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ORIGINAL PAPER

Microalgal species variation at different successional stages in biological soil crusts of the Gurbantunggut Desert, Northwestern China

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Abstract Biological soil crusts (BSC), most notably lichen crusts, develop and diversify in the Gurbantunggut Desert, the largest fixed and semi-fixed desert in China. Four different successional stages of BSC, including bare sand, microalgal crusts, lichen crusts, and moss crusts, were selected to determine successional changes in microalgal species composition and biomass and formation of BSC. A 10×10-m observation plot was established in an interdune region of the Gurbantunggut Desert and data were collected over an 8-year study period. The main results were: (1) different successional stages of BSC significantly affected the content of soil organic C and total and available N but not the total and available P and K content of soil; (2) composition of microalgal communities differed among the four successional stages; (3) significant differences in microalgal biomass were observed among the four successional stages; (4) bare sand was mainly uncompacted sand gains; (5) filamentous cyanobacteria, particularly *Microcoleus vaginatus*, were the dominant species in the early phase of crust succession. The presence of fungal mycelium and moss rhizoids prevented water and wind erosion.

Keywords Gurbantunggut Desert · Biological soil crusts · Successional stages · Microalgal crusts

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Introduction

Biological soil crusts (BSC) present unique soil communities of arid and semi-arid environments and show different physical, chemical, and biological properties with respect to those of the uncompacted sand (Belnap et al. 1994; West 1990; Zhang 2005). A variety of studies have indicated that BSC are widely represented in many desert environments and can withstand harsh conditions such as drought, extreme temperatures (up to 70°C), and high pH (Belnap 1995; Belnap and Gardner 1993; Chen et al. 2005). BSC play an important role in the biogeochemistry and geomorphology of arid regions (Evans and Belnap 1999). They reduce soil erosion, contribute to the content of organic carbon, may fix nitrogen, and either promote or retard the survival and growth of vascular plant seedlings (Bhatnagar et al. 2008).

Microalgae in BSC have attracted considerable attention due to their importance in the desert ecosystem and as aquatic organisms living in such a dry hostile environment (Grondin and Johansen 1995). They play a significant role in reducing wind and water erosion, retarding water, and promoting soil succession (Booth 1941; Johansen 1993; Mazor et al. 1996). In addition, microalgal crusts can improve soil structure and soil fertility by excreting extracellular substances and retaining soil moisture and can resist salt stress (Bowker and Belnap 2004; Mazor et al. 1996; Xie et al. 2007). Most of studies on microalgae

in the deserts have focused primarily on classification (Cardon et al. 2002; Flechtner 1999; Tirkey and Adhikary 2006), species composition (Flechtner et al. 1998; Hawkes and Flechtner 2002), ecology (Bhatnagar et al. 2008; Fritz-Sheridan 1988; Hu et al. 2003), sand fixation abilities (Chen et al. 2006; Xie et al. 2007), physiology (Gray et al. 2007; Pandey et al. 1992), and molecular biology (Billi et al. 1998; Redfield et al. 2002). Additional works have addressed BSC recovery patterns after disturbance (Eldridge and Greene 1994; Yamano et al. 2006; Zhang et al. 2007). Eldridge and Greene (1994) identified three types of BSC (cryptomorphic, perimorphic, and hypermorphic crusts). Redfield et al. (2002) examined cyanobacterial diversity and species community composition in three types of predominant soil crusts using terminal restriction fragment length polymorphism analysis and 16 S rDNA sequence analysis. Variation of nitrogen fixation in different types of BSC has been also investigated in some desert areas (Belnap 2002) as well as the carbon and nitrogen content of different successional stages of BSC (Housman et al. 2006). However, to our knowledge, little is known about the successional changes in species composition and microalgal biomass during the development of BSC.

The purpose of this study was to elucidate the species composition and roles of microalgae in different BSC successional stages in the Gurbantunggut Desert, so as to better understand the formation of BSC in desert environments, which can lead to the use of BSC for preventing desertification.

Materials and methods

Study area, field site, and sampling

The Gurbantunggut Desert, located in the center of the Jungger Basin (44° 11′–46° 20′ N, 84° 31′–90° 00′ E), Xinjiang Uygur Autonomous Region of China, is the largest fixed and semi-fixed desert in China, occupying an area of 488,000 km^2. Because of the rain shadow effect of the Himalayan Range, moist air currents from the Indian Ocean fail to reach the area, and thus mean annual precipitation is less than 150 mm, with even less (70–100 mm) in the desert hinterlands; it mainly occurs during spring, and mean annual evaporation exceeds 2,000 mm. Average temperature ranges from 6°C to 10°C, while the maximum temperature is over 40°C. Annual mean active accumulated temperature (≥10°C) is 3,000–3,500°C. Average relative humidity is 50% to 60%, but it is usually lower than 45% from May to August. Sub-shrubs and half-arbors composed of *Haloxylon persicum* and *Haloxylon ammodendron* are common in the region. Due to a long steady snow period in winter and increased precipitation in spring, ephemeral and ephemeroid plants are present at low frequency.

Abundant BSC are present on the desert sand surface, growing especially in cool periods (fall and early spring) and during wet periods such as during dew, fog, or temporary rainfall. Usually, three well-developed BSC types are present in the crust (Zhang et al. 2007). One 10×10-m permanent sampling plot was established in an interdune area in September 2000. All BSC were removed from the sand surface to initiate the study and they were allowed to reestablish naturally, so as to study succession during the recovery period. Soil samples were collected during predefined stages (bare sand, microalgal crusts, lichen crusts, and moss crusts) in September 2000, 2002, 2005, and 2007, respectively (Zhang 2005; Zhang et al. 2007). In order to protect the structure of BSC, the soil surface was moistened prior to sampling. We used a sterile spatula to collect surface (0–2 cm) soil samples. Twenty soil samples were collected and stored in sterilized plastic bags (Acea et al. 2003; Rivera-Aguilar et al. 2006). Samples were transferred to the laboratory in 2 days, air-dried, and stored at 6–10°C.

Analysis

Soil samples were analyzed by the soil physiochemical analysis laboratory at the Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, according to standard soil methods (Chen et al. 2007). Soil organic carbon was determined using the $K_2Cr_2O_7$ method, total N by the $CuSO_4$-Se powder diffusion method (GB7848-87), total P by the NaOH Melting-Mo Te Sc colorimetric method (GB7852-87), total K by the NaOH melting–flaming luminosity method (GB7854-87), available P by the 0.5 mol·L^{-1} $NaHCO_3$ leaching-Mo Te Sc colorimetric method, available N by the alkali hydrolysis–diffusion method, and available K by 1 mol·L^{-1} NH_40Ac leaching–flaming luminosity.

Microalgal culturing methods and taxonomic identification were conducted as reported by Hawkes and Flechtner (2002). Authoritative references used for algal identification included Anagnostidis and Komarek (1988, 1990) and Komárek and Anagnostidis (1999, 2005). Species composition and dominant species were determined by direct observation and solid cultivation. For direct observation, three temporary slices were prepared from each sample and ten observations were done for each slice. Each sample was crushed and sieved (0.1 mm); then, 5 g of the prepared material were added to 99 mL of sterile distilled water; 0.1 mL of this suspension were spread in triplicate on agar solidified BG_{11} medium and incubated for 3 weeks to quantify the number of cyanobacteria;

0.1 ml of the suspension was spread on Bold's basal medium for determining non-diatomaceous eukaryotic microalgae (often incubation of half a month; Fermani et al. 2007; Tirkey and Adhikary 2006). All media were incubated under controlled condition (25±1°C, 3,000 lx, 16:8 light cycles). Number of species was expressed per gram of soil. The percentage of occurrence of each species with respect to total occurrences was expressed as relative density (RD) and dominant species were determined according to RD.

Chlorophyll a concentrations were determined by the LS-50B fluorescence spectrophotometer after immediate extraction of the sample with 90% acetone and dimethyl sulfoxide (Catford et al. 2007; Stork and Shuber 1979).

Samples for thin sections were dried at 45°C for 48 h to remove the free water without killing microalgae, lichen, and moss (Chen et al. 2008). The unbroken-structure crusts were air-pumped at 685 mmHg (gauge pressure) to remove the air trapped within the samples and then impregnated with epoxy resin and acetone mixture (8:2 ratio by volume). Air pumping preceded the addition of resin. A hardening agent, methyl ethyl ketone peroxide (ten drops per 1,000 mL of mixture), and a fluorescent dye (Uvitex OB, Ciba-Geigy, Ardsley, NY 3 g per 1,000 mL of mixture) were added to the mixture. The mixture was poured around the soil blocks at a rate of about 1 cm day^{-1} until the samples were completely covered with the resin. After 30 min, the resin level was checked and topping-off mixture was added if needed. Then saturated samples were dried at 65°C for 24 h. The blocks of hardened soil were cut into 3×3-cm soil slices with a thickness of 0.03 mm. Finally, soil slices were examined and photographed under an Olympus BX51 digital microscope (Singh et al. 1991; Chen et al. 2008).

Observations under the dissecting microscope were performed as follows: intact BSC representing different successional stages were incubated in Petri dishes containing sterilized distilled water for 1 h. Then, samples were photographed under a Motic-DMBA400 dissecting microscope.

SPSS 8.0 (Chicago, IL, USA) statistical package was used to process data. All data represented mean values of 20 replicates. The levels of variation among samples and levels of significance, if present, were estimated by a one-way analysis of variance (ANOVA) and a multiple comparisons test (Tukey's honestly significant difference). Relationships between soil chemical properties and microalgal biomass were determined using Pearson's correlations coefficient test at 0.05 levels (two-tailed).

Results

Soil physiochemical properties varied among different successional stages (Table 1). ANOVA indicated significant differences in contents of organic carbon ($p<0.01$), total N ($p<0.05$), and available N ($p<0.05$) among soils sampled from different successional stages. No significant differences were observed for total P, total K, and available P. The contents of organic carbon and total N were the lowest in the bare sand and increased with the development of BSC reaching the highest values in lichen crusts. On the contrary, the available N content reached the highest value in soil sampled from the moss crusts.

Microalgal diversity varied slightly during different BSC successional stages. Thirty-four microalgal species representing 23 genera and 17 families were identified in bare sand. In algal crusts, 35 microalgal species representing 22 genera and 15 families were detected. Lichen crusts supported 36 microalgal species representing 23 genera and 15 families. Thirty-eight microalgal species of 22 genera, comprising 14 families, were observed in moss crusts. Cyanobacteria dominated in different successional stages and the number of cyanobacterial species in bare sand, microalgal, lichen, and moss crusts was 25, 25, 28, and 31, respectively. Green microalgae, diatoms, and euglenoids were also detected, but they were less abundant than cyanobacteria.

Each successional stage showed changes in microalgal species composition according to successional expectations. The most common species supported by bare sand were *Fragilaria* sp., *Amphora ovalis*, *Oscillatoria sancta*, *Microcoleus vaginatus*, *Phormidium okenii*, and *Palmellococcus miniatus*. Diatoms, especially a

Table 1 Soil physicochemical properties in different successional stages of BSC

Physicochemical properties	Bare sand	Algal crusts	Lichen crusts	Moss crusts
Organic carbon ($g \cdot kg^{-1}$)	1.41±0.15BCc	1.62±0.13ABbc	2.48±0.30Aa	2.26±0.92ABab
Total N ($g \cdot kg^{-1}$)	0.15±0.04c	0.16±0.03bc	0.25±0.05a	0.24±0.10ab
Total P ($g \cdot kg^{-1}$)	0.41±0.04	0.41±0.06	0.43±0.05	0.41±0.04
Total K ($g \cdot kg^{-1}$)	17.82±0.28	17.90±0.50	17.91±0.46	18.00±1.13
Available N (mg kg^{-1})	12.54±3.30bc	15.36±3.51bc	21.26±4.10ab	27.87±15.59a
Available P (mg kg^{-1})	5.03±1.14	4.05±1.44	3.67±0.42	8.65±5.94

Data are reported as means±SD. For each of the same physiochemical property presented in Table 1, lowercase letters indicate $p<0.05$ and uppercase letters indicate $p<0.01$ ($n=20$)

Table 2 Algal species composition in different crust types

Algae species	Bare sand	Algal crusts	Lichen crusts	Moss crusts
Cyanophyta				
Anabaena sp.	++	−	−	−
Aphanocapsa banaresensis	−	−	−	+
Aphanocapsa montana	−	+	−	−
Aphanocapsa sp.	+	+	−	+
Chroococcus minutus	+	+	+	+
Chroococcus turgidus	+	−	+	+
Chroococcus turgidus var. *solitarius*	−	−	+	+
Chroococcus westii	−	−	−	+
Cyanothece aeruginosa	+	+	+	+
Gloeocapsa sp.	+	−	−	−
Hydrocoleus sp.	−	+	−	−
Jaaginema pseudogeminata	+	−	+	+
Limnothrix sp.	+	+	+	+
Lyngbya gracilis	−	−	+	+
Lyngbya majuscula	−	−	+	+
Microcoleus paludosus	−	−	−	+
Microcoleus vaginatus	□	■	■	□
Nodularia spumigena	−	+	−	−
Nodularia sp.	+	+	+	+
Nostoc commune	+	−	−	+
Nostoc sp.	+	−	+	+
Oscillatoria amoena	−	+	+	−
Oscillatoria chlorina	+	+	+	+
Oscillatoria cortiana	−	−	+	+
Oscillatoria formosa	+	+	+	+
Oscillatoria martini	+	+	+	+
Oscillatoria sancta	++	−	−	−
Oscillatoria subbrevis	+	++	+	+
Oscillatoria tenuis	+	+	−	+
Oscillatoria willei	+	+	++	−
Phormidium allorgei	−	−	+	+
Phormidium attenuatum	+	+	+	+
Phormidium calcicola	−	+	−	+
Phormidium irriguum	+	++	□	+
Phormidium okenii	++	+	+	−
Phormidium retzli	−	++	++	++
Planktothrix cryptovaginata	+	−	+	−
Porphyrosiphon martensianus	−	+	+	−
Scytonema ocellatum	−	−	□	■
Synechocystis crassa	+	+	+	++
Synechococcus parvus	−	++	+	++
Tychonema granulatum	+	++	−	+
Chlorophyta				
Chlamydomonas sp.	+	−	−	−
Chlorella vulgaris	−	+	+	−
Chlorococcum humicola	+	+	++	+
Palmellococcus miniatus	++	++	++	■
Volvox sp.	−	+	−	−

Table 2 (continued)

Algae species	Bare sand	Algal crusts	Lichen crusts	Moss crusts
Bacillariophyta				
Amphora ovalis	++	++	+	+
Cymbella sp.	−	+	−	−
Fragilaria sp.	■	□	+	+
Hantzschia amphioxys	+	+	+	+
Pinnularia borealis	+	+	−	+
Pinnularia sp.	−	−	+	+
Euglenophyta				
Euglena sp.	+	+	+	−
Petalomonas sp.	+	−	−	−
Total	34	35	36	38

■ dominant species, □ sub-dominant species, ++ common species, + existent species, − not detected

species of *Fragilaria*, were more abundant in bare sand than in other successional stages. *M. vaginatus* was abundant in all samples but at a lower extent than *Fragilaria*. *Synechococcus parvus*, *Oscillatoria subbrevis*, *Phormidium retzli*, *Phormidium irriguum*, *Tychonema granulatum*, *M. vaginatus*, *P. miniatus*, *Fragilaria* sp., and *A. ovalis*, which were common in microalgal crusts (Table 2). In lichen crusts, *Oscillatoria willei*, *P. retzli*, *M. vaginatus*, *Scytonema ocellatum*, *P. miniatus*, and *Chlorococcum humicola* were the most common species with a prevalence of *M. vaginatus*, *S. ocellatum*, and *P. irriguum*. In most cases, *M. vaginatus* was the first colonizer. With the exception of *S. parvus*, the common species of lichen crusts were also common in moss crusts. Generally, *S. ocellatum* or *P. miniatus* were the initial colonizers, and *M. vaginatus* the second (Table 2).

Some species were specific of the successional stage. For example, *Gloeocapsa* sp., *O. sancta*, *Anabaena* sp., *Chlamydomonas* sp., and a species of *Petalomonas* were restricted to bare sand, whereas *Aphanocapsa montana*, *Hydrocoleus* sp., *Nodularia spumigena*, *Volvox* sp., and a species of *Cymbella* characterized the algal crusts. Moss crusts were characterized by the presence of *Chroococcus westii*, *Aphanocapsa banaresensis*, and *M. paludosus* (Table 2).

Some species such as *Chroococcus minutus*, *Cyanothece aeruginosa*, *Synechocystis crassa*, *Limnothrix* sp., *Oscillatoria formosa*, *Oscillatoria chlorina*, *Oscillatoria martini*, *O. subbrevis*, *P. irriguum*, *Phormidium attenuatum*, *M. vaginatus*, *Nodularia* sp., *P. miniatus*, *C. humicola*, *Fragilaria* sp., *Hantzschia amphioxys*, and *A. ovalis* occurred in all successional stages (Table 2).

Microalgal biomass was the lowest in bare sand (1.6×10^{-4}-mg g^{-1} dry weight), increased with BSC development, and reached the highest value in lichen crusts (13.3×10^{-4}-mg g^{-1} dry weight). ANOVA indicated that there were highly significant differences in microalgal biomass in the different successional stages ($p<0.01$). Tukey's multiple-range test showed highly significant differences between the microalgal biomass of bare sand and that of the other successional stages ($p<0.01$), whereas no significant differences were observed in the other three successional stages ($p>0.05$; Fig. 1).

Soil slice microstructure indicated that bare sand was largely composed of uncompacted sand grains. Few filamentous cyanobacteria were detected in bare sand (Fig. 2a), and their presence, particularly that of *M. vaginatus*, increased in microalgal crusts (Fig. 2b, c). Filamentous cyanobacteria, which can form crusts due to their sand-fixing abilities, were integrated with uncompacted sand grains and were distributed in the upper layer of lichen crusts (Fig. 2d, e). As lichen crusts were transformed in moss crusts, filamentous cyanobacteria and the dominance of *M. vaginatus* gradually declined, and moss rhizoids rapidly increased. Moss rhizoids and filamen-

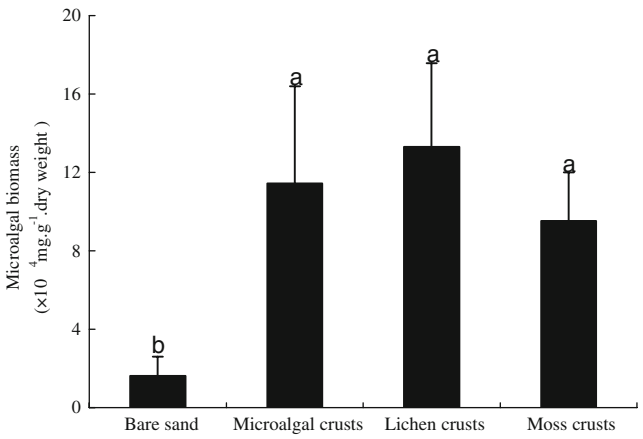

Fig. 1 Variation of microalgal biomass in different crust types

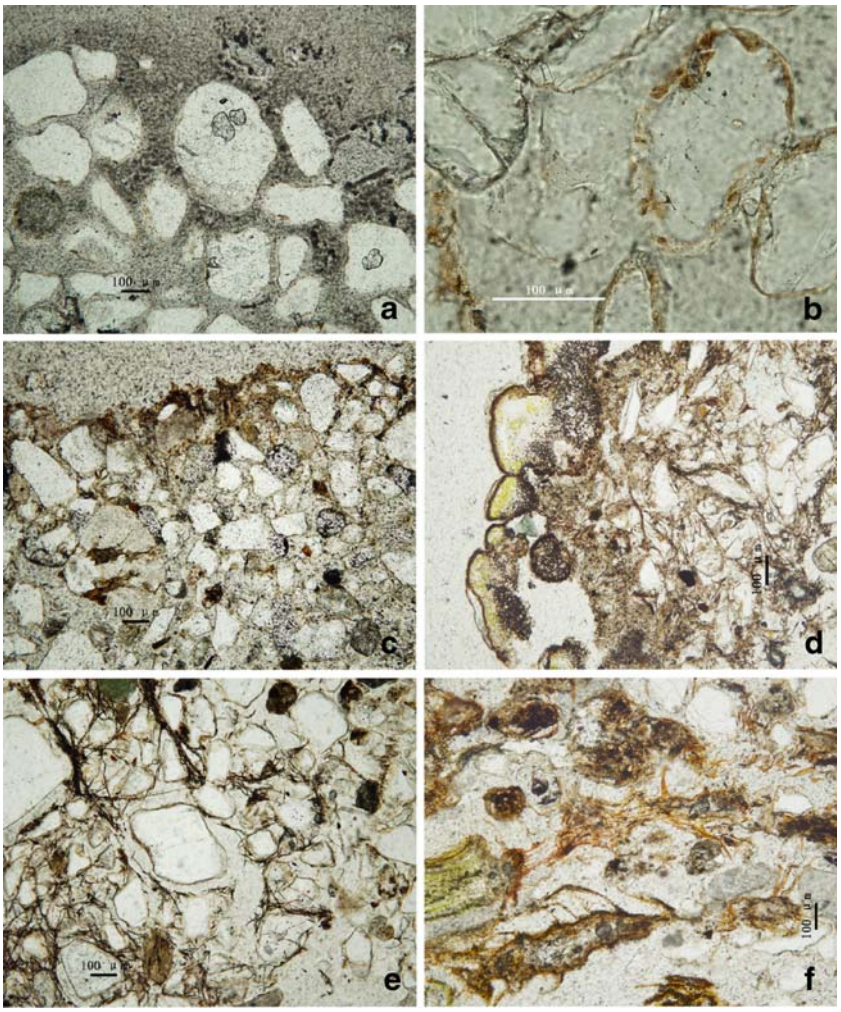

Fig. 2 Soil sections in different successional stages of biological soil crusts (**a** bare sand; **b** early stage of microalgal crusts; **c** lateral stage of algal crust; **d** microstructure of surface layer in lichen crust; **e** much mycelium in lichen crust; **f** filamentous cyanobacteria and moss rhizoid in moss crust)

tous cyanobacteria bound to sand particles were important components of the BSC community (Fig. 2f).

Microscope observations confirmed the results of soil slices because filamentous cyanobacteria were not detected in bare sand, but they were found in soil crusts, with dominance of *M. vaginatus* in microalgal crusts and lichen crusts (Fig. 3), whereas *M. vaginatus* decreased in moss crusts due to the increase in moss rhizoids.

Discussion

The chemical composition of soil was not affected in the first two successional stages, probably because the activity of cyanobacteria, microalgae, microfungi, and other bacteria presented in these crusts was not sufficiently high to change soil properties. As succession proceeded, communities of cyanobacteria, lichens, and mosses become more widespread,

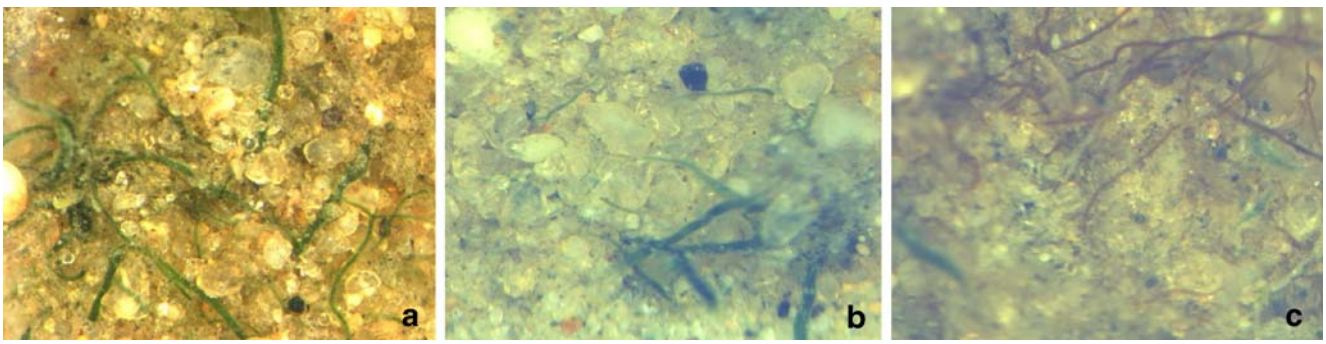

Fig. 3 Microstructure of different successional stages of biological soil crusts by dissecting microscope (**a** microalgal crusts; **b** lichen crusts; **c** moss crusts)

covering all surfaces not occupied by vascular plants or rock (Belnap et al. 2001). Later successional crusts had greater C and N fixation than early successional crusts (Housman et al. 2006). Thus, soil chemical properties were significantly different with respect to those in early successional stages. Rates of C fixation by *Microcoleus*-dominant crusts were generally low due to their low cyanobacterial biomass and chlorophyll content (Housman et al. 2006). The action of extracellular polysaccharides released by microalgae is important in promoting the release of nutrient from insoluble compounds (Metting 1981). Smith et al. (1978) provided laboratory evidence that microalgae extract orthophosphate from naturally occurring apatite.

N and C fixation rates of the BSC depend on species composition, biomass, and physical structure of the crust. For example, nitrogen fixation depends on the presence of cyanobacteria and cyanolichens (Belnap and Gardner 1996). The composition of microalgal community of the desert crust was changed by changing soil (Hu and Liu 2003). In the bare sand, C and N contents were lower than at later successional stages and dominant microalgal species included diatoms, such as *Fragilaria* sp. and *A. ovalis*, among others. *M. vaginatus* replaced diatoms as the dominant species as BSC developed into microalgal crusts and microalgal biomass rapidly increased as well as C fixation. In turn, accumulation of organic C probably changed microalgal composition and biomass. In addition, filamentous cyanobacteria, which were highly mobile, such as *M. vaginatus* and the number of coccoid green microalgal and cyanobacteria taxa (such as *P. miniatus*, *C. humicola*, and *S. ocellatum*) increased. Some coccoid green microalgae or heterocystic cyanobacteria (*Scytonema* sp. and *Nostoc* sp., etc.) could associate fungus into lichens (Belnap et al. 2001), and in this case the BSC was probably a lichen crust. At that stage, *M. vaginatus* was still the dominant species, whereas the abundance of the diatom was low. When BSC developed into moss crusts, either *S. ocellatum* or *P. miniatus* prevailed over *M. vaginatus*.

Microalgal biomass was positively correlated with the organic C(r=1, P=0), and available N (r=0.619, P=0.004) contents, whereas it was negatively correlated with total P and K contents.

Microalgal biomass was the lowest in the bare sand. The presence of diatoms such as *Fragilaria* sp. and *A. ovalis* and the presence of filamentous cyanobacteria probably enriched the sand with nutrients, thus creating favorable conditions for BSC succession (Metting 1981). The presence of low-nutrient bacteria, such as *Bacillus* sp., could be also important for the foundation of the crust. Indeed, these bacteria can secrete exopolysaccharides, which can glue sand grains together (Zhang 2005).

Filaments of *M. vaginatus*, which was dominant in the early stages, were often present as bundles surrounded by gelatinous sheaths, which can also bind and cement sand particles. Filamentous cyanobacteria, sand particles, and air dust-fall formed smooth compact crusts (Zhang 2005). The number of diatoms in microalgal crusts decreased whereas the number of *Oscillatoria* sp. and coccoid green microalgae gradually increased. These filamentous cyanobacteria play a role in the formation and maintenance of BSC. The increase in microalgae number increased organic C content and N fixation with consequent enhancement of soil properties including enzyme activity (Issa et al. 2007; Metting 1981).

In lichen crusts, *M. vaginatus* was initially the dominant species, and then *P. miniatus* and *S. ocellatum* became dominant. Filamentous cyanobacteria, mainly distributed in the upper lichen crust layer, with fungal mycelium could bind sand grains and thus could thicken crusts. In addition, the highest C and N fixation of the lichen crusts made this environment suitable for the establishment of mosses, which appeared in interdune areas (Belnap et al. 2001; Metting 1981; Shields and Dcrrell 1964; Housman et al. 2006). The presence of mosses further changed soil properties with further accumulation of organic C (Vitt 1989). Mosses gradually increased and, in some cases, developed into a monomorphic population.

In conclusion, BSC strength and the prevention of wind erosion were highest in moss crusts. Mosses continued to improve the soil structure and some permanent fixed sand dunes were created. Therefore, BSC facilitated the formation of conditions favorable for vascular plants, and mosses were the main contributors to sand dune stabilization (West 1990).

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