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Biological soil crust and disturbance controls on surface hydrology in a semi-arid ecosystem

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Abstract. Biological soil crust communities (biocrusts) play an important role in surface hydrologic processes in dryland ecosystems and can be dramatically altered with soil surface disturbance. In this study, through a simulated rainfall experiment, we examined biocrust hydrologic responses to disturbance (trampling and scraping) at different developmental stages on sandy soils on the Colorado Plateau. Our results showed that all disturbance treatments of the early-successional light cyanobacterial biocrusts reduced runoff after 10 min of cumulative rainfall. Scraped and scraped + trampled treatments also reduced runoff after 30 min in the light biocrust when compared to the intact controls but runoff in the trampling treatments was not significantly reduced. Light biocrust sediment loss trended toward a decrease in total amount of sediment lost in all disturbance treatments but not significantly so. In contrast, trampling well-developed dark cyano-lichen biocrusts demonstrated an opposite response than the less-developed light biocrusts and increased runoff after 30 min of cumulative rainfall and in total sediment loss relative to intact controls. Scraping in dark crusts did not increase runoff, implying that soil aggregate structure was important to the infiltration process. Well-developed, intact dark biocrusts generally had lower runoff and sediment loss and highest aggregate stability, whereas the less-developed light biocrusts were highest in runoff and sediment loss after disturbance when compared to the controls. These results suggest the importance of maintaining the well-developed dark biocrusts, as they are beneficial for lowering runoff and reducing soil loss and redistribution on the landscape. These data also suggest that upslope patches of light biocrust may either support water transport to downslope vegetation patches or alternatively this runoff may place dark biocrust patches at risk of disruption and loss, given that light patches increase runoff and thus soil erosion potential.

Key words: biological soil crust; disturbance event; drylands; rainfall simulation; runoff; sediment loss; soil surface.

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Introduction

Biological soil crusts (hereafter referred to as "biocrusts") are found in many ecosystems across the globe with a strong presence in arid and semi-arid drylands (Belnap et al. 2001, Belnap 2006). Biocrusts colonize the uppermost surface of the soil and contain a broad range of microorganisms such as fungi, cyanobacteria, lichens, and mosses. Although biocrusts have long been recognized as having a strong role in runoff and erosion dynamics in dryland environments, biocrusts do not have a single, uniform impact on surface runoff, infiltration rates, or sediment production (Williams et al. 1999, Belnap 2006, Herrick et al. 2010, Chamizo et al. 2012*a*, 2015, Bu et al. 2015, Rodríguez-Caballero et al. 2015, Chamizo et al. 2016, Chamizo et al.

2017). Abiotic factors such as climate and soil physical characteristics create diverse microtopographic features on soil surfaces and influence water flow paths. In cool desert ecosystems, biocrusts generally increase infiltration and reduce runoff (Li et al. 2002, Barger et al. 2006), which may then enhance soil water gain (Berdugo et al. 2014). Well-developed biocrusts in these environments more often have high microtopographic relief and surface roughness relative to hot desert biocrusts, which are generally level at the soil surface with less roughness (Belnap 2006). Higher topographic relief of the cool desert biocrusts can result in more indirect water flow paths, increasing travel time at the soil surface and thus reducing runoff rates (Belnap 2006).

Runoff and infiltration rates of biocrusted soils may also depend on soil texture. Biocrust organisms swell upon wetting, which can then reduce available pore spaces for water to infiltrate (Fischer et al. 2010). This effect may be most apparent on sandy soils with large pores and high hydraulic conductivity (Warren 2001). Infiltration rates on fine-textured soils are inherently lower and can be further reduced by dispersion of soil silts and clays where biological aggregation agents are absent (Cantón et al. 2003, Chamizo et al. 2015). Thus, the swelling effect of biocrust organisms on finer-textured soils may be offset by the binding of soil particles and limited dispersion of soil fines by biocrusts, resulting in no loss or even an increase in pore space and infiltration capacity (Eldridge and Greene 1994, Kidron et al. 1999, 2012).

Disturbance of biocrust communities at the soil surface may alter runoff and infiltration dynamics and can be highly dependent on levels of biocrust development (e.g., Warren 2001, Belnap 2006, Chamizo et al. 2012*a*, *b*, 2016). Trampling is a common disturbance in these landscapes due to grazing or recreational use. These disturbances can break up the intact biocrusts, increasing infiltration (Bowker et al. 2011, Chamizo et al. 2012*a*). However, these downward compressional forces may also cause a higher bulk density compacting the soil, increasing runoff and decreasing infiltration.

This relationship between biocrusts, physical disturbance, and erosion is further complicated as biocrusts are often found as a mosaic of developmental phases across a landscape. Following disturbance, biocrusts develop through successional phases (Belnap 2003) in which filamentous cyanobacteria are early colonizers on unstable soils. These early colonizers begin the process of soil surface stabilization, which is followed by darker-pigmented cyanobacteria (Belnap and Eldridge 2001). In the later stages of development, mosses and lichens establish, increasing photosynthetic capacity, nutrient exchange, moisture retention, and continued soil stability (Belnap and Eldridge 2001, Barger et al. 2006, 2016).

Across successional phases, as well as desert types, biocrust biomass and ecosystem functioning can vary and thus influence soil stabilization which, together with their effects on runoff, can control sediment flux (Belnap 2006). The later biocrust successional stages, with the highest level of development, often have the highest soil stability (Belnap 2006). This increased stability can likely be contributed to the higher biomass of organisms holding the soil together and potentially through additional cementing agents (e.g., shifting of clay particles) that occur over periods of soil immobilization (Amézketa 1999). However, the stability attained by later-successional biocrusts (Bowker et al. 2008), and prolonged soil immobilization, may be lost after a disturbance, which could increase the amount of sediment redistribution in a landscape.

In this study, we examined the effects of biocrust type and subsequent disturbance on runoff and sediment loss on fine sandy soils common in many arid and semi-arid regions of the world. We asked the questions: (1) What are the effects of disturbance of biocrusted soils on runoff and sediment loss? (2) Does the effect of disturbance differ between well-developed dark cyano-lichen biocrusts compared to weakly developed (light) cyanobacterial biocrusts? We conducted a series of rainfall simulations and biocrust disturbance manipulations to answer these questions. Due to the nature of these sandy soils, we predicted that runoff would be lower in the later-successional biocrusts because the greater surface roughness would overwhelm the potentially negative impacts on porosity of greater organismal biomass. In contrast, trampling was predicted to increase runoff relative to the intact plots in the dark crusts due to the reduction in circuitous runoff paths. In the dark biocrust scraped plots, we predicted that runoff will be increased because of a similar smoothing mechanism found

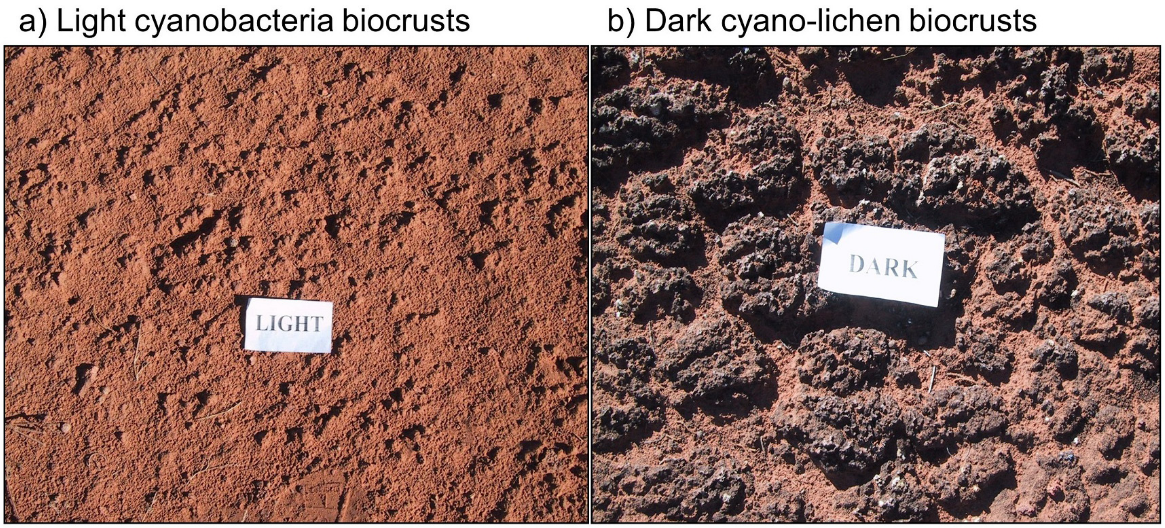

Fig. 1. Representative photographs of (a) intact less-developed light cyanobacteria-dominated biocrusts and (b) intact well-developed dark cyano-lichen-dominated crusts. Photo credit: N.N. Barger.

in the trampled treatment, and in contrast, the light crusts could demonstrate a decrease in runoff because of the removal of the biocrust filaments holding the soil together.

Methods

Site description

Experiments were conducted on lands managed by the Bureau of Land Management on the Colorado Plateau, near the Island-in-the-Sky District of Canyonlands National Park, Utah (also described in Barger et al. 2006). All plots were located (38°11′ N, 109°49′ W) within a 2.5 km radius of each other, ranged from 1767 to 1813 m elevation, and had a 50-yr mean annual precipitation of 215 mm. All plots were located on the Semi-Desert Shallow Sandy Loam (Utah juniper, blackbrush) ecological site as characterized by the U.S. Department of Agriculture Nature Resources Conservation Service (035X Y233UT; USDA NRCS, http://www.nrcs.usda.gov). Dominant vascular plant species at the sites were *Coleogyne ramosissima* (blackbrush), *Pinus edulis* (pinyon pine), *Juniperus osteosperma* (Utah juniper), and *Yucca harrimaniae* (Harriman's yucca). Soils at all plots were classified as Arches loamy fine sands (mixed, mesic Lithic Torripsamments) (Lammers 1991), confirmed by examination of a soil profile and laboratory soil texture measurements at each plot (N = 1 per plot). Depth to sandstone bedrock ranged from 20 to 53 cm and the loamy fine sand texture was uniform throughout the profiles. Vegetation cover was patchy, with litter accumulation beneath plants, but with little accumulation on biocrusts in the interspaces. Plant interspaces at these sites showed some level of biocrust development, except where they have been very recently disturbed. Two broad categories of cyanobacteria-dominated biocrust types that differ in their development and stability occur in a mosaic across the plant interspaces. The less-developed light biocrusts (Fig. 1a) are generally weakly stabilized by *Microcoleus vaginatus* with no or low levels of the darker-pigmented cyanobacterial species (Belnap and Eldridge 2001, Barger et al. 2006). In contrast to the light biocrusts, the relatively well-developed dark biocrusts (Fig. 1b) are dominated by the cyanobacterium *M. vaginatus*, but also contain other smaller darker-pigmented cyanobacteria *Scytonema myochrous* and *Nostoc commune* and soil lichens *Collema tenax* and *Collema coccophorum*.

Treatments

In October of 2001, we located seven 2 × 3 m dark biocrust plots with uniform crust coverage and microtopographic features where vascular plants were absent. Average slope of these plots was 3.6% ± 1.7. Each of the 2 × 3 m plots was then divided into three 0.71 × 0.71 m (0.5 m^2) subplots, all of which received the rainfall treatment at the same time. We randomly assigned treatments to the dark biocrust subplots: (1) control-intact, (2) trampled, and (3) scraped. The control-intact plots were left undisturbed to serve as a reference. In the trampled disturbed treatment, we made 100 passes over the plot by foot (two people jogging in hard-soled hiking boots) moving from the downslope to the upslope side of the plot on each pass. Since trampling affects both the biological and physical structure of the soil, we implemented a scraped treatment to remove the biocrust while maintaining the plot elevational characteristics. In the scraped treatment, we identified the lowest point in the plot and carefully removed the top 1 cm of soil in addition to all biocrust pinnacles (which can protrude upward 5–10 cm) above the soil surface with a straight-edged flat trowel, leaving the subsurface soil structure intact. Rainfall simulations were completed within six hours of treatment application to prevent interactions with aeolian processes.

We conducted a second experiment the following summer (June 2002) to test the effects of disturbance on light biocrusts. These light biocrusts were more weakly stabilized than dark biocrusts, as they had a lower cyanobacteria biomass and lacked any lichens (Belnap and Eldridge 2001). For comparison purposes, light biocrust plot locations were chosen to mimic the dark crust plots in soil texture, aspect, and slope as closely as was feasible. This experiment was conducted on eight light biocrust plots that were divided into four subplots and received treatments: (1) control-intact, (2) trampled, (3) scraped, and (4) scraped + trampled. We conducted the treatments in the same manner as described for the dark biocrusts with the addition of a combination of scraped + trampled treatment. In the scraped + trampled treatment, we first removed the biocrusted surface soils (top 1 cm) and then immediately trampled the scraped surface using the same techniques as the dark biocrust. As with the dark biocrust experiments, we conducted rainfall simulations within six hours of implementing the light treatments.

Pre-simulation soil measurements

We completed soil sampling following treatment application and prior to simulation. In order to not disrupt the plot treatments, all pre-simulation measurements were made adjacent (immediately above and below) to the plots with the appropriate treatment type applied. Here, we measured bulk density (core method), soil texture (hydrometer method; Gee and Bauder 1979, Gee and Or 2002), and antecedent moisture content on one 0–5 cm deep sample per treatment plot, composited from four 44 mm diameter cores. On these initial samples, we also generated an index of soil aggregate stability for the top 2–3 mm of the soil for eight samples per plot using a field soil stability test (Herrick et al. 2001 modified to a 1–6 scale as described in Herrick et al. 2005). Each 6–8 mm diameter crust fragment was immersed in deionized water on a 1.5-mm sieve for 5 min, then pulled completely out of the 2.5 cm deep water five times at a rate of one cycle every two-seconds, and rated on a scale from 1 to 6 with 1 being least stable and 6 being most stable. Erosion bridge measurements were used to understand surface roughness.

Erosion bridges were placed on the approximate edge of each plot, leveled, and pins dropped to establish heights at 20 different locations along the bridge, and photographed. The standard deviation of the pin drop heights (mm) was calculated for each photograph; thus, the larger the SD, the greater the surface roughness reported. We measured soil chlorophyll *a* content (μg/g of soil), which we used as a general indicator of photosynthetic biomass, on one sample per plot composited from 12, five mm deep soil cores. We chose to use μg/g of soil rather than by area as we did not obtain a known bulk density specifically in the top 5 mm of the soil surface; however if we were to run, this method again would report chlorophyll *a* per unit area, which could only serve to strengthen the treatment differences (Lan et al. 2011). In the laboratory, chlorophyll *a* soil samples were ground to a fine powder with a mortar and pestle. Quantitative and qualitative HPLC analyses were performed according to the method of Karsten and Garcia-Pichel (1996).

Rainfall simulation

We applied water simultaneously to all 71 × 71 cm treatment subplots in each plot for

Table 1. Pre-rainfall simulation soil measurements for the light and dark biocrust field trials.

Parameters	Light intact control	Light scraped	Light trampled	Light scraped + trampled	Dark intact control	Dark scraped	Dark trampled
Texture							
% sand	79.6 (1.3)	79.5 (2.3)	77.6 (1.1)	81.3 (2.0)	79.02 (0.67)	81.21 (0.86)	79.54 (1.49)
% silt	14.1 (1.2)	14.4 (2.2)	16.0 (0.9)	12.3 (1.9)	13.76 (1.70)	10.91 (0.62)	13.22 (1.34)
% clay	6.3 (0.3)	6.2 (0.4)	6.5 (0.5)	6.4 (0.4)	7.22 (1.03)	7.82 (0.53)	7.24 (0.45)
Bulk density (g/cm^3)	1.61 (0.05)	1.59 (0.06)	1.87 (0.03)	1.96 (0.02)	1.69 (0.03)	1.70 (0.03)	1.95 (0.03)
Soil stability class	1.78 (0.13)	1.28 (0.09)	1.02 (0.02)	1.00 (0.0)	5.09 (0.24)	1.16 (0.11)	1.00 (0.00)
Chlorophyll *a* (µg/g soil)	1.84 (0.26)	0.70 (0.09)	0.81 (0.15)	0.55 (0.09)	11.40 (1.82)	0.72 (0.14)	2.67 (0.16)
% soil moisture	0.5 (0.1)	0.6 (0.1)	0.6 (0.1)	0.6 (0.1)	0.6 (0.1)	0.7 (0.1)	0.7 (0.1)
Surface roughness	6.7 (0.6)	4.9 (0.4)	9.2 (0.4)	8.8 (0.4)	13.4 (1.2)	5.84 (0.7)	8.9 (0.9)

Notes: Values are means ± 1 SE (dark crust treatments N = 7 and light crust treatments N = 8). Dark biocrust metrics also described in Barger et al. (2006).

30 min at an average rate of 227 mm/h for the dark biocrust treatments and 222 mm/h for the light biocrust treatments based on measurements from rain gauges spaced evenly around the periphery of the plots. Rates were also similar across disturbance treatments. Runoff coefficients were adjusted, as appropriate, for the minor differences (<10 mm/h) measured. The high rainfall simulation rate, which is similar to that used by Thurow et al. (1988), was needed to produce runoff on these coarse-textured soils. We recognize this is a high-intensity event, and it is these events that are often responsible for redistributing sediment and structuring the landscape, especially in arid and semi-arid systems (Osterkamp and Friedman 2000). Widespread rills, water flow patterns, and fluvial litter deposits indicated that runoff has occurred in the area (Pyke et al. 2002).

Water was applied with a VeeJet 80/100 nozzle located 2.0 m above the soil surface. To generate a uniform spatial distribution of water, we controlled water pressure at 31.0 kPa and the nozzle was moved once across the plots every four-seconds using a hand-pulley system. The coefficient of variation of the 15 precipitation gauges located in the plots was generally less than 5%. We continuously collected runoff, and volume was measured and recorded every minute of the 30-min simulation. We used application rates at the plot level and a three-minute average runoff rate to calculate runoff rates at 10 and 30 min. We report results at both 10 and 30 min because 10 min is representative of the period that the simulated rainfall intensities would occur, while 30 min allows for runoff rates to stabilize and may more accurately reflect changes in the physical structure of the soil. Sediments from runoff samples were measured every minute for the first five minutes and every five minutes thereafter. Sediments were collected in runoff water in the field, brought to the laboratory, flocculated with a 1% alum solution, and then oven-dried at 105°C. All sediment masses are reported as oven-dry weights.

Statistical analysis

Because we were primarily interested in the responses of each of the two different biocrust types, dark and light treatments were analyzed as separate experiments using one-way ANOVAs for each response variable, with treatments blocked by plot, representing a single rainfall simulation across each of the three disturbance treatments. We used the Anderson-Darling test ($P > 0.05$) to test for normality. For significantly different models, we ran pairwise post hoc Tukey's honest significant difference tests. Because environmental conditions such as temperature and antecedent soil moisture (Table 1) were extremely similar within each of the experimental dates, we conducted pairwise comparisons and regressions across intact biocrusts, but conservatively chose not to statistically compare across the different biocrust type treatments due to potential unaccounted for differences.

We calculated percent runoff coefficient (runoff volume / added rainfall volume x 100; Schlesinger et al. 1999) at 10 and 30 minutes of simulated rainfall and tested for treatment differences through one-way ANOVAs and pairwise Tukey HSD tests. Sediments in runoff were collected each minute in

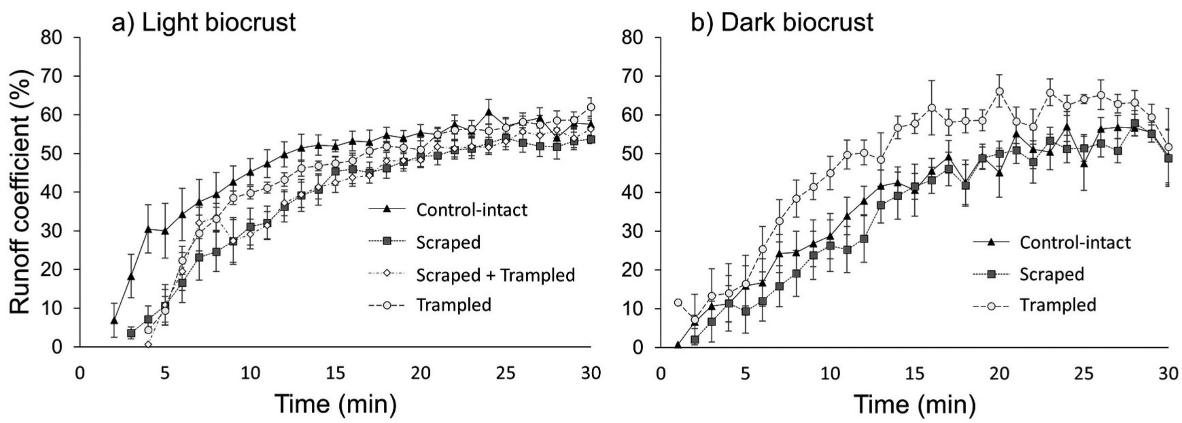

Fig. 2. Mean runoff coefficient (% runoff as determined by amount of water added) over time for light (a) and for dark biocrusts (b). Error bars represent ±1 SE.

the first five minutes of the rainfall simulation and every five minutes thereafter. We calculated total sediment flux by summing sediment loss in the first five minutes and then estimated sediment loss between the 5-min time periods with a linear estimate between time points. We summed total sediment loss after 30 min to obtain grams of sediment loss per m^2 and obtained sediment concentration in runoff by dividing total sediment by runoff (g/L). Data were transformed if the 30-min sediment data did not meet assumptions of normally distributed data (Anderson-Darling test, $P > 0.05$). Sediment data were analyzed using one-way ANOVAs for biocrust type and treatment blocked by plot for each biocrust type and through a t test to compare across intact light and dark biocrusts. Finally, chlorophyll a was regressed against grams of sediment loss per L of runoff (m^2) of the intact biocrust types; both were transformed to meet assumptions of normality. We conducted all analyses in R (RDC 2014, Vienna, Austria) and used a standard α of 0.10.

Results

Treatment effects on soils

Chlorophyll a (a proxy for biomass of photosynthetic organisms) reflected differences in biocrust types and treatments. As expected, chlorophyll a was higher in intact dark soil biocrusts (mean 11.40 ± 1.82 μg/g soil) compared with the light intact biocrusts (1.84 ± 0.26 μg/g soil). The trampling treatments reduced chlorophyll a by nearly 80% in the dark crusts (2.67 ± 0.16 μg/g soil) and by just over half in the light biocrusts (0.81 ± 0.16 μg/g soil). Scraping of both dark and light biocrusts resulted in low chlorophyll a levels (~0.7 μg/g soil). The combination of scraping and trampling of light biocrusts had the lowest concentration across all treatments (0.55 ± 0.09 μg/g soil). Loss of soil surface structure, associated with trampling, in these dry sandy soils lead to increased compaction and higher soil bulk density (Table 1). Bulk density (top 5 cm) in scraped plots was indistinguishable from those of intact controls (Table 1); however because bulk density values are the aggregated values for both crust and underlying soil, the differences between them may not have been detected due to the lack of separation between the two. Soil stability was higher in dark biocrusts relative to the light and was greatly reduced by trampling and scraping for both biocrust types. Antecedent soil moisture and soil texture were extremely similar across treatments for both dark and light biocrusts (Table 1). Erosion bridge measurements showed that the intact dark crust had the greatest soil surface roughness and the dark scraped was less rough than the trampled. Trampling the light crust increased roughness compared to the intact and scraped that showed a generally low level of surface roughness (Table 1).

Runoff

All treatments showed rapidly increasing runoff coefficients followed by stabilization as the saturated hydraulic conductivity of the soil was approached. Fig. 2 demonstrates runoff for both

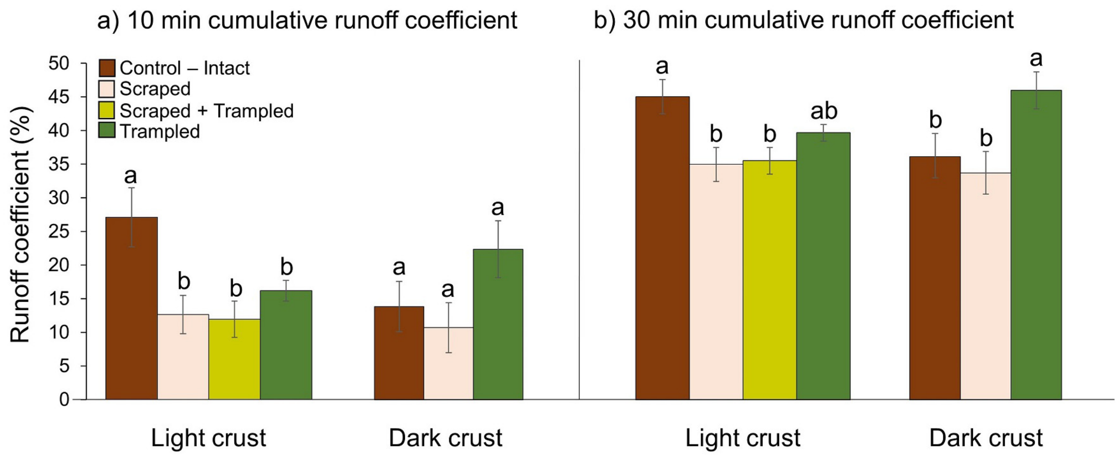

Fig. 3. Cumulative volumetric runoff coefficient (% runoff of total as determined by amount of water added) for both light and dark biocrusts after 10 min of rainfall simulation (a) and after 30 min (b). Letters indicate significant differences ($P < 0.10$) between treatments within a biocrust type as determined by ANOVA and post hoc Tukey's HSD tests. Error bars represent ±1 SE from the mean.

light (Fig. 2a) and dark (Fig. 2b) biocrusts. After 10 min of rainfall simulation, the light crust runoff coefficient was significantly higher than that of the dark crust intact controls (27% ± 4% vs. 14% ± 4%, respectively; *t* test $P = 0.04$). This trend continued to hold true after 30 min of rainfall simulation where two intact crust types remained significantly different (*t* test $P = 0.06$) with the light crust runoff coefficient at 46% ± 3% and the intact dark crust runoff coefficient at 37% ± 3%. Treatment effects differed between light and dark biocrusts and were not uniform in their runoff coefficients (Fig. 3). From the start until 10 min of water application, control plots in the light biocrust showed greater runoff than their disturbed treatments, these control plots had the highest percent runoff (27% ± 4% of total water applied), whereas runoff from the other light biocrust treatments ranged from 16% to 12% of total water applied. Conversely, the dark biocrust plots showed no significant differences in percent runoff across treatments after 10 min. After 30 min of rainfall simulation, the intact light biocrusts trended toward higher runoff coefficients (46% ± 3%) than trampled treatments (40% ± 1%) and were significantly higher when compared to the scraped (35% ± 3%) and scraped + trampled treatments (36% ± 2%) as shown in Fig. 3. The highest runoff in the dark crust plots occurred in the trampled plots (46% ± 3%), whereas the intact controls and scraped plots demonstrated lower general runoff percentages (37% ± 3% and 34% ± 3%, respectively).

Sediment loss

The cumulative sediment loss results illustrate a contrasting pattern of sediment loss across biocrust types and treatments. Across biocrust types, the intact dark crusts had roughly 2.5 times lower sediment loss than the intact light crusts (Fig. 4; *t* test $P = 0.07$). We saw no significant difference in total sediment loss among treatments in the light biocrust plots (Fig. 4a). Contrary to the light biocrust treatment responses to sediment loss, the dark biocrust did demonstrate significant difference (Fig. 4b). Trampling the dark biocrusts increased total sediment loss by nearly four times compared to the intact controls (1555 ± 594 g/m^2 and 398 ± 148 g/m^2, respectively) over the entire 30-min simulated precipitation event. Even with the presence of high variability across plots within the treatments, this trend was significant ($P = 0.09$). There was no significant difference between the control and the scraped dark biocrust.

We also tested how chlorophyll *a*, used as a proxy of biocrust biomass, may influence sediment concentrations through a linear regression

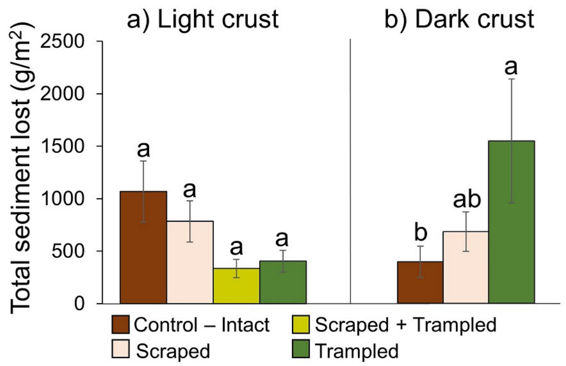

Fig. 4. Total mean sediment lost (g/m^2) over 30 min of rainfall simulation for the (a) light and (b) dark biocrusts. Letters represent significant differences ($P < 0.10$) between treatments within each biocrust type. Error bars represent ±1 SE from the mean.

including both the light and dark intact biocrusts (Fig. 5). After log transforming the data, the relationship was found to be significant ($P = 0.07$); however with a low R^2 ($R^2 = 0.23$), this trend was not strongly supported. Upon a qualitative comparison across the biocrust types, the light biocrusts generally demonstrated a greater variability of sediment loss and lower chlorophyll *a* levels than the dark biocrusts (Fig. 5). Alternatively, the dark crusts demonstrated a higher range of chlorophyll *a* concentration than the

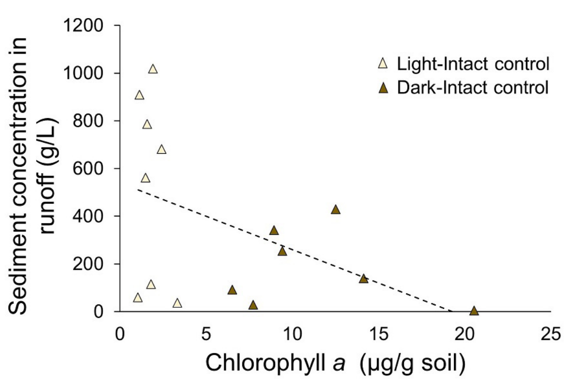

Fig. 5. Sediment concentration in runoff (g/L) over the 30-min rainfall simulation as determined by chlorophyll *a* content across intact dark and light biocrusts. Original data shown for clarity, statistical analysis ran on transformed data to meet assumptions of normality (linear regression on transformed data $P = 0.07$, $R^2 = 0.23$).

light biocrust, yet less variability in their sediment loss (Fig. 5).

Finally, we tested total sediment concentration in runoff levels (after 30 min) to better understand erosion. Here, we observed very similar trends to total sediment loss. The intact light biocrusts did not have a significant difference in their sediment loss by runoff. While not significant, the intact light controls displayed a higher general sediment loss as related to runoff (521 ± 141 g/L) than the scraped, scraped + trampled, and trampled (433 ± 116, 158 ± 41, and 191 ± 59 g/L, respectively). The dark crust also had a similar trend to its total sediment loss where the trampled plots were significantly higher in their sediment loss (702 ± 251 g/L) than the intact dark controls (183 ± 61 g/L), but not significantly higher than the scraped dark treatments (362 ± 115 g/L).

Discussion

In this study, we sought to understand how soil disturbance affects surface hydrologic processes in both light, less-developed and dark, more well-developed biocrusts. Here, we manipulated these biocrusts by either (1) trampling or (2) scraping and compared these manipulations to the intact controls. We originally hypothesized that the intact dark biocrusts would have the lowest runoff and sediment production of plot types, and that any disturbance would increase runoff and sediment, regardless of biocrust type. Interestingly, our findings were not directly in line with our hypotheses. The greatest observed treatment effect was the response to compressional forces, in this case trampling, and in that it was not uniform across the biocrust types. The intact light crusts generally, while not statistically significant, had higher runoff and more sediment loss than any of the associated disturbance treatments. Alternatively, trampling the more developed dark biocrusts generally had a greater runoff and sediment loss than when the dark biocrusts were left intact.

Surface hydrology may be explained by a suite of interacting biological and physical properties and processes. These include biocrust development, including soil surface roughness (Herrick et al. 2010, Chen et al. 2013, Chamizo et al. 2015), soil texture and physical structure (Warren 2001), and soil moisture (Bowker et al. 2008). Many (Eldridge 1993, Warren 2001, Belnap 2006, Chamizo et al. 2012*a*, Zaady et al. 2014) argue that much of the variability in the literature can be explained by physical site conditions, especially soil characteristics, and disturbance history. A grazing study (Eldridge 1993), and rainfall simulation studies conducted in sandy soils (~80% sand) with combined lichen and moss cover ranging from 1% to 84%, concluded that variability in biocrust cover has a negligible effect on infiltration and runoff rates and it was the physical properties controlling these metrics (Eldridge et al. 1997). Their argument that the large pore space found in sandy soils can decrease runoff levels is analogous to that offered by other studies (Warren 2001, Williams et al. 2012, Zaady et al. 2014). Yet, it has also been found that with increasing biocrust succession, an increased porosity and decreasing bulk density occurred across different soil types (Guo et al. 2008, Zaady and Offer 2010, Miralles-Mellado et al. 2011, Lan et al. 2012, Felde et al. 2014). These works plus others (e.g., Chamizo et al. 2015, 2016, 2017) suggest that on structurally degraded soils, microbiota found in biocrusts can increase infiltration by binding soil particles and preventing dispersion, while on intact soils their contribution is inconsequential (Eldridge and Greene 1994). The effect may, however, depend on the type of physical degradation. J. E. Herrick and J. W. Van Zee (*unpublished data*) found no effect of disturbance on infiltration for loamy soils where a moderately developed cyanobacterial and lichen biocrust was present on top of a weak vesicular horizon. In this case, it is likely that the subsurface (0.5–3 cm) vesicular horizon limited infiltration across all treatments (Felde et al. 2014).

In the light biocrusts, the presence of cyanobacteria may be smoothing the soil surface and filling in the pores of the high sand content soils (~80%) as suggested by Warren (2001), thus causing higher runoff when compared to the intact biocrusts that have a higher roughness. The importance of soil structure and pore space is supported by the fact that scraping, but not necessarily trampling, decreased runoff after 30 min of rainfall simulation. This may be because the act of scraping removed the cyanobacterial filaments while maintaining the soil aggregate structure and removing residual hydrophobicity (Fischer et al. 2010), allowing for increased pore space and thus increased infiltration (Chamizo et al. 2012*a*, Bowker et al. 2013). In contrast, trampling both destroyed the aggregate structure and disrupted the integrity of crusts potentially allowing for decreased runoff.

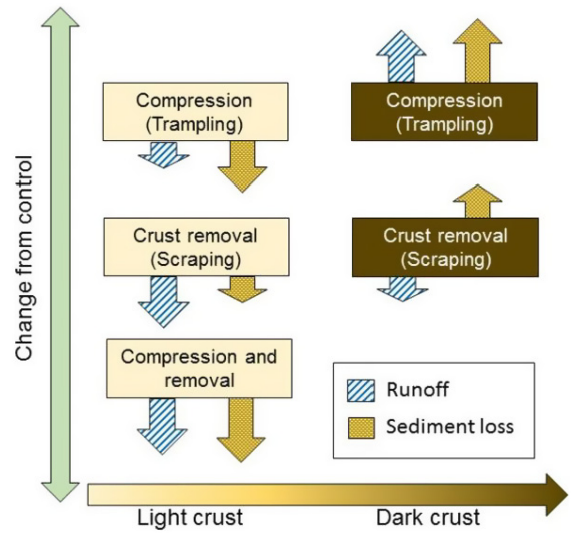

Fig. 6. Overview of directional trends after disturbance from the intact control of both light and dark biocrusts.

The well-developed dark biocrusts displayed a different pattern of runoff and sediment loss than the light (Fig. 6). The presence of dark biocrusts roughening the soil has long been understood as a strong influence on local infiltration, runoff, and sediment yield (Belnap 2006, Turnbull et al. 2012, Chen et al. 2013). In our two treatments, trampling and scraping had distinct effects on the dark biocrust roughness. The trampling and scraping lessened the soil surface roughness by compressing or removing the biocrust-caused pinnacles. However, the dark intact biocrusts had the highest surface roughness and consequently exhibited low runoff and sediment loss. Here, water had further to move along the surface and had more time for infiltration to occur (Belnap 2006, Chen et al. 2013), unlike the smoother light biocrusts. In the scraped treatments, the soil aggregate structure was left intact likely allowing for water to be absorbed and decreasing runoff amounts (Zaady et al. 2014). In addition to a decreased roughness lessening travel distance and decreasing amount of time water spent on the soil surface in the trampled plots, biomass was reduced and the soil aggregates disrupted. Other drivers potentially increasing the runoff in the trampled plots are that the hydrophobic components of the biocrust were left in place rather than removed, as was the case in the scraped plots, and that the rainfall simulation coupled with compressional forces caused by trampling could cause a physical soil sealing, thus increasing runoff as compared to the controls (Eldridge 1998, Eldridge et al. 2000, Chen et al. 2013). The dark biocrust results suggest that the presence of intact biocrust biomass, and the microtopographic features it creates are important in decreasing runoff, yet the soil aggregate structure remains critical in preventing soil loss.

Chlorophyll *a* is a commonly used proxy for biocrust development, where the higher the concentrations of chlorophyll *a,* the greater amount of biocrust biomass, and thus the benefits that accompany the presence of biocrust. Our results demonstrated a relationship, albeit weak, between chlorophyll *a* concentrations and sediment loss (Fig. 5). This relationship bolsters the long-held belief that late-successional, well- developed crust phases help reduce sediment loss and maintain stability (e.g., Belnap et al. 2007, Bowker et al. 2008) through high levels of biomass holding the soil together. In addition, our data suggest that the light crusts generally contained lower biomass levels and the amounts of sediment produced were highly variable and thus not a predictor of sediment creation. These data suggest that there may be a threshold where physical processes are proportionally more influential on hydrologic processes than the limited biomass of biocrust, and warrant future studies directly testing this threshold.

Conclusions

Biocrusts are commonly found in a mosaic pattern across the landscape through different disturbance events and levels of development. This mosaic pattern, coupled with variable hydrologic responses that depend on biocrust and disturbance type, can create a complex network of varying levels of runoff and sediment redistribution. In our study, we found that different biocrust and disturbance types resulted in very different runoff and erosion responses (Fig. 6). With intact well-developed dark biocrusts demonstrating high soil stability, lower soil redistribution, and generally decreased runoff relative to trampled plots, these biocrusts remain highly desirable on the landscape. Alternatively, the intact less-developed light biocrusts had much more variable runoff rates than the intact dark biocrusts. The transport of water from the light biocrust patches may in fact be beneficial if downslope vegetation is available to receive additional water. However, it is thought that historically a large proportion of soil surfaces were likely covered with dark biocrusts, as is still seen today in areas that were never grazed by livestock (e.g., Kleiner and Harper 1977). Our study suggests that the disturbance of dark well-developed biocrusts through anthropogenic forces (Belnap and Eldridge 2001, Duniway et al. 2010, Duniway and Herrick 2011) may have greater adverse effects than the disturbance of less-developed light biocrusts. Additionally, the presence of light biocrust patches upslope of dark biocrust patches, and with minimal vegetation in between, may place the latter at risk of sediment deposition, especially during extreme rainfall events, as greater water quantity or velocity can increase potential soil loss.

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