Biocrust effects on soil infiltrability in the Mu Us Desert: Soil hydraulic properties analysis and modeling

Hongjie Guan^{1,2,3*}, Xinyu Liu⁴

¹ Yanchi Research Station, School of Soil and Water Conservation, Beijing Forestry University, Beijing 100083, China.

² Key Laboratory of State Forestry Administration on Soil and Water Conservation, Beijing Forestry University, Beijing 100083, China.

³ Beijing Engineering Research Center of Soil and Water Conservation, Beijing Forestry University, Beijing 100083, China.

⁴ State Key Laboratory of Earth Surface Processes and Resource Ecology, MOE Engineering Research Center of Desertification and Blown-sand Control, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, China.

* Corresponding author. E-mail: guanhong311@163.com

Abstract: The presence of biocrusts changes water infiltration in the Mu Us Desert. Knowledge of the hydraulic properties of biocrusts and parameterization of soil hydraulic properties are important to improve simulation of infiltration and soil water dynamics in vegetation-soil-water models. In this study, four treatments, including bare land with sporadic cyanobacterial biocrusts (BL), lichen-dominated biocrusts (LB), early-successional moss biocrusts (EMB), and late-successional moss biocrusts (LMB), were established to evaluate the effects of biocrust development on soil water infiltration in the Mu Us Desert, northwest of China. Moreover, a combined Wooding inverse approach was used for the estimation of soil hydraulic parameters. The results showed that infiltration rate followed the pattern BL > LB > EMB > LMB. Moreover, the LB, EMB, and LMB treatments had significantly lower infiltration rates than the BL treatment. The saturated soil moisture (θ_s) and shape parameter (α_{VG}) for the EMB and LMB treatments were higher than that for the BL and LB treatments, although the difference among four treatments was insignificant. Water retention increased with biocrust development at high-pressure heads, whereas the opposite was observed at low-pressure heads. The development of biocrusts influences van Genuchten parameters, subsequently affects the water retention curve, and thereby alters available water in the biocrust layer. The findings regarding the parameterization of soil hydraulic properties have important implications for the simulation of eco-hydrological processes in dryland ecosystems.

Keywords: Cyanobacteria; Lichen; Moss; Infiltration; Inverse approach; Hydraulic parameter.

1 INTRODUCTION

Dryland landscape is usually characterized by woody plant patches, which is separated by open patches (Ludwig et al., 2005). The surface of these open patches is usually occupied by biocrusts (also named biological soil crusts), which result from a configuration between soil particles and cyanobacteria, algae, fungi, lichens, and mosses within the upper millimeters of the soil (Belnap, 2006; Eldridge et al., 2020; Weber et al., 2016). Biocrusts change physicochemical properties of topsoils and have a significant impact on water infiltration (Chamizo et al., 2016; Jiang et al., 2018).

A few studies have been performed to evaluate the effects of biocrusts on water infiltration. Nevertheless, contradicting results exist regarding the roles of biocrusts on soil water infiltration (Warren, 2003; Weber et al., 2016). Biocrusts modify soil infiltrability through different pathways. Biocrusts increase soil porosity, roughness and aggregate stability and improve physical structure, which in turn increase soil water infiltration (Felde et al., 2014; Jiang et al., 2018). On the other hand, biocrusts increase water repellency and cause pore clogging due to exopolysaccharide excretion, which impede soil water infiltration (Keck et al., 2016; Kidron et al., 2020; Xiao et al., 2019). These contradictory results were attributed to the difference in soil properties (soil structure and texture), biocrust characteristics (cover, morphology, and composition), and climate (mainly rainfall characteristics) (Weber et al., 2016). Therefore, further studies are necessary to test these contradicting results in other areas, such as the Mu Us Desert where the

soil, climate, and biocrusts differ from other areas. In this area, a large number of shrubs died with the occurrence of late-successional biocrusts, possibly due to the reduced soil water infiltration caused by biocrusts (Guan and Liu, 2019; Xiao and Hu, 2017). However, no conclusive data are yet available and our understanding of the mechanisms of biocrusts in altering soil hydrology remains unknown.

In addition, the presence of biocrusts alters soil physical properties, and subsequently influences soil hydrological processes, and thus changes plant growth (Havrilla et al., 2019; Kidron, 2019; Xiao and Hu, 2017). Improved knowledge of the hydraulic properties of biocrusts and estimation of soil hydraulic parameters are crucial for improving simulation of infiltration, soil water dynamics, and soil water uptake in vegetation-soil-water models (Coppola et al., 2011; Wang et al., 2007; Yu et al., 2010), and have important implications for the simulation of eco-hydrological processes in dryland ecosystems (Chen et al., 2018). We hypothesized that biocrust development has a negative influence on water infiltration. Accordingly, the purposes of our study were: (1) to evaluate whether biocrust development influence soil water infiltration; (2) to estimate the hydraulic parameters in biocrust-covered soils.

2 MATERIALS AND METHODS

2.1 Experimental site

This study was undertaken at the Yanchi Research Station, Ningxia Province, northwestern China (106°30'–107°47' E and 37°04'–38°10' N, 1550 m above the sea level). The site is lo-

cated on the southwestern fringe of the Mu Us Desert and is characterized by a mid-temperate semi-arid climate with mean annual temperature of 8.1 °C. Mean annual precipitation in this area is 287 mm, most of which occurs from July to September. Soil texture is classified as sand. The average sand, silt, and clay content in the shallow soil profile (0- to 10-cm depth) are 79.1%, 18.5%, and 2.4%, respectively. The mean percentages of sand, silt and clay in lower soil (10- to 60-cm depth) are 93.0%, 4.3%, and 2.7%, respectively. The dominant shrubs are *Artemisia ordosica*, *Caragana korshinskii*, *Salix psammophila*, and *Hedysarum mongolicum*, which are distributed in patches covering 30–70% of the soil surface. The inter-canopy soil surface is commonly covered by biocrusts.

2.2 Experimental design

In this study, infiltration experiments were conducted in August 2017 to evaluate the influence of biocrust development on water infiltration. In this experiment, four treatments, including bare land with sporadic cyanobacterial biocrusts (BL) (Fig. 1A), lichen-dominated biocrusts (LB) (Fig. 1B), early-successional moss biocrusts (EMB) (Fig. 1C), and late-successional moss biocrusts (LMB) (Fig. 1D), were established to evaluate the effects of biocrust development on soil water infiltration. Five replicates with similar soil and topographic conditions were established for each treatment, thus totalling 20 experimental sites.

There are three main types of biocrusts in this area: cyanobacteria, lichens, and mosses. The cyanobacterial biocrusts are

consisted of *Microcoleus vaginatus*. The lichen-dominated biocrusts are mainly composed of *Collema tenax* species with a low cover of cyanobacteria. The moss-dominated biocrusts, in addition to *Byumargenteum* p., include a certain amount of lichens and cyanobacteria. A vernier caliper and line intercept transects were used for measuring the thickness and cover of biocrusts, respectively. Biocrust samples, which were manually screened through a 2-mm screen and dried at 65 °C for 24 h, were used for measuring the biomass. The polysaccharide content of biocrust samples were also measured by the phenol-sulfuric acid method. Additionally, particle size distribution of the biocrust layer and the subsurface (at 5-cm depth under biocrust layer) was determined.

2.3. Infiltration experiments

The infiltration experiments were performed using a disc infiltrometer with a 15 cm-diameter disc. The height and diameter of the water reservoir tower was 100 and 3.5 cm, respectively. In order to estimate van Genuchten parameters, three pressure heads (h) of –3, –6, and –12 cm at each infiltration point were used. Prior to each measurement, a layer of fine sand with thickness of 2 mm was laid on soil surface at each infiltration point and then the disc infiltrometer was put on the fine sand. The water level in the reservoir tower was recorded until it reached steady state. The time interval for observation was 10 s during the first 3 min of the infiltration experiment. However, the time interval for observation was 30 s when the infiltration time reached 3 min.

Fig. 1. Landscapes with the four treatments for study including (A) bare land with sporadic cyanobacterial biocrusts (BL), (B) lichen-dominated biocrusts (LB), (C) early-successional moss biocrusts (EMB), (D) late-successional moss biocrusts (LMB).

2.4 Calculation of soil hydraulic parameters

The following method was adopted to analyze the infiltration data. Over time, the infiltration from a circular source with a constant pressure head can be described by the Wooding's solution (Wooding, 1968):

$$Q = \pi r_0^2 K(h) \left[1 + \frac{4\lambda_c}{\pi r_0} \right] \quad (1)$$

with λ_c is calculated according to White and Sully (1987):

$$\lambda_c = \frac{bS^2}{[K(h)(\theta_{fin} - \theta_{ini})]} \quad (2)$$

where r_0 is the radius of the disc (cm); h is the pressure head (cm), which was -3, -6, and -12 cm; λ_c is the macroscopic capillary length; $K(h)$ is the unsaturated conductivity under a given pressure head (cm min^{-1}); Q is the steady-state infiltration rate ($\text{cm}^3 \text{ min}^{-1}$); b is a shape parameter between 1/2 and $\pi/4$ (Smettem and Clothier, 1989); θ_{fin} is the final soil water content ($\text{cm}^3 \text{ cm}^{-3}$); θ_{ini} is the initial surface soil water content ($\text{cm}^3 \text{ cm}^{-3}$); and S is the sorptivity ($\text{cm min}^{-1/2}$).

The Q can be calculated as the following form by substituting Eq. (2) into (1):

$$\frac{Q}{\pi r_0^2} = K(h) + \frac{4bS^2}{[\pi r_0(\theta_{fin} - \theta_{ini})]} \quad (3)$$

with i_c is expressed as:

$$i_c = \frac{Q}{\pi r_0^2} \quad (4)$$

From Eqs. (3) and (4), the $K(h)$ can be calculated as the following form by replacing Q with constant infiltration rate (i_c , cm min^{-1}) (White and Sully, 1987):

$$K(h) = i_c - \frac{4bS^2}{[\pi r_0(\theta_{fin} - \theta_{ini})]} \quad (5)$$

In Eq. (5), S is estimated by the intercept of the regression line between $\Delta I/\Delta t^{1/2}$ and $t^{1/2}$ according to Vandervaere et al. (1997), where $\Delta t^{1/2}$ is the variable quantity of the square root of time (min) and ΔI is the variable quantity of cumulative infiltration (cm); and i_c is calculated by the slope of the linear fitted cumulative infiltration curves with the stable infiltration data.

According to the quasi-linear Gardner model (Gardner, 1958), the $K(h)$ (cm min^{-1}) could be expressed as:

$$K(h) = K_s e^{\alpha_{GRD} h} \quad (6)$$

where K_s is the saturated hydraulic conductivity (cm min^{-1}); and α_{GRD} is the exponential slope.

The K_s can be expressed using Eqs. (5) and (6).

$$K_s e^{\alpha_{GRD} h} = i_c - \frac{4bS^2}{[\pi r_0(\theta_{fin} - \theta_{ini})]} \quad (7)$$

The K_s and α_{GRD} in Eq. (7) are only the two unknown parameters, which could be calculated by two consecutive pressure heads. The approach assumes that parameter α_{GRD} is constant over the interval between two consecutive pressure heads

(Coppola et al., 2011).

The microscopic pore radius (λ_m , mm) was calculated through Eq. (8) according to White and Sully (1987).

$$\lambda_m = \frac{\sigma \alpha_{GRD}}{\rho g} \quad (8)$$

where σ is the surface tension (N m^{-1}); ρ is the density of water (kg m^{-3}); and g is the acceleration due to gravity (N kg^{-1}).

2.5 Estimation of van Genuchten parameters using a combined Wooding inverse approach

Soil hydraulic properties are usually expressed by the soil hydraulic conductivity ($K(h)$) and water retention curve ($\theta(h)$). The most important work in determining the functional relationships between the soil hydraulic conductivity, water content, and matric potential is to obtain van Genuchten parameters, which are estimated using a coupled Wooding inverse approach that combined the results from Wooding's analytical solution with a parameter estimation method using a numerical solution of the Richards equation (Coppola et al., 2011; Lazarowitch et al., 2007).

The following form of the Richards equation is usually used to characterize the radially symmetric isothermal Darcian flow in a variably saturated isotropic rigid porous medium (Warrick, 1992):

$$\frac{\partial \theta}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} (rK(h) \frac{\partial h}{\partial r}) + \frac{\partial}{\partial z} (K(h) \frac{\partial h}{\partial z}) - 1 \quad (9)$$

where t is time; r is the radial coordinate; and z is the vertical coordinate positive downward. Initial and boundary conditions that are appropriate for a disc tension infiltrometer experiment are expressed by the following equations (Šimůnek and van Genuchten, 2000):

$$h(r, z, t) = h_{ini}(z) \quad t = 0 \quad (10)$$

$$h(r, z, t) = h_0(t) \quad 0 < r < r_0, z = 0 \quad (11)$$

$$\frac{\partial h(r, z, t)}{\partial z} = 1 \quad r > r_0, z = 0 \quad (12)$$

$$h(r, z, t) = h_{ini} \quad r^2 + z^2 \rightarrow \infty \quad (13)$$

where h_{ini} is the initial pressure head (cm); r_0 is the disc radius (cm); and h_0 is the time-variable supply pressure head (cm).

The van Genuchten model (van Genuchten, 1980) was chosen to express the soil water retention, $\theta(h)$, and hydraulic conductivity, $K(\theta)$:

$$S_e = \frac{\theta - \theta_r}{\theta_s - \theta_r} = [1 + |\alpha_{VG} h|^n]^{-m} \quad (14)$$

$$m = \frac{n-1}{n} \quad (15)$$

$$K(S_e) = K_s S_e^l [1 - (1 - S_e^{1/m})m]^2 \quad (16)$$

where θ_s and θ_r are the saturated and residual soil moisture ($\text{cm}^3 \text{ cm}^{-3}$), respectively; α_{VG} (cm^{-1}), m and n are the shape parameters; S_e is the effective fluid saturation; and l is the tortu-

osity parameter, which is usually fixed at 0.5 (Mualem, 1976).

The transient tension disc infiltration data, together with initial and final soil moisture, were used for the numerical inverse determination of van Genuchten parameters, by fixing K_s at the value obtained using Wooding's analytical solution. Given that all optimizations initially gave θ_r estimates very close to zero, we decided to fix θ_r to zero for all cases. The objective function, Φ , for the numerical inverse approach is:

$$\Phi(\beta) = \sum_{i=1}^M W_i [I_i^*(t_i) - I(\beta, t_i)]^2 \quad (17)$$

where M is the number of measurements in a particular set; β is the vector of optimized parameters; W_i is the weight of a particular measured point; I_i^* (cm) is the measured cumulative infiltration at time t_i ; and I_i (cm) is the simulated cumulative infiltration at time t_i .

Water retention curves can be obtained through the estimated van Genuchten parameters. The plant available water, which was defined as the difference in soil moisture ($\Delta\theta$) within a pressure head ranged from -1 to -1000 cm, was estimated by water retention curves (Wang et al., 2007).

2.6 Data analyses

A two-way ANOVA was used for analyzing the effects of biocrust type and pressure head on the soil water infiltrability at the 5% probability level. The differences in soil hydraulic parameters among these treatments were analyzed using the least significant difference (LSD) tests at the 5% probability level. All statistical analyses were performed using the SPSS 19.0 software (SPSS, Chicago, IL, USA).

3 RESULTS

3.1 Characteristics of biocrusts

Generally, with the development of biocrusts, the cover, thickness, and biomass of the biocrusts significantly increased; however, the difference in biocrust cover between the EMB and LMB treatments was insignificant at the 0.05 level (Table 1). In comparison to the bare land, biocrusted soils had more silt and clay content. Moreover, higher fine content (i.e., silt and clay) was observed in the moss-covered biocrusts compared to lichen-covered biocrusts (Table 1).

3.2 Effects of biocrust development on water infiltration

As shown in Fig. 2, from initial to steady state, the BL treatment had significantly higher infiltration rates than the other treatments. Furthermore, infiltration rate was similar for

the EMB and LMB treatments, but significantly lower than for the LB treatment. Specifically, the i_c under the pressure head of -3 cm followed the pattern $BL > LB > EMB > LMB$. Furthermore, for the BL treatment under the pressure head of -3 cm, the i_c was 92.3% higher than that for the LB treatment ($P < 0.05$) (Table 2). The i_c for the LB treatment under the pressure head of -3 cm was 25.8% and 38.7% higher than that for the EMB and LMB treatments, although there was no significant difference in the infiltration rate among the three treatments (Table 2).

In addition, the $K(h)$, S , K_s , and λ_c for the BL treatment were obviously higher than that for the other treatments. In detail, the $K(h)$ and K_s for the BL treatment under the pressure head of -3 cm were significantly higher than that for the LB treatment by 2.0- and 2.1-fold, respectively (Table 2). Similarly, the S averaged over three pressure heads followed the pattern $BL > LB > EMB > LMB$. On the contrary, the λ_m followed the pattern $BL < LB < EMB < LMB$, although the difference among them was insignificant. The two-way ANOVA results indicated that the influences of biocrust type or head on i_{ini} , i_c , S , $K(h)$, K_s , and λ_c were significant at the 0.01 or 0.05 level; however, the influence of biocrust type on λ_m was insignificant at the 0.05 level (Table 3). In addition, the influences of the interaction between the biocrust type and pressure head on i_{ini} , i_c , S , $K(h)$, and K_s were insignificant at the 0.05 level.

3.3 Determination of van Genuchten parameters

As can be seen in Table 4, the θ_s and α_{VG} increased with biocrust development. More specifically, the θ_s and α_{VG} for the EMB and LMB treatments were higher than that for the BL and LB treatments, although the difference among four treatments was insignificant. For instance, the θ_s for the LMB treatment was 28.0% higher than that for the LB treatment. Moreover, there was no significant difference in θ_s and α_{VG} between the BL and LB treatments. In addition, the relation between the parameter of the n and biocrust development was found to be non-unique. In detail, the BL and EMB treatments had slightly higher n than the LB and LMB treatments. Furthermore, there was no obvious difference in n between the BL and EMB treatments or between the LB and LMB treatments. The one-way ANOVA results indicated that the influences of biocrust development on θ_s , α_{VG} and n were insignificant at the 0.05 level (data not shown).

As shown in Fig. 3, biocrust development had a significant influence on water retention and hydraulic conductivity. Water retention increased with biocrust development at high-pressure heads, whereas the opposite was observed at low-pressure heads (Fig. 3A and B). In detail, water retention at high-pressure heads followed the pattern $LMB > EMB > BL > LB$.

Table 1. Characteristics of the biocrusts in the four treatments.

Treatments	Cover (%)	Thickness (mm)	Biomass (mg cm ⁻²)	Polysaccharide content (μg mg ⁻¹)	Sand (%)	Silt (%)	Clay (%)
Bare land with sporadic cyanobacterial biocrusts (BL)	–	–	–	–	85.79±5.09 a	12.71±1.51 b	1.50±0.16 b
Lichen-dominated biocrusts (LB)	70±9.7 b [†]	4.8±0.9 c	0.81±0.08 c	2.26±0.03 b	84.59±4.43 a	13.53±2.21 b	1.88±0.13 b
Early-successional moss biocrusts (EMB)	76.8±3.5 a	8.9±0.7 b	1.84±0.36 b	3.76±0.05 a	77.50±5.26 b	20.60±2.56 a	1.90±0.21 b
Late-successional moss biocrusts (LMB)	95.8±1.8 a	15.2±0.8 a	2.94±0.57 a	3.94±0.02 a	75.34±4.82 b	21.33±2.29 a	3.33±0.18 a

[†] Different letters in the same column indicate significant differences at the probability level of 0.05.

Fig. 2. Infiltration rate of the four treatments including bare land with sporadic cyanobacterial biocrusts (BL), lichen-dominated biocrusts (LB), early-successional moss biocrusts (EMB), and late-successional moss biocrusts (LMB).

On the contrary, Water retention at low-pressure heads followed the pattern $LB > BL > LMB > EMB$. Hydraulic conductivity for the BL treatment, as shown in Fig. 3C, was obviously higher than that of the other treatments. Furthermore, there was no obvious difference among the LB, EMB, and LMB treatments, and the difference was dependent on the pressure head.

In addition, the development of biocrusts influences the water retention curve, and thus alters the available water. In detail, $\Delta\theta$ for the moss-covered treatments were obviously higher than that for the cyanobacteria- or lichen-covered treatments. For example, the available water increased from $\Delta\theta = 0.251 \text{ m}^3 \text{ m}^{-3}$ and $\Delta\theta = 0.214 \text{ m}^3 \text{ m}^{-3}$ for the BL and LB treatments to $\Delta\theta = 0.281 \text{ m}^3 \text{ m}^{-3}$ for the EMB treatment. Moreover, for moss biocrusts, the available water increased from $\Delta\theta = 0.281 \text{ m}^3 \text{ m}^{-3}$ for the EMB treatment to $\Delta\theta = 0.290 \text{ m}^3 \text{ m}^{-3}$ for the LMB treatment. However, the available water decreased from $\Delta\theta = 0.251 \text{ m}^3 \text{ m}^{-3}$ for the BL treatment to $\Delta\theta = 0.214 \text{ m}^3 \text{ m}^{-3}$ for the LB treatment (Fig. 3A and B).

4 DISCUSSION

4.1 Influence of biocrust development on water infiltration

Our study shows that the presence and development of biocrusts had a negative effect on water infiltration when com-

pared to the bare land (Table 2; Fig. 2). The negative biocrust effects on water infiltration are likely due to the higher amount of clay and silt in the biocrusted soils, which could reduce soil pores and result in a decrease in water infiltration (Table 1). Additionally, the biocrust effects could be attributed to the higher biocrust thickness and the polysaccharide content (Table 1). We should note that the polysaccharides measured in this study is different from exopolysaccharides (EPS), and it can only serve as a measure for biocrust biomass (similar to chlorophyll content). Namely, the polysaccharides cannot be an indication of the capacity of the biocrusts to absorb water. Although not measured in this study, the involvement of the EPS cannot be neglected. Given that the ability of the EPS to absorb copious amounts of water (Chenu, 1993; Colica et al., 2014; Mazor et al., 1996), the cyanobacterial capacity to excrete copious amounts of EPS (Kidron et al., 2003), and the fact that cyanobacteria also inhabit the lichen- and moss-dominated biocrusts (Gentili et al., 2005; Paulsrud and Lindblad, 1998; Rossi et al., 2018), an efficient impediment of infiltration is expected. This issue deserves further research.

Our results correspond to the results of other authors (Coppola et al., 2011; Xiao et al., 2019; Yang et al., 2016), who concluded that the lichen- and moss-covered biocrusts led to a decrease in water infiltration (Table 5). However, some other studies have shown the opposite: biocrusts increased water infiltration (Jiang et al., 2018; Kakeh et al., 2021) (Table 5). The difference in soil surface roughness caused by biocrusts could partly explain these contradictory results (Warren, 2003). In detail, rugose or smooth biocrusts such as cyanobacteria are common in the areas without frost-heaving, thus resulting in a low surface roughness. Nevertheless, in the areas where soils freeze, frost-heaving of biocrusted surfaces results in a highly roughened surface. Higher roughness allows more residence time, and thus leads to an increased infiltration (Warren, 2003). In this study site with no obvious frost-heaving, low surface roughness resulted in a negative effect of biocrusts on water infiltration.

Additionally, our results concluded that moss-dominated biocrusts had much lower soil infiltrability compared to the lichen-dominated biocrusts (Table 2; Fig. 2). In comparison to lichen-covered biocrusts, higher cover, thickness, biomass, and

Table 2. Soil hydraulic parameters of biocrusts and bare soil under the different biocrust development.

Pressure head	Treatments	i_{mi} (mm min ⁻¹)	i_c (mm min ⁻¹)	$K(h)$ (mm min ⁻¹)	S (mm min ^{-1/2})	K_s (mm min ⁻¹)	λ_c (mm)	λ_m (mm)
-3 cm	BL	1.36±0.37 bc [†]	0.75±0.09 a	0.79±0.10 a	0.89±0.48 ab	1.44±0.18 b	4.87±3.27 bc	21.79±13.05 b
	LB	1.00±0.28 bc	0.39±0.06 b	0.39±0.06 b	0.18±0.06 b	0.70±0.11 c	0.54±0.24 c	453.81±390.96 b
	EMB	0.93±0.15 bc	0.31±0.04 bc	0.31±0.04 bc	0.11±0.02 b	0.57±0.08 c	0.14±0.05 c	168.72±109.64 b
	LMB	1.05±0.32 bc	0.27±0.07 bc	0.26±0.07 bc	0.09±0.06 b	0.48±0.13 c	0.31±0.26 c	3603.71±2192.01 a
-6 cm	BL	1.36±0.26 bc	0.72±0.19 a	0.69±0.16 a	0.61±0.34 b	2.30±0.52 a	3.89±3.01 bc	108.74±95.49 b
	LB	0.99±0.37 bc	0.33±0.07 b	0.32±0.07 b	0.25±0.04 b	1.07±0.23 bc	0.85±0.19 c	12.18±4.02 b
	EMB	0.49±0.16 c	0.23±0.06 bc	0.24±0.06 bc	0.07±0.02 b	0.79±0.19 c	0.13±0.08 c	1667.40±1192.36 ab
	LMB	0.49±0.13 c	0.18±0.05 bc	0.19±0.06 bc	0.12±0.04 b	0.64±0.20 c	0.35±0.14 c	187.57±162.26 b
-12 cm	BL	2.95±0.70 a	0.20±0.05 bc	0.12±0.02 c	1.20±0.29 a	1.32±0.19 bc	63.96±26.20 a	0.47±0.25 b
	LB	1.61±0.47 b	0.11±0.03 c	0.08±0.02 c	0.69±0.19 ab	0.91±0.18 bc	25.63±11.06 b	0.55±0.19 b
	EMB	0.79±0.26 bc	0.05±0.02 c	0.05±0.01 c	0.32±0.10 b	0.53±0.15 c	7.27±3.30 bc	1.78±0.51 b
	LMB	0.91±0.29 bc	0.06±0.02 c	0.05±0.01 c	0.37±0.12 b	0.57±0.16 c	12.40±5.96 bc	1.80±0.73 b

Note. [†] Different letters in the same column indicate significant differences at the probability level of 0.05. BL: bare land with sporadic cyanobacteria biocrusts; LB: lichen-dominated biocrusts; EMB: early-successional moss biocrusts; LMB: late-successional moss biocrusts.

Fig. 3. Water retention (A and B) and hydraulic conductivity (C) of the four treatments including bare land with sporadic cyanobacterial biocrusts (BL), lichen-dominated biocrusts (LB), early-successional moss biocrusts (EMB), and late-successional moss biocrusts (LMB).

polysaccharide content for the moss-covered biocrusts could explain this phenomenon (Table 1; Kidron et al., 2003; Chamizo et al., 2012). Furthermore, higher fine content (i.e., silt and clay) in the moss-covered biocrusts may reduce soil infiltrabil-

ity when compared to the lichen-covered biocrusts (Table 1; Xiao et al., 2019). Similarly, Wu et al. (2012) concluded that soil infiltrability was lower for the moss-covered biocrusts compared to the lichen-covered biocrusts. On the contrary, some other studies have found that infiltration increased when biocrusts shifted from cyanobacteria or algae to lichens or mosses, which is usually characterized by increased biomass (Barger et al., 2006; Chamizo et al., 2012). The different response of infiltration to biocrust type was dependent upon surface roughness. In these regions, greater roughness which may have been caused by frost-heaving for lichen- or moss-dominated biocrusts than those for the cyanobacteria or algae could explain the contradictory results (Belnap et al., 2013).

It should be noted that the use of a disc infiltrometer does not adequately reflect water flow under natural conditions. Firstly, it does not reflect surface roughness, because a layer of fine sand was laid on soil surface before infiltration experiments were performed. Therefore, the use of a disc infiltrometer could alleviate the influence of surface roughness caused by biocrusts on water infiltration. Secondly, unlike one-dimensional vertical flow under natural conditions, the unconfined three-dimensional infiltration (vertical and lateral flow) usually take place under tension condition when using a disc infiltrometer (Vandervaere et al., 1997). Although there are some above-mentioned limitations, the disc infiltrometer under tension condition can still reflect biocrust effect on soil infiltrability, as verified by a similar study of Xiao et al. (2019) that reported consistent results of the double-ring infiltrometer and the disc infiltrometer. Considering the above-mentioned issues, further research is needed to evaluate the difference between the double-ring infiltrometer and disc infiltrometer in our study site.

4.2 Determination of van Genuchten parameters

Parametrization of hydraulic properties on biocrusted soils and estimation of soil hydraulic parameters are crucial for improving simulation of infiltration and soil water dynamics in vegetation-soil-water models (Coppola et al., 2011; Yu et al., 2010), and thus the understanding of eco-hydrological processes in dryland ecosystems (Rodríguez-Caballero et al., 2015). Among them, the most important factor is to estimate the parameters of van Genuchten model. Our results indicated that moss-covered soils had lower K_s than lichen-covered soils; however, the θ_s for the moss-covered soils was higher than that for lichen-covered soils, although the differences were insignificant. This result could be attributed to the higher fine content and polysaccharide content of the moss-covered soils when compared to lichen-covered soils (Table 1). Furthermore, similar to our simulation study, the results of field experiments by Guan and Liu (2019) also found that well-developed moss-covered biocrusts had higher θ_s than lichen-covered biocrusts, suggesting a higher retention capacity for the moss-covered biocrusts.

Table 3. P values from the two-way ANOVA to test the influences of biocrust type and pressure head as well as their interaction effects on soil hydraulic parameters.

Effects	i_{ini} (mm min ⁻¹)	i_c (mm min ⁻¹)	S (mm min ^{-1/2})	$K(h)$ (mm min ⁻¹)	K_s (mm min ⁻¹)	λ_c (mm)	λ_m (mm)
Biocrusts	0.001**	<0.001**	<0.001**	<0.001**	<0.001**	0.013*	0.175
Pressure head	0.015*	<0.001**	<0.001**	0.024*	0.023*	<0.001**	0.133
Biocrusts × Pressure head	0.188	0.149	0.020*	0.431	0.949	0.031*	0.040*

Note. i_{ini} , initial infiltration rate; i_c , steady-state infiltration rate; S , sorptivity; $K(h)$, unsaturated hydraulic conductivity at h pressure head; K_s , saturated hydraulic conductivity; λ_c , macroscopic capillary length; λ_m , microscopic pore radius. * Effect is significant at .05 level of probability. ** Effect is significant at .01 level of probability.

Table 4. Water retention and hydraulic conductivity parameters for the biocrusted soils under the different biocrust development.

Treatments	θ_s	α_{VG} (cm ⁻¹)	n
Bare land with sporadic cyanobacterial biocrusts (BL)	0.28±0.02 a [†]	0.11±0.03 a	1.72±0.14 a
Lichen-dominated biocrusts (LB)	0.25±0.01 a	0.12±0.03 a	1.51±0.07 a
Early-successional moss biocrusts (EMB)	0.30±0.02 a	0.21±0.04 a	1.72±0.08 a
Late-successional moss biocrusts (LMB)	0.32±0.04 a	0.27±0.09 a	1.54±0.07 a

[†] Different letters in the same column indicate significant differences at the probability level of 0.05.

Table 5. Regional difference in the biocrust effects on soil water infiltrability (in increasing order of annual precipitation).

Locations	Climate (annual precipitation in mm)	Soil texture	Biocrust type	Measured parameters	Biocrust effects on infiltration	References
Heihe River Basin	Hyper arid (71)	Silty loam		Infiltration rate	Decreasing	Yang et al. (2016)
Central-Western Negev Desert	Hyper arid (90)	Sand	Cyanobacteria	Infiltration rate	Increasing under tension; no significant effect under ponding	Eldridge et al. (2000)
Western Negev Desert	Hyper arid (95)	Sand	Cyanobacteria	Runoff yield	Decreasing	Kidron (2016)
Mojave Desert	Arid (101)	Sand; loamy sand	Cyanobacteria	Infiltration rate	Decreasing	Herrick et al. (2010)
Tengger Desert	Arid (191)	Sand	Mosses	Infiltration rate	Increasing	Coppola et al. (2011)
Tabernas Desert	Semiarid (200–235)	Silty loam; sandy loam	Cyanobacteria; lichens; mosses	Infiltration rate	Decreasing with biocrust development	Chamizo et al. (2012)
Colorado Plateau	Semiarid (215)	Loamy sand	Cyanobacteria; cyanolichens	Runoff coefficient	Decreasing	Faist et al. (2017)
Southeastern Spain	Semiarid (220–235)	Silty loam; sandy loam	Cyanobacteria	Runoff coefficient	Decreasing with biocrust development	Cantón et al. (2020)
Western New South Wales	Semiarid (244)	Sand	Cyanobacteria; lichens; mosses	Infiltration rate	Increasing	Bowker et al. (2013)
Northern Chihuahuan Desert	Semiarid (250)	Sandy clay loam	Cyanobacteria	Infiltration depth	Increasing	Chung et al. (2019)
Quara Qir range-lands	Semiarid (273)	Loamy	Lichens; mosses	Infiltration rate	Increasing	Kakeh et al. (2021)
Qinghai-Tibet Plateau	Semiarid (389)	Silty loam	Mosses	Infiltration rate	Increasing	Jiang et al. (2018)
Loess Plateau	Semiarid (409)	Loamy sand	Cyanobacteria; mosses	Infiltration rate	Decreasing	Xiao et al. (2019)

Additionally, our results indicated that the shape parameter of α_{VG} followed the pattern LMB > EMB > LB > BL. This result suggests that the shape parameters of α_{VG} increased with biocrust development. A higher α_{VG} corresponds to a lower air entry value, and implies a lower water holding capacity near saturation (van Genuchten, 1980). Moreover, this result indicates that the higher α_{VG} was consistent with a higher content of clay and silt. On the contrary, Wang et al. (2007) reported that the shape parameter of α_{VG} declined as the time since stabilization increased, and the lower α_{VG} was related to a higher proportion of silt- and clay-sized particle. The difference in the inverse method and model uncertainty may lead to this discrepancy.

The development of biocrusts leads to different van Genuchten parameters, which alter the $\theta(h)$ and $K(h)$ curves. Our results indicate that $\theta(h)$ on the moss-covered soils was higher than on the lichen-covered soils at high-pressure heads; however, the opposite was observed at low-pressure heads (Fig. 3B). In addition, moss-covered soils had lower $K(h)$ than the lichen-covered soils. Decrease in $K(h)$ and increase in $\theta(h)$ are likely due to the characteristics of biocrusts when compared to bare land. In comparison to the bare land, greater water-holding capacity on the biocrust-covered soils could lead to an improved water conditions on the soil surface (Fig. 3B; Guan and Liu, 2019). Furthermore, the anchoring structures on lichen-

covered soils allows for a longer residence time of the water, which could improve water retention at the soil surface. Moreover, higher content of clay and silt in the moss-covered biocrusts reduce the soil pores, and lead to a decrease in soil hydraulic conductivity. Accordingly, the presence of lichen or moss biocrusts on the soil surface enhances water retention, but inhibits soil hydraulic conductivity.

The occurrence and development of biocrusts change van Genuchten parameters and affect the water retention curve, and subsequently alters the available water in the biocrust layer. We found that available water in the biocrust layer increased with a shift in biocrusts from cyanobacteria to lichens or mosses (Fig. 3A and B). It is noted that available water mentioned above focused on the soil surface (i.e., biocrust layer). The increased water content on the soil surface implies a lower soil water content of the shrub root layer. This suggests that the presence and development of biocrusts could facilitate the growth of annual plants, but inhibit the growth of vascular plants. Moreover, higher soil surface water content has important implications for dryland productivity. Therefore, our results provide strong support for the explicit inclusion of biocrusts in hydrological and ecohydrological models.

Our study focused on the effects of biocrust development on soil infiltrability. The presence and development of biocrusts

change the water infiltration during rainfall events and alter soil evaporation during the drying periods, and consequently have the potential to influence plant water uptake, and eventually impact plant growth (Xiao and Hu, 2017; Zhang and Belnap, 2015; Zhuang et al., 2015). In addition, biocrusts are very fragile and are susceptible to disturbance, which could affect water infiltration during rainfall events (Barger et al., 2006; Chamizo et al., 2012). However, how the biocrust development and its disturbance influence soil water availability and shrub growth have not yet been well understood (Chamizo et al., 2016; Kidron and Aloni, 2018). Accordingly, further studies are necessary to evaluate the role of the biocrust development and its disturbance in soil water uptake and growth of vascular plants in drylands.

5 CONCLUSIONS

Infiltration rate decreases and saturated soil moisture increases with biocrust development, especially with the presence of moss biocrusts. Water retention increases with biocrust development at high-pressure head, whereas the opposite is found at low-pressure heads. The biocrust development influences van Genuchten parameters, subsequently affecting the water retention curve, and thereby altering the available water in the biocrust layer. The findings regarding the parameterization of soil hydraulic properties have important implications for the simulation of eco-hydrological processes in dryland ecosystems.

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