardless of SWC . Photosynthesis provide substrates to roots and rhizosphere microbes
214 (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011; Han et al., 2014). Temperature directly drives
215 enzymatic kinetics of respiratory metabolism in organisms (Van’t Hoff, 1898; Lloyd and Taylor, 1994). Photosynthesis is
216 directly driven by radiation (specifically, photosynthetically active radiation). Temperature is also driven by radiation, but
217 through heating of the surface and subsequent air and soil layers. Thus, diel patterns in temperature continuously lagged
218 behind those of photosynthesis by a few hours (as indicated in Fig. 2). The interactions between photosynthesis and
219 temperature led R_s to lag behind photosynthesis, but temperature lagged behind R_s (Fig. 2). This sequence of events may
220 explain the difference in the direction of hysteresis observed here, in contrast to that reported in Phillips et al. (2011). Such
221 explanation is different from the explanations for forest ecosystems, where the transport of photosynthates and influence of
222 turgor and osmotic pressure may be responsible for the specific coupling observed between current photosynthesis and R_s ,
223 (Steinmann et al., 2004; Högberg et al., 2008; Hölttä et al., 2006, 2009; Mencuccini and Hölttä, 2010). Variations in
224 coupling dynamics may occur because of differences in vegetation height among ecosystems (Kuzyakov and Gavrichova,
225 2010; Mencuccini and Hölttä, 2010). Unlike forest ecosystems, low-statured vegetation in shrub systems (~0.5 m), may elicit
226 a few minutes of delay in the transportation of photosynthates and influence of turgor and osmotic pressure (Kuzyakov and
227 Gavrichkova, 2010). Such small time lags cannot be easily identified in hourly measurements, resulting in an apparent
228 temperature-dominated control of photosynthesis and R_s .

229 **4.3 Influences of soil water content on seasonal variation in diel hysteresis**

230 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
231 decreased from this value, diel R_s varied more closely with photosynthesis, leading to increased diel hysteresis between R_s
232 and T_{surf} . These results suggest that SWC played a more important role in regulating the relative control of photosynthesis
233 and temperature on diel R_s over the growing season, supporting our second hypothesis.

234 A possible explanation for SWC regulating hysteresis might be associated with changes in substrate supply. During the
235 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
236 microbes (Curiel Yuste et al., 2003; Jarvis et al., 2007). Amount of substrate to roots and rhizosphere microbes is also
237 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
238 substrates provided by current photosynthesis and soil organic matter. Consequences of diel R_s may vary repeatedly in
239 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
240 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
241 microbes (Jassal et al., 2008) and also suppresses photosynthesis (supported by Fig. 2g, h). As a result, R_s may be limited by
242 C substrates under dry conditions. It has been reported current photosynthesis can account for about 65-70% of total R_s over

243 the growing season (Ekblad and Högberg et al., 2001; Högberg et al., 2001). Thus, diel R_s may vary more closely to
244 photosynthesis during dry and hot phases over the growing season (Fig. 2h), resulting in increased hysteresis with decreasing
245 SWC below $0.08 \text{ m}^3 \text{ m}^{-3}$ (Fig. 6b).

246 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
247 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
248 responses of R_s to temperature (Palmroth et al., 2005; Jassal et al., 2008). For example, R_s in an 18-year-old temperate
249 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
250 temperature for low SWC was due to a shift in control from temperature to photosynthesis. Our work provides urgently
251 needed new knowledge concerning causes/mechanisms involved in defining variation in diel hysteresis in desert shrubland.
252 Based on our work, we suggest that photosynthesis should be considered in simulations of diel R_s in drylands, especially
253 when SWC falls below $0.08 \text{ m}^3 \text{ m}^{-3}$.

254 **5 Conclusions**

255 Soil water content regulated the relative control between photosynthesis and temperature on diel R_s by changing the relative
256 contribution of autotrophic and heterotrophic respiration to total R_s , causing seasonal variation in diel hysteresis between R_s
257 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 as
258 SWC decreased below this SWC threshold. Incorporating photosynthesis into R_s -temperature-based models reduces diel
259 hysteresis and increases the overall level of goodness-of-fit. Our findings highlight the importance of biological mechanisms
260 in diel hysteresis between R_s and temperature and the importance of SWC in plant photosynthesis-soil respiration dynamics
261 in dryland ecosystems.

262

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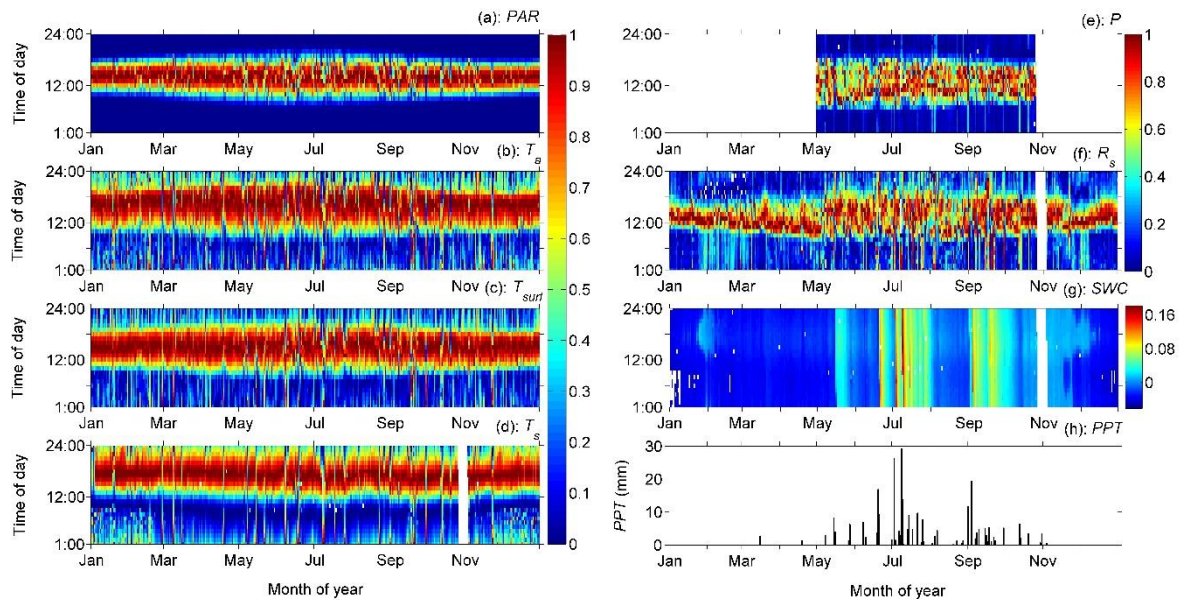
401 **Table 1.** Analysis of mean monthly diel cycles of soil respiration (R_s), air temperature (T_a), soil-surface temperature (T_{surf}), soil
402 temperature at a 10-cm depth (T_s), and photosynthesis (P) in a dominant desert-shrub ecosystem, including correlation coefficients and
403 time lags times 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
404 bold.
405

		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		

406 **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 dry month (August)
 407 in 2013. Variables T_{surf} ($^{\circ}\text{C}$) refers to the soil-surface temperature; P photosynthesis in the dominant shrub layer; R^2 the coefficient of
 408 determination; and $RMSE$ the root mean squared error.

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

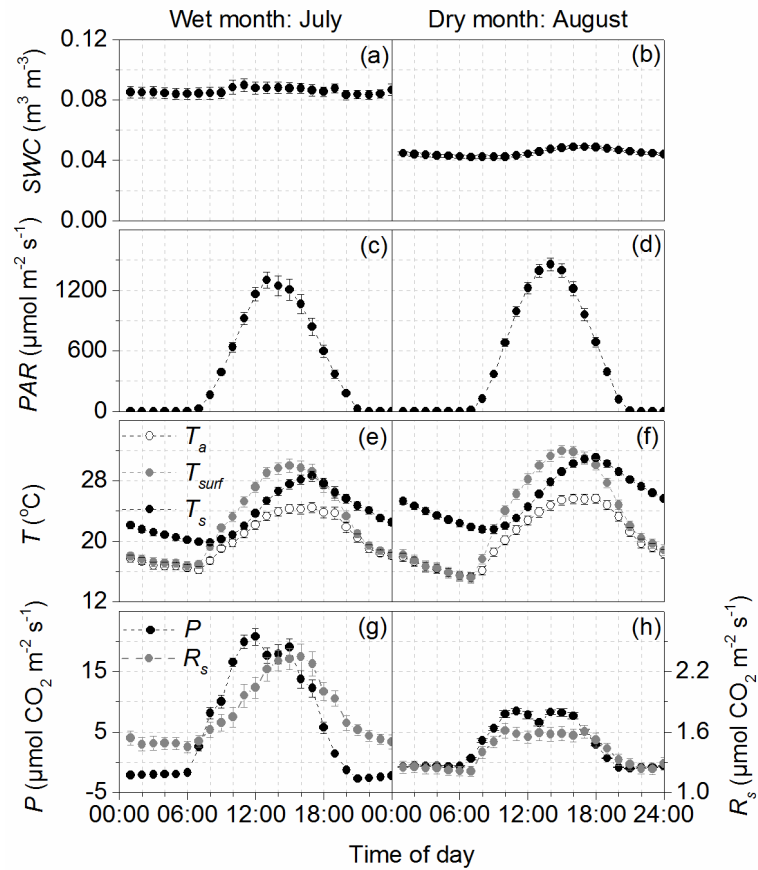
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411 **Figure 1.** Seasonal variation in incident photosynthetically active radiation (*PAR*), temperature [i.e., air (T_a), soil-surface (T_{surf}), and soil
 412 temperatures (T_s)], photosynthesis (P), and soil respiration (R_s) at an *Artemisia ordosica*-dominated site, and seasonal variation in soil
 413 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.
 414 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
 415 daily minimum value.

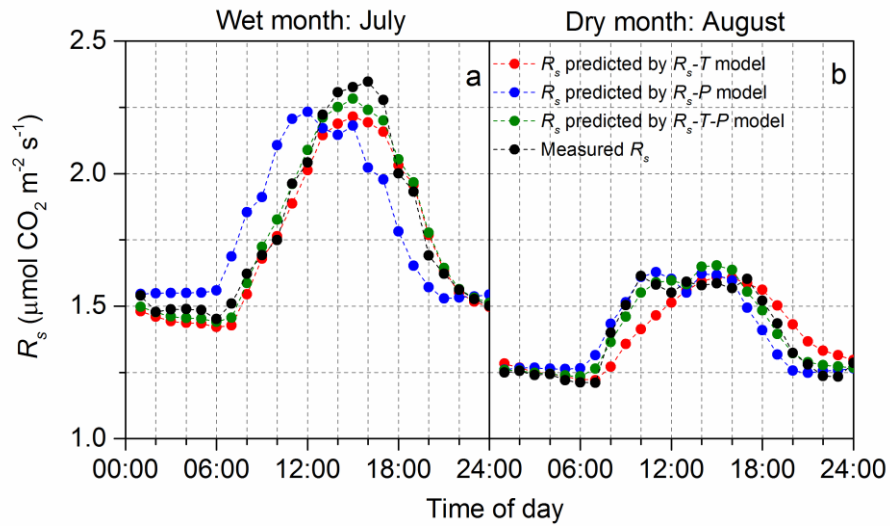
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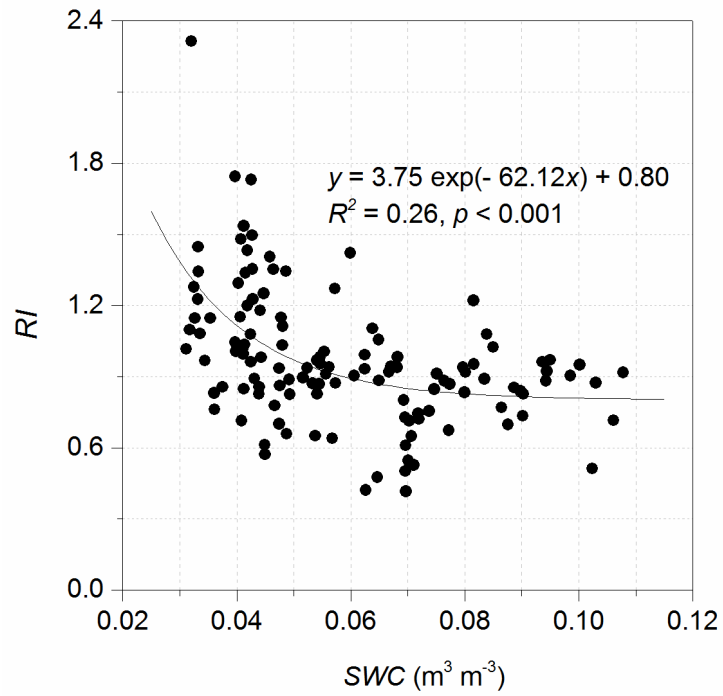
417

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

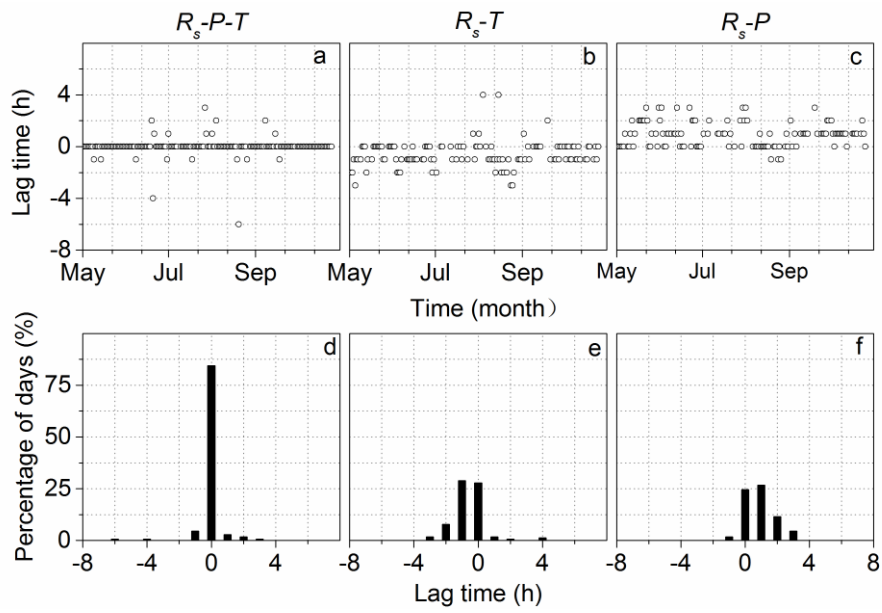
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 423 **Figure 3.** Diel variation of measured soil respiration (R_s) and modeled R_s by using temperature and photosynthesis as input variables in the
 424 calculation of R_s for both a wet and dry month (i.e., July and August, respectively); R_s - T function (Eq. 1), R_s - P function (Eq. 2), and R_s - T - P
 425 function (Eq. 3).
 426



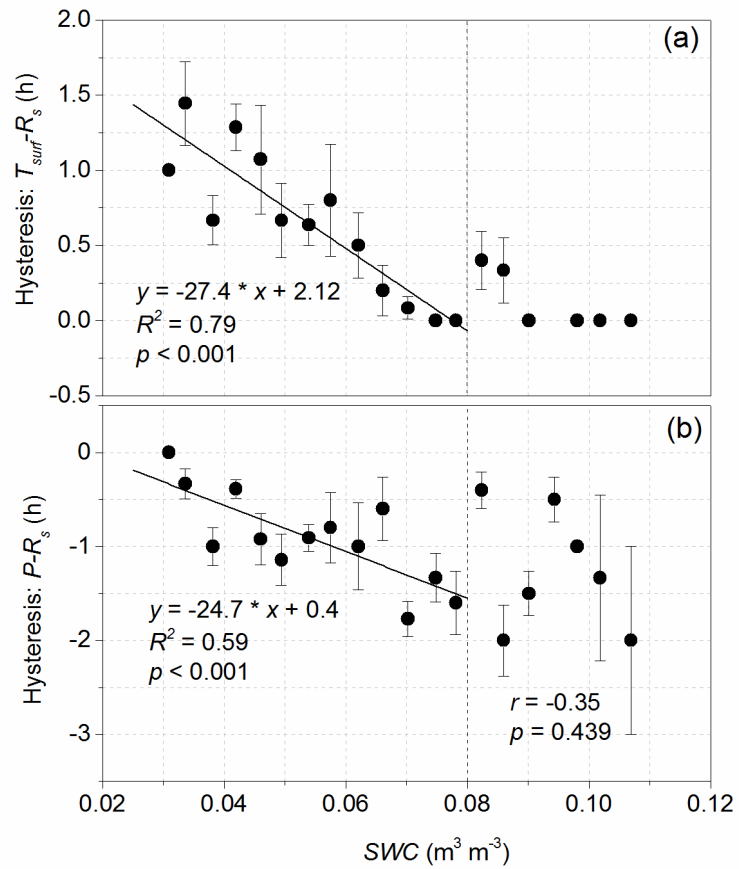
427
 428 **Figure 4.** Relationship between soil water content (SWC) and the relative importance (RI) of soil-surface temperature and photosynthesis
 429 at an *Artemisia ordosica*-dominated site as a function of soil respiration (R_s).
 430



431

432 **Figure 5.** Time lags between measured and modeled soil respiration by means of soil-surface temperature and photosynthesis over the

433 growing season; R_s-T function (Eq. 1), R_s-P function (Eq. 2), and R_s-P-T function (Eq. 3).



434

435 **Figure 6.** Time lags between soil respiration (R_s) and soil-surface temperature (T_{surf}), R_s , and photosynthesis at an *Artemisia ordosica*-

436 dominated site with respect to soil water content (SWC). Time lags were bin-averaged using SWC-intervals of $0.004 \text{ m}^3 \text{ m}^{-3}$