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Hydrological function of rapidly induced biocrusts

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Abstract

In dryland ecosystems, land degradation and erosion pose severe threats to ecosystem productivity and human well-being. Bio-inoculation of degraded soils with native biological soil crusts ("biocrusts") is a promising yet relatively untested means to improve soil stability and hydrological function (i.e., increase infiltration and reduce run-off). In a degraded semiarid grassland on the Colorado Plateau, we studied the establishment and hydrological function (via simulated rainfall) of induced biocrusts grown with and without an organic soil stabilizer (psyllium, derived from *Plantago* sp.), after a period of 4 months. We found evidence of biocrust establishment, including significantly higher biocrust cover, chlorophyll *a*, and exopolysaccharides in inoculated plots compared with controls. Plots inoculated with biocrust had higher run-off and sediment yields than controls during rainfall simulation. However, this effect was mitigated in plots where stabilizer was added, resulting in greater soil aggregate stability and higher levels of infiltration (reduced total run-off). The time to ponding was significantly greater than control for all inoculated plots, suggesting that induced biocrusts may be most effective at improving infiltration under low-intensity, smaller precipitation events. Notably, the biocrusts in this study lacked rough surface microtopography, which is common in well-developed biocrusts regionally and likely instrumental in slowing overland flow and increasing infiltration for larger rain events. These results highlight the temporal lag that may exist between apparent and functional restoration of biocrusts. In addition, the simultaneous additions of stabilizing amendments with biocrust inoculum may work collectively to achieve both short- and long-term restoration targets.

KEYWORDS

biological soil crust, bioremediation, Colorado Plateau, cyanobacteria, EPS, erosion, lichen, microbial inoculation, moss, psyllium

1 | INTRODUCTION

In drylands, a broad range of soil surface properties are important determinants of local-scale water balance and erosion risk (Branson, Gifford, Renard, & Hadley, 1981). Many properties such as texture, aggregate stability, surface crusting, bulk density, and ground cover are sensitive to both management activities and climatic events (Tugel et al., 2005) and are potential indicators of ecosystem transitions towards alternative states (Suding, Gross, & Houseman, 2004). In particular, reductions in vegetative cover or aggregate stability from soil surface disturbances may initiate ecohydrological feedbacks, which result in persistent degraded conditions (Williams et al., 2016; Turnbull et al., 2011). Destabilized and exposed soils may become vulnerable to erosive energy from raindrop impacts and overland flow (Branson & Owen, 1970; Duniway, Geiger, Minnick, Phillips, & Belnap, 2018), resulting in topsoil loss. Soil loss may lead to declines in productivity and shifts in plant communities towards barren, woody, or annual-dominated states (Miller, Belote, Bowker, & Garman, 2011; Schlesinger et al., 1990). The development of reliable, cost-effective, and persistent means for restoration of both vegetative cover and soil surface integrity remains a priority, given projected increases in aridity and human disturbance in drylands globally (Huang, Yu, Guan, Wang, & Guo, 2016).

Overcoming the physical processes that maintain degraded states (e.g., soil and water loss) is often a critical step for restoration of ecosystem functionality in dryland systems (Fick, Decker, Duniway, & Miller, 2016; Whisenant, 1999). A broad range of strategies such as the use of organic soil amendments (Larney & Angers, 2012; Tordoff, Baker, & Willis, 2000; Wong, 2003), synthetic soil stabilizers (Green & Stott, 1999), and physical alterations to the soil surface (Bainbridge, 2007) have been deployed to improve infiltration in highly degraded sites and thereby facilitate vegetative recovery. The use of microbial inoculants to improve soil stability and infiltration is a relatively recent development, although microbial inoculations have been discussed extensively in the context of bioremediation and engineering (DeJong et al., 2009; Vogel, 1996). One such application of bio-inoculation for restoring degraded dryland hydrological function is the use of biological soil crust (hereafter biocrust) propagules on disturbed soil surfaces (Antoninka et al., 2017). Biocrusts are consociations of lichens, mosses, cyanobacteria, algae, and fungi, which form throughout the top 1–2 cm of soil surfaces and are found across drylands globally (Belnap, Weber, & Büdel, 2016). Biocrusts dramatically improve soil resistance to erosion and contribute to dryland soil fertility (Belnap, 2003). However, biocrusts are also sensitive to physical disturbance, such as trampling by livestock or off-road vehicle tracks, and absence of biocrust can be indicative of site degradation (Duniway et al., 2016; Ferrenberg, Reed, & Belnap, 2015; Miller et al., 2011).

Although biocrusts yield demonstrable improvements to wind erosion resistance (Belnap & Gillette, 1998; Marticorena, Bergametti, Gillette, & Belnap, 1997), their influence on hydrology varies by environmental context, biocrust community composition, and scale of observation (Chamizo, Belnap, Eldridge, Cantón, & Issa, 2016; Warren, 2001). In general, well-developed biocrusts dominated by dark-pigmented cyanobacteria, lichens, and/or mosses are associated with increased infiltration, reduced run-off, and reduced soil loss (Barger, Herrick, Van Zee, & Belnap, 2006; Belnap, Wilcox, Van Scoyoc, & Phillips, 2013; Bu, Wu, Han, Yang, & Meng, 2015; Chamizo, Cantón, Lázaro, Solé-Benet, & Domingo, 2012; Faist, Herrick, Belnap, Van Zee, & Barger, 2017; Gao et al., 2017; Kidron, Yair, Vonshak, & Abeliovich, 2003; Wei, Yu, & Chen, 2015; Xiao, Wang, Zhao, & Shao, 2011). By contrast, biocrusts dominated by early colonizing light-pigmented cyanobacteria tend to be associated with heightened run-off and erosion rates (Belnap, 2006; Faist et al., 2017; Yair, Almog, & Veste, 2011). In arid regions such as the Negev and Australian deserts, run-off from these smooth-surfaced biocrusts may be important for concentrating water in run-on locations and supplying much needed water to downslope plant communities (Ludwig, Wilcox, Breshears, Tongway, & Imeson, 2005; Yair et al., 2011). Regardless of biocrust type, soil texture and rainfall intensity play important moderating roles (Belnap, 2006; Chamizo et al., 2016), with finer textured soils and higher intensities associated with lower infiltration, sometimes even in the presence of well-developed biocrusts (Chamizo et al., 2012; Li et al., 2008; Zhao & Xu, 2013).

The high variability in run-off generation observed across studies may be due in part to the differing mechanisms by which biocrusts either enhance or reduce infiltration and sediment yield (Chamizo et al., 2016; Warren, 2001). Biocrusts may increase water and sediment retention by creating surface microtopography, limiting overland flows of water (Kidron, 2007; Rodríguez-Caballero, Cantón, Chamizo, Afana, & Solé-Benet, 2012; Rodríguez-Caballero, Cantón, Chamizo, Lázaro, & Escudero, 2013), especially during low- to moderate-intensity precipitation events. Biocrusts are also associated with improved resistance to kinetic energy of raindrops (Zhao, Qin, Weber, & Xu, 2014) and increased soil aggregate stability (Bowker, Belnap, Bala Chaudhary, & Johnson, 2008; Carpenter & Chong, 2010), which serves to maintain pore space and limit the formation of sealed physical surface crusts (Le Bissonnais, 1996). However, biocrust organisms as well as the extracellular polymeric substances (EPS) secreted by these organisms are often hydrophobic (Fischer, Veste, Wiehe, & Lange, 2010), repelling water and potentially leading to higher run-off. Soil EPS and biocrust structures also tend to swell during wetting and may effectively clog the pores of sandy soils (Kidron & Büdel, 2014; Rossi, Potrafka, Pichel, & De Philippis, 2012; Warren, 2001). Ultimately, the influence of biocrusts on run-off and erosion is strongly influenced by biocrust species and morphology.

Given the importance of biocrusts for ecosystem functioning and their slow recovery rates following disturbance (extending years to decades), there has long been interest in actively restoring biocrusts, primarily by overcoming propagule limitation via inoculation (Belnap, 1993; St Clair, Johansen, & Webb, 1986). The majority of published studies dealing with biocrust restoration have been conducted in the laboratory or greenhouse, with a focus on optimizing biocrust propagation. In general, these studies show that biocrust growth is enhanced under frequent watering followed by a period dry down, moderate air temperature, shading to reduce ultraviolet and water stress, and an increase available nutrients through fertilization (Antoninka, Bowker, Reed, & Doherty, 2015; Ayuso, Silva, Nelson, Barger, & Garcia-Pichel, 2017; Doherty, Bowker, Antoninka, Johnson, & Wood, 2017). These results confirm earlier investigations of biocrust physiology (Lange, 2001), indicating that biocrust establishment may occur rapidly given adequate propagules and environmental conditions. Under greenhouse conditions, relatively well-developed surfaces of biocrust have been grown in a period of months from scattered source inocula (Antoninka et al., 2015).

Despite these advances, there have been fewer studies of biocrust restoration in the field, where establishment success has been highly variable. Notable successes include dune stabilization efforts in Inner Mongolia and the Tengger Desert (Chen et al., 2006; Hu, Liu, Song, & Zhang, 2002; Wang, Liu, Li, Hu, & Rao, 2009), the Colorado Plateau

(Belnap, 1993), the Mojave Desert (Chiquoine, Abella, & Bowker, 2016), and Great Basin (Condon & Pyke, 2016). Many of the recorded successes correspond with periods of greater moisture availability, such as Chen et al. (2006) who implemented large-scale continuous irrigation. Other studies have found little difference from natural recovery (Antoninka et al., 2017) or outright failure of establishment (Chandler, Day, Madsen, & Belnap, 2018; Young, Bowker, Reed, Duniway, & Belnap, in press). Given publication bias towards significant results in ecology (Møller & Jennions, 2001), it is likely that more unsuccessful biocrust restorations exist than are reported in the literature.

The combined use of soil-stabilizing amendments with bio-inoculants is a promising new approach for improving soil stability and infiltration, which hedges the short-term uncertainty and potential long-term benefit of biocrust inoculation against the short-term efficacy and long-term degradation of stabilizing compounds. The hydrological effects of both natural biocrusts and soil stabilizers have been studied extensively in the field (Belnap & Büdel, 2016; Lee, Gantzer, Thompson, & Anderson, 2011; Tümsavas & Kara, 2011), although often independently. Studies combining biocrust inoculations with stabilizers such as sodium alginate (Peng et al., 2017), hydrogels, and tackifiers (Park, Li, Jia, & Hur, 2016) have found synergistic effects on soil stability and inoculant growth in the laboratory within the short-term durations of these experiments. Other amendments, such as NaCl or polyacrymalide, have had positive effects on soil stability with neutral effects on biocrust development (Chandler et al., 2018; Davidson, Bowker, George, Phillips, & Belnap, 2002).

Most studies documenting the effects of biocrusts on infiltration, run-off, and sediment yield rely on comparisons to control surfaces where existing biocrust has been recently removed (as by scraping) or nearby areas where biocrust is naturally absent (Chamizo et al., 2016). However, in both cases, these surfaces may not be truly representative of control conditions due to their altered physical properties and environmental contexts. Comparing the hydrological properties of degraded soils with induced biocrusts to neighbouring degraded soils without any added inoculum thus offers the opportunity to isolate the effects of biocrust on infiltration and sediment yield without confounding factors related to soil disturbance, circumstances of measurement (e.g., antecedent weather), or other environmental differences among sites. Furthermore, characterizing the functionality of induced biocrusts (and actions that might improve this functionality such as simultaneous application of stabilizer) is relevant for planning and weighting costs in a restoration setting. In this experiment, we examine the hydrological responses of short-term induced biocrusts (4 months) with and without an added psyllium soil stabilizer to simulated rainfall. On the basis of the influence of biocrust composition and morphology on run-off characteristics, we expected that plots with inoculated biocrusts would have reduced sediment yield and run-off compared with control, given adequate levels of biocrust development. We expected to see further reductions in run-off and sediment with the addition of soil stabilizer, assuming the stabilizer would not negatively impact biocrust development.

2 | METHODS

2.1 | Study site

Experiments were conducted at an abandoned field at Dugout Ranch, part of the Canyonlands Research Center in south-eastern Utah (38.070, −109.564; https://canyonlandsresearchcenter.org/). The ranch is located in the Colorado Plateau physiographical region, composed predominantly of broad, gently sloping valleys surrounded by sandstone outcrops and cliffs. The climate is cool desert, with a mean annual temperature of 15°C and a mean annual precipitation of 197 mm (Urban, 2017). Approximately 50% of precipitation falls in the cool season (October–May) as frontal storms and 50% falls in the warm season as monsoonal thunderstorms (June–September). Interannual variability in precipitation is high, ranging from 124 to 319 mm (coefficient of variation = 0.25).

Soils at the site are sandy loams (50–65% sand, 30–44% silt, and 4–6% clay) belonging to the Mivida series (Ustic Haplocalcid) and are attributed to the Semidesert Sandy Loam Fourwing Saltbrush ecological site by the U.S. Department of Agriculture Natural Resources Conservation Service (035XY215UT; U.S. Department of Agriculture [USDA] Natural Resources Conservation Service, 2009). The Mivida soil series of the region contain low amounts of organic matter (~1.5%, USDA Natural Resources Conservation Service, 2009). The area has been used for grazing domestic livestock for over 100 years and has been periodically irrigated through approximately 2003 (though the specific study site likely was not irrigated due to slope), leading to dominance by invasive annual weeds including *Salsola* sp. and to a lesser extent *Bromus tectorum*. The specific hillslope selected for rainfall simulation experiments had also been used as a corridor for motor vehicle traffic and showed signs of recent disturbance, including imprints from tyre tracks (Figure 1a). Surfaces exhibited symptoms of highly erosive soils for the region, with patchy deposits of mobile sediment and litter temporarily forming across otherwise bare exposures of finer textured subsoils. There was no evidence of biocrust development on any surface (Figure 1a,b), likely related to the highly unstable and degraded conditions at the site. The area was devoid of any native perennial vegetation but, based on ecological site characteristics and uncultivated areas nearby, would likely support a mix of C3 and C4 perennial bunch grasses (*Achnatherum hymenoides*, *Plueraphis jamesii*, and *Sporobolus* spp.) and shrubs (*Atriplex canescens* and *Sarcobatus vermiculatus*). Due to the absence of biocrusts and native perennial vegetation at the site as well as the prevalence of bare soil and exotic annuals, it is likely that the site exists in a persistent degraded "annualized-bare" ecological state described and mapped for this region (Duniway et al., 2016; Miller et al., 2011; Poitras et al., 2018).

2.2 | Plot establishment and rainfall simulation

Biocrust used for inoculation was collected from two locations within 5 km of the experimental site: (a) a location with well-

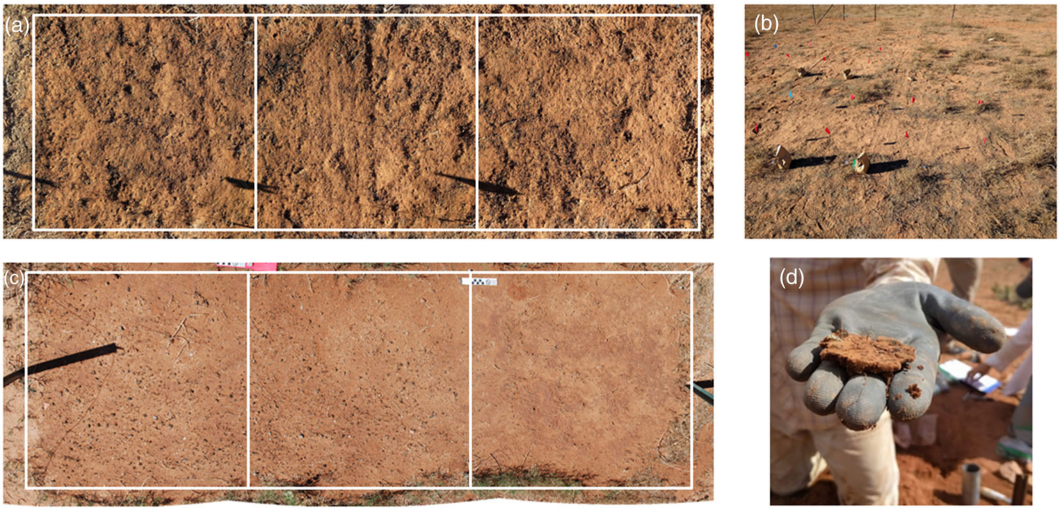

FIGURE 1 Images of example experimental plots. (a) Typical experimental plot prior to inoculation in February 2018. Approximate plot boundaries demarcated in white. (b) Overview of same plot area before inoculation. (c) The same plot at the end of the experiment, prior to rainfall simulation. Plots from left to right were treated with biocrust inoculum, biocrust inoculum and stabilizer, and control. (d) Example plate of light-pigmented cyanobacteria-dominated induced crust, following rainfall simulation

developed dark crust containing a rich assemblage of lichen species and (b) a location characterized by more disturbed biocrust with higher moss and light-pigmented cyanobacteria prevalence. In this region, light-pigmented biocrusts are dominated by *Microcoleus vaginatus*, whereas dark-pigmented crusts tend to have a higher prevalence of N-fixing species such as *Nostoc* and *Scytonema* spp. (Yeager et al., 2004). Crust samples were air dried to halt metabolic activity (Belnap, Büdel, & Lange, 2003; Reed et al., 2012) and then crumbled to roughly "pea"-sized particles (1- to 2-cm diameter) to facilitate even spreading during inoculation. Crumbled particles were sieved, rejecting sand particles <1 mm, to limit the amount of loose sand in the inoculum mix and maximize potential exposure of photosynthetic surfaces after inoculation. Biocrust particles were portioned on the basis of mass/area ratios estimated from stratified samples across inoculum stocks, calculated from the mass of Petri dishes filled to a depth of approximately 1 cm. Crusts were dry stored for approximately 2 weeks before inoculation.

Treatments were applied to 0.65 m^2 (0.81 m on a side) plots cleared of any extant litter or debris. Plots received no surface amendments (control), biocrust inoculation (40% aerial cover, 1.4 kg m^{-2}), or biocrust inoculation combined with an organic soil stabilizer, "M-Binder" (Ecology Controls, Carpinteria, CA, USA), at a rate of 60 g m^{-2}. M-Binder consists primarily of psyllium, a mucilaginous compound extracted from the seed coat of *Plantago insularis*. Treatments were randomly assigned to one of three contiguous plots aligned perpendicular to the slope line to facilitate simultaneous rainfall simulations of each treatment. Eight blocks of three plots were established at various locations across the hillslope. Treatments were applied in early February 2018 by hand-distributing preweighed mixed inoculum and powdered soil stabilizer across plot surfaces and then lightly watering (1 mm added) after application.

Plots were watered frequently throughout the winter and spring, with breaks between waterings 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 transported from municipal facilities in Moab, UT, which was then charcoal filtered prior to application to remove chlorine that may inhibit biocrust growth. Length of exposure to hydrated conditions has been linked to biocrust biomass growth, and short pulses of hydration are often detrimental to biocrust organisms (Reed et al., 2012). To prolong the duration of hydrated conditions following manual watering and natural precipitation events, a canopy of 40% transmittance shadecloth (ultraviolet polyethylene knitted shade cloth—60% green, DeWitt, Sikeston, MO) was suspended over plots in early March. Plots were hand weeded in the spring (April–May) as needed to remove seedlings in plots.

A high-resolution topographical survey was conducted using ground-based lidar and total station ground control at the study area in March 2018. The lidar survey used a Riegl VZ1000 scanner (Riegl Laser Measurement Systems, Horn, Austria). Lidar data were registered and georeferenced using reflective targets located at surveyed ground control points. Each survey produced a dense point cloud (mean point density >80,000 points per m^2, standard deviation = 1.2×10^5) with a ground-control registration accuracy ≤1 cm. The survey data were postprocessed to remove vegetation using topographical and proximity filters within RiscanPro software (Riegl, Horn, Austria). The filtered point data were converted to a 5-cm raster digital elevation model. Plot slope was derived from the digital elevation model. Slope for each plot was taken as the average change in elevation between the upslope and downslope corners, divided by their horizontal distance.

In early June 2018, immediately prior to each rainfall simulation, plots were sampled for soil surface characteristics. Surface cover was assessed using a 0.71 × 0.71-m pinframe with a grid of 7 × 7 sampling intersections (49 points per plot) following classes described in Herrick, Van Zee, Havstad, Burkett, and Whitford (2005), with modifications used by the National Wind Erosion Research Network (Webb et al., 2016). Roughness was assessed by comparing the apparent overhead length of a 54-mm jewellery chain laid flush against the soil surface to its true length to create a roughness index (Saleh, 1993). The index was calculated as one minus the mean of two perpendicular measurements across each plot. Soil aggregate stability was assessed with six samples per plot with a field aggregate stability test kit (Seybold & Herrick, 2001). We excavated and oven dried a 5.8-cm diameter × 5-cm soil core from the perimeter of each plot to obtain presimulation bulk density and volumetric water content. Five ~2-g soil samples were taken from the top 1 cm of the soil surface for chlorophyll *a* and EPS analysis. We collected all presimulation soil samples (aggregate stability, soil cores, chlorophyll, and EPS) from the perimeter of each plot, outside of the area used for rainfall simulations. Plot characteristics are summarized in Table 1.

Rainfall simulations were conducted between June 5, 2018, and June 11, 2018, using a carriage-mounted VeeJet 95/70 nozzle suspended on a track 2 m above the ground. The sampled area of each plot was 0.71 × 0.71 m, demarcated with heavy metal flashing and collection troughs. A small number of divots and exposed patches of loose soil caused by recent rodent disturbance were filled prior to simulations with a mix of silicone and turpentine, hardened for at least 1 hr before simulation. Filled regions never exceeded 0.5% of a plot's total area. The nozzle was maintained at a pressure of 21 kPa and passed across the block of three plots every 4 s for 30 min, pausing for 2 s outside the plot areas on each pass. The estimated application rate was approximately 75 mm hr^{-1}. This rate corresponds to the 95th percentile of local rain intensities measured for the area in the past 10 years (USGS, unpublished data) and is comparable with other rainfall simulations throughout the area (Belnap et al., 2013). Initial trials with lower intensity settings were found to be inadequate for reliably producing run-off. Water input was measured using an array of 1.5-cm-diameter rain gauges spread across the sampling area. The time at which ponding was first observed on the soil surface (standing water persisting for two "passes" of the overhead nozzle) and the time to first observed run-off were recorded for each plot. Run-off was collected each minute, weighed, then dried, and weighed again to determine the yield by mass of water and sediment. Sediment remaining on collection troughs at the conclusion of each simulation was rinsed and processed in the same manner and included in estimates of total accumulated sediment.

Immediately after rainfall simulations were completed, wetting depth and volumetric water content (VWC) from the top 5 cm of soil were determined at three locations (top, middle, and bottom) within each plot using a 5.8-cm-diameter core. VWC samples were placed in a sealed container and transported to the laboratory, and wet weights were obtained immediately. VWC samples were dried for 96 hr at 60°C and weighed to obtain a dry weight. Gravimetric water contents were converted to VWC using measured bulk densities. Additionally, five soil surface texture samples (0–1 cm) were collected within each plot using a 5.8-cm-diameter core. Surface soil texture samples were composited for each plot and analysed for particle size using the pipette sedimentation method for clay content and wet sieving through a 53-μm mesh for sand content (Gee & Or, 2002; USDA Natural Resources Conservation Service, 2004; Soil Survey Staff, 2014).

The five presimulation subsamples for chlorophyll *a* and EPS were pooled prior to laboratory analysis. Chlorophyll *a* was extracted by grinding 1 g of soil with a mortar and pestle in 3 ml of 90% acetone for 3 min. The sample and solvent mixture were brought up to 10 ml with 90% acetone, and the sample was vortexed for 2 min and incubated in the dark at 4°C for 24 hr. After incubation, the sample was centrifuged for 12 min at 4,000 rpm and 15°C. The absorbance of the supernatant was recorded at 663 nm using an Ocean Optics CHEMUSB4-VIS-NIR spectrophotometer (400–950 nm) and at 1,000 nm for background adjustment. We used the adjusted absorbance and soil sample mass to determine chlorophyll *a* content

TABLE 1 Prerainfall simulation soil measurements

Variable	Control	Biocrust only	Biocrust + stabilizer
Bulk density (g cm^{-3})	1.401 (0.036)	1.395 (0.019)	1.397 (0.016)
% soil moisture (gravimetric)	1.601 (0.658)	1.537 (0.623)	1.02 (0.126)
Stability class	2.208 (0.321)	2.5 (0.435)	3.904 (0.427)$_a$
Chlorophyll *a* (μg g^{-1} soil)	0.727 (0.137)	1.932 (0.459)$_a$	2.745 (0.586)$_a$
Total EPS (μg g^{-1} soil)	120.102 (12.804)	162.176 (10.755)$_a$	266.81 (26.531)$_b$
Colloidal EPS (μg g^{-1} soil)	7.591 (3.728)	15.853 (3.314)$_a$	50.723 (9.047)$_b$
Tightly bound EPS (μg g^{-1} soil)	113.971 (9.006)	146.323 (9.01)$_a$	216.087 (19.102)$_b$
Roughness index	0.018 (0.002)	0.021 (0.002)	0.022 (0.003)
Biocrust cover (%)	0 (0)	18.076 (1.632)$_a$	18.076 (1.692)$_a$
Loose material cover (%)	12 (2.911)	14.143 (3.166)	15.286 (2.337)
Physical crust cover (%)	32.143 (2.549)	20.714 (2.688)$_a$	19.571 (2.553)$_a$
Slope (%)	9.923 (0.868)	10.458 (0.587)	10.246 (0.654)

Note. Values are means ± 1 standard error (n = 8). Values with different letters were significantly different.

Abbreviation: EPS, extracellular polymeric substance.

using calculations outlined in Ritchie (2006). EPSs from colloidal and tightly bound fractions were extracted and quantified following a modified version of De Brouwer and Stal (2001) using 50-mg soil samples, 15-min room temperature initial extraction time combined with vortexing, and 8,000 × *g* centrifugations. Absorbances were read on an Ocean Optics CHEMUSB4-VIS-NIR spectrophotometer (400–950 nm) at 490 nm along with a 1,000-nm background reading, which was subtracted as the baseline. It is important to note that this methodology does not distinguish between extracellular polysaccharides derived from biocrust organisms or other sources (e.g., psyllium stabilizer or other organisms). For brevity and simplicity, we refer to this collection of carbohydrates as EPS.

2.3 | Analysis

Chlorophyll *a* concentrations, total EPS concentrations, aggregate stability scores, standard deviations in aggregate stability scores, roughness indices, and visual cover percentages were compared by treatment using R package emmeans (Lenth, 2018) and Tukey's adjustment (α = .05), from fitted linear mixed models with treatment as a factor and simulation run (block) as random effect in the R package lme4 (Bates, Mächler, Bolker, & Walker, 2015). Indices were checked for normality with a Shapiro–Wilk test and log transformed as necessary. Standard deviation in aggregate stability was included to capture the variability in soil stability across the plot scale.

Rainfall simulation response variables included accumulated sediment after 10 min, accumulated run-off divided by accumulated water input after 10 min, total sediment (including wash from the trough), total run-off divided by total input, time to ponding, time to run-off, mean wetting depth, and mean postsimulation volumetric water content. For determination of run-off ratios, run-off values were divided by estimated plot-level rainfall, as assessed by the average rain gauge values within and surrounding each plot. Response variables were tested for normality with a Shapiro–Wilk test and log transformed as appropriate. Responses were first modelled as a function of treatment, including simulation event as a random effect using the function lmer from the R package lme4. Model fit and significance of treatments were tested using the r.squaredGLMM function in the package MuMIn (Barton, 2018) and the analysis of variance and summary functions from the package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017), respectively. Treatment coefficient degrees of freedom and *t* statistics were assessed using the default Satterthwaite's method.

To explore potential mechanisms underlying treatment responses, we used backwards stepwise model selection to identify parsimonious groups of explanatory variables related to each hydrological measurement. Relationships between response variables and ancillary data, including slope, chlorophyll *a*, total EPS (colloidal + tightly bound), mean and standard deviation in aggregate stability, per cent sand, biocrust cover, physical crust cover, loose material cover, and roughness index, were first fit with mixed effects models, including simulation event as a random effect. These response variables were chosen because they are commonly related to hydrological processes (e.g., slope, texture, surface cover, and stability) or indices of biocrust function (chlorophyll *a* and EPS; Branson et al., 1981; Chamizo et al., 2016). Using initial Akaike information criterion-based model reduction strategies, it was found that certain pairs of variables were highly collinear, leading to high variable inflation scores (colloidal, with tightly bound EPS fractions, and physical crust cover with loose material cover, see correlations in the Supporting Information). Because single variables within each of these groups contained >80% of the information in the others, only single variables (total EPS and physical crust) were included in subsequent model selections. All variables were standardized to a zero-mean and unit-variance scale prior to fitting. Due to the high number of potential explanatory variables relative to data (data were further truncated as one set of plots was missing cover data), we applied backward stepwise regression to "full" models with all variables to identify subsets of predictors most related to each response, using the R function "drop1" (R Development Core Team, 2015) and dropping nonsignificant terms at a threshold of α > .1, starting with the least significant terms.

3 | RESULTS

3.1 | Biocrust establishment

Biocrust establishment, as assessed by visual cover and chlorophyll *a* content, 4 months after inoculation was higher in inoculated plots than control (Figure 2). Estimated biocrust cover values were between 15% and 20% for inoculated plots, whereas no biocrust organisms (lichens, mosses, and dark cyanobacteria) were observed on control plots. The majority of biocrust cover was composed of lichen (88%), followed by dark cyanobacteria (11%), with only a single pin-hit of moss found across all plots. Control plots also had higher levels of physical crust cover (Figure 3). Average aggregate stability and total EPS were greater in plots with soil stabilizer than either control plots or biocrust-only plots (Figure 2). However, biocrust-only plots did have greater EPS values than control plots (contrast estimate = −0.321, standard error = 0.123, adjusted *p* = .0511). Other variables, including surficial loose material, roughness, and standard deviation of aggregate stability, did not vary significantly by treatment (Figure 3).

3.2 | Rainfall simulation

Water application rates averaged 73 mm hr^{-1} per plot, with an average within-run coefficient of variation among gauges equalling 25%. Plot slopes ranged from 5.6% to 13%, with an average grade of 10%. Average prerun volumetric soil moisture content was 2.1% (standard deviation = 1.97%).

Means and standard errors for erosion responses are reported in Table 2. Times to ponding were highly variable, ranging from 48 to 215 s. Plots with soil stabilizer had longer times to ponding than control plots (46 s longer on average, *p* = .003, Tables 2 and 3), with

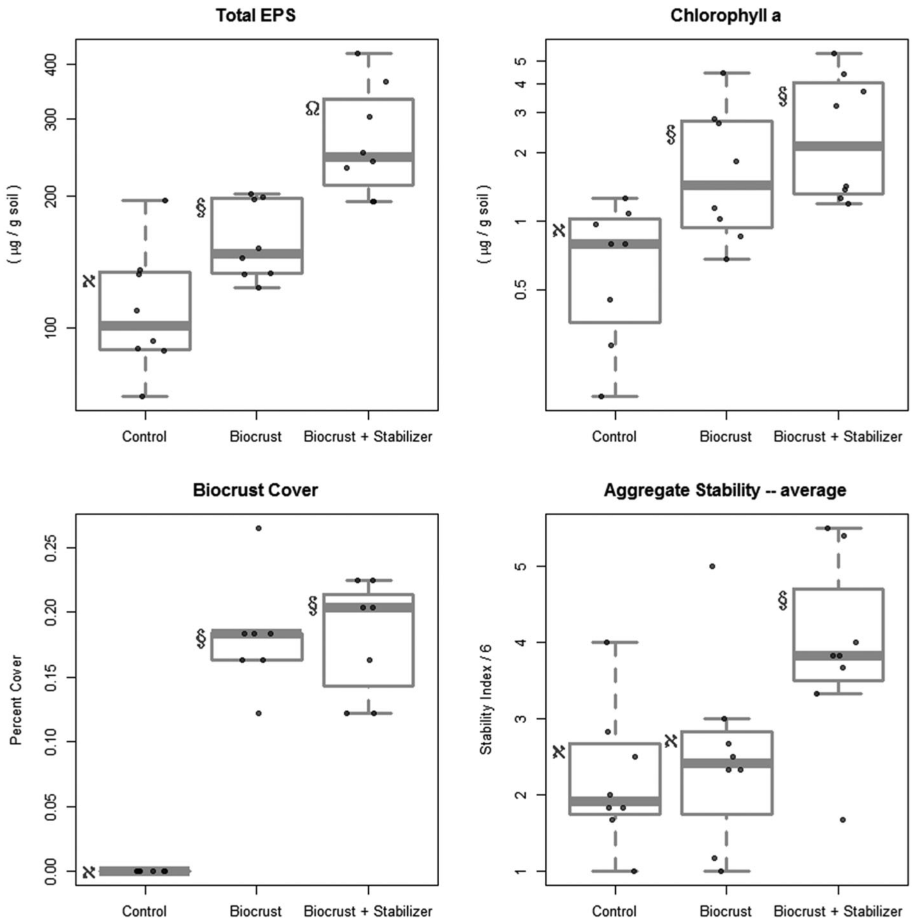

FIGURE 2 Boxplots of biocrust-related variables by experimental treatment. Treatments sharing the same symbol not significantly different according to Tukey's honestly significant difference tests of mixed effect models with treatment as fixed effect and block as random effect. Aggregate stability is scored using an index with increasing values indicating greater stability. EPS, extracellular polymeric substance

biocrust-only plots having intermediate times to ponding. Times to run-off ranged between 103 and 417 s and showed a similar pattern among treatments to that of ponding, although mean differences were not significant (Table 3). Response variables for sediment yield and run-off tended to be positively correlated (Figure S1).

Temporal trends in average run-off and sediment output per input rainfall followed saturating curves, with sharp increases within the first 10 min followed by stable or slowly increasing rates in the last 20 min of the simulation (Figure 4). Run-off rates continued to rise at the end of simulations, whereas sediment rates remained relatively stable after 10 min. For 10-min cumulative run-off ratio, total run-off ratio, and total sediment yield, biocrust-only plots had significantly higher values than controls (Tables 2 and 3, p = .04, .04, and .03, respectively). Although run-off rates and sediment yields for soil-stabilizer plots and controls were similar and not statistically different, plots with stabilizer tended to have slightly lower yields overall (Figure 4).

Average wetting depth following simulation was shallower on average for biocrust-only plots (though not significantly so, Table 3). Postsimulation mean volumetric water content was slightly lower in the biocrust-only plot than control, although differences were not significant (Table 3). There was high variance in sediment and run-off yields among replicate simulation runs, with the ranking of treatments in terms of sediment and run-off outputs reversed in a few instances (Figure S2).

For all models, the portion of the variance explained by simulation runs was greater than the variance explained by treatment (difference between marginal and conditional R^2, Table 3), emphasizing the importance of block-level plot characteristics (slope and soils), variation in simulation intensity and amounts, or both.

3.3 | Explanatory variables

Although there were few significant pairwise correlations between hydrological responses and soil surface variables (Figure S3), several important explanatory variables were identified in stepwise multiple regression (Figure 5). For all estimates of sediment yield and run-off ratios, total EPS was negatively associated with water and sediment outputs (Figure 5). Within-plot variance in aggregate stability, which is an indicator of small-scale patchiness in soil properties, was positively related to outputs (Figure 5). The negative associations between EPS and erosive outputs were strongest for sediment yields (standardized coefficients double that of run-off, Figure 5). For 10 min and total sediment yields, both surface sand content (post simulation) and

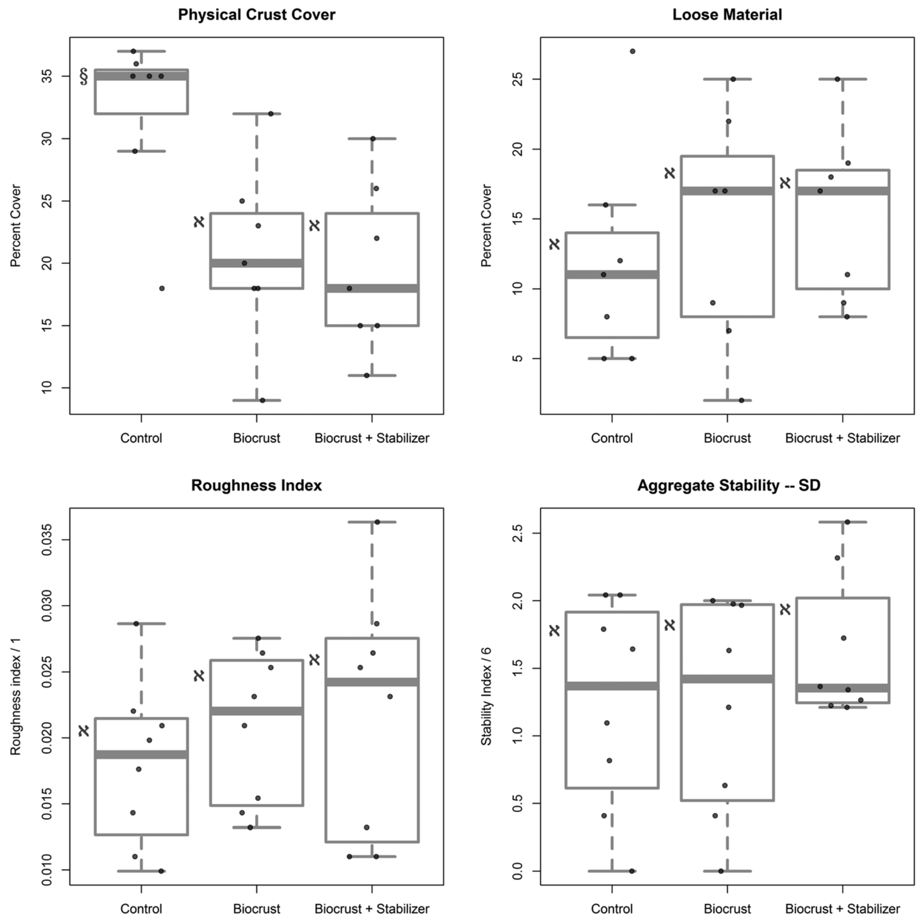

FIGURE 3 Boxplots of biocrust-related variables by experimental treatment. Treatments sharing the same symbol are not significantly different (Tukey's honestly significant difference). Tests performed on mixed effect models with treatment as fixed effect and block as random effect. Higher roughness index values indicate greater surface microtopography (calculated as 1—difference in length of a jewellery chain fully extended vs. draped over the soil surface). Aggregate stability—*SD* indicates the plotwise standard deviation in aggregate stability index score

TABLE 2 Rainfall simulation response variables

Variable	Control	Biocrust only	Biocrust + stabilizer
10-min sediment (g m^{-2})	19.738 (6.001)	26.116 (5.013)	12.703 (3.052)
Total sediment (g m^{-2})	157.862 (24.225)	248.263 (46.098)	184.817 (28.622)
10-min run-off (%)	17.156 (3.155)	23.397 (2.68)	15.004 (2.931)
Total run-off (%)	30.23 (3.615)	37.034 (3.055)	27.711 (3.263)
Time to ponding (s)	81.875 (11.632)	115.25 (15.717)	129.5 (11.269)
Time to run-off (s)	166.625 (13.948)	180.125 (16.085)	212.625 (31.259)
Wetting depth (cm)	10.846 (0.913)	9.567 (0.576)	10.896 (0.511)
Volumetric water content (%)	17.244 (1.058)	16.096 (0.676)	17.094 (0.614)

Values are means ± 1 standard error (n = 8).

biocrust cover were positively associated with sediment output (Figure 5). The total run-off ratio was positively associated with slope (Figure 5). Only physical crust cover was found to be (negatively) associated with time to ponding. Wetting depth was found to be positively related to average aggregate stability but negatively related to variance in aggregate stability and slope.

4 | DISCUSSION

4.1 | Rapid biocrust establishment

Within the 4-month time period of this study, we observed evidence of enhanced biocrust colonization relative to controls (equivalent to

TABLE 3 ANOVA and summary results for mixed effects models of treatment with simulation event as random effect

Variable	R^2m	R^2c	Sum squared	Mean squared	NumDF	DenDF	*F* value	*Pr* (>*F*)	Intercept	Biocrust only	Biocrust + stabilizer
10-min sediment[a]	0.148	0.351	2.326	1.163	2	14	2.62	0.108	1.93 (<.001)	0.51 (.15)	−0.24 (.484)
Total sediment[a]	0.144	0.458	0.884	0.442	2	14	3.06	0.079	4.29 (<.001)	0.46 (.029)	0.16 (.401)
10-min run-off	0.162	0.634	0.03	0.015	2	14	5.08	0.022	0.17 (<.001)	0.06 (.039)	−0.02 (.445)
Total run-off	0.155	0.654	0.037	0.019	2	14	5.16	0.021	0.3 (<.001)	0.07 (.04)	−0.03 (.416)
Time to ponding	0.206	0.646	8240.459	4120.23	2	12.91	6.6	0.011	84.95 (<.001)	26.19 (.07)	45.58 (.003)
Time to run-off[a]	0.088	0.141	0.183	0.092	2	13.01	1.17	0.34	5.09 (<.001)	0.07 (.608)	0.21 (.156)
Wetting depth	0.094	0.406	9.081	4.541	2	14	1.82	0.198	10.85 (<.001)	−1.28 (.127)	0.05 (.95)
VWC[a]	0.052	0.631	0.021	0.01	2	14	1.63	0.232	−1.77 (<.001)	−0.06 (.138)	0 (.982)

Note. R^2m and R^2c represent the marginal and conditional coefficients of determination (pseudo-R^2), respectively, for mixed effects models, following Nakagawa and Schielzeth (2013). The marginal R^2 represents variance explained by fixed effects, and the conditional R^2 represents variance explained by both fixed and random effects. *Pr* (> *F*) indicates the overall significance of the treatment term, and intercept, biocrust, and biocrust + stabilizer represent the coefficients for treatment effects (control included in intercept), with *p* value in parentheses.

Abbreviations: ANOVA, analysis of variance; VWC, volumetric water content.

[a]Responses log transformed.

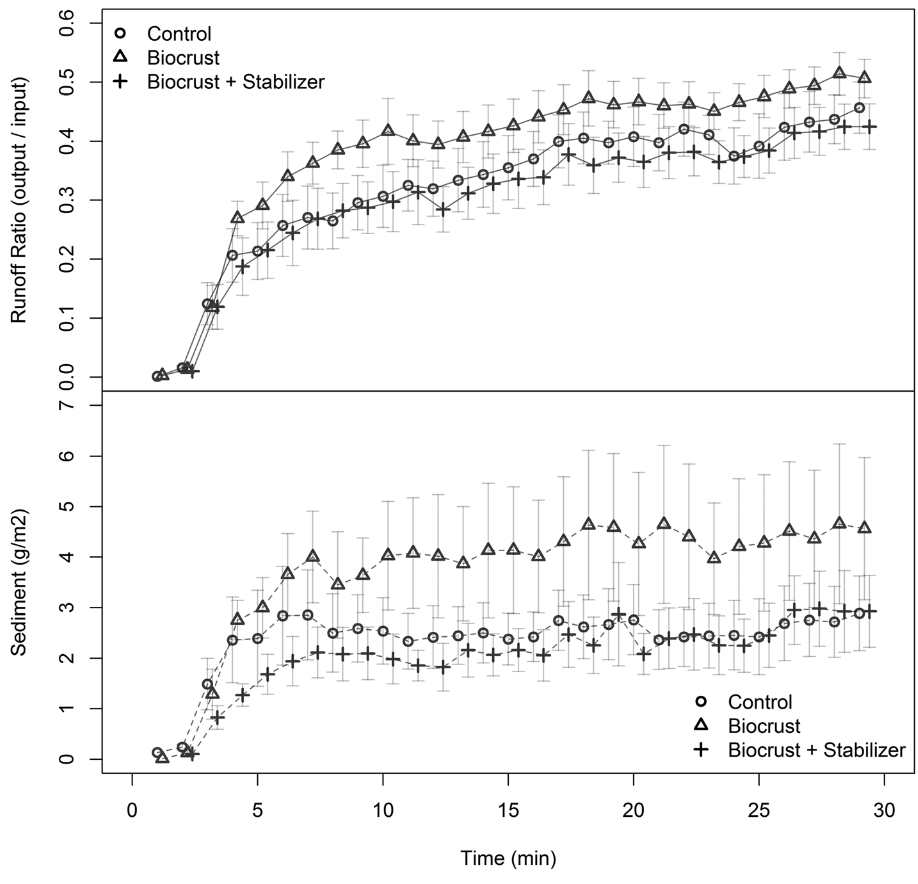

FIGURE 4 Average run-off and sediment yield over the duration of the simulation by treatment. Error bars represent ±1 standard error

an early to midlevel of development; Belnap et al., 2013). Resultant biocrusts consisted of small embedded fragments of lichen and dark cyanobacteria inoculum fragments within a matrix of smooth, light-coloured crusted soil (Figure 1c). Areal biocrust cover estimates for inoculated plots were 18% on average, approximately half of the rate applied at the initiation of the experiment (40%). Inoculum mortality rates around 50% may be expected because a significant portion of crust aggregates land “face down” by chance during aerial application (S. Fick, personal observation) and many obligate photoautotroph biocrust organisms die when exposed to moisture and deprived of light (Jia, Li, Liu, Gao, & Li, 2008; Reed et al., 2012). Furthermore, visual cover assessments only counted lichens, mosses,

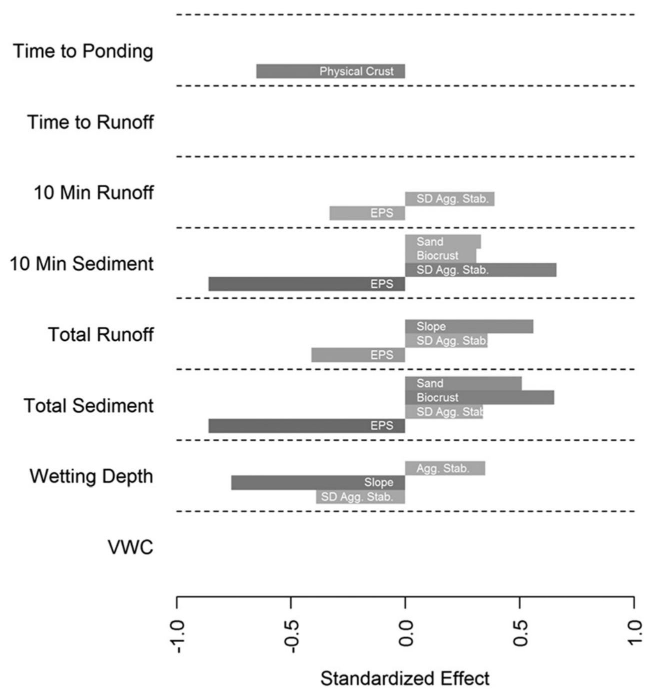

FIGURE 5 Backwards stepwise selection model coefficients. Other forms of extracellular polymeric substance (EPS; colloidal and tightly bound EPS fractions) and loose material not entered into the model due to high correlations with other predictors. SD Agg. Stab., standard deviation in aggregate stability scores; VWC, volumetric water content

and darkened cyanobacteria. It is likely that a significant portion of light cyanobacterial crust was also extant in these plots as well, as indicated by chlorophyll *a* and EPS values and visual evidence of cyanobacterial crust fragments after simulation (Figure 1d).

In the short period of biocrust establishment in this experiment, we did not succeed in developing some key functional characteristics of biocrust, including roughened surface microtopography or macroaggregate stability (in the absence of soil stabilizer amendments). Estimates of roughness were less than half that of comparable reference roughness indices for early successional biocrusts in nearby locations and less than 20% of well-developed biocrusts (Miller et al., 2011). Biocrust surface roughness in cold desert environments is thought to be related to the effects of shrink-swell and frost heaving throughout the winter months (Belnap, 2001). The biocrusts in this experiment were only subjected to such conditions for a minimal time period (months of February and early March), during which biocrust establishment would have been minimal. For aggregate stability values, estimates from biocrust-only plots were similarly well below references for early successional biocrusts in similar soils (Miller et al., 2011). The low levels of aggregate stability and surface roughness observed in these plots are likely due to the extremely short timeframe of this experiment, and levels would likely increase with more time for biocrusts to develop.

4.2 | Biocrust restoration and erosion processes

On the basis of the high cover of light-pigmented cyanobacterial crust in plots inoculated with biocrust only (no additional stabilizer), it was somewhat expected that these plots would have higher levels of run-off than controls (Figure 2 and Table 3). High rates of run-off have been observed among such cyanobacterially dominated biocrusts in other rainfall simulation experiments in this area (Barger et al., 2006; Belnap et al., 2013; Faist et al., 2017) and in sandy soils from other contexts (Kidron & Büdel, 2014; Yair et al., 2011). For example, in a rainfall simulation conducted at a nearby location on the Colorado Plateau, intact light-pigmented cyanobacterial crusts (dominated by species such as *M. vaginatus*) had much higher rates of run-off and sediment yield than neighbouring light-pigmented crusts that had been scraped of their top layer or other more developed biocrusts (Faist et al., 2017). The authors hypothesized that the smooth, crusted surfaces of these soils, underlain by cyanobacterial filaments and associated EPS, may have been driving this effect. Cyanobacteria are known to be prolific EPS producers, and field and laboratory studies consistently show that EPS can reduce hydraulic conductivity at the soil surface (Colica et al., 2014; Kidron & Büdel, 2014; Mazor, Kidron, Vonshak, & Abeliovich, 1996). However, it has also been suggested that EPS can improve infiltration by maintaining the integrity of macropores (Rossi et al., 2012). Interestingly, in the only other rainfall simulation using induced biocrusts we are aware of (in mesocosms; Sadeghi, Kheirfam, Homaee, Darki, & Vafakhah, 2017), cyanobacterial crusts dramatically reduced run-off compared with control. Similarly, in the Tabernas Desert of Spain, cyanobacterially-dominated biocrusts had reduced run-off compared with lichen-dominated biocrusts during intense rain events, a result attributed in part to hydrophobicity of lichen surfaces (Chamizo et al., 2012; Rodríguez-Caballero et al., 2013). In both of these cases, underlying soil textures were finer than in our experiment (silty clay loam and 80% silt, respectively), and the effects of EPS on improving infiltration are thought to be stronger in fine-textured soils (Chamizo et al., 2016; Kidron, Monger, Vonshak, & Conrod, 2012).

On the Colorado Plateau, well-developed lichen, moss, and dark-pigmented biocrusts tend to have greater levels of aggregate stability and surface roughness than biocrusts dominated by light-pigmented cyanobacteria (Fischer et al., 2010; Warren, 2001), which are often considered early successional (Belnap et al., 2013, but see Kidron, 2018). The enhanced roughness and stability of well-developed biocrusts likely counteract the effects of hydrophobicity and pore clogging on infiltration by biocrust biomass (as both filamentous cyanobacteria and other organisms are abundant in these biocrusts), but this may depend on rainfall intensity (Rodríguez-Caballero et al., 2013). Despite containing patches of dark-pigmented inoculum, the rapidly induced biocrusts of this experiment lacked both the levels of overall roughness and aggregate stability characteristic of more developed crusts. This early developmental state, combined with potentially higher supplies of sediment derived from loose inoculum fragments, may explain the increased sediment and run-off yields observed in these plots.

The increase in sediment and run-off observed in biocrust-inoculated plots was reversed in plots that received the psyllium-based soil stabilizer (Figure 4). Plots with soil stabilizer had the longest time to ponding, indicating higher rates of infiltration, at least initially.

The most notable differences between plots with stabilizer and others were the significantly higher levels of both EPS and aggregate stability (Figure 2), variables that were highly correlated (R^2 = 0.58, p = .002). As our EPS assay measured all extracellular carbohydrates (rather than those exclusive to biocrust organisms), the high concentrations of EPS observed in plots with stabilizer may have resulted from the psyllium-based soil amendment itself, which is primarily composed of highly branched, fibrous carbohydrates (Anderson & Fireman, 1935; M. H. Fischer et al., 2004). EPS can bind soil particles together and promote stability of soil aggregates (Issa et al., 2006; Mazor, Kidron, Vonshak, & Abeliovich, 1996), which are instrumental in maintaining infiltration and reducing suspended sediment in precipitation events (Le Bissonnais, 1996). EPS may also occur in a variety of morphologies and configurations within the soil matrix, dependent on species and conditions (Rossi, Mugnai, & De Philippis, 2017). Given the relatively consistent effect of cyanobacterial filament-derived EPS in promoting run-off in cyanobacterial-dominated soils, it is reasonable to assume that the psyllium amendment mitigated run-off and sediment yield through its enhancement of surface aggregate stability, rather than stimulation of cyanobacterial growth.

The combined application of biocrust inoculant with soil stabilizing amendments is a promising technique for dryland soil stabilization and restoration. Repeated observations of aggregate stability in soils amended with M-Binder suggest that the treatment retains its efficacy for at least a year (USGS unpublished data). The fact that the psyllium stabilizer improved infiltration and reduced sediment yield while not inhibiting biocrust development suggests that the temporal lag observed between crust establishment (visible crusts and chlorophyll *a* abundance) and functional stabilization (surface roughness and aggregate stability) may be ameliorated with the use of stabilizers in the short term (Figure 6). Other studies have found neutral to improved cyanobacterial growth when simultaneously inoculated with stabilizers (Chandler et al., 2018; Davidson et al., 2002; Park, Li, Jia, & Hur, 2014; Peng et al., 2017), and in plots sampled for this study, microbiotic chlorophyll was marginally greater in plots with both biocrust and stabilizer. More studies are needed to determine the mechanisms by which soil-stabilizing amendments may facilitate microbiotic growth, such as by anchoring inoculum (Ballesteros, Ayerbe, Casares, Cañadas, & Lorite, 2017), providing microsubstrate for improved growth (Zaady, Katra, Barkai, Knoll, & Sarig, 2016), or improving water status or nutritional conditions (Park et al., 2016).

4.3 | Surface properties and water erosion processes in biocrusted soils

In this study, there were a number of associations between soil surface variables and hydrological responses (setting aside treatment) identified following variable selection. Some associations were expected, such as the relationship between slope and increased total run-off, as well as reduced wetting depth, or the negative association between physical crust cover and time to ponding (Figure 5). Postsimulation sand content was positively associated with sediment yields, after accounting for biocrust cover, variation in aggregate stability, and EPS. This may reflect the preferential movement of finer soil fractions in overland flow (Hillel, 1998) resulting in higher concentrations of sand remaining on plot surfaces.

Other associations highlight the importance of dynamic surface properties such as EPS and variability in surface aggregate stability for determining run-off and sediment yield (Figure 5). As noted above, EPS in cyanobacterially dominated biocrusts is typically associated with greater run-off due to swelling and pore clogging (but see Rossi et al., 2012), and thus, the EPS signal in the regression is likely due to the strong effect of the psyllium stabilizer (a polysaccharide). The selection of variability in aggregate stability as a predictor for sediment yield suggests that some level of spatial consistency in soil properties at the subplot scale may be important for determining erosion potential. Although extrapolations across scales in run-off experiments are notoriously difficult (Parsons, Brazier, Wainwright, & Powell, 2006; Wilcox, Breshears, & Allen, 2003), the effects of small-scale spatial heterogeneity in surface stability may have emergent

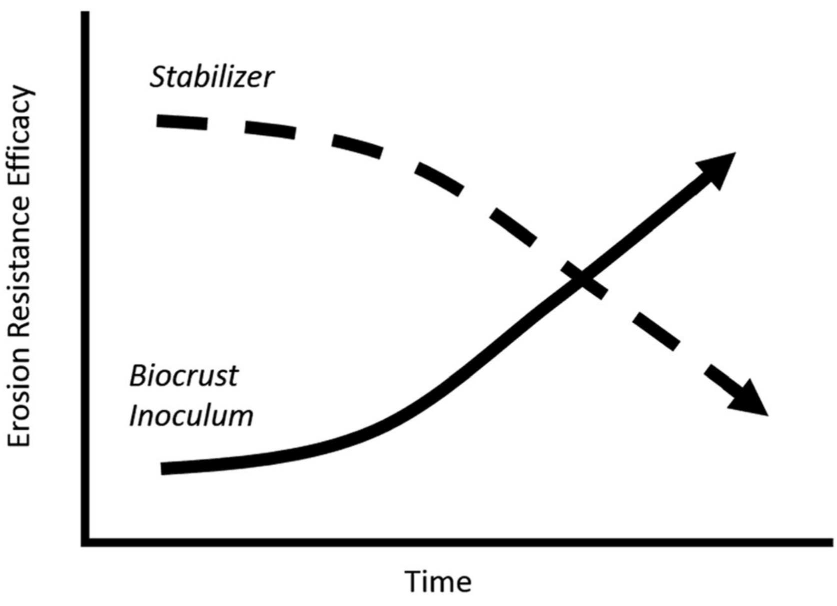

FIGURE 6 Heuristic representation of complementarity between biocrust inoculation and addition of soil stabilizer across time

effects on water and sediment yields (e.g., interpatch interactions). This result would have direct implications for sampling methodology, because many studies rely on estimates of mean conditions (through either averaging or composited samples), which may obscure important within-site variation in soil condition (Herrick & Whitford, 1995).

Biocrust cover was positively associated with sediment yields, after accounting for EPS, variation in aggregate stability, and texture in stepwise multiple regression. This again highlights the fact that the biocrust surfaces created in this experiment lack important functional qualities found in more developed biocrusts that reduce erosivity, particularly surface roughness and aggregate stability (Miller et al., 2011). Furthermore, much of the increased sediment observed in biocrust-only plots could be from unstabilized inoculum, such as the ~50% aggregates landing photosynthetic side down. Notably, sediment losses in plots with psyllium stabilizer, which had the same quantities of inoculum fragments added at the outset, had the lowest sediment yield of all plot types. It should be noted as well that frequent watering of plots (including controls) during the biocrust development phase of the experiment may have altered surface properties, potentially compacting and inadvertently redistributing loose soils, although care was taken to avoid ponding and run-off during irrigation.

As the induced biocrusts developed in this experiment were mosaics of well-developed dark cyanobacteria and lichen aggregates interspersed among light cyanobacterial and bare soil (Figures 1c and S4), they likely have few natural analogues. Nevertheless, patterns in run-off and erosion of induced biocrusts without additional psyllium stabilizer were similar to that of other early successional, cyanobacterial biocrusts found throughout the region (Barger et al., 2006; Chamizo et al., 2016; Faist et al., 2017). Given more time to develop (particularly with exposure to freeze–thaw cycles to induce roughness), it is likely that hydrological function of these biocrusts would approach that of more mature biocrusts in the region (Belnap et al., 2013). The clear benefits of adding a relatively inexpensive stabilizer to biocrust inoculum suggest that rehabilitation activities may greatly benefit from its use. The considerable costs related to collecting and watering biocrusts in this study are unrealistic for most management settings, except possibly small high-priority areas or areas near infrastructure. However, as methods for inducing biocrust in the field become more efficient, simultaneous applications of inoculum and stabilizer will likely be an effective treatment.

It is important to note that the rainfall intensities used in simulations were very high (among the upper 95% quantile) and that the hydrological function of biocrusts may qualitatively different in high- versus low-intensity rain events (Chamizo et al., 2012; Rodríguez-Caballero et al., 2013). Indeed, all induced biocrusts had significantly greater time to ponding than controls, indicating higher infiltration rates for low-volume events. In addition to the particulars of our experimental methodology, factors such as the scale of the plots, soils, and composition of the biocrust organisms make generalizations across spatial scales or to other contexts imperfect (Chamizo et al., 2016). Contingencies related to experimental methods, rainfall intensity, soil texture, and biocrust community, combined with inherent noisiness of run-off and sediment yield data itself, likely underlie many apparently contradictory results in the literature (Chamizo et al., 2016). Properly contextualized, our results support the idea that the hydrological function of induced biocrusts, like naturally occurring biocrusts, depends largely on the composition and morphology of biocrust organisms present.

5 | CONCLUSIONS

- Biocrust was rapidly established in the period of 4 months, as evident in elevated levels of chlorophyll *a*, EPS, and biocrust cover in inoculated plots. However, functional improvements to soil stability, sediment yields, and run-off were only attained in plots that also received a psyllium-based soil stabilizer. Although patches of lichens and dark cyanobacteria were present in biocrust plots, overall erosion behaviour was similar to light-pigmented cyanobacterial crusts, which were the dominant type of biocrust cover.
- It is recommended that soil stabilizer be added to biocrust inoculations to mitigate run-off and erosion in the short term. It is expected that once crusts establish and develop, they will gradually become more resilient to water erosion as the effects of added soil stabilizer degrade over time.
- This study highlights the potential lag between apparent biocrust establishment and restoration of biocrust function, which may depend on properties such as surface roughness and aggregate stability.

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SUPPORTING INFORMATION

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