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Formation of litter crusts and its multifunctional ecological effects in a desert ecosystem

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Abstract. Desertification is one of the major issues in global environmental change, and it is of great concern to scientists and policy-makers in the world. Litter crusts can be of great importance for the restoration and management of desert ecosystems. The formation of litter crusts and its ecological effects on desert surface microhabitats were studied in a wind–water erosion crisscross desert region. It was found that litter crusts, especially the four-year litter crusts, exhibited a better soil storage capacity and temperature regulating ability when compared to the bare land, biocrusts, and two-year litter crusts; the four-year litter crusts significantly increased soil total porosity, soil water storage, and soil organic carbon content, but reduced soil bulk density. Furthermore, species richness, coverage, and plant height of seedlings in litter crusts were significantly greater than those in bare land and biocrusts. Although the bare land had the greatest total number of seedlings, the survival rate of seedlings was lowest there. Our findings revealed that litter crusts had significantly positive effects on soil moisture, soil temperature, soil physicochemical properties, and seedling establishment. The multifunctional ecological effects of litter crusts are more positive than lichen- and moss-dominated biocrusts in desert ecosystems.

Key words: desert ecosystem; litter crusts; microhabitats; moisture; physicochemical properties; seedling establishment; temperature; water storage capacity.

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Introduction

Drylands cover about 41% of the Earth's land surface, and many dryland regions around the world are affected by desertification. Desertification can result in rapid changes in soil properties, vegetation cover, plant community composition, and hydrologic conditions (D'Odorico et al. 2013), and these changes can further influence ecosystem balance and sustainable livelihoods. Therefore, as one of the major issues in global environmental change, desertification has attracted widespread attention from scientists and policy-makers in the world (Prince et al. 1998).

Eolian desertification is one of the most serious eco-environmental problems (Wang et al. 2012, Li et al. 2013). Among the regions with high risks of desertification in arid Asia, the Mu Us Desert is a representative area which has suffered wind and water erosion (Wang et al. 2017). With the occurrence of desertification, nutrients such as nitrogen (N), phosphorus (P), and potassium (K) in the soil are lost (Larney et al. 1998), and soil fertility declines (Lyles and Tatarko 1986, Field et al. 2010); consequently, the regional ecosystems are affected (Munson et al. 2011, Álvarez et al. 2012, Field et al. 2012, Wang 2013). Succeeding desertification and vegetation loss will result in degradation of a few soil physicochemical properties (Li et al. 2012). A series of means and measures, such as setting of mechanical sand barriers (Bo et al. 2015), afforestation (Zeng et al. 2009), and establishment of artificial terrace cropping systems (Wei et al. 2007), have been taken in an effort to modify the sand surface and restore soil fertility and have taken effects on controlling desertification.

Surface crusting has a strong impact on a number of soil properties even at small spatial scales, which ultimately determine various ecosystem functions (Assouline 2004). Soil surfaces in deserts are generally covered with biological soil crusts, which are composed of a group of organisms dominated by cyanobacteria, lichens, and mosses (Belnap 2003). Biocrusts have been described as a major contributor to the conservation of dryland ecosystems (Gao et al. 2017). These tiny organisms are very important to many processes in desert ecosystems despite their unassuming appearance (Li et al. 2011). Belnap (2003) illustrated that biocrusts were vital in creating and maintaining fertility in infertile desert soils, and they can fix both carbon (C) and N, capture nutrient-rich dust, and stimulate plant growth. Incidentally, we found another soil crust type in the Mu Us desert. The Mu Us desert, located in north-central China, has complicated soils and landforms, and sparse vegetation cover, and the land use there is unreasonable. Wind erosion and water erosion occur alternatively and accelerate each other when the weather changes dramatically in this area. In the bare sandy land of the wind–water erosion crisscross regions, some plant litter can be brought together occasionally due to the superposed interaction of wind and water erosion. In the case of rain erosion and wind burial, plant litter is embedded in sand; through the decomposition and decay of litter in consecutive years, a distinctive landscape characteristic is formed (Fig. 1B). Here, we define this kind of soil crust as "litter crust," which refers to the cohesiveness of the soil surface created by litter and soil. The long-term decomposition of litter results in abundant organic matters in the uppermost soil layers, which links loose particles together to form larger soil aggregates. Topsoil structure and morphology in the range of millimeters to a few centimeters are strongly influenced by the formation of litter crusts.

Biocrusts and litter crusts (Fig. 1A) were both major contributor to improve the surface micro-environmental conditions across the Mu Us Desert in response to the cessation of disturbance and restoration of vegetation, but the ecological functions of two crusts types showed some difference. As an integral component of near-soil surface characteristics, biocrusts occur on or within the top few centimeters of the soil surface. In arid regions, water availability limits most vascular plant cover, whereas these communities created an almost continuous living skin that mediates most inputs, transfers, and losses across the soil surface boundary. Biocrusts can highly influence soil physicochemical properties and hydrology by determining soil surface structure and morphology (Belnap et al. 2012, Gao et al. 2017, Wang et al. 2017). However, the biocrust-forming organisms are easily damaged by soil surface disturbance and are very slow to recover (Belnap 2003), whereas evidence testifies that the functional attributes of plant litter can have important implications for ecosystem properties where productivity is nutrient limited, for example, plant decomposition and nutrient availabilities (Hobbie 1992, Wardle et al. 1997, Eviner and Chapin 2003). This influence may be via impacts on the decomposition of species' litters in plant-litter layers. The above- and belowground plant-litter input constitutes the main resource of energy and matter for an extraordinarily diverse community of soil organisms connected by highly complex interactions (Hättenschwiler et al. 2005). Besides, the effects of litter layer on water evaporation reduction (Murphy et al. 2004), soil moisture regulation, and seedling establishment (Reader 1993) have also been confirmed. Previous research has mostly focused on the effects of biocrusts on miocrohabitats, and little research has paid attention to the formation and ecological functions of the litter crusts in the wind–water erosion crisscross regions. Consequently, it is essential to define and study litter crust in desert ecosystems.

In the present study, we studied the effects of litter crusts on soil properties in desert surface

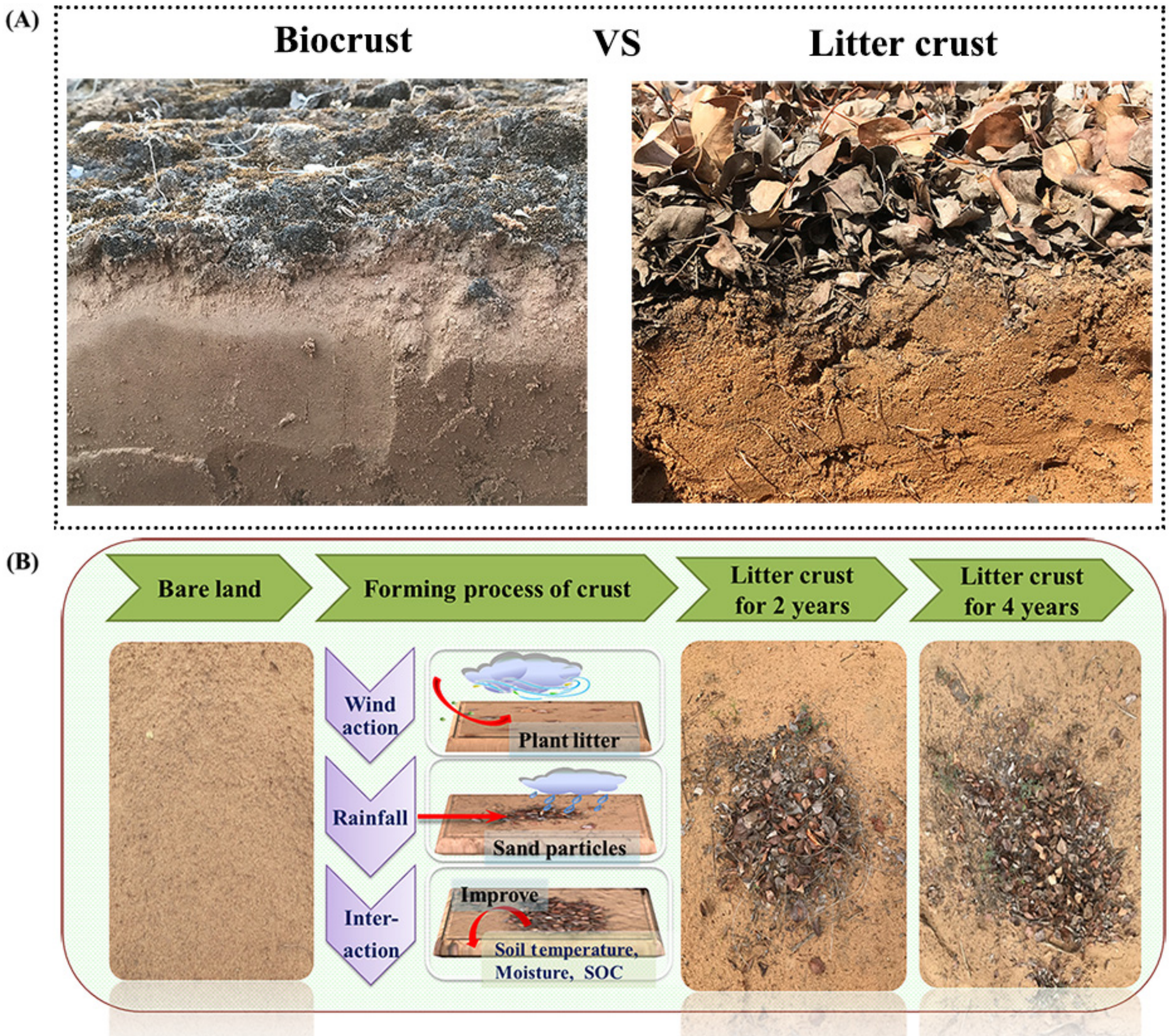

Fig. 1. The vertical soil profiles in biocrusts and litter crusts (A). The formation processes of litter crusts (B).

microhabitats and seedling establishment in the wind–water erosion crisscross region in the Mu Us desert and compared the influence of bare land, biocrusts, and litter crusts of different development stages on microhabitats. The objectives of this study were to (1) investigate the formation process of the litter crusts in the wind–water erosion crisscross region in the desert and (2) assess the ecological effects of the litter crusts on desert surface microhabitats, for example, maintaining soil moisture, regulating soil temperature, improving soil physicochemical properties, and promoting seedling establishment. The results are essential for the development of the framework of the litter crusts and its multifunctional ecological effects in desert ecosystems, and can provide a foundation for future work on litter crusts in desert ecosystems.

Methods

Study area

The study was carried out at Liudaogou (110°21′–110°23′ E, 38°46′–38°51′ N; 1080–1270 m altitude) located in the southern part of the Mu Us Desert, Shaanxi Province, China (Fig. 2). The study area is part of the water–wind erosion crisscross zone, with a typical continental

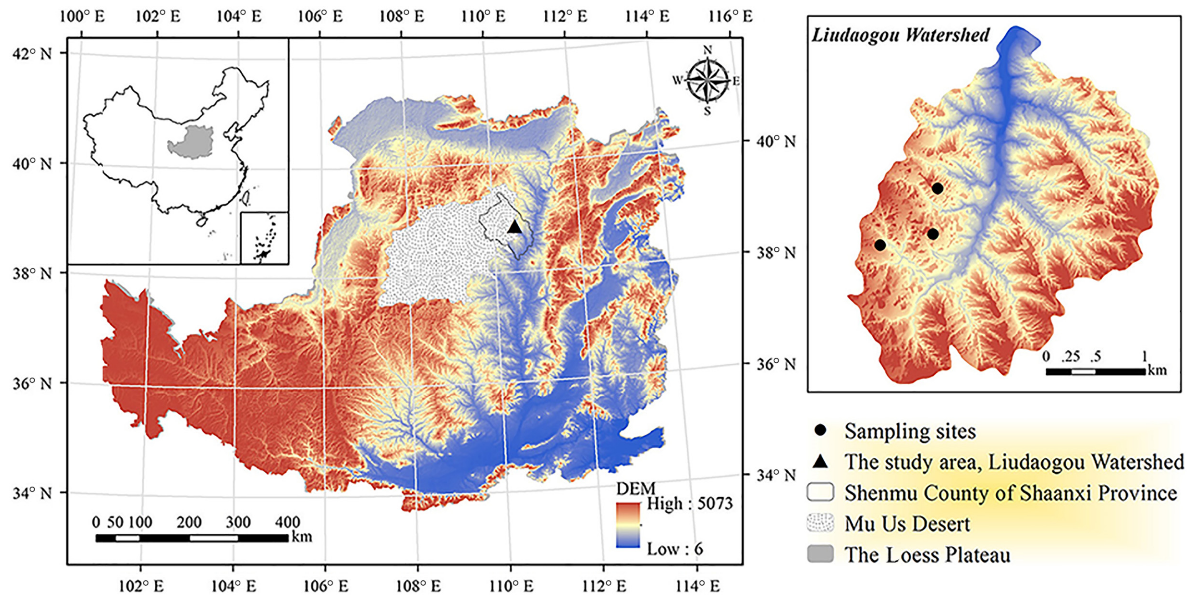

Fig. 2. Map of the study area and experimental sites in the Liudaogou watershed, China.

semi-arid monsoonal climate. The annual average precipitation is 437 mm, with 60–80% of the precipitation occurring concentratedly between June and September (Jia et al. 2015). The annual mean temperature is approximately 8.4°C, with the minimum monthly temperature ranging from −9.7° to –12.0°C in January, and the maximum monthly temperature ranging from 22.0° to 24.0°C in July. The annual average wind speed is about 2.2 m/s, northwest wind of which the speed is greater than 5 m/s occurs more than 200 d/yr, and wind erosion dominates in winter and spring. The mean annual potential evaporation is approximately 785 mm, and the mean index of aridity is 1.8. The landscape is characterized by typical desert ecosystems, where the mobile, the semi-fixed, and the fixed dunes coexist. The soil in the study area is a typical eolian sandy soil, which is highly vulnerable to water–wind erosion. The content of soluble nutrients in surface soil is around 5.10 g/kg, and vegetation succession faces severe challenges due to low soil fertility and harsh living environment. Dominant plant species in this area are mainly psammophytic shrubs and herbaceous plants, including *Artemisia ordosica*, *Salix cheilophila*, *Artemisia sphaerocephala*, *Astragalus adsurgens*, and *Lespedeza davurica.*

Experimental design and measurements

Field experiment was conducted in a flat ground of sands with a few arbors growing nearby in the southern part of the Mu Us Desert. Biocrusts and litter crusts are typical crust types in the study area. The coverage of biocrusts reached about 40%, while that of litter crusts which existed for one year or several years reached approximately 30%. In the study area, biocrusts were dominated by lichen and moss, while litter crusts were mainly composed of tree leaves from *Populus simonii* and other species. Three sites with similar environmental conditions were selected in this area, and the distance between each site was about 500 m. In order to compare the effects of biocrusts and litter crusts of development stages on microhabitats and seedling establishment, four treatments were designed, that is, bare land, biocrusts, two-year litter crusts (LC 2 yr), and four-year litter crusts (LC 4 yr), with the age of the litter crusts (LC 2 yr or LC 4 yr) determined according to the color of the litter and the adhesion degree of soil–litter mixture. Three replicate plots (1×1 m^2) were selected for each treatment at each site.

In April 2017, soil moisture and temperature in the 0- to 5-cm and 5- to 10-cm soil layers in each treatment were measured for ten days continuously, by using a Parrot Flower Power Wireless Indoor/Outdoor Bluetooth Smart Plant Sensor with a free dedicated app (Green, France). Soil moisture and temperature were recorded in the apparatus, from which the data were downloaded after ten days. During the ten-day measuring period, a rainfall event occurred and was recorded. The first five days (as whole days), soil moisture data were picked for the calculation of average soil moisture during a drying period, while the data around noon time (11:00–12:00 a.m.) of the fifth day were taken to represent the minimum soil temperature change of one day. The data of three whole days before the rainfall event and three whole days after the rainfall event were picked for the calculation and comparison of the mean soil moisture and temperature at different time.

Seedling investigations and soil sampling

In each treatment, a 50 × 50 cm quadrat at each site was selected. The number of species, the total number of green herbaceous seedlings, and dead individuals in each quadrat above the bare land and crusts' surface were recorded. Plant height, plant coverage, and crust thickness in each quadrat selected were measured.

Soil bulk density of the 0- to 5-cm and 5- to 10-cm soil layers was measured using the volumetric ring method. Soil samples were collected using a soil auger of 1 cm inner diameter, and then, air-dried subsamples were sieved through a 0.25-mm sieve. Subsamples of the soil were used for the determination soil organic carbon (SOC) content using the dichromate oxidation method. Soil total porosity and soil water storage were calculated using the following functions:

$$\mathrm{TP} = \left(1 - \frac{\mathrm{BD}}{\mathrm{ds}}\right) \times 100$$

where TP is the total soil porosity (%), BD is the soil bulk density (g/cm^3), and ds is the soil density (g/cm^3).

$$\omega = h \times \theta \times \mathrm{BD} \times 10^{-1}$$

where ω is the soil water storage (mm), h is the soil depth (cm), θ is the gravimetric water content (%), and BD is the soil bulk density (g/cm^3).

Data analysis

All data were expressed as mean ± standard error (SE) of mean. The Kolmogorov–Smirnov and Levene's tests were used to test the normality of data and the equality of variance. We conducted a combination of analysis of variance (ANOVA) on a subset of data. The Tukey's honestly significant difference (HSD) test was used to analyze the differences in soil physicochemical properties in the same soil layer within the different crusts type or in different soil layers within the same crusts type. The differences in seedling total number, coverage, and plant height of various crust types were tested using HSD. Two-way ANOVA was conducted to examine the main and interactive effects of various crusts treatment and soil depths on soil properties. Significant differences were evaluated at the 0.05 level. Correlation analysis was used to study the correlations among three-decomposed layer thickness of litter and seedling indexes. All statistical analyses were performed using the software program SPSS, version 12.0 (SPSS, Chicago, Illinois, USA), Figs. 3, 4 were drawn using Origin version 8.0, and Figs. 2, 5 were created using Revolution R Enterprise 8.0 (R Core Team 2014).

Results

Effects of crusts on soil moisture and temperature

The results of two-way ANOVA showed that soil moisture and temperature were significantly affected by the main effects of various crusts treatment and soil depths during sunny days (all $P < 0.01$; Table 1). Soil moisture in the 0- to 5-cm soil layer of bare land and crusts land was significantly lower than that in the 5- to 10-cm soil layer, but soil temperature exhibited the opposite results (Fig. 3). Meanwhile, soil moisture of the bare land and crusts showed contrasting results during sunny days. Soil moisture in the 0- to 5-cm soil layer of the bare land was 3.6% lower than that of the biocrusts, and soil moisture of the biocrusts and bare land was consistently lower than that the litter crusts, irrespective of the development stage of the litter crusts (Fig. 3A). Moreover, soil moisture in the 5- to 10-cm soil layer of LC 4 yr (18.64%) was significantly higher than that of the bare land, biocrusts, and LC 2 yr (Fig. 3A). As presented in Fig. 3B, soil temperature differed significantly

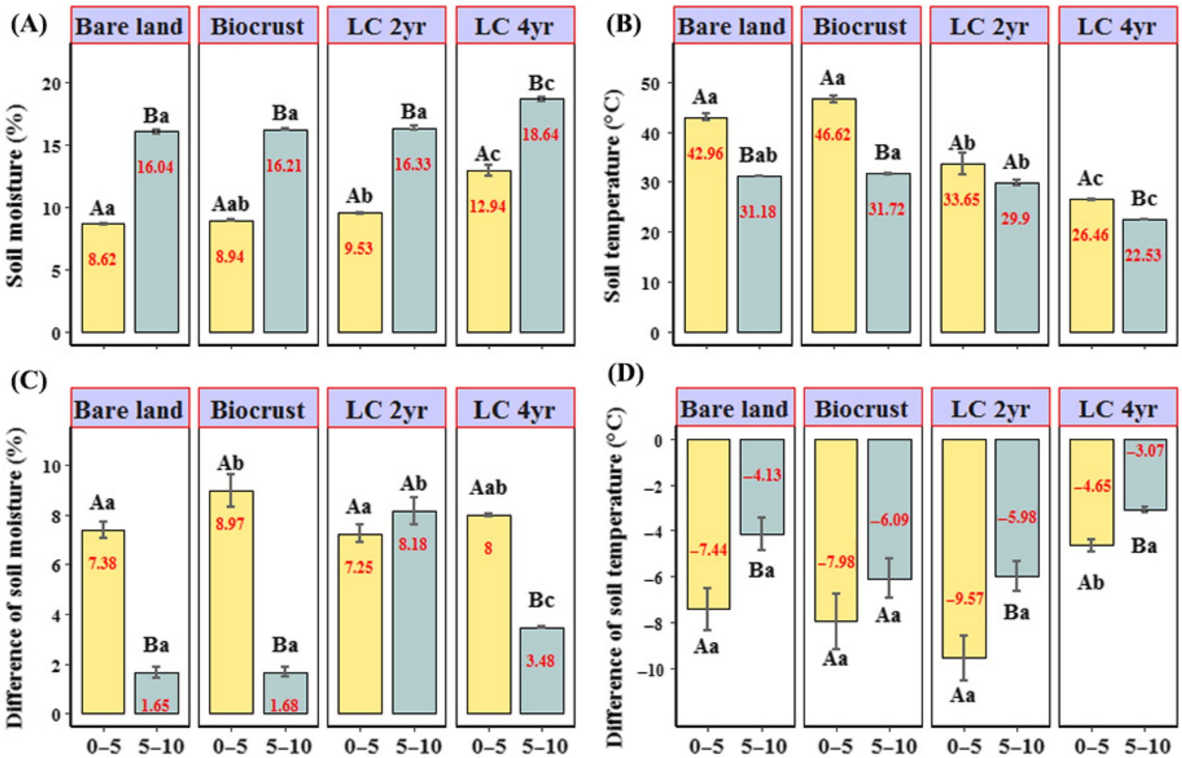

Fig. 3. Soil moisture and soil temperature of two soil layers (0–5 and 5–10 cm) during a drying period among the bare land, biocrusts, two-year litter crusts (LC 2 yr), and four-year litter crusts (LC 4 yr; A and B). The differences in soil moisture and temperature in both the 0- to 5-cm and 5- to 10-cm soil layers between the before-rain and post-rain period (C and D). Different lowercase letters indicate significant differences among the various crust lands in the same soil layer at the level of $P < 0.05$, and different uppercase letters indicate significant differences among the soil layers at the level of $P < 0.05$. Error bars indicate standard errors.

among treatments. Litter crusts presented lower soil temperature in both the 0- to 5-cm and 5- to 10-cm soil layers compared to the bare land and biocrusts. As a result, the four-year litter crusts showed the highest soil moisture but the lowest temperature among treatments.

After an occasional rainfall, the differences in soil moisture and temperature in both the 0- to 5-cm and 5- to 10-cm soil layers between the before-rain and post-rain period were marked, as what are shown in Fig. 3C, D. Differences in soil moisture and temperature in the 5- to 10-cm soil layer between the before-rain and post-rain were significantly lower than that in the 0- to 5-cm soil layer over treatments. Biocrusts exhibited a higher soil moisture changes in the 0- to 5-cm soil layer compared to the bare land and litter crusts, but the soil moisture fluctuation in the 5- to 10-cm soil layer of litter crusts was significantly higher than the bare land and biocrusts. Moreover, LC 4 yr showed the lowest soil temperature changes compared to other groups for both the 0- to 5-cm and 5- to 10-cm soil layers. Compared with the bare land and biocrusts, litter crusts, especially the LC 4 yr, exhibited a better soil water storage capacity and temperature regulating ability.

Effects of crusts on soil physicochemical characteristics

The interaction between crust types and soil layer was significant for soil bulk density, soil water storage, soil total porosity, and SOC content (Table 1). For both the 0- to 5-cm and 5- to 10-cm soil layers, soil bulk density in the LC 4 yr treatment was significantly lower than that of the bare land, biocrusts, and the LC 2 yr treatment (Fig. 4A). For the 0- to 5-cm soil layer, the soil

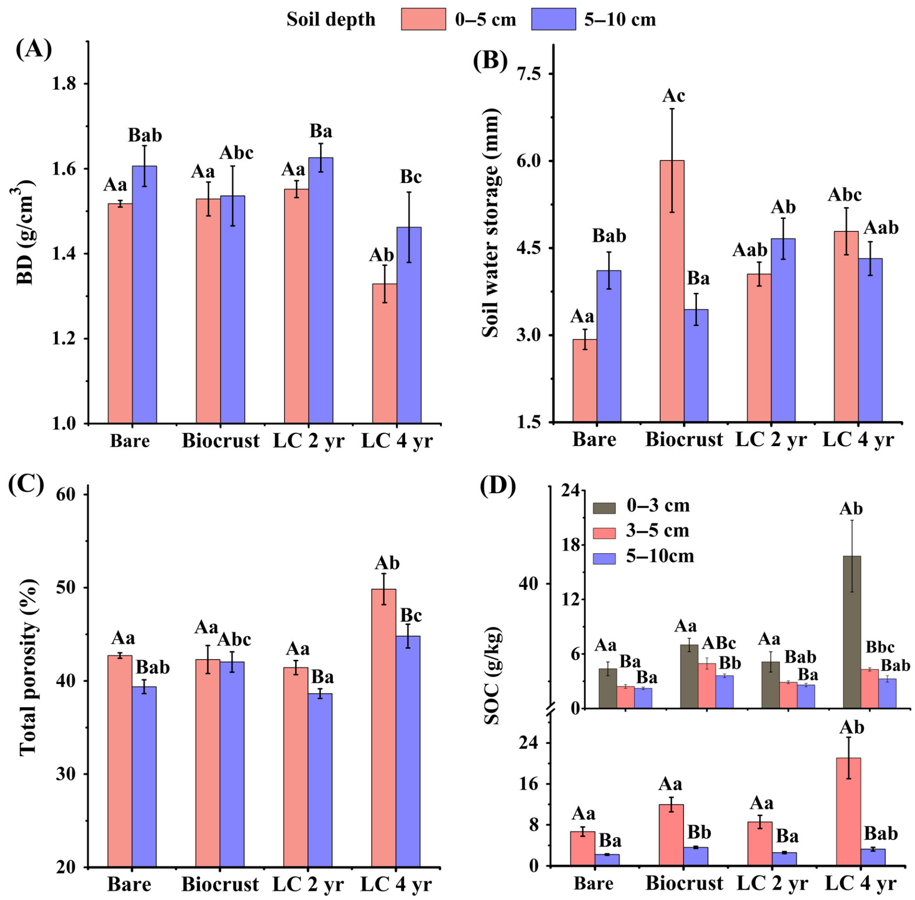

Fig. 4. Differences in soil physical properties of two soil layers (0- to 5-cm and 5- to 10-cm) among the bare land, biocrusts, two-year litter crusts (LC 2 yr), and four-year litter crusts (LC 4 yr). Different lowercase letters indicate significant differences among the various crust lands in the same soil layer at the level of $P < 0.05$, and different uppercase letters indicate significant differences among the soil layers at the level of $P < 0.05$. Error bars indicate standard errors.

water storage of biocrusts (6.0%) was about three times as much as that of the bare land, while the soil water storage of the litter crusts was about two times greater than that of bare land (Fig. 4B). Conversely, for the 5- to 10-cm soil layer, the soil water storage of biocrusts was the lowest among treatments. Moreover, the LC 4 yr treatment showed the highest soil total porosity, which was 17.8% and 13.8% higher than that of the bare land and other crust types in the 0- to 5-cm and 5- to 10-cm soil layer, respectively (Fig. 4C).

The content of SOC in the 0- to 5-cm soil layer of LC 4 yr was significantly higher than that of other treatments (Fig. 4D). Content of SOC in the 0- to 5-cm soil layer was the highest in LC 4 yr (3.5 times as much as the bare land), followed by biocrusts (two times as much as the bare land). Content of SOC in the 5- to 10-cm soil layer was at least 50% lower than that in the 0- to 5-cm soil layer; there was no significant difference in SOC content between the bare land and LC 2 yr, but both the bare land and LC 2 yr showed lower SOC contents than biocrusts and LC 4 yr.

Differences in seedling establishment between the bare land and crusts

The differences in seedling establishment indexes between the bare land and crust types were significant, as presented in Fig. 5. The lowest species richness, coverage, and plant height

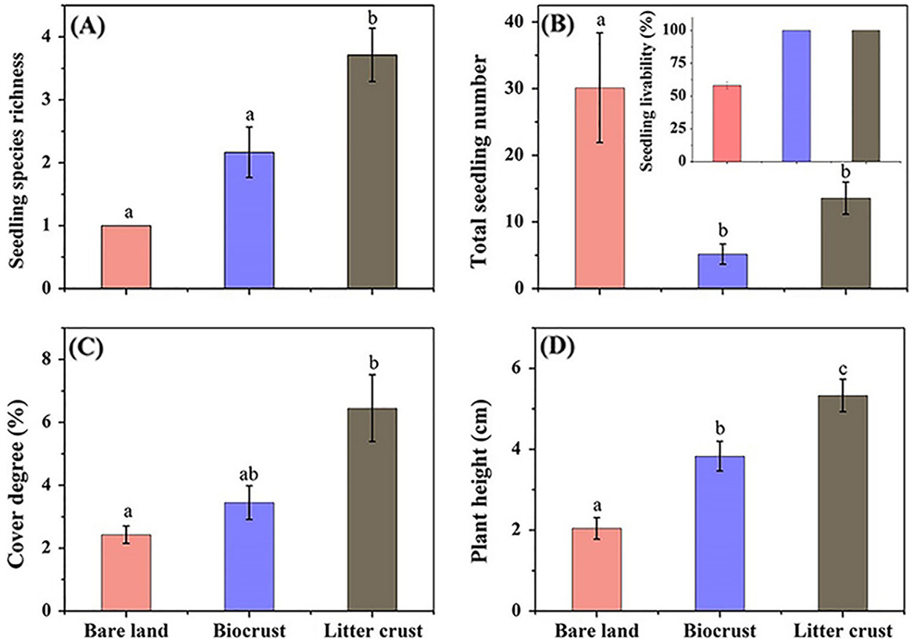

Fig. 5. Differences in seedling establishment indexes (A, seedling species richness; B, total seedling number; C, cover degree; D, plant height) among the bare land, biocrusts, and litter crusts. Means with different letters are significantly different ($P < 0.05$) between three groups as determined by ANOVA. Error bars indicate standard errors.

were recorded in the bare land. Although the total seedling number of the bare land was significantly higher than that of biocrusts and litter crusts, seedling survival rate of the bare land was the lowest. Species richness, coverage, and plant height of the biocrusts were 117%, 42.1%, and 87.2% higher than that of the bare land, respectively. Total seedling number of biocrusts was about six times lower than that of the bare land, but seedling survival rate was two times greater than that of bare land. Moreover, species richness, total seedling number, coverage, and plant height of biocrusts were 41.7%, 61.9%, 46.5%, and 28.2% lower than that of litter crusts, respectively. Furthermore, the relevance between seedling indexes and three-decomposed layer of litter is shown in Fig. 6. Results showed that the correlation coefficient between semi-decomposed layer with total number of seedling, species richness, and coverage was 0.74, 0.72, and 0.7, respectively, and the correlation coefficient between decomposed layer with total number of seedling, species richness, and coverage was 0.55, 0.81, and 0.7. But there was no significant relevance between non-decomposed layer of litter and seedling indexes. Therefore, litter crusts significantly promoted seedling establishment in the desert that was benefited by a long-term decomposition of litter.

Discussion

Formation process of litter crusts

Litter could provide a significant amount of substrate for decomposition and play an important role in biogeochemical cycling of nutrients (Loydi et al. 2013). Generally, soluble forms of nutrients are leached from the litter, and nutrient immobilization and mineralization occur in soil. Changes in soil texture take place with the ongoing litter decomposition (Aerts and Chapin 1999), which results in the gradual formation of litter crusts. The interaction between the sandy soil and the litter decomposition effectively improved the physicochemical characteristics of the soil (Fig. 4) and promoted the evolution of sand into loam, thus making nutrients available for seedlings. Formation of litter crusts improved the microenvironments around them, which favored seed germination and promoted the

Table 1. Results of two-way ANOVAs using various crusts soil treatment and soil depths as fixed factors.

Soil property	Statistical parameter *F*	Statistical parameter *P*	Soil depth 0–5 cm *F*	Soil depth 0–5 cm *P*	Soil depth 5–10 cm *F*	Soil depth 5–10 cm *P*
Moisture (%)						
Treatment	152.00	***	86.67	***	67.69	***
Depth	2720.45	***	–	–	–	–
Treatment: depth	8.89	**	–	–	–	–
Temperature (°C)						
Treatment	124.72	***	64.88	***	203.4	***
Depth	214.97	***	–	–	–	–
Treatment: depth	23.11	***	–	–	–	–
$\text{Temperature}_{\text{Dif}}$ (°C)						
Treatment	9.52	***	5.14	**	5.25	**
Depth	21.78	***	–	–	–	–
Treatment: depth	0.829	–	–	–	–	–
$\text{Moisture}_{\text{Dif}}$ (%)						
Treatment	27.68	***	3.59	*	100.80	***
Depth	257.95	***	–	–	–	–
Treatment: depth	47.77	***	–	–	–	–
Bulk density (g/cm^3)						
Treatment	18.10	***	10.63	***	8.73	***
Depth	14.06	***	–	–	–	–
Treatment: depth	1.68	–	–	–	–	–
Soil water storage (mm)						
Treatment	3.23	*	6.49	**	2.74	ns
Depth	1.08	–	–	–	–	–
Treatment: depth	7.71	***	–	–	–	–
Soil total porosity (%)						
Treatment	18.10	***	10.63	***	8.73	***
Depth	14.06	***	–	–	–	–
Treatment: depth	1.68	–	–	–	–	–
Soil organic content (g/kg)						
Treatment	13.20	***	11.55	***	11.73	***
Depth	89.74	***	–	–	–	–
Treatment: depth	9.91	***	–	–	–	–

Note: $\text{Temperature}_{\text{Dif}}$ and $\text{Moisture}_{\text{Dif}}$ indicates that the differences in soil temperature and moisture between the before-rain and post-rain period.

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$, ns $P > 0.05$.

establishment of seedlings (Fig. 1). Our results supported the hypothesis that litter crusts could modify the surface microhabitats of sand by maintaining soil moisture, regulating soil temperature, and improving soil physicochemical properties, thus promoting the establishment of herbaceous plant species. Compared to lichen- and moss-dominated biocrusts, litter crusts exhibited a better ability of regulating microhabitats and promoting seedling establishment in the sand. The microhabitats improved by litter crusts increase seedling formation, which in turn forms the pattern of vegetation succession in the water–wind erosion desert regions.

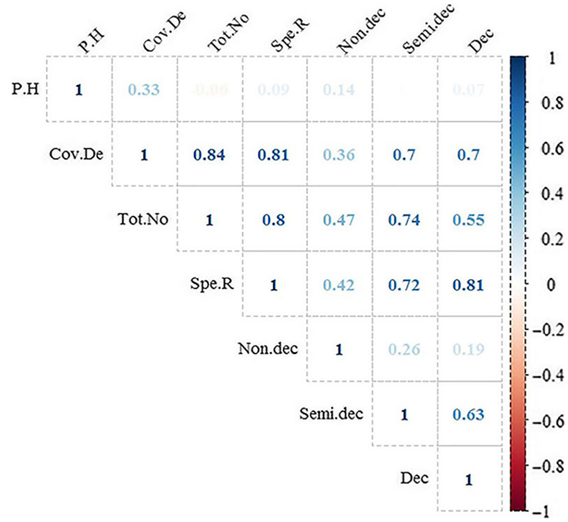

Fig. 6. The relevance between three-decomposed layer thickness of litter and seedling indexes (including total number of seedling, species richness, plant height, and coverage factors). P.H, plant height; Cov.De, coverage degree; Tot.No, total number of seedling; Spe.R, species richness; Non.dec, non-decomposed layer; Semi.dec, semi-decomposed layer; Dec, decomposed layer.

Multifunctional ecological effects of litter crusts

The triggering of key ecological processes in arid and semi-arid areas is strongly related to soil moisture and temperature, which is not only driven by rainfall and sunlight, but also by the type of soil and the covering above the soil (Noy-Meir 1973). In this sense, the presence of litter crusts and biocrusts modifies the surface soil characteristics, thereby finally conditioning soil moisture and temperature. In this study, we found that the most developed litter crusts showed the highest moisture but the lowest temperature in the sublayer soil when compared to the bare land and biocrusts. Meanwhile, after an occasional rainfall event, biocrusts exhibited the most significant changes in soil moisture in the upper soil layer (0–5 cm), but the moisture fluctuation in the 5- to

10-cm soil year of biocrusts was less significant than that of the litter crusts. Moreover, the four-year litter crusts showed the least significant changes in soil temperature in both the 0- to 5-cm and 5- to 10-cm soil layers. In general, the most development litter crusts exhibited a better soil water storage capacity and temperature regulating ability than the bare land and biocrusts, consistent with previous studies which have reported that one of the most important effects of litter seems to be the maintenance of soil moisture (Boeken and Orenstein 2001) and the reduction in temperature fluctuations beneath the litter layer (Eckstein and Donath 2005). A number of studies have been conducted to study the effects of biocrusts on water infiltration, most of which have shown that biocrusts can reduce the infiltration of water into sandy soils (Bisdom et al. 1993, Eldridge et al. 2000). Li et al. (2010) illustrated the presence of biocrusts which facilitated the maintenance of a higher water content in the upper soil layer than in the deeper soil layer may result in the reduced infiltration, and our study showed similar results (Fig. 3C). There are some studies showing that the reduction in water infiltration in response to biocrusts likely occurred as a result of improved topsoil structure (Li et al. 2006) and differences in rainfall amount (Li et al. 2010). Overall, compared with lichen- and moss-dominated biocrusts, the presence of litter crusts played a more positive role in soil moisture retention and soil temperature regulation, and in the improvement of the microhabitats on the extreme sand surface in the arid region.

Crusts can affect many soil properties involved in primary ecosystem processes in drylands, including hydrological processes and nutrient cycling. Hence, crusts have a great effect on components changes in soil textures, by aggregating soil stability (Schulten 1985), increasing water retention (Malam Issa et al. 2009), and OC and N content (Rogers and Burns 1994). Most studies have explored the effects of biocrusts on soil properties, and few previous publications have reported the changes in soil properties in the litter crusts and their underlying soils, with taking the development stage of the crusts into consideration. In terms of the development stage of litter crusts, we examined the effects of litter crusts on soil properties. Our results showed that four-year litter crusts significantly increased soil total porosity, soil water storage capacity, and SOC content, but reduced soil bulk density. Decomposition of plant litter plays a key role in the productivity and community composition of desert ecosystems (Aerts and Chapin 1999). The formation of soil organic matter from decomposition of plant litter contributes to the microhabitat improvement in sands, and the interaction between sandy soil and litter promotes the evolution of sand into loam. Therefore, the litter crusts effectively improved the soil physicochemical characteristics than lichen- and moss-dominated biocrusts (Fig. 4).

The establishment of seedling depends not only on the availability of seeds but also on seed dispersal and germination conditions. Generally, seed is transported to the surface of soil by wind and animal action, and then, subsequent movement of seeds over the surface of soil takes place (Watkinson 1978, Chambers and Macmahon 1994). Favorable conditions (light, temperature, soil moisture, and nutrition) should be provided for seed germination to increase the survival rate of seedlings and enhance seedling growth (Chambers and Macmahon 1994). Crusts are important for the establishment processes of new species at the soil–atmosphere boundary, which eventually affect the microhabitats on desert surface and seedling performance in drylands (Collins et al. 2008, Loydi et al. 2013, Chamizo et al. 2016). The results of the present study showed that the species richness, coverage, and plant height of seedlings in litter crusts were significantly greater than that in the bare land and lichen- and moss-dominated biocrusts. For the bare land, although it had the highest total seedling number, its seedling survival rate was the lowest, very likely due to the high soil temperature, low soil moisture, extreme light identity, and low soil fertility of the bare land. Previous studies have shown that seedling establishment in dry environments is facilitated by improvements in soil properties such as higher soil moisture (Fowler 1986), reduced light intensity (Boeken and Orenstein 2001), appropriate shading on the desert surface (Eckstein and Donath 2005), and the aggregation of soil nutrients (Facelli and Pickett 1991). Litter crusts significantly increased the survival rate and establishment of seedlings through improving the extreme soil conditions of the bare land. The positive effects of litter crusts on soil were more significant than those of lichen- and moss-dominated biocrusts (Figs. 3, 4). Therefore, litter crusts were identified as more suitable microhabitats for seedling establishment (Fig. 5).

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