Received: 26 April 2024 | Accepted: 18 September 2024

DOI: 10.1002/2688-8319.12389

Ecological Solutions and Evidence | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Comparing greenhouse and field biocrust cultivation methods in the Sonoran Desert

A. Antoninka[1] | H. Rowe[2,3] | J. Weser[4] | D. Langenfeld[3] | J. Brady[3] | T. Sprague[3] | N. Day[5]

[1]School of Forestry, Northern Arizona University, Flagstaff, Arizona, USA

[2]School of Earth and Sustainability, Northern Arizona University, Flagstaff, Arizona, USA

[3]McDowell Sonoran Conservancy, Scottsdale, Arizona, USA

[4]Department of Life Sciences, Scottsdale Community College, Scottsdale, Arizona, USA

[5]USGS, Colorado Water Science Center, Grand Junction, Colorado, USA

Correspondence
A. Antoninka
Email: anita.antoninka@nau.edu

Funding information
City of Scottsdale

Handling Editor: Marcio Leite

Abstract

1. Developing methods to use biocrusts in restoration is becoming more important as land use and climate change impact the health and intactness of high-stress ecosystems. Methods of cultivation to maximize the production of biocrusts for use in restoration activities are necessary because salvage opportunities are limited. Our objective for this research was to determine an optimal method for scalable biocrust cultivation.
2. We tested two Field and one Greenhouse cultivation methods. The Field cultivation methods had a base layer of weed cloth, soil and irrigation with either (1) shade cloth immediately over the surface (Quesadilla method) or (2) with shade cloth over a 1 m tall hoophouse (Hoophouse method). The Greenhouse method had nested basins with water wicking up to the soil surface and biocrust from below, with shade cloth attached to basins. We crossed these methods with the addition of native soil or sand and with and without a base of jute using salvaged biocrusts from the Sonoran Desert.
3. All methods led to at least doubling biocrust cover in 11 weeks. The Greenhouse method led to the highest cover of cyanobacteria and mosses, whereas the field Quesadilla method and the addition of native soil in all cultivation methods led to higher abundance of lichens. There were interactions of cultivation method and soil type, with Greenhouse cultivation and native soil promoting the highest cyanobacteria cover and chlorophyll a. We measured exopolysaccharide sheaths (EPS) in native soil and all cultivation conditions, finding no differences for tightly bound sheath fractions, but higher quantities of the loosely bound EPS in the Greenhouse. We also quantified native and non-native plants in cultivation, finding few plants in Greenhouse cultivation, but high abundance in both Field methods, and particularly with native soil and without jute for native plants.
4. *Practical implication*: Together, these results demonstrate that all three cultivation methods are successful for bulking biocrust materials for restoration, and preference should be given to the method that is the easiest and most accessible for practitioners.

KEYWORDS
biocrust, biocrust cultivation, citizen science, cyanobacteria, lichen, moss, restoration, Sonoran Desert

1 | INTRODUCTION

Biological soil crusts (biocrusts) are an integral component of all ecosystems where sunlight reaches bare soil (Weber et al., 2022), covering an estimated 12% of the Earth's terrestrial surface (Rodriguez-Caballero et al., 2018). This complex community, consisting primarily of cyanobacteria, algae, bryophytes and lichens, lives in and binds the top millimetres of mineral soil together. They are critically important in stabilizing soil (Felde et al., 2018), influencing hydrology (Eldridge et al., 2020) and plant community assembly (Havrilla et al., 2020) and contributing to N and C fixation and cycling (Elbert et al., 2012; Porada et al., 2014). Biocrusts and the functions they provide are threatened by land use changes and climate change. In drylands, which are among the most degraded ecosystems and make up more than 40% of the Earth's terrestrial surface, biocrusts are often dominant ground cover (Prăvălie, 2016).

Biocrusts are sensitive to both physical disturbances and climate perturbations (Ferrenberg et al., 2015). Climate change, including altered precipitation, and land use activities is expected to reduce biocrust cover by 25%–40% over the coming decades (Rodriguez-Caballero et al., 2018). While resilient to long periods of hot, dry conditions, biocrusts hydration and metabolic activity are highly sensitive to higher temperatures, especially when coupled with reduced precipitation (Ferrenberg et al., 2015). Similarly, activities that disrupt the soil surface through compression (e.g. cattle grazing or driving heavy machinery) or removal of the soil surface (e.g. mining and chaining) damage biocrust communities. The extent of damage depends on climate, soil type and nature of the disturbance (Zhao et al., 2016). In some cases, natural recovery can occur by removing the disturbance, but often intervention is required (Antoninka et al., 2020; Bowker, 2007).

Biocrusts should be included in ecosystem rehabilitation and planning because of the myriad of ecosystem functions they provide. Biocrust recovery without intervention can be slow or sometimes impossible (Weber et al., 2016). However, recent advances in biocrust cultivation and reintroduction methods suggest that we might be able to speed up recovery of lost biocrust communities (e.g. Antoninka et al. 2016, 2017, 2019; Bowker & Antoninka, 2016; Chock et al., 2019; Faist et al., 2020; Giraldo-Silva et al., 2019). There is considerable desire to reintroduce cultivated, full communities of biocrusts into field settings, rather than individual taxa, because increases in community composition of biocrusts correlates with increased biocrust functions (Bowker et al., 2011, 2013). Methods for cultivating mixed communities in greenhouses have been successful, (Antoninka et al., 2016; Doherty et al., 2015), however the published results of applying cultivated biocrusts to field setting have been decidedly mixed (reviewed in Zhao et al., 2016, also eg. Antoninka et al. 2017, 2019; Faist et al., 2020; Giraldo-Silva et al., 2019), especially when cultivating and inoculating with full communities of lightly and darkly pigmented cyanobacteria, mosses and lichens. Cultivation methods that result in establishment and persistence of biocrust communities in field restoration settings and at scales that meet restoration goals are needed.

The goal of this project is to compare methods to cultivate biocrusts for use in restoration with high establishment rates. Multiple factors are assumed to influence the success and failure of biocrust cultivation techniques including (1) optimal environmental conditions, (2) presence of native soil organisms and (3) initial soil stability. We set up an experiment to test cultivation method (two fields and one greenhouse approach) crossed with native soil or sand, and to enhance stability, with and without burlap jute netting under soil. We used mixed community inoculum salvaged from a site slated for development in the Sonoran Desert of Arizona. We tracked biocrust cover and measured chlorophyll *a* content and exopolysaccharide (EPS) content before the inoculated pairs were placed in the field over the 11-week cultivation. We hypothesized: (1) What are the differences in cyanobacteria, lichen and moss cover, chlorophyll *a* content and exopolysaccharide (EPS) content of greenhouse-cultivated and two field-cultivated biocrusts of the same origin? Based on results from previous experiments, we hypothesized that greenhouse cultivation would yield the highest biomass and cover of mosses due to more consistent and lower temperatures and higher relative humidity and field cultivation would yield lower biomass, but higher cyanobacteria and lichen cover. (2) Does biocrust cover, chlorophyll *a* content and EPS content remain consistent, increase or decrease through time for each cultivation type, and are the rates of change the same? Because greenhouse-cultivated crusts are presumably experiencing optimal growing conditions for biocrust growth, we expected both greenhouse-cultivated biocrust to increase more over time compared to field-cultivated biocrust. (3) Does native soil enhance biocrust establishment? Because biocrusts are in close association with the soil microbial community and adapt to local edaphic conditions, we expected the highest biocrust establishment in native soil compared to sand. (4) Does providing supplemental stability through burlap jute netting change the trajectory of greenhouse-cultivated or field-cultivated biocrust? Stability is critical to biocrust establishment post disturbance and has aided field establishment of cultivated biocrust (Bowker et al., 2007, 2020), leading us to hypothesize additional stability provided by jute would lead to increases in total cover and function in the form of increase chlorophyll *a* content and EPS content of biocrusts through time.

2 | METHODS

2.1 | Site description and harvest methods

Citizen Scientists salvaged soil biocrusts from Fraesfield trailhead (33.741528, −111.7882963) in the McDowell Sonoran Preserve, Scottsdale, USA prior to trailhead improvement work in July 2018.

The site has a mixture of Eba—very gravelly loam and Pinaleno—Tres Hermanos Complex 1 soils and a mixed vascular community of *Ambrosia deltoidea—Parkinsonia microphylla*—mixed scrub Association and *Ericameria laricifolia—P. microphylla*—mixed scrub Association (Brown et al., 1979). The mean annual temperature is 21.3°C and annual mean precipitation is 334.62 cm (30 years normal, 1991–2020, interpolated climate data at a resolution of 800 m, from https://prism.oregonstate.edu/explorer/, accessed July 1, 2022).

Citizen Scientists were trained to identify and harvest biocrusts. Harvest was conducted in July 2018 using hand trowels or flat shovels, where biocrust was scraped from the soil surface and added to buckets after a cleaning step to save only the top 0.5-1 cm of soil and biocrust. Biocrust collections were a mix of lichens (~50%), mosses (~20%) and cyanobacteria (~30%) based on a random survey of functional groups while harvesting. Iin this site, biocrust is dominant across the interspace, likely with higher cyanobacteria cover than noted in surveys. Biocrusts were then sieved through a 5 mm mesh screen to remove rocks and break up biocrusts into fragments 5 mm diameter and smaller, then homogenized by mixing and stored indoors in the dark until experimental set up.

2.2 | Experimental design

To test the best cultivation method, we compared two field cultivation methods on the grounds of Scottsdale Community College and one greenhouse cultivation method at the Northern Arizona University Research Greenhouse Complex. The experiment was set up as a fully replicated experiment with cultivation type (three cultivation systems: two in the field (Quesadilla, Hoophouse) and one in the Greenhouse, described below), crossed with jute treatment (two factors: jute burlap or no jute; here after referred to as jute), and soil substrate (two factors: native soil or commercial play sand). All factors were replicated five times, with the exception of controls and jute plots. Double the number of jute plots were created to harvest in two unique ways (scraping or intact) for the next stage of field establishment trials post-cultivation. One full replicate of all treatment combinations without inoculation was added for controls. Again, this was doubled for jute plots. Thus, the experiment includes a total of 108 plots: 5 replicates of each crossed treatment (jute/no jute and native soil/sand for inoculated plots = 20), plus another set of all combinations of inoculated jute plots (=10), one replicate of all combinations without inoculum (=4) and an extra combination of uninoculated controls (=2) on jute across three cultivation systems. The non-inoculated control plots were included to account for natural colonization of biocrust organisms. Inoculated plots received 375 mL of dry homogenized biocrust by volume.

At the Scottsdale Community College cultivation site, we prepared the area for the experiment by clearing weeds and debris and levelling the ground for the Hoophouse and Quesadilla treatments. Within each cultivation type, we layered each of the 0.25 m^2 plots with the following elements: (1) synthetic light grey landscape fabric across soil surface of each cultivation area to keep vegetation out (used as the base layer in the greenhouse units), (2) 1 L of substrate (native soil collected from near the biocrust collection area and sieved to remove rocks or commercial play sand; Quikrete graded and washed coarse sand) spread out thinly for each 0.25 m^2 plot, (3) fine woven jute burlap fabric (only in jute treatment; Viagro 100% natural burlap) cut to cover the 0.25 m^2 area and (4) biocrust inoculum was mixed thoroughly and often to avoid settling, and added by sprinkling low over the surface at calculated rate of 20% cover of the surface area to 1 cm depth (50 mL per unit by volume).

The *Field Quesadilla* cultivation plots were additionally layered with ½ inch drip emitter PVC tubing on top then covered with shade cloth (tan woven UV stable polyethylene, 62% shade) and pinned to the ground with landscaping staples. Irrigation for these plots was two rows of drip emitter tubing with two emitters stationed at each plot and attached with ground staples (Figure 1a).

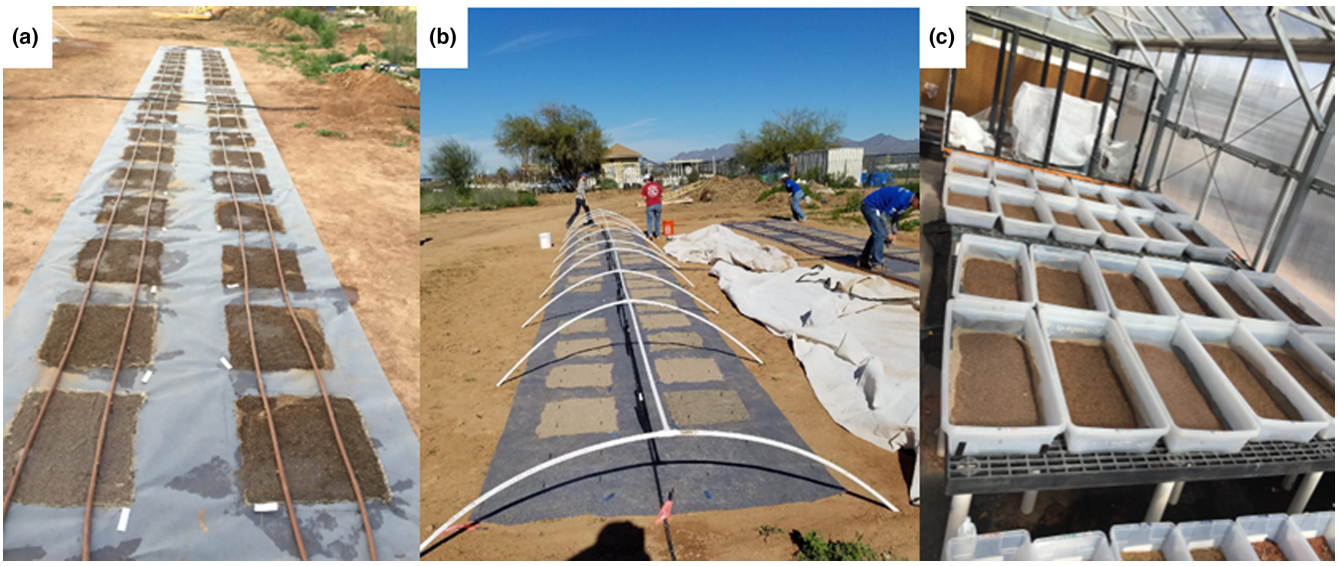

FIGURE 1 Biocrust cultivation experimental design: (a) Quesadilla: In-line irrigation covered with shade cloth just above the surface, (b) Hoophouse: 360° low sprinkler heads under a low hoophouse and (c) Greenhouse: Wicking irrigation in the NAU greenhouse.

Field Hoophouses were constructed with ½ inch PVC pipe bent and staked into the ground with rebar to a height of 1 meter. PVC cross beams were added with PVC joints every 2 m attached with ties to the PVC. The same shade cloth used in the Quesadilla covered the Hoophouse and was attached to the ground using landscaping staples (20 cm depth) around the whole perimeter. Irrigation was set up with an ½ inch centre line with one aboveground 360° DIG microjet adjustable jets (300B) per four plots placed 15 cm above the soil surface. Emitters were adjusted to cover the full area and to provide the equivalent watering as the drip tape (saturation without puddling, or field capacity). Temperatures at the Scottsdale Community College Field Cultivation study site ranged from 8C to 29C with an average temperature of 15C (SCC weather station, weather underground; https://www.wunderground.com/dashboard/pws/KAZSCOTT198/graph/2019-01-15/2019-01-15/monthly).

The Greenhouse cultivation used a nested wicking system described by Doherty et al. (2015) in the same area as field cultivation (Figure 1c). Each bottom container had a drain hole and an ¼ inch irrigation tube entering the basin. The top basin has small wicking holes drilled into it. The bottom is covered with a wicking weed cloth (same as in field cultivation), with or without the addition of jute, a layer of sand or soil and then the inoculum at the same rate as the field plots. We used rectangular containers for underbed storage of the same area (85 cm X 30 cm), allowing the same inoculation rate, density and survey area as for field plots. Containers were also covered with the same shade cloth attached to basins with binder clips. The greenhouse was maintained at 20°C ± 2°C, with a relative humidity varying between 20% and 45%. Greenhouse and field cultivation systems were watered with charcoal-filtered water on an automated system that ran weekdays, three times per day during daylight hours, with the amount of watering time adjusted as needed to accommodate changing temperature and precipitation conditions. For the majority of time, the watering ran at 6 AM, 12 PM and 4 PM for 30-second intervals. This was sufficient water to keep plots hydrated to field capacity during daylight hours equally across all cultivation types. The experiment was stopped when the ambient temperature hit 26°C for three consecutive days at the field cultivation site, which equalled 11 weeks (Jan-April 2019).

2.3 | Measurements

At installation and at the end of the experiment, per cent soil crust and plant cover of each unit was estimated within the center 25 cm × 25 cm of the plot using a grid point intercept method with 20 points. We put nails into opposite corners so the frame could be placed in the same spot for each sampling effort. We recorded cyanobacteria, moss and lichen cover. Anything not encountered but present in the plot was recorded and given a 2.5% cover designation. We measured plant cover to species or genus as possible using the following cover classes: 0%, 0%–0.1%, 0.1%–1%, 1%–2%, 2%–5%, 5%–10%, 10%–25%, 25%–50%, 50%–75%, 75%–95% and greater than 95% (Peet et al., 1998). We collected and homogenized three 0.5 cm depth by 1 cm diameter cores from designated spots outside the sampling area in each plot at the end of the experiment. From these, we extracted chlorophyll a on all plots, which is a proxy for biocrust biomass using methods from Castle et al. (2011). We used the same cores for exopolysaccharides (EPS) extraction, which is a measure of growth and soil binding capacity of biocrusts, from a subset of plots because of cost and time constraints (all cultivation types on native soil only for a total of 15 plots, with 5 replicates and run in triplicate). We extracted multiple EPS components, including loosely bound (LB-EPS), tightly bound (TB-EPS) and sheath (G-EPS), which according to the previous study (Chen et al., 2018), likely have different functional roles. We extracted the different fractions using the methods described by Rossi et al. (2017). Following the extraction of the three fractions, we used the phenol-sulfuric acid assay to quantify them as detailed by Dubois et al. (1956).

2.4 | Analysis

Data were assessed for homogeneity of variance and normal distribution and transformed arcsine square root for all variables. We used a three-way factorial ANOVA design with main factors and interaction terms: cultivation environment (three levels: Greenhouse, Field Quesadilla and Field Hoophouse), jute (two levels: jute and no jute) and soil type (sand and native soil) as the factors. We report summary statistics on the controls (plots without biocrust inoculum) in Table 1, but they are not included in the models because they were not fully replicated. Response variables were total biocrust cover, the different biocrust components, chlorophyll a and EPS fractions, and plant cover (total plant, nonnative and native plant cover). Plants did not grow well in the greenhouse, therefore we excluded Greenhouse from the plant analyses. We used Tukey's post hoc treatments to compare among groups with more than two levels. We analysed the relationship between total biocrust and plant variables using regression (bivariate analysis function). We also tested relationships among plant and biocrust variables to determine if there were interactions of interest. All statistics were performed in JMP 16.0 (JMP®, Version 16.0. SAS Institute Inc., Cary, NC, 1989–2023) and all figures were created in Microsoft excel.

3 | RESULTS

Across all plots, there was a two to fourfold increase in biocrust cover from 17.27 ± 3.05% starting cover at project installation to 45%–79% by the end of 3 months. The uninoculated control plots had very low colonization, with the exception of the native soil in the Greenhouse, which had 35% ± 7% colonization of cyanobacteria and moss (Table 1). The cultivation method had a strong effect on

TABLE 1 Mean, SE and sample size for response variables by treatment.

Cultivation type	Soil type	Jute/no	Inoculum	Reps	% Bare soil	% Cyanobacteria	% Lichen	% Moss	% Late succession	% Total biocrust	Chlorophyll a (μg/g soil)	% Plants	% Native plants	% Non-native plants
GH	Native	Jute	Biocrust	10	4.8 (1.0)	5.0 (0.9)	0.0 (0.0)	17.6 (1.6)	17.6 (1.6)	22.6 (1.9)	57.5 (9.5)	3.9 (0.3)	2.3 (0.2)	1.6 (0.2)
GH	Native	Jute	Control	2	8.0 (4.0)	1.0 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.0 (1.0)	126.6 (19.2)	0.0 (0.0)		
GH	Native	No Jute	Biocrust	5	6.8 (2.5)	8.0 (2.2)	0.0 (0.0)	13.6 (2.7)	13.6 (2.7)	21.6 (1.0)	24.7 (6.5)	3.5 (0.2)	1.9 (0.2)	1.6 (0.2)
GH	Native	No Jute	Control	1	8.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	40.5 (0.0)	0.0 (0.0)		
GH	Sand	Jute	Biocrust	10	4.8 (0.7)	5.2 (1.0)	0.0 (0.0)	20.4 (3.0)	20.4 (3.0)	25.6 (3.2)	35.0 (4.4)	3.3 (0.3)	1.9 (0.2)	1.5 (0.2)
GH	Sand	Jute	Control	2	2.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	86.3 (0.5)	0.0 (0.0)		
GH	Sand	No Jute	Biocrust	5	4.0 (1.1)	4.8 (1.4)	0.0 (0.0)	12.0 (4.6)	12.0 (4.6)	16.8 (4.6)	34.4 (5.2)	2.8 (0.6)	1.2 (0.3)	1.6 (0.3)
GH	Sand	No Jute	Control	1	2.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	99.9 (0.0)	0.0 (0.0)		
Quesadilla	Native	Jute	Biocrust	10	8.0 (1.8)	7.6 (1.1)	0.4 (0.3)	4.2 (1.2)	4.6 (1.1)	12.2 (1.6)	32.6 (5.9)	40.2 (4.1)	13.5 (2.3)	15. (6.1)
Quesadilla	Native	Jute	Control	2	34.0 (30.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	67.3 (5.5)	0.0 (0.0)		
Quesadilla	Native	No Jute	Biocrust	5	1.6 (1.0)	14.4 (3.7)	1.2 (0.8)	2.0 (0.9)	3.2 (0.5)	17.6 (3.8)	25.8 (5.2)	67.7 (6.3)	20.1 (3.3)	16.5 (2.9)
Quesadilla	Native	No Jute	Control	1	44.0 (0.0)	0.0 (0.0)	2.0 (0.0)	0.0 (0.0)	2.0 (0.0)	2.0 (0.0)	57.3 (0.0)	0.0 (0.0)		
Quesadilla	Sand	Jute	Biocrust	10	0.4 (0.4)	8.6 (1.3)	1.4 (0.5)	1.8 (0.8)	3.2 (0.6)	11.8 (1.6)	34.8 (5.7)	49.9 (4.5)	6.5 (1.1)	11.8 (3.4)
Quesadilla	Sand	Jute	Control	2	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	45.1 (26.8)	0.0 (0.0)		
Quesadilla	Sand	No Jute	Biocrust	5	0.8 (0.8)	10.4 (1.6)	1.6 (1.0)	1.6 (0.7)	3.2 (0.5)	13.6 (1.5)	39.9 (5.7)	49.7 (4.9)	17.3 (2.9)	11.2 (4.0)
Quesadilla	Sand	No Jute	Control	1	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (3.1)	68.3 (0.0)	0.0 (0.0)		
Hoop	Native	Jute	Biocrust	10	27.2 (9.8)	11.0 (2.1)	2.4 (1.6)	4.0 (0.7)	6.4 (1.4)	17.4 (2.7)	27.7 (3.5)	28.4 (7.8)	19.9 (1.4)	20.3 (4.)
Hoop	Native	Jute	Control	2	18.0 (6.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	97.1 (15.2)	12.5 (12.5)		
Hoop	Native	No Jute	Biocrust	5	8.8 (4.3)	10.4 (1.6)	11.6 (7.2)	4.4 (1.5)	16.0 (6.3)	26.4 (7.4)	34.0 (11.8)	36.6 (6.0)	30.7 (4.7)	37. (3.7)
Hoop	Native	No Jute	Control	1	160.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	5.7 (0.0)	0.0 (0.0)		
Hoop	Sand	Jute	Biocrust	10	6.4 (2.2)	10.0 (3.4)	0.8 (0.8)	3.0 (0.7)	3.8 (1.0)	13.8 (4.1)	23.7 (3.8)	18.5 (3.4)	20.0 (2.1)	29.7 (3.3)
Hoop	Sand	Jute	Control	2	2.0 (2.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	38.8 (15.2)	0.0 (0.0)		
Hoop	Sand	No Jute	Biocrust	5	26.4 (21.5)	3.6 (1.3)	6.4 (3.2)	3.2 (0.5)	9.6 (3.2)	13.2 (3.3)	24.8 (8.1)	28.5 (3.3)	18.5 (4.1)	31.2 (4.2)
Hoop	Sand	No Jute	Control	1	4.0 (0.0)	0.0 (0.0)	2.0 (0.0)	0.0 (0.0)	2.0 (0.0)	2.0 (0.0)	61.6 (0.0)	0.0 (0.0)		

total biocrust cover and relative cover of different biocrust taxa and plants.

Greenhouse and Field Quesadilla cultivated biocrusts attained higher per cent cover than the Field Hoophouse conditions (Figure 2). Cyanobacteria cover was highest in the Field Quesadilla, followed by Greenhouse and then Field Hoophouse (Tables 1 and 2; Figure 3). Lichen cover was higher in Field Quesadilla and Field Hoophouse compared to Greenhouse and moss was highest in the Greenhouse compared to the Field Quesadilla or Field Hoophouse (Tables 1 and 2; Figure 3).

In a few cases, we saw that soil type affected biocrust growth. Lichens grew better on native soil and chlorophyll a was higher on native soil (Tables 1 and 2). Cyanobacteria, chlorophyll a and total biocrust cover responded to interaction with soil type and cultivation method (Tables 1 and 2; Figures 3 and 4). For cyanobacteria and total biocrust cover, native soil and sand in both Greenhouse and Field Quesadilla cultivation were similar, but for Field Hoophouse biocrust growth, while lower than Greenhouse and Quesadilla, had higher growth in native soil than sand (Figure 3).

Chlorophyll a was greater in the Greenhouse compared to both Field cultivation methods (Tables 1 and 2; Figure 4). For chlorophyll a, values were two times or greater in Greenhouse native soil compared to any other cultivation/soil combination (Figure 5). Exopolysaccharides (EPS) only varied in the loosely bound fraction, with greater abundance in the Greenhouse. Tightly bound EPS, sheath EPS and total EPS did not vary among treatments (Table 3; Figure 5). Jute only affected moss cover, with greater moss cover on plots with jute present (Tables 1 and 2).

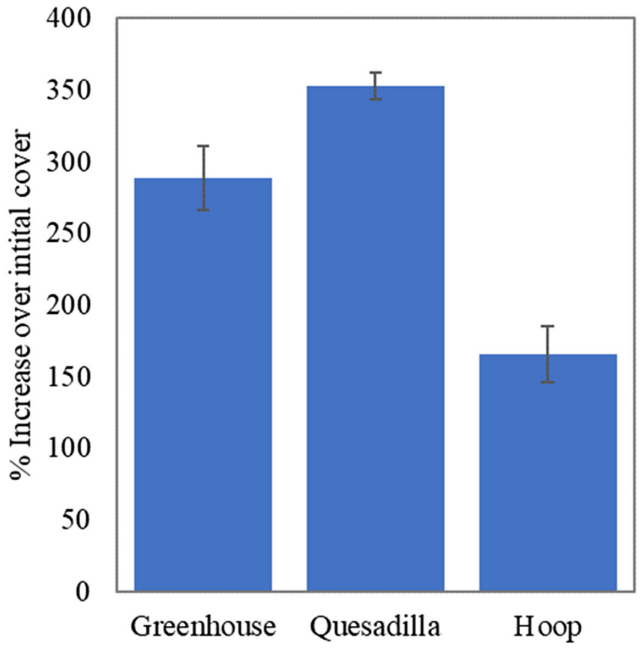

FIGURE 2 Percent biocrust cover increase from the initial cover value calculated as: (End cover-original cover)/initial cover × 100). Error bars represent one standard error of the mean. Lowercase letters represent Tukey's post hoc comparisons.

TABLE 2 *F* and *p* values (*F*(*p*-value)) for response variables and treatment combinations.

Treatment	df	% Bare	% Cyanobacteria	% Lichen	% Moss	% Total biocrust	Chlorophyll a	% Total plants	% Native plants	% Non-native plants
Cultivation	2	**57.9 (<0.0001)**	**50.4 (<0.0001)**	**7.2 (0.001)**	**58.7 (<0.0001)**	**70.2 (<0.0001)**	**22.9 (<0.0001)**	**101.6 (<0.0001)**	**22.0 (<0.0001)**	**22.6 (<0.0001)**
Soil	1	**21.3 (<0.0001)**	0.5 (0.5)	**5.9 (0.02)**	0.3 (0.6)	**3.1 (0.08)**	**18.5 (<0.0001)**	2.7 (0.1)	**9.8 (0.003)**	0.03 (0.9)
Jute	1	0.1 (0.8)	0.2 (0.7)	2.6 (0.1)	**4.4 (0.04)**	0.02 (0.9)	2.6 (0.1)	**7.2 (0.01)**	**15.3 (0.0003)**	**3.0 (0.09)**
Cultivation × Soil	2	**18.8 (<0.0001)**	**5.1 (0.01)**	0.8 (0.5)	0.3 (0.7)	**7.5 (0.001)**	**8.4 (0.0004)**	0.8 (0.5)	0.03 (0.9)	0.8 (0.4)
Cultivation × Jute	2	1.0 (0.4)	0.2 (0.9)	2.4 (0.09)	**3.1 (0.05)**	0.9 (0.4)	2.0 (0.1)	2.2 (0.1)	**4.2 (0.05)**	0.5 (0.5)
Soil × Jute	1	2.4 (0.1)	0.5 (0.5)	2.8 (0.09)	0.1 (0.7)	2.1 (0.2)	0.2 (0.9)	2.4 (0.1)	0.3 (0.6)	2.3 (0.1)
Soil × Jute × Cultivation	2	**4.0 (0.02)**	**3.0 (0.05)**	0.3 (0.8)	0.7 (0.5)	2.3 (0.1)	0.7 (0.5)	3.0 (0.06)	**5.6 (0.02)**	0.2 (0.7)

Note: Bolded values represent significant values at the level of $p < 0.05$.

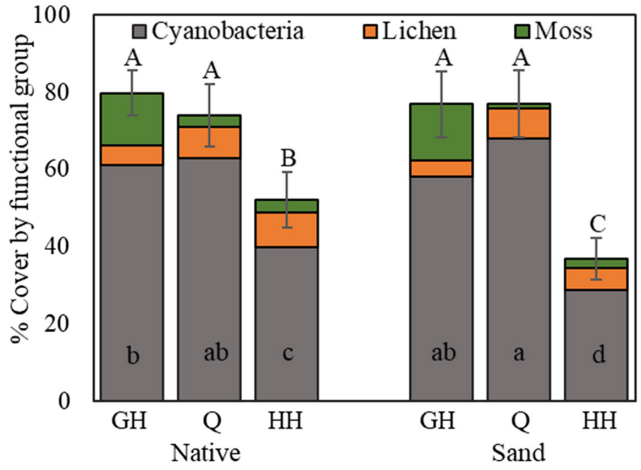

FIGURE 3 Biocrust cover by functional group. The overall bar represents total biocrust cover. Lower case letters represent Tukey's post hoc comparisons for cyanobacteria and upper case for overall biocrust cover. Other groups were not different across both soil and cultivation method. Error bars represent one standard error of the mean for total biocrust cover.

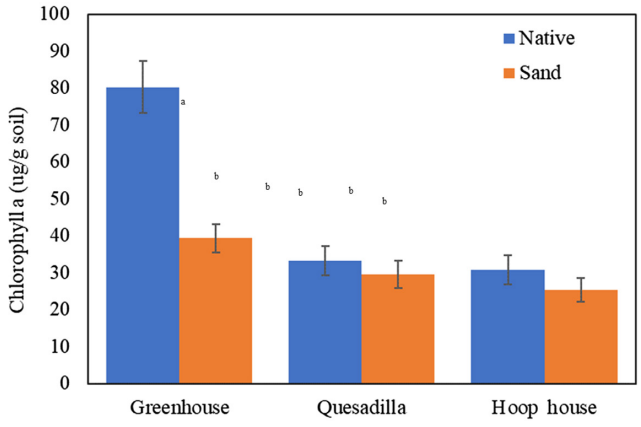

FIGURE 4 Chlorophyll a by cultivation method and soil type (native in blue, sand in orange). Lowercase letters represent Tukey's post hoc comparisons cultivation by soil type. Error bars represent one standard error of the mean.

The mean total plant cover across all treatments was 38.03 ± 2.59% (mean and SE; comprised of native plant cover: 17.19 ± 1.15% and nonnative plant cover: 20.78 ± 1.86%). Per cent cover of total plants, native plants and nonnative plants were all higher in the field Quesadilla compared with the field Hoophouse (Table 2; Figure 6). Native plants had a three-way interaction among soil type, jute and cultivation method such that native plants preferred native soil without jute in the Field Quesadilla environment (Figure 4). Nonnative and total plant cover responded in the same way to these treatments as native plants, but differences were not significant.

Biocrust and plant cover were positively correlated. We found total plant cover ($R^2 = 0.14$, $p < 0.05$) exotic ($R^2 = 0.07$, $p < 0.05$) and native plants ($R^2 = 0.17$, $p < 0.05$) had higher cover with increasing biocrust cover. We only tested for these patterns in the field cultivation methods because plant cover was minimal in the Greenhouse.

4 | DISCUSSION

4.1 | All cultivation methods effective

With all three cultivation methods, we were able to at least double the biocrust cover in only 11 weeks. Cyanobacteria was the majority of the cultivated biocrust in all cultivation environments. In contrast, lichens dominated the original source collections. It seems likely that we underestimated cyanobacteria cover in our collection at the salvage site, as the site had a high cover of cyanobacteria in all adhering soil, which is notably difficult to detect at the surface. Regardless, the growth of cyanobacteria was notable and lichen cover was low in comparison to other groups. This follows from past experiments where lichens are generally much harder to cultivate than other taxa (eg. Bowker et al., 2017).

In the Greenhouse, we had higher moss cover than in both Field cultivation methods, and lichens were more abundant, particularly in the Field Quesadilla cultivation. This suggests that mosses do better with the more constant, cooler and higher RH conditions in the Greenhouse compared to the Field, and lichens prefer warmer and drier conditions. Both of these make sense in the context of moss and lichen biology and past cultivation experiments demonstrating that mosses like longer hydration periods compared to lichens (Antoninka et al., 2016; Ayuso et al., 2020; Bowker & Antoninka, 2016).

Among the three methods, biocrust cover was highest in Greenhouse and Field Quesadilla environments, suggesting these methods are more efficient than Field Hoophouse cultivation. However, we noted more erosion in the Field Hoophouse plots compared to the Field Quesadilla plots, likely because of the different irrigation methods combined with increased soil and inoculum retention associated with the shade cloth close to the soil in the Quesadilla. It is possible that using the same irrigation system as used in the Quesadilla would have reduced erosion in the Hoophouse. Even so, the Quesadilla is much easier and less expensive to set up and is more resistant to wind, and therefore may remain the preferred field cultivation method.

Of the three exopolysaccharide (EPS) sheath fractions, only loosely bound EPS were higher in the Greenhouse, which may correspond to the higher abundance of cyanobacteria and observed. The presence of EPS helps cyanobacteria survive in conditions of high UV and frequent soil dry-down events and helps to keep organisms in place and stabilize soils (Chamizo et al., 2019; Chock et al., 2019; Fick et al., 2020; Kidron, 2021). Because all cultivation methods promoted EPS formation, we can expect this will aid establishment of cultivated biocrusts under field conditions.

4.2 | Native soil boosts some biocrust components

Although chlorophyll a levels were higher in the Greenhouse, this was largely driven by the native soil treatments compared to sand. It is likely that there were cyanobacteria present in the native soil, and the growth was best promoted in the Greenhouse compared to other cultivation methods. Mosses may also have influenced

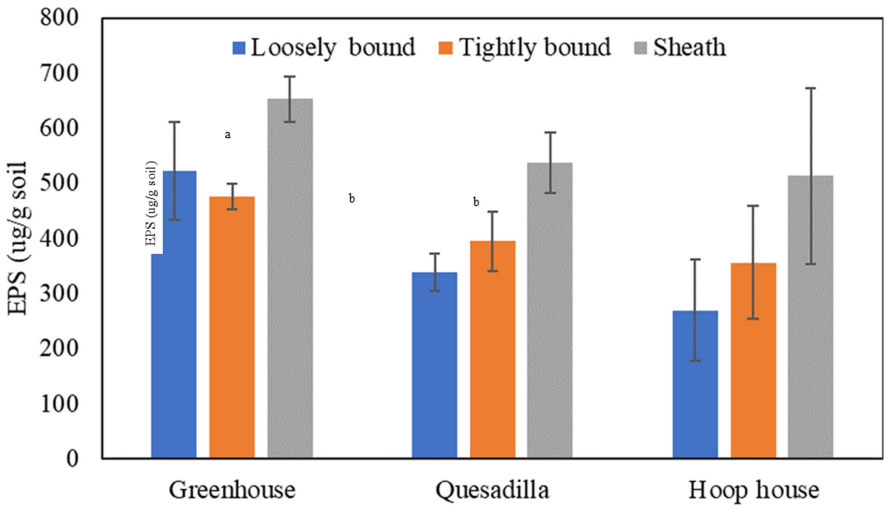

FIGURE 5 Exopolysaccharide (EPS) in different sheath fractions. Lower case letters represent Tukey's post hoc comparisons for fractions that were affected by cultivation method. Error bars represent one standard error of the mean.

TABLE 3 Mean, SE and *F* and *p* values for the three EPS categories.

Cultivation type	Replicates	Loosely bound EPS (g/g soil)	Tightly bound EPS (µg/g soil)	Sheath EPS (g/g soil)
GH Mean (SE)	3	522.4 (88.5)	475.6 (22.8)	652.6 (40.9)
Quesadilla Mean (SE)	3	338.9 (53.1)	395.2 (95.0)	537.6 (99.5)
Hoop Mean (SE)	3	269.9 (91.0)	356.2 (102.6)	512.9 (160.1)
Cultivation type (*F* ratio (*p*-value)	df = 2	3.0 (0.6)	0.8 (0.6)	1.4 (0.3)

Note: All are native soil with jute.

the higher level of chlorophyll a a in the greenhouse. We found higher cyanobacterial cover overall in the Greenhouse compared to other methods and in the native soil in particular. Lichen cover was also greatest with native soil, even though lichens are particularly difficult to culture (Bowker & Antoninka, 2016; Ficko et al., 2023). It is also possible that the sand substrate was less favourable than native soil because of the soil physical properties and presence of the native microbial community that can promote nutrient exchange and cycling (Delgado-Baquerizo et al., 2013). The high cover of cyanobacteria should translate to high establishment in field sites because cyanobacteria are early successional and have been shown to establish best in the field (Antoninka et al. 2017; Belnap, 2003; Giraldo-Silva et al., 2019). Overall, our results suggest that native soil was not necessary for successful biocrust cultivation, but could be helpful for certain components of the biocrust community.

4.3 | Jute creates biocrust "fabric"

In other field trials we have found jute to be a helpful element to contain biocrust and offer added protection in establishment (Bowker et al., 2020; Condon & Pyke, 2016). Here we found that jute increased the cover of mosses, but not other components of the biocrust community. We did not directly measure soil loss, but it is likely that jute treatments retained soil and biocrust better than controls, particularly in the field. A goal of this experiment was to create biocrusts that could be transported to disturbed areas for restoration. The addition of jute facilitates good binding when plant cover increased, allowing units to be moved in one piece with less disturbance to the biocrust than without jute, which is promising as a technique to restore islands of biocrust.

4.4 | Plants like Quesadillas, native soil and no jute

Plant cover was higher in the Quesadilla compared to the Hoophouse and positively correlated with biocrust cover. Plants did not grow well in the Greenhouse, likely because the Greenhouse conditions were different than needed for Sonoran Desert plant germination. Plants grew preferentially in native soils over sand. The increase of plants with native soils is likely due to the additional seed bank and/or native microbial symbionts in the native soils compared with the sand. However, the three-way treatment interaction for native plants suggests that jute seemed to suppress plant establishment from the native soil, likely because the jute is placed over the native soil and acts as a weed barrier. The responses of biocrust and plant growth were correlated, but

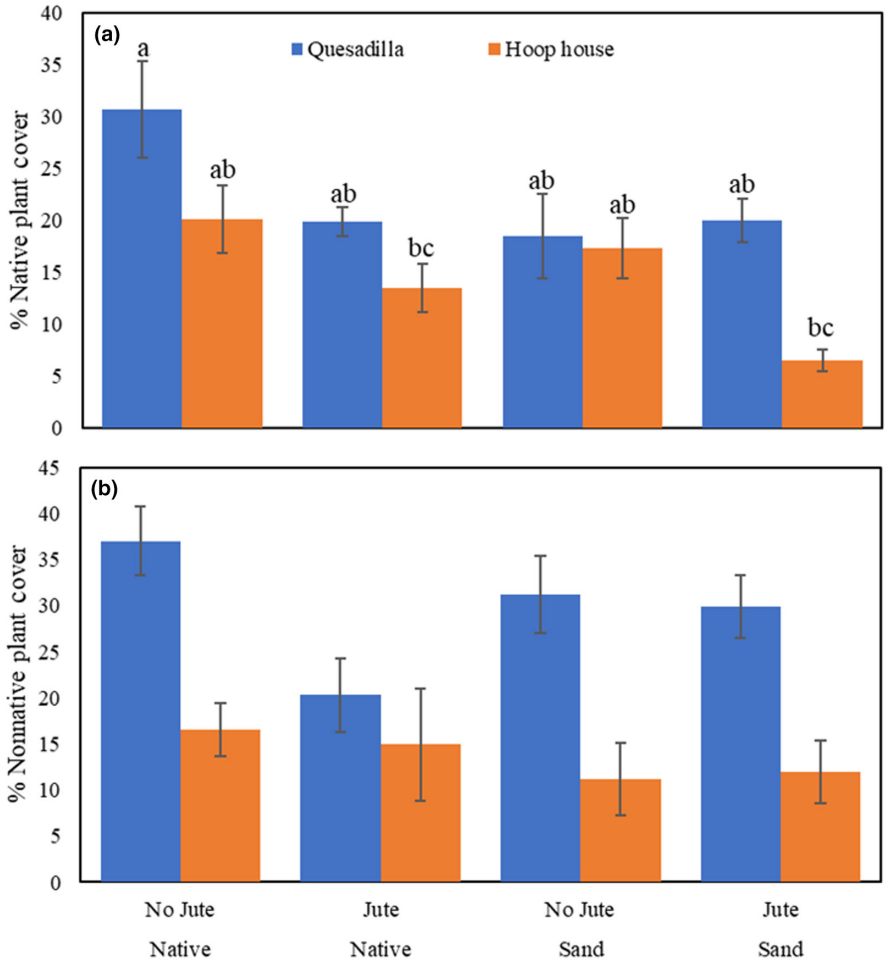

FIGURE 6 Percent native (A) and non-native (B) plant cover by cultivation method (blue: Quesadilla, orange: Hoophouse) plants as affected by jute and soil type. Lower case letters represent Tukey's post hoc comparisons of cultivation by soil type. Error bars represent one standard error of the mean.

not strongly so, likely because while jute improved moss growth, it inhibited plant growth from the native soil. One of the goals of cultivating biocrusts can be to remove the weed seed bank. If the goal is to enhance native plant establishment, then nonnative plants could be weeded out of the sods during cultivation and the native plants could be left to flower and re-seed. Alternatively, all plants could be weeded out during cultivation if a plant-free sod was desired.

4.5 | Scaling up is possible

Our results demonstrate that a variety of biocrust cultivation methods are possible in the field or Greenhouse. The ability to grow biocrust directly on the ground in the field with weed cloth, a small layer of soil, simple irrigation and shade is beneficial for a few reasons. First, we can scale up biocrust restoration efforts for application at large disturbed sites (Antoninka et al., 2020). Second, the use of a weed cloth with shallow soil allows cultivation without the introduction of nonnative plants from the cultivation field soils. The non-native plants that germinate within the cultivated biocrusts can be cut or pulled easily to remove the threat of introducing weeds into field plots. Depending on goals, native plants can be left to re-seed or removed. The Greenhouse culturing methods can also be scaled up, limited only by the greenhouse space. Thus, practitioners can choose a method most appropriate to their biocrust community, available resources and size needs.

4.6 | Next steps

The ultimate test of these methods is whether these cultivated biocrusts can survive and be established in the field. Field trials are underway to determine overall biocrust survival and if cultivation methods affect the establishment of the original biocrust community. This is an important step for successful restoration because previous repeat cultivation of biocrust cyanobacteria in the Greenhouse led to significant drift from the original community after only two rounds (Bethany et al., 2019). We anticipate that since the field cultivated biocrusts largely mimic the field salvaged biocrusts, that this drift will be minimal. Hardening trials have had very mixed results (Antoninka et al., 2019; Bowker et al., 2020; Faist et al., 2020; Giraldo-Silva et al., 2019), but we anticipate that field-grown biocrusts will be better "hardened" to field conditions because of the higher temperature and RH variation and UV exposure. Finally, a critical pinch point for biocrust restoration is finding biocrust inoculum without disturbing intact biocrust communities. We were able to salvage biocrusts from an area slated to be disturbed, but

that is not always possible. Creating sustainable harvest and cultivation technologies is necessary for the future of restoration (Tucker et al., 2020). Interactions with citizen scientists was critical to make this work happen, and we encourage others to adopt programs that interact and train community members.

AUTHOR CONTRIBUTIONS

Anita Antoninka and Helen Rowe conceived the experiment. All coauthors helped to set up the experiment. John Weser provided the SCC space and maintained the experiment. Debbie Langenfeld and Jane Brady monitored the experiment. Natalie Day performed EPS analysis. Tiffany Sprague helped with data collection and archiving. Anita Antoninka wrote the first draft of the manuscript. Anita Antoninka and Helen Rowe did the analysis. All coauthors edited the manuscript and provided significant intellectual contributions.

ACKNOWLEDGEMENTS

This work was funded through a grant from the City of Scottsdale and was conducted in partnership with the Citizen Science program at the McDowell Sonoran Conservancy. We are also grateful for the facilities support from Scottsdale Community College.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12389.

DATA AVAILABILITY STATEMENT

Data is publicly available at Zenodo: https://doi.org/10.5281/zenodo.13829769 (Antoninka et al., 2024).

ORCID

A. Antoninka https://orcid.org/0000-0001-6583-9892

REFERENCES

Antoninka, A., Bowker, M. A., Barger, N. N., Belnap, J., Giraldo-Silva, A., Reed, S. C., Garcia-Pichel, F., & Duniway, M. C. (2019). Addressing barriers to improve biocrust colonization and establishment in dryland restoration. *Restoration Ecology*, *28*, S150–S159. https://doi.org/10.1111/rec.13052

Antoninka, A., Bowker, M. A., Chuckran, P., Barger, N. N., Reed, S., & Belnap, J. (2017). Maximizing establishment and survivorship of field-collected and greenhouse-cultivated biocrusts in a semi-cold desert. *Plant and Soil*, *429*, 213–225. https://doi.org/10.1007/s11104-017-3300-3

Antoninka, A., Bowker, M. A., Reed, S. C., & Doherty, K. (2016). Production of greenhouse-grown biocrust mosses and associated cyanobacteria to rehabilitate dryland soil function. *Restoration Ecology*, *24*, 324–335. https://doi.org/10.1111/rec.12311

Antoninka, A., Faist, A., Rodriguez-Caballero, E., Young, K. E., Chaudhary, V. B., Condon, L. A., & Pyke, D. A. (2020). Biological soil crusts in ecological restoration: Emerging research and perspectives. *Restoration Ecology*, *28*, S3–S8.

Antoninka, A., Rowe, H., Weset, J., Langenfeld, D., Brady, J., Sprague, T., & Day, N. (2024). Data from: Comparing greenhouse and field biocrust cultivation methods in the Sonoran Desert. *Ecological Solutions and Evidence*, *Zenodo*. https://doi.org/10.5281/zenodo.13829769

Ayuso, S. V., Giraldo-Silva, A., Barger, N. N., & Garcia-Pichel, F. (2020). Microbial inoculum production for biocrust restoration: Testing the effects of a common substrate versus native soils on yield and community composition. *Restoration Ecology*, *28*, S194–S202. https://doi.org/10.1111/rec.13127

Belnap, J. (2003). Biological soil crusts in deserts: A short review of their role in soil fertility, stabilization, and water relation. *Archiv für Hydrobiologie-Supplements*, *148*, 113–126.

Bethany, J., Giraldo-Silva, A., Nelson, C., Barger, N. N., & Garcia-Pichel, F. (2019). Optimizing the production of nursery-based biological soil crusts for restoration of arid land soils. *Applied and Environmental Microbiology*, *85*, e00735-19. https://doi.org/10.1128/AEM.00735-19

Bowker, M. A. (2007). Biological soil crust rehabilitation in theory and practice: An underexploited opportunity. *Restoration Ecology*, *15*, 13–23. https://doi.org/10.1111/j.1526-100X.2006.00185.x

Bowker, M. A., & Antoninka, A. J. (2016). Rapid ex situ culture of N-fixing soil lichens and biocrusts is enhanced by complementarity. *Plant and Soil*, *408*, 415–428. https://doi.org/10.1007/s11104-016-2929-7

Bowker, M. A., Antoninka, A. J., & Durham, R. A. (2017). Applying community ecological theory to maximize productivity of cultivated biocrusts. *Ecological Applications*, *27*(6), 1958–1969.

Bowker, M. A., Antoninka, A. J., & Chuckran, P. F. (2020). Improving field success of biocrust rehabilitation materials: Hardening the organisms or softening the environment? *Restoration Ecology*, *28*, S177–S186. https://doi.org/10.1111/rec.12965

Bowker, M. A., Maestre, F. T., & Mau, R. L. (2013). Diversity and patch-size distributions of biological soil crusts regulate dryland ecosystem multifunctionality. *Ecosystems*, *16*, 923–933. https://doi.org/10.1007/s10021-013-9644-5

Bowker, M. A., Mau, R. L., Maestre, F. T., Escolar, C., & Castillo-Monroy, A. P. (2011). Functional profiles reveal unique ecological roles of various biological soil crust organisms. *Functional Ecology*, *25*, 787–795. https://doi.org/10.1111/j.1365-2435.2011.01835.x

Brown, D. E., Lowe, C. H., & Pase, C. P. (1979). A digitized classification system for the biotic communities of North America, with community (series) and association examples for the southwest. *Journal of the Arizona-Nevada Academy of Science*, *14*(Suppl. 1), 1–16.

Castle, S. C., Morrison, C. D., & Barger, N. N. (2011). Extraction of chlorophyll a from biological soil crusts: A comparison of solvents for spectrophotometric determination. *Soil Biology and Biochemistry*, *43*(4), 853–856.

Chamizo, S., Adessi, A., Mugnai, G., Simiani, A., & de Philippis, R. (2019). Soil type and cyanobacteria species influence the macromolecular and chemical characteristics of the polysaccharidic matrix in induced biocrusts. *Microbial Ecology*, *78*, 482–493. https://doi.org/10.1007/s00248-018-1305-y

Chen, J., Yin, C., Jin, J., Wu, K., Yu, Z., & Deng, C. (2018). Characteristics of different molecular weight EPS fractions from mixed culture dominated by AnAOB and their role in binding metal ions. *Environmental Science and Pollution Research*, *25*, 5491–5500.

Chock, T., Antoninka, A. J., Faist, A. M., Bowker, M. A., Belnap, J., & Barger, N. N. (2019). Responses of biological soil crusts to rehabilitation strategies. *Journal of Arid Environments*, *163*, 77–85. https://doi.org/10.1016/j.jaridenv.2018.10.007

Condon, L. A., & Pyke, D. A. (2016). Filling the interspace—Restoring arid land mosses: Source populations, organic matter, and overwintering govern success. *Ecology and Evolution*, *6*, 7623–7632. https://doi.org/10.1002/ece3.2448

Delgado-Baquerizo, M., Morillas, L., Maestre, F. T., & Gallardo, A. (2013). Biocrusts control the nitrogen dynamics and microbial functional diversity of semi-arid soils in response to nutrient additions. *Plant and Soil*, *372*, 643–654. https://doi.org/10.1007/s11104-013-1779-9

Doherty, K. D., Antoninka, A. J., Bowker, M. A., Ayuso, S. V., & Johnson, N. C. (2015). A novel approach to cultivate biocrusts for restoration and experimentation. *Ecological Restoration*, *33*, 13–16. https://doi.org/10.3368/er.33.1.13

Dubois, M., Gilles, K. A., Hamilton, J. K., Rebers, P. A., & Smith, F. (1956). Colorimetric method for determination of sugars and related substances. *Analytical Chemistry*, *28*, 350–356.

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M. O., & Pöschl, U. (2012). Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience*, *5*, 459–462. https://doi.org/10.1038/ngeo1486

Eldridge, D. J., Reed, S., Travers, S. K., Bowker, M. A., Maestre, F. T., Ding, J., Havrilla, C., Rodriguez-Caballero, E., Barger, N., Weber, B., Antoninka, A., Belnap, J., Chaudhary, B., Faist, A., Ferrenberg, S., Huber-Sannwald, E., Malam Issa, O., & Zhao, Y. (2020). The pervasive and multifaceted influence of biocrusts on water in the world's drylands. *Global Change Biology. Bioenergy*, *26*, 6003–6014. https://doi.org/10.1111/gcb.15232

Faist, A. M., Antoninka, A. J., Belnap, J., Bowker, M. A., Duniway, M. C., Garcia-Pichel, F., Nelson, C., Reed, S. C., Giraldo-Silva, A., Velasco-Ayuso, S., & Barger, N. N. (2020). Inoculation and habitat amelioration efforts in biological soil crust recovery vary by desert and soil texture. *Restoration Ecology*, *28*, S96–S105. https://doi.org/10.1111/rec.13087

Felde, V. J. M. N. L., Chamizo, S., Felix-Henningsen, P., & Drahorad, S. L. (2018). What stabilizes biological soil crusts in the Negev Desert? *Plant and Soil*, *429*, 9–18. https://doi.org/10.1007/s11104-017-3459-7

Ferrenberg, S., Reed, S. C., & Belnap, J. (2015). Climate change and physical disturbance cause similar community shifts in biological soil crusts. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 12116–12121. https://doi.org/10.1073/pnas.1509150112

Fick, S. E., Day, N., Duniway, M. C., Hoy-Skubik, S., & Barger, N. N. (2020). Microsite enhancements for soil stabilization and rapid biocrust colonization in degraded drylands. *Restoration Ecology*, *28*, S139–S149. https://doi.org/10.1111/rec.13071

Ficko, S. A., McClymont, A., Haughland, D. L., & Naeth, M. A. (2023). Optimizing growth chamber conditions for maintaining Arctic lichen-dominatedbiocrusts. *Restoration Ecology*, *31*, e13876. https://doi.org/10.1111/REC.13876

Giraldo-Silva, A., Nelson, C., Barger, N. N., & Garcia-Pichel, F. (2019). Nursing biocrusts: Isolation, cultivation, and fitness test of indigenous cyanobacteria. *Restoration Ecology*, *27*, 793–803. https://doi.org/10.1111/rec.12920

Havrilla, C., Leslie, A. D., Di Biase, J. L., & Barger, N. N. (2020). Biocrusts are associated with increased plant biomass and nutrition at seedling stage independently of root-associated fungal colonization. *Plant and Soil*, *446*, 331–342. https://doi.org/10.1007/s11104-019-04306-4

Kidron, G. J. (2021). The role of biocrust-induced exopolymeric matrix in runoff generation in arid and semiarid zones—A mini review. *Journal Of Hydrology And Hydromechanics*, *69*, 360–368.

Peet, R. K., Wentworth, T. R., & White, P. S. (1998). A flexible, multipurpose method for recording vegetation composition and structure. *Castanea*, *63*, 262–274.

Porada, P., Weber, B., Elbert, W., Pöschl, U., & Kleidon, A. (2014). Estimating impacts of lichens and bryophytes on global biogeochemical cycles. *Global Biogeochemical Cycles*, *28*, 71–85. https://doi.org/10.1002/2013GB004705

Prăvălie, R. (2016). Drylands extent and environmental issues. A global approach. *Earth-Science Reviews*, *161*, 259–278. https://doi.org/10.1016/j.earscirev.2016.08.003

Rodriguez-Caballero, E., Belnap, J., Büdel, B., Crutzen, P. J., Andreae, M. O., Pöschl, U., & Weber, B. (2018). Dryland photoautotrophic soil surface communities endangered by global change. *Nature Geoscience*, *11*, 185–189. https://doi.org/10.1038/s41561-018-0072-1

Rossi, F., Mugnai, G., & De Philippis, R. (2018). Complex role of the polymeric matrix in biological soil crusts. *Plant and Soil*, *429*, 19–34.

Tucker, C., Antoninka, A., Day, N., Poff, B., & Reed, S. (2020). Biological soil crust salvage for dryland restoration: An opportunity for natural resource restoration. *Restoration Ecology*, *28*, S9. https://doi.org/10.1111/rec.13115

Weber, B., Belnap, J., Büdel, B., Antoninka, A. J., Barger, N. N., Chaudhary, V. B., Darrouzet-Nardi, A., Eldridge, D. J., Faist, A. M., Ferrenberg, S., Havrilla, C. A., Huber-Sannwald, E., Malam Issa, O., Maestre, F. T., Reed, S. C., Rodriguez-Caballero, E., Tucker, C., Young, K. E., Zhang, Y., … Bowker, M. A. (2022). What is a biocrust? A refined, contemporary definition for a broadening research community. *Biological Reviews and Biological Proceedings of the Cambridge Philosophical Society*, *97*, 1768–1785. https://doi.org/10.1111/BRV.12862

Weber, B., Bowker, M., Zhang, Y., & Belnap, J. (2016). Natural recovery of biological soil crusts after disturbance. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands* (pp. 479–498). Springer International Publishing.

Zhao, Y., Bowker, M. A., Zhang, Y., & Zaady, E. (2016). *Biological soil crusts: An organizing principle in drylands*. B. Weber, B. Buedel, & J. Belnap (Vol. *226*, pp. 499–523). Springer-Verlag. https://doi.org/10.1007/978-3-319-30214-0

How to cite this article: Antoninka, A., Rowe, H., Weser, J., Langenfeld, D., Brady, J., Sprague, T., & Day, N. (2024). Comparing greenhouse and field biocrust cultivation methods in the Sonoran Desert. *Ecological Solutions and Evidence*, *5*, e12389. https://doi.org/10.1002/2688-8319.12389