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Artificially Accelerating the Reversal of Desertification: Cyanobacterial Inoculation Facilitates the Succession of Vegetation Communities

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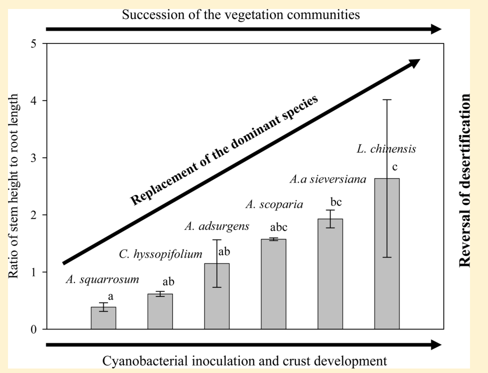
Supporting Information

ABSTRACT: Desertification has been recognized as a global environmental problem, and one region experiencing ongoing desertification is the eastern edge of Qubqi Desert (Inner Mongolia). To investigate the facilitating effects of cyanobacterial inoculation technology on the desertification control along this steppe-desert transition region, artificial cyanobacterial crusts were constructed with two filamentous cyanobacteria 3 and 8 years ago combined with *Salix* planting. The results showed that no crusts formed after 3 years of fixation only with *Salix* planting, whereas after cyanobacterial inoculation, the crusts formed quickly and gradually succeed to moss crusts. During that course, topsoil environments were gradually improved, providing the necessary material basis for the regeneration of vascular plants. In this investigation, total 27 species of vascular plants had regenerated in the experimental region, mainly belonging to *Asteraceae*, *Poaceae*, *Chenopodiaceae* and *Leguminosae*. Using space time substitution, the dominant species along with the application of cyanobacterial inoculation technology succeeded from *Agriophyllum squarrosum* ultimately to *Leymus chinensis*. In addition, it was found that the shady side of the dunes is more conducive to crust development and succession of vegetation communities. Conclusively, our results indicate artificial cyanobacterial inoculation technology is an effective and desirable path for desertification control.



■ INTRODUCTION

Drylands cover 33.6−52.3% of the terrestrial land surface and are home to 35−38% of the world's population.[1,2] It is reported that as much as 70% of the drylands may suffer from desertification, and the total dryland area may continue to increase as a result.[3] The United Nations has long focused on drylands and desertification, notably in 1992 adopting the Convention to Combat Desertification.[2] As a serious threat, desertification affects the livelihood of more than 25% of the world's population, and results in long-lasting and observable loss of vegetation coverage and bareness of soil surface for the environment itself.[4] In short, desertification leads to the loss of productivity and ability to retain resources, such as nutrients and water, bringing considerable economic, social, and environmental problems to the local residents. Therefore, finding a viable approach to reverse desertification has become such an urgent problem for humanity.

According to the visual characteristics of desertification, topsoil stability and vegetation regeneration are two important issues in desertification control. In desertified regions, vascular plants are severely restricted by the extreme desert environmental stresses, such as drought, salinity, wind, and sand-scouring. Additionally, the sparse surviving vegetation cannot completely cover and stabilize the soil surface, and the gaps between vegetation patches remains a source of sand and dust. To the contrary, biological soil crusts (BSCs), because of their unique physiological and ecological characteristics, can survive and attain higher coverage in these areas.[5] BSCs form and directly cover on soil surfaces, stabilizing topsoil and decreasing erosion effectively, therefore the recovery of BSCs is considered to have an important role in desertification control.

BSCs are a complex association of microorganisms and soil particles within the uppermost millimeters of topsoil, in which cyanobacteria (especially the filamentous ones) first settle and grow, then other organisms, such as bacteria, fungi, eukaryotic algae, lichens, and mosses emerge after the topsoil is stabilized.[6,7] On the basis of the different dominant species and developmental levels, BSCs are categorized into different successional stages, in sequence including cyanobacterial crusts,

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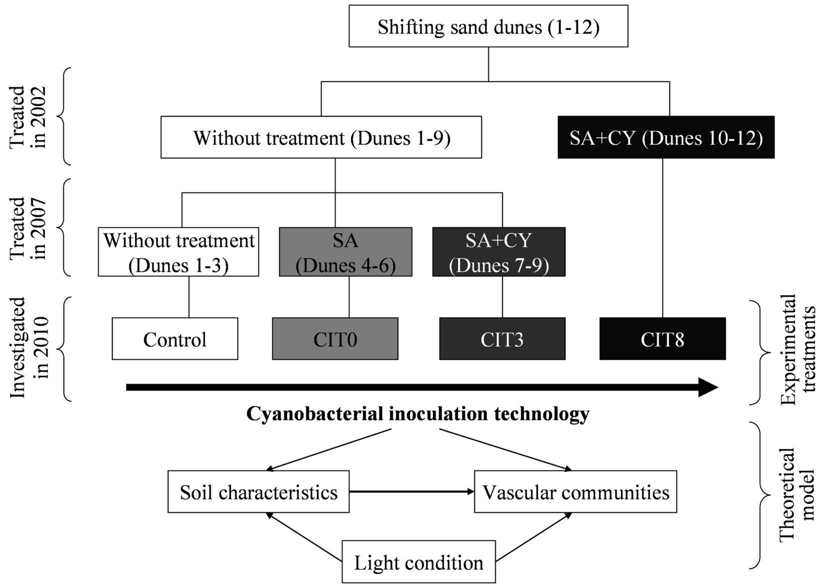

Figure 1. The experimental design and theoretical model for demonstrating the facilitating effects of cyanobacterial inoculation technology on desertification control. The different shading within boxes represents the different experimental treatments. SA: dunes fixed by planting *Salix*; SA +CY: dunes fixed by planting *Salix* and inoculating cyanobacteria. In the experimental treatments, the black arrow represents the using time of cyanobacterial inoculation technology from control to 0, 3, and 8 years (CIT0, CIT3, and CIT8 respectively). The priori theoretical model indicates the effects of cyanobacterial inoculation and light condition on soil characteristics and vascular communities.

lichen crusts, and moss crusts.[6−8] Cyanobacterial crusts normally represent the primary successional stage, light, flat, and brittle. However, they play an important role in facilitating crust succession to later stages due to their ability to improve the surface microenvironments and enhance the probability of colonization and survival of later successional species.[6,9] Therefore, artificially accelerating the formation of cyanobacterial crusts is proposed by many researchers for the reconstruction of soil ecosystem function.[9−11]

Several projects to accelerate the formation of cyanobacterial crusts, including inoculating crust slurry and dry-crumbled crusts have been proposed,[12,13] but these technologies are not widely used because of the limited inoculum. Then others focused research on cyanobacterial inoculation, and the reliability was verified at both the laboratory level and field scale.[14−16] On the premise of such results, our research group began to artificially construct cyanobacterial crusts via inoculating two mixed filamentous cyanobacteria in Dalate Banner of Inner Mongolia (at the eastern edge of Qubqi Desert) in 2002, and the scale has attained over 30 km^2 as of December 2010. To our knowledge, at present, it is the first and only attempt worldwide to construct artificial cyanobacterial crusts on a large scale via cyanobacterial inoculation. In our experimental region, with cyanobacterial inoculation, cyanobacterial crusts formed quickly and in some micoenvironments gradually succeeded to moss crusts 2−3 years later.[17,18] In the survey of Wang et al.,[19] it was found the diverse vegetation communities (17 species of vascular plants in total) were established on the different sides of dunes after 3 years of cyanobacterial inoculation. However, the mechanisms of formation, development, succession of BSCs, revegetation of vascular plants, and succession of vegetation communities after cyanobacterial inoculation are still unknown.

As an effective approach for desertification control, cyanobacterial inoculation we speculate not only accelerates the development of BSCs and increases soil available resources, but also promotes the succession of vegetation communities, and ultimately improves the regional ecological environment. Therefore, in this study, artificial cyanobacterial inoculation technology (cyanobacterial inoculation alongside with *Salix* planting) was conducted in Dalate Banner of Inner Mongolia, in order to accomplish the following: (1) study the facilitating effects of cyanobacterial inoculation technology on the recovery of BSCs and improvement of soil available resources and (2) investigate the successional mechanism of vascular vegetation communities after using the cyanobacterial inoculation technology. In addition, this study also compared the effects of light conditions on development of BSCs and succession of vascular vegetation communities. The results not only would be of important application value in desertification control, but also be of great theoretical significance for ecosystem reconstruction in desertified regions.

MATERIALS AND METHODS

Study Region. Our study was conducted in Dalate Banner of Inner Mongolia Autonomous Region, at the eastern edge of Qubqi Desert (40°21′N, 109°51′E), where desertification was quite severe due to long-term excessive graze. Now the large areas in this region are barren shifting sand dunes with a relative height of 5−8 m. The sparse natural plants mainly are *Agriophyllum squarrosum* (Linn.) Moq. and *Corispermum hyssopifolium* L. As a steppe-desert transition zone, this region is a typical continental monsoon climate with an elevation of 1040 m, where the average temperature is 6.1 °C (the lowest is −34.5 °C and the highest is 40.2 °C). Mean annual precipitation is 240−300 mm, falling predominantly in July−September. The annual potential evapotranspiration during growing season (May−September) is approximately 2400 mm. The average wind velocity is 3.3 m s^{-1}, predominantly from the northwest, and windy days (wind velocity >5 m s^{-1}) occur more than 180 d y^{-1}.

Field Experiment. In 2002, 12 shifting sand dunes were randomly selected to interpret the facilitating effects of cyanobacterial inoculation technology on the recovery of BSCs and establishment of vegetation communities (Figure 1). From this pool of dunes, we randomly assigned 3 without any treatment as Control and 3 to treatment *Salix* (*mongolica*) planting and cyanobacterial inoculation in 2002 (CIT8). The other 6 dunes were treated in 2007, when 3 dunes were treated with *Salix* planting and cyanobacterial inoculation (CIT3), and the remaining 3 were treated with only *Salilx* planting but without cyanobacterial inoculation (CIT0). The details about *Salix* planting and cyanobacterial inoculation (generally the two filamentous cyanobacteria *Microcoleus vaginatus* and *Scytonema javanicum* were inoculated with a proportion of 10:1) are described in the previous studies.[16−19] In September 2010, we characterized the vegetation communities and BSCs of each dune replicating per treatment, and then we were able to investigate the recovery of BSCs and establishment of vegetation communities with cyanobacterial inoculation. It is worth stressing that the cyanobacterial inoculation technology used in our windy experimental region must include *Salix* planting (or other means) to initially stabilize the shifting sand dunes before cyanobacterial inoculation. Therefore, in our experiment the dunes fixed for 3 years by planting *Salix* without cyanobacterial inoculation were regarded as 0 year after using artificial cyanobacterial inoculation technology (CIT0); the dunes fixed for 3 and 8 years by planting *Salix* and inoculating cyanobacteria were respectively regarded as 3 (CIT3) and 8 years (CIT8) after using this technology. Then the change of soil characteristics and successional mechanism of vegetation communities could be studied using space time substitution across the different dunes where cyanobacterial inoculation technology was used 3−8 years ago.

In addition, in order to compare the effects of light conditions on the development of BSCs and succession of vascular vegetation communities, both sunny (Su) and shady (Sh) sides of each dune were investigated in this study. Both sides of shifting sand dunes before using the cyanobacterial inoculation technology were regarded as uniform experimental condition (Control), because the soil physicochemical characteristics and vegetation communities were similar between the two sides, as it had been demonstrated in the preliminary experiments. Therefore, a total of 7 experimental conditions in the 4 types of dunes were designed in our experiment (Supporting Information, SI, Table S1).

Survey of Vascular Plants. For vascular plant survey, five 5×5 m^2 or 1×1 m^2 survey quadrats were established on each side of the treated dunes, the survey quadrats of subshrubs were 5×5 m^2, whereas those of herbs were 1×1 m^2. In each quadrat, vascular vegetation coverage (%), number of species, height (cm), root length (cm), density (ind m^{-2}) and biomass (dry weight; g m^{-2}) for each species were recorded. For the vascular vegetation communities, average height, root length, total density, and biomass were evaluated. For each species, relative importance value (IV) was calculated as follows:[20]

$$\mathrm{IV} = (\text{relative height} + \text{relative density} + \text{relative biomass})/3$$

Among the vascular plants, only those with IV > 0.2 were considered as dominant species; those with 0.1< IV < 0.2 were identified as subdominant species.

To evaluate the diversity of vascular vegetation communities in the different dune conditions, Shannon−Wiener index (H'), Simpson index (DS), Pielou evenness index (JP), and Margalef richness index (Ma) were used in our experiment as described by Li et al.:[21,22]

$$H' = -\Sigma P_i \ln P_i$$

$$\mathrm{DS} = 1 - \Sigma P_i^2$$

$$\mathrm{JP} = -\Sigma P_i \ln P_i / \ln S$$

$$\mathrm{Ma} = (S - 1)/\ln N$$

Here, P_i is the IV of species i, S is the species number in a certain quadrat, and N is the sum of individual numbers of all species in the quadrat.

In addition, the ratios of stem height to root length in several dominant species derived in our experiment were used to evaluate the succession of vascular vegetation communities.

Analysis of Soil Samples. Soil sampling was also conducted in September 2010, and the experimental region did not receive any rainfall in the past three days. Soil samples including BSCs and shifting sand were collected from the interspaces between shrubs (0.2 m away from the planted *Salix*), and at least 10 similar soil samples were collected randomly on each side of the investigated dunes, mixed together and kept in sterilized paper bags.[8] Then these samples were carried to the laboratory as soon as possible for the subsequent analysis, and also at least three replications were prepared for each analysis.

For microscopic observation of cyanobacterial and algal composition, the soil samples were passed through 0.1 mm (pore size) sieve first, and then 0.1 g of each sample was diluted in 10 mL sterile distilled water. The mixtures were shaken carefully and placed in darkness for 12 h. For each sample, 0.1 mL of the mixture was then observed directly with a microscope and another two 0.1 mL mixtures were inoculated on solid BG11 and BBM mediums, respectively (1.3% agar; Eiken, Tokyo, Japan). The inoculations were placed in a greenhouse (25 ± 2 °C) and illuminated with cool white fluorescent light at 40 μE m^{-2} s^{-1}.[17,18] Fifteen to 20 days later, the cyanobacterial and algal colonies were identified and the dominant species were determined as the method described by Lan et al.[18]

Soil physical properties including water content, crust thickness, compressive strength, bulk density, porosity, and soil texture were measured by the standard methods described by Xie et al.[23] and Lan et al.[6,15] Chl-a was taken as a measure of the photosynthetic biomass and determined with spectrophotometer after extraction in ethanol.[15] Exopolysaccharide content was determined according to the phenol-sulphuric acid method as described by Li et al.[24] Soil organic carbon (C), total nitrogen (N), and total phosphorus (P) were also measured with the standard soil analysis methods described by Nanjing Institute of Soil Research.[25]

Statistic Analysis. Variance of each parameter in the experiment was analyzed with One-way ANOVA at 95% using SPSS 13.0 software. Principal components analysis (PCA) was performed to highlight similarities and differences of soil characteristical variables and vegetation community variables between different experimental conditions using CANOCO 4.5 software. Highly correlated (Pearson, $P < 0.001$) variables were removed from the PCA. Then the first axes of PCA were used in constructing structural equation model (SEM) representing soil charateristics and vegetation communities respectively. The

Table 1. Change of Soil Physicochemical Characteristics in the Different Experimental Conditions

	control	CIT0+Su	CIT0+Sh	CIT3+Su	CIT3+Sh	CIT8+Su	CIT8+Sh
biomass (μg Chl-a cm^{-2})	0 a[a]	0 a	0 a	7.04 ± 0.68 b	18.77 ± 2.44 c	7.06 ± 0.94 b	31.91 ± 5.44 d
exopolysaccharide content (mg g^{-1})	0.03 ± 0.01 a	0.04 ± 0.00 a	0.05 ± 0.01 a	0.71 ± 0.02 b	1.84 ± 0.15 c	0.75 ± 0.08 b	3.31 ± 0.35 d
water content (%)	0.24 ± 0.03 a	0.24 ± 0.03 ab	0.25 ± 0.03 ab	0.29 ± 0.02 ab	0.45 ± 0.04 c	0.29 ± 0.01 b	0.44 ± 0.04 c
crust thickness (mm)	0 a	0 a	0 a	4.36 ± 0.80 b	8.33 ± 0.15 c	3.90 ± 0.35 b	9.05 ± 0.67 c
compressive strength (N cm^{-2})	0 a	0 a	0 a	29.57 ± 2.77 b	66.74 ± 2.54 c	35.54 ± 1.81 d	106.00 ± 4.13 e
bulk density (g cm^{-3})	1.60 ± 0.05 a	1.53 ± 0.02 a	1.55 ± 0.03 a	1.34 ± 0.13 b	1.05 ± 0.01 c	1.36 ± 0.09 b	1.01 ± 0.02 c
porosity (%)	33.82 ± 1.32 a	35.37 ± 1.18 a	36.77 ± 2.04 a	36.88 ± 1.97 a	48.76 ± 1.55 b	38.17 ± 4.71 a	50.79 ± 1.19 b
sand (%)	99.50 ± 0.25 a	98.76 ± 0.73 a	98.44 ± 0.49 a	92.65 ± 0.80 b	84.50 ± 2.29 c	91.19 ± 1.42 b	83.83 ± 6.83 c
silt (%)	0.33 ± 0.29 a	1.06 ± 0.69 a	1.33 ± 0.50 a	6.00 ± 1.97 b	14.15 ± 4.26 c	7.46 ± 1.42 b	14.86 ± 6.95 c
clay (%)	0.17 ± 0.04 a	0.18 ± 0.04 a	0.23 ± 0.04 a	1.35 ± 0.55 b	1.35 ± 0.03 b	1.36 ± 0.13 b	1.31 ± 0.12 b
organic C (g kg^{-1})	0.51 ± 0.04 a	0.57 ± 0.06 a	0.63 ± 0.17 a	5.02 ± 0.21 b	11.47 ± 0.21 c	7.28 ± 0.14 d	17.09 ± 0.26 e
total N (g kg^{-1})	0.08 ± 0.02 a	0.10 ± 0.02 a	0.13 ± 0.03 a	1.10 ± 0.64 b	1.38 ± 0.53 b	1.63 ± 0.47 b	1.77 ± 0.40 b
total P (g kg^{-1})	0.06 ± 0.05 a	0.06 ± 0.04 a	0.06 ± 0.01 a	0.19 ± 0.10 ab	0.17 ± 0.07 ab	0.18 ± 0.04 ab	0.23 ± 0.06 b

[a]The different letters represent the difference for a given parameter is significant at 0.05 level ($P < 0.05$). CIT0, CIT3, and CIT8 respectively represent the using time of cyanobacterial inoculation technology from 0, 3, to 8 years; Su: sunny sides of dunes; Sh: shady sides of dunes.

priori hypothesized theoretical model was given in Figure 1, and SEM analysis was carried out using AMOS 17.0 software.

RESULTS

Development of BSCs and Change of Soil Characteristics. After cyanobacterial inoculation, cyanobacterial crusts formed quickly (in about one week) in the case of adequate moisture conditions, but the newly formed crusts were very thin, light in color, flat, fragile, and easily blown away (SI Figure S1). Then the cyanobacterial crusts gradually developed with increased thickness, darker color, rough surface, and strong compressive strength. On the sandy sides of dunes, mosses began to germinate 2−3 years later after cyanobacterial inoculation, and cyanobacterial crusts gradually succeeded to moss crusts there (CIT3+Sh; Table 1). However on the sunny sides, the crusts entered the later cyanobacterial stages with slow growth approximately 2−3 years later (CIT3+Su; Table 1). Even 8 years after inoculation, scarcely any mosses were found on the sunny sides, while the shady sides had already developed to moss crusts accounting for more than 60% of the soil surface (SI Figure S1 and Table S1).

Different from the above results, it was found on the dunes only fixed by planting *Salix* (without cyanobacterial inoculation; CIT0), no cyanobacterial crusts formed after 3 years, and the soil physicochemical properties were not improved yet ($P > 0.05$). However, with the inoculation of cyanobacteria and formation of cyanobacterial crusts on dunes CIT3 and CIT8, photosynthetic biomass and exopolysaccharide content in the topsoil gradually accumulated; organic carbon and total nitrogen content were improved significantly ($P < 0.05$; Table 1). As expected after the formation of cyanobacterial crusts, soil texture became finer with an increasing percent of fine soil particles (clay content), therefore the bulk density decreased, although soil porosity and water content were not improved significantly on dunes CIT3 ($P > 0.05$; Table 1). In addition, along with crust development, cyanobacterial crusts gradually succeeded to moss crusts (CIT3+Sh and especially CIT8+Sh), where photosynthetic biomass and exopolysaccharide content further accumulated, crust thickness and compressive strength further increased, and soil texture and water condition were also further improved (Table 1).

It was also found that with crust development, the community structure of soil cyanobacteria and algae changed simultaneously (SI Table S2). Three years after inoculation, cyanobacterial and algal species number increased from the initial 2 (inoculum) to 10 (CIT3+Su) and 13 (CIT3+Sh) on the sunny and shady sides, respectively, and this number further increased to 11 (CIT8+Su) and 15 (CIT8+Sh), respectively, 8 years later. Currently, 15 species of cyanobacteria and algae found in the restored region mostly belonged to cyanobacteria, accounting for 46.67% of the total. *Microcoleus*, *Scytonema*, *Nostoc*, and *Phormidium* were the main dominant cyanobacterial species in the BSCs (SI Table S2).

Regeneration of Vascular Plants. At present, as many as 27 species of vascular plants had naturally colonized the restored region, belonging to 21 genera and 8 families (SI Table S3). The main families were *Asteraceae* (11 species), *Poaceae* (5 species), *Chenopodiaceae* (3 species), and *Leguminosae* (3 species), accounting for 81.48% of the total species. Among the present vascular plant species, the main dominant species in the different communities were *Agriophyllum squarrosum*, *Corispermum hyssopifolium*, *Astragalus adsurgens*, *Artemisia scoparia*, *Artemisia sieversiana*, and *Leymus chinensis*. According to the species composition and dominance, the vascular vegetation communities in the restored region could be divided into several relatively steady small community types, in which some patches only dominated by single species, whereas others formed with subdominant or codominant species, such as *C. hyssopifolium* + *A. adsurgens*, *C. hyssopifolium* + *Setaria viridis*, *A. scoparia* + *A. sieversiana*, and *A. scoparia* + *A. sieversiana* + *C. hyssopifolium*. As for the life-form, almost all the naturally colonized vascular vegetation components belonged to the herbaceous species, including the annual, biennial, and perennial, occasionally companioned by a few subshrubs such as *Artemisia ordosica* and *Cynanchum komarovii*. Overall, in the restored region *Artemisia* communities at present took the dominant status.

Succession of Vascular Vegetation Communities. The constructed SEM model rejected the null hypothesis ($P < 0.05$), although the model could explain about 80% of variance in soil characteristics, and 95% of variance in vegetation communities. Therefore, we just accepted the model as a causal model, and the relationship profile among cyanobacterial inoculation, light condition, soil characteristics, and vegetation

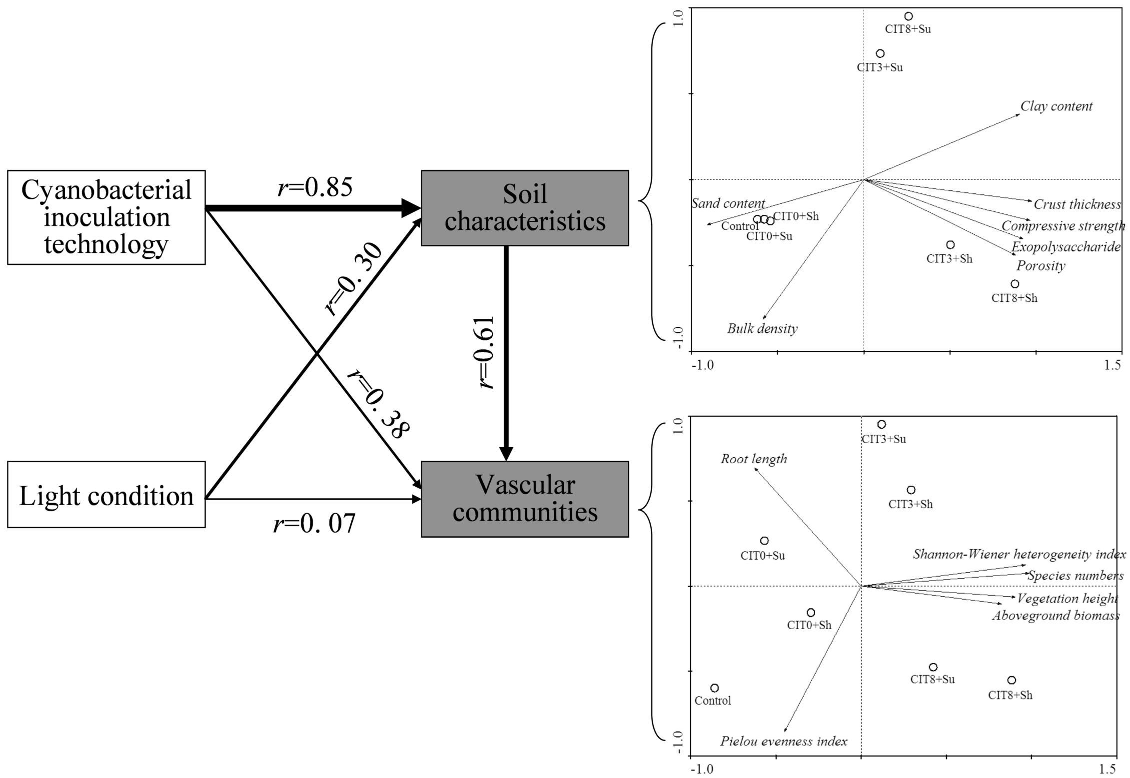

Figure 2. The facilitating effects of cyanobacterial inoculation technology on the succession of vegetation communities. Unidirectional arrows in the causal model (left) indicate a hypothetical causal relationship, and the arrow width indicates the strength of causality, which is accordance with the path coefficients which appear adjacent to arrows. The variables in the shading boxes were represented by the first axes in the principal components analysis of soil characteristical variables (top right) and vegetation community variables (bottom right). The first axes explain 78.9% and 66.7% of the total soil characteristical and vegetation community variables, respectively.

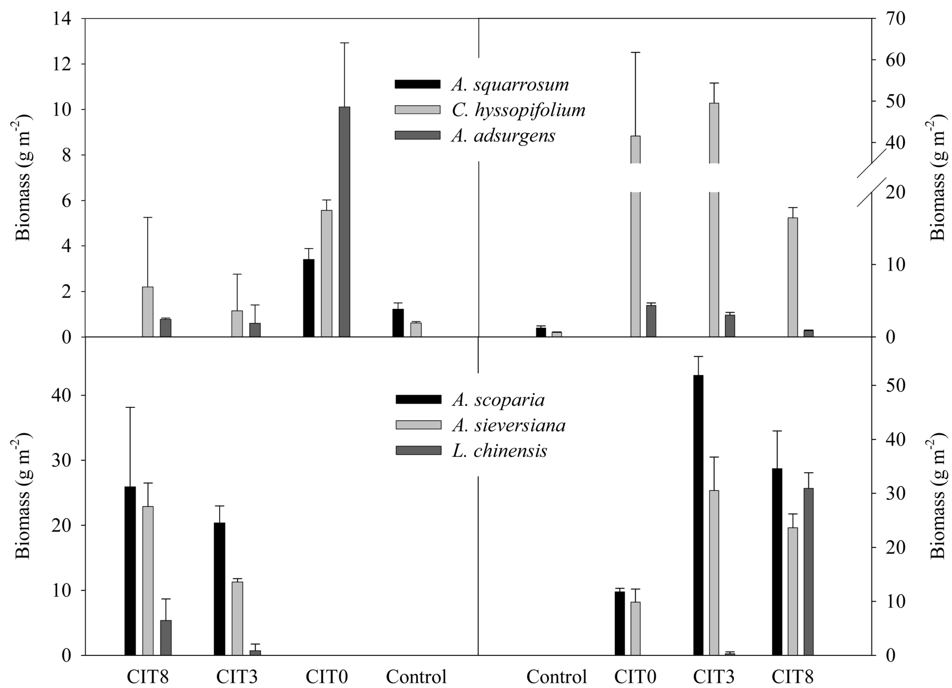

Figure 3. Biomass change of *A. squarrosum*, *C. hyssopifolium*, *A. adsurgens* (top), and *A. scoparia*, *A. sieversiana*, *L. chinensis* (bottom) in the different experimental conditions. The figures on the Left represent the data on the sunny sides of dunes, while the right the data on the shady sides. CIT0, CIT3, and CIT8 respectively represent the using time of cyanobacterial inoculation technology from 0, 3, to 8 years.

communities was given in the causal model (Figure 2). The model indicated cyanobacterial inoculation technology mainly indirectly facilitated the succession of vegetation communities through improving soil available resources ($P < 0.01$), which directly promoted the succession of vegetation communities ($P < 0.001$).

On the shifting sand dunes (Control), only two typical pioneer species *A. squarrosum* and *C. hyssopifolium* survived, while their coverage and biomass were severely limited due to the unconsolidated sand surface (Figure 3; SI Table S3). When fixed via planting *Salix* (CIT0), the unconsolidated sand surface was relatively stabilized, although no crusts formed there. Since then, some other vascular plants began to grow on the dunes and vegetation coverage, density, and heterogeneity increased on both sides of dunes ($P < 0.05$; Table 2). Comparing CIT0 and CIT3, when looking at the sunny sides of dunes, the effects of cyanobacterial inoculation on vegetation heterogeneity and evenness were obvious ($P < 0.05$), while looking at the shady sides, vegetation coverage and biomass were higher with inoculation ($P < 0.05$; Table 2). Moreover, with the time further elapsing (comparing CIT3 and CIT8), the vegetation communities on the sunny sides of dunes had an obvious increase in coverage and evenness; while the communities on the shady sides had a significant increase in vegetation height and density ($P < 0.05$). Overall, compared with the sunny sides of dunes, the shady sides had higher vegetation coverage, biomass, density, and species number (Table 2).

After using cyanobacterial inoculation technology, the dominant vascular plant species also experienced a changing process (Figure 3; SI Table S3). As pioneers, *A. squarrosum* and *C. hyssopifolium* were the dominant species on shifting sand dunes. When the dunes were fixed by planting *Salix* (CIT0), *A. squarrosum* withdrew its dominant status from the vegetation communities (although its biomass presented a brief increase on the sunny sides; Figure 3; SI Table S3). At this time, *C. hyssopifolium* was the sole dominant species on the shady sides of dunes, while *C. hyssopifolium* and *Astragalus adsurgens* were the codominant species on the sunny sides (SI Table S3), and both *C. hyssopifolium* and *A. adsurgens* had their highest biomasses on the dunes CIT0 (Figure 3). *Artemisia scoparia* and *A. sieversiana* appeared after the dunes were fixed by planting *Salix* (CIT0) and their blooms arrived on the dunes CIT3 (Figure 3; SI Table S3). Subsequently, on the shady sides (Sh) of dunes CIT8, the biomasses of *A. scoparia* and *A. sieversiana* decreased as large numbers of *L. chinensis* grew flourishingly there. As the special dominant species, *L. chinensis* only appeared on the crust surface, and possessed a low biomass (0.27–0.72 g m^{-2}) even after 3 years of cyanobacterial inoculation (Figure 3; SI Table S3). Up to 8 years after the inoculation, *L. chinensis* began to propagate in a large number on the shady sides and formed some dominated community patches. In addition, it was interesting to find that the ratio of stem height to root length showed an increasing trend from *A. squarrosum* to *L. chinensis* ($P < 0.05$; SI Figure S2). *Agriophyllum squarrosum* with the minimum ratio about 0.37 was ultimately replaced by *L. chinensis*, whose ratio was about 2.64, about 6.14 times higher than the ratio in *A. squarrosum*.

■ DISCUSSIONS

Change of Soil Available Resources. In the cyanobacterial inoculation technology, *M. vaginatus* and *S. javanicum* were chosen as inocula, because the two filamentous cyanobacteria not only occupy masses of crust biomass, but also play significant roles in the formation of BSCs in natural settings.[5,6,14] After inoculation, on the one hand, cyanobacterial filaments directly bound soil particles through growing and moving. On the other hand, the secreted exopolysaccharides in association with cyanobacterial growth further conglutinated additional soil particles to form firmer soil conglomerations and

Table 2. Characteristics of Vascular Vegetation Communities in the Different Experimental Conditions

	control	CIT0+Su	CIT0+Sh	CIT3+Su	CIT3+Sh	CIT8+Su	CIT8+Sh
species, genus and family numbers	2, 2, 1	5, 5, 4	8, 7, 5	14, 12, 6	19, 16, 8	17, 13, 6	23, 17, 7
vegetation height (cm)	13.17 ± 6.33 a[a]	17.65 ± 12.59 ab	16.32 ± 4.55 ab	29.81 ± 15.06 abc	20.80 ± 0.57 ab	31.22 ± 9.02 bc	39.45 ± 12.14 c
root length (cm)	19.17 ± 1.54 a	20.76 ± 10.90 a	19.17 ± 7.75 a	19.72 ± 7.42 a	19.97 ± 1.67 a	17.41 ± 5.38 a	17.45 ± 0.88 a
vegetation coverage (%)	1.23 ± 0.75 a	12.60 ± 2.82 b	27.60 ± 7.21 c	19.87 ± 2.16 b	83.27 ± 4.97 e	41.03 ± 6.61 d	89.27 ± 1.55 e
aboveground biomass (g m^{-2})	1.87 ± 0.28 a	74.79 ± 13.55 ab	100.31 ± 41.67 ab	42.04 ± 6.80 ab	300.62 ± 72.62 c	161.56 ± 16.64 b	335.20 ± 144.68 c
vegetation density (ind m^{-2})	2.90 ± 1.10 a	71.70 ± 24.90 b	135.32 ± 13.72 bc	79.22 ± 56.78 b	200.54 ± 4.26 c	136.96 ± 1.04 bc	282.63 ± 78.31 d
Shannon–Wiener heterogeneity index (H')	0.67 ± 0.02 a	1.31 ± 0.06 b	1.72 ± 0.25 bc	1.93 ± 0.14 cd	2.11 ± 0.15 cde	2.21 ± 0.33 de	2.50 ± 0.10 e
Simpson heterogeneity index (DS)	0.47 ± 0.02 a	0.70 ± 0.01 b	0.79 ± 0.05 c	0.81 ± 0.06 c	0.83 ± 0.01 cd	0.87 ± 0.05 cd	0.90 ± 0.00 d
Pielou evenness index (JP)	0.96 ± 0.03 a	0.88 ± 0.05 abc	0.89 ± 0.04 ab	0.69 ± 0.00 d	0.78 ± 0.04 cd	0.86 ± 0.00 bc	0.87 ± 0.07 abc
Margalef richness index (Ma)	0.94 ± 0.00 a	0.82 ± 0.17 a	1.22 ± 0.29 ab	2.40 ± 0.81 abc	2.74 ± 0.93 bc	2.54 ± 1.01 abc	3.10 ± 1.13 c

[a]The different letters represent the difference for a given parameter is significant at 0.05 level ($P < 0.05$). CIT0, CIT3, and CIT8 respectively represent the using time of cyanobacterial inoculation technology from 0, 3, to 8 years; Su: sunny sides of dunes; Sh: shady sides of dunes.

cyanobacterial crusts, which ultimately stabilized the soil surface.[15,23]

The formation of cyanobacterial crust also accelerated the succession of soil community structure and crust type. Liu et al.[16] reported cyanobacteria diversity had increased 22 days after inoculation. In the present study, we further found the diversities of chlorophytes, diatoms, and mosses increased with crust development. In our other experiments, it was also found that bacteria, fungi, and actinomycetes increased similarly, along with the development of BSCs.[7,26] Among these crust organisms, those photosynthetic species such as cyanobacteria, algae, and mosses resulted in substantial inputs of carbon (C) into the soil layer, increasing the soil organic matter, and those nitrogen-fixing species such as *Scytonema* and *Nostoc* fixed nitrogen (N), providing the necessary soil N nutrition. Crust organisms also promoted the conversion of sand into soil by increasing soil nutrients and improving topsoil texture.[6,18] In addition, the increased dust deposition on crust surface also could increase soil organic matters and nutrients. [27]

Succession of Vascular Vegetation Communities. The important driving factors for succession of vascular vegetation communities are the colonizing capacity in plants and excess resources in soil.[28−31] Bare and shifting sand dunes are the peak of vegetation degradation and the process of regeneration would experience a gradual change from shifting sand dunes to the fixed ones.[32−34] When only *Salix* were planted to fix the sand dunes in our experiment (CIT0), the sand surface was relatively stabilized within a short time, when the soil texture and nutrition had not been improved, so only a number of vascular plants could survive at this time. However, after cyanobacterial inoculation, the developed artificial BSCs provided not only a more stable soil surface, but also the favorable nutritional conditions for the survival and succession of vascular vegetation communities. Therefore, compared with the shifting sand dunes (Control) and the fixed ones with *Salix* planting (CIT0), the higher vegetation coverage, biomass, and diversity occurred on the dunes covered with BSCs (CIT3 and CIT8). At present, in the experimental region 27 species of naturally colonized vascular plants were found. Compared with the 17 species in the report of Wang et al. (3 years after inoculation),[19] more plant species colonizing the experimental region may be due to the further accumulation of soil available resources.

Comprehensively analyzing the succession sequence of vascular vegetation communities along with the application of cyanobacterial inoculation technology, it was found the dominant species succeeded along the following sequence: *A. squarrosum*, *C. hyssopifolium*, *A. adsurgens*, *A. scoparia*, *A. sieversiana*, and *L. chinensis*, that is from *Chenopodiaceae*, *Leguminosae*, and *Asteraceae* to *Poaceae*. As a pioneer species, Chenopod *A. squarrosum* often first colonizes sand surface due to its unique characteristics:[29,35,36] (1) the small and flat seeds are propitious to resistance to wind erosion and good retention in sandy soil; (2) after germination, its embryo roots can develop a deep root system as fast as possible, maintaining the seedling in sandy soil against wind erosion; (3) *A. squarrosum* also can well adapt to the barren and low-fertility sandy soils. As another pioneer species, *C. hyssopifolium* in our experiment had a lower IV value than *A. squarrosum* on the shifting sand dunes, although *C. hyssopifolium* also could well acclimatize itself to the adverse dune environments.[37,38] However, as annuals, both *A. squarrosum* and *C. hyssopifolium* have to experience a series of vital processes every year, including bearing fruit, seed dispersal, and germination, etc. During each process, any environmental condition of uncertainty could decrease their probability of propagation.[39] Therefore, these two pioneer species subsequently withdrew from the vegetation communities due to their weaker competitive ability compared with later colonized species. [40] In the relatively stabilized dunes where only *Salix* were planted previously, the increased *A. adsurgens* might be related to the nitrogen-fixing of the legume rhizobia.[41] However *A. adsurgens* experienced a decrease when BSCs formed on the dunes, which might suggest that the nitrogen input had transferred mostly from legume rhizobia to crust cyanobacteria. At present, the experimental region as a whole was dominated by *Artemisia* plants, such as *A. ordosica*, *A. argyi*, *A. scoparia*, and *A. sieversiana*. In the degraded grassland ecosystems, *Artemisia* plants often form dominant communities due to their advantages in resisting grazing pressure, including their hard stems and unpleasant volatile.[28,42,43] In the regeneration process of vegetation communities, the biennial and perennial *Artemisia* plants can accumulate more aboveground biomass and play an active role in stabilizing soil surface, and thus have been recognized as important transition species.[40] Eventually, *Artemisia* plants (*Asteraceae*) were replaced by those of the grass family (*Poaceae*) along the direction of succession. That is because those grasses (such as *L. chinensis*) have higher aboveground biological productivity and clonal colonizing capacity in the underground rhizomes, and can thereby effectively expand their root systems to the surroundings and occupy more community resources and space, which is just characteristic of constructive species in climax communities.[44]

Interestingly, along the succession sequence, the ratios of stem height to root length showed an increasing trend in the dominant species. As the underground parts, plant roots play an important role in anchoring plants to the soil layer. Especially on dunes, the anchoring would be an important guarantee to the survival of plants.[29,32] That may be the reason why the investigated dominant species at the early successional stages had the smaller ratios of stem height to root length. With the application of cyanobacterial inoculation technology, the environmental conditions in our experimental region were gradually improved as described above, so the same depth of root system could support the higher vegetation communities and the ratio of stem height to root length increased along with the replacement of dominant species. In addition, Zhang et al.[29] found the ratio of aboveground to belowground biomass showed a decreasing trend with the succession of vegetation communities. Those results imply to us that with the succession of vegetation communities, the underground roots gradually expand to the surrounding soil to compete for more available resources, while the aboveground stems shoot upward, elongating to obtain sufficient light and growth space.

Effect of Light Conditions on the Development of BSCs and Succession of Vegetation Communities. As two different habits, the two sides of dunes have attracted much attention due to their different environmental conditions and biological components.[19,45,46] In our experimental region, it was found that the succession models of both BSCs and vascular vegetation communities were different between the two sides of dunes. On the shady sides, BSCs completely evolved from cyanobacterial crusts to moss crusts after 8 years of inoculation (CIT8+Sh), which may be due to the more favorable soil microenvironments there, such as water conditions, soil texture, and nutrition. However, on the sunny sides of the same dunes, scarcely any mosses were found and BSCs still stopped at the stage of cyanobacterial crusts (CIT8+Su). Similar results were also observed in the natural BSCs in the Negev Desert, where the shady slopes exposed to less direct solar radiation had more water availability, as a result hastened the establishment of mosses and facilitated the crust succession.[45,46] In addition, the vegetation communities on the shady sides of our experimental regions with an obvious increase in vegetation coverage, biomass, density, and species number also might be due to the more favorable environmental conditions there. Overall, the shady sides of dunes were more conducive to crust development and vegetation succession. Therefore, 8 years after using cyanobacterial inoculation technology, the climax vegetation communities—*Leymus chinensis* communities—appeared on the shady sides of dunes.

Artificial Technologies to Reverse Desertification. To reverse desertification, topsoil stability and vegetation regeneration are two important issues, although this progress is quite slow in natural settings.[47] Olson estimated that from bare shifting sand dunes to steady forest communities would experience a succession process of about 1000 years on southern Lake Michigan sand dunes.[48] However, human involvement can accelerate this process. Some researchers even suggested that human impact on the succession was much more important than all other natural factors.[49] In China, the technology to reverse desertification by setting up sand barriers and erecting straw checkerboards was first applied in Shapotou region (at the southeast edge of Tengger Desert) in large-scale.[27] Their results showed 4 years after the dunes were fixed, the aeolian sediment crusts gradually evolved to BSCs, which began to play an important role in the stabilization of dunes. In our experimental region, the vascular vegetation coverage, density, and heterogeneity had a certain increase on the dunes only fixed by planting *Salix*, although no BSCs formed yet 3 years after the dunes were fixed. All these results to some extent support the point of view that artificially accelerating the reversal of desertification is possible. Nevertheless, through setting up sand barriers or erecting straw checkerboards, dunes are only relatively stabilized at the beginning. At this time, the sand surface is still unconsolidated and does not form a whole, so some sand particles would still be carried away and fly everywhere in windy weather. Generally, the sand barriers and straw checkerboards can only last 4−5 years.[27] If BSCs cannot form during this period, the dunes would return to the moving situation. By contrast, our results showed that cyanobacterial crusts could form quickly after using cyanobacterial inoculation technology, making the original unconsolidated sand particles cement together with each other, providing more stable soil surface microenvironments for vegetation communities, and ultimately facilitating the succession of vegetation communities, which demonstrates that the technology via inoculating cyanobacteria to construct artificial cyanobacterial crusts is an effective and desirable model for desertification control in China and elsewhere.

■ ASSOCIATED CONTENT

Ⓢ Supporting Information

All the treatments designed in the experiment (Table S1); variations of cyanobacterial and algal species diversity after using cyanobacterial inoculation technology on dunes (Table S2); vascular plant components and their relative important values (IV) under the different experimental conditions (Table S3); developmental and successional model of BSCs after the cyanobacterial inoculation on dunes (Figure S1); and ratios of stem height to root length in several dominant species (Figure S2) are given as supporting information.This information is available free of charge via the Internet at http://pubs.acs.org.

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Notes

The authors declare no competing financial interest.

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