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Original article

Precipitation intensity is the primary driver of moss crust-derived CO_2 exchange: Implications for soil C balance in a temperate desert of northwestern China

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ABSTRACT

Precipitation is the major driver of ecosystem functions and processes in semiarid and arid regions. Although re-wetting pulses generate a significant portion of the total annual CO_2 exchange between atmosphere and soil, there has been little recognition of the importance of photosynthetic and respiratory activities of biological soil crusts (biocrusts) in desert soil CO_2 exchange. In this study in the Gurbantunggut Desert of northwestern China, our objective was to determine the extent to which precipitation intensity could influence soil CO_2 exchange of the desert ecosystem and the role played by moss crust in soil C balance during this process. In field experiments, net CO_2 exchange (NCE) was measured in moss crusted soil and in bareland once a month from March to November in 2013. In laboratory experiments, simulated precipitation treatments (0 mm, 2 mm, 5 mm, 10 mm and 15 mm) were applied to moss crust, and NCE of moss crusted soil and its three flux components (crust photosynthesis, crust respiration, and subsoil respiration) were measured. Temporal variation of NCE varied with soil moisture and temperature. Soil moisture alone can explain 71–74% of variation in NCE. Soil type (moss crusted soil or bareland) also had a significant effect on NCE ($P < 0.01$), but this was dependent on soil moisture which is directly linked to precipitation pulse. The response of NCE to precipitation pulse in moss crust differed significantly from that of bareland. After a 2 mm precipitation pulse, the crust gross photosynthetic rate (GPc) was lower than the crust respiration rate (Rc), resulting in C efflux. When precipitation intensity was equal to or greater than 5 mm, GPc fully offset total respiration, resulting in an increase in C uptake. C gain was positively correlated with intensity of precipitation pulse. Regardless of different precipitation intensities, Rc was significantly higher than that of subsoil respiration. Thus, precipitation primarily drives moss crust-derived CO_2 exchange, which significantly influences the balance of soil-level CO_2 exchange in desert ecosystems. Overall, this study demonstrates that in desert ecosystems, the regulation of atmospheric-soil C balance by moss crusts depends on the intensity of precipitation.

1. Introduction

Ecosystem processes in arid regions are principally dependent on water, the most limiting factor determining the activity of desert organisms [1]. Water availability is directly linked to precipitation and the majority of precipitation events occur as small (<5 mm) short-duration events [2]. Therefore, the majority of arid ecosystems exhibit a pulse-dynamic response to precipitation, and soils which are almost continuously dry are sporadically interrupted by transitory periods of saturation following precipitation events [3]. Individual precipitation events can provide brief pulses of resource availability for desert organisms [4]. In such water-limited ecosystems, pulsed water inputs directly control soil CO_2 exchange through a series of soil drying and rewetting cycles [5].

Although re-wetting pulses generate a significant portion of the total annual CO_2 exchange of desert soils, communities of

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heterotrophic and autotrophic micro-organisms in biological soil crusts provide an additional and important contribution to soil CO_2 exchange [6]. Biological soil crusts (biocrusts) are composed of various combinations of cyanobacteria, algae, fungi, lichens and mosses intermixed with mineral grains and colonize the top several millimeters of the soil surface in many arid and semi-arid ecosystems [7]. Biocrusts can completely cover plant inter-space surfaces in undisturbed areas and thus can constitute as much as 70% of the living cover in dryland areas [7]. Autotrophic organisms that comprise biocrusts have the potential to fix atmospheric C during photosynthesis, at rates ranging from 0.1 to 11.5 μmol m^{-2} s^{-1} [8], thus making them the main source of C input to desert ecosystem [9]. Photosynthetic and respiratory activity in biocrusts can be triggered by very small amounts of moisture, including dew and fog and can be sustained over a wide range of moisture conditions, and influence soil CO_2 exchange in arid and semi-arid regions [10].

The soil net CO_2 exchange of desert ecosystems is determined principally by the difference between CO_2 fixation by gross photosynthesis (GPc) of autotrophic soil crust, and combined respiration of soil crusts (Rc) and soil heterotrophs (Rs). Precipitation patterns in deserts determine the tradeoff between C uptake (photosynthesis by autotrophs in biocrusts) and C efflux (respiration by heterotrophs or light respiration from photoautotrophs) [4]. Specifically, both magnitude and duration of C exchange are related to precipitation intensity [4]. Given that biocrusts are concentrated within the first few centimeters of the surfaces of arid soils, biocrusts in hyperarid regions reduce precipitation infiltration [11]. Autotrophic and heterotrophic processes in surface strata can be initiated by small precipitation events [6]. Larger precipitation events are required to initiate belowground root and heterotrophic microbe activity [6]. For example, after a small precipitation pulse, crusts contributed 80% of soil-level CO_2 efflux to the atmosphere in the Sonoran Desert; following a large pulse event, roots and soil microbes contributed nearly 100% of the soil-level efflux [6]. Therefore, precipitation intensity appears to determine the relative contribution of both crust and subsoil to soil-level CO_2 exchange, with important implications for C balance in arid and semiarid ecosystems.

Moss crust is a characteristic type of biocrusts found in arid lands. Biocrust mosses play a major role in crust structure and function, and appear to be particularly sensitive to environmental change [12]. Change in the intensity of precipitation is predicted to significantly affect desert moss C balance and belowground processes [13]. In North America desert, biocrust moss (such as *Syntrichia caninervis*) displays higher C balances in winter than in summer [14]. However, little is known about the way in which biocrust mosses affect soil surface C flux in central Asia arid deserts, especially, the contribution of moss crust to ecosystem C flux and how it balances soil-level CO_2 exchange following precipitation pulses.

The Gurbantunggut Desert is a typical temperate desert, which is located at the central Asia. In the desert, biological soil crusts cover more than 40% of the land surface and moss crust is one of the dominant types of soil crust [15]. Special geographic location cast dry climate and conditions, which has been becoming more extreme in the summer months. Precipitation events are usually small, isolated and sporadic; the period between precipitation events lasts at least several days and may extend to many weeks in the desert [16]. Global climate models predict that annual precipitation in this area will increase by 25% by the next century [17], therefore, a better understanding of the contribution made by moss crust to C flux in the desert is essential for evaluating desert C balance.

We carried out experiments on moss crusted soil in the field and in the laboratory. The objectives of this study were (1) to explain the temporal variation in soil net CO_2 exchange in both moss crusted soil and in bareland; (2) to gain an understanding of the way in which precipitation intensity and moss crust influence soil CO_2 exchange and soil C balance. We hypothesized that (1) biocrusts significantly drive soil net CO_2 exchange after precipitation pulses; and (2) the contribution of biocrust CO_2 exchange to ecosystem C exchange is dependent on pulse intensity.

2. Material and methods

2.1. Study area

An *in situ* experiment was conducted in the Gurbantunggut Desert (44°11′–46°20′N, 84°31′–90°00′E), in the Junggar Basin of the Xinjiang Uygur Autonomous Region of China. The area is characterized as a temperate desert ecosystem. Annual precipitation varies from 70 mm to 160 mm; mean potential annual evaporation is 2606.6 mm. The average annual temperature is 7.26 °C. Natural vegetation is dominated by *Haloxylon ammodendron* (C.A. Meyer) Bunge and *Haloxylon persicum* Bunge ex Boissier & Buhse (Amaranthaceae), as well as shrubs and small semi-shrubs including *Ephedra distachya* L., *Calligonum leucocladum* (Schrenk) Bunge, *Artemisia campestris* subsp. *inodora* Nyman (syn. *Artemisia arenaria* D.C.) and *Seriphidium terrae-albae* (Krasch.) Poljakov. In spring and early summer, ephemerals and ephemeroids can grow vigorously and cover extensive areas. Vegetation cover can be as high as 40% in May [15]. Biocrusts are widely distributed on soil between shrubs and cover more than 40% of the whole desert. They are most abundant in the central and southern regions of the desert where there are two dominant crust types based on species composition: lichen/cyanobacteria crusts and moss crusts [18]. Lichen/cyanobacteria crusts are usually dominant throughout the desert, with the exception of the crests of high dunes. Moss crusts are typically found in the inter-dune areas where they form a patchwork mosaic with lichen/cyanobacteria crusts, the thickness of moss crust is about 2–2.5 cm. Moss crusts are usually dominated by *S. caninervis* Mitt., together with *Bryum argenteum* Hedw. and *Tortula muralis* Hedw [15].

2.2. In situ experiment: measurement of net CO_2 exchange in moss crusted soil and in bareland

In March 2012, one year prior to the start of CO_2 exchange measurement, a site with well-developed moss crust was selected in the southern part of the desert. The site, 10 m × 15 m, was fenced to protect the ground from disturbance by people and/or animals prior to the commencement of the study. Twelve 1 m × 1 m plots

Table 1
Soil organic matter content (SOC), soil microbial biomass carbon (MBC), soil total nitrogen content (TN), bulk density (BD), and chlorophyll *a* content (Chl *a*) in moss crusted soil and bare soil at soil layers of 0–3 cm.

Soil type	SOC (g kg^{-1})	MBC (μg g^{-1})	TN (g kg^{-1})	BD (g cm^{-3})	Chl *a* (10^{-3} mg/g)
Moss crusted soil	8.47 ± 1.34	486.22 ± 45.15	1.67 ± 0.23	1.46 ± 0.12	2.22 ± 0.50
Bare soil	2.66 ± 0.43	10.22 ± 1.82	0.83 ± 0.33	1.76 ± 0.06	0.35 ± 0.17

were randomly established within the enclosure. The experimental design was planned to ensure that there were enough plots to account for between-plot variability and to avoid spatial interdependencies between the plots (pseudo-replication). Six plots were established for moss crusted soil (with moss crust covering >80% ground surface); 6 plots for bareland from which the biological soil crusts had been removed prior to fencing. A frame (inside diameter: 0.49 m × 0.49 m, external diameter: 0.52 m × 0.52 m) was installed in each plot for net C exchange (NCE) measurements. The soil (0–3 cm below the surface) was tested prior to commencement of the experiment and there were considerable differences between moss crusted soil and bareland in terms of soil organic C content, soil microbial biomass C, total nitrogen content, soil bulk density and soil chlorophyll *a* content (Table 1).

In 2013, NCE was measured once a month on clear days from March through to November (Fig. 1). Measurements were not taken in winter (December, January and February) when the soil was frozen and C flux was minimal. Since soil C exchange in the morning between 9:00–11:00 (local time) can represent the mean daily value as demonstrated in our previous studies [18] and in field observations in northern China [19], the measurements for this study were also conducted in the morning between 9:00–11:00 (local time), using an infrared gas analyzer (IRGA; LI-6400, Li-Cor, Lincoln, NE, U.S.) attached to a transparent polyvinylchloride chamber (0.5 m × 0.5 m and 0.25 m tall). The chamber consisted of five parallel-piped transparent polyCate walls (1.5 mm thick, allowing 92% of photosynthetically active radiation to pass into the plots) held together by a narrow metallic angular frame. During measurement, the chamber was sealed with water to the surface of the frame. Two small electric fans were installed and these operated continuously in the chamber to promote mixing of air during measurement. This method has been validated by several previous studies [18,20,21]. As soon as steady-state conditions were achieved within the chamber, nine consecutive CO_2 concentration recordings were taken at 10 s intervals over a 90 s period. During the time measurements were taken, air temperature within the chamber increased by <0.2 °C. Only the data from the last 60 s were used to calculate C exchange. The soil C exchange was computed using the following equation:

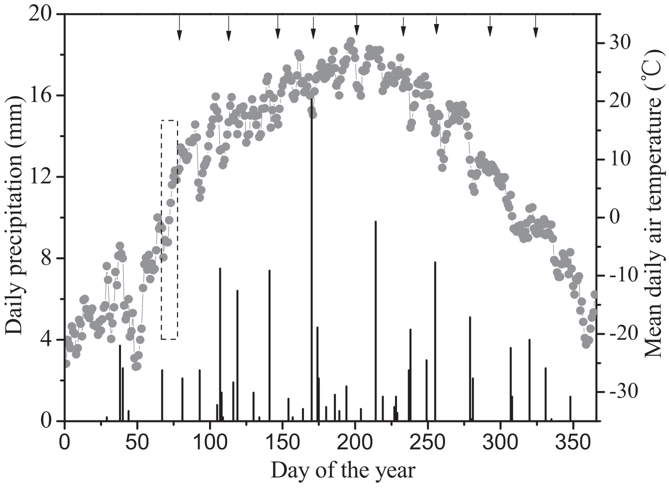

Fig. 1. Daily precipitation (mm) and mean daily air temperatures (°C) for 2013 at the study site. Arrows indicate the days on which soil CO_2 exchange was measured. The dotted box indicates snowmelt period.

$$F_c = \frac{10\ VP_0(1-W_0)}{RS\ (T_0+273.15)}\frac{\partial C}{\partial t}$$

where F_c is the C exchange rate (μmol m^{-2} s^{-1}); a positive value indicates C efflux. V is the volume of the assimilation chamber (cm^3), P_0 is the initial pressure (kPa), W_0 is the initial water vapor mole fraction (μmol mol^{-1}), R is the universal gas constant (8.312 kJ mol^{-1} K^{-1}), S is the soil surface area (cm^2), T_0 is the initial air temperature (°C), and $\partial C/\partial t$ is the slope of least square linear regression of CO_2 concentration.

Soil volumetric water content (SVWC) and soil temperature at 0–5 cm soil layer in each plot were measured using a portable TDR (HH_2-Delta T device moisture meter, UK) at the same time as the C exchange measurement [18]. During periods of drought stress, the volumetric water content was determined with the use of a handheld TDR moisture meter in conjunction with a sensor that measured 65 mm deep × 45 mm wide (WET-2, Delta-T Devices). We also compared the correlation between volumetric water content and gravimetric water content. The correlation coefficient can reach 0.89. Meteorological data (precipitation and air temperature) was from the Fukang Station of Desert Ecology, Chinese Academy of Sciences (44°17′N, 87°56′E and 475 m a.s.l.), about 20 km south from the study site.

2.3. *Laboratory experiment: separating soil net CO_2 exchange into crust and subsoil components*

In the southern Gurbantunggut Desert, moss crust, usually 2–2.5 cm thickness, is well developed between shrubs. Biocrusts described here are defined as the top layer of moss crust which can be easily and readily stripped from the soil surface. Before sampling, one PVC column with a diameter of 10 cm and a height of 20 cm was cut into two parts: one 4 cm high (column A) and the other 16 cm high (column B). The two parts were reconnected with plastic tape (Fig. 2A).

Sampling was conducted in September 2013. In the field, the surface of moss crust was dampened, the thickness of the moss crust was determined by a ruler. Once the depth of the crust layer had been measured, the column was pushed into the ground to the depth of the crust layer +16 cm to collect undisturbed whole soil columns with a cover of *S. caninervis*. The crust layer was then fully located within column A and the subsoil within column B (Fig. 2B). The base of each column was then sealed with metal plates and plastic tapes. A total of 20 soil columns were collected and carefully transported to the Fukang Station of Desert Ecology, Chinese Academy of Sciences. In order to make comparable C exchange measurements, we pretreated all the samples before carrying out the simulated precipitation experiment. All samples were kept dry in a growth chamber where they underwent 6-days of pretreatment (daytime conditions: photosynthetically active radiation (PAR) ~300 μmol m^{-2} s^{-1}, 20 °C, relative humidity (RH) ~40%, day length of ~12 h; nighttime conditions: PAR = 0, 12 °C, RH ~ 45%).

Precipitation in this desert is small and brief (≤2–5 mm). Small precipitation events (≤5 mm) account for 87.5% of the total precipitation frequency and 47.5% of the precipitation amount, while large precipitation events (10–15 mm) account for 4.3% of the precipitation frequency and 26.6% of the precipitation amount [16]. Five levels of simulated precipitation, (0 mm, 2 mm, 5 mm, 10 mm and 15 mm), were applied to the moss crust on the evening. Samples were gently moistened with distilled water using a sprinkling and there was no runoff. Our previous studies indicated that net C exchange and soil respiration in biologically crusted soil reached to a steady state after approximately 12 h after precipitation pulse [18]. In addition, we aimed to separate the contribution

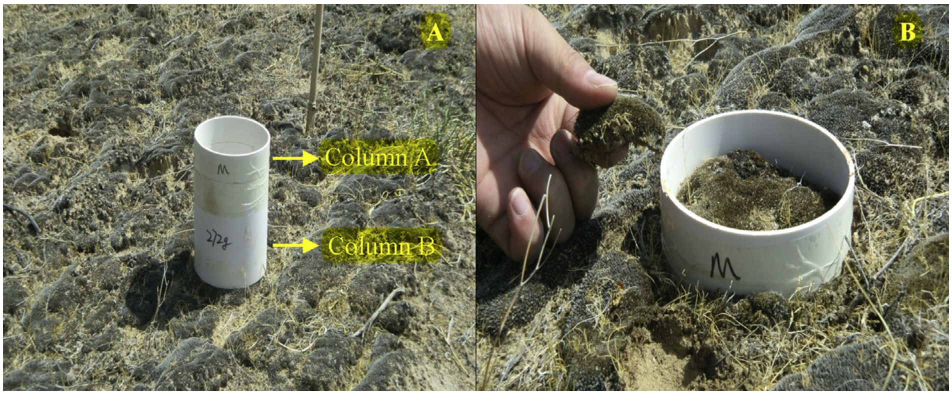

Fig. 2. (A) The PVC column used to collect moss-crusted soil; (B) field sample collection.

of moss crust layer from the entire soil-level CO_2 exchange, and measurements in the steady state can simplify this process. Therefore, in the next morning (about 12 h after precipitation treatment), gas exchange measurements were conducted in the growth chamber using an infrared gas analyzer (IRGA; LI-6400, Li-Cor, Lincoln, NE, U.S.) with the custom chamber that fitted over the soil collar. Natural light was transmitted (>93%) through the 154 cm^2 clear polyCate chamber top and air temperature remained within 1 °C of ambient conditions [21]. In order to adequately simulate natural conditions and maintain high photosynthetic activity, the climatic conditions within the chamber during C exchange measurements were maintained at ~800 $\mu mol\ m^{-2}\ s^{-1}$ PAR and ~65% relative humidity, and air temperature was controlled at 20 ± 0.5 °C [14]. The entire soil column (column A [crust layer] together with column B [subsoil]), was used to measure the overall net CO_2 exchange in light. Then the whole soil column was covered with an opaque cloth to determine the total respiration (Re). Gross photosynthesis of the moss crusted soil (GPc) can be calculated by formula GPc = NCE-Re. Later, column A was lifted off, the crust layer was naturally and integrally separated from the subsoil with the help of adhesion caused by PVC. There was no disturbance to the structure of either the crust layer or the subsoil during the separation process. Subsequently, respiration was measured in the crust layer (Rc) and in the subsoil (Rs). These gas exchange rates were calculated on a surface area basis as $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ (where upward CO_2 fluxes are considered positive).

2.4. Data analysis

In addressing the first objective in this study (understanding the temporal variation in soil net CO_2 exchange), repeated measures ANOVA was used to evaluate the primary and interactive effects of the measured time (month) versus soil type, with soil type as a subject factor. One-way ANOVA was performed to test the effect of soil types on soil C flux within each month, and means were compared with Tukey's honest significant difference test. Values were ln-transformed prior to analysis to normalize their distribution. Subsequently, stepwise regression analysis was used for determining the relative importance of temperature and moisture on seasonal variation of NCE.

To address the second main objective in this study (understanding how precipitation intensity influences soil CO_2 exchange and the role of biocrusts in soil C balance), laboratory data were used for the following analysis. One-way analysis of variance (ANOVA) was performed to test the effect of precipitation intensity on NCE and Re. One-way ANOVA was also used to assess differences in GPc, Rc and Rs among precipitation treatments. Duncan's new multiple range tests were performed to test for treatment effects. T-tests were performed to test the difference between Rc and Rs within each precipitation levels. Statistical analyses were performed using SPSS software (SPSS for Windows, version 13, Chicago, IL).

3. Results

3.1. Field experiment: temporal variation of net CO_2 exchange in moss crusted soil and in bareland

NCE differed significantly among measurement dates ($p < 0.01$) and temporal variation in NCE varied with soil moisture and

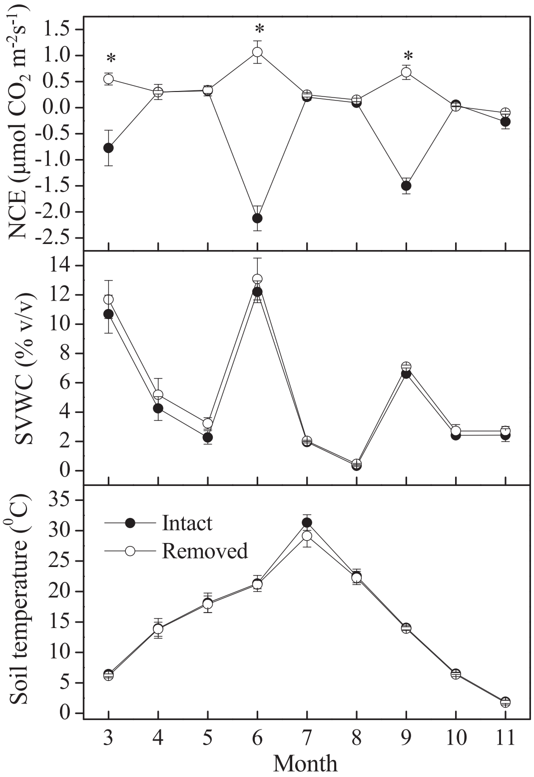

Fig. 3. Mean net carbon exchange (NCE), soil temperature (ST) and soil volumetric water content (SVWC) for control (moss crust intact) and treatment (moss crust removed) plots from March to November 2013 in field experiment. A single asterisk indicates a significant difference (p < 0.01) between control and treatment plots. Values are presented as the mean and standard error of values. Positive values for NCE indicate carbon efflux.

temperature. In both moss crusted soil and bareland, the maximum NCE rates were recorded in June (Fig. 3) when soil moisture levels were at their highest (more than 12% v/v) and soil temperatures more than 20 °C. C exchange rates were also very high in March and September when soil moisture levels were relatively high (more than 12% and 6%, respectively), but soil temperatures were relatively low (close to 5 °C and 15 °C, respectively). The lowest C exchange rates occurred in October when soil temperatures were low (<6.5 °C) and soil moisture content was less than 3% v/v (Fig. 3). When stepwise regression analysis, using soil temperature and soil moisture as independents, was used to evaluate the relative importance of temperature and moisture on soil CO_2 exchange, we found that soil moisture was more important than soil temperature ($R^2 = 0.71–0.74$, soil moisture alone; $R^2 = 0.84–0.89$, moisture plus temperature).

Soil type also had a significant effect on NCE ($F = 317.25$, $p < 0.01$), but the effect was dependent on measurement date. The interaction between time and soil type significantly influenced NCE ($F = 79.20$, $p < 0.01$). There were significant differences in NCE between moss crusted soil and bareland in March ($p < 0.01$), June ($p < 0.01$) and September ($p < 0.01$) when soil volumetric water content exceeded 6%. However, in the months when soil volumetric water content was less than 6%, there were no differences (Fig. 3). In June and September, one day before measurement, precipitation was 15.8 mm and 7.6 mm respectively (Fig. 1); soil moisture content was very high and net CO_2 exchange in moss crusted soil showed C uptake, at rates of −2.13 μmol $CO_2\ m^{-2}\ s^{-1}$ and −1.51 μmol $CO_2\ m^{-2}\ s^{-1}$, respectively. However, again for June and September, NCE in bareland was 1.07 μmol $CO_2\ m^{-2}\ s^{-1}$ and 0.68 μmol $CO_2\ m^{-2}\ s^{-1}$, showing C efflux to atmosphere. In March, one day prior to measurement, the snow melted completely (Fig. 1), soil moisture exceeded 10%, and soil net CO_2 exchange was −0.77 μmol $CO_2\ m^{-2}\ s^{-1}$ for moss crusted soil, and 0.55 μmol $CO_2\ m^{-2}\ s^{-1}$ for bareland. In other months (April, May, July, August, October, November), there was no recorded precipitation for at least three days prior to measurement (Fig. 1), resulting in much lower levels of soil moisture. In these months, net CO_2 exchange from moss crusted soil and bareland both showed C efflux and there was no significant difference between them, except for minimal C fixation in November.

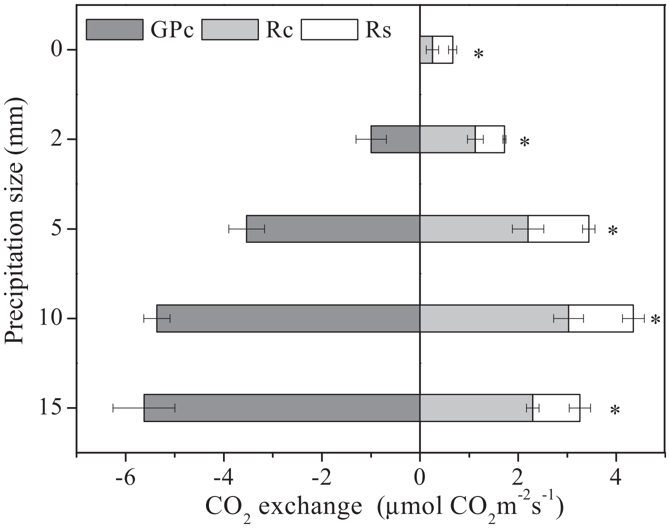

Fig. 5. The response of crust gross photosynthesis (GPc), crust respiration (Rc) and subsoil respiration (Rs) to different precipitation treatments (0 mm, 2 mm, 5 mm, 10 mm and 15 mm). Data are presented as the mean ± SE of four replicates each. Asterisks indicate significant differences ($p < 0.01$) between Rc and Rs within each precipitation treatments. A positive value indicates carbon release, negative value indicates carbon fixation.

3.2. Laboratory experiment: CO_2 exchange of moss crusted soil, crust and subsoil

Precipitation intensity significantly influenced soil NCE ($F = 217.26$, $p < 0.001$). When the precipitation intensity increased substantially, net C exchange in moss crusted soil changed markedly from positive to negative, from 0.64 ± 0.06 μmol $CO_2\ m^{-2}\ s^{-1}$ to −2.55 ± 0.11 μmol $CO_2\ m^{-2}\ s^{-1}$. C efflux following 2 mm precipitation was slightly higher than that of the 0 mm precipitation treatment, but there was no significant difference. However, when precipitation intensity was equal to or greater than 5 mm, net C exchange showed a positive C uptake which significantly increased with increasing precipitation intensity (Fig. 4a). Total soil respiration (Re) also varied significantly with precipitation pulse size ($F = 67.66$, $p < 0.001$). Re firstly increased and then decreased with

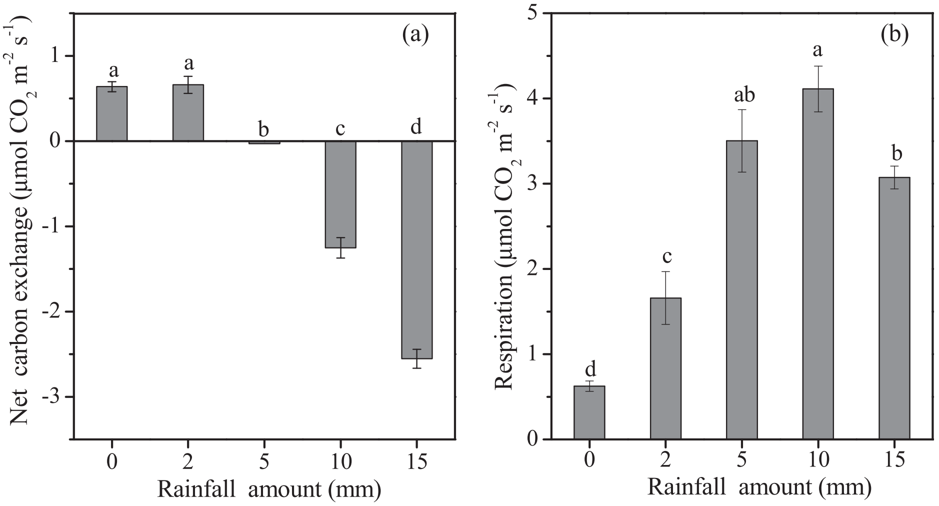

Fig. 4. The response of net carbon exchange (NCE) and total respiration (Re) for moss crusted soil to different precipitation treatments (0 mm, 2 mm, 5 mm, 10 mm and 15 mm). Data are presented as the mean ± SE of four replicates each. A positive value indicates carbon release, negative value indicates carbon fixation. Different letters indicate significant differences ($p < 0.01$) between precipitation treatments.

the increase in precipitation intensity. The rate of Re was lowest (0.63 ± 0.07 μmol CO_2 m^{-2} s^{-1}) when the precipitation intensity is 0 mm. The highest respiration rate was 4.11 ± 0.27 μmol CO_2 m^{-2} s^{-1}, following 10 mm precipitation treatment (Fig. 4b).

Crust gross photosynthesis (GPc) increased substantially with increasing precipitation. However, crust respiration (Rc) and subsoil respiration (Rs) increased at first then decreased with the increase in precipitation intensity. Crust respiration (Rc) was significantly higher than that of subsoil respiration (Rs) regardless of precipitation pulse size (excluding 0 mm) (Fig. 5). There were significant differences in GPc ($F = 184.93$, $p < 0.001$), Rc ($F = 56.10$, $p < 0.001$), and Rs ($F = 20.03$, $p < 0.001$) between precipitation intensities of 2 mm, 5 mm, 10 mm and 15 mm. In the absence of precipitation, photosynthetic activity was completely inhibited, C exchange in moss crusted soils resulted from respiration, and Rs contributed 61% of the total CO_2 efflux. Although photosynthetic activity was triggered by moisture, after the 2 mm precipitation pulse, the moss crust photosynthetic rate was less than its respiration rate. Following the 5 mm precipitation treatment, C efflux originating from Rc and Rs accounted for 62% and 35% of their total C uptake (GPc), respectively (Fig. 5). Following 10 mm precipitation pulse, maximum Rc and Rs were recorded. However, GPc exceeded the total C efflux (Rc + Rs). When precipitation exceeded 10 mm, GPc continued to increase while there was a decrease in Rc and Rs.

4. Discussion

4.1. Temporal variation of soil net CO_2 exchange

The temporal variation in soil net CO_2 exchange was evident, and varied with soil moisture and temperature. Variations in soil moisture alone can explain 71–74% of variance in NCE, clearly indicating that soil moisture can determine temporal variations in soil CO_2 exchange. It is well known that ecosystem processes in arid areas are primarily dependent on water, often the most limiting factor for desert organisms [1]. Only when soil moisture levels are favorable, is soil C flux mediated by soil temperature [19,22]. In this study, when soil moisture levels rose above ca 6% v/v, soil CO_2 exchange increased with increasing soil temperature. These results are consistent with those of other studies in arid lands [23,24].

In arid regions, soil moisture is directly linked to precipitation patterns. A high frequency of limited precipitation events has the potential to interrupt drought in continuously dry soils, and subsequently have a profound effect on C efflux by moistening the soil surface where microbes and labile soil organic C are abundant [4]. In this study, soil moisture and soil net CO_2 exchange increased significantly after natural precipitation pulses in March, June and September (Figs. 1 and 2). In the other months (April, May, July, August, November), when there was no precipitation for at least three days before measurements were taken, the soil surface was dry and net CO_2 exchange rate was low. Thus, soil moisture driven by precipitation pulse significantly influences temporal variation in net CO_2 exchange.

The characteristics of the soil surface are the primary factors that determine soil net C exchange. We found that soil cover types (moss crust, bareland) significantly affect the soil net CO_2 exchange rates. These results are in agreement with other dryland ecosystem studies, which have established that soil respiration rates were higher in microsites dominated by biocrusts than in bareland [25]. Such differences are not surprising given in the difference in soil fertility [25], microbial abundance [26] and soil environmental conditions [25]. Interestingly, the C exchange rate was significantly higher in moss crusted soil than in bareland only when soil volumetric water content exceeded 6%, the point at which moss crusted soil showed C uptake (Fig. 2). These differences cannot be explained by differences in soil temperature and soil moisture, as there were no differences in soil temperature between moss crusted soil and bareland and soil moisture was comparatively lower in moss crusted soil than in bareland. We found chlorophyll *a* concentration in moss crusted soil (2.22×10^{-3} mg/g) was significantly higher than in bareland (0.35×10^{-3} mg/g) (Table 1). Therefore, photosynthetic activity may explain the result obtained.

When soil moisture was less than 6%, there was no significant difference in net C exchange between the two soil types. The results may be explained by the following two mechanisms. Firstly, the surface soil is dry and biocrusts are dormant when there is no precipitation for seven days prior to measurement. Secondly, when soil water content is comparatively low, photosynthetic activity in biological soil crusts is relatively low, and is unable to, or can barely, offset respiration after small precipitation events [27]. Therefore, precipitation pulse is the primary driver of moss crust-derived CO_2 exchange, and influences the soil net CO_2 exchange in desert ecosystems. This supports our first hypothesis that the presence of biocrusts significantly changes the response of soil net CO_2 exchange to precipitation pulse.

4.2. Biocrusts and subsoil contribution to soil net CO_2 exchange

From our field observations, we can conclude that net C exchange can be significantly influenced by the presence of biocrusts. However, whether biocrusts change the response of soil net CO_2 exchange to precipitation pulse is dependent on the relative contribution of crust photosynthesis, crust respiration and subsoil respiration to soil net CO_2 exchange. In this study, increases in the intensity of precipitation (from 2, 5, 10–15 mm) resulted not only in a significant increase in the three C flux components (GPc, Rc and Rs) but also, a shift from C losses to C gains for the net C exchange. This suggests that photosynthetic activity in biocrusts can be triggered by a wide range in size of precipitation pulse and that the effect of photosynthetic activity on soil C balance depends on precipitation pulse size. This supports our second hypothesis that precipitation intensity determines the relative contribution of crust and subsoil to soil net CO_2 exchange, with important implications for C balance.

Biocrust microphytes are poikilohydric organisms in which the water content of cells is in equilibrium with the surrounding environment [10]. Mosses possess neither vascular tissue nor roots and are thus disconnected from belowground water sources and their cellular water status is determined by hydration from precipitation pulses [14]. In natural condition, biocrust mosses inhabit in the first few centimeters of soil surface, which could reduce water infiltration and influence soil moisture [11]. Thus, in order to simulate the field environment, we took the entire soil at the depth of 0–20 cm and then separated CO_2 exchange in biocrust mosses from the subsoil at the steady state. In the absence of precipitation, mosses are desiccated and inactive [10] and subsoil respiration dominated the soil-level CO_2 exchange (Fig. 4). Following 2 mm precipitation pulse, photosynthesis in moss crust was less than respiration, thus small precipitation events caused a negative C balance for moss crust, and soil net CO_2 exchange showed C efflux (Fig. 3). Precipitation events of less than 2 mm may not allow mosses to fully hydrate [28], and this may lead to pigment degradation if recurrent [29]. Similarly, small precipitation events resulted in C deficits for *S. caninervis* in Colorado Plateau [14], and may even reduce moss cover from 25% of total surface cover to <2% after only one growing season [13].

After comparatively large precipitation events, photosynthetic activity in moss crust remained high, resulting in C gains sufficient to compensate for respiratory C loss [14]. Our results suggest that there is a minimum precipitation event size of about 5 mm required to sustain C balance. When the precipitation intensity exceeded 5 mm, net C exchange was negative, indicating C uptake. In desert ecosystems, the majority of precipitation events occur as small (<5 mm) shot-duration events [2]; this may be the reason that in such systems, biologically-crusted soil (inferring soil covered by biocrusts) showed a net C efflux most of the time in field observations [18]. When the precipitation intensity exceeded 10 mm, both subsoil and crust respiration begun to decrease, but this was accompanied by an increase in crust photosynthesis. Precipitation is predicted to be increasing over the next 30 years in northern China, and the lager precipitation event would be more frequent in the Gurbantunggut Desert [17]. Thus, this higher precipitation density scenario would result in favorable C gain for biocrust mosses, sequentially have profound impacts on soil C balance in the desert.

Lastly, when crust respiration (Rc) was compared to subsoil respiration (Rs), Rc contributed most of the total soil respiration irrespective of the intensity of precipitation (Fig. 4). Small precipitation pulses (2 mm) activate the soil crust rather than plant roots and soil microbes [6] and organic C is preferentially concentrated at the crust layer in the Gurbantunggut Desert (Table 1). Thus, after the 2 mm precipitation pulse, Rc was significantly greater than Rs and constituted the largest component of total respiration (Re), an outcome consistent with findings in the Sonoran Desert [6]. Since water infiltrates deep into the soil profile, relatively large precipitation pulses have the potential to influence subsoil microbes. Following larger precipitation pulses (5, 10, 15 mm), subsoil respiration increased significantly (Fig. 4). However, Rc was still significantly higher than Rs. In contrast [6], have shown that subsoil respiration contributed nearly 100% of the soil-level CO_2 efflux following a 25.4 mm pulse event in the Sonoran Desert. In the biocrust areas of the Gurbantunggut Desert, vascular plant cover is sparse and root growth minimal. Soil organic matter and soil microbes are concentrated in the biocrusts and not evenly distributed through the soil profile [18]. Therefore, nutrient levels, soil organic matter and soil microbes are insufficient to generate high subsoil respiration even when there is adequate moisture at deep soil levels. Similarly, in the Iberian Peninsula, biocrusts have been shown to be the major contributor of the total C released by soil respiration [25] thus confirming that our results show that precipitation pulse primarily drives crust CO_2 exchange and the largest C gains are associated with the largest precipitation events.

5. Conclusion

Our results indicate that the manner in which soil CO_2 exchange responds to precipitation is crucial in accurately estimating the role of the C cycle at the soil level in arid lands. Large differences in soil CO_2 exchange were found between biocrusts-covered areas and those devoid of biocrusts, suggesting that the presence of biocrusts significantly changes the response of soil net CO_2 exchange to precipitation pulse. Our partitioning experiments further demonstrate that biocrusts are the main contributor to the total C released by soil respiration after a precipitation pulse. However, larger precipitation pulses are able to fully activate photosynthesis in biocrusts and completely offset crust respiration and subsoil respiration, resulting in C uptake by moss crusted soil. Therefore, precipitation pulse is the primary driver of soil crust CO_2 exchange that balances soil-level CO_2 exchange in desert ecosystem. Given the large areas covered by BSCs in arid and semiarid lands, the unequivocal consideration of crust-derived CO_2 exchange in future empirical and modeling studies may greatly contribute to the understanding of the global C cycle and enable better prediction of the effects of global environmental change on soil C balance.

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