Pedosphere **28**(1): 103–113, 2018
doi:10.1016/S1002-0160(17)60307-2
ISSN 1002-0160/CN 32-1315/P

Published by Elsevier B.V. and Science Press

PEDOSPHERE

www.elsevier.com/locate/pedosphere

Soil Respiration of Biologically-Crusted Soils in Response to Simulated Precipitation Pulses in the Tengger Desert, Northern China

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(Received July 25, 2016; revised January 15, 2018)

ABSTRACT

Soil respiration (SR) is a major process of carbon loss from dryland soils, and it is closely linked to precipitation which often occurs as a discrete episodic event. However, knowledge on the dynamic patterns of SR of biologically-crusted soils in response to precipitation pulses remains limited. In this study, we investigated CO_2 emissions from a moss-crusted soil (MCS) and a cyanobacteria-lichen-crusted soil (CLCS) after 2, 4, 8, 16, and 32 mm precipitation during the dry season in the Tengger Desert, northern China. Results showed that 2 h after precipitation, the SR rates of both MCS and CLCS increased up to 18-fold compared with those before rewetting, and then gradually declined to background levels; the decrease was faster at lower precipitation amount and slower at higher precipitation amount. The peak and average SR rates over the first 2 h in MCS increased with increasing precipitation amount, but did not vary in CLCS. Total CO_2 emission during the experiment (72 h) ranged from 1.35 to 5.67 g C m^{-2} in MCS, and from 1.11 to 3.19 g C m^{-2} in CLCS. Peak and average SR rates, as well as total carbon loss, were greater in MCS than in CLCS. Soil respiration rates of both MCS and CLCS were logarithmically correlated with gravimetric soil water content. Comparisons of SR among different precipitation events, together with the analysis of long-term precipitation data, suggest that small-size precipitation events have the potential for large short-term carbon losses, and that biological soil crusts might significantly contribute to soil CO_2 emission in the water-limited desert ecosystem.

Key Words: biological soil crusts, C cycling, CO_2 emission, desert ecosystem, precipitation amount, soil water content

Citation: Li X J, Zhao Y, Yang H T, Zhang P, Gao Y P. 2018. Soil respiration of biologically-crusted soils in response to simulated precipitation pulses in the Tengger Desert, northern China. *Pedosphere*. **28**(1): 103–113.

INTRODUCTION

Arid and semiarid ecosystems cover about 40% of the Earth's land surface (Reynolds *et al.*, 2007), and store 15.5% (equivalent to 232.5 Pg C) of the world's total soil organic carbon (SOC) (Lal, 2004). They have long been considered as carbon (C) sources in the terrestrial C cycle due to the low vegetation coverage (Schlesinger, 1990; Wang *et al.*, 1999; Conant *et al.*, 2000; Liu *et al.*, 2002). Soil respiration (SR) is a major process of C loss from dryland soils (Conant *et al.*, 2000), and changes in SR can slow or accelerate the increase of atmospheric CO_2 concentrations (Raich and Schlesinger, 1992; Trumbore *et al.*, 1996; Cox *et al.*, 2000; Raich *et al.*, 2002), and have a large impact on soil C storage and fertility, since these soils have relatively low organic C contents (West *et al.*, 1994; Castillo-Monroy *et al.*, 2011). Thus, quantifying likely responses of soil CO_2 emission to controlling factors is critical to our understanding of C budgets in dry ecosystems and their significance to global C cycling and balance.

In arid and semiarid ecosystems, soil water availability, which is directly linked to precipitation, is the principle variable driving ecosystem processes (Noy-Meir, 1973), including C dynamics (Bowling *et al.*, 2011). Precipitation in these regions often occurs as a discrete episodic event. Dry soils are irregularly interrupted by precipitation pulses that elevate water availability for short periods and drive C effluxes (Sponseller, 2007; Munson *et al.*, 2010). Previous studies have reported that, after wetting, SR increases up to 30 times (Sponseller, 2007), and is several times greater than that of soil kept continually moist (Fierer and Schimel, 2003; Thomas and Hoon, 2010). This pulse-induced CO_2 emission may contribute a significant portion of the total annual CO_2 release from soil, since the soil in drylands often remains relatively dry for prolonged periods (Fierer and Schimel, 2003; Sponseller, 2007; Thomas *et al.*, 2008; Thomas and Hoon, 2010). Consequently, investigations on C cycling in drylands should focus on the implications of such eve-

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nts (Reynolds *et al.*, 2004). However, precipitation affects SR in complex ways in water-limited ecosystems. First, the size of rain-triggered respiration pulses is linked directly to the amount, intensity, and frequency of precipitation. Generally, small pulses only initiate the activities of microorganisms within the first few centimeters of topsoil, while large pulses could wet deeper soil (Bowling *et al.*, 2011; Thomas *et al.*, 2011). Repeated drying-rewetting cycles may reduce the pulsing effects due to the decay of the accessible organic matter pool (Degens and Sparling, 1995; Fierer and Schimel, 2003). Less intense precipitation events often generate CO_2 emission pulses with a slower rise, shorter duration, and smaller magnitude than more intense events (Fierer and Schimel, 2003; Ma *et al.*, 2012). Second, the response of SR to rewetting does not only depend on the amount of precipitation, but also on antecedent conditions (Bowling *et al.*, 2011). Cable *et al.* (2008) reported that the response of SR to precipitation pulses was amplified when dry antecedent conditions occurred and was dampened under wet antecedent conditions. Finally, distinct spatial heterogeneity of vegetation and soil properties in drylands makes SR particularly difficult to quantify, for example, the patchy distribution of vegetation, the stratification of soil which is composed of a surface layer relatively rich in organic matter (typically biological soil crusts (BSCs), often the major source of organic C in dryland soils) covering a subsoil with limited organic matter (Li *et al.*, 2004; Li *et al.*, 2008). These are likely to add complexity to the response of SR to precipitation pulses (Maestre and Cortina, 2003; Thomas and Hoon, 2010; Thomas *et al.*, 2011; Su *et al.*, 2012).

Although, pulsing CO_2 emissions after rewetting of dry soils have been recognized for decades (Birch, 1958), and have been observed in a variety of ecosystems (Birch, 1958; Liu *et al.*, 2002; Austin *et al.*, 2004; Sponseller, 2007; Song *et al.*, 2012), most studies have focused on the ecological implications of long-term fluctuations in water availability (Huxman *et al.*, 2004), and the dynamic behavior of SR in response to precipitation pulses remains poorly understood in drylands for lack of data from these ecosystems (Raich and Schlesinger, 1992; Conant *et al.*, 2000; Huxman *et al.*, 2004; Castillo-Monroy *et al.*, 2011; Ma *et al.*, 2012). Moreover, previous studies have not assessed the contribution of SR induced by small events to the C dynamics of drylands (Zhao *et al.*, 2009), because small events only wet the first few centimeters of topsoil (Austin *et al.*, 2004), and the response of SR to these events is rapid and short-lived (Sponseller, 2007; Cable *et al.*, 2008). However, such ignorance may result in underestimated SR in water-limited ecosystems where resources and microbes are concentrated within the surface strata and small precipitation events account for a large proportion of the received precipitation (West and Skujins, 1978; Huxman *et al.*, 2004). More importantly, climate models have predicted that precipitation patterns will likely intensify in mid-latitude regions in the future, with increasing total precipitation, increased duration of drought periods, and increased frequency of extreme precipitation events (Huntington, 2006; IPCC, 2007). This may alter the dynamics of soil water availability and intensify the dependence of ecosystem processes on moisture pulses (Knapp *et al.*, 2008), further adding to the uncertainty of C cycling in water-limited regions (Fay *et al.*, 2008). However, current understanding of SR in drylands remains limited, and prediction of the effects of these changes on SR is still uncertain (Thomas *et al.*, 2011). However, identification of the dynamic patterns of SR following a precipitation pulse is a key step toward a mechanistic understanding of soil C fluxes in arid conditions (Liu *et al.*, 2002).

In this study, a simulated precipitation experiment was conducted to characterize the dynamic pattern of CO_2 release from two biologically-crusted soils in response to precipitation pulses during the dry season of 2012 in the Tengger Desert, northern China. The changes in SR and soil water content (SWC) after the rewetting were monitored continually over a short-term period. The aim of this study was to examine: 1) the response of SR of crusted soils to simulated precipitation, 2) the relationship between the duration of pulse-driven soil CO_2 release and total CO_2 emission with precipitation, and 3) the effects of BSC type on the relationships between precipitation event size and SR. A further purpose of this study was to contribute to an understanding of the significance of precipitation-induced SR to C budget and balance in water-limited ecosystems.

MATERIALS AND METHODS

Study site

The experimental site, named Hongwei (37°26′ N, 104°30′ E), was located at the southeast fringe of the Tengger Desert in Northern China, 22 km west of the Shapotou Desert Research and Experiment Station (SDRES) of Chinese Academy of Sciences (Fig. 1). According to long-term meteorological records of the weather station of SDRES, the mean annual air temperature in this region is 10.0 °C, with daily minimum and maximum values of −25.1 and 38.1 °C, respectively. The mean annual precipitation is 180.2 mm, with approximately 80% falling between May and September, with a coefficient of variation as high as 46%. Rain is the only source of soil water replenishment because the groundwater is too deep to be used by plants. The potential evapotranspiration during the growing season (from April to October) is 2 300–2 500 mm (Li *et al.*, 2004).

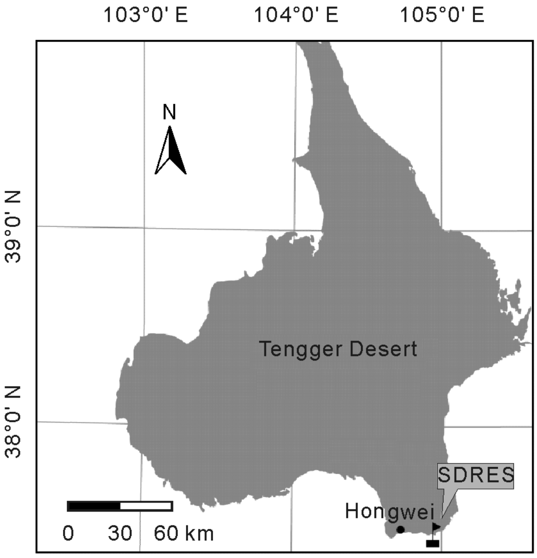

Fig. 1 Geographic location of the study site (Hongwei) in the Tengger Desert, North China. SDRES = Shapotou Desert Research and Experiment Station.

Natural vegetation on stabilized dunes is dominated by shrubs, semishrubs, forbs, and grasses, including *Caragana korshinskii* Kom, *Artemisia ordosica* Krasch., *Ceratoides latens* Reveal et Holmgren, *Stipa breviflora* Griseb., *Cleistogenes songorica* Ohwj, *Eragrostis poaeoides* Beauv., and *Artemisia capillaris* Thunb., with an average coverage of 30%. The common BSCs in this region are mainly predominated by mosses (*Bryum argenteum* Hedw., *Didymodon constrictus* (Mitt.) Saito., *Tortula bidentata* Bai Xue Liang, and *Tortula desertorum* Broth.), algae (*Anabaena azotica* Ley, *Euglena* sp., *Hantzschia amphioxys* var. *capitata* Grum, *Oscillatoria obscura* Gom., *Oscillatoria pseudogeminate* G. Schm., and *Scytonema javanicum* (Kutz) Bornet Flash), cyanobacteria (*Microcolous vaginatus* Gom., *Hydrocoleus violacens* Gom., *Lyngbya crytoraginatus* Schk., *Phormidium amblgum* Gom., *Phormidium autumnale* (Ag.) Gom., *Phormidium foveolarum* (Mont.) Gom., and *Phormidium luridum* (Kutz) Gom.), and lichens (*Collema tenax* (Sw.) Ach., *Endocarpon pusillum* Hedw.), or any combination of these organisms, with an average cover of 68% (Li *et al.*, 2003). The entire site has been fenced for > 30 years to exclude grazing (Li *et al.*, 2008).

Experiment

In April of 2012, three plots (5 m × 5 m) were set up on a flat area of stabilized dunes at the study site to investigate SR of two biologically-crusted soils following the application of simulated precipitation events. In each plot, two subplots (0.5 m × 0.5 m) were set up, with one subplot for a moss-crusted soil (MCS) and the other for a cyanobacteria-lichen-crusted soil (CLCS). In each subplot, five small polyvinyl-chloride (PVC) pipes (10 cm in diameter and 10 cm in length) were inserted 8 cm into the soil. To exclude the disturbances of SWC measurement and soil sampling, two other big PVC pipes (25 cm in diameter and 10 cm in length) were inserted 8 cm into MCS and CLCS, respectively. All PVC pipes were inserted at least 1 month prior to the initiation of the experiment to minimize possible disturbance.

Artificial precipitation events were applied to the plots on June 23, 2012; prior to this, no measurable precipitation occurred within 30 d. Distilled water was applied to PVC pipes within each plot to simulate precipitation pulse events in increasing amounts (2, 4, 8, 16, and 32 mm) at 07:30 am. Identical precipitation pulse treatments were applied to MCS and CLCS. Simulated precipitations were applied by spray bottles, and the application rates were kept consistent among treatments and adjusted to prevent overland flow; consequently, the duration of water addition varied with precipitation size (Sponseller, 2007).

Soil respiration rate was measured 1 h before rewetting, then at 30 min and 1, 2, 4, 12, 24, 36, 48, 60, and 72 h following rewetting using a Li-6400-09 soil chamber (LI-COR, Lincoln, USA). We placed the chamber on the small PVC collars and programmed the LI-6400 such that each measurement was made according to the CO_2 concentration in the chamber. For each measurement, consecutive recordings of SR rate were taken at 2-s intervals for 30 s until steady state conditions were achieved within the chamber. Three measurements were successively carried out for each sampling PVC collar, and all the small PVC collars were measured in the sequence of water addition. At the same time each measurement was made, soil temperature at 0–10 cm depth was measured with a thermocouple connected to the LI-6400, and soil samples at 0–10 cm depth were also taken with a soil auger (3-cm inner diameter) and dried at 105 °C for 48 h to measure gravimetrical SWC.

Before the field experiment was conducted, the coverage and thickness of BSCs were investigated. Soil bulk density (BD) (0–10 cm) was measured by the core method (Su *et al.*, 2012). Soil organic C, total nitrogen (TN), and grain size distribution were measured for each plot. Three samples (0–10 cm) were taken for two biologically-crusted soils at each plot; a total of 18 samples were collected. The soil collected from a given plot for each crust type was mixed to form a composite soil sample, and a total of six composite samples were obtained. Each composite sample was air dried and sieved to remove coarse plant debris (> 2 mm). Soil TN was analyzed with the Kjeltec system 2 300 distilling unit (FOSS Inc., Hillerød, Denmark). Soil organic C was measured using the Walkley and Black dichromate oxidation method (Nelson and Sommers, 1982).

To evaluate the response magnitude of SR to precipitation, three parameters were used: 1) the time-weighted average SR rate over the first 2 h (SRR_2, g C m^{-2} h^{-1}); 2) the average SR rate during the entire experiment period (72 h) (SRR_{72}, g C m^{-2} h^{-1}); 3) the total CO_2 emission over the duration of the experiment (E_{total}, g C m^{-2}). Total CO_2 emission was determined for each plot from the area under curves relating SR to time.

Statistical analysis

The differences in SR rate and SWC among precipitation pulses were examined using a repeated-measures analysis of variance (ANOVA). Two-way ANOVAs were used to identify the effects of precipitation amount and BSC type, and their interactions on SRR_2, SRR_{72}, and E_{total}. Bivariate regression analyses, using data from each plot, were conducted to determine how these parameters varied with increasing precipitation amount. Regression analysis was also used to evaluate the possible relationships between SR rate and either SWC or soil temperature of two biologically-crusted soils. All statistical analyses were performed using the SPSS program (SPSS for Windows, Version 13, SPSS Inc., Chicago, USA).

RESULTS

Soil properties of the study site

The coverage of moss crust was significantly less than that of cyanobacteria-lichen crust, while the thickness of moss crust was significantly greater ($P < 0.05$) than that of cyanobacteria-lichen crust (Table I). The contents of SOC, TN and silt of MCS were significantly greater ($P < 0.05$) than those of CLCS, while sand content of MCS was remarkably smaller ($P < 0.05$) than that of CLCS (Table I). There were no significant differences ($P > 0.05$) in C:N ratio, pH, clay content, and bulk density between two crusted soils (Table I).

TABLE I

Selected properties of a moss-crusted soil (MCS) and a cyanobacteria-lichen-crusted soil (CLCS) of the study site

Property[a]	MCS	CLCS
Crust coverage (%)	31.51 ± 1.65[b]b[c]	42.08 ± 4.17a
Crust thickness (mm)	33.08 ± 3.77a	6.11 ± 0.47b
SOC (g kg^{-1})	3.44 ± 0.27a	2.43 ± 0.21b
TN (g kg^{-1})	0.58 ± 0.04a	0.39 ± 0.08b
C:N ratio	5.94 ± 0.18a	6.21 ± 0.11a
pH	8.85 ± 0.06a	8.97 ± 0.09a
Clay (%)	7.28 ± 0.52a	6.65 ± 0.13a
Silt (%)	20.36 ± 2.83a	13.56 ± 1.68b
Sand (%)	72.35 ± 1.08b	79.79 ± 1.49a
BD (g cm^{-3})	1.34 ± 0.08a	1.42 ± 0.11a

[a] SOC = soil organic carbon; TN = total nitrogen; BD = bulk density.

[b] Mean ± standard error.

[c] Values with different letters are significantly different between the two biologically-crusted soils ($P < 0.05$).

Responses of gravimetric SWC and SR to simulated precipitation

Gravimetric SWC at the study site was significantly influenced by the simulated precipitation treatments (Fig. 2). Before water addition, gravimetric SWC was 1.88% ± 0.68% and 2.07% ± 0.55% for MCS and CLCS, respectively, and no statistical differences ($P > 0.05$) were found between the two crusted soils. Upon rewetting, gravimetric SWC increased in both biologically-crusted soils, ranging from 3.57% ± 0.63% to 25.85% ± 3.08% in MCS, and from 3.35% ± 0.87% to 24.12% ± 2.74% in CLCS. After that, gravimetric SWC gradually declined and remained higher for a longer period with increasing precipitation magnitude (Fig. 2). Gravimetric SWC returned almost to background levels 12 h after 2 mm of precipitation for both soils, 24 h after 4 mm of precipitation, 48 h with 8 mm, and 60 h with 16 mm (Fig. 2a–d). With 32 mm precipitation, gravimetric SWC remained high, at 5.02% in MCS at 72 h (Fig. 2e).

Results of repeated-measures ANOVA showed that SWC over the whole experiment was significantly affected by crust type, precipitation amount, and their interactions ($P < 0.01$) (Table II). For all treatments, the gravimetric SWC of MCS and CLCS showed similar patterns (Fig. 2). The gravimetric SWC was greater in MCS than in CLCS in the same precipitation size, and the differences between MCS and CLCS became larger and more significant with increasing precipitation amount (Fig. 2).

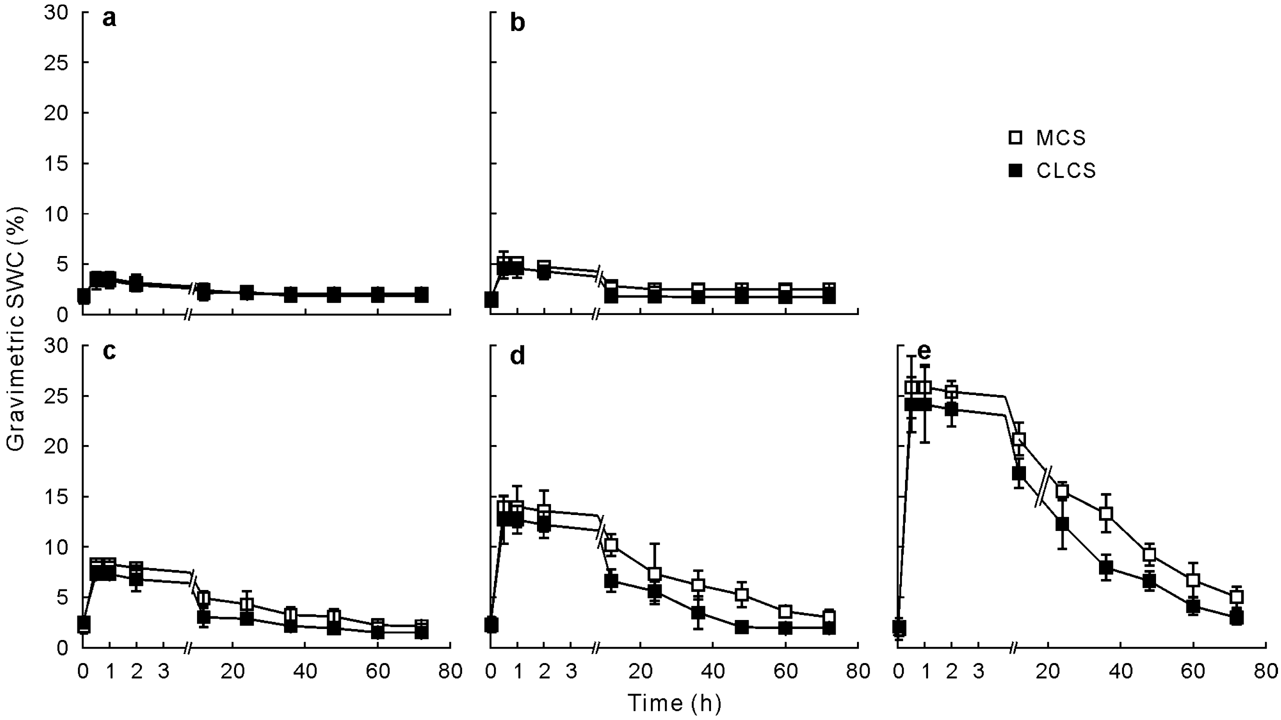

Fig. 2 Dynamic patterns of gravimetric soil water content (SWC) of a moss-crusted soil (MCS) and a cyanobacteria-lichen-crusted soil (CLCS) following different amounts of simulated precipitation: 2 mm (a), 4 mm (b), 8 mm (c), 16 mm (d) and 32 mm (e). Vertical bars are the standard errors of means.

TABLE II

Results of the effects of crust type (T), simulated precipitation amount (A), and their interaction on gravimetric soil water content (SWC) and soil respiration (SR) rate using repeated-measures analysis of variance

Variable	Source	Type III sum of squares	df[a]	Mean square	F value	P value
Gravimetric SWC	T	131.19	1	131.19	139.07	< 0.01
	A	7 233.95	4	1 808.49	1 916.98	< 0.01
	T × A	67.68	4	16.92	17.94	< 0.01
SR rate	T	15.22	1	15.22	87.92	< 0.01
	A	17.00	4	4.25	24.54	< 0.01
	T × A	10.85	4	2.71	15.67	< 0.01

[a] Degree of freedom.

Precipitation stimulated SR in all five treatments of both biologically-crusted soils (Fig. 3). Before rewetting, the SR rates of MCS and CLCS were 0.27 ± 0.02 and 0.19 ± 0.08 μmol CO_2 m^{-2} s^{-1}, respectively. In response to simulated precipitation, SR rate increased rapidly and considerably. At the first measurement after rewetting, SR rates ranged from 1.44 to 1.99 μmol CO_2 m^{-2} s^{-1} and 0.89 to 1.63 μmol CO_2 m^{-2} s^{-1} for MCS and CLCS, respectively. For all five treatments, the peak values were observed at 2 h after rewetting for both MCS and CLCS, and were 18-times higher than the background levels (Fig. 3). After SR rate peaked, it gradually decreased, and the decrease was faster at the lower water levels and slower at higher water levels. With 2 mm of precipitation, the SR rate returned almost to background levels in 12 h. With 4, 8, and 16 mm of precipitation, the SR rate decreased to background levels at 24, 48, and 60 h, respectively. With 32 mm of precipitation, the SR rate remained as high as 0.89 and 0.34 μmol CO_2 m^{-2} s^{-1} in MCS and CLCS at 72 h, respectively (Fig. 3e).

Results of repeated-measures ANOVA showed that SR significantly differed between the two biologically-crusted soils, and among simulated precipitation treatments, and the interactions between crust type and precipitation amount were significant ($P < 0.01$) (Table II). Temporal variations in SR rate after 2 and 4 mm of precipitation were similar (Fig. 3a, b), while SR rates in MCS after 8, 16, and 32 mm of precipitation were significantly greater than those in CLCS before these values returned to background levels (Fig. 3c–e). Comparisons among the five levels of precipitation

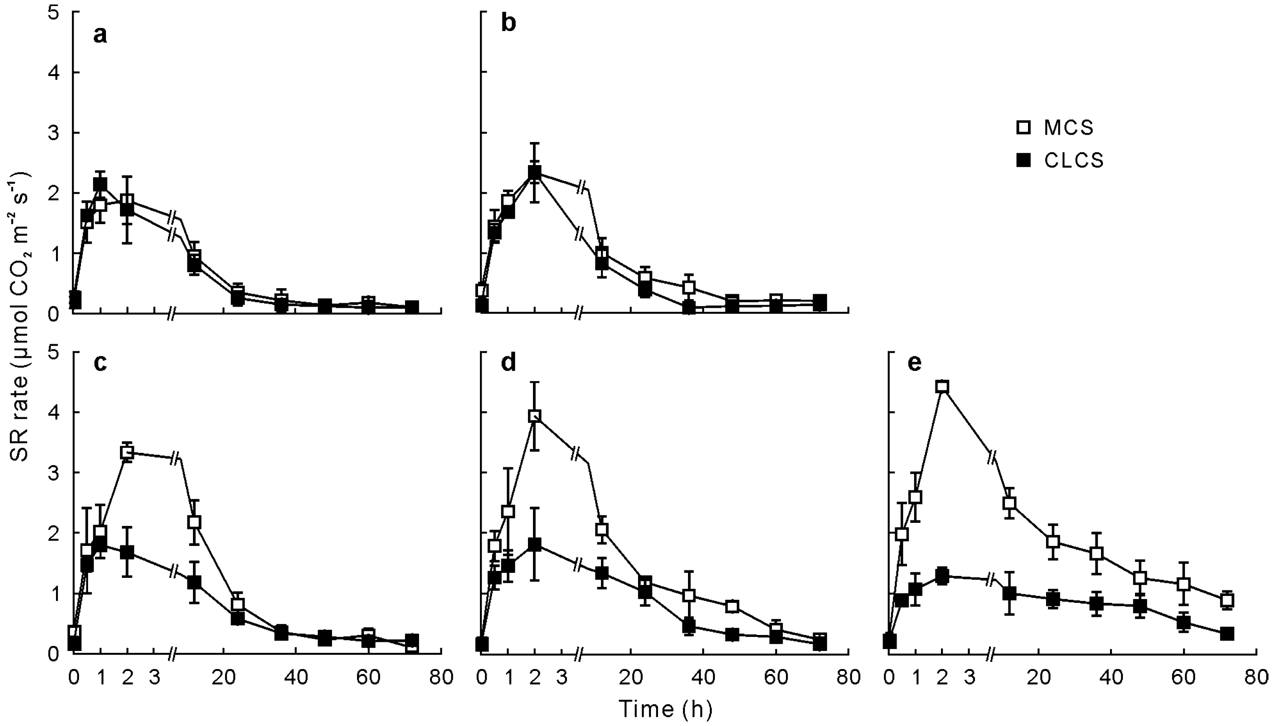

Fig. 3 Dynamic patterns of soil respiration (SR) rates of a moss-crusted soil (MCS) and a cyanobacteria-lichen-crusted soil (CLCS) following different amount of simulated precipitation: 2 mm (a), 4 mm (b), 8 mm (c), 16 mm (d), and 32 mm (e). Vertical bars are the standard errors of means.

treatments indicated that the peak SR rate in MCS was the highest (4.43 ± 0.08 μmol CO_2 m^{-2} s^{-1}) with 32 mm and the lowest (1.88 ± 0.09 μmol CO_2 m^{-2} s^{-1}) with 2 mm of precipitation; this increased with increasing precipitation amount. However, the peak SR value in CLCS was the highest (2.34 ± 0.18 μmol CO_2 m^{-2} s^{-1}) with 4 mm and the lowest (1.29 ± 0.14 μmol CO_2 m^{-2} s^{-1}) with 32 mm of precipitation (Fig. 4).

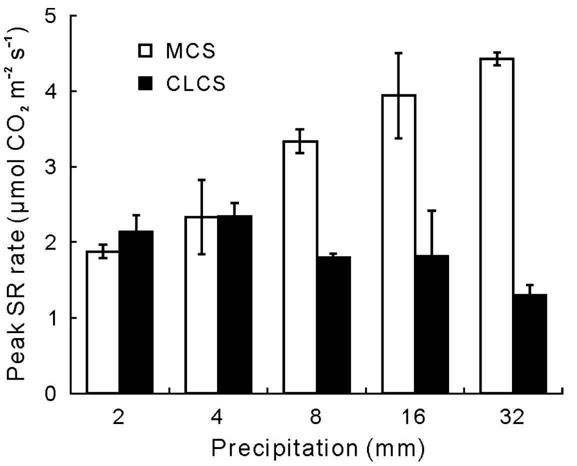

Fig. 4 Peak soil respiration (SR) rates of a moss-crusted soil (MCS) and a cyanobacteria-lichen-crusted soil (CLCS) following different amounts of simulated precipitation. Vertical bars are the standard errors of means.

Average SR rate over the first 2 h (SRR_2) and over the whole 72-h experiment (SRR_{72}), and total CO_2 emission during the experiment (E_{total}) all significantly differed between the two biologically-crusted soils and remarkably varied with precipitation treatments ($P < 0.05$) (Table III). The SRR_2 ranged from 0.08 to 0.16 g C m^{-2} h^{-1} in MCS, and from 0.06 to 0.08 g C m^{-2} h^{-1} in CLCS; SRR_{72} ranged from 0.39 to 1.56 g C m^{-2} h^{-1} and from 0.32 to 0.88 g C m^{-2} h^{-1} for MCS and CLCS, respectively; E_{total} ranged from 1.35 to 5.67 g C m^{-2} and from 1.11 to 3.19 g C m^{-2} for MCS and CLCS, respectively. The SRR_2, SRR_{72}, and E_{total} values in MCS were statistically greater than those in CLCS, and they increased with increasing precipitation amount as a nonlinear function, except for SRR_2 of CLCS (Fig. 5). Both SRR_2 and SRR_{72} were closely related to E_{total} ($P < 0.05$). As much as 11.01%–29.64%

TABLE III

Significance (F values) of the effects of crust type (T), precipitation amount (A), and their interactions on peak soil respiration (SR) rate, average SR rate over the first 2 h (SRR_2) and over 72 h (SRR_{72}), and total CO_2 emission during the experiment (E_{total}) using two-way analysis of variance

Source	Peak SR rate	SRR_2	SRR_{72}	E_{total}
T	109.549*	101.510*	103.931**	102.512**
A	9.058**	127.065**	5.489*	127.062**
T × A	20.133**	20.480**	14.345**	20.480**

*, **Significant at $P < 0.05$ and $P < 0.01$, respectively.

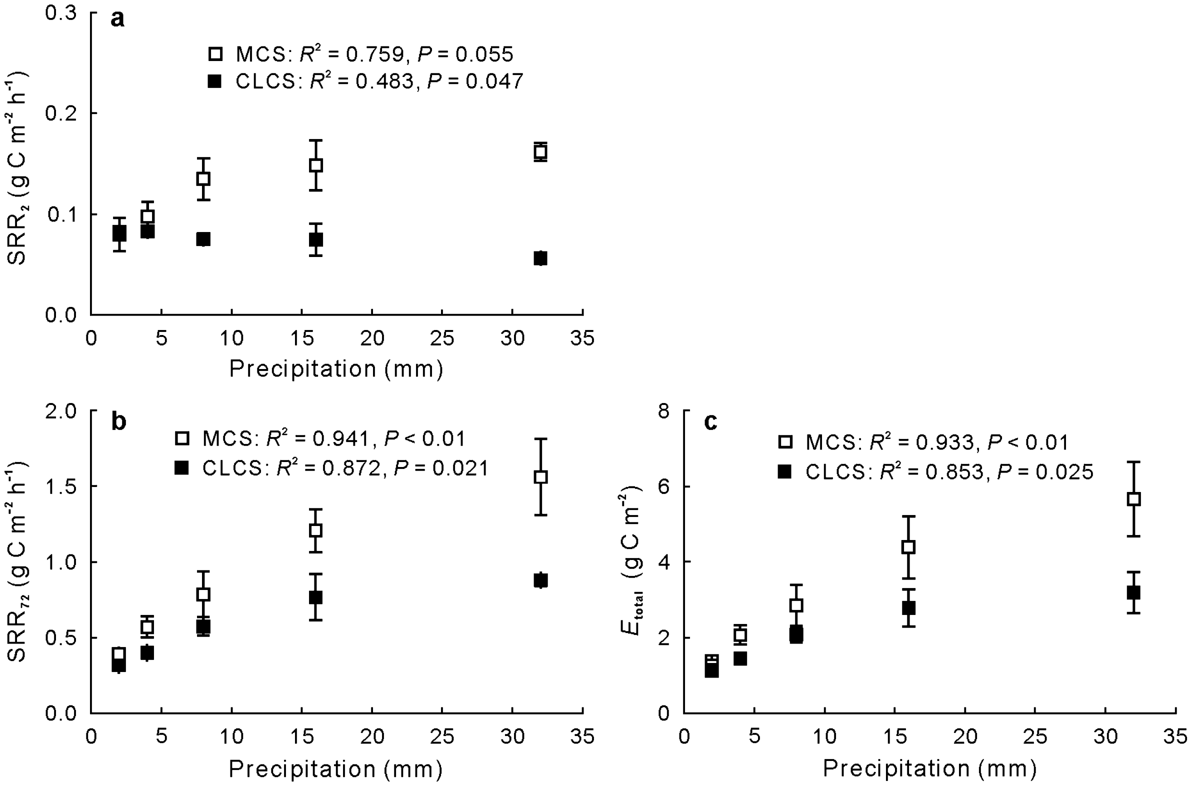

Fig. 5 Relationships of average soil respiration rate over the first 2 h (SRR_2) (a) and over 72 h (SRR_{72}) (b), and total CO_2 emission during the experiment (E_{total}) (c) with simulated precipitation amount for a moss-crusted soil (MCS) and a cyanobacteria-lichen-crusted soil (CLCS). Vertical bars are the standard errors of means.

and 6.80%–25.10% of the total C loss over the duration of the experiment occurred during the first 2 h for MCS and CLCS, respectively.

Relationships of SR with gravimetric SWC and soil temperature

We plotted individual data points of the SR rate and gravimetric SWC or soil temperature measured on all plots over the duration of the experiment and found that the relationship between SR and gravimetric SWC could be well described by logarithmic functions ($P < 0.01$) (Fig. 6a). Gravimetric SWC alone could explain more than 60% of the variation in SR rate following rewetting. However, no statistical relationships were observed between SR rate and soil temperature ($P > 0.05$) (Fig. 6b).

DISCUSSION

Responses of SR to simulated precipitation

In this study, we found that SR rate rapidly increased to reach a peak after rewetting, and then gradually returned to near background values, which confirmed that microbial activities were primarily limited by moisture. The peak SR rate varied with precipitation amount, and the decline in SR following the appearance of peak values was fast with less precipitation and slow with more precipitation (Figs. 3 and 4). These results were in consistent with those of previous studies conducted in drylands (*e.g.*, Liu *et al.*, 2002; Sponseller, 2007; Chen *et al.*, 2008; Zhao *et al.*, 2009; Su *et al.*, 2012). Pulsing CO_2 emissions after rewetting of dry soil may be induced by multiple factors. First, infiltration of water may physically displace the CO_2 accumulated in soil pore spaces during the dry period, and cause a significant increase in CO_2 emission (Liu *et al.*, 2002; Huxman *et al.*, 2004). Second, activation of microbial activity in both BSCs and underlying soil by rewetting may result in increased SR (Steenwerth *et al.*, 2005). Third, addition of water to an extremely dry soil may induce CO_2 release from the microbial biomass pool (Fierer and Schimel, 2003; Huxman *et al.*, 2004).

In this study, the peak SR rate was 18-times greater than that prior to rewetting. This was greater than the 15-fold increase observed in the Gurbantunggut Desert, and less than the 30-fold increase observed in the Sonoran Desert (Sponseller, 2007; Su *et al.*, 2012). These differences could be explained by the differences in precipitation amounts and patterns (Sponseller, 2007; Thomas and Hoon, 2010), as well as in substrate pools supporting microbial biomass, and plant

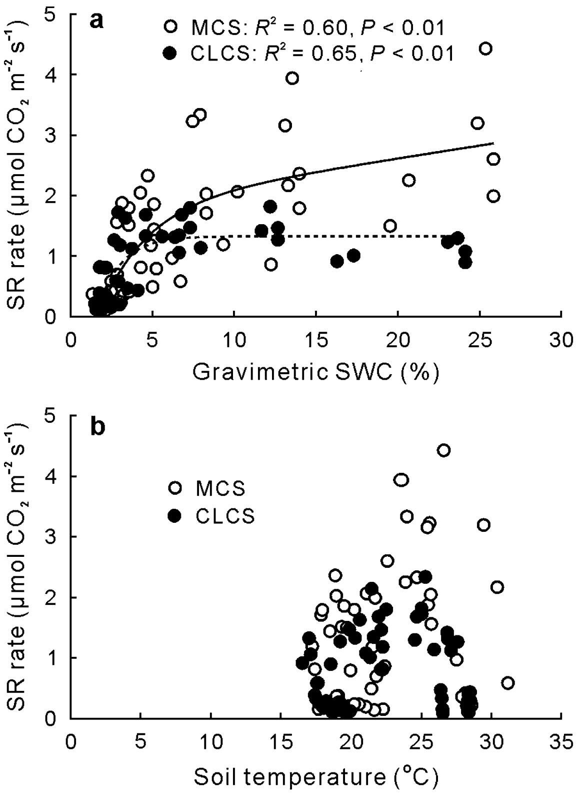

Fig. 6 Relationships of soil respiration (SR) rate of a moss-crusted soil (MCS) and a cyanobacteria-lichen-crusted soil (CLCS) with gravimetric soil water content (SWC) (a) and soil temperature (b).

root biomass (McCulley *et al.*, 2007). Nevertheless, according to long-term meteorological records of the weather station of SDRES, the average time interval between precipitation pulses from May to September at this study site is 6.15 d, which is much shorter than the duration of dry period before this experiment. More regular rewetting events may result in pulsing CO_2 emissions that are smaller than those observed in this study, since prolonged drought prior to our measurements being made could have increased the response magnitude (Meisner *et al.*, 2013).

In general, SR in water-limited ecosystems is regulated mainly by soil water availability when temperature is favorable (Luo and Zhou, 2006; Song *et al.*, 2012). In this study, the SR rates of both MCS and CLCS were significantly correlated with the gravimetric SWC, which could account for 60% and 65% of the variation in SR, respectively (Fig. 6a). However, no statistical relationship was observed between SR rate and soil temperature (Fig. 6b), suggesting the complexity in mechanisms mediating soil C dynamics (Liu *et al.*, 2002). This is consistent with the findings of Sponseller (2006) and Su *et al.* (2012), who found that soil temperature failed to account for any of the variation in SR. One possibility is that low SWC limits the response of SR to changes in soil temperature (Fernandez *et al.*, 2006; Castillo-Monroy *et al.*, 2011). In general, the patterns of SR may closely follow the increments in soil temperature when SWC is not a limiting factor for plants and microorganisms, while changes in the track of SWC when SWC is limited (Luo and Zhou, 2006; Castillo-Monroy *et al.*, 2011; Song *et al.*, 2012). On the other hand, variability in SR magnitude in response to different amounts of precipitation may mute the effects of soil temperature (Thomas *et al.*, 2011), and lead to the differentiation of SR rates. In addition, compared with light rainfall, the prolonged evaporation after heavy rainfall may reduce soil temperature (Song *et al.*, 2012).

Differences between two biologically-crusted soils

Unlike MCS, peak SR values and SRR_2 in CLCS did not increase with precipitation amount, and the maximum values occurred with 4 mm of precipitation (Figs. 4 and 5). At this study site, moss-dominated crusts were significantly thicker than cyanobacteria-lichen-dominated crusts (Table I), and the amount of rainwater required to saturate moss crusts is greater than that needed by cyanobacteria-lichen crusts. Higher amounts of water may not increase the CO_2 emission from cyanobacteria-lichen crusts, and may even restrain it (Liu *et al.*, 2002). Another explanation for these observations is that polysaccharides secreted by cyanobacteria expand rapidly when saturated soon after water addition (Li *et al.*, 2008), and then physically impede CO_2 transport through the soil profile and from the surface, thereby inhibiting soil CO_2 emission (Liu *et al.*, 2002; Sponseller, 2007; Thomas *et al.*, 2008).

Additionally, the magnitude of SR of CLCS in response to rewetting was smaller than that of MCS despite no differences in soil temperature and SWC between the two soils. This difference could be partly attributed to lower contents of SOC and TN in CLCS than in MCS (Table I), and smaller soil microbial biomass in CLCS than in MCS. For example, Liu *et al.* (2013) found that microbial biomass C and N in MCS were both significantly greater than those in CLCS. This could also be ascribed to greater SWC of MCS than that of CLCS with the same precipitation amount, which was mainly due to the difference of hydraulic conductivity between two soils (Wang *et al.*, 2008). In addition, these observed results could be caused by the difference in SR between crusts. This hypothesis has been confirmed by both manipulative and field experiments at this study site (Zhao, 2013), which is consistent with the findings of Belnap and Lange (2003), who reported that crusts dominated by mosses enhanced CO_2 flux in comparison with cyanobacterial crusts. In short, SR in response to rewetting at this study site could be due to the joint effects of biotic and abiotic factors, representing the combined physiological reactions of crusts and underlying soils.

Implications for soil C in the Tengger Desert

Soils in the Tengger Desert consist of a surface layer relatively rich in organic C (typically in a BSC layer) overlying a subsoil with limited organic C (Li *et al.*, 2003; Wang *et al.*, 2008). Microbes are concentrated within the top few millimeters of soils (Liu *et al.*, 2013). This suggests that larger events delivering water to deeper soils do not definitely induce stronger SR compared with events that only wet the topsoil (especially the BSC layer). In this study, total CO_2 emission following 2, 4, and 8 mm of precipitation accounted for 26%–74% and 22%–65% of that with 16 and 32 mm of precipitation, respectively, and 44%–53% on average (Fig. 5).

Importantly, it has been extensively proven that BSCs significantly contribute to SR in dryland ecosystems (Cable and Huxman, 2004; Castillo-Monroy *et al.*, 2011; Thomas *et al.*, 2011). For example, Cable and Huxman (2004) found that BSCs contributed 80% of soil CO_2 emission following small-size precipitation events in the Sonoran Desert. Castillo-Monroy *et al.* (2011) modelled SR in Mediterranean semiarid areas and found that vegetated and BSC-dominated microsites accounted for 37% and 42% of the yearly CO_2 released by SR, respectively. In this study, the addition of water to the BSCs (rainfall in small amount) and to the whole soil (rainfall in big amount) triggered increases in the magnitude and range of SR of the two biologically-crusted soils (Fig. 3). However, long-term data on precipitation throughout the growing season for the study site indicated that small-size precipitation events (less than 5 mm) were predominant across the Tengger Desert (Li *et al.*, 2004; Wang *et al.*, 2008), and will have a significant effect on SR and total C loss. Because organisms in BSCs can utilize very small amounts of water, even in the form of dew, which is unavailable for microbes in the subsoil, the contributions of BSCs could account for the majority of SR after light rainfall, and will be the greatest when soil is initially dry (Thomas *et al.*, 2011). Respiration partitioning experiments at this study site indicated that BSCs could contribute 75%–80% of soil-level CO_2 emission to the atmosphere following small-size precipitation events (Zhao, 2013). Considering the response magnitude of SR to different-size precipitation events, together with long-term precipitation data, our results suggest that CO_2 production from BSCs may have important contribution to ecosystem CO_2 emission in the Tengger Desert.

CONCLUSIONS

Both MCS and CLCS were quite responsive to simulated precipitation pulses. The simulated precipitation pulses led to increased short-term soil CO_2 emissions, and SR rate was logarithmically relevant to SWC, but no statistical relationships were found between SR rate and soil temperature, which suggested that water was the dominant factor for SR during the dry season of desert regions. Soil respiration of MCS and CLCS showed distinct responses to simulated precipitation, the magnitude and range of rain-triggered respiration pulses of MCS were greater than those of CLCS, which could be attributed to the variations in the biotic and abiotic properties and the regulating effects between different types of crusts. The response magnitude to SR to different-size precipitation events together with historical precipitation data suggest that CO_2 emission in small-size precipitation events and from BSCs might have important contribution to C cycling in the temperate desert ecosystems.

ACKNOWLEDGEMENTS

This study was financially supported by the National Natural Science Foundation of China (No. 41171078) and the Main Direction Program of Knowledge Innovation of Chinese Academy of Sciences (No. KZCX2-EW-301-2).

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