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RESEARCH ARTICLE

Microsite enhancements for soil stabilization and rapid biocrust colonization in degraded drylands

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In dryland ecosystems, natural recovery of biological soil crusts (biocrusts) following disturbance may be slow or inhibited, necessitating active restoration practices. While biocrusts can be readily propagated under environmentally controlled conditions, rehabilitation in the field is complicated by environmental stresses which may be particularly acute in degraded, destabilized soils with harsh climatic conditions at the soil surface. In this study, we first present the results of a field trial at a severely degraded rangeland site examining the stabilizing effects of various soil amendments (polysaccharide glues and polyacrylamides) in combination with biocrust inoculum. We found that a psyllium compound was the only amendment to maintain effectiveness after 19 months, and the only treatment that maintained biocrust inoculum throughout the trial. In a subsequent short-term experiment where plots were shaded and watered, we examined how biocrust inoculation rate (0, 20, and 40% initial cover) and the psyllium-based amendment affected biocrust growth. After 4 months, visible biocrust cover in inoculated plots was greater than in controls, but only chlorophyll *a* exhibited a dosage-response to inoculum application rate, indicating preferential establishment of cyanobacteria. Psyllium did not affect biocrust development but did improve soil stability. Shade and watering buffered against temperature extremes (up to 15°C) and increased the duration of moist surface conditions necessary for biocrust growth by up to 30%, mimicking conditions more common in the fall and winter months. Our results suggest that inducing early successional biocrusts on a highly degraded site is possible with suitable microclimate conditions.

Key words: aggregate stability, bioinoculation, biological soil crust, Colorado plateau, microenvironment, psyllium, soil amendments

Implications for Practice

- Combined application of biocrust inoculum with soil stabilizer is a promising technique for biocrust restoration at degraded sites. We found applications of psyllium stabilizer with biocrust to be most effective at increasing soil aggregate stability.
- Induction of early successional biocrusts in highly degraded sites may be possible with suitable microsite conditions (stability, shade, moisture).
- Shading or watering may be unfeasible at large scales but effective for smaller high-priority areas, or areas near suitable infrastructure.
- Timing of biocrust inoculations with suitable climate conditions may facilitate success with fewer inputs. For our field location (cold desert) we identified high intra-annual variation in estimated biocrust activity, with the most suitable conditions for inoculation occurring in the fall.

Introduction

Biological soil crusts ("biocrusts") are communities of lichens, mosses, cyanobacteria, and other microorganisms that develop on the top 1–2 cm of soil surfaces and are critically important functional components of dryland systems across the Earth. In cool desert systems, biocrusts are often associated with increased soil nutrient and water retention—resources that are highly limiting to plant productivity (Barger et al. 2016; Chamizo et al. 2016). Biocrusts stabilize soil surfaces against wind and water erosion (Belnap & Gillette 1997; Chamizo et al. 2016; Faist et al. 2017), and some intact biocrust surfaces may be essentially impervious to naturally occurring wind velocities (Belnap et al. 2009). Intact and diverse biocrust communities are taken to be an indicator of soil health (Herrick et al. 2002) and the decline or loss of biocrusts may be an indicator of an ecosystem shift to a degraded state (Belnap et al. 2001; Miller et al. 2011). Biocrusts are highly susceptible to compressional forces, such as those generated from livestock grazing and foot

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and vehicle traffic (Belnap & Eldridge 2003). Due to their relatively slow recovery rates and importance for ecosystem health, assisted biocrust recovery may be an important step to restoring ecosystem function in degraded dryland systems (St Clair et al. 1986; Belnap 1993; Bowker 2007; Zhao et al. 2016).

Natural recovery of biocrusts may occur without significant management intervention simply by removing activities that disturb the soil surface (Weber et al. 2016*b*; Duniway et al. 2018). In heavily degraded sites, however, the lack of propagules, suitable environmental conditions, and a stable soil surface for colonization by microorganisms may pose significant barriers to natural recovery of the biocrust community (Bowker 2007). In recent years, substantial efforts have been made in developing inoculum to increase availability of biocrust propagules and promote more rapid recovery of these communities (Velasco Ayuso et al. 2017; Bethany et al. 2019; Giraldo-Silva et al. 2019). Grown under controlled environmental conditions, biocrust biomass may reach levels observed in intact field populations in as little as 3 to 7 weeks (Bethany et al. 2019). Transfer of both field-collected inoculum and inoculum propagated in the laboratory or greenhouse to disturbed or degraded soils without any irrigation or modification to the site has been met with more limited success (Chen et al. 2006; Antoninka et al. 2017; Faist et al. this issue; Antoninka et al. this issue). Interestingly, in some studies the natural recovery of experimentally disturbed surfaces has kept pace with inoculated plots (Antoninka et al. 2017) when abundant natural inoculum was available in surrounding areas. These findings suggest that at recently disturbed sites, biocrust propagules are either present in the soil or are blown or washed into sites, and even at low levels may be sufficient to induce recovery. However, it is clear that environmental factors such as nutrient limitation, soil instability, and erosion in the field can significantly constrain biocrust recovery rates, especially in highly degraded settings with limited propagule abundance (Young et al. 2019).

A broad range of factors limit biocrust establishment and confound restoration outcomes under especially stressful environmental conditions. Numerous studies on inoculum development under controlled conditions have shown the importance of continuous periods of surface moisture followed by a drying cycle, moderate temperatures, and reductions in UV exposure, consistent with the photosynthetic requirements of nonvascular, slow-growing poikilohydric organisms (Lange 2001; Antoninka et al. 2015; Doherty et al. 2015; Velasco Ayuso et al. 2017). Because of these environmental constraints to biocrust growth, time periods in which biocrusts may be active in the field are relatively short (Lange 2001; Belnap 2002). Thus, altering field conditions in a way that lengthens periods of biocrust activity through water additions, inoculating during cooler time periods, and reducing UV exposure is likely to lead to more rapid recovery (Chock et al. 2019; Sorochkina et al. 2018; Antoninka et al. this issue).

At highly degraded sites, unstable soil surfaces may also constrain biocrust recovery (Bowker 2007). Soil detachment and sandblasting from erosive winds and even bioturbation by animals may bury early biocrust pioneers (Jia et al. 2008; Kidron & Zohar 2014). In the absence of soil stabilization by physical crusting or other means, colonization by cyanobacterial pioneer species will be limited by continual disturbance of the soil surface (Weber et al. 2016*b*). Thus, artificial stabilization of the soil surface before inoculation may also be an important step to promote biocrust recovery. A number of strategies have been used to decrease soil erosion and stabilize soils surfaces such as the use of straw checkerboards (Li et al. 2006) and artificial soil stabilization products such as polyacrylamides (Davidson et al. 2002; Park et al. 2014, 2016; Chock et al. 2019).

In this study, we examined the relative importance of biocrust inoculation and soil stabilization amendments in promoting soil stability and biocrust growth at a degraded rangeland site. First, we performed a field trial using different types of stabilizers, testing for stabilization effectiveness and any potential effects on biocrust development. Using the findings from this field trial, we implemented an expanded experiment involving two levels of biocrust inoculation and a psyllium-based product for soil stabilization. In the expanded experiment we also alleviated water and UV stress through frequent irrigation and shading of the soil surface, measuring effects on surface temperature and hydration. We hypothesized that both soil stabilization and biocrust inoculation are needed to increase the rate of biocrust recovery at highly degraded sites, even with reductions in stress associated with temperature and hydration status.

Methods

Study Area

Experiments were conducted at the Canyonlands Research Center (CRC) in southeastern Utah (38.070°, −109.564°; https://canyonlandsresearchcenter.org/). The study area is located in the Colorado Plateau physiographic region of the southwestern United States at an altitude of 1,627 m above sea level. The climate is characterized as cool desert, with a mean annual temperature of 15°C and a mean annual precipitation of 197 mm (Urban 2017). The landscape at the CRC has been subject to grazing by domestic livestock for over 100 years, with some areas receiving irrigation for livestock forage cultivation. Many of these previously cultivated areas have severely truncated soils and are dominated by invasive annual weeds including *Salsola* sp., *Erodium cicutarium*, and *Bromus tectorum*. The sites selected for this study (see below) were exemplars of such heavily impacted sites, characterized by relatively unstable soils, a lack of native perennial vegetation, and no sign of incipient biocrust growth on any soil surface. Expected biocrust communities in the area contain a mix of mosses, lichens, and dark-colored cyanobacterially dominated surfaces ("dark-pigmented" cyanobacterial crust) as well as some smoother, early successional light-colored patches dominated by cyanobacteria such as *Microcoleus vaginatus* ("light-pigmented" cyanobacterial crust; Yeager et al. 2004).

Stabilizer Trial

In July 2016, trials were established to identify amendments that would enhance soil stability, and screen for any

impacts on biocrust growth. Soils at the site selected for trials were sandy loams, belonging to the Redbank soil series (Ustic Torrifluvents) and attributed to the Semidesert Sandy Loam Fourwing Saltbrush ecological site description (ESD) by the US Department of Agriculture Natural Resources Conservation Service (035XY215UT; USDA NRCS 2009). Ten soil stabilization amendments (including controls) were randomly applied to plots located along five replicate transects ($N = 50$). Plots were 0.5×0.5 m and surrounded by metal flashing 10 cm in height. Treatments included two polysaccharide glues: "M-Binder" psyllium-based soil stabilizer (Ecology Controls, Carpinteria, CA, U.S.A.) and xanthan gum (Bob's Red Mill, Milwaukee, OR, U.S.A.) and two polyacrylamides: Terraloc (MonoSOL, Merrillville, IN, U.S.A.) and Dirt Glue (Dirtglue Enterprises, Salem, NH, U.S.A.). Each amendment was applied alone and with biocrust inoculum. Control plots with no stability amendment and a biocrust-only amendment were also located in each transect.

Prior to application, plots were cleared of plant debris and raked by hand. Liquid amendments, including DirtGlue and Terraloc, were diluted to 10% with deionized water and applied evenly over the surface with a backpack sprayer (2 L/m^2). Dry amendments, including M-Binder (60 g/m^2) and Xanthan gum (40 g/m^2), were spread evenly across the soil surface and lightly hand raked into the soil. Biocrust inoculum with a well-developed biocrust community comprised of lichens, mosses, and dark- and light-pigmented cyanobacterial crust was collected from a location approximately 60 km from the field site near Moab, UT. The inoculum was collected dry from the top 2 cm of the soil surface, crumbled to fragments roughly 0.5–2 cm in diameter and spread evenly across the plot. One liter of water was added after treatment application (corresponding to 4 mm or a rain event in the 80% quantile) with no additional water added during the trial. In April 2017 (9 months after establishment) and February 2018 (19 months after establishment), plots were sampled for soil aggregate stability with a field aggregate stability test kit (Seybold & Herrick 2001). Two replicates were collected at each plot for a total of 10 replicates per amendment at each time point. For each sampling date, we recorded whether any moss, lichen, or dark cyanobacterial crust were present on a plot.

Average aggregate stability scores among treatments at each time point were compared using analysis of variance and Tukey's test in the "multcompView" package (Graves et al. 2015) in R (R Development Core Team 2015). The association between persistence of biocrust cover across both sampling periods and amendment type was tested with a chi-square contingency test.

Establishment Experiment

In early 2018 we established a factorial field experiment at a separate site within the CRC studying the effects of inoculation rate and stabilization on biocrust growth. Soils at the site were sandy loams (50–65% sand, 30–44% silt, 4–6% clay), belonging to the Mivida series (Ustic Haplocalcid), and are attributed to the same ESD as the field stability trial (Semidesert Sandy Loam Fourwing Saltbrush). In January 2018, biocrust inoculum was collected from two areas within 5 km of the study site: (1) a mesa top protected from grazing with a well-developed biocrust community dominated by lichens and dark-pigmented cyanobacterial crusts and (2) a valley floor subject to grazing containing light-pigmented biocrust dominated by cyanobacteria such as *M. vaginatus*. The top 2 cm of soil was collected. The two biocrust community types were then mixed together and air dried to stop metabolic activity. Dried inoculum particles were then fragmented to 0.5–2 cm pieces to facilitate even distribution across plots. Inoculum particles were then passed through a 1-mm mesh sieve to remove loose sand particles from biocrust biomass. To calculate inoculum mass per surface area for application rates, samples of processed inoculum were spread across a 9-cm diameter petri dish at a consistent depth of 1 cm (0.75 kg/m^2 for 20% cover, 1.5 kg/m^2 for 40%).

Inoculum community composition was estimated by spreading the sieved inoculum on a tray at a consistent depth of 1 cm, ensuring the photosynthetic side of aggregates was facing up. A 15×15-cm grid was then used to make 50 pin drop observations. Lichens and moss were recorded to the species level, while all other hits were recorded as cyanobacterial crust, assuming that sieving removed unbound sediment. This process was repeated for six samples of inoculum stock to find the average percent cover for each biological type. A species accumulation curve was used to estimate the efficiency of species richness sampling (Fig. S1).

Biocrust inoculation plots were established as part of a larger set of experiments (Fick et al. 2019*a*, 2019*b*). We present here pooled data focused on indicators of biocrust development for these studies. Treatments consisted of a factorial combination of three levels of crust inoculation (0, 20, and 40%, or 0, 0.75, and 1.5 kg/m^2) crossed with two levels of M-Binder psyllium-based soil stabilizer, either 0 or 60 g/m^2. One set of plots were slightly larger than the others (0.81×0.81 m vs. 0.71×0.71 m), arranged in blocks of three plots (as opposed to blocks of 18), and consisted of three treatment types: control (no additions), 40% biocrust, and 40% biocrust with 60 g/m^2 M-binder ($N = 8 \times 3$ vs. $N = 18 \times 6$, total = 132). Prior to treatment application, all plot surfaces were cleared of litter and loose sediment. Treatments were applied in early February 2018 by distributing pre-weighed mixed inoculum and powdered soil stabilizer across plot surfaces, which was followed by a light watering after application. In plots with both inoculum and stabilizer, materials were mixed prior to application.

Plots were watered frequently throughout the winter and spring, with breaks between watering not exceeding 1.5 weeks (Table S1). On watering days, plots were repeatedly sprayed by hand with a low-pressure sprinkler nozzle to the point of surface saturation but not ponding. Water was charcoal filtered prior to application. In early March, a canopy of 40% transmittance shade cloth was suspended over plots (Fig. S2) to extend the duration of hydrated conditions suitable for crust growth following manual watering and precipitation events (UV Polyethylene Knitted Shade Cloth—60% Green, DeWitt, Sikeston, MO, U.S.A.). Plots were hand-weeded in the spring (April–May) as needed to remove seedlings in plots. Most

seedlings were *Salsola* sp., which were easy to remove without significant surface disturbance.

In early June 2018, all plots were sampled for soil surface characteristics. Soil aggregate stability was assessed for six samples per plot with a field aggregate stability test kit (Seybold & Herrick 2001). Surface cover was assessed using a 0.71 × 0.71-m pin-frame with a grid of 7 × 7 sampling intersections (total of 49 points per plot) following classes described in Herrick et al. (2005), with modifications used by the National Wind Erosion Research Network (Webb et al. 2016). For chlorophyll *a* and exopolysaccharides (EPS), a subset of plots was sampled (Table S2). From selected plots, five soil subsamples (each ~2.5 g) were taken from the top 1 cm of the surface. Subsamples were pooled prior to extraction, except for a subset of 49 plots where extractions on individual subsamples were run, then averaged per plot. Details on extraction procedures for EPS and chlorophyll *a* are available in Supplement S1. We note that the EPS extraction method assays all extracellular polysaccharides, which may include residues from the M-binder stabilizer. We hereafter refer to this collection of polysaccharides as EPS.

Response variables (cover values, EPS, chlorophyll *a*, and aggregate stability) were modeled as a function of treatments and their interactions, with block and plot type (from either Fick et al. 2019*a* or Fick et al. 2019*b*) as nested random effects using the lme4 package (Bates et al. 2015) in R (R Development Core Team 2015). Treatment least-squared means were compared using the package emmeans (Lenth 2018), adding a Tukey's adjustment for multiple comparisons and setting alpha at 0.05. Variables including chlorophyll *a* and EPS were log-transformed prior to analysis and all other variables were arcsine-transformed. Plot properties including biocrust cover and chlorophyll *a* were compared with Pearson's product moment correlations. Average chlorophyll *a* and EPS values expressed in units of mass per area are presented in Table S3.

Environmental Conditions

In early February 2018, a set of nine soil surface moisture probes (Weber et al. 2016*a*) were installed across nine plots in one block in the establishment experiment. A set of three additional probes were installed in an adjacent area which was cleared of litter and debris but not subject to any further modifications (inoculation, shading, watering) for comparison. Potential active time for experimental plots (shaded + watered) and these additional control locations were calculated as the cumulative amounts of time average surface conductance exceeded 1 S and the sun was above the horizon.

To assess general periods of potential biocrust activity at the field site, we used 15-year hourly time series data from a climate station located 6 km from the site with a similar elevation and topographic setting (Urban 2017). We assumed that surface moisture would persist until the cumulative evaporative demand following a precipitation event exceeded the storm's precipitation volume. While this approximation would be inappropriate for estimating moisture deeper in the soil profile, due to downward movement of water and buffering from evaporative demand at the surface, it reasonably represents an upper bound for surface conditions. For each rain event (hourly precipitation events with gaps less than 24 hours), we calculated the cumulative evaporative demand (potential evapotranspiration) for the days following the event following Priestley and Taylor (1972). We then calculated the fractional days (starting at the first instance of rain) until post-rainfall evaporative demand equaled total rainfall volume. We then calculated the fraction of this time window (rainfall initiation to predicted onset of dry conditions) for which the sun was above the horizon and air temperatures were greater than 0°C, assuming that biocrust organisms need sunlight and non-freezing temperatures for carbon fixation (Lange 2001). Evapotranspiration was calculated using the R package "Evapotranspiration" (Guo et al. 2017), and sun angle was calculated with the R package "suncalc" (Thieurmel & Elmarhraoui 2019).

Results

Stabilizer Trial

Nine months after the initiation of the stabilizer trial, biocrust inoculum was visible in all inoculated plots and measurable differences in aggregate stability existed among the soil surfaces of treated plots (Fig. 1). In some plots treated with TerraLoc, aggregate stability was lower relative to biocrust-only inoculated control plots, suggesting that the addition of polyacrylamide did not improve aggregate stability compared to biocrust inoculation alone (Fig. 1). Soil aggregate stability differences were less clear at a 0.95 confidence level among other treatments.

Nineteen months after plot establishment, biocrust-inoculated plots with psyllium M-Binder had significantly greater soil aggregate stability than all other treatments (Fig. 1). Amendment type was significantly related to the presence of biocrust through both sampling periods ($X^2 = 19.05$, $df = 4$,

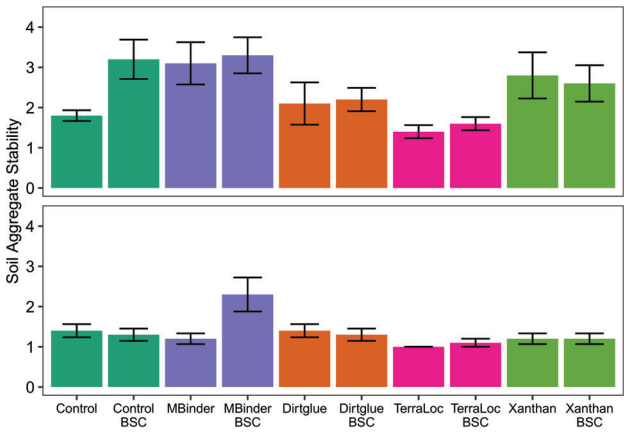

Figure 1. Average aggregate stability of stabilizer and biocrust (BSC) treatments (± 1 SE) 9 and 19 months after application (top and bottom panels, respectively). Different letters (within sampling date) indicate significant differences among treatments ($\alpha = 0.05$). The combination of biocrust and psyllium-based M-binder had significantly greater aggregate stability than any other treatment after 19 months. $N = 5$ per observation.

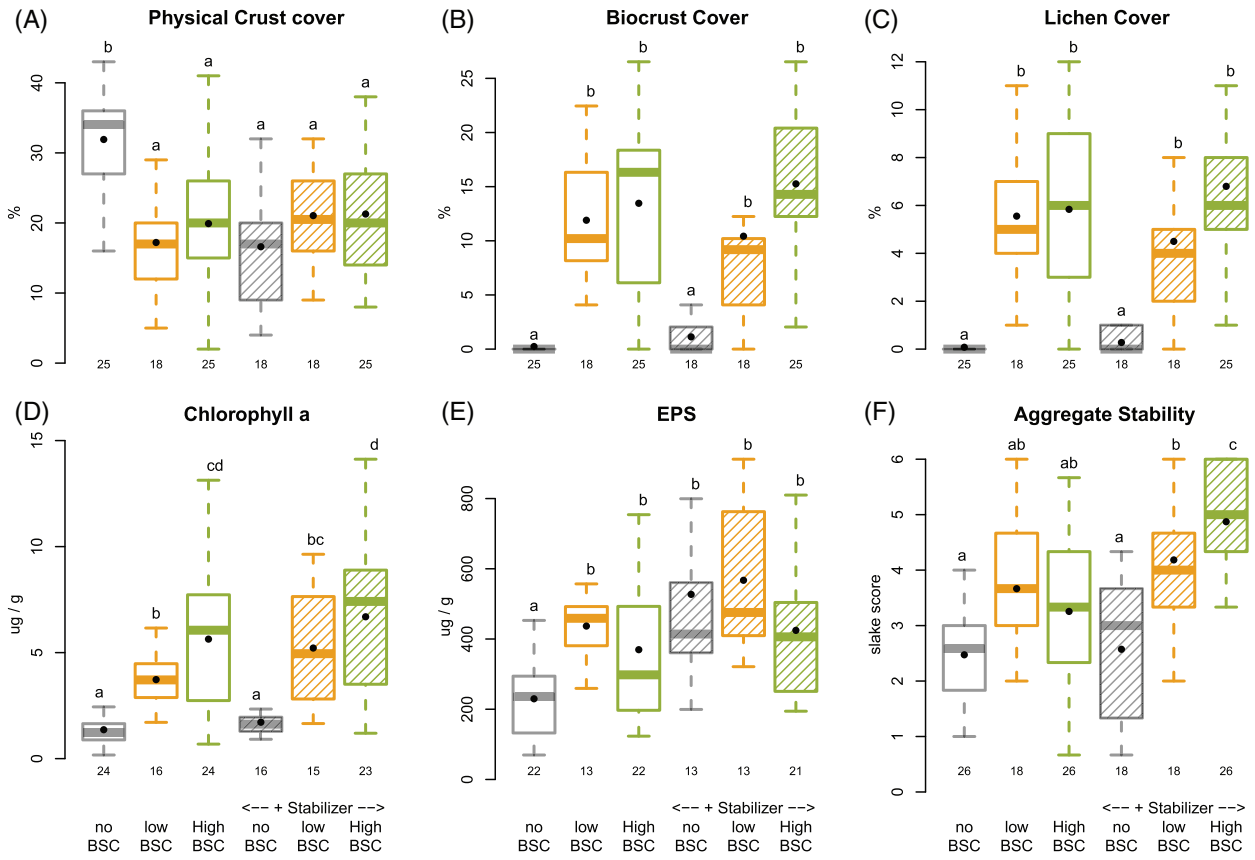

Figure 2. Relationships between restoration treatments and indicators of biocrust development. Filled dot indicates mean value per group, horizontal line indicates median, boxes represent 25th and 75th quantile, and whiskers indicate 5th and 95th quantile. Least-squared means of treatments sharing letters are not significantly different according to Tukey's HSD ($\alpha = 0.05$). Number of replicates is printed below each box.

$p < 0.001$). Only inoculated plots with M-Binder had any biocrust remaining at the end of the trial. Biocrusts were present in these plots at much lower densities than what was initially applied N. Day, personal observation, although this was not quantified. Based on the results of this trial, we included the psyllium stabilizer as a treatment factor in subsequent experiments.

Establishment Experiment

In the full biocrust establishment experiment, biocrust-inoculated plots contained a mix of mid- to large-sized biocrust particles (0.5–1.5 cm diameter) integrated into the soil surface at the end of 4 months. Visual scores of biocrust cover from pin-frame surveys identified that biocrust cover was significantly greater than control (Fig. 2), although estimated cover values were far lower than amounts applied. Average final cover estimates were 14 and 11% for high and low (40 and 20%) inoculation rates, respectively. The effect of inoculation rate on establishment was not influenced by the presence of stabilizer (lack of significant interaction). The majority of biocrust cover was identified as lichen (88%), compared to dark-pigmented cyanobacterial crust (12%) or moss (<0.2%), somewhat mirroring initial inoculum composition (Table 1).

Table 1. Community composition of biocrust types prior to inoculation.

Biological Type	*Percent Cover*
Cyanobacteria	64.3
Cyanolichens	
Collema coccophorum	11.0
Collema tenax	3.3
Peltula richardsii	3.0
Chlorolichens	
Candelariella citrina	0.6
Fulgensia braceata	1.0
Placidium lacinulatum	0.6
Placidium squamulosum	6.0
Psora decipiens	3.6
Psora tuckermanii	0.3
Squamarina lentigera	3.0
Toninia sedifolia	1.0
Mosses	
Syntichia caninervis	2.0

Initial biocrust inoculum surveys identified 12 species of lichen and one species of moss, with richness values comparable to a late-successional biocrust community with minimal historic disturbance (Belnap et al. 2006).

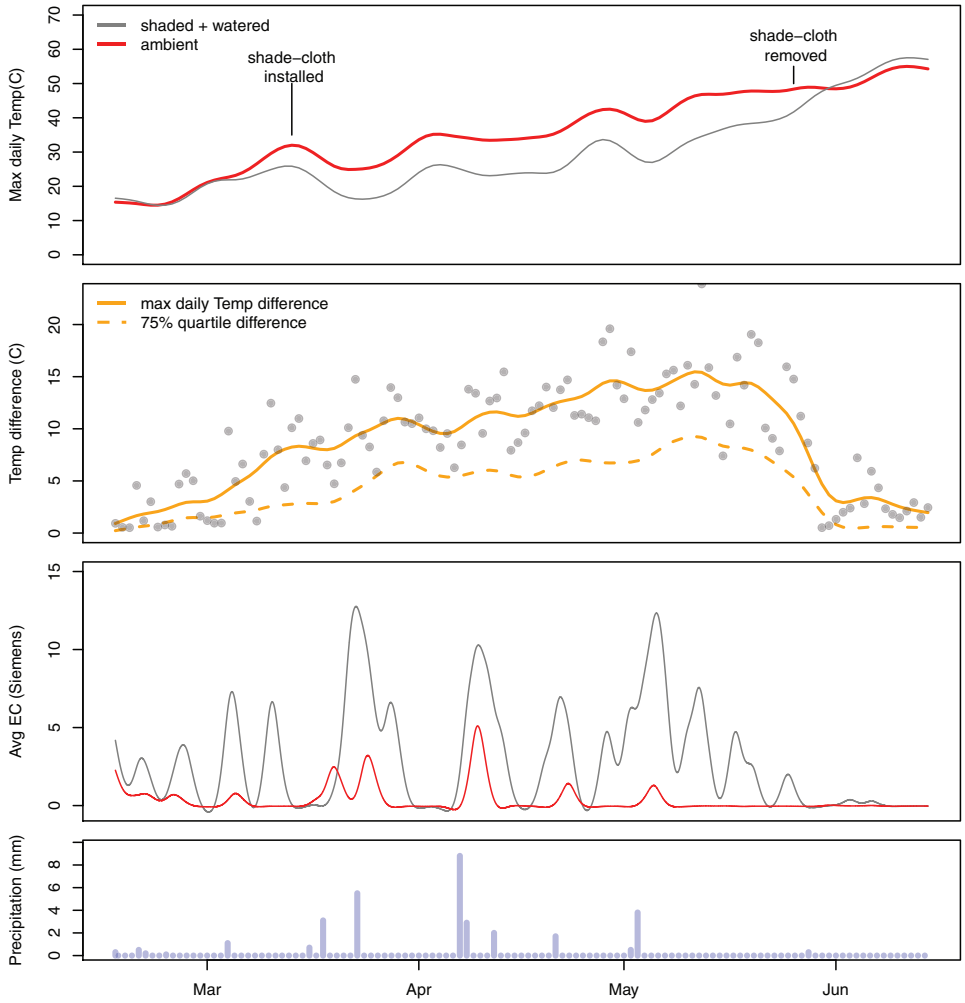

Figure 3. Average sensor readings from select plots subject to watering and shading during the spring of 2018. EC indicates electrical conductivity. Shaded and watered cloths clearly experience reduced surface temperatures (maximum daily temperature [top panel] and temperature difference [ambient minus shaded and watered temperature; second panel]), and extended periods of saturation (third panel, water present when EC >0).

Chlorophyll *a* values were also significantly greater (by a factor of 2–4) in inoculated plots than in controls, and plots with a high inoculation rate had approximately 85% greater average chlorophyll *a* content than those with low inoculation rates (Fig. 2, Table S3). As with visual biocrust cover, there were no significant interactions between inoculation rate and addition of stabilizer. The correlation coefficient between chlorophyll *a* and surface biocrust cover was 0.47 ($p < 0.001$).

Total EPS concentrations in inoculated or stabilized plots were all approximately 50% greater than in controls but did not differ among each other (Fig. 2, Table S3). For aggregate stability, there was a positive interaction between high inoculation rate and addition of soil stabilizer (Fig. 2).

Influence of Shading, Watering, and Local Climate Variability

Shading and periodic watering extended the timeframe plots experienced moist conditions and reduced the surface temperature of the soil (Fig. 3). Soil temperature was reduced by 10–15°C in shaded and watered plots for much of the hottest period of the experiment in May (Fig. 3). Although there is evidence that shade cloth may have repelled moisture for small precipitation events (e.g. reduced surface moisture in covered plots during the mid-March storms in Fig. 3), it likely lengthened surface soil moisture following larger storms (e.g. the early April storm in Fig. 3). Similarly, because the edges of the shade cloth coverings were flush to the ground, wind movement and sandblasting of plot surfaces was likely reduced, although this effect was not measured. Based on the difference between surface soil moisture measured under treated and ambient locations, it is estimated that watering and shading tripled potential biocrust activity time, resulting in active conditions 33% of the time versus 9% for ambient locations, corresponding to an additional 350 hours of potential activity.

We found strong seasonal variation in estimated potential active time for biocrusts at our site, related to the interplay of precipitation volumes mediated by post-rainfall evapotranspiration, daylight hours, and temperatures above freezing (Fig. 4).

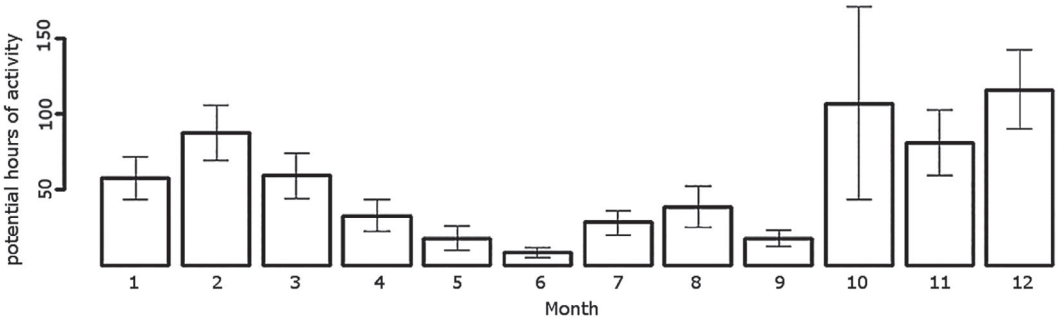

Figure 4. Estimated potential active time (± SE) for biocrusts at the field site based on a 15-year meteorological time series. Activity was calculated based on the duration of periods following rainfall with a net positive water balance (storm precipitation > cumulative potential evapotranspiration) in the time series, excluding times with the sun below the horizon or air temperatures below freezing (<0°C).

Fall and winter were found to have longer periods of potential activity than spring or summer, despite the high volumes of average precipitation during the late summer monsoons (Fig. 4). Interannual variation in potential active hours was relatively high (CV = 0.35 across years studied), ranging from a minimum of 323 hours in 2012 to 907 hours in 2009 (Fig. S3).

Discussion

Stabilization

In this study, we found positive effects of biocrust inoculation and soil stabilization amendments, particularly psyllium-based M-binder, in promoting soil stability and biocrust establishment at a highly degraded rangeland site. We applied soil stabilizer to prevent burial of photosynthetic organisms and displacement of inoculum through ambient erosion by wind and water. In both the stabilizer trial and full establishment experiment, we were not able to detect any negative effects of the addition of psyllium stabilizer on the development of biocrusts, and in the trial, psyllium was the only amendment which maintained visible biocrust organisms through 19 months. In both the field trial and establishment experiment, the combination of psyllium-based stabilizer with biocrust inoculum maintained a significantly greater aggregate stability than other treatments. Similar increases in aggregate stability have been found when combining cyanobacterial inoculum with polysaccharide glues derived from plant seeds in a lab context (Park et al. 2016) or with other types of amendments (Park et al. 2014; Zaady et al. 2017).

We attribute the interactive effect of biocrust inoculation and psyllium stabilizer in part to the physical mixing of stabilizer with biocrust material (particularly in the main establishment study), which helped distribute the stabilizer within the soil surface and avoid the development of self-adhering flakes that formed when stabilizer was added by itself (Fick et al. 2019*b*). The biopolymers in psyllium M-binder consist of highly branched, fibrous carbohydrates (Fischer et al. 2004) which may mimic the particle-binding effects of cyanobacterial EPS (and reactivity to the EPS assay), although the structure of biocrust-derived EPS is likely to vary by environment and species composition (Rossi et al. 2018). Xanthan gum, the other EPS-like polysaccharide glue used in the trial, did not have comparable effects to psyllium, despite signs of effectiveness after 9 months.

It is important to consider that the physical conditions at the establishment site were harsh and indicative of a degraded "annualized bare-ground" state at the initiation of the establishment experiment (Miller et al. 2011; Duniway et al. 2016). In contrast to other studies where intact biocrusts are crushed or removed and then reinoculated (Belnap 1993; Antoninka et al. 2017), the soils of this study were physically crusted, compacted, and devoid of both perennial vegetation and biocrust at the start of the experiment. Before shading structures were installed, plots experienced high winds which carried sediment that was observed to bury and/or sandblast biocrust in some plots (Fig. S4). Stabilizer may have served to anchor biocrust aggregates in the initial stages of the experiment, when loose fragments may be blown away in the wind. The use of soil stabilizers to provide short-term erosion resistance while simultaneously not inhibiting biocrust development is a promising approach to restoration involving biocrust inoculation.

Differential Establishment Among Biocrust Functional Groups

Inoculation methodology likely plays a large role in the initial survival of biocrust inoculum (Velasco Ayuso et al. 2017). After 4 months, levels of lichen, moss, and dark-pigmented cyanobacterial biocrust cover in the main experiment were greater than control, but lower than the applied rate, indicating significant mortality of visible biocrust material. We attribute much of this low biocrust cover to our application method, which consisted of scattering biocrust aggregates across the soil surface. Using this approach, approximately half of the biocrust aggregates landed photosynthetic-side-down, indicating effective inoculation rates of 10 and 20% for low and high density treatments, respectively. These values are much closer to the observed average cover rates of 11 and 14% for low and high inoculation rates, respectively.

The lack of growth observed in surface-dwelling, sessile biocrust organisms (lichens and mosses) suggests that the additional hours of potential active time afforded by shading and watering efforts were not sufficient to induce net growth in in these organisms, at least in the timeframe of this study.

Lichens tend to grow slowly under most undisturbed field conditions (Belnap 1993; Duniway et al. 2018), and efforts to extend physiologically active time may have merely enabled the establishment and/or acclimation of biocrust aggregates to their transplanted environment. By contrast, early colonizing cyanobacteria such as *M. vaginatus* have means to avoid stressful surface conditions by moving along filaments throughout the soil (Sorochkina et al. 2018), potentially making them better able to take advantage of the shading and watering additions in this study. Nevertheless, as with other slow-growing organisms with longer generation times, small initial densities of lichens may translate to future abundance (i.e. transient population dynamics; Shriver et al. 2019). Additionally, the high level of species richness of the inoculum may lead to a more resilient community. Species richness in biocrust communities has been shown to positively influence ecosystem functions such as soil nutrient cycling and other indicators important to long-term health (Bowker et al. 2014).

Given the difficulty of discriminating between light-colored cyanobacterial crusts and physical surface crusts, we did not include lightly pigmented biocrusts in our cover estimates from the experiment and thereby likely underestimated the amount of cover of incipient biocrusts. This hypothesis is supported by the concentration of soil surface chlorophyll *a*, which exhibited a positive dosage response to inoculation rate (whereas surface cover did not). Although chlorophyll *a* is not a direct measure of biocrust biomass (Belnap & Gardner 1993), it does incorporate cyanobacteria not readily estimated visually in cover assessments, which may explain the modest (but significant) correlation between cover estimates and chlorophyll *a*. Greater cyanobacterial content in response to higher inoculation levels also indicates that cyanobacteria are somewhat propagule limited in this context (O'Malley 2008; Warren et al. 2019).

Microclimate Effects of Shading and Watering

The effects of shade and watering dramatically reduced surface temperatures and extended the periods of soil-surface hydration by an estimated factor of three. At the soil surface, temperatures are generally hotter than the air (Jin & Dickinson 2010), and moisture levels tend to be more transient than deeper in the soil profile (Tucker et al. 2017), making the biocrust microenvironment potentially more extreme than that experienced by vascular plants. In many arid and semi-arid contexts, biocrusts are often found at the base of shrubs (St Clair et al. 1993; Duniway et al. 2018), suggesting that shrubs may be facilitating biocrust growth through mitigating these stresses via the "nurse-plant" phenomenon (Niering et al. 1963; Flores & Jurado 2003). Shading treatments to reduce evaporation have been used in other arid restoration contexts, including some biocrust restorations, to varying effect (Li et al. 2006; Fick et al. 2016; Antoninka et al. 2017). Mitigating stresses related to evaporative demand and erosive winds through techniques such as installing shading structures is likely to be essential to rehabilitation of biocrusts in degraded sites where natural recovery is inhibited (Bowker 2007), in addition to timing inoculations to be coincident with favorable environmental conditions (Sorochkina et al. 2018; Giraldo-Silva et al. this issue).

At the main experimental site, the expected potential active time of biocrusts varied across seasons and across years. While the absolute estimates of active time should be considered approximate, based on the coarse nature of the modeling exercise, estimates in a relative sense may be valuable for inferences about biocrust ecology and management. Seasonal variation in potential active time at the site matched other observations of biocrust activity (Darrouzet-Nardi et al. 2015), and thus mirrors broader climatic patterns which are thought to explain the biogeographic distribution and composition of biocrusts: that is, the cool, moist conditions which characterize fall and winter on the Colorado Plateau are thought to facilitate the enhanced growth of biocrust biomass relative to hot deserts with abundant summer rainfall (Belnap et al. 2003). In this cold-desert context, restorationists would do well to plan inoculations mid-fall, and to expect strong year-effects in restoration success related to weather patterns. Multiple years of inoculations and/or simultaneous use of stabilizer to anchor inoculum could be one option to buffer against these effects.

Biocrust Restoration and Abiotic Processes

In the 4 months of the establishment experiment, we observed successful establishment of light-pigmented cyanobacterial crusts and survival of inoculated dark-pigmented cyanobacterial and lichen biocrust aggregates to the soil surface. Research on the association of biocrust level of development and indicators of resistance to water erosion suggests that these types of crusts (level of development 2 or 3; Belnap et al. 2008) provide some reductions in runoff and sediment loss (Belnap et al. 2013; Faist et al. 2017). Companion studies examining the resilience of our induced biocrust to simulated wind and rain storms suggest that the application of biocrust aggregates combined with soil stabilizer reduces soil loss from wind and rain, and increases time to ponding (Fick et al. 2019*a*, 2019*b*). However, the simulation results for both wind and rain also suggest that even the most successful treatment combinations would only improve soil conservation under relatively moderate storm intensities, but this would likely improve through time.

Mitigating abiotic processes that limit establishment of target organisms is a prerequisite in ecological restoration (Whisenant 1999), especially in destabilized or degraded soils. Our results indicate that for these settings, simultaneous inoculation of biocrusts with a stabilizer such as psyllium may be critical for anchoring aggregates to the surface and limiting abrasion from nearby eroded sediment. Establishment of long-term viable biocrusts based on the approaches tested here would also likely entail (1) a longer period of microclimate conditions favorable to biocrust growth and (2) the absence of high wind or intense rain events. At our study site, these conditions are most likely to occur over the winter (Darrouzet-Nardi et al. 2015), providing further support for a late fall/early winter application. Synchronizing the timing of inoculations with favorable conditions could be particularly important for large-scale restorations, where modifying the surface microclimate may be impossible

(unlike in our small-scale study). Additionally, as with restoration using vascular plant seeds (Shriver et al. 2018), recurrent applications of biocrust inoculum and stabilizer across years may greatly increase the probability of inducing a successful biological soil crust community.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Species accumulation curve (SAC) generated in R using the specaccum function, in the R package "vegan" (Oksanen et al. 2018).

Figure S2. Shade structures for study plots, built by suspending 60% shade cloth across guywires suspended above the ground by half-length T-posts.
Figure S3. Meteorological conditions and estimated potential active time for biocrusts at the field site, based on a 15-year time series.
Figure S4. Climatic conditions at the site. Boxes represent 20-year quantiles, red dots indicate 2018 values.

Table S1. Dates and times shaded and watered plots were irrigated, including volume added, effective precipitation depth, air temperature, and wind speed.
Table S2. Number of plots sampled for EPS and chlorophyll *a* compared to total plots, by treatment.
Table S3. Chlorophyll *a* and EPS values by experimental treatment expressed in units of estimated mass per area.
Supplement S1. Supplemental methods.

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