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Biocrusts enhance non-rainfall water deposition and alter its distribution in dryland soils

Shenglong Li [a,b], Matthew A. Bowker [c], Bo Xiao [a,b,*]

[a] College of Land Science and Technology, China Agricultural University, Beijing 100193, China
[b] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling 712100, China
[c] School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA

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ABSTRACT

Non-rainfall water deposition is an important water resource, critical for the survival of dryland vegetation and soil biota and maintaining dryland water balance. As a "living skin", biocrusts are attracting increasing attention due to their potentially positive impacts on non-rainfall water deposition. However, the magnitude and underlying mechanisms of biocrust regulation of non-rainfall water are still unclear. In this study, we investigated the non-rainfall water deposition and distribution through continuous weighing micro-lysimeters (0–3, 3–6, and 6–10 cm depths) with bare soil and three types of biocrusts (cyanobacterial crusts, cyanobacterial-moss mixed crusts, and moss crusts) in a semiarid region of the Chinese Loess Plateau. Our results showed that the biocrusts were associated with significantly greater non-rainfall water deposition capacity (~13%–22%) in contrast to the bare soil, and biocrust type strongly influenced the daily non-rainfall water amount in the order: moss crusts > mixed crusts > cyanobacterial crusts > bare soil. Biocrusts were also associated with faster rates of non-rainfall water formation (42%; $F \geq 2.87$, $P \leq 0.04$), which may be linked to faster nighttime cooling in comparison to the bare soil. Atmospheric vapor condensation was the primary water source for non-rainfall water deposition at the 0–10 cm depth, as opposed to soil vapor condensation. Biocrusts had higher condensation from both sources, and had relatively more deposition from the atmosphere: atmospheric vapor condensation was greater by 114%-143% and soil vapor condensation was greater by 20%–30%. Moreover, >69% of the total non-rainfall water amount occurred in the top 3 cm of soil. The strong biocrust influence in the uppermost centimeters ($F = 45.34$, $P < 0.001$) appears to primarily drive the contrasts in non-rainfall water deposition in soils. Furthermore, all of the apparent effects of biocrusts on non-rainfall water deposition and distribution were reasonably attributed to the biocrust influences on soil physicochemical properties, especially the contents of fine particles, organic matter, high soil roughness, daily temperature difference, and moss morphology. In conclusion, biocrusts are associated with much greater non-rainfall water deposition capacity, and change non-rainfall water distribution along with soil depth, implying that they play a critical role in surface soil water balance of dryland ecosystems.

1. Introduction

Drylands are widespread terrestrial ecosystems in which precipitation is counterbalanced by evaporation from surfaces and transpiration by plants, often making them fragile (Huang et al., 2015; Reynolds et al., 2007). In dryland ecosystems, water availability is the most vital limiting factor in soil physical, chemical, biological, and ecological processes (Zhang et al., 2009), and any sources of water can have important impacts (Kidron, 2010; Xiao et al., 2009). Non-rainfall water is a common and natural meteorological phenomenon which comprises fog, dew, and water vapor sorption, and it plays a significant role in the water balance of dryland ecosystems (Florentin and Agam, 2017; Uclés et al., 2016). Compared with rainfall and evaporation, the daily non-rainfall water amount is assumed to be very small, i.e., usually a fraction of a millimeter, but it is an indispensable water source for biocrusts, insects, small animals, and certain plants during drought periods (Jacobs et al., 1999; Xiao et al., 2009). Consequently, non-rainfall water is a crucial water supplement and significantly contributes to the water

* Corresponding author at: College of Land Science and Technology, China Agricultural University, No. 2, Yuanmingyuan West Road, Haidian District, Beijing 100193, China.
E-mail address: xiaobo@cau.edu.cn (B. Xiao).

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cycle in near-surface soil (Florentin and Agam, 2017).

As a natural physical process, non-rainfall water has been investigated in some arid and semiarid regions, humid tropical islands, and even in cold alpine areas (Kidron, 2010; Xiao et al., 2009). Usually, the deposition of non-rainfall water may in turn modify surface reflective properties, influence larger-scale atmospheric moisture levels, and consequently recharge soil moisture levels (Agam and Berliner, 2006; Pan et al., 2018). Furthermore, because of the lack of rainfall in arid and semiarid areas during dry spells, the accumulation of non-rainfall water (e.g., monthly means and seasonal means) may account for a large percentage of total water inputs (Kidron, 2010; Li et al., 2018). For example, studies in Israel and South Africa estimated that non-rainfall water may comprise more than a third of, or even exceed, the annual rainfall (Kidron and Tal, 2012; Maphangwa et al., 2012). On account of the long, stable vapor periods favoring condensation, non-rainfall water contributes greatly to the water budget and plays a vital role in the water balance of some vascular plants (Agam and Berliner, 2004).

Generally, the free atmosphere and vapor emitted from the topsoil are the main water sources for non-rainfall water deposition on the soil surface (Agam and Berliner, 2006; Fischer et al., 2012). However, a major limitation in evaluating the ecological role of non-rainfall water is difficulty of measurement, especially for assessing its long-term variability (Zhuang and Zhao, 2017). Therefore, various methods and instruments have been developed for the measurements of non-rainfall water deposition in the past decade, such as automated weighing lysimeters (Xiao et al., 2009, 2013), micro-lysimeters (Pan et al., 2010), the cloth-plate method (Kidron and Temina, 2017), electrical impedance grids (Pedro and Gillespie, 1981), and leaf wetness sensors (Scherm and van Bruggen, 1993). The weight method using weighing micro-lysimeters is the most common and convenient way to continuously obtain weight changes during dew formation process (Agam and Berliner, 2006). Despite the availability of these technologies, non-rainfall water deposition in drylands remains undermeasured and thus underappreciated.

Biocrusts are communities of cyanobacteria, lichens, mosses, fungi, and other organisms that are commonly distributed on surface soil in drylands (Belnap, 2006; Bowker et al., 2013). Although the thickness of biocrusts is usually very thin (a few millimeters or centimeters; Xiao et al., 2019c), these organisms strongly impact surface soil characteristics, including soil texture, roughness, structure, aggregation, micro- and macro-porosity, as well as fertility (Belnap, 2006; Xiao et al., 2019a). More importantly, as an important ecosystem engineer, biocrusts significantly regulate soil hydrological, ecological, biological, and chemical processes, acting as pioneering species to accelerate the progress of vegetation restoration (Bowker et al, 2008; Li et al, 2018). Therefore, it is well supported that biocrusts have an essential role in regulating local water balance and surface hydrology in arid and semiarid climate regions (Chamizo et al., 2012b; Eldridge et al., 2020).

At present, some studies have found that biocrusts have a significant impact on non-rainfall water deposition in dryland ecosystems (Fischer et al., 2012; Zhang et al., 2009). It has been reported that biocrusts improved non-rainfall water deposition capacity by changing the soil properties (Chamizo et al., 2012a) and regulating the microtopography of surface soil (Fischer et al., 2012), however, few studies focus on biocrust effects on non-rainfall water deposition capacity and distribution along soil depth. Most research on this subject focuses on the difference in physical and chemical soil processes during non-rainfall water formation (Fischer et al., 2012), and some of the outcomes of non-rainfall water pulses such as the response of carbon and nitrogen (Delgado-Baquerizo et al., 2013; Kidron et al., 2014). However, the biocrust effects on dryland water balance through facilitation of non-rainfall water input have not been reported to date. What is the effect of biocrusts on non-rainfall water distribution at different soil depths? Do different types of biocrusts play different role in non-rainfall water deposition? These questions require further exploration and hence, any additional knowledge about non-rainfall water deposition modulation by biocrusts (such as dew or vapor condensation) may improve our understanding regarding the complex interrelations responsible for water balance in drylands.

In this study, we hypothesized that the presence of biocrusts would significantly affect non-rainfall water deposition and distribution in drylands. Based on this hypothesis, we conducted non-rainfall water deposition measurements for bare soil and different types of biocrusts (cyanobacterial crusts, cyanobacterial-moss mixed crusts, and moss crusts) in a semiarid climate on the Chinese Loess Plateau. The specific objectives of this study were: (i) to determine the effects of biocrusts on non-rainfall water deposition and their relationships with microclimate factors; (ii) to clarify the main water sources of non-rainfall water induced by biocrusts and quantify the biocrust effects on non-rainfall water formation processes; (iii) to compare the variations of non-rainfall water amounts along a soil depth gradient in biocrusts and bare soil, and (iv) to explain the biocrust effects on non-rainfall water deposition based upon their influences on surface soil properties.

2. Materials and methods

2.1. Study site

We conducted our study at the Liudaogou watershed (110°21′-110°23′ E, 38°46′-38°51′ N; Fig. 1a-b) in the Shenmu county on the northern Loess Plateau, China. This area covers about 6.89 km^2 and ranges in altitude from 1081 to 1274 m. It is situated at the center of the "Wind-Water Erosion Crisscross Region" in which both wind and water erosion processes are prevalent, and has a typical semiarid continental monsoonal climate. The potential evaporation is 1337 mm, and the mean annual temperature is 8.4 °C, which ranges from −9.7 °C in winter to 23.7 °C in summer (Xiao and Veste, 2017). The average annual precipitation in this area is 409 mm with 70%–80% falling during the summer (June to September).

Water is the most limited resource in ecological restoration and agricultural production in this area (Jia et al., 2019; Xiao and Veste, 2017). The soil was highly susceptible to water and wind erosion before the implementation of "Grain for Green" project which imposed limits on grazing and tillage practices (Zhang et al., 2011). In the past decades, extensive shrub planting has been undertaken to conserve soil and water (Xiao et al., 2019b). The common vegetation in this region is comprised of *Bothriochloa ischaemum* (Linn.) Keng., *Festuca ovina* Linn., *Artemisia desertorum* Spreng., *Cotoneaster horizontalis* Dcne., and *Hippophae rhamnoides* Linn. (Gao et al., 2017). In this watershed, biocrusts widely developed spontaneously on the stabilized soil surfaces and now cover >30% of the land, and sometimes as much as 70%–80% (Xiao et al., 2019a). The biocrust types are variable and comprised of both cyanobacterial and moss-dominated types and intermediates, with mosses being the dominant autotrophs.

2.2. Experimental design

Bare soil (soil without any biocrusts) and three representative types of biocrusts were investigated in this study, which include cyanobacteria crusts (cyano crusts; cyanobacterial cover was >90%; Fig. 1e), cyanobacteria and moss mixed crusts (mixed crusts; both cyanobacterial and moss cover were ~ 50%; Fig. 1f), and moss crusts (moss cover was >90%; Fig. 1g).

In this study, the non-rainfall water amount refers to the sum of atmospheric vapor condensation and soil vapor condensation. The non-rainfall water measurements included three experiments applied for the above four treatments focused on: (i) daily non-rainfall water amount and its formation processes; (ii) partitioning and measuring the amount of atmospheric vapor condensation and soil vapor condensation; and (iii) non-rainfall water distribution at different soil depths.

We weighed cylindrical PVC micro-lysimeters to obtain the accurate non-rainfall water amount of different types of biocrusts and bare soil,

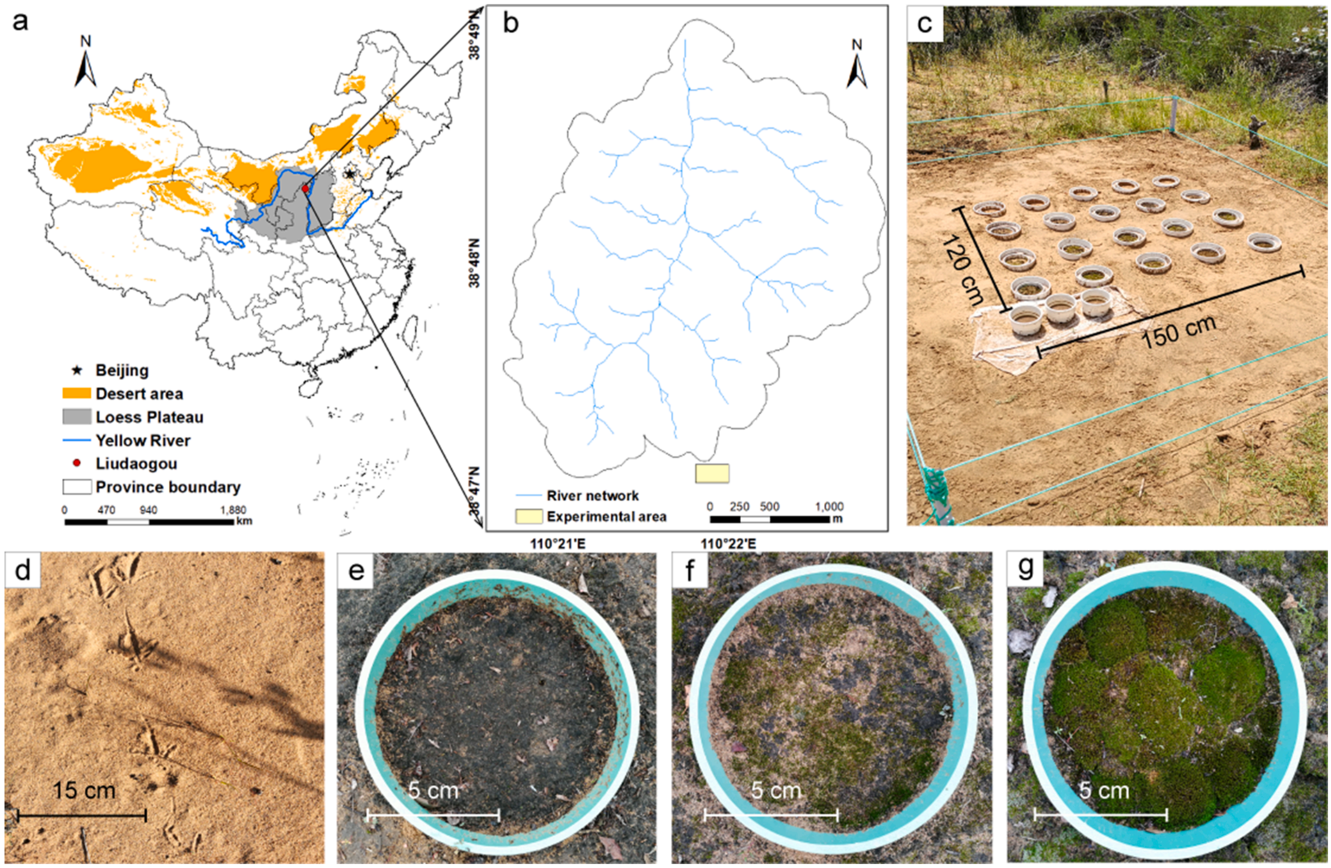

Fig. 1. Location of experimental region and photos of bare soil and different types of biocrusts. (a) Liudaogou watershed; (b) Experimental area; (c) Measurements of daily non-rainfall water deposition; (d) Bare soil; (e) Cyanobacteria biocrusts(cyano crusts); (f) Cyanobacteria and moss mixed biocrusts (mixed crusts); (g) Moss biocrusts (moss crusts).

using established methods similar to those in previous studies (Liu et al., 2006; Zhang et al., 2009). To test for possible artifacts caused by lysimeter-induced changed in soil temperature, we conducted a pilot study in which we simultaneously measured the soil temperature in micro-lysimeters and natural nearby soils at 2, 5, and 10 cm depths from 6:00 to 20:00. The results showed that the micro-lysimeters did not induce changes soil temperature (Fig. S1). Furthermore, different types of micro-lysimeters were used in these experiments (Table 1). Before sampling, we investigated and chose an open and flat place (~50 m × 50 m) without any vascular plant cover, and all experiments and associated measurements were conducted in this common location (Fig. 1b). In order to reduce the non-rainfall water loss through evaporation during the weighing process, each micro-lysimeter was taken out to weigh and put back immediately after the measurement (within 10 s).

2.3. *Measurements of non-rainfall water amount*

2.3.1. *Measurements of daily non-rainfall water amount and its formation processes*

The experimental non-rainfall water measurements were conducted from July to October 2019. The in-situ daily non-rainfall water amount was collected in Type A cylindrical PVC micro-lysimeters (in 5 replicates; Table 1). All the micro-lysimeters were pushed into the soil carefully to collect soil to a depth of 0–10 cm in an intact core for each treatment. Before installing micro-lysimeters, e.g., 10 cm-long micro-lysimeters, we installed larger PVC cylinders (15.5 cm in inner diameter and ~ 11 cm in height; see Fig. S2) about 1 cm above the ground surface and removed the soil within. Micro-lysimeters were installed within the PVC cylinders, flush with the level of the soil outside of the cylinders. Finally, the interspace between the inner and outer PVC cylinders of each micro-lysimeter was filled with polystyrene foam (the

Table 1
Detailed description of different types of micro-lysimeters for non-rainfall water measurements.

Type of micro-lysimeter	Inner diameter (cm)	Height (cm)	Type of top cover	Type of bottom cover	Number of replicates	Measurements	Measurement period	Data
A	10.5	10	None	300-mesh nylon net	5	Daily non-rainfall water amount, non-rainfall water formation process	July 1-October 11	Figs. 2–5, Fig. S7, Table 3, Table 5
B	10.5	10	Plastic wrap	300-mesh nylon net	5	Soil vapor condensation	August 10–11	Figs. S8 and S9, Table 4
C	10.5	10	None	Rubberized fabric	5	Atmospheric vapor condensation	August 10–11	Figs. S8 and S9, Table 4
D	10.5	3 + 3 + 4	None	300-mesh nylon net	5	Non-rainfall water distribution along soil depths	August 8-October 11	Fig. 6, Table S1

thickness is 2 cm; see Fig. S2) to diminish thermal convection. Moreover, the bottom and side face of micro-lysimeter was fit tightly to the underlying soil and polystyrene, respectively. Thus, the soil in the micro-lysimeter was only lit by direct sunlight striking the surface, resulting in a similar thermal regime as a natural soil column. The same general method was used to install the other types of lysimeter as well, detailed below.

The daily non-rainfall water amount (mm) for a micro-lysimeter was calculated as the difference between the weights of the morning (~7:00) and previous sunset (~19:00). In addition, all measurements were carried out only on clear days and were stopped if rainfall events occurred. All of the micro-lysimeters were manually weighed with an electronic balance (±0.01 g, equaling ± 0.001 mm of water). Overall, the non-rainfall water amount was calculated in mm of liquid water through Eq. (1).

$$h = 10m/\rho\pi r^2 \tag{1}$$

Where h is non-rainfall water amount, in mm; m is the increased weight of micro-lysimeter, in g; ρ is the density of water, which is 1.0 g cm^{-3}; r is the inner radius of micro-lysimeter, which is 5.25 cm.

Furthermore, all the micro-lysimeters (Type A) were weighed consecutively within 48 h in intervals of 2 h from 18:00 to accurate quantify the biocrust effects on non-rainfall water formation and evaporation processes. These experiments took place on several continuous clear days. The rates of non-rainfall water formation and evaporation were calculated as the change in mass per hour through Eq. (2).

$$h_r = h_i/t \tag{2}$$

Where h_r is rates of non-rainfall water formation and evaporation, in mm h^{-1}; h_i is the changed weight during a period, in mm; t is the time interval, which is 2 h in this study.

2.3.2. Measurements of vapor condensation from atmosphere and deep soil

In order to analyze the biocrust effects on water sources in non-rainfall water deposition at 0–10 cm depth, two types of sealed micro-lysimeters were designed (Types B and C, both in 5 replicates; Table 1) to collect non-rainfall water. In the case of Type B, the top of the micro-lysimeter was sealed by plastic film to prevent water vapor exchange with the surface soil atmosphere, but a 300-mesh nylon net formed its bottom (see Fig. S3); thus, the soil vapor condensation (i.e., vapor condensation of deep moist soil) was the main water source of non-rainfall water in micro-lysimeter. Most importantly, the top-sealed micro-lysimeter was covered by plastic film only at night, and the plastic film was completely removed during daytime to make sure it received the same solar radiation as the other micro-lysimeters. In the case of Type C, the bottom of the micro-lysimeter was sealed by a rubberized fabric to exclude the water vapor exchanging from deep moist soil (see Fig. S3), which means that the atmospheric vapor condensation (i.e., vapor condensation from the atmosphere) is the main input water source.

The total non-rainfall water amount at the 0–10 cm depth was calculated as the sum of separately measured atmospheric vapor condensation and vapor condensation from deep moist soil. Consequently, the fraction of water source inputs was calculated through Eq. (3).

$$P = h_n/_{h_t} \times 100\% \tag{3}$$

Where P is percentage of the total non-rainfall water amount composed by either atmospheric or soil vapor condensation, in %; h_n is the daily non-rainfall water amount of either atmospheric vapor condensation or soil vapor condensation (depending on the type of lysimeter), in mm; h_t is the total daily non-rainfall water amount, calculated as the sum of atmospheric vapor condensation and soil vapor condensation in this study, in mm.

2.3.3. Measurements of non-rainfall water distribution by soil depths

In order to distinguish the effects of biocrusts on non-rainfall water distribution at different soil depths, the Type D micro-lysimeter similar to that of Pan et al. (2018) was installed to measure the non-rainfall water amount at the 0–3, 3–6 and 6–10 cm depths, respectively (in 5 replicates; Table 1 and Fig. S4). In brief, we assembled the Type D micro-lysimeters by stacking three small micro-lysimeters (10.5 cm inner diameter and 3 or 4 cm in height; bottom covered by 300-mesh nylon net). All micro-lysimeters were used to collect undisturbed soil samples carefully at a depth of 0–10 cm, and they were stacked making sure the bottom of micro-lysimeters were fit closely to the top of underlying soil surface (see Fig. S4). During the experiments, we weighed the soil samples from top to bottom at sunrise and sunset and repositioned them immediately. To avoid the influences of rainfall, we used a rainfall exclusion shelter (~2.0 m in width, ~2.0 m in length, and 1.0 m in height) during rainfall events. A transparent and colorless plastic film covered the top of shelter during rainfall events and was removed in between them. The sides of the shelter were open with good ventilation. The fraction of non-rainfall water at the different depths was calculated in Eq. (3), and the non-rainfall water amount at the 0–10 cm depth in this part was the sum of non-rainfall water at the 0–3, 3–6, and 6–10 cm depths.

2.4. Measurements of soil properties and meteorological factors

Before soil sampling, ~2 m × 2 m of each treatment was demarcated and used to estimate the cover of biocrusts by processing digital photographs in the ImageJ (Wayne Rasband, National Institutes of Health). The soil surface was photographed under daylight conditions beneath a whitish opaque foil (light tent) to diffuse the light and avoid direct radiation, and we applied rigorous and repeatable methods of image processing to determine the biocrusts coverage through following procedures. Firstly, a geometric correction of the photos was implemented by establishing a relationship between the location of pixels in the image and the corresponding coordinates on the soil surface. Secondly, the color threshold between biocrusts and bare soil was adjusted by visual check and then the biocrusts cover area was separated from the bare soil. Lastly, a binary picture was obtained and the biocrust cover was automatically calculated by ImageJ (in 5 replicates).

In addition, Petri dishes (9 cm in diameter and 2 cm height) were used to collect the biocrust layer and underlying soil to measure moss density and total biomass (Xiao et al., 2019c). The surface soil roughness was measured through the chain method (Jester and Klik, 2005). Furthermore, intact soil cores (5 cm height and 100 cm^3 in volume) were collected for each treatment in 6 replicates to measure soil bulk density and particle composition. In the laboratory, the thickness of the biocrust layer was measured using a digital Vernier caliper, and moss plants were separated from the soil with water through a 2 mm sieve and dried at 65 °C for 24 h for the measurement of moss biomass (Xiao et al., 2019c). The particle size distribution was measured using a laser particle size analyzer (Malvern, Mastersizer 2000, England), and soil organic matter content was measured by the dichromate redox titration method.

During the measurements of the non-rainfall water formation processes, the surface temperature of the biocrust layer and bare soil (0–3 cm depth) were measured using an infrared thermometer (Fluke MT4MAX, with a measurement range of −30–400 °C and an accuracy of ± 1 °C). The air temperature, dew point, and relative humidity at a height of 2.0 m were monitored by an automatic weather micro-station throughout the whole experimental period (see Figs. S5-S6).

2.5. Data analysis

The experimental data were analyzed based on descriptive statistics and the differences among the four treatments. All statistical analyses were conducted using IBM SPSS Statistics 22.0. After normality and equality of variance tests, repeated-measures ANOVA was used to test the differences in the daily, monthly, minimum, maximum and total non-rainfall water amount between the bare soil and different types of biocrusts. We did not have a temporal hypothesis to test, but rather used this method to account for temporal auto-correlation because these data were re-measured many times. We used one-way ANOVA with a least significant difference (LSD) post-hoc test at the $P < 0.05$ level of significance to test for differences among the soil physicochemical properties between the bare soil and different types of biocrusts. We used Pearson correlation analysis to determine the degree to which soil temperature and meteorological factors (air temperature, relative humidity, and dew point) associated with non-rainfall water formation, with each 2 h interval across a 48-h measurement period serving as a replicate.

3. Results

3.1. Biocrust effects on surface soil physicochemical properties

The biocrusts decreased soil bulk density but increased the surface roughness and the contents of clay and organic matter at 0–5 cm-depth. The bulk density of the biocrusts was 10.0%-26.9% lower than that of bare soil (Table 2). This was especially true for the moss crusts; the bulk density was decreased by 0.35 g cm^{-3} in comparison to the bare soil (Table 2). However, the fine particles content (clay and silt) of biocrusts was ~ 4-fold higher, with the clay content being 1–3-fold higher in the biocrusts than that in the bare soil. Moreover, the organic matter content of the biocrusts was up to 28.5 g kg^{-1}, which was ~ 2.5-fold higher than that of the bare soil (Table 2). Furthermore, the surface roughness of the biocrusts was 9.2%-361.4% greater than bare soils, and it was highest in the mixed crusts which was ~ 4.4-fold rougher than the bare soil.

3.2. Biocrust effects on surface soil non-rainfall water deposition

Biocrusts had a significantly higher daily mean and total non-rainfall water amount as compared with the bare soil ($F \geq 4.64$, $P \leq 0.022$; Fig. 2 and Table 3). Specifically, the daily mean non-rainfall water amount of the biocrusts averaged 13.0%-21.7% higher than that of the bare soil at the 0–10 cm depth (Table 3). Especially, the daily mean non-rainfall water amount of moss crusts and mixed crusts was higher ($F = 4.82$, $P \leq 0.003$; Table 3) than that of the bare soil. In comparison to bare soil, biocrusts significantly increased total non-rainfall water amount by 10.1%–24.4% at the 0–10 cm depth from July to October, and the total non-rainfall water amount of moss crusts averaged 1.2 times higher (21.18 vs. 17.52 mm; Table 3) than that of the bare soil. Additionally, the monthly non-rainfall water amount reached a peak in August and then declined in October (Table 3). The daily non-rainfall water amount of moss crusts was the highest in August (0.32 mm), which was higher by 17.9%, 6.7%, and 3.2% than that of the bare soil, cyano crusts, and mixed crusts, respectively (Fig. 3 and Table 3).

3.3. Biocrust effects on non-rainfall water formation and evaporation processes

Biocrusts significantly increased the rates of non-rainfall water formation and evaporation at the 0–3 cm depth compared to bare soil ($F \geq 2.867$, $P \leq 0.039$; Figs. 4-5). Biocrusts increased non-rainfall water formation by 41.7% (0.017 vs. 0.012 mm h^{-1}; Fig. 5) on average and increased non-rainfall water evaporation rate by 52.6% (0.029 vs. 0.019 mm h^{-1}; Fig. 5) on average compared to the bare soil. The non-rainfall water accumulation amount of the biocrusts was higher by 0.04–0.09 mm (with a maximum of 0.20 mm; Fig. 4) compared to bare soil. For the moss crusts, the non-rainfall water accumulation amount was higher by 93.3%-122.2% in comparison to that of the bare soil (Fig. 4). Correspondingly, the biocrusts enlarged the daily surface soil temperature differences between the crusted and uncrusted soils during the non-rainfall water formation processes, specifically, they increased the surface soil temperature by 2.6–8.4 °C during daytime in comparison to the bare soil; however, they cooled rapidly at night and did not differ from the bare soil from 18:00–6:00 (Fig. S7).

3.4. Biocrust effects on water sources of non-rainfall water

The biocrusts had a significantly higher amount of atmospheric vapor condensation and soil vapor condensation as compared with the bare soil ($F \geq 6.13$, $P \leq 0.001$; Table 4 and Fig. S8). During the experimental period, the biocrusts had a higher soil vapor condensation amount by 20.0%-30.0% and a higher atmospheric vapor condensation amount by 114.3%-142.9% than that of the bare soil at the 0–10 cm depth (Table 4). Particularly, the soil vapor condensation amount of the mixed crusts and moss crusts was significantly higher (0.13 vs. 0.10 mm; Table 4) than that of the bare soil. The biocrusts entrapped a greater proportion of water vapor from the atmosphere than surface soil (Fig. S8), and the atmospheric vapor condensation of the bare soil was lower (0.07 vs. 0.10 mm; Fig. S9a) than soil vapor condensation. Furthermore, the atmospheric vapor condensation amount of the mixed crusts and moss crusts was more than double that of the bare soil (0.16 vs. 0.07 mm; Table 4). For moss crusts, the soil vapor condensation amount was higher by up to 149.9% (0.17 vs. 0.7 mm; Fig. S9b) compared to the bare soil.

3.5. Biocrust effects on non-rainfall water distribution along soil depths

The daily mean non-rainfall water amount was highest at the 0–3 cm depth (>0.22 mm) and the biocrusts significantly increased the non-rainfall water amount at that depth (>69.4% in total; Fig. 6 and Table S1). During the experimental periods, the daily non-rainfall water amount at 0–3 cm followed the order of moss crusts > mixed crusts > cyano crusts > bare soil ($F = 45.34$, $P < 0.001$; Table S1). The differences were slight in deeper soils ($F \leq 4.35$, $P \geq 0.08$; Table S1), and the

Table 2
Soil physical properties of bare soil and different types of biocrusts.

Measurements	Bare soil	Cyano crusts	Mixed crusts	Moss crusts	n	F	P
Bulk density (0–2 cm) (g cm^{-3})	1.65 ± 0.02 a [†]	1.41 ± 0.07b	1.31 ± 0.15c	1.22 ± 0.02 d	6	19.35	<0.001
Percentage of clay (<2 μm) (%) [‡]	0.24 ± 0.01 d	0.27 ± 0.01c	0.34 ± 0.04b	0.71 ± 0.01 a	6	522.64	<0.001
Percentage of silt (2–20 μm) (%) [‡]	2.19 ± 0.07b	8.9 ± 0.10 a	9.10 ± 0.17 a	9.15 ± 0.06 a	6	1927.65	<0.001
Percentage of sand (20–2000 μm) (%) [‡]	97.77 ± 0.10 a	90.82 ± 0.10b	90.56 ± 0.18b	90.14 ± 0.06c	6	1831.75	<0.001
Organic matter content (0–2 cm) (g kg^{-1})	8.24 ± 0.43b	27.83 ± 0.16 a	28.34 ± 1.15 a	28.47 ± 1.30 a	6	246.88	<0.001
Surface roughness	2.77 ± 0.89 d	7.22 ± 2.23b	12.12 ± 3.06 a	5.33 ± 1.13c	6	148.493	<0.001
Biocrust thickness (mm) [§]	–	6.43 ± 1.67c	12.28 ± 1.33b	13.69 ± 0.90 a	6	74.26	<0.001
Total biomass (g cm^{-2})	–	0.10 ± 0.03b	0.17 ± 0.07 a	0.21 ± 0.02 a	6	10.81	0.002
Color	Pale brown	Black and grey	Black, grey, and green	Green	–	–	–
Dominant species	Without cyanobacteria filament	Cyanobacteria	Cyanobacteria and mosses	Mosses	–	–	–

[†] Different letters (a–d) presented within the same row indicate significant differences among soil treatments at the 5% probability level.
[‡] Classification of soil particle size is based on the soil texture classification system of the FAO/UNESCO.
[§] Biocrust thickness includes biocrust layer and the soil that was naturally adhered to the biocrust layer.

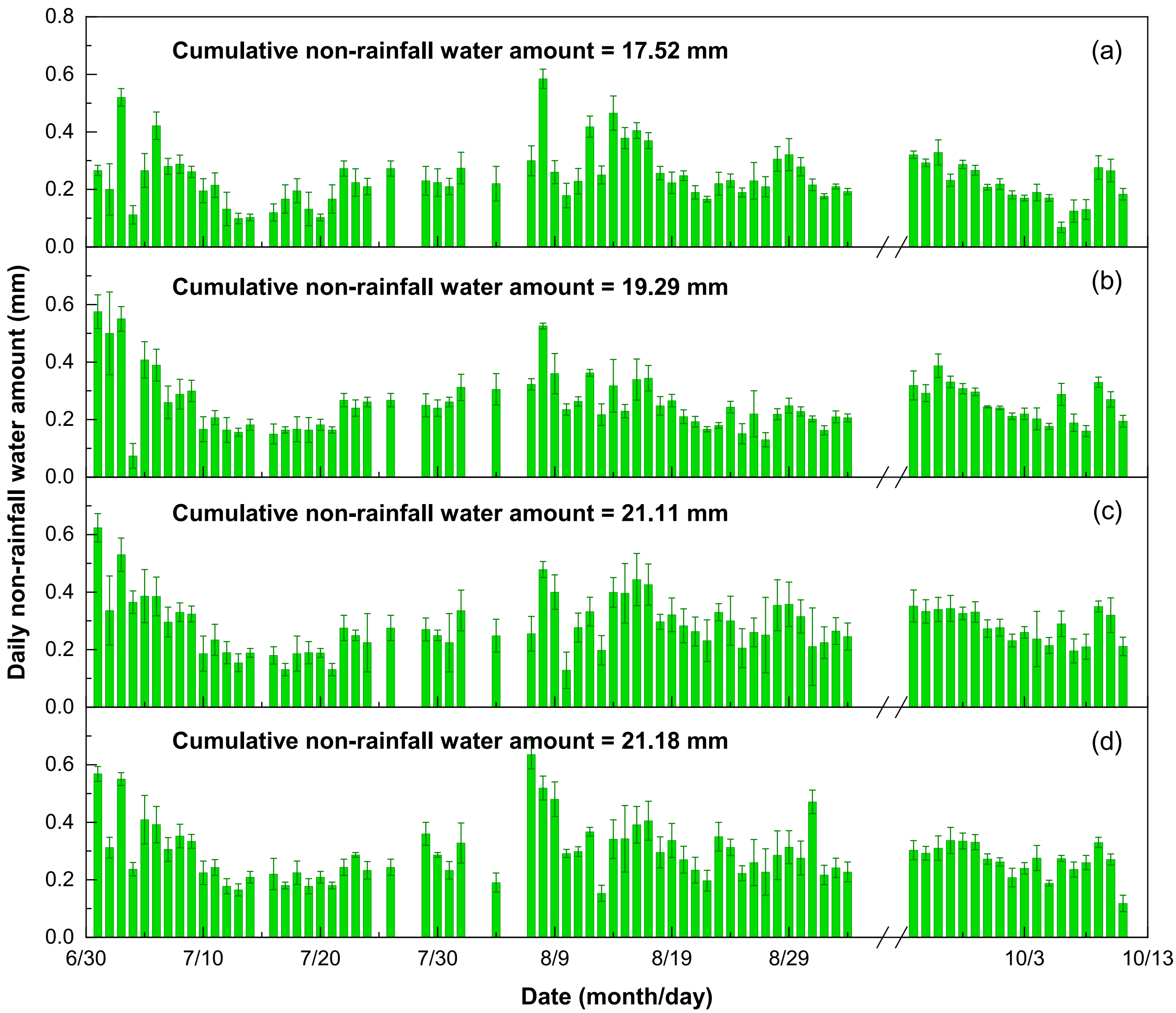

Fig. 2. Daily mean non-rainfall water amount of bare soil and different types of biocrusts at the 0–10 cm depth. (a) Bare soil; (b) Cyano crusts; (c) Mixed crusts; (d) Moss crusts.

non-rainfall water amount at the 3–6 and 6–10 cm depths declined rapidly compared to the surface, averaging <0.10 mm (<25.8% in total; Fig. 6 and Table S1). As compared with the bare soil, the biocrusts increased the daily mean non-rainfall water amount at the 0–3 cm depth by 1.7-fold higher (~0.17 vs. 0.10 mm), and the percentage in total of the biocrusts was up to 10.8% higher than that of bare soil on average (69.9% vs. 59.1%; Table S1).

4. Discussion

4.1. Biocrust effects on soil non-rainfall water deposition and their underlying mechanisms

In our study, non-rainfall water in biocrusts was substantially higher than in bare soil (Fig. 3 and Table 3), suggesting that biocrust colonization on the Loess Plateau of China has enhanced the capture of this water source. This improvement of non-rainfall water deposition capacity can be reasonably attributed to the biocrust effects on soil physicochemical properties (Gao et al., 2017; Kakeh et al., 2018), i.e., the decreasing percentage of coarse particles and bulk density as well as the increasing percentage of fine particles, organic matter content, and roughness of the biocrusts in comparison to bare soil (Table 2).

Therefore, biocrust effects on non-rainfall water deposition can be explained by the following three processes. First, the biocrusts strongly regulate surface soil properties. In this study, the biocrusts enriched fine particles (clay and silt), especially moss crusts. Elevated amounts of fine particles in biocrusts may come from the capture and fixation of mineral dust mobilized by off-site wind erosion (Reynolds et al., 2001; Rozenstein et al., 2014), or through superior protection of fines from erosion (Abed et al., 2013; Gao et al., 2017). The biocrusts layer has a greater mineral specific surface area because of the higher fine particle contents and therefore provide more surface for non-rainfall water deposition in comparison to bare soil (Grismer, 1987; Schneider and Goss, 2012). Furthermore, the organic matter content of biocrusts was markedly higher than that of bare soil due to the ability of biocrusts to fix atmospheric carbon through photosynthesis and deposit carbon in soil, for example as extracellular polymeric substances (Kakeh et al., 2018; Zhang et al., 2018). Specifically, extracellular polymeric substances (EPS) and other forms of organic matter may have prolonged near surface water saturation, enhancing the onset of the phase transition from vapor to liquid water (Adessi et al., 2018; Schneider and Goss, 2012). Consequently, the biocrusts likely changed multiple surface soil

Table 3
Daily non-rainfall water amount of bare soil and different types of biocrusts measured by Type A micro-lysimeter.

Non-rainfall water	Bare soil	Cyano crusts	Mixed crusts	Moss crusts	*F*	*P*
Minimum (mm)	0.09 ± 0.12 a [§]	0.10 ± 0.02 a	0.12 ± 0.04 a	0.12 ± 0.03 a	0.318	0.812
Maximum (mm)	0.47 ± 0.03 a	0.53 ± 0.01 a	0.53 ± 0.06 a	0.52 ± 0.50 a	0.999	0.427
Mean in July (mm)	0.20 ± 0.07b	0.25 ± 0.11 ab	0.26 ± 0.10 a	0.26 ± 0.08 a	2.377	0.074
Mean in August (mm)	0.28 ± 0.08b	0.30 ± 0.08 ab	0.31 ± 0.08 ab	0.32 ± 0.09 a	2.456	0.067
Mean in September (mm)	0.25 ± 0.05b	0.30 ± 0.04 a	0.30 ± 0.04 a	0.29 ± 0.04 ab	2.384	0.085
Mean in October (mm)	0.18 ± 0.05b	0.23 ± 0.05 ab	0.25 ± 0.05 a	0.24 ± 0.05 a	3.842	0.017
Mean in July-October (mm)	0.23 ± 0.09b	0.26 ± 0.09 ab	0.28 ± 0.09 a	0.28 ± 0.10 a	4.827	0.003
Total amount (mm)	17.52 ± 0.59b	19.29 ± 1.42 ab	21.11 ± 2.01 a	21.18 ± 1.16 a	4.642	0.022

[§] Different letters (a-b) presented within the same row indicate significant differences among soil treatments at the 5% probability level.

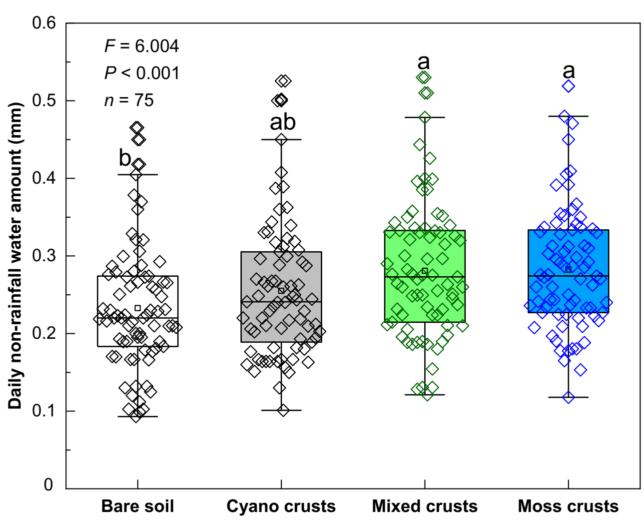

Fig. 3. Daily mean non-rainfall water amount of bare soil and different types of biocrusts. Different letters indicate significant differences among different soil treatments at a 0.05 level of probability.

properties that favored greater capacity to capture and hold water.

Second, the macromorphological changes caused by, e.g., freezing and thawing, influence the development of soil roughness over time (Wang et al., 2017). Because the stability of biocrusts preserves this microtopography, biocrusts have higher surface soil roughness compared to bare soil, and can present a greater soil surface area for dew and fog precipitation (Kidron et al., 2002; Wang et al., 2017).

Third, moss morphology in particular plays a triggering role in non-rainfall water deposition (Kidron et al., 2002; Pan et al., 2016). In our study, mixed crusts and moss crusts have much more non-rainfall water deposition than either cyano crusts or bare soil (Fig. 3). Although the moss plants are only several millimeters above the surface, mosses absorb water directly through stems, leaves and awns from rain, clouds, fog, and dew (Fig. S10) (Nejidat et al., 2016; Zhang et al., 2009). Mosses can enhance all of the soil properties discussed above, often more strongly than cyanobacterial crusts, because they fix greater amounts of carbon and enhance roughness and surface area particularly well by protruding above the surface leading to better capture of fines. Furthermore, the specific surface structures of moss stems, leaves and awns are the sites of nucleation of non-rainfall water, which means that they may be important in terms of water collection and transport (Holder, 2012; Pan et al., 2016; Tao and Zhang, 2012). As reported by Pan et al. (2016) and Tao and Zhang (2012), the presence of awns alone, e.g., in *Syntrichia caninervis*, has been experimentally demonstrated to boost non-rainfall water collection by 20%. Additionally, the mosses have papillae and lamellae on their costae, as well as moss cushions and the rhizoids (root-like structures) that anchor the plants to the ground, which play an important part in water collection, imbibition, transportation, and storage (Tao and Zhang, 2012). Consequently, the successional transition from cyanobacterial to moss biocrusts should be expected to strongly increase non-rainfall water condensation capacity, signaling a key functional shift.

4.2. Biocrust influences on the non-rainfall water formation rate and soil temperature range

In this study, we were able to show that the biocrusts significantly increased the non-rainfall water deposition capacity of the surface by the use of micro-lysimeter (Figs. 4–6). Yet, the non-rainfall water deposition was mostly being temperature-dependent, and some studies pointed out that preferential nocturnal cooling through the walls of the micro-lysimeter was shown to significantly increase the amount of vapor condensed (Kidron and Kronenfeld, 2017). However, the effects of micro-lysimeter on soil temperature at daytime are slight as compared to ambient conditions in this study (Fig. S1). Albeit the soil temperature maybe different at night and changed the non-rainfall water formation rate, however, by using concomitantly biocrusted and uncrusted soil columns within the micro-lysimeter, the inherent drawback of the micro-lysimeter, i.e., their tendency to influence the actual values at the intact soil was avoided.

In addition to higher amounts of non-rainfall water, our results showed that biocrusts were also associated with higher non-rainfall water formation rates, particularly when mosses were co-dominant or dominant (Fig. 5). In general, non-rainfall water occurs when the surface temperature falls below the dew point and is primarily influenced by vapor pressure, air temperature, radiation exchange on the Earth's surface, the heat and vapor transport in the underlying soil, among other factors (Agam and Berliner, 2006; Kidron, 2010; Zhang et al., 2009). In this study, the non-rainfall water amount was negatively correlated with soil temperature, air temperature, dew point, and surface temperature, while it was positively correlated with the relative humidity (Table 5). It is often reported that biocrusts increase soil temperature through decreasing surface albedo and increasing the absorption of solar radiation due to their higher biomass and dark color (Belnap, 1995; Xiao et al., 2016). For example, Xiao and Bowker (2020) recently documented a decrease in albedo of 43% in moss biocrusts compared to bare soil.

The biocrust effects on soil temperature is also mediated through modification of soil physical properties (Kidron, 2010; Xiao et al., 2019b). Although the biocrust layer is usually several millimeters to centimeters thick at most, bulk density, water content, macro-aggregation, fine particle content, and organic matter content are all modified (Niu et al., 2017; Yang et al., 2019). These modifications result in higher heat capacity, thermal conductivity, and thermal diffusivity than bare soils under the same conditions (Xiao et al., 2016, 2019b).

Because of the elevated heat gain of biocrusts during the day, the heat loss at night is more precipitous than in bare soils. More rapidly cooling surfaces can trigger a phase transition of water vapor into liquid (Zhang et al., 2009). Hence, the biocrusts increase the rate of temperature rise and subsequent fall, and this expands the diurnal range of temperature on the soil-atmosphere interface as compared with bare soil (Kidron and Tal, 2012; Xiao et al., 2019b). This result is consistent with the reports by Liu et al. (2006), Zhang et al. (2009), and Jia et al. (2014),

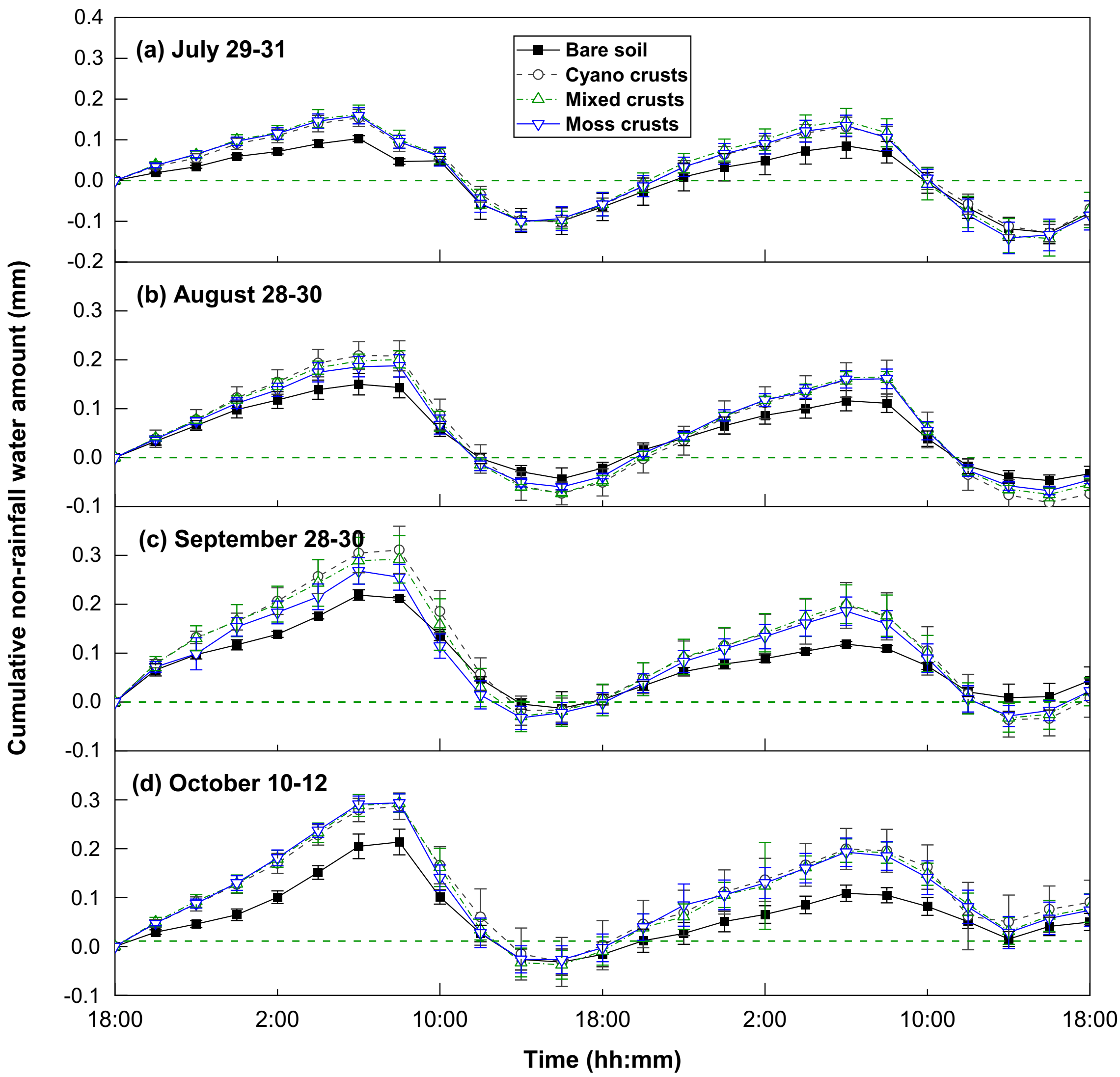

Fig. 4. Non-rainfall water formation and evaporation processes of bare soil and different types of biocrusts at the 0–3 cm depth during representative periods. (a) July 29–31; (b) August 28–30; (c) September 28–30; (d) October 10–12.

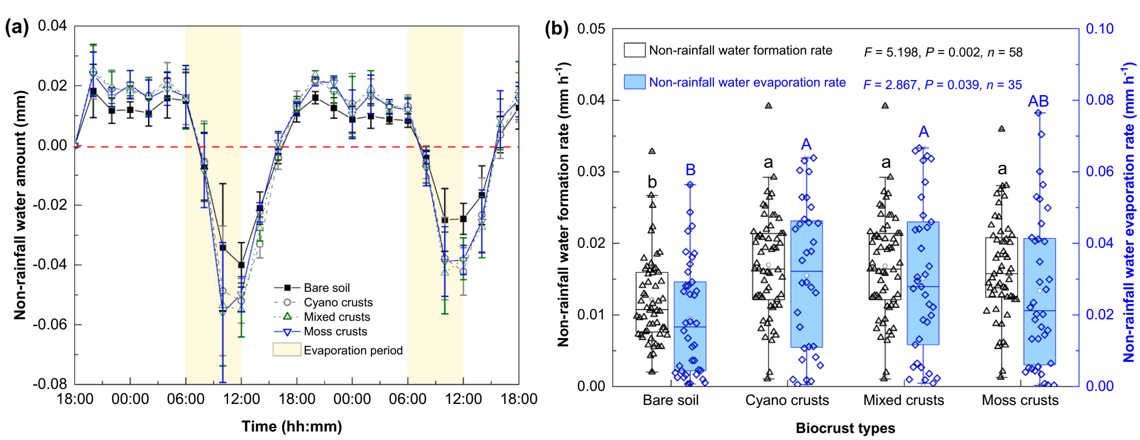

Fig. 5. Hourly mean non-rainfall water amount (a) and rates of non-rainfall water formation and evaporation (b) of bare soil and different types of biocrusts. Different letters in upper or lower case indicate significant differences among different soil treatments at a 0.05 level of probability.

who concluded that the biocrusts enlarge the diurnal range of surface temperature, which is believed to be one of the key factors in enhancing non-rainfall water amounts.

Table 4
Non-rainfall water formation from atmospheric vapor condensation (bottom-covered micro-lysimeter) and soil vapor condensation (top-covered micro-lysimeter) of bare soil and different types of biocrusts from August to October.

Vapor sources	Non-rainfall water	Bare soil	Cyano crusts	Mixed crusts	Moss crusts	*F*	*P*
Atmosphere	Maximum (mm)	0.17 ± 0.01b §	0.22 ± 0.04 ab	0.24 ± 0.05 a	0.22 ± 0.02 ab	2.784	0.110
	Minimum (mm)	0.02 ± 0.01b	0.04 ± 0.02 ab	0.05 ± 0.01 a	0.05 ± 0.01 a	3.619	0.065
	Mean (mm)	0.10 ± 0.04b	0.12 ± 0.04 ab	0.13 ± 0.05 a	0.13 ± 0.04 ab	5.593	0.001
	Total amount (mm)	5.63 ± 0.21b	6.79 ± 0.41 a	7.35 ± 0.84 a	6.92 ± 0.31 a	50.49	0.030
	Percentage in total (%)	58.88	44.76	45.45	43.09	–	–
Soil	Maximum (mm)	0.15 ± 0.04b	0.27 ± 0.06b	0.40 ± 0.08 a	0.42 ± 0.05 a	9.583	0.005
	Minimum (mm)	0.01 ± 0.01b	0.02 ± 0.00b	0.03 ± 0.01 ab	0.05 ± 0.01 a	4.190	0.047
	Mean (mm)	0.07 ± 0.04b	0.15 ± 0.05 a	0.16 ± 0.06 a	0.17 ± 0.06 a	39.176	<0.001
	Total amount (mm)	3.96 ± 0.68b	8.38 ± 0.29 a	8.82 ± 0.19 a	9.14 ± 0.20 a	78.420	<0.001
	Percentage in total (%)	41.12	55.24	54.55	56.91	–	–
Atmosphere + soil	Maximum (mm)	0.30 ± 0.03c	0.41 ± 0.03b	0.47 ± 0.02 a	0.44 ± 0.02 ab	30.330	<0.001
	Minimum (mm)	0.04 ± 0.02b	0.06 ± 0.02b	b0.09 ± 0.02 a	0.10 ± 0.02 a	10.020	<0.001
	Mean (mm)	0.17 ± 0.06b	0.27 ± 0.07 a	0.29 ± 0.08 a	0.29 ± 0.06 a	33.540	<0.001
	Total amount (mm)	9.59 ± 0.42b	15.03 ± 0.69 a	15.92 ± 1.19 a	15.78 ± 1.12 a	43.938	<0.001
	Percentage in total (%)	100	100	100	100	–	–

§ Different letters (a–c) presented within the same row indicate significant differences among soil treatments at the 5% probability level.

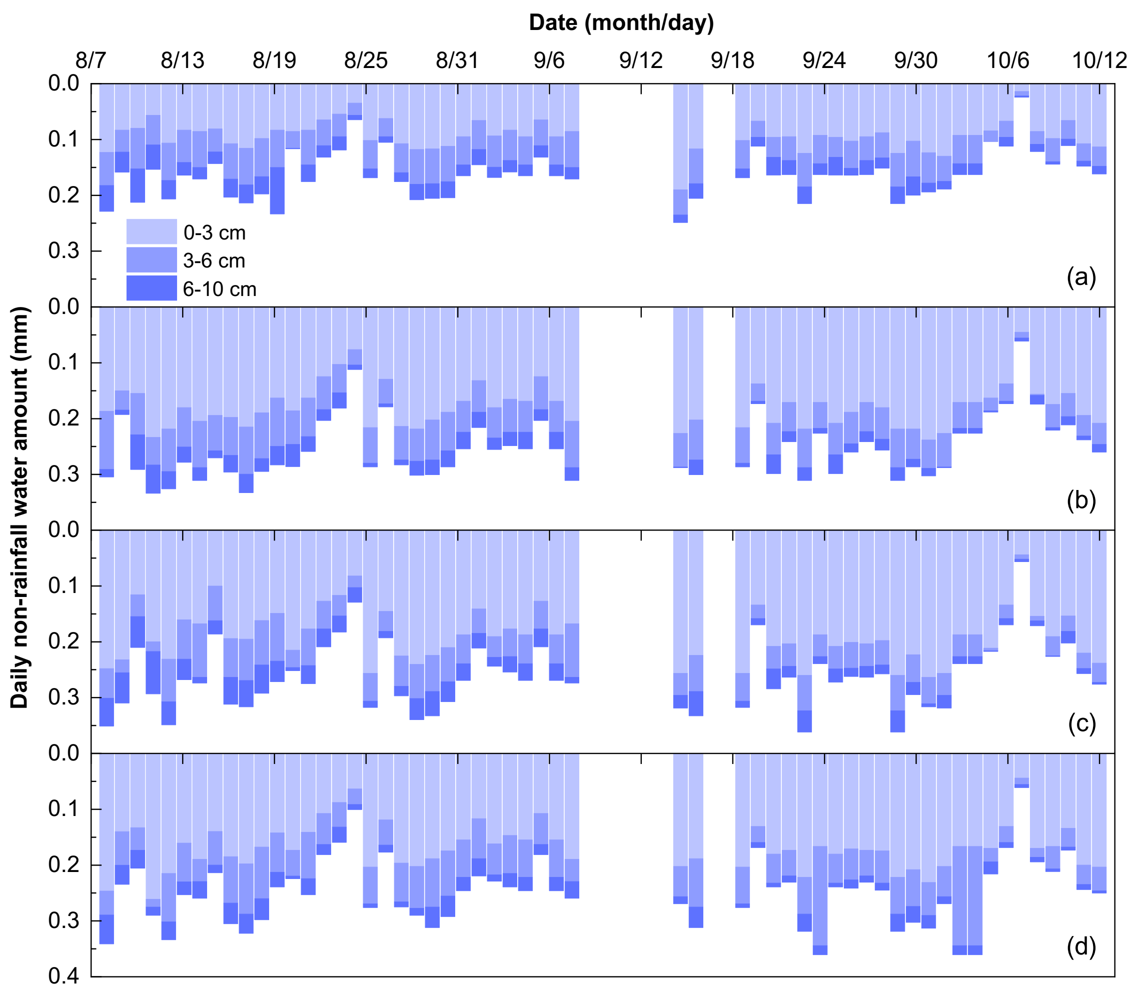

Fig. 6. Daily mean non-rainfall water amount of bare soil and different types of biocrusts at the 0–3, 3–6, and 6–10 cm depths. (a) Bare soil; (b) Cyano crusts; (c) Mixed crusts; (d) Moss crusts.

4.3. Biocrusts alter the sources of non-rainfall water from atmosphere and deep soil

In this study, atmospheric vapor condensation was the primary moisture source for non-rainfall water deposition as opposed to soil vapor condensation, and biocrusts exhibited higher atmospheric vapor condensation amounts by up to 149.9% in contrast to bare soils (Table 4); this contrast became more pronounced as mosses became more prevalent (Figs. S8-S9). Under normal conditions, the free atmospheric vapor and moisture from deep soil are two main water sources

Table 5
Pearson's correlation coefficients (significance in bracket) between the non-rainfall water amount and meteorological factors or surface soil temperature from 18:00–6:00 (next day).

Factors	Bare soil	Cyano crusts	Mixed crusts	Moss crusts
Air temperature	−0.759 (<0.001)	−0.758 (<0.001)	−0.781 (<0.001)	−0.801 (<0.001)
Relative humidity	0.713 (<0.001)	0.722 (<0.001)	0.757 (<0.001)	0.757 (<0.001)
Dew point	−0.279 (0.006)	−0.260 (0.010)	−0.252 (0.013)	−0.294 (0.004)
Surface soil temperature	−0.746 (<0.001)	−0.749 (<0.001)	−0.775 (<0.001)	−0.791 (<0.001)

that contribute to non-rainfall water formation (Fischer et al., 2012; Pan et al., 2018). The soil water content is low in drylands and water transmission is primarily due to the slow process of vapor diffusion to the atmosphere, bringing moisture to the surface. On account of lower soil moisture content compared with atmospheric water vapor in arid and semiarid climate regions, the water vapor amount from the deep soil migrating to the surface under the temperature gradients is generally small (Pan et al., 2018). However, biocrust-induced changes in underlying soil properties can result in a higher water holding capacity, and thus we would expect that more vapor from deep soil would be available for condensation (Adessi et al., 2018; Fischer et al., 2012; Xiao et al., 2019b). This expectation is not inconsistent with our data, but the greater influence of biocrusts appears to be enhancement of non-rainfall water from atmospheric sources.

Generally, the atmospheric water vapor includes water vapor within the air near the soil surface and from plant transpiration and respiration, and soil water vapor is found within pores below the soil surface (Pan et al., 2018). Correspondingly, because biocrusts significantly increased the atmospheric vapor condensation amount, this important water sources is also the main supplemental water for biocrusts (Zhang et al., 2009; Zheng et al., 2018). Especially, the moss colonization stage biocrusts (e.g., mixed crusts and moss crusts) can directly absorb water through moss stems, leaves, awns, cushions and rhizoids, and so on (Pan et al., 2016; Tao and Zhang, 2012). Therefore, on account of the condensing atmospheric vapor, moss biocrusts visibly become green in the morning, conducting photosynthesis (Delgado-Baquerizo et al., 2013), and possibly contributing to nitrogen and carbon cycling processes (Belnap, 2002; Belnap et al., 2004).

4.4. Biocrusts alter non-rainfall water distribution by depth, concentrating it in the surface

In our study, the biocrusts changed the non-rainfall water distribution by soil depth and significantly increased the non-rainfall water amount at the 0–3 cm depth (>69.4%) as compared with bare soil (Fig. 6 and Table S1), which means biocrusts condensed more water vapor primarily in shallow soil. The different non-rainfall water amounts between surface and substratum was probably mostly attributable to temperature gradients (Saito et al., 2006; Xiao et al., 2016). Generally, the liquid water and vapor fluxes are both affected by the soil temperature (Du et al, 2018), and the movement of liquid water and water vapor in the subsurface is driven by both pressure head and temperature gradients (Saito et al., 2006). Because surface soils dramatically change temperature (Du et al, 2018; Saito et al., 2006), whereas subsurface soils maintain more stable temperatures, temperature gradients are established (Du et al., 2018; Zeng et al., 2011). Physical distance and moderate temperature shifts mean that substratum soil is unlikely to obtain much water vapor from the atmosphere directly. Rather, the vapor condensed from moist deeper soil should be expected to be the main water source for non-rainfall water formation below the surface (Fischer et al., 2012; Pan et al., 2018). Namely, during the non-rainfall water formation process, the surface soil created a pivotal non-rainfall water formation region as compared with substratum soil (Pan et al., 2018).

Although biocrusts are only a surficial phenomenon, they drastically affected the distribution of non-rainfall water by depth in our study. Biocrusts greatly enlarged the differences in non-rainfall water amount between the surface 0–3 cm and deeper soil (6–10 cm; Fig. 6 and Table S1). They likely did so by more than one mechanism. As elaborated previously, their enhancement of diurnal temperature fluctuation and nighttime cooling rate at the surface likely boosted non-rainfall water from atmospheric sources, and did so especially strongly in the surface 3 cm. Another mechanism is a mulching effect in which they stabilize temperatures at depth (Xiao et al., 2016, 2019a, 2019b, 2019c). Consequently, even as the surface soil temperature changes more dramatically, the subsoil temperature of biocrusts was dampened making it more difficult to reach the dew point to condense water vapor from deep soil. These two contrary forces induced by biocrusts likely resulted in the strong contrast between surface and subsurface non-rainfall water that we saw.

4.5. Implication of biocrust effects on non-rainfall water deposition in dryland water balance

From our results, we conclude that the biocrusts significantly increased non-rainfall water deposition capacity in the semiarid portion of the Loess Plateau of China. It was known that the biocrust influences on non-rainfall water deposition strongly depend on meteorological factors, soil texture, biocrust types, moss morphology, and so on (Ouyang et al., 2017; Zheng et al., 2018). Nonetheless, it is still challenging to evaluate the biocrust effects on non-rainfall water deposition and its role in the water balance in dryland ecosystems. Accordingly, we reviewed the biocrust effects on non-rainfall water deposition (including dew formation and vapor condensation) in different regions in Table 6. The non-rainfall water is an indispensable source of liquid water and even greater than ephemeral rainfall events in extreme drought regions, e.g., the Alexander Bay of South Africa, the Negev Desert of Israel and other Chinese desert areas (Kidron, 2010; Maphangwa et al., 2012; Pan et al., 2010). In an extreme case (Maphangwa et al., 2012), the non-rainfall water intercepted by bare gypsum soil was ~ 10 times greater than the measured rainfall amount (510.0 vs. 43.0 mm), and that solely by lichens was up to 3 times greater than the rainfall amount (152.0 vs. 43.0 mm). Consequently, that biocrusts significantly increase the soil non-rainfall water deposition capacity is broadly supported in the available literature.

In this study, although we have not estimated the annual cumulative non-rainfall water in the Chinese Loess Plateau, the 4 months cumulative non-rainfall water amount of biocrusts was about 5% of annual rainfall in Chinese Loess Plateau (21.2 vs. 409.0 mm). Therefore, there is no doubt that the non-rainfall water makes a substantive contribution to the water budget through the long, stable periods favoring vapor condensation (Agam and Berliner, 2004; Pan et al., 2018).

Although the non-rainfall water amount was usually smaller in quantity, ancillary water wets and dries the upper soil surface more frequently than rainfall in arid areas, and strongly influences organisms that dwell on the soil surface (Jia et al., 2014; Pan et al., 2018). According to the studies of Kappen et al. (1979) and Pan et al. (2018), the minimum non-rainfall water amount of 0.03 mm is the threshold value for the non-rainfall water to become available to microorganisms. In our study, the mean amount of daily non-rainfall water in both biocrusts and bare soils was higher than 0.03 mm, meaning that a typical deposition event in the region is likely to induce biological activity. Though the effect of biocrusts on non-rainfall water is significant and meaningful, this important phenomenon is still undervalued in drylands. The entire literature on biocrust effects on non-rainfall water is only a few papers by a few research groups in a few locations. A recent *meta*-analysis by Eldridge et al. (2020) about the influence of biocrusts on water in the world's drylands did not account for non-rainfall water at all, likely because of the paucity of studies. The *meta*-analysis shows a pervasive

Table 6
Regional differences of biocrust effects on non-rainfall water deposition based on literatures.

Location	Annual rainfall (mm)	Biocrust characteristics		Measurement method	Dimension of measurement device (diameter/(length × width) × height) (cm)	Daily non-rainfall water amount (mm)		Reference
		Type	Thickness (mm)			Biocrusts	Bare soil	
Alexander Bay, South Africa	46	Lichen	–	Micro-lysimeter	24.0 × 3.5	~0.42	~1.40	Maphangwa et al. (2012)
Almería, Spain	220	Cyanobacteria, lichen	–	Micro-lysimeter	15.0 × 9.0	~0.10	~0.07	Uclés et al. (2016)
Gurbantunggut Desert, China	80	Cyanobacteria, lichen, moss	2.8–22.0	Micro-lysimeter	6.0 × 3.5	~0.09–0.14	~0.08	Zhang et al. (2009)
Hobq Desert, China	293	Algae, moss	4.7–13.7	Micro-lysimeter	5.0 × 1.0	0.04–0.22	0.04	Ouyang et al. (2017)
Hobq Desert, China	293	Cyanobacteria	1.1–2.7	Cloth-plat	6.0 × 6.0 × 0.2	0.02–0.35	~0.08	Rao et al. (2009)
Hobq Desert, China	293	Cyanobacteria, cyano-moss mixed, moss	3.1–14.3	Micro-lysimeter	5.4 × 5.0	~0.10–0.20	~0.08	Zheng et al. (2018)
Lieberose, Germany	569	Green algae, algae-moss mixed	1.5–4.5	Micro-lysimeter	–	0.06–0.18	~0.06	Fischer et al. (2012)
Negev Desert, Israel	95	Lichen	–	Cloth-plat	15.0–20.0 × 15.0–20.0	~0.18–0.20	0.04–0.18	Kidron (2000)
Negev Desert, Israel	95	Cyanobacteria, moss	1.0–10.0	Cloth-plat	6.0 × 6.0 × 0.15	0.03–0.20	~0.10	Kidron et al. (2002)
Negev Desert, Israel	95	Cyanobacteria, lichen	5.0–10.0	Cloth-plat	6.0 × 6.0 × 0.15	0.03–0.15	–	Kidron et al. (2014)
Negev Desert, Israel	95	Cyanobacteria, lichen	–	Cloth-plat	6.0 × 6.0 × 0.15	0.10–0.20	~0.03–0.10	Kidron and Temina (2017)
Negev Desert, Israel	95	Lichen	–	Cloth-plat	~10 × 10 × 5	~0.10–0.20	~0.10–0.20	Temina and Kidron (2015)
Tengger Desert, China	186	Moss	8.6–15.0	Micro-lysimeter	10.0 × 3.5	~0.09–0.13	~0.09	Jia et al. (2014)
Tengger Desert, China	186	Cyanobacteria, lichen, moss	–	Micro-lysimeter	10.0 × 10.0 × 5.0	~0.10–0.20	–	Li et al. (2018)
Tengger Desert, China	186	Algal, moss	2.0–20.0	Micro-lysimeter	10.0 × 10.0	~0.02-	~0.07	Liu et al. (2006)
Tengger Desert, China	186	Algae, lichen, moss	–	Micro-lysimeter	10.0 × 3.0	~0.30–0.40	–	Pan et al. (2010)
Tengger Desert, China	186	Algae-lichen mixed, moss	2.0–20.0	Micro-lysimeter	10.0 × 9.0	~0.30–0.40	–	Pan et al. (2018)
Tengger Desert, China	186	Moss	–	Micro-lysimeter	40.0 × 30.0	~0.03–0.40	~0.03–0.11	Wang et al. (2017)

influence of biocrusts on many properties and processes related to soil water, and a better understanding of biocrust effects on non-rainfall water would help us complete the puzzle. We should seek to better understand how the effect of biocrusts on non-rainfall water may play a critical role in many ecosystem processes (Xiao et al., 2009; Zhang et al., 2009), and how much of dryland ecosystem function can be directly attributed to non-rainfall water pulses.

5. Conclusion

In this study, we analyzed the differences of non-rainfall water deposition between bare soil and different types of biocrusts (cyano crusts, mixed crusts, and moss crusts) in a dryland ecosystems. Our results indicated that biocrusts greatly increased non-rainfall water amount by about 70% due to the higher contents of fine particles and organic matter, higher daily soil temperature differences and moss morphology. Moreover, the presence of biocrusts significantly increased the rates of non-rainfall water formation and evaporation, and boosted the condensation of both soil-sourced and, especially, atmospherically-sourced vapor. All of these effects showed that biocrusts are playing an important role in regulating surface soil water balance in dryland ecosystems. We can conservatively estimate that in our study area, the capture of non-rainfall water by biocrusts increases ecosystem water inputs by about 5% and does so in periods of time when rainfall is scarce. Because most non-rainfall water deposition events are typically sufficient to activate biocrusts and other soil microbiota, it appears that this understudied water input may be important for biological activity and therefore ecosystem function in our study system, and perhaps other water-limited regions.

CRediT authorship contribution statement

Shenglong Li: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing - original draft, Writing - review & editing. **Matthew A. Bowker:** Writing - original draft, Writing - review & editing. **Bo Xiao:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhydrol.2021.126050.

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