Carbon fixation and influencing factors of biological soil crusts in a revegetated area of the Tengger Desert, northern China

Lei HUANG^{1,2*}, ZhiShan ZHANG^{1,2}, XinRong LI^{1,2}

¹ Shapotou Desert Research and Experimental Station, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China;

² Key Laboratory of Stress Physiology and Ecology in Cold and Arid Regions of Gansu Province, Lanzhou 730000, China

Abstract: Biological soil crusts (BSCs) are an important type of land cover in arid desert landscapes and play an important role in the carbon source-sink exchange within a desert system. In this study, two typical BSCs, moss crusts and algae crusts, were selected from a revegetated sandy area of the Tengger Desert in northern China, and the experiment was carried out over a 3-year period from January 2010 to November 2012. We obtained the effective active wetting time to maintain the physiological activity of BSCs basing on continuous field measurements and previous laboratory studies on BSCs photosynthesis and respiration rates. And then we developed a BSCs carbon fixation model that is driven by soil moisture. The results indicated that moss crusts and algae crusts had significant effects on soil moisture and temperature dynamics by decreasing rainfall infiltration. The mean carbon fixation rates of moss and algae crusts were 0.21 and 0.13 g C/(m²·d), respectively. The annual carbon fixations of moss crusts and algae crusts were 64.9 and 38.6 g C/(m²·a), respectively, and the carbon fixation of non-rainfall water reached 11.6 g C/(m²·a) (30.2% of the total) and 8.8 g C/(m²·a) (43.6% of the total), respectively. Finally, the model was tested and verified with continuous field observations. The data of the modeled and measured CO₂ fluxes matched notably well. In desert regions, the carbon fixation is higher with high-frequency rainfall even the total amount of seasonal rainfall was the same.

Keywords: moss crusts; algae crusts; soil moisture dynamics; non-rainfall water; effective wetting time

Citation: Lei HUANG, ZhiShan ZHANG, XinRong LI. 2014. Carbon fixation and influencing factors of biological soil crusts in a revegetated area of the Tengger Desert, northern China. *Journal of Arid Land*, 6(6): 725–734. doi: 10.1007/s40333-014-0027-3

Biological soil crusts (BSCs) are vital features of arid desert regions. BSCs are widespread communities of diminutive organisms, such as cyanobacteria, green algae, lichens, mosses and other organisms that are closely integrated with particles of the surface soil. Therefore, these communities form a cohesive, thin horizontal layer over the desert landscape (Belnap and Lange, 2003; Li et al., 2004). BSCs are considered desert ecosystem engineers and cover up to 40%–70% of the landscape (Bowker, 2007), especially in extreme environments with low interference. Several studies have confirmed that BSCs are vital carbon sinks in a desert ecosystem because of their consider-

able photosynthetic capacities (Evans and Lange, 2001; Wilske et al., 2009; Su et al., 2011; Li et al., 2012). For example, under the optimal conditions of hydration and light, the photosynthetic rates of *Collema tenax* are in the upper range of or even higher than the maximal area-related leaf net photosynthesis rates of the plants that characterize the phanerogamous vegetation of the collection site (Lange et al., 1998). Beymer and Klopatek (1991) estimated that the potential annual carbon contribution of lichen soil crusts is 12–37 g C/(m²·a). Lange et al. (1994) estimated that lichen crusts in Namibia contribute 16 g C/(m²·a). Therefore, the photosynthetic aspect of BSCs-related

*Corresponding author: Lei HUANG (E-mail: mathecology@163.com)

Received 2013-11-07, revised 2014-03-20, accepted 2014-04-18

© Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Science Press and Springer-Verlag Berlin Heidelberg 2014

carbon fixation should be considered in carbon budget allocations at local and regional scales (Li et al., 2010).

An estimated total of 1.0×10^{16} g of carbon is contained in deserts throughout the world (Saugier et al., 2001). Approximately 5.6×10^{13} g of the total carbon is stored in cyanobacteria (Garcia-Pichel et al., 2003). The effects of various types of BSCs have been well studied in arid and semi-arid environments, such as desert areas in the United States, Australia, Israel, temperate grasslands in Europe, the north and south poles and the sub-arctic zones (Harley et al., 1989; Sonesson et al., 1992; Davey, 1997; Zotz et al., 2000). Such studies have mainly focused on the relationships between the BSCs structure, spatial distribution, taxonomic composition, physiological characteristics (e.g. BSCs photosynthetic rate, stomatal conductance and chlorophyll content), and biological/environmental factors (e.g. soil moisture and temperature) (Brostoff et al., 2002). Furthermore, these studies were often restricted to intermingling communities rather than monoculture species. In fact, species with different thallus structures and physiological features can lead to the dominance of certain life forms on long-time scales, during which their carbon inputs into the ecosystem can be altered (Lang, 2000). For example, the accumulated carbon fixation of cyanobacterial-algal crusts increased from 2.9 to 35.4 g C/m² over 15 years at the restoration site in the Tengger Desert (Su et al., 2011).

Numerous findings have identified soil moisture as one of the most important environmental factors in the BSCs carbon fixation (Li et al., 2010; Su et al., 2011; 2012). This is attributed to the dominance of poikilohydric plants in the BSCs group (Zotz et al., 2000), which are extremely sensitive to moisture, especially in arid environments. Once getting a small amount of water, these plants quickly begin metabolic activity despite their typical dry, dormant state. Researchers have proven that BSCs possess a strong photosynthetic capacity after 10-min water uptaking in the semi-arid areas of eastern Australia (O'Neill, 1994). Additionally, some types of BSCs can maintain maximum photosynthetic capacity with 0.2 to 0.3 mm of rainfall. Therefore, we hypothesize that non-rainfall water, such as dew, fog and high air humidity, can supply an adequate amount of water for BSCs (e.g. green algae and lichens) photosynthesis in some areas

(e.g. Israel's Negev Desert) (Lange et al., 1998; Wilske et al., 2008). Solar radiation and temperature also directly affect photosynthetic activities, chlorophyll content and rubisco content of BSCs. Given sufficient moisture and light, the optimum temperature for the carbon fixation of BSCs generally ranges from 20°C to 30°C (Li et al., 2013).

Studies on BSCs carbon fixation models mainly focused on photosynthesis and its impacts (Jeffrise, 1993; Evans and Lange, 2001; Brostoff et al., 2005; Wilske et al., 2009; Su et al., 2011; Li et al., 2012). Annual carbon fixation was extrapolated from the empirical models. Based on the empirical models, the reported estimates of the carbon input of BSCs to the entire ecosystem range from 0.4 to 37 g C/(m²·a) (Lange, 2003). The large variation among studies was partially caused by different crust types. For example, cyanolichen crust had the highest fixation rates, but it did not differ significantly from darkened moss crust. Light algal crust, incipient algal-fungal crust and fungal crust exhibited substantially lower fixation rates than that crusts containing moss and/or lichen species (Pietrasiak et al., 2013), but the results were usually restricted to certain areas. Furthermore, most of the previous estimations based on laboratory studies lacked the long-term monitoring of BSCs carbon fixation under natural conditions (Evans and Lange, 2001; Brostoff et al., 2002). Some research has recognized the importance of the water availability for the estimation of the carbon fixation of BSCs (Lange et al., 1977, 1994; Belnap et al., 2005; Su et al., 2011; Li et al., 2012), but it is difficult to determine the exact wetting time and the contribution of BSCs carbon fixation from rainfall and non-rainfall sources by using previous models. For example, the BSCs in the Tengger Desert often have low activity for a few months per year (Li et al., 2010). Lange et al. (1992) reported that BSCs activity from rainstorms at the Nizzana sand dune area lasted for several days. The net carbon sequestration in ecosystems requires careful consideration because overestimations or underestimations of the activity periods can lead to relatively large deviations.

The Tengger Desert, which is located in northern China, is the fourth largest desert in the country. Local moss crusts and algae crusts developed with the sand dune stabilization and displayed very good formation

in this area. Therefore, this area presents a valuable opportunity to study the carbon exchange of BSCs with different species compositions (Su et al., 2012). In the current study, we obtained soil moisture calculated by BSCs carbon fixation model basing on fixed long-term continuous field observations, laboratory works on BSCs photosynthesis and a respiration model with soil moisture dynamics. Unlike the previous model, the model is continuous and has a clear physical mechanism. The model is also more complex because the BSCs photosynthesis, respiration and related factors (e.g. soil moisture, soil temperature, solar radiation, and in particular, the effective wetting time to maintain the BSCs activity) were emphasized. The daily CO₂ fluxes of the moss crusts and algae crusts were calculated, after which the annual carbon fixation was extrapolated. Our results confirmed the important role of BSCs carbon input in stabilizing sand dunes, thereby providing useful information concerning carbon cycling in aeolian desert ecosystems.

1 Materials and methods

1.1 Study area

The study area is at Shapotou Desert Research and Experimental Station, Chinese Academy of Sciences, located in the Shapotou region at the southeastern Tengger Desert (37°32'N, 105°02'E). The study area falls into the transitional zone from desert steppe to steppified desert and is a transitional belt between oasis and desert environments. The elevation of the area is 1,330 m. The mean annual precipitation is 188.2 mm (according to meteorological records from 1956 to 2009), which mostly falls between June and September. The potential evapotranspiration during the growing season (May–September) is 2,300 to 2,500 mm (observed by an evaporation pan of type E-601). The annual mean temperature is 9.6°C. The mean temperature is −6.9°C in January and 24.3°C in July. The annual mean wind velocity is 2.6 m/s, and the annual mean number of dust-storm days is 59. The soil surface is loose, poorly aggregated mobile sand dunes with moisture content of 2%–3%.

For protecting the Baotou–Lanzhou railway line from sand burial, a non-irrigated vegetation protection system was established in 1965. After 50 years, the planted shrub vegetation was gradually replaced by

dominant shrubs, such as *Artemisia ordosica*, *Caragana korshinskii*, *Hedysarum scoparium* and herbaceous plants due to the decreasing deep soil water content (Li et al., 2004). Meanwhile, BSCs colonized and developed on the stabilized dunes once the sand-binding vegetation were established, after which the crusts were converted from the initial cyanobacteria dominated crusts to lichen and moss dominated crusts (Li et al., 2011).

1.2 Sampling and data collection

Intact crust samples with 100% coverage of moss crusts (*Bryum argenteum* Hedw. dominated) and algae crusts (*Microcoleus vaginatus* Gom. dominated) were randomly collected from the revegetated zones. Three moss crusts and three algae samples were collected. The size of each sample was 50 cm×50 cm×50 cm. For each collected sample, the soil water content and temperature were measured by a time-domain reflectometer (TDR) soil moisture and temperature probe which was placed (model 6050X1, Trase System I, Soilmoisture Equipment Corp., USA) at the depth of 3 cm below the sampled moss and algae crusts. The probe had three 20 cm rods spaced 2.5 cm apart. For installing the probe, a pit with sufficient width was dug in the ground. The probes were inserted into the soil from interior of the pit and the probes were placed horizontally in the direction of the maximum slope of the terrain. Once the probes were inserted, the pit was carefully refilled to avoid perturbations and the surface was contoured similarly to the surrounding slope. We used three probes at each site to estimate the average soil moisture content. The value obtained from each probe was weighted with the assumption that it represents soil moisture over a depth of 0–3 cm. The soil temperature was directly measured at the 0 cm soil surface. The net solar radiation (CNR-1, Kipp & Zonen, Delft, the Netherlands) was measured by the microclimate station, which was railed 15 m away from the sample plot. The data were computed every 30 min from January 2010 to November 2012 and were recorded by Campbell CR30X data loggers. Data on the relationships between photosynthesis, respiration rate and soil moisture were obtained from the publications by Jia (2009) and Su et al. (2011). The equations of the regression analysis were listed in Table 1.

Table 1 Relationship between photosynthetic rates (Pn), dark respiratory rates (Rd) and soil water contents of moss crusts and algae crusts

Crust type		Equation	R^2	p
Moss crust	Pn	$Pn = -0.00141x^2 + 0.14779x - 0.67839$	0.573	<0.0001
	Rd	$Rd = -0.00203x^2 + 0.22602x - 0.38639$	0.841	<0.0001
Algae crust	Pn	$Pn = -0.000192x^2 + 0.02656x + 0.14749$	0.778	<0.0001
	Rd	$Rd = -0.000247x^2 + 0.03242x - 0.08253$	0.692	<0.0001

Note: Pn, photosynthetic rates ($\mu\text{mol}/(\text{m}^2\cdot\text{s})$); Rd, dark respiratory rates ($\mu\text{mol}/(\text{m}^2\cdot\text{s})$); x, soil water moisture (V/V, %).

To measure the photosynthesis of the two BSCs in the field, we placed ten 10-cm diameter soil collars in the soil at a depth of 2 cm for each sample. The net photosynthesis (Pn) for all of the plots was then measured every 2 h from sunrise to sunset. Gas exchange was measured through two Licor 6400 portable photosynthesis systems (LI-COR Inc. Lincoln, NE, USA) with custom chambers that fit over the soil collar. First, we measured the gross photosynthesis in the light (Pg). Then an opaque foil cover was placed over the collar to determine respiration (Re). The readings for Pg and Re were recorded until the values became stable. Net photosynthesis was then calculated by $Pn = Pg - Re$, and the photosynthetic rates ($\mu\text{mol CO}_2/(\text{m}^2\cdot\text{s})$) were finally calculated by the surface area.

1.3 Model description

The aim of the model is to simulate the annual carbon fixation held in BSCs in the desert. The rate of CO_2 exchange (flux, simulated: $FS(w, t, l)$) of the crusted soils was the key component of the model. The model includes the following state variables: photosynthesis ($FS_p(t, l)$), respiration ($FS_r(t)$) rate of BSCs with temperature (t) and net radiation (l), the trigger that activates the BSCs photosynthesis $f_p(w)$ and respiration $f_r(w)$ activity with soil moisture (w) dynamics, and the effective wetting time (N_p , N_r). The major assumptions and conditions used in the model formulation were discussed next.

The functional relationship of $FS_p(t, l)$ and $FS_r(t)$ with light and temperature can be obtained from an existing algorithm that describes the reaction kinetics for poikilotherm development (Sharpe and DeMichele, 1977) and the volatile organic compound flux emission (Schuh et al., 1997). Wilske et al. (2009) have modified the algorithm to simulate the BSCs-related CO_2 emissions and deposition fluxes, which are expressed by:

$$FS_r(t) = \exp\left(\frac{cT_p}{R} \times \frac{T_{ssb} - T_s}{T_{ssb} \times T_s}\right), \quad (1)$$

$$FS_p(t, l) = cL \times \frac{a \times l}{\sqrt{1 + a^2 \times l^2}} \times \frac{\exp\left(\frac{cT_1}{R} \times \frac{T_{ssb} - T_s}{T_{ssb} \times T_s}\right)}{1 + \exp\left(\frac{cT_2}{R} \times \frac{T_{ssb} - T_M}{T_{ssb} \times T_s}\right)}. \quad (2)$$

Where T_{ssb} is the BSCs-affecting temperature, $T_{ssb} = (T_{s3} + T_a)/2$, T_{s3} is the soil temperature at a 3 cm soil depth below the crusts, and T_a is the soil surface temperature. $cT_p = 130$, $R = 8.314$, $cL = 1.1974$, $a = 0.003829$, $cT_1 = 30$, $cT_2 = 9$, $T_s = 20$, and $T_M = 10$ are all empirical constants that modulate photosynthesis and respiration as presented by Wilske et al. (2009).

The simulated rate of the daily CO_2 exchange of the crusted soils can be obtained from the following equation:

$$FS(w, t, l) = FS_p(t, l) \times \frac{f_p(w)}{\sum N_{pi}} \times N_p + FS_r(t) \times \frac{f_r(w)}{\sum N_{ri}} \times N_r. \quad (3)$$

The BSCs-related photosynthesis $f_p(w)$ and respiration $f_r(w)$ rates with soil moisture were determined by separate experiments from the previous researches and the regression equations were listed in Table 1. N_p and N_r are the BSCs-related effective wetting times, which are defined as the duration (daytime and nighttime hours) when the surface soil (BSCs and nearly active crust organisms were included) moisture content exceeds 1% of the volumetric water content (Belnap et al., 2005) that available for BSCs physiological processes and respiration. This corresponds to 0.73% of the gravimetric water content of the crustal soil in the Shapotou region (Li et al., 2012). $\sum N_{pi}$ and $\sum N_{ri}$ are the daily accumulative effective wetting times. Then the daily CO_2 flux was transformed to a unit for net carbon fixation of BSCs (A , $\text{g C}/\text{m}^2$). Thus, the annual carbon fixation is the sum of the carbon fixation in all days.

$$A = FS(w, t, l) \times 12(g/mol) \times 10^{-6} \times 3600. \quad (4)$$

Our BSCs carbon fixation model is similar to the precipitation-driven activity model (PdAM) by Wilske et al. (2009) but extended to the importance of non-rainfall pulses and the effective wetting time. And the activity periods of the BSCs-related effective wetting times are varied, depending on the amount and/or frequency of rain/humidity events, rather than using the empirical constants stated in Wilske's PdAM model (2009). Furthermore, the photosynthetic and respiration rates of BSCs are a function of soil moisture in our experiment. Thus, we need to model these variables in more detail (Eq. 3). By continuously monitoring the soil moisture dynamics, the daytime effective wet periods for BSCs carbon fixation were determined. Therefore, the daily and annual totals of carbon fixation were accurately estimated. Matlab 7.0 (The MathWorks, Natick, MA, USA) and Origin 7.0 (OriginLab, Northampton, MA, USA) software were used for the data simulation and analysis.

2 Results

2.1 Effects of BSCs on rainfall infiltration, soil moisture and soil temperature

During three years of continuous monitoring of soil water and soil temperature dynamics in moss and algae crusts, the amount of precipitation was 113.9, 189.8 and 195.3 mm in 2010, 2011 and 2012, respectively. Rainfall of 5–10 mm accounted for 80% of the total precipitation (Fig. 1a). In general, the infiltration depth was positively correlated with the one-off rainfall amount despite the crusts covering over the sand dunes. The approximate infiltration depths of the moss and lichen crusts were 1.56 and 1.75 cm for every 1 mm of rainfall. However, the presence of BSCs had little influence on infiltration when the one-off rainfall was close to or greater than 20 mm (Fig. 1b). The soil water volume within the moss crusts (1% to 1.5%) was slightly higher than that within algae crusts (0.8% to 1.3%) in the drought seasons, but the difference was not significant. However, such differences were dramatically altered on rainy days. To determine the influence of BSCs on soil moisture and soil temperature during various rainfall amounts, we examined two specific cases under natural conditions: soil moisture and soil temperature dynamics in moss and

algae crusts during a typical precipitation of 4.4 mm on 20 May 2011 (Fig. 1c) and 13.7 mm on 2 June 2011 (Fig. 1d). The soil water content for each rainfall event dramatically increased initially, and then decreased smoothly to a normal level. However, the rate of decline in the algae crusts was faster due to its low water holding capacity and high evaporation rate. Meanwhile, the growth rate in the algae crusts was approximately 2 to 3 times higher than that of the moss crusts within 3 to 5 days after the rainfall. The soil temperature changed regularly with the climate variations of the inter-annual time scale during the three-year observation period. However, at the daily time scale, the soil temperature had significant fluctuations and dynamics and was significantly lower in rainy days than in sunny days. Moreover, the temperature in the topsoil of the algae crusts was higher than that of the moss crusts because the darker algae crusts were expected to absorb more solar radiation than that the lighter moss crusts. However, the minimum temperature of the algae crusts was smaller than that of the moss crusts, which suggested a relatively larger amplitude range. Thus, the temperature of algae crusts varied greatly between day and night.

2.2 Model simulation

The simulation algorithm contained the data input and calculated results from Table 1 and Eqs. 1–2. The physiological and respiration active times of the BSCs were determined by using the soil water content threshold. The CO₂ fluxes were derived from Eq. 3. The annual carbon fixations of the two types of BSCs per unit area and time were simulated. The results are presented in Fig. 2. Positive values, which often occurred during daytime, revealed the carbon fixation of the BSCs, whereas negative values indicated CO₂ emission. A zero-value indicated that the carbon fixation was equal to the CO₂ emission. Therefore the two were approximately canceled out. Figure 2 indicated that the BSCs-related CO₂ flux was similar to the trend of soil moisture dynamics on an annual time scale. Moreover, the average CO₂ fluxes of moss crusts and algae crusts were 0.49 and 0.29 μmol/(m²·s), respectively. The daily simulated CO₂ fluxes of the BSCs were in a dormant state in which weak photosynthesis and respiration rates occurred during the drought days. However, in most rain-free days of the year, the simulation results revealed that the CO₂ flux

Fig. 1 Precipitation during January 2010 to November 2012 (a), the effects of different crusts on the infiltration depth (b) and dynamics of the soil moisture and soil temperature in response to typical precipitation of 4.4 mm on 20 May 2011 (c) and 13.7 mm on 2 June 2011 (d).

Fig. 2 The modeled net CO₂ fluxes of moss crusts and algae crusts from January 2010 to November 2012

of moss crusts was significantly larger than that of the algae crusts, most likely due to the non-rainfall water (e.g. dew, fog and condensation) in the early morning, which was absorbed by the moss crusts. This phenomenon was also confirmed by other researchers (Wilske et al., 2008; Li et al., 2009). High photosynthesis did not occur during the rainy days and often had a time delay of 1 to 2 days. Due to the evaporation of soil moisture, the activity of BSCs carbon sequestration gradually decreased. Therefore, the non-rainfall water stimulus plays a very important role in the carbon sequestration potential of the BSCs, especially in the arid desert regions. However, rainfall frequency and duration were not considered in the model. This shall be discussed in future studies.

The daily carbon fixation of the moss crusts was

greater than that of the algae crusts for most of the time during our experimental period (Fig. 3). Compared with the soil moisture dynamics shown in Fig. 1, the reasons may be attributed to the greater water-holding capacity that prolongs the available wetting time for photosynthesis. The mean carbon fixation rates of the two types of crusts from January 2010 to November 2012 were 0.21 and 0.13 g C/(m²·d), respectively, and the total carbon fixations were 194.8 and 115.7 g C/m², respectively. The annual carbon fixations of the moss crusts and algae crusts were 64.9 and 38.6 g C/(m²·a), respectively.

To test and verify the simulation results, we continuously measured the net CO₂ flux during the periods of 2010–2012 (Fig. 4). The model output of net photosynthesis matched the experiment data very well.

However, for both moss crusts and algae crusts, the modeled CO_2 fluxes were greater than the measured CO_2 fluxes. This was attributed to the definition of the effective wetting time, which not only depended on soil moisture but also depended on other factors (e.g. air temperature, humidity or light). For both types of crusted soils, the magnitude of the CO_2 variations was relatively larger in the rainy days (i.e. 5 mm precipitation on 7 June 2010, 4.8 mm precipitation on 25 June 2011 and 19.2 mm precipitation on 17 July 2012) than in the sunny days. The CO_2 fluctuations of algae crust were significantly greater than those of the moss crusts, which might be due to the soil physical characteristics that induced different soil water redistributions and rainfall infiltrations (Fig. 1). The average estimated daily carbon fixation rates of moss and algae crusts during the rainfall period were 0.31 and

0.19 $\text{g C}/(\text{m}^2\cdot\text{d})$, which were significantly higher than those values in the sunny days (0.05 and 0.02 $\text{g C}/(\text{m}^2\cdot\text{d})$) (Fig. 4). However, this difference was not significant during other rainfall intensity periods, such as the 5-mm precipitation on 7 June 2010 (daily carbon fixations of 0.32 and 0.20 $\text{g C}/(\text{m}^2\cdot\text{d})$ for moss crusts and algae crusts, respectively), and the 19.2-mm precipitation on 17 July 2012 (daily carbon fixation rates of 0.35 and 0.22 $\text{g C}/(\text{m}^2\cdot\text{d})$ for moss crusts and algae crusts, respectively). Thus, we concluded that there was not a significant increase in the carbon fixation as the rainfall intensity increased because the increased soil moisture not only triggered the BSCs photosynthesis but also the respiration. Therefore, the net carbon fixation of BSCs in the non-rainfall days requires extra attention and may play an important role in the annual BSCs carbon fixation.

Fig. 3 The daily modeled carbon fixations of moss crusts and algae crusts from January 2010 to November 2012

Fig. 4 The daily dynamics of the measured and modeled net CO_2 fluxes of moss crusts and algae crusts on 6–9 June 2010, 24–27 July 2011 and 17–21 July 2012

3 Discussion

The carbon fixation of BSCs is an important complementarity to the global carbon cycle in desert regions. In this study, an integrated dynamic modeling framework was established for investigating the daily and annual carbon fixations of BSCs. Based on the model estimations, the annual carbon fixations of moss and algae crusts were 64.9 and 38.6 g C/(m²·a), respectively, which were greater than those estimated for temperate Central European steppes (0.4 to 2.3 g C/(m²·a) for cyanobacteria BSCs and 12–37 g C/(m²·a) for lichen BSCs (Belnap et al., 2005), and 11.36 g C/(m²·a) for cyanobacteria-algae dominated crusts and 26.75 g C/(m²·a) for lichen-moss dominated crusts (Li et al., 2012).

The high carbon input of the BSCs in this study can be attributed to several factors. First, there were a high coverage of BSCs, a high proportion of mosses in the moss-dominated BSCs, and the appearance of several lichens with high carbon gains, such as *Collema tenax* in the algae-dominated BSCs (Li et al., 2012). In European steppe sites, the BSCs communities only colonize in plant-free interspaces (Evans and Lange, 2001). Thus, when we considered the total carbon input in different ecosystems, a coefficient of the BSCs area index should be implemented in certain study areas or be extrapolated to regional scales. Second, carbon fixation in winter seasons was not considered because the carbon gains and losses of crusted soils were always considered in balance proven by previous studies (Kappen, 1993; Belnap et al., 2005; Li et al., 2012). However, the photosynthesis and respiration rates of moss crusts can reach 0.91 and −0.75 μmol/(m²·s), respectively, in the Tengger Desert (Jia, 2009). So the net moss crusts related CO₂ flux was 0.16 μmol/(m²·s), which accounted for the 0.007 g C/(m²·d) carbon fixation rates that should not be ignored. The dark color of the algae crusts might make them and the underlying soils relatively warmer in the cold days, leading to more favorable temperatures for photosynthesis and hence a substantial amount of carbon fixation. And higher frequencies of rains during the winter have also displayed important synergisms for CO₂ deposition fluxes (Wilske et al., 2008). Third, the physiological active times differed in different studies. Researchers had their own evaluation methods, mainly

because of regional differences in climate or BSCs types (Li et al., 2012), and the amount, timing and intensity of precipitation are highly variable and create pulses of activity in soils and vascular plants that also vary on both spatial and temporal scales in arid desert areas (Sala and Lauenroth, 1982; Belnap et al., 2005). Jeffries et al. (1993) assumed 10 h of metabolic activity per day and 50 and 180 wet days per year in the *Scytonema*-dominated and *Microcoleus*-dominated crusts. Garcia-Pichel and Belnap (1996) assumed 100 h of activity during a winter season. Wilske et al. (2009) used precipitation records as the main factor for driving BSCs activity and obtained 992 h of BSCs activity, including 617 h of nighttime activity and 375 h of daylight activity between 2001 and 2002. In this study, a total of 922 days of BSCs carbon fixation were simulated from January 2010 to November 2012. The activity periods of moss crusts and algae crusts were 756 days (82% of the total) and 716 days (78% of the total). These values were much higher than those of previous studies; however, they varied with soil moisture dynamics. The range of carbon fixation rates for moss crusts and algae crusts were 0.002–0.509 and 0.0002–0.529 g C/(m²·d), and the averages were 0.26 and 0.19 g C/(m²·d), respectively.

The model discussed here was extremely simplified, and the physiological active time was obtained using a TDR method. Whether in wet or dry seasons, the total diurnal wet time is continuously counted until the BSCs moisture reaches the lowest limit of 1%. This method has the advantage of counting the wet times induced by non-rainfall events (e.g. fog or dew), but the times when the photosynthesis was inhibited at supersaturated water contents was limited. Using our model, the annual carbon fixations of moss crusts and algae crusts were 38.4 and 20.2 g C/(m²·a), respectively, without considering carbon fixation during the winter season. When combined with the study conducted by Li et al. (2012), which stated that carbon fixation was only driven by rainfall, it can be concluded that the carbon fixations by non-rainfall water reach 11.6 g C/(m²·a) for moss crusts (30.2% of the total) and 8.8 g C/(m²·a) for algae crusts (43.6% of the total), respectively. Given that the average daily dew on the BSCs was 0.37 mm in the research area and an amount within 0.03 mm could mark the threshold of dew availability for microorganisms (Kappen et al., 1979), the higher dew amount should be favorable to

the photosynthetic activity of the BSCs (Pan et al., 2010). This conclusion has also been verified by Lange et al. (1994), who estimated that the annual C gain for lichen crusts is $32 \text{ g C}/(\text{m}^2 \cdot \text{a})$ on foggy days when the rainfall is negligible. Thus, the effect of moisture on BSCs carbon fixation is versatile. Based on our field measurements, the modeled and measured CO_2 fluxes matched very well. Both datasets clearly showed that carbon fixation decreased as the moisture dropped, despite favorable temperature and light conditions. With sufficient soil moisture, rising temperatures increased carbon fixation values continuously and then stabilized after reaching a maximum value. However, the photosynthesis was virtually inhibited at supersaturated water content of crustal thallus (Li et al., 2012), so there should exist a threshold value for the BSCs related CO_2 flux under certain conditions (e.g. the interaction of different soil temperatures and soil moistures), under which the carbon fixation is optimized. Although the major carbon fixation occurred during the rainy period, it did not increase with the increasing one-off rainfall intensity. Thus, the carbon fixation was larger in the case of more frequent rainfall events when the value of the total seasonal rainfall volume is the same in desert regions. Therefore, BSCs carbon fixation should be estimated carefully if it is assumed to be fully concentrated in a wet season with constant or intermittent rain.

4 Conclusions

Assessment of BSCs contributions to carbon assimilation can improve scientific understanding of the carbon source-sink exchange in the revegetated desert ecosystem. In this study, we established a soil-driven carbon fixation model of BSCs based on the long-term continuous field measurements of soil moisture dynamics and laboratory studies of BSCs photosynthesis and respiration rates. The mean carbon fixation rates of moss crusts and algae crusts from January 2010 to November 2012 were 0.21 and $0.13 \text{ g C}/(\text{m}^2 \cdot \text{d})$, respectively, whereas the total carbon fixations were 194.8 and $115.7 \text{ g C}/\text{m}^2$, respectively. The carbon fixations of non-rainfall water reached $11.6 \text{ g C}/(\text{m}^2 \cdot \text{a})$ (30.2% of the total) and $8.8 \text{ g C}/(\text{m}^2 \cdot \text{a})$ (43.6% of the total) for moss crusts and algae crusts, respectively. The validity of the carbon fixation model was tested and verified with field measurements. The data of the

modeled and measured CO_2 fluxes matched notably well, and the carbon fixation was larger in the case of more frequent rainfall events than that having the same amount of total seasonal rainfall in desert regions. The results confirmed that BSCs in dry areas can have profound influence on the carbon balance between the atmosphere and the soil, which suggests that ecological restoration in desert ecosystems, especially for desertified areas impacted by sand burial, has great potential to contribute to the carbon input. And it also is of great ecological significance in the field that BSCs carbon fixation effects would become stronger as the precipitation events worldwide are predicted to become more frequent because of global climate changes.

Acknowledgements

This work was supported by the Knowledge Innovation Project of the Chinese Academy of Sciences (KZCX2-EW-301-3), the National Program on Key Basic Research Project (2013CB429905) and the National Natural Scientific Foundation of China (41201084; 31170385). Thanks to two anonymous reviewers for their suggestions and helpful comments.

References

- Belnap J, Lange O L, 2003. Biological Soil Crusts: Structure, Function, and Management. Berlin: Springer-Verlage, 3–30.
- Belnap J, Welter R, Grimm N B, et al. 2005. Linkages between microbial and hydrologic processes in arid and semiarid watersheds. *Ecology*, 86: 298–307.
- Beymer R J, Klopatek J M. 1991. Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands. *Arid Soil Research and Rehabilitation*, 5: 187–198.
- Bowker M A. 2007. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity. *Restoration Ecology*, 15: 3–23.
- Brostoff W N, Sharifi M R, Rundel P W. 2002. Photosynthesis of *cryptobiotic* crusts in a seasonally inundated system of pans and dunes at Edwards Air Force Base, western Mojave Desert, California: Laboratory studies. *Flora*, 197: 143–151.
- Brostoff W N, Sharifi M R, Rundel P W. 2005. Photosynthesis of *cryptobiotic* soil crusts in a seasonally inundated system of pans and dunes in the western Mojave Desert, CA: Field studies. *Flora*, 200: 592–600.
- Davey M C. 1997. Effects of continuous and repeated dehydration on carbon fixation by bryophytes from the maritime Antarctic. *Oecologia*, 110: 25–31.
- Evans R D, Lange O L. 2001. Biological soil crusts and ecosystem nitrogen and carbon dynamics. In: Belnap J, Lange O L. Biological Soil Crusts: Structure, Function, and Management. Berlin: Springer-Verlage, 263–280.

- Garcia-Pichel F, Belnap J. 1996. Microenvironments and microscale productivity of *cyanobacterial* desert crusts. *Journal of Phycology*, 32: 774–782.
- Garcia-Pichel F, Belnap J, Neuer S, et al. 2003. Estimates of global *cyanobacterial* biomass and its distribution. *Archive for Hydrobiology/Algological Studies*, 109: 213–227.
- Harley P C, Tenhunen J D, Murray K J, et al. 1989. Irradiance and temperature effects on photosynthesis of tussock tundra *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia*, 79: 251–259.
- Jeffries D L, Link S O, Klopatek J M. 1993. CO₂ fluxes of *cryptogamic* crusts I. response to resaturation. *New Phytologist*, 125: 163–173.
- Jia R L. 2009. Photosynthetic ecophysiological characteristics of moss crusts in a revegetated area of the Tengger Desert. PhD Dissertation. Beijing: Graduate School of Chinese Academy of Sciences.
- Kappen L, Lange O L, Schulze E D, et al. 1979. Ecophysiological investigations on lichens of the Negev Desert. IV. Annual course of the photosynthetic production of *Ramalina maciformis* (Del.) Bory. *Flora*, 168: 85–105.
- Kappen L. 1993. Plant activity under snow and ice, with particular reference to lichens. *Arctic*, 46: 297–302.
- Lange O L, Geiger I L, Schulze E D. 1977. Ecophysiological investigations on lichens of the Negev Desert. V. A model to simulate net photosynthesis and respiration of *Ramalina maciformis*. *Oecologia*, 28: 247–259.
- Lange O L, Kidron G J, Budel B, et al. 1992. Taxonomic composition and photosynthetic characteristics of the biological soil crusts covering the sand dunes in the western Negev Desert. *Function Ecology*, 6: 519–527.
- Lange O L, Meyer A, Zellner H, et al. 1994. Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. *Function Ecology*, 8: 253–264.
- Lange O L, Belnap J, Reichenberger H. 1998. Photosynthesis of the *cyanobacterial* soil-crust lichen *Collema tenax* from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO₂ exchange. *Function Ecology*, 12: 195–202.
- Lange O L. 2000. Photosynthetic performance of a gelatinous lichen under temperate habitat conditions: Long term monitoring of CO₂ exchange of *Collema cristatum*. *Bibliotheca Lichenologica*, 75: 307–332.
- Lange O L. 2003. Photosynthesis of soil-crust biota as dependent on environmental factors. In: Belnap J, Lange O L. *Biological Soil Crusts: Structure, Function, and Management*. Berlin: Springer-Verlag, 217–240.
- Li X R, Xiao H L, Zhang J G, et al. 2004. Long-term ecosystem effects of sand-binding vegetation in Shapotou region of Tengger Desert, northern China. *Restoration Ecology*, 12: 376–390.
- Li X R, He M Z, Stefan Z, et al. 2010. Micro-geomorphology determines community structure of BSCs at small scale. *Earth Surface Processes and Landforms*, 35: 932–940.
- Li X R, Jia R L, Chen Y W, et al. 2011. Association of ant nests with successional stages of biological soil crusts in the Tengger Desert, Northern China. *Applied Soil Ecology*, 47: 59–66.
- Li X R, Zhang P, Su Y G, et al. 2012. Carbon fixation by biological soil crusts following revegetation of sand dunes in arid desert regions of China: a four-year field study. *Catena*, 97: 119–126.
- Li X R, Zhang Z S, Huang L, et al. 2013. Review of the ecohydrological processes and feedback mechanisms controlling sand-binding vegetation systems in sandy desert regions of China. *Chinese Science Bulletin*, 58: 1483–1496.
- O'Neill A L. 1994. Reflectance spectra of microphytic soil crusts in semi-arid Australia. *International Journal of Remote Sensing*, 15: 675–681.
- Pan Y X, Wang X P, Zhang Y F. 2010. Dew formation characteristics in a revegetation-stabilized desert ecosystem in Shapotou area, Northern China. *Journal of Hydrology*, 387: 265–272.
- Pietrasiak N, Regus J U, Johansen J R, et al. 2013. Biological soil crust community types differ in key ecological functions. *Soil Biology and Biochemistry*, 65: 168–171.
- Sala O E, Lauenroth W K. 1982. Small rainfall events: an ecological role in semiarid regions. *Oecologia*, 53: 301–304.
- Saugier B, Roy J, Mooney H A. 2001. Estimations of global terrestrial productivity: converging towards a single number? In: Roy J, Saugier B, Mooney H A. *Global Terrestrial Productivity*. San Diego: Academic Press, 541–555.
- Schuh G, Heiden A C, Hoffmann T, et al. 1997. Emissions of volatile organic compounds from sunflower and beech: dependence on temperature and light intensity. *Journal of Atmospheric Chemistry*, 27: 291–318.
- Sonesson M, Gehrke C, Tjus M. 1992. CO₂ environment, microclimate and photosynthetic characteristics of the moss *Hylocomium splendens* in a subarctic habitat. *Oecologia*, 92: 23–29.
- Su Y G, Li X R, Chen Y W, et al. 2011. Carbon fixation of *cyanobacterial-algal* crusts after desert fixation and its implication to soil organic carbon accumulation in desert. *Land Degradation and Development*, 24: 342–349.
- Su Y G, Li X R, Qi P C, et al. 2012. Carbon exchange responses of *Cyanobacterial-Algal* crusts to dehydration, air temperature, and CO₂ concentration. *Arid Land Research and Management*, 26: 44–58.
- Wilske B, Burgheimer J, Karnieli A, et al. 2008. The CO₂ exchange of biological soil crusts in a semiarid grass shrubland at the northern transition zone of the Negev desert, Israel. *Biogeosciences*, 5: 1411–1423.
- Wilske B, Gurgheimer J, Maseyk K, et al. 2009. Modeling the variability in annual carbon fluxes related to biological soil crust in a Mediterranean shrubland. *Biogeosciences Discussion*, 6: 7295–7324.
- Zotz C G, Schweikert A, Jetz W, et al. 2000. Water relations and carbon gain are closely related to cushion size in the moss *Grimmia pulvinata*. *New Phytologist*, 148: 59–67.