

# Effects of covering sand with different soil substrates on the formation and development of artificial biocrusts in a natural desert environment

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## ABSTRACT

In recent years, artificial biological soil crusts (BSCs)—i.e., the inoculation of soil with cyanobacteria—have become one of the most promising biotechnological strategies for preventing soil erosion and restoring soil functionality in degraded drylands. In order to use this biotechnology on a large scale, researchers must explore methods that enable rapid and largescale propagation of soil inoculum, as well as testing methods for developing artificial BSCs in the field. To help do this, we tested the effects of four soil substrates on the development of artificial BSCs in the Tengger Desert. Each soil substrate was collected from a different area in Zhongwei city in northern China and had different particle sizes and nutrient contents. We measured artificial BSCs characteristics according to the coverage, thickness, and wind erosion resistance of the BSCs analyzed. After 12 months, incubated artificial BSC coverage in incubated soils rose from 6% to 20%, and thickness rose from 2.94 to 4.06 mm. Incubated BSC coverage was positively correlated with fine material content (i.e., soil particle size less than 0.10 mm). There was also a positive relationship between coverage and soil organic matter, total nitrogen, and total phosphorus. Artificial BSC inoculation significantly improved soil resistance to wind erosion. These findings indicate that soil substrates improve BSC recovery rate over sand substrates by enhancing sand surface stabilization, increasing initial silt and clay content and nutrient content, especially soil organic matter content. Considering the scarcity of soil resources and the advantages of reusing soil resources, we suggest that left-over soils dredged from irrigation channels and abandoned farmlands can be used as substrate for the propagation of BSC inoculum.

## 1. Introduction

Biological soil crusts (BSCs) are a community of interacting autotrophic and heterotrophic organisms that are associated with cyanobacteria, algae, fungi, lichens, and mosses (West, 1990). BSCs are commonly referred to as a “living skin” on the soil surface and are found in many low-productivity ecosystems around the world. It is estimated that BSCs cover approximately 12% of the Earth's land surface (Rodríguez-Caballero et al., 2018). As ecosystem engineers associated with both abiotic and biotic processes, BSCs play a particularly vital role in ecological restoration, since they help stabilize soils (Zhao et al., 2019; Zhao et al., 2021), improve carbon and nitrogen fixation and nutrient cycling (Eldridge and Delgado-Baquerizo, 2019; Hu et al., 2020; Zhao and Zhang, 2021), mediate hydrological processes (Kidron and Yair, 1997; Li et al., 2021; Xiao and Hu, 2017), adjust soil microbe abundance

and community diversity (Xiao and Veste, 2017; Zhao et al., 2020) and enhance plant survival by increasing essential nutrients (Belnap and Lange, 2003). Obviously, BSCs health is closely associated with important ecological functions in arid and semi-arid ecosystems (Antoninka et al., 2020a; Chiquoine et al., 2016).

According to Rodríguez-Caballero et al. (2018), it is thought that climate change and land-use intensification will lead to a decline in BSCs coverage by approximately 25–40% within the next 65 years. It is expected that the loss of BSCs will negatively affect ecosystem functioning in multiple ways, including an increase in soil dust and a decrease in carbon and nitrogen fixation, which will lead to increasing CO<sub>2</sub> emissions and reductions in soil nitrogen availability (Antoninka et al., 2020a; Chiquoine et al., 2016; Ferrenberg et al., 2017). Due to their key ecological roles in dryland ecosystems, artificial BSCs (i.e., the inoculation of soil with cyanobacteria) (Antoninka et al., 2020b; Román et al.,

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2018; Xiao et al., 2019) have become one of the most promising biotechnological strategies for decreasing abiotic stress and restoring soil functionality in degraded desert ecosystems (Antoninka et al., 2020b; Chamizo et al., 2018; Chock et al., 2019). Importantly, BSCs can be rapidly incubated in both laboratory and field conditions, making it easy to develop and implement them over a variety of different regions. In laboratory conditions, Park et al. (2014) used cyanobacteria combined with a superabsorbent polymer to successfully cultivate BSCs over a period of three months. In a greenhouse setting, Antoninka et al. (2016) found that cultivated BSCs were able to establish in sand rapidly, attaining ~82% coverage in one year. In the Tengger Desert, northern China, Park et al. (2017) showed that a combination of cyanobacteria and soil-fixing chemicals was an effective way to facilitate artificial cyanobacterial crust growth and development in the field. Meanwhile, Bu et al. (2018) and Xiao et al. (2015) successfully cultured moss crust in degraded area in Loess Plateau. However, restoration of ecosystem functions using BSCs remains challenging at large scales (Antoninka et al., 2020a; Román et al., 2020; Zhou et al., 2020).

Numerous studies have indicated that establishing BSCs in the field requires stable soil surfaces (Faist et al., 2020; Young et al., 2019; Zhao et al., 2021). In order to allow BSCs to successfully establish in sand surface, a broad range of soil stabilizing methods must be tested. Possible methods include using mechanical barriers (e.g., straw checkerboard barriers) (Antoninka et al., 2020a; Bowker et al., 2020; Faist et al., 2020), which increases surface roughness and reduces wind erosion (Zhao and Wang, 2019), or synthetic soil stabilization products (e.g., Tacki-Spray<sup>TM</sup> and Modified water-borne polyurethane) (Park et al., 2017; Zhao and Wang, 2019), polysaccharide glues and polyacrylamides (Fick et al., 2020), or polyacrylamide gels (Chandler et al., 2019; Faist et al., 2020). Furthermore, covering soils with a clay barrier is also an effective way to stabilize sand surfaces, and is widely used for dryland restoration across China (Wu, 2009). However, it remains unclear how clay barrier methods benefit the establishment of artificial BSCs in field conditions.

Soil properties are another key factor that influence both artificial and natural BSC colonization (Antoninka et al., 2020a; Chamizo et al., 2018; Li et al., 2017). In the Great Basin Desert (a cool desert ecosystem), Chock et al. (2019) demonstrated that the highest BSC coverage occurred on clay soils rather than on sandy clay loam soils. Román et al. (2018) compared coverage of artificial cyanobacteria crusts that were cultivated with Amoladeras, El Cautivo (in Tabernas desert, hot desert) and Gádor quarr-developed soils in southeastern Spain. They found that Amoladeras-developed soils showed the highest cyanobacteria crust coverage in 3 months inoculation period in laboratory. Zaady et al. (2017) examined the effects of adding coal fly-ash and bio-inoculant to sand surfaces on the cultivation of filamentous cyanobacteria crust. They showed that the treatments with sand + BSC inoculum + coal fly-ash performed significantly better than the sand-only treatment. Giraldo-Silva et al. (2020) and Velasco Ayuso et al. (2020) used two texturally different soils from the cool Great Basin Desert and the hot Chihuahuan Desert to cultivate BSCs, demonstrating that native soils can inoculate whole natural BSC communities or individual isolates. In each of these examples, soil substrates were selected according to differences in soil conditions, including physicochemical properties, which might cause different responses during BSC cultivation (Antoninka et al., 2020a; Román et al., 2018). Soil properties must be taken into account when assessing BSC restoration treatments (Chock et al., 2019). However, almost all of these studies occurred in hot and cold deserts. There is relatively little data describing the effects of soil substrate on the colonization and development of artificial cyanobacteria crust in temperate desert ecosystems.

Here, we investigated the effects of four soil substrates collected from the southeast edge of the temperate Tengger Desert in northern China on the colonization and development of artificial BSCs. The specific objectives were: 1) to test how clay barrier methods influence the establishment of artificial BSCs in a natural desert environment; 2) to evaluate

the effects of different soil substrate fine material and nutrient contents on the colonization and development of artificial BSCs; and 3) to select the ideal soil substrate used to cultivate artificial BSC organisms in temperate desert ecosystems.

## 2. Materials and methods

### 2.1. Study site

We conducted our experiment within the Shapotou Desert Research and Experiment State Station, which is located on the southeastern edge of the Tengger Desert in northern China (37°27'36.8"N, 105°00'42.7"E). The station is at an elevation of 1339 m and the primary soils in the region are orthic sierozem and aeolian sandy soils (Li et al., 2010). The mean annual air temperature and wind velocity are 9.6 °C and 2.9 m s<sup>-1</sup>; mean annual rainfall is 186.6 mm. Most rainfall occurs from June to September (Li et al., 2005). The dominant vegetation consists of shrubs, forbs, and grasses. Common species include *Artemisia ordosica* Krasch., *Reaumuria soongorica* Maxim, *Salsola passerina* Bunge, *Oxytropis aciphylla* Ledeb., *Caragana korshinskii* Kom., *Ceratoides latens* Reveal et Holmgren, *Stipa breviflora* Griseb., *Carex stenophylloides* Krecz., and *Cleistogenes songorica* Ohw. Total vegetation cover are about 1% and 30% on aeolian sandy and orthic sierozem soils, respectively (Li et al., 2004).

Open areas between perennial plants are colonized by well-developed BSCs that are dominated by cyanobacteria, algae, lichens, and mosses. Dominant cyanobacteria include *Anabaena*, *Hydrocoleus*, *Lyngbya*, *Microcoleus*, *Oscillatoria*, *Phormidium* and *Scytonema*. Common mosses include *Bryum* and *Didymodon*. The lichen primarily include *Collema* and *Endocarpon* (Li, 2012; Wang et al., 2020).

### 2.2. Field soil and BSCs collection

We used four soil substrates collected from four different areas in the Zhongwei city, Ningxia Hui Autonomous Region, on the southeastern edge of the Tengger Desert (northern China; Fig. 1). The four sites are described as follows: Site 1: Xiaohong Mountain (37°29'47.00"N, 104°25'32.99"E) is at an elevation of 1657.0 m, and has light gray soil color with a pH of 8.1; Site 2: Shapotou Station experimental area (37°27'04"N, 105°00'21"E) is at an elevation of 1250.0 m, with grayish yellow soil color and a pH of 7.9; Site 3: abandoned farmland in Heilin village of Zhongwei city (37°27'22.9"N, 105°03'33.49"E) at an elevation of 1198.2 m, with yellow brown soil color and pH of 8.4; Site 4: dredged soil from Meili irrigation channel next to an abandoned farmland (37°27'21.66"N, 105°03'25.18"E) at an elevation of 1201.0 m, with yellow brown soil color and pH of 8.3 (Fig. 1). Other soil properties are described in Fig. 2. Soils were collected from 0-10 cm depth. Soil samples were sieved to 2 mm to remove herbs, roots and other fragments.

We also collected naturally developed cyanobacteria and cyanobacteria-lichen crusts along the southeastern edge of the Tengger Desert. Sixteen natural cyanobacteria-lichen crusts and 16 natural cyanobacteria crust samples were taken, each with 600 cm<sup>2</sup> (equivalent to 6% coverage in a 1 m<sup>2</sup>-plot). Average diameters of the natural cyanobacteria crust and cyanobacteria-lichen crust fragments were 17.52 ± 1.20 mm and 17.08 ± 1.49 mm, respectively.

### 2.3. Experimental design

In August of 2017, we established experimental plots in mobile dunes, where no BSCs had developed on the sand surface. We flattened the dunes so their sand surfaces were level (not curved or sloping) and free of rock fragments and vascular plant vegetation and litter. We covered the experimental plots with the different soil substrates that we had collected from different areas in Zhongwei city, covering the sand surface with 100% coverage and a 2-cm thickness. We followed a full-factorial design with 4 soil substrates and with and without cyanobacteria or cyanobacteria-lichen crust additions, generating a total of 12

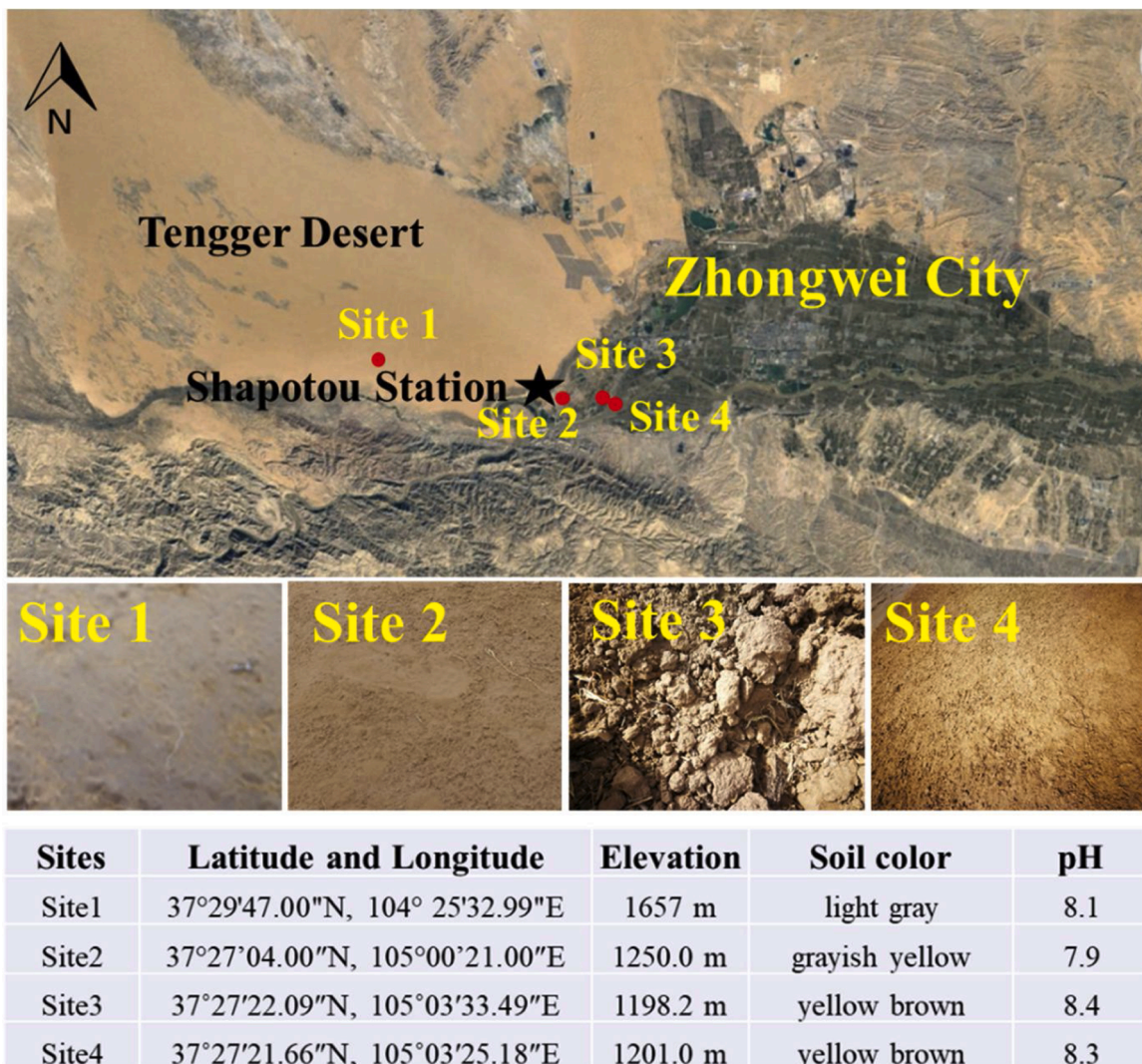


Fig. 1. Map of soil substrate collection locations and soil characteristics. Site 1: Xiaohong Mountain; Site 2: the sandy Shapotou Station experimental plot; Site 3: abandoned farmland in Heilin village; Site 4: a dredged area of the Meili irrigation channel.

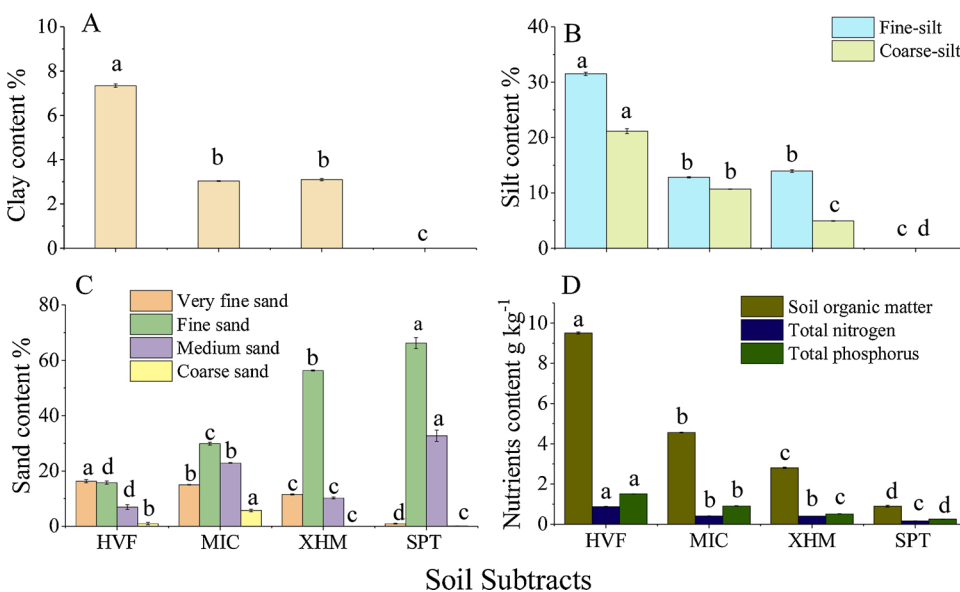


Fig. 2. Soil particle size distribution characteristics—clay content (A), silt content (B), sand content (C), and soil organic matter, total nitrogen and total phosphorus contents (D)—in soils collected from abandoned farmland in Heilin village of Zhongwei city (HVF); a dredged area of the Meili irrigation channel (MIC); Xiaohong Mountain (XHM); and the sandy Shapotou Station experimental area (SPT). Different letters indicate statistically significant differences ( $p < 0.05$ ) between soil substrates. Bars represent one standard error.

different treatments. We randomly assigned treatments to plots and replicated each treatment 4 times, creating a total of 48 1-m<sup>2</sup> (1 × 1 m) plots. We spread (through random broadcast sowing) collected natural cyanobacteria-lichen fragments (NCL) and natural cyanobacteria fragments (NC) on each plot once. During the broadcast-dispersal process, NCL and NC fragments disaggregated and homogeneously spread across the plot surface, covering each plot with 600 cm<sup>2</sup> (equivalent to 6% cover in a 1-m<sup>2</sup> plot). We did not add supplemental water to any of the plots and rainfall during study was the only source of water.

#### 2.4. Field measurements

We measured artificial BSC coverage in October 2017 and in September 2018 using a point sampling frame (Li et al., 2010). We also measured the thickness of BSCs in September 2018 using vernier calipers. To measure wind erosion thickness, we placed 48 steel chisels (0.5 m length and 0.02 m diameter) randomly inserted into the soil within each plot. We measured the height of the steel chisels 2 times: at the start of the experiment (August 2017) and in September 2018.

We measured soil particle size of each soil substrate using the pipette method (Loveland and Walley, 2001). We also measured soil organic matter, total nitrogen, and total phosphorus using standard soil analysis methods described by the Nanjing Institute of Soil Research (1980).

Estimates of daily wind direction, daily average wind speed, and maximum wind speed at 1-m height were obtained from a meteorological station (MILOS 520, Vaisala Company, Helsinki, Finland) located 300 m from the experimental plots (Fig. S1 and S2). The primary wind direction was westward during most of the study period (Fig. S1). Daily average wind speed ranged from 0.69 m s<sup>-1</sup> to 2.89 m s<sup>-1</sup>, with an average speed of 1.40 m s<sup>-1</sup> (Fig. S2A). Daily maximum wind speed ranged from 1.63 m s<sup>-1</sup> to 6.51 m s<sup>-1</sup>. Maximum wind speed exceeded 4.0 m s<sup>-1</sup> (wind speed of sand movement) a total of 248 days, and wind speeds exceeding 5.0 m s<sup>-1</sup> and 6.0 m s<sup>-1</sup> were observed 128 days and 33 days, respectively (Fig. S2B).

#### 2.5. Data analyses

We used a one-way ANOVA to assess differences in soil and BSC variables among the 12 different treatments. A two-way ANOVA was used to assess the effect of soil substrates and incubated BSC types on the coverage and thickness of artificial BSCs. A post-hoc test was conducted using Duncan's multiple range test when the assumption of equal variance was met. When this assumption was not met, we used Tamhane's T2. We analyzed the relationships between incubated BSC properties and wind erosion resistance and soil properties using linear regression. BSC coverage and thickness were treated as dependent variables, while wind erosion resistance and soil particle size and nutrient content were treated as independent variables. In addition, we conducted stepwise linear regression analysis using incubated BSC coverage and thickness as dependent variables, and with soil particle size and nutrient content as independent variables. Finally, we used structural equation modeling (SEM) to evaluate the effects of soil particle size and soil nutrients content on the coverage and thickness of the incubated biocrusts. All of the statistical analyses were performed using the SPSS 16.0 statistical software (SPSS Inc., Chicago, IL, USA). SEM analyses were conducted using AMOS 2.1 software.

### 3. Results

#### 3.1. Soil substrate particle size and nutrient content

Soils collected from an abandoned farmland had clay, fine- and coarse-silt contents of 7.34%, 31.51% and 21.13%, respectively; higher than soils dredged from an irrigation channel (3.04%, 12.8% and 10.68%) and soils from Xiaohong Mountain (3.09%, 13.90% and 4.92%) ( $p < 0.05$ ) (Fig. 1). We found almost no clay or silt in the sandy soils from

Shapotou Station experimental area. Very fine sand content from abandoned farmland soils was 16.30%, followed by dredged soils (15.00%), Xiaohong Mountain soils (11.50%) and sandy Shapotou Station soils (0.96%). Sandy Shapotou Station soils had the highest fine- and medium- sand content (66.24% and 32.71%), higher than dredged soils, Xiaohong Mountain soils, and abandoned farmland soils ( $p < 0.05$ ) (Fig. 2A-C).

Abandoned farmland soils had the highest organic matter content (9.50 g kg<sup>-1</sup>), followed by dredged soils (4.56 g kg<sup>-1</sup>), Xiaohong Mountain soils (2.81 g kg<sup>-1</sup>) and sandy soils (0.89 g kg<sup>-1</sup>). Total nitrogen content in abandoned farmland soils was 0.88 g kg<sup>-1</sup>, which was significantly higher than for dredged soils (0.41 g kg<sup>-1</sup>), Xiaohong Mountain soils (0.40 g kg<sup>-1</sup>), and sandy Shapotou Station soils (0.16 g kg<sup>-1</sup>;  $p < 0.05$ ). The highest total phosphorus content occurred in abandoned farmland soils (1.51 g kg<sup>-1</sup>), followed by 0.91 g kg<sup>-1</sup> in dredged soils, 0.51 g kg<sup>-1</sup> in Xiaohong Mountain soils, and 0.25 g kg<sup>-1</sup> in sandy Shapotou Station soils. Soil nutrient levels in the sandy Shapotou Station soils were significantly lower than for the other 3 soil substrates (Fig. 2D).

#### 3.2. Coverage, thickness, and wind erosion resistance of incubated BSCs

Within most treatments, BSC coverage increased rapidly during the first two months of incubation in the field before leveling off over the next 10 months. Exceptions included sandy Shapotou Station soils with NC and NCL treatments, where coverage declined during the last 10 months (Fig. 3A). After 12 months of development, all treatments had significantly more BSC coverage than did control plots (CK), which had little to no cyanobacterial crust development. BSCs had higher coverage in soils with incubated treatments (i.e., dredged soils, Xiaohong Mountain soils, and abandoned farmland soils with NC and NCL) compared to the sand-incubated cyanobacterial treatments (sandy Shapotou Station soils with NC and NCL; Fig. 3A).

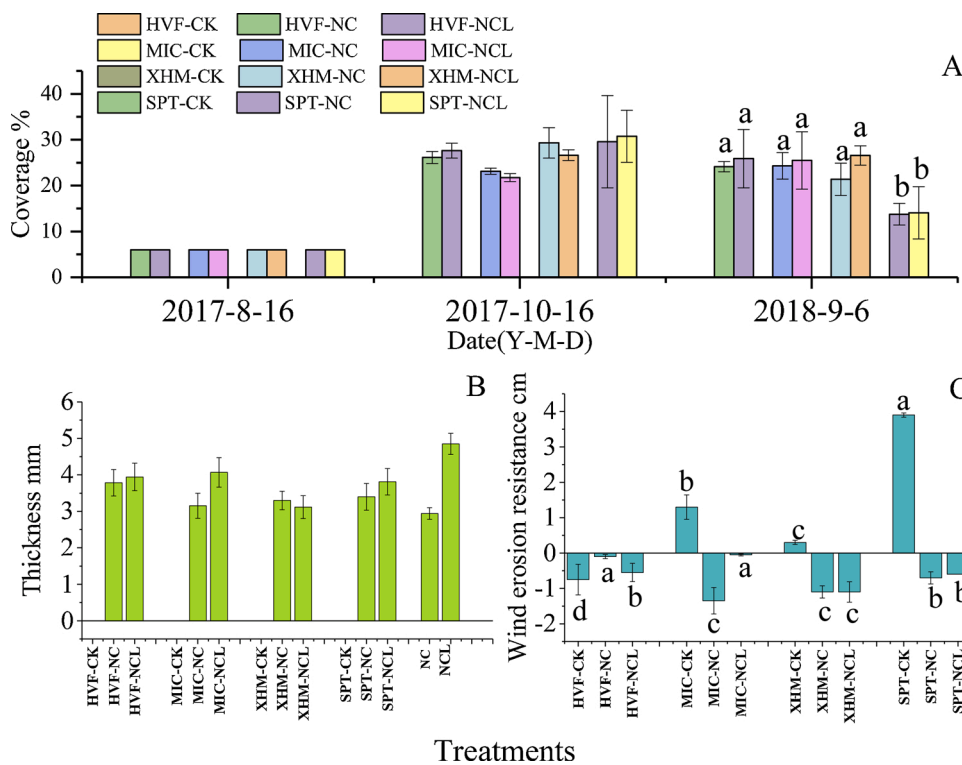
After 12 months, the thickness of the incubated BSCs in the dredged soils, Xiaohong Mountain and abandoned farmland soils with NC treatments were greater than the initial thickness of the NC (2.94 mm). However, the thickness of BSCs in the dredged soils, Xiaohong Mountain soils, and abandoned farmland soils with NCL treatments were lower than the initial thickness of the NCL (4.85 mm; Fig. 3B).

Wind erosion resistance (here lower values reflect greater resistance to wind erosion) was worst in the sandy Shapotou Station soils treatment (3.90 cm), followed by the dredged soils, Xiaohong Mountain soils, and abandoned farmland soils treatments (1.30, 0.30 and -0.75 cm, respectively; Fig. 3C). Twelve months after incubated BSCs were colonized, wind erosion resistance was best in the dredged soils with NC (-1.35 cm) and Xiaohong Mountain soils with NCL (-1.10 cm) treatments (Fig. 3C). Coverage and thickness of incubated BSCs both showed positive relationships with wind erosion resistance ( $R^2 = 0.36$  and  $0.35$ ,  $p = 0.040$  and  $0.041$ ; Fig. 4A and B).

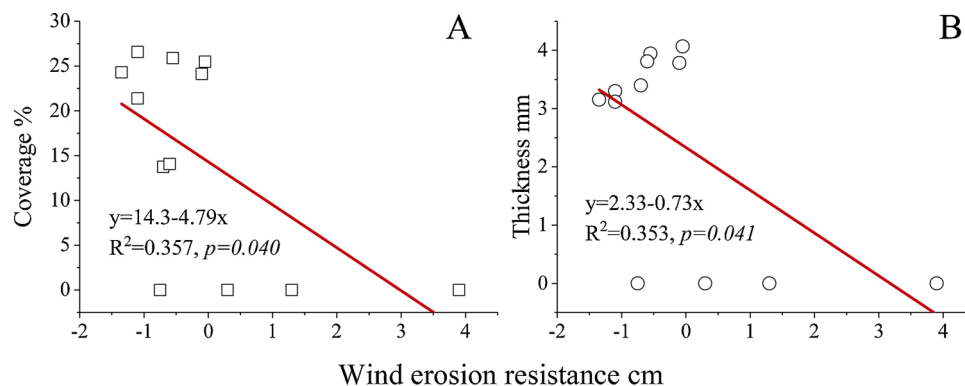
#### 3.3. Relationship between incubated BSC characteristics and soil properties

Soil particle size was positively related to coverage of incubated BSCs ( $R^2 = 0.35$ ,  $0.35$ ,  $0.31$  and  $0.55$ ,  $p < 0.001$ ; Fig. 5 A-D). Fine sand and medium sand content were negatively related to coverage ( $R^2 = 0.38$  and  $0.32$ ;  $p < 0.100$ ; Fig. 5 E and F). For soil nutrients content, soil organic matter, total nitrogen, and total phosphorus were positively related to coverage of incubated BSCs ( $R^2 = 0.28$ ,  $0.28$  and  $0.30$ ;  $p = 0.002$ ,  $0.002$  and  $0.001$ ; Fig. 6). However, there was no relationship between thickness of incubated BSCs and all soil properties (Table S1). Stepwise regression analyses suggested that very fine sand content explained 55.7% of the variation in coverage ( $F = 37.7$ ,  $R^2 = 0.56$ ,  $p < 0.001$ ; Table 1 and Table S2).

The two-way ANOVA analysis showed that soil substrate ( $F = 12.86$ ,  $p < 0.001$ ), incubated BSC types ( $F = 215.74$ ,  $p < 0.001$ ) and the



**Fig. 3.** Coverage (A), thickness (B), and wind erosion resistance (C) of biocrusts incubated on soil substrates collected from abandoned farmland in Heilin village of Zhongwei city (HVF); a dredged area of the Meili irrigation channel (MIC); Xiaohong Mountain (XHM); and the sandy Shapotou Station experimental area (SPT). For wind erosion resistance, lower values reflect better resistance to wind erosion. Bars for natural cyanobacteria crust fragments (NC) and natural cyanobacteria-lichen crust fragments (NCL) reflect initial thickness prior to applications of those treatments. Different letters reflect statistically significant differences ( $p < 0.05$ ) between treatments. Bars represent one standard error.



**Fig. 4.** Linear regression analyses showing coverage (A) and thickness (B) of incubated biocrusts with wind erosion resistance. For wind erosion resistance, lower values reflect better resistance to wind erosion.

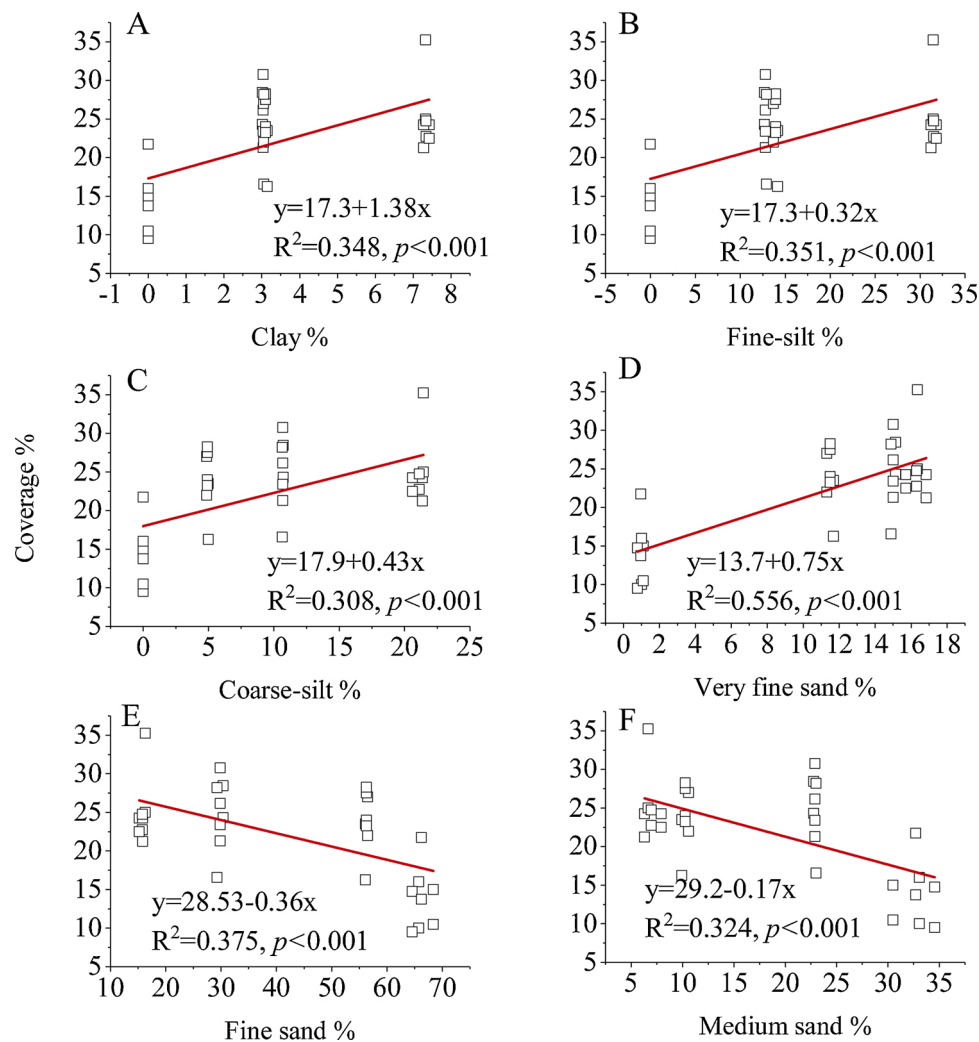
interaction between soil substrate and incubated BSC types ( $F=3.59, p = 0.007$ ) significantly affects artificial BSC coverage. Together, these variables explained 93.2% of the variation in BSC coverage. However, only incubated BSC types ( $F=208.27, p < 0.001$ ) had a significant impact on artificial BSCs thickness. This variable alone explained 92.2% of the variation in BSCs coverage (Table 2).

In addition, our SEM explained 65.8% and 14.6% of the variations in coverage and thickness of the incubated biocrusts. Clay (Standardized Coefficients = 0.591;  $p < 0.001$ ), fine-silt (Standardized Coefficients=0.434;  $p = 0.001$ ), coarse-silt (Standardized Coefficients=0.389;  $p = 0.001$ ), very fine sand (Standardized Coefficients=0.808;  $p < 0.001$ ) and soil organic matter (Standardized Coefficients=0.219;  $p < 0.05$ ) had positive effects on artificial BSC coverage; coarse-silt and fine sand (Standardized Coefficients=0.252 and -0.515;  $p < 0.10$  and  $<0.05$ ) had positive and negative effects on artificial BSCs thickness (Fig. 7 and Table S3).

#### 4. Discussion

##### 4.1. Covering soil substrate on sand surface was benefit to artificial BSCs colonization and development

Wind is a major erosive force in deserts. Multiple studies have demonstrated that the successful colonization of BSCs in harsh dryland environments depends on the stability of the sand soil surface; wind erosion is an intermittent disturbance event that limits the colonization of BSCs (Li et al., 2016; Park et al., 2016). The study from Negev Desert showed that abrasion and flaking lead to BSC destruction and degradation and to sand mobilization. High-speed wind may impede BSC establishment and wind erosion increases BSCs vulnerability, reflected by declines in BSC cover (Kidron et al., 2020; Kidron et al., 2017). In the Gurbantunggut Desert, Zhang et al. (2006) found that disturbance of sandy soil surfaces by wind greatly decreases soil resistance and disadvantages BSC establishment. In a field study, Zhao and Wang (2019) also found BSC coverage was significantly negatively related to wind erosion.



**Fig. 5.** Linear regression analyses showing coverage of incubated biocrusts with soil particle size. Clay content (%), A), Fine-silt content (%), B), Coarse-silt content (%), C), Very fine sand content (%), D), Fine sand content (%), E) and Medium sand content (%), F).

Our results agree with previous findings that wind erosion is negatively related to coverage and thickness of incubated biocrusts.

Relatively faster biocrust recovery rates occur on stable sand or soil substrates, even if after small disturbances (Rodríguez-Caballero et al., 2018; Xiao et al., 2019). To stabilize sand surfaces, many researchers and restoration managers use mechanical barriers, such as straw checkerboard barriers and clay barriers, and chemical sand fixing to stabilize soil surfaces (Bo et al., 2015; Bowker et al., 2020; Peng et al., 2017). Covering sand with soil substrates (clay barriers) is a traditional sand fixing method used widely in northern China (Collin et al., 2002; Sun et al., 2012; Wu, 2009). A 6-year field study in the Badain Jaran Desert, showed that clay barriers can significantly reduce 0-20 cm sand surface wind speed and sand transport rate by 80% compared to bare sand. Clay barriers kept good shape for the first 3 years, and were just 20% damaged in sixth year (Sun et al., 2012; Wu, 2009). Thus, using clay barriers to stabilize sand surfaces can reduce the risk of soil wind erosion over short time periods, up to at least 3 years. Compared to coarser textured soils, finer soil textures are more stable due to their higher surface area-to-volume ratio, which enhances their ability to bind to minerals and organic matter (NRCS, 1996). In our own study, even though wind speeds greater than  $4.0 \text{ m s}^{-1}$  (threshold value of sand movement) were observed in 248 days, we still found that covering sand by soils significantly improved their resistance to wind erosion. Also, the three soil substrate-covering treatments with clay and silt components (abandoned farmland soil collected from Heilin village, dredged soil

from Meili irrigation channel, and Xiaohong Mountain soils) had higher wind erosion resistance and higher BSC coverage than sand (sandy Shapotou Station soils) plots after 12 months (Fig. 3C). These results suggest that covering sand dunes with substantially more consolidated soil substrates can drastically reduce sand erosion. These stabilized sand surfaces can provide a good environment for BSC formation and therefore assist crust recovery in natural desert habitat. More importantly, if artificial biocrusts successfully colonize, the restored area will have less risk of secondary soil wind erosion.

#### 4.2. Fine material and nutrient contents in soil substrates significantly influence the development of artificial BSCs

BSC development and recovery were tightly with soil habitats (Kidron et al., 2020). Numerous studies have reported positive feedbacks between natural BSCs and fine particle content of soils (Belnap and Lange, 2003; Li, 2012). Likewise, clay, silt and fine sand particles are recognized for their importance in the establishment, development, and recovery of BSCs (Belnap and Lange, 2003). For example, based on field investigation, Li et al. (2017) found that total BSC coverage was significantly positively correlated with silt and the clay content. Zaady et al. (2017) showed that cyanobacteria use fine particles of coal fly-ash as bridges for growing toward and adhering to larger sand particles. Faist et al. (2020) and Chock et al. (2019) both showed that BSC recovery was faster within finer-textured sites than in coarser-textured

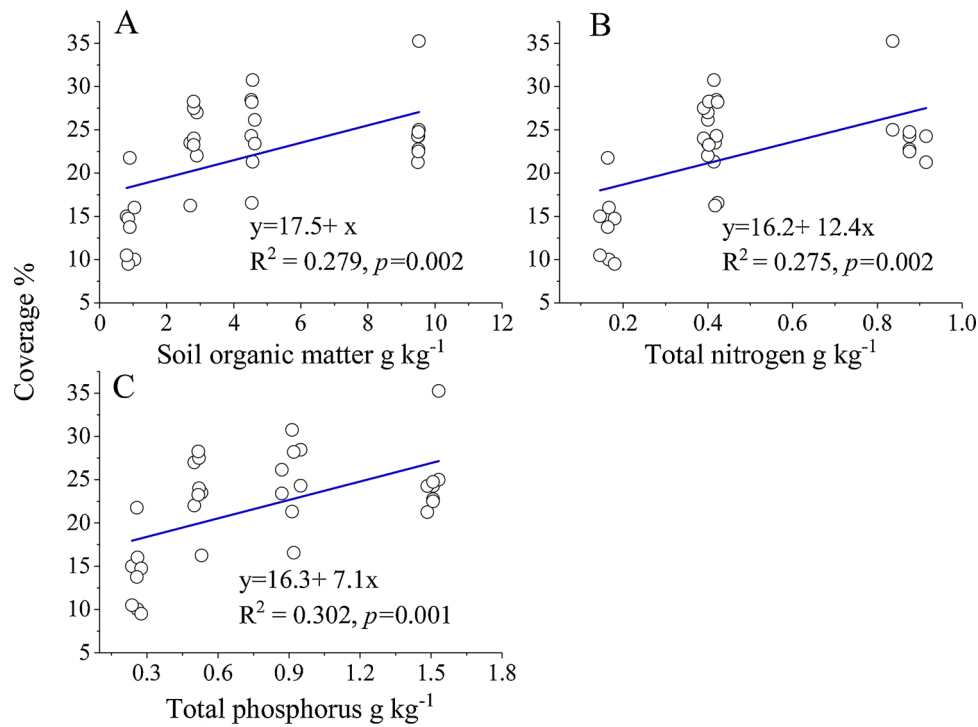


Fig. 6. Linear regression analyses showing coverage of incubated biocrusts with soil nutrient content. Soil organic matter ( $\text{g kg}^{-1}$ ; A), Total nitrogen ( $\text{g kg}^{-1}$ ; B) and Total phosphorus ( $\text{g kg}^{-1}$ ; C).

Table 1

Stepwise regression analysis showing the effects of soil particle size on the coverage of incubated biological soil crusts. Bold type mean significance at  $p < 0.05$  level.

Dependent Variable	Constant	Very fine sand %	R <sup>2</sup>	F	p
Coverage %	13.70	0.76	0.557	37.73	<0.001

Table 2

Two-Way ANOVA showing the effect of soil substances and incubated biological soil crusts (BSCs) types on artificial BSCs coverage and thickness. Bold types mean significance at  $p < 0.05$  level.

Source	Type III Sum of Squares	Mean Square	F	p
Coverage				
Corrected Model	5904.47 <sup>a</sup>	536.77	44.69	<0.001
Intercept	10293.09	10293.09	856.99	<0.001
Soil substances	463.25	154.42	12.86	<0.001
Incubated BSCs types	5182.46	2591.23	215.74	<0.001
Soil substances × Incubated BSCs types	258.76	43.13	3.59	0.007
Error	432.39	12.01		
Thickness				
Corrected Model	139.98 <sup>b</sup>	12.73	38.71	<0.001
Intercept	272.18	272.18	827.84	<0.001
Soil substances	1.17	0.39	1.19	0.328
Incubated BSCs types	136.95	68.47	208.27	<0.001
Soil substances × Incubated BSCs types	1.87	0.31	0.95	0.473
Error	11.84	0.33		

a.  $R^2 = 0.932$  (Adjusted  $R^2 = 0.911$ ); b.  $R^2 = 0.922$  (Adjusted  $R^2 = 0.898$ ).

sites. In our own study, clay, fine-silt, coarse-silt, and very fine sand content were positively correlated with coverage of incubated BSCs. Very fine sand content alone explained 55.7% of the variation in BSC coverage. Cyanobacteria colonize quickly on finer textured soils, probably because of the greater ability of cyanobacterial trichomes to bridge

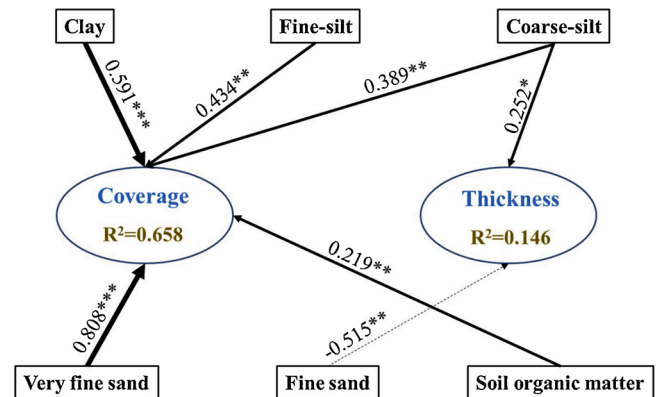


Fig. 7. Structural equation model fitted to the coverage and thickness of the incubated biocrusts derived from soil particle size and soil nutrients content. Numbers adjacent to arrows are standardized path coefficients of the relationship.  $R^2$  = the proportion of variance explained.  $p$  values are as follows: \*  $< 0.01$ ; \*\*  $< 0.05$  and \*\*\*  $< 0.001$ . Solid and dash lines are positive and negative relationships, respectively.

smaller spaces between soil particles (Belnap and Lange, 2003; Chock et al., 2019).

In the current study, incubated cyanobacteria and cyanobacteria-lichen crusts grew better in soil substrates than in sandy substrates. Our observations are supported by previous reports indicating that clay soil substrates had higher recovery rates than sandy clay loam substrates in the Great Basin Desert (Chock et al., 2019). In addition, our results are consistent with Román et al. (2018), suggesting that artificial cyanobacteria crust developed better in soil substrates derived from Amoladeras and Gádor quarr soils, which have more fine material than the Tabernas Desert soil substrate in southeastern Spain. Our results indicate that cultivation of artificial BSCs through inoculum additions and selected soil substrates with high initial fine material should be prioritized on sand substrate.

Growth and development of BSCs usually are limited by soil nutrients (Li, 2012). The field study by Antoninka et al. (2016) indicated that slow growth in artificial BSC organisms might result from resource limitations. Soil organic matter, total nitrogen, and total phosphorus were significantly positively correlated with the growth and development of BSCs in the Negev Desert (Kidron et al., 2010) and Tengger Desert (Li et al., 2017). Bu et al. (2018) observed that increasing soil nutrients increased incubated BSC coverage by 40–50% compared to controls. Nutrients have also been promoted cultivated BSCs development as has been demonstrated in Antoninka et al. (2016). Our results are in line with previous reports showing that soil organic matter, total nitrogen, and total phosphorus were positively correlated with coverage of incubated cyanobacteria crust (Chamizo et al., 2018). In summary, rapid growth of BSC organisms can be achieved if soil nutrient limitations are removed (Antoninka et al., 2016). Importantly, our findings indicate that increasing initial soil substrate nutrient content, especially soil organic matter content, will help the recovery of BSCs.

Additionally, fine material (clay and silt) in soil substrate increases the specific surface area, facilitating the adsorption of large quantities of monolayer water and hygroscopic water relative to sand (Li et al., 2021; Li et al., 2017). The organic matter covers the sand particles, increasing the effective surface area available for higher vapor sorption (Li et al., 2021), holding more moisture and facilitating BSC development (Kidron et al., 2020). A study in the Ulan Buh Desert found that covering sand with soil substrates increased soil surface moisture content 3.77–8.65% relative to sand (Zhang et al., 2018). Importantly, the duration of soil surface wetness is positively related to biocrust colonization and growth (Kidron et al., 2020; Xiao et al., 2016), another potential explanation for why artificial biocrusts developed better in soil substrates than in sand.

#### 4.3. Soil substrate selection for future BSCs cultivation in temperate desert

BSC inoculation significantly enhanced the recovery of BSC communities and soil stability on severely disturbed soil surfaces (Antoninka et al., 2020b; Chiquoine et al., 2016). Local BSC fragments can serve as an effective inoculum for artificial BSC cultivation in natural systems (Chiquoine et al., 2016; Young et al., 2019), in part because local BSCs are adapted to local soil environments and climate conditions (Chiquoine et al., 2016). In a field environment, Antoninka et al. (2018) observed that field-collected cyanobacteria crust established well, and reached ~55% cover after 14 months. Likewise, in an open field study, 50–90% coverage of BSCs developed on disturbed soil surfaces using naturally developed BSC fragments within 2 months in a Loess Plateau ecosystem (Bu et al., 2018). Our results indicate that broadcasting BSC inoculum on different soil substrates was an efficient way to accelerate cyanobacteria crust restoration in a short period. Likewise, our current study showed that BSCs can be stabilized one year after artificial BSCs reached 15.0–20.0% coverage. This is likely due to the fact that field-collected inoculum was well-suited to field conditions as it was collected, crumbled and reapplied to its home site within a few days (Antoninka et al., 2018). Our study provides evidence that BSCs can be successfully reestablished in dryland field conditions through use of BSC fragments collected from the field. In the current study, incubated biocrusts in the first two months (between August and October) after inoculation in all treatments had reached high coverage, largely due to water input from rainfall events, which are typical for this time of year (Zhao et al., 2019). However, all treated soils retained high coverage at the finally measurement while that of the sand decreased. This phenomenon perhaps can be explained by the lower nutrients available and the less stable surface environment in sand than in soil substances (Román et al., 2018; Zhao et al., 2021). Our study demonstrated that adding BSC fragments can accelerate biocrusts recovery rate in a natural condition.

Collecting on-site for a 10% cover reapplication can translate into a relatively large new disturbance (Antoninka et al., 2018). Therefore, directly using field-collected material is not always satisfactory, as it

places too much pressure on natural intact BSCs. Specifically, large amounts of naturally grown BSCs would need to be collected for large-scale projects, which would then lead to degradation of natural areas (Zhou et al., 2020). As such, a protocol for the rapid and mass propagation of BSC inoculum material is needed (Faist et al., 2020; Li et al., 2016). Specifically, it will likely be necessary to effectively cultivate BSCs for reintroduction (Antoninka et al., 2018; Bowker et al., 2017).

For larger scale restoration projects requiring large amounts of BSC fragments as inoculum (Antoninka et al., 2020b; Zhao et al., 2019; Zhao et al., 2021), more BSC inoculum material and larger amounts of soil substrates are needed. Our current study describes methods that could be used. This is supported by the fact that soil substrates have significant advantages over sand substrate in terms of BSC cultivation (Chock et al., 2019; Giraldo-Silva et al., 2020; Velasco Ayuso et al., 2020). However, soil substrates collected from both cool and hot deserts were very limited, due to being developed under natural conditions. A lack of soil resources presents a barrier to current technology used for large scale ecological restoration projects.

In northern China, the deposition of sediments can block irrigation channels, creating serious problems in the Yellow River water diversion irrigation district (Wang et al., 2016). Wu (2017) report that more than 2000 m<sup>3</sup> km<sup>-1</sup> of alluvial soil is deposited each year in these irrigation channels. To guarantee proper flow, the Chinese government invests a great deal of money to dredge sediment from the channels each year. We expect that dredged sediment from the Yellow River could be used for restoration projects, which could solve many of the problems associated with lack of material for restoration. And because irrigation channel systems are widely distributed throughout arid and semi-arid regions in northern China, alluvial soils are abundant and easy to collect (Wang et al., 2016). Meanwhile, abandoned farmlands are common around the world (Wei and Ying, 2019), particularly in China, occupying 12% of farmlands (total 135 million hectares of farmland area in 2016) across 25 provinces (Jiao et al., 2014; Wang et al., 2016; Xue et al., 2013).

Ultimately, our study shows that three of the soil substrates that we collected facilitated higher artificial BSC coverage than sandy substrates, which indicates that they are ideal substrates for the production of BSC inoculum material. However, considering the scarcity of soil resources and the value of reusing soils, as well as the relatively low acquisition cost and high quality of incubated artificial BSCs, we expect that sediment from dredged irrigation channels and abandoned farmlands could provide ideal substrates for the culture of artificial BSCs or inoculant in arid and semi-arid regions.

The survival and establishment of artificial biocrusts inoculants was closely related to the initial properties of the inoculated soil substrates (Román et al., 2018). So far, our findings provide valuable insights for improving BSC recovery rates in desert regions by covering sand with soil substrates and ameliorating soil conditions. Tests similar to our current study have conducted at small scales, such as in the Tabernas Desert in southeastern Spain (Román et al., 2018), in Great Basin Desert in USA (Chock et al., 2019) and in the western Negev Desert in Israel (Zaady et al., 2017). Further experiments will examine the applicability and scope of application of current methods in different deserts or regions with degraded soils, including at large scales. For example, experiments will test uses of soils from dredged irrigation channels, abandoned farmlands, and other sources to cover sand or combine with other methods for ameliorating soil conditions and culturing different BSC types.

## 5. Conclusion

Overall, we have shown that broadcasting natural cyanobacteria and cyanobacteria-lichen crust fragments can lead to successfully cultivated artificial BSCs in field conditions. Artificial BSCs developed well on all covering soil treatments, reaching 15–20% coverage and 2.94–4.06 mm thickness after 12 months of incubation. Our study indicates that



covering sand with soil substrates improved BSC recovery rates in the field conditions. Covering sand with soil substrates created more ideal soil habitats because soil substrates have higher sand surface stability, greater initial finer material content and greater nutrient content, and delayed soil surface wetness duration than sandy substrates. Considering the scarcity of soil resources and the value of reusing soil resources, our results suggest that left-over soils from dredged irrigation channels and abandoned farmlands can provide a good substrate to culture BSC inoculum material. These can provide potential materials for large-scale ecological restoration projects in temperate dryland regions in the future.

### Declaration of Competing Interest

The authors report no declarations of interest.

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### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.still.2021.105081>.

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