

Moss-dominated biocrusts decrease soil moisture and result in the degradation of artificially planted shrubs under semiarid climate

Bo Xiao^{a,b,*}, Kelin Hu^a

^a Department of Soil and Water Sciences, China Agricultural University, Beijing 100193, PR 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, Yangling, Shaanxi 712100, PR China

ARTICLE INFO

Article history:

Received 24 November 2016

Received in revised form 21 December 2016

Accepted 4 January 2017

Available online xxxx

Keywords:

Biological soil crust

Microbiotic crust

Soil water regime

Soil water balance

Artemisia ordosica

Vegetation degradation

ABSTRACT

The relationships between biocrusts and shrubs in semiarid areas, are of great importance, however, not yet sufficiently investigated. It is unknown whether or not biocrusts will decrease soil moisture and result in the degradation of artificially planted shrubs in semiarid climates. In a semiarid watershed on the Loess Plateau of China, we selected 18 sampling sites in artificial shrublands and measured at each the soil moisture from 0 to 200 cm depth under bare land, moss-dominated biocrusts, artificially planted *Artemisia ordosica*, *A. ordosica* with biocrusts, and dead *A. ordosica* with biocrusts. We also estimated the water-holding capacity and infiltrability of the soil with and without biocrusts. The *A. ordosica* with biocrusts had 24.4% lower biomass and 18.9% lower leaf area index than those without biocrusts, suggesting negative effects of biocrusts on these shrubs. Moreover, the biocrusts underneath *A. ordosica* decreased soil moisture 14.8% on average (2.6% vs. 3.1%; $p < 0.01$) due to their significant higher water-holding capacity ($\geq 21.6\%$) and lower infiltrability (50.4%), compared to the area without biocrusts. Most importantly, the area with biocrusts and dead *A. ordosica* had similar soil moisture to the area with biocrusts and live *A. ordosica*, suggesting that the decreased soil moisture under the biocrusts persists after the death of *A. ordosica*. Our results suggest that biocrusts reduce soil water resources available to the artificially planted shrubs, thus increasing the risks of shrub mortality and further land degradation. The high coverage of moss-dominated biocrusts appears to be a dominant factor in soil moisture variations in artificial shrublands under semiarid climates, making the soil water balance more vulnerable in this region.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Desertification represents one of the most significant environmental problems in arid and semiarid climate regions all over the world, due to climate change and human activities (Johnson et al., 2006; Thai et al., 2007; Helldén and Tottrup, 2008; Verstraete et al., 2009). In order to combat land degradation and desertification, several large scale ecological projects, such as the Three-North Shelterbelt Forest Program and the Grain for Green Project, have been implemented to restore vegetation through afforestation in northwest China in recent decades (Cao et al., 2009; Wang et al., 2010). During these projects, a large number of native shrubs, including *Artemisia ordosica* Krasch. (Asteraceae), *Caragana korshinskii* Kom. (Leguminosae), and *Salix psammophila* C. Wang et Chang Y. Yang (Salicaceae), have been artificially planted due to their outstanding performance in drought tolerance as well as soil and water conservation (Li et al., 2006; Xu et al., 2007; Lai et al., 2016).

Owing to the stabilization of land surface (against wind erosion) reinforced by these artificially planted shrubs, biocrusts (known also as

biological soil crusts or microbiotic crusts (Belnap and Lange, 2003)) gradually and extensively developed underneath the shadow of shrubs and in the interspaces between them (Xiao et al., 2010; Zhao et al., 2011; Bu et al., 2016). Biocrusts are formed by a highly specialized community of living microorganisms (including moss, lichen, green algae, cyanobacteria, fungi, and bacteria) and their by-products in dry environments, creating a crust of soil particles bound together by organic materials on land surface (Belnap and Lange, 2003). Such biocrusts, together with the artificially planted shrubs, successfully conserved soil and water in regions threatened by desertification by preventing water and wind erosion (Zhang et al., 2006; Bowker et al., 2008; Rodríguez-Caballero et al., 2012; Tisdall et al., 2012), as well as changing water infiltration, runoff, and evaporation (Belnap, 2006; Xiao et al., 2011; Kidron and Tal, 2012; Rodríguez-Caballero et al., 2012). Biocrusts are recognized as a component that exerts a major influence on arid and semiarid ecosystems (Belnap, 2006; Maestre et al., 2011).

It seems that the occurrence of biocrusts is closely related to the establishment of artificially planted shrubs in semiarid climates, especially on the Loess Plateau of China; however, their relationships have not yet been sufficiently investigated. It has been reported that biocrusts facilitated seed entrapment by increasing soil surface roughness (Su et al., 2007; Rodríguez-Caballero et al., 2012), and promoted (sometimes not; e.g.,

* Corresponding author at: Department of Soil and Water Sciences, China Agricultural University, No. 2, Yuanmingyuan West Road, Haidian District, Beijing 100193, PR China.
E-mail addresses: xiaobo@cau.edu.cn, xiaoboxb@gmail.com (B. Xiao).

Pando-Moreno et al. (2014)) seedling emergency, survival, rooting, establishment, and growth by offering favorable soil moisture, temperature, and nutrients (Deines et al., 2007; Langhans et al., 2009; Funk et al., 2014; Pando-Moreno et al., 2014). However, it was also found that biocrusts decreased deep soil moisture, and would possibly reduce the soil water resources available to vascular plants and subsequently lead to vegetation degradation (e.g., Almog and Yair, 2007; Li et al., 2010). Consistent with this competition hypothesis, a few landscape surveys have found a negative relationship between biocrusts and vascular plant cover (e.g., West, 1990; Eldridge, 1993). In northwest China, the potential negative effects of biocrusts on soil moisture and artificially planted shrubs are of great interest, because a large proportion of the artificially planted shrubs have died from drought stress. It seems that the existence of biocrusts may have decreased soil moisture and caused the death of the artificially planted shrubs (Zhang and Belnap, 2015; Zhuang et al., 2015); however, till now no direct and sufficient evidence is available.

In this study, we hypothesized that moss-dominated biocrusts decreased soil moisture and resulted in reduced growth and even mortality of the artificially planted *A. ordosica* in the semiarid region of the Loess Plateau of China. Based on these hypotheses, we conducted a multi-location sampling experiment for soil moisture under a semiarid climate on the Loess Plateau of China. In a representative watershed, we selected 18 sampling sites with similar conditions (e.g., texture, structure, organic matter content, and orientation) in artificial shrublands and measured at each the soil moisture from 0 to 200 cm depth under bare land, moss-dominated biocrusts, *A. ordosica*, *A. ordosica* with biocrusts, and degraded *A. ordosica* with biocrusts. We also estimated the water-holding capacity and infiltrability of the soil with and without biocrusts. From the experimental data, the relationships between the biocrusts and artificially planted shrubs in the utilization of soil moisture were analyzed. Our results are helpful for a better understanding of the competitive relationships between biocrusts and vascular plants in semiarid climate regions.

2. Materials and methods

2.1. Study area

The study was conducted in a 6.89 km² watershed named Liudaogou (38°46′–38°51′ N, 110°21′–110°23′ E; Fig. 1a), which has 409 mm

average annual precipitation (about 80% of it occurs in summer) and 1337 mm average annual water evaporation (pan evaporation). Due to the serious degradation of natural vegetation, artificially planted shrubs including *A. ordosica* and *C. korshinskii* were widely planted in this watershed about 30 years ago. Nowadays, these shrubs (Fig. 2a) are distributed in patches covering 20–30% of the watershed; whereas moss-dominated biocrusts have extensively developed (initially recorded around 20 years ago) covering approximately 70–80% of the watershed. A large number of the artificially planted shrubs died (non-natural mortality) in the past 5 years, especially *A. ordosica* which has a shallower root system compared to *C. korshinskii*. Biocrusts often fully covered the ground surface around the dead shrubs. The dominant soil in the watershed is arenosols in FAO soil classification or psamment in USDA soil taxonomy, and its texture was sandy loam with 81% sand, 14% silt, and 5% clay (Xiao et al., 2014).

2.2. Experimental design and measurement

Five treatments, including bare land (Fig. 2b), biocrusts (Fig. 2c), *A. ordosica* (Fig. 2d), *A. ordosica* with biocrusts (Fig. 2e), and dead *A. ordosica* with biocrusts (Fig. 2f), were considered in this study; and each treatment had 18 replicates.

According to the experimental design, eighteen sampling sites (Fig. 1b) with similar conditions (e.g., texture, structure, organic matter content, and orientation) for each treatment were selected in the artificial shrublands in and around the watershed. Owing to the sparse shrubs and mosaic distribution of biocrusts, it was easy to find adjacent sampling points for the five treatments, respectively, at each sampling site. The dead *A. ordosica* plants selected in this study died and dried out in 2005 (the moss-dominated biocrusts already colonized the soil around the shrubs before they died) according to our records.

The measurements were grouped in the following five categories: (1) the plant cover (estimated using a grid method), height and canopy breadth (measured by a flexible rule), above- and below-ground biomass (dried at 65 °C for 24 h), root distribution (measured through the trench-profile method (Cheng et al., 2008)), and leaf area index (measured by a LI-3000A Portable Leaf Area Meter (Yin et al., 2009)) of the *A. ordosica*; (2) the biocrust cover (using line intercept transects), thickness (measured by a digital caliper), moss biomass (washed out with a 2 mm screen and dried at 65 °C for 24 h), moss density

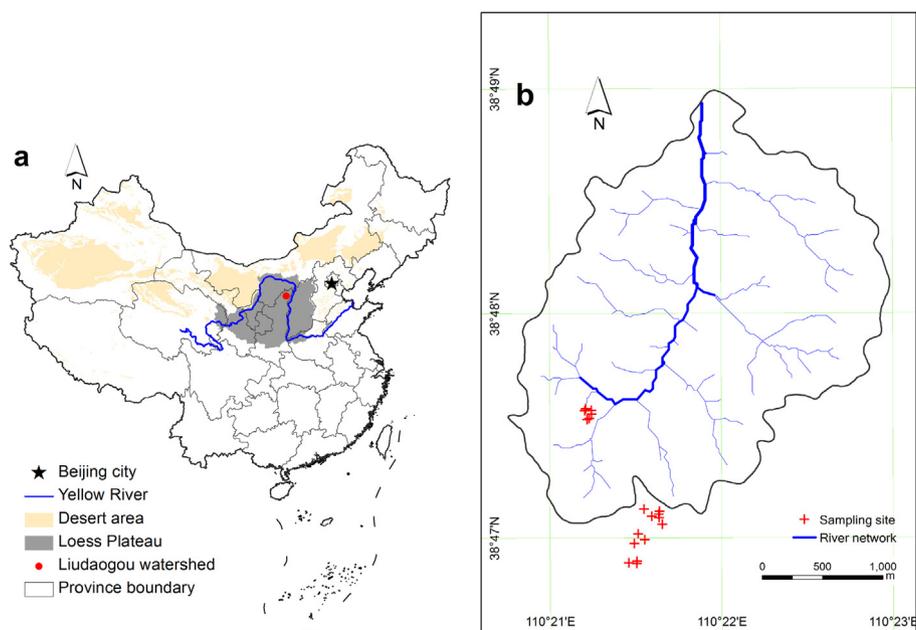


Fig. 1. Location of (a) the Liudaogou watershed and (b) sampling sites on the Loess Plateau of China.

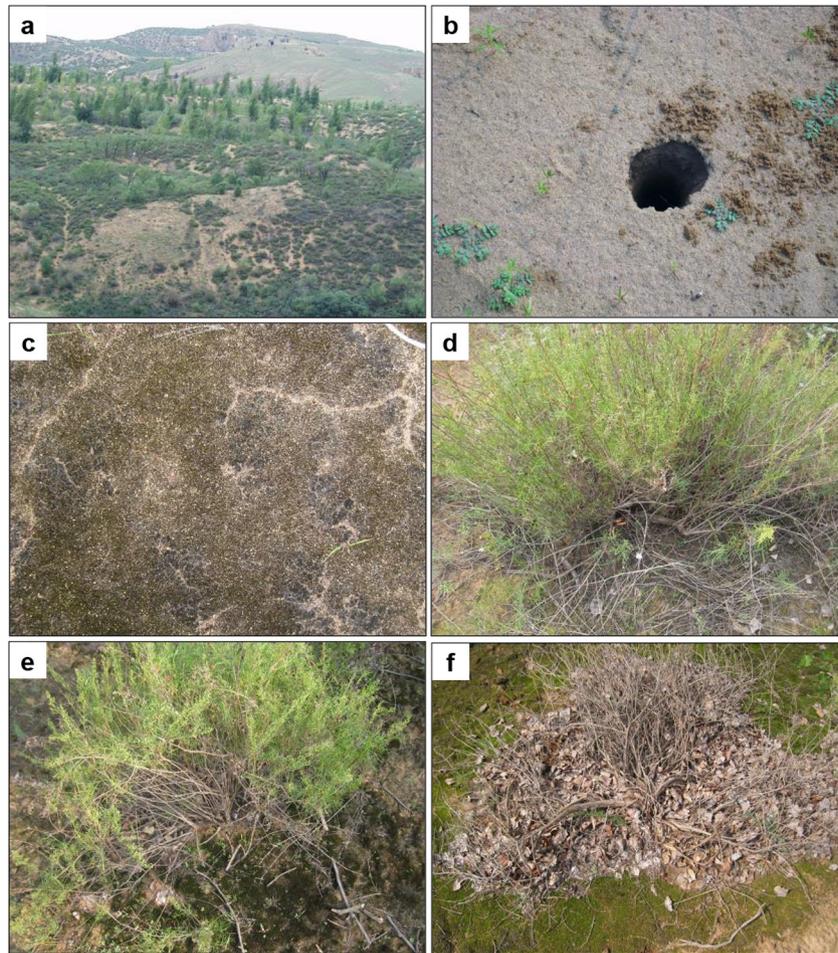


Fig. 2. Landscapes with (a) well-developed biocrusts and sparse artificial shrub patches; and the five treatments for study including (b) bare land, (c) biocrusts, (d) *A. ordosica*, (e) *A. ordosica* with biocrusts, and (f) dead *A. ordosica* with biocrusts.

(calculated from the total moss gametophytes in a 20 mm square sample), and species (identified according to their general appearance, size, color, and habitats) of the biocrusts; (3) the water-holding capacity of the biocrust layer and bare land (0–5 cm), including the saturated soil moisture (saturated in distilled water for 24 h and determine the gravimetric soil moisture through oven-drying) and field capacity (drained away excess water for 24 h after the saturation, and then determine the gravimetric soil moisture through oven-drying); (4) the soil infiltrability indicated by the saturated hydraulic conductivity of the biocrusts and bare land, measured by a disk infiltrometer at suction of 0, –3, –6, and –15 cm water, respectively (Logsdon and Jaynes, 1993); and (5) the gravimetric soil moisture for 0–200 cm depth at interval of 10 cm, through sampling by an auger and oven-drying for 24 h at 105 °C. The experiment was performed from Aug. 4 to Aug. 13 in 2011, without rainfall during this period.

2.3. Data analysis

The experimental data were analyzed based on the descriptive statistics in IBM SPSS Statistics 22, and the final results of each treatment were averaged from the 18 replicates and expressed as the mean \pm standard error. The differences between the paired treatments (biocrusts vs. bare land; *A. ordosica* with biocrusts vs. *A. ordosica*; dead *A. ordosica* with biocrusts vs. live *A. ordosica* with biocrusts) were statistically evaluated at 5% probability level by the paired-samples *t*-test after normality tests in IBM SPSS Statistics 22. The representation and graphical fits of experimental data were obtained by using OriginPro 9.2.

3. Results

3.1. Characteristics of biocrusts and artificially planted shrubs

The biocrusts were generally about 20 years old according to our records, and were mainly constituted by the mosses *Bryum argenteum* Hedw., *B. arcticum* (R. Brown) B.S.G., *B. caepiticium* Hedw., *Didymodon vinealis* (Brid.) Zander, *D. nigrescens* (Mitt.) Saito, *Barbula vinealis* Brid., and *B. perobtusa* (Broth.) Chen. However, biocrusts associated with *A. ordosica* were significantly different from biocrusts without shrubs in their thickness, biomass, and moss density. Compared to the biocrusts without shrubs, the thickness, biomass, and moss density of biocrusts were decreased by 49.7% ($t = 12.24$, $p < 0.01$), 46.1% ($t = 9.06$, $p < 0.01$), and 17.3% ($t = 3.90$, $p = 0.03$), respectively, as in association with the live *A. ordosica* (Table 1). Whereas they were increased by 58.0% ($t = 1.44$, $p = 0.25$), 55.3% ($t = 2.33$, $p = 0.10$), and 16.7% ($t = 0.91$, $p = 0.43$), respectively, as in association with the dead *A. ordosica* compared to the biocrusts with alive *A. ordosica* (Table 1). The results suggest that the development of biocrusts was significantly inhibited by the artificially planted *A. ordosica*; and these hindering effects gradually disappeared along with the dying of the artificially planted *A. ordosica*.

The selected *A. ordosica* plants were generally about 30 years old, 30–40% in cover, 30–45 cm in height, and 45–60 cm in canopy breadth. Their roots reached up to about 70 cm depth; however, most (>89%) of them were distributed in 0–40 cm depth, especially when they were associated with biocrusts (Fig. 3). The *A. ordosica* without biocrusts consistently had higher ($t \geq 2.21$, $p \leq 0.05$) root biomass than the live or dead *A.*

Table 1
Characteristics of the biocrusts and artificially planted *A. ordosica* in different treatments.

Treatments	Biocrusts				<i>A. ordosica</i>					
	Cover (%)	Thickness (mm)	Moss biomass (mg cm ⁻²)	Moss density (count cm ⁻²)	Cover (%)	Height (cm)	Canopy breadth (cm)	Above-ground biomass (g clump ⁻¹)	Below-ground biomass (g clump ⁻¹)	Leaf area index
Biocrusts	93.9 ± 0.5a*	17.5 ± 0.5a	14.1 ± 1.8a	184.2 ± 15.9a	0	–	–	–	–	–
<i>A. ordosica</i>	0	–	–	–	41.4 ± 1.7a	41.5 ± 6.4a	59.5 ± 7.8a	186.5 ± 25.1a	66.3 ± 11.4a	0.95 ± 0.15a
<i>A. ordosica</i> with biocrusts	81.6 ± 0.8a	8.8 ± 0.6b	7.6 ± 0.5b	152.4 ± 16.7b	29.9 ± 0.5a	36.3 ± 7.5b	51.1 ± 7.2b	149.2 ± 35.4b	47.2 ± 13.2b	0.77 ± 0.12b
Dead <i>A. ordosica</i> with biocrusts	87.9 ± 0.8a	13.9 ± 0.4b	11.8 ± 0.6a	177.8 ± 18.7a	20.9 ± 1.3a	19.4 ± 8.8c	44.6 ± 7.5c	60.3 ± 15.9c	30.9 ± 10.8c	–

* Different letters in the same column indicate significant differences at 5% probability level.

ordosica with biocrusts in root zone, especially in the upper soil. Although the distribution of root biomass had great differences among the three treatments in Fig. 3a, the distribution of the percentage of root biomass was quite similar in Fig. 3b. The *A. ordosica* plants were generally less vigorous when they were surrounded by the biocrusts. Compared to the *A. ordosica* without biocrusts, the plant height, canopy breadth, above-ground biomass, below-ground biomass, and leaf area index of the *A. ordosica* with biocrusts were decreased by 12.5% ($t = 8.64$, $p < 0.01$), 14.1% ($t = 16.39$, $p < 0.01$), 20.0% ($t = 34.92$, $p < 0.01$), 28.8% ($t = 11.04$, $p < 0.01$), and 18.9% ($t = 4.95$, $p = 0.02$), respectively (Table 1). The results implied that the biocrusts negatively affected the growth of the artificially planted *A. ordosica*.

3.2. Effects of biocrusts on soil water-holding capacity and infiltrability

As presented in Fig. 4, the saturated soil moisture of the biocrusts (Fig. 4a) was 5.5% and 25.6% higher ($t = 2.83$, $p = 0.014$) than the bare land in absolute and relative terms, respectively; while their field capacity (Fig. 4b) was 2.7% and 21.6% higher ($t = 2.56$, $p = 0.023$) than the bare land in absolute and relative terms, respectively. However, the saturated hydraulic conductivity of the biocrusts (Fig. 4c) was 9.8% and 50.4% lower ($t = 4.43$, $p = 0.001$) than the bare land in absolute and relative terms, respectively. Thus, the biocrusts significantly increased soil water-holding capacity as indicated by their increasing effects on saturated soil moisture and field capacity, and they significantly decreased soil infiltrability as indicated by their decreasing effects on saturated hydraulic conductivity.

3.3. Effects of biocrusts on soil moisture

As shown in Fig. 5 and Table S1, the biocrusts consistently had lower (2.0% vs. 3.3%; $t > 3.32$, $p \leq 0.01$) soil moisture at 0–200 cm depths compared to the bare land (Fig. 4a). Similarly, the *A. ordosica* with biocrusts consistently had lower (2.6% vs. 3.1%; $t > 4.80$, $p < 0.01$) soil moisture compared to the *A. ordosica* without biocrusts (Fig. 4b); whereas the dead *A. ordosica* with biocrusts had similar soil moisture (2.6% vs. 2.5%; $t < 1.90$, $p > 0.08$) to the live *A. ordosica* with biocrusts (Fig. 4c). In other words, the soil moisture was significantly decreased by 1.3% and 38.1% in absolute and relative terms due to the biocrusts without vegetation, whereas it was significantly decreased by 0.5% and 14.8% in absolute and relative terms due to the biocrusts with the artificially planted *A. ordosica*. On average, the soil water storage (using bulk density = 1.5 g cm⁻³ as a mean value for the whole profile) for the 0–200 cm layer was decreased by 37.9 mm in the open space due to the biocrusts and 14.2 mm underneath the artificially planted *A. ordosica* due to the biocrusts.

4. Discussion

The symbiotic or competitive relationships between biocrusts and vascular plants are of great interest and importance in the utilization of limited soil water resources (e.g., Belnap, 2006; Li et al., 2010), which is the main determining factor of vegetation restoration in arid and semiarid ecosystems (Chen et al., 2007). In our study, the establishment of artificially planted shrubs facilitated the development of

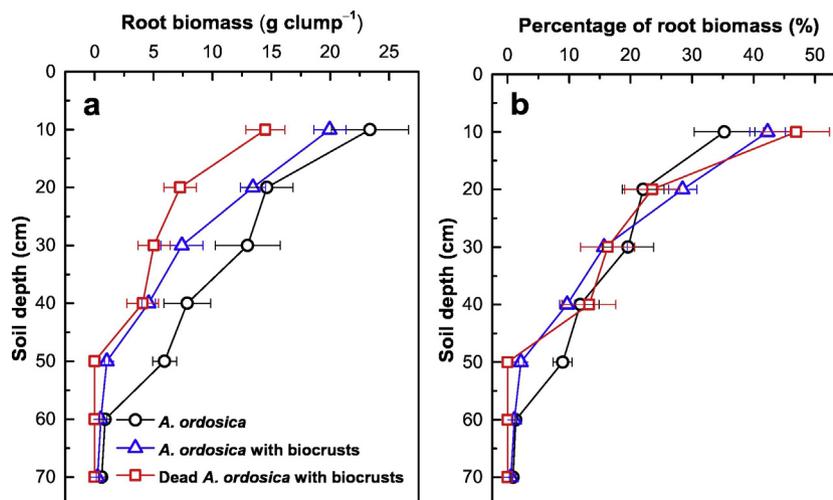


Fig. 3. Vertical root distribution of *A. ordosica*. (a) Root biomass vs. soil depth; (b) percentage of root biomass vs. soil depth.

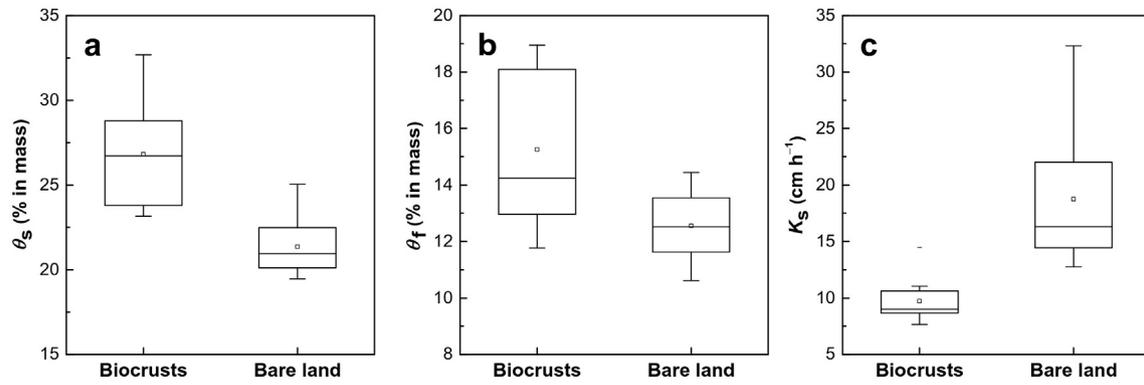


Fig. 4. Saturated soil moisture (θ_s), field capacity (θ_f), and saturated hydraulic conductivity (K_s) of the biocrusts and bare land.

biocrusts at early stage (Li et al., 2004; Li et al., 2010); however, afterwards they inhibited the further development of these biocrusts. As reported by other studies, the artificially planted shrubs usually generated positive effects on the establishment of biocrusts at early successional stage, possibly because they firstly protected the live microbial organisms from soil surface disturbance and sand burial in water and wind erosion (Li et al., 2004), and secondly provided a favorable environment with rich moisture and moderate temperature from the shadow of shrub canopies (Xiao et al., 2016). However, in the middle or late successional stage, the artificially planted shrubs generally produced negative effects on the development of biocrusts possibly due to the interception of rainfall (accounting for 6.9%–17.1% of the overall precipitation, especially in small rainfall events) and sunshine by both shrub canopies and plant litters (Wang et al., 2005; Mousaei Sanjerehei, 2013; Zhang et al., 2016).

On the other side, our results suggested that the soil moisture was significantly decreased by the existence of biocrusts in lands with artificially planted shrubs of *A. ordosica*; and the decreased soil moisture was not replenished after the death of the artificially planted *A. ordosica*. In other words, the occurrence and development of biocrusts increasingly deteriorated soil water conditions, and likely contributed to shrub mortality. These results fully supported our hypothesis that the moss-dominated biocrusts decreased soil moisture and resulted in reduced growth and even mortality of the artificially planted *A. ordosica* in the semiarid regions on the Loess Plateau of China. It has been reported that well-developed biocrusts inhibited the growth and survival of artificially planted shrubs by their negative effects on soil moisture in other regions

(Zhang and Belnap, 2015; Zhuang et al., 2015), because biocrusts decreased the amount and depth of rainfall infiltration due to their lower infiltrability and higher water-holding capacity, which was supported by Li et al. (2010) and also confirmed by our results in Fig. 4. Some studies also found that biocrusts intensified soil water evaporation due their high water content and surface temperature (Xiao et al., 2010; Xiao et al., 2013), but other studies have not shown these effects (e.g., Zhang et al., 2008; Chamizo et al., 2013a). In addition to these surface effects, this study showed that biocrusts consistently decreased soil moisture, not only on the surface but also up to the 200 cm soil depth. Prior studies reported that biocrusts only decreased soil moisture in about upper 60–80 cm soil depths and reduced the growth of shrubs with shallow root system in other regions (e.g., Li et al., 2004; Li et al., 2010; Yair et al., 2011). These regional differences, as listed in Table 2, were possibly caused by our moss-dominated biocrusts which had greater thickness and larger biomass compared to cyanobacterial- or lichen-dominated biocrusts (thus enabling stronger influences on soil moisture). The greater impact on soil moisture at depth in our study may also be due to the relatively abundant precipitation (>400 mm) in the semiarid climate region of this study, where the annual precipitation was much higher than the arid climate regions in other studies (<250 mm; e.g., Li et al. (2010)), thus biocrusts in our study may have affected more water through infiltration and evaporation.

An additional mechanism that may contribute to the reduced soil moisture under biocrusts is related to preferential flow. Wang et al. (2007) found that the rainfall infiltration increased due to preferential flow associated with the root tunnels in shrubland without biocrusts,

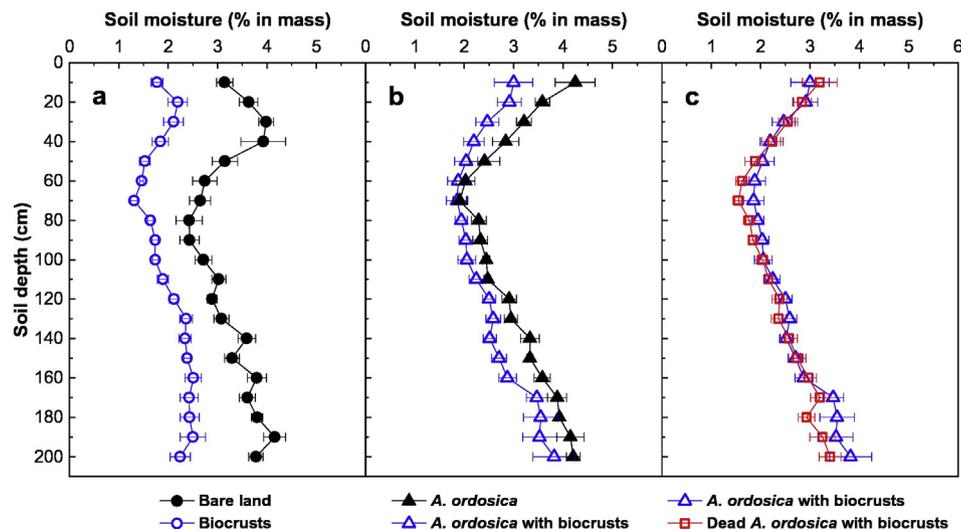


Fig. 5. Soil moisture variation of the five treatments at 0–200 cm depths. (a) Biocrusts vs. bare land; (b) *A. ordosica* with biocrusts vs. *A. ordosica*; and (c) dead *A. ordosica* with biocrusts vs. *A. ordosica* with biocrusts.

Table 2
Regional differences of biocrusts and their effects on soil moisture and vascular plant.

Region		Biocrusts				Effects of biocrusts on soil moisture and vascular plant
Location	Climate	Dominant community	Dominant species	Thickness (mm)	Biomass (mg cm ⁻²)	
Northern Loess Plateau, China	AP = 409 mm, APE = 1337 mm	Moss	<i>Bryum argenteum</i> , <i>B. arcticum</i> , <i>B. caepiticium</i> , <i>Didymodon vinealis</i> , <i>D. nigrescens</i> , <i>Barbula vinealis</i> , <i>B. perobtusata</i>	8.8–17.5	7.6–14.1 ^a	Biocrusts consistently decreased soil moisture at 0–200 cm depth and resulted in the degradation of artificially planted <i>A. ordosica</i> (this study)
Mu US Sandland, China	AP = 250–450 mm, APE = 1800–2500 mm	Moss	<i>B. dichotomum</i> , <i>B. argenteum</i> , <i>D. vinealis</i>	10–16.1	2.82 ^a	Biocrusts may negatively affect local vegetation because they (1) had higher soil moisture in surface layer (0–10 cm) and lower soil moisture in deep soil layer (30–55 cm) under high water conditions; and (2) had lower soil moisture at 5–40 cm under low water conditions (Gao et al., 2010; Yin et al., 2013). Compared with the bare sand, the <i>A. ordosica</i> and moss crusts decreased soil moisture from 0 to 160 cm depth in the dry and rainy seasons by 8.4% and 5.7%, respectively; and the proportional contribution of moss crusts was 46.4% and 82.5%, respectively (Yang et al., 2014)
Shapotou of Tengger Desert, China	AP = 186 mm, APE = 1830 mm	Moss	<i>B. argenteum</i> , <i>D. vinealis</i> , <i>D. tectorum</i> , <i>Syntrichia bidentata</i> , <i>D. nigrescens</i> , <i>S. caninervis</i>	9.0–36.0	1.64–9.46 ^a	Biocrusts limited water infiltration depth (0–40 cm) and subsequently changed the plant community from xerophytic shrubs to annual plants and herb communities (Xu et al., 2003; Li et al., 2004; Li et al., 2010)
Western Negev Desert, Israel	AP = 95 mm, APE = 2600 mm	Cyanobacteria and moss	<i>Microcoleus</i> sp., <i>Scytonema</i> sp., <i>Oscillatoria</i> sp., <i>B. dunense</i> , <i>Tortula brevissima</i>	1.1–10.3	1.67–5.32 × 10 ^{-3b}	Biocrusts are able to absorb and retain large rain amounts, limiting the depth to which water can penetrate, and therefore water availability for the perennial plants (Almog and Yair, 2007; Yair et al., 2011); Biocrusts had higher moisture content and longer wetness duration at 0–40 cm (Kidron and Tal, 2012)
Gurbantunggut Desert, China	AP = 79.5 mm, APE = 2607 mm	Lichen and moss	<i>Collema tenax</i> , <i>Psora decipiens</i> , <i>Xanthoria elegans</i> , <i>Acarospora strigata</i> , <i>Lecanora argopholis</i> , <i>T. desertorum</i> , <i>B. argenteum</i> , <i>Crassidium chloronotos</i> , <i>T. muralis</i> , <i>B. capillare</i>	12.9–22	7.2–9.9 ^c	Moss and lichen crusts had significant greater amount of dew at dawn than bare sand; thus they play a vital role in providing an essential source of water for plants (Zhang et al., 2009; Zhang et al., 2010)

AP = Annual precipitation; APE = Annual potential evaporation.

^a Biomass was weighted directly after washing and drying of all the biological components (mainly mosses), in mg cm⁻².

^b Biomass was indicated by chlorophyll *a* concentration, in mg m⁻².

^c Biomass was indicated by chlorophyll *a* concentration, in g g⁻¹ dry soil.

which implies that biocrusts possibly may restrict infiltration through blocking preferential water flow through root tunnels of vascular plants. Generally, preferential flow of water occurs in the root channels (1) formed by dead or decaying roots, (2) formed by decayed roots but newly occupied by living roots, and (3) formed around live roots (Ghestem et al., 2011). In our study, the root systems of *A. ordosica* may have created networks of preferential flow paths, which facilitated deeper soil water storage. The presence of biocrusts may have increasingly blocked these root channels and eventually resulted in the deterioration of deep soil water storage, and subsequently the mortality of *A. ordosica*. According to our records, the dead *A. ordosica* plants died in 2005, possibly due to the extreme drought at that time (annual precipitation = 279.8 mm; 31.6% less than the average of regular years). In the study region, the vulnerable soil-water balance between the biocrusts and artificially planted *A. ordosica* could be barely maintained in a year with regular precipitation; however, it would be totally broken if significantly

lower precipitation occurs in a dry year (e.g., 2005), which is supported by the results from Veste et al. (2011) and Siegal et al. (2013) in the Northern Negev desert. Shrubs with deeper root systems (e.g., *Caragana korshinskii* and *Salix psammophila*) may be less responsive to the decreasing precipitation than *A. ordosica*. The shrubs with a taproot system are able to take up water from deeper soil layers, where water is stored even during the dry season (Ohte et al., 2003; Veste et al., 2008).

In addition, our study indicated that the death of the artificially planted shrubs further improved the development of biocrusts underneath the shadow of the shrubs; however, shrub mortality did not restore the soil water condition, which was deteriorated by the biocrusts earlier. These results implied that the dominant factor of soil moisture in the artificial shrublands had been transferred from vascular plants to biocrusts (Li et al., 2010; Xiao et al., 2014; Xiao et al., 2016); therefore, the death of artificially planted shrubs did not affect the soil water regime controlled by biocrusts.

In our study, the moss-dominated biocrusts decreased soil moisture and resulted in the reduced growth of artificially planted shrubs under semiarid climate on the Loess Plateau of China. However, it does not mean that such degradation of shrubs will definitely lead to desertification in this region, because the land surface released from the shrubs would be still protected by biocrusts against wind-water erosion (In another viewpoint, the replacement of vascular plants by biocrusts, together with a lower soil moisture, can be considered also as a form of degradation although the biocrusts defend the soil against erosion). For example, Siegal et al. (2013) reported that an average of 27% and 68% of the shrubs in the fixed sand dunes had wilted by 2009 in the southern and northern Negev Desert, respectively; however, a such vast decrease of shrub cover is not expected to induce dune remobilization because the existing biocrust cover is not negatively affected by the drought. In the Tengger Desert of China, Fearnough et al. (1998) also found that the xerophytic shrubs were replaced by widespread biocrusts, with shrubs declining from 12 to only 3% cover after 37 years of stabilization due to the decreased moisture penetration and subsequent desiccation of the deeper dune sands. In other words, biocrusts took over the ecological functions of vascular plants when they wilted; subsequently, biocrusts, in the long term, may play more important ecological and functional roles than vascular plants in arid and semiarid ecosystems, especially in conserving soil surface against water and wind erosion (Bowker et al., 2011; Maestre et al., 2011; Chamizo et al., 2013b; Kidron, 2015).

5. Conclusions

The moss-dominated biocrusts significantly reduced the limited soil water resources available to the artificially planted shrubs under semiarid climates, and subsequently resulted in reduced growth and eventual mortality of the artificially planted shrubs. Moreover, the deteriorated soil water conditions did not restore, even after the artificially planted shrubs had been dead for several years. Biocrusts can become a dominant factor for the determination of soil moisture under semiarid climates, making vascular plants in this region more vulnerable to drought. However, it should be noted that our results were obtained from the shrublands with very well-developed moss-dominated biocrusts (coverage >80%). In other words, these negative effects of biocrusts on soil moisture and artificially planted shrubs may be greater than those for other types of biocrusts (dominated by cyanobacteria/green algae or lichen) or moss-dominated biocrusts with lower coverage. In addition, although biocrusts have negative effects on the survival of artificially planted shrubs and on soil water, they also have positive effects such as reducing surface erosion (water and wind) and improving soil fertility (carbon and nitrogen). Thus, the ecological functions of biocrusts are both positive and negative in semi-arid climates; but we should pay more attention to their negative effects on soil water and the survival of shrubs based on the results of our study. These findings contribute to a better understanding of the competitive relationships between biocrusts and vascular plants, not only on the Loess Plateau of China but also in semiarid climate regions throughout the world.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.geoderma.2017.01.009>.

Acknowledgments

This study was supported by the National Natural Science Foundation of China (41671221) and the Open Fund from the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau (A314021402-1513). We give our thanks to Dr. Tyson Ochsner from the Oklahoma State University, Dr. H. J. Wang from the Chinese Academy of Agricultural Sciences, and two anonymous reviewers for their invaluable comments on improving the manuscript.

References

- Almog, R., Yair, A., 2007. Negative and positive effects of topsoil biological crusts on water availability along a rainfall gradient in a sandy area. *Catena* 70, 437–442.
- Belnap, J., 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrol. Process.* 20, 3159–3178.
- Belnap, J., Lange, O.L., 2003. *Biological Soil Crust: Structure, Function, and Management*. Springer, Berlin & Heidelberg.
- Bowker, M.A., Belnap, J., Bala Chaudhary, V., Johnson, N.C., 2008. Revisiting classic water erosion models in drylands: the strong impact of biological soil crusts. *Soil Biol. Biochem.* 40, 2309–2316.
- Bowker, M.A., Mau, R.L., Maestre, F.T., Escobar, C., Castillo-Monroy, A.P., 2011. Functional profiles reveal unique ecological roles of various biological soil crust organisms. *Funct. Ecol.* 25, 787–795.
- Bu, C.F., Zhang, P., Wang, C., Yang, Y.S., Shao, H.B., Wu, S.F., 2016. Spatial distribution of biological soil crusts on the slope of the Chinese loess plateau based on canonical correspondence analysis. *Catena* 137, 373–381.
- Cao, S.X., Chen, L., Yu, X.X., 2009. Impact of China's grain for green project on the landscape of vulnerable arid and semi-arid agricultural regions: a case study in northern Shaanxi Province. *J. Appl. Ecol.* 46, 536–543.
- Chamizo, S., Cantón, Y., Domingo, F., Belnap, J., 2013a. Evaporative losses from soils covered by physical and different types of biological soil crusts. *Hydrol. Process.* 27, 324–332.
- Chamizo, S., Cantón, Y., Lázaro, R., Domingo, F., 2013b. The role of biological soil crusts in soil moisture dynamics in two semiarid ecosystems with contrasting soil textures. *J. Hydrol.* 489, 74–84.
- Chen, L.D., Huang, Z.L., Gong, J., Fu, B.J., Huang, Y.L., 2007. The effect of land cover/vegetation on soil water dynamic in the hilly area of the loess plateau, China. *Catena* 70, 200–208.
- Cheng, X.R., Huang, M.B., Shao, M.A., Warrington, D.N., 2008. A comparison of fine root distribution and water consumption of mature *Caragana korshinskii* Kom grown in two soils in a semiarid region, China. *Plant Soil* 315, 149–161.
- Deines, L., Rosentreter, R., Eldridge, D., Serpe, M., 2007. Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. *Plant Soil* 295, 23–35.
- Eldridge, D.J., 1993. Cryptogams, vascular plants, and soil hydrological relations: some preliminary results from the semiarid woodlands of eastern Australia. *Great Basin Naturalist* 53, 48–58.
- Fearnough, W., Fullen, M.A., Mitchell, D.J., Trueman, I.C., Zhang, J., 1998. Aeolian deposition and its effect on soil and vegetation changes on stabilised desert dunes in northern China. *Geomorphology* 23, 171–182.
- Funk, F., Loydi, A., Peter, G., 2014. Effects of biological soil crusts and drought on emergence and survival of a Patagonian perennial grass in the Monte of Argentina. *Journal of Arid Land* 6, 735–741.
- Gao, S., Ye, X., Chu, Y., Dong, M., 2010. Effects of biological soil crusts on profile distribution of soil water, organic carbon and total nitrogen in Mu Us Sandland, China. *J. Plant Ecol.* 3, 279–284.
- Ghestem, M., Sidle, R.C., Stokes, A., 2011. The influence of plant root systems on subsurface flow: implications for slope stability. *Bioscience* 61, 869–879.
- Heldén, U., Tottrup, C., 2008. Regional desertification: a global synthesis. *Glob. Planet. Chang.* 64, 169–176.
- Johnson, P.M., Mayrand, K., Paquin, M., 2006. *Governing Global Desertification: Linking Environmental Degradation, Poverty and Participation*. Ashgate Publishing Company, Burlington, Ontario, Canada.
- Kidron, G.J., 2015. The role of crust thickness in runoff generation from microbiotic crusts. *Hydrol. Process.* 29, 1783–1792.
- Kidron, G.J., Tal, S.Y., 2012. The effect of biocrusts on evaporation from sand dunes in the Negev Desert. *Geoderma* 179–180, 104–112.
- Lai, Z.R., Zhang, Y.Q., Liu, J.B., Wu, B., Qin, S.G., Fa, K.Y., 2016. Fine-root distribution, production, decomposition, and effect on soil organic carbon of three revegetation shrub species in northwest China. *For. Ecol. Manag.* 359, 381–388.
- Langhans, T.M., Storm, C., Schwabe, A., 2009. Biological soil crusts and their microenvironment: impact on emergence, survival and establishment of seedlings. *Flora* 204, 157–168.
- Li, X.Y., Gao, S.Y., Xu, H.Y., Liu, L.Y., 2006. Growth of *Caragana korshinskii* using runoff-collecting microcatchments under semiarid condition. *J. Hydrol.* 328, 338–346.
- Li, X.R., Ma, F.Y., Xiao, H.L., Wang, X.P., Kim, K.C., 2004. Long-term effects of revegetation on soil water content of sand dunes in arid region of northern China. *J. Arid Environ.* 57, 1–16.
- Li, X.R., Tian, F., Jia, R.L., Zhang, Z.S., Liu, L.C., 2010. Do biological soil crusts determine vegetation changes in sandy deserts? Implications for managing artificial vegetation. *Hydrol. Process.* 24, 3621–3630.
- Logsdon, S.D., Jaynes, D.B., 1993. Methodology for determining hydraulic conductivity with tension infiltrometers. *Soil Sci. Soc. Am. J.* 57, 1426–1431.
- Maestre, F.T., Bowker, M.A., Cantón, Y., Castillo-Monroy, A.P., Cortina, J., Escobar, C., Escudero, A., Lázaro, R., Martínez, I., 2011. Ecology and functional roles of biological soil crusts in semi-arid ecosystems of Spain. *J. Arid Environ.* 75, 1282–1291.
- Mousaei Sanjerehi, M., 2013. Annual gross primary production and absorption of solar energy by *Artemisia* sp. in arid and semiarid shrublands. *Appl. Ecol. Environ. Res.* 11, 355–370.
- Ohte, N., Koba, K., Yoshikawa, K., Sugimoto, A., Matsuo, N., Kabeya, N., Wang, L., 2003. Water utilization of natural and planted trees in the semiarid desert of Inner Mongolia, China. *Ecol. Appl.* 13, 337–351.
- Pando-Moreno, M., Molina, V., Jurado, E., Flores, J., 2014. Effect of biological soil crusts on the seed germination of three plant species under laboratory conditions. *Botanical Sciences* 92, 273–279.

- Rodríguez-Caballero, E., Cantón, Y., Chamizo, S., Afana, A., Solé-Benet, A., 2012. Effects of biological soil crusts on surface roughness and implications for runoff and erosion. *Geomorphology* 145–146, 81–89.
- Siegal, Z., Tsoar, H., Karnieli, A., 2013. Effects of prolonged drought on the vegetation cover of sand dunes in the NW Negev Desert: field survey, remote sensing and conceptual modeling. *Aeolian Res.* 9, 161–173.
- Su, Y.G., Li, X.R., Cheng, Y.W., Tan, H.J., Jia, R.L., 2007. Effects of biological soil crusts on emergence of desert vascular plants in North China. *Plant Ecol.* 191, 11–19.
- Thai, K.V., Rahm, D., Cogburn, J.D., 2007. *Handbook of Globalization and the Environment*. CRC Press, Boca Raton, FL, USA.
- Tisdall, J.M., Nelson, S.E., Wilkinson, K.G., Smith, S.E., McKenzie, B.M., 2012. Stabilisation of soil against wind erosion by six saprotrophic fungi. *Soil Biol. Biochem.* 50, 134–141.
- Verstraete, M.M., Scholes, R.J., Smith, M.S., 2009. Climate and desertification: looking at an old problem through new lenses. *Front. Ecol. Environ.* 7, 421–428.
- Veste, M., Breckle, S.W., Eggert, K., Littmann, T., 2011. Vegetation pattern in arid sand dunes controlled by biological soil crusts along a climatic gradient in the Northern Negev desert. *Basic and Applied Dryland Research* 5, 1–16.
- Veste, M., Staudinger, M., Küppers, M., 2008. Spatial and temporal variability of soil water in drylands: plant water potential as a diagnostic tool. *Forestry Studies in China* 10, 74–80.
- Wang, X.P., Li, X.R., Xiao, H.L., Berndtsson, R., Pan, Y.X., 2007. Effects of surface characteristics on infiltration patterns in an arid shrub desert. *Hydrol. Process.* 21, 72–79.
- Wang, X.P., Li, X.R., Zhang, J.G., Zhang, Z.S., Berndtsson, R., 2005. Measurement of rainfall interception by xerophytic shrubs in re-vegetated sand dunes. *Hydrol. Sci. J.* 50, 897–910.
- Wang, X.M., Zhang, C.X., Hasi, E., Dong, Z.B., 2010. Has the Three Norths Forest Shelterbelt Program solved the desertification and dust storm problems in arid and semiarid China? *J. Arid Environ.* 74, 13–22.
- West, N.E., 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. In: Begon, M., Fitter, A.H., Macfadyen, A. (Eds.), *Advances in Ecological Research*. Academic Press, pp. 179–223.
- Xiao, B., Hu, K.L., Ren, T.S., Li, B.G., 2016. Moss-dominated biological soil crusts significantly influence soil moisture and temperature regimes in semiarid ecosystems. *Geoderma* 263, 35–46.
- Xiao, B., Wang, H.F., Fan, J., Fischer, T., Veste, M., 2013. Biological soil crusts decrease soil temperature in summer and increase soil temperature in winter in semiarid environment. *Ecol. Eng.* 58, 52–56.
- Xiao, B., Wang, Q.H., Zhao, Y.G., Shao, M.A., 2011. Artificial culture of biological soil crusts and its effects on overland flow and infiltration under simulated rainfall. *Appl. Soil Ecol.* 48, 11–17.
- Xiao, B., Zhao, Y.G., Shao, M.A., 2010. Characteristics and numeric simulation of soil evaporation in biological soil crusts. *J. Arid Environ.* 74, 121–130.
- Xiao, B., Zhao, Y.G., Wang, H.F., Wu, J.Y., 2014. Natural recovery of moss-dominated biological soil crusts after surface soil removal and their long-term effects on soil water conditions in a semi-arid environment. *Catena* 120, 1–11.
- Xu, J., Bai, X.L., Yang, C., Zhang, P., 2003. Study on diversity and binding-sand effect of moss on biotic crusts of fixed dunes. *Acta Phytoecologica Sin.* 27, 545–551 (in Chinese with English abstract).
- Xu, D.H., Li, J.H., Fang, X.W., Wang, G., 2007. Changes in soil water content in the rhizosphere of *Artemisia ordosica*: evidence for hydraulic lift. *J. Arid Environ.* 69, 545–553.
- Yair, A., Almog, R., Veste, M., 2011. Differential hydrological response of biological topsoil crusts along a rainfall gradient in a sandy arid area: Northern Negev desert, Israel. *Catena* 87, 326–333.
- Yang, Y.S., Bu, C.F., Mu, X.M., Shao, H.B., Zhang, K.K., 2014. Interactive effects of moss-dominated crusts and *Artemisia ordosica* on wind erosion and soil moisture in Mu Us Sandland, China. *Sci. World J.* 2014, 649816.
- Yin, J., He, F., Qiu, G., Xiong, Y., Zhao, S., He, K., Tian, J., Zhang, W., Liu, J., 2009. Characteristics of leaf areas of plantations in semiarid hills and gully loess regions. *Frontiers of Forestry in China* 4, 351–357.
- Yin, R.P., Wu, Y.S., Zhang, X., Ha, S., Tian, X.M., Li, Z.K., Wang, J., Miao, H.L., Ren, J., 2013. Effects of biological crusts on dew deposition and evaporation in the southern edge of the Mu Us Sandy Land, northern China. *Acta Ecol. Sin.* 33, 6173–6180 (in Chinese with English abstract).
- Zhang, Y.M., Belnap, J., 2015. Growth responses of five desert plants as influenced by biological soil crusts from a temperate desert, China. *Ecol. Res.* 30, 1037–1045.
- Zhang, Z.S., Liu, L.C., Li, X.R., Zhang, J.G., He, M.Z., Tan, H.J., 2008. Evaporation properties of a revegetated area of the Tengger Desert, North China. *J. Arid Environ.* 72, 964–973.
- Zhang, Y.M., Wang, H.L., Wang, X.Q., Yang, W.K., Zhang, D.Y., 2006. The microstructure of microbial crust and its influence on wind erosion for a sandy soil surface in the Gurbantunggut Desert of Northwestern China. *Geoderma* 132, 441–449.
- Zhang, Y.M., Wu, N., Zhang, B.C., Zhang, J., 2010. Species composition, distribution patterns and ecological functions of biological soil crusts in the Gurbantunggut Desert. *Journal of Arid Land* 2, 180–189.
- Zhang, J., Zhang, Y.M., Downing, A., Cheng, J.H., Zhou, X.B., Zhang, B.C., 2009. The influence of biological soil crusts on dew deposition in Gurbantunggut Desert, Northwestern China. *J. Hydrol.* 379, 220–228.
- Zhang, Z.S., Zhao, Y., Li, X.R., Huang, L., Tan, H.J., 2016. Gross rainfall amount and maximum rainfall intensity in 60-minute influence on interception loss of shrubs: a 10-year observation in the Tengger Desert. *Sci. Rep.* 6, 26030.
- Zhao, H.L., Guo, Y.R., Zhou, R.L., Drake, S., 2011. The effects of plantation development on biological soil crust and topsoil properties in a desert in northern China. *Geoderma* 160, 367–372.
- Zhuang, W.W., Serpe, M., Zhang, Y.M., 2015. The effect of lichen-dominated biological soil crusts on growth and physiological characteristics of three plant species in a temperate desert of northwest China. *Plant Biol.* 17, 1165–1175.