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ORIGINAL ARTICLE

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Biological soil crusts influence carbon release responses following rainfall in a temperate desert, northern China

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Abstract How soil cover types and rainfall patterns influence carbon (C) release in temperate desert ecosystems has largely been unexplored. We removed intact crusts down to 10 cm from the Shapotou region, China, and measured them in PVC mesocosms, immediately after rainfall. C release rates were measured in soils with four cover types (moss-crusted soil, algae-crusted soil, mixed (composed of moss, algae, and lichen)-crusted soil, and mobile dune sand). We investigated seven different rainfall magnitudes (0–1, 1–2, 2–5, 5–10, 10–15, 15–20, and >20 mm) under natural conditions. C release from all four BSCs increased with increasing rainfall amount. With a rainfall increase from 0 to 45 mm, carbon release amounts increased from 0.13 ± 0.09 to 15.2 ± 1.35 gC m^{-2} in moss-crusted soil, 0.08 ± 0.06 to 6.43 ± 1.23 gC m^{-2} in algae-crusted soil, 0.11 ± 0.08 to 8.01 ± 0.51 gC m^{-2} in mixed-crusted soil, and 0.06 ± 0.04 to 8.47 ± 0.51 gC m^{-2} in mobile dune sand, respectively. Immediately following heavy rainfall events (44.9 mm), moss-crusted soils showed significantly higher carbon release rates than algae- and mixed-crusted soils and mobile dune sands, which were 0.95 ± 0.02, 0.30 ± 0.03, 0.13 ± 0.04, and 0.51 ± 0.02 μmol CO_2 m^{-2} s^{-1}, respectively. Changes in rainfall patterns, especially large rain pulses (>10 mm) affect the contributions of different soil cover types to carbon release amounts; moss-crusted soils sustain higher respiration rates than other biological crusts after short-term extreme rainfall events.

Keywords Arid regions · Biological soil crusts · Extreme rainfall event · Rainfall pattern · Tengger Desert

Abbreviations

BSCs	Biological soil crusts
C	Carbon
EPS	Extracellular polysaccharide
MDS	Mobile dune sand
Rs	Soil respiration
SOC	Soil organic carbon

Introduction

Biological soil crusts (BSCs) are globally widespread communities of diminutive organisms such as cyanobacteria, green algae, lichens, mosses and other organisms. BSCs are closely integrated with surface soil particles, resulting in the formation of a cohesive thin-layer; they may constitute as much as 40 % of the living cover in arid and semi-arid ecosystems. These soil organisms can significantly improve soil stability and fertility by alleviating soil erosion, contributing greatly to carbon (C) assimilation and nitrogen fixation, and creating favorable microhabitats for other organisms (Belnap and Lange 2003; Bowker et al. 2006; Li 2012).

BSCs are major players in the global C cycles, in terms of C uptake from and release to the atmosphere (Elbert et al. 2012). The high photosynthetic C fixation potential of BSCs, such as lichen crusts, makes them an important C uptake pathway (C sink) in desert ecosystems. Thus, researchers have recently become interested in studying BSCs, and their role in C cycling (Zaady et al. 2000; Huxman et al. 2004a, b; Li et al. 2012). BSCs also contribute to C release in desert ecosystems; however, many studies neglect this role (Thomas et al. 2008; Thomas and Hoon 2010; Gao et al. 2012; Li et al. 2012). Castillo-Monroy et al. (2011) found that BSC-domi-

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nated sites accounted for 43 % of total C release by soil respiration (37 % from vegetation and 20 % from bare soil) in a semi-arid steppe ecosystem on the Iberian Peninsula. They concluded that BSC-dominated areas are the main contributors to the total C release by soil respiration in desert ecosystems. Furthermore, the vast BSC surface area on the Colorado Plateau has increasing CO_2 release rates related to 2 °C elevated soil temperatures and additional 2 and 30 mm summer rainfall events. This enhanced CO_2 flux in soils covered with BSCs indicates that the contribution of BSCs to atmospheric CO_2 is projected to increase (Zelikova et al. 2012). Relatively few studies have assessed the role of BSCs in ecosystem C release; C release from soils covered with different BSC types under natural conditions is especially poorly understood (Thomas et al. 2008; Grote et al. 2010; Coe et al. 2012; Li 2012).

Spatial and temporal patterns in water availability limit biological processes in arid and semi-arid ecosystems (Noy-Meir 1973). There is a growing appreciation that the magnitude of rainfall in these areas influences ecosystem processes, including C dynamics (Bowling et al. 2011). The C release in desert BSCs is ultimately water-limited (Sponseller 2007; Grote et al. 2010). Because of low, unpredictable rainfall and their proximity to the soil surface, desert BSCs are dry and inactive >90 % of the time (Lange et al. 1994). Therefore, they do not contribute to the C exchange for much of the time (Wilske et al. 2008). Once wetted, BSCs immediately release CO_2 through non-metabolic and metabolic pathways (Smith and Molesworth 1973; Farrar and Smith 1976). Optimal water levels can strongly stimulate CO_2 release in BSCs (Belnap and Lange 2003; Huxman et al. 2004a, b). Rainfall magnitudes and patterns in deserts also influence C release (Huxman et al. 2004b). Responses of C release by desert plants (e.g., Sala and Laurenroth 1982; Schwinning et al. 2002), soil microbial communities (Austin et al. 2004), short grass steppes (Munson et al. 2010), and hot desert ecosystems (Sponseller 2007) to rainfall events are well documented. However, there is still little information on the effects of rainfall magnitude on C release from BSC-covered soil in temperate deserts (Belnap et al. 2004; Li et al. 2012).

In the re-vegetated fixed sand dune area in the Shapotou region of the Tengger Desert in China, moss, algal and mixed crusts are the three predominant soil crust types. These crusts form a dense green bio-carpet, covering large areas that amount to more than 95 % of the regional surface; they stabilize the mobile sand (Li et al. 2005, 2012). The present study was conducted in this region to answer three questions: (1) How does C release amount vary with different soil cover types? (2) How does rainfall magnitude influence C release amounts and patterns in different soil cover types? (3) How does C release from different soil cover types respond to extreme rainfall events?

Materials and methods

Study site

The Shapotou region is located on the southeast edge of the Tengger Desert in northern China (37°33′N, 105°02′E) at an elevation of 1,339 m AMSL. The area is a typical transitional zone between desert and desert oasis. The natural vegetation is dominated by Sweetvetch (*Hedysarum scoparium*) and Sand Rice (*Agriophyllum squarrosum*), with a cover of approximately 1 %. Most of the area is covered by high, dense, and continuous reticulate barchan dunes. The soil substrate is loose and impoverished mobile sand. The mean annual air temperature is 9.6 °C, with extreme minimum and maximum temperatures of −25.1 and 38.1 °C, respectively. Mean annual rainfall is 186.6 mm and mean annual wind velocity is 2.9 ms^{-1}. To insure smooth operation of the Baotou-Lanzhou Railway in the sand dune area, a vegetation protective system was established along the railway line in 1956 by the Chinese Academy of Sciences and related departments (Li et al. 2005).

Establishment of the vegetation protective system involved an initial stage with a "sand barrier" made of woven willow branches or bamboo to act as a windbreak. Behind the sand barrier, straw checkerboards (1 m × 1 m) were established. The straw was inserted to a depth of 15–20 cm, so that it protruded approximately 10–15 cm above the dune surface. These barriers remained intact for 4–5 years, allowing time for xerophytic plants to establish. During this period, a number of native shrubs, including Peashrub *Caragana korshinskii*, Sagebrush *Artemisia ordosica*, and *H. scoparium*, were planted within the checkerboards. North of the railway line, a 500 m-wide protective belt was set up, while on the south side, a 200 m-wide protective belt was established; thus, the total length of the protective system was 16 km. The vegetation in this system plays a vital role in soil rehabilitation and production of this desert ecosystem by stabilizing dune surfaces, preventing wind erosion and thus stabilizing the local desert ecosystem. In addition, surface BSCs have expanded to cover 60 % of the vegetation protection system during the past 54 years (Li et al. 2005).

Experimental design and carbon release measurements

We selected the four most frequent soil cover types in the 1956 re-vegetated area for measurement of C release rate from April to October in 2011 and 2012: (1) moss-crusted soil (with more than 90 % moss crust cover), (2) algae-crusted soil (with more than 70 % algal crust), (3) mixed (moss/algae/lichen)-crusted soil (with 45 % moss crust, 45 % algal crust, and 10 % lichen crust), (4) mobile dune sand (with no biological soil crust cover). Consistent with other deserts (Sala and Laurenroth

1982; Lauenroth and Bradford 2009), rainfall in this desert is small and brief (≤ 10 mm). Rainfall events of less than 10 mm magnitude account for 85 % of the total annual rainfall frequency and 49 % of the annual rainfall amount; while 10–20 mm rainfall events account for 11 % of the annual rainfall frequency and 30 % of the annual rainfall amount, and rainfall events exceeding 20 mm account for 4 % of the total annual rainfall frequency and 21 % of the annual rainfall amount (Li et al. 2010). Thus, we defined seven rainfall magnitudes in this study: 0–1, 1–2, 2–5, 5–10, 10–15, 15–20, and >20 mm.

Sample collection and carbon release measurements

To avoid terrain and vegetation influences on crust development, all samples were randomly collected from undisturbed soil in the spaces between shrubs. Samples were collected in October 2010 using PVC tubes, with 10.4 cm-inner diameter, and a height of 12 cm. All samples had a surface area of 85 cm^2 and a thickness of approximately 10 cm to ensure that active rhizines and organisms, as well as most of the surface soil organic matter layer in the crust were included. The samples were taken to the nearby experimental station and randomly buried in soil (still in the PVC tubes), keeping the BSC surfaces at the same level as the local soil surface. To keep the test conditions close to those in the natural environment, we maintained natural soil water and air cycles, and we kept the base of the PVC tubes open for drainage.

Post rainfall CO_2 release rate in collected samples was measured between April and October in 2011 and 2012, using a Li-6400-09 Soil Chamber (LI-COR, Lincoln, NE, USA). Measurements were taken immediately after rainfall and repeated daily between 9:00 to 10:00, 14:00 to 15:00 and 20:00 to 21:00 (GMT + 8) until the C release rate returned to the pre-rainfall level. For each measurement, soil respiration rates were recorded at 4 s intervals over a 40 s period, once steady state conditions were achieved within the chamber. If the rainfall magnitude was less than 2 mm, then measurements were taken immediately after rainfall, and repeated hourly (because sample surfaces dried rapidly) until the respiration rate returned to the pre-rainfall level. Rainfall distribution in the Shapotou region during these experimental periods is shown in Fig. 1.

To assess temporal variation in C release rates after rainfall, we compared the rates measured at 9:00–10:00 am on different days. Additionally, a temperature correction algorithm was used to standardize all measurements to 20 °C, according to Parkin and Kaspar (2003):

$$CO_2\,release\,rate\,at\,20\,^{\circ}C\;=Rs\;\times\;Q(20-T)/10 \qquad (1)$$

where Rs was the measured CO_2 release at a specific hour, T was the soil temperature at 5 cm-soil depth at the time Rs was measured, while Q was the Q_{10} obtained from laboratory incubations of different soil types at different temperatures (5–35 °C). For moss-, algae- and mixed-crusted soils, and MDS, these Q_{10} values were determined to be 2.20, 1.88, 1.93, and 1.32, respectively.

We first calculated the daily and hourly mean values of C release amount during the measurement period, and then added these values to obtain the total C release amount from moss, algae, and mixed-crusted soils, and MDS for each rainfall magnitude. To avoid the effects of continuous rainfall on cumulative C release calculations, we only used data from rainfall events when C release rates returned to baseline before subsequent rainfall. This resulted in 36 events (0–1 mm, n = 13; 1–2 mm, n = 7; 2–5 mm, n = 6; 5–10 mm, n = 3; 10–15 mm, n = 3; 15–20 mm, n = 2; and > 20 mm, n = 2).

Chlorophyll a and b concentrations were estimated after sample collection in 2010. Pigments were extracted with 98 % ethanol in a dimly lit room. The absorptions of the extracted solutions were measured at wavelengths of 649 and 665 nm using a spectrophotometer (UV-1700 PharmaSpec, Japan). Concentrations were calculated according to the following relationships (Chappelle et al. 1992; Hui et al. 2013):

$$Chlorophyll\,a\,concentration\,\left(\mu g\,cm^{-2}\right) = 12.7A_{665} + 2.69A_{649} \qquad (2)$$

$$Chlorophyll\,b\,concentration\,\left(\mu g\,cm^{-2}\right) = 22.9A_{649} - 4.68A_{665} \qquad (3)$$

where A_{649}, and A_{665} were the absorption values at 649 and 665 nm, respectively.

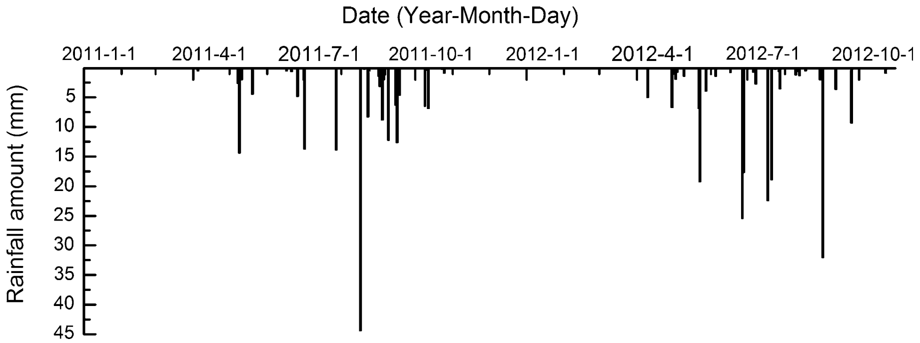

Fig. 1 Rainfall distribution during the experimental periods from April to October in 2011 and 2012 in the Shapotou region of the Tengger Desert, northern China

Soil organic carbon (SOC) was measured using the $K_2Cr_2O_7$ method, which is described in the Agriculture Chemistry Specialty Council, Soil Science Society of China (1983).

Statistical analysis

To test for significant effects of different soil cover type and rainfall magnitude on C release, we used a two-way ANOVA. The Duncan post hoc test was conducted when variances were equal, while Tamhane's T2 test was carried out when variances were not equal. Nonlinear regression analyses were used to examine the relationships between C release in soils with different cover types and after different rainfall magnitudes. All of the ANOVA and regression analyses were performed using the SPSS 16.0 statistical software (SPSS Inc., Chicago, IL, USA).

Results

Carbon release amount in the four soil cover types

Contributions to mean C release amount differed significantly among soil cover types: it was highest for moss-crusted soil, and lowest for MDS. The C release amount ranged from 0.13 ± 0.09 to 15.2 ± 1.36 gC m^{-2} in moss-crusted soil, which was significantly higher than in all other soil cover types. While the C release amounts ranged from: 0.08 ± 0.06 to 6.43 ± 1.23 gC m^{-2} in algae-crusted soil; 0.11 ± 0.08 to 8.01 ± 0.50 gC m^{-2} in mixed-crusted soil; and 0.06 ± 0.04 to 8.47 ± 0.51 gC m^{-2} in MDS. The C release amounts from all soil cover types increased with increasing rainfall magnitude. However, when the rainfall magnitude exceeded 15 mm, C release amounts did not increase further in algae- or mixed-crusted soils. Similarly, no difference in C release amount was observed between the 15–20 and > 20 mm rainfall magnitudes in algae-crusted soil and MDS (Fig. 2; Table 4). Hence, there were differences in C release amounts among crust types for different rainfall magnitudes.

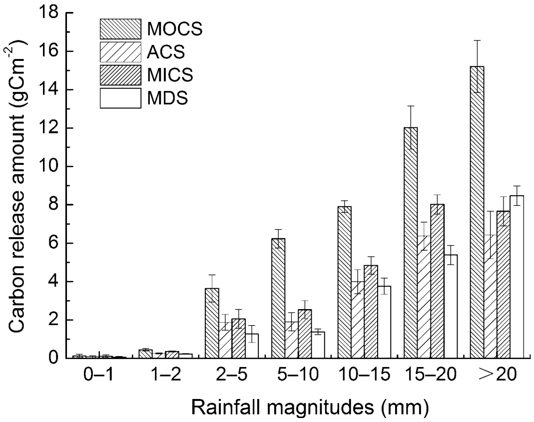

Fig. 2 The contribution of rainfall magnitudes (0–1 mm, n = 13; 1–2 mm, n = 7; 2–5 mm, n = 6; 5–10 mm, n = 3; 10–15 mm, n = 3; 15–20 mm, n = 2; > 20 mm, n = 2) to carbon release rate (gC m^{-2}; mean ± SE) in different soil cover types: moss- (MOCS), algae- (ACS), and mixed-crusted soils (composed of moss, algae, and lichen; MICS), and mobile dune sand (MDS), respectively

Temporal variation in carbon release amounts

Following small (4.8 mm) to moderate (13.7 mm) rainfall events, C release rates in all four types of BSCs showed similar trends; namely a high C release rate immediately following rainfall, followed by a gradual decrease. However, immediately following heavy rainfall events (44.9 mm), moss-crusted soils had higher C release rates (0.95 ± 0.02 μmol CO_2 m^{-2} s^{-1}) than algae- and mixed-crusted soils, and MDS, with rates of 0.30 ± 0.03, 0.13 ± 0.04, and 0.51 ± 0.02 μmol CO_2 m^{-2} s^{-1}, respectively. The C release rate for moss-crusted soils showed a gradually decrease after heavy rainfall events. Algae- and mixed-crusted soils, on the other hand, first showed a gradual increase and then decrease in C release after heavy rainfall. The highest C release rates from algae- and mixed-crusted soils occurred on the sixth day following heavy rainfall. Hence, for all rainfall magnitudes, different soil crust types can be ordered from highest to lowest C release rates, as follows: moss-crusted soils > mixed-crusted soils > algae-crusted soils > MDS (Fig. 3).

Using the two-way ANOVA, the model variables explained 98.9 % of the variation in C release rate. Both soil cover type and rainfall magnitude had significant effects on the C release amount ($F_{BSC} = 497.756$, $p < 0.001$; $F_{Rainfall} = 616.552$, $p < 0.001$; $F_{BSC \times Rainfall} = 26.375$, $p < 0.001$; Table 1). Nonlinear regression analyses suggested significant correlations between rainfall magnitude and C release. The fitted models accounted for a substantial part of the variation in soil respiration rates (rainfall magnitude explained more than 95 % of C release in moss-crusted soils and MDS, more than 90 % in algae-crusted soils, and more than 85 % in mixed-crusted soils; Table 2).

Chlorophyll a + b concentration and SOC content

Our study showed that moss-crusted soil had significantly higher chlorophyll a and b concentration (3.81 ± 0.42 μg cm^{-2}) than algae- and mixed-crusted soils, with concentrations of 2.07 ± 0.31 and 2.90 ± 0.22 μg cm^{-2}, respectively. Moss-crusted soil also had significantly higher SOC content (9.53 ± 1.52 g kg^{-1}) than and mixed-crusted soils, and MDS, with contents of 5.74 ± 0.81, 6.61 ± 1.07, and 3.24 ± 0.73 g kg^{-1}, respectively (Table 3).

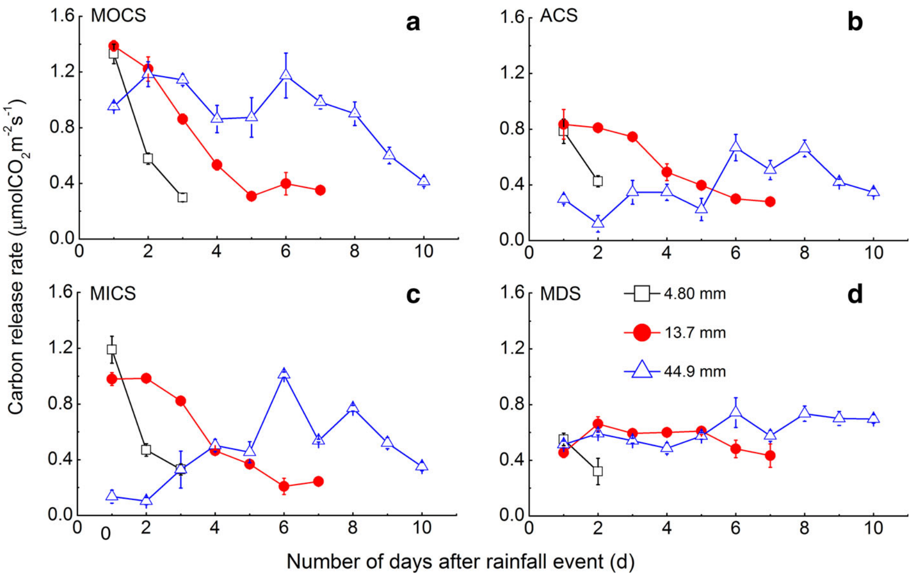

Fig. 3 Temporal variation in carbon release rate (μmol CO_2 m^{-2} s^{-1}; mean ± SE) in different soil cover types: **a** moss- (MOCS), **b** algae- (ACS), and **c** mixed-crusted soils (composed of moss, algae, and lichen; MICS), and **d** mobile dune sand (MDS), after small (4.8 mm), moderate (13.7 mm) and extreme (44.9 mm) rainfall events, respectively. To compare between events, the number of days after each rainfall event is used on the x-axis. All rates were standardized to 20 °C

Table 1 Two-way ANOVA analysis on effects of soil cover types (moss, algae, and mixed encrusted soils, and mobile dune sand) and rainfall magnitudes (0–1 mm, n = 13; 1–2 mm, n = 7; 2–5 mm, n = 6; 5–10 mm, n = 3; 10–15 mm, n = 3; 15–20 mm, n = 2; >20 mm, n = 2) on carbon release amount

Source	Mean square	F	*p*
Corrected model[a]	45.112	191.583	<0.001
Intercept	2579.831	10956.190	<0.001
Soil cover types	117.205	497.756	<0.001
Rainfall magnitudes	145.178	616.552	<0.001
Soil cover types × rainfall magnitudes	6.211	26.375	<0.001

R^2 values give the variation explained using a three-way ANOVA model

[a] $R^2 = 0.989$ (adjusted $R^2 = 0.984$)

Table 2 Multiple step-wise regression analyses of carbon release amount (R_s) for different soil cover types with variable rainfall magnitudes (W): moss (MOCS), algal (ACS), and mixed (composed of moss, algae, and lichen) crusted soils (MICS), and mobile dune sand (MDS), respectively

Soil cover types	Predicted model	R^2	*p*
MOCS	$R_s = 0.20\ W^2 + 0.97\ W - 1.43$	0.976	0.001
ACS	$R_s = 0.09\ W^2 + 0.50\ W - 0.74$	0.923	0.006
MICS	$R_s = 0.10\ W^2 + 0.70\ W - 1.03$	0.871	0.013
MDS	$R_s = 0.26\ W^2 - 0.74\ W + 0.65$	0.989	0.001

Table 3 Chlorophyll a + b concentration and organic carbon content for different soil cover types: moss (MOCS), algal (ACS), and mixed (composed of moss, algae, and lichen) crusted soils (MICS), and mobile dune sand (MDS), respectively

Soil cover types	Chlorophyll a + b (μg cm^{-2})	Organic carbon content (g kg^{-1})
MOCS	3.81 ± 0.42a	9.53 ± 1.52a
ACS	2.07 ± 0.31c	5.74 ± 0.81b
MICS	2.90 ± 0.22b	6.61 ± 1.07b
MDS	–	3.24 ± 0.73c

Values are mean ± SE; a–c denote significant differences at $p < 0.05$ level

Discussion

BSCs are a prominent component of and play an important role in the C cycle of most arid and semi-arid terrestrial ecosystems (Belnap and Lange 2003). Li et al. (2005) found that, through more than 50 years of continuous monitoring of the southeastern edge of the Tengger Desert, colonization and succession of BSCs proceed from MDS to physical crust to algal crust then mixed crust, and finally moss crust. Our results suggest that C release amounts increase along with this successional process. Numerous laboratory and field studies have shown C release amounts to be closely related to biomass or chlorophyll content of BSC organisms (Lange et al. 1998; Thomas et al. 2008). Our study showed that chlorophyll a and b concentration increased during BSC succession. This suggests that the biotic components of BSCs influence C release. Our findings are supported by Grote et al. (2010), who also found that dark respiration rates measured in field and laboratory conditions were significantly greater in dark (late succession) vs. light (early succession) BSCs collected from the Canyonlands National Park, Utah, USA. Therefore, BSC colonization and development on land surfaces enhance soil C release and change C release patterns in desert ecosystems. We surmise that late succession BSCs are the main contributors to C release in BSC-covered land in arid and semi-arid regions. Li et al. (2012) measured the annual amount of fixed C at our study site, and found that late succession crusts (lichen- or moss-dominated crusts) had a higher carbon input than early succession crusts (cyanobacteria- algae-dominated crusts) due to a higher chlorophyll content in the late succession crusts. Thus, a more developed successional ecosystem releases more C and uptakes more C due to its higher production rates.

Like most other biological activities, the ability of BSCs to release C depends on the presence of sufficient water. As dry and inactive BSCs can release little CO_2 (Lange et al. 1994), the physical distribution of soil water following rainfall links ecosystem C exchanges to rainfall patterns (Huxman et al. 2004b). In our study, rainfall magnitudes, especially moderate and heavy rainfall events, translate into dramatic increases in C release amounts, as well as changes to C release patterns in BSC-covered soils and MDS. This result is in agreement with other studies carried out in Sonoran, Chihuahuan, and Mojave Deserts, (Cable and Huxman 2004) and the Colorado Plateau (Coe et al. 2012). These studies found that the contribution of crusts to ecosystem CO_2 exchange is potentially large and increases with rainfall magnitude. Su et al. (2013) measured dark respiration after rainfall in cyanobacteria/lichen-crusted soil in Gurbantunggut Desert. They found that accumulated C release amounts were 2.09, 3.59 and 5.59 gC m^{-2} after 2, 5, and 15 mm rainfall events, respectively. Compared with our study, the C release amounts from the Su et al. study were higher for all crust types following a 2 mm-rainfall event; and higher for algae- and mixed-crusted soil following 5 and 15 mm-rainfall events. In contrast, our algae- and mixed-crusted soil C release rates following 5 and 15 mm-rainfall events were higher than those of Su et al. These discrepancies are most likely due to biotic differences in crust types, particularly in biomass or chlorophyll content of the BSC organisms.

Usually, BSCs do not contribute to the C exchange while they are dry and inactive (Wilske et al. 2008). However, the physiological inactivity of BSC organisms, such as mosses, does not mean that the soils as a whole are inactive. In fact, these soils are likely still respiring carbon even when they are fairly dry (Bowling et al. 2011). This is one circumstance, when the removal of soils from their soil profile could influence experimental results. For instance, if deeper rooted plants have root systems that extend beyond their plant canopies, they could contribute to C fluxes where the crusts are present, i.e., the C source could originate from below 10 cm-depth. Therefore, in future studies, C release during dry conditions also should be measured.

Our results also showed that C release amounts did not increase in algae- and mixed-crusted soils, when the rainfall magnitude exceeded 15 mm. One explanation for this observation is that substrate (SOC pool) limitation on rewetting constrains the duration (Huxman et al. 2004b; Bowling et al. 2011), rate, and amount of C release (Sponseller 2007; Miralles et al. 2013). Statistical relationships between microbial respiration and the SOC pool suggest that biotic activity, rather than abiotic processes, was responsible for patterns of soil CO_2 efflux observed at the time scales described in Kieft et al. (1987) and Fierer and Schimel (2003). In our study, moss-crusted soil had significantly higher SOC content than algae- and mixed-crusted soils, and MDS. Low SOC content was also shown to limit C release amounts after larger rainfall magnitudes in algae- and mixed-crusted soils, and MDS. However, the majority of rainfall events in our study region were small pulse events (<10 mm) (Li et al. 2010). This study suggests that changes in rainfall patterns, such as a trend toward large pulse events (>10 mm), will alter total C release and the proportional contribution of different soil cover types to total C release in this ecosystem.

The effects of climate change on terrestrial ecosystems are of wide scientific and public concern. The increasing incidence of extreme rainfall events is one of the obvious effects of climate change (Christensen and Hewitson 2007). At regional and small scales, extreme rainfall events have increased (except in Antarctica) (New et al. 2001). Recently, Jiang et al. (2012) used the IPCC-AR4 model to predict that extreme rainfall events in China will increase in frequency. Zhao et al. (2013) used World Meteorological Organization (WMO) standards to define extreme weather events in the Shapotou region, as any event with a magnitude of more than 30 mm. Our study demonstrates that C release rates increase with rainfall magnitude in all soil crust types (Fig. 2). However, C release is inhibited for several days after an extreme rainfall event, and then increases only in algae- and mixed-crusted soils. Soil water content has been shown to be the most important factor influencing soil C release rate. Too much soil water can inhibit soil respiration (Kidron et al. 1999; Huxman et al. 2004b; Sponseller 2007) because water fills soil pores, replacing CO_2 and decreasing soil permeability. This increases the resistance to soil CO_2 diffusion, causing reduced soil CO_2 emissions (Kursar 1989). Rainfall events cause accumulation of large amounts of water on the land surface (Christensen and Hewitson 2007), resulting in poor soil permeability and resistance to CO_2 release. Soil pores reopen as soil dries in algae- and mixed-crusted soils (Chamizo et al. 2013), resulting in an increase in C release. Additionally, BSC-covered soils can become hydrophobic, due to metabolites of some fungi and extracellular polysaccharide (EPS) secretions of some algae and cyanobacteria (Mager and Thomas 2011). EPS blocks topsoil pores (Avnimelech and Nevo 1964), increasing the water content of algal and mixed crust-covered soils. This leads to water accumulation in the surface layer after heavy rainfall (moss tissue can play a role in water conduction, inhibiting large amounts of water accumulation on the soil surface) (Frey and Kürschner 1991; Chamizo et al. 2012). EPS is a major source of soil C in arid and semi-arid regions (Mager and Thomas 2011); microorganisms use it as an energy source (Fischer 2009). As EPS decomposes, soil pores will reopen, resulting in increases in C release from algae- and mixed-crusted soils. Extreme rainfall events have less influence on respiration in moss-crusted soils, potentially because mosses have higher porosity (a higher number of macropores) and infiltration rates, such that water percolates deep into the soil (especially in sandy soils). Thus, more water may be needed to saturate the crust and block soil pores. Indeed, moss-crusted soils have higher water retention capacities and maintain higher soil moistures at the surface than algal and mixed crusts (Li et al. 2010; Chamizo et al. 2012). Our results indicate that in later succession stages, moss-crusted soils adapt well to extreme rainfall events in the short term; they, maintain ecosystem C balance and protect ecosystem structure and stability. Although we only document two extreme rainfall events in our study, we believe these results reflect natural trends.

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Appendix

See Table 4.

Table 4 Effects of rainfall magnitude on carbon release from the same soil cover type (significant variation denoted by lower case letters a–f; $p < 0.05$) and effects of the different soil crust types: moss (MOCS), algal (ACS), and mixed (composed of moss, algae, and lichen; MICS) crusted soils, and mobile dune sand (MDS) on carbon release following the same magnitude rainfall event

Rainfall magnitude (mm)	MOCS	ACS	MICS	MDS
0–1	fA	dC	eB	fD
1–2	fA	dC	eB	fC
2–5	eA	cC	cdB	eC
5–10	dA	cBC	cB	dC
10–15	cA	bC	bB	cD
15–20	bA	aC	aB	bC
> 20	aA	aC	aBC	aB

significant variation denoted by capital letters A–D; $p < 0.05$

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