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Litter crusts promote herb species formation by improving surface microhabitats in a desert ecosystem

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ABSTRACT

The degradation of soil and vegetation substantially damages ecosystem functions. Litter crusts play an active role in the vegetation restoration and management in desert ecosystems. In this study, the effects of litter crusts on surface microhabitats and species formation on sandy land were studied in the wind-water erosion crisscross region in the Mu Us Desert, northwest China. Soil microhabitat features including moisture, temperature, and organic matter content were measured in different positions of litter crusts and bare sand, seedling species richness, and total seedling number of all species were recorded in litter crusts on the sand's surface. The results showed that there were significant differences between litter crusts and bare sand in terms of soil moisture, temperature, organic matter content, and light intensity. Compared with that of bare sand, soil moisture below litter crusts was increased by an average of 17.0% overall, soil organic matter content was increased by 77.5% at the 0–5 cm depth and by 80.8% at the 5–10 cm depth. Litter crusts decreased soil temperature and light intensity by an average of 16.6% and 31.6%, respectively. Seedling species richness and total seedling number of all species were significantly higher in litter crusts than those in bare sand. Our findings revealed that litter crusts modify the surface microhabitats of sand by maintaining soil moisture, regulating soil temperature, increasing soil nutrients, and reducing light intensity, thus promoting species establishment in the wind-water erosion crisscross region.

1. Introduction

Drylands cover approximately 41% of the Earth's land surface (Reynolds et al., 2007), and 25% of these areas are affected by the changes in soil properties, hydrological conditions, vegetation cover or plant community composition that are often termed “desertification” (D'Odorico et al., 2013). Land desertification in arid and semi-arid areas is a global ecological and environmental problem. Depending on the geographic setting, desertification can result in the loss of soil resources, the salinization of soil, increases in bare soil or shifts in vegetation structure (Todd, 2006), which substantially damage ecosystem functions (Ravi et al., 2010).

In arid and semi-arid regions, deserts with crossing rivers usually suffer from complex soil erosion by wind and water. According to the survey report published by the World Meteorological Organization and the United Nations Environment Program (WMO-UNEP), over 17.5% of the total land area of the Earth is subjected to soil erosion by wind and water. Among the regions with high risks of desertification in arid Asia, the Mu Us Desert is a representative area that has suffered wind and water erosion (Wang et al., 2017). Difficulties in the recovery and management of sandy ecosystems hinder the restoration of degraded land in these regions. Previous studies of land recovery mainly focused on aspects of artificial systems (e.g., artificial terraces and alley cropping systems; Wei et al., 2007) and natural processes (e.g., biocrusts and physical crusts; Bu et al., 2014; Gao et al., 2017) which have essential influences on the interface of plant and soil.

There are evidences that the functional attributes of plant species can have important implications for the properties of ecosystems where productivity is nutrient-limited (Hobbie, 1992; Wardle et al., 1997; Eviner and Chapin, 2003). Such influences may be via impacts on the

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decomposition of species' litters in plant litter layers. Studies confirmed that the litter layer supplies substrate for decomposition and plays an important role in biogeochemical nutrient cycling (Aerts and Chapin, 1999; Brearley et al., 2003). Incidentally, we found a kind of soil crust type in the Mu Us desert, which was defined as “litter crust” and referred to the cohesiveness of the soil surface created by litter and soil (Jia et al., 2018). In the wind-water erosion crisscross regions, some plant litter can be brought together and embedded in sand due to the superposed interaction of rain erosion and wind burial; After consecutive years decomposition and decay of litter, litter crust landscape characteristics is formed. Because plant establishment is characteristically limited by water and nutrients in arid and semi-arid zones, some researches showed the effects of litter layer on water evaporation reduction (Murphy et al., 2004), soil moisture regulation, and seedling establishment (Reader, 1993). Usually a long-term decomposition of litter contributes toabundant organic matters in the uppermost soil layers, and topsoil structure and morphology are strongly influenced by the formation of litter crusts. Additionally, we found the growth of seedlings in the surface of litter crust area, which may be a response to the improvement of microhabitats in litter-soil interface. As a consequence, investigation of litter crust in desert ecosystems is necessary.

Here, we studied the effects of litter crusts on surface microhabitats characteristics including soil moisture, temperature, organic matter content, and light intensity, and on vegetation species establishment in the sand of the water–wind erosion crisscross region. Different positions at the litter crust patch may exhibit diverse characteristics due to the special microenvironment. Therefore, we designed an experiment to measure relevant parameters of different positions of litter crust patch and bare sands to determine the ecological effectiveness of litter crust, meanwhile we documented the crusts size and seedling characteristics to explore the relationships between species establishment with surface microhabitats in desert ecosystem. Our main objectives were to examine whether: 1) litter crusts can modify the surface microhabitats of sand by maintaining soil moisture, regulating soil temperature, accumulating organic matter, and reducing light intensity; and 2) litter crust increase species richness by improving the surface microhabitats of sand. We hypothesized that soil moisture and organic matter content would be higher beneath the litter crusts than in soil with no litter coverage, but that soil temperature beneath the litter crusts and light intensity on the surface of litter crusts would be lower compared with bare sand.

2. Material and methods

2.1. Study site and design

The study was conducted in the Liudaogou watershed (110°21′–110°23′E, 38°46′–38°51′N; 1080–1270 m a.s.l.) in Shenmu County, Shannxi Province, China. The study site is located in the southern part of the Mu Us desert, which is the largest mobile sand dune system with poor nutrient and dry conditions, and a typical water-wind erosion crisscross zone, i.e. the regions that suffer from complex soil erosion by wind and water, in northwestern China. The climate of this region is a typical continental semi-arid monsoonal climate. The mean annual daily temperature is 8.4 °C, and average daily temperatures range from −9.7 °C in January to 23.7 °C in July. Annual total solar radiation is 141–153 W m^{-2}, and the mean number of annual sunshine hours is approximately 2800–3100 h (Yang et al., 2014). Mean annual precipitation is 437 mm, with 60–80% of the precipitation concentrates in the period from June to September. Mean annual potential evaporation is approximately 785 mm, and the mean index of aridity is 0.56. The prevailing wind in this region is from the northwest and has an average annual wind speed of 2.2 m s^{-1}; wind of speeds > 5 m s^{-1} occurs > 200 days per year. Wind erosion dominates in winter and spring, while water erosion occurs in summer and autumn due to frequent rainfall. On the Loess Plateau in the water-wind erosion crisscross region, the amount of soil erosion is over 10,000 t km^{-2} yr^{-1} (She et al., 2014). The soil in the study region is a typical Aeolian sandy soil, and the landscape is characterized by fixed and semi-fixed sand dunes. The total content of soluble nutrients in surface soils in this region was 5.10 g kg^{-1}, with total N being 0.60 g kg^{-1}, and total P being 0.82 g kg^{-1}. Therefore, barren soil nutrients, low sand stability, high light intensity, and shortages of soil moisture all restrict seed germination and vegetative growth in this region. The representative vegetation of the study region consists of herbaceous plants and scattered shrubs such as *Artemisia ordosica*, *Salix cheilophila*, *Artemisia sphaerocephala*, and *Lespedeza davurica*.

The experiment was conducted on a sandy land (clay, < 0.002 mm, 0.88%; silt, 0.02–0.002 mm, 1.29%; sand, 2–0.02 mm, 97.84%) with a few arbors growing nearby in the southern part of the Mu Us desert. The coverage of litter crusts reached about 20% in the study region and was mainly composed of tree leaves from *Populus simonii*. Litter crusts was formed naturally and had existed for approximately more than two years. We chose three study sites with similar environmental conditions in terms of underlying bedrock, subsoil, microtopography, and soil hydrology, and the distance between each site was > 100 m. Litter crusts of 20–50 cm diameter and 2–5 cm thickness were selected for the study. We investigated the effects of different positions of litter crust on the characteristics of sand surface microhabitats, and four treatments were implemented. Bare sand was set as the control, while three sampling locations of litter crust were defined, i.e. (1) the center of the litter crust patch (Center), (2) halfway between the center and the edge of the litter crust patch (Middle), and (3) the outer edge of the litter crust patch (Edge) (Fig. 1). We selected a total of 27 patches of litter crusts at three sampling locations, with nine replications for each location.

2.2. Experimental setup

Soil moisture, soil temperature, and light intensity were measured at each sampling site of litter crusts and bare sands using a Parrot Flower Power Wireless Indoor/Outdoor Bluetooth Smart Plant Sensor with a free dedicated app – (Green, France). The apparatus was vertically inserted into the soil surface to measure soil moisture and soil temperature.at a depth of 0–10 cm. Simultaneously, the sensors were placed close to the surface of litter crusts or the bare sand to obtain light intensity precisely. At different sampling site of each patch, we used four apparatuses to measure the variables in different positions of the litter crust. These measurements were conducted around noon time (11:00 am–12:00 pm) to represent the minimum soil temperature change of one day.

The number of species and the total seedling number of all annual and perennial plants above the surface of the litter crusts were documented, and the patch diameter of each litter crust was measured. Meanwhile, the characteristics of seedlings were documented in bare sand using a 1 × 1 m frame quadrat. In order to explore the difference in soil organic matter content among treatments, soil samples at the depths of 0–5 and 5–10 cm were collected using a soil auger of 4-cm inner diameter. Soil samples were air-dried and then sieved at 2 mm to determine soil organic matter content by the dichromate oxidation method (Walkley and Black, 1934).

2.3. Data analysis

Data are expressed as the mean ± standard error (SE). The Tukey's honestly significant difference (HSD) test was used to analyze the differences in soil moisture, soil temperature, soil organic matter content, and light intensity between bare sand and three different positions of litter crust patches. Significant differences were evaluated at the 0.05 level. Regression lines were plotted to express the relationships between litter crust size and seedling species richness or total seedling numbers. All data were analyzed, and figures were created using Revolution R Enterprise 8.0 (Microsoft Corporation R version 3.2.2 2015). Shapiro-

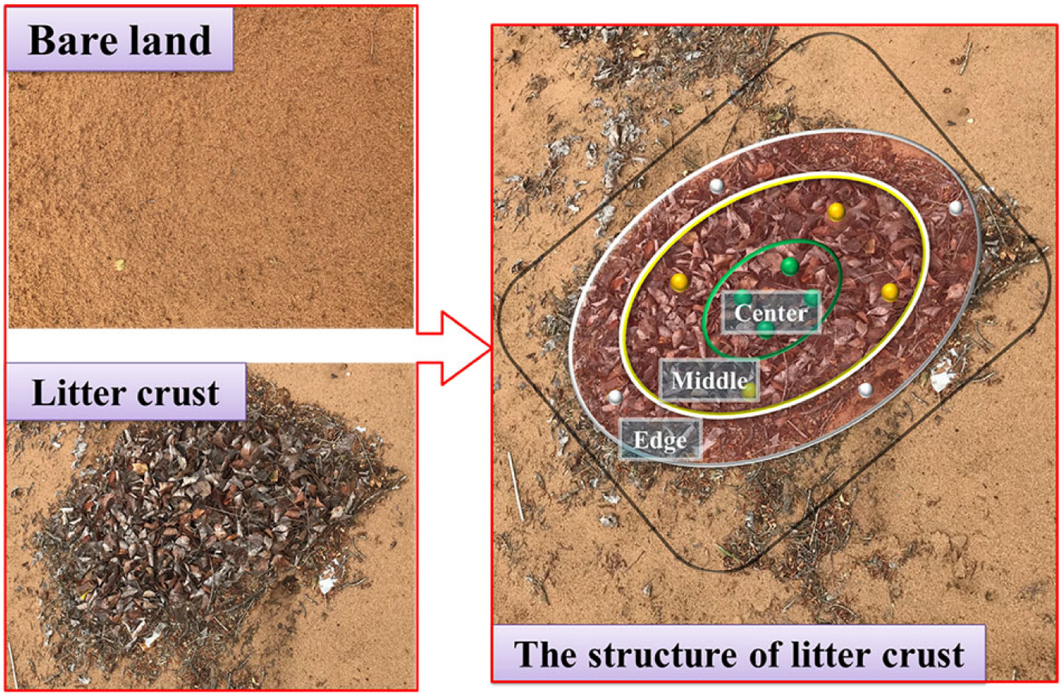

Fig. 1. Soil sampling locations: bare sand with no coverage (Bare), the center of the litter crust (Center), halfway between the center and the edge of the litter crust (Middle), and the outer edge of the litter crust (Edge).

Wilk normality test of different characteristics on microhabitat between bare sand and litter crust were performed and listed in Appendix B.

3. Results

3.1. Effects of litter crusts on surface microhabitats

Litter crusts had accumulated and decomposed for approximately two years according to our records in this study. The results showed that litter crusts were significantly different from bare sand in terms of soil moisture, temperature, organic matter content, and light intensity (Table 1). Compared with that of bare sand, soil moisture below the litter crusts was increased by an average of 17.0% ($F = 200$, $P < 0.01$, Fig. 2A), soil organic matter content was increased by 77.5% at the 0–5 cm depth ($F = 55.35$, $P < 0.01$) and by 80.8% at the 5–10 cm depth ($F = 17.86$, $P < 0.01$, Fig. 2D). Litter crusts decreased soil temperature and light intensity by an average of 16.6% ($F = 75.19$, $P < 0.01$, Fig. 2B) and 31.6% ($F = 45.17$, $P < 0.01$, Fig. 2C), respectively. In addition, soil moisture was lower in the center than in the edge of the litter crust, and soil organic matter was higher in the middle of the litter crust than in the center or the edge, nevertheless light intensity was the lowest in the middle of the litter crust (Fig. 2).

Table 1
Statistical results of one-way ANOVAs comparing soil parameters between litter crusts and bare sand: soil moisture, soil temperature, light intensity, and soil organic matter content.

Parameter	*df*	Litter crusts	Bare land	*F*	*P*
		Mean	Mean		
Soil moisture (%)	2	14.00	11.97	200	< 0.001
Soil temperature (°C)	2	22.21	26.62	75.19	< 0.001
Light intensity (Klux)	2	60.82	88.89	45.17	< 0.001
SOM (0–5 cm g kg^{-1})	2	6.80	3.83	55.35	< 0.001
SOM (5–10 cm g kg^{-1})	2	2.99	1.64	17.86	< 0.001

Note: SOM refers to soil organic matter content.

3.2. Effects of litter crusts on seedling establishment

The species richness and total number of annual and perennial plants were significantly higher in litter crusts than in bare sand (Fig. 3). Total seedling number reached approximately 16 plant in the litter crust patches but was only five plant in bare sand. Seedling species richness was on average five in litter crusts, which was approximately three times greater than that in bare sand. The seedling species were showed in appendix A.

Whereas multiple seedling characteristics were influenced by a series of environmental variables, seedling establishment in our study is mainly attributable to litter crust area. Litter crust area explained most of the variation in total seedling number ($R^2 = 0.70$, $P < 0.001$; Fig. 4A), while part of the variation in seedling species richness ($R^2 = 0.21$, $P < 0.05$; Fig. 4B). The slope of the relationship between litter crust area and total seedling number was estimated to be 0.011, which was higher than the estimate between litter curst area and seedling species richness (0.0015).

4. Discussion

Litter crusts affect soil surface properties by improving microhabitats in sand, including regulation of soil physical conditions and nutrient cycling. Numerous studies have reported the functions of litter in soil such as evaporation reduction (Murphy et al., 2004), water retention, nutrient release (Brearley et al., 2003), and the facilitation of seedling establishment (Reader, 1993). Our experimental results confirm that both surface microhabitats and seedling emergence are strongly affected by the formation of litter crusts in the water-wind erosion crisscross region.

In this study, light intensity at the surface of litter crusts was 16.6% lower on average than that of bare sand, and correspondingly, soil temperature at a depth of 0–10 cm beneath litter crusts was significantly lower than that in bare sands. Light intensity is probably related to the spectral reflectance of soil and vegetation, the "colour" and the amount of water (darkness) of litter result in its lower reflectance, thus litter crusts exhibited lower light intensity compared

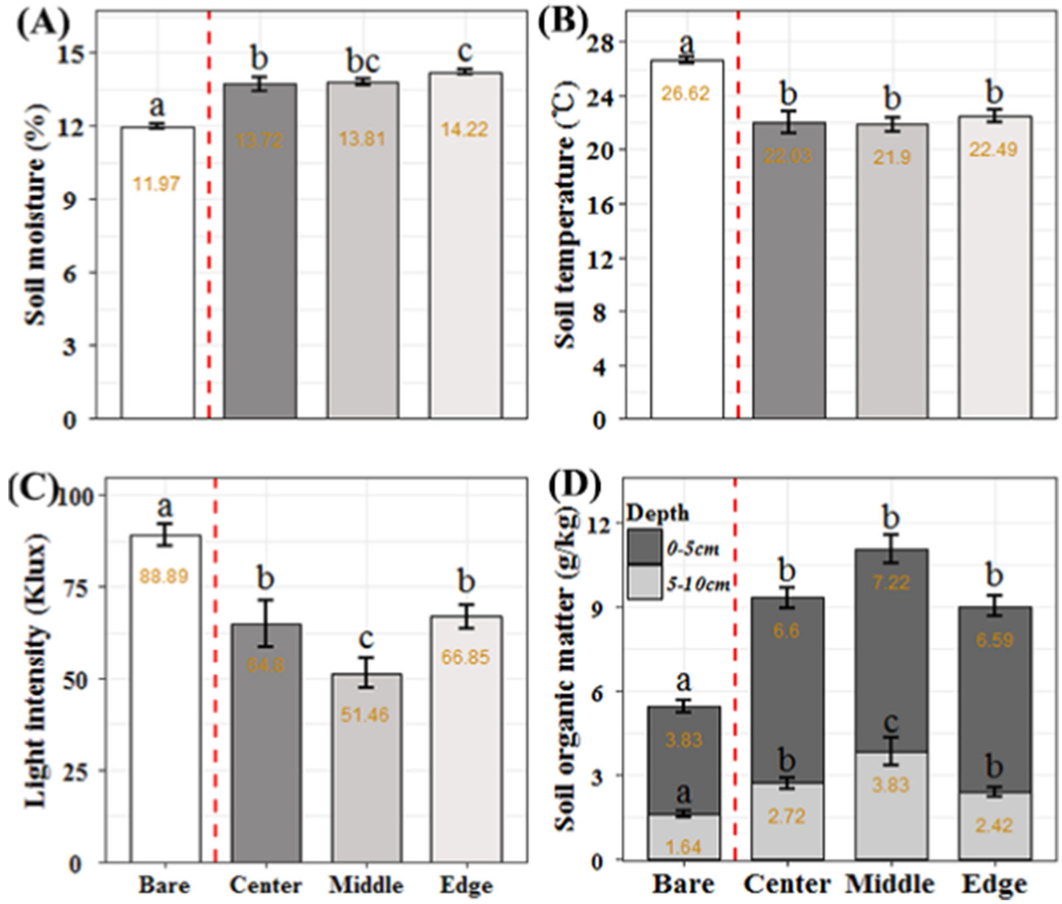

Fig. 2. Soil moisture, temperature, and organic matter content in mineral soil (0–10 cm in depth) in three different positions of the litter crusts (center, middle, and edge) and bare sand, and light intensity at the surface of litter crusts and bare sand. Means with different letters are significantly different ($P < 0.05$) between sampling locations as determined by ANOVA. Error bars indicate standard errors. Bare: bare sand with no coverage; Center: the center of the litter crust; Middle: halfway between the center and the edge of the litter crust; Edge: the outer edge of the litter crust.

with bare sands. We speculated that light intensity had a strong effect on soil temperature, especially near the soil surface where lower radiation was associated with a decreasing soil temperature. Eckstein and Donath (2005) reported that one of the most important effects of litter seems to be the maintenance of soil moisture and the reduction in temperature fluctuations beneath the litter layer. Our results confirmed these effects, since soil moisture beneath the litter crusts was significantly higher than that of bare sand, which may be relate to the lower soil temperature beneath litter crusts. In addition, three different positions of litter crust also showed differences in soil moisture, light intensity and organic matter content. Soil moisture was lower in the center than in the edge of the litter crust, probably due to the higher evaporation in the center; organic matter content was higher in the middle of the litter crust than in the center or the edge, possibly because of the lower light intensity and organic matter mineralization rate in the middle of the litter crust.

Litter could provide a substrate for decomposition, and play an important role in nutrient cycling and community composition in desert ecosystems (Aerts and Chapin, 1999). Compared with that of bare sand, soil organic matter content beneath litter crusts was increased by an average of 77.5% at a depth of 0–5 cm and by 80.8% at a depth of 5–10 cm; the higher soil organic matter content in the surface soil of litter crusts is mainly attributed to the decomposition of litter. Cotrufo et al. (2015) proposed two pathways of litter decomposition contributing to soil organic matter formation, i.e. (1) a dissolved organic matter-microbial path occurs early in decomposition when litter loses mostly non-structural compounds, which are incorporated into microbial biomass at high rates, resulting in efficient soil organic matter formation, and (2) an equally efficient physical-transfer path occurs when litter fragments move into soil. These two pathways result in soil organic matter stabilization, thus improving soil surface properties. Due to the presence of litter crusts, soil moisture retention, soil temperature regulation, reduced light intensity, and high soil nutrient content improved the harsh environment and surface properties of sands in the wind-water erosion crisscross region.

The establishment of new seedlings depends not only on the availability of seeds but also on the dispersal and germination position of seeds. Seed dispersal usually involves two phases (Watkinson, 1978; Chambers and Macmahon, 1994): transport from the mother plant to the soil surface by abiotic and biotic factors (Watkinson, 1978), and the subsequent movement of seeds over the soil surface. Aguiar and Sala (1997) illustrated that microsites covered by litter had higher seed density than bare-soil microsites, indicating that litter crusts play an important role in intercepting seeds. In this study, total seedling number and seedling species richness in litter crusts were significantly greater than that in bare sand, indicating the positive influences of litter crusts on seedling establishment. 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 soil surface (Eckstein and Donath, 2005), and the aggregation of soil nutrients (Facelli and Pickett, 1991). As litter crusts can effectively improve the poor soil conditions of sands, they can increase the survival rate and establishment of seedlings. Moreover, litter crusts of larger size facilitate an increase in total seedling number and seedling species richness, indicating that seedling establishment

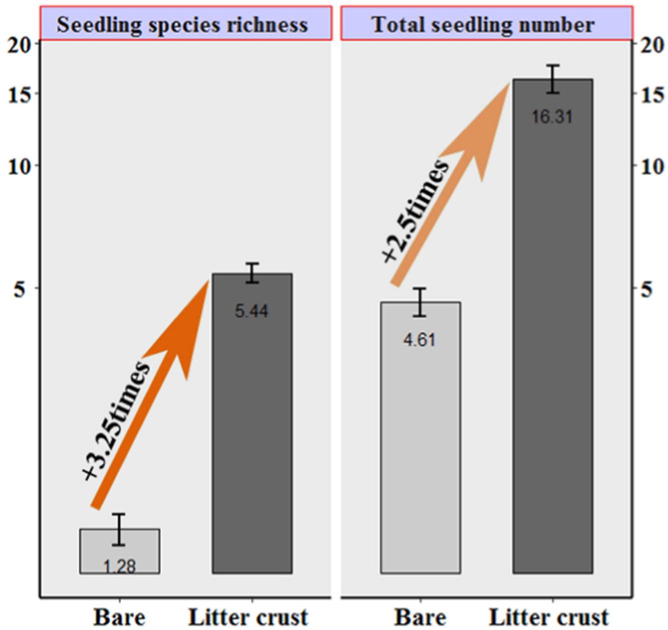

Fig. 3. Differences in seedling species richness and total seedling number between bare sand and litter crust patches. Means are significantly different ($P < 0.05$) between bare sand and litter crusts as determined by ANOVA. Error bars indicate standard errors. The upward arrow represents the multiplicative increase in seedling species richness or total seedling number between bare sand and litter crusts.

strongly requires a large litter crusts area. Meanwhile, the number of individual seedlings living in the litter crust surface is more easily restricted by crust area than seedling species richness is. These effects of increased litter crust area are mostly caused by a longer time for litter accumulation and decomposition, which can concentrate more nutrients, improve soil surface properties and provide a preferable habitat for seedling establishment. In summary, litter crusts play a positive role in seed germination, and provide favorable conditions for vegetation species formation by improving surface microhabitats of sand in the wind-water erosion crisscross region.

5. Conclusion

Litter crusts can be of great importance to sand recovery, given their critical roles in the surface microhabitats improvement and vegetation formation in the desert ecosystem. These results confirmed our hypothesis that litter crusts improved the surface microhabitats of sand by maintaining soil moisture, regulating soil temperature, releasing nutrients, and reducing light intensity, thus promoting herb species establishment. The presence of litter crusts is important for the restoration and management of sands in semi-arid regions. The microhabitats formed by litter crusts increase seedling establishment, which in turn forms the pattern of vegetation succession. In the desert ecosystem region studied here, each pattern in the cycle of vegetation succession benefited from the previous stage.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2018.07.024.

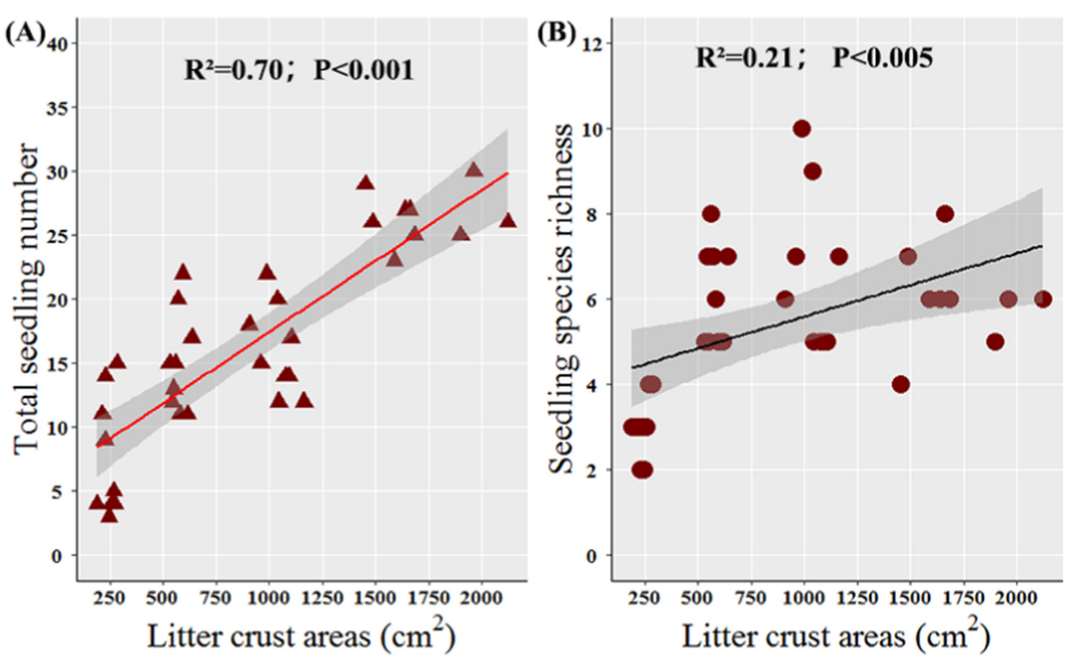

Fig. 4. Relationships between litter crust area and (A) total seedling number, or (B) seedling species richness. Circles and triangle indicate means of replicate plots; the lines (brownish-red line and black line) and gray shadows represent linear regressions fit through the plot data and 95% confidence intervals around the regressed means, respectively. R^2 values and P values apply to the linear regression fits in each panel. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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