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

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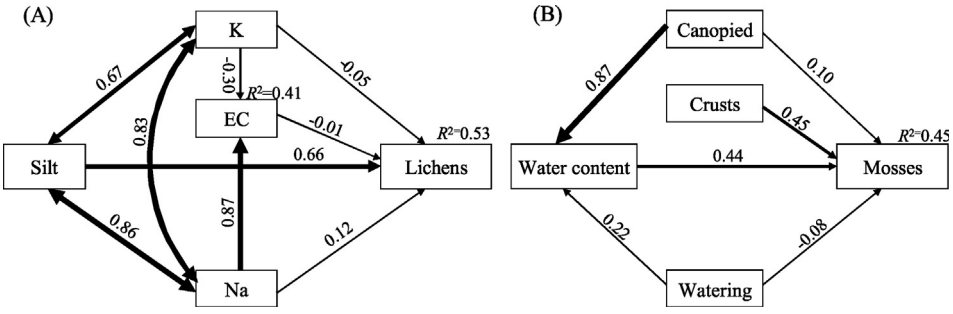
HIGHLIGHTS

- 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.

GRAPHICAL ABSTRACT



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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.

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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

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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 (Castenholz and Garcia-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 southeast 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 *Byum* 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* Gom. 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 cm^2 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.

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