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ORIGINAL ARTICLE

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Growth responses of five desert plants as influenced by biological soil crusts from a temperate desert, China

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Abstract In almost all dryland systems, biological soil crusts (biocrusts) coexist alongside herbaceous and woody vegetation, creating landscape mosaics of vegetated and biocrusted patches. Results from past studies on the interaction between biocrusts and vascular plants have been contradictory. In the Gurbantunggut desert, a large temperate desert in northwestern China, well-developed lichen-dominated crusts dominate the areas at the base and between the sand dunes. We examined the influence of these lichen-dominated biocrusts on the germination, growth, biomass accumulation, and elemental content of five common plants in this desert: two shrubs (*Haloxylon persicum*, *Ephedra distachya*) and three herbaceous plants (*Ceratocarpus arenarius*, *Malcolmia africana* and *Lappula semiglabra*) under greenhouse conditions. The influence of biocrusts on seed germination was species-specific. Biocrusts did not affect percent germination in plants with smooth seeds, but inhibited germination of seeds with appendages that reduced or eliminated contact with the soil surface or prevented seeds from slipping into soil cracks. Once seeds had germinated, biocrusts had different influences on growth of shrub and herbaceous plants. The presence of biocrusts increased concentrations of nitrogen but did not affect phosphorus or potassium in tissue of all tested species, while the uptake of the other tested nutrients was species-specific. Our study showed that biocrusts can serve as a biological filter during seed germination and also can influence growth and elemental uptake. Therefore, they may be an important trigger for determining desert plant diversity and community composition in deserts.

Keywords Biological soil crusts · Seed germination · Seedling growth · Element uptake · Temperate desert

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Introduction

Seed dispersal and germination, and seedling emergence, are defining points in the successful establishment of a plant and thus determine the initial stages of plant distribution and community composition. For this reason, many studies have focused on how seed traits (e.g., mass, shape, and external morphology such as appendages) interact with microsite characteristics (e.g., climate, soil moisture, existing plants, and physical soil properties) (Grubb 1977; Baskin and Baskin 1998) to affect these processes. External seed morphology is believed to influence germination via effects on water absorption (Baskin and Baskin 1998; Fenner and Thompson 2005) and to affect dispersal through either enhancing seed movement (e.g., to escape competition or predation) or inhibiting it (e.g., retention in a favorable environment) (Boeken and Shachak 1994; Fenner and Thompson 2005; Gros et al. 2006). In all desert ecosystems, scant and highly variable precipitation also exerts strong selective pressures on all aspects of plant development, including seeds (Noy-Meir 1973).

Biological soil crusts (biocrusts) typically consist of a mixture of mosses, lichens, algae, cyanobacteria, bacteria, fungi, and microfauna. Owing to their extraordinary abilities to survive extreme conditions such as complete desiccation, high temperatures (up to 70 °C), solar radiation, and high soil pH and salinity, biocrusts occur in deserts worldwide and can constitute as much as 70 % of the living ground cover (Belnap 2003). As documented by numerous studies, biocrusts play significant ecological roles in desert ecosystems (Eldridge and Greene 1994; Belnap 2003). These communities can benefit soil structure (Zhang et al. 2006; Chen et al. 2009), stability, and fertility (Kidron 2007; Belnap et al. 2008; Li et al. 2008; Zhang et al. 2009); affect surface hydrology (Belnap 2006); increase carbon (Li et al. 2012) and nitrogen (N) in soils (Evans and Ehleringer 1993; Housman et al. 2006; Wu et al. 2009), as well as enrich the diversity and abundance of soil fauna (Lalley et al. 2006; Li et al. 2006).

Biocrusts can affect germination and establishment of vascular plants, although their influence can be positive, negative, or neutral, depending on the species of plant and the external morphology and composition of the biocrust community (Zaady et al. 1997; Prasse and Bornkamm 2000; Gutterman 2003; Hawkes 2004; Li et al. 2005; Serpe et al. 2006; Deines et al. 2007; Escudero et al. 2007). Studies show biocrusts can have a positive influence on the colonization of vascular plants in the field in many settings, including polar (Anderson and Bliss 1998; Bliss and Gold 1999; Cooper et al. 2004; Breen and Levesque 2006), cool (Harper and Belnap 2001), and hot arid areas (DeFalco et al. 2001; Scott and Morgan 2012).

Experiments under laboratory conditions have shown that biocrusts can facilitate seed germination (St Clair et al. 1984; Rivera-Aguilar et al. 2005) and increase plant height and biomass (Belnap 2003). Studies have also shown negative correlations between vascular plant success and biocrusts across various biocrust types, including lichen-dominated (Deines et al. 2007; Serpe et al. 2008), moss-dominated (Serpe et al. 2006), and cyanobacterial ones (Zaady et al. 1997; Prasse and Bornkamm 2000). Other researchers have reported that the occurrence of biocrusts has negligible effects on germination and seedling growth compared with bare soil (Li et al. 2005; Rivera-Aguilar et al. 2005; Serpe et al. 2006; Deines et al. 2007). Studies have also shown the presence of biocrusts can alter nutrient concentrations in plant tissue, especially N (DeFalco et al. 2001; Pendleton et al. 2003; Langhans et al. 2009, 2010). In this study, a series of greenhouse experiments were used to test the hypothesis that biocrusts affect vascular plants differentially at various life stages, depending on seed morphology, life form, and species.

Materials and methods

Study site description

The Gurbantunggut Desert is situated in center of the Junggur Basin in the Xinjiang Uygur Autonomous Region of northwestern China. It is the second largest desert in China with an area of 48.8×10^3 km^2. Mean annual precipitation is approximately 79 mm, falling predominantly during spring. Mean annual evaporation is 2606 mm. Average temperature is 7.3 °C. Wind speeds are greatest during late spring, being 11.2 m s^{-1}, and are predominantly in WNW, NW and N directions. Natural vegetation is dominated by the shrubs *Haloxylon ammodendron* and *H. persicum*, with a total vegetative cover of less than 30 %. The area is covered by large and dense semi-fixed sand dunes. Abundant biocrusts cover all soil surfaces except the top half of sand dunes (Zhang et al. 2007).

Plant selection and seed collection

We conducted an initial field survey to determine the frequency and abundance of vascular plant species in our study area. Using this data, we chose the 15 most common plant species. At least 100 seeds were collected from at least 20 individuals of these species at the end of June and August of 2011. The collected seeds were then tested for germinability on filter paper. For each species, we placed 20 seeds in five replicate 90 mm Petri dishes containing filter papers continuously moistened with distilled water. Seeds were incubated in a growth chamber with a constant temperature of 20 °C. Of the 15 species tested, we then selected *H. persicum*, *Ephedra distachya*, *Ceratocarpus arenarius*, *Malcolmia africana* and *Lappula semiglabra* for further study, as they all had consistently high (>80 %) germination and best met our desired range of plant life form (herbaceous and woody plants) and seed traits (size, shape, and weight). We then characterized a subset of the seeds from these species for their size, shape, weight and the presence or absence of seed appendages. The rest of the seeds were then stored under dry conditions at 5 °C until used for the greenhouse experiment.

Biocrust and bare soil sample collection for greenhouse experiments

Lichen-dominated biocrusts are the prevalent biocrust type in the Gurbantunggut Desert (Zhang et al. 2006, 2007). In October, 2012, we selected a typical interdune area with an approximate size of 30 m x100 m in southern part of this desert, where the most dominant lichen species is *Collema tenax*, and low growing forms of other lichen species such as *Caloplaca* and *Placidium*, and the moss *Syntrichia caninervis* occur. Within this sampling area, we also randomly selected a 10 × 10 m sub-site where biocrusts and the top 5 cm of underlying soil were removed to create bare soil for future sample collecting; the rest of the interdune area was not disturbed. After seven months' treatment (April 2013), we returned and excavated biocrust and soil samples for the greenhouse experiment in open interspaces between perennial vegetation. Using cylindrical collecting augers (15 cm in diameter, 17 cm in height), we randomly collected 25 intact biocrusted samples and 25 bare soil samples where the biocrust had been previously removed.

Greenhouse experiments

The experiment was carried out in a shade-net greenhouse in the Fukang Desert Station of Chinese Academy of Sciences, which is located in the southern fringe of the Gurbantunggut Desert. The biocrusted and crust-removed samples were taken to the greenhouse. In order to exhaust the seed bank in the samples, we watered the dishes daily and removed all seedlings that appeared. After seven consecutive days with no seedlings, we considered the soil samples seedless and used them for our seed germination experiment. For each of the five plant species, we used five replicates of biocrusted and five replicates of biocrust-removed pots for a total of 10 pots per species and 50 pots for the experiment. Twenty seeds of each species were spread randomly on the surface of each pot, without inserting them into the soil, to imitate the first stages of natural dispersal. Every second day 150 ml of water was applied as a fine mist to each pot. Radicle emergence from the seed was recorded daily and used to calculate percent germination. We also measured seedling height of five marked seedlings in each pot every 5 days. The greenhouse experiment lasted for 2 months. At the end of the experiment, we harvested leaves and stems for above ground biomass and roots for below ground biomass separately for each species. Materials were then oven-dried at 70 °C and weighed.

Measurement of element concentrations in plant tissues

Plant tissue element analyses were performed by the Key Laboratory of Biogeography and Bioresources, Chinese Academy of Sciences. Plant tissue samples were prepared and analyzed using the traditional methods as described in Harper and Pendleton (1993).

Data analysis

For each species, the effects of both biocrusted soil and crust-removed soil on percent emergence, seedling growth rate, shoot height, ending biomass accumulation and root:shoot ratios were analyzed using one-way ANOVA to determine whether there were significant differences among treatments. Differences among treatments were detected with Tukey's HSD test. All the statistical analyses were performed using SPSS, version 9.0 (SPSS, 1998).

Results

Seed traits

The main seed traits and seed morphology of five tested species are shown in Fig. 1. Three of the tested species had appendages. Seeds of *H. persicum* have membra-

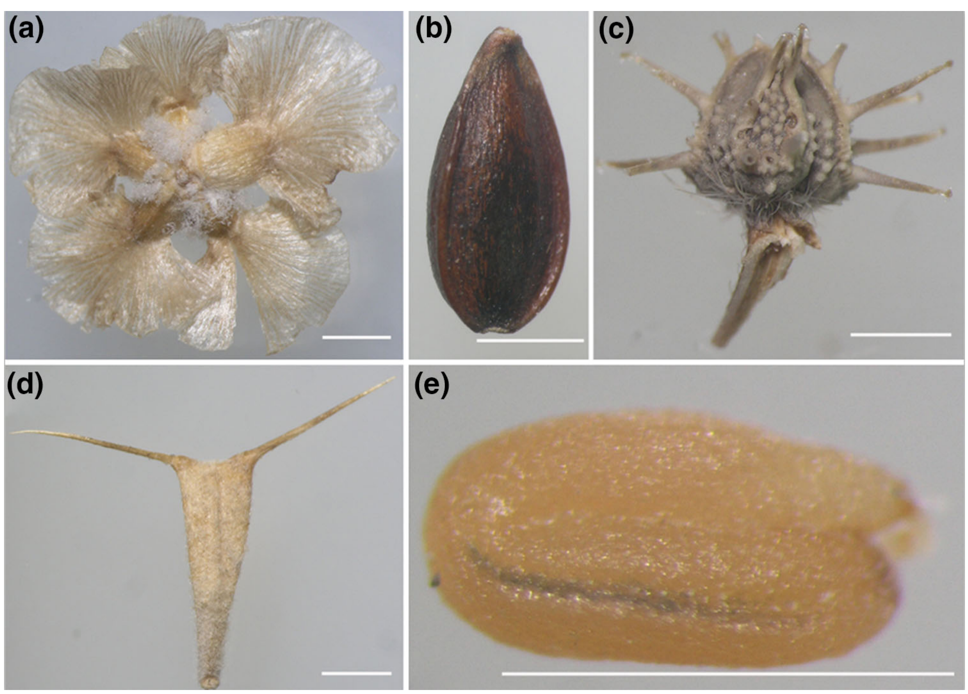

Fig. 1 Seed morphology of five plant species. **a** *Haloxylon persicum*; **b** *Ephedra distachya*; **c** *Lappula semiglabra*; **d** *Ceratocarpus arenarius*; **e** *Malcolmia africana*. *Scale bar* 1 mm. Three of them have seed appendages and two of them have smooth surface

nous winged appendage around the seeds, whereas seeds of *L. semiglabra* have structures on the opposite side of the germination pore, with several short thorns on the center of this side. Seeds of *C. arenarius* are wrapped in a cuniform utricle that is covered by stellate hairs. In addition, there are needle-like thorns in two corners. However, unlike *H. persicum* or *L. semiglabra*, seeds of *C. arenarius* are flat. In contrast, the seeds of *M. africana* and *E. distachya* have no appendages and their surfaces are smooth. Therefore, we had woody and herbaceous seeds with and without appendages.

Seed germination

Biocrusts affected percent germination differently among the five tested plant species (Fig. 2). Percent germination was the same on biocrusted and biocrust-removed soils for the two plants whose seeds lack appendages: the woody *E. distachya* and the herbaceous *M. africana* ($P > 0.05$). In contrast, the emergence of *H. persicum*, *C. arenarius* and *L. semiglabra* were all significantly inhibited by biocrusts ($P < 0.05$) and all three have relatively large seed appendages.

For *E. distachys* and *M. africana,* both of which have smooth seeds but are of greatly disparate life form, seed size, and seed weight, there was no significant difference in germination between seeds planted in biocrusted and biocrust-removed soil. In contrast, biocrusted soil inhibited germination in *H. persicum*, *C. arenarius*, and *L. semiglabra*, all of which have appendaged seeds ($P < 0.05$), whereas there was no effect when grown without biocrusts. Seed weight and size varied widely among these species, but neither trait showed any correlation with the ability to germinate on biocrusted soils.

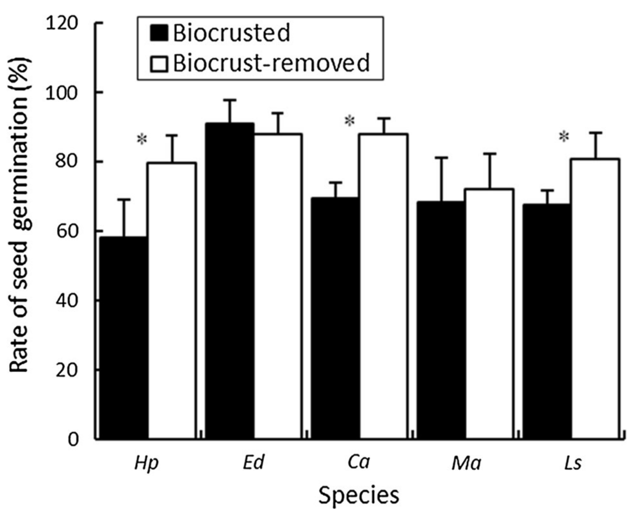

Fig. 2 The influence of biocrusts on seed germination of five desert plants. (An *asterisk* (*) indicate statistical significances of $P < 0.05$). Germinations of seeds with appendages were significantly inhabited by existence of biocrusts, regardless of shrub or herbaceous species. (*Hp*: *Haloxylon persicum*; *Ed*: *Ephedra distachya*; *Ca*: *Ceratocarpus arenarius*; *Ma*: *Malcolmia africana*; *Ls*: *Lappula semiglabra*)

Seedling growth

Shoots of the shrub *E. distachys* were taller on biocrusted soils when compared to biocrust-removed soils until day 20 (Fig. 3, $P < 0.05$). Two (*M. africana*, *L. semiglabrata*) of the three herbaceous plants were taller at all measurement times on the biocrusted than biocrust-removed soil. There were no significant differences at any time for the shrub *H. persicum* or the herbaceous *C. arenarius*.

Ending seedling biomass

The effects of biocrusts on biomass accumulation varied among plant species at the end of the experiment (Fig. 4). Above-ground, below-ground, and total biomass of the herbaceous *M. africana* and *L. semiglabra* were significantly greater when growing in biocrusted than biocrust-removed soils ($P < 0.05$). In contrast, there was no difference observed for *H. persicum, E. distachya*, or *C. arenarius* for any biomass category.

No significant differences in root:shoot ratios were found between biocrusted and biocrust-removed soils within five tested plat species (Fig. 5). The species *E. distachya* showed the highest root-shoot ratio among all the species, while the lowest value was found in *M. africana*.

Element concentrations

All five species growing in the biocrusted soils had significantly greater N concentrations in their tissue than plants growing in biocrust-removed soils (Table 1). In contrast, biocrusts had no influence on tissue concentrations of phosphorus (P), potassium (K), or magnesium (Mg) in any of the tested species. Effects of biocrusts on the other nutrients was species specific: calcium (Ca) increased in the shrub *H. persicum* and the herbaceous *C. arenarius*, but decreased in *E. distachya* and *L. semiglabra*, whereas biocrusts reduced sodium (Na) absorption in *H. persicum*, *E. distachya* and *L. semiglabra*, while increasing Na in *C. arenarius*.

Biocrusts only affected copper (Cu) uptake in *M. africana*, while strongly inhibiting uptake of maganese (Mn) in *M. africana* and *L. semiglabra*. Absorption of iron (Fe) was slightly decreased by biocrusts in *E. dis-*

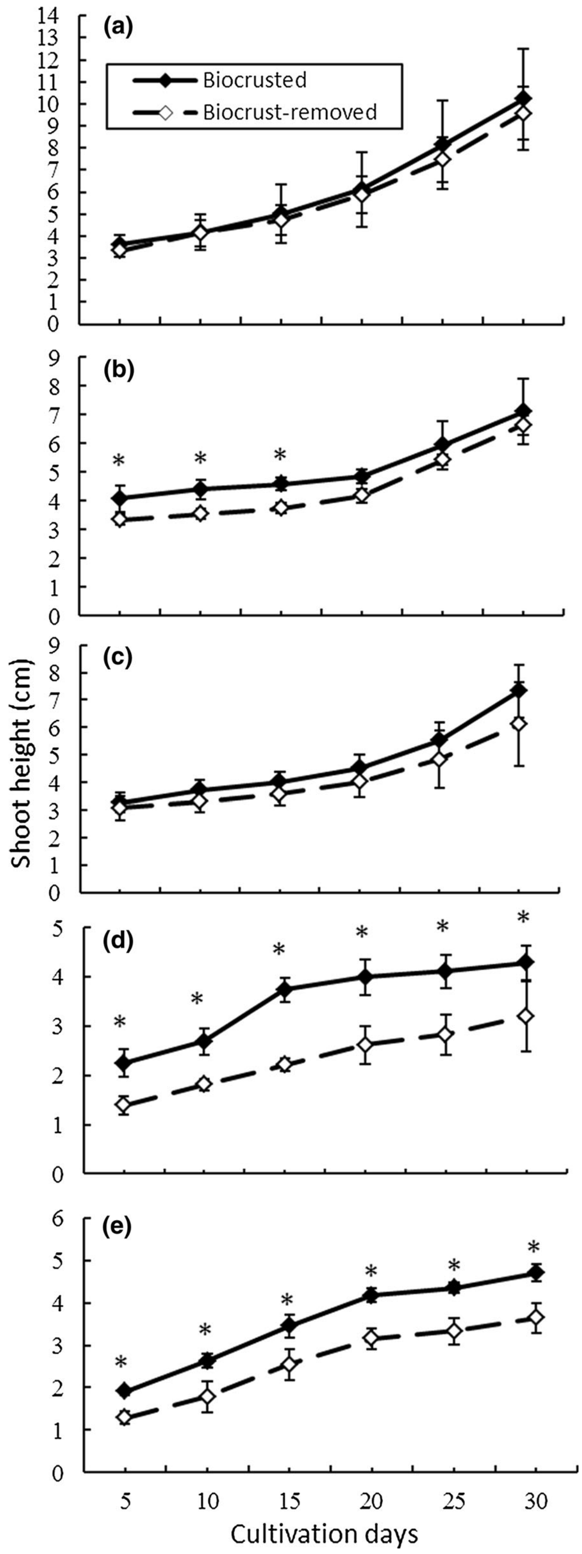

Fig. 3 Variations in shoot height for the five plant species at different cultivation times. An *asterisk* (*) indicate statistical significances of $P < 0.05$. The growth of herbaceous species were significantly enhanced when grew on biocrust-coverd soils. **a** *Haloxylon persicum*; **b** *Ephedra distachya*; **c** *Ceratocarpus arenarius*; **d** *Malcolmia africana*; **e** *Lappula semiglabra*

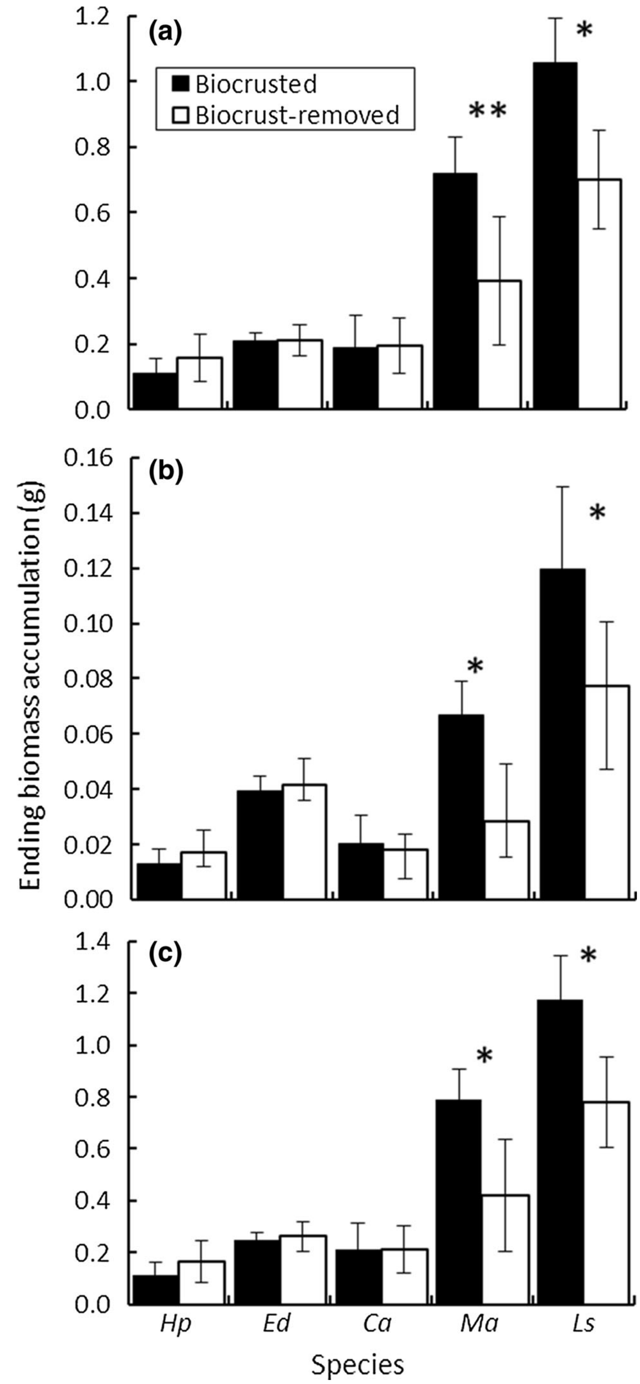

Fig. 4 Effect of biocrusts on ending biomass of the five plant species. *Asterisks* (* and **) indicates significant differences $P = 0.05$ and $P = 0.01$, respectively. The existence of biocrusts could significantly enhance ending biomass accumulations of herbaceous species, and no differences were observed among shrub species. **a** Above ground biomass; **b** below ground biomass; **c** above + below ground biomass

tachya, while being greatly increased in *C. arenarius*, *M. africana,* and *L. semiglabra*. Biocrusts also reduced Zn uptake in *H. persicum* while increasing it in *E. distachya, M. africana* and *C. arenarius*.

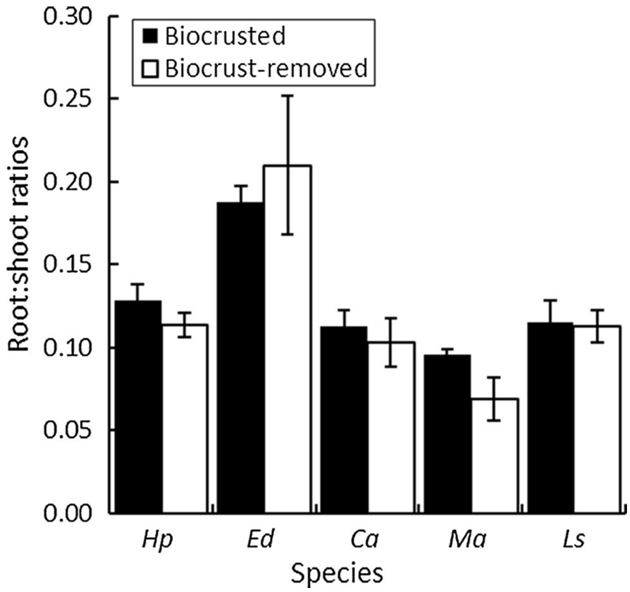

Fig. 5 Effects of biocrusts on root:shoot ratios of the five plant species. No significant differences were observed among all tested plants. (*Hp*: *Haloxylon persicum*; *Ed*: *Ephedra distachya*; *Ca*: *Ceratocarpus arenarius*; *Ma*: *Malcolmia africana*; *Ls*: *Lappula semiglabra*)

Discussion

Plant germination and growth

Germination is the first bottleneck plants must pass through for successful establishment. Therefore, any factors that influence this step can be critical in determining plant community composition. Because biocrusts can influence many soil factors such as soil surface roughness, porosity, structure, moisture, pH, nutrient availability, and temperature, there are multiple ways biocrusts could influence the germination of seeds and seedling growth. This range of responses may be attributed to other effects of biocrusts on the soil such as moisture, which influence the availability of cations and other nutrients (Concostrina-Zubiri et al. 2013; Wu et al. 2013; Zhao et al. 2014) and influence the availability of water and nutrients reaching nearby plants (Boeken and Orenstein 2001). In semiarid Negev ecosystems, seedling establishment in annuals benefits from biocrust disturbance and removal because these disturbance increases seed capture and water infiltration rates (Eldridge et al. 2000).

Biocrust composition was held constant in this study, and thus the differential response we saw in seed germination is most likely attributable to traits of the seeds we used. Our results show that the size, shape, or weight of seeds did not determine whether a seed would more successfully germinate on biocusted soils when compared to soils where the biocrusts had been removed. However, when appendages such as those found on *H. persicum*, *L. semiglabra*, and *C. arenarius* were present, germination was negatively affected.

There are several ways in which appendages can negatively affect seed germination under greenhouse and field condition. First, appendages can reduce or eliminate contact between the seed and the soil surface, reducing absorption of water and nutrients (Eldridge and Greene 1994). During our pre-testing, all seeds were grown on filter paper and kept wet constantly by misting. Under these conditions, we obtained high and consistent germination. However, when seeds with appendages were placed on biocrusted soils, they had only minimal contact with the soil surface. As a likely consequence, we observed seeds did not stay wet as long as seeds on bare soils or those in greater contact with the soil surface. Second, under field settings, it is likely that because appendages make the propagule larger, they inhibit seeds from slipping into the small cracks commonly found on biocrusted surfaces. In deserts, seed burial can be important, as seeds remaining on the soil surface have access to less moisture and nutrients than buried seeds and are exposed to higher predation rates

Table 1 Influence of biocrusts on tissue concentrations of nutrients in five desert plants (μg g^{-1})

Elements	*H. persicum*		*E. distachya*		*C. arenarius*		*M. africana*		*L. semiglabra*	
	Biocrust	Biocrust removed	Biocrust	Biocrust removed	Biocrust	Biocrust removed	Biocrust	Biocrust removed	Biocrust	Biorust removed
N	29.0**	18.0	20.0*	18.0	24.0*	19.0	32.0**	22.0	26.0*	21.0
P	4.7	4.8	4.0	4.2	4.8	3.9	5.4	5.7	4.1	4.9
K	59.0	52.0	51.0	54.0	73.0	59.0	51.0	52.0	41.0	40.0
Mg	7.2	7.3	1.3	1.4	2.5	2.3	2.0*	2.9	1.8**	2.0
Ca	9.3**	7.1	4.1**	4.7	16.0*	12.0	10.0**	22.0	17.0	15.0
Na	3.0	3.3	1.4*	1.5	2.7*	2.0	1.5**	1.9	1.6*	1.9
Cu	4.0	4.4	2.5	2.7	9.8	9.8	5.1*	7.6	9.1	8.4
Mn	53.0	50.0	23.0	25.0	110.0	91.0	25.0**	139.0	25.0**	142.0
Fe	228.0	210.0	168.6**	199.0	1090.0**	673.0	465.7**	177.0	1177.0**	691.0
Zn	278.0*	319.0	273.0*	212.0	740.0**	454.0	35.0*	31.0	254.0	293.0

N nitrogen, *P* phosphorus, *K* potassium, *Mg* magnesium, *Ca* calcium, *Na* sodium, *Cu* copper, *Mn* manganese, *Fe* iron, *Zn* zinc
Single (*) and double (**) asterisks indicate significant differences of $P = 0.05$ and 0.01 levels, respectively

(Boeken and Shachak 1994). Third, appendages can facilitate (e.g., adhering to animal fur) or inhibit (e.g., anchoring to soil surface) seed dispersal. Depending on the specific situation, this can have positive or negative effects on seed germination and subsequent plant establishment. For example, in cool deserts such as the Gurbnatunggut Desert and the Colorado Plateau Desert in the US, biocrusts roughen the soil surface and thus can increase seed retention in plant interspaces which are considered safe sites for seeds (Eckert et al. 1986). In contrast, the smooth hard biocrusts found in hot deserts can facilitate seed movement to the nearest obstruction and thus decrease germination in the interspace (Prasse and Bornkamm 2000).

Plant shoot height and ending biomass

In the current study, we found that plant life form did not predict response to the presence of biocrusts, as the woody plant *E. distachya* and the herbaceous plants (*M. africana* and *L. semiglabra*) were taller in biocrusted soils, whereas the other woody shrub *H. persicum* or the other herbaceous species did not respond at any point.

Most studies from many different climate zones show biocrusts either a positive or neutral effect (Li et al. 2005; Deines et al. 2007; Serpe et al. 2008). For instance, in a cool desert, Harper and Pendleton (1993) found plants growing in biocrusts had four times greater biomass than those in uncrusted soils. Another study showed that the biomass of *Festuca octoflora* was two times higher in biologically crusted soil than in soil without biocrusts (Belnap and Harper 1995).

Only a few studies have addressed the effect of biocrusts on the root:shoot ratio of plants. Bliss and Gold (1999) and Pendleton et al. (2003) reported lower root:shoot ratios of plants associated with biocrusts compared to those growing without crusts. Langhans et al. (2009) found that root:shoot ratios decreased with biocrust age, indicating less allocation to roots with improved fertility. Furthermore, Thiet et al. (2014) showed that seedlings in biocrusts had shorter roots than bare ground controls. In this present study, however, we found no significant difference in root:shoot ratios in any of the five tested species when biocrusted and biocrust-removed soils were compared.

Elemental content

The biocrust on the fixed sand increased the organic matter and total N content of the soil, but only on the upper 5 cm (Gao et al. 2010). This unequal effect of the biocrust on N content may lead to differences in N uptake among plant species. Plants with shallow roots usually benefit more from the biocrust presence (DeFalco et al. 2001; Yan 2009).

Higher P availability beneath the biocrust is associated with higher concentrations of P in plant tissues. For example, in southeastern Utah foliar levels of P in *Festuca octoflora* were 78 % higher in plants growing in biocrust covered soil than uncrusted soil (Belnap, 2011). Positive effects of biocrusts on plant P uptake were also observed in the Kubuqi deserts, although the extent of this effect varied among plant species; overall, the enhancement of P uptake was greater for herbaceous than shrub species (Yan 2009). We found all plant species had an increase in N plant tissue concentration when growing in biocrusted soil compared to biocrust-removed soil. This is a common finding among studies: biocrusts fix N and much of the N they fix is leaked to underlying soils. Therefore, more N is likely available for plant uptake (Belnap et al. 2003; Langhans et al. 2009, 2010). Stable isotopes have shown that biocrusts can be the dominant source of N in desert soils (Evans and Ehleringer 1993). In addition, it has been found that cyanobacterial polysaccharides of biocrusts can improve nitrate reductase activities and root vigor, and thus stimulate the root growth and uptake of nitrate–N and ions for plants, although very high levels of polysaccharides could suppress these responses (Xu et al. 2013). Some studies do not report enhanced N concentrations in plants growing in biocrusted soil (DeFalco et al. 2001). Biocrusted soils generally support greater shoot biomass and density of plants than bare soils. Therefore, if a study does not take this into account, nutrient concentrations can be diluted in an individual plant.

The effects of biocrusts on plant uptake of cations have ranged from negative to positive (Harper and Belnap 2001; Pendleton et al. 2003). In addition, competition for nutrients with microbes in biocrusts might cause lower cation concentrations. Although conflicting results are found in the literature, the uptake of some cations including Cu, K, Mg, and Zn tends to increase in the presence of biocrusts (Harper and Belnap 2001; Pendleton et al. 2003). In contrast, plant Fe uptake appears to be lower in soil covered with biocrusts. For other cations including Ca, Mn, and Na positive, minimal, and negative effects of biocrusts on plant uptake of these cations have been reported (Harper and Belnap 2001; Pendleton et al. 2003). Like for P and N, differences in cation uptake among plant species reflect in part differences in root architecture.

In this study, we did not see any effect on P and K concentrations in any species. Levels of the micronutrients Fe and Zn and the macronutrient Ca was affected in four of the five species, although not always in the same direction. The micronutrients Cu and Mn and the macronutrients Mg and Na were only affected in 1–2 of the species, but again not always in the same direction. The shrub *H. persicum*, with concentrations of three of the ten nutrients affected, was the least responsive to the presence of biocrusts. The shrub *E. distachya* had five of the ten nutrients affected. Zinc and Ca also responded in both species, but the response was opposite in sign. Interestingly, the herbaceous *C. arenarius* had an almost identical response pattern to the shrub *E. distachya*. The herbaceous *M. africana* showed the greatest response of the five species, with eight of the ten nutrient levels different in biocrusted soils. There were also similarities between *L. semiglabra* and *M. africana*, although several nutrients that were different in *M. africana* were not significantly so in *L. semiglabra*, despite tending in the same direction.

Given the complexity of response we observed in cations and micronutrients in this study, explaining the data is difficult. In addition, only a few studies have been done to provide background for our results. Belnap et al. (2003) summarized these studies, reporting that 50 % showed biocrusts enhanced Ca, Mn and Na, and 70 % showed an enhancement of Cu, K, Mg and Zn with a concomitant reduction of P and Fe.

There are many reasons to believe that biocrusts differentially affect absorption of elements by plants in multiple ways. Biocrusts could fix C, increasing levels in soils (Belnap 2003). Increased organic matter stimulates soil fauna and thus decomposition rates, thereby increasing soil fertility. Biocrusts alter pH and secrete phosphatase, likely affecting the bioavailability of micronutrients. Indeed, several studies have shown micronutrient concentrations, especially Fe, in plants growing in biocrusts are often higher than those in uncrusted soils (Harper and Pendleton 1993; Harper and Belnap 2001). Biocrusts also alter hydrologic relations and thus nutrient availability. Lastly, plants in biologically crusted soils have a greater rate of mycorrhizal fungal infection compared with plants growing in adjacent soil without biocrusts (Pendleton et al. 2003).

However, very few of the manipulative experiments needed to directly test the mechanisms of the relationship between biocrusts and plant tissue concentrations have been done, making it impossible to elucidate any general patterns and or make predictions about this relationship at this time. Of all aspects of biocrust ecology, this is one of the most critical areas for future investigations.

Conclusion

Our results show that the influence of biocrusts on seed germination can be species-specific. Biocrusts negatively affected the germination of seeds with appendages. Once seeds had germinated, the effect of biocrusts on growth rate and ending biomass (aboveground, belowground, and total) depended on plant life form rather than seed traits. Two of the three herbaceous plants were stimulated by the presence of biocrusts, whereas neither woody species responded (although *E. distachys* did respond initially). The presence of biocrusts increased concentrations of N and did not affect P or K in all tested species, whereas the uptake of other tested nutrients was species-specific. Our study showed that biocrusts can favor germination of certain species over others and also can influence growth and elemental uptake. Therefore, they may be an important trigger for determining desert plant diversity and community composition in deserts.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict interest.

References

Anderson DG, Bliss LC (1998) Association of plant distribution patterns and microenvironments on patterned ground in a polar desert, Devon Island NWT, Canada. Arct Antarct Alp Res 30:97–107

Baskin CC, Baskin JM (1998) Seeds. Ecology, biogeography, and evolution of dormancy and germination. Academic Press, New York

Belnap J (2003) Factors influencing nitrogen fixation and nitrogen release in biological soil crusts. In: Belnap J, Lange OL (eds) Biological soil crusts: structure, function, and management. Ecological studies, vol 150. Springer, Berlin, pp 241–262

Belnap J (2006) The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrol Process 20:3159–3178

Belnap J (2011) Biological phosphorus cycling in dryland regions. Phosphorus Action 26:371–406

Belnap J, Harper KT (1995) Influence of cryptobiotic soil crusts on elemental content of tissue of 2 desert seed plants. Arid Land Res Manag 9:107–115

Belnap J, Prasse R, Harper KT (2003) Influence of biocrusts on soil environments and vascular plants. In: Belnap J, Lange OL (eds) Biocrusts: structure, function, and management. Springer, Berlin, pp 281–300

Belnap J, Phillips SL, Witwicki DL, Miller ME (2008) Visually assessing the level of development and soil surface stability of cyanobacterially dominated biological soil crusts. J Arid Environ 72:1257–1264

Bliss LC, Gold WG (1999) Vascular plant reproduction, establishment, and growth and the effects of cryptogamic crusts within a polar desert ecosystem, Devon Island, N.W.T., Canada. Can J Botany 77:623–636

Boeken B, Orenstein D (2001) The effect of plant litter on ecosystem properties in a Mediterranean semi-arid shrubland. J Veg Sci 12:825–832

Boeken B, Shachak M (1994) Changes in desert plant communities in human-made patches and their implications for management of desertified landscapes. Ecol Appl 4:702–716

Breen K, Levesque E (2006) Proglacial succession of biological soil crusts and vascular plants: biotic interactions in the High Arctic. Can J Botany 84:1714–1731

Chen RY, Zhang YM, Li Y, Wei WS, Zhang J, Wu N (2009) The variation of morphological features and mineralogical components of biological soil crusts in the Gurbantunggut Desert of Northwestern China. Environ Geol 57:1135–1143

Concostrina-Zubiri L, Huber-Sannwald E, Martinez I, Flores Flores JL, Escudero A (2013) Biological soil crusts greatly contribute to small-scale soil heterogeneity along a grazing gradient. Soil Biol Biochem 64:28–36

Cooper EJ, Alsos IG, Hagen D, Smith FM, Coulson SJ, Hodkinson ID (2004) Plant recruitment in the High Arctic: seed bank and seedling emergence on Svalbard. J Veg Sci 15:115–124

DeFalco LA, Detling JK, Tracy CR, Warren SD (2001) Physiological variation among native and exotic winter annual plants associated with microbiotic crusts in the Mojave Desert. Plant Soil 234:1–14

Deines L, Rosentreter R, Eldridge DJ, Serpe MD (2007) Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. Plant Soil 295:23–35

Eckert RE, Peterson FF, Meurisse MS, Stephens JL (1986) Effects of soil-surface morphology on emergence and survival of seedlings in big sagebrush communities. J Range Manag 39:414–420

Eldridge DJ, Greene RSB (1994) Microbiotic soil crusts—a review of their roles in soil and ecological processes in the rangelands of Australia. Aust J Soil Res 32:389–415

Eldridge DJ, Zaady E, Shachak M (2000) Infiltration through three contrasting biological soil crusts in patterned landscapes in the Negev, Israel. Catena 40:323–336

Escudero A, Martinez I, de la Cruz A, Otalora MAG, Maestre FT (2007) Soil lichens have species-specific effects on the seedling emergence of three gypsophile plant species. J Arid Environ 70:18–28

Evans RD, Ehleringer JR (1993) A break in the nitrogen-cycle in aridlands—evidence from δN^{15} of soils. Oecologia 94:314–317

Fenner M, Thompson K (2005) The ecology of seeds. Cambridge University Press, Cambridge

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

Gros A, Poethke HJ, Hovestadt T (2006) Evolution of local adaptations in dispersal strategies. Oikos 114:544–552

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52:107–145

Gutterman Y (2003) The inhibitory effect of Negev Desert loess soil on the fast germinating caryopses of *Schismus arabicus* (Poaceae). J Arid Environ 54:619–631

Harper KT, Belnap J (2001) The influence of biological soil crusts on mineral uptake by associated vascular plants. J Arid Environ 47:347–357

Harper KT, Pendleton RL (1993) Cyanobacteria and cyanolichens: can they enhance availability of essential minerals for higher plants? Great Basin Nat 53:59–72

Hawkes CV (2004) Effects of biological soil crusts on seed germination of four endangered herbs in a xeric Florida shrubland during drought. Plant Ecol 170:121–134

Housman DC, Powers HH, Collins AD, Belnap J (2006) Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. J Arid Environ 66:620–634

Kidron GJ (2007) Millimeter-scale microrelief affecting runoff yield over microbiotic crust in the Negev Desert. Catena 70:266–273

Lalley JS, Viles HA, Henschel JR, Lalley V (2006) Lichen-dominated soil crusts as arthropod habitat in warm deserts. J Arid Environ 67:579–593

Langhans TM, Storm C, Schwabe A (2009) Biological soil crusts and their microenvironment: impact on emergence, survival and establishment of seedlings. Flora 204:157–168

Langhans TM, Storm C, Schwabe A (2010) Regeneration processes of biological soil crusts, macro-cryptogams and vascular plant species after fine-scale disturbance in a temperate region: recolonization or successional replacement? Flora 205:46–60

Li XR, Jia XH, Long LQ, Zerbe S (2005) Effects of biological soil crusts on seed bank, germination and establishment of two annual plant species in the Tengger Desert (N China). Plant Soil 277:375–385

Li XR, Chen YW, Su YG, Tan HJ (2006) Effects of biological soil crust on desert insect diversity: evidence from the Tengger Desert of northern China. Arid Land Res Manag 20:263–280

Li XJ, Li XR, Song WM, Gao YP, Zheng JG, Jia RL (2008) Effects of crust and shrub patches on runoff, sedimentation, and related nutrient (C, N) redistribution in the desertified steppe zone of the Tengger Desert, Northern China. Geomorphology 96:221–232

Li XR, Zhang P, Su YG, Jia RL (2012) Carbon fixation by biological soil crusts following stabilization of sand dune in arid desert regions of China: a four-year field study. Catena 97:119–126

Noy-Meir I (1973) Desert ecosystems: environment and producers. Annu Rev Ecol Syst 4:25–52

Pendleton RL, Pendleton BK, Howard GL, Warren SD (2003) Growth and nutrient content of herbaceous seedlings associated with biological soil crusts. Arid Land Res Manag 17:271–281

Prasse R, Bornkamm R (2000) Effect of microbiotic soil surface crusts on emergence of vascular plants. Plant Ecol 150:65–75

Rivera-Aguilar V, Godinez-Alvarez H, Manuell-Cacheux I, Rodriguez-Zaragoza S (2005) Physical effects of biological soil crusts on seed germination of two desert plants under laboratory conditions. J Arid Environ 63:344–352

Scott AJ, Morgan JW (2012) Early life-history stages drive community reassembly in Australian old-fields. J Veg Sci 23:721–731

Serpe MD, Orm JM, Barkes T, Rosentreter R (2006) Germination and seed water status of four grasses on moss-dominated biological soil crusts from arid lands. Plant Ecol 185:163–178

Serpe MD, Zimmerman SJ, Deines L, Rosentreter R (2008) Seed water status and root tip characteristics of two annual grasses on lichen-dominated biological soil crusts. Plant Soil 303:191–205

St Clair LL, Webb BL, Johansen JR, Nebeker GT (1984) Cryptogamic soil crusts—enhancement of seedling establishment in disturbed and undisturbed areas. Reclam Reveg Res 3:129–136

Thiet RK, Doshas A, Smith SM (2014) Effects of biocrusts and lichen-moss mats on plant productivity in a US sand dune ecosystem. Plant Soil 377:235–244

Wu N, Zhang YM, Downing A (2009) Comparative study of nitrogenase activity in different types of biological soil crusts in the Gurbantunggut Desert, Northwestern China. J Arid Environ 73:828–833

Wu Y, Rao B, Wu P, Liu Y, Li G, Li D (2013) Development of artificially induced biological soil crusts in fields and their effects on top soil. Plant Soil 370:115–124

Xu YH, Rossi F, Colica G, Deng SQ, De Philippis R, Chen LZ (2013) Use of cyanobacterial polysaccharides to promote shrub performances in desert soils: a potential approach for the restoration of desertified areas. Biol Fert Soils 49:143–152

Yan DR (2009) The effects of biocrusts on the nutrient absorption of vascular plants. J Arid Land Res Environ 23:177–181

Zaady E, Gutterman Y, Boeken B (1997) The germination of mucilaginous seeds of *Plantago coronopus*, *Reboudia pinnata*, and *Carrichtera annua* on cyanobacterial soil crust from the Negev Desert. Plant Soil 190:247–252

Zhang YM, Wang HL, Wang XQ, Yang WK, Zhang DY (2006) The microstructure of microbiotic crust and its influence on wind erosion for a sandy soil surface in the Gurbantunggut Desert of Northwestern China. Geoderma 132:441–449

Zhang YM, Chen J, Wang L, Wang XQ, Gu ZH (2007) The spatial distribution patterns of biological soil crusts in the Gurbantunggut Desert, Northern Xinjiang, China. J Arid Environ 68:599–610

Zhang BC, Zhang YM, Zhao JC (2009) Microalgal species variation at different successional stages in biological soil crusts of the Gurbantunggut Desert, Northwestern China. Biol Fert Soils 45:539–547

Zhao Y, Zhu Q, Li P, Zhao L, Wang L, Zheng X, Ma H (2014) Effects of artificially cultivated biological soil crusts on soil nutrients and biological activities in the Loess Plateau. J Arid Land 6:742–752