Biol Fertil Soils (2011) 47:473–480
DOI 10.1007/s00374-010-0521-5

SHORT COMMUNICATION

Effects of inoculated *Microcoleus vaginatus* on the structure and function of biological soil crusts of desert

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Received: 8 February 2010 / Revised: 10 November 2010 / Accepted: 13 November 2010 / Published online: 1 December 2010

Abstract *Microcoleus vaginatus* Gom., the dominant species in biological soil crusts (BSCs) in desert regions, plays a significant role in maintaining the BSC structure and function. The BSC quality is commonly assessed by the chlorophyll a content, thickness, and compressive strength. Here, we have studied the effect of different proportions of *M. vaginatus*, collected from the Gurbantunggut Desert in northwestern China, on the BSC structure and function under laboratory conditions. We found that when *M. vaginatus* was absent in the BSC, the BSC coverage, quantified by the percentage of BSC area to total land surface area, was low with a chlorophyll a content of 4.77×10^{-2} mg g^{-1} dry soil, a thickness of 0.86 mm, and a compressive strength of 12.21 Pa. By increasing the percentage of *M. vaginatus* in the BSC, the BSC coverage, chlorophyll a content, crust thickness, and compressive strength all significantly increased ($P<0.01$). The maximum chlorophyll a content (13.12 mg g^{-1}dry soil), the highest crust thickness, and the compressive strength (1.48 mm and 36.60 Pa, respectively) occurred when the percentage of inoculated *M. vaginatus* reached 80% with a complex network of filaments under scanning electron microscope. The BSC quality indicated by the above variables, however, declined when the BSC was composed of pure *M. vaginatus* (monoculture). In addition, we found that secretion of filaments and polymer, which stick sands together in the BSC, increased remarkably with the increase of the dominant species until the percentage of *M. vaginatus* reached 80%. Our results suggest that not only the dominant species but also the accompanying taxa are critical for maintaining the structure and functions of the BSC and thus the stability of the BSC ecosystems.

Keywords *Microcoleus vaginatus* Gom. · Biological soil crusts (BSCs) · Gurbantunggut Desert · Northwestern China

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Introduction

Approximately 30% of lands globally consist of arid and semiarid landscapes where biological soil crust (BSC) is a predominant ecosystem generally exceeding the total coverage of grasses and shrubs (Nash et al. 1979; Belnap 1995; Redfield et al. 2002; Eldridge and Leys 2003; Bowker and Belnap 2004). However, the BSC has only been studied in the past years due mainly to its small biomass and remote distribution. It has recently been found that the BSC plays a pivotal role in desert stabilization and ecosystem restoration

(Schulten 1985; Eldridge and Bradstock 1994; Hu et al. 2002; Zhang 2005). Due to land degradation and desertification in most arid areas in the world, environmental issues, such as dust storms, have become more sever, particularly in northwestern China where the rich sand materials have been the primary sources to the dust storms in the past decades (Guan et al. 1995; Chen et al. 2005; Zhang et al. 2007; Wu et al. 2009; Zheng et al. 2009).

Based on the dominant species, BSCs can be classified as microalgal crusts, lichen crusts, and moss crusts (Belnap 2003; Housman et al. 2006; Zhang et al. 2009). The microalgal crusts are the pioneer stage of the BSC succession because microalgae, being able to fix solar energy through photosynthesis, can improve the biotic and abiotic environments for lichens and mosses, both occurring in the late stages of the BSC succession (Zhang 2005; Housman et al. 2006; Zhang et al. 2006; Zhao et al. 2009). Additionally, the microalgal crust plays a vital role in biogeochemical cycles and geomorphological processes in desert ecosystems (Booth 1941; Eldridge and Greene 1994; Belnap and Lange 2001; Belnap 2003; Zhang et al. 2009). Therefore, many studies have focused on microalgal crust for restoring and reconstructing vegetations in arid and semi-arid regions (Belnap and Gardner 1993; Issa et al. 1999, 2001; Belnap 2002; Hu and Liu 2003; Xie et al. 2007; Zhang et al. 2009). However, the species composition and its effects on the structure and function of BSCs are poorly understood (Redfield et al. 2002; Savage et al. 2007; Wang et al. 2009).

Microcoleus vaginatus, a predominant species in microalgal crusts, is widely distributed in the deserts over the world due to its proliferated ability under harsh and variable environments (Mazor et al. 1996; Redfield et al. 2002; Hawkes and Flechtner 2002; Chen et al. 2002; Zhang et al. 2009). *M. vaginatus* is also a biofertilizer and soil conditioner during the restoration process of degraded ecosystems by forming extracellular polymer secretions (EPS) which can bind and cement sand particles (Hu et al. 2002; Hokputsa et al. 2003; Zhang et al. 2009; Wu et al. 2010). For these reasons, *M. vaginatus* is considered as a keystone species in various BSC ecosystems (Mazor et al. 1996; Issa et al. 2001; Nisha et al. 2007; Issa et al. 2007). Soil inoculation with cyanobacteria including some of the microalgal species in microalgal crusts, significantly improved the physical and biochemical properties of the crust (Rao and Burns 1990; Belnap 2003; Zhao et al. 2010), promoted microbial diversity (Rogers and Burns 1994; Acea et al. 2001) and enhanced soil fertility (Zimmerman 1993; Osman et al. 2010). So far, to our knowledge, few studies have estimated the influences of microalgal proportion, especially the percentages of the dominant species *M. vaginatus* on the BSC structure and functions (Falchini et al. 1996; Issa et al. 2001; Wang et al. 2009). The objective of the current study is to examine the effects of different percentages of *M. vaginatus* on the BSC structure and functions under controlled environments. In order to evaluate if it is possible to use *M. vaginatus* for degraded desert ecosystem restoration, we measured chlorophyll a content, thickness, and compressive strength of the BSCs; these properties have been commonly used for estimating BSC quality in many studies (Falchini et al. 1996; Zhang 2005). This is because chlorophyll a content is related to the photosynthesis capacity of BSCs in desert ecosystems (Zhang et al. 2009); the thickness is related to the ecosystem production, biomass and proportion of microalgae in the BSC complex (Zhang 2005; Wang et al. 2009); and the compressive strength is a good indicator against physical stresses, such as wind erosion and the momentum from raindrops (Chen et al. 2006; Issa et al. 2007). These indicators have been commonly used for characterizing the structure and functions of BSCs and also for evaluating the quality of desert BSCs.

Materials and methods

Field sampling

Field BSC samples were collected in July of 2007 at the Fukang Desert Ecological Research Station (44°35′ N, 88°14′ E) in the Gurbantunggut Desert, the largest fixed and semi-fixed desert in China with an area of 4.88×10^5 km^2. The desert is located in the center of the Jungger Basin (44° 11′–46° 20′ N, 84° 31′–90° 00′ E), Xinjiang Uygur Autonomous Region, China. The desert climate has an annual precipitation of 79.5 mm and an annual pan evaporation of 2,000 mm; annual mean temperature ranges from 6°C to 10°C, while the maximum temperature is over 40°C. The sampling area is covered (<30%) by sparse vegetation and the dominant vascular plants include *Haloxylon ammodendron* and *Haloxylon persicum*. Microalgal crusts, lichen crusts, and moss crusts are commonly found in this area with the microalgal crusts mostly present in areas where vascular plants are absent.

Microalgal isolation and incubation

The samples were first ground to pass the 0.1-mm mesh sieve and then mixed with sterilized water. We added 1 mL of the mixed solution to a BG-11 agar medium in a culture vessel with a diameter of 5 cm. After 2 weeks at 26°C, with relative humidity of 60% and light intensity of 50 μE·m^{-2} s^{-1}, microalgal taxa were isolated under a stereo light microscope before the individual microalgae grew together. We isolated six major microalgal species from the field samples according to their abundance in the micro-

Table 1 Microalgal inoculum inoculated into the sand soil

Inoculum	*Microcoleus vaginatus* (%)	*Scytonema ocellatum* (%)	*Phormidium* sp. (%)	*Ulothrix tenerrima* (%)	*Synechococcus* sp. (%)	*Chlorococcum humicola* (%)
1	0	20	20	20	20	20
2	20	16	16	16	16	16
3	40	12	12	12	12	12
4	60	8	8	8	8	8
5	80	4	4	4	4	4
6	100	0	0	0	0	0

algal crust (Table 1). Each of these isolated species was cultivated with BG-11 liquid medium in a growth chamber (temperature 26°C, relative humidity 60%, and light intensity 50 μE m^{-2} s^{-1}) for 2 months; then the microalgae were filtered, air-dried, and ground for further experiments.

Microalgal inoculation and incubation

We added 0.3 g ground powders of each species into 30 mL sterilized water before the six microalgal suspensions were mixed based on the percentages listed in Table 1. One milliliter of each of the mixture with a concentration of 0.01 g/mL was added to the sterilized soils, collected from the Gurbantunggut Desert. Each treatment was replicated three times. The inoculated soils were kept moist with sterilized water (5 mL per day for each inoculated soil) in the first 5 days before they were incubated for 20 days in growth chambers at 26°C, with relative humidity of 60% and light intensity of 50 μE m^{-2} s^{-1} (Xie et al. 2007, 2008).

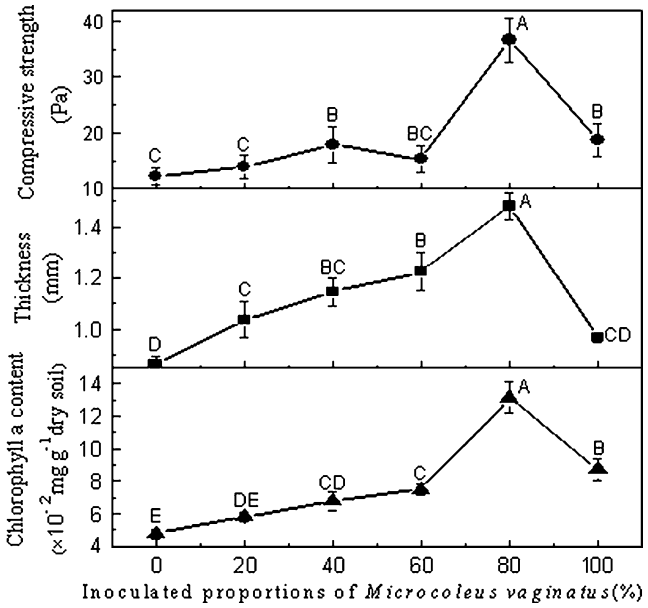

Fig. 1 Changes of BSC properties with different inoculated percentages of *M. vaginatus* (*different letters* indicate $P<0.01$ and the *same letters* indicate $P>0.01$)

We randomly took six samples from each treatment (proportional combination of different species) to assess the quality of the BSCs after an incubation of 20 days when the BSCs featured similar thickness and morphology to those growing in the desert.

The chlorophyll a content was measured with an LS-50B fluorescence spectrophotometer after immediate extraction of the sample with 90% acetone and dimethyl sulfoxide as reported by Catford et al. (2007). The crust thickness was measured using a vernier caliper as shown by Wang et al. (2009), and the compressive strength was measured using a soil sclerometer as reported by Xie et al. (2007). A piece of the BSC (about 5×5 mm) was randomly removed from each incubated BSC for evaluating its microscopic structures by an S-570 Scanning Electron Microscope (SEM, HITACH Corp, Japan) (Zhang 2005).

Statistical analysis

The SPSS 13.0 (Chicago, IL, USA) statistical package was used for data analysis. The one-way analysis of variance (ANOVA) followed by a multiple-comparison test (Tukey's test) was used to test the differences among the six treatments involving combination of the species with different proportions.

Results

Our results showed that the proportion of *M. vaginatus* in the incubated BSCs significantly affected the BSC structure and function ($P<0.01$). When the *M. vaginatus* was absent (treatment 1) in the BSCs, the average chlorophyll a content, thickness, and compressive strength were 4.77×10^{-2} mg g^{-1} dry soil, 0.86 mm, and 12.21 Pa, respectively. These properties increased with the addition of *M. vaginatus* to the BSC combinations until the percentage of *M. vaginatus* reached 80% (treatment 5). The BSC quality as shown by the measured properties increased slowly when the *M. vaginatus* increased from 0% to 60% with a rapid increase from 60% to 80% (Fig. 1).

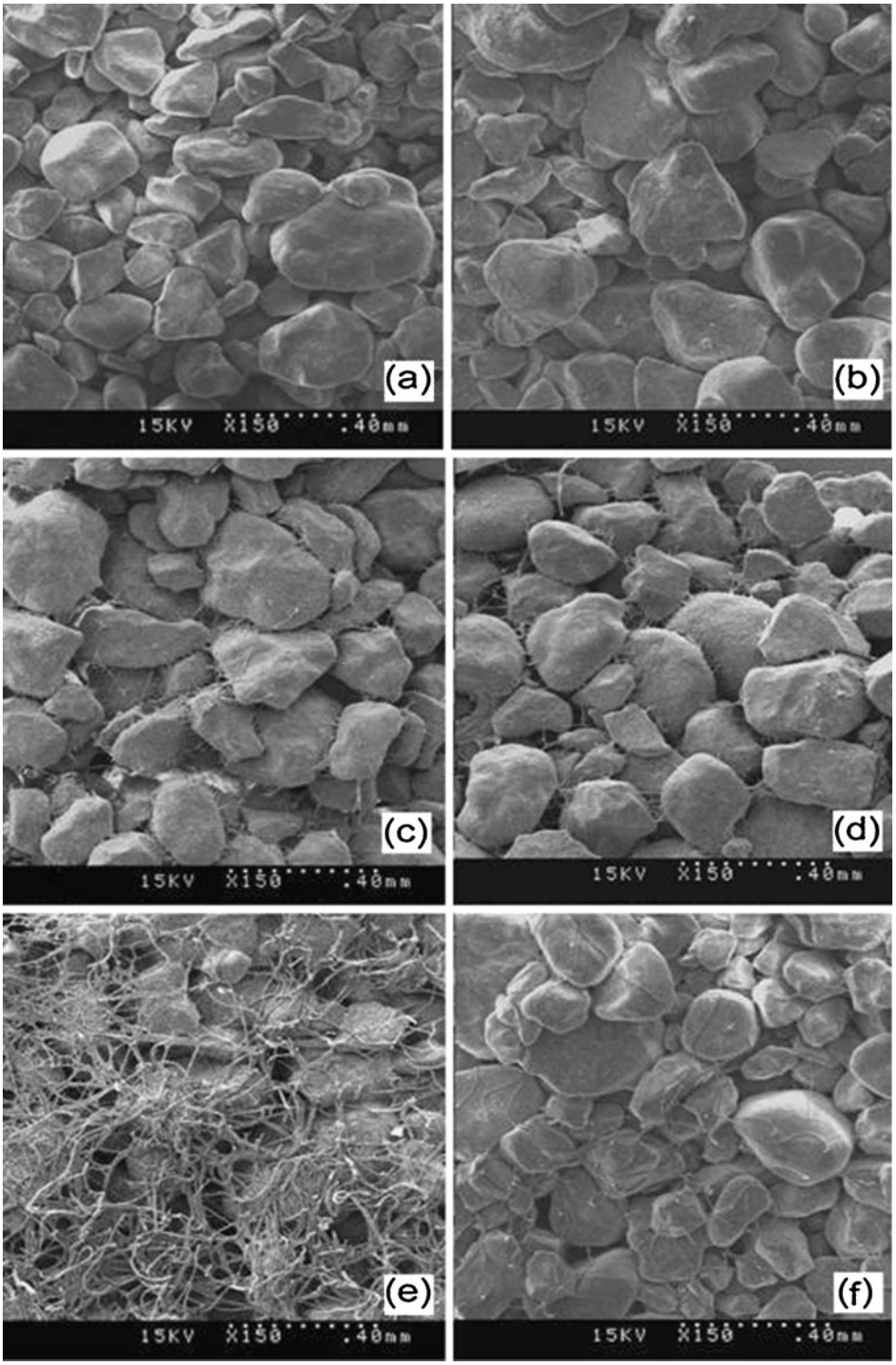

Fig. 2 Variations of the microstructure in BSC with different inoculated percentages of *M. vaginatus* (**a**–**f** indicate the microstructural images of treatment *1*–*6*)

The structure and function of the BSC ecosystems were determined not only by the percentage of the *M. vaginatus* but also by the interactions between the *M. vaginatus* and other species. By comparing treatment 1 (absence of *M. vaginatus*) and treatment 6 (only presence of *M. vaginatus*), we found that the BSCs only composed of *M. vaginatus* had a better quality than that made of the other five species with even percentages. The chlorophyll a content and the compressive strength in treatment 6 almost doubled those in treatment 1, while the thickness was slightly higher in treatment 6 than in treatment 1 (Fig. 1). Interestingly, the best BSC quality did not occur at 100% (treatment 6), but at

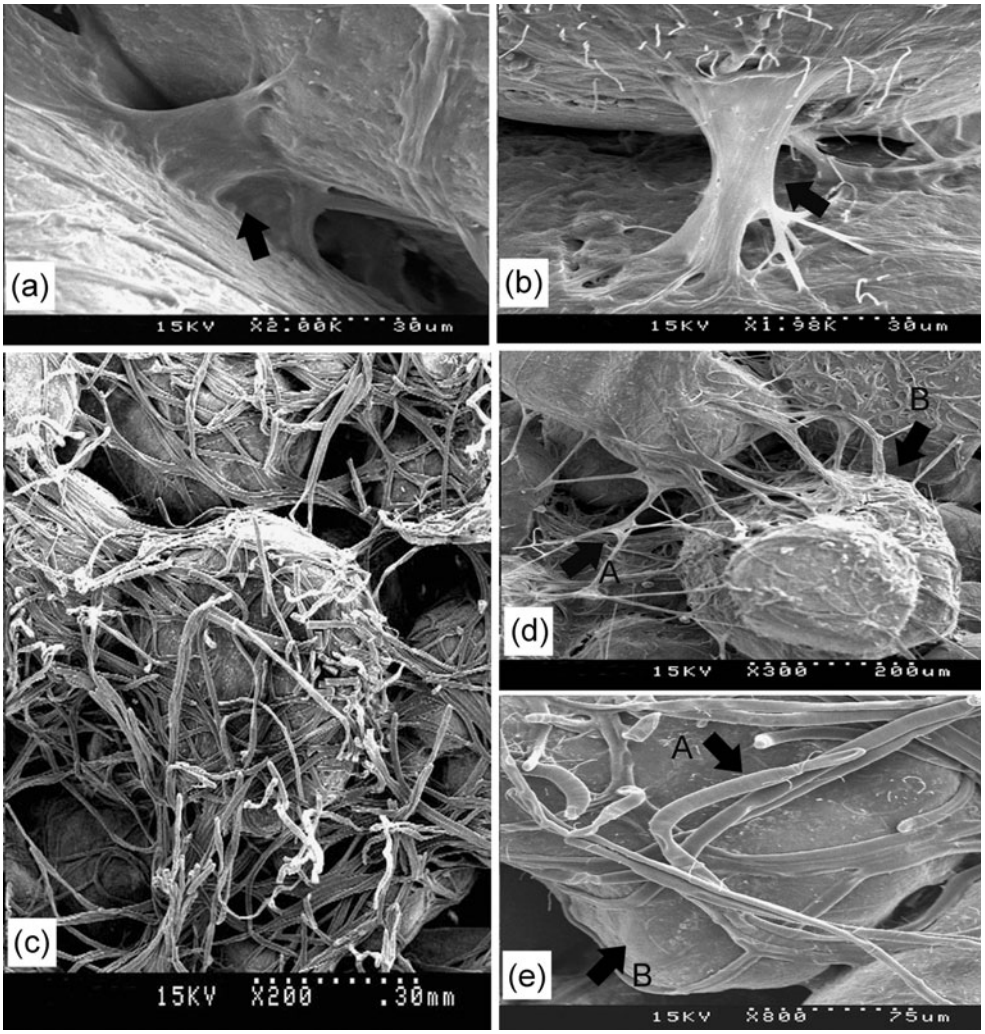

Fig. 3 Interactional images between *M. vaginatus* filaments and sand grains: **a** and **b** indicate sand grains linked with each other by glutinous EPS secreted from *M. vaginatus* (*arrow* shows the link sites between sand grains). **c**, **d**, and **e** indicate sand grains entrapped and bind by filaments of *M. vaginatus* (*arrow A* shows filaments and *arrow B* shows sand grains)

80% (treatment 5) of *M. vaginatus*, which indicated that the interactions between the *M. vaginatus* and other species are also important to improve the BSC quality.

Our ANOVA results also indicated that differences in chlorophyll a content, thickness, and compressive strength among all the treatments were statistically significant ($P<0.01$; Fig. 1). Tukey's multiple-comparison tests showed that treatment 5 was significantly different from all the other treatments for all the three measured variables ($P<0.01$). According to the chlorophyll a content, we found that the differences among all the treatments were statistically significant different ($P<0.01$) except for the difference between treatments 1 and 2, and treatments 3 and 4 ($P>0.01$). The multiple-comparison results of thickness showed significant differences among treatments 1, 2, 4, 5 ($P<0.01$); but no significant differences between treatment 6 and treatments 1, 2, and 3 and between treatment 3 and treatments 2 and 4 ($P>0.01$). Based on the compressive strength, we found that only the differences among treatments 1, 5, and 6 were statistically significant ($P<0.01$).

The above results that the microalgal taxa composition and proportion affect the BSC quality were also confirmed by our direct microscopic observations of the BSC microstructures. We observed that the number of filaments and the amount of the EPS apparently increased with the increasing percentage of *M. vaginatus* presented in the BSC (Figs. 2 and 3). When the percentage of *M. vaginatus* increased to 80% (treatment 5), a complex network of filaments formed to wrap around sands tightly (Fig. 3). However, we found that treatment 6 (only *M. vaginatus)* had less filaments and EPS than treatment 5 (80% of *M. vaginatus*), confirming the decline of BSC quality with reduced species diversity (Fig. 2).

Discussion

Usually the dominating (keystone) species affect ecosystem functions and processes (Tilman 1996; Loreau et al. 2001; O'Connor and Crowe 2005; Koellner and Schmitz 2006; Savage et al. 2007; Goudard and Loreau 2008; Lewis 2009)

and maintain the structure and function of communities (Mills et al. 1993; Paine 1995; Estes et al. 1998). Munzbergova and Ward (2002) demonstrated that three *Acacia* species acted as keystone species in maintaining the species diversity and soil quality in the Negev desert ecosystems. Jefferey and William (1994) found that the endemic keystone species *Acanthosicyos horridus* dominated the ecosystem processes and functions in providing various nutrients and sources for the Namib Desert. Our results suggest that the *M. vaginatus* is also a keystone species in the Gurbantunggut Desert for its role in stabilizing BSC in the degraded desert ecosystems.

Our results that the accompanying microalgal taxa enhanced the BSC structure and function also support conclusions from previous studies that the species diversity and species interactions might play an important role in maintaining the ecosystem function and stability (Garcia-Pichel et al. 2003; Nagy et al. 2005; Gundlapally and Garcia-Pichel 2006; O'Bryan et al. 2009; Bates and Garcia-Pichel 2009). The effect of species diversity in maintaining ecosystem functions, such as productivity, had been reported for forest (Bunker et al. 2005; Wills et al. 2006), cropland (Huang et al. 2005), and grassland (Tilman et al. 2001; Loreau et al. 2001) ecosystems. In the case of desert ecosystems, most studies have focused on the diversity of vascular plants (Paine 1995; Estes et al. 1998; Wall and Virginia 1999; Munzbergova and Ward 2002), and only few studies have evaluated the effect of the non-vascular plant diversity on ecosystem functions and processes (Evans and Johansen 1999; Langhans et al. 2009). Our results suggested that the interactions between the *M. vaginatus* and other species are important for functions of BSC. To our knowledge, our finding is the first supporting the biodiversity–productivity theory in the BSC ecosystems. Further studies are needed to elucidate the mechanisms of the interactions among the microalgal taxa in the BSC ecosystems.

Microalgal crusts are a complex assemblage consisting of multiple microalgal communities such as cyanobacteria, diatoms, and green algae (Mazor et al. 1996; Belnap and Lange 2001; Zhang et al. 2009). These microalgal communities play an important role in improving soil fertility and promoting soil succession in degraded desert ecosystems (Booth 1941; Evans and Johansen 1999; Acea et al. 2003; Bowker and Belnap 2004; Zhang et al. 2009; Osman et al. 2010). Our results suggested that the dominant species in microalgal crusts (*M. vaginatus*) substantially affected soil structure by forming a complex network of filaments which wrap sand particles together and fertility by excreting extracellular substances which can promote the release of nutrient from insoluble compounds (Smith et al. 1978; Metting 1981; Hokputsa et al. 2003; Chen et al. 2009).

It is difficult to isolate all the individual species from the field microalgal crusts due to the small size of individual microalgae which are usually not visible. Hence, we have used a common method with five steps: isolation; incubation; mixing; inoculation; and re-incubation as reported in previous studies (Acea et al. 2001, 2003; Pandey et al. 2005; Wu et al. 2010). This method worked well for the cultivation of five cyanobacteria and one green algae species from the Gurbantunggut Desert in northwest China. The success of this laboratory-based experiment suggests that it is possible to extend this method for massive BSC production for ecosystem restoration in desert regions.

Acknowledgments We thank Prof. Paolo Nannipieri and the anonymous reviewer for their constructive comments and suggestions on revising the manuscript. This research was partially supported by the Natural Science Foundation of China (31070184; 30770411) and the Natural Science Foundation of Hebei Province (2008000158). The Chinese Academy of Sciences also supported Ming Xu's work through the Bairen Program. The authors gratefully acknowledge the assistance of Dr. Zhang Bingchang and Prof. Zhang Yuanming.

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