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Responses of temporal and spatial variation in soil  
respiration to biotic and abiotic factors in a desert  
shrubland in northwest China

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Academic dissertation

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## ABSTRACT

The aim of this work was to analyze the responses of temporal and spatial variation in soil respiration to biotic and abiotic factors in a desert shrubland in Ningxia, northwest China. For this purpose,  $R_s$  together with abiotic (soil temperature ( $T_s$ ), soil water content ( $SWC$ ), precipitation ( $PPT$ )) and biotic (root biomass, litter fall, leaf area index, soil nitrogen) factors were measured, and plant phenophases were recorded over a typical sand dune in 2012-2014. The specific aims of this study were to: (1) quantify the diurnal and seasonal variation of  $R_s$  and its controlling factors, and to understand the influences of  $SWC$  on the temperature sensitivity of  $R_s$  (Paper I); (2) explore the mechanisms controlling the spatial heterogeneity in  $R_s$  and the plant effects on spatial variation of  $R_s$  in different phenophases (Paper II); (3) examine the seasonal variation of diel hysteresis in  $R_s$ - $T_s$  relationship and its controlling factors ( $SWC$  and photosynthesis) (Papers I and III); and (4) explore the influences of biological soil crusts on  $R_s$  and its climatic ( $T_s$ ,  $SWC$ ,  $PPT$ ) responses (Paper IV).

As a result, both diurnal and seasonal variation in  $R_s$  were controlled dominantly by  $T_s$ , but the diurnal and seasonal response of  $R_s$  to  $T_s$  was modified by  $SWC$  and biological soil crusts (Papers I, III and IV). At diel scale,  $R_s$  was strongly regulated by  $T_s$  at moderate and high  $SWC$ , but decoupled from  $T_s$  under low  $SWC$ , due to significant diel hysteresis between  $R_s$  and  $T_s$  (Papers I and III). This diel hysteresis varied seasonally with  $SWC$ , showing increasing lag time with decreasing  $SWC$  (Papers I and III). Variation in the diel hysteresis with changing  $SWC$  was regulated by photosynthesis of the dominant shrub species (Paper III). At seasonal scale,  $R_s$  significantly correlated with  $T_s$  at  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$  (Paper I). In addition, the temperature sensitivity of  $R_s$  increased with increasing of  $SWC$  (Paper I). The  $R_s$  at both non-cruste (NCS) and lichen-cruste (LCS) soils increased with increasing  $T_s$ , opposite to that on moss-cruste soil (MCS), where  $R_s$  declined with increasing  $T_s$  as  $T_s > \sim 20^\circ\text{C}$  (Paper IV). Root biomass of shrubs and grasses, litter fall and soil nitrogen affected the topographic variation in  $R_s$  (Paper II). During the flowering-bearing phase of the dominant shrub, root biomass affected  $R_s$  the most, whereas during the leaf coloration-defoliation phase, soil nitrogen content affected  $R_s$  the most, explaining 72 and 56% of the total variation, respectively (Paper II).

To conclude,  $SWC$ , biological soil crusts and shrubs exert strong influences on the temporal and spatial responses of  $R_s$  to  $T_s$  in a desert shrubland. These results highlight the necessity to account their interactive effects in estimation of carbon balance for desert ecosystems and in modelling of global carbon cycle in order to increase the accuracy of model predictions.

**Keywords:** Soil  $\text{CO}_2$  flux, phenology, hysteresis, microtopographic variation, *Artemisia ordosica*

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Joensuu, April 2017

Ben Wang

## LIST OF ORIGINAL ARTICLES

The thesis is a summary of the following papers referred to in the text with Roman numbers I-IV. Articles I and II are reprinted with the kind permission of the publisher. Articles III and IV are the author's version of the submitted manuscript.

- I Wang B., Zha T.S., Jia X., Wu B., Zhang Y. Q., Qin S. G. (2014). Soil moisture modifies the response of soil respiration to temperature in a desert shrub ecosystem. *Biogeosciences* 11: 259-268.  
<http://doi.org/10.5194/bg-11-259-2014>
- II Wang B., Zha T.S., Jia X., Gong J. N., Wu B., Bourque C. P. A., Zhang Y., Qin S. G., Chen G. P., Peltola H. (2015). Microtopographic variation in soil respiration and its controlling factors vary with plant phenophases in a desert-shrub ecosystem. *Biogeosciences* 12: 5705-5714.  
<http://doi.org/10.5194/bg-12-5705-2015>
- III Wang B., Zha T.S., Jia X., Gong J. N., Bourque C. P. A., Wu B., Zhang Y., Feng W., Peltola H. (2017). Soil water regulates the control of photosynthesis on diel hysteresis between soil respiration and temperature in a desert shrub land. Manuscript.
- IV Wang B., Zha T.S., Jia X., Gong J. N., Wu B., Bourque C. P. A., Zhang Y., Qin S. G., Chen G. P., Peltola H. (2017). Influences of biological soil crust on CO<sub>2</sub> exchange in a desert shrub ecosystem. Manuscript.

The present author, Ben Wang, was mainly responsible for field measurements, data processing and analyses, and manuscript writing for Articles I - IV. The co-authors contributed to the articles via work related to the experiment design, field measurements, support for data analyses and manuscript revisions.

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## ABBREVIATIONS

<b>Symbol</b>	<b>Unit</b>	<b>Description</b>
AIC	/	Akaike information criterion
CART	/	Class and regression tree analyses
$C_{eff}$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Soil CO <sub>2</sub> efflux
$C_{inf}$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Soil CO <sub>2</sub> influx
LAI	$\text{m}^2 \text{m}^{-2}$	Leaf area index
LCS	/	Lichens crusted soil
MCS	/	Mosses crusted soil
NCS	/	Non-crusted soil
PAR	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Incident photosynthetically active radiation
PPT	mm	Precipitation
$R_s$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Soil respiration
SWC	$\text{m}^3 \text{m}^{-3}$	Volumetric soil water content
$T_a$	°C	Air temperature
$T_s$	°C	Soil temperature at 10 cm depth
$T_{surf}$	°C	Soil surface temperature





# 1. INTRODUCTION

## 1.1 Importance of soil respiration in drylands to global carbon cycle

Arid, semiarid and dry-subhumid ecosystems (drylands), occupying 41% of the earth's land surface (Reynolds, 2001; Safriel and Adel, 2005), are rapidly expanding due to human population growth and global climate change (Geist and Lambin, 2004). Based on recent studies, the carbon (C) turnover rates are high in drylands and closely coupled to variabilities in temperature and precipitation. Thus, C cycle in drylands is sensitive to climatic variations and changes, and could affect largely the global C variability and trends (Poulter et al., 2014; Ahlström et al., 2015). Global climate change is also associated with an increase of temperature and precipitation variability, which may exacerbate aridity in some desert ecosystems (Lioubimtseva and Henebry, 2009). Therefore, for accurate estimation of the global C balance under changing climate, the climatic control on C cycle in drylands should be better understood (Cable et al., 2011).

Soil respiration ( $R_s$ ) accounts for about 50-90% of ecosystem respiration (Schimel et al., 2001; Ryan and Law, 2005; Jassal et al., 2007; Gaumont-Guay et al., 2008), and its global integral is an order of magnitude larger than anthropogenic CO<sub>2</sub> releases from burning fossil fuels and land-use change (Marlan et al., 2008). Even relatively small increases in  $R_s$  may have a profound impact on atmospheric CO<sub>2</sub> concentrations, exerting a positive feedback to global warming (Schlesinger and Andrews, 2000; Davidson and Janssens, 2006; Luo, 2007). Previous studies have reported that  $R_s$  exhibits strong spatiotemporal heterogeneities, which makes it difficult to estimate soil C release (Bond-Lamberty and Thomson, 2010; Luo et al., 2012; Ja et al., 2013). Furthermore, such heterogeneity in  $R_s$  depends strongly on biotic factors (e.g., soil organic matter and living biomass, Martin and Bolstad, 2009; Geng et al., 2012; Nago et al., 2012) and abiotic factors (e.g. soil temperature ( $T_s$ ) and soil water content (SWC); Marrin and Bolstad, 2009; Ngao et al., 2012). Thus, to predict in an accurate way the alteration in C balance at both regional and global scales under the changing climate, we need to understand in detail the biotic and abiotic control on temporal and spatial variation in  $R_s$  in drylands (Grote et al., 2010). However, currently  $R_s$  is not yet well understood for drylands, partly due to their low productivity (Chen and Tian, 2005).

## 1.2 Biotic and abiotic control on temporal variation in soil respiration

Temporal variation in  $R_s$  and its controlling factors have been widely studied in forest and grassland ecosystems. Both  $T_s$  and SWC have been considered as the primary abiotic factors in controlling the seasonal variation in  $R_s$ , due to their strong influences on the decomposition of soil organic matter (Jassal et al., 2008; Liu et al., 2009; Moyano et al., 2012), roots (Palta and Nobel, 1989; Bouma et al., 1997) and microbial activity (Linn and Doran 1984; Skopp et al., 1990; Hallett and Yong, 1999; Drenovsky et al., 2004). Generally,  $T_s$  dominantly controls  $R_s$ , because it regulates the kinetics of microbial decomposition, diffusion of enzymes and substrates (Jassal et al., 2008). However, different from forest and grassland ecosystems, SWC in drylands may have greater influences than  $T_s$  in controlling the temporal variation in  $R_s$ . This is because drylands are characterized with shorter wet

periods and longer intervals of periodic drought. During the drought periods, biological activities in drylands are suppressed by the limited soil water (Noy-Meir, 1973), resulting restriction of microbe access to C substrate, reduction of C substrates and extracellular enzymes diffusion, and limitation of microbial mobility (Yuste et al., 2003). Therefore, future studies are needed to clarify the control of  $T_s$  and  $SWC$  on temporal variation in  $R_s$  in drylands.

Beyond the controls of  $T_s$  and  $SWC$ , biological soil crusts (e.g., mosses, lichens, cyanobacteria and algae), which dominate about 40-70% of the interspace between plants in drylands (West, 1990; Belnap and Lange, 2003), have also been reported to exert strong influences on  $R_s$  (Castillo-Monroy et al., 2011; Su et al., 2011; Feng et al., 2014). Biological soil crusts switch from inactive during a drought period to active in a wet period, resulting in significant  $CO_2$  uptake. Such  $CO_2$  influxes ( $C_{inf}$ ) make the responses of  $R_s$  to climatic factors (e.g.  $T_s$  and  $SWC$ ) complex. Biological soil crusts are also inactive and exhibit C release most (90%) of the year to withstand extreme environment conditions (Miralles et al., 2012). They are metabolically active and exhibit  $CO_2$  uptake within 20 min after moistened by dew, fog or rainfall (Lange et al., 2001; Barker et al., 2005; Grote et al., 2010; Su et al., 2011). Their  $C_{inf}$  could offset  $CO_2$  efflux ( $C_{eff}$ ) respired by other organisms beneath (e.g., microbes and roots), resulting in much lower  $R_s$  in the field compared to that predicted by the commonly used  $T_s$ - $R_s$  models. To well understand the climatic control on  $R_s$  in drylands, we need to better understand the influences of biological soil crusts on  $R_s$ .

The influences of biological soil crusts on  $R_s$  may also vary with crust types. Previous studies have reported that biological soil crusts exert strong influences on  $T_s$ ,  $SWC$ , soil nitrogen, microbial community and activity underground (Belnap, 2002; Sedia and Ehrenfeld, 2005; Castillo-Monroy et al., 2011; Delgado-Baquerizo et al., 2010), and thus also on autotrophic and heterotrophic soil respiration. The influences of biological soil crusts on these factors differ among crust types. Water infiltration is lower for higher successional stage (Zaady et al., 2012). Lichens grow slowly (Rogers, 1990), which coupled to low mortality rates and low standing crop biomass (During, 1992), results in low organic matter input for lichen-crusting microsites. Lichens inhibit also the microbial activity (Sedia and Ehrenfeld, 2005). In contrast, mosses have higher biomass and grow faster, resulting in higher inputs of organic matter for moss-crusting microsites (During, 1992). Mosses also enhance the microbial activity (Sedia and Ehrenfeld, 2005). Moreover, studies from recent warming and water regulation experiments suggest that different biological soil crusts types respond differently to changing climatic conditions (Reed et al., 2012; Zelikova et al., 2012; Maestre et al., 2013; Escolar et al., 2014; Escolar et al., 2015). Warming substantially decreases lichens cover but slightly increases mosses cover (Escolar et al., 2014). Rainfall frequency alterations promote also shifting from mosses to cyanobacteria (Reed et al., 2012; Zelikova et al., 2012). The alteration in biological soil crusts cover and composition will affect recalcitrant C sources, such as the aromatic compounds and the abundance of fungi related to bacteria. Consequently, it may affect the C cycle response to climate change in drylands (Maestre et al., 2013). Therefore, we need to better understand the influences of different biological soil crust types on  $R_s$  in drylands.

### 1.3 Biotic and abiotic control on spatial variation in soil respiration

Active, semi-active aeolian, and fixed sand dunes are the primary landscape features of desert ecosystem. Soil respiration has been reported to exhibit high spatial variation in desert ecosystem (Mahall et al., 1992; Gold et al., 1995; Xie et al., 2001). Generally,

hydrometeorological factors, especially  $T_s$  and SWC (Xu and Wan, 2008; and Liu et al., 2010), are the primary controls of such high spatial variation in  $R_s$  in desert ecosystem. This is because  $T_s$  and SWC control temporal variation in  $R_s$  (Lloyd and Taylor, 1994; Davidson et al., 1998; Wang et al., 2014). They both exhibit high spatial variation over sand dunes, due to the influence of topography in governing the amount of solar radiation received and the re-distribution of surface and shallow subsurface water (Kang et al., 2003; Liu et al., 2010). However, heterogeneity in micro-hydrometeorological factors affect largely the formation and patchy distribution of vegetation growing in an area and C sources (fertility islands), respectively (Richerson and Lum, 1980; Parker, 1991). The plant-scale processes, such as plant-facilitated entrapment of soil particles and organic matter propelled by wind or rain droplets, canopy shading, hydraulic lift, and accumulation and decomposition of litterfall, all induce enrichment of water, nutrients, and root biomass in the vicinity of plant canopy (Hook et al., 1991; Schlesinger and Raikes, 1996). Such plant effects also constrain the spatial variation in soil respiration over sand dunes. Therefore, plant controls on spatial variation in soil respiration may nest within micro-hydrometeorological controls. Further studies need to clarify the micro-hydrometeorological controls and plant control on spatial variation in  $R_s$  over sand dunes in drylands.

Previous studies have reported that both micro-hydrometeorological and plant control could vary with plant phenophases (Fu et al., 2002; Dungan et al., 2003; Tang et al., 2005; Asaeda and Rashid, 2015; Osono, 2014). This is because current photosynthate supply and decomposition and supplementation of litterfall change over time. For example, Fu et al. (2002) reported that root activity and rhizosphere processes could vary with plant phenophases. Yuste et al. (2004) and DeForest et al. (2006) argued that such changes potentially alter the relationship between  $R_s$  and  $T_s$ . However, further understanding on the seasonal effects of plants on the spatial variation in  $R_s$  is still needed in drylands.

#### 1.4 Diel hysteresis between soil respiration and soil temperature

Diel hysteresis, which appears as an elliptical loop in the relationship between diel  $R_s$  and  $T_s$ , has been widely reported for forests (Tang et al., 2005; Gaumont-Guy et al., 2006; Vargas and Allen, 2008), grasslands (Carbone et al., 2008; Barron-Gafford et al., 2011) and drylands (Feng et al., 2014). However, theoretical models for  $R_s$  (e.g. Lloyd-Taylor, Arrhenius, and van) cannot estimate the diel hysteresis, thus resulting in errors in predicted hourly  $R_s$  and uncertainties on temperature sensitivity in  $R_s$  (Gaumont-Guay et al., 2008; Phillips et al., 2011; Darenova et al., 2014). Most previous studies have found that the diel hysteresis varies seasonally with soil water content (Vargas and Allen, 2008; Gaumont-Guay et al., 2008; Phillips et al., 2011; Darenova et al., 2014). Two main lines of reasoning have been proposed to explain the causes of diel hysteresis. The first one is based on the physical processes of heat and gas transport in soil (Vargas and Allen, 2008; Phillips et al., 2011; Zhang et al., 2015) and soil CO<sub>2</sub> production is expected to be an integrated response to a non-uniform  $T_s$  profile. The  $T_s$  used in theoretic models is likely different in phase from the  $T_s$  forcing CO<sub>2</sub> production out of soil (Phillips et al., 2011), resulting in time lag between diel  $R_s$  and  $T_s$ . High SWC blocks CO<sub>2</sub> gas and thermal diffusion through soil, resulting in large hysteresis loops (Riveros-Iregui et al., 2007; Zhang et al., 2015). The other line is based on biological processes of photosynthate supply (Tang et al., 2005; Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011). In this line, aboveground photosynthesis supply is expected to be substrate for roots and rhizosphere microbes,

resulting in peak  $R_s$  at midday (e.g., 11:00-13:00), unlike in  $T_s$  which usually peaks in the afternoon (e.g., 14:00-16:00). Low  $SWC$  and high vapour pressure deficit induces partial plant stomata closure, resulting in peak photosynthesis in early morning (e.g., 9:00-11:00) and suppressed photosynthesis in mid-afternoon, as a consequence of large hysteresis loops (Tang et al., 2005; Vargas and Allen, 2008; Carbone et al., 2008). Currently, our understanding on the mechanism of diel hysteresis between  $R_s$  and  $T_s$  is still limited and should be studied more in details in drylands.

### 1.5 Aims of the study

In this work, the main aim was to study the responses of temporal and spatial variation in soil respiration to biotic and abiotic factors in a desert shrub ecosystem in northwest China. The specific objectives were:

- (i) To quantify the diurnal and seasonal variation in  $R_s$  and its controlling factors, and to understand the influences of  $SWC$  on the temperature sensitivity of  $R_s$  (Paper I);
- (ii) To explore the mechanisms controlling the spatial heterogeneity in  $R_s$ , and the plant effects on  $R_s$  in different phenophases (Paper II);
- (iii) To examine the seasonal variation in diel hysteresis in  $R_s$ - $T_s$  relationship and its controlling factors ( $SWC$  and photosynthesis) (Papers I and III);
- (iv) To explore the influences of biological soil crusts on  $R_s$  and its climatic ( $T_s$ ,  $SWC$ ,  $PPT$ ) responses (Paper IV).

The hypotheses of this study were:

- (i) The  $R_s$  is in a desert shrubland highly limited by  $SWC$  but less sensitive to  $T_s$ , and  $SWC$  affects the response of  $R_s$  to  $T_s$  both seasonally and diurnally (Paper I);
- (ii) Topographic heterogeneity in  $R_s$  depends largely on substrate supplied by plant photosynthesis and nitrogen compounds during leaf-fall, and the drivers of topography heterogeneity vary with plant phenology of the dominant shrub (Paper II);
- (iii) Photosynthesis dominantly controls diel hysteresis between  $R_s$  and  $T_s$ , and  $SWC$  regulates such control of photosynthesis on hysteresis and its variation over the growing season (Paper III);
- (iv) Biological soil crusts change the responses of  $R_s$  to climatic factors, and such influences differ among crust types (Paper IV).

To undertake this work,  $R_s$  together with different climatic ( $T_s$ ,  $SWC$ ) and abiotic (e.g., root biomass, litter fall, soil nitrogen content, photosynthesis) factors were continuously measured, and phenophases of the dominant shrub species recorded over a typical fixed sand dune in a desert shrub ecosystem in 2012-2014 in northwest China.

## 2. MATERIALS AND METHODS

### 2.1 Study site description

The measurements of this study were performed at Yanchi Research Station of Beijing Forestry University, Ningxia, northwest China (37.68° - 37.73° N, 107.20° - 107.26° E, 1550 m a.s.l). The station is located at the southern edge of Mu Us desert in the transition between the arid and semi-arid climatic zones. Based on 51 years (1954-2004) data from the meteorological station of Yanchi Country, the mean annual precipitation is 292 mm (with a range of 250-350 mm), of which 62% falls between July and September. The mean annual total potential evaporation is 2024 mm.

At the experimental site, the soil was of sandy type, with a bulk density of  $1.54 \pm 0.02 \text{ g cm}^{-3}$ . The water-filled pore space across all the microsites was  $23.42 \pm 0.92\%$ . Soil organic matter, soil nitrogen and pH were 0.21 - 2.14  $\text{g kg}^{-1}$ , 0.08 - 2.10  $\text{g kg}^{-1}$ , and 7.76 - 9.08, respectively. The vegetation was regenerated from aerial seeding that took place in 1998 and is currently dominated by a semi-shrub species, *Artemisia ordosica*, averaging about 50 cm tall with a canopy size of about 80 cm times 60 cm. The coverage percentage of plants ranged from 30 to 60%. The mosses are dominated by *Byumargenteum*, and the lichens by *Microcoleus vaginatus*, *Oscillatoria chlorine* and *Collema tenax*.

### 2.2 Experiment design

Measurements were made over a shrub dominant sand dune (Figure 1a), which was of typical size for the study area, (i) 2.9 m high, (ii) 7.6m long leeward slope, (iii) 15.6 m long windward slope, (iv) 13.3 m long north-facing slope and (v) 13.4 m long south-facing slope (Figure 1; Figure 2). The measurements were taken on windward in the east, leeward in the west, and north- and south-facing slopes of the sand dune (Figure 2). On each slope, lower, upper and top positions were used for the measurements (Figure 2). The positions of measurements were located at about 3 to 5 m apart along the line transects. Besides the positions in the line transects, measurements also involved the microsites of lichen-cruste soil (LCS, Figure 1b), moss-cruste soil (MCS, Figure 1c) and *Artemisia ordosica* covered soil (Figure 1d) over the sand dune (Figure 2).



### 2.3 Measurements of soil respiration, and biotic and abiotic factors

Permanent collars were installed at approximately 3 m spacing in March 2012, three months before the first  $R_s$  measurements. The collars were 20.3 cm in diameter and 10 cm in height, with 7 cm inserted into the soil. Three transparent chambers (model LI-104C, LI-COR, Nebraska, USA) were used to measure  $\text{CO}_2$  exchange at LSC, MCS and *Artemisia ordosica* covered soil. The rest of the positions were measured by opaque chambers (model LI-104, LI-COR, Nebraska, USA). The  $R_s$  was measured in situ using a LI-8100A automated soil gas flux system (model Li-8100A, equipped with Li-8150 multiplexer, LI-COR, Nebraska, USA). Instrument maintenance was carried out bi-weekly during the growing season, including removing plant-regrowth in the opaque chambers, and cleaning to avoid blackout conditions associated with the transparent chamber.

Biotic factors measured were root biomass ( $\text{kg m}^{-3}$ ), litterfall ( $\text{kg m}^{-2}$ ), total soil nitrogen content ( $\text{g kg}^{-1}$ ) within the first 25 cm of the soil and leaf area index (LAI,  $\text{m}^2 \text{m}^{-2}$ ). Alive roots and litterfall samples were analysed after oven dried at 70 °C to a constant weight. Total nitrogen in the soil was determined with a Kjeldahl Total Nitrogen Apparatus (FOSS 2200, Foss, Denmark). LAI was measured near each chamber within one hour immediately after sunset using LI-COR 2000 (LI-COR, Nebraska, USA) with a 90° view cap, twice or three times every month during the measurement period. In addition, the phenological phases of *Artemisia ordosica* were observed and recorded over the growing season at weekly intervals.

The  $T_s$  and SWC at 10 cm soil depth were hourly measured in 10 cm away from each chamber using a LI-8150-203 temperature sensor and an  $\text{EC}_{\text{H}_2\text{O}}$  moisture sensor (LI-COR, Nebraska, USA), respectively. The other environmental factors were half-hourly recorded using the sensors mounted at 6-meter-tall flux tower 800 m away from our soil  $\text{CO}_2$  flux measurement site. Air temperature ( $T_a$ , °C) was measured by a thermohygrometer (HMP155A, Vaisala, Finland). Soil surface temperature ( $T_{\text{surf}}$ , °C) was measured by an infrared temperature sensor (model SI-111, Campbell Scientific Inc., USA). Incident photosynthetically active radiation (PAR) was measured using a quantum sensor (PAR-LITE, Kipp and Zonen, the Netherlands). Precipitation (PPT, mm) was measured by three tipping-bucket rain gauges (model TE525MM, Campbell Scientific Inc., USA) 50 m around the flux tower (Jia et al., 2014).

### 2.4 Data processing and statistical analysis

The measured  $R_s$  data were screened using limit-checking. In order to exclude the influence of chamber gas leakage, plant budding, and insects invasion, hourly  $R_s$  over the range of -30 to 30  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  were considered to be abnormal and were removed from our data set. After limit-checking, for every 3 days, hourly  $R_s$  which beyond three times of the standard deviation were excluded as outliers. Regression and correlation analyses were used to evaluate the relationship between  $R_s$ , and biotic and abiotic factors (Papers I - IV). Class and regression tree analyses (CART) were used to explore the biotic and abiotic control on spatial variation in  $R_s$  (Breiman et al., 1984) (Paper II). Cross-correlation analysis was used to estimate diel hysteresis between  $R_s$ , and temperature and photosynthesis (Papers I and III). Akaike information criterion (AIC) (Paper I, Eq 1) was used to evaluate the goodness of  $R_s$  models (Posada and Buckley, 2004). All statistical analyses were performed in Matlab (R2010b, Mathworks Inc., Natick, MA, USA). The significant level of statistical analysis

was set at 0.05.

### 3. RESULTS

#### 3.1 Diel and seasonal variation in soil respiration and its response to biotic and abiotic factors (Papers I, III and IV)

Diel  $R_s$  pattern varied corresponding to diel  $T_s$ , but  $T_s$  lagged behind  $R_s$  with 0 - 8 hours (Paper I, Figure 3). After synchronizing diel  $R_s$  and  $T_s$ , diel  $R_s$  increased significantly with increasing  $T_s$  ( $p < 0.05$ ; Paper I, Figure 4). The  $T_s$  alone explained over 95% variation in diel  $R_s$ . Besides the controls of  $T_s$ ,  $SWC$  modified the diel patterns of  $R_s$ . Under high  $SWC$ , diel  $R_s$  varied consistently with soil surface temperature ( $T_{surf}$ ) (Paper I, Figure 2; Paper III, Figure 2). Under moderate  $SWC$ ,  $R_s$  followed the variation in photosynthesis, which increased in response to increasing  $T_s$  in the early morning but then plateaued at high  $T_s$  during the midday, before declining with declining  $T_s$ . Under low  $SWC$ , diel  $R_s$  varied consistently with diel photosynthesis but out of phase of diel  $T_s$ . It reached the maximum value at the lowest  $T_s$  value (Paper I, Figure 2).

Seasonal pattern of  $R_s$  followed the variation in  $T_s$  (Paper I, Figure 5; Paper IV, Figure 1). Rainfall events caused large pulse of  $R_s$  during the growing season.  $T_s$  dominantly controlled the seasonal variation in  $R_s$ , but  $SWC$  modified the seasonal response of  $R_s$  to  $T_s$ . During the growing season, daily  $R_s$  increased with increasing  $T_s$ , when  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$  ( $p < 0.05$ ), which alone explained 76% of the seasonal variation in daily  $R_s$  (Paper I, Figure 6, Table 2). In contrast, when  $SWC < 0.08 \text{ m}^3 \text{ m}^{-3}$ , daily  $R_s$  decoupled from  $T_s$ . Besides, temperature-normalized respiration increased with increasing  $SWC$  ( $p < 0.05$ ; Paper I, Figure 8). Over the growing season, the bivariate models with  $T_s$  and  $VWC$  as independent variables, produced a better fit than the model with  $T_s$  only (Paper I, Table 3). The temperature sensitivity of  $R_s$  ( $Q_{10}$ ) decreased with increasing  $T_s$ , but increased with increasing  $SWC$  ( $p < 0.05$ ; Paper I, Figure 8).

Besides the controls of  $T_s$  and  $SWC$ , biological soil crusts also exerted strong influences on  $R_s$ , and such influences varied with crusts types. First, biological soil crusts induced significant  $\text{CO}_2$  uptake and  $\text{CO}_2$  influx ( $C_{inf}$ ) (Paper IV, Figure 1 and Figure 5). Total annual  $C_{inf}$  at moss crusted soil (MCS) were the highest, i.e. 58.0 and 62.1  $\text{g C m}^{-2}$  in 2013 and 2014, respectively (Paper IV, Table 4). Annual  $C_{inf}$  at lichen crusted soil (LCS) were 29.9 and 24.4  $\text{g C m}^{-2}$  in 2013 and 2014. Annual  $C_{inf}$  at non-crusts soil (NCS) were only 10 and 15  $\text{g C m}^{-2}$  in 2013 and 2014. Biological soil crusts changed the response of  $C_{eff}$  to  $T_s$  and  $SWC$ . The  $C_{eff}$  at both NCS and LCS increased with increasing  $T_s$  (Paper IV, Figure 2). In contrast,  $C_{eff}$  at MCS increased with increasing  $T_s$ , when  $T_s < \sim 20^\circ\text{C}$ , but decreased with higher  $T_s$  being greater than this turning point. The normalized  $C_{eff}$  at MCS increased with increasing  $SWC$ , when  $SWC < 0.15 \text{ m}^3 \text{ m}^{-3}$ , but decreased with higher  $SWC$  in both 2013 and 2014. In contrast, the corresponding turning points of  $SWC$  were 0.09 - 0.10  $\text{m}^3 \text{ m}^{-3}$  and 0.11 - 0.13  $\text{m}^3 \text{ m}^{-3}$  at NCS and LCS, respectively. Third, biological soil crusts also changed the response of  $C_{inf}$  to  $SWC$  and  $PPT$ . The  $C_{inf}$  at MCS and LCS was dominantly controlled by both  $SWC$  and  $PPT$ , whereas  $C_{inf}$  at NCS was dominantly controlled by  $PPT$  (Paper IV, Figure 6).



### 3.2 Spatial variation in soil respiration and its response to biotic and abiotic factors (Paper II)

Over the growing season, the coefficient of variation in  $R_s$  over the sand dune was 23.5% (Paper II, Table 1). Topographic heterogeneity in  $R_s$  correlated positively with the plant-related factors, like root biomass of the dominant shrub and grasses, litterfall and soil nitrogen content, but not with the microhydrometeorological factors (e.g.  $T_s$  and  $SWC$ ) (Paper II, Table 3). However, the controls of these plant-related factors on topographic heterogeneity in  $R_s$  varied with plant phenophases of the dominant shrub. During flower-bearing phase, the spatial variation in  $R_s$  over the sand dune correlated with the spatial variation in root biomass, litter fall and soil nitrogen. Over 61% of the variation in  $R_s$  over the sand dune was explained by the variation in root biomass, litterfall and soil nitrogen content. After using CART analysis to eliminate the co-correlation effects, the spatial variation in  $R_s$  during flower-bearing phase was affected the most by root biomass, which alone explained 72% spatial variation in  $R_s$  over the sand dune (Paper II, Figure 7 and Table 3). In contrast, spatial variation in  $R_s$  correlated strongly to the spatial variation in root biomass and soil nitrogen content during leaf coloration-defoliation phase (Paper II, Table 3). Soil nitrogen content and root biomass explained 56 and 39% of the variation in  $R_s$  over the sand dune, respectively. The CART analysis showed that the soil nitrogen content was the most significant factor affecting the spatial variation in  $R_s$  during leaf coloration-defoliation phase (Paper II, Figure 7 and Table 3).

### 3.3 Diel hysteresis between soil respiration and soil temperature (Papers I and III)

Diel  $R_s$  patterns were out of phase with diel temperature, resulting in significant diel hysteresis in  $R_s$ -temperature relationship (Paper I, Figure 1; Paper III, Figure 3). Diel  $R_s$  patterns were highly variable during the growing season, peaking between 10:00 AM - 16:00 PM (Paper III, Figure 1). In contrast, diel air temperature ( $T_a$ ), soil surface temperature ( $T_{surf}$ ) and  $T_s$  patterns remained stable, peaking at ~ 12:00 PM, ~16:00 PM, and ~17:00 PM, respectively. The hysteresis between diel  $R_s$  and  $T_s$  influenced the accuracy of  $R_s$  predicting models. For modelling  $R_{ss}$ ,  $R^2$  values (12 - 20%) derived from the data set with synchronized  $R_s$  and  $T_s$ , were higher than that without synchronization (Paper I, Table 3).

Diel photosynthesis patterns of the dominant shrub were similar to diel  $R_s$ . Diel photosynthesis was also highly variable during the growing season, peaking between 10:00 AM - 16:00 AM (Paper III, Figure 1). Over the growing season, diel hysteresis in  $R_s$ - $T_{surf}$  relationship was the lowest among the relationships between temperatures measured ( $T_a$ ,  $T_{surf}$ ,  $T_s$ ) (Paper III, Figure 2). Seasonal variation in the relative importance ( $RI$ ) between photosynthesis and  $T_{surf}$  in controlling diel  $R_{ss}$ , and diel hysteresis between  $R_s$  and  $T_{surf}$ , varied with  $SWC$  (Paper I, Figure 3; Paper III, Figures 4 and 5). The  $RI$  decreased with increasing  $SWC$  ( $p < 0.05$ ; Paper III, Figure 4). The diel hysteresis between  $R_s$  and  $R_{surf}$  decreased with increasing  $SWC$ , when  $SWC < 0.08 \text{ m}^3 \text{ m}^{-3}$ . With  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ , no hysteresis was observed (Paper III, Figure 5).

## 4. DISCUSSION

### 4.1 Response of diurnal variation in soil respiration to biotic and abiotic factors

In this study, the variation of diel  $R_s$  was out of phase with diel  $T_s$ , but highly correlated with diel  $T_s$  after synchronization (Papers I and III). The predominant control of  $T_s$  on diel  $R_s$  was in line with many previous studies in forest and grassland ecosystems (Tang et al., 2005; Gaumont-Guay et al., 2006; Vargas and Allen, 2008; Carbone et al., 2008). This was due to its strong controls on enzyme activities (Gaumont-Guay et al., 2006; Sotta et al., 2007; Jassal et al., 2008; Liu et al., 2009), which strongly influenced roots and microbial processes in soil. Furthermore, the results of this study showed strong correlations between lag hours and  $SWC$ . During the growing season, lag hour increased with decreasing of  $SWC$  (Paper I, Figure 3; Paper III, Figure 5). These results suggested that  $SWC$  can modify the diel variation in  $R_s$ . This result is different from a previous study on a forest ecosystem, which reported that  $SWC$  had no effects on diel variation in  $R_s$  (Tang et al., 2005).

The results of this study also showed that diel  $R_s$  followed diel variation in photosynthesis under low  $SWC$  ( $< 0.08 \text{ m}^3 \text{ m}^{-3}$ ), resulting in a large diel hysteresis between  $R_s$  and  $T_s$  (Paper III, Figure 2). However, no diel hysteresis was observed, when  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$  (Paper III, Figure 5). These results suggested that soil water regulates the control of photosynthesis on diel hysteresis between  $R_s$  and  $T_s$ , and supported the assumption that biological processes could regulate such diel hysteresis in drylands. Such result is different from forest ecosystems, in which physical processes have dominant roles (Riveros-Iregui et al., 2007; Zhang et al., 2015). The contradictory findings may attribute to the differences in soil properties. For example, forest soils are dense, therefore diel hysteresis can be influenced by the gas transport within soil. High  $SWC$  tends to block gas transport, leading to larger hysteresis than under low  $SWC$  in forest ecosystem (Riveros-Iregui et al., 2007; Zhang et al., 2015). In contrast, sandy soils in desert shrubland like in this study have much higher soil porosity, which have weak influences on within-soil gas transport processes.

In desert shrublands, soil C pool and microbes often concentrate in the surface soil layer (Fisher et al., 1987), and are sensitive to changes in surface  $SWC$ . Whereas, roots distributed deep in soil, and are less sensitive to changes in surface  $SWC$ . Hence, wetting of shallow soil (e.g.  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$  in our study) could largely accelerate heterotrophic respiration, without significantly affecting autotrophic respiration in the deeper soil. In this condition,  $R_s$  is dominated by heterotrophic respiration and primarily controlled by soil surface temperature (Lloyd and Taylor, 1994; Winkler et al., 1996). In contrast, when soil surface dries and  $SWC$  decreases, heterotrophic respiration could be largely suppressed (Borken et al., 2006), leading to greater contribution from autotrophic respiration to total  $R_s$ . In this condition, plant photosynthesis, roots activity and respiration could firmly associate with each other (Liu et al., 2006; Baldocchi et al., 2006; Högberg and Read, 2006; Kuzyakov and Gavrihkova, 2010). In our case, lower photosynthesis at midday (12:00 - 14:00) than in the morning (9:00 - 11:00) was associated with lower  $R_s$  on dry days, leading to greater diel hysteresis between  $R_s$  and  $T_s$  than that on wet days.

## 4.2 Response of seasonal variation in soil respiration to biotic and abiotic factors

In this study,  $T_s$  predominantly controlled the seasonal variation in  $R_s$ , and  $SWC$  modified the responses of  $R_s$  to  $T_s$ .  $T_s$  explained 76% of the variations in  $R_s$ , when  $SWC > 0.08 \text{ m}^3 \text{ m}^{-3}$ , but did not correlate with  $R_s$  when  $SWC < 0.08 \text{ m}^3 \text{ m}^{-3}$  (Paper I, Figure 6). The short-term  $Q_{10}$  of  $R_s$  decreased with decreasing  $SWC$  (Paper I, Figure 8). These results are in line with many previous studies in other ecosystems (Chen and Tian, 2005; Palmroth et al., 2005; Gaumont-Guay et al., 2006; Jassal et al., 2008; Zhang et al., 2010). As  $SWC$  decreased from the willing point value of  $0.08 \text{ m}^3 \text{ m}^{-3}$ , plant and microbe activities were suppressed, availability and diffusion of C substrates and extracellular enzymes were reduced, due to limited soil water (Gaumont-Guay et al., 2006; Sotta et al., 2007; Jassal et al., 2008; Liu et al., 2009). Such changes resulted in the increase of recalcitrant C pool (Reichstein et al., 2002) and lower  $R_s$ . Consequently,  $R_s$  and  $T_s$  were decoupled and short-term  $Q_{10}$  was lower under high  $T_s$  and low  $SWC$ .

Besides the abiotic controls, biological soil crusts also exerted large influence on  $R_s$  in this studied desert shrubland. Biological soil crusts significantly induced  $C_{inf}$  (Paper IV, Figure 1). Annual  $C_{inf}$  at MCS ( $58 - 62 \text{ g C m}^{-2} \text{ year}^{-1}$ ) was up to two times greater than that at LCS ( $24 - 30 \text{ g C m}^{-2} \text{ year}^{-1}$ ), and up to four times greater than that at NCS ( $10 - 15 \text{ g C m}^{-2} \text{ year}^{-1}$ ) (Paper IV, Table 4). Biological soil crusts showed strong influences on  $C_{inf}$ , as they are sensitive to rainfall and can photosynthesize once being moistened enough (Lange et al., 1998; Tuba et al., 1996; Nash 1996; Belnap et al., 2004). In this study, seasonal variation in  $C_{inf}$  at LCS and MCS were strongly related to both  $SWC$  and  $PPT$ . In contrast,  $C_{inf}$  at NCS could be mainly due to the processes of  $\text{CO}_2$  dissolving and saline/alkaline absorption after rainfall (Fa et al., 2015).  $PPT$  controlled dominantly the seasonal variation in  $C_{inf}$  at NCS.

Different types of biological soil crusts influenced also the response of  $C_{eff}$  to  $T_s$  (Paper IV, Figure 2). For NCS, plant roots extended to a wide and deep range in soil, resulting a good access to water sources. Lichens thallus is also encased in fungal tissue, which protects lichens from water loss (Lange, 2003). Thus,  $C_{eff}$  at LCS and NCS increased with increasing  $T_s$ . In contrast, mosses thallus has a large surface-volume ratio and direct contact with air, and thus mosses are more vulnerable to water loss (Lange, 2003). In this study,  $C_{eff}$  at MCS decreased, when  $T_s > \sim 20 \text{ }^\circ\text{C}$ , i.e. to decrease water loss during hot and dry periods.

## 4.3 Response of spatial variation in soil respiration to biotic and abiotic factors

This study reported predominant control of abiotic factors ( $T_s$  and  $SWC$ ) on temporal variations in  $R_s$  (Papers I and III). However, the spatial variations in  $R_s$  over the sand dune was closer related to soil nitrogen content, root biomass, and litter fall (Paper II). This result was in line with previous studies in desert ecosystems (Sponseller and Fisher, 2008), but different from that in forests (Kang et al., 2003; Liu et al., 2010). Desert ecosystems are characterized by limited distributions and high spatial heterogeneities of soil C pools, microbes and nutrients around shrubs (fertility island effect). Photosynthate of shrubs provides C resources for roots and rhizosphere respiration (Högberg et al., 2001; Tang et al., 2005; Han et al., 2014), and provides litterfalls for heterotrophic respiration (Reichstein et al., 2002; Zhou et al., 2013). These processes are influenced by soil nitrogen (Allison et al., 2008; Deng et al., 2010). Thus, the areas with higher soil nitrogen, root biomass and litterfall have higher  $R_s$ , than that of bareland even it is usually hotter in a desert ecosystem.

The effects of plant-related factors change with plant phenophases (Fu et al., 2002; Dungan et al., 2003; Kang et al., 2003; Yuste et al., 2004; Tang et al., 2005; Tamai, 2010; Asaeda and Rashid, 2014; Osono, 2014). Therefore, their controls on spatial variation in  $R_s$  in a desert shrubland also change with plant phenophases. In this study, the most important factor driving topographic heterogeneity in  $R_s$  was root biomass at the flowering and bearing phase (phase II), and soil nitrogen content (Paper II) at the leaf coloration and defoliation phase (phase III). The influences of plant phenophases on the controlling factors of topographic heterogeneity in  $R_s$ , may be due to the changes in C substrate supply and the relative contribution between autotrophic and heterotrophic respirations to total  $R_s$ . During phase II, high shrub photosynthesis can result in higher contribution of root respiration to total  $R_s$  (Lebret et al., 2001; Regina, 2001; Ochieng and Erfemeijer, 2002; Tu et al., 2013; Zhou et al., 2014). Root biomass depends also on the topographic heterogeneity in  $R_s$  over the sand dune in phase II. However, from phase II to phase III, additional liable fresh litterfall and suppressed shrub photosynthesis (as declined photosynthetic pigments) results in larger contribution of heterotrophic respiration to total  $R_s$  (Fu et al., 2002; Sey et al., 2010; Mauritz and Lipson, 2013). Also soil nitrogen content contributes strongly to the litterfall decomposition process (Yan et al., 2010; Sayer et al., 2011).

## 5. CONCLUSIONS

In this study, diel  $R_s$  was dominantly controlled by temperature, but the diel hysteresis between  $R_s$  and temperature were also regulated by  $SWC$  and plant photosynthesis. Diel hysteresis between  $R_s$  and  $T_s$  was limited by the relatively small contribution of autotrophic respiration to total  $R_s$  under high  $SWC$  condition. Seasonal  $R_s$  was also controlled dominantly by temperature, but the response of  $R_s$  to temperature was modified by both  $SWC$  and biological soil crusts. Seasonal  $R_s$  was decoupled from  $T_s$  under low  $SWC$ . Temperature sensitivity of  $R_s$  increased with increasing  $SWC$ . The response of  $R_s$  to  $T_s$  differed also among crust types. These results highlight the importance of biological mechanism in diel hysteresis between  $R_s$  and temperature, and the importance of  $SWC$  in soil respiration dynamics in a desert shrubland. The observed influences of  $SWC$  on  $R_s$  also indicate a potentially negative feedback to climate warming along with a decrease of  $SWC$  in desert shrublands. Topographic heterogeneity in  $R_s$  was also largely controlled by plants, due to the substrate supply from photosynthesis. Also, several other drivers on topographic heterogeneity in  $R_s$ , such as root biomass, litterfall and soil nitrogen, varied with plant photosynthesis. These results highlighted the importance of plants in controlling spatial variation in  $R_s$ , and suggested that both the temporal and spatial effects of plants should be considered in desert shrublands. To conclude, these results highlight the necessity to account the interactive effects of temperature,  $SWC$ , biological soil crusts, and shrubs in estimation of carbon balance for desert ecosystems and in modelling of global C cycle in order to increase the accuracy of model predictions.

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