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Biocrust islands enhance infiltration, and reduce runoff and sediment yield on a heavily salinized dryland soil

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ABSTRACT

Salinity and sodicity are major forms of land degradation in drylands worldwide, reducing soil function, and threatening pastoral livelihoods. Dryland soils are often dominated by biocrusts, surface aggregations of lichens, bryophytes, fungi and other minute organisms that stabilize surface soils. Biocrusts could have a role in maintaining hydrological functions in heavily salinized areas, but there have been few studies, and the mechanisms are poorly understood. We tested whether biocrust mosses and lichens enhanced infiltration, and reduced runoff and sediment yield, on biocrusted islands scattered among extensive patches of bare highly saline soils in northeaster Iran. Biocrusted soils had greater cumulative infiltration and hydraulic conductivity, less runoff, which commenced later, and lower sediment yields than bare soils. The water content of biocrusted soils was greater than bare soils, but only at low matric potentials. Biocrusted surfaces were alkaline, more sandy, had lower levels of sodium, chloride, and calcium-plus-magnesium ions, and a lower sodium absorption ratio than bare soils. Structural equation modelling showed that increasing salinity was associated with a suppression of the negative effect of biocrusts on runoff. Potential mechanisms for reduced runoff likely relate to enhanced soil aggregation and porosity of biocrusted soils leading to greater retention of soil water content at low matric potentials, as well as an ability of mosses and lichens to capture and store surface water or to permit infiltration into the uppermost surface layers. Overall, our findings reveal a strong association between moss- and lichen-dominant biocrusts and soil hydrological processes, and suggest that these crusts play an important role in maintaining hydrological function in heavily salinized soils.

1. Introduction

Land degradation is an issue of major global significance (Ghassemi et al., 1995; Ravi et al., 2010; Jendoubi et al., 2019). It reduces soil and environmental quality, and manifests itself as, among other things, increasing salinity and sodicity, erosion, unregulated flooding, altered soil nutrient status, and reduced soil surface stability (D'Odorico and Ravi, 2016; Eldridge et al., 2017). The outcome of land degradation is therefore a reduction in the capacity of the land to maintain critical ecosystem functions and provide essential ecosystem services that support humans and other organisms (Reynolds et al., 2007). Land degradation has a number of causal agents such as overgrazing by livestock and deforestation; land use practices that push the land beyond its productive capacity. Globally, land degradation affects almost a quarter of the terrestrial land area, which supports about 1.5 billion people (D'Odorico and Ravi, 2016; Jendoubi et al., 2019).

Salinity and sodicity are major forms of land degradation worldwide (Ghassemi et al., 1995), and estimated to affect about 4% of Earth's land area (D'Odorico and Ravi, 2016). For example, salinity and sodicity influence soil hydrology by reducing soil aggregate stability and water holding capacity, and by increasing surface sealing (Yang et al., 2016). Consequently, salinization often leads to increased runoff and reduced infiltration, and declining plant cover and productivity. Increased runoff is most strongly felt in drylands (arid and semi-arid environments) where water scarcity is a major challenge due to low and unreliable rainfall, and high evaporation (Davies et al., 2016). Understanding how

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salinization affects hydrological processes is critically important in drylands because water is a scarce resource, driving plant productivity and sustaining the lives of millions of people and their cultures (Davies et al., 2016; Nachshon, 2018).

Biocrusts, complex associations between the surface soil and a number of soil-borne organisms such as cyanobacteria, algae, fungi, lichens and bryophytes, are important elements of dryland soils. Biocrusts can affect many basic soil physicochemical properties including soil hydrological function (water absorption and retention, water infiltration rate, runoff, evaporation; Rodríguez-Caballero et al., 2012; Belnap and Büdel, 2016; Chamizo et al., 2016; Eldridge et al., 2020), soil aggregation and stability (Belnap and Büdel, 2016) and the availability of soil nutrients (Zhang et al., 2016). Biocrusts also have a role in reducing salinity (Kakeh et al., 2018 and 2020), though the mechanisms are poorly understood. Greater levels of infiltration and therefore water holding capacity in biocrusted soils would be expected to leach soluble salts and cations deeper into the soil profile (Kakeh et al., 2018). On bare unvegetated soils, however, high levels of salinity would likely prolong the unvegetated state (Wang et al., 2017a; Kakeh et al., 2018). Biocrusts could also provide sites where salinity in the uppermost layers is low, thereby acting as 'infiltration islands' where vascular plants can reestablish. There have been few studies of the effects of biocrusts on saline soils (though see Kakeh et al., 2018), and the extent to which they might moderate any negative effects of salinity or sodicity on ecosystem functions such as runoff and infiltration are poorly known. This lack of evidence makes it difficult to manage saline soils and to advocate sustainable management of saline areas where biocrusts might provide a strong moderating influence.

Ion uptake is critically important for the growth of plants and biocrust organisms in both saline and non-saline environments (Wang et al., 2008). Sodium and chloride, the predominant ions in saline environments, are required to regulate the osmotic potentials of plants and nonvascular organisms, but excess amounts can result in ionic imbalance, dehydration, osmotic stress, and eventually, death (Sabovljevic and Sabovljevic, 2007; Wang et al., 2008; Zhang et al., 2019). Although high salinity levels have a negative effect on moss development (Zhang et al., 2019), some mosses such as members of the families Pottiaceae, Bryaceae, Amblystegiaceae and Mniaceae can tolerate high levels of salt (Flowers et al., 2010) by being biological inactive for a few years (Carroll, 2003; Sabovljevic and Sabovljevic, 2007), or by synthesizing xanthophyll pigments to protect their photosystems (Zhang et al., 2019). Like mosses, some lichens have an ability to accumulate small quantities of sodium ions, thereby allowing them to survive in saline environments (Figueira et al., 2001). For example, lichens contain many metabolites, typically osmolytes, which allow them to adjust their osmotic potential and prevent intracellular water loss, a consequence of salt stress (Mahajan and Tuteja, 2005).

Here we describe a study where we examined the impacts of biocrusts on runoff, infiltration and sediment yield from a sodic soil in northeastern Iran. Salt-induced land degradation is a major environmental problem in Iran, where about 23 million ha is affected (Siadat et al., 2018). Although salinity occurs naturally due to differences in geology, climate and saline groundwater (Siadat et al., 2018), human-induced salinity and salinisation has increased markedly over the past 50 years due to overgrazing by livestock, removal of vegetation and loss of surface soils. We expected that the physical and chemical properties of biocrusted surfaces would differ from bare soil surfaces, and that these differences would lead to lower levels of runoff and sediment, and greater soil moisture and infiltration on biocrusted soils. Our reasoning is that biocrusts have been shown to maintain the integrity of soil micropores (Young et al., 2004), enabling infiltration of water. Equally, because biocrusts aggregate surface soils (Belnap and Büdel, 2016), we would expect greater structural stability, less dispersion of salts, and reduced surface sealing, resulting in less runoff (more infiltration) from biocrusted surfaces. We tested our prediction by applying simulated rainfall to 30 sites, half of which were dominated by biocrusts and the other half bare, and measured changes in infiltration with a disk permeameter.

2. Methods

2.1. The study area

Our research was conducted in the Quara Qir rangelands around Alagol Lake, Golestan province, Northern Iran (37°15′ to 37°23′ N and 54°33′ to 54°39′ E). The Qara Qir rangelands into the Gorgan Plain is connected in the north with the Karakum Deserts in Turkmenistan, in the east with the Koppeh Dagh Mountains, in the south with the Hyrcanian mixed forests, and in the west with the Caspian Sea lowland wetlands (Kakeh et al., 2018). The climate is semi-arid to arid, with a mean annual precipitation of 273 mm, the greatest rainfall occurring in January and February, and the lowest in July and August (Iranian Meteorological Organization). The mean annual temperature is 19.1 °C, and absolute maximum and minimum temperatures are 40 and −5.36 °C, respectively. Annual potential evaporation is 1700 mm. The study area, near Alagol Lake, is dominated by aeolian deposits of Holocene age (Rahimzadeh et al., 2019), so the soils are susceptible to erosion. Slopes range from 3 to 5% and the area is 15 to 47 m above the sea level. The soils are relatively deep (~3 m), derived from loess deposits (Rahimzadeh et al., 2019), have loamy surface textures (Sodic Haplogypsids, Soil Survey Staff, 1999) and are naturally saline (Moser, 2009). Compared with bare soils, biocrusted soils had more silt (57 *cf.* 52%), less clay (13.4 *cf.* 24.4%) and lower bulk densities (1.30 *cf.* 1.56 Mg m^{-3}, Table 1).

The main vegetation community is grassland-forbland dominated by the members of the families Poaceae, Asteraceae, Fabaceae, Lamiaceae and Brassicaceae (Kakeh et al., 2018). Total ground cover is relatively sparse (~35%), due to historic and current overgrazing. Common lichens in the biocrust include *Psora decipiens* (Hedw.) Hoffm., *Diploschistes diacapsis* (Ach.) Lumbsch, *Collema tenax* (Sw.) Ach, *Fulgensia bracteata* (Nyl.) Poelt, *Squamarina cartilaginea* (With.) P. James, *Toninia sedifolia* (Scop.) Timdal and *Caloplaca tominii* Savicz (lichens). Common mosses in the biocrusts include *Tortula revolvens* (Schimp.) G.Roth, *Aloina bifrons* (DeNot) Delgad, *Aloina aloidas* (Schultz.) Kindb and *Barbula trifaria* (Kakeh et al, 2018). Bare soils at all sites had no biocrusts or plants. Biocrusted plots were dominated by mosses (mean: 67.3%), followed by lichens (20.1%) and vascular plants (12.6%; Kakeh et al., 2020).

2.2. Rainfall simulations and soil sampling

We selected 30 plots on summit positions of a large sand dune. Half of the plots were bare and the others supported biocrusts (Fig. 1a and 1b). Moss cover ranged from 60 to 71% and lichen cover from 6 to 16%. The plots were separated by at least 500 m and had similar climate, geology, topography, slope, vegetation cover, and biocrust composition. In order to avoid the impact of topography on soil water redistribution and interception by vascular plants, all rainfall simulation plots we selected were relatively level, and had a sparse cover of perennial vascular vegetation (Fig. 1c). Rainfall simulation and soil collection were carried out between May 2017 and January 2018. Photographs were taken of each plot prior to rainfall simulation, and the cover of lichens, mosses and vascular vegetation assessed using ENVI software (Version 4.3). We used a pressurized drop-type rainfall simulator which delivered raindrops of 2.0 ± 0.8 mm in diameter from a height of 2 m at intensities of 40 mm h^{-1} over a period of 90 min (Fig. 1d). We measured total runoff (L) after 90 min from a flume at the base of each rainfall simulation microplot (0.5 m^2) and calculated the time for run-off to initiate, runoff volume and sediment yield according to in Holden and Burt (2002) and Gregory (2004). We acknowledge the issues associated with using small plots with artificial rainfall, where overland flow is constrained, rather than large, gauged catchments. Nonetheless, a small

Table 1
Description of soil physical and chemical properties of biocrusted and bare soils from the study area.

Surface type	Depth (cm)	Clay (%)	Silt (%)	Sand (%)	Organic carbon (%)	Nitrogen (%)	Bulk density (Mg m^{-3})
Biocrust	0–5	11.5	60.0	28.6	1.51	0.15	1.28
	5–10	15.3	57.3	27.4	1.15	0.06	1.32
Bare	0–5	24.9	51.7	23.3	0.95	0.06	1.62
	5–10	24.0	51.7	24.4	0.65	0.05	1.51

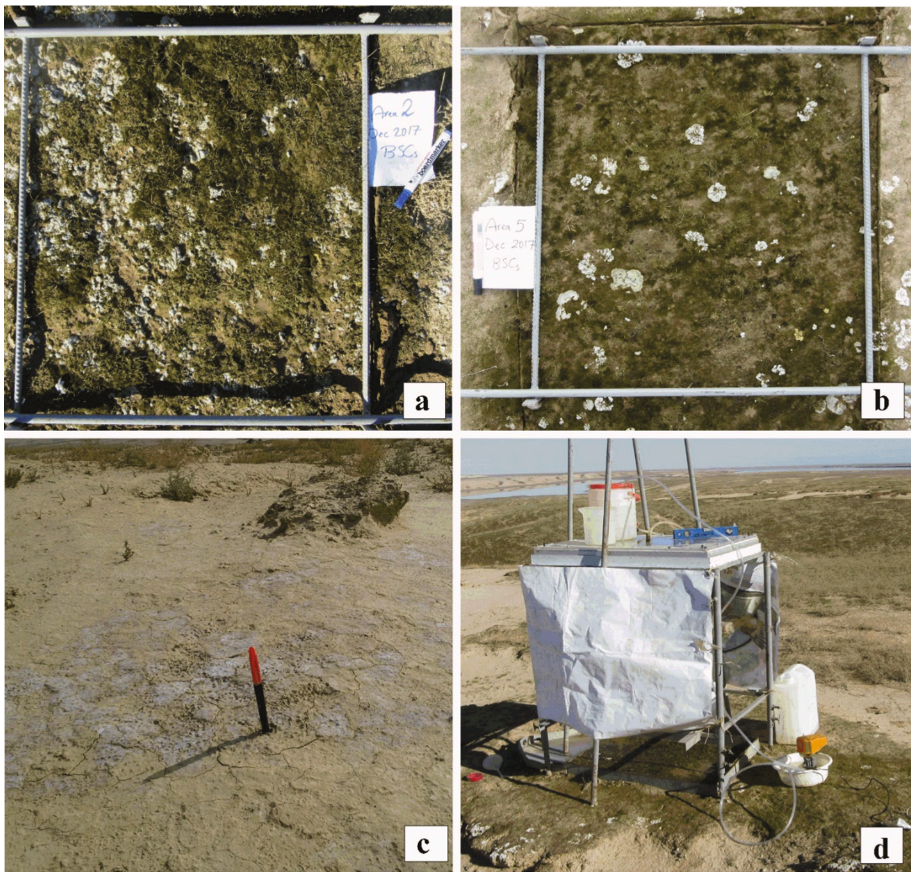

Fig. 1. Images of (a & b) biocrusted plots, (c) bare soil with accumulation of salt during the dry season, and (d) the rainfall simulator. Photographs: Jalil Kakeh.

rainfall simulator was used because the scale of measurement (0.5 m^2) aligns closely with a spatial scale of biocrust organisms, enabling us to select plots that were either dominated by biocrusts or biocrust free.

2.3. Infiltration measurements

As well as runoff and sediment yield, we assessed infiltration using a disk infiltrometer with a diameter of 20 cm at matric potentials of 0, −2 and −10 cm on 15 biocrusted and 15 bare plots. The disk infiltrometer was placed on the topsoil at and measurements started at 0 cm, increasing to −2 and −10 cm matric potential. Transient infiltration was examined until steady-state conditions were reached. For each plot, measurements were made at three replicate locations of each of biocrusted and bare surfaces. At the start and end of each infiltration measurement we collected samples in order to determine the early and final water contents. Samples to determine initial water content were taken from outside, but adjacent to the plot to avoid any disturbance of the soil during the measurements. The final sample for water content determined was collected from directly beneath the disk infiltrometer at the end of the infiltration measurement after the −10 cm matric suction (Coppola et al., 2011; Wang et al., 2017b; Xiao et al., 2019). Cumulative infiltration, hydraulic conductivity and soil water content were calculated using appropriate methods described in Appendix S1. All hydrological measurements were made once, between May and the following January. Because seasonal conditions were consistently relatively dry over that period. Therefore, we would not expect major differences in hydrological response due to different collection times.

2.4. Soil analyses

Surface soil (0–5 cm) was collected from each plot following rainfall simulations. These soils were oven dried, sieved (<2 mm fraction), and analysed for gravimetric soil water content (soil moisture: Topp, 1993), the percentage of fine soil particles (silt + clay%) using the hydrometer method (Gee and Bauder, 1986), electrical conductivity, and pH on a 1:5 soil: water extract (Rhoades, 1982). Potassium (Knudsen et al., 1982) and sodium (Na^+) were analysed with flame photometry (Rhoades, 1982), calcium (Ca^{2+}) and magnesium (Mg^{2+}) by the EDTA volumetric method (Lanyon and Heald, 1982), chloride (Cl^-) and bicarbonate (HCO_3^-) by silver nitrate titration and neutralization titration, respectively (Ryan, 2017). From these analyses we calculated the sodium adsorption ratio (SAR; U.S. Salinity Laboratory Staff, 1954).

2.5. Statistical analyses

We examined differences in soil physical, chemical and hydrological properties between biocrusted and bare soils using one-way ANOVA. Data were checked for homogeneity of the residuals (Levene's Test) prior to analyses. Pearson's correlation was used to examine the correlation between runoff and sediment yield. We then used Structural Equation Modelling (SEM; Grace, 2006) to examine the direct and indirect effect of biocrusts and soils on runoff. In our models, we depicted 'soils' as the percentage of sand (sand%), soil water and 'salinity'. To derive a measure of 'salinity', we used a multifunctionality index whereby we averaged the standardized values for EC, sodium, potassium, calcium + magnesium, chloride and the sodium adsorption ratio to calculate a vector that represents increasing salt content. The 'salinity' value was highly correlated with these six values ($r > 0.88$, $P < 0.001$). The total cover of mosses and lichens was used as our measure of biocrust. We then developed an *a priori* model of the hypothesized effects of biocrust cover and soils on runoff and predicted direct and indirect effects of biocrust cover on both runoff and soil water content, consistent with studies from Spain (Cantón et al., 2011, Rodríguez -Caballero et al., 2013) and Australia (Graetz and Tongway, 1986). We also predicted direct effects of soil particle size (sand) on runoff, and indirect effects of sand on runoff (Chamizo et al., 2015) *via* its effect on biocrust cover. Finally, we expected to detect direct effects, and indirect effects *via* biocrust cover, of increasing salinity on runoff (Mamedov et al., 2002). We compared the expected *a priori* model with the variance–covariance matrix of our data in order to estimate an overall goodness-of-fit, using the χ^2 statistic. The goodness of fit test estimates the likelihood of the observed data given the *a priori* model structure. Thus, high probability values indicate that these models are highly plausible causal structures underlying the observed correlations. Models with low χ^2, high Goodness of Fit Index [GFI], high Normal Fit Index [NFI] and low Root Mean Error of Approximation (RMSEA < 0.05) were interpreted as showing the best fit to our data. Because we had few data points ($n = 30$), we used the Bollen-Stine bootstrap test to improve goodness of fit when variables and to account for any variables that might not be normally distributed. A model with a good fit is represented as 0.10 < bootstrap $P \leq 1.00$ (Schermelleh-Engel et al., 2003). Analyses were performed using the AMOS 22 (IBM, Chicago, IL, USA) software.

3. Results

Biocrusted surfaces were associated with soils with significantly less runoff ($F_{1,28} = 72.4$, $P < 0.001$), a smaller mass of sediment ($F_{1,28} = 157.8$, $P < 0.001$; Fig. 2). Runoff commenced significantly earlier on bare (19.2 ± 1.21 min; mean ± SE) than biocrusted (36.2 ± 7.3 min; $F_{1,28} = 5.25$, $P = 0.03$) surfaces (Fig. 2). Across all plots, sediment yield and runoff were highly correlated ($r = 0.82$). Because of the strong dichotomy between biocrusts and bare soils, the relationship appears as two separate clusters (Fig. 3a). The runoff coefficient (runoff as a percentage of applied rainfall) was markedly lower on biocrusted (10.1 ± 8.3%; mean ± SE; range: 0–23%) than bare (45.2 ± 3.5%; mean ± SE; range: 23–64%) surfaces (Fig. 2). Sediment yield was significantly greater on bare (98.6 ± 11.4 g m^{-2}) than biocrusted (5.2 ± 3.9 g m^{-2}) surfaces (Figs. 2 and 3a).

The cumulative infiltration rate increased with increasing matric suction over time for both biocrusted and bare soils (Fig. 3b). When we compared the two curves, we found significantly greater cumulative infiltration for biocrusted than bare soil when data were averaged across all matric potentials ($P < 0.001$). Soil water content declined with increasing matric potentials for both biocrusted and bare soils (Fig. 3c). Although there was no overall difference in soil water content across all matric potentials ($P = 0.59$; Fig. 4), water content for biocrusted soils was significantly greater than that on bare soils at the ($P < 0.001$) at the lowest matric potential (1 cm) but converged at potentials greater than about 1000 cm (Fig. 3c). Finally, hydraulic conductivity declined with increasing matric potentials for both biocrusted and bare soils and was significantly greater for biocrusted soils at all levels of matric potential ($F_{1,28} > 12.1$, $P < 0.001$; Fig. 3d).

Biocrusted soils were more sandy ($F_{1,28} = 13.0$, $P = 0.001$) and pH values were slightly more alkaline ($P = 0.002$). Biocrusted surfaces had lower EC, sodium, chloride, calcium + magnesium, and HCO_3^- ions, and a lower sodium adsorption ratio ($P < 0.01$; Fig. 4). We then examined the direct effects of biocrust cover, salinity, and sand on runoff, and the indirect effects of biocrusts on runoff *via* soil water. Biocrusted soils were associated with a strong suppression of runoff (Fig. 5). Increasing salinity increased runoff, both directly, but also indirectly, by

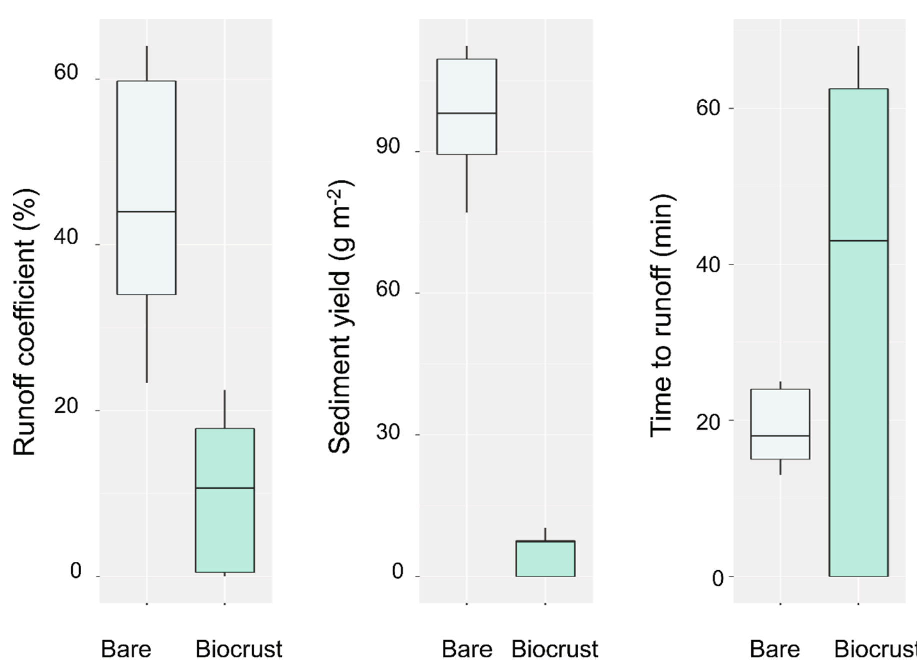

Fig. 2. Boxpots of the differences in the runoff coefficient (%), sediment yield (g m^{-2}) and time to runoff (mins) between bare and biocrusted surfaces.

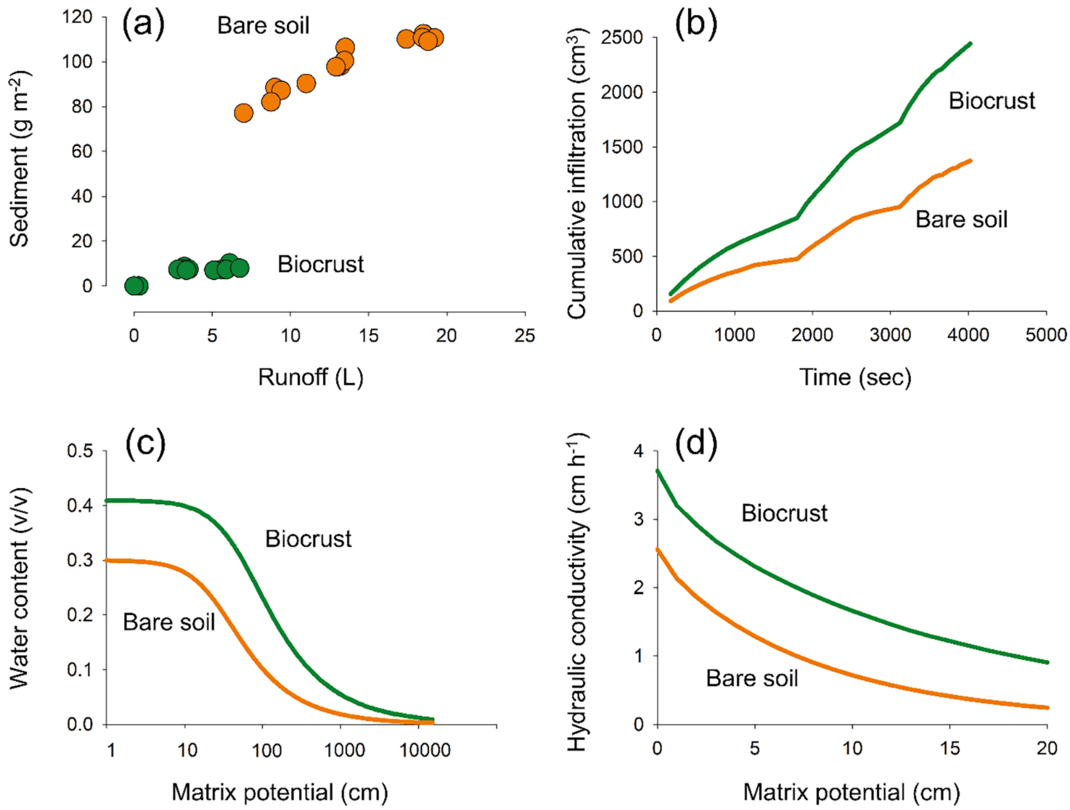

Fig. 3. (a) relationship between runoff and sediment yield, and plots of (b) cumulative rainfall over time, and (c) water content and (d) hydraulic conductivity in relation to matric potential for biocrusted and bare soils.

suppressing the negative effect of moss and lichen cover on runoff. Further, the percentage of sand reduced runoff indirectly *via* its negative association with increasing salinity (Fig. 5).

4. Discussion

In our study we found that biocrusted surfaces were less saline, had more sand, and less runoff and sediment yield. Further, infiltration and hydraulic conductivity were greater on biocrust surfaces, and there was greater retention of soil water content under conditions of low matric potential. In comparison, bare soils had higher SAR and clay contents, which together increase soil aggregate dispersion, reduce saturated hydraulic conductivity, and increase the likelihood of physical and chemical soil crust formation (Fang et al., 2007, Amini et al., 2016). There are few studies of the effects of highly saline soils on biocrust organisms (e.g., Fox et al., 2009; Schulz et al., 2016; Zhou et al., 2016; Sommer et al., 2020). Our study is novel because it improves our understanding of the functional role of biocrusts on highly saline soils; an area of research that has been little studied to date. A greater understanding of the links between soil salinization, biocrust cover and hydrology can lead to improved management of saline soils where biocrusts are significant surface features.

We envision two principal mechanisms to account for delayed onset in runoff: greater likelihood that captured water will infiltrate, and reduced sediment yield in biocrusted soils (Chamizo et al., 2016; Whitney et al., 2017; Eldridge et al., 2020; Kakeh et al., 2020). First, biocrusts enhance soil aggregation and porosity, reducing the effects of physical crusting, thereby enhancing hydrological functioning (Eldridge et al., 2020). The results of our study suggest that the mechanisms relate to a greater retention of soil water content at low matric potentials, and differences in the structure of biocrusted surfaces and the composite organisms that result in a rougher surface, and retention of water within crustal organisms and the uppermost surface layers. Second, biocrusts may have a competitive advantage over vascular plants in hyper-saline soils simply because they are able to tolerate higher levels of Na^+ ions or are able to engineer the surface to allow them to tolerate high salinity levels.

4.1. Retention of water in the uppermost soil and biocrusted surfaces

Greater cumulative infiltration, hydraulic conductivity and lower runoff are likely due to greater water retention on the soil surface or in the uppermost layers. Although we detected no difference in soil water content between biocrusted and bare soils using a coarse gravimetric field-based approach (Fig. 4), changes in water content across different matric potentials indicated major differences at low (1–10 cm) but not high (>1000 cm) matric potential (Fig. 3c). This greater soil water content under low matric potentials suggests more biocrust micropores for conducting water. These micropores are likely created by the rootlike structures of mosses (rhizoids) and lichens (rhizines) that provide entry points for water into the upper soil layers (Wang et al., 2017b; Shi et al., 2018; Kakeh et al., 2020). They are also likely responsible for the leaching of Na^+ ions. From an ecological perspective, differences in matric potentialshow the extent to which biocrusts can hold water in the upper soil layers and increase unsaturated hydraulic conductivity; processes that are critical for local hydrological regimes.

Greater hydrological function on biocrusted surfaces could also be due to idiosyncratic soil effects. Our structural equation model suggests that increasing sand content has an indirect suppressive effect on runoff through its association with less saline soils. This is generally consistent with the notion that increasing sand leads to greater hydraulic conductivity, greater soil leaching potential, and reduced runoff. Highly saline soils, particularly those where the electrical conductivity exceeds 3 dS m^{-1} are associated with extremely dispersible clay particles (Singer et al., 1982) that block surface soil pores (King and Bjorneberg, 2012), reducing porosity, and leading to reduced hydraulic conductivity (Yang

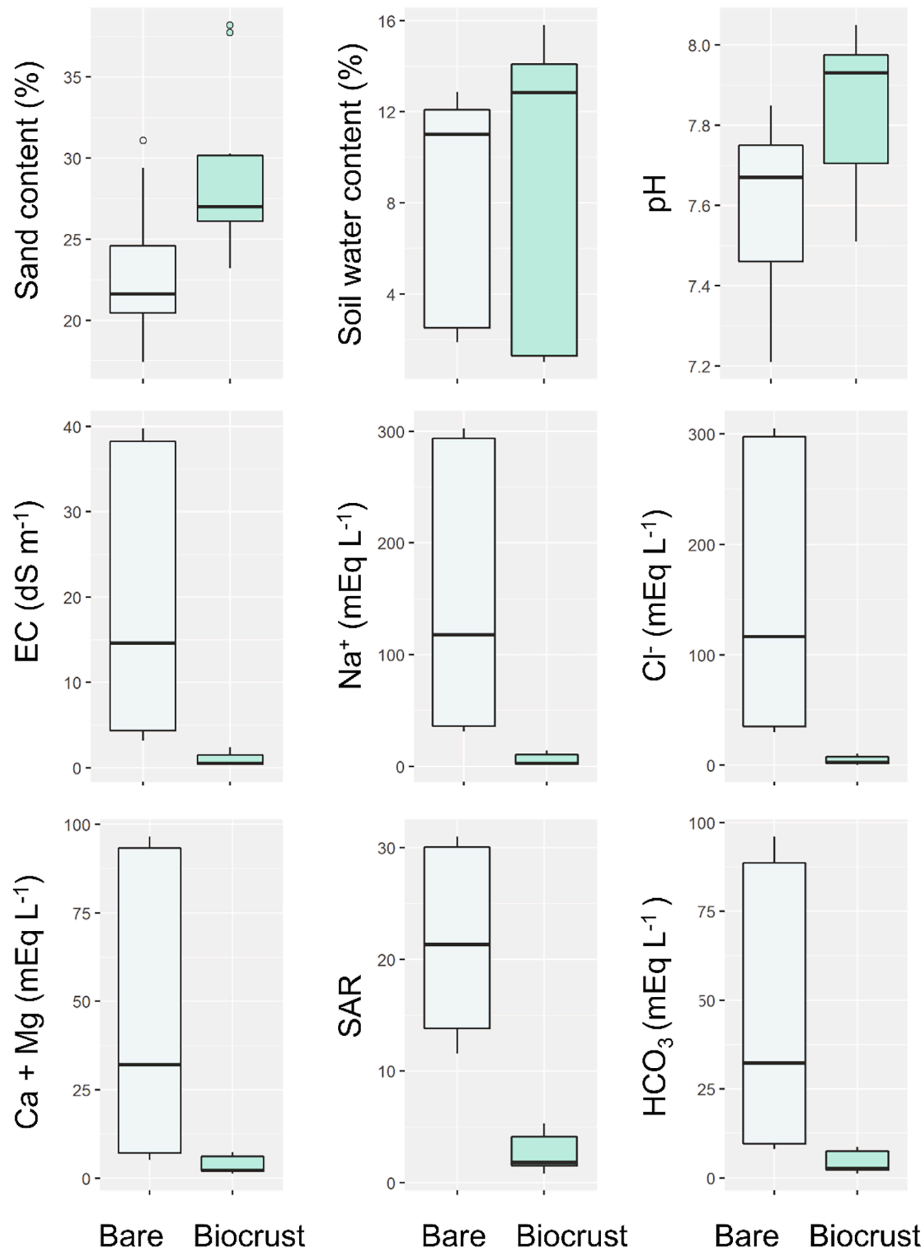

Fig. 4. Boxpots of the differences in soil physico-chemical attributes between bare and biocrusted surfaces. Bare and biocrusted surfaces were significantly different ($P < 0.05$) for all but saturated soil water content. SAR = sodium absorption ratio.

et al., 2016) and greater runoff. Higher levels of organic carbon in biocrusted soils (Table 1) would be expected to lead to greater soil aggregation and therefore more stable macropores, enhancing infiltration at low matric potentials (Fig. 3d). Finally, biocrusts can increase infiltration and soil water content by buffering the effects on evapotranspiration losses and runoff (Whitney et al., 2017).

The physical structure of mosses and lichens also has a role in moderating hydrological inflows and outflows. Mosses have specialized structures on their leaves such as hair points and water retaining cells (papillae, lamellae) that enhance the capture and retention of water, potentially reducing the volume available for runoff, and enhancing water storage in the uppermost layers (Eldridge et al., 2020). The surface of lichens is typically roughened and elevated above the soil surface. This enhances surface water storage (Faist et al., 2017), increases the microscale leaching of sodium ions, reduces runoff (Eldridge et al., 2020), and elevates these organisms above the highly saline surface (Garbary et al., 2009). Greater capture of even small amounts of rainfall at the surface by both mosses and lichens would likely explain the longer time taken for runoff to commence on biocrusted soils (Rodríguez-Caballero et al., 2013).

4.2. A capacity to survive on highly saline surfaces

One of the mechanisms linking biocrusts to runoff also relates to Na^+ ions, with a negative correlation between salinity and biocrust cover, and specifically, increasing salinity reducing the negative effect of biocrusts on runoff. Under tension, which often occurs early stages of infiltration, enhanced infiltration through biocrusts can potentially increase the leaching of Na^+ ions (Kidron, 2016) in the soil. Under tension, biocrusts can also reduce capillary rise and therefore the further ingress of Na^+ ions into surface soils. Despite these potential coping mechanisms, mosses and lichens cannot tolerate very high levels of salinity (Chandler et al., 2019) because this can disrupt cell functions such as intracellular pH and osmotic regulation, protein synthesis, and enzyme

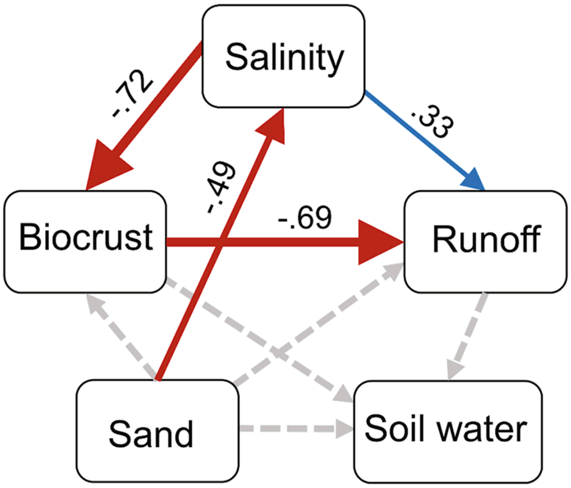

Fig. 5. Structural equation modeling of the direct and indirect effects of Biocrust cover (%), Soil sand content (%), Soil water content (%) and Salinity (unitless) on Runoff (L). Salinity is the average standardized (z-transformed) values for electrical conductivity, sodium, potassium, calcium + magnesium, chloride and the sodium adsorption ratio that represents increasing 'salt' content. Standardized path coefficients, adjacent to arrows, are analogous to partial correlation coefficients, and indicative of the effect size of the relationship. Continuous blue and red lines represent positive and negative correlations, respectively, and dashed lines indicate non-significant relationships. Model fit: $\chi^2 = 0.50$, df = 1, $P = 0.479$, RMSEA = 0, Bootstrapped $P = 0.44$. Model variance: R^2 (runoff) = 0.84.

activation, and generate hyperosmotic shock and oxidative stress (Evelin et al., 2009). The eventual outcome of such high levels of salinity on biocrust taxa is dessication *via* the loss of intracellular water (Delmail et al., 2013). However, lichens such as *Wahlenbergiella striatula* (Gasulla et al., 2019), *Niebla homalea* (Yamamoto et al., 2001), *Collema* spp., *Heppia lutosa* (Ach.) Nyl. and *Catapyrenium lacinulatum* (Ullmann & Büdel, 2001) may be able to accumulate small amounts of Na^+ ions in their thallus, thereby reducing sodium concentrations in the near surface soil layers (Figueira et al., 2001). Despite low salt tolerance in bryophyes (Flowers et al., 2010), they are able to survive in relatively highly salinity soils, due to a combination of dessication tolerance (O'Mahony and Oliver, 1999) and perhaps their capacity to form dense mats away from areas of high salinity (Garbary et al., 2009). Biocrust taxa may indeed be able to reduce salinity levels in the uppermost few millimetres of the soil, though this would need to be tested using finer scale methods than used in this study.

5. Conclusions

In conclusion, we have shown that, compared with bare highly saline soils, biocrusted soils have the capacity to retain more water at the surface and redistribute it to deeper layers, therefore leading to improved hydrological function across a large area of drylands where historic overgrazing has resulted in extensive secondary salinisation (Amini et al., 2016). Given the strong role of biocrusted soils under low matric potentials, we would expect that their effects would be most important during drought conditions or where groundwater is insufficient to support vascular plants. Overall, the maintenance of a stable biocrust cover may provide a means of remediating sparsely vegetated saline soils by providing islands of greater hydrological function within an environment of severe salinization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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