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Contrasting diel hysteresis between soil autotrophic and heterotrophic respiration in a desert ecosystem under different rainfall scenarios

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Weimin Song^{1,2}, Shiping Chen², Yadan Zhou², Bo Wu³, Yajuan Zhu³, Qi Lu³ & Guanghui Lin¹

Diel hysteresis occurs often between soil CO₂ efflux (R_s) and temperature, yet, little is known if diel hysteresis occurs in the two components of R_s , i.e., autotrophic respiration (R_A) and heterotrophic respiration (R_H), and how diel hysteresis will respond to future rainfall change. We conducted a field experiment in a desert ecosystem in northern China simulating five different scenarios of future rain regimes. Diel variations of soil CO₂ efflux and soil temperature were measured on Day 6 and Day 16 following the rain addition treatments each month during the growing season. We found contrasting responses in the diel hysteresis of R_A and R_H to soil temperature, with a clockwise hysteresis loop for R_H but a counter-clockwise hysteresis loop for R_A . Rain addition significantly increased the magnitude of diel hysteresis for both R_H and R_A on Day 6, but had no influence on either on Day 16 when soil moisture was much lower. These findings underline the different roles of biological (i.e. plant and microbial activities) and physical-chemical (e.g. heat transport and inorganic CO₂ exchange) processes in regulating the diel hysteresis of R_A and R_H , which should be considered when estimating soil CO₂ efflux in desert regions under future rainfall regime.

Soil CO₂ efflux, the second largest terrestrial carbon flux following photosynthesis, has received widespread attention during the past decades due to its vulnerability and high sensitivity to climate change^{1–3}. On a diel, seasonal and annual scale, soil temperature is widely recognized as a primary abiotic factor affecting soil CO₂ efflux, and the relationship between soil CO₂ efflux and soil temperature is often expressed as Arrhenius or van't Hoff exponential functions^{4–6}. However, describing and predicting soil CO₂ efflux using these simple reaction functions lead to many uncertainties, because various biotic and abiotic factors, such as plant physiological activity, soil physical properties, and soil moisture^{4,7–9}, can also considerably influence the relationship.

In recent years, many field studies have shown that, on the diel and seasonal scales, soil CO₂ efflux and soil temperature are decoupled, showing an elliptical hysteresis loop^{10,11}. For example, soil CO₂ efflux may increase more quickly in response to rising soil temperature in the morning compared to decreasing soil temperature in the evening, resulting in a clockwise diel hysteresis. Diel hysteresis (in some references also as “diurnal hysteresis”) has been observed in the soils of forests^{12–15}, savanna grasslands^{16,17}, and crop fields^{18–20}. The mechanistic explanation for such hysteresis phenomenon of soil CO₂ efflux is still lacking,

¹Ministry of Education Key Laboratory for Earth System Modeling, Center for Earth System Science, Tsinghua University, Beijing 100084, China. ²State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China. ³Institute of Desertification Studies, Chinese Academy of Forestry, Beijing 100091, China. Correspondence and requests for materials should be addressed to G.L. (email: lingh@tsinghua.edu.cn)

although two possible hypotheses have emerged. The first one focuses on the biological mechanism associated with photosynthate transport such that recent photosynthates are periodically transported to the roots zone, where they can alter the magnitude and timing of soil CO₂ efflux, leading to the phenomenon that soil CO₂ efflux is out of sync with soil temperature^{13,15,21}. For example, by comparing the relationship between soil CO₂ efflux and soil temperature under tree canopies and in an open area, Vargas and Allen¹³ proposed that photosynthesis is the main contributor to the diel hysteresis phenomenon of soil CO₂ efflux. The second hypothesis relies on the physical mechanisms associated with heat transport and CO₂ diffusion processes. The direction of heat transport is opposite in daytime to that in nighttime, which can influence the velocities of CO₂ diffusion along soil profiles when soil warms and cools^{10,15}. The biological and physical mechanisms are not mutually exclusive, and both are likely to play important roles in formulating diel hysteresis of soil CO₂ efflux¹⁰. In addition, many researchers have suggested that without considering diel hysteresis, a large bias will likely be present in the estimation of soil CO₂ efflux and soil C loss^{15,17,22}. In a montane conifer forest, for example, Riveros-Iregui *et al.*¹⁵ found that a representative model without considering diel hysteresis could overestimate the total soil CO₂ efflux of the growing season by 19%. Thus, proper interpretation and evaluation of diel hysteresis of soil CO₂ efflux is critical to accurate estimation and prediction of regional and global C budgets.

Soil rewetting following a rainfall event has been shown to be an important controlling factor for regulating soil CO₂ efflux, especially in desert and semiarid regions^{8,23,24}. Global climate models predict that the desert and semiarid regions such as those in northern China will undergo more extreme climate changes characterized by increasing amount of total precipitation and higher frequency of extreme rainfall events in the 21st century^{25–27}. Given that water is the primary driver of biological activity in desert and semiarid areas²⁸, such alterations of the hydrological cycle will potentially alter soil CO₂ efflux. In addition, by changing soil moisture, precipitation increase can influence heat transport and gas diffusion processes, since diffusion of gas in the gas phase is much higher than in the liquid phase²⁹. Therefore, any change in precipitation regions under the climate change scenarios can potentially influence diel hysteresis of soil CO₂ efflux. Thus, it is very important to evaluate possible responses of diel hysteresis of soil CO₂ efflux to changes in soil water availability associated with rainfall events, as any change in diel hysteresis of soil CO₂ efflux may affect the evaluation of possible response of soil CO₂ efflux to future precipitation change.

Soil CO₂ efflux has two components: the autotrophic respiration (R_A) of roots and the associated rhizosphere community, and the heterotrophic respiration (R_H) from the decomposition processes of soil microbes^{9,30}. However, most previous field studies mainly focused on diel hysteresis between total soil CO₂ efflux and soil temperature^{12–17,19}. Research concerning the diel hysteresis of the two respiration components is still rare¹⁸ and represents a gap in our knowledge of the response of soil CO₂ efflux to temperature. In addition, we are not aware of any study conducted to distinguish the differential response of diel hysteresis between the two components of soil CO₂ efflux *in situ* during rain pulses over an entire growing season. Modeling studies have shown differential responses of R_A and R_H to climate change such as increasing temperature³¹, indicating that the responses would be accompanied by varying changes in the magnitude of diel hysteresis of the two respiration components. Thus, partitioning soil CO₂ efflux into its two components, and analyzing the different responses of diel hysteresis are urgently needed for more accurate modeling of regional and global C budgets under future climate change scenarios.

We conducted a manipulative field experiment to simulate five scenarios of future rain regimes (0%, 25%, 50%, 75% and 100% increase over local annual mean precipitation (115 mm)) in a desert ecosystem of northwestern China dominated by the shrub species *Nitraria tangutorum*. The rain addition treatments were applied equally each month during the growing season (May–September). The effects of rain addition amount and timing on soil CO₂ efflux in this arid ecosystem have been reported previously^{8,32}. Although this study used some of the same dataset as our previous study³², the current study focused on the diel hysteresis phenomenon of two soil respiration components and their differential responses to rain additions, which is quite different from our previous paper in term of the scientific questions we addressed and the methods we used to analyze the data. The main objectives of this paper were to evaluate: (1) the diel relationship of the two components of soil CO₂ efflux with soil temperature, and (2) the possible responses of the diel hysteresis of the two components to rain increase. We hypothesized that the responses of diel hysteresis to rain addition would differ between the two components of soil CO₂ efflux because roots and microbes often have different response mechanisms to rain pulses of varying size, considering that small rainfall events can only enhance microbial respiration and larger rainfall events can increase both microbial and root respiration with different response time and duration^{24,32,33}.

Materials and Methods

Study site description. The experimental site (38° 34' N, 102° 58' E) was located in a sandy land area between Badain Jaran Desert and Tengger Desert in Minqin County, Gansu province, China. This area has a temperate arid continental climate with a mean annual temperature of 7.8 °C. The temperature during the warmest and coldest months is 23.2 °C and −9.6 °C, respectively. Mean annual precipitation is 115 mm mainly from July to September. The dominant soil type is aeolian sandy soil (Entisols in the USDA soil taxonomy system) with pH about 8.6. The dominant species is *Nitraria tangutorum* Bobr. More detailed information on the physical and chemical properties of soil can be found in Song *et al.*⁸.

Experimental design. The experiment was carried out in a patchy landscape with *N. tangutorum* interspersed with sand dunes, oriented in a northwest-southeast direction and composed of two distinct types of soil cover. The northwest area was covered with *N. tangutorum* plants, while the southeast area was bare soil. The mean height of the dunes was 0.9 m and the area was 14.2 m². Vegetation cover was approximately 35% at the entire study site.

A completely random design was used in this experiment, with five precipitation treatments and four replicates for each treatment (113 m² per plot, 20 plots in total). During the growing season (from May to September) of 2009, five precipitation treatments were designed to simulate a rain increase of 0% (CK), 25% (+25%PPT), 50% (+50%PPT), 75% (+75%PPT) and 100% (+100%PPT) over long-term average annual precipitation at the study site (115 mm). The precipitation addition treatments were applied every month and the precipitation amount added each time was 0, 5.8, 11.5, 17.3 and 23.0 mm for the five addition treatments, respectively. Water was pumped into a tank from a well near the plots and used to irrigate the plots via an irrigation system composed of a water-pump, water meter and spraying arms. In order to reduce water evaporation, precipitation treatments were carried out only in the morning. More detailed information on this experiment is provided in Song *et al.*⁸.

Soil CO₂ efflux measurements. Soil CO₂ efflux was measured on Day 6 and Day 16 after each rain addition for each month during the growing season (May to September). According to the general model of ecosystem carbon exchange following rain pulses^{24,33,34}, shrubs in desert ecosystems are generally characterized by long lag time and long duration relative to microbes in responding to an effective rainfall. Huang and Nobel³⁵ found that desert plants initialized new root growth c. 7 days after rewetting. The rate of soil CO₂ efflux of vegetated soils in water irrigated plots showed a significant difference from that in control plot only about 1 week after the water addition treatment⁸. In addition, the soil moisture data also showed that the effects of the rain addition treatments could last as long as 15 days after the rain addition treatment⁸. Thus, we chose Days 6 and 16 after the rain addition treatment for the soil CO₂ efflux measurements in this study.

At the beginning of the experiment, two PVC soil collars (80 cm² in area and 5 cm in height) were installed into the vegetated and bare soils to a depth of 3 cm in each plot for measuring soil CO₂ efflux. The rate of soil CO₂ efflux was determined using an automated soil CO₂ flux system (LI-8100, LI-COR Inc., Lincoln, NE, USA). Soil CO₂ efflux was measured on Days 6 and 16 after rain addition each month during the growing season (May to September). On each measurement day, soil CO₂ efflux rate was measured on each pre-installed collar repeatedly at an interval of 3 h from 6:00 AM to 6:00 AM of the following day. To achieve a more accurate estimate of soil CO₂ efflux, we visited the 20 plots in the same sequence on every occasion that measurements were taken. As the rate of soil CO₂ efflux was being measured, soil temperature (Ts) was measured at a depth of 10 cm with a thermocouple connected to the LI-8100 system. On each given measurement day, we also measured daily soil gravimetric water content (SWC) of the top 10 cm of the soil column in all plots by the oven drying method. We chose to measure soil temperature at 10 cm depth based on the compromise that most microbes were concentrated in the upper layers (0–10 cm). However, most roots biomass was found in the 10–30 cm soil layers.

Partition of soil CO₂ efflux components. At the study site, no obvious root biomass existed in the bare soils, and grasses and forbs were scarce enough to be negligible. Thus, the soil CO₂ efflux in the bare soils would mainly come from the decomposition of soil organic carbon - microbial respiration or heterotrophic respiration (R_H). There were no differences in soil organic matter, soil nitrogen content or microbial biomass between the two vegetation cover types⁸. In addition, there were no differences in soil temperature or moisture between the two vegetation cover types during the experimental period. Thus, autotrophic respiration (R_A) could roughly be determined by the difference in soil CO₂ efflux measured in the vegetated and bare soils:

$$R_S = R_H + R_A \quad (1)$$

where R_S is soil CO₂ efflux in the vegetated soil; R_H is soil CO₂ efflux in the bare soil; and R_A is autotrophic respiration.

Quantification of the diel hysteresis for soil CO₂ efflux. For each measurement day of the growing season, we fitted the relationship between soil CO₂ efflux and soil temperature during the night time (21:00–06:00) using a van't Hoff exponential function. The parameters of the function were then adopted to calculate soil CO₂ efflux during the daytime (09:00–18:00). Diel hysteresis was determined by the maximum difference of the daytime soil CO₂ efflux measured and calculated.

$$DH = R_{Sm} - R_{Sc} \quad (2)$$

where the degree of diel hysteresis (DH) is the maximum difference between the soil CO₂ efflux measured (R_{Sm}) during the daytime and the efflux calculated by the exponential function (R_{Sc}) that was extracted from the relationship between the nighttime soil CO₂ efflux and soil temperature. In this study, the

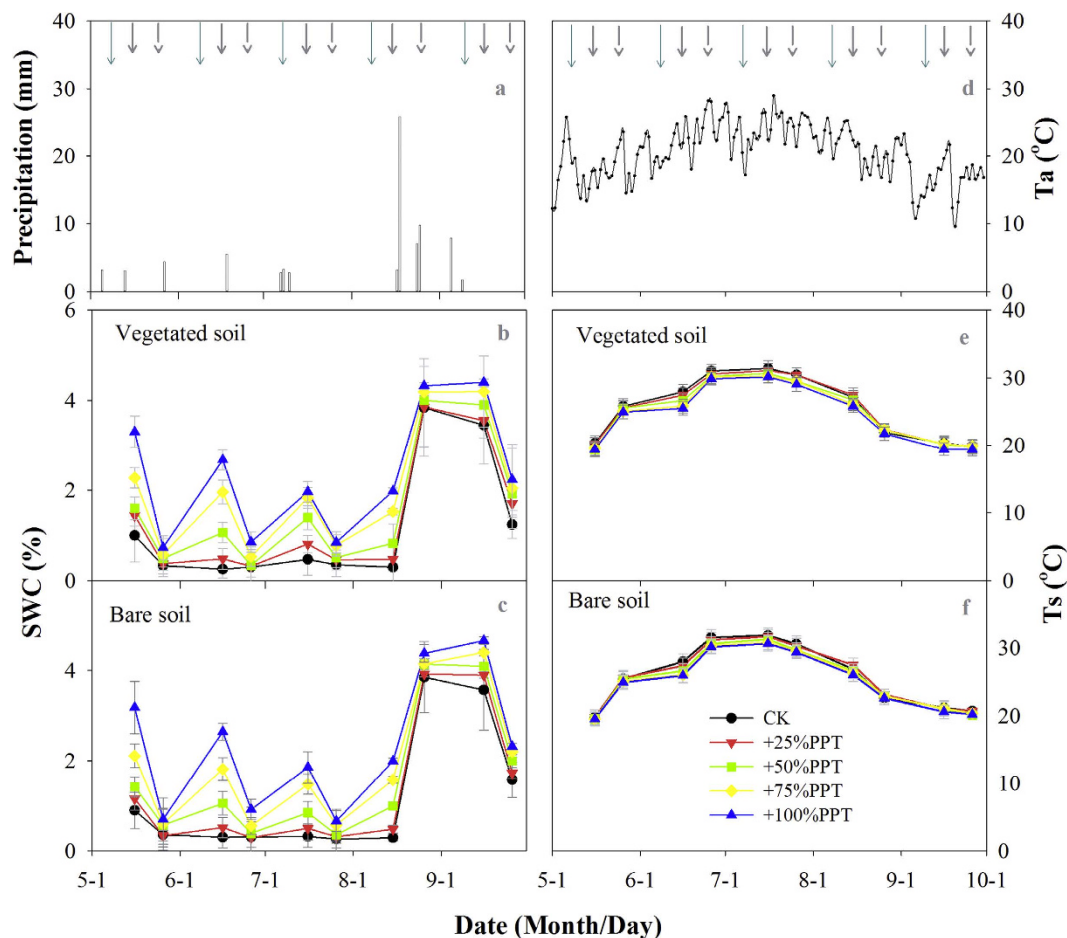


Figure 1. (a) Daily precipitation during the experimental period from 1 May to 1 October. (b,c): Soil water content (SWC) at 10 cm depth in vegetated soil and bare soil of a *N tangutorum* dominated desert ecosystem. (d) Daily mean air temperature (T_a) during the experimental period. (e,f): Soil temperature at 10 cm depth (T_s) in vegetated and bare soils. Long solid arrows represent the timing of rain addition treatments; short solid and dashed arrows represent the measurement time on Day 6 and Day 16 after the rain addition treatments, respectively.

maximum difference occurred at 12:00 for each measurement day. Positive values of diel hysteresis represent clockwise loop (higher CO_2 efflux during soil warming period).

Statistical analyses. We performed the repeated measurement analysis of variance (ANOVA) to test the differences in the degree of diel hysteresis of R_s , R_H and R_A on Days 6 and 16 after different rain addition treatments. Two-way ANOVA tests were used to examine the effect of rain addition time and rain addition amount on diel hysteresis of R_s , R_H and R_A on Days 6 and 16 after rain addition. Linear regression analysis was conducted to examine possible relationships between diel hysteresis and daily soil moisture. All statistical analyses were performed using SPSS 17.0 (SPSS for Windows, Version 17.0, Chicago, IL, USA).

Results

Soil water content and temperature under different rain additions. We measured the surface (0–10 cm) soil water content (SWC) on Days 6 and 16 following the rain addition treatments each month. As expected, SWC was strongly affected by rain addition treatments in both vegetated and bare soils (Fig. 1). The magnitude of change in SWC depended on the amount of rain added and the measurement day. Day 6 usually showed a higher increase in SWC than Day 16 during the growing season except for August due to a heavy natural rainfall event on 25th August (25.8 mm). There was no significant difference in SWC between the vegetated and bare soils under a given rain addition treatment on each measurement day³².

The seasonal trend in daily mean surface (0–10 cm) soil temperature (T_s) was similar for both vegetation cover types during the entire growing season (Fig. 1). Daily mean T_s at each measurement day did not show any significant differences among the five rain addition treatments³². Moreover, there was no

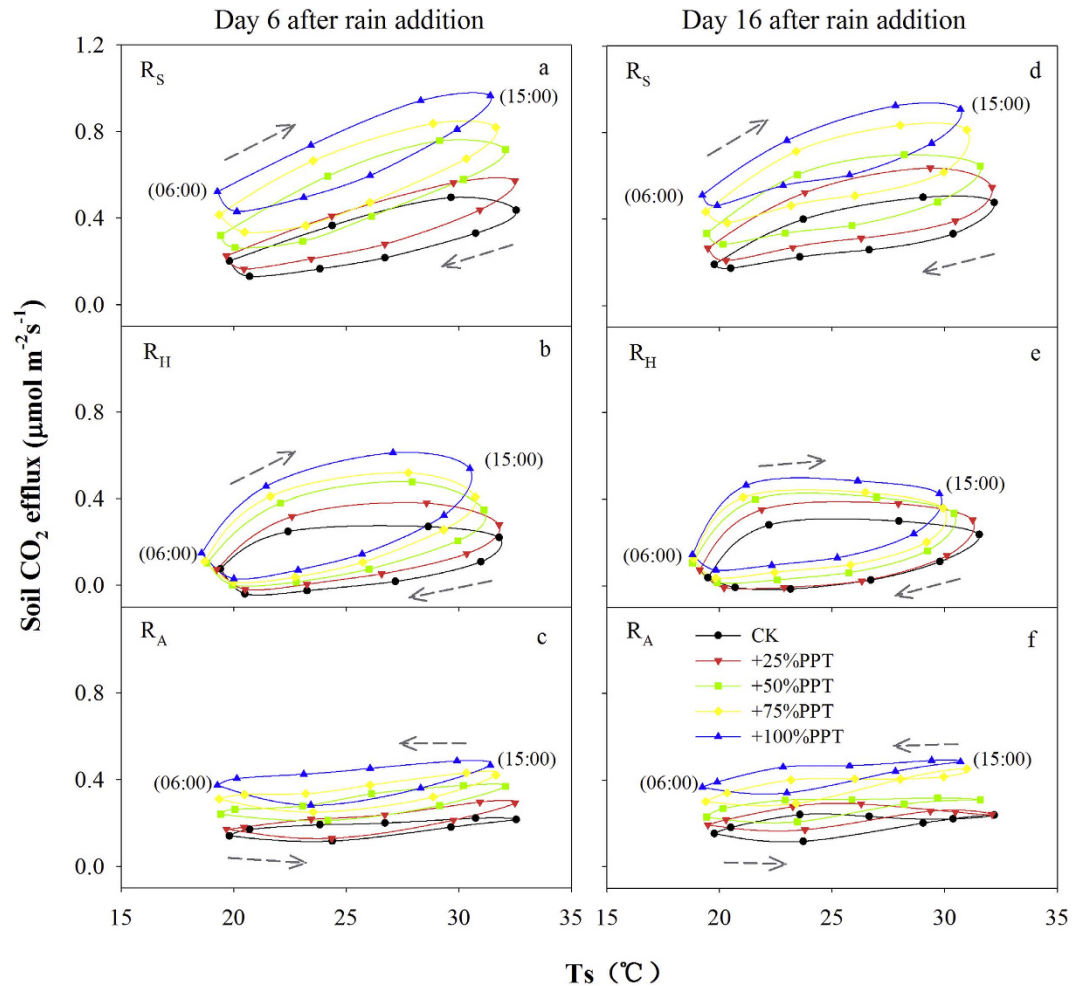


Figure 2. Relationships between diel soil CO₂ efflux and soil temperature at 10 cm soil depth on Days 6 and 16 after the rain addition treatments during the growing season. (a,d) Soil CO₂ efflux in the vegetated soils (total soil CO₂ efflux, R_S), (b,e) soil CO₂ efflux in the bare soils (heterotrophic respiration, R_H), (c,f) calculated autotrophic respiration (R_A). Dotted arrows indicate the directions of the hysteresis loop.

difference in daily mean T_s between the vegetated and bare soils under a given rain addition treatment on each measurement day³².

Relationship between diel soil CO₂ efflux and soil temperature. Plots of the diel dynamics of R_S, R_H and R_A against soil temperature on Day 6 and Day 16 following the rain addition treatments are shown in Fig. 2. A clockwise diel pattern of hysteresis with respect to soil temperature was found for R_S and R_H on both measurement days, with higher rate of R_S and R_H when soil temperature was increasing during daytime, and lower rate when temperature was decreasing during nighttime (Fig. 2a,b,d,e). The rate of R_S and R_H reached the maximum value between 12:00–15:00 and then gradually decreased to minimum value between 3:00–6:00. However, the maximum rate of R_A occurred between 18:00–21:00, and the minimum occurred between 6:00–9:00 despite the increase in soil temperature (Fig. 2c,f). Diel rate of R_A exhibited a counter-clockwise effect with soil temperature, that is, for a given temperature, the rate of R_A at nighttime was higher than at daytime.

Effect of rain addition treatments on diel hysteresis of soil CO₂ efflux. During the growing season, the diel hysteresis of R_S and R_H was positive while the diel hysteresis of R_A was negative (Fig. 3). The values of diel hysteresis of R_S and R_H showed significant seasonal variations, with the minimum diel hysteresis of R_S and R_H occurring on June 26th and the maximum on August 26th (Fig. 3a,b). However, the diel hysteresis of R_A were relatively stable during the growing season (Fig. 3c).

On Day 6, the rain addition had no influence on the diel hysteresis of R_S (Fig. 4a), but significantly increased the amplitudes of diel hysteresis of the two respiration components (Fig. 4b,c). On Day 16, the rain addition had no significant effect on the diel hysteresis of R_S and its components (Fig. 4d-f). There

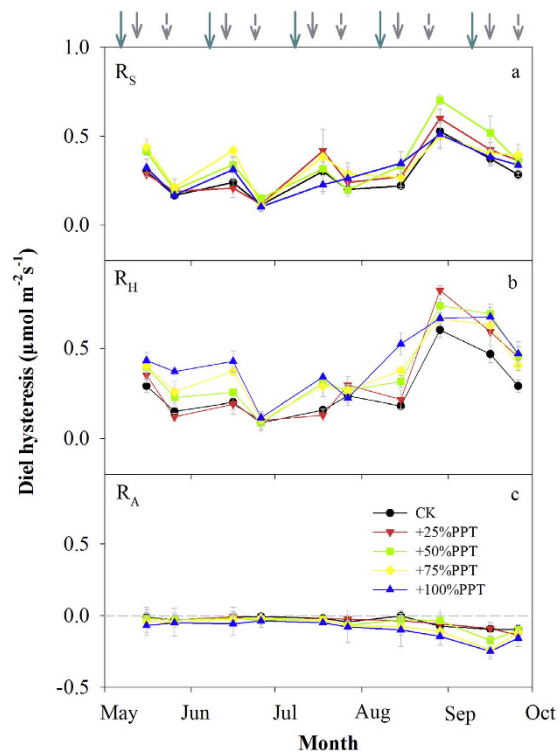


Figure 3. Seasonal variations in the diel hysteresis of soil CO₂ efflux (R_S) and its components (R_H and R_A). Long solid arrows represent the timing of rain addition treatments; short solid and dashed arrows represent the measurement time on Day 6 and Day 16 after the rain addition treatments, respectively.

was no significant interaction effect of rain addition amount and rain addition time on the diel hysteresis of R_A and R_H on either Day 6 or 16 (Table S1). The value of diel hysteresis for R_H was always higher than for R_A on both measurement days. In addition, the amplitude of diel hysteresis positively corresponded with the increase in daily SWC for R_S and its components on both measurement days (Fig. 5).

The method of using nighttime soil CO₂ efflux data to predict daytime soil CO₂ efflux, a common method in eddy covariance studies, resulted in significant error in the estimation of daily total soil CO₂ efflux (Table 1). During the growing season, there was an underestimation of daily flux by 10–32% for R_S and 41–62% for R_H , but an overestimation of R_A by 5–12% in this desert ecosystem. Rain addition changed the value of the error, and the magnitude of the change depended on the date of measurement (Table 1). On Day 6, rain addition significantly decreased the magnitude of the error for R_S and R_H but had no influence for R_A . On Day 16, however, there was a significant decrease in the magnitude of error for R_S but had no change in the two respiration components.

Discussion

Numerous studies have investigated diel hysteresis between soil CO₂ efflux and temperature, but reached contrasting conclusions on the mechanisms for the occurrence of such phenomenon^{12–20,36}. In addition, these results mainly focused on diel hysteresis of total soil CO₂ efflux and so far research concerning the diel hysteresis of two respiration components is still rare¹⁸. Furthermore, how diel hysteresis will respond to climate change, particularly precipitation change, is still poorly understood. To best of our knowledge, this is the first study focused on the differential responses of the diel hysteresis between the two components of soil CO₂ efflux *in situ* to rain pulses over an entire growing season. Our results from this field manipulation experiment offer new insights into how soil CO₂ efflux responds to temperature and soil moisture.

In this study, we found that a distinct diel hysteresis existed between R_A and R_H in terms of their responses to soil temperature. The rate of R_A was higher when soil temperature was decreasing than when soil temperature was increasing, producing a counter-clockwise hysteresis loop. In contrast, the rate of R_H increased more quickly in response to rising soil temperature in the morning compared to decreasing soil temperature in the evening, showing a clockwise hysteresis loop. These results suggest that both biological and physical mechanisms should be responsible for the diel hysteresis of soil CO₂ efflux in this desert ecosystem, and also indicate that variables that control diel behaviour of R_A in response to changes in soil temperature are different from the variables that control diel behaviour of R_H .

Several field studies have found a strong connection between plant photosynthesis and R_A at diel and seasonal scales^{16,21,37}. The time required to transport photosynthetic C to roots was found on the order

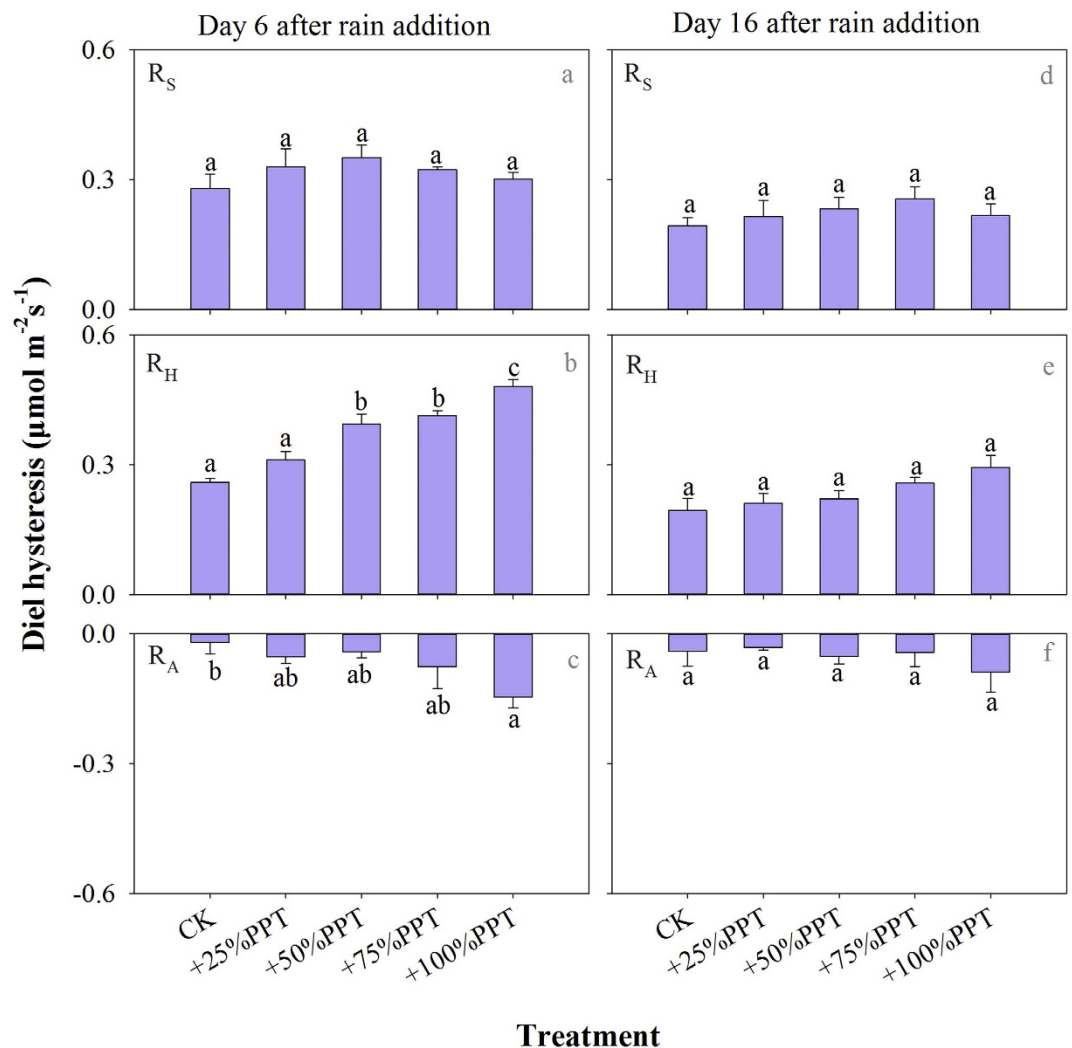


Figure 4. Mean values of diel hysteresis of soil CO₂ efflux (R_S) and its components (R_H and R_A) on Day 6 and Day 16 after different rain addition treatments during the growing season in 2009 ($n=4$). The different letters indicate significant differences between rain addition treatments at $P < 0.05$.

of many hours to a few day^{10,13,15,38}. For instance, Tang *et al.*¹⁶ reported that the time for photosynthetic products to be transported to the roots and be respired is less than 1 day. Similarly, by *in situ* ¹³CO₂ pulse labelling of shrubs, Carbone and Trunbore³⁹ demonstrated that a part of photosynthetic C can be rapidly transported to belowground and be quickly metabolized by roots within a few hours. In this study, peak R_A occurred at between 18:00–21:00, which was about 3 h after peak 10 cm soil temperature, 6 h after peak PAR. The high correlation between daily mean PAR and daily mean R_A (Fig. S1) suggested that the C respired by roots may be related to the same day's photosynthesis. We speculate that accumulated photosynthetic C during daytime was periodically transported to the roots and metabolized at night, which could have contributed to the counter-clockwise diel hysteresis of R_A (Fig. 6a). However, in this study site, most roots biomass was concentrated in the 10–30 cm soil layers, which suggested that the diel hysteresis of R_A could have also been modified by physical processes. According to model analysis, Phillips *et al.*¹⁰ demonstrated that the effect of CO₂ diffusivity on diel hysteresis can be bypassed because it does little to shift diel oscillation of R_A considering the high porosity of sandy soil, which is similar to the soil type in this study. In contrast to CO₂ diffusivity, model based on physical first principles (Table 1 and Fig. 3 in Phillips *et al.*¹⁰) proved that thermal transport plays an important role in controlling the diel hysteresis of soil CO₂ efflux by controlling the speed of air temperature propagated through soil and by changing the synchronicity of diel variations of soil temperature and efflux¹⁰. The asynchronous diel patterns between soil temperature and efflux could result in a clockwise hysteresis loop within an approximate rate (e.g. $1 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}$ based on measurements of a sandy loam soil) of thermal diffusivity for sandy soils experiencing normal field moisture level¹⁰ (Fig. 6a). Thus, although the clockwise effect of physical processes had no influence on the rate of R_A and the rotational direction of hysteresis loop, it could have modified the orientation of the principal axes of the hysteresis loop of R_A

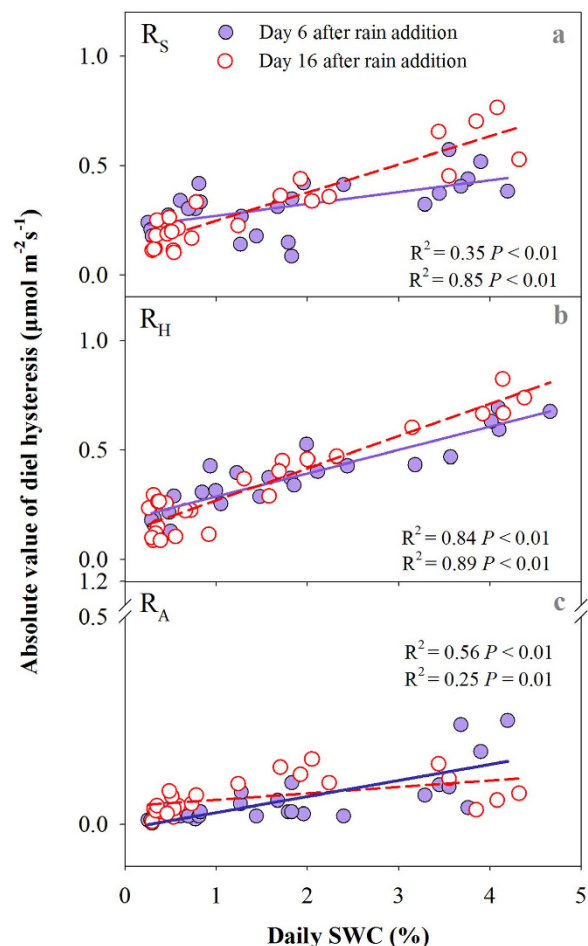


Figure 5. Relationships between absolute values of diel hysteresis and daily soil water content (SWC).

	R_S			R_H			R_A		
	Measured	Calculated	Error	Measured	Calculated	Error	Measured	Calculated	Error
Day 6 after rain addition									
CK	0.31 (0.06)	0.21 (0.06)	-32 (3) ^a	0.11 (0.02)	0.04 (0.02)	-62 (2) ^a	0.20 (0.04)	0.21 (0.04)	6 (2) ^a
+25%PPT	0.44 (0.07)	0.31 (0.06)	-29 (2) ^{ab}	0.15 (0.03)	0.07 (0.03)	-56 (2) ^{ab}	0.19 (0.04)	0.21 (0.04)	10 (2) ^a
+50%PPT	0.51 (0.06)	0.40 (0.06)	-21 (2) ^b	0.20 (0.03)	0.09 (0.02)	-49 (3) ^b	0.31 (0.03)	0.32 (0.03)	4 (2) ^a
+75%PPT	0.67 (0.11)	0.59 (0.11)	-12 (3) ^c	0.22 (0.02)	0.11 (0.02)	-51 (1) ^b	0.45 (0.09)	0.47 (0.09)	5 (3) ^a
+100%PPT	0.73 (0.10)	0.66 (0.09)	-10 (3) ^c	0.27 (0.03)	0.13 (0.03)	-52 (2) ^b	0.47 (0.10)	0.50 (0.09)	6 (2) ^a
Day 16 after rain addition									
CK	0.33 (0.04)	0.26 (0.04)	-20 (2) ^a	0.13 (0.02)	0.07 (0.01)	-46 (2) ^a	0.20 (0.03)	0.23 (0.03)	15 (2) ^a
+25%PPT	0.40 (0.06)	0.31 (0.05)	-21 (3) ^a	0.15 (0.03)	0.08 (0.01)	-47 (2) ^a	0.25 (0.03)	0.27 (0.03)	8 (2) ^a
+50%PPT	0.48 (0.06)	0.39 (0.06)	-18 (2) ^a	0.20 (0.02)	0.11 (0.02)	-45 (1) ^a	0.28 (0.03)	0.31 (0.03)	11 (2) ^a
+75%PPT	0.58 (0.06)	0.49 (0.06)	-15 (2) ^{ab}	0.24 (0.02)	0.13 (0.02)	-44 (1) ^a	0.34 (0.05)	0.36 (0.05)	6 (3) ^a
+100%PPT	0.69 (0.06)	0.63 (0.06)	-12 (3) ^b	0.27 (0.01)	0.16 (0.01)	-41 (1) ^a	0.42 (0.05)	0.47 (0.05)	12 (3) ^a

Table 1. A comparison of measured and calculated daily soil CO₂ efflux (R_S) and its components (R_H and R_A) (g C m⁻² d⁻¹) that was based on the relationship between nighttime efflux and soil temperature on Days 6 and 16 after different rain addition treatments. Error = (Calculated-Measured) × 100%/Measured. A positive value of the Error represents an overestimation of the soil CO₂ efflux, and *vice versa*. Values are presented as the mean (SE). The different letters within the Error column on each day indicate significant differences among the five rain addition treatments ($P < 0.05$).

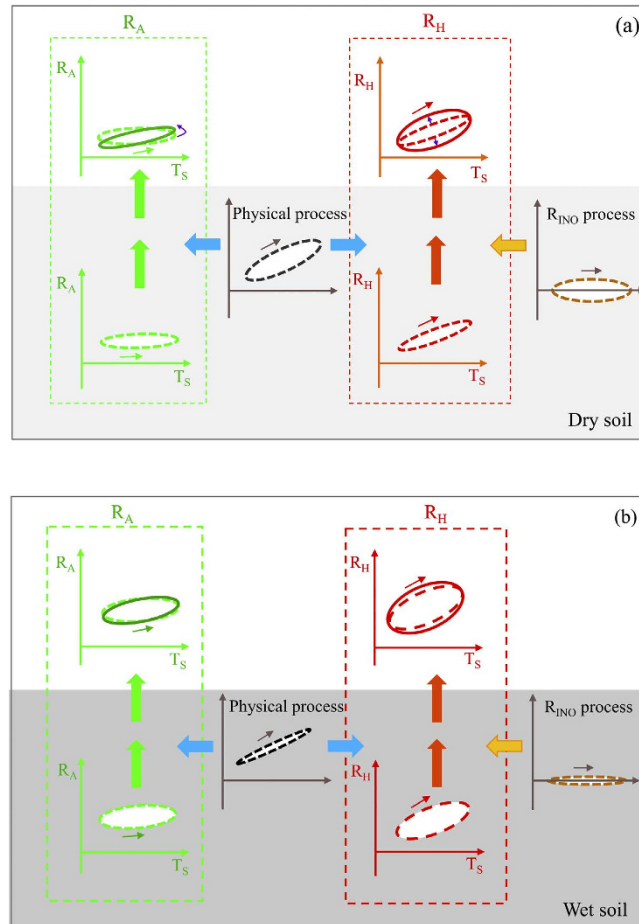


Figure 6. Conceptual illustration of factors controlling diel hysteresis patterns of soil CO₂ efflux (R_s) and its components (R_A and R_H) in responding to soil temperature in dry (a) and wet (b) soils. The effect of physical (mainly heat) transport processes on the diel hysteresis of R_A and R_H is same. Besides physical process, the diel hysteresis of R_H is also modified by chemical (inorganic CO₂ efflux, R_{INO}) process. In dry soil condition (a), the effects of physical and chemical processes to the diel relationship between soil CO₂ efflux and soil temperature are pronounced, while the effects are limited under wet soil condition (b). See the text in the Discussion for more details.

(Fig. 6a). Consequently, the co-occurrence of biological mechanism (diel photosynthetic carbon supply) and physical processes, particularly thermal transport, could have contributed to the counter-clockwise diel hysteresis of R_A in this desert ecosystem.

On the other hand, the clockwise hysteresis effect of R_H could not be associated with carbon supply mechanism because there were no obvious root biomass in the bare soils. The explanation for the diel hysteresis of R_H is still unclear, but three possible mechanisms may account for it. First, physical processes associated with heat transport and CO₂ diffusion mentioned above may be responsible for the diel hysteresis of R_H (Fig. 6a). Second, many previous studies have reported that in arid ecosystems with saline/alkaline soils, there is a chemical (i.e. carbonate precipitation and dissolution) process (inorganic CO₂ efflux, R_{INO}) influencing the diel variation of soil CO₂ efflux because R_{INO} shows a positive value during daytime (CO₂ emission) and a negative value (CO₂ absorption) at nighttime^{40–43} (Fig. 6a). Based on the diel relationship between R_{INO} process and soil temperature in Fig. 6a, which is redrawn based on results of Liu *et al.*⁴³ and Ma *et al.*⁴⁰ in saline/alkaline soil desert ecosystems located near our study site, we suggest that the diel variation in R_{INO} could have affected the observed diel hysteresis of R_H by modifying the rate of R_H and the roundness of hysteresis loop. However, the diel variation R_{INO} would have no influence on the orientation of the principal axes of the hysteresis loop of R_H and the rotational direction of hysteresis loop. Third, in desert ecosystems, microbial communities such as bacteria and fungi usually have different vertical distribution to compete for available substrates^{44–46}. The differential temperature sensitivities of microbial components^{47–49} may have contributed to the diel hysteresis of R_H . In addition, the growth rates of bacteria and fungi usually have optimum temperatures around 25–30 °C⁴⁹. The higher temperature (above 33 °C) at noon at this site could have inhibited the activity of microbes, leading to a clockwise hysteresis loops. We propose that the above three mechanisms together resulted in the

clockwise diel hysteresis of R_H (Fig. 6a). However, we found that R_H had a strong temporal coincidence with photosynthetic active radiation (PAR) (Fig. S2), which reached a maximum at 12:00. This is earlier than the soil temperature maximum, which occurred around 15:00, indicating that diel pattern of R_H in this desert ecosystem may be more closely related to near surface soil temperature. However, it does not necessarily imply that all microbial respiration occurs in surface soils, as microbial respiration at deep soils certainly occur.

In addition, a clockwise hysteresis loop of R_S was observed in responding to diel change of soil temperature, which is similar to that of R_H but distinct from that of R_A . The clockwise diel pattern could be attributed to the high contribution of R_H to R_S , particularly when soil temperature was increasing. Many previous studies suggest that the diel hysteresis between soil CO_2 efflux and soil temperature is an artifact due to an arbitrary selection of a reference soil depth, which can produce an unrealistic relationship between efflux and soil temperature^{19,50}. By exploring the relationship between soil CO_2 efflux and its two components with air temperature (Fig. S3), we found a distinct, elliptical diel hysteresis, suggesting a potential occurrence of diel hysteresis of soil CO_2 efflux in responding to soil temperature at different depths, and also highlighting the complexity of understanding the processes controlling the relationship between soil CO_2 efflux and temperature. Thus, we argue that, in order to accurately understand the temperature dependence of R_S , it is necessary to include measurements of soil temperature at several depths.

Rain addition resulted in a larger magnitude of diel hysteresis of R_A on Day 6 when soil moisture was higher. Many studies have shown that an effective rainfall can infiltrate into deep soils and be absorbed by plants with deep-rooted systems, leading to an increase in photosynthesis, especially in desert and semiarid ecosystems^{24,51}. In this study, photosynthesis of *N. tangutorum* significantly increased after rain addition treatments (unpublished data). This higher photosynthesis of plants implied that a larger portion of photosynthetic C was transported into belowground and metabolized by roots^{33,37}, which was of sufficient magnitude to alter diel patterns of R_A ^{32,52}. However, increased soil water moisture following rain addition could have altered the effects of physical processes by increasing the rate of heat diffusivity and decreasing the rate of CO_2 transport. The change in the two physical transport processes have consistent effect on diel hysteresis that cause clockwise diel hysteresis to become less pronounced¹⁰. Therefore, the limited effect of physical mechanism could have contributed to the change of diel hysteresis of R_A because physical processes had contrasting effect on the orientation of hysteresis loop. We found that rain addition had no effect on the diel hysteresis of R_A on Day 16 when soil was drier. The different effect of rain addition for the two days was most likely a consequence of variation in soil water content. On day 16, the lower soil water availability could have weakened the activity of plants and reduced the coupling between plant photosynthesis and belowground processes by reducing the movement of recent photosynthates to phloem loading sites and by changing the flow rate of photosynthates from the shoots into the roots^{33,54}. This would potentially stifle the effects of rain addition on diel hysteresis of R_A on Day 16. In addition, the increasing effect of physical processes following soil drying could be responsible for the consistent values of diel hysteresis among treatments on Day 16.

Similarly, soil water availability is a vital factor in controlling microbial activity in desert and semiarid ecosystems^{55–57}. After rewetting following simulated rain addition, microbial activity recovered quickly due to increased substrates availability and favorable environmental conditions^{23,51,58}, leading to a large production of CO_2 gas. In addition, the change in the two physical transport processes under rain addition treatments could have caused clockwise diel hysteresis to become less pronounced (Fig. 6b) because physical processes have a consistent effect on the orientation of hysteresis loop. Furthermore, increasing soil water content could decrease the effects of R_{INO} on diel hysteresis because the wetter the saline/alkaline soils are, the less effect R_{INO} will have on the diel pattern of R_H ^{40–42}. Therefore, compared with dry soil (Fig. 6a) or control plots (CK), rain addition treatments could have diminished the effects of physical processes and R_{INO} on the diel hysteresis of R_H .

Why was there an increase in the diel hysteresis of R_H on Day 6 after rain addition? We propose two possible mechanisms for this phenomenon. First, the high soil moisture enhanced the diffusion of organic molecules through soil water films and increased substrate availability for microbial mineralization^{23,59}. This would have affected microbial activity differently in various soil layers because microbial communities have a vast vertical distribution and thus have different moisture sensitivities^{47–49}, increasing the diel hysteresis of R_H on Day 6. Second, rain addition eliminated environment stress and provided a favorable (cool, wet) microclimate for microbial activity at a diel scale, particularly at noon³². The higher R_H rate and lower soil temperature at daytime resulted in an increase in the diel hysteresis of R_H . Whereas on Day 16 when the soil was drier, the diel hysteresis of R_H decreased and showed no significant difference among treatments. Previous studies have shown that an effective rainfall event could trigger a rapid pulse response of microbial activity, and the response would gradually decrease due to exhaustion of accessible organic matter^{55,60,61}. The declined substrate availability on Day 16 could have also inhibited the temperature response of microbial activity, particularly at midday when temperature reached maximum value, leading to a consistent diel hysteresis value of R_H among treatments. In addition, the consistent value could be attributed to the increasing role of physical mechanism discussed above. Our findings are consistent with other research showing that soil water availability can modify the magnitude of diel hysteresis between soil CO_2 efflux and soil temperature¹⁵. In addition, we found that the change in soil moisture would only change the diel magnitude of R_H with no effect on orientation. These results derived from field experiment is consistent with theoretical analysis¹⁰.

Surprisingly, we found that rain addition had no influence on the diel hysteresis of R_S on the two measurement days, although the daily mean rate of R_S significantly increased by rain addition treatments on both days during the growing season³². In this study site, the increased size of clockwise hysteresis loop of R_H would be offset by the increased size of counter-clockwise hysteresis loop of R_A , which could have resulted in the consistent value for diel hysteresis of R_S among the five rain addition treatments during the growing season.

In addition, we found that, without considering diel hysteresis, significant error would occur in the estimation of daily soil CO_2 efflux based on a relationship between efflux and temperature. Thus, diel hysteresis should be considered in terrestrial ecosystem models for predicting regional C cycles in desert regions. The method of using nighttime soil CO_2 efflux data to predict daytime soil CO_2 efflux, a common method in eddy covariance studies, resulted in an underestimation of daily R_S and R_H by 10–32% and 41–62% respectively, but an overestimation of daily R_A by 5–12% in this desert ecosystem. However, in a Chihuahuan desert shrubland, Hamerlynck *et al.*⁶² showed an overestimation of daily soil CO_2 efflux by 9–19% based on temperature-derived functions that do not consider diel hysteresis. Similarly, Riveros-Iregui *et al.*¹⁵ found an overestimation of growing season total soil CO_2 efflux by 19% in a montane conifer forest when diel hysteresis was not considered. These results indicate that in different ecosystems with varying relative contribution of the two respiration components to the total efflux, the value of the error would be different. Thus, in order to accurately estimate ecosystem C budgets under future climate scenarios, we should consider the different responses of R_A and R_H to climate change, particularly to rainfall variability.

Implications and limitations. The results from our field experimental studies have important implications for regional carbon cycle simulations. First of all, one can no longer confidently capture an entirety of temperature response in soil CO_2 efflux by only measuring soil CO_2 efflux late morning because of the present of hysteresis. At the ecosystem-scale, eddy covariance-based studies often use nighttime respiration data to predict daytime rates of respiratory efflux in accordance with exponential temperature extrapolation⁶³. The results of this study underscore that the failure to account for possible hysteresis of soil CO_2 efflux at diel and/or seasonal scales may result in under- or overestimation of ecosystem respiration^{36,64}, which is composed of both soil and aboveground component efflux. In addition, the occurrence of diel hysteresis suggests a potential problem in the usage of constant temperature sensitivity of soil CO_2 efflux for gap filling procedures and in ecosystem carbon cycling models⁶⁵. Lastly, higher soil water content results in a larger amplitude of diel hysteresis, implying that the role of soil water content in controlling the relationship between soil CO_2 efflux and soil temperature should be considered in the modeling of production and efflux of CO_2 from the soils in desert and semiarid ecosystems subjected to severe seasonal changes in soil water availability.

Although we investigated the effects of experimental rain addition on diel hysteresis of soil CO_2 efflux and its components (R_H and R_A) in a desert ecosystem, this study was limited by several uncertainties. First, the calculation of diel hysteresis was based on the relationship between soil CO_2 efflux and temperature at a soil depth of 10 cm. It is worth noting that the soil temperature used in our analysis is crucial because the phase and peak of soil temperature in different soil layers vary due to altered heat transport rate^{19,50}, despite finding a distinct diel hysteresis between soil CO_2 efflux and air temperature. Therefore, to understand exactly the diel hysteresis, several soil depth samples should be taken into account in further experiments. Second, the method of calculating R_A in our study was based on the difference in the rate of soil CO_2 efflux between the vegetated soil and the bare soil; however, this method may ignore the presence of rhizosphere respiration. Thus our method may over- or under-estimate the diel response of R_A to soil temperature and result in a calculated deviation in diel hysteresis of R_A . However, it should be noted that among the different partitioning methods reviewed by Hanson *et al.*⁶⁶ and Kuzyakov⁶⁷, our approach seems to be the most appropriate method for separating R_A and R_H in this desert ecosystem. Third, several previous studies suggested that a rainfall pulse after a period of drought can result in a quick response in microbial activity within several hours and the response is often short-lived in desert and semiarid regions^{24,33}. In this study, we measured diel variations in soil CO_2 efflux on Days 6 and 16 after the rain addition, which may not capture such quick response of microbial activity to the rain addition. Therefore, to fully understand the response of diel hysteresis to rainfall pulse, continuous soil CO_2 efflux measurements following rainfall events should be performed in further experiments. Finally, this study was conducted in a desert ecosystem, and whether other ecosystems, such as grassland or forest ecosystems have a similar response in diel hysteresis of soil CO_2 efflux and its components to rain addition is still unclear. Therefore, more experimental studies with better approaches (e.g. stable isotope labeling) are needed to better understand the diel hysteresis of soil CO_2 efflux and its components as well as to accurately model soil C loss from terrestrial ecosystems under future climate scenarios.

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Author Contributions

S.P.C., B.W., Q.L. and G.H.L. conceived and designed the experiments. W.M.S., S.P.C., Y.D.Z. and Y.J.Z. performed the experiments. W.M.S., S.P.C. and G.H.L. analysed the data and wrote the manuscript.

Additional Information

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