Analysis of environmental factors determining development and succession in biological soil crusts

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HIGHLIGHTS
• There is heterogeneity in crust development and succession in the different regions.
• K, Na, silt contents and prior biomass accumulation mainly affect lichen emergence.
• Early crusts and water holding content provide the guarantee for moss germination.
• A positive feedback mechanism forms between crust development and soil environments.
• A negative feedback mechanism forms between free living algae and crust succession.

ABSTRACT

Biological soil crusts play important ecological functions in arid and semi-arid regions, while different crust successional patterns appeared in different regions. Therefore in this study, the environmental conditions between Shapotou (with cyanobacterial, lichen and moss crusts) and Dalate Banner (with only cyanobacterial and moss crusts) regions of China were compared to investigate why lichen crusts only appeared in Shapotou; at the same time, artificial moss inoculation was conducted to find out the environmental factors promoting crust succession to moss stage. The results showed lichen crusts always developed from cyanobacterial crusts, which provide not only the stable soil surface, but also the biomass basis for lichen formation; furthermore, addition of crust physicochemical characteristics (primarily silt content) play a facilitating effect on lichen emergence ($R^2 = 0.53$). The inoculation experiment demonstrated early crust soil surface and enough water holding content (>4%) provided the essential guarantee for moss germination. Our results show that there is heterogeneity in crust succession in different regions, which may be mainly affected by the ambient soil microenvironments. It is concluded that a positive feedback mechanism is expected between crust succession and ambient soil microenvironments; while a negative feedback mechanism forms between crust succession and free living cyanobacteria and algae.

1. Introduction

In arid and semi-arid regions, many types of vegetation are restricted to the severe environmental conditions, while biological soil crusts (BSCs) appear commonly there, and even occupy more than 70% of the
living coverage in some regions (Eldridge and Greene, 1994; Belnap and Lange, 2001; Hu et al., 2012). BSCs are the complex biological-soil mosaic layers within the top millimeters of soil surface, composed of photoautotrophic cyanobacteria, algae, lichens, mosses and heterotrophic bacteria and micro-fungi (Belnap and Lange, 2001; Hu and Liu, 2003; Lan et al., 2012a). As the special life beings, BSCs play important ecological functions in desert ecosystems, such as effectively reducing soil erosion, promoting soil formation, changing soil water and nutrient cycling (Hu et al., 2002; Acea et al., 2003; Lan et al., 2010a). Furthermore, BSCs also influence the establishment and performance of higher plants, the distribution and behavior of soil animals, and even development and succession of the whole soil ecosystem (Belnap and Lange, 2001; Hu and Liu, 2003; Bowker et al., 2010). Collectively BSCs perform significant ecosystem services, however, the different crust developmental levels or successional stages still affect those services. At present, based on the difference of dominant organisms, BSCs are generally categorized into three different successional stages along with the developmental sequence, including: cyanobacterial, lichen and moss crusts (Housman et al., 2006; Su et al., 2009; Wu et al., 2011; Lan et al., 2012a).

In a desert ecosystem, once the soil surface is stabilized, BSCs will begin to develop (Brostoff, 2002; Stradling et al., 2002; Kidron et al., 2008). Cyanobacterial crusts form firstly due to the special performance of the filamentous cyanobacteria, including relatively rapid growth, migration, and their extraordinary adaptation ability to the extreme environmental conditions (Zaady et al., 2000; Garcia-Pichel and Pringault, 2001; Zhang et al., 2006; Lan et al., 2010b). Cyanobacterial crusts normally represent a primary successional stage of BSCs; however, they can facilitate crust succession to the later stages due to their ability in improving soil microenvironments and enhancing the probability of survival of later successional species (Acea et al., 2003; Hu and Liu, 2003; Kidron et al., 2008; Langhans et al., 2010). In a crust soil microsystem, the life activities of various crust organisms would inevitably lead to the continuous development of BSCs, and eventually lead to the succession. Early successional cyanobacterial crusts are light in color, with a small part of fine particles, low protective ability to water and wind erosion, poor nutrients and water retention (Housman et al., 2006; Lan et al., 2010a,b). With crust development and succession, dark-colored lichens or mosses later colonize the soil surface (Lange et al., 1992; Zaady et al., 2000; Lan et al., 2010a). Compared with cyanobacterial crusts, later successional lichen or moss crusts have the higher biological metabolic efficiency and protective ability; hence better topsoil microenvironments are expected in the later BSCs (Castañholz and García-Pichel, 2000; Redfield et al., 2002; Housman et al., 2006).

It has been proposed that crust successional pathways would be affected by many environmental factors, such as radiation intensity, topographic traits, soil structure and types (Zaady et al., 2000; Lan et al., 2012a); limited availability of resources (such as water, nutrients, and space) would stop the successional progress at a certain stage (Pickett and McDonnell, 1989; Zaady et al., 2000). Based on our previous observations, in Shapotou region (at the southeastern edge of Tengger Desert) BSCs generally succeed from cyanobacterial crusts to lichen and moss crusts along a pathway of “cyanobacterial crusts, cyanobacterial-lichen crusts, lichen crusts, lichen-moss crusts and moss crusts” (Lan et al., 2012a, 2013). However in Dalate Banner region (mainly in Jiefangtan; at the eastern edge of Qubqi Desert), BSCs directly succeed from cyanobacterial crusts to moss crusts (Lan et al., 2012b, 2014). As a whole, three different successional stages including cyanobacterial, lichen and moss crusts are found in Shapotou region, while only cyanobacterial and moss crusts appear in Dalate Banner region. Therefore in order to investigate why lichen crusts only occur in Shapotou region, instead of Dalate Banner region, further to understand the mechanism about crust development and succession, the climate and soil characteristics between Shapotou and Dalate Banner regions were compared in this study. In addition, via artificially inoculating moss plants onto different environmental conditions, this study would also particularly reveal the environmental driving factors about BSCs succeeding to moss crusts. The results will not only help us understand the development, succession and ecological adaptation of BSCs in desert environmental conditions, but also provide some useful information for the maintenance and management of BSCs in desertification control.

2. Materials and methods

2.1. Experimental regions

The experimental regions of this study include Shapotou and Dalate Banner regions (Fig. 1). The climate and vegetation conditions in those regions are listed in Table 1, in which all the data are cited from the reports of Hu and Liu (2003), Li et al. (2004) Xie et al. (2007), Jia et al. (2008), Rao et al. (2009), Lan et al. (2010a) and Li et al. (2010).

In Shapotou region, to insure the smooth operation of the Baotou–Lanzhou railway through the sand dune area, a 16 km long by 0.7 km width (0.5 km on the north side and 0.2 km on the south side of the railway) vegetation protective system was established in 1956 by setting up sand barrier and erecting straw checkerboard. Once the sand surface had been stabilized, xerophytic shrub species were planted in the sand barrier squares, such as Artemisia ordosica, Caragana koshinskii and Hedysarum scoparium. Half a century had elapsed when our experiment was conducted; the environment of this region had been improved, and substantial BSCs had covered more than 80% of soil surface, including cyanobacterial (about 10%; dominated by Microcoleus vaginatus), lichen (50–60%; dominated by Collema sp.) and moss crusts (20–30%; dominated by Bryum sp.; Li et al., 2003; Hu et al., 2004; Wu et al., 2011).

In Dalate Banner region, to accelerate the formation and recovery of BSCs, two mixed filamentous cyanobacteria (M. vaginatus Com. and Scytonema javanicum (Kütz) Born et Flah.) were mass cultured and spray-inoculated (10: 1 w/w) onto the shifting sand dunes in 2002, where sand barriers of straw checkboards (1 m × 1 m) or Salix mongolica had been previously set up. After cyanobacterial inoculation, the sandy soil was irrigated with groundwater for 1–2 weeks. More than 7 years elapsed since the cyanobacterial inoculation, the environment in this restored region had been much improved at this experimental time, and the established BSCs (more than 80% in coverage) included cyanobacterial (60–70%; dominated by M. vaginatus) and moss crusts (20–30%; dominated by Didymodon sp.; Xie et al., 2007; Rao et al., 2009; Lan et al., 2012b).

2.2. Sampling

BSCs in the two experimental regions were sampled in June 2009, and the sampling regions had not received any rainfall in the past 72 h. Intact BSCs including different developmental and successional stages (Table S1) were randomly collected from the interspaces between shrubs (0.2 m away from the shrubs). Before the sampling, cracking sections were first made in BSCs, and then pieces of crusts in their natural thickness (4–15 mm; without the soil beneath) were carefully sampled along the polygonal cracking sections with a sharp shovel. Each piece of crusts was collected as 10–20 cm² and placed into the sterilized plastic Petri-dishes (or paper bags). The samples were then carried to the laboratory as soon as possible, air dried in shade condition and kept in desiccators for subsequent analysis. For each crust developmental and successional stage, at least three independent crust samples were prepared for replication.

2.3. Crust biomasses

Before the determination of fungal biovolume and microbial (including bacterial and fungal) CFU (colony forming units), the crust samples were first passed through 0.1 mm (pore size) sieve, and then 0.1 g of each sample was diluted in 10 ml sterile distilled water.
For the determination of fungal biovolume, 0.1 mL of the crust–water mixture was directly observed with a microscope, then the biovolume of fungal hyphaes were recorded and expressed as mm³ g⁻¹ crusts (Hu and Liu, 2003). For the determination of microbial CFU, a certain amount of crust–water mixture was inoculated on Beef extract-peptone and Martin’s mediums respectively to cultivate bacterial and fungal colonies (1.5% agar; Eiken, Tokyo, Japan). Then bacterial and fungal inoculations were placed at 37 °C and 28 °C (±2 °C) respectively. Three to 5 days later, the microbial colonies were counted and expressed as CFU g⁻¹ crusts (Lan et al., 2013).

Chl-a content was taken as a measure of photosynthetic biomass in our experiment, and Chl-a content determination was conducted according to the description of Lan et al. (2011). For lichen and moss crusts, two subsamples were prepared respectively. In one set of subsamples, lichen thalli and moss plants were removed, and the other reserved. Chl-a content of the two subsamples respectively represented the free-living cyanobacterial and algal biomass and total photosynthetic biomass. In addition, the relative coverages of lichens and mosses were visually estimated on the sampled crust surface, as described by Wu et al. (2011).

2.4. Physicochemical characteristics

Crust physical properties including crust thickness, texture and water content were measured by the standard methods described by Lan et al. (2010a, 2012a) and Rao et al. (2012). Crust total organic carbon (TOC), total nitrogen (TN) and total phosphorus (TP) were also measured with the standard soil analysis methods described by Nanjing Institute of Soil Research, Chinese Academy of Sciences (1980) Crust pH and electrical conductivity (EC) were measured in...
were scattering-inoculated (0.05 m² moss crusts m⁻²) isolate moss plants from soil substrate. Then the isolated moss plants were collected and passed through 0.1 mm (pore size) sieve. Cyanobacterial crusts (the collected cyanobacterial crusts from shifting sand); 3) shifting sand. After inoculation, the experimental plots and treatments designed for inoculating moss plants in each experimental site. Three different colors indicated the three different inoculating habitats, in which path coefficients and R² were evaluated using AMOS 17.0 software.

### 2.5. Artificially inoculating moss plants

This part of experiment was conducted on shifting sand of Dalate Banner region. Before the experiment, the local moss crusts were collected and passed through 0.1 mm (pore size) sieve firstly to isolate moss plants from soil substrate. Then the isolated moss plants were scattering-inoculated (0.05 m² moss crusts m⁻² plot) onto the following three habitats: 1) cyanobacterial crusts (transplanted from crust covered areas before this experiment); 2) crumbled cyanobacterial crusts (the collected cyanobacterial crusts from crust covered area were firstly passed through 0.1 mm sieve, and then the sieved and crumbled crust soil was evenly scattered to the similar area of shifting sand); 3) shifting sand. After inoculation, each habitat was dealt with three treatments including Watering and canopied, Watering but no canopied and No watering and canopied, in which canopy was carried out by covering a black nylon net (about 50 cm over the ground) over the experimental spot. In each experimental site, 9 plots were designed as shown in Fig. 2, and each plot was enclosed independently. Since the moss plants were inoculated, the watering groups (including treatments Watering and canopied and Watering but no canopied) were irrigated with 20 mm groundwater once every other day at about 17:00. The next day after watering, the surface temperature and light intensity in each treatment were measured synchronously during an intensive observation period at 2 h intervals. After about 24 h since from the watering, the water content of topsoil (water holding content) in each treatment was measured according to the methods described by Lan et al. (2010a, 2012a). One month later, watering was stopped, and the moss coverage was estimated in each plot after 3 months of inoculation. In this part of experiment, total three experimental sites (27 plots) were randomly chosen for replication.

### 2.6. Data analysis

Variance of each parameter among different crust types or experimental treatments was analyzed by One-way ANOVA at 95% using SPSS 13.0 software. The relationships between emergence of lichens or mosses and associated environmental conditions were constructed in causal models, in which path coefficients and R² were evaluated using AMOS 17.0 software.

### Table 1

Comparison of climate and vegetation conditions between Shapotou and Dalate Banner regions.

<table>
<thead>
<tr>
<th></th>
<th>Shapotou</th>
<th>Dalate Banner</th>
</tr>
</thead>
<tbody>
<tr>
<td>Desert</td>
<td>Tengger Desert</td>
<td>Qubej Desert</td>
</tr>
<tr>
<td>Latitude and longitude</td>
<td>37°32’N, 105°02’E</td>
<td>40°21’N, 109°51’E</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>1339</td>
<td>1040</td>
</tr>
<tr>
<td>Climate</td>
<td>Typical continental monsoon pattern</td>
<td>Typical continental monsoon pattern</td>
</tr>
<tr>
<td>Mean annual precipitation (mm)</td>
<td>About 180</td>
<td>240–300</td>
</tr>
<tr>
<td>Mean annual evaporation (mm)</td>
<td>About 2800</td>
<td>About 2400</td>
</tr>
<tr>
<td>Average, lowest and highest air temperatures (°C)</td>
<td>10.0; –25.1; 38.1</td>
<td>6.1; –34.3; 40.2</td>
</tr>
<tr>
<td>Average wind velocity (m s⁻¹)</td>
<td>2.9</td>
<td>3.3</td>
</tr>
<tr>
<td>Wind day (&gt;5 m s⁻¹)</td>
<td>About 200</td>
<td>&gt;180</td>
</tr>
<tr>
<td>Relative high-variation (m)</td>
<td>15–20</td>
<td>About 5</td>
</tr>
<tr>
<td>Average groundwater depth (m)</td>
<td>&gt;0.60</td>
<td>2–4</td>
</tr>
<tr>
<td>Vegetation coverage (%)</td>
<td>20–30</td>
<td>30–60</td>
</tr>
<tr>
<td>Dominant plants</td>
<td>Artemisia ordosica, Bassia dasyphylla, Corispermum spp., Eragrostis poroides and Salsola spp.</td>
<td>Agriophyllum squarrosum, Artemisia spp., Astragalus adsurgens, Corispermum hyssopifolium, Leymus chinensis and Salix mongolica</td>
</tr>
</tbody>
</table>

### 3. Results

#### 3.1. Comparison of climate conditions and soil characteristics between the two experimental regions

As already pointed out, the BSCs included cyanobacterial, lichen, and moss crusts in Shapotou region; while in Dalate Banner region, no lichen crusts were found by now, and cyanobacterial crusts directly succeeded to moss crusts in some microhabitats (Fig. 1). Although different crust successional models appeared, climatic conditions are similar between the two experimental regions (Table 1), belonging to the typical continental monsoon climate zone, with largely fluctuated air temperature. Windy days (wind velocity > 5 m s⁻¹) occur more than half a year, and sand storms or blowing dusts occur predominantly in spring. In these regions, generally annual precipitation is very little (less than 300 mm) and uneven, falling predominantly between July and September, while the annual potential evapotranspiration is more than 2000 mm, although...
it was recorded as the mean ± standard deviation of triplicates, and the different superscript letters indicate the differences are significant at 0.05 level (*P < 0.05).

Table 2
Comparison of soil physicochemical characteristics between Shapotou and Dalate Banner regions.

<table>
<thead>
<tr>
<th>Locations</th>
<th>Shapotou</th>
<th>Dalate Banner</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil types</td>
<td>Shifting sand</td>
<td>Algae crusts</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water content (%)</td>
<td>0.23 ± 0.02 **</td>
<td>0.40 ± 0.05 ab</td>
</tr>
<tr>
<td>Crust thickness (mm)</td>
<td>0 a</td>
<td>4.73 ± 0.65</td>
</tr>
<tr>
<td>Sand (%)</td>
<td>99.49 ± 0.05 a</td>
<td>86.90 ± 2.58 c</td>
</tr>
<tr>
<td>Silt (%)</td>
<td>0.34 ± 0.04 a</td>
<td>12.63 ± 2.44 c</td>
</tr>
<tr>
<td>Clay (%)</td>
<td>0.17 ± 0.00 d</td>
<td>0.48 ± 0.15 c</td>
</tr>
<tr>
<td>TOC (g kg⁻¹)</td>
<td>0.48 ± 0.02 a</td>
<td>6.28 ± 1.53 a</td>
</tr>
<tr>
<td>TN (g kg⁻¹)</td>
<td>0.16 ± 0.04 b</td>
<td>0.57 ± 0.10 a</td>
</tr>
<tr>
<td>TP (mg kg⁻¹)</td>
<td>0.03 ± 0.00 a</td>
<td>0.14 ± 0.02 a</td>
</tr>
<tr>
<td>pH</td>
<td>7.65 ± 0.01 ab</td>
<td>7.60 ± 0.09 a</td>
</tr>
<tr>
<td>EC (ms cm⁻¹)</td>
<td>0.05 ± 0.00 a</td>
<td>0.24 ± 0.01 bc</td>
</tr>
<tr>
<td>K (mg kg⁻¹)</td>
<td>203.79 ± 0.80 a</td>
<td>222.43 ± 2.80 b</td>
</tr>
<tr>
<td>Na (mg kg⁻¹)</td>
<td>33.37 ± 0.77 a</td>
<td>47.85 ± 0.52 b</td>
</tr>
<tr>
<td>Ca (mg kg⁻¹)</td>
<td>398.02 ± 10.0 a</td>
<td>567.25 ± 15.4 a</td>
</tr>
<tr>
<td>Mg (mg kg⁻¹)</td>
<td>30.73 ± 1.71 a</td>
<td>32.65 ± 0.19 a</td>
</tr>
<tr>
<td>Mn (mg kg⁻¹)</td>
<td>30.08 ± 3.95 a</td>
<td>60.00 ± 3.74 b</td>
</tr>
</tbody>
</table>

*Data are represented as mean ± standard deviation of triplicates, and the different superscript letters indicate the differences are significant at 0.05 level (*P < 0.05).
41.88% compared with the situations in the other two groups (Fig. 4A). As a result, the water content in Watering and canopied group was highest, and significantly higher than that in the other two groups ($P < 0.05$; Fig. 4B). In other words, sole watering could not significantly improve soil water condition in the long period. Therefore moss plants only well germinated on cyanobacterial crusts in Watering and canopied group, where the moss coverage accounted for 32.27 ± 1.36% of soil surface after 3 months of inoculation, significantly higher than the coverage in other cases ($P < 0.05$). In Watering but no canopied group, although moss plants could germinate on the cyanobacterial crusts, the moss coverage was still very low after 3 months of inoculation (about 1%). While in the group No watering and canopied, no moss plants germinated yet 3 months later (Fig. 4C).

The relationship between moss emergence and associated environmental conditions was given in the causal model (Fig. 3B), which can explain nearly half of variance in moss emergence ($R^2 = 0.45$). From the model, it was also found early crusts were important for the emergence of mosses. In addition, both canopy and watering indirectly facilitated the emergence of mosses on crust surface via improving soil water condition, which promoted the emergence of mosses more directly.

3.4. Biomass change with crust development and succession

In Shapotou region, lichen thalli firstly emerged on cyanobacterial crusts, although this stage might not be recognized with the naked eyes (Lan et al., 2012a). With the reproduction of lichens and increase of lichen coverage, BSCs succeeded to lichen crusts. The lichen crusts in Shapotou region were dominated by Collema tenax at present and interspersed on the soil surface with an obvious dark discoloration, up to 60–70% coverage in some areas during the dry periods, and even 100% coverage when the soil surface was moistened. In addition, cyanobacterial and algal biomass (including the free-living and symbiotic) and also fungal biomass (including the free-living and symbiotic) increased significantly from cyanobacterial crusts to lichen crusts ($P < 0.05$; Fig. 5A), although the free-living cyanobacteria and algae and cultured microbial CFU decreased about 41% and 35% respectively (data in Lan et al., 2013). Moss crusts in Shapotou region developed and succeeded from either cyanobacterial crusts or lichen crusts, and the biomass change during those developmental courses has been given in our previous report (Lan et al., 2013).

In Dalate Banner region, after inoculating the two filamentous cyanobacteria, cyanobacterial crusts formed quickly and gradually...
succeed to moss crusts on the shady side of dunes 2–3 years later (Lan et al., 2012b). With the development and succession from cyanobacterial crusts to moss crusts, moss coverage gradually increased, photosynthetic biomass and microbial CFU also increased significantly ($P < 0.05$), while cyanobacterial and algal biomass decreased ($P < 0.05$; Fig. 5B).

4. Discussion

In desert regions, such as Shapotou and Dalate Banner regions, once BSCs have formed, their development and succession would be a natural process, which generally begins from the stage of cyanobacterial crusts (Eldridge and Greene, 1994; Zaady et al., 2000; Garcia-Pichel and Pringault, 2001; Zhang et al., 2006). As the special crust type in Shapotou region, lichen crusts develop and succeed from cyanobacterial crusts, and that process might include two stages of lichen emergence and reproduction. Our results showed that some soil characteristics including K, Na and silt contents are significantly different between Shapotou and Dalate Banner regions. Therefore, we speculate K, Na and silt contents are most likely to be the important factors affecting lichen emergence, although it cannot be excluded the emergence of lichens promoting the increase of K, Na and silt contents in crusts. That silt content is a limiting factor for lichen emergence may be due to the following two reasons: 1) on the one hand, fine particles provide a source of nutrition for some crust lichens (Danin et al., 1989; Kidron et al., 2008); 2) on the other hand, the silt can adsorb more moisture (Lan et al., 2012a), which provides a more suitable water environment for the emergence of lichens. Both K and Na contents restricting the emergence of lichens may be because these ions play an important role in regulating water content of lichen thalli (Stocker-Wörgötter and Türk, 1991). In addition, in other researches it has been reported that Mn and Zn (DTPA extracted) may also be the important limited nutrients for some lichen species (Bowker et al., 2005, 2006), while higher P availability and CaCO$_3$ support lower lichen coverage (Bowker et al., 2006).

Other researchers’ and our results demonstrated that lichen crusts always developed and succeeded from cyanobacterial crusts (Eldridge and Greene, 1994; Lan et al., 2012a). And it was proposed that the stabilized soil surface and abundant nutrients might be the main causes that lead to the emergence of lichens (Eldridge and Greene, 1994; Bowker et al., 2005). Our results showed that cyanobacterial crusts might also provide an important biological basis for the emergence of lichens, such as fungal, cyanobacterial and algal biomass. In the long-time experiment of Belnap (1993), little cyano-lichen Collema established in the plots where BSCs had been ‘scraped’ 9 years ago, although the abundant lichen propagule source was just 0.25 m away. Davidson et al. (2002) suggested the poor colonization of Collema on thescraped plots might be because the environment for Collema was somehow more favorable with abundant cyanobacteria and their fibers present. During the course of artificial constructing cyano-lichen Pettiglera praetextata, Stocker-Wörgötter and Türk (1991) also found the lichens formed after the sufficient growth of cyanobacteria and fungi, which might be because the enough cyanobacterial and fungal biomasses provided a guarantee for the interaction between cyanobacteria and fungi.

Once lichens have emerged, lichen reproduction would promote the succession from cyanobacterial crusts to lichen crusts. During that process, both cyanobacterial and algal biomass and also fungal biomass (include the free living and the symbiotic) further accumulate, although the free living cyanobacterial and algal biomass has been demonstrated to decrease (Lan et al., 2012a). The increased photosynthetic biomass result in substantial carbon (C) fixation into the soil layer, increasing the soil organic matter, and some increased nitrogen-fixing species such as Scytonema and Nostoc fix nitrogen (N) into the soil, providing the necessary soil N resource (Lan et al., 2012b, 2013). In addition, those increased crust organisms also promote the conversion of sand into soil by increasing soil nutrients and improving topsoil texture (Hu and Liu, 2003; Lan et al., 2012a). As a return, the improved micro-environments further promote the development and succession from cyanobacterial crusts to lichen crusts, and thus a positive feedback mechanism is expected.

As the later successional stage of BSCs, moss crusts develop and succeed from either cyanobacterial crusts or lichen crusts (Lan et al., 2012a), and also some studies reported that in artificially controlled conditions, mosses could directly emerge on the sandy soil surface (Xu et al., 2008), but as we know no such phenomenon has been found in the field. In our experiment of artificially inoculating moss plants in Dalate Banner region, it was found that mosses could only emerge on cyanobacterial crusts, which represented a stable soil surface with a higher compressive strength. Cyanobacterial crusts in our inoculation experiment or lichen crusts elsewhere, with the uneven or coarse crust surface, could successfully intercept moss plants (sometimes maybe only some moss spores) on the soil surface, avoiding the moss plants being blown away. Then the trapped and intercepted moss plants would germinate on crust surface under adequate water conditions, such as Watering and canopied group in our experiment. In Watering but no canopied group, although at beginning topsoil gained the same water content, moss plants did not get enough water for germination due to the rapid evaporation resulting from the higher solar radiation, consistent with the field observation (Kidron et al., 2008; Lan et al., 2014).

Mosses reproduce and extend mainly by mean of dispersal of moss plants or spores. When the dense mosses dominate crust surface, BSCs succeed to moss crusts. At this time, as the important photosynthetic taxa, mosses contribute most of the crust photosynthetic and also total biomass (Büdel et al., 2008; Lan et al., 2012a, 2013). With the emergence and reproduction of mosses, crust photosynthetic biomass increased gradually, further fixing more carbon (C) into the soil layer and increasing the soil organic matter. Although the biomass of nitrogen-fixing species such as Scytonema and Nostoc decrease at this stage (Redfield et al., 2002; Lan et al., 2012b), moss crusts have accumulated enough soil N resource, which even is higher than that in previous crust stages. In addition, the carpet-like coarse surface of moss crusts captures more dusts with rich nutrient substances, and moss multi-celled rhizoids interweave together with each other forming the web structure, intercepting more fine soil particles to form the thicker crusts, in which soil texture became finer with an increasing nutrient and water content. Those improved environmental conditions promote the growth of bacteria and fungi (Rao et al., 2009), further improving the microenvironments, which in turn promote the reproduction of mosses and accelerate the development and succession to moss crusts, thus forming another positive feedback mechanism.

Except for the soil microenvironments, climate and also vegetation appeared to have an effect on crust development and succession, because different crust species response variously to those influencing factors (Belnap et al., 2006; Bowker et al., 2006), among which some factors may directly affect crust metabolism (eg. solar radiation, although radiation also changes soil temperature and water content), while the others affect BSCs via changing the ambient soil microenvironments, such as soil water availability. Comparing the climate and vegetation conditions between our two experimental regions, the higher water availability is expected in Dalate Banner region, because the higher annual precipitation, lower evaporation rate, shallower groundwater depth and higher vegetation coverage (canopy decreasing the evaporation induced by solar radiation) were found there. All those conditions facilitate crust succession to the late moss stage, therefore in Dalate Banner region BSCs likely succeed to moss crusts more easily, which may also affect the development of lichen crusts there to some extent.

5. Conclusions

BSCs widely distribute in arid and semi-arid regions and perform vital ecological services there. In this study crust successional patterns between Shapotou and Dalate Banner regions of China were compared, and the environmental factors determining crust succession
were analyzing. As the pioneer and colonizer of BSCs, cyanobacteria and algae fix carbon and nitrogen into crust soil through photosynthesis and nitrogen fixation. At the same time they improve other crust characteristics (such as Na, silt and water contents) through a variety of metabolic activities. All those facilitate the emergence of lichens or mosses and succession from cyanobacterial crusts to lichen or moss crusts. As a return, the emergence of lichens and mosses on the one hand further improves the soil microenvironments, and thus accelerates crust succession to later lichen or moss stages, forming a positive feedback mechanism; on the other hand deprives free living cyanobacterial and algal living spaces and restricts the movement of cyanobacterial and algal cells, leading to the decrease of free living cyanobacterial and algal biomass, forming a negative feedback mechanism.

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Appendix A. Supplementary data

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References